

ON *HASTULA CINEREA*

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(with 5 plates)

During our studies of sand-burrowing olivids a terebrid called our attention by its ability to move in the sand. In July 1958 we began to study this snail in order to become acquainted with the anatomy of the Toxoglossa, the most highly specialized prosobranchs. Though the material obtained near Cananéia and Ubatuba was abundant, and the snails collected in November copulated in a laboratory dish, they did not lay eggs. Nor did we succeed to observe other biological aspects. The snails endured in the aquarium, but lived there with reduced functions. Also the biology of another toxoglossan family, the Conidae, of general interest because some are poisonous to man, has only been worked out recently.

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SYSTEMATIC NOTE

The auger shell common in the area of Santos is called *Hastula cinerea* (Born, 1780) by the South American conchologists v. Ihering (1897, p. 170), Lange de Morretes (1949, p. 110), Gofferjé (1950, p. 250), Carcelles (1953, p. 14), and L. and E. H. Buckup (1957, p. 33). According to Smith (1877, p. 229-230) Lamarck was right when he united *cinerea* Born and *aciculina* Lamarck (1822, p. 290; 1844, p. 250), but not every material called *aciculina* Lm. is *cinerea* (Born) (see Smith, l. c.). Bouvier's (1887, p. 324) *Terebra aci-*

culina Lm., for example, differs in details of the outer oral region and the central nervous system from our species. The latter agrees, on the other hand, with Bergh's *Hastula aciculina* Lm. (1908, p. 124) from Santos. We are, however, not quite certain that our species can be called *cinerea*. This species described, among others, by Reeve (1860, pl. 9, spec. 35) and Abbott (1955, p. 266) has 45-50 riblets per whorl against 28-36 in our shells and in *Terebra salleana* Deshayes (1859, p. 287). As the latter species differs from ours by size, colour, and punctuations, we call our material *cinerea* till further conchological studies.

According to Carcelles and Abbott the range of *cinerea* extends from SE Florida and the West Indies to S Brazil, Sta. Catarina. Coomans (1958, p. 101) reported it from Margarita Island on the Caribbean coast of Venezuela. Some indications of *cinerea* from the coast of Texas (Johnston 1934, p. 134; Behre 1950, p. 36) possibly refer to *salleana*.

The conchologically characterized subgenus *Hastula* H. and A. Adams, 1853, was considered as a genus by Troschel (1866, p. 29-35) because of particularities of its fore-gut. Among others, Bergh (1908, p. 124), Thiele (1931, p. 375), Joyce Allan (1950, p. 195), and A. Myra Keen (1958, p. 494) follow Troschel. By its shell *Hastula cinerea* belongs to the subgenus, in Thiele "sectio", *Impages* E. A. Smith (1873, p. 263).

OCCURRENCE

The snails live burrowing in clean and fine sand of the gradually sloping beaches of the State of São Paulo, from Ubatuba to Cananéia. Near the Station of Ubatuba they live near the low water-line in the zone that Gerlach (1957, p. 418) calls "Nerine-Zone". Here the polychaete *Nerinides agilis* (Verrill 1873, p. 346, 600) widely distributed along the American Atlantic coast (Hartman 1956, p. 291) occurs. Its vertical burrows extend farther down than the worms are long. In our material their length corresponds to that of *N. minuta*, according to Hartman (1951, p. 81) identical with *agilis*. Miner (1950, p. 336) applies another synonym, *heteropoda*. As we found typical setae in the gut of *Hastula cinerea*, we conclude that the snail regularly feeds on this spionid. On the sandy beaches of

the islands in front of Cananéia the snails are most frequent in the zone that Gerlach (l. c.) calls "Prallhang" and feed principally on an opheliid.

Hastula cinerea occurs chiefly in the intertidal zone, but was sometimes obtained also over the mean high water-line. It can be dug up from about 3-5 cm depth in the sand. It is easier to collect the animals at low tide, when their trail is visible on the sand, or when they are washed out by a wave and glide straight against the reflux water, "with the spire at the posterior mid point" (Morton 1958a, p. 7). When attained by the next wave they generally have dug the pedunculate foot sufficiently deep into the sand to maintain their place. For burrowing the shape of the shell is perhaps less fit than the torpedo-form of the genus *Olivella* (G. E. and N. MacGinitie 1949, p. 355), but the efficiency of the foot of *Hastula cinerea* compensates a possibly not quite as perfect adaptation of the shell-shape.

SHELL

The shell is medium-sized, with subulate spire. The whorls are nearly plane; 11-13 adult ones are topped by 3-4 of the protoconch (Fig. 1), frequently broken off, even in living snails. The protoconch of the species that Yen (1935, p. 263, pl. 11, f. 19) calls *Hastula lepida* (possibly *strigilata*) is much shorter. In *Hastula cinerea* the larval shell is 1 mm long, hence of considerable size. Due to its thick conchiolinous coat it is brown. It is filled up by secondary calcification as are the 3-4 following whitish whorls. The remaining whorls of living snails are bluish grey, sometimes olive grey. These colours are brought about by colourless layers of calcium carbonate alternating with dark brown conchiolinous ones. The periostracum is extremely thin. The inside of the shell and the strong columella are brown. Around the body whorl, a little below its middle, runs a white zone which is also distinctly seen within the brown aperture. Wrigley (1942, f. 21) figured this band in *H. anomala*. Dead shells whose outer calcareous layer is worn are light brown.

As in many sand-burrowers the surface of the shell is smooth, shining, though under a lens minute pricks appear which form more than 100 fine spiral rows. The apical half of the whorls bears flat axial riblets whose number is 28-36 per whorl. As calcareous thi-

kenings the ribs are whiter than the furrows between them, and sometimes the light and dark pattern is even more pronounced than could be expected from the sculpture. The sutures are concealed by the apical borders of the whorls and only recognizable where these, as frequently, are broken.

The aperture is broadened in front (below). A siphonal notch separates the thin outer lip from the columella. The latter projects in front and bears two quite low folds. The parietal wall (inner lip) is dark brown and contiguous with a white parietal callus on the body whorl. The length of our shells is up to 55 mm, the breadth up to 11 mm; the aperture of our longest shells is 11 mm high, 6 mm broad.

We obtained the biggest living snails in April, August, November, and the last week of January (greatest number of them) near Ubatuba. In July and the last week of January specimens from Cananéia did not surpass 32 mm in length.

In many shells local breaks are somewhat irregularly repaired. In July 1958 we frequently found eggs of *Turbellaria Proseriata* densely set in a single layer on the shell of living snails, several colonies of the membraniporid *Conopeum commensale* (Kirkpatrick and Metzelaar, 1922), and *Hydractinia*.

HEAD AND FOOT

Foot and siphon are the principal organs which come out of the shell; in the laboratory dish also the head with everted labial tube and once the proboscis were observed outside the shell. When preserved most of our anaesthetized motionless snails retracted foot, siphon and anterior tube, but when we crushed the shell of narcotized animals with a vise, many more remained stretched.

Siphon (vi) and head are richly pigmented. Only the folds around the outer mouth (m) are light as well as a stripe on the left side of the head which leads into the mantle cavity. The eyes are 40μ in diameter, their lens 25μ ; they lie in the connective tissue of the bases of the tentacles (t). These are low, blunt cones. Bergh's statement "no tentacles" (1908, p. 124) must have been occasioned by macerated specimens.

The borders of the muscular siphon are papillate (Bergh 1908, pl. 10, f. 5) and close the canaliculated organ to form a tube. The

outer opening bears some cilia, the lumen is nonciliate. Six principal longitudinal nerves whose origin is described in the chapter on the central nervous system occur in the siphon. At the base the borders of the siphon are thickened and produce a funnel leading to the tip of the osphradium (ov.). The lobate appendage which can close the siphon of *Conus lividus* (Alpers 1931, p. 591-592) is not developed.

The foot is 25 mm long in a snail with a 48 mm long shell; it is slightly pointed in front and rounded behind. Its most contractile zone lies in front of two slight folds which appear transitorily on both sides under the head. These folds allusively separate propodium and metapodium and are better marked in the living than in the preserved snail. Other pedal folds do not occur, also the anterior border is entire, not bilabiate and notched as in *Conus* (Bergh 1896, p. 74-75). Except for this border which is light, sole and back of the foot are richly pigmented. As the columellar and nervous connection between visceral hump and foot is thin, peduncle-like, the amplitude of the movements of the foot is wide. In the laboratory dish we often saw the foot moving in direction of the spire, and the shell swinging into normal position only after some time.

Behind the columellar connection the operculum (or) is attached on about half its length to the back of the foot. The operculum is oval, light yellow, horny, and thick; 3 mm long, 1,6 mm broad. Its border is convex, smooth; its nucleus, terminal. The operculum does not seal the aperture. Even in animals preserved without anaesthetization, hence maximally withdrawn, it does not close the shell. In these snails the frilled rim of the foot and the tip of the siphon stand out around the operculum.

The origin of the columellar muscle (cz) lies on the level of the posterior border of the anterior digestive diverticulum (1). In adult full-grown snails whose 4 larval and 4 first definitive whorls are filled up by calcification, the visceral hump ascends to the ninth whorl. Five to six further whorls contain the viscera. The retracted "Kopffuss" (Ankel 1936, p. 10, 11) occupies the two foremost whorls.

The sole of the foot is densely ciliated, the back is ciliated only in front under the mouth and in the stripe of the egg-guide (zo) described later on. The anterior border of the foot is amply supplied

with sensory cells connected by a nerve net which contains accessory ganglia. As in other burrowing prosobranchs, e. g. *Natica* and the olivids, the anterior border of the foot is an important sense organ. The glandular equipment of the foot is however weak. Scattered unicellular blue-staining glands occur in the epidermis of the foot and chiefly in that of the sole, but subepidermal insunk glands are restricted to the pedal borders mainly in front, in the middle of the fore end. They correspond to the anterior pedal mucus gland (Graham 1957, p. 141) and discharge to the anterior border and the dorsal surface of the foot, not to the sole. *Conus* has a concentrated anterior pedal gland (Houssay 1884, p. 266).

Penis, egg-guide, and ventral female gland are described with the reproductive organs.

