OBSERVATIONS ON THE CILIARY CURRENTS OF THE JELLY-FISH *AURELIA AURITA* L.

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(Text-figs. 1–7)

The common jelly-fish *Aurelia aurita* has been a popular species for the study of medusan physiology, for its abundance, transparency and docility make it easy to observe. Unfortunately, studies of the animal as a whole are rare, many investigators having confined themselves to isolated parts or functions, and it is sometimes difficult to combine the accounts in the literature. Such a difficulty arose on attempting to assess the role of ciliary currents in feeding. Widmark (1913) described only the internal currents, Orton (1922) the external currents, Gemmill (1920) the currents of the ephyra stage, while Henschel (1935) investigated the reactions of the oral arms alone. A study of the external and internal currents of the whole animal cleared up certain apparently conflicting details in these accounts, and disclosed several new features (Southward, 1949). It is now possible to give an account of a more complete investigation of the ciliary currents, both in the adult and in the larval stages of *Aurelia*, and to correlate some points of morphology with the currents.

In accordance with established use, the term 'ciliary currents' has been used to describe what are strictly flagellar currents. There is no ciliated epithelium as the term is understood in the higher metazoa; instead, as in most medusae (Hyman, 1940; Krasinska, 1914), a proportion of the ecto-dermal cells bear single flagella. In formalin-preserved material the flagella vary from 9 to 18 μ in length, somewhat longer than the cells themselves.

Observations on the living *Aurelia* were made at Liverpool in 1947 and 1948 on specimens from the Mersey estuary; at Port Erin in 1947–51 on specimens from the west coast of the Isle of Man; and at Plymouth in 1954 on specimens from the Tamar estuary. The external currents were investigated by adding suspensions of carmine or graphite particles to the water in which the specimens were kept, or by feeding with diatom cultures, mixed plankton or various proteins. The finer details of the currents were observed on speci-mens restricted in small dishes, but without narcosis, and were sometimes checked on isolated parts. Similar procedures often sufficed to show the internal currents, but it was sometimes necessary to inject suspensions directly into the canals and pouches.

Material was fixed in calcium-formalin, and much structure could be made out by simple sagittal sections. For more microscopic detail, standard paraffin

14

embedding proved unsatisfactory due to shrinkage of both cells and mesogloea, and sections were cut by the gelatin-freezing method (Baker, 1944) and the glycol wax procedure (Miles & Linder, 1952). The gelatin-freezing method produced least shrinkage of the mesogloea, and was found satisfactory for grosser detail, while the glycol wax procedure was preferable for cytological detail. All material was bulk-stained with Mayer's haemalum, but sections were sometimes reinforced with iron haematoxylin and eosin.

The figures are based on camera-lucida drawings of the fixed or sectioned material, to which the details of currents were added later from rough sketches of the living material.

The External Ciliation of the Adult

The Umbrellar Surfaces

The cilia of both the ex-umbrellar and sub-umbrellar surfaces beat centrifugally, towards the edge of the disc. Particles and food material are trapped in mucus, which accumulates in rolls and travels gradually to the umbrella margin.

