GROSS ANATOMY OF THE SPECIMENS OF THE SHELLED SACOGLOSSAN *VOLVATELLA* (=*ARTHESSA*) COLLECTED FROM OKINO-ERABU ISLAND, SOUTHERN KYUSHU, JAPAN (NUDIBRANCHIA)

KIKUTARÔ BABA

Biological Institute, Osaka Gakugei University

With Plates VII–X

This paper was formed as a summary of my observation on two preserved specimens of a shelled sacoglossan presented to me by the courtesy of Prince HITACHI of the Emperor's Family who has collected them from Okino-erabu Island, Southern Kyushu, during his visit to that Island in July, 1961.

With the provisional identification of the specimens to *Arthessa* EVANS, 1950, a work has been commenced in order to demonstrate the various features of this genus by figures of dissection. During the course of this procedure *Volvatella* PEASE, 1860 has also been taken into careful consideration, and finally I was inclined to have doubts about the separation of the two genera in the classification of the shelled sacoglossans. At about the close of this study I was told from my friend, Dr. J.J. GONOR (Marine Science Laboratory, Oregon State University) of his finding of live specimens of *Arthessa* at Fiji in May, 1965, from *Caulerpa*. Then there occurred an interchange of informations between us, and as a consequence both of us agreed in taking *Arthessa* as a complete synonym for *Volvatella*. For my part I gained especial benefit from him, and thus I was allowed to identify exactly the paired structures on the contracted head of my specimens.

I acknowledge here my deepest obligations to Prince HITACHI of Japan and Dr. GONOR of the Oregon State University for their generosities extended to me.

Anatomical Accounts

Material: Two specimens (Sp. A and Sp. B) collected by Prince HITACHI from Okino-erabu Island of the Amami Group, Southern Kyushu, Japan, on July 12, 1961.

The specimens were handed to me in a good state of preservation each. As preserved, the soft part showed a general colour of grayish white. No data of the animals in life were taken. The shell-length measured was about 14 mm in Sp. A and 10 mm

in Sp. B. After an inspection from without, the Sp. A was prepared in serial horizontal sections for internal morphology, and the Sp. B was opened in order to detect the pharynx, radula and penial organ.

External Morphology: Presumably it is not easy to find out a specific peculiarity from such a thin and elastic shell as that of *Volvatella* (PEASE, 1868, p. 73; see also the statement by MARCUS & MARCUS, 1956, on p. 119). On the present material of shells the periostracum which extends beyond the underlying calcareous layer is ashy yellow with fine growth lines of dark brown. The calcareous layer itself is thin, fragile and whitish. The involuted spire is entirely hidden by the swollen body whorl. A protoconch could not be detected from outside at the apex of the spire.

On the head of the animals there are paired oral tentacles and paired rhinophores[1]. The rhinophores are seemingly simple, without an outer groove, and relatively smaller in size than the oral tentacles. At the rear of each of the rhinophores the lateral margin of the head forms a ridge on the under side of which are seen a row of about 5 folds. This part of foldings, though weak in development, corresponds to the HANCOCK's organ. The presence in *Volvatella* of the HANCOCK's organ was already noticed by EVANS, 1950 (p. 105). A thick concentration of ganglionic cells occurs in the entire length of the lateral ridge. Below the ridge there is a deep furrow which extends forward to near the tip of the oral tentacle on its outer side. The male orifice is situated close to the posterior end of the furrow. The female genital papilla consisting of a female orifice and a vaginal pore is located far back at the right anterior corner of the visceral sac. The external oviducal groove which was noted by me (BABA, 1961, p. 42) in *Berthelinia* arises in *Volvatella* from a point immediately in front of the genital papilla, and passes below the male orifice up to the outer base of the right oral tentacle. The paired eyes, kept apart from one another, are situated behind the rhinophores. They lie deep in the integument, and are not visible from the surface. The foot is sub-triangular, widest in front, and narrowed behind to form a short tail. The sole is flat and presumably adapted for creeping.

The visceral sac, contained in the hollow of the shell, is asymmetrical in construction. The dorsal mantle arising from the left side of the visceral sac is destined to overhang it. On the right side the mantle-margin is freed so as to open the mantle cavity to the exterior. A gill characteristic of the primitive sacoglossans is on the under side of the dorsal mantle. The heart lies to the right of the median line, and linked posteriorly with the gill. The gill is also accompanied by an unpaired osphradium. On histological examination the tissue of kindey is found within the mantle just above the belt of the gill-folds (cf. kidney of *Cylindrobulla*, MARCUS & MARCUS, 1956, p. 121). And the remaining part of the mantle is almost everywhere packed with branching diverticula of the liver. Ciliated ridges were not detected in *Volvatella*.

