

ON *TRICOLIA AFFINIS CRUENTA*

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(with 6 plates)

Thanks to the Director of the Oceanographic Institute of São Paulo, Dr. Ingvar Emilsson, we could continue our studies on marine gastropods at the Base of Research, Bay of the Flamengo near Ubaituba (23° 27' S. 45° 6' W.), whose Head, our friend Dr. Edmundo Nonato, received us with habitual hospitality.

While collecting columbellids we found a trochacean in great numbers together with them. As the small Trochacea are anatomically little known, and this Super-Family is phylogenetically central, we decided to study these snails.

The species belongs to the Phasianellidae. According to Robertson's monograph of the Western Atlantic phasianellids (1958) it is the subspecies *cruenta* Robertson, 1958, of *Tricolia* (*Tricolia*) *affinis* (C. B. Adams, 1850). *T. concinna* (C. B. Adams, 1850) published two pages behind *affinis* is the same species. The references to *concinna* from the coast of São Paulo and Paraná (Lange de Morretes 1949, p. 62; Gofferjé 1950, p. 232) evidently belong to *affinis cruenta* (Robertson 1958, p. 268). The distribution of the subspecies comprises the Caribbean coast of northern South and Central America, ranging as far north as the Grenadines in the Lesser Antilles and south along the coast of Brazil to the State of Sta. Catharina. Sporadically it occurs on the shores of the western Gulf of Mexico (Robertson). The holotype was collected at the same place where we found the snails.

These live a little below the mean low water-line principally on *Sargassum cymosum stenophyllum*, but also on *Galaxaura stipicaulon*, *Acanthophora spicifera* and others. On *Padina* they are very rare. They inhabit mainly the lower regions of the *Sargassum* where the growth of Hydrozoa, Bryozoa, Tunicata and others is especially thick.

In July 1960 we found 40 two to seven millimeters long snails on a tuft of about 40 stems growing from one holdfast and up to 40 cm high.

SHELL AND OPERCULUM

The following description refers exclusively to the present material of several 1.000 snails of all sizes that we have seen.

Shell solid, ovoid, up to 8 mm in length, 4,5 mm in width. Colour pattern (Fig. 1) consisting in spiral rows of variously sized red spots. If these are small, 40-80 μ in diameter, there occur 32 rows or more on the body whorl; if they are big, 0,15 to 0,3 mm, there are about 20 rows. Between the red spots sometimes opaque white dashes lie over light ground colour. In worn shells the red dots appear as pits; severely worn shells are uniformly pink or quite white. The ground colour is olive or green to cream, or even dark purple. In front of the suture and at the periphery there may be whitish or darker, reddish, greenish or even dark brown axial blotches. Only over the whitish of these blotches occur the above-mentioned white dashes. The presutural and peripheral blotches may fuse, or zig-zag lines or variously shaped ones may occur. Among all our snails we found about ten melanistic shells with black dots on dark grey ground colour. Also the red dots on coloured ground may be substituted by black ones.

Whorls 7 1/2, two of which belong to the white depressed protoconch. The first whorl in front of the protoconch is dark with fine axial pink pattern. Whorls inflated, evenly rounded and smooth. Spire produced at an angle of from 45° to 90° (Fig. 3). Aperture oval, outer lip prosocline. Columellar callus moderately thin, white. Umbilicus of adult shells reduced to a chink. Suture impressed. Operculum (Fig. 4) white, dark olive-green or brown at the margin, paucispiral (oligogyrous), nucleus nearly marginal.

Robertson stressed "regularly spaced large red spots" and "usually low spire (65°-75°)" as characters of the subspecies, but these are not constant. The low spire was already restrained by Robertson who found an elongate spire (about 50°) in two specimens from Pernambuco. In big shells of our material the spire is higher than in smaller ones. In spite of these restrictions we maintain *cruenta* as a subspecies, because its combined characters allow for a separation

from Robertson's other subspecies of *affinis*. Among these only *T. a. beaui* overlaps the range of *cruenta* in the southernmost Lesser Antilles and differs by colour pattern and spiral striae on all postnuclear whorls.

The smallest preserved shell (Fig. 2) is 0,3 mm long and 0,5 mm in greater diameter. It has 2 white nuclear whorls and pale red dots on the following half whorl. The latter, and in older shells the entire first postnuclear whorl, bears convex spiral lines separated by furrows. The apex of young shells is quite, flat, nearly insunk. The angle of the spire is 130° and more. The umbilicus is a deep hole. The operculum is imperforate unlike that of *T. bella* (1958, p. 250, 274), and circular, 0,18 mm in diameter. As it has 4 whorls, it corresponds to the centre of the 0,45 mm long operculum of Fig. 4. The youngest operculum is not calcified yet; its outer surface is slightly depressed so that in this special case the centre is thinnest, and the periphery with its spirals thicker.

Juvenile shells agree with a not yet analyzed species of *Gabrielona* from the Island of São Sebastião (*Eulithidium brevissimum* in Lange's catalogue, p. 62) in several characters (Robertson, p. 259). Therefore we examined radulae (Fig. 8) and opercula of our young snails (Fig. 5) and found dentate (in *Gabrielona*, smooth) lateral teeth and opercula with generally smooth outside (in *Gabrielona*, spirally ridged externally) and thickest in the centre (in *Gabrielona*, thinnest).

JAWS AND RADULA

The radula (ra) works against a pair of jaws (j) which are colourless and united dorsally by cuticle. The mandibular plates are entire, not made up of two portions (Randles 1904, p. 49; Frank 1914, p. 433) as in some trochids. As the jaws are composed of rather flat lying rods, their surface appears scaly. These scales are most conspicuous and jutting in front and in the middle, smaller and flatter on the sides and behind.

The adult radula (Fig. 6) has 43 rows of 58.4.1.4.58 teeth. The rhachidian tooth is a nearly rectangular or more or less rounded plate with smooth borders and without any cusp. The lateral teeth are strongly dentate. They have a principal cusp and inner as well as outer

denticles on the 2 inner, only outer denticles on the 2 outer teeth. The numbers of these denticles are: on the innermost lateral tooth 4 inner and 4 outer ones, on the second 4-5 inner and 4 outer ones, on the third 4-6, and on the fourth 4 outer denticles.

The innermost tooth is broad and has an external wing. Robertson (p. 247) considered this dilatation as a character of Eastern Pacific species of *Tricolia*. Its appearance in our subspecies of *T. affinis* which occurs farthest towards the West, from Colombia (Cartagena) and Panama to Honduras, Mexico and Texas, may point at the Tertiary sea-connection in Central America. The base of the second lateral tooth is roundish. The cusp of the third is specially broad. The base of the fourth is long and expanded on the inner side.

We cannot confirm the existence of a "lateromarginal" plate (Robertson, p. 247) without cusp between the outermost lateral and the innermost marginal tooth and think it must be eliminated from the diagnosis of the subgenus (p. 261). This plate is actually the base of the innermost marginal tooth (Fig. 7). Powell (1951, p. 88, 105) stressed the difficulty to interpret the rhipidoglossid radula owing to the large number and the intricate overlapping of the teeth. The cusp of the first marginal tooth bears 5 outer denticles; that of the three following teeth is broader. From the fourth marginal tooth outwards the cusps decrease. The number of denticles augments to 12 and they are longer and thinner. The outermost marginal teeth are thin and curved plates.

The radula (Fig. 8) of a quite young snail with 0,6 mm long shell has about 17 rows of 11.2.1.2.11 teeth. The median tooth of the oldest rows has a complete cusp with up to 5 denticles on either side. In the younger rows the denticles disappear gradually, and the cusp shortens. The difference between lateral and marginal teeth is less pronounced than in the adult radula. The inner marginal teeth have pointed cusps with 8 outer denticles.

COLOUR, HEAD, EPIPODIUM AND FOOT

The colour of the flesh is green, especially intense on the roof of the mantle cavity. The epidermis bears spots which may be red, brown or black. Some snails have a uniform dark skin. Lighter or darker skin is not correlated with the tone of the shell. The upper

side of the foot is striped or spotted, the sole always light. The green colour is dissolved in alcohol, not the red spots.

The head is distinctly separated from the foot (f) and has a pattern of symmetrical black spots in some specimens (Fig. 10). The cylindrical tentacles (t) are pointed at the end and beset with two rows of sensory papillae which resemble those of *Incisura lytteltonensis* (Bourne 1910, p. 29, pl. 5, f. 27, 28). Equal papillae are rare on the stalks of the eyes (ee) and much more numerous on the epipodial appendages (ei). The cilia of all these papillae are immobile as Robertson (1958, p. 249) indicated correctly.

The eyes are highly developed for an archaeogastropod. They are closed as in the mentioned *Incisura* (l. c., p. 4), fissurellids and turbinids, not open as in the trochids. The shape of the eyes is globular, and they contain a refractive vitreous body. They lie immediately under the epidermis, without a separating precorneal blood sinus, so that inner and outer pellucid (corneal) layer are contiguous in the middle over the convex vitreous body. As in other archaeogastropods there is no lens differentiated within the vitreous humour. The retina agrees with that of *Astraea rugosa* (Hesse 1902, p. 580), but the roundish nuclei of the sensory cells are basal, the longish ones of the pigmented cells are more apical as in the trochid *Gibbula cineraria* (Frank 1914, p. 471-472, text-fig. 55), and contrary to the turbinid studied by Hesse (pl. 35, f. 10).

