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"*Helix*" *sororcula* BENOIT 1859 and its relationships to the genera *Vallonia* RISSO and *Planogyra* MORSE

(Pulmonata: Pupilloidea).[1])

By

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With 10 figures.

Introduction.

For several years now one of the authors (GIUSTI 1971, 1973) has engaged in friendly dispute with Dr. E. GITTENBERGER of Leiden (Holland) (GITTENBERGER 1972, 1977a) regarding the genus to which the south-European and Algerian species "*Helix*" *sororcula* BENOIT 1859[2]) should be assigned.

Many similarities resulted in the anatomy of the reproductive apparatus of "*H.*" *sororcula* and *Vallonia costata* (MÜLLER 1774), the only *Vallonia* that occasionally presents a genital apparatus comprising the male tract. GIUSTI (1971, 1973) therefore placed BENOIT's species in the genus *Vallonia* RISSO 1826 conferring minor importance to its peculiar conchological characteristics: shell thin and fragile, lacking a thick, reflected peristome (= mouth-edge), and consequently refused to include the species in the north-American genus *Planogyra* MORSE 1864. Infact its type species, *P. asteriscus* (MORSE 1857) described by PILSBRY (1948: 1038, fig. 406/1-3, fide BAKER), although possessing a similar genital apparatus seemed to display an

[1]) Research supported by C.N.R. grant ("Gruppo di Biologia Naturalistica").

[2]) The exact year of publication for "*H.*" *sororcula* is not 1857 but 1859. The BENOIT's "Illustrazione sistematica critica iconografica dei Testacei della Sicilia Ulteriore e delle isole circostanti" was published in four parts. The first (pp. I-XVI + 1-52) and the second one (pp. 53-116) in 1857, the third one (pp. 117-180) in 1859 and the fourth one (pp. 181-248) in 1862. The description of "*H.*" *sororcula* is found in the third part published in 1859 (: 149).

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unbranched penial retractor muscle, and therefore different from that of all the Valloniidae described in the literature (see GIUSTI 1971). GITTENBERGER (1972), however, assigned BENOIT's species to the genus *Planogyra* on the basis of the affinity between the shell microsculptures of *P. asteriscus* and "*H.*" *sororcula* as seen with the SEM.

Moreover, GITTENBERGER (1977a), considered "*H.*" *sororcula* to be different from *Vallonia*, because it showed an "epiphallic" papilla which was apparently absent in *V costata*. The same author also relegated to second place the apparent unbranching of the penial retractor muscle described by BAKER in PILSBRY, as a character differentiating *Planogyra* both from *Vallonia* and "*H.*" *sororcula*. Although accepted by many (KERNEY & CAMERON 1979; GITTENBERGER in KERNEY & CAMERON, 1980; GITTENBERGER, MENKHORST & RAVEN 1980; PRIETO, GOMEZ & MARTIN 1982; COLES, HOLYOAK & PREECE 1983; KERNEY, CAMERON & JUNGBLUTH 1983), the assignement of "*H.*" *sororcula* to the genus *Planogyra* remained a moot point. This situation was due mainly to the lack of a more accurate anatomical analysis determining the detailed structure of the genital tract in *Vallonia* and *Planogyra*.

This is the task that we have taken on in order to obtain a resolution to the problem, free of any previous bias. In addition we hoped to determine the importance of the conchological and anatomical characters for the supraspecific systematics of the problematic family of the Valloniidae.

As will become evident, the case is rather complicated and does not offer easy solutions. It should be emphasized the absurdity of certain associations between taxa that are based on single variable conchological characters that often result from convergence phenomena.

The structure of the reproductive apparatus in "*Helix*" *sororcula*, *Vallonia costata* and in *Planogyra asteriscus*.

Drawings by GIUSTI (1969: fig. 2) and GITTENBERGER (1972: figs. 1-2; 1977: fig. 3) offer incomplete information on the genital tract of "*H.*" *sororcula*.[3]) Precise data that would consent a more exact definition to the species have always been lacking. Our investigations of specimens gathered at Foce di Cardeto (Apuane Alps, Tuscany) and in Cansiglio Mountains (Treviso, Venetum) (Fig. 1CD) has revealed:

a) The presence of a rather long and pointed conical penial papilla (glands?) situated at the apex of the epiphallus extending into the proximal part of the penis.

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[3]) The noteworthy conchological similarities between the species of BENOIT and some species of other genera as well as the concordance with other species described in the past, have resulted in its being referred to by various other names: *Spelaeodiscus astoma* (O. BOETTGER) (GITTENBERGER 1967, 1969; ZILCH 1969); *Pleuropunctum micropleuros* (PAGET) (GIUSTI 1969, GIUSTI & MAZZINI 1970); *Vallonia astoma* O. BOETTGER (GIUSTI 1971); *Planogyra astoma* (O. BOETTGER) (GITTENBERGER 1972, FALKNER 1974).

b) The presence of a short, wide papilla in the basal portion of the penial appendix, usually disposed laterally. A thin and circonvoluted canal arises from the papilla and runs in the lumen of the penial appendix.
c) The penial retractor terminates in two short branches of unequal length: the longer branch is attached to the wall of the penial appendix where the papilla is found; the shorter branch is attached to the wall of the proximal portion of the penis in the portion that encircles the penial papilla. Among the different specimens there exist slight differences in the location of the two branches of the penial retractor, due to the greater or lesser development of the genital apparatus and, perhaps, to differing degrees of post-mortem contraction.
d) The ductus of the gametolytic gland (= bursa copulatrix) shows a slender diverticulum.

Numerous Valloniidae, including the type species of *Vallonia*, *V. pulchella* (MÜLLER 1774), present a genital apparatus that lacks the male tract (penial complex – penial retractor). *V. costata*, however, is one of the species that occasionally has populations in which rare individuals possess a complete genital apparatus.

Undoubtedly that is why there is little anatomical information available on such a diffuse species and it is usually limited to the scheme first outlined by STEENBERG (1917: 9-13, figs. 5-6), (see PILSBRY 1948: 1021, fig. 544; DAMJANOV & LIKHAREV 1975: 133, fig. 69; AKRAMOWSKI 1976: 148, fig. 66)[4]). More recently GITTENBERGER (1977a: 195, fig. 4) described the genital tract in some specimens of *V. costata* gathered at Wolvega (Friesland, Pays Bas), sustaining that they lacked a penial papilla (= "papille epiphallienne"). Our analysis (Fig. 2CD) is of the only specimen in the GIUSTI Collection, possessing a complete genital tract and found in the xerothermic oasis of Pondel (Aosta Valley). It revealed:

a) The presence of a long and pointed conical penial papilla (glans?) situated at the apex of the epiphallus and extending into the proximal portion of the penis.
b) The presence of a long, slender papilla in the basal portion of the penial appendix. No evidence of a canal within the penial appendix was found.
c) The penial retractor terminates in two long branches of unequal length: the longer branch is attached to the wall of the penial appendix where the papilla is found; the shorter branch is attached to the wall of the epiphallus, underneath the proximal portion of the penis where the papilla is situated.
d) The ductus of the gametolytic gland (= bursa copulatrix) lacks a diverticulum.

The literature offers very little information on the structure of the genital tract of the species of the genus *Planogyra*. The only description known to us is that of the type species, *P. asteriscus*, reported by PILSBRY (1948: 1038, figs. 460/1-2). BAKER, the author of the anatomical research, has described and drawn a genital tract with a simple retractor muscle that terminates on the wall of proximal portion of the penis, with a penial appendix that has a long papilla at its apex and with a scarcely developed penial papilla.[5])

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[4]) WATSON's drawing of the genital tract of *V. costata* (1920: pl. 2 fig. 5) does not correspond to reality, displaying a sort of diverticulum annexed to the distal portion of the penis.

