BASTERIA, 64: 29-32, 2000

Alternative pathways in the development of the clausilial apparatus in shells of *Albinaria* and *Isabellaria* (Gastropoda, Pulmonata, Clausiliidae)

E. GITTENBERGER

Institute of Evolutionary and Ecological Sciences & National Museum of Natural History, c/o P.O. Box 9517, NL 2300 RA Leiden, The Netherlands

In *Albinaria* and *Isabellaria* the step-wise development of a G-type instead of an N-type clausilial apparatus starts with the formation of a lamella fulcrans instead of a lamella spiralis, shortly after the initial formation of the lamella columellaris. The other lamellae as well as the full-grown clausilium are formed later on. It is hypothesized that the genetic background of such an early shift in the developmental programme might be relatively simple, facilitating both parallel evolution and introgression.

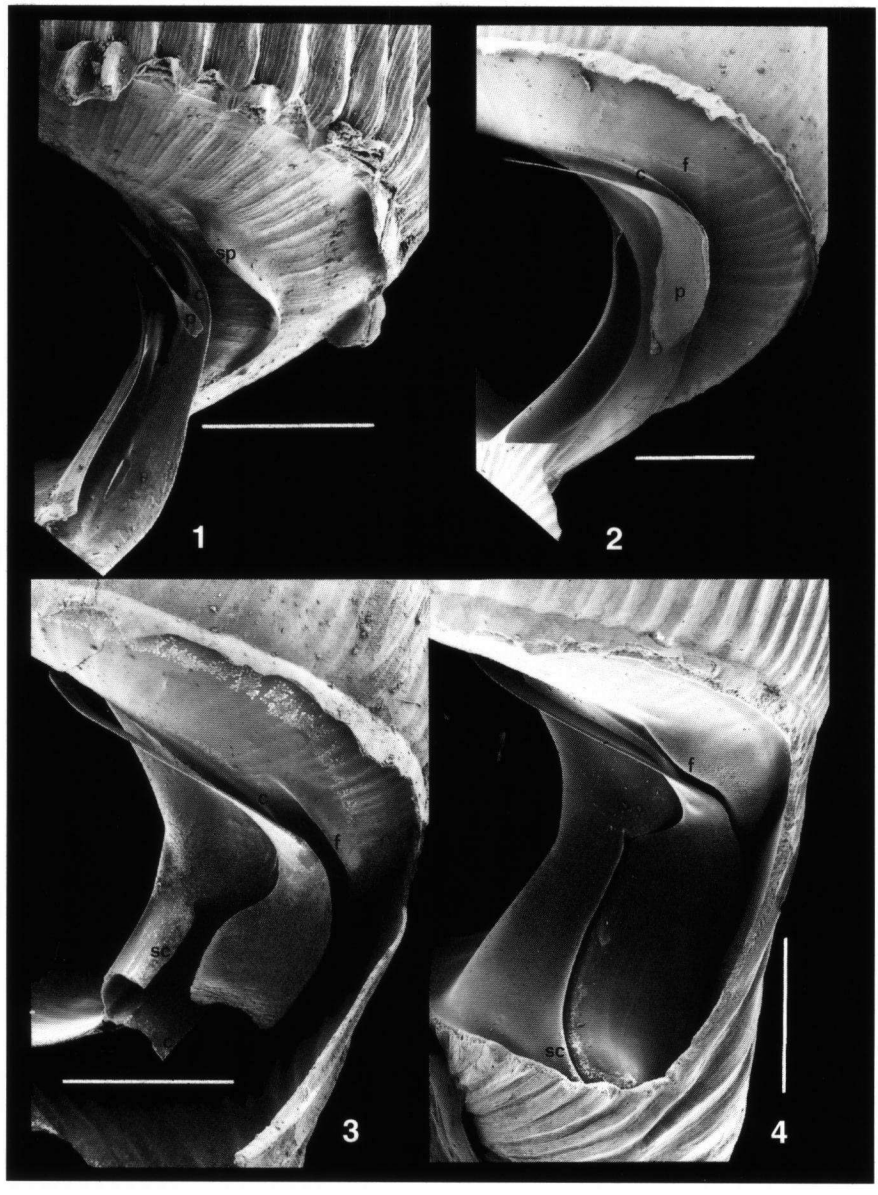
Key words: Gastropoda, Clausiliidae, *Albinaria*, *Isabellaria*, clausilial apparatus, parallelism, introgression.

