NOTES ON THE GENUS GAEOITIS
SHUTTLEWORTH, 1854
(MOLLUSCA, GASTROPODA, BULIMULIDAE)

by

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SUMMARY

This paper contains redescriptions of the four species of Gaectis, while photographs of all the types are presented for the first time. The anatomy is described from a single specimen of Gaectis sp. and the relationships of this genus with Amphibulina, Pellucula and Petella are discussed.

INTRODUCTION

The genus Gaectis was described by Shuttleworth in 1854, with three species, G. nigrolimata, G. flavolineata and G. albopunctulata. Eland & Binney (1873) and Binney (1884) reported on the jaw and radula of Gaectis nigrolimata. Pilkey compiled all data in the Manual of Conchology (1899) and described a new species, Gaectis malleata. The genus seems to be restricted to Puerto Rico.

Recently the type specimens of these four species, as well as a specimen of Gaectis sp. preserved in alcohol, became available. This enables me to give a review of the material, to study the anatomy in greater detail and to investigate the relationships of this genus to Amphibulina and Pellucula, genera occurring on the Lesser Antilles.

MATERIAL AND METHODS

The following abbreviations are used in the text to refer to the locations of the specimens:

ANSP  Academy of Natural Sciences, Philadelphia.

MCZ   Museum of Comparative Zoology, Cambridge (Mass.).

NMBN  Naturhistorisches Museum, Bern.


NRS   Naturhistoriska Riksmuseet, Stockholm.

RMNH  Rijksmuseum van Natuurlijke Historie, Leiden.

UF    Florida State Museum, University of Florida, Gainesville.

UMMZ  Museum of Zoology, University of Michigan, Ann Arbor.

ZSBS  Zoologische Sammlung des Bayerischen Staates, München.

The following numbers of specimens were studied: Gaectis albopunctulata 4, G. flavolineata 2, G. malleata 1, G. nigrolimata 21. The low number of available specimens makes it hardly possible to study the variation and to judge on the specific status of the taxa. Until more intensive collecting will make a solution of this problem possible, the present author prefers to give the taxa the benefit of the doubt.

The radulae were studied with a Cambridge scanning electron microscope (SEM).

Histological investigations were performed on a single specimen of Gaectis sp., as well as on specimens of Amphibulina patula from Guadeloupe. Data on Pellucula were taken from Van Mol (1971), those on Petella from Hieron (1886). After embedding in paraffin the material was sectioned at 6 μ and stained with 1% Alcian Blue after kaliumpermanganate oxidation, followed by staining with Haemalum and 0.5% Phloxine. The slides were mounted in malinol.

The measurements taken are (Figs 1-2): convexity (C); greater diameter (GD); lesser diameter (LD). Due to the aberrant form of the shell the height can not be measured as usual. Shuttleworth introduced measuring with the concave side of the shell down on a flat surface, for which measurement Pilkey used the term convexity. All measurements are given in Table I.

Drawings were made with a camera lucida attachment to a Wild M5 microscope or with a drawing prisma attached to a Wild compound microscope (M20).

SYSTEMATICS

Genus Gaectis Shuttleworth, 1854

SHUTTLEWORTH, 1854: 34. Type-species by subsequent designation (Thele, 1951): Gaectis nigrolimata Shuttleworth.

Diagnosis. – Shell depressed, fragile and hardly calcified. Protoconch
flat, almost smooth. Aperture very oblique. Lower surface completely open. Peristome with the basal margin reflexed and membranous.

Distribution.—Puerto Rico.

Fig. 3. Distribution of Gaeotis on Puerto Rico.

