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ON SOME ACTEONIDAE (GASTROPODA, OPISTHOBRANCHIA)

EVELINE D. B.-R. MARCUS

ABSTRACT

A study of five species of Acteonidae from the West Atlantic and the East Pacific changes the systematic position of some of them. The figures of the North and South American "Acteon" punctostriatus *are indistiguishable (Figs. 1, 2). However, their radulae belong to different types. The Brazilian species with the formula* $\infty.0.\infty$ *is a true* Acteon *and is called* A. pelecais *Marcus, 1971. The North American species with the formula 5.0.5 is removed to* Rictaxis *Dall, 1871. The type of that genus is* R. punctocaelatus. *The African* Pseudactaeon *Thiele, 1925, type species* albus *(Sowerby, 1873), is a junior synonym to* Rictaxis. *The outermost tooth of* R. punctostriatus *changes its shape with age (Figs. 23-25).* Acteon traski *from the East Pacific is a true* Acteon. Acteon cumingii *from the West Atlantic has the formula n.O.n as the African* Alexandria natalensis *Tomlin, 1922, and is transferred to the genus* Tomlinula *Strand, 1932, substituted for Tomlin's* Alexandria *(1926) and* Alexania *Strand, 1930, which are preoccupied.*

INTRODUCTION

While classifying a collection of opisthobranchs from Solomons, Md., I found that the radula of specimens which looked like *Acteon punctostriatus* (C. B. Adams, 1840) was quite different from that of the Brazilian snails we had determined as *A. punctostriatus*, conforming with the figures of Gould and Verrill (Marcus, 1956: 32, figs. 8-10). The Brazilian radula is compatible with that of *A. tornatilis* (L.), figured by G. O. Sars in 1878 (Pilsbry, 1893-1895, pl. 49, fig. 2). Pilsbry (l. c., p. 135) based his family diagnosis upon this radula, as it was the only one known at his time. Later on Bergh (1902: 317, pl. 27, fig. 9-10), Gabe and Prenant (1952, 1953), and Pruvot-Fol (1956: 301-307) also studied the radula of *A. tornatilis*. It is composed of a great many longitudinal rows, each with a vast number of uniform teeth (Pruvot-Fol, 1956: 303). Since Pilsbry's diagnosis (1894: 147-148) several radulae of Acteonids have been described. Due to the different types of radulae the species must be divided onto several genera. The formula 5.0.5 was found in *Pupa* (= *Solidula*)

Caixa Postal 6994, 01000 São Paulo, Brasil.

solidula (Linné, 1758) with three varieties by Bergh (1902: 320, pl. 27). Habe described (1950b: 41-42, pl. 2) the radulae of *P. solidula, P. sulcata* (Gmelin, 1791) and *P. strigosa* (Gould, 1859), now called *Strigopupa* Habe (1958: 117), and *Rictaxis punctocaelatus* (Carpenter, 1864) (Habe, 1956: 99, fig. 3). *Pseudactaeon albus* (Sowerby, 1873) was studied by Thiele (1925: 223, pl. 34, figs. 3, 3a) and Barnard (1963: 317, fig. 28, h). Thiele also described the radulae of *Neactaeonina cingulata* (Strebel, 1908) and *N. fragilis* Thiele (1912: 219) and indicated the formula 7-8.1.7-8, which Hoffmann (1938: 1002, note 1) interpreted to be 8.0.8. *Tomlinula natalensis* (Tomlin, 1926: 288, fig. 2) has the formula 18.0.18.

Thiele was right to suppose (1925: 223): "that also otherwise (than in *Pseudactaeon albus*) within the family Acteonidae there will exist considerable differences. Unfortunately I do not have further material to ascertain this, but I want to consider the groups until now called subgenera, *Solidula, Microglyphis*, and *Rictaxis*, as genera. Of these only the first was examined for its radula. Presumably also species as *Actaeon exilis* and perhaps *A. punctostriatus* will have to be placed in genera of their own".

Habe (1956: 99) approximated the radula of *Acteon* (*Rictaxis*) *punctocaelatus* to that of *Pseudactaeon albus,* both with the formula 5.0.5, and raised *Rictaxis* to generic rank. He did not include *albus,* which certainly does belong to the same genus as *punctocaelatus. Pseudactaeon* is a junior synonym to *Rictaxis.*

Zilch (1959-1960: 6) notes that "in Acteonids the systematic importance of the shell is generally less than in many other families of gastropods. Everywhere, where an anatomical study has not been carried out, or, as in the genera only known as fossils, cannot be accomplished, the exact systematic allotment of the respective forms remains more or less doubtful". Hence I do not treat the species and the genera of the Acteoninae known only by their shell (Zilch, 1959-1960: 7-10): *Acteonina; Bullina* (after Habe, 1950a: Hydatinidae); *Japonactaeon; Kleinella; Leucotina* (Pyramidellidae); *Lissactaeon* = *Crenilabrum; Metactaeon; Microglyphis* (after Steinberg, 1963: 114-115: Ringiculidae); *Ovulactaeon; Punctactaeon,* and *Rictaxiella* Habe (1958: 118, fig. 5); and of course much less the fossils.

I obtained the radulae of the following Acteonidae:

"Acteon" punctostriatus (C. B. Adams, 1840) from Maryland and Florida.

"Acteon" cumingii A. Adams, 1854, from Brazil, Ubatuba.

Rictaxis punctocaelatus (Carpenter, 1864) from California, Collection Los Angeles County Museum, and Pacific Marine Station, Dillon Beach, California.

Acteon traski Stearns, 1897, from California and Mexico, Collection Los Angeles County Museum.

Acteon pelecais Marcus, 1971, from Brazil, Ubatuba, own collecting and Museum of Zoology, University of São Paulo.

A *Pupa* species from Cook Island, Collection of the Smithsonian Institution, Washington, D. C., was compared. Its radula corresponds to the known figures.

Due to the scarcity of my material and to the unsatisfactory state of preservation I cannot give a complete comparative study of the anatomy. I have to restrict my statements to the mantle, the pallial caecum, the male organ, the jaw elements, the radula, and the prostate, which all show distinct differences.

My thanks are due to Rosalie M. Vogel and David G. Cargo, Solomons, Md., Liliana Forneris, São Paulo, Dennis Opresto, Miami, Fla., Gale Sphon and James H. McLean, Los Angeles, Harald A. Rehder, Joseph P. Rosewater and Walter J. Byas, Washington, D. C., Fred G. Thompson, Gainesville, Fla., Miriam and Talbot Murray, and Leslie G. Williams, Dillon Beach, Cal., Lícia Penna and José Luiz Moreira Leme, São Paulo, for helping me with material, and to Mr. Lawrence Reynolds, Los Angeles, for the photograph of five shells of *Acteon traski*.

Family Acteonidae

Diagnosis. — Opisthobranchia Cephalaspidea with spiral heterostrophic shell, sculptured with spiral striae, with corneous operculum, body with cephalic shield, non-invaginable penis, and free or adherent pallial caecum.

Remark. — The character of the radula given by Pilsbry (1893-1895: 135) was already invalidated by Bergh's findings (1902).

Key for the genera based upon their radula

1. Radula ∞.0.∞ equal teeth ..... *Acteon* Montfort, 1810
   Radula with less numerous teeth 2
2. Radula with more than 5 teeth per half-row 3
   Radula with 5.0.5 teeth 4
3. Radula with 8.0.8 teeth per half-row . *Neactaeonina* Thiele, 1912
   Radula with 18.0.18 teeth or more ..... *Tomlinula* Strand, 1932
4. Teeth of almost equal size ..... *Pupa* Roeding, 1798
   One tooth much larger than the rest ... *Rictaxis* Dall, 1871 ... 5
5. Outermost tooth largest . *Rictaxis punctocaelatus* (Carpenter, 1864)
   Penultimate tooth largest .. *R. punctostriatus* (C. B. Adams, 1840)

Genus **Acteon** Montfort, 1810

Operculate Acteonidae with a radula of very many rows containing very many small, uniform teeth (formula ∞.0.∞).

Type species *Acteon tornatilis* (Linné, 1758).

Now only three species are known to be true *Acteon*: *A. tornatilis, A. pelecais,* and *A. traski.* All others cannot with certainty be allotted to the genus *Acteon* before their radula has been described.