INTRODUCTION

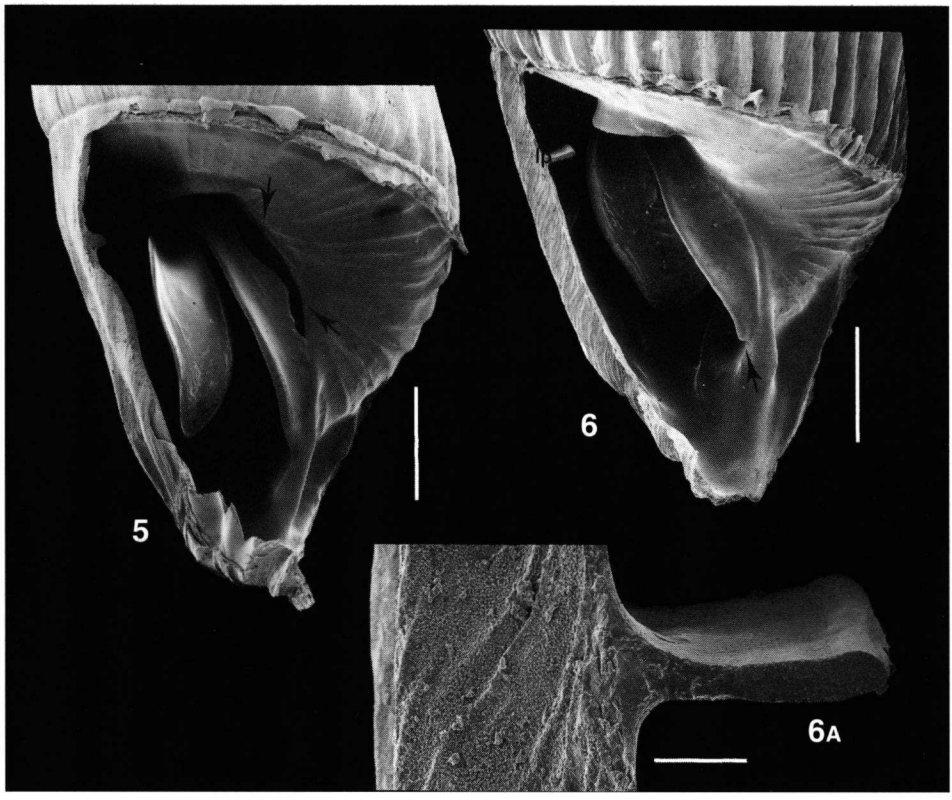
It is generally assumed that a clausilial apparatus (= CA) has originated only once in the course of evolution (Nordsieck, 1982), constituting an exemplary autapomorphic character. However, after its basic structures had formed, various adaptive refinements of the CA may have evolved independently more than once. The repetitive origin of species or subspecies with a G-type CA from N-type ancestors (Gittenberger & Schilthuizen, 1996; Douris et al., 1998; Gittenberger, 1998) is considered here, from both a developmental and a genetic point of view, on the basis of data published by Edlauer (1941) and personal observations on the ontogeny of both types of CA.

MATERIAL AND METHODS

The lamellae in both full-grown and subadult shells of G- and N-type *Albinaria* and *Isabellaria* species were compared in order to investigate at what stage the divergence between these two types becomes apparent during the formation of the CA. As complete growth-series of conspecific specimens were not available for study, the ontogeny of the CA had to be reconstructed on the base of specimens belonging to different species. Specimens from four samples are illustrated: 1, *Albinaria teres* (Olivier, 1801) subsp. [Greece, Crete, Lasithi, 7.5 km SE. of Pevkoi, 60 m alt.]; 2, id. [id., Lasithi, 6 km SSE. of Pevkoi, 50 m alt.]; 3, *A. adriani* (Gittenberger, 1987) [Greece, Peloponnisos, Arkadhia, 4 km SE. of Astros at Koutroufa, 20 m alt.]; 4, *Isabellaria saxicola* (L. Pfeiffer, 1848) subsp. [Greece, Attiki, Imittos mts., 10 km ESE. of Athinai]. The research material is kept at the National Museum of Natural History, Leiden.



Figs 1-4. The clausilium, seen from behind, in both a full-grown (4) and subadult specimens (1-3). 1, in addition to the straight clausilial stalk (s), the clausilial plate (p) begins to differentiate at its end; the columellaris (c) and the spiralis (sp) are already prominent (*Albinaria teres*, sample 2). 2, the clausilium already has its curvature, but the plate (p) is still relatively small; the fulcrans (f) is vaguely discernible (*Isabellaria saxicola*, sample 4). 3, the clausilial plate and the fulcrans (f) are prominently present, but the CA is not yet full-grown; the lower ends of both the columellaris (c) and the subcolumellaris (sc) are broken away (*Albinaria adriani*, sample 3). 4, the full-grown G-type CA, with the plate perfectly following the contours of the aperture, including the curvature of the subcolumellaris (sc) and the fulcrans (f) (*Albinaria adriani*, sample 3). Scale lines 1 mm. SEM-photographs by J. Goud (NNM, Leiden).