Key to the species of Gaeotis
1a Spire loosely coiled (Figs 4–6); shell convexity less than 5 mm; thin and translucent ............................................. 2
1b Spire closely coiled (Fig. 7); shell convexity 5 mm or more; rather solid and somewhat opaque .................................. G. albopunctulata
2a Surface with spiral striae hardly visible, or malleated; last whorl regularly rounded; aperture ovate ............................................. 3
2b Surface with irregular wrinkles and folds, giving it a crumpled appearance; last whorl subangular; aperture ovate-elongate ................. G. flavolineata
3a Surface sculptured with superficial spiral lines; suture margined at lower side ......................................................... G. nigrolineata
3b Surface with numerous superficial spiral and oblique, irregular lines, giving it a malleated appearance; suture margined at upper side ......................................................... G. malleata

Gaeotis nigrolineata Shuttleworth, 1854
Figs. 4, 8; Pl. I figs. 1–3
Gaeotis nigrolineata SHUTTLEWORTH, 1854: 35 (Description, measurements; type locality: Sierra de Luquillo; lectotype, here designated: NMBN 169).
PEIFER, 1856: 11; MARRENO, 1877: 323 (between Arceibo and Utuado); PEIFER & CLEBSCH, 1883: 228; COBB, 1892: 21; PILSBRY, 1899: 229, pl. 62 figs. 41–44 (Humacao); DALL & DAVIES, 1902: 377; THIEL, 1931: 667 (designated generotype); VAN DER SCHALCK, 1946: 91, pl. 8 fig. 5 (El Yunque); ZINCH, 1966: 515, fig. 1809.

Shell depressed, thin and translucent; colour pale tawny to glasy. Surface shining, sculptured with superficial spiral lines on upper part of whorl. Protoconch first 3/4 whorl, flat and minute, papillar. Whorls 2½, rapidly widening; stüture hardly impressed, margined at lower

Figs 4–7. Apical views in Gaeotis. 4, G. nigrolineata; 5, G. flavolineata; 6, G. malleata; 7, G. albopunctulata.—suture; margin;—"upper" whors seen through last whorl's transparency.

Fig. 8. General pattern of growthlines in Gaeotis (lectotype of G. nigrolineata).
side. Aperture very oblique, ovate. Peristome with slightly sinuous palatal margin; basal margin broadly and sharply reflexed, membranous. Spire loosely coiling.

Measurements of lectotype: convexity 4 mm, greater diameter 14 mm, lesser diameter 11 mm. See also Table I.

**Table I**

Measurements in *Gaetis* (in mm).

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<th>Species and location</th>
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<th>GD</th>
<th>LD</th>
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<td>15.6</td>
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<td>(paratypes)</td>
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<td>3</td>
<td>17.5</td>
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**Gaetis flavolineata** Shuttleworth, 1854

Shuttleworth gave the following data on the living animal: pale greenish-buff, pellucid, ornamented with very fine black lines. Liver a vivid and deep rust colour.

*Gaetis nigrolineata* differs from the sympatric *G. albopunctata* by its smaller size and less convexity, from *G. flavolineata* by its smaller size and its relatively smooth surface. *Gaetis malleata*, which is about equal in size, differs from this species by the sculpture of the surface and by the margin of the suture, which in *G. nigrolineata* is at the lower side. Locality records for this species are mainly from eastern Puerto Rico.

There are indications of its occurrence in the western mountain mass (viz., between Buena Vista and Santa Ana, Baker in Van der Schalie, 1948), which are, however, not confirmed by any material.

Material examined.—Puerto Rico, [Sierra de] Luquillo, 5 sp. NMNB 168 (incl. lectotype); 1 sp. ANSP 4959; 1 sp. NRS; 1 sp. ZSB5.—Humacao, 1 sp. ANSP 4614.

—Puerto Rico, 1 sp. ANSP 26051; 1 sp. MCZ 57134; 2 sp. MCZ 90479; 1 sp. NMW; 2 sp. NMW 2945; 1 sp. NRS; 1 sp. RMNH; 3 sp. UMMZ 147629.

**Gaetis flavolineata** Shuttleworth, 1854

Fig. 5; P. I. Figs 8–10

*Gaetis flavolineata* Shuttleworth, 1854: 35 (Description, measurements; Sierra de Luquillo and at Rio Blanco; type locality: Rio Blanco; lectotype, here designated: NMNB 168).—Perrier, 1903: 11; Perrier & Clevis, 1881: 228; Crosse, 1892: 22 (between Arecibo and Utuado); Priestley, 1899: 229; Dall & Simpson, 1902: 370.