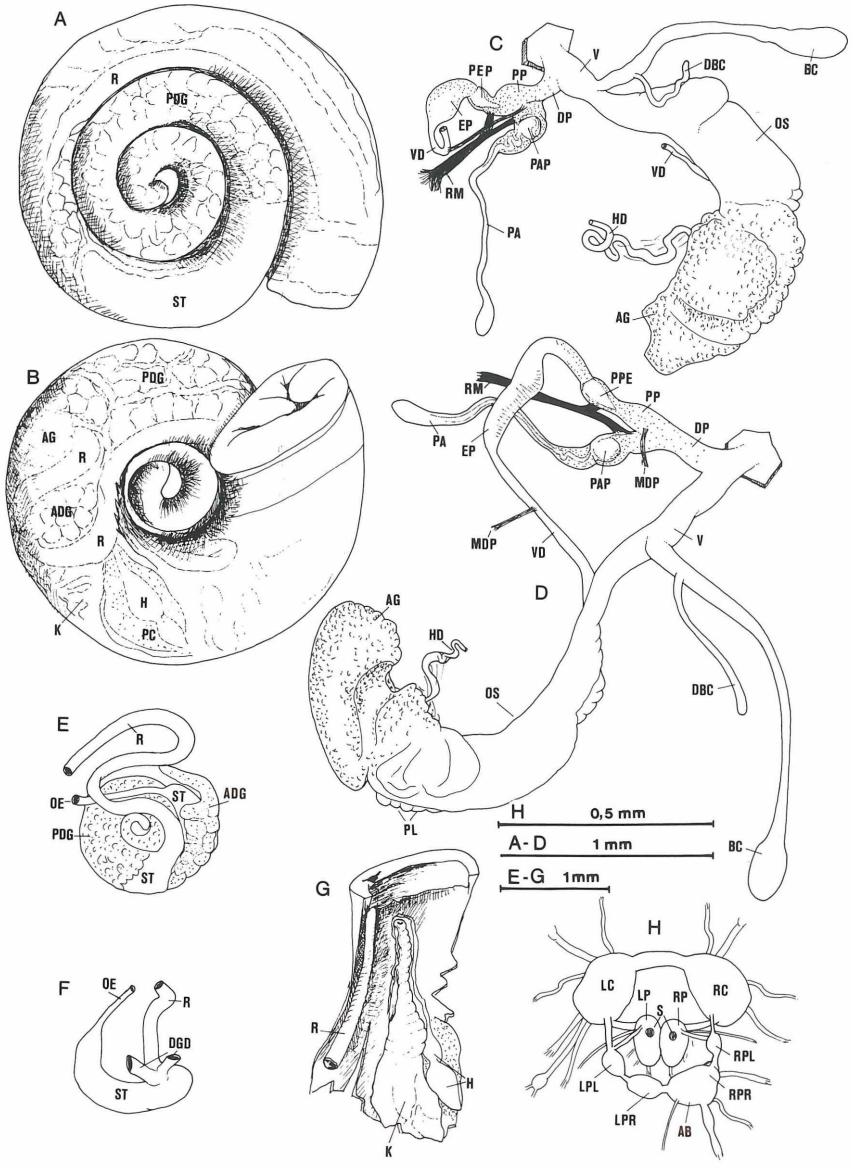
[5]) GITTENBERGER (1977a: 196) says that PILSBRY did not indicate the presence of a papilla inside the epiphallus (= proximal portion of the penis).

Table 1. The main anatomical characters in the species discussed in the text. The penial flagellum is here considered to be the structure on which one of the two arms of the penial retractor ends.

		Branches of the penial retractor: long = A, short = B				Papilla of the penial appendix: long A, short B	Penial papilla: long = A, short B	
Vallonia costata present paper								
Acanthinula aculeata present paper								
Planogyra asteriscus present paper								
"Helix" sororcula present paper								
Zoogenetes harpa (from PILSBRY 1948)		B						
Spelaeodiscus hauffeni (from BOLE 1965)								
Spelaeodiscus unidentatus (from BOLE 1965)								
Spelaeodiscus triarius (from SOOS 1917; HUDEC 1970)		B						
Virpazaria deelemanorum (from GITTENBERGER 1975)		B						
Klemmia magnicosta (from GITTENBERGER 1975)		B						
Klemmia sinistrosa (from GITTENBERGER 1975)								
Lauria cylindracea (from STEENBERG 1925)								
Pupilla muscorum (from STEENBERG 1925)								

▶

Fig. 1. *Gittenbergia sororcula* (BENOIT). Soft parts of some specimens collected at Foce di Cardeto (Apuane Alps, Tuscany) (A-C, E-H) and on the Cansiglio Mountains (Treviso, Venetum) (D). — A-B) two views of same specimen to show the position of the main organs; C-D) genital apparatus; E) the stomach, intestine and digestive gland lobes; F) the stomach; G) the kidney; H) main ganglia. AB abdominal ganglion, ADG anterior lobe of the digestive gland, AG albumen gland. BC gametolytic gland (= bursa copulatrix), DBC diverticulum of the gametolytic gland duct, DGD digestive gland ducts, DP distal portion of the penis, EP epiphallus, H heart, HD hermaphrodite duct, K kidney, LC left cerebral ganglion, LP left



pedal ganglion, LPL left pleural ganglion, LPR left parietal ganglion, MDP small muscle connecting vas deferens to the penial wall, OE oesophagus, OS ovispermiduct, PA penial appendix, PAP papilla of the penial appendix, PC pericardial cavity, PDG posterior lobe of the digestive gland, PEP penial papilla, PL prostatic lobes, PP proximal portion of the penis, R rectum, RC right cerebral ganglion, RM retractor of penial complex, RP right pedal ganglion, RPL right parietal ganglion, S statocyst, ST stomach, T talon, V vagina, VD vas deferens.

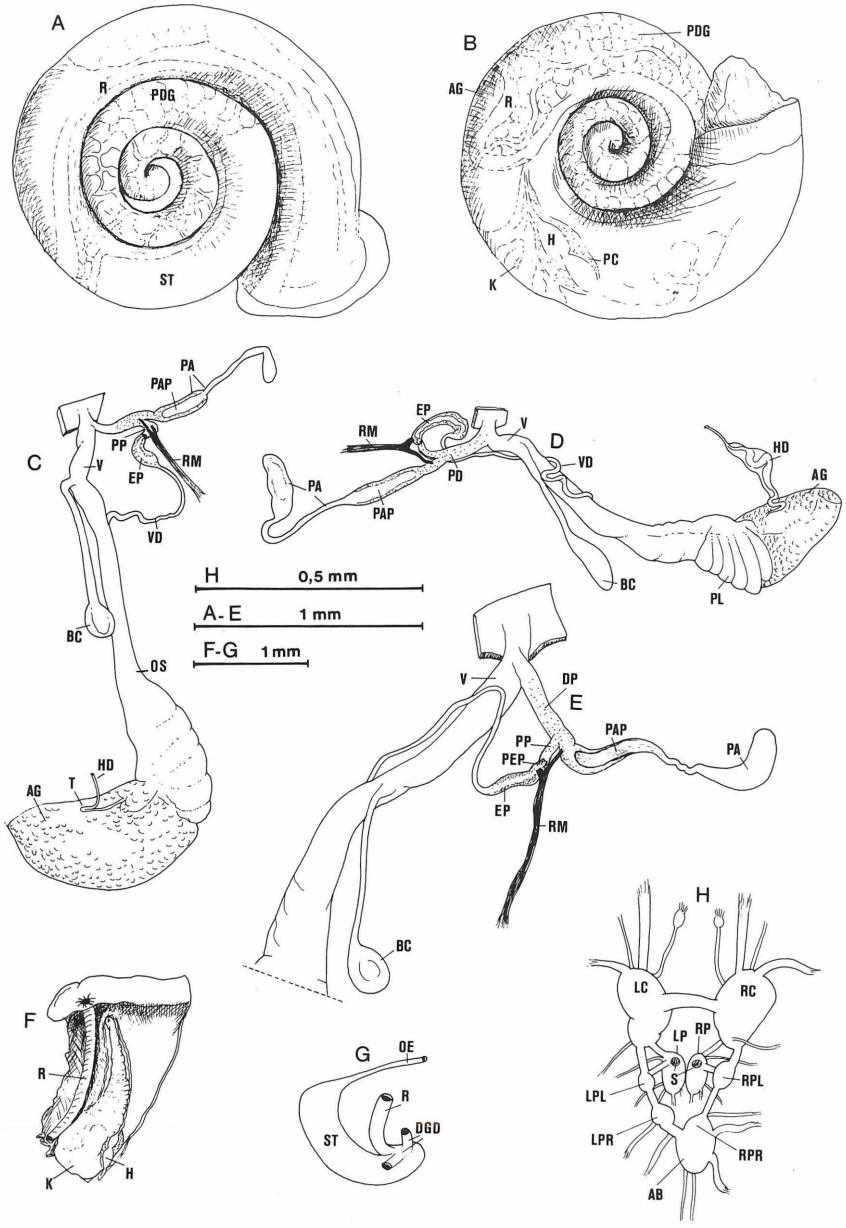


Fig. 2. Soft parts of *Vallonia costata* (MÜLLER) (A-F, H), specimens collected in Pondel (Aosta Valley), and *V. "excentrica"* STERKI (G), specimens collected in Woods Hole (Massachussets, U.S.A.) — A-B) two views of the same specimen to show the position of the main organs; C-D) two views of the same genital apparatus; E) the stomach; F) the kidney; G-H) the main ganglia. Symbols as in Fig. 1.

