

Calma Glaucoides: A study in adaptation.

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With Plate 11 and 3 Text-figures.

A DETAILED description of certain portions of the anatomy of a small British mollusc is here submitted, not so much as an extension of our knowledge of molluscan structure, as on account of the general biological interest of a unique metabolic type.

Whilst retaining the shape and general structural plan of an aeolidiomorph Nudibranch, *Calma* presents a combination of important departures from that type which may all be directly or indirectly referred to its specialized diet, namely, the eggs and embryos of the smaller shore fishes. So close is the external resemblance to the Aeolid that Alder and Hancock originally (1, Pl. xxii, letterpress) placed it in Cuvier's genus *Eolis*, whereas the modifications to be described are in some respects so great as to be comparable with those associated with a parasitic life.

The genus has been recorded only from European waters, and contains *Calma glaucoides* of Alder and Hancock, commonly taken at Plymouth, Roscoff, and Concarneau, the *Eolis albicans* of Friele and Hansen (5) from the North Atlantic, and the *Forestia mirabilis* of Trinchese (9) from the Mediterranean. All three will probably be found on re-examination to belong to one species, *C. glaucoides*.

At Roscoff, Hecht (6) found the animal feeding during June and July on developing eggs of *Cottus*, *Lepadogaster* and *Liparis* under stones, and in September in the swollen radical

sacs of *Laminaria flexicaulis*. The cavities of these sacs are rendered accessible to the smaller fish by the boring activities of various Prosobranchs, notably *Helecion*. The author collected *Calma* in August at Concarneau on *Lepadogaster* eggs in *Laminaria* sacs, while Dr. Allen reports that at Plymouth the animal is taken during the summer months on eggs of *Blennius ocellaris* and *Gobius minutus*.

EXTERNAL APPEARANCE (fig. 1).

When full grown *Calma glaucoides* is about half an inch in length, specimens obtained from Plymouth varying from 0.25 cm. to 1.3 cm. The body is depressed except when much distended with food. The very broad foot (0.3 cm. in large specimens) has a curved thick anterior rim, passing laterally into processes capable of extension. The rhinophores (*rh.*) and cephalic tentacles (*c.t.*) are smooth and of moderate length. Linear cerata, sometimes thrown into a pyriform shape by the contained food, are arranged in ten or eleven pairs of lateral groups, varying in number of cerata from four in front to two or one behind. The members of a group are not arranged in a row as in the *Aeolididae*, but irregularly, the smaller ones being ventral. In even quite young individuals the pale yellowish rosettes of the gonads (*g.*) can be seen in the angles between the bases of the groups of cerata, the grey centre of the rosette being the large male acinus, round which the numerous female acini are set. The pericardial hump (*pc.*) lies on the right opposite the space between the second and third groups of cerata, and with a strong lens the renal opening (*r.o.*) can be made out to the right of it in front. This was mistaken by Trinchese for the anal opening. With the exception of silvery white dots on the tentacles and cerata, representing gland-cells, and the opaque whiteness of the pedal glands which are especially richly distributed anteriorly, the integument is transparent, and the colour of the animal varies with the condition of the stomach contents and the gonads. In general, it is a dull greyish white in which the pigment of embryonic eyes may show as black dots. Hecht (*loc. cit.*) makes much of the protective value

of this inevitable colour resemblance of Calma to the spawn on which it feeds, and in one English text-book the argument for protective coloration is enhanced through careless quotation of Hecht, the fish spawn being thereby represented as laid on stones and roots of Laminaria. As, however, the spawn is laid under the stones and within the radical sacs, the value of the colour resemblance seems very questionable, especially if the cause of it be also considered.

INTERNAL ANATOMY.