Shell depressed, thin and translucent; colour pale tawny to glassy. Surface shining, with fine, spiral cords and irregular wrinkles on upper side and irregular folds giving a crumpled appearance on lower side of last whorl. Protoconch first 3/4 whorl, flat and minute, papillar. Whorls 1-2, rapidly widening, last whorl subangulate; suture hardly impressed, margined at lower side. Aperture very oblique, ovate-elongate. Peristome with slightly sinuous palatal margin; basal margin broadly reflexed, slightly reflexed, membranous. Spire loosely coiling.

Measurements of lectotype: convexity 3.5 mm, greater diameter 18 mm, lesser diameter 12.5 mm.

According to Shuttleworth (1854) the animal is ornamented with very fine yellow lines.

*Gaetis flavolineata* differs from the other species mainly by its subangular last whorl and crumpled surface.

One of the syntypes of *Gaetis flavolineata* (NMNB 167, Sierra de Luquillo) appeared to be a specimen of *G. albopunctata*.

The type locality is a small village at the foot of the Sierra de Luquillo.

Van der Schalie (1948: 91) has put this species in the synonymy of *Gaetis nigrolineata* without further remarks, but referring to Dall & Simpson (1902). These authors, however, considered *Gaetis flavolineata* a distinct species, an opinion also held by the present author.

Material examined.—Puerto Rico, Rio Blanco, 1 sp. NMNB 168 (lectotype).—Tooro Negro, 1 sp. UMMZ 168806.
Gaeotis malleata  
Pilsbury, 1899

Fig. 6; Pl. I figs. 4–7

Gaeotis malleata  
Pilsbury, 1899: 220, pl. 62 figs. 36–40 (Description, measurements; type locality: near San Juan; holotype: ANSP 26052).—Dall & Simpson, 1902: 378; Van der Schalie, 1948: 91.

Shell depressed, thin and milky-translucent; colour tawny. Surface shining, with numerous superficial spiral lines crossed by superficial, oblique and irregular lines at lower part of last whorl, giving a malleated impression. Protoconch first 3/4 whorl, slightly projecting, minute, papillar. Whorls 2 1/2, rapidly widening; suture slightly impressed, margined at upper side. Aperture very oblique, ovate. Peristome with slightly sinuous palatal margin; basal margin broadly and sharply reflexed, membranous. Spire loosely coiling.

Measurements of holotype: convexity 3.5 mm, greater diameter 13 mm, lesser diameter 9.7 mm.

Gaeotis malleata closely resembles G. nigromeata, but differs in the malleated surface and in the suture, which is margined at upper side.

Material examined.—Puerto Rico, near San Juan, 1 sp. ANSP 26052 (holotype).

Gaeotis albopunctulata  
Shuttleworth, 1854

Fig. 7; Pl. I figs. 11–13

Gaeotis albopunctulata  
Shuttleworth, 1854: 36 (Description, measurements; type locality: near Humacao; lectotype, here designated: NMBN 166).—Pfeiffer, 1866: 12; Pfeiffer & Clemens, 1881: 228; Chace, 1892: 22; Pilsbury, 1899: 230, pl. 62 figs. 45–48; Dall & Simpson, 1902: 378; Van der Schalie, 1948: 91.

Shell rather depressed, rather thin, somewhat translucent, opaque; colour tawny. Surface shining, with numerous fine and irregular lines, giving a slightly malleated impression. Protoconch first 3/4 whorl, hardly projecting, minute, papillar. Whorls 2 1/2, rapidly widening; suture hardly impressed, margined at lower side. Aperture very oblique. Peristome with sinuous palatal margin; basal margin broadened, reflexed, membranous. Spire closely coiling.

Measurements of lectotype: convexity 6 mm, greater diameter 19 mm, lesser diameter 14 mm.

Animal pellucid, while, spotted with opaque white dots. Liver pale greenish (Shuttleworth, 1854).

Gaeotis albopunctulata differs from the other species by its greater convexity and closely coiling spire. Gaeotis malleata, the only other species with malleated surface (though somewhat differently composed), is separable by its smaller size and lesser convexity.

This species and Gaeotis nigromeata seem to be sympatric.

Material examined.—Puerto Rico, prope Humacao, 2 sp. NMBN 166 (including lectotype).—Sierra de Luquillo, 1 sp. NMBN 167.—Humacao, 1 sp. ANSP 4613.