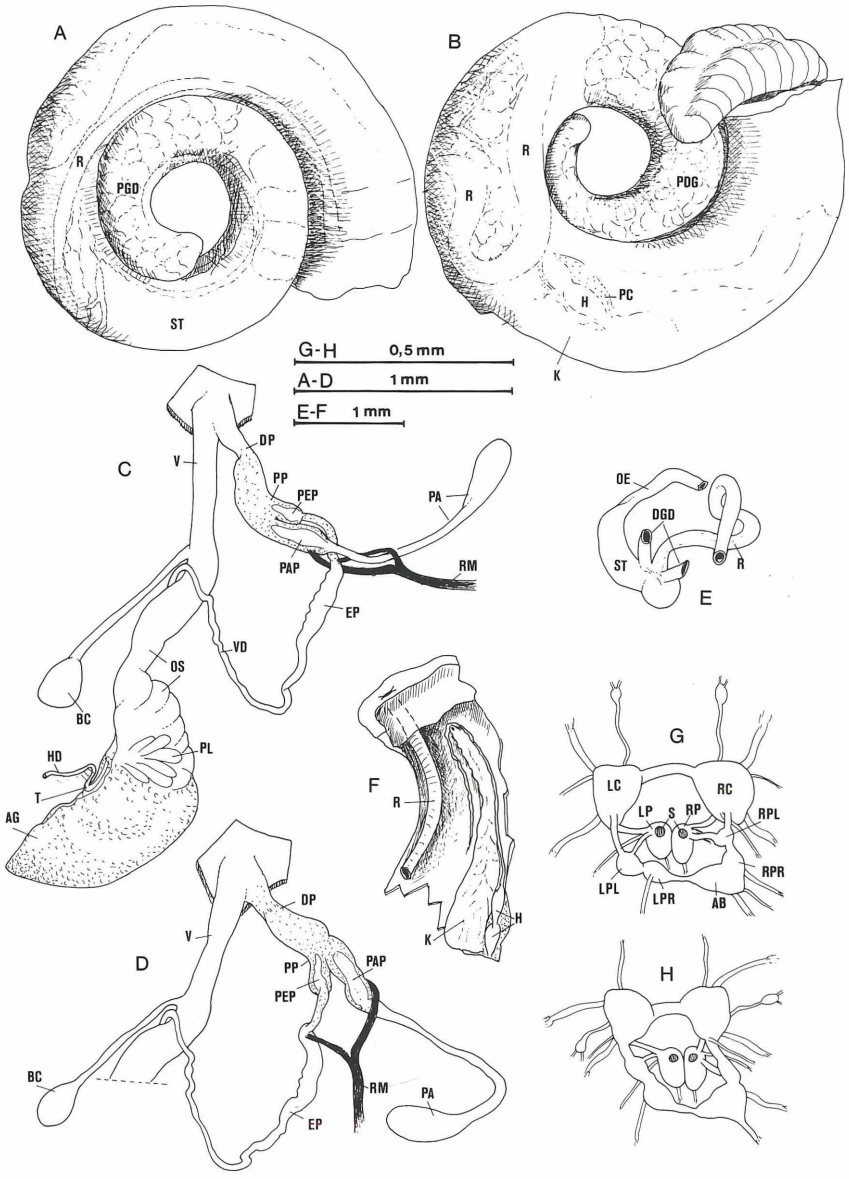


Fig. 3. *Planogyra asteriscus* (Morse). Soft parts of some specimens collected at Carp Creek (Douglas Lake, U.S.A.) (from ANSP Collection, A-1820 F). — A-B) two views of the same specimen to show the position of the main organs; C-E) three genital ducts; F) the kidney; G) the stomach; H) the main ganglia. Symbols as in Fig. 1.

Our studies (Fig. 3 C-E) of numerous specimens of *P. asteriscus*, kindly provided by Dr. G. M. DAVIS of the Academy of Natural Sciences of Philadelphia (U.S.A.) and gathered at Carp Creek (Douglas Lake, U.S.A.) revealed:

a) The presence of a very small penial papilla, perfectly corresponding to that described by BAKER in PILSBRY (1948).

b) The presence of a long, thin papilla in the basal portion of the penial appendix. There was no evidence of a canal in the penial appendix.

c) The penial retractor muscle terminates in two short branches of unequal length: the longer branch is extremely thin and is attached to the wall of the penial appendix where the papilla is situated; the shorter branch is attached to the wall of the proximal part of the penis in proximity to the base of the short penial papilla.

d) The ductus of the gametolytic gland (= bursa copulatrix) lacks a diverticulum.

The radular structure in "*Helix*" *sororcula*, *Vallonia costata* and *Planogyra asteriscus*.

Reference to the radula of "*H.*" *sororcula*, occurs in the literature only in a drawing published by GIUSTI (1969: fig. 1).

This drawing corresponds perfectly to the images we obtained with the SEM of the radula of specimens gathered in the Reatini Mountains (Jaccio Crudele, 1700 m, Central Apennines) (Fig. 4 A-C). The structure of the radula can be thus summarized:

a) Each row of teeth is constituted of 25-31 teeth according to the formula: $\frac{C}{3}+\frac{5-6L}{2}+\frac{1-2LM}{3}+\frac{6-8M}{4-6}$

b) The central tooth displays a long, slender mesocone and two small ectocones. The mesocone is almost as long as the basal plate and the mesocone of the first lateral teeth. The wide and square basal plate has two lateral vertices each of which is raised so as to form a slight point.

c) The lateral teeth present a mesocone and an ectocone. The mesocone is long as the basal plate and has a rather sharp point. The vertex of the external side of the basal plates is raised to form an evident and fairly sharp tip.

d) The doubling of their ectocone distinguishes the latero-marginal teeth from the lateral ones. Their wide basal plate distinguishes them from the marginal teeth.

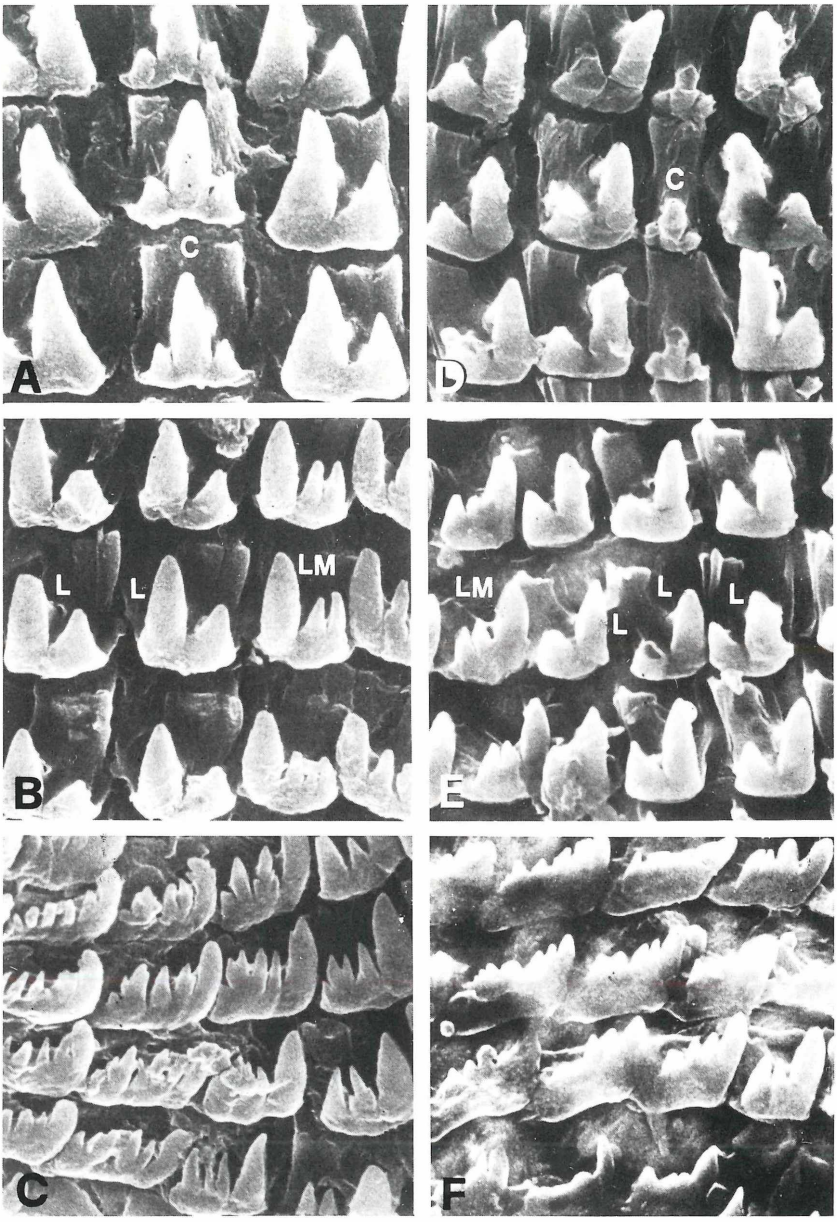
e) The marginal teeth display a mesocone that becomes gradually smaller and less sharp, and the ectocone split into a series of 3-5 small points.