Although Alder and Hancock (1) had referred to the simple wide alimentary tract and the regular lateral repetition of the gonads, the only considerable description of the internal anatomy is that of Trinchese (9). Excluding certain errors such as the identification of the renal pores as the anus, and the saccular kidney as the great dorsal vein, Trinchese's account, so far as it goes, applies well to the British species. His description of the radula and the contents of the gut added to that of the external features places the generic identity of Forestia and Calma beyond question. In fact there appears to be no reason for giving the Mediterranean form separate specific rank. It is curious that Trinchese did not recognize the spheres which he saw in the semi-digested food as the lenses of embryonic fishes. Hecht (6) gives a faithful description of the kidney in its relation to the pericardium, but represents the former as extending to the end of the body, whereas in all the numerous specimens examined for this paper the kidney lay entirely in front of the seventh ceratal group. Sir Charles Eliot's revision of the genus (3 and 4) served to establish its generic character, to collect together the scattered Calmas of the literature and to exclude from among them Calma cavolini of various authors which possesses none of the special anatomical characters of a Calma. He emphasized the peculiar nature of the radula, the great size of the stomach, the absence of cnidosacs, and the mode of grouping of the gonadial units as modifications correlated with the specialized diet. To him the author's thanks are due for an introduction

to Calma. In the account that follows the digestive system claims first place, not only because it shows the most extensive aberration from type but because it provides the key to the meaning of other topographical and histological changes.

The Digestive System.—The facial aspect of the animal in repose is rather flat and directed forwards and downwards. Below the middle of its smooth surface is a conical depression leading to the small oval mouth. In the act of eating the face fits like a hood on the egg and is capable of considerable extension. In this position the animal looks very aggressive, especially when the pressure which results in the swallowing of the embryo is exerted. In the meanwhile the narrow odontophore bearing the saw-like radula has been protruded into the oral opening and the act of slitting the egg-membrane performed. This muscular odontophore (fig. 2, *rad.*), which is very narrow at the protruded edge, is broadly based behind and on the floor of the buccal cavity. It is covered by a cuticle which is continuous under the radula and with the general buccal lining. Laterally the buccal cavity is largely occupied by a pair of muscular pads bearing smooth jaws, which are local thickenings of the buccal cuticle (*j.*). These come into action in the act of swallowing. Between them is a strongly cuticularized ventral groove in which the odontophore moves. The groove continues forward into a cavity in the ventral lip which acts as a reservoir for the very massive buccal glands.

Previous descriptions of the radula (fig. 3) have represented it as a continuous ribbon finely serrated at the edge like a bent saw, thus contrasting it strongly with other uniseriate radulae consisting of separate teeth carried on a basal dentigerous strip. The examination of transverse sections, however, shows that the profile view obtained in potash preparations is misleading, and that this radula is less of a neomorph than was supposed. It is constructed on the fret-saw principle, teeth not unlike those of the Aeolids being borne on a stout bent cylindrical rod (*b.r.*) secreted by the bed-cells of the radular sac. The teeth are as usual formed by the roof-cells of the sac and sit

closely equitant on the rod. In sections stained with iron haematoxylin and acid fuchsin this rod, which is the homologue of the basal membrane of other radula, takes the acid dye, while the teeth are a deep black. Even in potash preparations the faint lines of demarcation of the individual teeth can be made out under an oil immersion lens (see fig. 4). To the stoutness of the basal rod is due the fact that the radula is always obtained complete and undistorted in preparations, as well as its efficiency as a cutter of membranes. The most interesting feature of the Calma radula, however, is the preservation at its anterior end of the small first-formed teeth to the number of four or more. These minute persistent teeth (fig. 4, 1-5) are spaced out on their thin basal membrane and closely resemble those of the uniseriate radula of Favorinus, being without lateral denticulations. The basal membrane is continuous in front with the thick rod of the later radula. Between this early normal Aeolidian radula and that of the adult is a gap in which the dentigerous strip is already thickening, but the teeth themselves are imperfect. Numbers 5 and 6 of the figure look like imperfect Aeolidian teeth, while the remainder of the gap contains irregular serrulations suggesting the incipient adult structure. As this sequence is remarkably constant, it is evident that here in the radula of Calma we have a concise record of the change that occurs in the feeding methods of the animal, for it is unimaginable that the minute adult at the beginning of its career is capable of feeding on the eggs of fishes. It is still more interesting as the preserved record of the evolution of the Calma type from a more generalized carnivorous Aeolid.