PALLIO-PERICARDIAL COMPLEX

The pallial cavity is deep and narrow; the half apical angle which indicates its breadth (Fretter 1951, p. 584) is small, 7-7,5°. The border of the mantle cavity is light, the anterior region of the roof deep black, except for osphradium and gill; the floor is dark in some places, light in others. When the shell is removed, a sutural fold (so) appears as a sharp edge on the right side between pallial roof and bottom. This fold, Bergh's "Kapuze des Mantelgebrämes" in *Conus* (1896, p. 75-76, pl. 1, f. 5, c; explanation: p. 200), is thickened by vesicular tissue. Also in the visceral cavity this interstitial tissue is richly developed, wrapping the coils of the poison gland, salivary gland, radula-sac, central nervous system, and other organs.

The inhalant current produced by the branchial cilia passes over the osphradium. Big particles were seen to be retained by the papillae of the outer opening of the siphon. The exhalant current was observed on the roof of the pallial cavity on the right side, on some parts of the hypobranchial gland and on a ciliated streak on the floor, which is underlain by the pallial spermiduct in the male.

As generally in the *Stenoglossa* (Simrøth 1907, p. 1029) the slightly pigmented light brownish osphradium (ov) is large, 8 mm long, 2 mm broad, bipectinate, and has about 50 filaments on either side. The great size of this presumed chemoreceptor is evidently associated with carnivorous life (Morton 1958b, p. 72); whether besides

it is correlated with much sediment in the respiratory water (Hulbert and Yonge 1937; Yonge 1942, p. 200; 1947, p. 510) is discussed (Morton, l. c.; Clark 1958, p. 58-59). Of course only systematically related groups should be compared. Within the *Toxoglossa* certain conids show an osphradial-sedimental correlation. *Conus lividus* found on reefs (Alpers 1931, p. 588), hence in clean water, is about the same length (25-50 mm) as *Hastula cinerea*; its osphradium comprises only about 15 filaments on either side (l. c., f. 2). *Conus mediterraneus* which burrows in sand, is about 20 mm (Alpers 1932, p. 439), maximally 38 mm long (Bergh 1896, p. 166). Its osphradium is 6-8 mm long, 3-4 mm broad and has 50-60 filaments on either side.

The enlarged surface of the osphradium can be understood if the function is tactile (Yonge 1947, p. 512), but just as well if the snail is "macrosmatic". The sedimentary particles might exercise a mechanical stimulus to which the osphradial cells could react with accelerated divisions and therewith increase the size of the osphradium, even if its sensory cells are chemoperceptive as hitherto supposed by Crofts (1929, p. 44), Ankel (1936, p. 143), Kohn (1956, p. 170), Morton (1958a, p. 4-5) and others, though not proven (Bernard 1890, p. 128; Stork 1934, p. 98).

In *Hastula cinerea* the osphradium lies at the extreme left of the pallial roof. It is nearly symmetrical as in *Conus* (Bergh 1896, f. 30), contrary to *Buccinum* (Dakin 1912, p. 78). The leaflets are flattened in antero-posterior direction (Fig. 3) nearly rectangular, and fastened to the roof along their entire upper border which is very thin. The lower border hanging free into the mantle cavity is almost straight and covered with mantle epithelium containing some blue-staining gland cells. The same epithelium coats the outer border of the leaflet.

The surface of each leaflet is subdivided into 3 bulges by furrows (ur) which run from the outer border inwards on the anterior and posterior side. The dorsal bulge is longest, the ventral one shortest. The epithelium of the furrows is low, while the faces of the bulges are occupied by the sensory areas. The question whether the principal elements are epithelial sensory cells (Bernard 1890, p. 150-151) of indifferent cells with free nerve endings between them (Dakin 1912, p. 181) has been decided in favour of Bernard (Yonge 1947,

p. 511). We did not analyze the sensory areae, only verified that they contain some ciliated but no pigment-bearing cells. The border of the bulges bears a broad band of ciliated cells (cs). Beside these cells, on their inner side, courses a stripe of lower cells containing brown pigment (mo). Cilia and pigment continue over the ventral border of the leaflet which is covered with the already mentioned mantle epithelium with mucus glands (xc). A special layer of glands dorsally to the ciliated cells as in *Buccinum* (Dakin 1912, p. 79) is not developed; the epithelium beside the attachment of the leaflets is quite low mantle epithelium with scattered blue-staining glands.

A well delimited blood space (oc) runs along the axis of the osphradium. According to Bernard's injections (1890, p. 156-157) this vessel-like space communicates with the efferent branchial vessel only by lacunae. It is accompanied by 2 cartilage-like rods (ca) which consist of vesicular cells enveloped in muscle fibres; Bernard (p. 171-172) found comparable thickenings in trochids. These rods contain pigment which in life seen from the upper side appears blood red. The central osphradial blood space supplies blood lacunae on the upper border of the leaflet, and these are connected with blood lacunae of the cavity of the leaflet as well as with such on the outer border. The latter penetrate between the furrows of the leaflet.

Ventrally the central blood space extends the enormous osphradial ganglion (ow) whose mass, about 0,16 mm³, surpasses by far that of all the central ganglia together. The osphradial nerve enters this ganglion in its middle. From the ganglion a nerve (n) coated with glia cells goes into each leaflet and gives one branch to each bulge as in *Conus mediterraneus* (Bernard, p. 205, pl. 8, f. 31). The secondary nerves which supply the sensory cells on the anterior and posterior surface of the leaflet are paired.

The white gill (k) lies to the right of the osphradium, begins at about the same level and extends farther inwards. It is 15 mm long, 2 mm broad, and contains about 200 lamellae. Separated from the ctenidium by a smooth interspace the light yellow, opacous hypobranchial gland (xi) attains the intestine. It belongs to the right half of the pallial roof, from whose low epithelium the 0,2 mm thick cushion is sharply set off. In some preserved specimens the secretion was reddish violet as in *Terebra muscaria* Lm. (Risbec, 1953, p. 577).

RENAL ORGAN

Inwards to the ctenidium the pigmentfree kidney (h) lies over the pallial roof as a dorso-ventrally flattened sac. In front it is extended to the posterior end of the gill on the left, and to the anterior border of the hypobranchial gland to the right side; behind it ends over the stomach. Contrary to Bergh's statement for *Hastula coerulelescens* (1908, p. 128) the intestine does not run through the cavity of the kidney, though the renal sac overlies the intestine (i) intimately. The transverse section of the kidney is triangular with the smallest side left, where the renal gland (vv) is apposed to the pericardium. In the anterior part the inner surface of the ventral wall is smooth. Here the renal aperture (x) is located, a long slit between thick muscular lips. A little behind passes the ciliated funnel of the reno-pericardial duct (y) into the pericardium (er).

In the region behind the mantle cavity the ventral wall of the kidney bears transverse folds which are, contrary to *Lintricula auricularia* (E. and E. Marcus 1959, f. 58), restricted to the renal bottom. From the abdominal blood sinus emerges the muscular afferent renal vessel and branches into the folds. Besides there are also direct communications between sinus and folds, not developed in *Olivella* (l. c., f. 56). Of the blood spaces in the folds that in the summit is largest. Here the high epithelial cells of the folds were sometimes seen to detach their apices as in *Olivancillaria brasiliensis* (l. c., f. 62). The blood from the folds is collected in peripheral coalescing lacunae and passes to the afferent branchial sinus.

Beside the reno-pericardial duct (y) the afferent vessel (uz) ascends through the renal cavity to the roof. Its outer wall is smooth, the inner bears muscular projections. Its ramifications on the roof supply the villosities (zn); then the blood flows to the nephridial gland (vv), whose sinus opens into the auricle (ic). In conids the vascular axis of the villous part, Perrier's left lobe (1889, p. 249), runs on the left side, near the border of the renal gland. In *Hastula cinerea* it is situated (va) in the middle, so that its branches to right and left are of equal length.

The low epithelium of the villosities differs widely from that of the folds. It contains some blue-staining gland cells. Also the con-

nective tissue is quite different from that of the folds. It leaves only quite narrow blood spaces free, and is in some places, in one case nearly everywhere, stuffed with the protein crystalloids described by Cuénot (1914, p. 281). Amoebocytes occur principally in the villousities, but also in the blood lacunae and in the folds.

Perrier (1889, p. 262) called attention to the minuteness of the blood spaces in the accessory system, the villousities, of his Pycnonephridia (Muricacea, Buccinacea, and others). In this system, the so-called left lobe, circulation is slow and irregular (p. 256). The same certainly applies to *Hastula cinerea*. This system is principally absorbent (Cuénot 1914, p. 281-282). The nephridial gland (vv) differs from the adjacent villous region (zn) by a much higher epithelium and less richly developed connective tissue.

CENTRAL NERVOUS SYSTEM

The nervous system of the Toxoglossa is best known by Bouvier's (1887), Bergh's (1896), and Shaw's (1914) studies of various species of *Conus*. The terebrids were less completely described by Bouvier (p. 316-325); Risbec added some observations (1953, p. 582-583). Bouvier's (p. 341) and Shaw's (p. 36) difficulty in removing the connective tissue (Fig. 9, 10, co) which surrounds and binds firmly together nerves, oesophagus and coils of poison gland in *Conus* was also experienced in *Hastula cinerea*. Therefore our results obtained by dissection were controlled and completed by microtomic sections.

Together with radula-sac (rs) and salivary gland (sa) the central nervous system (b) shows the effect of torsion, though less pronounced than in *Conus* and *Terebra cancellata* (Risbec, l. c.). In *Hastula cinerea* the position is somewhat oblique, as the anterior border is more ventral than the posterior. The cerebro-pedal and pleuro-pedal connectives of the right side are longer than the corresponding left connections. The pleuro-pedal connectives are a little thicker than the cerebro-pedal ones. Neuroglia cells as described of *Olivella verreauxii* (E. and E. Marcus 1959, f. 17, n) are developed in the connectives.

The longish pedal ganglia (1) lie far in front of the cerebral ganglia (2) and the radula-sac, approximately over the peduncle of the foot. The volume of the pedal ganglia surpasses a little that of the

cerebral ganglia. In some cleared total mounts the pedal ganglia were topped by propodial ganglia (1a), not recognizable in other preparations. The accessory pedal ganglia of *Terebra cancellata* (Risbec 1953, f. 11, pda) are dorsal to the pedal ganglia, not terminal as in our species. On their adjacent sides the pedal ganglia are fused together. Each ganglion gives 2 nerves (10) off on its anterior border which subdivide short after their beginning. They enter the foot through the peduncle and form a net of branching nerves with accessory ganglia which supply chiefly the anterior pedal border as in the likewise burrowing olivids. In the male the right pedal ganglion is a little bigger than the left and gives rise to a penial nerve (11) near the cerebro-pedal connective.

