On Phyllaplysia engeli
by
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The type of *Phyllaplysia, Ph. lafonti* (P. FISCHER, 1870, p. 3—4) had been introduced with 40 specimens (id. 1872, p. 299). But FISCHER has found this rich material only once, and also the slugs of the other species of the genus have rarely been found (CUÉNOT, 1927, p. 259). ENGEL (1936, p. 210) says: "Ces animaux sont si rares et si mal connus que la connaissance du genre a forcément un caractère provisoire". *Phyllaplysia engeli* Marcus (1955, p. 105), however, is frequent among algae, *Padina* and others, which grow on stones in the upper littoral of the coast of S. Paulo, and so we can complete our first description.

The cutaneous villi are sometimes arborescent, and even the rhinophores may bear papillae. The anterior border of the foot is occasionally bilabiate. Also in these cases it is connected with the lateral margins of the body, so that the difference against *Petalifera* with free anterior border of the foot (ENGEL, 1936, p. 200; ENGEL & HUMMELINCK, 1936, p. 48) continues to be valid.

The dorsal integument of *Phyllaplysia engeli* contains only simple, unicellular glands. Their bodies (ni) are subepithelial, and the secretion of most of them is basophilous (mucous glands). They correspond to LEMCHE's mucous cells (1956, p. 25). Acidophilous, so-called serous glands, are rare as in *Cylichna* (ibid., p. 26). This type of glands, with the same proportion between blue and red ones, occurs on the whole body. Numerous such cyanophilous and few erythrophilous unicellular glands are also crowded (o) on the inner side of the right parapodium near its free border, where they are restricted to the anterior half. The sole contains unicellular, blue-staining glands of different sizes which are chiefly subepithelial. The supra-pedal gland and the anterior pedal gland, as described by EALES (1921, p. 22), are also developed in *Phyllaplysia engeli*. While the former consists of only few clusters,

the anterior pedal gland occupies a large area and discharges its secretion on a 0,6 mm long stripe of the sole in a 6 mm long slug. Posterior pedal glands were not seen.

The genital aperture (g) lies outside the dorsal slit (Fig. 2), in contrast to *Ph. lafonti* (ENGEL, 1936, p. 200). The distance measures 0,18—0,25 mm, and sometimes the opening is connected with the entrance of the slit by a minute superficial fold. EALES (1944, p. 9) verified the genital pore outside the slit in a species of *Petalifera* and just within the mantle cavity in her *Phyllaplysia plana* (p. 11). Therefore she used this difference in the diagnoses of the genera (p. 17). But the literature contains records of an inner genital orifice in *Petalifera,* e.g., by BERGH (1900, p. 182; 1902, p. 369) and VAYS-SIÈRE (1906, p. 64). On the other hand BABA's statement (1937, p. 216) shows that EALES' observation of a genital aperture in front of the dorsal slit in *Petalifera* is not isolated. The position of this opening must be eliminated from the characterization of *Petalifera* (PRUVOT-FOL, 1954, p. 104) and, as *Ph. engeli* proves, from that of *Phyllaplysia* too. On the other hand, the length of the intestine and the shape of the gonad are very different in the two genera.

The parapodial slit (Fig. 2) lies to the right of the mid line. Of the parapodial lobes which restrict the centre of the slit the right one is bigger than the left. The position of the slit on the right side and the symmetrical insertion of the parapodia on the sides of the body cause different extension of the parapodial cavity. On the left side it is much more profound than on the right (Fig. 12).

Dorsally the parapodial cavity extends between the left parapodium and the cover of the visceral hump from the left side to the middle. This cavity begins 0,6 mm in front of the anterior border of the parapodial slit. The pericardium appears to the right of the anterior part of the parapodial cavity and extends so far backwards that part of the ventricle and the entire auricle lie in the roof of the pallial cavity. The kidney (ki) is located behind the heart, its anterior part belongs to the bottom of the parapodial cavity, its middle and posterior part to the roof of the mantle cavity.