The radula of *V. costata* is found in the literature only in descriptions and drawings by BOWELL (1915: 157-158, Fig.), WATSON (1920: 11-14) and PILSBRY

Fig. 4. Portions of the radula of *Gittenbergia sororcula* (BENOIT) (A-C) from specimens collected on the Reatini Mountains (Central Apennines) and of *Planogyra asteriscus* (MORSE) from specimens collected at Carp Creek (Douglas Lake, U.S.A.) (from ANSP Collection, A-1820 F) (D-F). — A) the central tooth of *G. sororcula* shows a square basal plate and a mesocone almost as long as the basal plate and the mesocone of the first lateral teeth (3000 ×). B) a group of lateral (L) and latero-marginal (LM) teeth (3000 ×). C) a group of extreme marginal teeth (3000 ×). D) the central tooth of *P. asteriscus* shows a rectangular basal plate and a very small mesocone (3000 ×). E) a group of lateral (L) and latero-marginal (LM) teeth (3000 ×). F) a group of extreme marginal teeth (3000 ×). ▶

(1948: 1020, fig. 543B after STEENBERG). Our studies (Fig. 5A-C) confirm this literature references and permit the following description:

a) Each row of teeth is constituted of 25-29 teeth, according to the formula: $\frac{C}{3}+\frac{4L}{2}+\frac{1LM}{2-3}+\frac{7-9M}{4-7}$.



b) The central tooth has a short, pointed mesocone and two very small ectocones. The length of the mesocone does not exceed half that of the basal plate, nor half that of the first lateral teeth. The basal plate is rectangular and presents two lateral vertices, each raised to form sharp point.
c) The lateral teeth present a mesocone and an ectocone. The mesocone is slightly longer than the basal plate and presents a very sharp tip. The ectocone is sharp and does not exceed half the length of the mesocone. The vertex of the external side of the basal plates forms a fairly sharp point.
d) A smaller basal plate and an ectocone that is sometimes split in two tips, are distinguishing features of the latero-marginal teeth.
e) The basal plate of the marginal teeth is not evident. Their mesocone becomes gradually reduced in size and the ectocone is split into a series of 3-6 small tips.

In *V. pulchella* the radula has essentially the same structure (WATSON 1920: 12, fig. 4d; PILSBRY 1948: 1020, fig. 543A). The only difference lies in the reduction of the number of the lateral teeth to 3. Our studies (Fig. 5D-F) do not confirm this, having demonstrated instead the presence of 4 lateral teeth in *V. pulchella.*

The radula of *P. asteriscus* is not well known. In the literatur the only reference to it is that of PILSBRY (1948: 1037). This author sustains that it follows the formula 13+1+13, presents a central tricuspidated tooth smaller than the lateral teeth, and cusps smaller than the basal plate.

Our SEM studies (Fig. 4D-F) partially confirm PILSBRY's report and permit the following description:

a) Each row of teeth is constituted of 27-29 teeth, according to the formula: $\frac{C}{3}+\frac{6L}{2}+\frac{1LM}{3}+\frac{6-7M}{4-6}$
b) The central tooth has a short pointed mesocone and two small ectocones. The basal plate is more than twice as long as the mesocone. It is rectangular, with two raised lateral vertices that each forms a tip.
c) The lateral teeth present a mesocone and an ectocone. The mesocone is as long as the basal plate and presents a sharp tip. The ectocone is small and pointed with a length that does not exceed half that of the mesocone. The external side vertex of the basal plate is raised to form a fairly sharp point.
d) The latero-marginal tooth is distinguished for its reduced basal plate and its ectocone split into two tips.
e) The basal plate of the marginal teeth is not evident and the ectocone is split into a series of 3-5 small, pointed tips.

Fig. 5. Portions of the radula of *Vallonia costata* (MÜLLER) from specimens collected nearby ▶ Verona (Venetum) (A-C) and of *Vallonia pulchella* (MÜLLER) from specimens collected nearby Siena (Tuscany) (D-F). — A) the central tooth of *V. costata* shows a rectangular basal plate and a very small mesocone (3000×). B) a group of lateral (L), latero-marginal (LM) and marginal (M) teeth. (2000×). C) a group of extreme marginal teeth (2000×). D) the central tooth of *V. pulchella* shows a rectangular basal plate and a small mesocone (3000×). E) a group of lateral (L) and latero-marginal (LM) teeth (3000×). F) a group of extreme marginal teeth (3000×).

Other anatomical characteristics of "*Helix*" *sororcula*, *Vallonia costata* and *Planogyra asteriscus*.

The dissection of numerous specimens of the three species did not reveal any differences worthy of note in the form and disposition of the different organs.

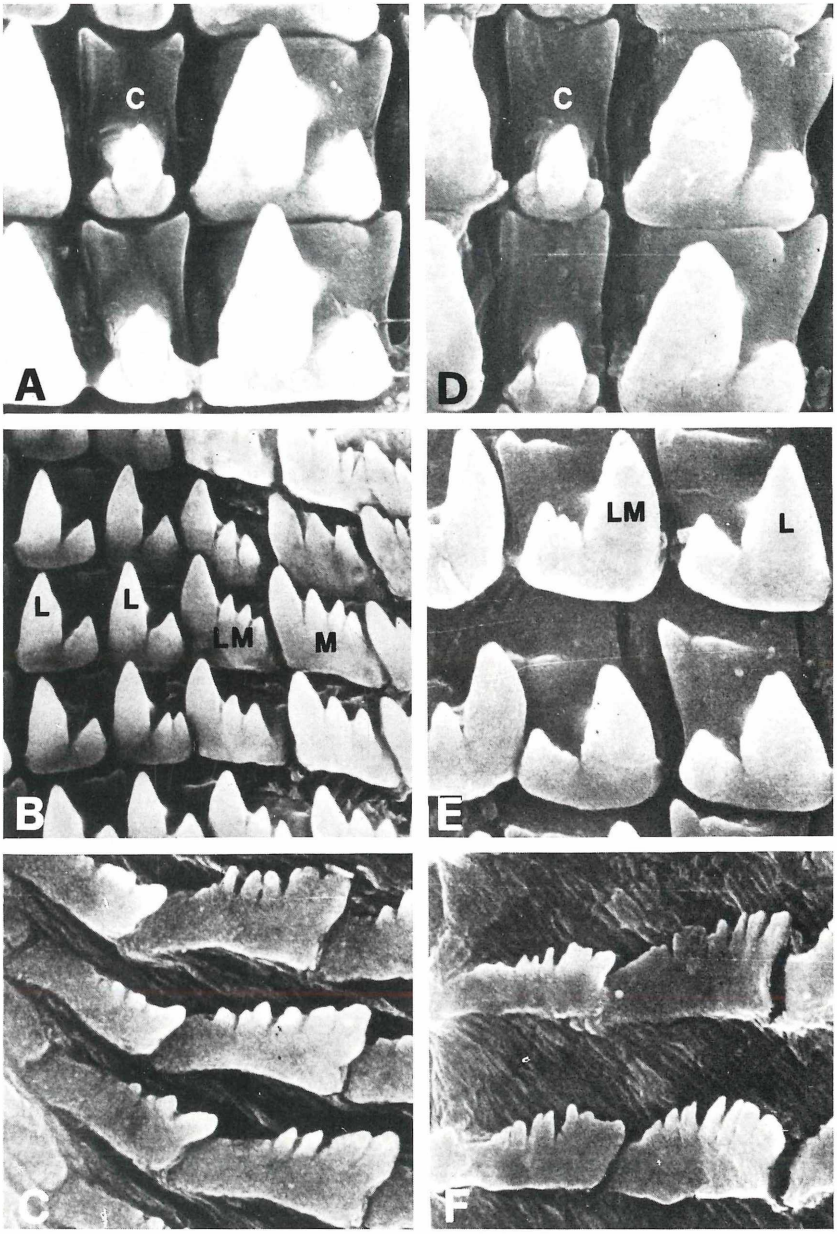


Table 2.
The radular formula and radular characters in the species discussed in the text.