The statocysts lie about 1 mm in front of the pedal ganglia under the anterior evaginable tube. Both are located in the same transverse plane. The diameter of the statocyst including its capsule is 0,2 mm, that of the statolith 0,08 mm. The extremely thin static nerves (12) can be followed backwards into the capsule of the pedal ganglia and farther to the pleuro-pedal connectives. Hence the static nerve reaches the cerebral ganglion as in *Buccinum* (Bouvier, p. 261), *Nassa* (p. 277), *Purpura* (p. 284), and *Conus virgo* (p. 333); in *C. tulipa* and *textile* (Shaw 1914, p. 33, 49) the static nerve runs through the cerebro-pedal connectives.

The broad cerebral ganglia (2) are separated from one another by a furrow; a true cerebral commissure is not developed. They cover the slightly smaller pleural ganglia (3), against which they are delimited by constrictions. The short buccal connectives of Bouvier's *Terebra aciculina* Lm. ("les ganglions buccaux sont très rapprochés des ganglions cérébroïdes", p. 325) contrast with those of *Hastula cinerea*. Also the long anterior tube (Bouvier, pl. 17, f. 81, X) and the short pleuro-subintestinal connective (f. 81, Cg, Sb) make it probable that Bouvier studied a different species.

Intimately connected with the static nerve (12) a nerve courses from the cerebral ganglia through the pleuro-pedal connectives forwards (13). Its twigs can be followed into the thick and loose layer of crossing muscle fibres under the outer mouth. Besides this cephalic integumentary nerve there are 3 labial nerves (14) on either side which issue from the cerebral ganglia farther backwards and outwards.

They enter the anterior tube (au) through its ventral attachment (xa) and spread into its wall. Behind these 3 labial nerves we only found 2 further cerebral nerves on either side, the thicker proboscidean nerve (16) and the thinner common nerve (15) for tentacle and eye. The proboscidean nerves trifurcate at the base of the proboscis, so that 6 principal nerves run in the inner muscle layer of the proboscis, chiefly on the ventral side. In correspondence with the smallness of tentacles and eyes and their insignificance for orientation of the burrowing snail tentacular and optic nerves are not separated, and their common trunk is tenuous.

As in *Conus* and the previously studied terebrids the buccal commissure is long. It is single as in *Terebra dimidiata* (Bouvier, p. 320), not double as in *Conus* (id., p. 340; Bergh 1896, f. 29, g, f. 31; Shaw 1914, p. 35), but also suboesophageal. As far as the 2 nerves (17) from each buccal ganglion (6) can be traced, they supply radula-sac and salivary gland; an unpaired nerve (18) from the right buccal ganglion enters between the coils of the poison gland (vo) where it was followed to the muscular bulb (q).

While there is no nerve given off from the right pleural ganglion in *Conus* (Bouvier, p. 337; Bergh, p. 80; Shaw, p. 44), such exists in *Buccinum* (Bouvier, p. 268: "grand nerf latéral droit"; Dakin 1912, p. 70). It goes out from the right pleuro-pedal connective and has its counterpart on the left side. The same disposition occurs in *Hastula cinerea*. The left nerve bifurcates soon into an anterior parietal (19) and a columellar (20) nerve. Also in the muricid *Concholepas peruvianus* Lm. the corresponding parietal nerve sends a branch to the columellar muscle. The right anterior parietal nerve (21) of *H. cinerea* does not divide for the length that was followed. From the left pleural ganglion the strong siphonal nerve (22) originates and divides into 6 branches in the root of the siphon. The dialyneurous connection (8) with the osphradial nerve (24) is distinct. Bouvier's indication of a columellar nerve coming from the "ganglion palléal droit" (p. 321) in *Terebra dimidiata* Lm. is a lapsus for "gauche", as his figure 82 shows (nerve 1). The same columellar nerve (23) exists in *Hastula cinerea*.

The left pleuro-subintestinal connective of *H. cinerea* is a little longer than that between right pleural and supra-intestinal ganglion.

This feature reminds of *Turris nodifera* Lm. (Bouvier, pl. 17, f. 78). The short right, stout zygosis (7) of *H. cinerea* and the beginning of the supra-intestinal branch of the visceral loop agree with Bouvier's figure of *Terebra aciculina* (f. 80).

The osphradial nerve (24) and the anterior branchial nerve (25) originate from the supra-intestinal ganglion (4); a posterior branchial nerve (26), together with the exit of the visceral loop from this ganglion. These nerves correspond to Bouvier's description of *Terebra dimidiata* (p. 321).

Three right posterior parietal nerves (27) course towards the right from the subintestinal ganglion (5), while the nerve (28) that goes out from the left and ventral surface of this ganglion seems to correspond to the parieto-columellar nerve in *Conus* (Shaw 1914, p. 43, pl. 4, f. 19, e).

The visceral loop contains 3 ganglia (9) as in the Conidae (Bouvier 1887, p. 332) and, according to Haller (quoted from Simroth 1901, p. 416, 418), the Muricidae. In the retracted snail of Figure 5 the visceral loop is twisted.

ALIMENTARY TRACT

On the level of the tentacles the integument of the head passes through the outer mouth (m) into the anterior tube (au), Bouvier's "gaine proboscidiennne". According to its innervation by labial nerves this tube corresponds to lips. In many of the preserved snails the labial tube is introverted. Annular muscles around the outer mouth are distinct, but no special glands besides the epidermal ones. The tube has thick muscular walls and can be extroverted through the outer mouth which in this condition constitutes the base of the tube.

Bouvier's two specimens classified as *Terebra aciculina* Lm. can hardly be our species, because their movable anterior tube is of approximately the same length as the proboscis (1887, p. 324, pl. 17, f. 81, X).

In living and preserved animals the tube was seen turned out. The snails possibly seize their food, polychaetes, with it, as Alpers (1932, p. 428 ff.) observed in *Conus mediterraneus*. Inner and outer epithelium of the tube contain more numerous gland cells than the

epidermis. The anterior tube bears a strong sphincter (r), dorsally less developed than ventrally. So a dorsal slit-like communication appears between the lumen of the tube and the spacious rhynchodaeum (ri), as Oswald (1893) called the cavity delimited by the proboscidean sheath. This slit is the "fente dorsale" of Bouvier (1888, quoted from Simroth 1897, p. 128-129), but its position varies according to the contraction of the sphincter. When the tube is everted, its opening is longer ventrally (Bergh 1908, pl. 10, f. 7), because the ventral wall of the tube is fastened to the bottom of the rhynchodaeum for a certain extent (xa). When the tube is evaginated, the inside of its dorsal wall is turned out completely, while the excursion of the ventral wall is restricted.

A tubular fold of the proboscidean sheath containing the buccal tube (uc) forms the proboscis (p), its anterior opening is the pharyngostome (Oswald 1893). As it functions as entrance of the gut, we call it inner mouth (im). The epithelium lining the rhynchodaeum is high in the portions apposed to the body wall. This epithelium contains numerous mucus gland cells; the subjacent muscle layer is thin. Retractors (s) of the proboscis originate on the lateral body walls and insert on the circle where the proboscis rises from the bottom of the rhynchodaeum.

Inner and outer epithelia of the proboscis are underlain by thick layers of longitudinal and diagonal muscles. These layers are connected by single radial fibres. Due to the longitudinal and diagonal fibres the retracted proboscis is bent and folded, not much contracted. Unfolded it is 10 mm long in adult snails. Annular muscles, principally in the outer layer, produce the lengthening of the proboscis. In our preserved snails the proboscis is never protruded beyond the evaginated anterior tube. In living animals we only once saw it project beyond this tube, when a polychaete was placed in front of the snail. We did not succeed to feed the snails, perhaps they prey only on worms that stick deep in the sand and maybe only at night as *Conus* (Kohn 1959, p. 69).

Six longitudinal nerves (Fig. 7, n.) run in the muscle layer of the buccal tube (uc). Near the inner mouth (im) these muscles form a sphincter (r), Hermitte's muscular collar (1946, p. 497) in *Conus*. Farther inwards the buccal tube is richly folded. At the level of the

proboscidean base the muscles around the buccal tube are thickened tightly forming a pharyngeal bulb (f).

The right ventral wall of the bulb is connected with the radula-sac (rs) by a short tube. The sac contains about 30 teeth fastened in two rows on the wall. The basal flange of every tooth is connected with the wall by a hyaline, acellular ligament (see Fig. 8). This band corresponds to a basement membrane (Pruvot-Fol 1926, p. 306). The tops of the older teeth are directed towards the lumen of the sac, those of the latest teeth point into the radular papilla. The rows of teeth begin proximally on the inner wall and pass to the outer wall in an S-curve. The hollow teeth are 0,54 mm long and 0,08 mm thick at the base or 0,11 mm when the flange is measured. The tooth bears a lancet-shaped tip and is rolled in along its whole length. The so-called pores are not holes, but bridges between the inner border and the outer wall of the tooth. These bridges produce the illusion of an inner spiral (Fig. 8). The shape of the tip is possibly correlated with the habit of feeding on burrowing polychaetes as Kohn (1959, p. 79) supposed for the terminal knob of the tooth in *Conus distans*.

Pruvot-Fol (1926, p. 306) compared the rolled up toxoglossan tooth with basally coalesced marginal rhipidoglossan teeth, e. g. of the Potamiasidae, but of course without phylogenetic claims.

Most of our snails show a tooth (za) in the buccal tube (uc) where its flange is fastened on an epithelial plug between inner mouth (im) and sphincter (r). We consider this position as normal and definitive, as long as the tooth functions. Its tip attains the inner mouth. In some of our sections the tooth lies proximally to the sphincter. We presume that such a tooth is being moved into place by peristalsis of the buccal tube. Hermitte (1946, p. 497) suggests that in *Conus* the transference of a fresh tooth from the radula-sac to the place where it functions is brought about by invagination of the proboscis, whose mouth grasps a tooth from the sac. Such is unlikely in *Hastula cinerea*, because we have seen normally directed teeth between pharyngeal bulb (f) and sphincter (r). Sometimes loose teeth with backwards directed tips were seen in the oesophagus. Probably such teeth had been engulfed together with the prey, as Kohn (1956, p. 170; 1959, p. 68) observed in piscivorous and certain

vermivorous cones. Alpers (1931, p. 650) found fragments of teeth mingled with the digested contents of the gut in *Conus lividus*. Though we did not observe a tooth right in the inner mouth like a stylet as in Amaudrut's figure of a *Terebra*-species (1898, pl. 3, f. 20) reproduced by Hescheler (1900, f. 265) and Simroth (1901, pl. 39, f. 6) we do not doubt its correctness for Amaudrut's species. In *Conus* it has been confirmed by Kohn (1956, f. 2).