From the following localities specimens without certain determination are known: Cayey (Martens, 1891), West Peak (MCZ 271642; animal in alcohol without shell). I have been unable to trace the latter location on the maps available to me. The former location is shown in Fig. 3.

ANATOMY

The following data are derived from the available material and completed by data from literature, which are discussed at the same time.

Jaw (Fig. 9).—Thin, transparent; ends attenuated. Divided by delicate ribs in about 45 narrow, platelike sections. Without median triangular space.

In Amphibulina and Petelita the jaw is composed of overlying plates, giving it a ribbed appearance. Median triangular plate (Figs 10–11). Höring (1886) described the same configuration for Petelita, although the median plate is reduced. This gives the jaw the appearance as if it is composed of two symmetrical parts.

Radula (Pl. II figs. 4–6, Pl. III figs. 1–6).—Transverse rows in V-shape (en chevron). Central teeth with a prominent, triangular to sagittal form, mesocone and two rudimentary denticles projecting anteriorly. In relation to the side teeth the centrals are situated more anteriorly on the basal membrane. First side teeth elongated, with a lancolate mesocone and one ectocone. Following side teeth uniformly trilobed. Mesocone small, more or less pointed, sometimes bifid. Ectocone and endocone larger than mesocone, bluntly-rounded and slightly asymmetrical. It is not certain whether the first side teeth must be called laterals and the following teeth marginal or that the first lateral is aberrant in form, while the others are indistinguishable from the marginals. At this moment the first hypothesis is accepted, giving the following radular formula: C 1 1 1 2 M 68 68 3.

The situation now observed differs somewhat from the data given in literature (Bland & Binney, 1873; Binney, 1884; Pilsbury, 1899). According to these authors the central teeth are similar to the marginals, although smaller. Also the elongated lateral is not mentioned by these authors (cf. Bland & Binney, 1873: pl. XI fig. 5).
In *Amphibulina* and *Pellicula* the radula shows the following characteristics (Pl. II figs 1–3): central teeth with a large mesocone and two smaller ectocones. Basal plate subquadrate, narrowing towards the center. Mesocone more or less pointed. Laterals with a large, blunt mesocone and a smaller, pointed ectocone, gradually changing in the

marginals which are described for *Gaecitis*. Centrals and laterals with supporting denticles. This supporting mechanism was previously described by Solem (1972) and Gittenberger (1973; "Stützähne").

According to Hering (1886) the radula of *Pellicula* is composed of straight rows. The central teeth are unicusp. Lateral and marginal teeth uniform with a prominent blunt mesocone, large endocone and a small ectocone, which is bident in the outer marginal teeth.

Genitalia (Fig. 12).—Genital atrium wide and short. Penis some-
what swollen, constricted at the transition to the epiphallus, which is about as long as the penis. Flagellum short, penis retractor distally attached. Vagina wide and short, about half the length of penis. Spermatheca without spermathecal duct (Fig. 15). Spermoviduct well developed. Ovotestis composed of digitiform tubes.

Fig. 15. Gaecotis sp. connection between spermatheca (SP) and vagina (V).

The genitalia of Ampsibulina and Pellicula (Figs 13–14) differ in the following respects: 1) components of penial complex more demarcated; 2) spermathecal duct long and slender; 3) vagina absent. According to Leve (1968: figs. 10, 16–17) the components of the penial complex of Pellicula are more or less demarcated, the spermathecal duct is about one third the length of spermoviduct and the vagina is very short.

The following histological data have been derived from a single specimen. As it was preserved in alcohol certain details could not be observed.

Flagellum (Fig. 16) characterized by a pseudo-stratified columnar epithelium with cilia and infoldings. It is surrounded by circular and longitudinal smooth muscle fibers with dispersed glandular cells, staining light blue.

Lumen of epiphallus lined by cubic epithelium with short cilia. Subepithelial glandular tissue with bright blue secretion. The epithelium and the homogenous subepithelial glands form villi-like folds in

Figs 16-22. Gaecotis sp., transversal sections through penial complex and schematic reconstruction. EP, epiphallus; FL, flagellum; P, penis; VD, vas deferens.
the lumen, whereas in the flagellum only the epithelium is folded. Epiphallus penetrating in distal part of penis (Figs 18, 22).