In the feeding snail mandibles and radula can be seen in ventral view. As in *Tricolia pullus* (Pelseneer 1899, p. 46) the left (ce) and right (rc) cervical (suborbicular) epipodial lobes are different. The left of *T. affinis cruenta* is pectinate, like the "siphon d'entrée" (l. c.) of the branchial side in trochids, the right one is entire, like the "siphon de sortie" of the anal side. In *Tricolia bella* only the pedunculate and digitate left cervical appendage is developed (Robertson 1958, p. 249). The left side comb of *T. affinis cruenta* has up to 7 projections. It does not alter its position, even if sediment is added to the water that is to be inhaled, nor did two nematodes moving about the inhalant opening provoke any noticeable reaction of the comb. This organ is innervated (Fig. 13, ce) but less muscular than the posterior epipodial tentacles (ei).

The latter are symmetrical structures, one in front of and one behind a fold (oe) beset with sensorial papillae. This lateral fringe is continued into a dorsal fold (oe) which hems in the anterior half of the operculum (oc), i. e. anterior in the creeping snail (Fig. 11). The epithelium that lies on the operculum is much higher than that of the back of the foot under the conchinous opercular base. Therefore we suppose that the high epithelium of the pouch secretes the lime of the operculum.

The sole of *T. affinis cruenta* (Fig. 9) does not have the longitudinal furrow that exists in *T. pullus* (Fretter 1955, p. 159) and other species of *Tricolia* and *Phasianella* (Robertson 1958, p. 25). The entire sole and the lateral borders of the foot bear mucus glands. The anterior pedal border is grooved transversely. From the middle of this anterior furrow a 0,18 mm long canal (wz) pierces the foot. Blue-staining glands open into the transverse groove as well as into the canal in its middle. Several trochids have similar structures (Randles 1904, p. 38; Frank 1914, p. 388-389). Mucus glands are accumulated near the posterior border of the foot, where their thick clusters (Fig. 11, oa) open into a shallow median groove.

LOCOMOTION

Corresponding to the undivided sole the muscular locomotion is only sometimes allusively ditaxic. We compared the available trochid *Tegula viridula* (Gm.); it protrudes the two halves of the sole alternately as *Trochus* (Weber 1924, p. 110). In *Tricolia* the position of the anterior border of the foot in relation to the shell is constant when the snail moves forward. It does not move by jerks as we know it of diggers (Olividae, *Hastula*) and climbers (*Anachis*). Our *Tricolia* did not move much about at the temperature of 20°C.

One can watch the snails gliding on the under side of a slide or on the surface film. Here they move by ciliary action on a ribbon of mucus (Kaiser 1959, p. 379) which begins at the anterior border of the foot whose glands were described. The glands of the posterior groove contribute to the ribbon of mucus securing the snails. When the snails glide on the surface film, parts of the sole shift their posi-

tion against others by muscular action. According to Kaiser (p. 375) this secures the contact of the foot with the surface.

If removed from the substratum our snails fall onto their aperture or onto their back. In the glass dish they cannot recover in the latter case nor if they are tilted a little to the right side. They try to attain the substratum, but the short foot is not sufficiently distensible. This insufficiency has probably no biological significance, as in the upper littoral the waves will soon roll the snails into a more favourable position with the inner lip nearer to the ground. Laid into the dish in this position the snails feel for a substratum with the anterior border of the foot. According to Weber (1926, p. 393) this is the simplest recovering action of prosobranchs. *Tegula viridula* behaves like *Tricolia affinis*; *Trochus* searches a hold and fixes itself preferably with the hind tip of the foot (l. c., p. 425-432). If the cephalic tentacles or the anterior pedal border of *Tricolia* come into contact with an object, e. g. the point of a needle, the border grasps it and draws the entire snail after. An equal stimulus touching the epipodial tentacles does not effect any visible reaction. In *Trochus* the epipodial tentacles are tactile (l. c., p. 427).

PALLIAL CAVITY

To the right of the middle the suprapallial border is somewhat recessed (mn) in front of the anus (ar), perhaps a vestige of the slit of *Incisura* (Bourne 1910, pl. 1, f. 2-4, m. s.) which disappeared with the loss of the right gill. An infrapallial narrow glandular fold (xu) runs between shell and operculum in the moving snail as in trochids (Randles 1904, pl. 6, f. 40, ma). The entire border of the mantle bears glands. In front and on the right side, that is under the growing edge of the body whorl, the glands (g) are especially numerous. This increase is brought about by 0,3 mm long ciliated tubular invaginations of the epithelium that lines the mantle furrow. The functioning glandular cells lie near the entrance of the tubules. These are parallel (Fig. 11, g) to the roof of the mantle, perpendicular to its edge (Fig. 12, g) and contiguous with one another. Similar structures occur in the trochid *Monodonta turbinata* (Frank 1914, p. 395-396) and with Frank we suppose that these glands se-

crete the shell or at least its periostracal conchiolin (Graham 1957, p. 136).

A big vessel (ve) accompanies the glands of the mantle furrow and is connected with the system of the efferent branchial vessel (ev). It comes from the lacunae in the foot, runs around the periphery of the mantle where its blood evidently becomes oxygenated. The vessel passes the osphradium (os) and enters the efferent branchial vessel. There are also vessels which come from the anterior margin of the mantle and enter the anterior pallial vein or the transverse pallial vein and therewith the afferent branchial vessel (ac). While these are frequently mentioned for the circulation of trochids (Robert 1900, p. 407; Randles 1904, p. 56-57; Fleure and Gettings 1907, p. 468; Frank 1914, p. 411), the vessel that comes from the roof of the pallial cavity and goes back to the left auricle through the efferent branchial vessel was only recorded by Fleure and Gettings (l. c., p. 468-469). It evidences a respiratory function of the mantle roof.

At the passage of the upper into the under mantle border a band of red staining glands runs into the mantle cavity and accompanies the suture on both sides to an extension of 1,2 mm. A vessel beneath the right glandular band can be followed nearly to the right auricle; it represents a vestige of the right efferent branchial vessel discovered by Thiele (1897, p. 641) in *Gibbula cineraria* and found in several trochids by Robert (1900, p. 405), Randles (1904, p. 57), Fleure and Gettings (1907, p. 467-468) and Frank (1914, p. 410). The last author found and described (p. 470) as glands several bulges in the right angle of the mantle cavity of *Gibbula cineraria*, but identified them with Thiele's sensory organs (1897, pl. 31, f. 8, so). Of this type occurs only one organ (Fig. 13, no) on the left side of the pallial cavity of *Tricolia affinis cruenta*, beside the button-like osphradium (os).

The size of the osphradium in relation to the ctenidium is not bigger than in *Tegula viridula* (Gm.), a trochacean common on rocks in the same region. According to Hulbert and Yonge's view (1937) that the osphradium is a tactile organ concerned with estimating the amount of sediment carried into the mantle cavity one would have expected a bigger osphradium in *Tricolia* than in *Tegula*. Mr. Edmund H. Smith, M. A. of Los Angeles who is at present working in

this Department on *Drupa nodulosa* (C. B. Ad.) and *Thais haemastoma* (L.) kindly informed that the first of these purpurines goes farther into turbid waters than the second and has a proportionally bigger osphradium.

The hypobranchial gland (y) of the present species is weakly developed. It lies to the right of the rectum over a pallial vein. In *Tricolia pullus* there is glandular tissue also to the left of the rectum (Fretter 1955, p. 161). Perhaps a strand of gland cells between anterior mantle border and osphradium can be considered as the left hypobranchial gland of *T. affinis cruenta*, though this gland lies much farther behind in *T. pullus*. Clark's table (1958, p. 61) shows the variation in the topography of the hypobranchial gland in Trochidae and Turbinidae as well as a correlation between an arcuate or straight course of the rectum and the development or absence respectively of a right hypobranchial gland. Also in the present species the right hypobranchial gland is associated with a more or less curved rectum.

The tip of the ctenidium (b) projects from the mantle cavity in some of the preserved snails. On the lower side there are about 50 lamellae hanging free into the cavity, whilst on the upper side they are a little less numerous. They are not placed symmetrically (Fig. 11, b). The hind part of the upper row is enclosed in a chamber formed by the roof of the pallial cavity and the afferent (am) and efferent membranes. These hold the gill for the greater part of its length as in *T. pullus* (Fretter 1955, p. 161). As in this species and contrary to three turbinids (Yonge 1947, p. 475; Clark 1958, p. 62) there is a weak supporting rod (or) in the free extremity of the ctenidium. Also the skeletal rod which bounds the branch of the efferent vessel within the leaflet occurs in our species as in the other Trochacea. Near the attachment to the rhachis every branchial leaflet has a small nick (ni), and these nicks "collectively form a groove which runs the length of the gill" (Clark 1958, p. 59). This feature noted by Clark in *Haliotis*, *Scutus* and numerous New Zealand trochids and turbinids has been object of a special study of Hatt (1927) who found it in many rhipidoglossan Diotocardia. Bourne (1910, p. 7) seems to be the first to have described it in *Incisura lytteltonensis*; he considered (p. 8) the cells of the ridge as secretory. Hatt

observed that they absorb Indian ink and dyes. Clark verified that they are not concerned with sediment disposal.

The branchial filaments on the lower side of the ctenidium are much more efficient to produce the inhalant current than those on the upper side. As in *Turbo* (Yonge 1947, f. 34 B on p. 498) there is also a forwardly directed axial current, carrying sediments from the left filament to the tip, besides the principal current from left to right. The axial current is intermittent. On the floor of the mantle cavity from the hind end forwards runs a streak of cilia (Fig. 10, ci). These beat upwards and forwards leading sediments dropped onto the floor into the exhalant current. Frequently these cilia discontinue beating. Functionally they correspond to those that produce the rejection current of many pectinibranchs and carry sediments along the floor of the mantle cavity (Yonge 1937, p. 693-694; 1938, p. 454-455; 1942, p. 200-201; 1947, p. 479). In sections of a small, 1,6 mm long snail the streak is 1 mm long and 0,1 mm broad. Generally the Trochacea live in clean water on rocks and reefs (Yonge 1947, p. 455). To the exceptions mentioned by Clark (1958, p. 59), trochids found on mud banks and fine sand flats, belong also the species of *Tricolia*, inhabitants of algae and grasses (Fretter 1955, p. 159; Robertson 1958, p. 252). In the bay where our abundant material occurs, sedimentation is intense in the rainy season. So a streak of special cilia under the gill seems to be functionally important.