Kohn's admirable photographs of feeding cones contradict Alpers' view (1931, p. 603, 650) that every occurrence of a tooth in the buccal tube of a toxoglossan (e. g., Bergh 1896, pl. 4, f. 70) is due to the violent contraction of the snail during preservation. According to Risbec (1953, p. 581) Alpers is possibly right to presume a normal function of the radula of *Conus lividus* in the way of his figure 28, VIII (1931). The anterior teeth which lie in the distal part of the radula-sac, the "quiver" (Alpers's "Köcher"), would act upon a worm while it passes through the pharyngeal bulb. In *Hastula cinerea*, however, the function of the radula must be similar to those conids that protrude the proboscis and harpoon their prey (Hermitte 1946; Kohn 1955; 1956). The fore-gut of the *Toxoglossa* varies in form and function and does not permit generalization. In *Conus mediterraneus* no function of the radula could be verified (Alpers 1932, p. 433, 445). Among the terebrids there are species without radula and without poison gland, others with radula and without gland, and still others, the genus *Hastula*, with radula and poison gland. Of course the various types feed differently.

Isolation of the numerous sympatric species of *Conus* in Hawaii is brought about, besides by the different habitats, subtidal reefs and marine benches, by the specificity of the preferred prey (Kohn 1959, p. 82 ff.).

A single salivary gland (Fig. 6, 9, sa) lies on the topographically left side. In some snails it is constricted in the middle, and its originally paired structure is evident in the sections. Its two ciliated ducts (wi) course above and below the gut, without passing through the nerve collar (b). In some snails the duct that emerges from the right half of the salivary gland runs under the oesophagus (e), and in others the left. The suboesophageal duct either goes around the radula-sac (Fig. 9, rs) or courses between it and the poison gland

(Fig. 6, vo). The salivary ducts open from both sides into the communication between pharyngeal bulb and radula-sac. The convolutions of the so-called poison duct (vo) lie principally on the topographically right side. The secretory part of this gland is the contorted long tube which passes through the nerve collar (b) and opens into the gut close to the radula-sac, immediately behind the pharyngeal bulb (f). The blind end of the gland is the bulb (q) composed of 4 muscle layers as in *Conus* (Shaw 1914, p. 24) and lined with a non-secretory epithelium (Fig. 10).

In the bulb of the poison gland the thick outer layer of spiral fibres is followed by a thin layer of annular ones. The third layer is also thick and spiral with parallel fibres as those of the outer layer, but crossing them. The fourth layer is annular and thicker than the middle annular one. The tubular part of the gland (vo), the poison duct of the literature, begins with a short muscular portion. The high cells of the tube contain rather big granules of secretion. From the structure we presume that the product of the gland cells is pumped into the proboscis by the muscular bulb (q). The same idea of the so-called poison gland as propulsive organ for the ejection of poison secreted in the so-called duct was for *Conus* first conceived by Hermitte (1946, p. 499) and independently by Kohn (1955).

Bouvier (1887, p. 323, 324, 329, f. 81, 83, 84), Bergh (1896, p. 89; 1908, p. 128), Amaudrut (1898, pl. 3, f. 20), and Shaw (1914, p. 14, 19) found a more or less distinctly bipartite salivary gland and two salivary ducts in *Terebra* and *Conus*. Alpers (1931) considered all these statements as erroneous, because he found only a single salivary duct in *Conus lividus* (f. 24). He homologized the poison gland with the second salivary gland, and Thiele (1935, p. 1049-1050) adopted this forced view. If the anterior limit of the oesophagus (e) is the point at which the radula-sac (rs) separates from the gut proper (Graham 1939, p. 76), the outlet of the poison gland (vo) lies in the foremost part of the oesophagus. Here the cilia begin and continue along the whole alimentary tract. The gland is comparable with the gland of Leiblein in the *Stenoglossa*, as Bouvier (1887, p. 330, 430, 473), Amaudrut (1898, p. 98), Dakin (1912, p. 32), Shaw (1914, p. 12) and Risbec (1955, p. 52) said. It is true that it opens into the anterior oesophagus, not into the mid-oesophagus as in

the *Stenoglossa*. This difference is brought about by the different formation of the preneural proboscides in *Stenoglossa* and *Toxoglossa*: in the first by a lengthening of the anterior oesophagus, in the second by that of the buccal tube, Hermitte's "prepharynx" (1946, p. 495).

The oesophagus is indistinctly separated from the stomach and about 15 mm long. Stomach and intestine together are of the same length. The oesophagus runs on the ventral side of the body cavity. At its origin from the pharyngeal bulb it forms a forward loop which is more or less straightened according to the state of protrusion or retraction of the proboscis. The oesophageal epithelium is thrown into 20-25 rather uniform longitudinal folds, particularly high in the region under the pericardium. Stronger dorsal folds or stretches with distinct accumulation of gland cells are not developed; the structure of the oesophagus is alike in front of the nerve collar and behind it. A dilatation was verified in many of the dissected specimens. Bergh (1908, p. 125) observed it in *H. coerulescens* (Lm.). It occurs on quite different levels of the oesophagus and is histologically not peculiar, hence only a temporary widening, not a true crop. Close in front of the diaphragm between cephalic and visceral body cavity the oesophagus is fastened to the ventral wall by a ring of muscle fibres as in *Oliva sayana* and *Lintrricula auricularia* (E. and E. Marcus 1959, p. 126, 129).

Some transverse gastric folds between the longitudinal ones of the oesophagus (e) indicate the region of the cardia. The thin-walled stomach is only a little wider than the oesophagus, tubular and quite without caecum, somewhat similar to that of the muricids studied by Graham, *Nucella*, *Ocenebra*, and *Urosalpinx* (1949, p. 748-749). The gastric portion of the mid-gut of *Hastula cinerea* (j) loops around the anterior, morphologically left liver (l), a spherical organ whose anterior border lies level with the pylorus. The hepatic ducts unite just before they open into the cardiac part of the stomach. The anterior duct (l) comes from the small anterior digestive diverticulum. The posterior duct (os) runs backwards under the stomach to the long posterior, morphologically right liver. This extends to the hindmost whorls, where it is topped by a knob of vesicular connective tissue. This liver is accompanied by the gonad and the latter's pigmented duct on its columellar side. Both digestive diverticula are brittle organs with smooth surface and very few nuclei. The volume of the visceral

hump varies considerably in our snails in correspondence with the size of the ovary before and after egg laying.

The longitudinal folds that run on the concave side of the oesophagus curve into the common hepatic duct and continue into the separate ducts. Some longitudinal folds course along the convex side of the stomach. Going out from the aperture of the digestive diverticula some folds follow the concave side of the stomach and constitute a kind of excurrent or intestinal groove (in). The upper or pallial wall of the stomach and the under or columellar wall are clothed with arched transverse folds. The 30-50 frequently bifurcate folds of the pallial wall may correspond to a major typhlosole (oa), those of the columellar wall which are straighter and less numerous (about 20) to a minor typhlosole (oi). Towards the intestine (i) the folds of the typhlosoles converge in some, not all examined snails on the convex side, but a true sorting area is not developed. This character, the anterior entrance of the oesophagus, and the absence of caecum and gastric shield are the same in *Hastula cinerea* and the above mentioned muricids.

Partly decomposed pieces of polychaetes were found in the stomach.

The beginning of the intestine (i) is characterized by a slight narrowing of the alimentary tube and the conversion of the transverse folds into longitudinal ones. The cilia of the epithelium continue; red-staining gland cells increase in number outwards, but rarify and finally disappear near the middle of the anal gland. This black gland (Fig. 13, 14, 17, an) is an up to 6 mm long, richly branched organ with narrow lumen and resembles that of the muricids (Fretter 1946, p. 129) and *Oliva peruviana* (Küttler 1913, p. 506-507). Contrary to the latter it is of equal size in males and females. Its ciliated epithelium contains brown concretions. As in the muricids studied by Fretter (l. c.) the anal gland of *Hastula cinerea* is combined with a histologically extremely simple digestive gland, and possibly assumes the function of an accessory excretory organ, as in the muricids. In one case the lumen of the gland contained a patch of brown granules on a lump of secretion. The epithelium on the side facing the granules was low and free of granules, thus proving recent excretion. A blood lacuna (oc) runs between gland and rectum. The latter projects into

the mantle cavity on the right side apposed to its roof, and the anus (ar) lies in the anterior third of the cavity. The anal gland opens into the anus or immediately beside it. As in *Oliva*, *Lintrricula*, and *Olivan-cillaria* the wall of the mantle cavity forms a tubular papilla (z) containing a nerve over the anus.

Masses of setae of polychaetes were observed in the rectum.

MALE ORGANS

The follicular testis (me) extends from the apical whorls forward on the columellar side of the posterior liver (os) and is continued into the coiled, nonciliate testicular duct (su) which functions as vesicula seminalis as in Muricidae, Buccinidae, and Olividae. There are no atypical sperms, as such are known from *Conus*, *Olivella*, and *Oliva*, neither in the testis and seminal vesicle, nor in the female organs. The straight and ciliated renal spermiduct (re) runs so closely approached to the pericardium that the presence or absence of a gonopericardial strand of connective tissue could not be verified.

The orange yellow pallial spermiduct (d) begins as a muscular pouch whose ciliate epithelium is surrounded by clusters of closely set subepithelial prostatic glands as drawn by Fretter (1941, f. 1). At its origin this pouch opens by a 0.5 mm long slit (sn) into the pallial cavity as in *Ocenebra lapillus* (l. c., p. 175), *Olivella*, *Oliva*, and *Lintrricula* (E. and E. Marcus 1959). In buccinids (Fretter 1941, p. 178, 180) this communication between prostate and mantle cavity is established by a duct. The dilated stretch of the pallial spermiduct in the roof of the mantle cavity is parallel to the sutural fold. The following thin tube curves from the roof to the floor, where its course produces a slight ridge.