Penis (Figs 19–21) with a large lumen. Epithelium less folded, consisting of glandular columnar cells without cilia. Cytoplasm with eosinophilic, granular secretion. In distal part of penis luma of bright blue secretion are observed between the eosinophilic granular cells, besides subepithelial glandular cells with same bright blue secretion. In these sections it is not clear whether the luma are glandular cells or ducts filled with secretion of the subepithelial gland.

In both Amphibulus and Pelleca the flagellum consists of columnar epithelium and homogenous subepithelial glands. The glandular cells are voluminous, with bright blue secretion. Penis without glandular cells in distal part (Figs 23–25). Comparable data are not available for Pellea.

Free retractor muscle system.—In Gaetopsis the same situation has been found as described by Van Mol (1971) for Amphibulus.

Pallial cavity (Fig. 26).—Nephridium disposed transversally, partially covering the adrenal (primary) ureter. Adrectal (secondary)

ureter passing below rectum, discharging into the urinary opening, which extended at the inner side of the pneumostome. Pericardium situated at the right side of the nephridium. Pulmonary vein abundantly ramified, but not dense. Region between pericardium and mantle posteriorly irrigated by fine capillaries, while anterior side seems to be without irrigation.

ECOLOGY

Data on the ecology of these species are very scarce. Blauner (in Shuttleworth) collected his specimens on the trunks and leaves of
trees, especially banana (Musasp). According to Baker (in Van der Schalie) the animals also occur on palm leaves. Van der Schalie (1948) found one specimen on a bridge along the road. There is, however, hardly any doubt that these species are wholly arboreal, which is supported by the structure of the radula (V-shaped rows).

RELATIONSHIPS

It is now supposed that Amphibulina, Gaetis, Pellicula and Petella compose a natural group. Whether this group must be given subfamilial rank or not will be left out of discussion at this moment, as the relationships to the other Bulimulidae are not quite clear. The following discussion gives the main characteristics of the genera.

The radular rows are V-shaped, except in Petella (Ihering, 1886: 64), where straight rows occur. The central teeth are tricuspid in Amphibulina and Pellicula, whereas Gaetis and Petella have unicuspid central teeth. Another characteristic of Gaetis (and Petella?) is the absence of supporting dentiles. Nothing can be said at this moment about the significance of the single lateral and uniform marginal teeth in Gaetis.

The genitalia also reveal several features which are of interest for this paragraph.

In Amphibulina, Pellicula and Petella the spermatheca is at the distal end of a more or less elongated spermathecal duct. This duct is absent in Gaetis.

The vagina is absent in Amphibulina and Pellicula, while the different components of the penial complex are clearly demarcated.

In Gaetis the flagellum is considerably reduced and the glandular cells are dispersed in the muscular tissue. The epiphallus tissue penetrates in the distal part of the penis, where subepithelial glandular tissue occurs.

The rectum is dilated in Pellicula and Petella (and Gaetis?) near the anus, forming a rectal sac. This condition is absent in Amphibulina.

These data are condensed in Fig. 27, which gives the hypothetical relationships of the four genera. When a better knowledge of the other Bulimulidae is achieved, it perhaps will be necessary to revise this grouping.

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REFERENCES


PLATE I

Gaetis nigolineata Shuttleworth—1–3, Puerto Rico, Sierra de Luquillo; lectotypus (NMNB 169).

Gaetis malleata Pilsbry—4–7, Puerto Rico, near San Juan; holotype (ANSP 260).

Gaetis flavolineata Shuttleworth—8–10, Puerto Rico, Rio Blanco; lectotypus (NMNB 168).

Gaetis albopunctata Shuttleworth—11–13, Puerto Rico, near Humacao; lectotypus (NMNB 166).

All figures about ×2, except details of shell surface.
Placa II

Pellicula appendiculata (Périfée)—1, central part of radula (× 500); 2, 36th to 38th marginal teeth (× 1000)—Guadeloupe, Baie Terre, 3 km N of St. Claude; UF.
Anomala beadula (Bouquière)—3, central part of radula (× 250)—Dominica, 1.3

Placa III

Ganelis sp.—1, central teeth (half) and first to fourth side teeth (× 500); 2, max

B