	Teeth on each row	Central tooth: short A long B	n lateral teeth	n latero-marginal teeth	n marginal teeth	cusps on the marginal teeth
Vallonia costata present paper	27–29	A	4	1	7–9	4–7
Vallonia pulchella present paper	27	A	4	1	8	3–7
Acanthinula aculeata (from BOWELL 1915)	31	A	6	1	8	4–8
Acanthinula aculeata (from WATSON 1920)	29	A	6		8	
Planogyra asteriscus present paper	27–29		6	1	6–7	4–6
"Helix" sororcula present paper	25–31	B	5–6	1–2	6–8	4–6
Zoogenetes harpa (from STEENBERG 1925)	33	B	5	1	10	4–7
Zoogenetes harpa (from PILSBRY 1948)	37	B	5	1	11	3–6
Spelaeodiscus hauffeni (from BOLE 1965)	31–37		4–5	0–1	10–13	3–7
Spelaeodiscus unidentatus (from BOLE 1965)	29		3–4	0–1	10	4–6
Spelaeodiscus triarius (from SOOS 1917)	33–39	A	5	1–2?	9–10	3–6?
Virpazaria deelemanorum (from GITTENBERGER 1975)	25	A	4–5		7–8	
Klemmia magnicosta (from GITTENBERGER 1975)	31	A	4	1	10	4–9
Klemmia sinistrorsa (from GITTENBERGER 1975)	35		4	1	12	4–9
Lauria cylindracea (from STEENBERG 1925)	39	B	7	2	10	5–9
Pupilla muscorum (from STEENBERG 1925)	27–29	B	5	2	7	4–6

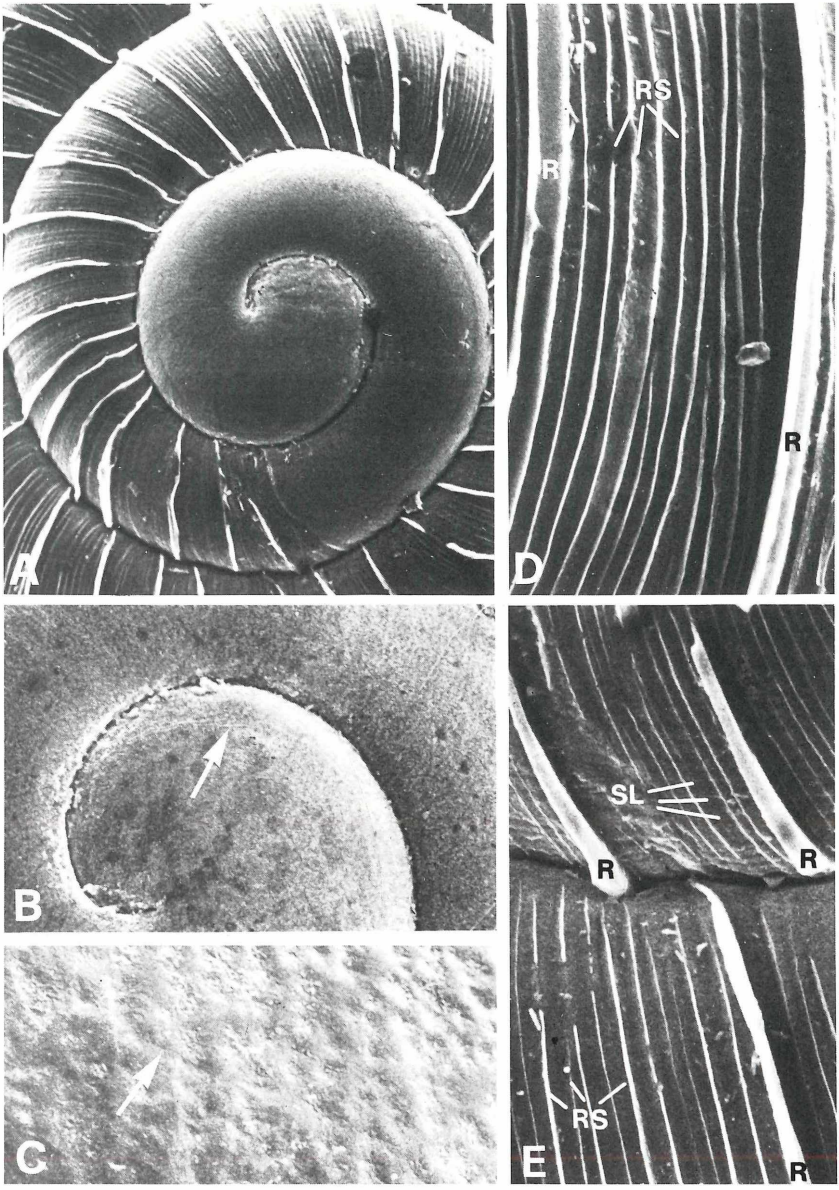


Fig. 6. *Gittenbergia sororcula* (Benoit). The external shell surface from specimens collected on the Cansiglio Mountains (Treviso, Venetum) (A-B, D-E) and on the Djurdjura Mountains (Great Kabilia, Algeria) (C). — A) a view of the protoconch and of the first whorls (100 ×); B) at its beginning the protoconch is malleated and shows thin spiral striae (arrows) (200 ×); C) in other parts the malleated protoconch shows shallow spiral grooves (arrow) (1000 ×); D) the teleoconch shows a periostracal layer with high ribs (R) and shorter radial striae (RS). Thin spiral lines (SL) run under the periostracal layer (300 ×); E) spiral lines (SL) are more evident in tangential images. R ribs, RS radial striae (300 ×).

The same form and dimensions are displayed in the orthurethrous type nefridium (Figs. 1G, 2F, 3F) and the digestive apparatus, especially the stomach (Figs. 1EF, 2E, 3G), of all three species.

The nervous system (Figs. 1H, 2GH, 3H) also shows a structure in the three species, which is similar in both the shape and disposition of the main ganglia. In *V costata* (as in *V. "excentrica"* STERKI), however, the left pleural ganglion and the left parietal ganglion seem to lie more closely to one another and so are less evidently distinguished with respect to those of *"H." sororcula* and *P. asteriscus.*

Shell structure and external surface microsculpture in *"Helix" sororcula*, *Vallonia costata* and *Planogyra asteriscus.*

The shell structure and microstructure of *"H." sororcula* are referred to in the literature principally in a note by GITTENBERGER (1972: 66, figs. 3, 8, 16). Our SEM studies (Fig. 6) confirm some of the published information and permit the addition of the following points:

a) The yellowish-white shell is rather fragile and thin; the peristome (= mouth-edge) is neither thickened nor reflected.

b) The protoconch displays an external surface which is malleated and traversed by thin spiral striae and rare, shallow spiral grooves.

c) The teleoconch has growth lines where the raised periostracum forms high ribs and lower radial striae. Between the two successive ribs 6-12 radial striae are interposed; they are discontinuous and generally unbranched. Spiral lines run over the surface of the whorls, under the periostracal layer.

The shell structure and microstructure of its external surface in *V. costata* are known through a paper by GITTENBERGER (1972: 63-64, figs. 9-11). Our investigations (Fig. 7) have permitted the following description:

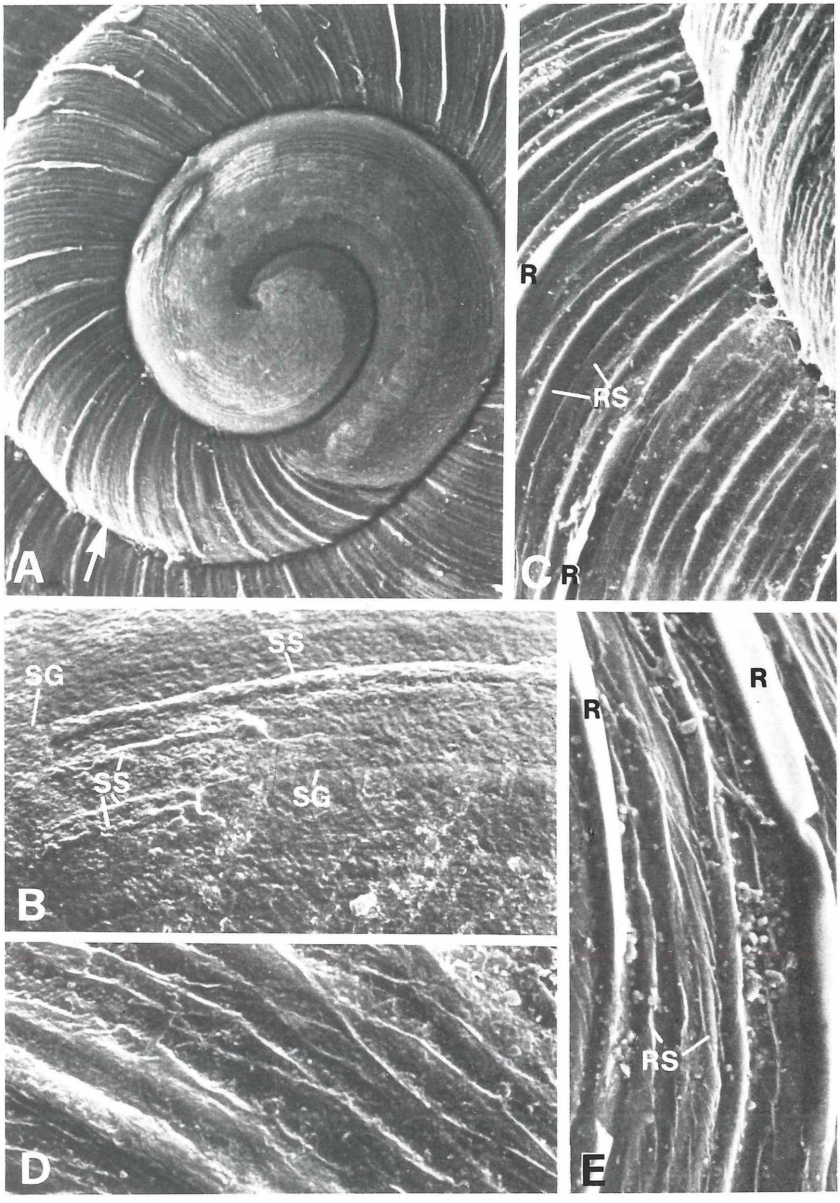
a) The milky-white shell is rather thick and resistant; the mouth-edge is thickened and reflected.

b) The protoconch shows a finely corrugated external surface, provided with numerous evident spiral striae. The latter are decaying, and when missing reveal the presence of corresponding narrow spiral grooves.

c) The teleoconch presents growth lines where the periostracum is raised to form high ribs and shorter radial striae. Between the two successive ribs there are 5-11 radial striae. These striae follow irregular paths and are more or less ramified.