1) The exact position of these cephalic structures was shown to me by GONOR on the basis of his observation on a live *Volvatella*. He informed me that there was no formation of a shield on the head of the animal.

The hypobranchial gland is diffuse as in *Berthelinia* (BABA, 1961, p. 43): the eosinophile gland cells are distributed on the posterior wall of the visceral sac as well as on the inner surface of the siphonal region of the mantle.

Internal Morphology: EVANS (1950, p. 105) mentioned correctly of the sacoglossan composition of the buccal apparatus in *Volvatella*. The pharyngeal bulb seen from above is barrel-shaped with an ascus on the ventral side. Posteriorly it is accompanied by a large muscular crop, spherical in shape. Serial horizontal sections of the crop show that this latter organ has paired lumina which pass forth into the common lumen of the pharyngeal bulb. The radula consists of a single row of articulating teeth, about 11 in the ascending series and 15 in the descending one. Each tooth is blade-like with a hooked apex and a series of about 20 pointed denticles[1] on either side of the blade. The salivary glands are long band-like and appear to open into the pharyngeal bulb at its junction with the oesophagus. The proximal portion of the oesophagus forms a straight tube which is coated with a rather thick circular muscle layer similar to that of the pharynx. Then follows a long and dilatable oesophagus with a ciliated lumen. There is no formation of an oesophageal diverticulum. The stomach is embedded in the visceral sac. The rectum is short, bearing strong cilia on the plicated epithelium. It rises up to the anus which lies on the back of the visceral sac at about the mid-length and slightly to the right of the median line. The main mass of the liver shows itself on the posterior half of the visceral sac, but actually it is more extensive, the branching diverticula passing into the dorsal mantle as the fact was cited elsewhere.

In *Volvatella* the head and neck are separated from the visceral sac by a thin diaphragmatic membrane consisting of muscle fibres. Immediately in front of this diaphragm there occurs a single adductor which is not strictly horizontal (cf. horizontal adductor in *Berthelinia*, BABA, 1961, p. 44) but runs more or less diagonally (cf. diagonal adductor in *Cylindrobulla*, MARCUS & MARCUS, 1956, p. 121). That is, the right insertion of the adductor to the shell is higher and more in advance than the left-sided insertion. The right and left foot retractors are so named after the cases in *Berthelinia* (BABA, 1961, p. 45); they are not strictly paired in situation. The posterior foot retractor (=columellar muscle) arising from above the root of the tail passes back through the visceral sac to about the involuted spire of the shell.

It seems necessary to make here a practical analysis of the streptoneury assigned by EVANS (1950, p. 105) to the nervous system of *Volvatella*. In so far as I am concerned, the nerve ring consisting of paired cerebro-pleural and paired pedal ganglia is found at about the half way of the length of the dilatable oesophagus. The visceral loop, though seemingly shortened in the contracted animal, is still distinct and triganglionated: The infra-intestinal ganglion is smaller than the supra-intestinal, and stands rather close to the nerve ring, and the visceral ganglion occurs as usual within the visceral sac. A small genital ganglion is formed in the course of the genital nerve.

1) Thanks to the information by Dr. GONOR I was able to confirm the exact shape of each of the denticles on my radula preparation.

The osphradial nerve is derived from the supra-intestinal and terminates in a small osphradial ganglion. Though there exist some small differences between the two, the streptoneurous nervous system of *Volvatella* does not differ materially from that in *Berthelinia* (cf. BABA, 1961, pp. 45–46).

As in the case of *Berthelinia* the genital system in *Volvatella* is especially characterized by the formation of an internal vas deferens leading into the penis and an external oviducal groove on which mention was made before. The penis in its proximal half is swollen in the middle and so as to say spindle-shaped with storage of sperms within the lumen; distally it passes into a looping, narrowed canal. In the animal of *Volvatella* there is found an armature of tubiform stylet at the apex of the penis. The stylet is fairly long, curved and almost colourless. The entire length of the penis lies within a sheath. The exact composition of the gonad could not be made out, but it appeared to me to be probable that the testis forms an ill-defined central mass which is covered by a considerable number of ovaries. The majority of these gonadial follicles are embedded in the liver-mass. The hermaphrodite duct has a mazy lumen. Distally it forms a roomy vesicle into which opens the bean-shaped ampulla. The proximal portion of the vas deferens is thick and makes up a marked structure of prostate gland. After leaving the prostate the narrowed vas deferens passes forwards to serve as an internal pathway of sperms. It was hardly possible to analyse the oviduct precisely; this latter proceeds ultimately to the female orifice. The accessory genital mass formed of an albumen and a mucous gland occupies the anterior half of the visceral sac. There is a single spermatheca which opens to the exterior through the vagina.