After its entrance into the penis (vr) the spermiduct (nv) becomes sinuous and continues so along the centre of the flattened copulatory organ. The hatchet-shaped, solid and muscular penis (Fig. 14, 15) is not as long as that of *Terebra (Subula) dimidiata* (Bouvier 1887, p. 319), nor dentate as in *T. (Oxymoris) maculata* (p. 322). The penial spermiduct opens on a small papilla which lies in the middle of a terminal concavity of the penis. The penis enters the terminal pouch in the mantle cavity of the female, where we found sperm. The muscular coat of the spermiduct (nv) can project the narrow

papilla and attain the bursa copulatrix and the ventral sperm channel through the pore-like outer opening of the capsule gland. At rest the penis is tucked into the mantle cavity, as Bouvier (1887) and Bergh (1908) already observed.

FEMALE ORGANS

The ovary lies on the columellar side of the posterior digestive diverticulum. The straight ovarian portion of the oviduct (ou) is about 5 mm long and lined with the same low epithelium as the ovary. The eggs in the oviduct measure $300 \times 150 \times 100 \mu$. As about 6 of these ovocytes were found descending the gonadal duct of one sectioned female, it is probable that several eggs are included in one capsule. In *Conus jaspideus* Gm. there are 3-7 eggs per capsule (Perry and Schwengel 1955, p. 180); in other conids many more (Risbec 1932, p. 366).

The renal oviduct (rv) curves in an almost right angle from the ovarian duct. A short gonopericardial duct (g) connects this angle with the pericardial cavity (er). This duct is ciliated, but the cilia are less developed than in the renal oviduct. Its opening into the pericardium is a pore, not a funnel. A sphincter is not present.

The beginning of the subepithelial glands marks the start of the pallial oviduct. Its innermost portion, the albumen gland (aa), is thinner along the ventral side of the duct. From the bound between albumen gland and capsule gland a canal (se) with high longitudinal folds leads to a wide, lobed pouch (rn). In the folds of the canal there are often sperms fastened with their heads to the low ciliate epithelium. The histological limit is sharp between this and the epithelium of the pouch whose reddish brown colour resembles that of the foliaceous organ of *Conus* (Bergh 1896, p. 98). The sperm masses included in it are disorderly, and the high nonciliate cells engulf sperms. The sperm pouch is obviously homologous to the receptaculum seminis of muricids, buccinids (Fretter 1941) and *Lintrricula auricularia* (E. and E. Marcus 1959, p. 143). In the last species as well as in *Nucella lapillus* and *Buccinum undatum* the duct of the receptaculum stores orientated sperm, while blind tubules going out from the duct function as ingesting gland.

Also the orange red capsule gland (c) of *Hastula cinerea* agrees with that of the *Stenoglossa* studied by Fretter (1941, f. 5). The different colourability of the glands in the dorsal, middle and ventral areas is indicated by different stippling in our Figure 18. The lumen of the capsule gland and its ventral sperm channel (sr) is lined by ciliate epithelium. The channel contains sperms; its epithelium is surrounded by muscles. Of the two longitudinal folds of the sperm channel present in Fretter's *Stenoglossa* only the left is developed in *Hastula cinerea*. This fold becomes higher towards the distal end of the capsule gland. The latter opens through a narrow pore (ec) into the outermost portion of the pallial oviduct.

Over the passage of the capsule gland into this outermost portion the lumen of the capsule gland forms an about 0,5 mm deep pouch, the bursa copulatrix (u). Its epithelium is glandular where it is continuous with the capsule gland and towards the fundus thrown into narrow folds of short ciliate cells without glands. Sperms were seen in the bursa of a snail preserved immediately after copulation. They lay as a small lump in the lumen.

The about 4 mm long outermost portion of the pallial oviduct is a colourless pouch (wo) open against the pallial cavity. Its walls form oblique folds; the epithelium is ciliate without glands. Its slit is bounded by thickened muscular lips. This terminal pouch of the oviduct ends behind the anal papilla (z). Its folds indicate that it is distensible by the egg capsule and also by the penis. Snails preserved after copulation had a loose mass of sperm lying in the terminal pouch without contact with its epithelium. The nutritive and protective coats of the eggs are already furnished by the glands of the pallial oviduct before the capsule enters the terminal pouch. Its slit may be correlated with the definitive size and firmness of the egg capsule as in *Pomatias elegans* (Creek 1951, p. 635). Topographically the terminal pouch corresponds to the jelly gland and the brood pouch in *Littorina* (Linke 1933, p. 33-35).

Except for the terminal pouch which has no counterpart in the known *Stenoglossa* the female organs of *Hastula cinerea* are very similar to those of this Order. A comparison with the Conidae was not possible, because we did not succeed to understand Bergh's descriptions (1896, p. 97-100, 175-177). It is possible that the elements

in *Hastula* and in *Conus* () are the same: terminal pouch (vulva), bursa copulatrix (Samenblase), capsule gland (Schleimdrüse), receptaculum seminis and ingesting gland (blättriges Organ), albumen gland (Fortsetzung der Schleimdrüse an der Hinterseite der Niere). This interpretation is tentative.

On the right side of females of *Hastula cinerea*, whose shell is at least 31-32 mm long, a nearly white 0,9 mm broad stripe (Fig. 2, zo) runs from the floor of the mantle cavity along the pedal peduncle and ends at the small marginal pedal fold that marks the limit between propodium and metapodium. This egg-guide is characterized by its much less intense pigmentation, a little higher epithelium, and principally by its 3 μ long cilia. The adjacent areas of the back of the foot are nonciliate.

In middle-sized and adult females a pigmentfree slit or circle about 1,3 mm in diameter, the ventral pedal or nidamental gland, lies about 2 mm behind the anterior border of the foot. This gland appears already in snails with 29 mm long shells. The blue staining gland cells extend 0,3-0,5 mm inwards. Among the strong muscles of the foot no special arrangement of fibres could be recognized related with this gland, nor a tract on the sole between it and the fold on the pedal border where the egg-guide (zo) ends.

The figures of ventral pedal glands of conids (Bergh 1896, pl. 1, f. 12, b; 22, a) refer to species of which the author had only females. In one case he mentioned a "posterior pedal gland" of a male lying "uncommonly far in front" (p. 108). This gland can hardly be the posterior pedal gland of Graham (1957, p. 142), because Bergh in other cases always mentions two glands, the anterior pedal mucus gland and the ventral pedal gland.

CONCLUSIONS

Among the Terebridae the genus *Hastula* with both radula and poison gland is less specialized than the other genera without gland or without gland and without radula. The proboscis of the Terebridae is highly specialized. The central nervous system attains a higher degree of specialization in conids than in any terebrids. It seems plausible to derive Terebridae and Conidae from the Turridae (Pleurotomidae), as Bouvier did (1887, p. 474) and not to consider the

last as a subfamily of the Conidae (Thiele 1931). The Turridae are better maintained as a separate family (Abbott 1955; Risbec 1955; A. Myra Keen 1958). Then the Toxoglossa would comprise Terebracea (Turridae, Conidae, Terebridae) and Mitracea, i. e., the Mitridae in their restricted range (Risbec 1928; 1955, p. 71-74, 76). The Turridae are anatomically and also systematically (e. g., N. MacGinitie 1959, p. 65) little known. Hence one cannot decide from which other stenoglossan family they should be derived, Volutidae (Bouvier 1887, p. 305-6, 315-316) or Muricidae (Thiele 1935, p. 1095). Perrier (1889, p. 241) considered the Conidae as Meronephridia and therewith nearer to the Volutidae, but the difference between Meronephridia and Pycnonephridia is gradual. A system based exclusively upon the anatomy of the kidney would lead to artificial results, viz. approach Cypraeidae to Volutidae (l. c., p. 239, 281) and Harpidae to Buccinidae (p. 264, 281).

RESUMO

Para a espécie das Terebridae comum nas costas de São Paulo, na areia fina das praias de declive gradual, usamos o nome *Hastula cinerea* (Born, 1780), apesar de nela ocorrerem 28-36 não 45-50 costelas axiais na margem apical de cada volta.

Os animais comem poliquetos. Tentáculos e olhos são pequenos; a margem anterior do pé e o grande osfrádio (Fig. 3), intensamente inervados. Como nos Pycnonephridia de Perrier os espaços sangüíneos do sistema renal acessório são diminutos.

O volume dos gânglios pedais (1) ultrapassa algo o dos cerebrais (2). O pé é como que pedunculado, extraordinariamente móvel. Corresponde à separação indistinta entre propódio e metapódio a irregularidade de gânglios propodiais (1a) separados. O nervo penial (11) sai do gânglio pedal perto do conectivo cérebro-pedal. Pelo mesmo conectivo o nervo estático (12) sai do gânglio cerebral. Os conectivos cérebro-buciais são compridos. Cada gânglio pleural (3) emite um nervo. A alça visceral contém 3 gânglios (9).

Pela inervação o tubo anterior evaginável (Fig. 6, au) é uma formação labial. Um dente da rádula (Fig. 7, za) no tubo bucal (uc), perto da boca interna (im), serve evidentemente para arpoar a presa. O chamado duto da glândula de veneno (vo) é secretor; o

bulbo (Figs. 6, 10, q), propulsor. A glândula salivar (sa) tem 2 dutos (wi). A glândula de veneno não corresponde a uma glândula salivar (Alpers; Thiele), mas à de Leiblein dos *Stenoglossa*. O estômago (Figs. 11, 12) é muito simples; a grande glândula anal (Figs. 13, 14, 17, an) é excretora.

O penis (Figs. 14, 15) entra na bolsa terminal (Figs. 16, 17, wo) do oviduto, podendo a papila penial chegar à bursa (u). Entre as glândulas albuminógena (Fig. 16, aa) e capsulígena (c) o órgão lobulado (rn) ingere espermatozóides alheios em excesso, servindo o canal (se) como receptáculo seminal. Os ovos passam pela faixa ciliada (Fig. 2, zo) da cavidade palial à margem da sola. Nesta, ocorre glândula nidamental nas fêmeas.

Conidae e Terebridae parecem ter evoluído das Turridae cuja ligação às Volutidae (Bouvier 1887) ou Muricidae (Thiele 1935) ainda não é possível definir.