NERVOUS SYSTEM

In its fundamental traces the nervous system of *Tricolia affinis cruenta* (Fig. 13) agrees with that of the Trochidae (Robert 1900; Randles 1904; Franck 1914), Turbinidae (Bouvier 1887) and, as far as studied, *Phasianella variegata* Lm. (Risbec 1939) whose name to-day is *Ph. rubens* Lm. (Robertson 1958, p. 249). It differs from that of trochids and turbinids by two ganglionar thickenings, one on each side of the abdominal ganglion (ao). Risbec has drawn a single right side ganglion in the supra-intestinal branch of the visceral loop (pl. 6, f. 64) and lettered it sb, suggesting a subintestinal ganglion. In the text (p. 286) however he called it visceral, i. e. abdominal ganglion. His topographic indication "à côté de l'orifice rénal droit"

shows that it corresponds to the abdominal ganglion of the present species.

The cerebral ganglia (ze) of *T. affinis cruenta* are voluminous; the tentacular and optic nerves have separate origins. The long and thin labial commissure (cm) goes out from a large ventrally directed labial lobe of each cerebral ganglion. The cerebral commissure (cz) is broad and posterior to the labial one. Independent from the latter the cerebro-buccal connectives come out from the cerebral ganglia as in *Phasianella rubens* (Risbec 1939, p. 286). The connectives are directed ventrally, they as well as the rather long buccal commissure have no nerve cells. The buccal ganglia (uc) are longish and angled, similar to those of *Turbo setosus* (Bouvier 1887, pl. 2, f. 5, B). They lie dorsal to the radula, ventral to the oesophagus, between these organs. Odontophore, salivary glands and crop are innervated by nerves from the buccal ganglia and the cerebro-buccal connectives.

The cerebro-pedal connectives (co) are shorter than the cerebro-pleural ones (cu). The latter are more lateral and include the static nerve. The pleural ganglia (ur) are fused to the dorsal surface of the pedal ganglia (en) and flank the big statocysts (sz) which contain numerous otoconia. The pedal ganglia are contiguous in the mid line. Each of them gives off a pair of anterior nerves which branch farther in front. Posteriorly each ganglion is continued into a broad cord (wo) coated with nerve cells. From the beginning of each cord spring two lateral epipodial nerves and farther behind several nerves principally to the ventro-lateral parts of the foot. The cords as well as the pedal ganglia are undivided, without a horizontal furrow. Three thin commissures connect the right and left cord. The purely pedal character of the cords first vindicated by Spengel (1881, p. 345) and Pelseneer (1899, p. 49) has been settled by Randles (1904, p. 61-64).

The pleural ganglia (ur) emit the branches of the visceral loop (ei, sv) and the mantle nerves (ne). The latter contain fibres which supply the two columellar muscles (mr, rr), run to the roof of the pallial cavity and unite on the anterior mantle border. A short nerve (ea) connects the nearly coalesced supra-intestinal (iu) and branchial (wa) ganglion with the left pallial nerve. This left zygois is developed in most Trochacea, but is absent in the calliostomine *Photinula*,

now *Photinastoma taeniatum* (Frank 1914, p. 461). The occurrence of one, exceptionally two (l. c., p. 459) right zygoes between sub-intestinal branch of the visceral loop and right pallial nerve is irregular in the Trochacea. Bouvier (1887, p. 32, pl. 1, f. 2, z¹) and Robert (1900, f. 500) found the right zygois in Turbinidae and Trochidae respectively. Frank (1914, p. 459) verified it in two of his trochids and stated its absence in the third, *Photinastoma taeniatum* (Wood, 1828). Randles (1904) had none in his numerous trochids, and also *Tricolia affinis cruenta* has no right zygois.

Between the branchial ganglion (wa) and the osphradium (os) lies the above-mentioned sense organ of Thiele (no). The abdominal ganglion is located in the fundus of the pallial cavity between right kidney and right columellar muscle. One of its nerves (on) goes to the gonopore, a second (ma) to the gut where it could be followed to the entrance of the oesophagus into the stomach.

Both branches of the visceral loop contain numerous nerve cells, as was observed by Frank (1914, p. 461). An accumulation of such evidently produced the sometimes developed ganglion in the supra-intestinal branch of *Phasianella rubens* (Risbec 1939, p. 286, pl. 6, f. 64, gn). In *Tricolia affinis cruenta* there are two such accumulations in the subintestinal branch, a right one in the right columellar muscle, and a left under the pallial floor. The nerve that connects this ganglion with the supra-intestinal loop runs under the above-mentioned streak of cilia (Fig. 10, ci). The occurrence of three visceral ganglia resembles the disposition in *Incisura lytteltonensis* (Bourne 1910, p. 27, pl. 1, f. 5), but the ganglia are not homologous.

SHELL MUSCLES

The present species has two columellar muscles (Fig. 14, mr, rr) as Fretter (1955, p. 159-160) discovered in *Tricolia pullus*. The right muscle is longer, thinner and attached to the spindle at the level of the hind end of the mantle cavity. The left muscle is shorter and thicker; its insertion lies farther in front, short behind the level of the osphradium. Also in *Incisura lytteltonensis* the right muscle extends farther back (Bourne 1910, p. 5). In the present state of knowledge (Crofts 1955, p. 740) this right muscle is the post-torsional typical columellar muscle. The presence of a left muscle is not

a novelty but a maintenance of the velum retractor muscle. It is generally considered as a functional adaptation to flattened shells, e. g., Hipponicidae and Cypraeidae. Though the body whorl is enlarged in *Tricolia*, its shell has attained full dextral coiling, it is not flattened, but has a conspicuous spire, and the animal can withdraw completely into the shell. Therefore its two shell muscles appear as a historical reminiscence which can be expected to be found also in other Trochacea.

Among the monobranchiate Aspidobranchia two columellar or shell muscles were hitherto only observed in *Tricolia* and the neritids. According to Bourne's opinion on the origin of the Neritacea quoted and shared by Yonge (1947, p. 492) the two muscles may perhaps be understood as characters which *Tricolia* and the Neritidae have retained independently from zeugobranchiate ancestors. To Robertson (1958, p. 249) it appears unlikely that these muscles indicate any close relationship between the two groups. Bourne's view concerning the origin of the Neritacea from the Zeugobranchia was not generally accepted. Thiele (1935, p. 1083) derives the Neritacea from the Trochacea, and in this sense the two muscles are certainly significant, as Fretter (1955, p. 160) suggested.

ALIMENTARY TRACT

The mouth (Fig. 11, m) is followed by a short oral tube which leads into the buccal cavity (mo). At the entrance of this cavity the mandibles (j) lie on the dorsal and dorso-lateral sides. The floor is occupied by the buccal mass whose anterior ventral and lateral parts are surrounded by diverticula of the cavity. The outer walls of the lateral diverticula are glandular. The buccal mass consists of a muscular sac containing the odontophoral cartilages. The muscles are transversely striated as described by Bourne (1910, p. 18, pl. 3, f. 15), Frank (1914, p. 399) and others. The cartilages are in two pairs whose dorsal mid line is occupied by the radula (ra). The long anterior cartilages (ca) are slightly concave on their inner side, the short posterior ones (sc) concave in front and firmly apposed to the posterior end of the anterior cartilages. These features are similar to those described by Amaudrut (1898, p. 57, pl. 4, f. 33) and Risbec (1939, p. 283, pl. 6, f. 70, not 71) for *Turbo setosus* and *Phasianella*

rubens respectively. The anterior end of the radula and its cushion lies under the jaws. The posterior end of the radula evidences the effect of torsion (Pelseneer 1899, p. 51; Randles 1904, p. 50) twisting around the cartilages and the oesophageal pouches towards the dorsal side (Fig. 15). Its slightly bifid blind end appears apposed to the topographically right wall of the oesophagus as in *Phasianella rubens* (Risbec, l. c.).

The oesophagus (o) begins rather far in front in the dorsal part of the buccal cavity at the level of the cerebral commissure (Fig. 14, cz). A little farther behind the tubular and simple salivary glands (sa) open into the oesophagus. In *Turbo porphyrites* (Risbec 1939, p. 271) and according to Risbec (1955, p. 47) generally in the Turbinidae the salivary glands are also inconspicuous and open immediately behind the cerebral commissure. Behind the entrance of the salivary glands the roof of the oesophagus is dilated transversely in *T. affinis cruenta* (Fig. 15), forming what Frank (1914, p. 431, 444) called "Dachfurche" in trochids. On both sides of the "Dachfurche" dorso-lateral diverticula (au) are developed whose fundi contain glandular epithelium. A glandular fold (zu) arises from the floor of the oesophagus and projects into the lumen as a principally backwards directed languet (Risbec 1939, p. 284: *Phasianella rubens*). Glandular are also the walls of the entrances of the posterior lateral oesophageal pouches (ou). These thin-walled diverticula communicate with the central lumen over a long stretch. Their walls form glandular papillae on their whole inner surface (Fig. 15). Farther behind the pouches unite over the oesophagus forming a crop. Transverse sections reveal the effect of torsion on this part of the anterior gut (Fig. 15) as Amaudrut (1898, p. 189-190, 265) and others described it for *Turbo* and other genera of the Trochacea. The oesophagus is displaced to the left and ventral side, thence also the left part of the crop attains a ventral position. The right part is turned dorsally and lies over the buccal mass. Unlike to the trochids (Robert 1900, p. 392, f. 499) the right pouch of *T. affinis cruenta* is not much bigger than the left.

