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Active Camouflage with Lichens in a Terrestrial Snail, *Napaeus (N.) barquini* Alonso and Ibáñez, 2006 (Gastropoda, Pulmonata, Enidae)

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***Napaeus barquini* Alonso and Ibáñez, 2006, from La Gomera, Canary Islands, lives most commonly on open rock faces covered with crustose lichens. In living specimens, the surface of the shell is covered with a lichen layer that is arranged in the form of protuberances, thereby considerably altering the appearance of the shell. Some of these protuberances may even extend beyond the tip of the shell. The way that these lichens are positioned on the shell and the manner in which they adhere were investigated. The snail grazes lichen material from the substrate and applies it to the surface of its shell in a standardized pattern of movements. The snail uses its mouth to place the moist material onto the shell and to form it into protuberances that adhere as they dry out. To do this, *Napaeus barquini* extends its body far beyond the shell margin so that it can reach the entire outer surface of the shell and cover it with protuberances, presumably as camouflage.**

Key words: Gastropoda, Pulmonata, Enidae, *Napaeus*, camouflaging behavior, active camouflage, lichens, La Gomera, Canary Islands

INTRODUCTION

The shells of land pulmonates show a great diversity of external ornaments, including spines, ribs and hairs, that are produced by the snail as part of the shell. However, the shells of some pulmonate species in a diverse array of families, including the Enidae, Chondrinidae, Cerastidae, Hygromiidae, Orculidae, Valloniidae and Succineidae, carry additional layers, mostly consisting of dust or soil (Fechter and Falkner, 1990; Falkner, 1992; Gittenberger and Menkhorst, 1993; Herbert and Kilburn, 2004).

In most cases, the manner in which such layers are positioned on the shell remains unknown. In addition, in museum collections, shells without extraneous layers may have been cleaned in the mistaken belief that the origin of the coating was secondary soiling. Consequently, research into the extraneous layers of shells must of necessity be carried out on living animals under natural conditions.

The genus *Napaeus* (Enidae) contains a number of species with extraneous layers (Alonso *et al.*, 1995, 2006; Bank *et al.*, 2002). *Napaeus,* a largely unknown taxon in terms of biology, is endemic to the Macaronesian archipelagos of the Azores and Canaries (Castillo *et al.*, 2006). The majority of the described species occur on Tenerife (18 species) and La Gomera (17 species) (Alonso *et al.*, 2006; Castillo *et al*., 2006). One of these species, *Napaeus barquini* Alonso and Ibáñez, 2006, from the Canary island of La Gomera, exhibits an impressive extraneous layer which is arranged in the form of prominent lichen protuberances on the shell (Allgaier, personal observations). *Napaeus barquini* snails live hidden on open rock faces with the shell camouflaged against the lichens on the rocks (Alonso *et al.*, 2006). To determine the mechanisms by which the shells become encrusted with lichens, the animals were observed in the field and in the laboratory. The morphology of the shell and the extraneous layer were investigated using various microscopic techniques.

MATERIAL AND METHODS

Study populations

Field observations were made on La Gomera Island on rock faces with a maximum elevation of about 900 m: Degollada de Peraza (900 m a.s.l., 28°05.591’N, 17°11.077’W), Casas de Enchereda (600 m a.s.l., 28°07.573’N, 17°09.591’W) and Vegaipala (900 m a.s.l., 28°05.010’N, 17°12.027’W). To confirm the species identity, two adult animals from each population with well-developed shell lips were dissected and features of the genital tract determined according to Alonso *et al.* (2006).

The rocks on which *N. barquini* lives face north and, as a result, become wet, mostly because of humid trade winds. The snail populations are concentrated on the steep rock faces, which are covered with a mixed lichen layer consisting primarily of crustose lichens. Approximately 20 snails occur on a rock area of 3×3 m.

Observation methods

Field observations were made during the period 7–21 March 2006 on La Gomera, but most of the behavioral data were obtained from snails transferred to two glass terraria (15×20×10 cm) in the laboratory, under the natural day-night light regime. The terraria contained stones and the snails were fed on foliose and crustose lichens. Observations were made after each terrarium had been

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moistened with distilled water, which was done at least once, for a period of 3 days, in three weeks. These observations continued until January 2007. Snail behavior was recorded with a Sony DCR-TRV80E digital video camera. The recordings were made under daylight and, for night observations, with the infrared mode of the camera. However, a flashlight directed at the snail from a distance of at least 10 cm had no visible effect on its behavior. The length of each behavioral phase was determined from the videotape time code.

Experimental setup

To test whether the behavior might be released by lichen substrate only, or if there is plasticity in camouflaging behavior with respect to materials different from pure lichens, the following experiment was set up. Fifty snails with clean, lichen-free shells from Casas de Enchereda were used. Clean shells were obtained by keeping the specimens crowded in a container without food, so that they thoroughly grazed the lichen layer off each other. The animals were randomly divided into two equal groups that were kept under moist conditions and natural daylight in translucent polyethylene boxes (18×12×9 cm). Snails in the first group had lichen-covered stones in their box; the other group had clean stones and finely ground material from the natural habitat, into which finely granulated pieces of lichen were mixed as food. Seven days after the experiment was set up, the animals were preserved in 70% ethanol and later prepared for investigation by scanning electron microscopy (SEM).