Fig. 7. *Vallonia costata* (MÜLLER). The external shell surface from specimens collected nearby Verona (Venetum) (A, C-D) and Siena (Tuscany) (B, E). — A) a view of the protoconch and of the first whorls. Note the numerous spiral striae (SS) which run on the protoconch. Traces of spiral lines are visible on tangential images of the first whorl of the teleoconch (arrow) (100×); B) the spiral striae (SS) of the protoconch when missing reveal the presence of corresponding narrow spiral grooves (SG) (arrows) (1000×); C) ribs (R) and radial striae (RS) are visible on the first whorl of the teleoconch; the radial striae are scarcely branched (200×); D) ribs (R) and branched radial striae (RS) are present on the last whorl of the teleoconch (300×); E) the branches of the radial striae (1000×). ▶

Their branches run between the growth lines. Spiral lines are not evident; nevertheless tangential images of the first whorls seem to reveal feeble traces of them (Fig. 7A).



In other *Vallonia* the external structure of the shell is altogether different. *V. "enniensis"* (GREDLER) (cfr. GITTENBERGER 1972: fig. 12)[6]) displays weak ribs on the teleoconch, and between these there appear weak, ramified radial striae that follow irregular paths. Spiral lines seem to be absent. *V. pulchella* (Fig. 8) and *V. "excentrica"* (Fig. 9) both display the same characteristics: protoconch with slight roughness and lined by numerous thin spiral grooves; teleoconch, furnished with growth lines, as well as rare, weak traces of branched periostracal striae, disposed irregularly. There are also thin spiral grooves, well visible in tangential images (Fig. 8C, 9C-D).

The structure of the shell and its external surface in *Planogyra* is already known through images published by GITTENBERGER (1972: figs. 4-7, 15) and SOLEM (1977: figs. 13-18) of *P. asteriscus* and *P. clappi* (PILSBRY).

Our research, carried out on *P. asteriscus* (Fig. 10) has confirmed the data permitting us to underline the following points:

a) The pale-brown shell is rather thin and fragile; the peristome is thickened only at the basal and columellar margins and is slightly reflected.

c) The protoconch shows an external surface which is malleated and lined by numerous spiral grooves.

c) The teleoconch shows prominent and radially disposed periostracal ribs. There are numerous radial striae found between the ribs. These striae are narrow, discontinuous, and rarely branched. The spiral lines are evident over the entire surface of the whorls. In the areas lacking the periostracal layer the mineralized shell wall presents evident spiral lines and radial growth lines. The latter are found in correspondence of the periostracal radial striae that develop between the ribs.

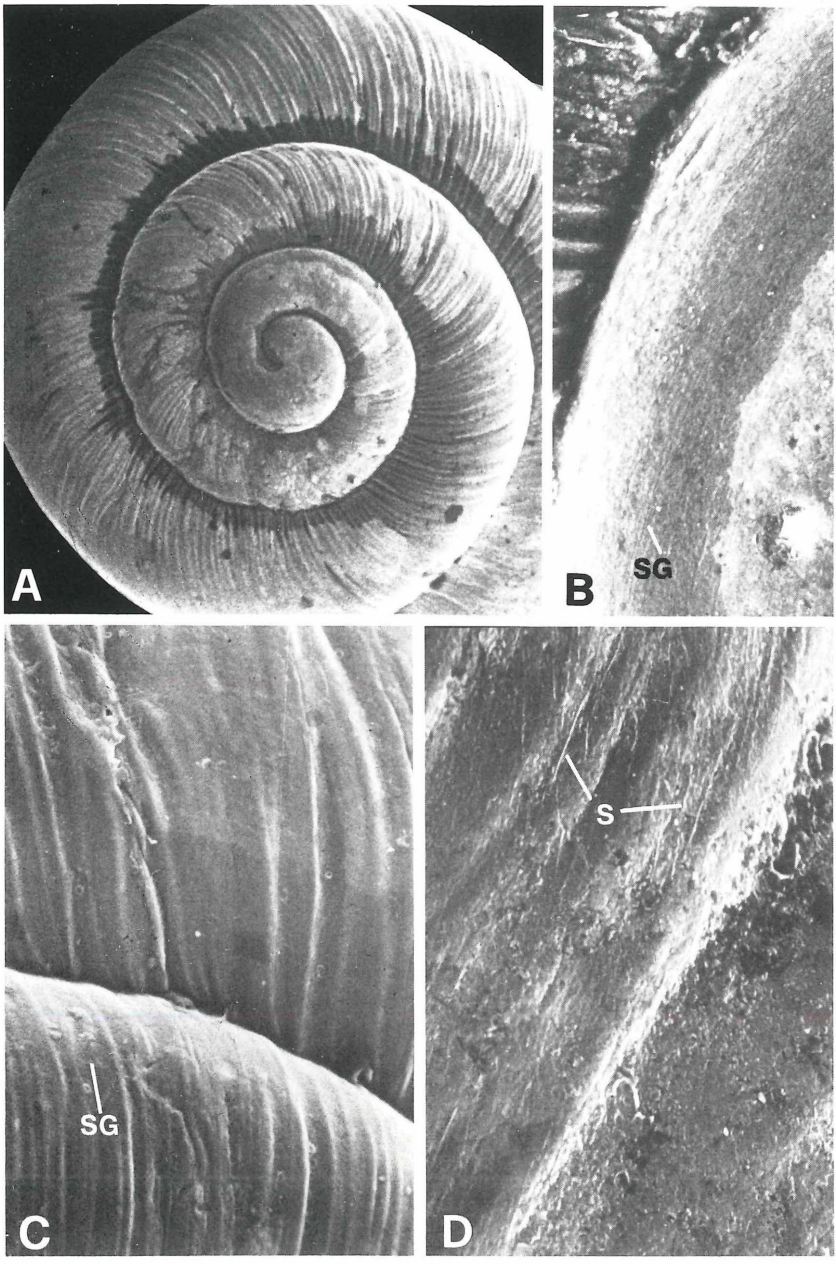
Discussion.

In our opinion this report, as summarized in Tables 1-3, demonstrates that *"Helix" sororcula,* while showing definite similarities to both *Vallonia costata* and *Planogyra asteriscus,* also displays significant distinguishing characters. Five of the

[6]) VARGA (1972) sustains that *V enniensis* could be recognized as a simple subspecies of *V. pulchella* (*V. pulchella enniensis*) and that *V excentrica* could be considered a synonym of *V. pulchella pulchella.* The present tendency to subdivide *Vallonia* into numerous species on the basis of weak conchological peculiarities seems rather subjective. The constant aphally of the *Vallonia* of the group *pulchella* suggests, in effect, that the group could be an aggregation of genetically distinct entities whose affinities are not distinguishable on a morphological basis. Populations that, in a given country result to be *V. pulchella* or *V. "excentrica"*, due to their shell form, cannot in fact correspond genetically to phenotypically corresponding populations living in other countries. It therefore seems more opportune to define them simply as *V. pulchella* "complex"

Fig. 8. *Vallonia pulchella* (MÜLLER). The external shell surface from specimens collected nearby Siena (Tuscany). — A) a view of the shell, note the presence on the teleoconch of regularly spaced growth lines (45×); B) narrow spiral grooves (SG) are visible on the protoconch (arrow) (500×); C) growth lines, sometimes giving rise to small radial striae, are present on the teleoconch. Tangential images reveal the presence of narrow spiral grooves (SG) (arrow) (200×); D) the periostracum on the growth lines of the teleoconch gives rise to weak branched periostracal striae, disposed irregularly (800×). ▶

eight anatomical characters displayed by "*H.*" *sororcula* and listed in Tab. 1 are common to both *P. asteriscus* and *V. costata.* It differs from the latter, however, in the short branches of the penial retractor, the shorter papilla of the penial appendix