Systematical Notes

The first record of the species of *Volvatella* from our southern seas was made conchologically by HABE (1946, p. 184) under the name of *V. kawamurai*, the type locality being Okinawa (=Ryukyu). Soon after this recording the distribution of the species was extended north to Amami (HABE, 1950). Lastly (HABE, 1965) *kawamurai* was synonymized with *vigourouxi* known from New Caledonia. When we follow to this identification the specific name of the specimens dissected for this report may be designated as *V. vigourouxi* (MONTROUZIER, 1861). This latter species, however, does not appear to me to be markedly separated from *V. fragilis* PEASE, 1860 that was known to occur in Hawaii. Further studies for the review of the species of *Volvatella* are expetecd to be done in future in different parts of the Indo-Pacific, preferably on live specimens.

In place of discussing the affinities of *Volvatella* to other members of the Sacoglossa, a revised synopsis of this Order will be given below (BABA, 1961, p. 50; cf. BOETTGER, 1962, pp. 430, 433):

A. Gill formed of a belt of thin, longitudinal folds on the under side of the mantle. With an osphradium. With a mantle cavity opening on the right side. Visceral sac distinct from foot.
   1. Fam. Cylindrobullidae [Cylindrobulloidea]. *Cylindrobulla.* An intermediate form between Cephalaspidea and Sacoglossa. With a medianly furrowed head-shield. With an external seminal groove. A somewhat streptoneurous nervous system. A presumed sacoglossan uniserial radula. Shell bulloid with a diagonal adductor.
   2. Fam. Volvatellidae [Volvatelloidea]. *Volvatella* (=*Arthessa*). Advanced as true sacoglossans but still showing a somewhat streptoneurous nervous system. Head with oral tentacles and rhinophores. There is no formation of a head-shield. Vas deferens internal, external seminal groove replaced by an oviducal groove. A typical sacoglossan radula. Shell bulloid with a posterior siphon (= spout). With a diagonal adductor.
   3. Fam. Juliidae [Julioidea]. *Julia, Berthelinia.* Specialized rather aberrantly in the formation of a bivalved shell and in the lateral compression of the body, but showing a close association with the Volvatellidae in other respects such as the streptoneury of nervous system and the possession of external oviducal groove in addition to internal vas deferens. Adductor horizontal. A sacoglossan radula.
   4. Fam. Oxynoidae [Oxynoidea]. *Oxynoe, Lobiger.* Possibly advanced in normal ways. A marked centralization of the nervous system. Shell bulloid or cap-shaped, tending to diminish in dimension. An adductor obsolete. An internal vas deferens; no external oviducal groove. Formation of parapodial lobes. A sacoglossan radula.

B. Most advanced in the Sacoglossa. Animal naked, and without a belt of gill-folds. Bilaterally symmetrical. A highly centralized nervous system. External aspects of body multiform: with parapodial lobes in the Elysiidae [Elysioidea], and rows of branchial papillae in the Stiligeridae [Stiligeroidea]. Arrangement of the other families is omitted here.

As was noted previously (BABA, 1961, pp. 39, 50) the genus *Berthelinia* (Juliidae) covers all of the bivalved sacoglossan species exclusive of those of *Julia.* As regards the recent species of *Berthelinia* from the world, actual differentiation appears to have taken place between them in certain ways. And when *Berthelinia* comes to be divided into subgenera, *Tamanovalva* does not mean an immediate synonym of *Edenttellina* (cf. KEEN & SMITH, 1961, pp. 51–52; BOETTGER, 1962, pp. 416–418). Many of the species that have denticulated radula teeth probably belong to *Tamanovalva. Edenttellina* is unusual in having a protoconch at the latter one-fourth of the shell-length, and especially in the possession of non-denticulated radula teeth (this character was re-assured exactly) each of which being deeply bifid at the tip. Conchologically *Midorigai* is distinct from *Tamanovalva. Berthelinia caribbea* EDMUNDS, 1963 has the radula type of *Tamanovalva,* but it shows peculiarities in the details of the pharynx and the ampulla of genitalia.

