THE MORPHOLOGY OF KALINGA ORNATA (Ald. & Han.).

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(From the University Zoological Research Laboratory, Madras).

(Plate III).

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Introduction.

My object in taking up this work was to furnish a detailed morphological account of a typical holohepatic Nudibranch Mollusc of the tropics; and for this purpose *Kalinga ornata* (Alder and Hancock), which is widely distributed in the Indian and the Pacific Oceans, has been chosen.

The present work has been carried out in the University Zoological Research Laboratory, Madras, and I am grateful to Professor R. Gopala Aiyar, Director of the Laboratory, for his kind suggestions and criticism; to Dr. B. Prashad, Director of the Zoological Survey of India, for having kindly lent me several books for reference; and to him and Dr. H. Srinivasa Rao for going through the manuscript and suggesting some improvements. My thanks are due to Mr. S. Ramaswami Iyengar of the Government Fisheries Station, Ennur, for having supplied some material for my work. To the Syndicate of the Madras University I am indebted for the award of a Research Studentship.

HISTORICAL RÉSUMÉ.

Alder and Hancock, from a collection of the Nudibranchiate Mollusca sent to them by Walter Eliot, described several new genera and new species including the present form. Eliot made these collections during 1853 and 1854 from Lawson's Bay in Waltair, near Vizagapatam in India, and sent them to the authors mentioned above, with a set of exquisite drawings in natural colours made by the Hindoo artists of the A single species of the genus Kalinga was described by the authors, and no new forms have since been added. The name of this genus has reference to one of the countries of the ancient Empire of Asoka, where it was first found. Perhaps the specific name ornata refers to its beautiful form beset with plumes and processes with variegated colours.

From the descriptions given by these authors of the external features, and from the life-like drawings made by the artists referred to, one can never go wrong in identifying the animal, especially when alive. far as the internal anatomy is concerned their description is very meagre. They placed the genus Kalinga in the family Polyceridae, and regarded it as intermediate between Euplocamus and Plocamopherus.

Bergh (1890), while studying a collection of Nudibranchs from Amboina in the Molucca Islands, came across a single specimen of this genus preserved in alcohol in the Leiden Museum. The buccal mass was completely everted, and most of the internal parts were very much damaged. He could not study the entire internal anatomy and doubted the identity of the form with Kalinga ornata.

In 1905 Farran described one young specimen of *Kalinga* from Professor Herdman's Collection of Opisthobranchiate Mollusca from the Gulf of Manaar. He gave an account of the radular teeth alone, as the radula was not in its normal position, but was found lining the under surface of the everted buccal-organ.

Sir Charles Eliot (1906) examined four very badly preserved specimens in the Hancock Museum in Newcastle-on-Tyne. He also found the same difficulty as the previous authors regarding the buccal parts, and like Bergh, he gave a brief anatomical description of these speci-In 1908 Bergh again published a short report on two more specimens captured alive in South Africa. Later, Eliot (1913), Baba (1933) from Japan, and Barnard (1927) from South Africa recorded the occurrence of this genus in their respective areas.

From the foregoing account it is evident that only two authors have so far described the anatomy of Kalinga from the insufficient and defective material available to them.

OCCURRENCE.

This Nudibranch has previously been recorded from the following places: (i) Lawson's Bay near Vizagapatam and near Madras in the Bay of Bengal—Eliot; (ii) near Amboina, Molucca Islands in the Pacific Ocean—Bergh; (iii) ten miles north of Cheval Paar in the Gulf of Manaar -Farran; (iv) near Amaticulu Conical Hill of South Africa in the Indian Ocean—Bergh; (v) Zululand coast of South Africa—Barnard; and (vi) Tateyama, Misaki, etc., in the Pacific coasts of Japan—Baba.

The material for my work was collected near Madras and at Ennur, ten miles north of Madras. From this it is evident that the animal is widely distributed throughout the Indian and the Pacific Oceans,

EXTERNAL FEATURES.

The animal is Dorid-like in appearance and measures, when full grown, about 10.4 cm. in length, 7.8 cm. in breadth and 3.5 cm. in height. foot is flat, oval, and pale yellowish-white in colour. The back, which is narrower than the foot, is tinted with shades of light green and pink. It is somewhat arched in front and its semilunar, free anterior margin bears fourteen small, pale-white, plumose tufts (pa. or.); the biggest of these lie on either side of the margin, and they become shorter and shorter towards the middle region. This anterior rim or the margin with the plumose tufts is usually spoken of as the 'oral veil' posterior end of the body is blunt and rounded. The back has an elevated position above the foot and slopes almost vertically along the sides. Anteriorly between the mantle and the foot just below the middle region of the oral veil is the slit-like mouth (or. s.) guarded by two large fleshy outer lips or labial folds (la.), each of which bears at its extremity a thin flat process, the oral tentacle. There is a slight constriction at a distance of 3.5 cm. from the oral veil dividing the back into two regions. anterior of these regions with the buccal mass, the rhinophores, the oral veil, and the labial folds in front, forms the head (Pl. III, figs. 1-4).

At a distance of 2 cm. from the front end are the two dorsal tentacles or rhinophores lodged within their sheaths about 2 cm. apart. The rhinophores (rh.) are somewhat conical, perfoliated structures with a stout, short pedicle. The margin of the rhinophore-sheath and the rhinophore stalk are crimson red in colour, while the perfoliated part is dull green with a crimson patch. The free edge of the rhinophore-sheath reveals very small, yellowish, papillated tufts with white tips.

Occupying most of the posterior dorsal region there are five pinnately branched gill-trees or branchiae (br.) with interspace between them. In this interbranchial area, almost equidistant from the five branchiae, the fimbriated anal opening (an.) is situated on a crimson coloured, raised papilla. Close to it, towards the right side, is the very minute renal opening (re. ap.). One of the gill-trees is median and situated in front of the anus at a distance of 1.2 cm.; the remaining four are placed two on either side of the anal papilla. The right posterior gill-tree is the largest. In the living condition, the gill-trees are greyish-green, bespeckled with crimson; they are extremely contractile and when touched or otherwise irritated measure only about a fourth to fifth of their original length. Unlike Doris and other allied genera Kalinga has no special peri-anal pockets; but the same amount of protection is afforded to the gills by their being contracted and closely pressed against the back.

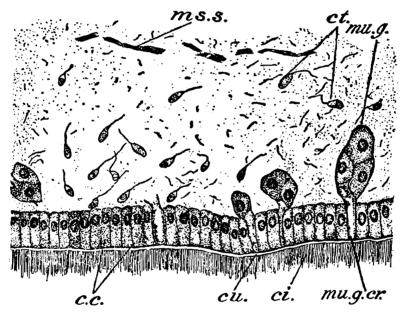
The mantle as well as the sides of the body are beset with small conical processes, very minutely papillated at the base and with a crimson or yellow, contractile tuft in the centre. The conical processes vary in size, almost microscopical to about 4 mm. in diameter. Those along the sides are less prominent, being smaller in size and lighter in colour than those on the back. On either side of the back there are four large conspicuous tufts, (l. pa.) each with a conical or a pyramidal stalk bearing on its sides smaller tufts of yellow and white. In between these

foar large tufts there are smaller tufts, all of them forming a ridge on either side of the back.

The genital vestibule is situated on the right side of the body between the mantle and the foot at a distance of about 3 cm. from the anterior end.

Гоот.

The foot (ft.) which is mainly a locomotor organ, is broad, oval, flat and muscular. It helps the animal to creep over and through the crevices of rocks on which it lives or to float freely with the current with its ventral surface upwards. When the animal is left in a spacious aquarium of sea-water, it secretes a copious quantity of mucus and creeps freely on the surface just like any other Gastropod. In such movements no muscular contractions and expansions of the foot are apparent, but the animal seems to glide. In captivity, Kalinga ornata, like most other Nudibranchs, has a tendency to float on the surface of the water with the ventral surface upwards.



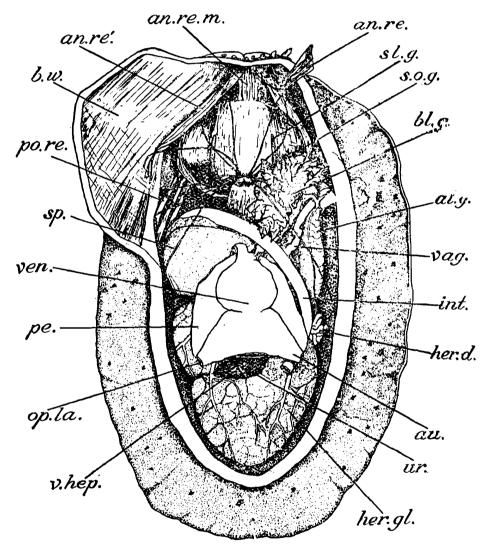
Text-fig. 1.—Transverse section of foot. ×600

c. c. columnar ciliated cells; ci. cilia; cu. cuticle; ct. connective tissue cells; ms. s. muscle strands; mu. g. mucous gland; mu. g. cr. crypt of the mucous gland.

A transverse section of the foot (text-fig. 1) reveals an outer epithelial layer of columnar ciliated cells (c. c.), the cilia (ci.) being nearly as long as the cells themselves. Beneath the ciliary epithelium there are small unicellular and multicellular mucous glands (mu. g.), which open to the exterior through minute crypts (mu. g. cr.) in the epithelium. The latter are numerous throughout the margin of the foot, and especially towards the extreme anterior and posterior regions, but in the middle region these are few and far between. They are club-shaped, and filled with minute granules which take basic stains very quickly. Separating the columnar cells from the row of cilia there is a thin hyaline cuticle (cu.). Underneath the ciliary layer there is the dermal connective tissue (ct.) with scattered nerve cells. Small nerve fibres pass from these nerve cells to supply the mucous glands. In the foot there are longitudinal and transverse strands of muscles (ms. s.) which are very irregularly arranged to form a network.

BODY-WALL.

The body-wall of the back and the sides of the animal is thick, soft, and flexible. It is devoid of spicules and cilia. A number of plumose contractile and highly sensitive processes of varying dimensions are scattered all over the surface. Anteriorly it bears the two rhinophores and posteriorly the branchiae. It lies somewhat loose over the internal organs except in the region of the rhinophores and the branchiae. In the region of the branchiae the great veins, the intestine and the ureter are connected with it; and in the region of the rhinophores the olfactory nerves pierce the wall of the back and enter the rhinophores. It is somewhat thin anteriorly. Internally, the body-wall has a silvery white appearance due to the close network of muscle strands. The outer



Text-fig. 2.—Viscera in situ.

al. g. albumen gland; an. re. anterior retractors of the first set; an. ré. same of the left side retaining their connection with the body-wall; an. re. m. anterior retractors of the second set (median and dorsal); au. auricle; b. w. body-wall; bl. g. blood gland; her. d. hermaphrodite duct; her. gl. hermaphrodite gland; int. intestine; op. la. opening of the lateral vein into the auricle; pe. pericardium; po. re. posterior retrators; sl. g. salivary glands; s. o. g. supra-oesophageal ganglionic mass; sp. spermatheca; ur. ureter; vag. vagina; ven. ventricle; v. hep. hepatic vein.

epithelium is glandular, followed by a dermal connective tissue of considerable thickness penetrated by a number of sinuses filled with blood,

which consequently give the body-wall a spongy appearance. The blood passing through these sinuses can be easily aerated, as it is separated from the outside water containing dissolved air only by a thin epithelial layer and the connective tissue. As in the foot, longitudinal and transverse strands of muscles are present in the connective tissue. Some of these strands enter the rhinophores, the contractile processes and the branchiae. The body-wall is partly respiratory and partly sensory. It is also protective as the outer epithelium and the branchiae lodge a number of secreting glands.