Morphological investigation

Specimens selected for SEM were preserved in 70% ethanol, dehydrated in a graded series of ethanol, critical-point dried in CO_2 in a Polaron E 3000 series II apparatus, coated with gold/palladium in a Balzers SCD 030 sputter coater, and examined under a Cambridge Stereoscan 250 Mk2 scanning electron microscope.

Geological thin sections were made to study the adhesion of the lichen layer to the shell. Portions from the lichen-covered third whorl of a specimen were broken with forceps, and the fragments were dehydrated in an increasing alcohol series, embedded in resin blocks (two-component Epoxidharz Körapox 439, Kömmerling Chemische Fabrik Pirmasens), mounted on a slide, and polished to a thickness of 10 µm. Lichen adhesion in 13 specimens and the shell layers of one subadult specimen with a fracture in the shell were also investigated by SEM.

Crustose lichens were collected from the habitat of *N. barquini* at Degollada de Peraza (10 March 2006) and air dried. The microstructure of lichens damaged by snail grazing was investigated by SEM. For this purpose, pieces of the lichen surface were critical-point dried and coated with Au/Pd alloy, as described above.

Terminology

The decoration of snail shells with foreign material is usually interpreted as camouflage, although critical experiments to test this assumed function have not yet been performed. In the present work, the term “camouflage” is used in the general sense of blending a snail with the background.

RESULTS

Behavior of *N. barquini*

Grazing behavior

During dry weather, the snails were often found in rock crevices or lichen thalli, withdrawn into the shell, with the shell aperture tightly adhering to the ground via an epiphragm of dried mucus. Only under moist atmospheric conditions, such as rain or intense fog, did they become active and start to graze lichens, their only food. If the conditions continued for several days, the snails were active primarily at night.

The crustose and foliose lichens on the rock faces of Degollada de Peraza belonged to 12 genera, with *Pertusaria* (Pertusariaceae) being one of the most abundant. In many cases, the upper surface and margins of the *Pertusaria* lichens consisted of isidia, protuberances of the thallus, some of which were granular and others finger-like or even ramified, ranging from 0.2–0.8 mm in diameter. The lichens on the rocks mostly consisted of a thin compact outer cortical layer. Inside the lichen, spongy hyphal threads were loosely interwoven into a fibrous layer. SEM images of lichens grazed by *N. barquini* showed shortened isidia with depressions resulting from bites, often connected by threads of mucus (Fig. 1A). On the plain thallus surfaces of grazed lichens, bite depressions with radular traces were visible in the grazed areas, the margins and faces of which were often covered by a layer of mucus (Fig.1B).

The trail of the bite depressions corresponds well with the observed grazing behavior of the snail. The snail starts by forming a scrape that is in line with its body. It then moves its head to one side and makes another scrape. It does this a few times, making a series of several scrapes almost parallel to each other in a shallow arc.

Camouflaging behavior

In addition to eating the lichen, the snails repeatedly applied sticky clusters of lichen material to their own shells, the entire outer surface of the shell becoming covered with lichen protuberances. In most cases, one cluster consisted of several granules. The size of the granules corresponded to the dimensions of the bitten-out cavities and isidia on the lichen surface (Fig.1C).

Camouflaging behavior as described above was established in 11 filmed scenes. The time data presented here focused on these 11 scenes, although many other cases were observed qualitatively but not filmed. All the sequences were of one basic type, representing a behavioral unit that proceeded continuously. For the purpose of time measurements, the behavior was divided into steps (Fig. 2), as follows.

Grazing: **(A)** Initial grazing and collection of bitten-off pieces in the oral cavity, often with the upper tentacles bent slightly downwards. Inside the mouth cavity, the pieces are lubricated with fluid.

Turning the head towards the shell: **(B)** Slight lifting of the head away from the substrate. **(C)** Turning of the head laterally towards the shell, buccal lobes extended. Simultaneous movement of the shell towards the head. **(D)** Touching the shell with the buccal lobes.

Applying and forming the protuberance: **(E)** Mounting the shell and crawling backwards in order to find a place to apply the lichen material. **(F)** The cluster of lubricated lichen material is applied. Depending on the place chosen, the body elongates, supported by the shell. **(G)** Slight retraction of the head and formation of the protuberance with the mouth. **(H)** The head is bent such that the mouth is retracted almost underneath the wrinkling sole, touching the base of the protuberance and scraping along the shell surface with the closed lips. This lubricates the shell and gives a smooth finish to the area in front of the protuberance. Subsequently, the head either reextends, but performs only slight shaping movements with the mouth, or reaches once again as far as the newly formed protuberance and repeats the shaping procedure.