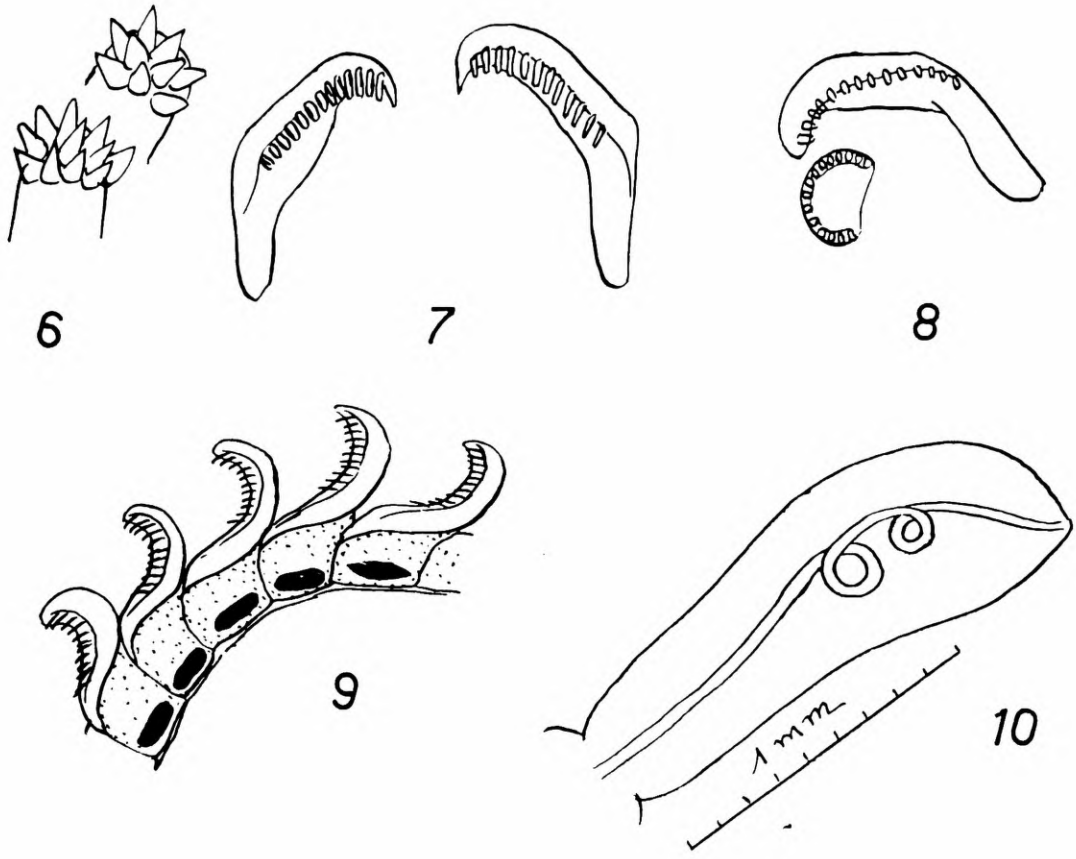
Acteon pelecais Marcus, 1971

(Figs. 1, 6-10)

Acteon punctostriatus; Marcus, 1956: 32, figs, 1-10.
? *Acteon punctostriatus*; Marcus, 1970: 924, fig. 5.
non *Actaeon punctostriatus* C. B. Adams, 1840; van Winkle Palmer, 1958: 238 (references).
Acteon pelecais Marcus, 1971: in press.

Material. São Paulo, Ubatuba, 4 specimens, 1955-1962. Ibid., 4 shells, Collection Museum of Zoology, University of São Paulo, nos. 2125, 2237, M 17 4 (5) III; A 73 3 (5) 7; Cananéia, E. São Paulo, one empty shell, 1969.

Descriptive notes. The present material contains one empty shell from Ubatuba, 9,5 mm high. For the measurements of the remaining shells see table 1 (p. 182). They are a little heavier than those of *Rictaxis punctostriatus*. The flat spiral striae are separated by narrow punctuate furrows. The operculum is 2.0 mm long, 1.1 mm broad, the width 55% of the lenghth.



Acteon pelecais: 6, jaw platelets; 7, innermost radular teeth; 8, normal and misformed tooth; 9, section of radula; 10, penis.

The re-examination of the radula of our old material confirms our classification as *Acteon*. The radular membrane is crumpled and cannot be properly extended for counting the rows of teeth (Pruvot-Fol, 1956: 303 and note **, fig. 1; Hurst 1965: 330, fig. 27). The teeth are 7-10 μ high (Figs. 7-9) and slightly different from those of *A. tornatilis* figured by Sars (Pilsbry, 1893-1895: 148, pl. 49, figs. 2, 3) and Bergh (1902: 317, pl. 27, fig. 9). For the discussion of Pruvot-Fol's (l. c.) and Gabe and Prenant's (1953: fig. 3) figures see Marcus (1956: 33). The uniform shape of the teeth and their great number justify the allocation of the species in *Acteon*.

The mantle border is pigmentfree. The prostate is a straight tube lined with a smooth layer of glandular epithelium with 60 μ high cells. Their nuclei are large, 10 μ in diameter. This epithelium is different from that of *A. tornatilis*, in which high longitudinal folds protrude into the prostatic lumen, covered with a rather flat, ciliated epithelium (Johansson, 1954: 224, figs. 1, 2, 3). The penial papilla (Fig. 10) is smooth, 1.4 mm long, 0.45 mm in diameter at its widest part, situated near the tip in the preserved specimen; the duct is coiled inside it.

Discussion. The Brazilian *"Acteon punctostriatus"* has a radula of the true *Acteon* type. When I found that the North American *punstostriatus* is really a *Rictaxis*, I had to give the Brazilian one a new specific name and called it *Acteon pelecais* (1971: in press). The shells of both are alike. Both are variable in thickness, ratio of diameter, height of spire, height of columellar fold, and extent of spiral striae. As their measurements and characters are the same it is practically impossible to classify them only by the shell. The Brazilian shells are perhaps a little heavier. Hence the "Further Distribution" cannot be determined, as long as the soft parts are not known from the respective region. Probably the shells from Bahia Blanca, Argentina (Carcelles and Parodiz, 1938: 261, pl. 1, fig. 3), and from Maranhão, Brazil (Marcus, 1970: 924, fig. 5) belong to the present species.

There are about thirty species of *"Acteon"* described from the Western Atlantic, only seven of which have a smooth upper half of the body whorl. Of these three, *exiguus* and *splendidulus* Mörch, 1875, and *semicingulatus* Dall, 1871, are not figured. The radulae of *semisculptus* E. A. Smith, 1890, and *A. candens* Rehder, 1939, are not known. *Acteon pelecais* Marcus, 1971, has a true *Acteon* radula like *A. tornatilis*, the type of the genus. *"Acteon" punctostriatus* is transferred to *Rictaxis* (p. 178).