The mantle cavity (Fig. 12, pa) is limited by the shelf which originates from the supra-pallial portion of the mantle and accompanies the bottom of the parapodial cavity. The mantle cavity begins 0,3 mm in front of the anterior border of the slit in the ventral part of the body. Numerous, unicellular opaline glands (glands of Bohadsch, x) lie beneath the floor of the entire mantle cavity, into which they discharge by their apertures. The right border of the mantle (ma) is free in the area of the slit, so that the pallial and the parapodial cavities communicate. In front the right border of the
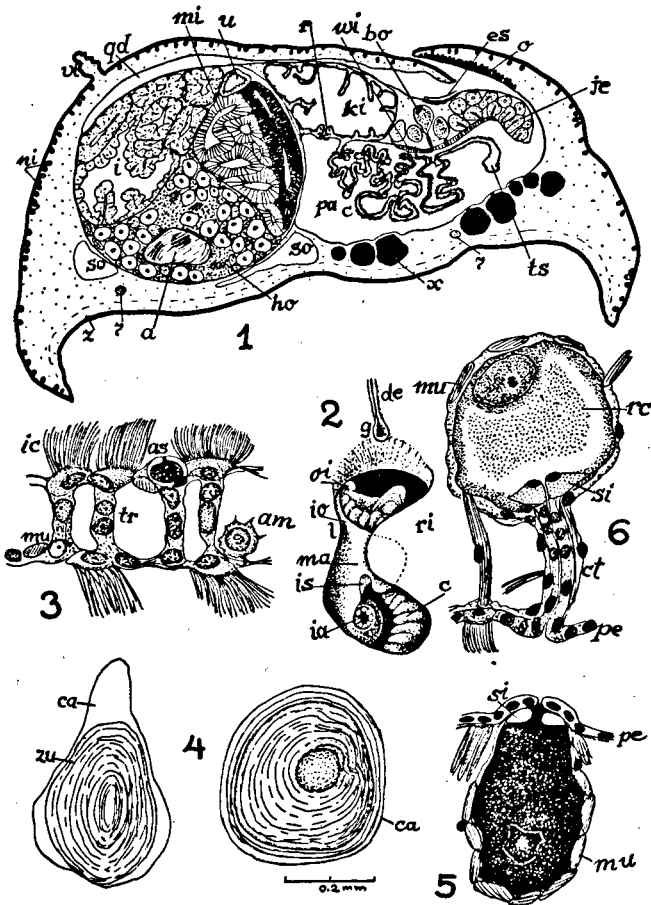
Fig. 1. Transverse section at level of renal pore. Fig. 2. Parapodial slit.
Fig. 3. Part of section through gill. Fig. 4. Secondary shells of 7 and 8 mm
long slugs. Fig. 5. Opaline gland cell. Fig. 6. Blochmann's gland cell from
roof of pallial cavity. For explanation of the abbreviations, see p. 64.

mantle is coalescent (io) with the left parapodium (1). At the
anterior border of the pallial cavity lies the osphradium (oi). The
ctenidium (c) appears almost at the anterior border of the slit; it is
entirely enclosed within the pallial cavity also in the living slugs. The
posterior border of the mantle forms a small cloacal fold (is), homo-
logous to the cloacal sipho of *Aplysia*. Behind it the rectum, which

ends with a rosette-shaped anus (ia), projects into the posterior opening of the slit. The pallial cavity extends a little backwards beyond the anus with opaline glands in its floor. Also the narrow parapodial cavity (qd) covers the hermaphrodite gland in this posterior region, it extends farther backwards than the pallial cavity.

The smallest preserved slug of our collection was 2 mm long alive, 1,5 mm preserved. It has a distinct shell-chamber in the roof of the mantle. This chamber is about 0,4 mm in diameter, its aperture approximately 0,27 mm. Its epithelium is glandular in the centre of the floor. In adult animals the fold that is the roof of the chamber is reduced without vestiges, but the epithelium of the former bottom is high. It is covered with cuticular scales (es) which stained with eosine in one of the sectioned specimens. In another there is a colourless membrane overlying the high epithelium. In a third, pre-served 5 mm long, mature slug the centre of the mantle is slightly deepened, and this concavity is covered with a cuticle incrusted with particles of detritus. Several slugs preserved in alcohol were dissected to find the shell in the total specimens. While a little plate (Fig. 4) was immediately freed in two big specimens (7 and 8 mm), there was no trace of it in two young ones (3 and 4 mm). In a 6 mm slug the roof of the mantle showed a vestige of a circular fold. Hence this shell is secondary. The plates measured 0,5 $\times$ 0,33 mm and 0,42 $\times$ 0,37 mm respectively. The larger one was decalcified, and a fine cuticula (zu), bigger than the calcareous centre (ca), was ob-tained. Structures in retrograde development, as are the shells of the Anaspidea, are known to vary very much concerning their degree of involution. PRUVOT-FOL (1954, p. 106) found a typical, primary shell with spire in a some millimeters long young specimen of *Ph. lafonti* (f. 29 d).