The thin oesophagus leaves the hind end of the left pouch of the crop, courses under the floor of the mantle cavity and passes into the posterior visceral cavity. Its course is rather straight; its epithe-

lium contains numerous blue staining, high, cup-shaped gland cells. The oesophagus comes from the left and enters the stomach (s) from the ventral side near its middle. One of the ducts (l) of the brown intestinal gland opens into the oesophagus short before its entrance into the stomach, the other into the stomach itself, a little farther behind.

As Fretter (1955, p. 161) observed, the stomach of *Tricolia* is similar to that of the trochid *Monodonta lineata* (Graham 1949, p. 747, f. 17). Different from *Phasianella rubens* (Risbec 1939, p. 285, pl. 7, f. 75, cs) the caecum of *T. affinis cruenta* is wide and not spiral. It contains the major typhlosole (ua) on the topographically right border of the intestinal groove (io). Where this groove is most distinct in transverse sections, it is formed by low cells which lie between the high, apically striated ones of the general gastric epithelium (Randles 1904, p. 54; Bourne 1910, p. 21). To the left of the groove come the ridges of the posterior sorting area (za) alongside of which runs the longitudinal fold (xo) that corresponds to the structure F in Graham's figures (1949). Farther in front the groove is bordered to the left by the minor typhlosole (ui). The two typhlosoles with the groove between them enter the topographically anterior tubular part of the stomach, the style sac, and continue along the whole intestine. For its most part the gastric wall is lined with a cuticle which is raised into a long and thick gastric shield (si) to the right of the major typhlosole. Evidently the cuticle of the shield is renewed from time to time, as it is quite loose in some snails (Fig. 16) and missing in several others. Also Risbec (1939, p. 285) found the cuticle loose in *Phasianella rubens*. The topography of the mucus-producing pouch (mu) and the gastric shield is somewhat different from that in *Monodonta lineata*. We compared the stomach of *Tegula viridula*; it has a long spirally coiled caecum as that of *Calliostoma conuloide* (Graham 1949, f. 18) and is also in further details similar with the latter.

The caecal end of the stomach of *Tricolia affinis cruenta* is apposed to the outer side of the visceral mass; the style sac to the floor of the mantle cavity. The snails browse on the surface of algae covered with detritus. The contents of the stomach are grey, evidently digested masses, in some cases mixed with mucus and including diatoms and animal material as eggs and Foraminifera, and sometimes stones.

At its egress from the style sac the intestine (Fig. 16, i) is directed to the topographically right side. Shortly after it curves to the left and runs backwards on this side. Then it bends to the right and passes through the ventricle (Fig. 12, v) near to the hindmost level attained by the gut (Fig. 14). The forward course on the right side of the mantle cavity is somewhat sinuate but in a variable degree according to contraction. From the level of the renal pores outward the intestine runs detached from the roof of the mantle cavity, on the right side.

Within the intestine the typhlosoles produce a longitudinal groove on the surface of the faecal pellets (ro), but as the folds stand quite near to one another, their two projections into the intestinal lumen bring forth only one incisure together, whilst there are two in the much bigger trochids (Moore 1932). Like *Tricolia pullus* and *Margarites helicinus* (Fretter 1955, p. 161) the present species has an anal gland (Fig. 17, an). It originates by fusion of the typhlosoles in the rectum and thickening of their epithelium. In *T. pullus* and the mentioned trochid (l. c., f. 1C, G) the anal gland is a groove communicating with the rectal lumen, while it is a closed canal in *T. affinis cruenta*. It runs on the side facing the floor of the pallial cavity; on the opposite side there is a short bulge (xi) of the outer side of the cylindrical anal papilla. This yellowish bulge bears a ciliated groove. Topographically the bulge corresponds to the anal gland of *Gibbula cineraria* (Pelseneer 1899, p. 51, f. 153, I; Frank 1914, p. 453), though this lies inside the rectum. Whether the anal glands of *Margarites* and *Tricolia* formed by the typhlosoles are homologous to the long siphons of fissurellids (Graham 1949, p. 754) is not certain; the function of the latter as well as that of the ventral and dorsal rectal structures is unknown.

UROGENITAL SYSTEM

The left kidney or papillary sac (Fig. 12, k) in its usual position, between intestine (i) and pericardium (p), is thin-walled, unlike that of the trochids examined by Randles (1904, p. 45). The number of the papillae increases with age; their structure is similar to that described by Frank (1914, p. 414) and Cuénot (1914, p. 272). An axial blood-space is surrounded by a thick layer of vesicular cells.

Their boundaries are distinct only at the scarcely ciliated surface where the nuclei are located. Some nuclei are farther inwards between the vesicular cells; these nuclei belong to phagocytic amoebocytes (lymphocytes). The nephridial gland (na) lies between kidney and pericardium on the auricular side; the ciliated reno-pericardial communication on the opposite, the right side; the renal pore in front (vo), to the left of the intestine. The outer walls of the left, bigger (ae) and the right, smaller (wr) auricle show slight knobby dilatations which constitute a pericardial gland.

The right kidney (zr) begins behind the pallial cavity where it is situated in front of and beside the stomach. This glandular or posterior lobe communicates with the tubular urinary chamber or ureter (rn) which runs forward in the roof of the pallial cavity to the right of the intestine. Its pore (x) lies level with the left nephropore.

In the females the slit-like urogenital pore opens in the centre of a large and smooth, colourless or orange button. This consists mainly of blue staining gland cells which secrete into the lumen. The bulge of glands around the female opening drawn in Figs. 12 and 18 (x) represents the maximum development of accessory glands in the present species. This contrasts with the sometimes enormous pallial appendage, the nidamental or albumen gland of the trochids that liberate their eggs in clumps or ribbons (Frank 1914, p. 420-21; Fretter 1946, p. 335; 1955, p. 162). Also *Monodonta turbinata* (Frank, text-fig. 25) has a bigger gland than *Tricolia affinis cruenta*, though it is said (Robert 1902, p. 294) to shed its eggs singly into the sea like *Monodonta lineata* and *Tricolia pullus* (Lebour 1937, p. 123, 124).

The male urogenital pore has no glands. In both sexes a narrow diverticulum communicates with the ureter, and the gonadial duct enters this communication short before it opens into the ureter.

Since Perrier (1889, p. 269) the communication of the right kidney with the pericardium was questioned. Ankel (1936, p. 115) indicated absence of the left reno-pericardial communication for the Trochidae, quoting Spillmann (1905). But this author had not found (p. 539) the right communication in *Gibbula cineraria*, as little as Robert (1900, p. 409) in *Monodonta turbinata*. Pelseneer (1899, p. 53) and Frank (1914, p. 421) verified its presence in the mentioned

species. Randles (1904, p. 47-48) observed the right communication in *Gibbula magus* and *Monodonta lineata*, so that its general occurrence in the Trochidae can be considered as settled as in all other Archaeogastropoda (Fretter 1946, p. 334). The left communication first described by Spengel (1881, p. 348) in *Haliotis* was found by all observers of trochids except Gersch (1936, p. 144-145).

The gonad lies in the spire, more on the outside of the whorls than the liver, and also farther apically. The liver does not extend beyond the outer half of the whorl that precedes the body whorl. In mature snails the gonad is much bigger than the digestive gland, unlike that of higher gastropods whose internal fertilization and accessory genital glands are correlated with a proportionally smaller gonad. To the right of the stomach the gonad is in front bordered by the right kidney which it enters with the gonadial duct. This duct is extremely thin-walled, especially in wholly mature snails. Our sectioned material of April 1960 contains spawning specimens with eggs or sperms in the ureter, as well as middle-sized and quite small, recently metamorphosized ones. Our embryological observations were all gathered in the first fortnight of July 1960 during a period of uncommonly cold nights. Evidently *Tricolia affinis cruenta* has no pronounced reproductive periodicity on the coast of Southern Brazil.

The glands around the urogenital aperture are already developed in young females. As far as known, the coverings of the egg of the Archaeogastropoda are produced in the ovary (Fretter 1946, p. 334). Hence the secretion of the accessory glands either hardens the coats or involves the eggs and flows them out of the pallial cavity (Fretter, l. c.). In *T. affinis cruenta* with a weakly developed hypobranchial gland and a gonopore rather distant from the mantle border the second function appears actually needed. Possibly the secretion of the glands around the female pore produces a substance attractive for the males. According to our observations of spawning snails this is however not probable.

The flat epithelium of the outer wall of the olive green ovary underlain by connective tissue and muscle fibres is thrown into high inner folds. There the epithelium is higher and quite distinct; the connective tissue contains blood-spaces. The growing ovocytes project

from the germinal epithelium into the cavity of the ovary. With the fold the germ cell is connected by an alimentary stalk through which pink yolk granules were seen to flow into the ovocyte. The nucleus of the latter lies opposite to the fixed pole. Unlike to *Tricolia pullus* (Lebour 1937, p. 110, f. 1 M) the freed eggs of *T. affinis cruenta* have only one thin membrane whose irregular gibbositities correspond to discoid pads which develop in the ovary. Already around ovocytes of 40 μ diameter these discoid pads appear. They are 5-8 μ thick in the middle, thinner at the margins, and about 15 μ across. Frequently, not always, they have a light spot in the centre. Ovocytes with half the definitive diameter have a complete egg membrane which is interrupted by the stalk, according to Frank (1914, p. 427-428) the future micropyle. Eggs in the ureter and freed ones are 0,12 mm across; free ones of *T. pullus* measure 0,14 mm (Lebour 1937, p. 124). The free eggs of *Gibbula cineraria* and *G. magus* are 0,115 mm in diameter according to Robert (1902, p. 295), whilst Gersch (1936, p. 136) indicated 0,144 mm without investment for those of *G. cineraria*.