Postscript

Following the suggestions given to me personally by Dr. GONOR, *Elysia grandifolia* KELAART, var. *orientalis* BABA, 1957 and *E. marginata* PEASE, var. *minor* BABA, 1957

have been re-identified here with *E. ornata* (SWAINSON, 1840) of which the type locality is West Indies. Also I intend to agree with him in recognizing three of the Indo-Pacific species of *Elysia*, viz. *E. ornata* (PEASE, 1860), *E. marginata* (PEASE, 1871) and *E. grandifolia* KELAART, 1858, as synonyms for *ornata* SWAINSON. On our specimens of *ornata*, they were revised and found to have each a denticulated type of radula teeth as one of the characteristics of the said species.

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EXPLANATION OF PLATES VII-X

Volvatella. Okino-erabu Island, Amami Group, Southern Kyushu, Japan (July 12, 1961), 2 specimens (Sp. A and Sp. B). Deposited in the Biological Laboratory, Imperial Household.

PLATE VII

Figs. A–B. Preserved animal from ventral and dorsal sides. Shell-length about 14 mm. Material: Sp. A.

Figs. C–D. Preserved animal from ventral and dorsal sides. Shell-length about 10 mm. Material: Sp. B.

PLATE VIII

Fig. 1. Preserved animal from dorsal side. Showing the shell. Material: Sp. B.

Fig. 2. Preserved animal from ventral side. Diagrammatized. Material: Sp. B. a. anterior shell aperture, b. body whorl, c. left lip, d. siphon (=spout), e. right lip, f. involuted spire hidden by the body whorl. The entire length of the shell aperture is slightly opened to show part of the visceral sac within.

Fig. 3. Preserved animal from latero-ventral side. Material: Sp. B. Showing scars of adductor (a) and right foot retractor (b).

Fig. 4. Head and neck from dorsal side. Part of the mantle is cut off. Material: Sp. B. a. oral tentacle, b. rhinophore. The cephalic structures are each bluntly conical, and seemingly they are frontal in position owing to the strong contraction of the head. There arose a shallow median furrow on the head, which may not be natural.

Fig. 5. Head and foot from ventral side. Material: Sp. B. a. lateral ridge of the head, b. part of the HANCOCK's organ, c. mouth, d. foot, e. anterior opening of the external oviducal groove, f. oral tentacle, g. rhinophore.

Fig. 6. Preserved animal within the shell, from dorsal side. Diagrammatized. Material: Sp. A. a. female genital papilla situated at the right anterior corner of the visceral sac, b. scar of the right foot retractor, c. right scar of the adductor, d. osphradium lying behind the right root of the adductor, e. ventricle and auricle, f. freed right margin of the dorsal mantle, g. anus lying on the back of the visceral sac, h. tissue of kidney which is included within the dorsal mantle just above the belt of gill-folds (i), j. left scar of adductor, k. scar of left foot retractor. Posteriorly the dorsal mantle is rolled to form an excurrent siphon.

Fig. 7. Head and neck from dorsal side. Mantle not shown. Material: Sp. A. a. external oviducal groove, b. paired eyes recognized by clarifying the specimen, c. male orifice, d. lateral ridge of head, e. rhinophore, f. oral tentacle.

The frontal region of the contracted head was raised up moderately and the oral tentacles and rhinophores were figured on the same flat plane. It was aimed to make easy the identification of the cephalic structures in Sp. A with those shown by PEASE, 1868, pl. 7, fig. 4, for live *Volvatella fragilis*.

Fig. 8. Head and neck from right side. Part of the mantle is cut off. Material: Sp. A. a. rhinophore, b. oral tentacle, c. anterior opening of the external oviducal groove (f), d. foldings of the HANCOCK's organ, e. male orifice, g. some of the ganglionic cells developed in the lateral ridge of head, h. female orifice (=oviducal orifice), i. vaginal pore, j. origin of the external oviducal groove. The frontal region of the head in the contracted state assumes a downward-facing position just as it was shown by EVANS, 1950, fig. 6, for *Arthessa cincta*.

Fig. 9. Part of the gill from above (×15). Material: Sp. A. a. tissue of kidney extending over the gill-folds (b).

Fig. 10. Preserved animal from ventral side. Diagrammatized. Material: Sp. A. a. scar of left foot retractor, b. left scar of adductor, c. part of visceral sac within the body whorl, d. belt of gill-folds, e. right scar of adductor, f. scar of right foot retractor. The shell aperture is slightly opened.

PLATE IX

Fig. 1. Preserved animal from ventral side. Diagrammatized. Material: Sp. A. Showing the interior of the mantle cavity. a. scar of left foot retractor, b. left scar of adductor, c. part of posterior foot retractor, d. free margin of ventral mantle, bearing papillae, e. freed right margin of dorsal mantle, bearing papillae, f. tissue of kidney extending over the gill-folds (g), h. female orifice (=oviducal orifice), i. vaginal pore, j. osphradium, k. right insertion of adductor, l. insertion of right foot retractor, m. outer oviducal groove.