The post-bulbar salivary glands (Text-fig. 1, *s.g.*) consist of a pair of simple tubes, the walls of the distal part of which contain very large granular cells. These bulge out singly or in groups of two or three, and their cell-contents stain deeply with the basic dyes. The salivary ducts pass through the nerve-ring to open into the buccal cavity at the posterior ventral edge of the lateral pads.

The oesophagus is short and narrow, but its walls are

thrown into longitudinal folds so that whole fish embryos pass through it unmutilated. Good serial sections of these are often obtained in microtome preparations.

The rest of the alimentary system consists of a spacious bag (Text-fig. 1, *g.s.*) extending to the end of the body together with its glandular diverticula into the cerata. In a well-fed specimen

TEXT-FIG. 1.

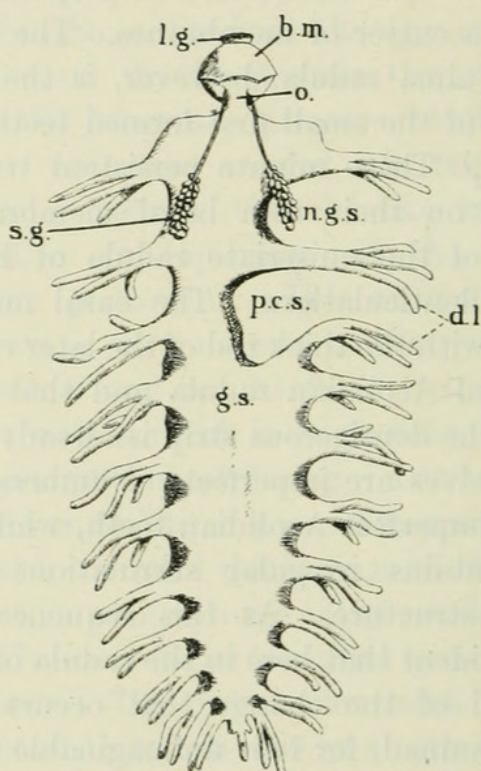


Diagram of the alimentary system. *b.m.*, buccal mass ; *d.l.*, hepatic diverticula ; *g.s.*, gastric sac ; *l.g.*, labial glands ; *n.g.s.*, space occupied by the nidamental part of the oviduct ; *p.c.s.*, space occupied by the pericardium and anterior part of the kidney ; *o.*, oesophagus ; *s.g.*, salivary gland.

this sac is so distended as to displace such loose structures as the salivary glands and the male duct into the head region above the brain and buccal mass, while the swollen ceratal diverticula may give the cerata an ovoid shape. The appearance of a common ceratal stalk observed by Alder and Hancock and suggested as a characteristic of *Calma* is also a temporary result of distension. On the right the sac is deeply constricted

and indented by the pericardium (*p.c.s.*) and anteriorly to that by the ootype (*n.g.s.*). Thus two chambers are connected by a narrow tube, but neither their histological structure nor their function justifies their being regarded as other than mechanically separated portions of a continuous food reservoir. The lining-cells of the gastric-sac are low and flat even when it is more or less empty, while the cells of the ceratal diverticula are very large and extensively vacuolated during active digestion. A comparison of these hepato-pancreatic cells in the active state (fig. 5, *d.c.*), and the tenuous squames that line the full stomach (fig. 8), strongly suggests that the former are responsible for the bulk of the digestive juices in Calma. The fish embryos (fig. 8, *s.e.*), whether very young or considerably developed when eaten, are, however, partly disintegrated in situ in the stomach, probably by enzymes delivered from the ceratal glands (fig. 8, *d.l.*), which at this stage are uninvaded by the food. Later the stomach contains a semifluid mass in which lenses of eyes (fig. 8, *l.*) and scattered lumps of undigested nuclei are the only remaining evidences of the nature of the food. During further digestion this thick fluid is continuously delivered into the cerata, where it undergoes solution (fig. 9, *d.l.*). An animal fixed at this stage is difficult to cut on account of the extremely hard consistency of the precipitated proteins. The gland-cells of the ceratal outgrowths (fig. 5, *d.c.*) project deeply into the food; no evidence of ingestion could be found, though fine brown granules similar to the eventual residuum in the whole system accumulate in them and are extruded into the lumen.