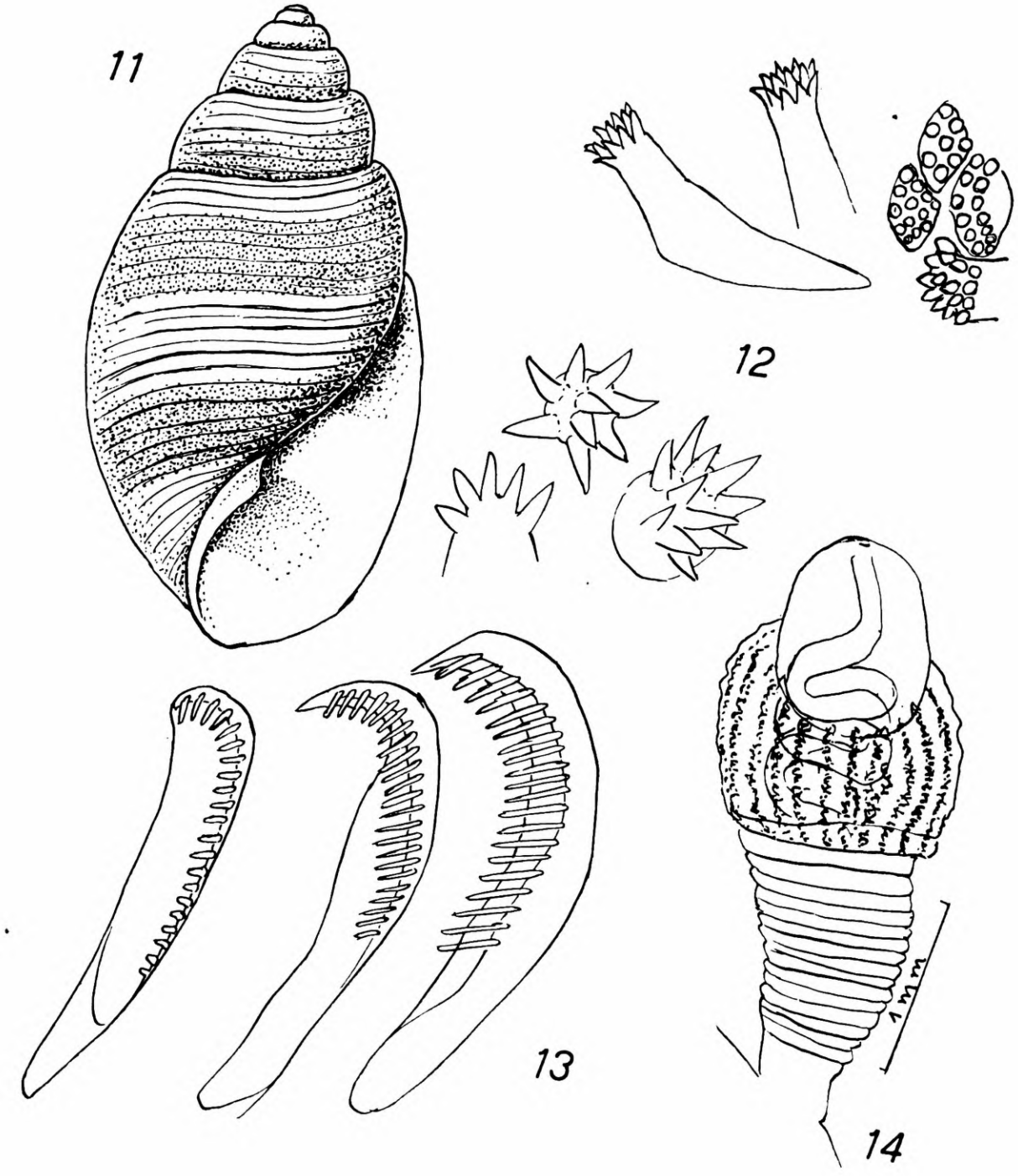
Acteon traski Stearns, 1897

(Figs. 3, 11-14)

Acteon traski; Stearns, 1898: 297, fig. on p. 8; Oldroyd, 1927: 24, pl. 1, fig. 12; Keen, 1958: 498, fig. 990.

Material. Mexico, Baja California, Bahia de Sta. Maria, 18-25 fms., grey sand, 19.I.1940, Allan Hancock Foundation no. 1031-40-D-2, 2 specimens, 11 × 6 mm and 6.8 × 3.8 mm. Madalena Bay, 5 dry shells (Fig. 3), one of which with radula, 18 × 9, 16 × 8, 15 × 7.5, 14 × 7, 11.4 × 5.7 mm.

Descriptive notes. The shell (Fig. 3, 11) has 6-7 whorls with distinct sutures. The aperture of the 18 mm shell is 10 mm high. The 30-35 convex spiral ribs are separated by narrow furrows. They are variable, in the largest shell they are strong, and there are irregular growth lines produced by radial folds, some of which are lighter



Acteon traski: 11, shell; 12, jaw platelets; 13, radular teeth; 14, penis.

than the ground colour of the shell. The shell is cream with two broad, spiral, mauve bands dividing the ground colour into tree narrower stripes. The columellar fold is distinct.

The roof of the mantle cavity has a pigmented area on the anterior border, wider in the sections corresponding to the colour bands of the shell. The pallial caecum accompanies one whorl. The penis is 3 mm in length and bears a glandular collar around its middle (Fig. 14).

The elements of the jaws are columns up to 68 μ high, crowned with 8-12 conical pointed spines (Fig. 12). The radula (Fig. 13) is similar to that of *Acteon pelecais*. Its membrane is so much twisted and torn, that it was not possible to count the numbers of rows and teeth. I estimate them at about 200 or more longitudinal rows with 200 teeth per half-row. The teeth are 15-18 μ long and have about 20 denticles along the outer side.

Tomlinula cumingii (A. Adams, 1854)

(Figs. 4, 15-18)

Acteon cumingii; Pilsbry, 1894: 162, pl. 19, figs. 16, 17; Johnson, 1934: 134; Marcus, 1970: 923, figs. 1, 2.

Material. Brazil, São Paulo, Ubatuba, May 1968, Liliana Forneris, one preserved specimen. In the collections of the Museum of Zoology, University of São Paulo, several empty shells from Ubatuba (no. 2237), Santos (no. 2936), and São Sebastião, and from the State of Rio de Janeiro, Angra dos Reis, 2 shells.

Further distribution: From Florida, 8 fms., to Brazil.

Descriptive notes. The largest shell measures 20 × 10.8 mm, the smallest 7.3 × 4 mm. The ovoid shell has a pointed apex and 6-7 whorls (Fig. 4). The periostracum is pinkish brown on the borders between the convex spiral ribs and the ca. 35 beaded furrows. The intensity of the colouring varies in radial bands, probably correlated with the rhythm of growth: while the shell grows fast, the border is pale, during periods of slow growth it becomes dark. There is a single columellar fold. The corneous operculum (Fig. 17) of the 14 mm specimen measures 6.5 × 2.7 mm, its breadth is 41.5% of the length. It is a little narrower than than that of *Acteon pelecais* (Marcus, 1956: 32, fig. 3).

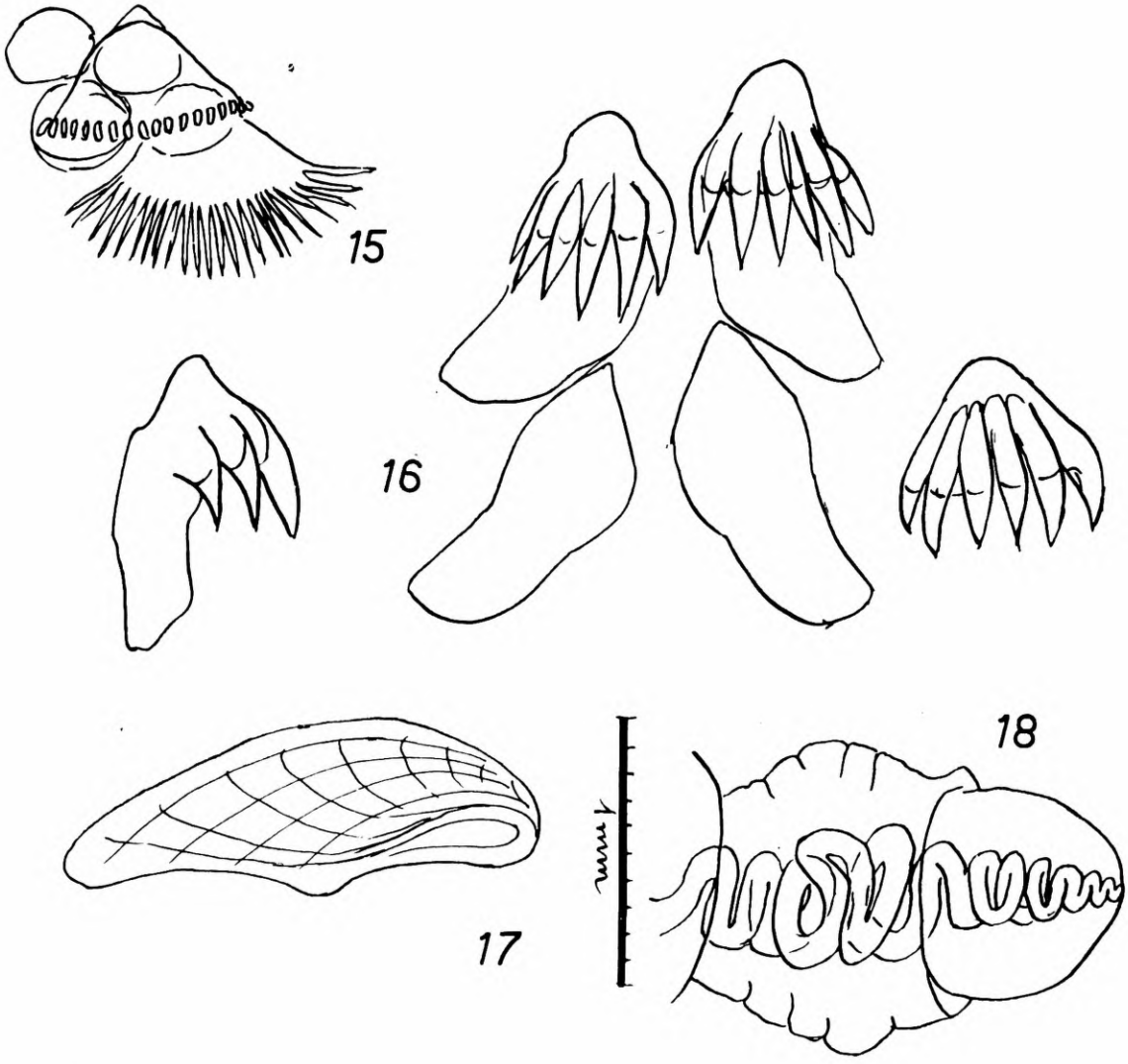
The pallial caecum of the mantle cavity is slender and accompanies one complete whorl. The penial papilla (Fig. 18) is 1.6 mm long. It has a collar around its middle, where the diameter is 1 mm. The efferent duct is densely coiled inside the papilla; probably it can be stretched considerably.