On removing the dorsal body-wall the internal organs are seen enveloped in a thin transparent membrane of fibrous material, the peritoneum of Hancock and Embleton (vide their description of the anatomy of Doris). As this membrane is only the dorsal wall of the haemocoel, the term peritoneum is not applicable; this was subsequently corrected by Hancock himself (1864) and has been accepted by other writers.

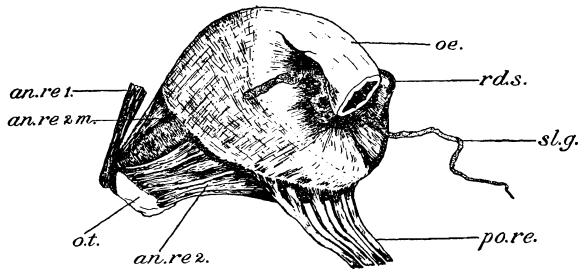
DIGESTIVE SYSTEM.

The mouth, which has already been described as a vertical slit between the mantle and the foot, is guarded by the outer lips and leads into a narrow passage, the oral tube (text fig. 3, o. t.) lined inside by a thin, fleshy, longitudinally folded inner lip or the second lip. Towards the posterior region of the oral tube there are well developed circular muscles forming a sphincter in front of the entrance to the buccal mass. Immediately following this is the huge bulb-like buccal mass (text-figs. 2, 3), narrow anteriorly and broad posteriorly, occupying the anterior third of the space in the body. The oesophagus (oe.) takes its origin from its posterior dorsal region. In the living animal the outer lip is of a pale white colour, while the oral tube is flesh-The buccal mass is of a rose colour anteriorly—this gradually intensifies posteriorly to bright crimson—but when preserved the whole structure appears pale yellow or white. A ventral view of the buccal mass reveals its bilateral symmetry. The lingual muscles starting from the floor of this organ divide it ventrally into two pad-like structures, while dorsally the buccal mass terminates in a small knob-like projection of the radular sac.

Retractor Muscles of the Buccal Mass.—The buccal mass and the oral tube have three sets of retractor muscles, two forming the anterior retractors and one the posterior (text-figs. 2, 3). The retractor muscles of Kalinga ornata do not appear to have been described previously.

Immediately below the body-wall we see a pair of fan-shaped muscles (an. re 1), each consisting of about half a dozen radiating strands of muscles, taking their origin dorso-laterally from the anterior end of the oral tube. Proceeding backwards and lying loosely above the buccal mass these muscles have their attachment with the body-wall in the region of the rhinophores, and are in fact a continuation of the longitudinal muscle strands of that region. These form the first set of anterior retractors.

On removing the above-mentioned muscle strands, lying under and in close contact with them we see two more strands of muscles, one on either side, each consisting of several bundles; these arise ventrolaterally from the middle region of the oral tube and extend to the posterior region of the buccal mass (an. re 2). These form the second set of anterior retractors for the shortening of the oral tube. Arising from the oral tube and attached to the anterior end of the roof of the buccal mass there is seen a short strip of a few strands of muscle (an. re. 2 m), which lies partly over the oral tube and partly over the labial disc. This probably assists the second set of anterior retractors in their action.



Text-fig. 3.—Side view of buccal mass.

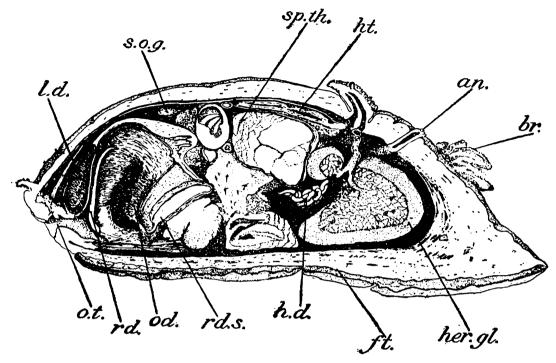
an. re. 1. anterior retractors; an. re. 2 anterior retractors of the second set (ventro-lateral); an. re. 2 m. anterior retractors of the second set (median dorsal); oe. oesophagus; o. t. oral tube; po. re. posterior retractors; rd. s. radular sac; sl. g. salivary gland.

The posterior retractors (po. re.) are two thick powerful strands of muscle, each consisting, like the previous sets, of four to five bundles of muscles which are inserted at the postero-lateral region of the buccal mass, and pass backwards to be fixed to the foot about its middle region. These are responsible for the retraction of the buccal mass as a whole.

Labial Disc.—In front of the buccal mass and guarding the entrance to it, a strong and powerful muscular hoop forms a sort of a collar which is well-developed along its roof and sides though its floor is soft. The corresponding structure in Doris has been differently named by different authors as the third lip, the prehensile collar, the buccal lip (Hancock and Embleton 1852), and the labial disc (Sir Charles Eliot 1910). In this paper I have adopted the term labial disc (text-figs. 4, 5, 7, l. d.). Like the buccal cavity the labial disc is lined by an epithelium of columnar cells, which secretes a stratified cuticular layer of varying thickness. It is particularly thick in the region of the labial disc which faces the odontophore. The labial disc of Kalinga ornata does not bear an armature.

Roof of the Buccal Mass.—Irregularly arranged bundles of muscles, both longitudinal and transverse, form the roof of the buccal mass, which is lined inside by the buccal epithelium of columnar cells, the secretory product forming a cuticle. The spaces between the muscle strands and the lining epithelium are filled by connective tissue. On

either side of the roof, the salivary glands (sl. g.) project forwards and open into the buccal cavity.



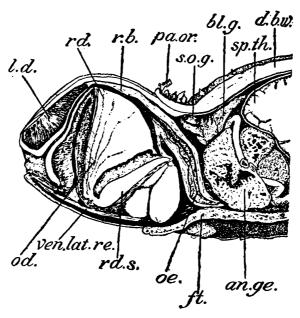
Text-fig. 4.—Median longitudinal section of the entire animal with the buccal mass in position.

an. anus; br. branchiae; ft. foot; h. d. hermaphrodite duct; her. gl. hermaphrodite gland; ht. heart; l. d. labial disc; od. odontophore; o. t. oral tube; rd. radula; rd. s. radular sac; s. o. g. supra-oesophageal ganglionic mass; sp. th. spermatheca.

Odontophore.—The odontophore (text-figs. 4, 5, od.) arises on the floor of the buccal mass as a highly muscular conical elevation, surmounted by the dentigerous membrane, the radula (rd.). Broadly speaking there are two sets of muscles that take part in the formation of the odontophore. Antero-ventrally where the odontophore faces the roof and the sides of the labial disc, one set of muscles forms a thick compact pad, which does not seem to be very much mobile; while a second set arising posteriorly from the base of the buccal mass consists of loosely arranged powerful muscles (text-fig. 7, msc. od.) which run forwards, laterally and upwards to form the muscular elevation. bring about the movements of the odontophore forwards and backwards, and play an important part in the eversion of the buccal mass. entire surface of the odontophore is lined by the epithelium and the cuticle, the latter being considerably thick in the anterior region of the odontophore facing the labial disc. Along the median line the odontophore has a deep longitudinal groove.

Radula.—The radula (text-fig. 4, rd.) lies closely pressed against the odontophore, and its membrane is almost fused with the cuticle lying underneath. It is also creased down along its middle line fitting into the median groove on the odontophore. Its shape is very much like the hood of a snake, expanded along the sides, narrowed down almost suddenly in front, and posteriorly folded longitudinally from side to side. Its surface is traversed by grooves, faint in front, more pronounced behind, where the radula becomes strongly narrowed down wards. It next takes an upward course to enter the radular sac, (rd. s.

where the grooves suddenly disappear. The radular sac is lined by special cells with deeply staining nuclei; and a large number of teeth are being continuously formed here.

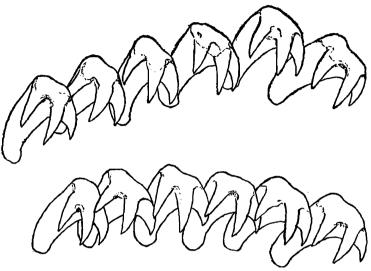


Text-fig. 5.—Median longitudinal section of the anterior region of the animal, in which the buccal mass is pushed out of the body preliminary to eversion.

an. ge. anterior genitalia; bl. g. blood gland; d. b. w. dorsal body-wall ft. foot l. d. labial disc; od. odontophore; oe. oesophagus; pa. or. papillae of the oral veil; r. b. roof of the buccal mass; rd. radula; rd. s. radular sac; sp. th. spermatheca; s. o. g. supra-oesophageal ganglionic mass; ven. lat. re. ventro-lateral retractors.

Numerous tricuspid microscopical teeth of almost the same shape and size are arranged in transverse rows on the radular membrane (textfig. 6). Each tooth shows a long curved root embedded in the substance of the membrane and a broad exposed crown bearing the three recurved The top portion of the root is held fast to the dentigerous membrane by a short connective tissue ligament. Along the median line of the radula there is the rachis devoid of teeth, but the transverse rows of either side sometimes come so close together that there appear, in certain areas, spurious rachidial teeth. The anterior-most rows of the teeth of the radula are close together and much worn out by use but the middle expanded portion reveals fairly big teeth in perfect condi-The radular formula given by Farran (1905) was 90. 0. 90. observations on several specimens show that the number of teeth varies from 85 to 100 in a row on each side. In the young specimen examined by Farran there were about 130 transverse rows of teeth, whereas in a full grown specimen I counted nearly 200 rows in the part of the radula lying outside the radular sac, and a great many more on the posterior part in the radular sac; this agrees more closely with what was found by Bergh (1908). Farran observed that the innermost tooth of each row differed from the rest in having one of its cusps shortened and the first few outermost teeth in having just one or two cusps only. description of Farran's agrees with the condition observed in some rows, but in many the innermost and the outermost teeth are quite perfect. In conclusion, it may be said that the radular formula of Kalinga ornata is 100. 0. 100, this being the maximum number of teeth seen in a row.