The ctenidium (c) is of the plicate type, and in transverse sections of the slug the aspect of the gill is similar to that in *Scaphander lignarius* (L.) (PERRIER & FISCHER, 1911, p. 82 text-fig. N; HOFF-MANN, 1940, f. 5 B), where the folding of the lamina is complicated by secondary and even tertiary folds. The ridges of the branchia of our species are somewhat dilated towards the ventral side. The broad base of the gill lies to the left under the kidney, deep in the pallial cavity, and the branchia curves to the right and backwards, where it ends with a free point. The branchial cells (Fig. 3) are more or less cubical, and many of them are ciliated (ic). Blue-staining mucous glands (as) lie between them, specially on the outer surface. The trabeculae (tr) between the epithelial sheets consist of contractile fibres with nuclei (FÖRSTER, 1934, f. 35); their length is very variable due to the different phases of contraction in the preserved animals.

Blood fluid with amoebocytes (am) circulates between the trabeculae. The afferent branchial sinus (ts) on the outer border of the ctenidium has an epithelium with many glands, underlaid by tubuliform muscle fibres. Also the finer branches of the sinus in the secondary folds have numerous muscle fibres, which are scarce in the surface of the gill.

The topography of the heart was described above. The auricle is thin-walled, the ventricle muscular. The arterial trunk shows the same elements that are known from *Aplysia*, but the disposition is not the same. The genital artery springs from the trunk at the root of the anterior aorta, quite near the ventricle on the right side and runs straight backwards. The posterior or abdominal aorta goes to the left side at the level of the trunk and curves backwards at a certain distance from the ventricle. The anterior aorta and the gastro-oeso-phageal artery spring from the trunk with nearly parallel roots, the latter in front of the former. The pericardial gland-cells which form the so-called crista aortae occupy the trunk between the origins of the one left and the three right vessels.

The pallial cavity is lined with a quite low epithelium which bears many tufts of cilia. Beneath the epithelium large blue-staining glands (x) are distributed over the whole bottom of the cavity. In spite of their diffuse distribution they must be homologized with the opaline glands (gland of Bohadsch) in the other Anaspidea. They are sur-rounded by connective tissue and muscles (Fig. 5, mu), and their apical sphincter (si) lies directly beneath the epithelium of the cavity (pe), generally in a small papilla. Young gland cells (Fig. 8, cy) are numerous in the connective tissue under the bottom of the pallial cavity.

Glands of a different type (Fig. 6) lie frequently between the opaline glands. They are typical Blochmann's glands (HOFFMANN, 1934, p. 422) with a multicellular duct. They are not restricted to the bottom of the pallial cavity, but occur also on its sides and on the roof, in the region of the kidney, and even farther to the right. Their secretion (rc) is yellowish, nearly colourless, or they are empty. There is a considerable layer of connective tissue nuclei (ct) around the epithelium of the duct in many of them. The gland-cells of Blochmann (bo) in the roof of the pallial cavity correspond to the purple gland of *Aplysia* and the glands of Blochmann in *Cylichna* (LEMCHE, 1956, p. 31).

To the right of the kidney occurs a third type of pallial glands (wi), similar to the "acidophil goblet cells" of *Cylichna* (ibid., p. 27). The area formed by these is here and there pierced by the ducts of the Blochmann's glands. The third glands are cylindrical, intra-epithe-

lial cells (Fig. 9, ao) with basophil secretion, between which the epithelium of the pallial cavity is transformed into high slender supporting cells (uc). The big nuclei of the cylindrical glands are basilar, those of the supporting cells apical. Evidently these glands are homologous to the hypobranchial gland of *Acteon tornatilis* (L.) (PERRIER & FISCHER, 1911, t. 5—6 f. 9; HOFFMANN, 1934, f. 322 B), though the literature (ibid., p. 436, 476—77) does not mention this gland in Anaspidea. Where the right mantle border coalesces with the left parapodium, the hypobranchial glandular epithelium passes a little on to the latter.