In the bright green testis the germinal epithelium on the folds or trabeculae is coated with a thick layer of developing sperms whose definitive minute heads are spherical. The number of male and even of female germ cells is extremely great.

During the first fortnight of July 1960 the snails emitted sperms and eggs every afternoon between 2 and 4 o' clock. This regular diurnal periodicity known of many gastropods (Pelseneer 1935, p. 472-473) was independent of the hour in which the snails were gathered and transferred from moved to still water, and of renewal of the water. Males and females cannot be distinguished externally, and several times all snails in one vial revealed to be only males or only females. Nevertheless they shed their spawn, both males and females, independently of the presence of the other sex. Also in the trochids studied by Gersch (1936, p. 140) the sexes do not exert a reciprocal influence for emission of their germ cells.

In the dish these sink to the bottom, in moved water this process is slower, and on the *Sargassum* part of them may adhere to the sticky film on the branched thallus. The great frequency of the snails proves that the absence of sexual attraction is compensated. The great

number of germ cells and their longevity counterweigh the loss of eggs that are not fertilized. A female sheds about 100 greyish green eggs at a time, as if it emptied a sac of marbles. After some minutes it gives off the same number again, and sometimes a third or fourth lot during the afternoon. The number of sperms in the "cloud of steam" (Robert 1902, p. 288) amounts to many thousands. At about 20°C. the germ cells are alive and fertilizable for 2-3 hours.

The above-mentioned egg-envelope of *Tricolia affinis cruenta* is a primary or "vitelline" membrane formed by the egg itself. It is separated from the cell already in the shed primary ovocyte by a peri-vitelline space which contains a liquid (Fig. 19). A micropyle is not visible. The polocytes are extruded when the ovocytes are discharged from the female body before fertilization. Several sperms pierce the egg membrane (Fig. 21), but only one spermatozoon enters the female cell. The spiral cleavage corresponds, as far as we accompanied it, to that of *Trochus* (Robert 1902), especially the size-relation between macromeres and micromeres is the same. The first six divisions are accomplished very rapidly so that 64-cell stages were reached one hour after fertilization.

The further development was much slower in our dishes where free-swimming trochophores were only found 16 hours after fertilization: probably the lack of suitable facilities had delayed the development. By deficient conditions our early veligers were even arrested (Crofts 1937, p. 226), they did not develop beyond the pre-torsional stage. Most of them had 16 ciliated cells of the prototroch (Fig. 22) and so corresponded to Crofts' stage of figure 41, c (1937). In *Tricolia affinis cruenta* these cells and the apical area are green, the shell is granular. Our veligers with an operculum died on the third day so that the torsion could not be observed. Young metamorphosized snails were found among algae; that whose shell is shown in Fig. 2 corresponds to Robert's figure 82 (1902, pl. 18), of course with different epipodial appendages.

GENERAL REMARKS

By suppression of the right ctenidium, foreshadowed in Halio-tidae and Scissurellidae, a left-right respiratory circulation is already established among the Archaeogastropoda (Yonge 1947, p. 491).

Therewith special arrangements for the exhalant current are dispensable, and accessory genital organs for internal fertilization (Neritacea, Meso- and Neogastropoda) could be developed. When the filaments of this left branchia are reduced to a single row an organisation is attained, whose extense ecological range and corresponding morphological diversification evidences its success.

Also a bipectinate single gill does not preclude its bearers from life in turbid water. Certainly most of them avoid water with much mud and silt, but they are not at all restricted to rocks and reefs. Many of them live, as so many other feeders on vegetable substance. in great numbers on seaweeds, e. g. kelp, and eel-grasse. Some are also inhabitants of sand flats, mud banks, mangrove swamps, or rather turbid brackish and fresh water, e. g., *Gibbula tumida* (Ankel 1936, p. 74) and occasionally other species of *Gibbula* (van Benthem Jutting 1947, p. 58), *Cantharidus huttoni* (Clark 1958, p. 59), *C. comtessei* (Dakin 1953, p. 243), *Monodonta subrostrata* (Clark, l. c.), *M. obtusata porcata* (Allan 1950, p. 65), sometimes *Tricolia pullus* (van Benthem Jutting 1947, p. 58), *Pictoneritina oualensis* (Allan 1950, p. 74), *Neritina virginea* (on mud flats on the coast of São Paulo) and other Neritinae, several species of the Valvatidae and Adeorbidae. The juvenile *Cyclostrema* from a locality rich in sediments (Emerson and Puffer 1957, p. 32) may be a turbinid, but this is not sure (see Fretter 1956, p. 379). Odd as it may seem, Thiele (1935, p. 1088) considered the bipectinate gill of the Adeorbidae as an adaptation to burrowing habits. Though few will accept this idea, also the opposite, an incompatibility of bipectinate gill and life in turbid water, cannot be stated. A muscular aspidobranch ctenidium can wipe itself against the floor of the pallial cavity and therewith remove sediment from its filaments (Clark 1958, p. 63). In *Valvata* the cilia of the pallial tentacle on the right side create a powerful outgoing current (Yonge 1947, p. 479).

Within the limits traced by their primitive reproductive organs the Trochacea with single long ctenidium and rasping rhipidoglossan radula have been successful. Fundamental uniformity and a great number of species characterize such groups, e. g. the Kalyptorhynchia of the Turbellaria or the Ascophora of the Bryozoa. In these cases natural subdivisions can be recognized only by detailed studies. Thus

Trochidae and Turbinidae differ in few characters, the conchinous and calcareous operculum, the open and closed eyes, and the presence and absence of the supporting rod in the free extremity of the ctenidium (Yonge 1947, p. 475; Clark 1958, p. 62). The difference concerning the branchial ciliation (Yonge, f. 34 B and C) cannot be used for the classification of preserved animals.

Of the 3 last subfamilies of the Trochidae in Thiele's system (1931, p. 58-63) the Stomatiinae were re-established as family (Risbec 1955, p. 65) and *Teinostoma* removed from the Skeneinae (Abbott 1955, p. 139), though not by all (Emerson and Puffer 1957, p. 34). Among the Turbinidae several authors consider the Liotiinae (Thiele 1931, p. 64; Abbott 1955, p. 121) as family (Strong 1934, p. 432; Powell 1951, p. 103; A. Myra Keen 1958, p. 264).

The lack of nacre in the shell of Thiele's Phasianellinae was after 1931 generally considered as sufficient to dissociate them from the Turbinidae. The presence of the skeletal rod in the gill is another character which parts at least *Tricolia* from the turbinids. Operculum and eyes separate *Tricolia* and *Phasianella* from the Trochidae. By far the most important feature is the occurrence of two shell muscles but this, too, was verified only in *Tricolia*. Risbec (1939) would have noted the two columellar muscles if they were developed in *Phasianella*. The presence of a post-torsional left muscle is not even probable in snails with a spire produced at an angle from 45° to 55° (Robertson 1958, p. 254). The correspondingly rather narrow mantle cavity (Fretter 1951, p. 583) would be still more restricted by this muscle and the function of the gill reduced.

Robertson (1958, p. 251) considers the Phasianellidae diphyletic in origin and quotes Woodring (1928) who distinguished two families, Tricoliidae and Phasianellidae. Certainly one should always try to subordinate systematic categories to one another, in place of coordinating them. But the presence of two shell muscles in *Tricolia*, or perhaps in *Tricolia* and *Gabrielona*, in our opinion outweighs an entirely porcellanous bulimoid shell, so that after the necessary examination Woodring's systematization may become necessary.

An evolution of the Trochacea from the Scissurellidae, as enounced by Thiele (1935, p. 1081) in a general manner, is suggested also by several similar details in the organization of *Incisura lytteltonensis*

and *Tricolia affinis cruenta*. This origin of the trochaceans can be conceived only from a common root with the scissurellids, not from the recent members of this family whose pedal nervous system is the most concentrated among all Rhipidoglossa (Bourne 1910, p. 34).

RESUMO

Tricolia affinis cruenta Robertson, 1958, é freqüente nas algas do litoral superior, principalmente em *Sargassum*, na Base Norte do Instituto Oceanográfico de São Paulo, 14 km. a oeste de Ubatuba.

O ângulo apical da concha (Fig. 2, 3) varia de 130° nos caramujos mais jovens observados, até 45° nos mais crescidos. Também a forma do opérculo (Fig. 2, 4) e o umbigo modificam-se com o crescimento.

Os animais alimentam-se do filme existente na superfície das algas. Deslizam principalmente por meio dos cílios da sola sobre a fita de muco produzida por glândulas do bordo pedal anterior (Fig. 11, uz). Glândulas da extremidade posterior do pé (oa) alongam a fita, segurando o animal. O bordo anterior e os tentáculos cefálicos (t) são tácteis; os animais não mostram reação quando os apêndices epipodiais (ei) são estimulados mecânicamente. Em oposição a *Trochus*, animais caídos viram-se com a parte anterior do pé, como o faz também *Tegula viridula*. O movimento ditáxico da última espécie ocorre apenas alusivamente em *Tricolia affinis cruenta*, cuja sola é indivisa (Fig. 9). Os olhos são fechados, possuem pelúcida externa e interna contíguas e corpo vítreo sem diferenciação de cristalino. O apêndice epipodial ramificado do lado esquerdo (ce) é pouco móvel, não filtra. Faixa de cílios (Fig. 10, ci) no fundo da cavidade do manto repele sedimentos; êstes cílios são incomuns nos Aspidobranchia, cuja ocorrência é mais freqüente em águas limpas. O influxo de sedimentos é intenso no lugar de achado, no verão.