Fig. 2. Digestive and nervous systems in the body, diagrammatic. Material: Sp. A. a. oral tract guarded by eosinophile gland cells, b. scar of right foot retractor, c. right scar of adductor, d. osphradium, e. diaphragm separating head and neck from visceral sac, f. anus, g. diverticula composing the main liver-mass, h. stomach, i. insertion of left foot retractor.

Fig. 3. Siphonal margin of the dorsal mantle (×35). Same specimen as Fig. 2. Showing distribution of the liver-diverticula (a) within the mantle-lobe, and the hypobranchial gland cells(b).

Fig. 4. Pharyngeal region from above. Material: Sp. B. a. pharyngeal bulb, b. salivary gland, c. muscular crop, d. dilatable part of oesophagus, e. muscular part of oesophagus, f. buccal ganglion.

Fig. 5. Pharyngeal region from right side. Material same as Fig. 4. a. pharyngeal bulb, b. radula ribbon, c. ascus, d. muscular crop, e. dilatable part of oesophagus, f. salivary gland, g. muscular part of oesophagus, h. buccual ganglion.

Fig. 6. Pharyngeal region in horizontal section (×10). Material: Sp. A. a. part of pharyngeal bulb containing odontophore (b), c. part of the common lumen of pharynx, d. paired lumina of the muscular crop (e).

Fig. 7. Pharyngeal region in horizontal section at lower level than in Fig. 6 (×10). a. pharyngeal bulb, b. muscular crop, c. common lumen of pharynx.

Fig. 8. Pharyngeal bulb in horizontal section at its lowest level (×25). a. pharyngeal bulb, b. common lumen of pharynx, c. descending series of radula, d. ascus.

Fig. 9. Radula. Material: Sp. B. a. entire row, b. teeth from the proximal end of the row, c. teeth from about the middle of the row.

Fig. 10. Cross section of rectum (×30). Material: Sp. A.

Plate X

Fig. 1. Oesophageal region in horizontal section (×30). Material: Sp. A. a. muscular part of oesophagus, b. salivary gland, c. buccal ganglion.

Fig. 2. Nervous system from above (×20). Material: Sp. A. a. pedal ganglion, b. cerebro-pleural ganglion, c. supra-intestinal ganglion, d. osphradial ganglion, e. visceral ganglion, f. genital ganglion, g. infra-intestinal ganglion. The nerves from the cerebro-pleural ganglia and the statocysts themselves were not determined. The fine structure of the osphradium needs to be re-examined on fresh material.

Fig. 3. Genital system in the body, diagrammatic. Material: Sp. A. a. male orifice, b. internal vas deferens, c. origin of the posterior foot retractor, d. external oviducal groove, e. female orifice (=oviducal orifice), f. scar of right foot retractor, g. right scar of adductor, h. osphradium, i. diaphragm, j. insertion of the posterior foot retractor, k. main liver-mass, l. mucous gland of the accessory genital mass, m. left insertion of the adductor, n. insertion of the left foot retractor, o. albumen gland of the accessory genital mass.

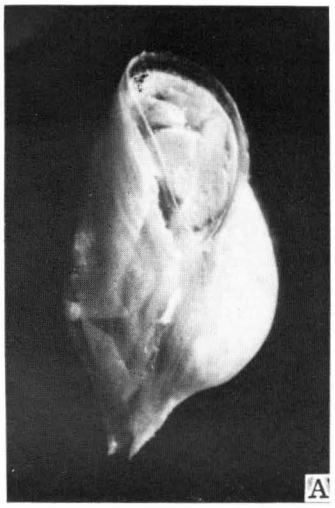
Fig. 4. Anatomy of the male organ (×20). Material: Sp. B. a. penis sheath, b. penis, c. apical stylet.

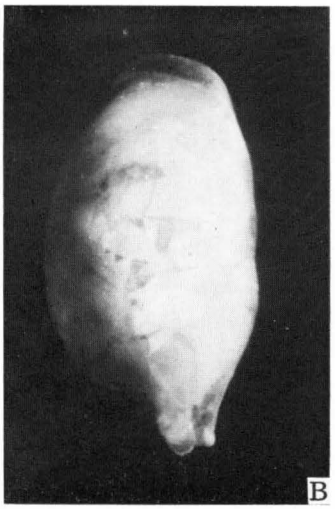
Fig. 5. Male organ in horizontal section, diagrammatic (×20). Material: Sp. A. a. male orifice, b. internal vas deferens, c. penis sheath, d. penis.