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).
- Alpers, Friedrich 1931, Zur Kenntnis der Anatomie von *Conus lividus* Brug., besonders des Darmkanals. *Jen. Ztsch. Naturwiss.* v. 65, p. 587-658, 40 text-figs. Jena.
- 1932, Über die Nahrungsaufnahme von *Conus mediterraneus* Brug., eines toxoglossen Prosobranchiers. *Pubbl. Staz. Zool. Napoli* v. 11 (3), p. 426-445, 15 text-figs. Roma & Berlin.
- Amaudrut, 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.
- Änkel, Wulf Emmo 1936, *Prosobranchia*. G. Grimpe & E. Wagler, *Tierwelt Nord- & Ostsee*, part IX b 1, 240 p., 222 figs. Leipzig (Akadem. Verlagsges.).
- Bchre, Ellinor H. 1950, Annotated list of the fauna of the Grand Isle region. *Occ. Pap. Mar. Lab. Louisiana State Univers.* n.º 6, p. 1-66. Baton Rouge.
- Bergh, Rudolph 1896, Beiträge zur Kenntnis der Coniden. *Nov. Act. Leopold.* v. 65 (2), p. 67-214, 13 pl. Halle a. S.
- 1908, *Malacologische Untersuchungen*, 6. Theil, 3. Lieferg., p. 118-178, pl. 9-12. Wiesbaden.

- Bernard, F. 1890, Recherches sur les organes palléaux des Gastéropodes prosobranches. Ann. Nat. Zool. sér. 7, v. 9, p. 89-404, pl. 6-15. Paris.
- 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.
- Buckup, Ludwig & Erica Helena 1957, Catálogo dos moluscos do museu Rio Grandense de ciências naturais. Iheringia n.º 1, p. 1-40. Pôrto Alegre.
- Carcelles, Alberto R. 1953, Nuevas especies de gastropodos marinos de las Repùblicas Oriental del Uruguay y Argentina. Com. Zool. Mus. v. 4 (70), p. 1-16, pl. 1-5. Montevideo.
- Clark, W. C. 1958, Notes on the mantle cavity of some trochid and turbinid Gastropoda. Proc. Malacol. Soc. v. 33 (2), p. 57-64, 7 text-figs. London.
- Coomans, H. E. 1958, A survey of the littoral Gastropoda of the Netherlands Antilles and other Caribbean islands. Stud. Fauna Curaçao, 8, p. 42-111, pl. 1-16.
- Creek, Gwendoline A. 1951, The reproductive system and embryology of the snail *Pomatias elegans* (Müller). Proc. Zool. Soc. v. 121 (3), p. 599-640, 18 text-figs. London.
- Crofts, Doris R. 1929, *Haliotis*. L. M. B. C. Mem. 29, VIII + 174 p., 17 pls. Liverpool.
- 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. 1912, *Buccinum* (The Whelk). L. M. B. C. Mem. 20, VIII + 115 p., 8 pls. London.
- Deshayes, G. P. 1859, A general review of the genus *Terebra* and a description of new species. Proc. Zool. Soc. v. 27, p. 270-321. London.
- Fretter, Vera 1941, The genital ducts of some British stenoglossan prosobranchs. Journ. mar. biol. assoc. Unit. Kingd. v. 25 (1), p. 173-211, 6 text-figs. Cambridge.
- 1946, The pedal sucker and anal gland of some British *Stenoglossa*. Proc. Malacol. Soc. v. 27 (3), p. 126-130, 2 text-figs. London.
- 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, 6 text-figs. Cambridge.
- Gerlach, Sebastian A. 1957, Die Nematodenfauna des Sandstrandes an der Küste von Mittelbrasilien. Mitteil. Zool. Mus. v. 33 (2), p. 411-459, 16 text-figs. 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 (Brasil).
- Graham, Alastair 1939, On the structure of the alimentary canal of style-bearing prosobranchs. Proc. Zool. Soc. ser. B, v. 109, p. 75-112, 10 text-figs. London.
- 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.
- Hartman, Olga 1951, The litoral marine annelids of the Gulf of Mexico. Publ. Inst. Mar. Sci. v. 2 (1), p. 7-124, 7 pls. Texas.
- 1956, Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. Bull. Amer. Mus. Nat. Hist. v. 109 (2), p. 239-310, pl. 21, New York.
- Hermitte, L. C. D. 1946, Venomous marine molluscs of the genus *Conus*. Tr. R. Soc. Trop. Med. & Hyg. v. 39 (6), p. 485-512, pls. 1-5. London.
- Hescheler, K. 1900, Mollusca. Arnold Lang, Lehrb. vergl. Anat. wirbelloser Thiere, 2. ed., v. 3 (1), VIII + 509 p., 410 text-figs. Jena (Gustav Fischer).
- Houssay, Frédéric 1884, Recherches sur l'opercule et les glandes du pied des Gastéropodes. Arch. Zool. expér. génér. sér. 2, v. 2, p. 171-288, pls. 7-14. Paris.
- Hulbert, G. C. E. B. & Yonge, C. M. 1937, A possible function of the osphradium in the Gastropoda. Nature v. 139 (3524), p. 840-841. London.
- Ibering, Hermann von 1897, A ilha de São Sebastião. Rev. Mus. Paul. v. 2, p. 129-171. São Paulo.
- Jehson, C. W. 1934, List of marine Mollusca of the Atlantic coast from Labrador to Texas. Proc. Bost. Soc. Nat. Hist. v. 40 (1), p. 1-204. Boston.
- Keen, A. Myra 1958, Sea Shells of Tropical West America. VIII + 626 p., 10 pls. University Press, Stanford, California.
- Kohn, Alan J. 1955, Studies on food and feeding of the cone shells, genus *Conus*. Ann. Rep. Americ. Malacol. Union, Bull. 22, p. 31. Buffalo, N. Y.
- 1956, Piscivorous gastropods of the genus *Conus*. Proc. Nat. Acad. Sci. v. 42 (3), p. 168-171, 7 figs. Washington, D. C.
- 1959, The ecology of *Conus* in Hawaii. Ecol. Monogr. v. 29, p. 47-90, 30 text-figs. Durham, N. C.
- Küttler, Arthur 1913, Die Anatomie von *Oliva peruviana* Lamarck. Zool. Jahrb. Suppl. v. 13 (Faun. Chil. v. 4), p. 477-544, 51 text-figs. Jena.
- Lamarck, Jean-Baptiste de 1822, Histoire naturelle des animaux sans vertèbres, éd. 1, v. 7. Paris.
- 1844, id., éd. 2, v. 10. Paris.
- Lange de Morretes, Frederico 1949, Ensaio de catálogo dos moluscos do Brasil. Arq. Mus. Paran. v. 7 (1), p. 5-216. Curitiba (Brazil).
- Linke, Otto 1933, Morphologie und Physiologie des Genitalapparates der Nordsee-litorinen. Wiss. Meeresunters. N. F., Abtlg. Helgoland, v. 19, Heft 2 (5), p. 1-60, pls. 1-8. Kiel & Leipzig.
- MacGinitie, G. E. & Nettie MacGinitie 1940, Natural history of marine animals. XII + 473, p., 282 figs. New York (McGraw-Hill Book Co.).
- Nettie 1959, Marine Mollusca of Point Barrow, Alaska. Proc. U. S. Nat. Mus. v. 109, p. 59-208, 27 pls. Washington, D. C.
- Marcus, Eveline & Ernesto Marcus 1959, Studies on Olividae. Bol. Fac. Fil. Univ., Zoologia n.º 22, p. 99-188, 11 pls. São Paulo.

- Miner, Roy Waldo 1950, Field book of seashore life. XV + 888 p., 251 pls. New York (G. P. Putnam's Sons).
- Morton, J. E. 1958a, Torsion and the adult snail, a re-evaluation. Proc. Malacol. Soc. v. 33 (1), p. 2-10, 4 text-figs. London.
- 1958b, Molluscs. 232 p., 23 figs. Hutchinson University Library, London.
- Oswald, A. 1893, Der Rüsselapparat der Prosobranchier. Jen. Ztschr. Naturw. v. 28, p. 119-162, 2 pls. Jena.
- 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.
- Perry, Louise M. & Schwengel, Jeanne S. 1955, Marine shells of the western coast of Florida. 318 p., 55 pls. Ithaca, N. Y. (Paleontol. Research Institution).
- Pruvot-Fol, Alice 1926, Le bulbe buccal et la symétrie des Mollusques I. La radula. Arch. Zool. expér. génér. v. 65, p. 209-343, pl. 4-7. Paris.
- Reeve, A. L. 1860, Monograph of the genus Terebra. Conchol. Icon. v. 12, 27 pls. London.
- Risbec, Jean 1928, Contribution à l'étude anatomique de quelques espèces de Mitres de la presqu'île de Nouméa. Bull. Mus. Hist. Nat. 1928, p. 105-112, pl. 1, 173-180, pl. 2, 225-227. Paris.
- 1932, Note sur la ponte et le développement de Mollusques Gastéropodes de Nouvelle-Calédonie. Bull. Soc. Zool. France, v. 57 (4), p. 358-374. Paris.
- 1953, Observations sur l'anatomie des Terebridae Néo-Calédoniens. Bull. Mus. Hist. Nat. sér. 2, v. 25 (6), p. 576-583, 14 text-figs. Paris.
- 1955, Considérations sur l'anatomie comparée et la classification des Gastéropodes Prosobranches. Jour. Conchyl. v. 95, p. 45-82, figs. 1-22. Paris.
- Shaw, H. O. N. 1914, On the anatomy of *Conus tulipa*, Linn., and *Conus textile* Linn. Quart. Jour. micr. Sci. n. ser. v. 60 (237), p. 1-60, 12 text-figs., pls. 1-6. London.
- Simroth, Heinrich 1896-1907, Gastropoda prosobranchia. Bronn, Kl. Ordn. v. 3, Abt. 2, VII + 1056 p., 63 pls. Leipzig (C. F. Winter).
- Smith, Edgar A. 1873, Remarks on a few species belonging to the family Terebridae, and descriptions of several new forms in the collection of the British Museum. Ann. Mag. Nat. Hist. ser. 4, v. 11, p. 262-271. London.
- 1877, Descriptions of some new species of Conidae and Terebridae. Ann. Mag. Nat. Hist. ser. 4, v. 19, p. 222-231. London.
- Stork, H. A. 1934, Beiträge zur Histologie und Morphologie des Osphradiums. Arch. Néerl. Zool. v. 1 (1-2), p. 71-99, 10 text-figs. Leiden.
- Thiele, Johannes 1931; 1935, Handbuch der systematischen Weichtierkunde, v. 1; 2, VI + V, 1154 pp., 897 text-figs. Jena (Gustav Fischer).
- Troschel, F. H. 1866, Das Gebiss der Schnecken zur Begründung einer natürlichen Classification untersucht. Vol. 2 (1), p. 1-48, pl. 1-4. Berlin (not seen).