Vasos do teto da cavidade palial (Fig. 12) evidentemente auxiliam na respiração, pois dêles o sangue passa à aurícula esquerda (ae); há vestígio do vaso branquial eferente direito. No sistema nervoso (Fig. 13) notam-se células nervosas na alça visceral e nos cordões pedais; os últimos não possuem sulco horizontal. Há zigose somente no lado esquerdo. O ramo subintestinal da alça visceral contém 3 gânglios, o abdominal (ao) e um de cada lado dêste. Além

do músculo columelar típico, direito depois da torsão (Fig. 14, rr), mantém-se, no lado esquerdo (mr), o retrator do velum larval. O esôfago é rico em glândulas e dilatações (Fig. 15); o ceco do estômago, curto, largo e reto (Fig. 14, ce). A cutícula gástrica, nomeadamente a do escudo (Fig. 16, si), é periodicamente renovada. Cada rim tem comunicação com o pericárdio. O poro urogenital da fêmea (Fig. 12, 18, x) é provido de glândulas. Entre o ovo e a membrana vitelina (Fig. 19-21) existe espaço peri-vitelino repleto de líquido. Gibosidades irregulares elevam-se na membrana vitelina. Machos e fêmeas emitiram as células germinativas independentemente da presença de indivíduos do outro sexo, na primeira quinzena de julho de 1960, sempre entre 2 e 4 horas da tarde. Os corpúsculos polares formam-se antes da fecundação. A clivagem espiral concorda com a de *Trochus*; a phase de 64 blastômeros alcança-se dentro de 1 hora (20°C.). A retardação ulterior parece ser devida às condições desfavoráveis de manutenção. Os últimos estádios vivos obtidos no aquário foram velígeres jovens, antes da torsão, com 16 células ciliadas do prototróquio (Fig. 22).

REFERENCES

- Abbott, R. Tucker 1955, *American Seashells*. XIV + 541 p., 40 pl. New York (D. van Nostrand Company, Inc.).
- Allan, Joyce 1950, *Australian Shells, etc.* XIX + 470 p., 44 pl. Melbourne (Georgian House).
- Amraudrut, Alexandre 1898, La partie antérieure du tube digestif et la torsion chez les Mollusques Gastéropodes. *Ann. Sci. Nat. Zool. sér. 8, v. 7, p. 1-291, pl. 1-10.* Paris.
- Ankel, Wulf Emmo 1936, *Prosobranchia*. G. Grimpe & E. Wagler, *Tierwelt Nord- & Ostsee, part IX b 1, 240 p., 222 figs.* Leipzig (Akadem. Verlagsges.).
- Bentham Jutting, Woutera 1947, Lijst van Gemeenten als Vindplaatsen van Nederlandse Mollusken. *Basteria v. 11, n.º 1-3, p. 54-86.* Lisse.
- Beurne, Gilbert C. 1910, On the anatomy and systematic position of *Incisura* (*Scissurella*) *lytteltonensis*. *Qu. J. micr. Sci. n. ser. v. 55, p. 1-47, pl. 1-5.* London.
- Bouvier, E. L. 1887, *Système nerveux, morphologie générale et classification des Gastéropodes prosobranches.* *Ann. Sci. Nat. Zool. sér. 7, v. 3, p. 1-510, pl. 1-19.* Paris.
- Clark, W. C. 1958, Notes on the mantle cavity of some trochid and turbinid Gastropoda. *Proc. Malacol. Soc. v. 33 (2), p. 57-64.* London.

- Crofts, Doris R. 1937, The development of *Haliotis tuberculata* with special reference to organogenesis during torsion. Phil. Tr. R. Soc. Lond. ser. B. — Biol. Sci. n.º 552, v. 228, p. 219-268, pl. 21-27. London.
- 1955, Muscle morphogenesis in primitive gastropods and its relations to torsion. Pr. Zool. Soc. v. 125 (3-4), p. 711-750, 30 text-figs. London.
- Cuénot, Lucien 1914, Les organes phagocytaires des Mollusques. Arch. Zool. expér. génér. v. 54 (9), p. 267-305, pl. 10-13. Paris.
- Dakin, William J. 1953, Australian Seashores. XII + 372 p., 99 pl. Sydney & London (Angus & Robertson).
- Emerson, William K. and Puffer, Elton L. 1957, Recent mollusks of the 1940 "E. W. Scripps" cruise to Clipperton Island. Am. Mus. Nov. n.º 1825, p. 1-57, textfigs. 1-2. New York.
- Fleure, H. J. and Gettings, M. M. 1907, Notes on common species of *Trochus*. Qu. J. micr. Sci. n. ser. v. 51, p. 459-472, pl. 28. London.
- Frank, Eduard Joseph 1914, Beiträge zur Anatomie der Trochiden. Jen. Ztschr. Naturw. v. 51 (3), p. 377-486, pl. 5. Jena.
- Fretter, Vera 1946, The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*. Journ. mar. biol. assoc. Unit. Kingd. v. 26 (3), p. 312-351, text-figs. 1-7. Cambridge.
- 1951, Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). Journ. mar. biol. assoc. Unit. Kingd. v. 29, p. 567-586, text-figs. 1-6. Cambridge.
- 1955, Some observations on *Tricolia pullus* (L.) and *Margarites helicinus* (Fabr.). Proc. Malacol. Soc. v. 31 (3-4), p. 159-162. London.
- 1956, The anatomy of *Circulus striatus* (Philippi) and a review of its systematic position. Pr. Zool. Soc. v. 126 (3), p. 369-381, text-figs. 1-5. London.
- Gersch, Manfred 1936, Der Genitalapparat und die Sexualbiologie der Nordseetrochiden. Ztsch. Morphol. Oekol. v. 31 (1), p. 106-150. Berlin.
- Gofferjé, Carlos N. 1950, Contribuição à zoogeografia da malacofauna do litoral do Estado do Paraná. Arq. Mus. Paran. v. 8, p. 221-282, pl. 31-35. Curitiba (Brazil).
- Graham, Alastair 1949, The molluscan stomach. Tr. R. Soc. Edinb. v. 61, part 3 (27), p. 737-778, 24 figs. Edinburgh & London.
- 1957, The molluscan skin with special reference to prosobranchs. Proc. Malacol. Soc. v. 32 (4), p. 135-144. London.
- Hatt, Pierre 1927, L'absorption d'encre de chine par les branches de *Diotocardes*. Bull. Soc. Zool. France, v. 52, p. 179-184, 4 text-figs. Paris.
- Hesse, Richard 1902, Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. VIII. Ztschr. wiss. Zool. v. 72 (4), p. 565-656, pl. 35. Leipzig.
- Hulbert, G. C. E. and Yonge, C. M. 1937, A possible function of the osphradium in the Gastropoda. Nature v. 139, n.º 3524, p. 840-841. London.

- Kaiser, Peter 1959, Die Leistungen des Flimmerepithels bei der Fortbewegung der Basommatophoren. *Ztschr. wiss. Zool.* v. 162 (3-4), p. 368-393, text-figs. 1-8. Leipzig.
- Keen, A. Myra 1958, *Sea Shells of Tropical West America*. VIII + 626 p., 10 pls. Stanford, California (University Press).
- Lange de Morretes, Frederico 1949, Ensaio de catálogo dos moluscos do Brasil. *Arq. Mus. Paran.* v. 7 (1), p. 5-216. Curitiba (Brazil).
- Lebour, Marie V. 1937, The eggs and larvae of the British prosobranchs with special reference to those living in the plankton. *Journ. mar. biol. assoc. Unit. Kingd.* v. 22 (1), p. 105-166, 4 text-figs. Cambridge.
- Moore, Hilary B. 1932, The faecal pellets of the Trochidae. *Journ. mar. biol. assoc. Unit. Kingd.* v. 18 (1), p. 235-241, 12 text-figs. Plymouth.
- Pelseeneer, Paul 1899, Recherches morphologiques et phylogénétiques sur les mollusques archaïques. *Mém. cour. Acad. Roy. Belg. (Sci. Nat.)* v. 57, p. 1-112, pl. 1-24. Bruxelles.
- 1935, *Essai d'éthologie zoologique d'après l'étude des mollusques*. 662 p. Bruxelles (Académie Royale de Belgique, Classe des Sciences).
- Perrier, R. 1889, Recherches sur l'anatomie et l'histologie des Gastéropodes prosobranches. *Ann. Sci. Nat. Zool. sér. 7*, v. 8, p. 61-315, pl. 5-13. Paris.
- Powell, A. W. B. 1951, Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. *Discovery Rep.* v. 26, p. 47-136, 130 figs., pl. 5-10. Cambridge (University Press).
- Randles, W. B. 1904, Some observations on the anatomy of the Trochidae. *Qu. J. micr. Sci. n. ser.* v. 48, p. 33-78, pl. 4-6. London.
- Risbec, Jean 1939, Recherches anatomiques sur les Prosobranches de Nouvelle-Calédonie. Deuxième partie (1). *Ann. Sci. Nat. Zool. sér. 11*, v. 2, p. 235-298, pl. 1-7. Paris.
- 1955, Observations sur l'anatomie comparée et la classification des Gastéropodes Prosobranches. *Jour. Conchyl.* v. 95, p. 45-82, figs. 1-22. Paris.
- Robert, A. 1900, *Le Troque*. Zoologie descriptive des Invertébrés, v. 2, chap. 30, p. 381-415, figs. 493-508. Paris (Octave Doin).
- 1902, Recherches sur le développement des Troques. *Arch. Zool. expér. génér. sér. 3*, v. 10, p. 269-538, pl. 12-42. Paris.
- Robertson, Robert 1958, The Phasianellidae in the Western Atlantic. *Johnsonia* v. 3, n.º 37, p. 245-284, pl. 136-148. Cambridge, Mass.
- Spengel, Johannes W. 1881, Die Geruchsorgane und das Nervensystem der Mollusken. *Ztschr. wiss. Zool.* v. 35 (3), p. 333-383, pl. 17-19. Leipzig.
- Spillmann, Jean 1905, Zur Anatomie und Histologie des Herzens und der Hauptarterien der Diotocardier. *Jen. Ztschr. Naturw.* v. 40, p. 536-588, pl. 19-21. Jena.
- Strong, A. M. 1934, West American species of the genus *Liotia*. *Tr. San Diego Nat. Hist.* v. 7 (37), p. 429-452, pl. 28-31. San Diego.
- Thiele, Johannes 1897, Beiträge zur Kenntnis der Mollusken. III. Hautdrüsen und ihre Derivate. *Ztschr. wiss. Zool.* v. 62 (4), p. 632-670, pl. 31-32. Leipzig.