There is no trace of anus or intestine. The small amount of undigested matter remains as a dark-brown core (fig. 9, *d.*) throughout the alimentary system, so that the shape of this system can be made out in a fasting animal by clearing alone. On account of a certain amount of compression of this faecal residue during the fast there is no admixture with a subsequent meal. In connexion with the digestive system must be mentioned certain special connective-tissue cells (figs. 8 and 9, *c.s.*) of the cerata which differ widely from those of the rest of the

body in structure and function. These, while retaining their connecting processes and their position as lining-cells of the ceratal blood-spaces (fig. 5, *b.s.*), are at times among the largest cells in the body and exhibit remarkable secretory activities during the period of digestion of a meal in the neighbouring gut diverticula. At the same time they increase greatly in size till, finally, their identity as cells of the connective tissue is obscured, and only a thin envelope continuous with the processes (fig. 6, *e.*) is free from accumulated secretion staining deeply with basic dyes. Simultaneously with the deposition of stainable material in the cytoplasm, a clear non-staining sphere (fig. 6, *n.b.*) grows within the nucleolus, which in fixed tissue is so hard as to be frequently displaced or torn out by the microtome knife. In specimens with empty stomachs these cells are found in various stages of reduction in size, an early stage of reduction and solution of the deuteroplasmic contents being shown in fig. 6, while fig. 5 shows normal, faintly granular cells in which the nucleolar body is absent. Hecht (*loc. cit.*) notifies these cells as 'cellules spéciales', the significance of which he discusses without offering a final judgement. He draws them as loose cells and seems not to have recognized their essential conjunctive nature, but compares them with the large rounded or oval cells found in the ceratal connective tissue of *Galvina* and other *Aeolidiomorpha* previously described by Herdman (7). Comparison of sections of animals at different stages of the alimentary cycle appears to provide convincing evidence that both the secretum of the cell-body and the refringent spherule of the nucleolus grow during digestion and disappear during a fast. On account of their structure, the readiness with which they take up both basic and acid dyes, their position, on the one hand close to the absorptive cells of the gut, and on the other on the walls of the blood-spaces, and lastly on account of the significant variation of their contents during a digestive cycle, it is here proposed to regard them as protein storage cells. The agreement in phase between the granular deuteroplasm and the nucleolar secretion is in keeping with this explanation, and

suggests a zymogenic character for the latter. The cell of fig. 6 is on the metabolic down-grade; the more centrally placed secretion has been brought into solution, and the streaming enzyme from the nucleus has also attacked the periphery. The necessity of means of storage must be present in all organisms depending on a precarious food supply, but a peculiar spatial relationship exists in Calma between gut and gonad, which makes it advisable to postpone the discussion of the utility of these cells until after the reproductive system has been described.

The Nervous System (fig. 7) resembles closely that of Facelina and other Aeolids with uniseriate radulae. The following points are to be noted:

- (1) The large dorsal ganglia (*cp.g.*) contain the cerebral centres and all the ganglionic elements of the visceral commissure. The short unbeaded visceral loop (*v.l.*) gives but one visceral nerve which sends a branch to the gastro-oesophageal anastomosis and continues into the reno-cardiac plexus, and probably the gonad.
- (2) The rest of the reproductive system is innervated from a stout nerve (*g.n.*) arising from the right dorso-pedal connective. This nerve consists of fibres derived chiefly from the dorsal ganglion, and some pedal fibres.
- (3) There are large rhinophorial ganglia (*rh.g.*), and the optic ganglia (*o.g.*) are also outside the dorsal mass.
- (4) The parapedal commissure (*pp.c.*) is distinct from the pedal.
- (5) The eyes and statocysts (*ot.*) are placed, as in most Aeolididae, dorso-laterally in the angle between the pedal and dorsal ganglia.