Retraction to original position: **(I)** Large retraction back-

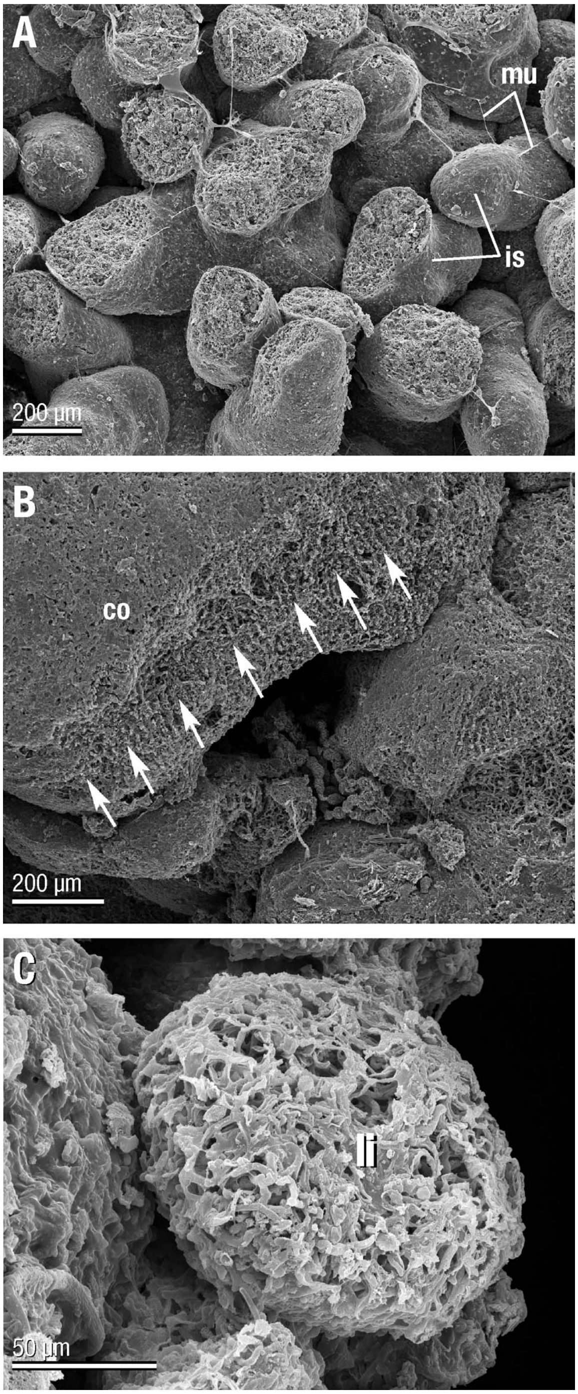

Fig. 1. SEM images of lichen material grazed by *Napaeus barquini*. **(A)** Surface of the lichen *Pertusaria* sp. with partially shortened isidia (is), connected by mucus threads (mu). **(B)** Plain surface of a lichen showing the cortical layer (co). Arrows point to the center of a bite depression revealing the fibrous layer. **(C)** Lichen granule (li), covered with mucus, attached in a cluster to the shell surface.

wards, causing major wrinkling of the sole, lips scraping on the shell surface. **(J)** Lateral sliding of the head keeps the sole in contact with the shell. **(K)** Lifting the head, turning forwards and detaching from the shell. Movement of the shell into the normal position in the direction opposite the movement of the head. **(L)** Realigning of the fore part of the body on the substrate.

After grazing (Fig. 2A), the start of the sequence is indicated by a slight lifting of the head (Fig. 2B) as soon as the snail has filled its mouth cavity completely with lichen material. Consequently, the snail may perform the sequence extending along the right side of the shell (as shown in Figs. 2, 3A). However, the animal can also perform the sequence with its body extending along the left side, depending on the starting position of the head during grazing (Fig. 3B).

The behavioral pattern always includes alternating short grazing and camouflaging behavior. Once started, the entire process of covering the shell proceeds continuously and may require an hour or more.

By frequent repetition of the sequence, the shell is covered with lichen material from the apex to the aperture (Fig. 3C, 3D), except for a tiny area of 1–2 mm² at the base of the body whorl close to the aperture. In spite of its ability to turn the shell half way around, the snail is not able to reach the base of the shell, consequently leaving this gap uncovered (Fig. 4A).

The behavior occurs in a stereotyped manner, but the duration of each step can vary. The time of the completed sequence of camouflaging behavior from the lifting of the head (Fig. 2B) to the realignment of the fore part (Fig. 2L) ranged from 1 min 10 s to 4 min 18 s (mean=2 min 34 s, SD=45 s; n=11; 1–16 sequences per individual). The grazing between two application events varied between 45 s and 7 min 50 s (mean, 1 min 54 s; SD=1 min 10 s; n=11; 2–16 sequences per individual). The times recorded for the steps of the sequence can be seen in Fig. 2 (n=11; 1–16 sequences per individual).

During a single sequence, three different ways of depositing lichen material were observed. (i) Material is applied in a punctiform manner on a bare place on the shell, possibly on the initially bare shell or between two existing lichen protuberances. (ii) Protuberances are extended by attaching additional material to the top of an existing protuberance. (iii) Smaller protuberances in the immediate vicinity may be removed, lubricated in the oral cavity, and fused into one single protuberance together with additional lichen material. As described above, the final result is a shell almost completely covered with dry encrustations, which may form prominent protuberances (Fig. 4A–C). Both newly hatched snails with embryonic shells and adults more than one year old had camouflaged shells (Fig. 4D).