- Verrill, Addison Emery 1873, Report upon the invertebrate animals of Vineyard Sound and adjacent waters, etc. Bull. U. S. Fish. Comm. 1871-72, p. 295-778, 38 pls. Washington, D. C.
- Wrigley, Arthur 1942, English Eocene *Hastula* with remarks on the coloration of the Terebridae. Proc. Malacol. Soc. v. 25 (1, 1941), p. 17-34, 30 text-figs. London.
- Yen, Teng-Chien 1935, Notes on protoconch and early conch stages of some marine gastropods of Japan. The Venus, v. 5 (5), p. 255-264, pl. 11. Kyoto.
- Yonge, C. M. 1942, Ciliary currents in the mantle cavity of the Atlantidae. Quart. Jour. micr. Sci. n. ser. v. 83, p. 197-203, 2 text-figs. London.
- 1947, The pallial organs in the aspidobranch Gastropoda and their 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 IN FIGS. 1-19

(Hastula cinerea Born)

aa — albumen gland	k — gill
am — amoebocyte	l — anterior liver duct
an — anal gland	m — outer mouth
ar — anus	me — testis
au — anterior tube	mo — pigment
av — afferent penial vessel	mr — mantle border
b — nerve collar	n — nerve
c — capsule gland	nv — penial spermiduct
ca — cartilage-like rod	oa — folds of pallial wall of stomach
co — connective tissue	oc — blood lacuna
cs — ciliate band	oi — folds of columellar wall of stomach
cz — columellar muscle	or — operculum
d — pallial spermiduct	os — posterior liver duct
e — oesophagus	ou — ovarian duct
ei — egg	ov — osphradium
eo — aperture of capsule gland	ow — osphradial ganglion
er — pericardium	p — proboscis
ev — efferent penial vessel	q — poison bulb
f — pharyngeal bulb	r — sphincter
g — gono-pericardial duct	re — renal spermiduct
h — kidney	ri — rhynchodaeum
i — intestine	rn — ingesting gland
ic — auricle	rs — radula-sac
im — inner mouth	rv — renal oviduct
iu — intestinal groove	
j — stomach	

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|---|---|
| s — retractor | 1a — propodial ganglia |
| sa — salivary gland | 2 — cerebral ganglia |
| sc — receptaculum seminis | 3 — pleural ganglia |
| sm — communication between
spermiduct and mantle
cavity | 4 — supra-intestinal ganglion |
| so — sutural fold | 5 — subintestinal ganglion |
| sr — sperm channel | 6 — buccal ganglia |
| su — testicular duct | 7 — right zygosis |
| t — tentacle | 8 — dialyneurous connection |
| u — bursa copulatrix | 9 — visceral ganglia |
| uc — buccal tube | 10 — pedal nerves |
| ur — osphradial furrows | 11 — penial nerve |
| uz — afferent renal vessel | 12 — static nerve |
| va — renal vascular axis | 13 — cephalic integumentary
nerve |
| ve — ventricle | 14 — labial nerves |
| vi — siphon | 15 — tentacular and optic nerve |
| vo — poison gland | 16 — proboscidean nerve |
| vr — penis | 17 — radular nerves |
| vv — nephridial gland | 18 — poison gland nerve |
| wi — salivary ducts | 19 — left anterior parietal nerve |
| wo — terminal pouch | 20 — columellar nerve |
| x — renal aperture | 21 — right anterior parietal
nerve |
| xa — ventral attachment of
anterior tube | 22 — siphonal nerve |
| xc — gland cells | 23 — columellar nerve |
| xi — hypobranchial gland | 24 — osphradial nerve |
| y — reno-pericardial duct | 25 — anterior branchial nerve |
| z — anal papilla | 26 — posterior branchial nerve |
| za — tooth | 27 — right posterior parietal
nerves |
| zn — villous part of kidney | 28 — right parieto-columellar
nerve |
| zo — egg-guide | |
| l — pedal ganglia | |

PLATES

PLATE 1

Hastula cinerea

- Fig. 1 — Tip of shell with protoconch.
- Fig. 2 — Anterior part of preserved snail extracted from shell and unrolled.
- Fig. 3 — Diagram of 4 pairs of osphradial filaments; on the left side, surface view; on the right side, cut in the middle.
- Fig. 4 — Transverse section of two osphradial filaments.

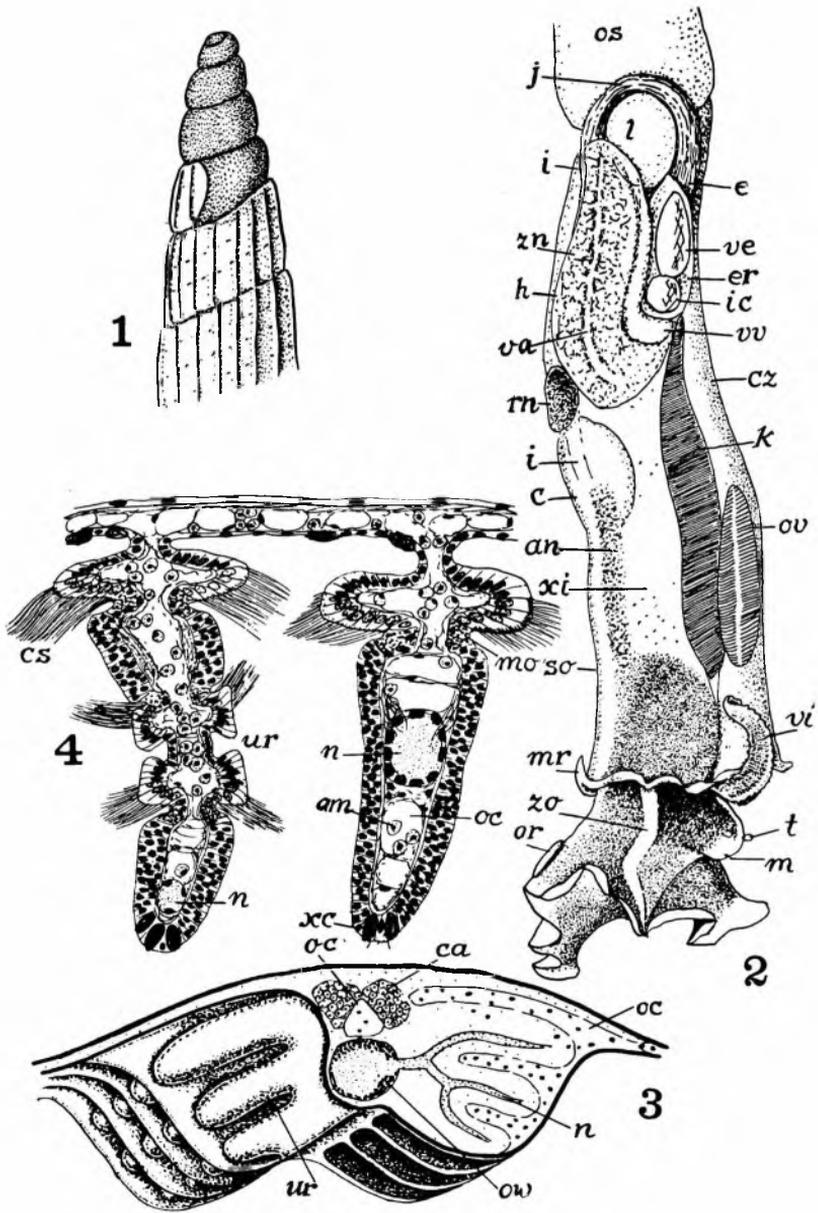


PLATE 2

Hastula cinerea

- Fig. 5 — Central nervous system.
Fig. 6 — Diagram of fore gut.
Fig. 7 — Section of tip of proboscis.
Fig. 8 — Radular tooth with ligament.

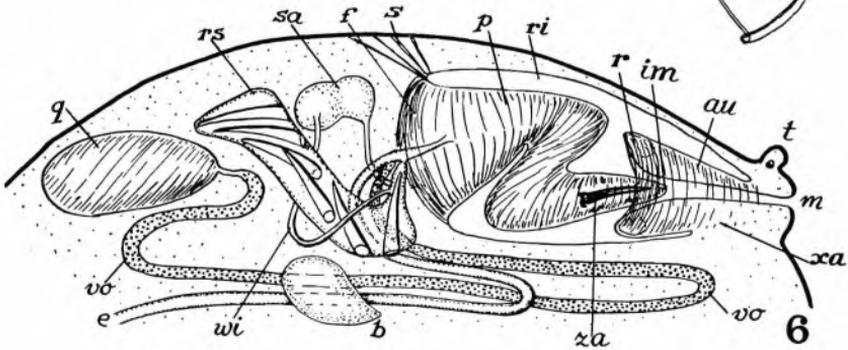
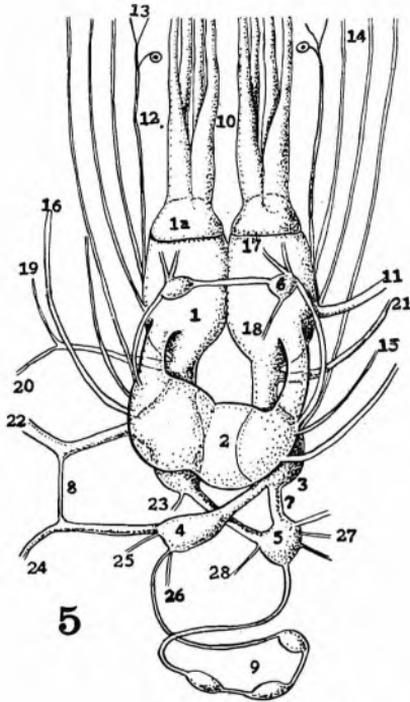


PLATE 3

Hastula cinerea

- Fig. 9 — Combined transverse section at level of salivary gland.
Fig. 10 — Section of bulb and beginning of poison gland.
Fig. 11 — Dorsal view of stomach.
Fig. 12 — Ventral view of stomach.