The jaw platelets (Fig. 15) have ovoid bases, 12 × 10 μ, arranged in quincunx, rising with a narrow neck to a broad, flattened sharp edge at the top, 30 μ broad, provided with about 25 spines, 5-8 μ long. The radula is composed of 112 rows with 36 teeth per half-row. These are almost uniform (Fig. 16), but the number of denticles, 6 on the innermost tooth, decreases to three on the outermost.

The salivary glands are a little longer than the buccal mass. The stomach contained a 6 mm long, 3 mm wide, undigested piece of a Sabellid with bundles of typical setae.

Discussion. *Tomlinula* Strand, 1932, is the new name for *Alexandria* Tomlin, 1926. *T. natalensis* Tomlin, 1926: 287, is nearest to *A. cumingii* due to its radular formula and the description of its jaw platelets. Tomlin's figure (pl. 16, fig. 2) of the teeth is unsatisfactory; their points may be unnaturally twisted (p. 288). However, Tomlin's comparison with the radula of *Hydatina* approximates *natalensis* to *cumingii*.

Tomlin's report compared the radula also to that of *Bullina*, which in Thiele (1931: 380) is indicated as unknown. Habe (1950a: 19)



Tomlinula cumingii: 15, jaw platelets; 16, radular teeth, innermost teeth; tooth from middle of half-row; lateral view of tooth; 17, operculum; 18, penis.

transferred *Bullina* without operculum to the Hydatinidae. The operculum of *Tomlinula* justifies its place in the Acteonidae.

The shell of *Acteon delicatus* Dall, 1889 (p. 5, 41, pl. 17, fig. 5), found from Barbados to Patagonia in 50-400 fms., is similar to that of *cumingii*. It has 6-7 whorls in a shell of 10 × 5.6 mm. The pink colour is strongest in an irregular flammulate pattern against the longitudinal striations of *cumingii*, reported from Cape Florida to Rio de Janeiro. The columellar fold is stronger in *cumingii* than in *delicatus*, and the spiral ridges of the robust shell stand out over the margin of the outer lip, so I call my material *Tomlinula cumingii*. The radula of *delicatus* is unknown; possibly it will be so similar to that of *cumingii*, that *delicatus* will turn out to be a synonym.

Acteon finlayi McGinty, 1955 (p. 81), reported from Palm Beach, Florida, to Rio Grande do Sul, Brazil, from 22 to 44 fms. (Rios, 1970: 130, pl. 49) has a pink shell similar to that of *cumingii*. It differs by the lattice like appearance of the shell sculpture.

Rictaxis puntocaelatus (Carpenter, 1864)

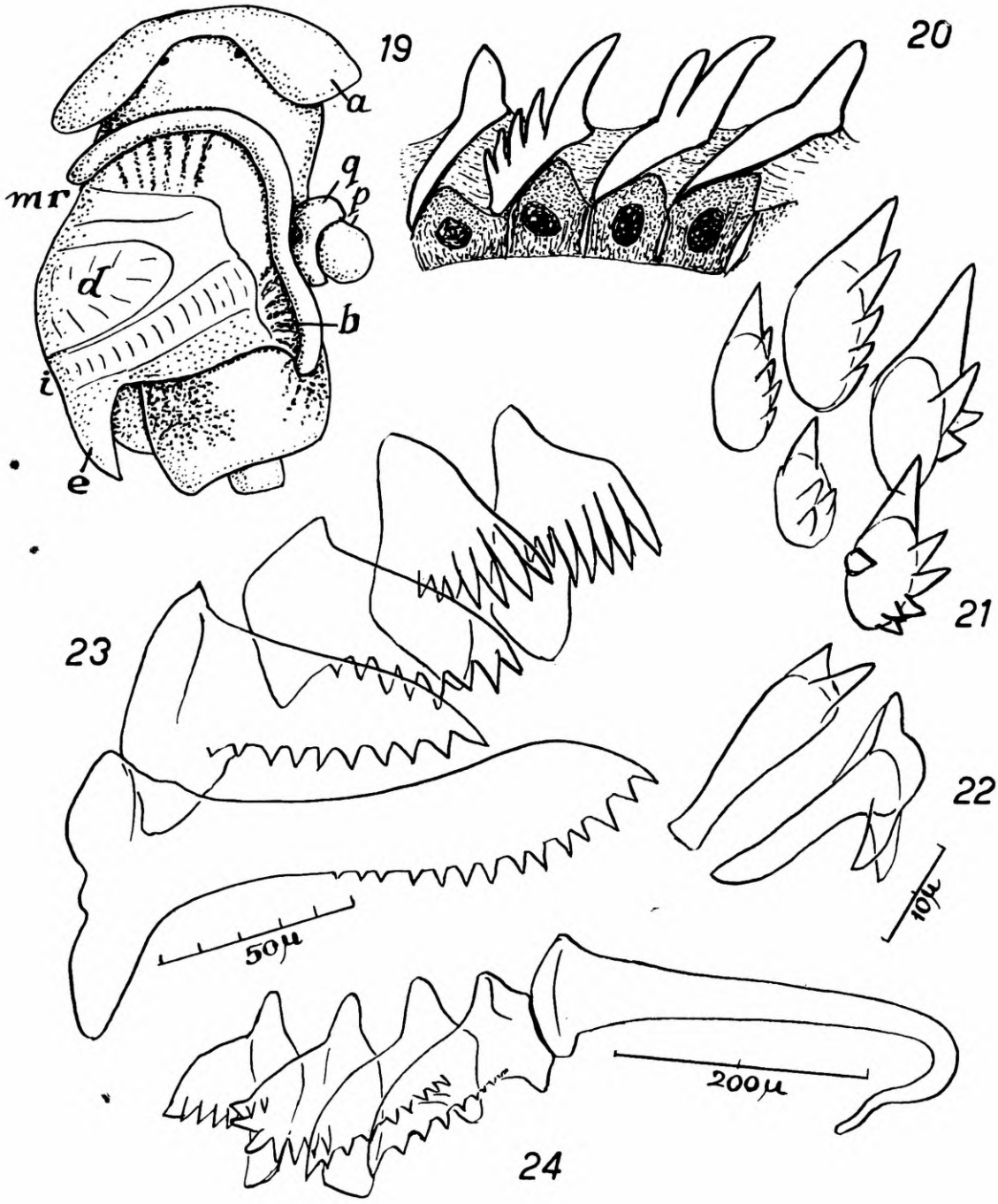
(Figs. 5, 19-29)

Acteon (*Rictaxis*) *punctocaelata*; Dall, 1871: 136.
Acteon (*Rictaxis*) *punctocaelatus*; Pilsbry, 1894: 166, pl. 49, fig. 24; Oldroyd, 1927: 24, pl. 1, figs. 17, 17a.
Rictaxis punctocaelatus; Habe, 1956: 99, fig. 3 (radula).
Actaeon punctocaelatus; McLean, 1969: 55, fig. 31, 1.