A smaller number of teeth may indicate loss due to use. The teeth are all similar, and the subsequent deformity of some of them may be due to accidental breakage of their cusps.

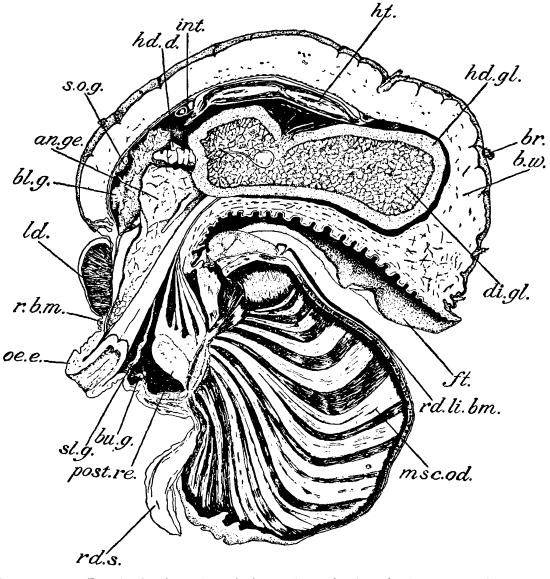


TEXT-FIG. 6.—Teeth of the Radula. ×300.

Eliot (1910) says of Doris that "the radula can be drawn backwards and forwards over the odontophore as over a pulley and thus tear to pieces any substance which may be pressed against it" and Embleton (1852) also expressed the same view as regards Doris and Eolis. According to Sedgwick (1909), however, it is very common in almost all the Gastropoda that the odontophore itself, with the radula lying upon it, is moved forwards and backwards. I have observed this feature in Kalinga ornata when alive. When the odontophore is thus moved with the radula, it rubs against the roof of the labial disc lined by the cuticle and crushes and rasps away any substance that comes The radula cannot apparently be moved independently of the odontophore as it is connected intimately with the cuticular layer mentioned already. Judging from the nature of the habitual eversion of the buccal mass to a very great extent, exposing the radula, it is probably right to suppose that it is of immense advantage to the animal to have the radula thus intimately united with the surface upon which it lies.

Condition of the Buccal organ when it is everted.—When the animal is suddenly plunged into a fixative, it undergoes convulsions before it dies, and the whole buccal mass is pushed out of the body as a bag of considerable dimensions, often larger than the individual itself. In such a condition the parts already described assume a peculiar shape and position. The odontophore as a whole, with the radula lying over it is pushed out through what was once the mouth, and the oesophagus remains partly everted as a short tube opening out externally about the middle region of the first half of the buccal mass. The rest of the oesophagus lies concealed and cannot be seen unless a longitudinal section of the animal along with the everted buccal organ is taken. Such a preparation made it possible for me to describe its parts very clearly. As shown in text-fig. 7, the oesophagus is continued into the stomach which is pulled forwards and consequently becomes thinner and longer.

Between the labial disc (ld.) which is a continuation of the anterior margin of the mantle, and the mantle itself is a fold which forms the roof of the

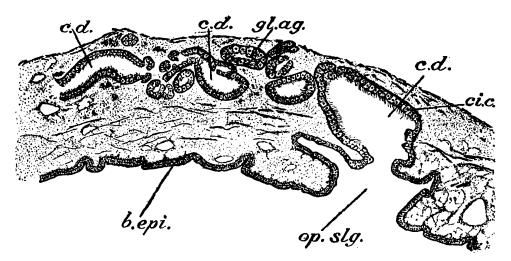


Text-fig. 7.—Longitudinal section of the entire animal with the completely everted buccal mass.

an. ge. anterior genitalia; bl. g. blood gland; br. branchiae; bu. g. buccal ganglia; b. w. body-wall; di. gl. digestive gland; ft. foot; hd. d. hermaphrodite duet; hd. gl. hermaphrodite gland; ht. heart; int. intestine; ld. labial disc; msc. od. muscles of odontophore; post. re. posterior retractors; r. b. m. roof of buccal mass everted; oe. e. part of oesophagus everted; rd. li. bm. radula lining the everted buccal mass; rd. s. radular sac torn; sl. g. salivary gland; s. o. g. supra-oesophageal ganglionic mass.

oral tube in its non-everted condition. The anterior end of the labial disc is in continuation of the everted roof of the buccal mass and also of the partly everted oesophagus. Ventrally the labial disc is less prominent. In the everted condition of the buccal mass, the radular sac lies at its free extremity, while the posterior retractors (post. re.) are beneath the oesophagus (oe.e.) proper attached to the lingual muscles at their origin. The latter proceed forwards and downwards arching along the sides of the buccal mass. The radula lies on the under surface of the everted buccal mass. It is extremely thick near the mouth region becoming gradually thinner towards the radular sac. The buccal ganglia (bu. g.) lie beneath the oesophagus in front of the insertion of the

posterior retractors. The salivary glands (sl. g.) are now found underneath the oesophagus, opening out to the exterior at the base of the tubular oesophageal projection of the buccal mass.



Text-fig. 8.—Section of the roof of the buccal mass showing the opening of the salivary gland. ×30.

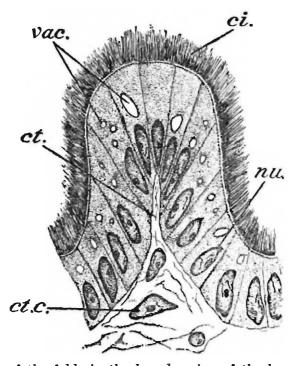
b. epi. buccal epithelium; c. d. central conducting duct; ci. c. ciliated cells of the conducting passage; gl. ag. glandular aggregations; op. slg. opening of the salivary duct into the buccal cavity.

Salivary Glands.—The salivary glands (text-fig. 2, 3, sl. g.) are two thin flat thread-like structures rather broad anteriorly and narrow posteriorly. They open on the roof of the buccal mass and passing through the circum-oesophageal nerve collar extend up to the liver mass. In sections the salivary gland reveals a central ciliated lumen of the conducting duct (text fig. 8, c. d.) into which aggregations of glandular cells (gl. ag.) open. A short portion of the duct just before it opens into the buccal mass is devoid of glandular cells.

Oesophagus.—The oesophagus (measuring 15 mm. by 10 mm. in a full grown specimen) takes its origin from the dorsal posterior region of the buccal mass, and bending slightly to the left of the radular sac runs downwards. It has a bright crimson colour and thick walls, with longitudinal plications lined by a thin cuticle. Posteriorly between it and the stomach there is a narrow constriction which, however, is not sharply marked off in large and full grown specimens.

Stomach.—It is a roughly "S" shaped saccular structure. From the point of its origin from the oesophagus it bends slightly to the left and then proceeding backwards in close contact with the inner wall of the foot, enters the mass of the digestive gland on its right side. It then becomes narrow, lies hidden in the furrow of the mass of the digestive gland, takes a crescentic curve there and finally emerges from its left top corner. The rest of the alimentary canal is continued as the intestine with a deep constriction separating the pyloric end of the stomach and the intestine proper. Piercing the curved floor of the stomach, there is a wide opening leading into a stout tubular portion, into which the duct of the supposed gall-bladder from the left side and the hepatic ducts from the anterior and the posterior regions of the digestive gland open.

Digestive Gland.—Occupying nearly the whole of the posterior half of the visceral cavity there is the mass of the digestive gland (text-fig. 7, di. gl.) or the hepato-pancreas surrounded by the follicles of the hermaphrodite gland. It is a dull greyish-green conical mass of glandular structure, spongy in appearance due to the blood vessels and the hepatic ducts which ramify in its tissue. Anteriorly, it is broad with a crescentic groove to accommodate the posterior portion of the stomach, which receives the hepatic ducts and the gall-bladder. The hepatic ducts are fairly wide where they open into the stomach, but are extremely narrow where they emerge from the hepatic lobules.

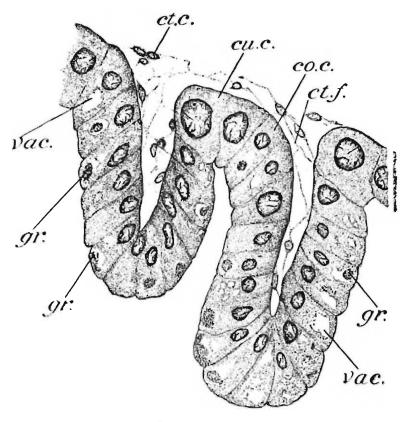


TEXT-FIG. 9.—One of the folds in the broad region of the hepatic ducts. ×750. ci. cilia; ct. connective tissue penetrating into the fold; ct. c. connective tissue cells; nu. nucleus of the ciliated cells of the lining membrane; vac. vacuoles of the ciliated cells.

Similar to the corrugations observed by Agersborg (1923) in the pyloric diverticulum of *Melibe leonina*, I find in *Kalinga ornata* crypts or villi-like projections in the broader regions of the hepatic ducts. These corrugations (text-fig. 9) are formed by the mucous layers being thrown into small folds into which the connective tissue (ct.) is continued. In a perfect transverse section of the broad region of the hepatic duct only the floor of the duct displays these corrugations while the roof does not. The latter consists of columnar ciliated cells with fairly large oval nuclei, and without vacuoles in the cytoplasm, while the former consists of cells with oblong nuclei (nu.) and vacuolated cytoplasm (vac.).

The hepatic lobules are lined by a glandular epithelium of cubical and columnar cells with granular contents (text-fig. 10). The former (cu. c.) are larger in size though fewer in number and have bigger nuclei. Some of the columnar cells (co. c.) show vacuoles and brown granules (gr.) probably of the nature of secretory products. There is one feature common to all these cells; that their cytoplasm is filled with minute

granules which are stained dark with haematoxylin. The epithelium formed of these cells projects in the form of folds into the lumen increasing



Text-fig. 10.—Section of the glandular epithelium of the digestive gland. ×600.

co. c. columnar cells—the difference in the contents of the adjacent cells may be noted; ct. c. connective tissue cells; ct. f. connective tissue penetrating into the folds; cu. c. cubical cells with large nuclei; gr. brown granules in the cytoplasm; vac. vacuoles in the cytoplasm.

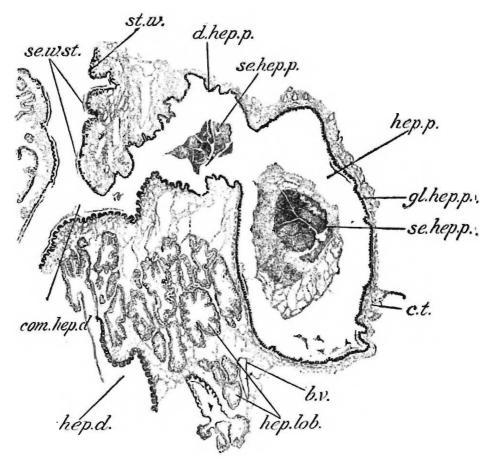
the surface. The connective tissue meshwork (ct. f.) penetrated by blood vessels and the sinuses fills up the interspaces between the various lobules and the ducts, holding them together as a compact gland.