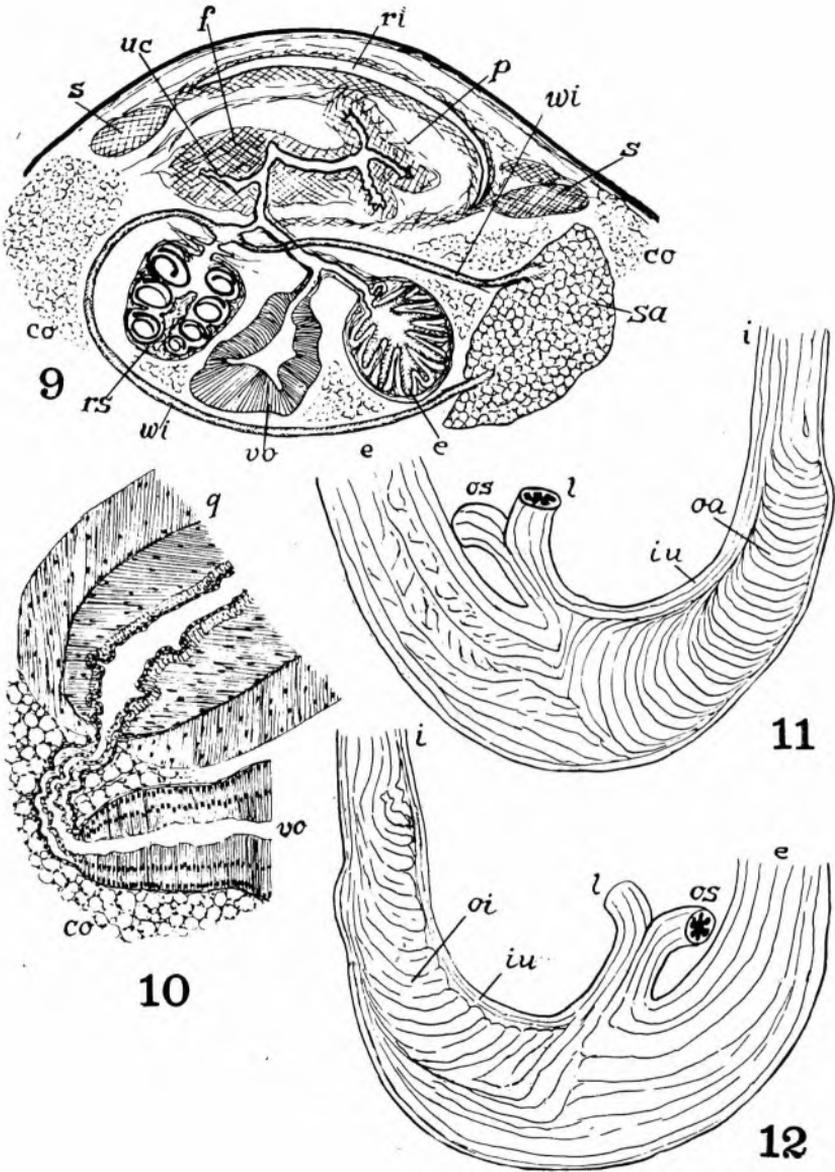


PLATE 4

Hastula cinerea

- Fig. 13 — Rectum and anal gland.
Fig. 14 — Diagram of male organs.
Fig. 15 — Transverse section of penis.

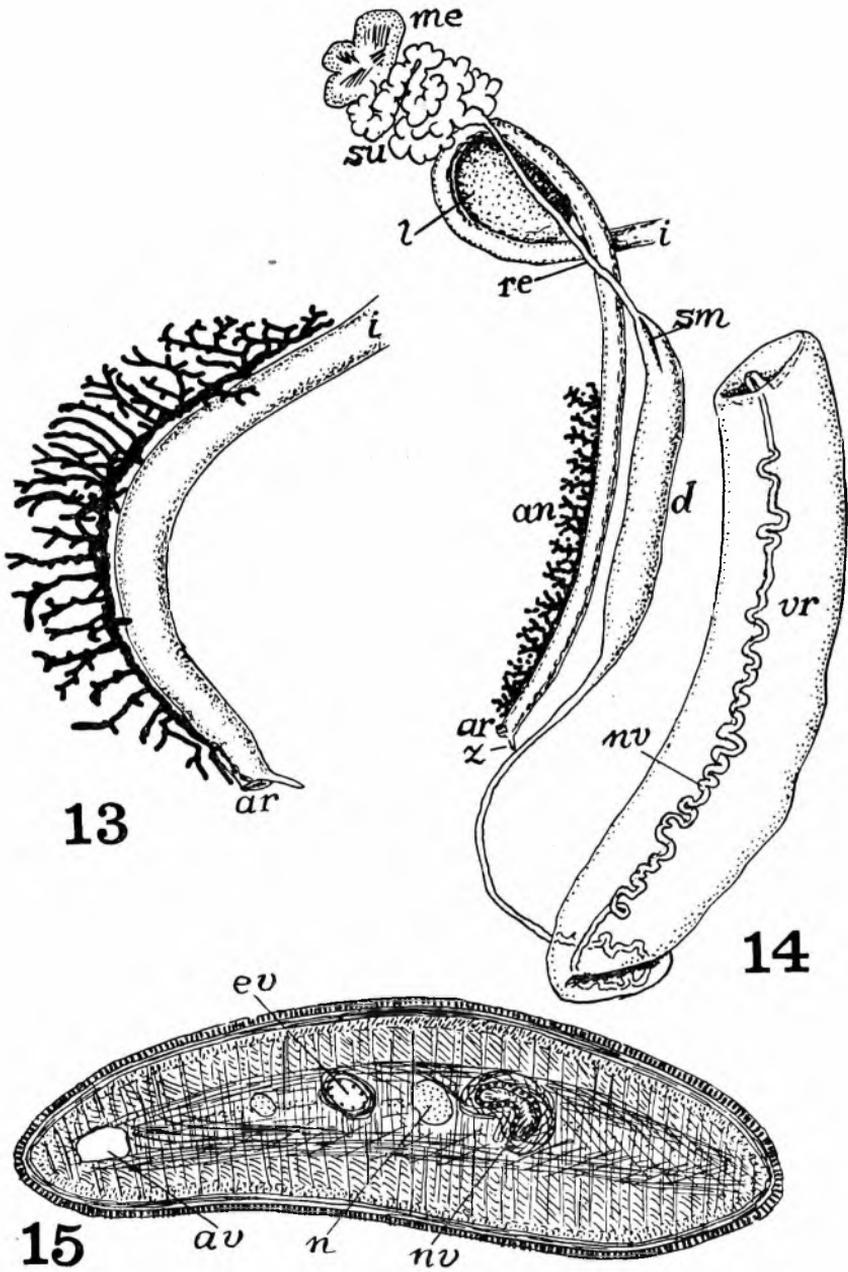
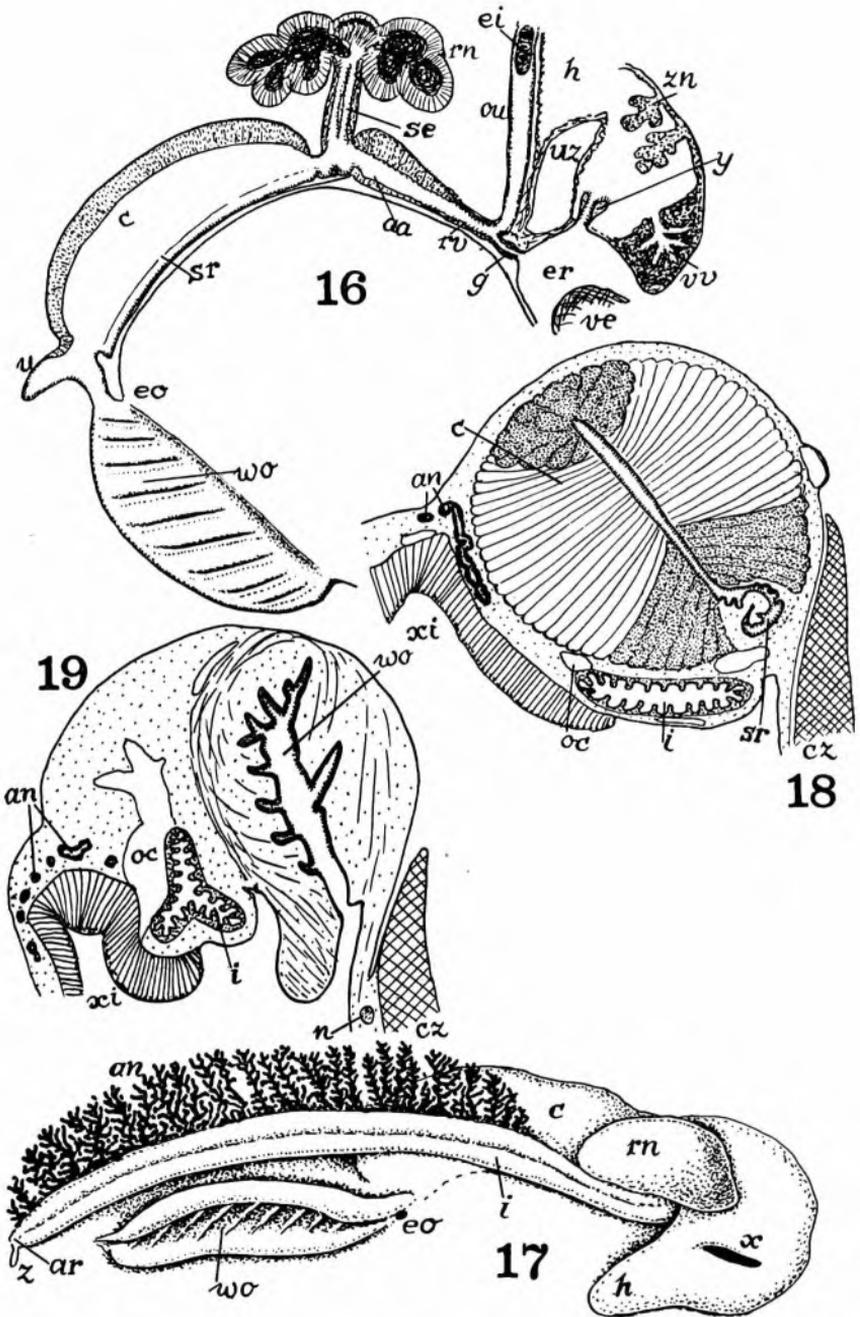


PLATE 5

Hastula cinerea

- Fig. 16 — Diagram of female organs.
Fig. 17 — Organs of right suture of mantle cavity of female.
Fig. 18 — Transverse section of capsule gland.
Fig. 19 — Transverse section of terminal pouch.



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