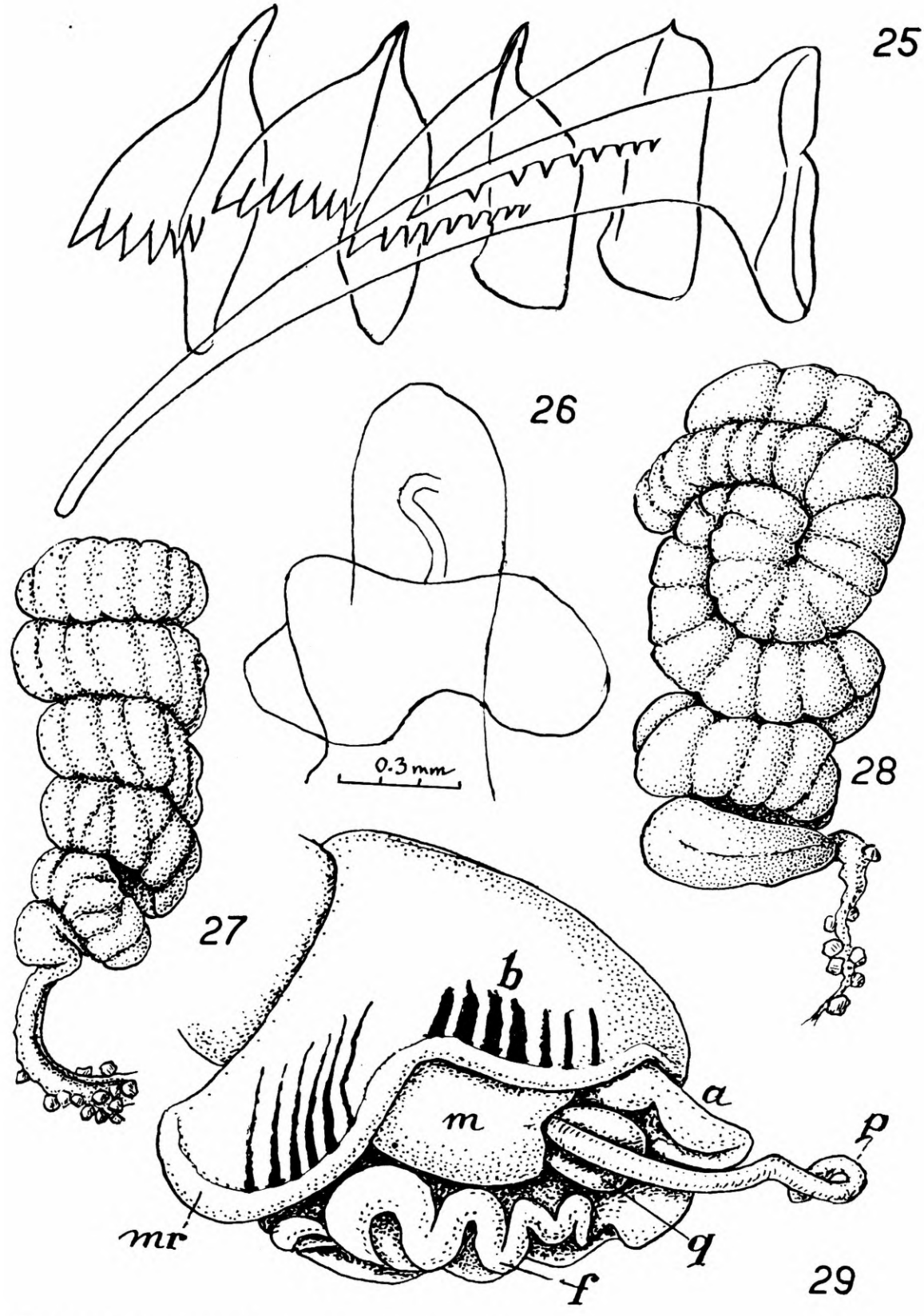
Material. California, Bodega Lagoon, Sonoma co., Allan Hancock Foundation no. 1799-49, one specimen, 16.5 × 8.2 mm, with radula. Dillon Beach, Marin co., Tomales Bay, Lawson's mudflat, 11.VII.1971, Talbot and Miriam Murray leg., 11 specimens, 9-13 mm long, and two spawns; 6.VIII.1971, Leslie Williams leg., 15 specimens, Sta. Barbara co., Sta. Cruz Island, 3 mi. NE San Pedro Point, 17.IX.1941, 87 m, on sand, two specimens, 8.2 × 4.5 mm and 9.1 × 4.3 mm, Los Angeles County Museum no. 1418-41. Doheny Park, Orange co., 1957, Mark Rogers leg., 15 shells, up to 16 mm long, with 2 radulae. Point Loma, San Diego co., 30.VII.1969, one empty shell.

Further distribution. From Alaska, Ketchkan, 55° 24' N, to Mexico, Madalena Bay, Baja California, 24° 30' N.

Descriptive notes. The delicate shells (Fig. 5) measure from 7.4 × 3.5 to 15.9 × 7.5 mm. The ratio varies from 1.79 to 2.25; in the present material the average lies over 2.00. The shells are so thin that the furrows between the spiral ribs appear as crests on the inner side of the shell. The number of dark stripes in the two bands on the body whorl is variable, in some shells there are more, total 5-8, in the frontal band than in the apical one with 5-7. On the border of the roof of the mantle cavity there are two groups of 5-8 black stripes each, corresponding to those in the pattern of the shell (Figs. 19, 29, b). The posterior flaps of the head shield are folded forward in the preserved, retracted snails, and cover the anterior border (Figs. 19, 29, a). All specimens have lost their operculum,



Rictaxis punctocaelatus: 19, animal extracted from shell (a, cephalic shield; b, pigment stripes; d, kidney; e, pallial caecum; i, gill; mr. border of mantle; p, penis; q, collar of penis); 20, section of jaw platelets; 21, jaw platelets; 22, smallest radular teeth; 23, half-row of juvenile teeth; 24, half-row of adult teeth of same animal.



Rictaxis punctocaelatus: 25, half-row of older radula; 26, penis; 27-28, spawns; 29, animal with everted penis (a, cephalic shield; b, pigment stripes; f, foot; m, bulge around female aperture; mr, border of mantle; p, penis; q, collar of penis).

but the pigmented opercular lobe is distinct. The pallial caecum is short, about one fourth of the body whorl.

The jaw platelets are up to 52 μ high; they have a conical tip and one to six small accessory points (Figs. 20, 21). The radula of *R. punctocaelatus* was described and figured by Habe (1956: 99, fig. 3). The present specimens have 27-35 rows of 5.0.5 teeth. In the oldest series only 1-2 of the inner teeth of the row are maintained, farther ectally the number of rows increases to the full five. The teeth in the half-row increase in length outwards, e.g., 50, 65, 80, 115, 300 μ. The number of denticles varies from 5 to 9 on the four inner teeth (Figs. 23-25). The smallest old teeth were 23 μ long with only two denticles (Fig. 22). The outermost tooth is quite different in young (Fig. 23) and older rows (Figs. 24, 25). The smallest fifth tooth measured 65 μ and had 4 denticles. In each following row the size increases, and there are up to 20 denticles. The number of denticles diminishes at a length of about 300 μ; the longest denticled tooth measured 340 μ; in another specimen a 300 μ tooth was smooth and flagelliform. The longest fifth tooth measured 460 μ. In a radula of 35 series 28 rows were complete. In these 17 of the outermost teeth bore denticles, the eleven newest ones were smooth and flagelliform. In another radula of 33 series the fifth tooth was present in eight, on one side all had denticles, on the other all were smooth.

The single radula I at first only had available, had retained 20 rows of fifth teeth, all with denticles, so that I could not identify it with Habe's figure. However, the rich material from Dillon showed the variability of the denticulation with age.

In all radulae of *punctocaelatus* the outermost tooth is the longest, as in *Rictaxis albus*, and different from *R. punctostriatus*, in which the fourth tooth is the longest.

The stomachs contained many tentacles of polychaetes, probably sabellids, as such were also found to be the food of *R. punctostriatus* and of *Tomlinula cumingii*.