Next to the free border of the mantle lie acidophil glands of a fourth type (je). These are crypt-shaped multicellular glands with pink-staining secretory cells, paler supporting cells, and a fine cover of connective tissue (Fig. 10). These densely packed clusters of mantle-border glands ("Mantelranddrüsen") extend from the level of the renal pore (Fig. 1, r) backwards to the rectum. They are homologous to the glands which BLOCHMANN (1883, p. 413—14 t. 22 f. 4—5; HOFFMANN, 1934, p. 492) discovered in *Dolabrifera dolabrifera* (Rang, 1828). In our young slugs they are not developed yet, while numerous opaline glands already exist.

The central nervous system (Fig. 11) agrees with the orthoneural type of the Aplysiidae Dolabriferinae, whose visceral loop is short. It tends to the gastroneural type (HOFFMANN, 1936, f. 583 D), but differs from this by the equal shortness of the cerebro-pleural and pleuro-pedal connectives. In the typical gastroneural system of *Notarchus* (GUIART, 1901, p. 120) the cerebro-pleural connectives are much longer than the pleuro-pedal ones. The biggest ganglia are the pedal ganglia (d). The next in size are the cerebral ganglia (kc), which are considerably bigger than each of the "visceral" ganglia. The latter together do not quite attain the volume of the cerebral ganglia. The cephalization (WIRZ, 1952, p. 164) reaches a high degree, the cerebralization (ibid.) a moderate one. With exception of the cerebral ganglia all are ventral, but also the cerebro-pedal connectives are short. The biggest cells with a diameter of 0,1 mm lie, as usual, in the "visceral" ganglia, viz. in the left pleural (p) and in the supraintestinal ganglion (s).

The cerebral ganglia (kc) are united by a short commissure, which is more distinct than in MAZZARELLI's figure (1901, p. 435 f. 1; HOFFMANN, 1936, f. 512 B) of *Ph. lafonti*. The six cerebral nerves spring from the antero-lateral portion of the cerebral ganglia close together. The innermost nerve (em) supplies the skin of the head and sends a branch (tu) to the oral lobes. The two next nerves have a common origin; the inner (m) ramifies and innervates the buccal,
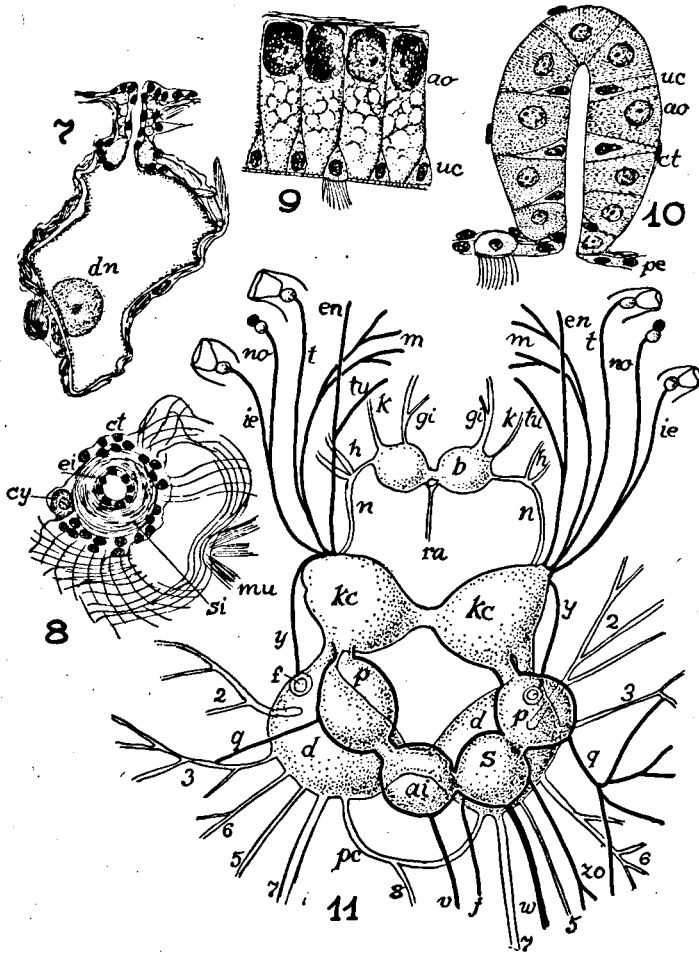
Fig. 7. Empty Blochmann's gland cell from floor of pallial cavity. Fig. 8. Tangential section of sphincter of empty Blochmann's gland cell. Fig. 9. Section of hypobranchial gland. Fig. 10. Multicellular gland of mantle border. Fig. 11. Central nervous system. For explanation of the abbreviations, see p. 64.

on the right side also the penial region. The outer (t) runs straight to the tentacular ganglion. This lies at the base of the tentacle-slit; the borders of the slit are lined with sensory cells, which also occur on the medial sides of the oral lobes and around the folds of the rhinophores. The following optic nerve (no) is thin and closely attached

to the rhinophoral nerve (ie). Each of these nerves ends with a gang-
lion; that of the rhinophore at the base of the fold is voluminous.
The slender static nerve (y) arises from the base of the rhinophoral
nerve.