In Gastropoda this digestive gland is, according to Barfurth (1883)*, both secretory and excretory in function. Frenzel (1886) described in Tethys three types of cells, the Kornzellen, the Keulenzellen and the Kalkzellen. Hecht* (1895) observed three kinds of definite cells, and a fourth which, according to him, may give rise to cells of any of the three types mentioned above. The three types he described are (i) Cellules vacuolaires excrétrices, (ii) Cellules excrétrices and (iii) Cellules The cubical cells without the vacuoles in Kalinga ornata á ferments. agree with the Cellules excrétrices of Hecht and the Kornzellen of Frenzel; while the vacuolated cells of either kind, i.e., those with and without the secretory products agree with the Cellules & ferments and Cellules vacuolaires respectively of Hecht, they are also identical with the Keulenzellen of Frenzel. I have not been able to make out cells which correspond to the Kalkzellen or the chalk cells of Frenzel. Eliot and Evans (1908) describe in Doridoeides gardineri certain free cells inside the lumen of the hepatic lobules. They believe that as some of the cells are filled with the excretory products they are detached from the

^{*} For reference to these authors see Agersborg (1923).

walls of the lobules and are dropped into the cavity. No doubt some of them discharge an excretory function; but I have not noticed any such cells lying free inside the hepatic lobules of *Kalinga ornata*.

Hepatic Pouch.—This is a roundish bag of 3 mm. diameter having thick glandular walls and a short, narrow passage 1 mm. long. It is placed just to the left of the common portion of the hepatic duct into which its cystic duct opens. As a result of the activity of the glandular cells lining the pouch a bluish-black granular secretion is derived. This secretion was considered by Eliot (1910) in Doris as forming a thin lining over the soft mucous layer of the stomach, the intestine and the wider portions of the hepatic duct to overcome the irritation caused by the spicules in the food of these Dorids. As a part of this secretion is also mixed with the contents of the alimentary canal, Evans (1914) believed that it acts also as a lubricant for the easy passage of the spiculose excrement down the intestine. As is seen in text-fig. 11, the secretion of the



Text-fig. 11.—Section of hepatic pouch with its cystic duct opening into common hepatic duct. ×40.

b. v. blood vessel; c. t. connective tissue; com. hep. d. common hepatic duct; d. hep. p. duct of the hepatic pouch; gl. hep. p. glandular wall of the hepatic pouch; hep. d. one of the hepatic ducts; hep. lob. hepatic lobules; hep. p. hepatic pouch; se. hep. p. secretion of the hepatic pouch; se. w. st. secretion of the hepatic pouch over the mucosal walls of the stomach; st. w. stomach wall.

hepatic pouch in this animal also forms a thin lining over the inner walls of the gut (se. w. st.) and the hepatic ducts; and, as has been

suggested by previous writers, it probably protects the inner lining of the digestive area.

Intestine.—From the termination of the stomach the alimentary canal is continued as the intestine, about 6.2 cm. in length, with an almost uniform calibre, rather flat and oval in section and with its interior thrown into close longitudinal ridges. From its origin it runs forwards, and turning to the left makes an arch in front of the heart; it is then continued backwards to the anus. The presence of food in varying states of digestion in the intestine, shows that it is the main absorptive region of the gut. The intestinal region nearest the stomach shows only partly digested food not completely absorbed; while the region near the anus reveals undigested calcareous shells and spicules. The intestine consists of an outer fibrous layer and an inner glandular layer with connective tissue between them. The latter layer is formed of columnar ciliated cells with oval nuclei. The outer fibrous layer reveals only a few muscle fibres here and there. The intestine is of an orange colour, when the animal is alive, and is uniformly ciliated throughout its length. There is no typhlosole of the type described in such forms as Melibe.

Rectum.—The terminal region of the intestine, which pierces the wall of the back in the interbranchial area and opens out by the anus (text-fig. 4, an.) situated to the left of the renal pore, may be reckoned as the rectum though it does not differ to any extent from the rest of the intestine in its histological structure. Near the anus there is a sphincter muscle.

CIRCULATORY SYSTEM.

The circulatory system of *Kalinga ornata* resembles that of other Doridiform Nudibranchiate Molluscs with gills, except for a few variations.

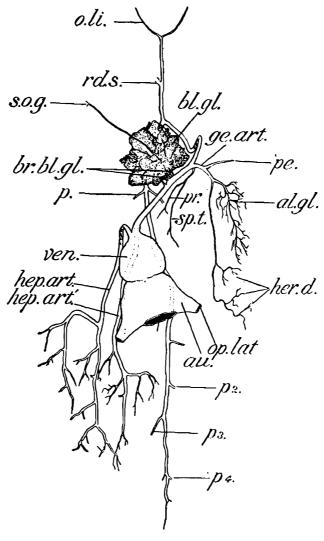
Heart and Pericardium.—The heart lies above the visceral organs just in front of the root of the median gill tree (text-fig. 4, ht.). Its pulsations can be seen through the translucent bodywall of the back, and vary from 48 to 50 per minute. It is a broad, muscular, two-chambered organ (text-figs. 2, 12) consisting of a thin-walled roughly triangular auricle (au.), and a comparatively thick-walled ventricle (ven.), enclosed in a thin transparent membranous pericardium (pe.), which is a continuation of the so-called peritoneum on all sides except in the hind region where the great veins communicate with the auricle. The latter, in its expanded condition, fills up a greater part of the lower half of the pericardial chamber, but the ventricle appears somewhat smaller. walls of the auricle are transparent and formed of delicate strands of muscle and fibrous tissue; whereas those of the ventricle are opaque and highly muscular. As has been noted in Aplysia there is no endothelium lining either the auricle or the ventricle, and their muscles are directly bathed in blood. The floor of the pericardium is pierced by the reno-pericardial duct in the right posterior corner and the syrinx renale is suspended freely in the pericardial chamber by fine short strands of

fibrous tissue arising from the auricular wall. I have not observed communication between the pericardial chamber and the perivisceral cavity. Since the pericardial cavity of Molluscs is coelomic and the perivisceral space is haemocoelic, the statements of some authors regarding the existence of such a communication in certain Dorids are obviously incorrect. The auriculo-ventricular opening, which is a wide transverse slit, is guarded by two semi-circular valves, which appear to be the continuation of the ventricular walls projecting inside. valves prevent the passage of the blood back into the auricle when the ventricle contracts. This is effected by slender papillated ligaments which connect the auricular wall with the valves. It is probable that when the auricle filled with the blood contracts, the valves rise like a hinge mechanism aided by the pressure of the blood; but when it resumes its original form, the ligaments pull down the valves so that their straight edges meet preventing the blood from going back. the entrance to the aorta there is another pouch-like valve which consists of a thin transparent membrane attached to the base of the aorta except anteriorly where it is free; the blood from the ventricle flows over the valve into the aorta and its branches, but as soon as it tries to flow backwards, the space between the valve and the lumen of the aorta gets filled and the passage is blocked.

Arterial circulation.—The main aorta arises above the ventricle (text-fig. 12) and divides immediately into three branches. The one lying to the left bends down, passes between the pericardium, and on reaching the mass of the hepatic gland divides into two branches, one ventral to the gland and the other dorsal. The right aortic branch has a similar course, reaching the digestive gland on its right side and giving off branches on the dorsal surface only. All these branches ramify in the hermaphrodite gland over the mass of the digestive gland and the ultimate minute branches enter the substance of this gland. Some of these minute branches are also in intimate connection with the kidney ramifications seen in the mass of the digestive gland.

The median branch or the anterior agrta at a distance of 1.2 cms. from its origin gives off from its left side about half a dozen minor branches which end in bunches of follicles of the blood gland (bl. gl.). One of these is considerably stouter than the others, and has some of its branches ending in follicles of this gland; but the main stem is continued forwards to supply the brain with blood. As the anterior agrta proceeds forwards slightly to the right, it gives off a branch (ge. art.) to the anterior genitalia. This artery gives off branches (her. d.) to the hermaphrodite duct, the albuminous gland (al. gl.) and the penis-sheath The branch to the albumen gland divides further to form a close network over that gland. Before the genital artery is given off there arises from the aorta another small artery which supplies the spermatheca and the prostate gland. Then the anterior agrta turns slightly to the left and bending over the anterior genitalia reaches the ventral side where it divides into two branches. An anterior branch running straight along the median line on the ventral surface of the buccal mass gives off a short branch to the radular sac (rd. s.) and proceeds forwards to reach the oral tube, where it bifurcates supplying the outer

lips and the surrounding parts (o. li.). The other branch of the anterior aorta proceeds posteriorly supplying the foot with blood.

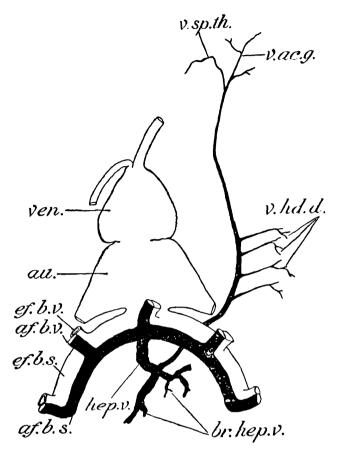


TEXT-FIG. 12.—Arterial system.

al. gl. branches to the albumen gland; au. auricle; bl. gl. blood gland; br. bl. gl. branches to the blood gland; ge. art. genital artery; hep. art. hepatic artery of the left side; hep. art. same of the right side; her. d. to the ampulla of the hermaphrodite duct; o. li. to the outer lips and the surrounding regions; op. lat. opening of the lateral vein into the auricle; p., p2, p3 and p4. branches of the pedal artery supplying the foot; pe. to the penis; pr. to the prostate; rd. s. to the buccal mass in the region of the radular sac; s. o. g. to the supra-oesophageal ganglionic mass; sp. t. to the spermatheca; ven. ventricle.