The penial papilla at rest (Figs. 19, 26) is about 1 mm long and 0.4 mm in diameter. It is surrounded by a thick and wide collar. The latter keeps its shape during erection, when the papilla lengthens to 5 mm, diminishing its diameter to about 300 μ (Fig. 29, p).

The two spiral spawns obtained at Dillon in July are coiled strings 3 mm in diameter. They are 8 mm (Fig. 27) and 10.5 mm high (Fig. 28), and fastened to the muddy substratum by a mucous thread. The egg string inside has a diameter of 1.2 mm, and contains eggs of 0.2 mm.

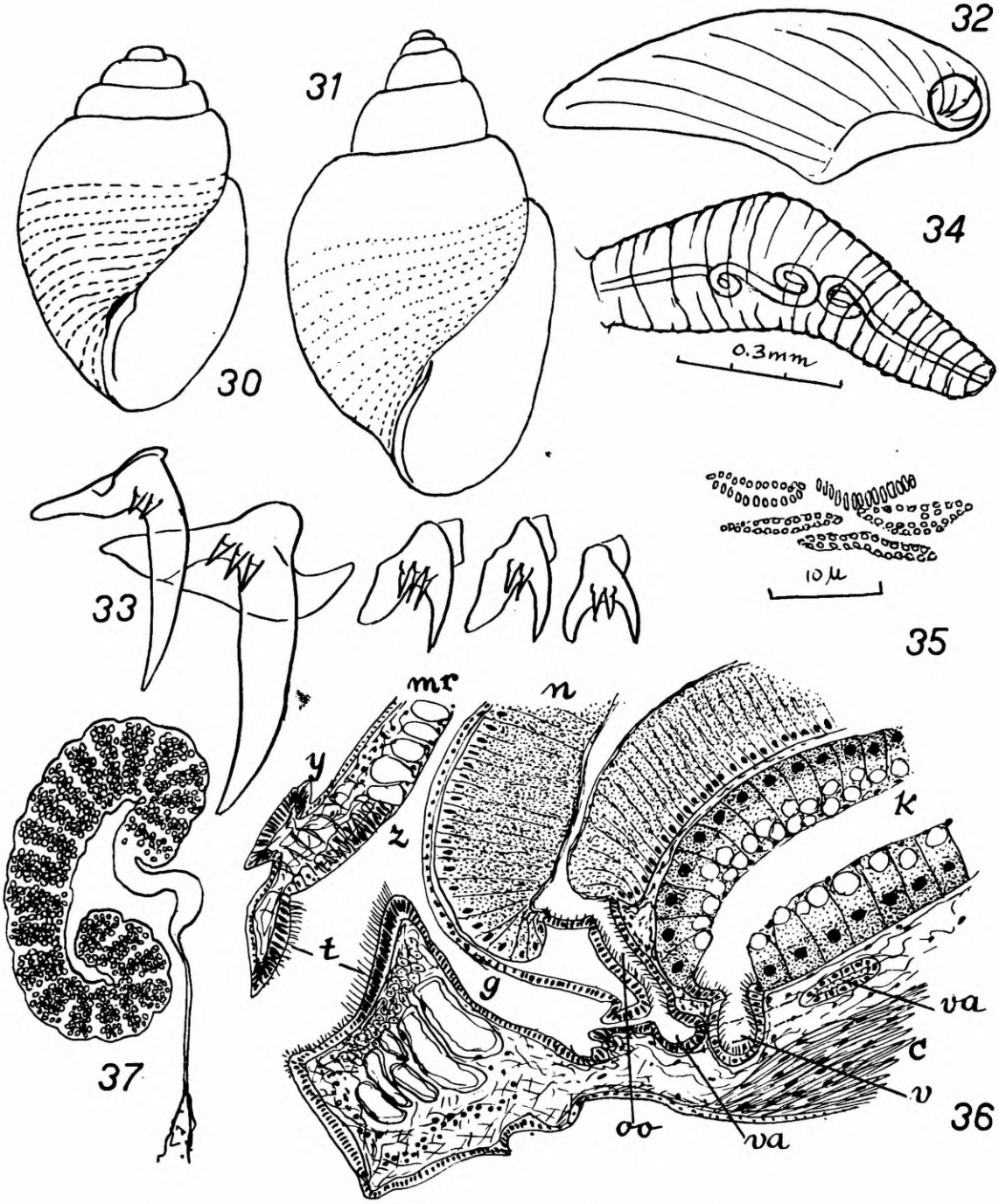
Rictaxis punctostriatus (C. B. Adams, 1840)

(Figs. 2, 30-37)

Tornatella puncto-striata; Gould, 1870: 224, fig. 515; Clench & Turner, 1950: 333, pl. 40, figs. 5, 6.

Actaeon punctostriatus; Pilsbry, 1894: 157, pl. 18, figs. 98-99 (from d'Orbigny), pl. 19, fig. 22 (from Gould), fig. 23 (from Verril, var.).

Acteon punctostriatus; Abbott, 1954: 275, pl. 26, fig. T; Warmke and Abbott, 1961: 140, pl. 28, fig. b.



Rictaxis punctostriatus: 30, shell from Solomons, Md., 3.8 mm high; 31, shell from Marco, Florida, 4.2 mm high; 32, operculum; 33, radula; 34, penis; 35, jaw platelets; 36, partial section of reprodutive organs; 37, spawn.

Rictaxis punctostriatus; Marcus, 1971: in press.
non *Acteon punctostriatus*; Marcus, 1956: 32, figs. 1-10.
? *Acteon punctostriatus*; Marcus, 1970: 924, fig. 5.

Material: Florida, Key Biscayne, Bay shore, on outer side of mangrove, among algae, 20.XI.1970, 7 specimens: Solomons, Md., X.1969, 8 specimens, three spawns.

Description. The fragile shells (Fig. 2, 30, 31) correspond to the descriptions and figures of *Acteon punctostriatus* in Pilsbry, by Abbott, and by Warmke and Abbott. The punctuate spiral furrows separate flat ridges. For measurements see tables 1 and 2. The shells form 4-5 whorls besides the protoconch. The whorls are convex, the suture is channeled. They are semitransparent with a thin, yellowish periostracum. The transparent operculum (Fig. 32) is flat, up to 2 mm long and 0.8 mm broad, that is 40% of the length. Its hind border, in creeping state, is convex, the anterior border has two slight concavities flanking a tip. The soft parts are cream-coloured. The big black eyes are visible at the root of the round cephalic lobes. The anterior border of the mantle roof is thickened, its outer surface over the mantle cavity is spotted with black pigment. The anterior foot border is bilobed, and a big foot gland opens over its notch. The hind end is pointed. The opercular lobes are prominent on both sides. The soft penis is cylindrical (Fig. 34). The infrapallial lobe is triangular with a median furrow. The ventral ciliated ridge, underlain by big glands, arises from the infrapallial lobe and turns inward in a semi-circle, following the mantle suture. It is accompanied by the dorsal ridge in the roof of the mantle cavity. Both ridges thin out entally and end in the suture near the innermost part of the mantle cavity, close to the anal opening. There is no free pallial caecum.

The mantle cavity occupies the entire body whorl. Its epithelium is for the most part glandular. The roof lodges the small folded gill and the wide kidney behind it, in front of the heart. The kidney has a long afferent vessel on its left side, giving off transverse, rib-like branches coated with high, folded epithelium.

The alimentary tract corresponds to that of *Acteon tornatilis* (Pelseneer, 1894, figs. 7, 11), except for the cuticular elements. The mouth cavity receives a pair of clustered cyanophilous ptyaline glands. The jaw elements are very delicate platelets, 13×4 μ, covered with tiny denticles (Fig. 35). The radula measures 2.3 mm in length and has 45-53 rows of 5.0.5 teeth (Fig. 33). The three inner rows have a pointed cusp arising from a narrow, high base, from which a delicate mediad plate diverges. There are 2-3 denticles on the outer side of each tooth. The fourth tooth is biggest; it has a heavy, transverse base 40 μ long, an equally long pointed cusp, and 2-3 outer denticles. The fifth, outermost tooth is smaller, with a longitudinal, narrow base and 3-4 outer denticles.

Where the oesophagus leaves the pharynx there is one pair of sac-shaped salivary glands which open to the sides of the buccal ganglia. The long and narrow oesophagus is continued into the wide stomach embedded in the digestive gland. A thin intestine goes out from the hind end of the stomach and opens into the innermost part of the mantle cavity near the end of the pallial ridges.