The left pleural ganglion (p) is bigger than the right one. This
indicates that it contains the subintestinal ganglion. Also the con-
nective between the left pleural and the following ganglion (ai) is
longer than those between the other ganglia of the visceral loop,
which are contiguous. The space between the left pleural and the
following "visceral" ganglion is of variable length, though in all
dissected slugs it is shorter than in MAZZARELLI's figure (1901, p.
435 f. 1). Each pleural ganglion emits one richly ramified nerve (q).
One of its branches anastomoses with one of the pedal nerves (3),
as PELSENEER (1894, p. 27) observed in *Petalifera petalifera* (Rang,
1828). From the supra-intestinal ganglion (s) arise three nerves. The
vulvar nerve (zo) supplies the common genital opening. The branchial
or osphradial nerve (w) runs to the osphradial ganglion and gives
off branches to the heart and the ctenidium. The third nerve which
goes out from the supra-intestinal ganglion is probably a spermathecal
nerve (j) which corresponds to nerve s4 (a5) of HOFFMANN's table
(1936, p. 709). A strong viscero-genital nerve (v) springs from the
abdominal ganglion (ai). External vestiges of parietal ganglia are not
developed.

The parapedal commissure (pc) is longer than the pedal commis-
sure. The pedal nerves in our Figure 11 were numbered after HOFF-
MANN's explanation (1936, f. 510 B; text p. 526—27) of VAYSSIÈRE's
drawing of *Petalifera gravieri* (1906, t. 4 f. 65). We did not find the
small nerves 1 and 4. The strongest of the pedal nerves is the posterior
pedal nerve (7), as in *Petalifera*. The next in size is the parapodial
nerve (5).

The buccal or stomato-gastric ganglia (b) lay obliquely over the
buccal mass in several cases. The buccal commissure may be a little
longer or a little shorter than in our Figure 11. As in *Dolabella*
(HOFFMANN, 1936, p. 721) the ventro-lateral pharyngeal nerve (h)
springs from the cerebro-buccal connective (n) and bifurcates. The
two roots of the radular nerve (ra) lie near the buccal commissure.
Two further nerves arise from either buccal ganglion. The strong,
bifurcate inner nerve (gi) corresponds to the salivary-oesophageal-
gastric nerve of *Aplysia* and *Dolabella*, the smaller outer one (k) to
the dorsal pharyngeal nerve.

The gut (Fig. 12) is similar to that of *Aplysia* (EALES, 1921, p. 24)
with exception of the much longer intestine. The mouth of *Phylla-
plysia engeli* is a longitudinal slit. HOFFMANN (1938, p. 884) was

evidently right, when he considered the broad mouth of *Ph. lafonti* in ENGEL's figure (1936, f. 1 b) as an effect of muscle contraction in the moment of preservation. Jaws and radula were described previously (MARCUS, 1955, p. 106). The radula-cushion contains muscles, vesicular cells and between the latter a blue-staining ground-substance similar to that occurring beneath the epithelium of the thin spines of the gizzard and the gastric valves (Fig. 14). The ducts of the salivary glands (sw) open into the cavity of the buccal mass (bu) at the same level on both sides. Behind the nerve ring, however, the left gland lies above, the right under the oesophagus (e). The cavity of the pharyngeal bulb passes to the short oesophagus that dilates into the spacious crop (cr).