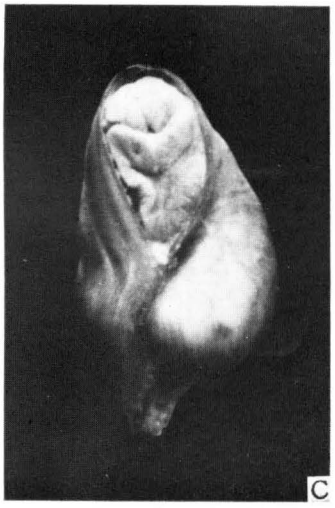
Fig. 6. Male organ in cross section (×30). Material: Sp. A. a. penis sheath, b. penis proper, c. connective tissue, d. longitudinal muscle fibres, e. circular muscle fibres, f. ciliated epithelium.

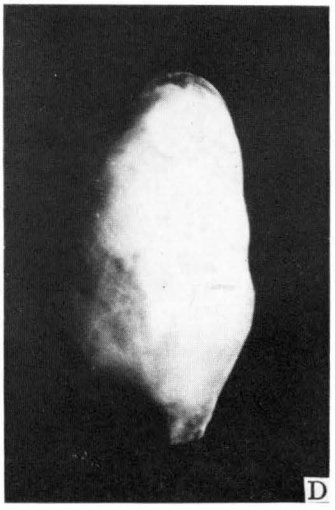
Fig. 7. Reconstructed genital system from above. Diagrammatic. Material: Sp. A. a. external oviducal groove, b. female orifice (=oviducal orifice), c. vaginal pore, d. oviduct, e. spermatheca containg sperms, f. mucous gland, g. vesicle at the end of hermaphrodite duct (i), h. testis, j. ovarian follicles, k. ampulla, l. prostate gland, m. albumen gland, n. genital ganglion, o. visceral ganglion, p. internal vas deferens. The winding course of the oviduct was not analysed exactly.

Fig. 8. Part of the prostate gland (×130). Material: Sp. A.









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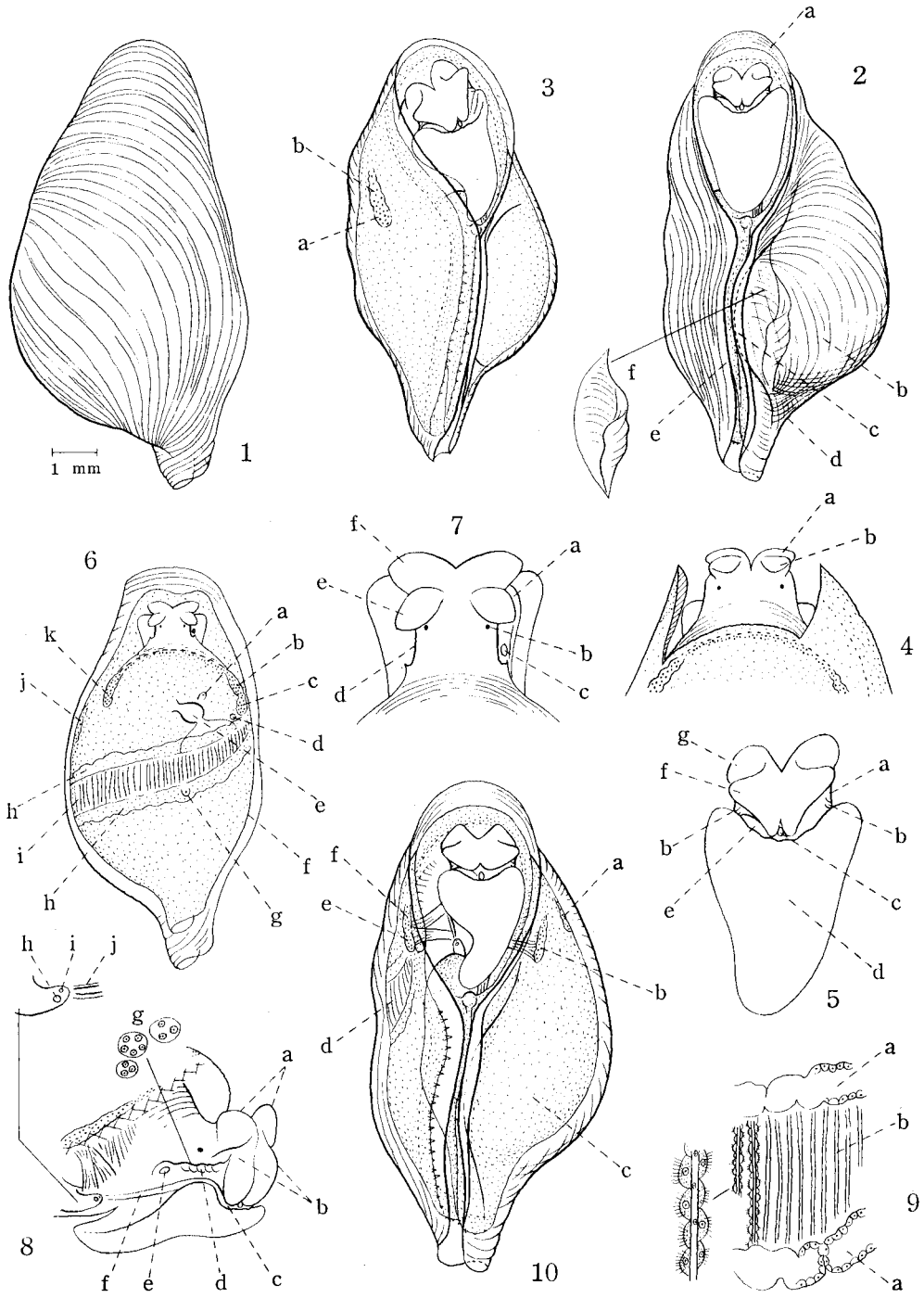