The reproductive organs are similar to those of *Acteon tornatilis* (Pelseneer, 1894: 9, 13; Fretter & Graham, 1954: 574; Johansson, 1954: 224, figs. 1-3). The ental follicles of the ovotestis contain

sperm, those in the outer part of the gland ova. The prostate differs from that of *A. tornatilis* by a smooth layer of big glandular cells 40-60 μ high with large basal nuclei, 10 μ long, and small apical epithelial cells with small nuclei (Fig. 36, k). It is much like that of *Acteon pelecais,* while in *A. tornatilis* the prostatic epithelium is rather thin and ciliated and thrown into deep longitudinal folds protruding into the lumen of the gland. The smooth penial papilla(Fig. 34) is 0.8 mm long and 0.25 mm in diameter.

The spawn (Fig. 37) is a mucous tube 6-9 mm long on a stalk standing out over the muddy substratum, so that the collector can see where he has to dig for the snails. The egg string in the tube forms about 27 loops on the largest spawn. The yolk of the eggs is 70-85 μ, the individual mucous capsule 100 × 120 μ, and the number of eggs in one spawn can be estimated to about 3000.

Discussion. In discussing our Brazilian Acteonid (1956: 34) we noted some differences between our material and Abbott's photograph, but we did not want to separate it based only on minute diversities of the shells. When Habe (1956: 99, fig. 3) studied the radula of *Acteon punctocaelatus* Carpenter, 1864, he found the formula 5.0.5, and established the generic validity of Dall's subgenus *Rictaxis* (1871: 136) with the type species *punctocaelatus*. Based on this same type of radula Thiele (1925: 223, pl. 34, figs. 3, 3a) created the genus *Pseudactaeon* for *Acteon albus* (Sowerby, 1873), so that *Pseudactaeon* becomes a synonym of *Rictaxis*. In both *punctocaelatus* and *albus* the fifth, outermost tooth is the longest. Though in the present *punstostriatus* the longest tooth is the fourth, it does not seen advisable to create a further genus for this Acteonid with the formula 5.0.5. I place it in *Rictaxis* Dall, till further radulae with the fourth tooth longest justify generic separation.

Among the western and central Atlantic species called *"Acteon"* seven have spiral grooves only in the lower half of the body whorl. Of these the Antillean *exiguus* and *splendidulus* Mörch, 1875, and the Floridian *semicingulatus* Dall (1927: 19) are unfigured. The measurements and the ranges of *"A." punctostriatus* (C. B. Adams, 1840) and *"A." candens* Rehder, 1939 (p. 21) overlap. The former was indicated from Cape Cod to Argentina, the latter from North Carolina to Cuba (Abbott, 1954: 275). The original locality of *punctostriatus* is Connecticut, and as the present shells agree with the original description of *punctostriatus,* I assume that they belong to that species. *"Acteon" semisculptus* E. A. Smith, 1890, from St. Helena has a longitudinal sculpture besides the spiral one. The seventh species is *Acteon pelecais* (see p. 170).

The shell of *"Acteon" melampoides* Dall (1881: 95) from the east coast of North America (Pilsbry, 1893-1895: 158, pl. 20, fig. 33) is similar to the present wide specimens (Fig. 33), but its spiral sculpture covers the whole body whorl.

I give a table of the shells in the previous descriptions (table 2) and of those that I could take myself of *R. punctostriatus* (table 1), of the Brazilian *Acteon pelecais,* of the type specimen of *"A." candens,* which I had the opportunity to examine thanks to the kindness of Harald A. Rehder and Joseph P. Rosewater in the Smithsonian Institution, and of 12 shells of *"A." candens* from the collection of the Florida State Museum, Gainesville, n.º 13.604, kindly entrusted to me by Fred Thompson. The measurements vary between almost the

same limits for all (see table 2). The sculpture is nearly identical, however, the shells of *candens* are heavier than those of *punctostriatus*.

Both *Pupa* and *Rictaxis* have 5.0.5 teeth, but the degree of difference between inner and outer teeth of the half-row varies. The inner teeth of *Pupa* have a very broad base and a long cusp with small

Table 1. Shells of *Rictaxis punctostriatus* from Solomons, Md.

specimen nº	length mm	width mm	ratio l:w	aperture mm	aperture %	spire mm	spire %
1	5.1	2.8	1.82	2.5	49	1.3	25.5
2	4.3	2.4	1.79	2.6	55.7	1.2	27.9
3	4.1	2.8	1.46	2.4	58.5	1.1	26.8
4	4.3	2.4	1.79	2.6	60.5	1.0	23.2
5	4.0	2.3	1.74	2.6	65	1.1	27.4
6	4.1	2.4	1.71	2.6	62	1.1	26.1
7	3.8	2.3	1.65	2.3	60	0.9	24.6
8	3.8	2.4	1.58	2.5	65	0.7	18.4
	2.3-5.1	2.3-2.8	1.46-1.82	2.3-2.6	49-65	0.7-1.3	18.4-27.9

Table 2. Shells of Western Atlantic Acteonidae with smooth top

Material	length mm	width mm	ratio l:w	aperture mm	aperture %	spire mm	spire %
Acteon = *Rictaxis punctostriatus* from literature	3.0-6.2	2.8-3.8	1.64-1.92	3-4	58-67	0.7-1.2	20-23
Rictaxis punctostriatus from Solomons	3.8-5.1	2.4-2.8	1.46-1.82	2.3-2.6	49-65	0.7-1.3	18.4-27.9
Rictaxis punctostriatus from Florida	3.5-4.3	1.9-2.4	1.73-1.79	1.6-2.7	47-64.3	0.8-1.5	21-31
"Acteon" candens Rehder, 1939 holotype	8	4.6	1.74	5.5	68.7	1.9	23.8
"Acteon" candens, Museum Gainesv	4.2-8.0	2.5-4.5	1.65-2.3	2.74-6.0	52.9-76.4	1.2-1.5	11.5-27.5
Acteon pelecais Brazil	4.5-6.2	2.8-3.8	1.61-1.69	3.0-4.0	64.5-66.5	1.2-1.5	22.8-26.6
Biggest empty shell *pelecais*	9.5	5.5	1.73	6.0	62.0	2.0	21.5
"Acteon punctostriatus" Carcelles & Parodiz,1938	8.0	4.6	1.74	5.5	68.7	1.9	24
Acteon semisculptus Smith, 1890	4.0	2.25	1.77	2.75	68.7	0.5	12.5

Note: Table 1, lowest line of "length", read 3.8-5.1 for 2.3-5.1. Table 2, second line of "width", read 2.3-2.8 for 2.4-2.8.

denticles (Bergh, 1902, pl. 27; Thiele, 1931, fig. 473). Habe (1950b, pl. 8, figs. 11-13) figures the radulae of *P. solidula* (Linné, 1758), *P. sulcata* (Gmelin, 1791), and *P. strigosa* (Gould, 1859). The two former have a broad base on all five teeth, while the latter has narrow bases with denticled cusps on the inner teeth and a long cusp on the fifth, outermost tooth, thus somewhat similar to the radula of *Rictaxis*. In *R. punctocaelatus* and *R. albus* the inner teeth have a narrow and high base and a short cusp with increasing denticles. The fifth, outermost tooth has no denticles and a long, soft cusp (Thiele, 1925: 356, pl. 34, figs. 3, 3a; 1931, fig. 472; Habe, 1956, fig. 3; Barnard, 1963, fig. 28h). In *Rictaxis punctostriatus* the broad base of the three inner teeth is inconspicuous and sometimes rolled around the shaft of the cusp. The fourth tooth having the longest cusp distinguishes *punctostriatus* from *Rictaxis punctocaelatus* and *albus*, and from *Pupa*. But, as long as the radulae of so few species are known, it does not seem to be advisable to create more genera for single species. Thiele (1931: 378) remarked that without knowledge of the animals the delimitation of *Actaeon* against several other genera is uncertain.

Comparative notes

The present forms do not only differ by radulae and jaw platelets. They also have different pigment of the mantle border, which is wanting in *Acteon pelecais* and *Tomlinula cumingii*. In *Rictaxis punctostriatus* the border of the roof the mantle is spotted with black; black spiral stripes corresponding to the spiral stipes of the shell occur in *R. punctocaelatus*. In *Acteon traski* there is a black area along the mantle border, widened under the two pink bands of the shell.