Like *Bulla* and *Aplysia*, but contrary to *Philine* (FÖRSTER, 1934, p. 16—17), our youngest *Phyllaplysia* already have big, pyramidal teeth in the gizzard. Fig. 13 shows that the broad tooth of the anterior gizzard of *Ph. engeli* originates as a whole, not by coalescence of thin spines. Our section of a gizzard tooth from a 2 mm long slug is very similar to LEMCHE's figure 153 (1956, t. 15). In older slugs the number of cells at the base of the teeth increases and widens their sockets. The musculature of the anterior gizzard (za) is very much thicker than that of the posterior gizzard (xi). The latter contains about 40 irregularly scattered papillae with long, slender spines (Fig. 14). These are specially numerous in the anterior part, and their size diminishes backwards. A cushion of blue-staining, rather consistent ground-substance, which contains some stellate connective tissue-cells, lies beneath the formative epithelium of the spine. The same type of matrix occurs under the high epithelium of the two gastric valves (av) at the end of the posterior gizzard.

As in many Opisthobranchs (FRETTER & GRAHAM, 1954, p. 572) cardia and pylorus are near one another in *Ph. engeli*. A straight glandular caecum (cn) evidently not developed in all species of the genus (EALES, 1944, p. 11), extends from the entrance of the stomach slanting to the left. The stomach (sy) has a richly folded ciliated epithelium. Stomach and intestine (u) contain diatoms. These were seen in great numbers in the young slugs, but are also present in full grown animals. *Ph. lafonti* feeds on *Zostera* and algae (P. FISCHER, 1870, p. 6—7; 1872, p. 300). The intestine is relatively longer than that of *Aplysia* and very much longer than that of *Petalifera gravieri* (VAYSSIÈRE, 1906, p. 60 t. 4 f. 61). It is first directed backwards, curves around the stomach and runs forward beyond the level of the valves, then bends backwards again and turns once more even farther forward, finally stretching backwards a little beyond the level of the posterior border of the parapodial slit. During all this course the

intestine runs on the surface of the liver-mass (i); then the rectum leaves the liver, passes to the right along the hinder margin of the mantle, and ends with the stellate anus (ia). The loops of the intestine were found rather constant in ten slugs.

The ovotestis (Fig. 15, ho) consists of about a dozen follicles. A lobate hermaphrodite gland occurs also in *Dolabrifera dolabrifera* (BERGH, 1902, p. 363: *Aplysiella pallida*; synonymy ENGEL & HUMMELINCK, 1936, p. 41), while that of *Aplysia* (EALES, 1921, t. 6 f. 20) and *Petalifera* (VAYSSIÈRE, 1906, t. 4 f. 62) is compact. The hermaphrodite duct (zi) opens into a short and wide ampulla (a) followed by an inconspicuous fertilization chamber (ce). The duct of the spacious spermatocyst (se) enters the spermoviduct (ut) ectally to the fertilization chamber. While the sperms are parallel and undulated within the ampulla, the alien spermatozoa are heaped without any order in the spermatocyst. The spermoviduct contains a ciliated seminal groove and an equally ciliated, glandular oviduct. The voluminous acidophil albumen (wa) and basophil mucus gland (mi) communicate with the spermoviduct by several connections.

Aplysia has a glandular appendage, called bursa seminalis by EALES, at the entrance of the spermathecal duct into the spermoviduct, which does not exist in *Ph. engeli*. On the other hand, a pink-staining, folded gland (ae) joins the strongly muscular outer part of the so-called "large hermaphrodite duct" or vagina (or uterus), perhaps better atrium (iv). Such a gland also exists in *Petalifera gravieri* (VAYSSIÈRE, 1906, p. 64 t. 4 f. 62, p), where it is called "glande prostatique" in the explanation of the figure (p. 90). The numerous diverticles of the atrial gland of the present species communicate with the atrium by a single ciliated duct (Fig. 16).