- 1931; 1935, *Handbuch der systematischen Weichtierkunde*, v. 1; 2, VI + V, 1154 pp., 897 text-figs. Jena (Gustav Fischer).
- Weber, Hermann 1924, Ueber arhythmische Fortbewegung bei einigen Prosobranchiern. *Ztschr. vergl. Physiol.* v. 2, p. 109-121, text-figs. 1-5. Berlin.
- 1926, Ueber die Umdrehreflexe einiger Prosobranchier des Golfes von Neapel. *Ztschr. vergl. Physiol.* v. 3, p. 389-474, text-figs. 1-22. Berlin.
- Yonge, C. M. 1937, The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.). *Journ. mar. biol. assoc. Unit. Kingd.* v. 21 (2), p. 687-703, text-figs. 1-6. Plymouth.
- 1938, Evolution of ciliary feeding in *Capulus ungaricus*. *Journ. mar. biol. assoc. Unit. Kingd.* v. 22 (2), p. 453-468, text-figs. 1-6. Cambridge.
- 1942, Ciliary currents in the mantle cavity of the Atlantidae. *Qu. J. micr. Sci. n. ser.* v. 83 (2), p. 197-203, text-figs. 1-2. London.
- 1947, The pallial organs in the aspidobranch Gastropoda and the evolution throughout the Mollusca. *Phil. Tr. R. Soc. ser. B. (Biol. Sci.)* n.º 591, v. 232, p. 443-518, 40 text-figs., pl. 18. London.

EXPLANATION OF LETTERS OF TRICOLIA AFFINIS CRUENTA

- | | |
|---------------------------------------|--|
| ac — afferent branchial vessel. | co — lateral epipodial fold. |
| ae — left auricle. | ev — efferent branchial vessel. |
| am — afferent membrane. | f — foot. |
| an — anal gland. | g — glands of mantle border. |
| ao — abdominal ganglion. | i — intestine. |
| ar — anus. | ie — subintestinal branch of
visceral loop. |
| au — anterior oesophageal
pouches. | io — intestinal groove. |
| b — gill. | iu — supra-intestinal ganglion. |
| ca — anterior buccal cartilage. | j — jaw. |
| cc — caecum. | k — left kidney. |
| ce — left cervical epipodial
lobe. | l — ducts of digestive gland. |
| ci — ciliary streak. | m — mouth. |
| cm — labial commissure. | ma — gastric nerve. |
| co — cerebro-pedal connective. | mn — incisure of mantle
border. |
| cu — cerebro-pleural connective. | mo — buccal cavity. |
| cz — cerebral commissure. | mr — left shell muscle. |
| ea — left zygosia. | mu — gastric mucus pouch. |
| ee — eye. | na — nephridial gland. |
| ei — epipodial tentacle. | ne — pallial nerve. |
| en — pedal ganglion. | ni — nick in branchial fila-
ments. |

- no — Thiele's sensory knob.
 nr — branchial nerve.
 o — oesophagus.
 oa — foot gland.
 oc — operculum.
 oe — dorsal epipodial fold.
 on — genital nerve.
 or — supporting rod.
 os — osphradium.
 ou — posterior oesophageal pouches (crop).
 p — pericardium.
 ra — radula.
 rc — right cervical epipodial lobe.
 rn — ureter of right kidney.
 ro — faecal mass.
 rr — right shell muscle.
 s — stomach.
 sa — salivary gland.
 sc — posterior buccal cartilage.
 si — gastric shield.
 sv — supra-intestinal branch of visceral loop.
 sz — statocyst.
 t — tentacle.
 ua — major typhlosole.
 uc — buccal ganglion and commissure.
 ui — minor typhlosole.
 ur — pleural ganglion.
 uz — canal of pedal gland.
 v — ventricle.
 va — vessel corresponding to afferent right branchial vessel.
 ve — vessel along glands of mantle furrow.
 vo — left nephropore.
 wa — branchial ganglion.
 wo — pedal cord.
 wr — right auricle.
 x — uro-genital aperture.
 xi — ciliated furrow of anal papilla.
 xo — longitudinal gastric fold.
 xu — glands of infrapallial border.
 y — hypobranchial gland.
 za — sorting area.
 ze — cerebral ganglion.
 zr — right kidney.
 zu — glandular fold of oesophageal floor.

PLATES

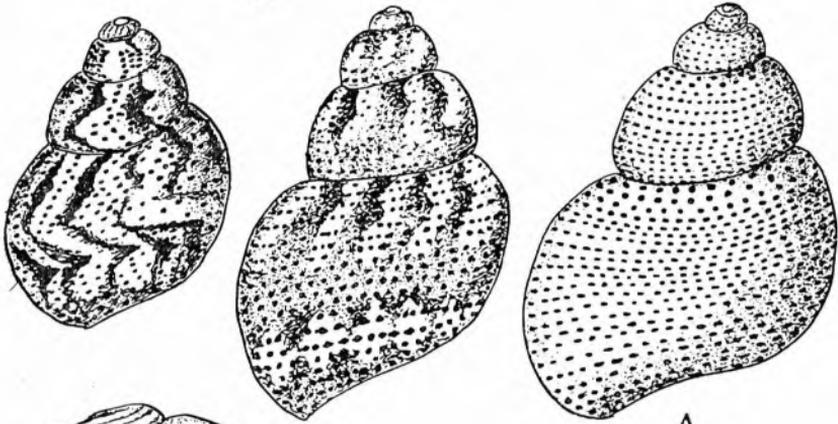
PLATE 1

Tricolia affinis cruenta

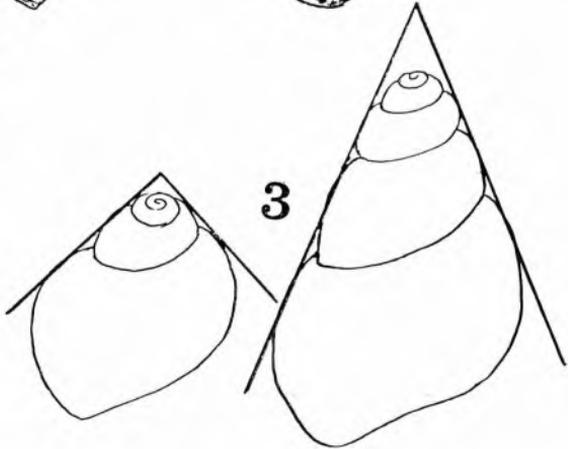
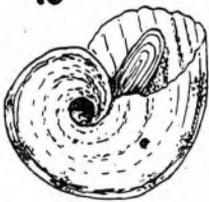
- Fig. 1 — Shells of living snails from typical locality.
Fig. 2 — Youngest snail in frontal view and from below.
Fig. 3 — Broad shell, 3,5 mm high, and narrow shell, 6,5 mm high.



1



2



3

PLATE 2

Tricolia affinis cruenta

- Fig. 4 — Surface view of full-grown operculum, 2,2 mm long.
- Fig. 5 — Inside of juvenile operculum, 0,45 mm. long.
- Fig. 6 — Part of adult radula.
- Fig. 7 — Innermost marginal tooth of adult radula.
- Fig. 8 — Part of young radula.
- Fig. 9 — Living snail.

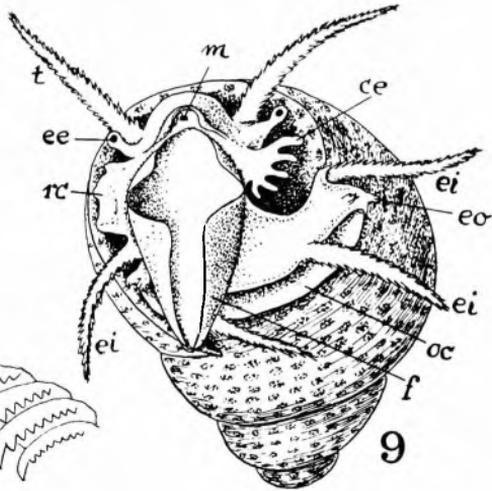
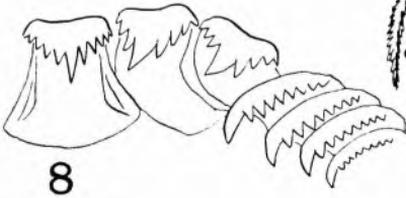
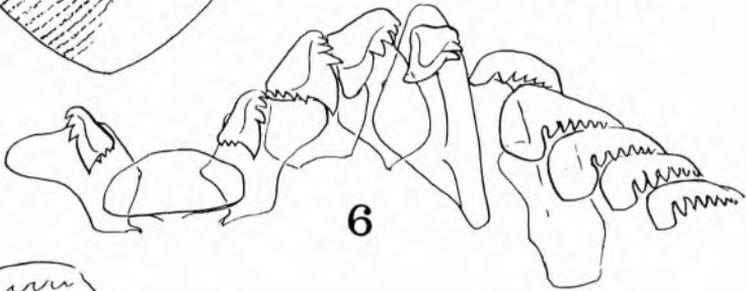
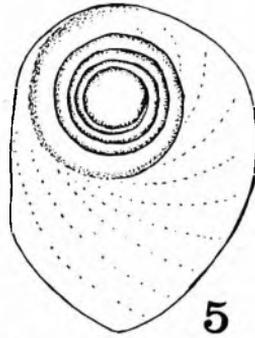


PLATE 3

Tricolia affinis cruenta

- Fig. 10 — Anterior part of snail, mantle cavity opened on right side.
Fig. 11 — Combined sagittal section.