The pallial caecum is adherent in *R. punctostriatus*, free in the other species. Its length is about one quarter of the body whorl in *Act. traski* and *R. punctocaelatus*, about one whorl long in *T. cumingii*, and one and a half whorl in *Act. pelecais*.

The penial papilla is a simple short muscular tube with the male duct coiled inside in *Act. pelecais* and *R. punctostriatus*. It has a narrow collar in *T. cumingii*, which is glandular in *Act. traski*, and a wide collar in *R. punctocaelatus*.

The prostatic epithelium is flat and thrown into longitudinal folds in *Acteon tornatilis* (L.) (Fretter and Graham, 1954: 574, fig. 7; Johansson, 1954: 224, textf. 1, 2, pl. 1, fig. 1). There is a simple tube of high glandular cells interspersed with small ciliated cells in *Act. pelecais* and *R. punctostriatus*. In *R. punctocaelatus* the prostatic tube forms many deep transverse pouches lined with a medium high epithelium. In *Acteon traski* and *Tomlinula cumingii* it was not studied.

The contents of the digestive tract were found to be parts of sessile polychaetes. In *Tomlinula cumingii* I found a piece of several undigested segments of a sabellid, in *Rictaxis punctostriatus* tentacles and some segments with bundles of setae, and in *R. punctocaelatus* great masses of coiled tentacles.

Conclusions

As Thiele (1925: 223) and Zilch (1959-1960: 6) supposed, the study of the soft parts of the Acteonidae makes a distribution of many of the known shells onto several genera necessary. The basic character is the radula. Until now there are three distinct types. *Acteon* has very many small and uniform teeth. There is a restricted number of rows of strong teeth in *Tomlinula,* and five teeth per half-row in *Rictaxis.* Probably the knowledge of more radulae will permit further distinctions.

Resumo

O estudo de cinco espécies de Acteonidae do Atlântico ocidental e do Pacífico oriental modifica a posição sistemática de algumas delas. As figuras das conchas de *"Acteon" punctostriatus* da América do Norte e do Sul são indistinguíveis (Figs. 1, 2). No entanto, as suas rádulas são de tipos diferentes. A espécie brasileira é um *Acteon* verdadeiro com fórmula $\infty.0.\infty$ e recebeu o nome *A. pelecais* Marcus, 1971. A espécie norte-americana, com a fórmula 5.0.5, é colocada no gênero *Rictaxis* Dall, 1871. O tipo dêste gênero é *R. punctocaelatus. Pseudactaeon* Thiele, 1925, com o tipo *albus* (Sowerby, 1873) é sinônimo de *Rictaxis.* O dente externo de *R. punctocaelatus* varia de forma com a idade (Figs. 23-25). *Acteon traski* do Pacífico oriental é mesmo *Acteon. Acteon cumingii* do Atlântico ocidental tem a fórmula n.0.n. como *Alexandria natalensis* Tomlin, 1926, e é transferida para o gênero *Tomlinula* Strand, 1932, que substitui *Alexania* Strand, 1928, e *Alexandria* Tomlin, 1926, nomes preocupados.

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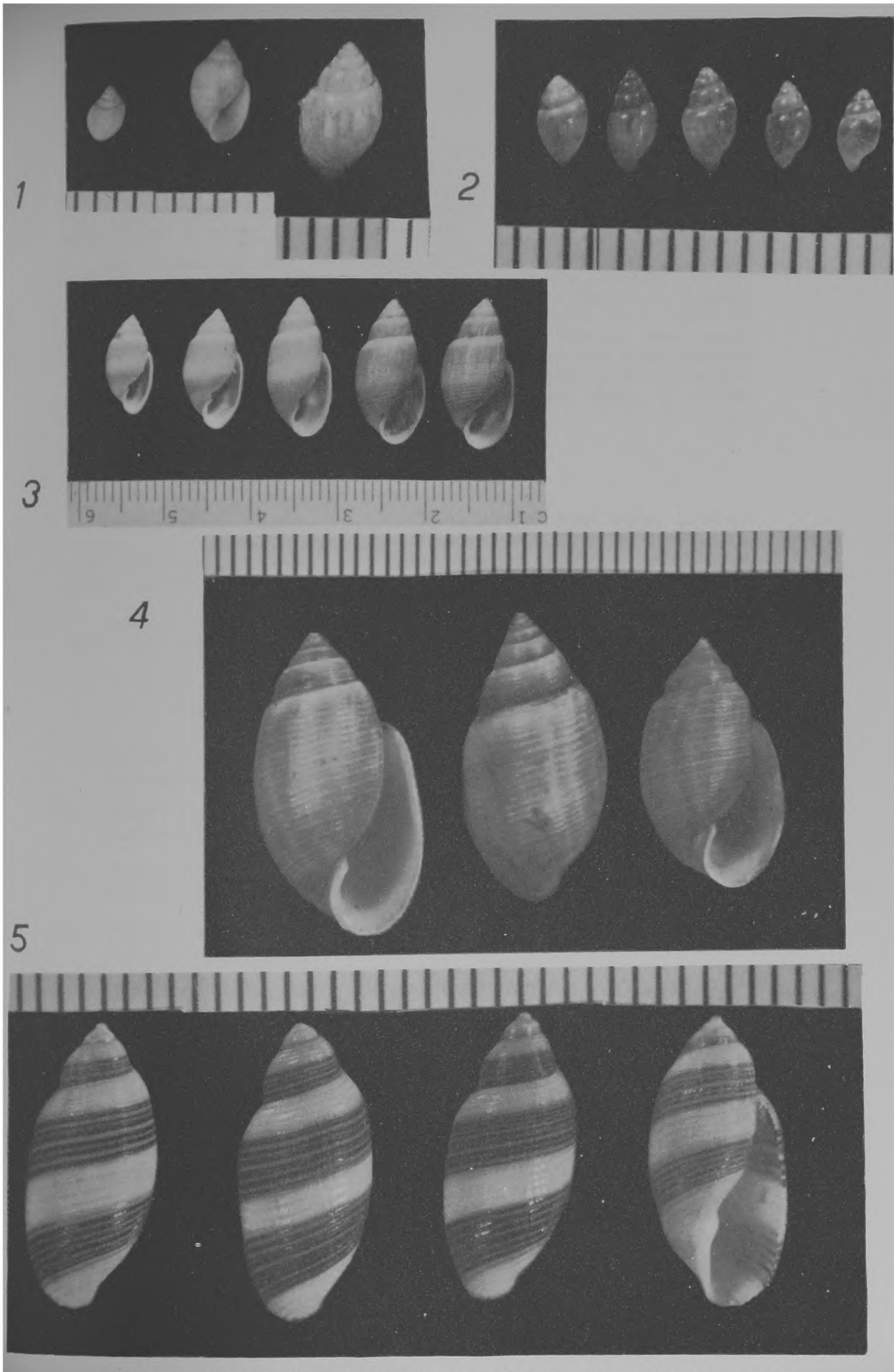
ADDENDUM

After the present paper had gone to press (17.IX.1971) I received two reprints from W. B. Rudman dealing with Acteonidae, issued September 1971. Rudman stresses the importance of the anatomy for the systematics of the Acteonidae. He found the operculum of *Bullina* and returned it to the Acteonidae, and described its jaw platelets and radula. In the second paper he creates a new genus *Maxacteon* for species with 13 or less teeth per half-row, his treated species have 8, 11, and 13 teeth respectively. Rudman discusses the genera of the Acteonidae. He considers *Pseudactaeon* Thiele as a probable synonym of *Rictaxis*. *Punctacteon* should be declared a nomen nudum. The radula of *Maxacteon* with 13 teeth or less differs from *Rictaxis* with five teeth in the known species, by equal shape and almost equal size of its teeth, while in *Rictaxis* the cusp of one tooth is much longer. From *Tomlinula* with 18 and 36 teeth *Maxacteon* is distinguished by the long and slender main cusp with few basal denticles, while the teeth of *Tomlinula* have uniform denticles and no main cusp.



1, *Acteon pelecais;* 2, *Rictaxis punctostriatus;* 3, *Acteon traski;* 4, *Tomlinula cumingii;* 5, *Rictaxis punctocaelatus.*