



## DEVELOPMENT OF CLAUSILIAR APPARATUS IN *VESTIA GULO* (E. A. BIELZ, 1859) (GASTROPODA: PULMONATA: CLAUSILIIDAE)

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**ABSTRACT:** Formation of clausiliar apparatus in *Vestia gulo* (E. A. Bielz) was analysed and illustrated with SEM photographs. The sequence of formation of apertural barriers is the following: 1) inferior and spiral lamellae, 2) superior lamella, subcolumellar lamella, clausilium, principal palatal plica, 3) lunella and other palatal folds. Under laboratory conditions the closing apparatus developed during two weeks. The shell development in *V. gulo* was compared with literature data on another clausiliid, *Herilla bosniensis*. Adaptive significance of the rapid development of apertural barriers is discussed in relation to the reproductive biology of Clausiliidae.

**KEY WORDS:** *Vestia gulo*, Clausiliidae, clausiliar apparatus, apertural barriers, shell development, sexual maturity

### INTRODUCTION

The sophisticated system of apertural folds, characteristic of clausiliids, is built during the growth of the ultimate shell whorl. This closing apparatus is often termed clausiliar apparatus (see NORDSIECK 2007). Its structure has a high taxonomic value and is useful for identification of species. Apertural barriers are believed to reinforce the aperture, provide protection against desiccation or predators, protect the pneumostome or stabilize the shell when climbing vertical surfaces (SUVOROV 1991, POKRYSZKO 1997). On the other hand, formation of teeth or folds is costly in terms of calcium and energy expenditure and may result in delayed growth and sexual maturity.

The sequence of development of clausiliid apertural barriers, which are probably among the most

complex in gastropods, has been described in *Herilla bosniensis* (L. Pfeiffer, 1868), subfamily Aloiinae (EDLAUER 1941). It has also been found that clausiliar apparatus develops rapidly, and the process takes only 2–3 weeks (LIKHAREV 1962).

In this paper the formation of clausiliar apparatus in another species – *Vestia gulo* (E. A. Bielz, 1859) (subfamily Baleinae) is described and illustrated. In *V. gulo* the clausiliar apparatus consists of: 1. clausilium (plate and stalk), 2. lamellae (spiral, superior, inferior, subcolumellar); 3. palatal folds (principal plica and lunella) (Fig. 1F) (for detailed description of adult clausiliar apparatus in *V. gulo* see LIKHAREV 1962).

### METHODS

Specimens of *Vestia gulo*, collected in Krościenko (Pieniny Mts, Poland), were kept in the laboratory at the Department of Invertebrate Zoology and Hydrobiology, University of Łódź (for description of laboratory culture see MALTZ & SULIKOWSKA-DROZD 2008). Juveniles (50 specimens hatched in laboratory) were

kept till the ultimate whorl formation. According to the shape of aperture the snails were classified as juvenile (J – before formation of ultimate whorl), subadult (SA – during formation of ultimate whorl) and adult (A – with thickened lip). Then, the animals were killed in boiling water and their soft parts were removed. To

show the development of apertural barriers, parts of the shell wall were cut out. SEM photographs were taken at the Department of Physics, University of Łódź

and at the Polytechnic of Łódź. The nomenclature of clausiliar apparatus follows NORDSIECK (2007).

## RESULTS

The juvenile shell of *V. gulo* has an open umbilicus, and a square aperture with thin edges (Fig. 1A). Based on the development of lamellae the subadult phase can be divided into several consecutive stages (Table 1). The change in the aperture shape and the complete sealing of the umbilicus are the first signs of the ultimate whorl formation (stage SA-1, Fig. 1B). Then (stage SA-2) the first lamellae are built: spiral and inferior (Fig. 1C). At this stage, the inner end of the spiral lamella reaches much deeper inside the shell than the inner end of the inferior lamella. At first, the lamellae are not prominent, they are paper-thin and low, they thicken and gain length during later stages. At the next stage (SA-3) the superior lamella develops, primary as a small protrusion (Fig. 1D). At the same stage a very thin, leaf-shaped clausilium can be observed, as well as the subcollumellar lamella and the first palatal fold – principal plica. The clausilium stalk separates from

the columella about 0.9–1 whorl from the ultimate aperture margin. The edges of the aperture are still not connected on the parietal wall. At stage SA-4 all the parts of the clausiliar apparatus are present (including lunella), the spiral lamella is so long that it usually joins the superior lamella (some adult specimens retain the gap between these two lamellae). The aperture edges are now connected, however the lip is still very thin and fragile (Fig. 1E). The pointed end of the clausilium plate is short and not upturned. Soon the inferior and subcollumellar lamellae come to reach the aperture margin, and sometimes additional interlamellar folds are built on the columellar wall. The lip thickens, and the callus is formed parallel to it. Inside the shell, the inner ends of the inferior and spiral lamellae are situated approximately at the same distance from the aperture. All the lamellae and folds have now reached their ultimate thickness, and the shell formation has been completed (Fig. 1F).