The Umbrella Margin

The margin of the umbrella, except in the region of the eight sense organs (rhopalia), bears an outer row of lappets, an intermediate row of tentacles, and an inner fold of ectoderm (Fig. 2 A); the latter, from its superficial resemblance to the velum of the hydromedusae, is called the velarium (Figs 1 and 2 A, *V*). The cilia on the tentacles beat distally, towards the tip, but the direction of travel of the material depends on the position of the tentacle. If the tentacle is relaxed and hanging free vertically the material is rejected, but if the tentacle is contracted, for example by stimulus of food, the material is caught up by the other structures of the margin. Each of the lappets has a peripherally directed current on the outer side and a centripetal current on the inner side: the result is that material collected by the lappets, and that reaching them from the ex-umbrellar surface, is passed between the lappets into the marginal groove (Fig. 2 A, *Mg*). Material collected on the sub-umbral surface is passed smoothly over the velarium and also accumulates in the marginal groove. In this groove the currents move away from the rhopalia and towards the regions of the adradial canals (Fig. 1, right half) and material accumulates beneath the adradial canals in slight widenings of the velarium, termed food pouches by Orton (1920). The marginal groove, the food pouches and the side of the velarium directed towards the marginal groove are all richly ciliated, and in section show tall columnar cells similar to those of the inner, endodermal surfaces of the oral arms.
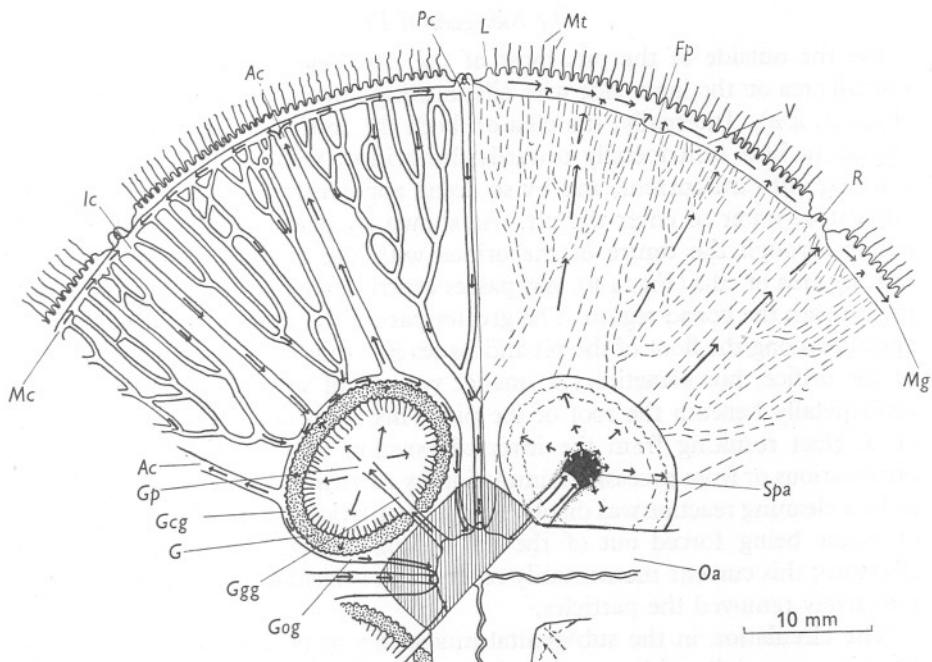
Fig. 1. *Aurelia*: part of the disc seen from the sub-umbrellar surface, with two of the oral arms removed (the cut bases hatched). The right side shows the currents on the sub-umbrellar surface and at the margin, while the left side shows the major currents in the canals and in one of the gastric pouches. *Ac*, adradial canal; *Fp*, food pouch; *G*, gonad; *Gcg*, gastro-circular groove; *Ggg*, gastro-genital groove; *Gog*, gastro-oral arm groove; *Gp*, gastric pouch; *Ic*, interradial canal; *L*, lappet; *Mc*, marginal canal; *Mg*, marginal groove; *Mt*, marginal tentacle; *Oa*, oral arm; *Pc*, perradial canal; *R*, rhopalium; *Spa*, aperture of sub-genital pit; *V*, velarium.
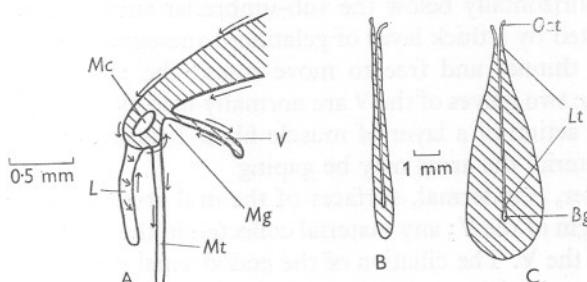
Fig. 2. *Aurelia*: diagrammatic sections of: (A) the umbrella margin; (B) the distal, and (C), the proximal regions of an oral arm. *Bg*, basal groove tract; *L*, lappet; *Lt*, lateral tract; *Mc*, marginal canal; *Mg*, marginal groove; *Mt*, marginal tentacle; *Oat* oral arm tentacle; *V*, velarium.

14-2

The Sub-genital Pits

On the outside of the pits most of the cilia beat outwards, but there is a small area on the inner side with cilia beating towards the aperture of the pit (Figs. 1, 4 B). Internally, the cilia on both the roof and the floor of the pit appear to beat centripetally towards the orifice; those on the floor set up a strong outward current, and by so doing apparently cause a compensatory current of water to enter the pit. As shown by particles in it, this current enters through the centre of the orifice with the assistance of the inward beating area of cilia (Fig. 4 B), and passes centrifugally to the periphery of the pit beneath the gonad region. The greater part of the water passes back to the aperture along the floor of the pit and issues in a thin layer around the margin of the orifice, but sometimes a smaller volume of water was seen to travel centripetally beneath the roof of the pit. This latter current may have been an artefact resulting from the inverted position of the animal during the observations or from excessive stimulation by particles. In fact, what appeared to be a cleaning reaction was displayed if many particles were present, a current of water being forced out of the pit by contraction of the sphincter-like aperture; this current momentarily reversed the normal ingoing current and effectively removed the particles.

The circulation in the sub-genital pits seems to be largely respiratory in function, especially with regard to the gonads. The latter are separated from the pits only by a single layer of thin ectoderm and the merest trace of genital epithelium.