Veins and Branchial Circulation.—The arterial blood, after circulation throughout the body tissues, is received into the auricle from two sources: (i) from the skin or the body-wall proper, and (ii) from the branchial system (text-fig. 13). The great hepatic vein (hep. v.), which has its ramifications in the mass of the digestive gland, collects the blood from the hermaphrodite gland, the kidney and the digestive gland after they receive their supply from the hepatic arteries. The blood from the ampulla of the hermaphrodite duct (v. hd. d.), the spermatheca and the prostate is collected by various minute branches which unite into a small vein to join the great hepatic vein at its origin. This vein from the ampulla of the hermaphrodite duct, the spermatheca and the prostate

is, I believe, described here for the first time. In regard to *Doris*, Hancock and Embleton (1852) say, "In the viscera except in the liver mass and the skin after repeated injections and examination, we have

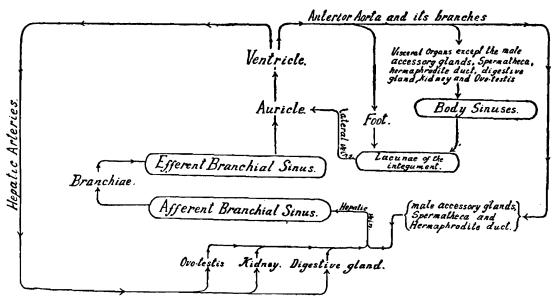


TEXT-FIG. 13.—Venous system.

au. auricle; af. b. s. afferent branchial sinus; af. b. v. afferent branchial vein; br. hep. v. branches of the hepatic vein; ef. b. s. efferent branchial sinus; ef. b. v. efferent branchial vein; hep. v. hepatic vein; v. ac. g. vein from the accessory reproductive gland; ven. ventricle; v. hd. d. veins from the hermaphrodite duct; v. sp. th. vein from the spermatheca.

failed to discover veins" Eliot (1910) verifying these results came to the same conclusion. The common hepatic vein after receiving all the branches comes up vertically through the hepatic groove and opens into a semi-circular afferent branchial loop or sinus (af. b. s.) lodged in the mantle in the region of the branchiae. In front this loop gives off the afferent branchial veins to the median, right and left anterior gilltrees; and its two ends are continued as the afferent branchial veins into the right and left posterior gill-trees. All these afferent branchial veins (af. b. v.) running along the inner side of the branchiae give off branches into the branchial pinnae. The blood passing through these membranous branchiae becomes aerated and is collected by the efferent branchial veins (ef. b. v.) lying along the external side of the gills. efferent vessels of the five gill-trees open into another semi-circular loop or sinus (ef. b. s.) lying externally to the one described above. external sinus communicates directly with the auricle by a median ventral opening; unlike Doris there is no efferent vein connecting the auricle and the sinus.

The blood from the anterior genitalia, the hermaphrodite duct, the liver, the kidney and the hermaphrodite gland is thus efficiently aerated in the branchiae and returned to the auricle. In all probability, blood from other regions of the body percolates, as has been suggested by Eliot and others, into a system of inter-visceral blood spaces or sinuses constituting the haemocoel, and passes into the lacunae in the integument, wherefrom it is collected by two lateral veins, one on either side, which open into the auricle posteriorly. Blood thus brought into the auricle through these veins is only partly aerated in the skin.



TEXT-FIG. 14.—Course of Circulation.

Blood Gland.—" It is a spongy glandular-looking organ analogous to some of the vascular ductless glands of the Vertebrata", say Hancock and Embleton in their description of the anatomy of Doris. Eliot (1910) says, "The functions of this gland have not been ascertained with preci-There are indications that it provides some of the constituents of the blood, as the colourless circulating fluid may be termed for brevity, and that it produces phagocytic cells which destroy pathogenic It is present in the Bullids and Pleurobranchus among microbes" the Tectibranchs, and in all Dorids among the Nudibranchiata; in Cladohepatica, however, it is rarely present. When it occurs, as in Bathydoris, in the region of the kidney it is said to be very primitive. In Kalinga ornata this gland (text-fig. 2, bl. g.), consisting of bunches of glandular follicles, lies slightly to the right side of the central nervous system, partly hides the anterior genital mass and communicates with the vascular system by the arterial branches arising from the anterior aorta. In Bouin-fixed material, stained with Mayer's haemalum, a number of loose cells with round nuclei are seen inside this gland and similar cells are also present free in the arterial branches. When observed fresh under a high power of the microscope the cells exhibit pseudopodial processes, and probably correspond to the phagocytic cells mentioned above.

The pericardial glands, which are generally present in the Gastropoda and whose function is supposed to be excretory, are absent in this form,

RESPIRATORY SYSTEM.

The chief respiratory organs are the branchiae, but the skin also has an accessory respiratory function. The branchiae are five, pinnately branched and arranged in a semi-circle in the region of the anus. Their colouration, arrangement and blood supply have already been described. In a transverse section (text-fig. 15) the branchiae show a non-ciliated epithelium, underlying which there is the loose connective tissue (l. ct.) with the afferent branchial veins (af. b. v.) running internally and efferent veins (ef. b. v.) externally. The two veins are separated by connective tissue through which, as shown in the figure, the muscle strands (l.s.m.) run lengthwise. There are no capillaries, and the blood passing through the fine branches in the minute plumes or pinnules is collected by similar branches of the efferent veins. Internally beneath the epithelium, there are numerous oval multicellular glands (gl. m.) with narrow ducts opening externally between the pinnules (pin.).



Text-fig. 15.—Transverse section of a branchial plume. xca. 35.

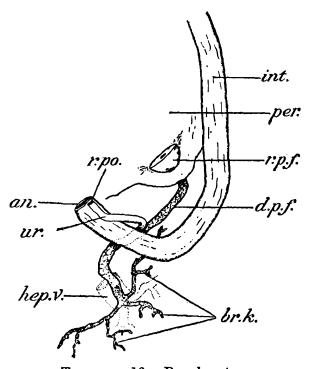
af. b. v. afferent branchial vein; b. n. one of the branchial nerves cut in section; b. pin. branch of the vein to the pinnules; br'. branch to the pinnules of the other side; ef. b. v. efferent branchial vein; gl. m. multicellular glands; l. ct. loose connective tissue; l. s. m. longitudinal strands of muscle; o. epi. outer epithelium; pin. pinnules.

The skin, being soft, free from spicules and beset with a number of papillated tufts, also acts as an accessory organ for the exchange of gases.

RENAL SYSTEM.

The renal system (text-fig. 16) consists of (i) the kidney with its ramifications spread in the mass of the digestive gland, (ii) the ureter (ur.) arising from the kidney and opening externally by the side of the anus and (iii) the reno-pericardial funnel (r. p. f.) with its duct communicating with the pericardial chamber on the one hand and with the ureter on the other.

Kidney.—The kidney consists of a few ramifications in the connective tissue, which fills up the interspaces between the follicles of the mass of the digestive gland. Its walls are supplied with blood from the branches of the hepatic arteries, and the waste products are extracted by special cells lining the kidney.



Text-fig. 16.—Renal system.

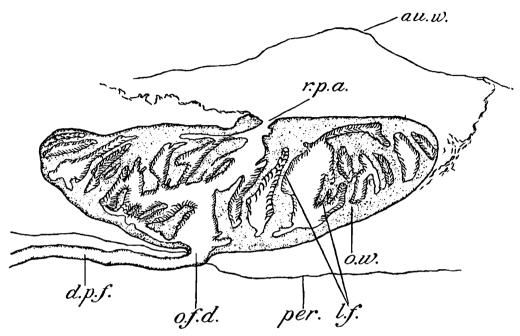
an. anus; br. k. ramifications of the kidney; d. p. f. duct of the reno-pericardial funnel; hep. v. hepatic vein; int. intestine; per. pericardium; r. p. f. reno-pericardial funnel; r. po. renal pore; ur. ureter.

The kidney in *Plocamophorus ceylonicus*, one of the Polyceridae, as described by Hancock (1864) extends between the anterior and the posterior lobes of the digestive gland in contact with the hepatic vein and terminates in a simple blind caecum; in *Doris tuberculata* it lies externally over the hermaphrodite gland; in *Melibe* the branches more or less follow the ramifications of the hepatic lobules which extend throughout the body-cavity; and in *Kalinga ornata* the ramifications are very few and lie well within the mass of the digestive gland.

Ureter.—The ureter (text-fig. 16, ur.) from the kidney is a thin semi-transparent duct about 8 mm. long. It follows the course of the hepatic vein, and piercing the wall of the back opens externally by the single pore (r. po.). About half way up it receives the duct of the reno-pericardial funnel. It is lined by an internal syncytial layer and an external thin fibrous layer. Near the cells of the internal layer there appear vacuoles of various sizes which seem to break up into the lumen of the ureter. Similar vacuoles were noticed in the ureter of Melibe leonina by Agersborg (1923), who suggested that the excretory product formed near the nuclei appears first in small vacuoles which later unite to form larger vacuoles and discharge their contents into the lumen of the ureter.

Reno-pericardial Funnel.—This structure has received different names such as the pyriform vesicle, the portal heart, the accessory renal or hepatic heart (Hancock and Embleton 1852), pericardial trichter

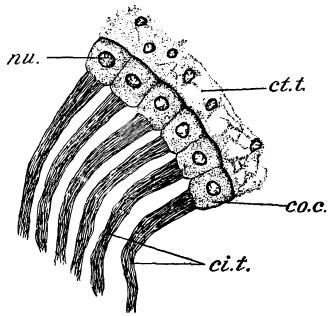
(Von Jhering), syrinx renalis or renal syrinx (Bergh), nierenspitze, etc. Some of these names are suggestive of its function, a few of its shape and position, while the others are mere misnomers. The terms, portal heart and accessory heart, applied by Hancock and Embleton introduce, according to Eliot (1910), confusion with regard to its function.



TEXT-FIG. 17.—Longitudinal section through the reno-pericardial funnel.

au. w. auricular wall; d. p. f. duct of the pericardial funnel; l. f. longitudinal folds bearing large tufts of cilia; o. f. d. opening of the funnel into its duct; o. w. outer wall of the funnel; per. pericardium; r. p. a. reno-pericardial aperture.

In Kalinga ornata the reno-pericardial funnel (text-fig. 16, r. p. f.) is an orange yellow, hollow, cup-shaped organ, 3.5 mm. by 2.5 mm., with its outer edge turned inwards to form a circular orifice. It lies in the right posterior corner of the pericardial chamber almost touching the auricular wall (text-fig. 17) where the right lateral vein enters the auricle and, as has been mentioned elsewhere, is held in position by a few fine fibrous strands arising from the auricular wall. In Doris and in Eolis figured by Hancock and Embleton (1848 and 1852) the funnel lies in apposition to the wall of the pericardium, and communicates with it, whereas in Kalinga ornata it lies within the pericardial chamber. From the narrow end of the funnel arises a thin translucent duct about 3-4 mm. long, and joins the ureter after piercing the pericardial wall. Unlike Tritonia hombergi (Hancock 1864) the wall of the funnel does not show any muscles. Internally as in all Nudibranchs, it is longitudinally plicated, the folds projecting into the lumen almost to the The lining membrane over these folds is formed of moderately long columnar cells (text-fig. 18, co. c.) with fairly large nuclei (nu.) and tufts of cilia (ci. t.) several times longer than the cells themselves. The ciliary tufts of the individual cells are separate. The lining membrane of the lower fourth of the funnel does not bear any cilia, and the duct arises from this region. External to the lining membrane, there is a fibrous wall showing rather round nuclei. There is a definite renopericardial aperture (text-fig. 17, r. p. a.) in Kalinga ornata unlike Melibe leonina in which Agersborg (1923) described a syncytial plate, which covers the reno-pericardial opening. In carefully prepared serial sec-



Text-fig. 18.—Ciliated cells lining the folds of the renal funnel. $\times 600$. ci. t. ciliary tufts; co. c. moderately tall columnar cells; ct. t. connective tissue of the outer wall of the funnel; nu. nuclei.

tions I did not find any such syncytial plate, but only a clear orifice communicating with the pericardial chamber. In this respect it agrees with *Dirona picta* where MacFarland (1912) describes such a communication.