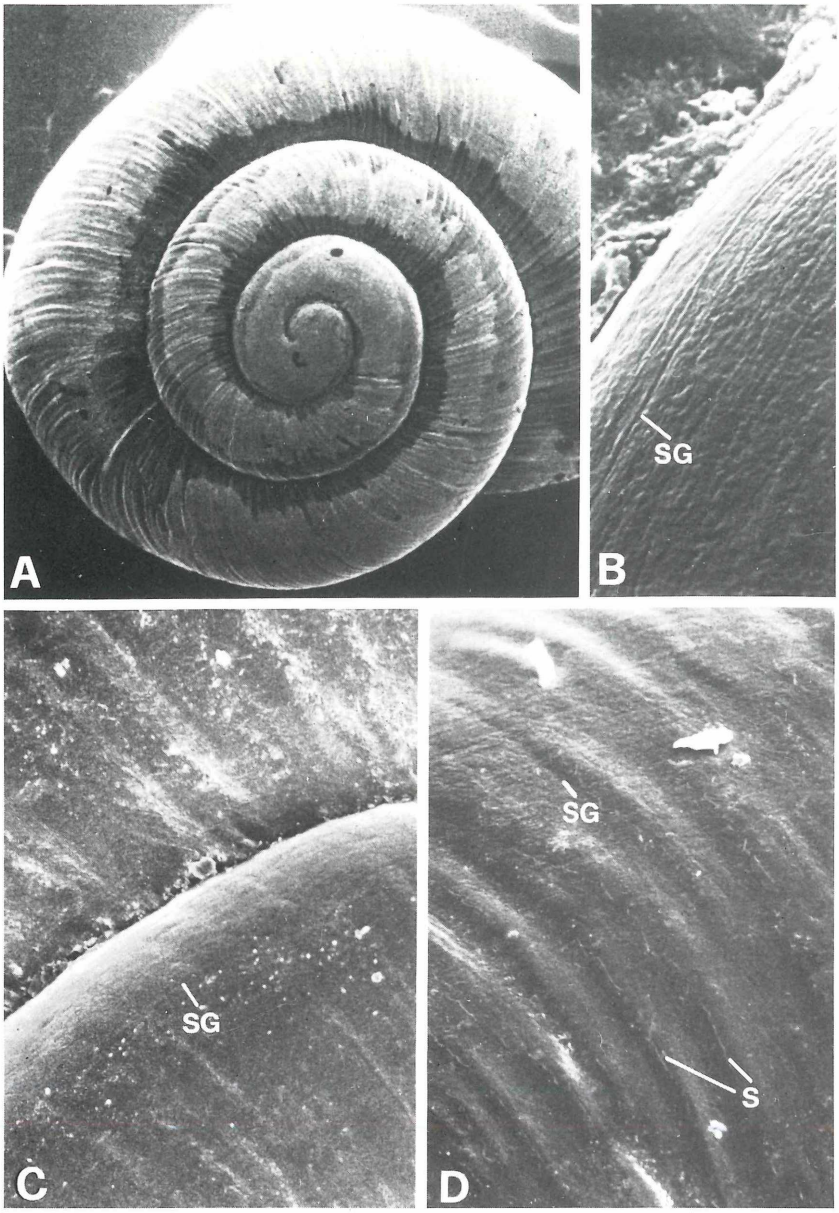


Fig. 9. *Vallonia "excentrica"* Sterki. The external shell surface from specimens collected nearby Siena (Tuscany). — A) a view of the shell to show the presence on the teleoconch of regularly spaced growth lines (45×); B) narrow spiral grooves (SG) are visible on the protoconch (1000×); C) tangential images reveal the presence of narrow spiral grooves (SG) on the teleoconch (arrow) (300×); D) spiral grooves (SG) and weak traces of periostracal striae (S) (arrows) are present on the teleoconch (300×).

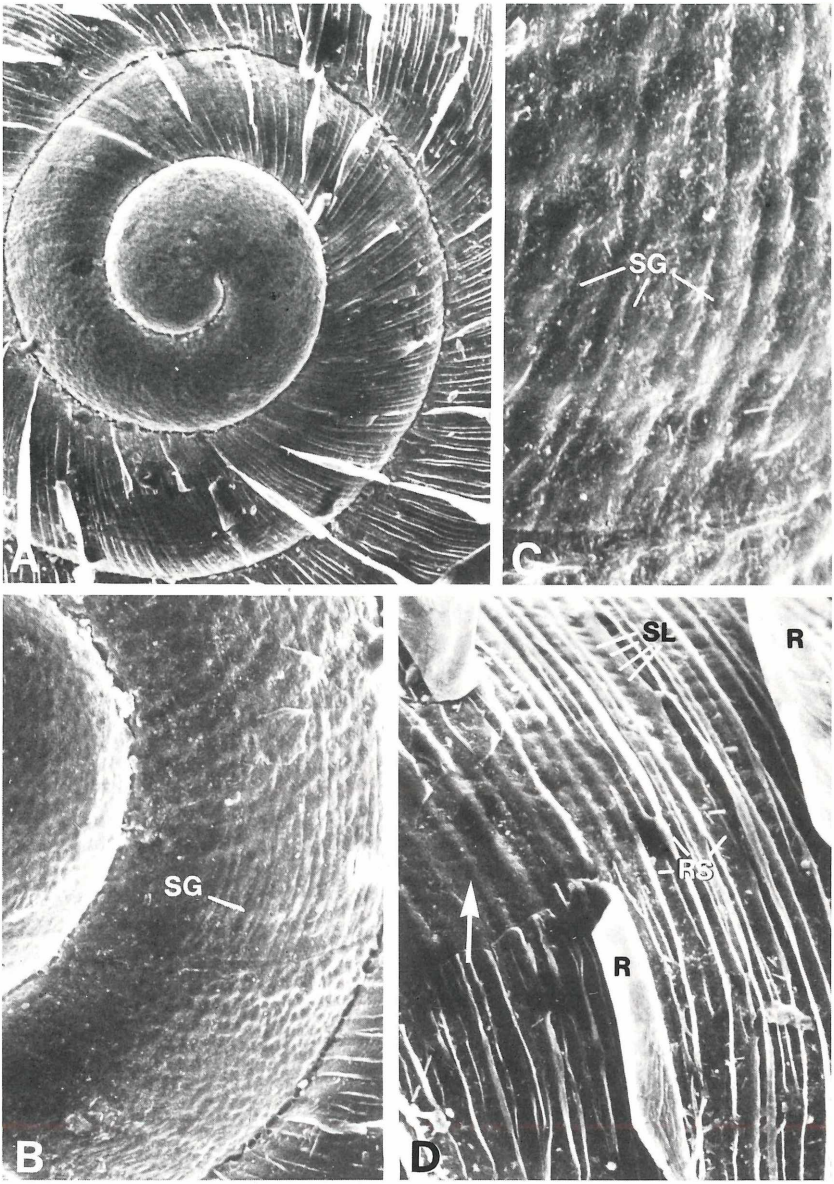


Fig. 10. *Planogyra asteriscus* (Morse). The external shell surface from specimens collected at Carp Creek (Douglas Lake, U.S.A.) (From ANSP Collection, A-1820 F). — A) a view of the protoconch and of the first whorls (100×); B) the protoconch is malleated and shows spiral grooves (300×); C) the grooves on the protoconch (1000×); D) ribs (R), radial striae (RS) and spiral lines (SL) are visible on the teleoconch. As is evident in areas lacking the periostracal layer (arrow) the mineralized shell wall shows spiral lines and growth lines. These last correspond to the periostracal radial striae and ribs (300×).

and the presence of a diverticulum in the bursa copulatrix duct (= gametolytic gland canal).[7])

It differs from *P. asteriscus* not only in the shorter papilla of the penial appendix and the presence of a diverticulum in the bursa copulatrix canal, but also in the longer penial papilla.[8]) The discovery in *P. asteriscus* of a bifurcated penial retractor (described and drawn incorrectly by BAKER in PILSBRY 1948: 1038, fig. 460/1-2) eliminates one of the characters previously cited in favour of a greater affinity between "*H.*" *sororcula* and *V. costata* (cfr. GIUSTI 1971). This does not however confirm the inclusion of "*H.*" *sororcula* in the genus *Planogyra*. The latter is distinguished, just as the *Vallonia,* by the absence of a diverticulum in the bursa copulatrix duct.

There is no substantial difference in the radular formula of the three species (Tab. 2). "*H.*" *sororcula,* however, is clearly distinguished by the structure of the central tooth. The latter shows a mesocone as long as the basal plate and therefore comparable in height to that of the first lateral teeth. In *V. costata* and in *P. asteriscus,* instead, the central tooth is reduced and presents cusps (mesocone) whose length does not exceed half that of the basal plate nor half of the mesocone of the lateral teeth.

As to the conchological characters, and in particular the microsculpture of the external surface of the whorls (Tab. 3), a greater correspondence is evident between "*H.*" *sororcula* and *P. asteriscus.* GITTENBERGER's (1972, 1977a) tendency to assign the two species to the same genus is therefore understandable. However, establishment of the genus is not feasible on the sole basis on the microsculpture of the shell's external surface.