Table 1. *Vestia gulo*. Development of apertural barriers

| Stages of shell development | Umbilicus | Aperture shape                | Spiral lamella | Inferior lamella | Superior lamella | Clausilium | Principal plica | Lunella | Lip                               |
|-----------------------------|-----------|-------------------------------|----------------|------------------|------------------|------------|-----------------|---------|-----------------------------------|
| J<br>Juvenile               | open      | straight                      | –              | –                | –                | –          | –               | –       | –                                 |
| SA-1<br>Subadult            | closed    | oblique, narrow               | –              | –                | –                | –          | –               | –       | –                                 |
| SA-2<br>Subadult            | closed    | oblique, narrow               | +              | +                | –                | –          | –               | –       | –                                 |
| SA-3<br>Subadult            | closed    | straight, broad (pear-shaped) | ++             | ++               | +                | +          | +               | –       | thin, not joined on parietal side |
| SA-4<br>Subadult            | closed    | straight, broad (pear-shaped) | ++             | ++               | ++               | ++         | ++              | +       | thin, joined on parietal side     |
| A<br>Adult                  | closed    | straight, broad (pear-shaped) | +++            | +++              | +++              | +++        | +++             | +++     | expanded with interlamellar teeth |

+ an initial stage of structure development; ++ middle stage of structure development; +++ ultimate stage of structure development