NERVOUS SYSTEM.

The nervous system of Kalinga ornata (text-figs. 2 and 19), as in other Dorids, can be divided into two parts (i) the central nervous system with its commissures and peripheral nerves, which can be compared, according to Hancock and Embleton (1852), to the excitomotor or the cerebro-spinal system of Vertebrata, and (ii) the sympathetic system or, as has been suggested by Sir Charles Eliot (1910), the accessory nervous system which forms an extensive network over the viscera where it reveals a number of sympathetic ganglia.

The central nervous system, consisting of a small ganglionic mass (text-figs. 2 and 19, s. o. g.) enclosed in a thin translucent capsule of connective tissue, is placed on the roof of the buccal mass, where the oesophagus takes its origin. With its enclosing capsule the dimensions of this supra-oesophageal mass are 3.5-4 mm. from side to side and 2.5-3 mm. from back to front in a full-grown specimen. It is completely surrounded by small capsules or globules of nerve matter the function of which is very little known. The actual ganglionic mass is much smaller. The brain of Kalinga ornata shows a very great concentration of ganglia as in Hexabranchus, and is extremely small in porportion to the size of the body though in such small forms as Eolis and Scyllea the ganglia in the brain can be made out easily with a hand-lens. For this reason, sections of the supra-oesophageal ganglionic mass were made by the

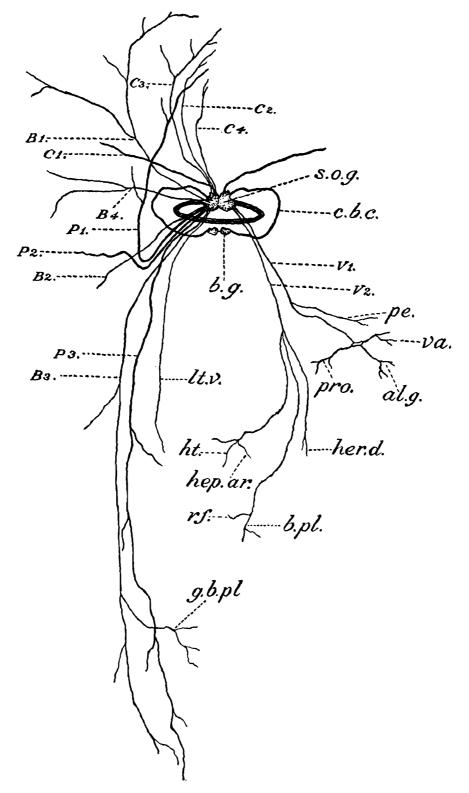
usual double embedding method, and stained with Delafield's Haematoxylin and eosin. The serial sections reveal a pair of small ovoid cerebral ganglia, a pair of branchial or pleural ganglia closely pressed against and almost fused with the cerebrals, and a pair of pedal ganglia. Since the cerebral and pleural ganglia are, as in many Dorids, more or less fused together, they may be called the cerebro-pleural in conformity with the terminology of several authors; its double nature, however, is seen clearly in transverse sections of the mass. ganglia lie posterior to and beneath the pleural. From the antero-dorsal region of the cerebral portion of the cerebro-pleural ganglion there arises the paired sessile rhinophoral or olfactory ganglion which is several times smaller than the cerebral. Lying beneath the posterior region of the right branchial and pedal ganglia is the unpaired visceral ganglion which is slightly smaller than the rhinophoral ganglion. The cerebrals are united by a very short commissure, while a distinct commissure does not exist between the cerebral and the pleural as they are almost fused; the pedal and the branchial are connected by commissure.

From behind the origin of the fourth pair of cerebral nerves, a pair of stout nerve trunks, the cerebro-buccal connectives arise, which passing round the oesophagus join the elliptical buccal ganglia (b. g.) to form a complete collar round the oesophagus. Close to this collar is another stouter collar consisting of three cords without ganglia on the inferior side of the oesophagus. Two of these cords connect the pedal ganglia while the third connects the left branchial on the one side and the unpaired visceral on the other. Whether the third collar is present in Kalinga ornata as in Archidoris is still to be verified.

Nerves from the Cerebral Ganglia.—A pair of stout nerves (C1) from the dorso-lateral region of the rhinophoral ganglia supplies the rhinophores. A second pair of cerebral nerves (C2) passing along the roof of the buccal mass supplies the anterior retractor muscles with branches. A third pair (C3) arising near the outer side of C2 supplies the oral tube, the oral tentacles and the outer lips. A fourth pair of cerebral nerves (C4) running down the buccal mass to near the oral tube supplies the buccal muscles. The nerves C2, C3 and C4, described above, all arise from the anterior region of the lower surface of the cerebral ganglion of either side. The next two pairs starting from these ganglia are extremely short and supply the eyes and otocysts.

Nerves from the Branchial Ganglia.—There are four pairs of pallial nerves arising from the branchial or the pleural ganglia. The first pair (B1) arises anteriorly from the branchials and passing forwards divides into two branches, which divide again to supply the papillae of the oral veil. The second pair (B2), arising from the postero-dorsal region of the branchials, supplies the middle region of the mantle. The third (B3), arising from about the same region, passes backwards to supply the mantle. The nerves of this pair in the region of the branchiae communicate with the branchial plexus of the sympathetic system. The fourth pair (B4) starts from about the middle region of the lower surface of the branchial and passing between the posterior retractor

muscles of the buccal mass divides into two branches which innervate the mantle region lying just behind the buccal mass. An unpaired



Text-fig. 19.—Nervous system.

C1 Rhinophoral nerve; C2, C3 and C4, other cerebral nerves.

B1, B2, B3 and B4, branchial nerves to the mantle. P1, P2 and P3, pedal nerves to the foot.

V1 and V2, first and second visceral nerves. tt. v. left visceral nerve starting from the left branchial ganglion.

al. g. nerve to the albumen gland; b. g. buccal ganglia; b. pl. branch from the visceral nerve to the branchial plexus; c. b. c. cerebro-buccal connective; g. b. pl. ganglion of the branchial plexus; her. d. to hermaphrodite duct; hep. ar. hepatic artery; ht. to heart; pe. to the penis sheath; pro. to the prostate; rf. branch to the renal funnel; s. o. g. supra-oesophageal ganglionic mass; va. to the vagina.

nerve from the left branchial, which is regarded as a visceral nerve, is described below.

Nerves from the Pedal Ganglia.—There are three comparatively stout pairs of pedal nerves (P1-3). The first bends under the posterior retractors of the buccal mass and supplies the anterior region of the foot; the second taking a similar course supplies the middle region; while the third passes backwards to innervate the whole of the middle and the posterior regions of the foot.

Nerves from the Visceral centres.—From the unpaired visceral ganglion mentioned above only two nerves were observed to take their origin. The first of these (V1) passes to the anterior genitalia and communicates with the sympathetic plexus of the genitalia innervating the vagina (va.), the albumen gland $(al.\ g.)$ and the prostate (pro.). This nerve sends a small branch about half-way down its course to the base of the penis sheath (pe.). The comparatively slender second visceral nerve (V2) gives a few branches to the blood gland and proceeds backwards dividing into three branches. One of them divides into branches at the base of the aorta supplying the heart (ht.), the pericardium and the hepatic arteries $(hep.\ ar.)$; the second, a slender nerve, supplies the reno-pericardial funnel (rf.) and finally joins the branchial plexus $(b.\ pl.)$ of the sympathetic system; while the third innervates the ampulla of the hermaphrodite duct $(her.\ d.)$.

A long slender visceral nerve (lt. v.) from the left branchial ganglion proceeds backwards to the hermaphrodite gland. Alder and Hancock (1845) describe a similar nerve in *Polycera quadrilineata*.

Nerves from the Buccal Ganglia.—A pair of buccal or infra-oesophageal or the stomatogastric ganglia (b. g.) is placed posteriorly on the buccal mass beneath the oesophagus. They are united by a short commissure and are connected to the cerebral ganglia by the cerebro-buccal connectives (c. b. c.). In some Nudibranchs there is a pair of gastro-oesophageal ganglia connected with the buccal ganglia. Alder and Hancock (1866) noted their absence in Kalinga ornata when they first described Three pairs of nerves arise from the buccal ganglia where the collar The first two pairs arise directly from the ganglia. nerves join them. whereas the third pair takes its origin from the collar. In one of the specimens examined, I found two pairs of nerves arising from the collar. The first pair passes slightly forward and divides into two branches, the posterior which proceeds along the oesophagus and the stomach to communicate with the sympathetic system and the anterior which runs forward on the roof of the buccal mass to supply the salivary glands and the muscles of the roof of the buccal mass. The next nerve arising from the ganglia supplies the roof of the buccal mass. The third pair, arising from the collar, supplies the muscles of the floor of the buccal mass. A pair of minute nerves, arising from the posterior region of the buccal ganglia, supplies the radular sac, and the posterior region of the buccal mass.

Sympathetic Nervous System.—This system in Kalinga ornata is neither as conspicuous as in Doris tuberculata nor so poorly developed as in Eolis and other forms; it is somewhat intermediate between the two types. It consists of various plexuses formed of nerve fibres and

minute ganglia, the latter being orange yellow in *Doris* and pale white in *Kalinga ornata*. One of the plexuses is seen over the anterior genitalia where it is connected with the central nervous system by the genital nerve of the visceral ganglion. A second plexus is seen over the stomach, the liver and the kidney communicating with the central nervous system through the gastro-oesophageal nerves arising from the buccal ganglia. A third is seen near the branchiae in the mantle forming what is known as the branchial plexus, which receives a branch from each of the third pair of branchial nerves. Serial sections of the entire animal reveal minute ganglia of this system all over the visceral organs and in the body-wall.

SENSE ORGANS.

The sense organs of *Kalinga ornata* comprise the eyes, the otocysts, the rhinophores, the labial folds, the lining of the oral tube, the general body-wall, and the papillated processes.