Figs 5-6. The developing CA, in frontal view. 5, the plate has not yet reached its final width and the columellaris is not yet completely fixed to the apertural wall (arrows) (*Albinaria teres*, sample 1). 6, the columellaris is full-grown but its origin as a separate addition to the apertural wall is still discernible at its base (arrow); the internal crystal structure of the principalis (lp) (fig. 6A) is also indicative of an independent origin of that lamella (*Albinaria teres*, sample 2). SEM-photographs by J. Goud (NNM, Leiden).

RESULTS AND DISCUSSION

According to Edlauer (1941), who studied the complicated CA of *Herilla bosniensis* (L. Pfeiffer, 1868) (Alopiinae), CA formation is a sequential process, taking place during the formation of the last whorl of the shell (figs 1-4). Only then the mantle of the snail forms a series of folds, one after the other, between which chalk is secreted. The lamellae are formed after the shell wall. They are secondarily added onto the wall, which becomes obvious when their formation has not yet been completely finished and a lamella is not yet fixed over its entire length (fig. 5). The internal crystal structure of both a lamella and the shell wall (fig. 6) suggests the same. CA formation starts with the columellaris. While this lamella is still growing, the spiralis and the clausilium begin to form. The parietalis follows and then the subcolumellaris. With the formation of the principalis and finally the palatal folds the CA is completed.

In *Albinaria*, as in *Herilla*, formation of the spiralis and the clausilium also starts early in development, at least in species with an N-type CA (fig. 1). In the *Isabellaria* species and in *Albinaria* species with a G-type CA however, the growing clausilium is formed together with the lamella fulcrans (figs 2-4), which apparently takes the place of the spiralis here. Maybe the combined development of either the clausilial and the spiralis mantle fold, or the clausilial and the fulcrans mantle fold, is decisive for the formation of a future N-type or a G-type CA. Because of the oblique fulcrans, the clausilium may become relatively broad early in development, before a principalis begins to form. Later on, there is hardly any space left for the principalis and a G-type CA is formed. The presence of a spiralis in early CA development might force the equally early developing clausilium further away from the palatal wall, leaving space for the subsequent formation of a prominent principalis, resulting in an N-type CA (fig. 1). Consequently, the genetic background for an evolutionary shift from one type of CA to another, may be a relatively simple mutation, related to position and formation of the fulcrans, replacing the spiralis.

When co-evolution of several independent CA-related morpho-genes is not required, it is not extremely unlikely that a G-type CA will develop from an N-type in various *Albinaria* species under high selection pressure, by parallel evolution or maybe even transspecific introgression (Gittenberger, 1998). It remains to be investigated how the two types of CA develop in other clausiliid taxa.

REFERENCES

CHRISTELOW, A.Q., 1992. The morphology and function of the clausilium of *Clausilia bidentata* (Ström) (Gastropoda, Pulmonata, Clausiliidae). — In: E. GITTENBERGER & J. Goud, eds, Proceedings of the Ninth International Malacological Congress: 107-113. Unitas Malacologica, Leiden.

DOURIS, V., R.A.D. CAMERON, G.C. RODAKIS, & R. LECANIDOU, 1998. Mitochondrial phylogeography of the land snail Albinaria in Crete: long-term geological and short-term vicariance effects. — Evolution 52: 116-125.

EDLAUER, E., 1941. Die ontogenetische Entwicklung des Verschlussapparates der Clausiliiden, untersucht an *Herilla bosniensis*. — Zeitschrift für wissenschaftliche Zoologie 155: 129-158.

GITTENBERGER, E., 1996. Adaptations of the aperture in terrestrial gastropod-pulmonate shells. — Netherlands Journal of Zoology 46: 191-205.

——, 1998. Transspecific introgression in *Albinaria* (Gastropoda Pulmonata). — In: R. BIELER & P.M. MIKKELSEN, eds, Abstracts, 1998 World congress of malacology, Washington DC: 122. Unitas Malacologica, Washington D.C.

——, & M. SCHILTHUIZEN, 1996. Parallelism in the origin of the G-type clausilial apparatus (Gastropoda, Pulmonata, Clausiliidae). — In: J.D. TAYLOR, ed., Origin and evolutionary radiation of the Mollusca: 295-300. Oxford University Press, Oxford.

NORDSIECK, H., 1982. Die Evolution des Verschlussapparates der Schliessmundschnecken (Gastropoda: Clausiliidae). — Archiv für Molluskenkunde 112: 27-43.