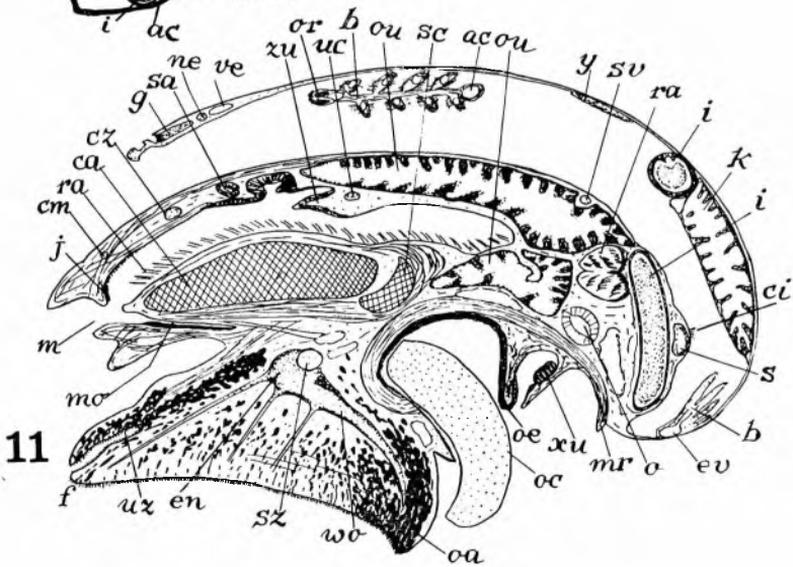
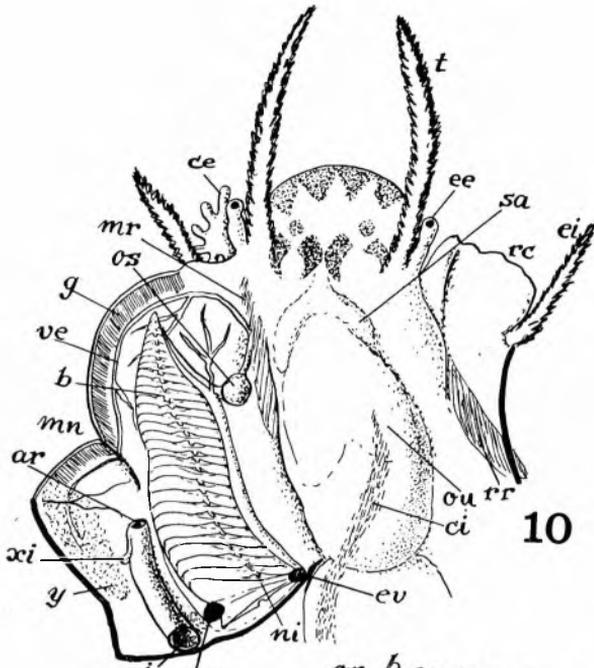


PLATE 4

Tricolia affinis cruenta

- Fig. 12 — Inside of pallial roof laid to right side.
Fig. 13 — Nervous system.

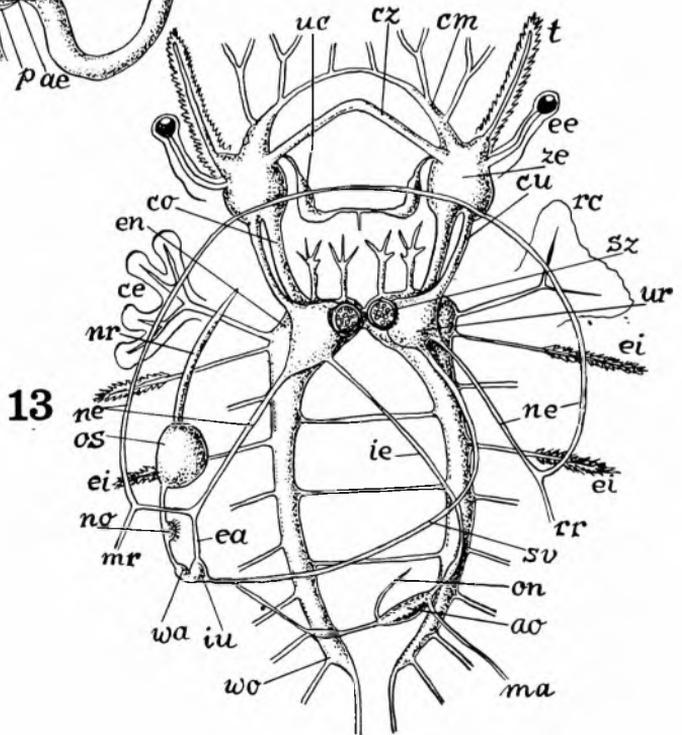
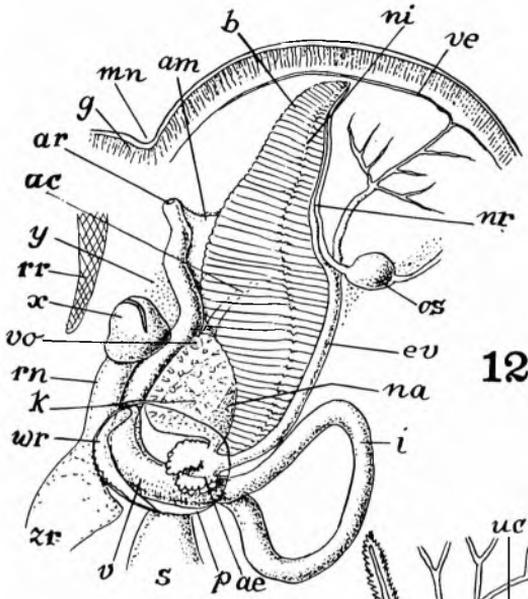
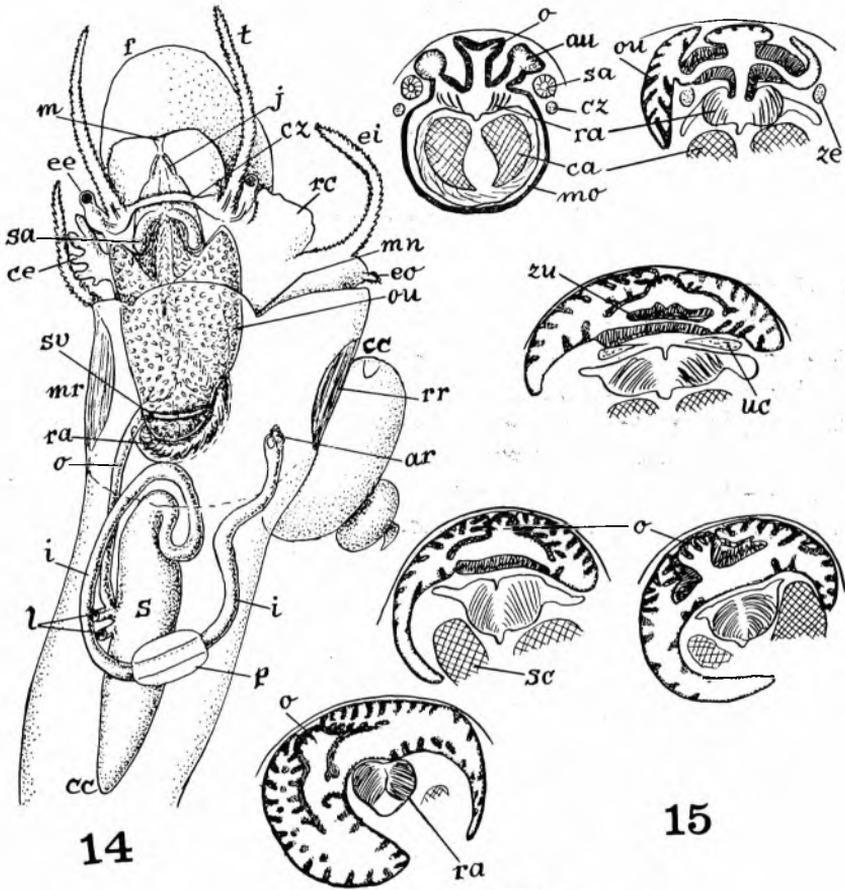


PLATE 5

Tricolia affinis cruenta

Fig. 14 — Topography of alimentary tract with body whorl drawn unrolled.

Fig. 15 — Transverse sections of anterior gut.



14

15

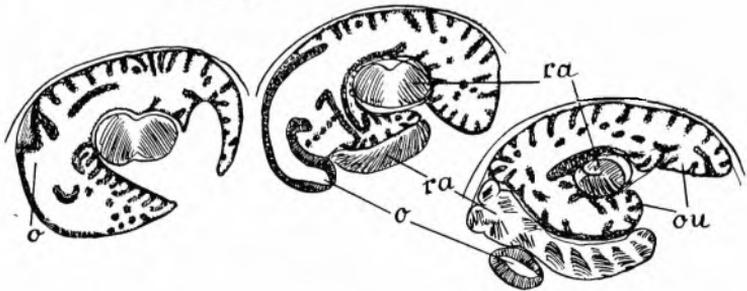


PLATE 6

Tricolia affinis cruenta

- Fig. 16 — Stomach.
- Fig. 17 — Transverse section of rectum.
- Fig. 18 — Section of renal apertures.
- Fig. 19 — Unfertilized egg one hour after being shed.
- Fig. 20 — Sperm swarming around egg; the tails are so fine that only their movement is visible.
- Fig. 21 — Sperms penetrating egg membrane.
- Fig. 22 — Young pre-torsional veliger.