Even the Vallonias display differences among themselves. Although all are lacking spiral lines on the teleoconch, some (*V. costata*) have evident periostracal ribs, while others (*V. pulchella* complex) are almost or completely lacking them. Moreover, *V. pulchella* and *V.* "*excentrica*" are almost completely lacking ramified radial striae, that are well developed in *V. costata* (and hardly evident in *V.* "*enniensis*") and present narrow spiral grooves on the teleoconch that are absent in *V. costata.*

The microsculpture of the protoconch is of no aid in assigning "*H.*" *sororcula* to *Vallonia* or to *Planogyra.* "*H.*" *sororcula* does not display the large spiral striae normally present in *V costata* and similar to those of *Acanthinula aculeata* (MÜLLER). This does not suffice to differentiate it from the *Vallonia* however. In fact, it displays traces of spiral grooves that seem similar to those present on the protoconch of *P. asteriscus* but which recall also the smaller ones present on the protoconch of the *Vallonia,* as well as *V. costata* that have lost the material covering them and forming the spiral striae.

In the final analysis the three species seem to belong to three different genera. "*H.*" *sororcula* is consequently elected the type species of the new genus described below.

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[7]) Perhaps due to its small size, the diverticulum escaped notice during previous anatomical studies (GIUSTI 1969, GITTENBERGER 1972, 1977a). GITTENBERGER (1972: fig. 2) indicated it in only one of the two specimens he examined.

[8]) It is interesting to note that a noteworthy anatomical affinity exists between *V. costata* and *P. asteriscus.* The two species concur in six of the eight characters listed in Tab. 1 and differ only in the length of the branches of the penial retractor and the length of the penial papilla.

Table 3.
The main shell characters in the species discussed in the text.

	Peristome (Mouth-edge): thickened and reflected ..... = A; slightly thickened and slightly reflected = B; not thickened nor reflected ..... = C; with denticles ..... = D	Teleoconch, spiral lines: well evident = A; absent ..... = B; traces ..... = C	Teleoconch, spiral grooves	Teleoconch, periostracal ribs: well evident ... = A; slightly evident = B; absent ..... = C	Teleoconch, radial striae: evident and ramified ..... = A; slightly evident and ramified = B; evident not ramified ..... = C; traces ..... = D	Protoconch: spiral striae ..... = A; spiral grooves well evident = B; malleated ..... = C; traces of spiral grooves .. = D
Vallonia costata (from GITTENBERGER 1972)	A	B	–	A	A	A
Vallonia costata present paper	A	C	–	A	A	A+B
Vallonia pulchella present paper	A	B	+	C	D	B
Vallonia "excentrica" present paper	A	B	+	C	D	B
Vallonia enniensis (from GITTENBERGER 1972)	A	B	–	B	B	?
Acanthinula aculeata (from GITTENBERGER 1977)	B	A	–	A	C	A
Planogyra asteriscus (from GITTENBERGER 1972)	B	A	–	A	C	B+C
Planogyra asteriscus (from SOLEM 1977)	B	A	–	A	C	B+C
Planogyra asteriscus present paper	B	A	–	A	C	B+C
Planogyra clappi (from GITTENBERGER 1972)	B	A	–	A	C	B+C
Planogyra clappi (from SOLEM 1977)	B	A	–	A	C	?B+C
"Helix" sororcula (from GITTENBERGER 1972)	C	A	–	A	C	C
"Helix" sororcula present paper	C	A	–	A	C	A+C+D
Spelaeodiscus triarius (from GITTENBERGER 1975)	A+D	B	–	A	A	C
Klemmia sinistrosa (from GITTENBERGER 1975)	B	B	–	A	B	C

Gittenbergia n. gen.

Description: Small, fragile shell milky-white or yellowish-white in colour. External surface of the protoconch malleated and with thin spiral striae and rare shallow spiral grooves. External surface of the teleoconch furnished with fairly evident periostracal ribs, interposed with narrow unbranched radial striae; spiral lines run over the whorls. Mouth-edge neither thickened nor reflected. Umbilicus opened.

Genital apparatus provided with a penial complex which shows a penial appendix whose base contains a short, wide papilla; widened epiphallus; proximal portion of the penis containing a long, pointed papilla; penial retractor subdivided into two short branches, the longest one terminates at the base of the penial appendix, the shortest on the proximal portion of the penis. Gametolytic gland duct provided with a thin tubular diverticulum. Aphally is unknown. Oviparous. Radula showing a tricuspid central tooth with mesocone as long as the basal plate and the mesocone of the first lateral teeth.

The new genus, dedicated to our friend and collegue Dr. E. GITTENBERGER from Leiden (Holland), seems to lie closer to the genus *Zoogenetes* than to *Vallonia* or to *Planogyra,* particularly when considering the structure of the central tooth of the radula.

Z. harpa (SAY), the only species extant, is not well known anatomically (see PILSBRY 1948: pp. 1041-1045, figs. 557-559; STEENBERG 1925: 102-104, pls. 28-29) but it seems to show anatomical and biological characteristics which are sufficiently different. It is, in fact, ovoviviparous; frequently aphallic; it shows a genital duct with longer branches of the penial retractor and a diverticulum of the gametolytic gland duct which arises very near the gametolytic gland. Notwithstanding this, the affinity between *Zoogenetes* and *Gittenbergia* is at least as evident as that between *Vallonia* and *Planogyra.* It therefore follows that the usual subdivision of the Valloniidae into the two subfamilies Acanthinulinae and Valloniinae[9]) based esclusively on conchological characters cannot be convalidated when the peculiarities of the genital duct and the radula are taken into account. In our opinion such a subdivision is to be abandoned, even if we are at present unable to say if *Gittenbergia* should be placed among the Valloniidae or not. We feel it necessary to point out that the distinction between Valloniidae and Pupillidae is a problem that has been neglected too long.

The Spelaeodiscinae, for example, presently included among the Pupillidae seem much closer to the Valloniidae than is *Gittenbergia* , because the central tooth of their radula is reduced and presents a mesocone shorter than the basal plate and shorter than the mesocone of the first lateral teeth.[10])

If we exclude convergence phenomena in the structure of the central tooth of the radula, *Gittenbergia* and *Zoogenetes* could easily be placed near to *Pupilla* and

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[9]) The subfamily Spelaeodiscinae, which has been included by ZILCH (1959, 1969) in the Valloniidae, has been considered by others to belong to the Pupillidae (BOLE 1965, GITTENBERGER 1967, 1969, HUDEC 1970, KERNEY, CAMERON & JUNGBLUTH 1983).

[10]) This phenomenon is evident in *Spelaeodiscus unidentatus* BOLE while it seems less evident in *S. hauffeni* (SCHMIDT) and *S. triarius* (ROSSMÄSSLER) (cfr. SOOS 1917; BOLE 1965). The central tooth is very reduced in *Virpazaria* and *Klemmia* (cfr. GITTENBERGER 1975).

Lauria (Pupillidae), while the Spelaeodiscinae could be placed near to *Vallonia, Acanthinula* and *Planogyra* (Valloniidae) (see Tab. 2).[11]) Moreover, *Gittenbergia* and *Zoogenetes* present a fairly developed diverticulum of the bursa copulatrix similar to that of numerous Pupillidae (excluding *Lauria*), which is absent, instead, in the Spelaeodiscinae, just as in *Vallonia, Acanthinula* and *Planogyra.*[12])

Only careful re-examination of the anatomical characteristics of the genera herein discussed can permit a fresh approach to the present problem. Only then can we determine the validity of the division between Pupillidae and Valloniidae, and to state to what family *Gittenbergia* belongs.

Summary

The analysis of the anatomical and conchological characteristics of *Vallonia costata, Planogyra asteriscus* and "*Helix*" *sororcula* has allowed us to ascertain that the last belongs to a separate new genus: *Gittenbergia*. The data of present research suggest the abolition of the subdivision of the Valloniidae into the Valloniinae and the Acanthinulinae. *Gittenbergia* n. gen. and other related genera seem to hold a place in between the Valloniidae and the Pupillidae. This underlines the need for further investigation of the distinction of the Valloniidae from the Pupillidae.

Addendum.

Whilst the present paper was in press, numerous specimens of *Zoogenetes harpa* (SAY) from Sweden (TED VON PROSCHWITZ leg.) have been studied. All of them were aphallic. In the female portion of the genital duct, the diverticulum of the gametolytic gland (= bursa copulatrix) is frequently poorly developed or totally absent.

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[11]) The peculiarity of the microsculpture of the shell's external surface are subject to convergence and so should not be taken into consideration for use in systematics at the genus level. For example *Punctum* (*Toltecia*) *pusillum* (LOWE) (Punctidae) displays a protoconch microsculpture similar to that of *V. costata* and a teleoconch microsculpture identical to that of the *Planogyra* (see GITTENBERGER 1972, GIUSTI 1973, SOLEM 1977).

[12]) The anatomical characters adopted by BOLE (1965) and HUDEC (1970) in distinguishing the Spelaeodiscinae, both from the Pupillinae, Lauriinae, and the Valloniidae, are subject to vary from one species to another and therefore lack sufficient significance. The penial diverticulum (= penial flagellum auctorum) for example, is present not only in *Pupilla* and in *Lauria*, but also in *Acanthinula* (see Tab. 1).

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