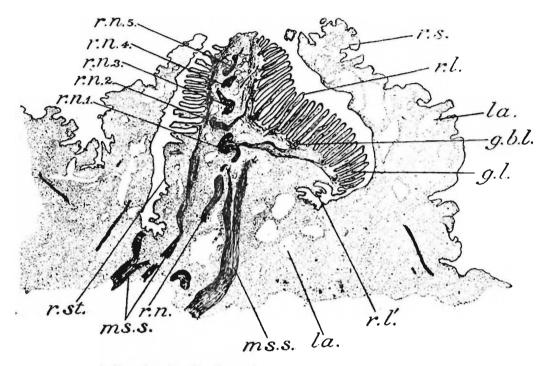
Eyes.—The eyes are present beneath the skin as two very minute black dots in the supra-oesophageal ganglionic mass close to the cerebral ganglia. They appear to be almost sessile on the cerebrals but carefully prepared serial sections reveal a very short nerve arising from the anterior face of these ganglia. Despite its very minute size and restricted function, the eye in Kalinga ornata is structurally well developed showing all the parts of a normally functioning Gastropod eye. Enclosed in a thin investing membranous capsule it consists of a cup-shaped pigmented retina accommodating a round globular lens over which lies a non-pigmented layer, the cornea. At the base of the retinal cup the optic nerve ends in a very small ganglion, from which radiate nerve fibres to supply the retinal cells. The skin that covers the eye being somewhat translucent, the animal can probably differentiate darkness from light, though perception of objects is not possible.

Otocysts.—Two tiny sacs placed dorsally on the cerebral ganglia reveal in each about 100 microscopical ovoid bodies, the otoliths or the otoconia, which when stained reveal a central and deeply stained part surrounded by a clear area. Each otocyst consists of a membranous capsule filled with a colourless fluid in which the otoliths float. These organs were for a long time supposed to be auditory in function but later Tschachotin (1908) in Heteropoda, and authors like Ilyn and Delage* on other Molluscs and Invertebrates in general, proved that they "maintain the equilibrium and regulate the exact position of the animal in space" For this reason these structures are appropriately termed statocysts and statoconia. The innervation of these organs as in other Nudibranchiata is from the cerebral ganglia.

Rhinophores.—The rhinophores or the dorsal tentacles are two club-shaped, retractile, lamellated and stalked structures situated on the back in the head region about 2 cm. from the oral veil. A description of their shape, appearance and colouration was included under the head 'External Features' of the animal. Their internal structure is rather complicated as they are traversed by nerve fibres, ganglia and muscle

^{*} As referred to by Prashad, Pila globosa, Mem. Ind. Mus. VIII, p. 145 (1925).

fibres. Serial sections of this organ reveal a conical lamellated part with a very much abbreviated stalk (text-fig. 20, r. st.) lodged in the sheath (r. s.). There are thirty-two well-formed lamellae (r. l.) and a few minor lobes (r. l.') at the base of the stalk. When the rhinophore is exserted the stalk is conspicuous, and the inner fold of the sheath is pulled out to form a real stalk, while the cavity of the sheath disappears.



Text-fig. 20.—Median longitudinal section of a rhinophore in its sheath drawn from a slide. $\times ca$. 35.

 $g.\ b.\ l.$ nerve ganglia at the base of the lamellae; $g.\ l.$ ganglia in the lamellae; la. lacunae; $ms.\ s.$ muscle strands; $r.\ l.$ lamellae of the rhinophore; $r.\ l.'$ minor lobes at the base of the rhinophore club; $r.\ n.,\ r.\ n1,\ r.\ n2,\ r.\ n3,\ r.\ n4$ and $r.\ n5$. rhinophoral nerve cut at various places as it passes in a slightly zigzag way; $r.\ s.$ rhinophore sheath; $r.\ st.$ rhinophore stalk.

The sheath is lined externally by the dermal epithelium which is a continuation of the epithelium of the body-wall. Underneath the epithelium there is loose connective tissue with lacunae (la.) filled with blood. The muscle strands (ms. s.) of the body-wall pass into the club-shaped head of the rhinophore and their fibres have their attachment near the bases of the lamellae, while a few pass into the lamellae also. Exsertion of the rhinophores is probably caused by the pressure of the blood which fills up the sinuses in the body-wall, and the retraction by the muscle strands described above. The rhinophoral nerve (r.n.) with its origin in the dorso-lateral region of the rhinophoral ganglion has a wavy course through the rhinophore to its very tip. A series of minute ganglia situated in and at the bases of the lamellae is connected by nerve fibres from the rhinophoral nerve. The epithelium lining the lamellae of Kalinga ornata is not ciliated.

The function of the rhinophores has not been definitely ascertained. Alder, Hancock and Embleton in describing various forms of Nudibranchs termed these structures as dorsal tentacles and attributed to them the sense of smell. Bergh called them 'rhinophores', a name which suggests their function to be olfactory. Eliot (1910) agreeing

with this view believed that the rhinophores enable these creatures to detect the presence of one another or of suitable food at a considerable distance. The reasons advanced by Hancock and Embleton (1852) in support of the view that these organs are olfactory in function are, that these organs are strongly innervated from the anteriormost regions of the cerebral ganglia, that the surface is laminated and that the epithelium bears vibratile cilia. While these facts show beyond doubt that these organs are highly sensitive and react to certain stimuli, it cannot be definitely said that they are discrete organs of smell or taste. who conducted several experiments on Nudibranchs says that it is safer to avoid such terms as the sense of smell or taste and believes that they respond to a general chemical stimulus, the power to respond to which is present all over the anterior part of the body-wall. Arey and Crozier* found that in Chromodoris the rhinophores are rheotropic in function, that when these organs are removed the animals lose their power of orientation while moving against the water currents. Agersborg (1922) in Hermissenda, however, observed that individuals deprived of these organs moved as easily against the current as the normal ones.

Other Sense Organs.—The labial folds and the lining of the oral tube are supposed to be the seat of sense of taste. The general body surface, especially the papillated processes and the branchiae, also respond to tactile stimulations.

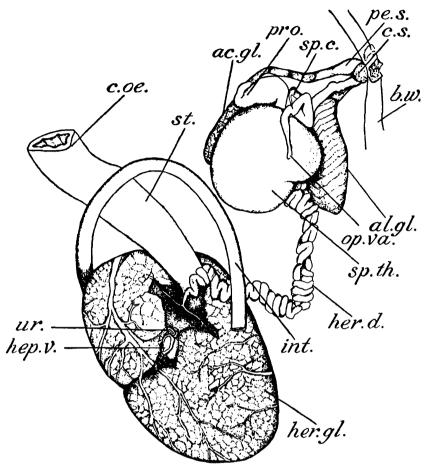
REPRODUCTIVE SYSTEM.

It consists of the hermaphrodite gland (text-fig. 21, her. gl.), the hermaphrodite duct (her. d.) and the anterior genital mass. All these parts, especially the anterior genitalia, attain considerable dimensions during the breeding season and occupy a very large space in the viscera. In its ducts it shows a typical triaulic condition.

Hermaphrodite Gland.—In a well-developed specimen the hermaphrodite gland (her. gl.) completely envelops the mass of the digestive gland excepting the region of the hepatic groove, and is profusely supplied with blood from the branches of the hepatic arteries. living animal this gland is externally deep brownish red and internally pale yellow in colour. In dorsal view it appears to be roughly divided into two lobes by the alimentary canal which fits into the hepatic groove, but ventrally it is continuous though compressed laterally to a certain extent between the stomach and the intestine. Sections of this gland fixed in Bouin's fluid, cut 6-7 \mu thick, and stained with iron haematoxylin and eosin reveal a number of acini of either sex, all intermingling and communicating at intervals as they run side by side. Such communications exist between the acini of the same sex as also of opposite sexes. Ova and spermatozoa in various stages of development can be recognized in different acini. In the Nudibranchs the real hermaphrodite gland was for a long time considered to be the ovarium and the vas deferens to be the testis, causing a great confusion in identifying the various parts of the reproductive system. According to Pelseneer

^{*} Arey and Crozier as referred to by Agersborg (1923).

(1895), it was Meckel who first showed the presence of the male and the female acini in the supposed ovarium, but he thought that the



Text-fig. 21.—Reproductive system showing the anterior genitalia and the hermaphrodite gland over the digestive gland. The stomach and the intestine are also shown.

ac. gl. accessory male gland; al. gl. albumen gland; b. w. body-wall; c. oe. cut end of the oesophagus; c. s. copulatory sac; hep. v. hepatic vein; her. d. hermaphrodite duct; her. gl. hermaphrodite gland; int. intestine; op. va. origin of the vagina from the spermatheca; pe. s. penis sheath; pro. prostate; sp. c. spermatocyst; sp. th. spermatheca; st. stomach; ur. ureter.

acini did not communicate with one another. Nordman* was the first to notice the intercommunication of the acini, but he supposed that the ovular acini opened into capsules full of spermatozoa. Like his predecessors he supposed the hermaphrodite gland to be the ovarium with capsules of spermatozoa which he called the fecundation pouches. A correct interpretation was, however, given by Leuckart for Eolis. He showed that the peripheral ovular acini open into the central acini, producing sperms. This was confirmed by Bergh, Pelseneer (1895) and others. In Kalinga ornata the arrangement of the acini is irregular, the male and the female acini running side by side and communicating with one another, but without distinct central and peripheral regions of exclusively sperm-producing and ova-producing acini respectively. A similar arrangement of the acini was also recorded by Eliot (1908) in the hermaphrodite gland of Doridoeides gardineri.

^{*} As referred by Pelseneer (1895).

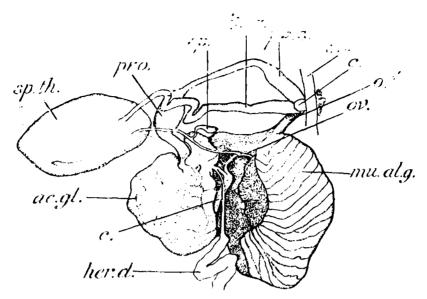
The gland is protandrous. In young specimens with very immature ova, the male acini clearly show well-developed sperms attached by their heads to the walls of the acini. Mature specimens reveal actual sperms as also fairly ripe ova in different acini. Along with these, spermatocytes and vocytes in various stages of growth are always present.

Hermaphrodite Duct.—Towards the anterior region of the hermaphrodite gland from each of its two lobes a minute duct is formed by a ramification of fine branches, which arise from the acini of the gland. These two ducts from the two lobes unite to form the hermaphrodite duct proper, which, very narrow at first, suddenly dilates into a broad duct (text-fig. 21, her. d.). It lies coiled to the right of the stomach between the anterior genital mass and the hermaphrodite gland. dilated part of the hermaphrodite duct, which is called the ampulla, is richly supplied with blood from a branch of the genital artery. its lumen fairly mature ova and a great number of spermatozoa are seen. A transverse section of the duct reveals an inner cellular layer and an outer fibrous layer. The cellular layer consists of ciliated columnar cells with fairly large oval nuclei. The hermaphrodite duct approaches the anterior genital mass and passes between the accessory male gland and the albuminous gland as a compressed narrow duct. On reaching the top region of these two glands, it suddenly bifurcates giving a very short left branch to the male genitalia and a right branch to the androgynous and the female genitalia.