From time to time, single specimens were observed thoroughly grazing off their own lichen layer, at least partially, leaving the glossy surface of the intact shell visible. This behavior was sometimes observed in snails sitting on a lichen-free substrate immediately after a dry period, before foraging on neighboring moist areas.

Although individuals under crowded conditions in containers started grazing lichen material from the shells of other snails, either for ingestion or during the course of camouflaging behavior, this was rarely observed in the field. The lichen layer could also be removed from the shell by hand, especially after the shell had been soaked.

Structure of the lichen layer on the shell

The lichen-free shell is glossy, with fine growth lines. Typical shell thickness is 20–30 µm. Examination of the frac-

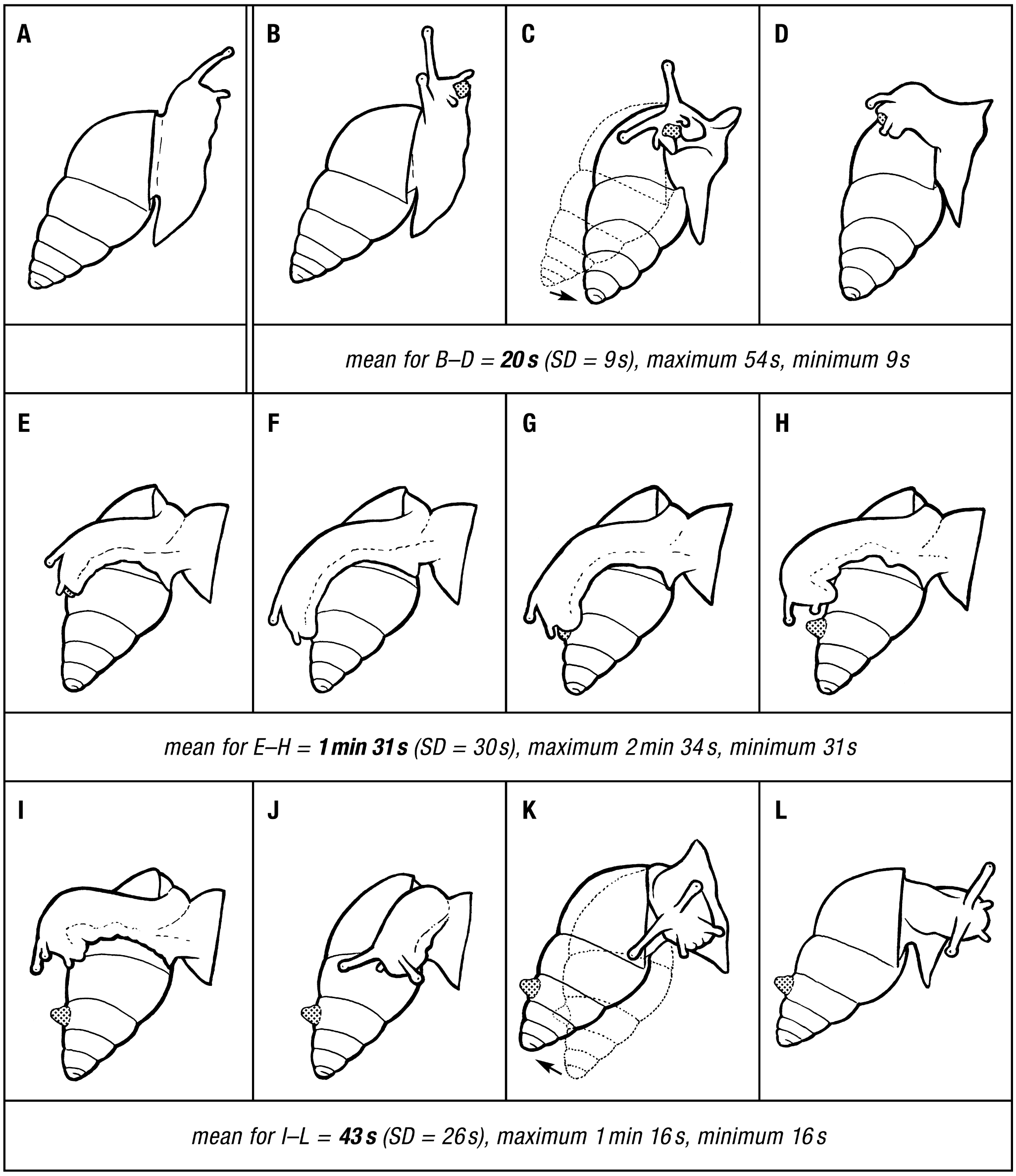

Fig. 2. Rigidly performed camouflaging behavior in *Napaeus barquini* and its duration. The sequence of movements (A–L) in this camouflaging behavior proceeds continuously as a behavioral unit but has been divided, for the purpose of time measurements, into four different steps: **(A)** grazing, **(B–D)** turning the head towards the shell, **(E–H)** applying and forming the protuberance, and **(I–L)** retraction to original position. For further explanation, see text.

tured shell by SEM and in thin sections shows that the shell is composed of two distinct layers, *i.e.*, an external periostracum and an underlying ostracum (Fig. 5A–C).