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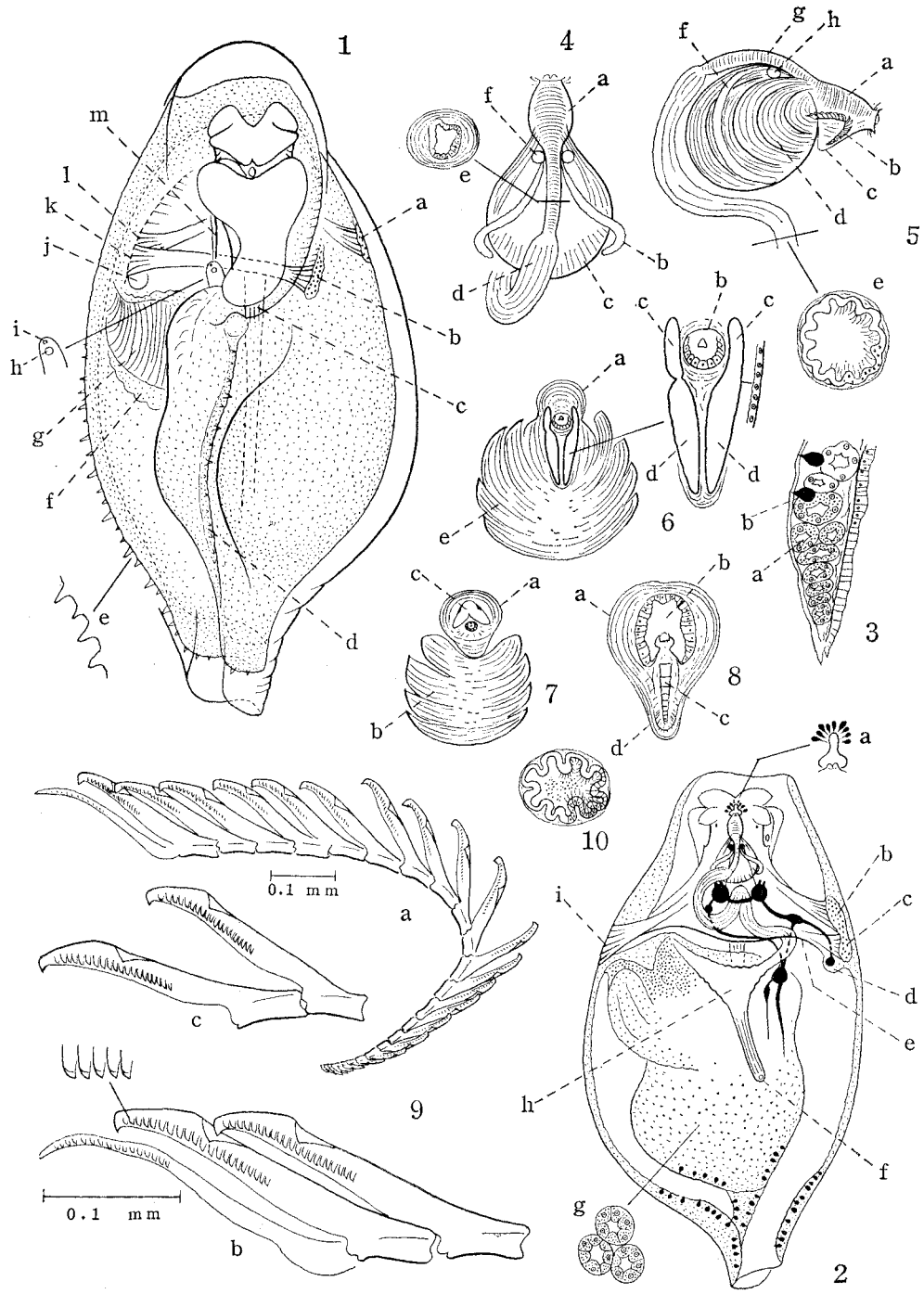