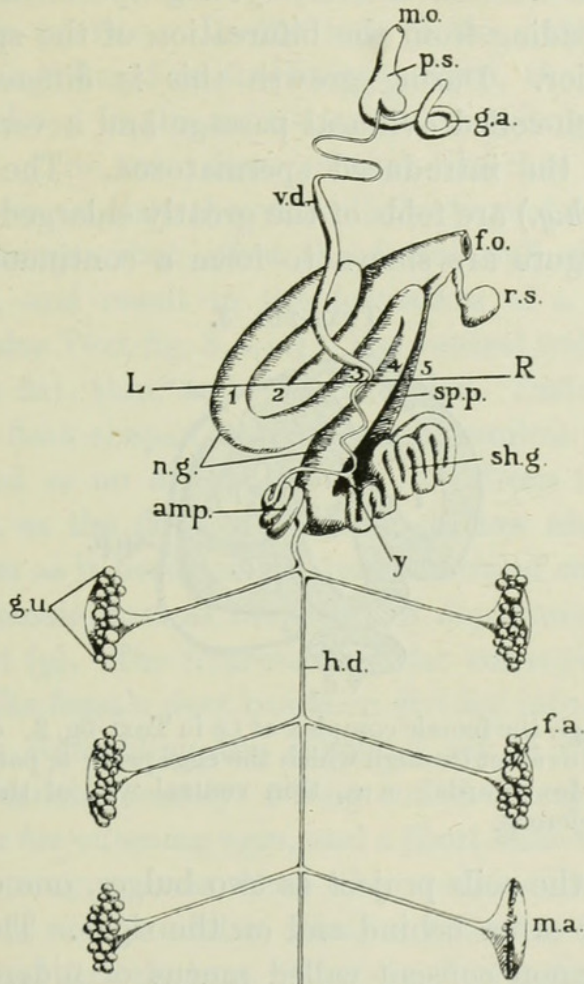
The vascular system does not call for special description, and the renal and pericardial coelomic spaces have, as Hecht (*loc. cit.*) has shown, the normal relations and openings, but the kidney is unusual in being a simple dorsal sac extending backward from the pericardium to the level of the sixth or seventh ceratal groups.

The Reproductive System (Text-fig. 2).—The works of Alder and Hancock, Bergh and Trinchese provide an abundance of surface views of incompletely dissected reproductive systems of the Aeolidiomorpha, but the complexity of the oviducal glands (ootype) is such that none is satisfactorily described. The attempted reconstruction of the oviduct of *Doto fragilis* by Dreyer (2) shows how a tangle may be made worse by this method. In *Calma*, however, the structure of the ootype is so simple that a little displacement of its parts, aided by reference to serial sections, is sufficient to disclose its mode of formation. With the knowledge thus gained as key it was found that the much more intricate ootypes of Aeolidia, Antiopella, and Pleurophyllidia are elaborations of the same general plan.

As in Aeolidiomorpha generally, the gonadial unit consists of a large central male acinus, bearing a number of female acini, first as solid outgrowths, later as hollow diverticula of its wall. Here, however, the gonadial units (*g.u.*) are not as elsewhere united together into a compact mass, but serially distributed in all the interceratal spaces except the first. Thus six to eight pairs are present according to the size of the animal. Paired efferent ducts (*e.d.*) lead into the spermoviduct, which swells into a coiled ampulla before the bifurcation into male and female ducts at *y*, Text-fig. 2. The vas deferens (*v.d.*) is very long, with a thick, glandular wall in its middle portion. All other Aeolidiomorpha have their male and female openings approximated in a common atrium, except *Fiona*, but the male opening of *Calma* is placed in front of and below the level of the right rhinophore (see fig. 1), while the female opening occupies the usual position between the first and second ceratal groups on the right. It is curious that, along with this primitive position, the male organ itself has a primitive structure reminiscent of the Bullids, especially *Haminea*. It is a partial pleurec-bolic introvert, the penis sac in the retracted condition containing the unchanged apex of the penis as a conical papilla on which opens the vas deferens. Close to the end the deferent duct receives that of a long tubular gland (*g.a.*) resembling the

organ named prostate in the Bullids. When retracted this gland lies along with the terminal coils of the vas deferens tucked away in the head above the brain, but is partly drawn

TEXT-FIG. 2.