As indicated by SEM, the lichen material has no deep rootage in the thin periostracum but is attached to the surface (Fig. 5A, 5D). Protuberances are stuck to the shell surface and are composed of loosely arranged lichen granules. The thin sections (Fig. 5C) show that neither the periostracum nor the ostracum is invaded by the lichen.

Single lichen protuberances are around 0.5–1.5 mm wide and up to 2 mm long. They consist of many lichen granules (Fig. 1C). The protuberances are up to 100 times taller than the thickness of the shell. The granules show no indications of hyphal growth. They consist of detached pieces coated with a layer of a mucus-like substance that provides structural stability to the protuberances and that glues the granules to the shell surface (Fig. 5D–E).

The nature of the adhesive mucus-like substance that later solidifies was not determined. In some cases, superimposed mucus-like fibers were visible, extending from lichen granules to the shell surface or from one protuberance to the next, possibly derived from mucus secreted by the pedal gland (Figs. 4B, 5F). The course of the fibers in the various levels presumably reflected the successive progress of construction, a layer of mucus initially coating the periostracum, with dry protuberances lying in the direction of retraction later being covered with mucus-like fibers. In areas of the shell without encrustations, flattened lichen hyphae and mucus-like fibers were stuck to the surface by a layer of mucus.

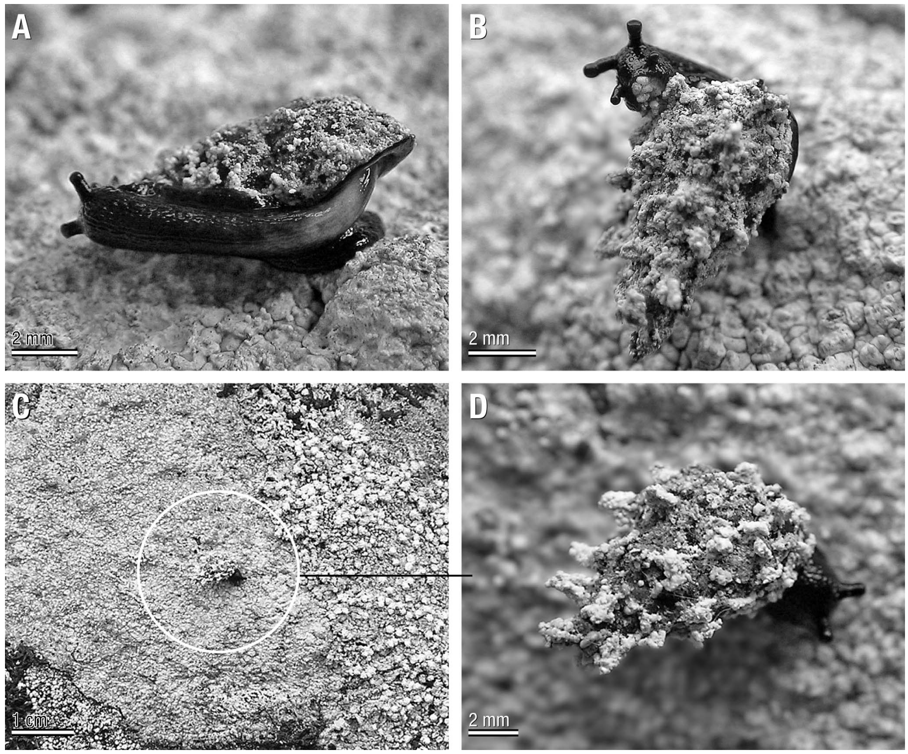

Fig. 3. **(A)** The camouflaging behavior of *N. barquini* extending its body to the right side of the shell and reaching the tip of the shell. The animal still adhers to the substrate with the hind part of its foot. **(B)** *N. barquini* at the moment of application of a cluster of moist lichen granules to the shell while extending to the left side. **(C)** *Napaeus barquini* grazing on crustose lichens in its natural habitat during the daytime (rock faces of Degollada de Peraza, La Gomera). **(D)** Enlarged detail showing the lichen protuberances on the camouflaged shell.