The Anterior Genitalia.—In the anterior genital mass (text-figs. 21 and 22) which lies just behind the buccal mass and in front of the ampulla of the hermaphrodite duct can be recognised the male, the female and the androgynous organs with their ducts and accessory glands, all greatly pressed and united by connective tissue membranes. A close examination of the genital vestibule reveals the male, the vaginal and the oviducal openings.

The Male Genitalia.—Mention has already been made about the bifurcation of the hermaphrodite duct. Its left branch, which is very short, communicates with a spongy-looking gland (ac. gl.) that lies closely pressed against the muco-albuminous gland or the nidamental gland (test-fig. 22, mu. al. g.). The spermatozoa, which have been observed lying free in the hermaphrodite duct, are now seen in this accessory gland grouped into round or ovoid clusters forming the spermatophores. From the top corner of this gland a short wide thin-walled duct leads into a large ovate expansion, the prostate (pro.). Its walls are thick and glandular. A thin flat duct, about 20 mm. long, starts from the narrow end of the prostate and joins the penis sheath (textfigs. 21 and 22, pe. s.) which is 1.2 cms. long. The vas deferens passes through this thin flat duct and is followed by the penis with its basal wall in continuation of the penis sheath. Close to the base of the penis there are two folds of skin. The penis is armed with spines or "hacken bewaffnung" described and figured by Bergh (1890). They vary greatly in size and shape and can be seen lining the inner wall of the penis in its retracted condition. When the penis is everted they come to lie on the outer surface of the penis, and serve to secure firm hold on the vaginal tube of the mate during copulation,

Androgynous and Oviducal Organs.—The second division of the hermaphrodite duct from its point of bifurcation slightly bends down to the



Text-fig. 22.—Anterior genitalia of the reproductive system showing the ducts. ac. gl. accessory male gland; b. w. body-wall; c. caecum; c. s. copulatory sac; her. d. hermaphrodite duct; mu. al. g. muco-albuminous gland; ov. oviduct entering the muco-albuminous gland; ov¹. oviduct emerging out from the muco-albuminous gland; pe. s. penis sheath; pro. prostate; sp. c. spermatocyst; sp. th. spermatheca; vag. vagina.

right and communicates with a moderately long caecum (c.) 3-3.5 mm. long which lies pressed against the surface of the albuminous gland. Though I have not examined its contents microscopically yet from its shape, and position, and from the analogous structure, "the fertilization chamber", of Polycera quadrilineata figured and described by Pohl (1905), I believe that its function is to receive eggs and spermatozoa for fertilization. After communicating with the caecum the branch of the hermaphrodite duct runs slightly forwards and upwards on the surface of the albuminous gland and receives a narrow but tough duct from the spermatheca. It next enters the opaque albuminous gland and is continued into the mucous gland as a fairly wide greatly coiled ciliated tube. Finally it emerges from that gland on its extreme right top corner and opens externally by the oviducal opening for the deposition of the spawn.

The spermatheca or the receptaculum seminis (text-fig. 22, sp. th.) is a large roundish bag of reddish brown colour measuring about 15 mm. in diameter when full. Two ducts lead away from it, the vagina (vag.) opening to the exterior and the thin narrow passage communicating with the caecum mentioned above. This second duct receives on its way a still narrower duct approximately 2 mm. in length arising from a small pear-shaped body, the spermatocyst (sp. c.). The histological structure of the spermatheca is peculiar. Externally there is a thin muscular layer beneath which lies a comparatively thicker layer of loose connective tissue. Internally it is lined by a closely plicated glandular layer of columnar cells with three-fourths of their length free, and united only at their bases. The nuclei of these cells are large and oval; and from their staining reaction appear to be in a very active state. These cells

in Kalinga ornata differ from similar cells in Melibe described by Agersborg (1923) in that the nuclei in all the cells of the former occupy the distal half whereas in the latter they are basal in the majority of cells. The spermatheca examined by Agersborg contained both spermatozoa and ova and for this reason he designated it as the ovi-spermatheca. In Kalinga ornata during the breeding season the contents are only spermatozoa which are either free or packed into clusters. It, therefore, differs from Melibe in this respect and agrees with the Dorids in general.

The vagina (vag.) arising from the spermatheca (text-fig. 21, op. va.) is a fairly long highly muscular duct with an inner lining of glandular layer formed of columnar ciliated cells; this layer forms complex projections into the lumen. At its opening to the exterior, on either side, there is a small ovate saccular organ, which according to Bergh (1890) is the copulatory sac (c. s.).

BIOLOGICAL NOTES.

Kalinga ornata inhabits crevices of rocks submerged in shallow waters of the sea. Eliot (1910) remarked that "the Cladohepatica and Polyceridae are much more agile than the Dorids," but Kalinga ornata which is undoubtedly a Polycerid is as sluggish as the Dorids on account of the Dorid-like build of its body, as contrasted with the long, tailed forms like Polycera, Plocamopherus, etc., of this group.

Kalinga ornata is mainly carnivorous. Its food, as revealed by the stomach contents, consists of sponges, young lamellibranchs such as Pecten and Cardium, small Gastropods, and bits of Holothurians and Echinoids. It is very doubtful whether Kalinga ornata, without any organs of offence or defence except for the distasteful secretion of its dermal glands, can tackle any active fair-sized living prey. Probably it feeds on living as well as decaying animal matter available on the substratum on which it lives. From the nature of its radula and oral parts and from observations made on living specimens, the following conclusions are drawn regarding the method of its feeding. The animal applies the mouth to the prey bringing it more ventrally by a contraction of the ventro-lateral strands of the second set of anterior retractor Further, as a result of the relaxation of the first set of anterior retractors and the sphincter, the oral tube is widened and shortened. Then as a result of the movements of the odontophoral muscles, the odontophore and the radula are set into motion, rubbing against the hard surface of the labial disc. The prey caught between these two hard surfaces is crushed and at the same time rasped; the resultant scrapings are directed towards the oesophagus by the movement of the odontophore.

The eversion of the buccal organ is a very peculiar feature, which has been regularly observed in preserved specimens by all who studied Kalinga ornata. Eliot (1906) says "It is therefore clear that the buccal parts are habitually protruded in preserved specimens. But it is impossible to say whether this protrusion is due to convulsive action at the moment of death or whether the living animal can protrude its radula voluntarily. Information as to the feeding habits is much to be desired,". I have noticed eversion of the buccal organ both

in living and preserved specimens. When a living specimen of Kalinga ornata and a fish were brought together to the Laboratory in a small pot, the Nudibranch, perhaps as a result of the constant annoyance caused by the fish, had partly everted its buccal mass, which measured as much as the animal itself. It was coloured crimson on its upper surface, while its lower surface was of a somewhat lighter hue. that this organ serves to warn or frighten the approaching enemy. Like most Nudibranchs Kalinga ornata must be unpalatable to fishes and other animals owing to the presence of large number of mucous glands in the foot, the body-wall and the branchiae; the inedibility of brightly coloured animals is a wide-spread and well-known feature. As in the instance cited above I have observed eversion occurring in a healthy specimen and it may be concluded that it is within the direct control of the animal. The withdrawal of the buccal organ is also under the control of the animal if eversion has been carried only so far as not to cause any injury to the animal. It may be noted here that the eversion of the buccal organ brought about by convulsions before death, though similar, is very violent, and consequently the parts are very much torn. The fact that such an eversion takes place only when the animal is irritated indicates that the explanation suggested above is tenable. Such a display of bright colouration to warn enemies, is not uncommon. A tropical Dorid, Hexabranchus, acts similarly. According to Eliot (1910) it spreads out its bright red mantle region at the approach of the enemy as a warning; but when pursued further by the enemy, it hides its bright colouration by folding the mantle, and disappears from view. No mollusc protruding its buccal organ to display a warning colouration of this kind has hitherto been recorded.

Autotomy of the respiratory organs or the cerata in Eolids is very Though this phenomenon is unknown among the British Dorids, Eliot (1910) observed that Discodoris fragilis and a few others from the tropics having lost the entire mantle margin "remain in apparent good health" In Kalinga ornata I have often seen the absence of some of the branchiae, the mantle being scooped out in those places. In a few forms that I have observed some of the branchial trees were very small when compared with the rest. It is probable that they were regenerating branchiae. Strictly speaking, the term autotomy cannot be applied to the phenomenon observed here. In Eolids, where they are shed off voluntarily at the mere sight of the enemy it is undoubted autotomy. In Kalinga ornata, I have never observed the branchiae being shed spontaneously, or any structural modification of the branchiae enabling the breakage of the organs to take place along a definite weak zone. It seems to me therefore that what has been observed here is only a case of regeneration following injury caused by enemies, or by accident.

Very few parasites seem to infest this animal. On the back of the animal a pycnogonid, probably Nymphon parasiticum, and a few Copepod parasites have been noticed.

The animals are protandrous, and even though mature sperms have been noticed almost throughout the year the eggs ripen during the early summer, i.e., January and February. During these months copulation also takes place as a result of which their spermathecae are full of sperms.

SUMMARY.

- 1. A study of the complete external and internal morphology of *Kalinga* ornata has been attempted.
- 2. The structure of the buccal mass is described in detail and drawings of the various parts of the buccal organ under normal and everted conditions are reproduced.
- 3. The radular formula of Kalinga ornata is 100.0.100. The teeth are all similar. The independent movement of the radula over the odontophore is impossible; the former moves with the latter by the action of the odontophoral muscles.
- 4. The peculiar histological structure of the hepatic ducts is described.

 The Kalkzellen of the disgestive gland are absent. It is suggested that the intestine is the main absorptive region.
- 5. There is no endothelium lining either the auricle or the ventricle, and the muscles of the heart are directly bathed in blood. The circulatory system is described, and the presence of a vein which brings blood from the spermatheca, the prostate and the hermaphrodite duct is recorded.
- 6. The kidney ramifications are few in number; they penetrate the connective tissue of the digestive gland. The reno-pericardial funnel lies within the pericardial cavity and communicates with it by a distinct orifice. There are no pericardial glands in this form.
- 7. The central nervous system shows a very great concentration of the various ganglia.
- 8. The ovo-testis is protandrous. Ova and spermatozoa are produced in different acini, but there is no definite arrangement of these acini. The genital vestibule shows three openings, viz., the male, the vaginal and the oviducal. In addition to the prostate there is an accessory gland in connection with the male genitalia. A small caecum communicates with the oviduct; and it acts in all probability, as a fertilization chamber.
- 9. Its habitat, food and the method of feeding are described. The animal protrudes its buccal organ to display a warning colouration. A Pycnogonid and a few Copepod Crustaceans on the back of the animal as external parasites are recorded.

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