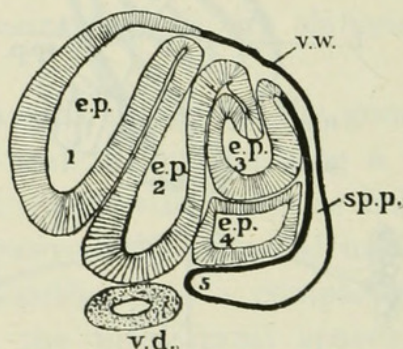
Dissection of the reproductive system of a small, nearly mature individual. *amp.*, ampulla of *h.d.*, the sperm-oviduct; *m.a.* and *f.a.*, male and female acini; *m.o.* and *f.o.*, male and female openings; *g.a.*, glandular appendage of the penis; *g.u.*, genital unit; *n.g.*, nidamental gland; *p.s.*, penis sac; *r.s.*, receptaculum seminis; *sh.g.*, shell-gland; *s.p.p.*, sperm-path from the receptaculum to the commencement of the oviduct at *y*; *v.d.*, vas deferens; 1.2.3.4.5, coils of the oviduct similarly numbered in Text-fig. 3.

into the everted penis, giving it its shape and firmness. The large cells lining it contain a clear secretion which, unlike the granular contents of the prostatic cells of the vas deferens,

takes up no dyes, acid or basic. The fact that no other Aeolidio-morph possesses such a glandular appendage of the penis adds to the interest of this coincident acquisition of primitive position and structure.

The female duct is in very young specimens a straight broad tube leading from the bifurcation of the sperm-oviduct to the exterior. During growth this is differentiated into a dorsal, much-coiled oviducal passage and a ventral straight pathway for the introduced spermatozoa. The dorsal coils (1.2.3.4 and *sh.g.*) are folds of the greatly enlarged female duct, and in the figure are shown to form a continuous tube. In

TEXT-FIG. 3.



Section through the female complex at LR in Text-fig. 2. *e.p.* 1.2.3.4, folds of the oviduct through which the eggs pass; 5, path of sperm migration downwards; *v.w.*, thin ventral wall of the oviduct; *v.d.*, vas deferens.

surface view the coils project as two bulges, one on the left in front and the other behind and on the right. The former has been by common consent called mucus or nidamental gland, and appears in pickled specimens of the Opisthobranchs as a brittle white mass, swelling in water, while the latter is named albumen gland. Many authors have stated or conveyed the impression that these lobes are dependent glands opening by ducts into the oviduct and pouring their secretion on the eggs as they pass. The long continuous tube here described, however, comprises both lobes, and is actually the functional oviduct through which the eggs pass, and in which they receive the successive layers of nidamentum. The first or posterior lobe (*sh.g.*) is composed of a coiled portion of the tube which is