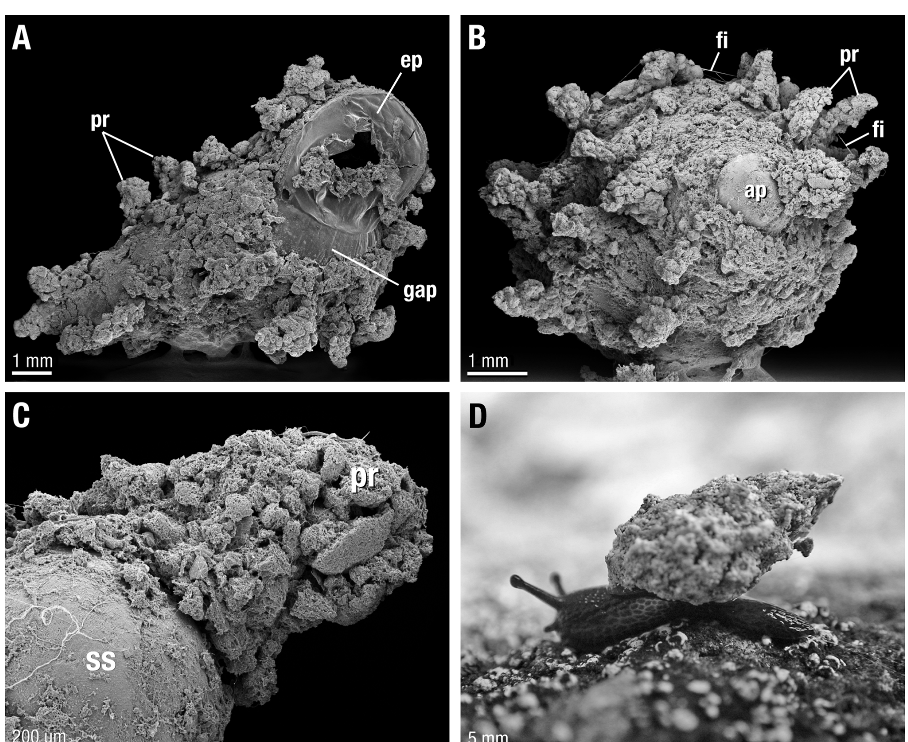

Fig. 4. Camouflaged shells of *N. barquini*. **(A)** SEM image of the lateral aspect of a shell with lichen protuberances (pr) and an uncovered gap (gap) near the shell aperture; the epiphragm (ep), a sheet of dried mucus, cements the shell aperture to the substrate. **(B)** SEM image of the lichen-free apex (ap). Note also the lichen protuberances (pr) and mucus-like fibers (fi). **(C)** Closer view of (B) showing a single protuberance (pr) consisting of lichen granules adhering to the shell surface (ss). **(D)** A living subadult.