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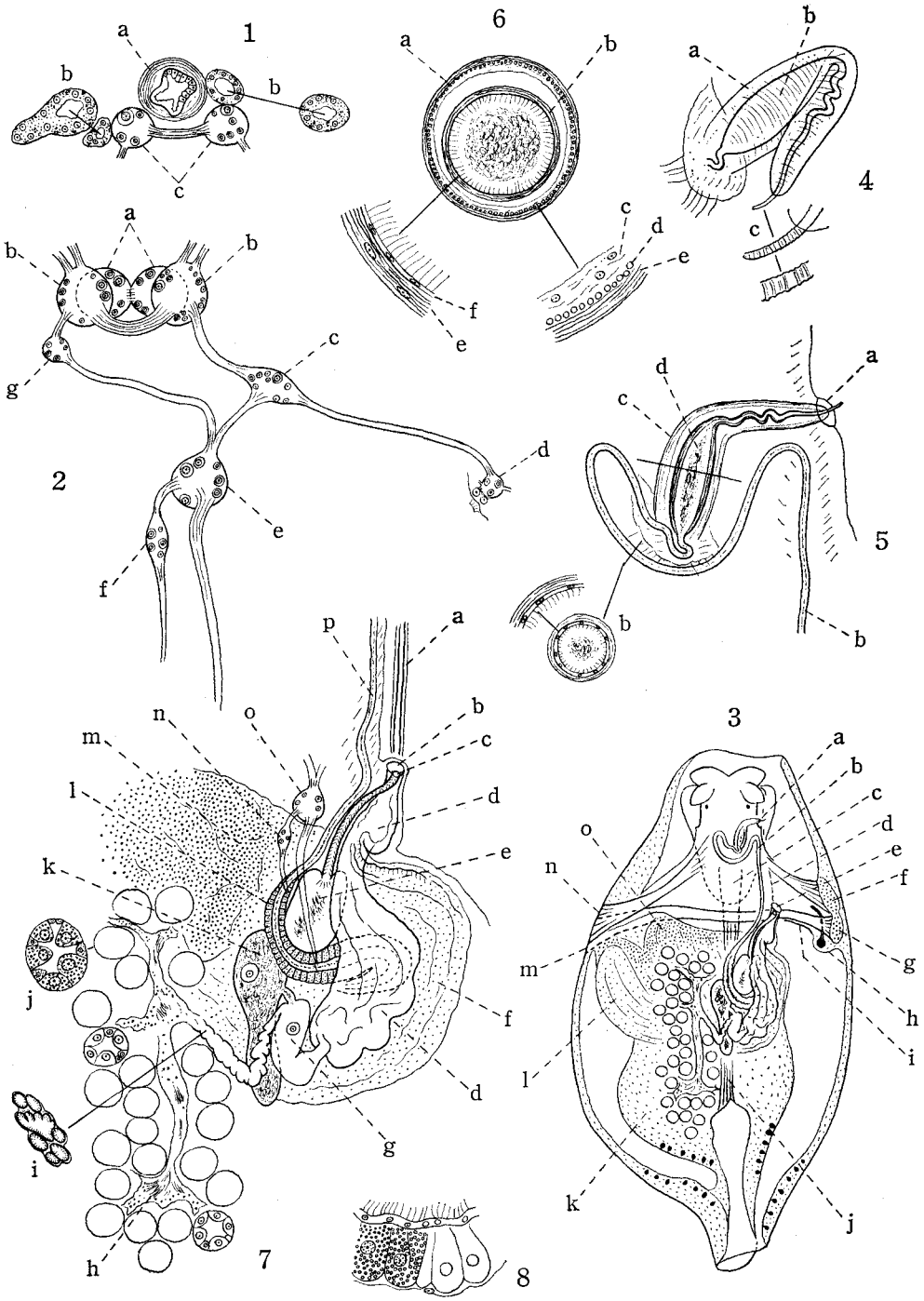

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