opaque in life and more slender than the rest. In it single eggs or small groups of eggs receive a separate investment of a substance giving the chemical tests for mucin. This is at first laid on in a fluid condition, while the later layers are dense and firm. Shell-gland would therefore perhaps be the appropriate name for this portion. In the rest of the oviducal passage (*n.g.*) which is pellucid in the living animal, the eggs in their shells are enclosed in the substance of the nidamental ribbon, also a mucin. The outer layer of this, like that of the shells, is firmer and denser than the rest. Hitherto we have considered only those changes that affect the dorsal wall of the original oviducal sac, and result in the formation of a twisted egg-passage (see also Text-fig. 3, *e.p.*). The ventral wall (Text-fig. 3, *v.w.*) remains flat, thin, and non-glandular. Distally, near the atrium, the flask-shaped receptaculum seminis (Text-fig. 2, *r.s.*) is formed as an evagination of it. From the atrium it extends back as the floor of a broad, shallow chamber (*sp.p.*) which narrows as it becomes continuous behind with the initial part of the female duct at the point of departure of the functional oviduct (*y*). The impression so far conveyed is that the original sac-like female duct has been divided into two passages by a process resembling the pinching off of the vertebrate semicircular canals, namely, a long coiled dorsal one, ciliated and glandular for outgoing eggs, and a short thin-walled ventral one for incoming sperms from the receptaculum, which is neither ciliated nor glandular. Such a complete female diauly is, however, not strictly true. Text-fig. 3 of a section through the nidamental region in the plane LR in Text-fig. 2 shows that three (1.2.3) out of the four oviducal loops thus cut across are incompletely separated from the vaginal chamber below, while the fourth or proximal loop (4) is a discrete tube. Thus for a considerable length of ribbon-forming oviduct a facultative but not a structural diauly is present. The tube of the shell-gland is, however, completely separated except at its commencement, as mentioned above. This is essential since it deals with loose eggs, or with eggs receiving a fluid envelope. The continuity at *y* of the undivided oviduct with the vaginal

channel (*sp.p.*) is also essential for the passage of the backwardly migrating spermatozoa. It is, therefore, seen that dialy of the female duct in *Calma* is just so far expressed as to constitute passages that are functionally efficient.

The foregoing rather detailed account of the female reproductive ducts, though a digression from the main thesis of the paper, has been introduced because the supposed female monaulity of the Aeolidiomorpha forms an important item in the definition of that group.

The reproductive system as a whole presents three anatomical departures from the Aeolidian type, namely (1) the displacement of the male opening and its accessories into the head, (2) the substitution for a muscular penis of one which derives its bulk from a gland which grows at sexual maturity, and (3) the breaking up of the massive aeolidian gonad into serially arranged pairs of gonadial units which are so placed as to intrude least on the body-space available for distention of the alimentary system. They are, moreover, placed where digestion of a meal begins, and in the path of food-laden blood from the cerata, so that their growth proceeds *pari passu* with the adjacent reduction in bulk of the stomach. All three modifications may be regarded as correlated with the demand for space to receive the maximum meal when food is plentiful. The last further enables *Calma* to replace that meal by its own enlarging gonads with the greatest structural convenience. Figs. 8 and 9 are sections through the interceratal regions of two animals of similar size at nearly opposite poles of the metabolic cycle. In fig. 8 digestion has begun, the gonads are small, and the special cells (*c.s.*) in the cerata are almost at minimum size, while in fig. 9 the meal has largely disappeared, the special cells are greatly enlarged, and the ovarian acini (*f.a.*) are distended with nearly full-grown eggs. In this specimen the black granular remains (*d*) of a previous meal are also visible on the floor of the gastric sac. As animals of various sizes are found in both of these metabolically antithetic conditions, it is almost certain that the rhythmic succession of alimentary and reproductive activity takes place several times in the individual lifetime. Dr. Orton (8) has shown by

his raft experiment that the life-cycle of such a much less advantageously placed animal as *Galvina* is far shorter than had been imagined. What must it be then in a case where food is plentiful if found at all, and its nutritive value so great that a hind-gut is useless; where, moreover, the chemical constitution of the food and the gonad which it nourishes must be so similar as to reduce the entailed metabolic conversion to a minimum? In fact, such an economical metabolic system is equalled only by parasites that absorb the gonads of their hosts.

As to the special cells of the cerata, the supposition that they act as reservoirs of food during a fast is supported by the incidence of their periods of growth and diminution, while the fact that only the connective tissue cells of the cerata are so employed agrees with the principle observed throughout in *Calma*, namely, that the whole available body-space should be reserved for the alternation of food and gonad.

GENERAL CONSIDERATIONS.