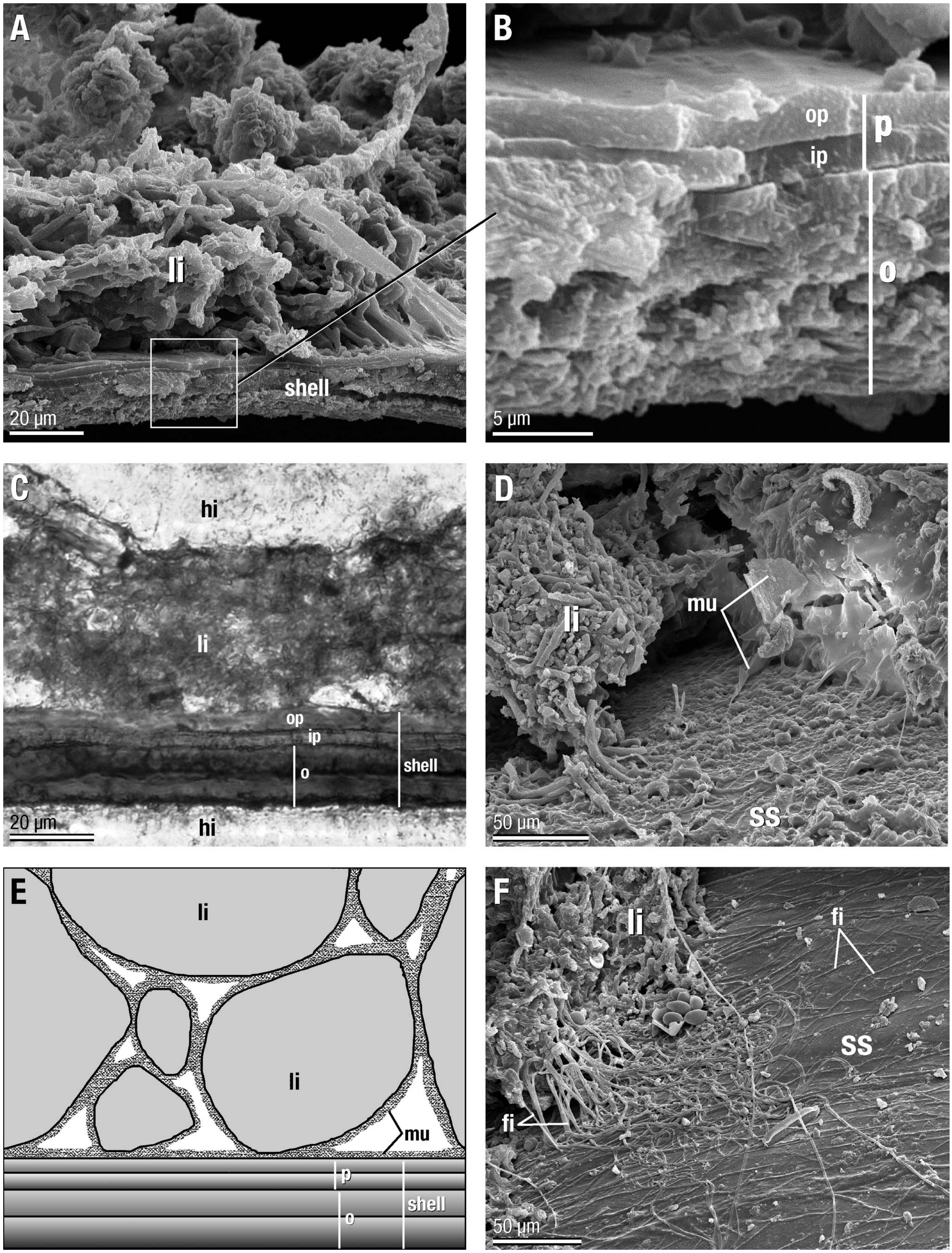

Fig. 5. The lichen-covered shell of *Napaeus barquini*. **(A)** SEM image of a fractured section through the shell with attached lichen layer (li). **(B)** Enlarged detail of the shell showing the periostracum (p) and the underlying ostracum (o). The periostracum is composed of an outer periostracum (op) and an inner periostracum (ip). **(C)** Light-microscope thin section of the shell with the lichen layer (li) lying above the outer periostracum (op). ip, inner periostracum; o, ostracum, hi, histological embedding medium. **(D)** SEM image of the contact zone showing the lichen granules (li) and the shell surface (ss) coated with partially shredded mucus-like sheets (mu). **(E)** Schematic diagram of a transverse section of lichen-covered shell illustrating the adhesion of the lichen to the shell surface. Lichen granules (li) covered with a mucus-like material (mu) are stuck to the periostracum (p), which is underlain by the ostracum (o). **(F)** SEM image of the shell surface (ss) with mucus-like fibers (fi) extending to lichen granules (li).

Influence of available material

In the experiment with the two different substrates, most of the initially lichen-free snails kept in a box with moist lichen-covered stones had lichen granules on their shells. The shaping of the lichen protuberances was, in general, poorly advanced. In contrast, the shells of animals from a second box with fine ground material mixed with lichen fragments were coated with a layer of soil. In some animals, protuberances of irregular shapes made of soil material were visible, and single fragments of lichens were embedded in the soil layer (Fig. 6). SEM revealed that the soil granules and granular crystals were held together by a fibrous mass of mucus-like substance.

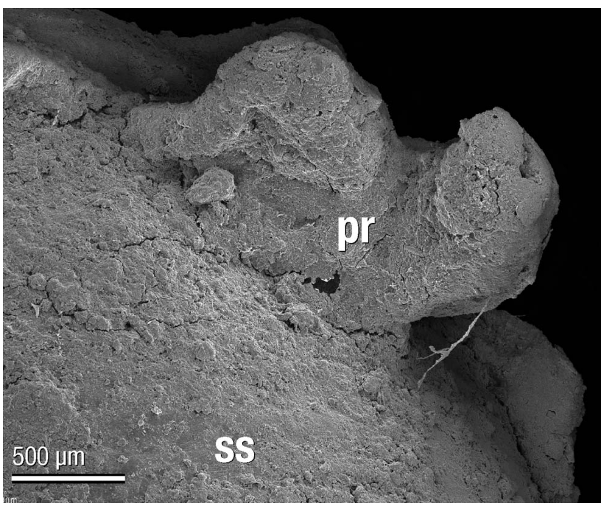

Fig. 6. SEM image of a protuberance (pr) of irregular shape made of soil material on a snail provided with fine ground material (see text). The shell surface (ss) is also covered by a soil layer.

DISCUSSION

Camouflage layers on gastropod shells are well known, despite the assumption that the camouflage layers of shells in museum collections might often have been removed by cleaning. Many species of pulmonates carry extraperiostracal encrustations, but this phenomenon has also been reported in a terrestrial prosobranch of the family Maizaniidae (Herbert and Kilburn, 2004).

To a large extent, the camouflage layer on the shell corresponds to the substrate on which the animal lives. Tree-inhabiting South African pulmonate bark snails (*Edouardia*, Cerastidae) carry a thick layer of bark debris (Herbert and Kilburn, 2004). Some European species of Chondrinidae are covered with a fine layer of stone dust of the same color as the rocks they inhabit (Fechter and Falkner, 1990). Mucus-bound coatings of soil or mud on the shell are known from many species of the pulmonate family Enidae (Gittenberger and Menkhorst 1993, Gittenberger, 1996). The coating of these enids is often seen only in subadult specimens and is usually lost in the adults (Falkner, 1992). Some pulmonates mask their shells with their own excrement (Fechter and Falkner, 1990; Falkner, 1992).

Although little is known about the biology of species of *Napaeus,* several previous observations suggest that camouflage is widespread in this genus. For example, the three species endemic to La Gomera (*N. inflatiusculus, N. berthelothi, N. servus)* carry soil layers on their shell in the subadult stages (Bank *et al.*, 2002; Allgaier, personal observations). Soil used as camouflage contrasts with carrying lichens, which form part of the food spectrum of *N. barquini*. *Napaeus beguirae* from La Gomera and *N. rufobrunneus* from Lanzarote camouflage their shells with the same lichens as those found on the rocks that they inhabit (Alonso *et al.*, 1995). Whether they produce the same elaborate structures as those of *N. barquini* or whether the camouflage consists of a uniform layer is unknown.