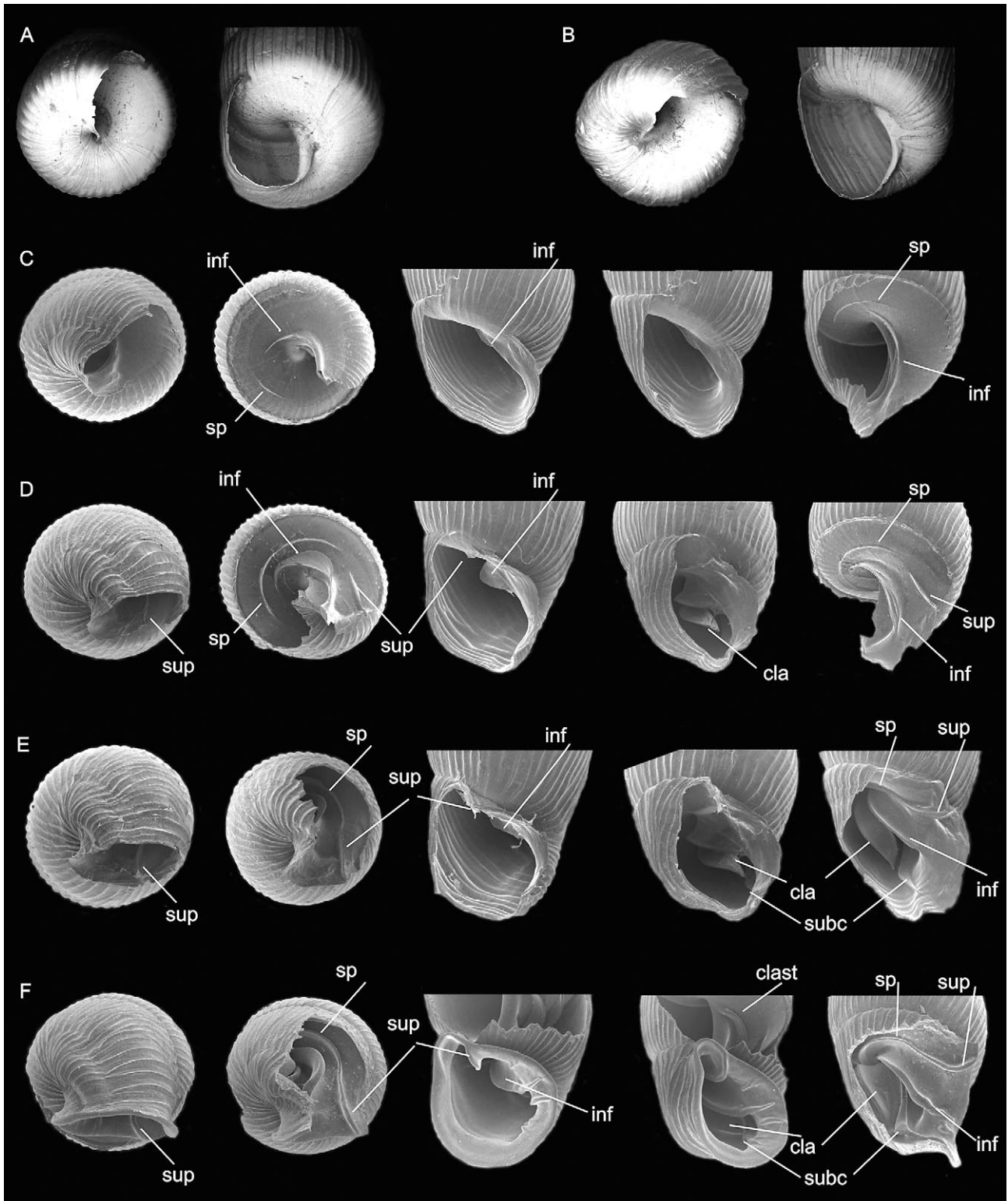


Fig. 1. *Vestia gulo*. Development of ultimate whorl: A – juvenile; B – subadult (SA-1); C – subadult (SA-2); D – subadult (SA-3); E – subadult (SA-4); F – adult; cla – clausilium, clast – clausilium stalk, inf – inferior lamella, sp – spiral lamella, subc – subcollumellar lamella, sup – superior lamella



## DISCUSSION

In *V. gulo*, like in most clausiliids, the shell growth is restricted to juvenile phase of life cycle. *Balea perversa* (Linnaeus, 1758) is the only exception in that it can grow during its reproductive life (BAUR & BAUR 1992). Under laboratory conditions the average time needed to complete the shell growth varies between three and six months, depending on the species (MALTZ & SULIKOWSKA-DROZD 2008). In *V. gulo* the average time needed to complete the growth from hatching was 148 days, the quickest growth took 81 days (SULIKOWSKA-DROZD, unpublished data). Formation of the ultimate whorl lasted ca. two weeks. This process is also very rapid in natural populations of *V. gulo* (SULIKOWSKA-DROZD, in preparation).

The formation of clausiliar apparatus in *V. gulo* can be compared with results of EDLAUER's study (1941) on *Herilla bosniensis*. According to EDLAUER (1941) at the beginning of the ultimate whorl formation the aperture becomes more narrow; resulting in the mantle edge folding and creating wrinkles or pockets, which take part in the formation of lamellae and clausilium. In *H. bosniensis* the sequence of lamellae development is as follows: 1) inferior lamella, 2) spiral and superior lamellae, 3) clausilium, 4) subcolumellar lamella, 5) principal palatal plica 6) lunella and other palatal folds. According to LIKHAREV (1962) the same pattern of the development of lamellae and main palatal plica occurs in other clausiliids, but the building of lunella and other palatal folds varies among species.

My observations on *V. gulo* confirm most of EDLAUER's (1941) results. The formation of clausiliar apparatus starts when the aperture becomes very narrow; the inferior lamella is the first to develop. The only difference concerns the formation of superior

lamella. In *V. gulo* this lamella is built significantly later than the spiral lamella.

Clausiliids start to reproduce only after the shell growth has been completed (LIKHAREV 1962). The formation of thickened lip is the sign of reaching ultimate size. Formerly, it was also regarded as tantamount to attaining sexual maturity (LIKHAREV 1962), however it was found that reproductive system developed a few months later (SCHILTHUIZEN & LOMBAERTS 1994, GIOKAS & MYLONAS 2002, MALTZ & SULIKOWSKA-DROZD 2008).

The ultimate whorl formation is costly in terms of energy and calcium expenditure. Moreover, the aperture margin at this stage is thin and fragile. During the body whorl formation, lamellae easily break at a touch. Any major damage at this stage results in deformation of shell, such as double mouthed shells, or others – various cases of shell deformation in clausiliids have been described in detail by JACKIEWICZ (1965).

In clausiliid development the body whorl formation precedes the maturation of the reproductive system, which is also energy demanding (MALTZ & SULIKOWSKA-DROZD 2008). The main advantage of such a development strategy rests on the reduction of time required to finish the shell growth (formation of the apertural barriers) and shortening the period when the shell is most susceptible to physical damage.

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