The *Aeolidiomorpha* are all carnivorous, and the *Aeolididae* all eat *Coelenterates*. The smaller ones live on *Hydrozoa*, but supplement that diet by eating other members of their own and neighbouring species or their eggs. Such are *Facelina* and *Favorinus*, and it was among these most probably that *Calma* arose, and, in spite of its extensive aberration from type, it is to be hoped that no systematist will think fit to separate it from them. The contours of the body are still typically *Aeolidian* in detail. Examination of the least plastic of bodily systems, the nervous system, by itself would place *Calma* in the genus *Facelina*. During the precarious early days of settling down on the sea bottom it is highly probable that the little animal actually uses its initially uniseriate *Aeolidian* radula as a generalized carnivore. All the departures from the *Aeolididae* in the structure of the alimentary and other systems have been shown to be closely associated with the adoption of a diet different from and even more specialized than that of its polyp-eating relatives. In doing this it provides an exception to the rule that, as Dr. Willey expresses it, the adoption of a specialized diet marks the culmination of a phyletic career.

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EXPLANATION OF PLATE 11.

Fig. 1.—Dorsal view of the mature animal. *a.m.f.*, anterior margin of the foot; *c.t.*, cephalic tentacle; *E.*, eye; *g.*, gonad seen through the integument; *pc.*, pericardium; *pe.*, extruded penis; *rh.*, rhinophore; *r.o.*, renal opening.

Fig. 2.—Buccal mass laid open dorsally by turning back the flap *f.* *j.*, muscular pads thinly chitinized, called jaws when the chitin is locally thickened; *m.*, mouth; *o.*, gullet; *rad.*, odontophore with radula.

Fig. 3.—Side view of the radula. *b.r.*, basal dentigerous rod.

Fig. 4.—Anterior end of the radula, highly magnified. 1.2.3.4.5, the primary teeth. Note the reduction in size from 1 to 4, and the loss of shape at 5.

Fig. 5.—Part of a section of a ceras. *a.g.*, epidermal gland-cell with contents taking acid dyes; *b.g.*, ditto taking basic dyes; *b.s.*, blood-space; *c.c.*, ciliated cell of the epidermis; *c.s.*, connective-tissue cell; *c.t.*, dense dermal connective tissue; *d.c.*, digestive cell; *f.*, food with vacuoles; *m.f.*, muscle-fibres.

Fig. 6.—A connective-tissue cell, special cell of Hecht, during solution of its contents. *e.*, clear envelope free from granular material; *n.b.*, nucleolar body.

Fig. 7.—Central nervous system. *cp.g.*, cerebro-pleural ganglion;

p.g., pedal ganglion; *st.g.*, stomatogastric ganglion; *o.g.*, optic ganglion; *g.o.g.*, gastro-oesophageal ganglion; *rh.g.*, rhinophorial ganglion; *a.p.n.*, anterior pedal nerve; *b.m.n.*, nerve to buccal mass; *bu.n.*, nerve to the lips; *E.*, eye; *g.n.*, genital nerve of cerebro-pleural origin, continuing beyond the genital complex as a pleural nerve; *n.c.t.*, nerve to cephalic tentacle; *ot.*, otocyst; *p.c.*, pedal commissure; *p.p.c.*, parapedal commissure; *pl.n.*, pleural nerves, innervating the cerata and the dorsal body-wall; *p.n.*, pedal nerves (*N.* no branches to the cerata from these were discovered); *rh.n.*, rhinophorial nerve; *s.n.*, nerve to salivary duct.

Fig. 8.—Section through an interceratal space of an animal killed shortly after a full meal.

Fig. 9.—Ditto of an animal of the same size taken when the meal was nearly all digested. *a.v.* and *e.v.*, afferent and efferent veins of the ceras; *c.s.*, the special cells of the ceratal connective tissue; *d.*, residual faecal mass on the floor of the gastric sac; *d.l.*, hepatic diverticulum; *f.a.* and *m.a.*, female and male acini; *h.d.*, sperm-oviduct; *pl.n.*, pleural nerve; *p.n.*, pedal nerve; *v.*, median dorsal vein leading to the auricle.



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