Unfortunately, in all these examples, no detailed observations have been made of the way in which the camouflage layers are formed. In most cases, the supposition seems to be that soil and debris are trapped because of the adhesive properties of the shell surface, resulting from its being covered by a layer of foot mucus. A few reports indicate that, shortly after manual cleaning of shells of living specimens, the snails reestablish their camouflage layer (Falkner, 1992; Herbert and Kilburn, 2004). Concerning the South African bark snails, *Edouardia* spp., Herbert and Kilburn (2004) noted, “The origin of this covering needs investigation: although it may prove to consist merely of loose particles glued to the shell with mucus, it is difficult to conceive how the foot can apply such mucus even to the apical whorls of the spire!”

Camouflaging behavior occurs in species of the marine prosobranch family Xenophoridae that bear foreign items, such as the empty shells of other gastropods, on their shells (Yonge and Thompson, 1976). *Xenophora conchyliophora* clasps foreign shells or fragments of coral between the proboscis and the head, raises them into position, and cements them to its own shell (Shank, 1969).

Our study has shown that the lichens on the shell of *N. barquini* are there only because of the actions of the snail. This behavior is more complex than previously assumed and results in the formation of elaborate protuberances. Both young snails and those more than one year old are camouflaged. Thus, the fixed behavior develops inherently after hatching, is maintained throughout life, and is presumably hereditary. Whether the camouflaging behavior of other enids involves a similar elaborate behavior, or the number of times such behavior may have evolved, is not known.

Cases of active camouflage must not be mistaken for examples in which the shells of living or dead animals provide a suitable substrate for epiphytes. As an example, lichens have been found on the shells of living marine snails (Klement, 1962; Peake and James, 1967) and on dead shells of land snails (Peake and James, 1967). In these cases, viable epiphytes settle on the shell without assistance of the snail, which remains passive.

The different steps of the camouflaging behavior in *N. barquini* are stereotyped and therefore show little time variation, except in the second step, viz. from mounting of the shell (Fig. 2E) to full eversion (Fig. 2H). This is a consequence of the variable distances that the snail has to cover and depends on the area in which the snail deposits material, *e.g*., at the margin or the apex of the shell.

In view of the stereotyped nature of the behavior, its flexibility with respect to the available building material is of particular interest. We have shown experimentally that the snails are also able to use soil material to shape protuberances on their shell. The protuberances are not as elaborate as those constructed from lichen (Fig. 6). Presumably, one important precondition for the snail to form long protuberances is the appropriate texture of the building material (Fig. 3D).

The length of the protuberances might be correlated with the weather and the duration of periods of high humidity. The behavioral patterns observed suggest that the ingestion of lichen food takes priority over camouflage. Snails recovering from a weather-dependent resting period appear to feed to a certain extent before the application behavior starts. Under conditions of lack of food, the snails are able to graze their own shell, showing the possible importance of the lichen layer as a food reserve.

As shown in the SEM images, the lichen material on the shell seems to consist of small bitten-off pieces, covered and held together with a mucus-like substance; anchorage organs of the lichen appear to be missing. This suggests that the lichen is no longer viable after deposition on the shell.

Since the snail processes the bitten-off pieces of lichen in its oral cavity before sticking them to the shell, the adhesive is presumably contained in the saliva. In many gastropods, a major role of salivary secretion is postulated to be the lubrication of food particles with mucus-containing fluid (Moura *et al.*, 2004). However, the possibility of the disgorgment of additional secretions together with ingested lichen material from the crop also exists.

Another type of mucus may be represented by the fibers connecting the lichen granules to the shell (Fig. 5F). These mucus-like fibers might be secreted from the pedal gland, which opens below the oral orifice. This could explain the behavior in which, after forming the protuberance, the head is bent in such a way that the mouthpart is retracted almost underneath the sole (Fig 2H). In so doing, the snail possibly uses its head as a “gluing stick” and applies additional mucus to the surface area of the protuberance and the shell. Compared to other terrestrial pulmonates, the shell of *N. barquini* is relatively fragile, as in the camouflaged shells of South African bark snails (Herbert and Kilburn, 2004). The thickness of the periostracum in molluscs probably varies depending on the species and the environment (Meenakshi *et al.,* 1969). *Napaeus barquini* has a periostracal thickness comparable to that of other terrestrial pulmonates, and the thinner shell mainly seems to be the result of the minor thickness of the ostracum (Allgaier, personal observations).

Snails inhabiting open rock faces during daylight are easily detectable by predators with good visual sense on the mostly light surface of crustose lichens. In La Gomera, *Anthus berthelotii* (Motacillidae), a possible bird predator of snails, can be observed on the rock faces, together with rock-inhabiting lizards (*Gallotia* spp.), representing the possible selective pressure that has lead to the camouflaging behavior. A comparable case seems to be *Solatopupa cianensis* (Chondrinidae), which is endemic to southern France and which possibly evolved, via selection by snail-hunting birds, to camouflage itself with reddish dust from the sandstone rock faces that it inhabits (Fechter and Falkner, 1990).

The breaking up of sharp body outlines by means of prominent protuberances in order to merge optically with the fissured surface of the lichens (Fig. 3C, 3D) could allow the snails to feed on the open rock faces during daylight as soon as moist weather arrives, without suffering losses from a higher predation rate. The supplementary movies for this article can be found online at “http://dx.doi.org/10.2108/zsj.24.869.s1” and “http://dx.doi.org/10.2108/zsj.24.869.s2”.

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