The collar of the penis bears only few spines; the number of the penial spines varies. Previously we had observed 7 spines (MARCUS, 1955, p. 56), now we found once 8, onze 13 spines.
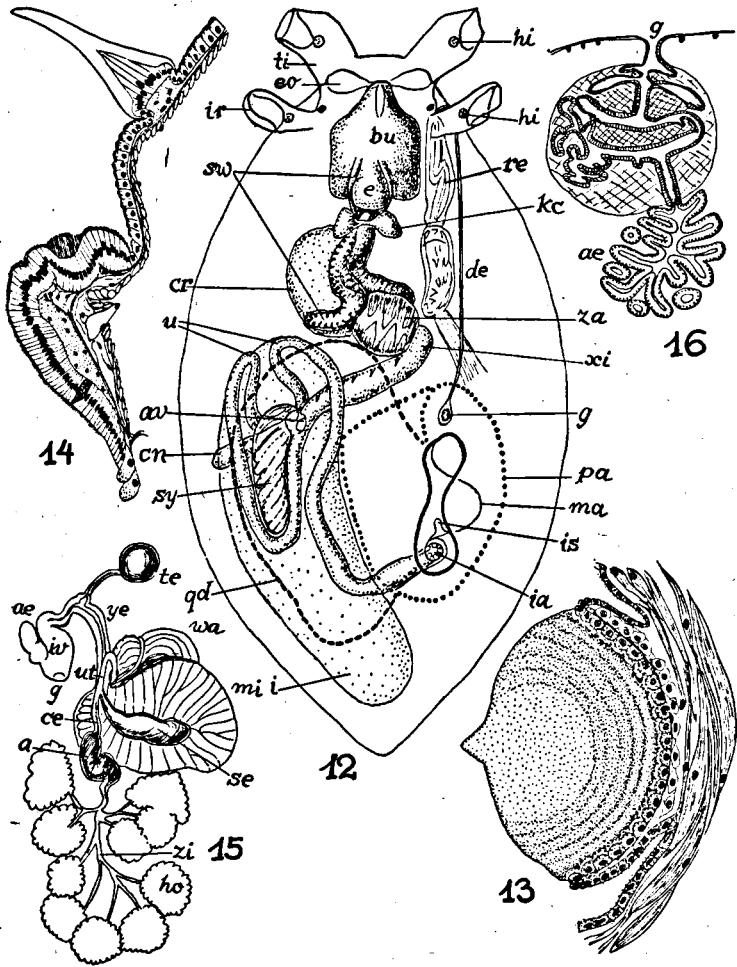
Fig. 12. Diagram of alimentary canal. Fig. 13. Section of gizzard tooth from 2 mm long slug. Fig. 14. Section of triturating stomach with spine and valve. Fig. 15. Ventral aspect of generative organs. Fig. 16. Section of gonoduct near opening. For explanation of the abbreviations, see p. 64.

ABBREVIATIONS USED IN THE FIGURES

a: ampulla; ae: atrial gland; ai: abdominal ganglion; am: amoebocyte; ao: gland cell; as: mucous gland cell; av: valves of stomach; b: buccal ganglion; bo: gland cells of Blochmann; bu: buccal mass; c: ctenidium; ca: calcareous part of shell; ce: fertilization chamber;. cn: caecum; cr: crop; ct: connective tissue; cy: young gland cell; d: pedal ganglion; de: seminal furrow; dn: degenerated nucleus; e: oesophagus; ei: epithelium of glandular duct; en: nerve to head skin; eo: oral lobes; es: secondary shell; f: statocyst; g: common genital opening; gi: salivary-oesophageal-gastric nerve; h: ventro-lateral pharyngeal nerve; hi: tentacular and rhinophoral ganglion; ho: ovotestis; i: liver; ia: anus; ic: ciliated cell; ie: rhinophoral nerve; io: concrescence of mantle with left parapodium; ir: rhinophore; is: cloacal fold; iv: atrium; j: spermathecal nerve; je: glands of mantle border; k: dorsal pharyngeal nerve; kc: cerebral ganglia; ki: kidney; l: left parapodium; m: nerve of buccal and penial region; ma: mantle; mi: ·mucus gland; mu: muscle fibre; n: cerebrobuccal connective; ni: cutaneous mucous and serous glands; no: optic nerve; o: gland on inner side of right parapodium; oi: osphradium; p: pleural ganglion; pa: pallial cavity; pc: parapodial commissure; pe: epithelium of pallial cavity; q: pleural nerve; qd: parapodial cavity; r: renal pore; ra: radular nerve; rc: colourless secretion; re: penis; ri: right parapodium; s: supraintestinal ganglion; se: spermatocyst; si: sphincter; so: blood sinus; sw: salivary gland; sy: stomach; t: tentacle nerve; te: spermatheca; ti: tentacles; tr: trabecula; ts: afferent branchial sinus; tu: nerve to oral lobes; u: intestine; uc: supporting cell; ut: spermoviduct; v: viscero-genital nerve; vi: cutaneous villus; w: branchial and osphradial nerve; wa: albumen gland; wi: hypobranchial gland; x: opaline gland; xi: posterior gizzard; y: static nerve; ye: large hermaphrodite duct (EALES); z: sole; za: anterior gizzard; zi: little hermaphrodite duct (EALES); zo: nerve to genital opening; zu: cuticular part of shell.

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