THE INTERNAL CURRENTS OF THE ADULT

The Oral Arms

The oral arms of the adult jelly-fish are formed by elongation of the four corners of the simple mouth of the ephyra stage. They are V-shaped in section, and extend horizontally below the sub-umbrellar surface, the proximal part being supported by a thick layer of gelatinous mesogloea (Fig. 2 C), while the distal half is thinner and free to move round the margin of the umbrella (Fig. 2 B). The two halves of the V are normally held close together, apparently partly by the action of a layer of muscle fibres beneath the ectoderm, for in preserved material the arms may be gaping.

On the outer, ectodermal, surfaces of the oral arms the cilia beat towards the open margin of the V; any material collected in the mucus passes over into the groove of the V. The ciliation of the endodermal surfaces of the groove is more complex. At the extreme base there is a continuous distally-moving current, the basal groove current, which is largely excretory, for the particles carried by it have usually passed through the gastric pouches and canals (Fig. 3, *Bg*). This tract of cilia seems distinct from the remaining cilia of the groove which can act in two ways. Food material, including the mucous

masses picked up from the marginal food pouches, travel proximally along the arm in a tract formed by the apposition of the two sides of the groove (Fig. 3, *Lt*), and is passed on to the gastric pouches. The width of the lateral tract involved varies with the amount of food in it; in some cases the whole of the groove, with the exception of the basal tract, may be seen moving food towards the gastric pouches. These two opposing tracts have never been seen to mix in a healthy jelly-fish, yet they are apparently separated only by the close apposition of the two halves of the V, which must nevertheless leave room for the cilia to work.
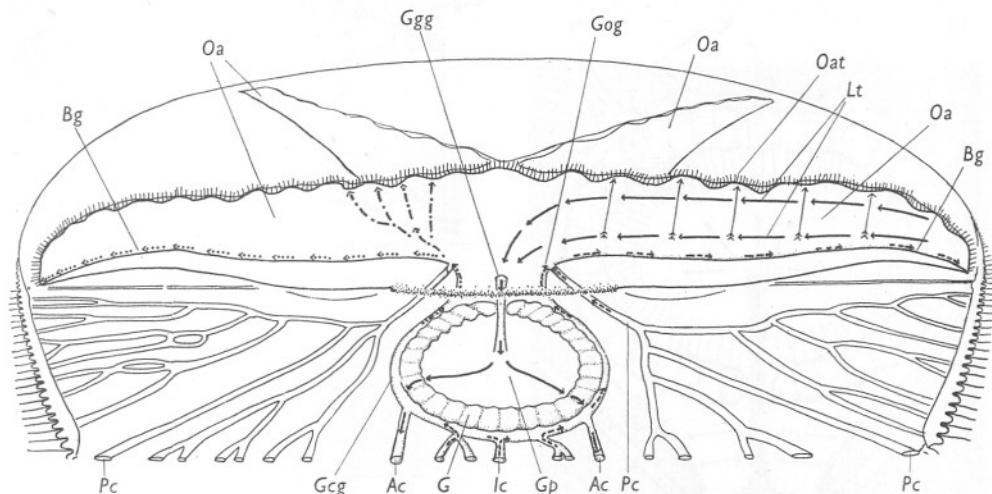

Fig. 3. *Aurelia:* oblique view of part of the disc from the sub-umbrellar surface, showing some of the currents in two of the four oral arms and in one of the four gastric pouches. The right side shows the path of food (solid arrows) in the lateral tract, and of excretory matter (broken arrows) in the basal groove, while the left side illustrates the main paths of the gametes at spawning (path of sperm in male shown by dotted arrows, path of eggs in female shown by dotted and dashed arrows). The feathered arrows represent the rejection reaction in the lateral tract. *Ac*, adradial canal; *Bg*, basal groove tract; *G*, gonad; *Gcg*, gastro-circular groove; *Ggg*, gastro-genital groove; *Gog*, gastro-oral groove; *Gp*, gastric pouch; *Ic*, interradial canal; *Lt*, lateral tract; *Oa*, oral arm; *Oat*, oral arm tentacle; *Pc*, perradial canal.

In the absence of food the lateral tract rejects nearly all inert particles placed in it. More rarely inert material may be picked up and passed a short distance proximally, but sooner or later there comes a marked change in the current, and the inert material is carried laterally to the margins of the V and rejected (Fig. 3, feathered arrows).

THE GASTRIC POUCHES

The currents in the gastric pouches are more complex than suggested by Widmark (1913), for selection mechanisms are present as in the oral arms. Food from the lateral tracts of the oral arms passes into the gastric pouches by

the gastro-genital grooves (Figs. 3, 4, *Ggg*). These grooves, first noted by Goodey (1908, 1909), have two tracts of cilia beating in different directions. In the upper part of the groove, between the roof of the gastric pouch and the sides of the groove, there is an ingoing food-bearing current continuous with the lateral tracts of the oral arms (Fig. 4 B, D, *Gggu*). In the lower part of the groove, the cilia beat outwards towards the mouth, but this is not noticed
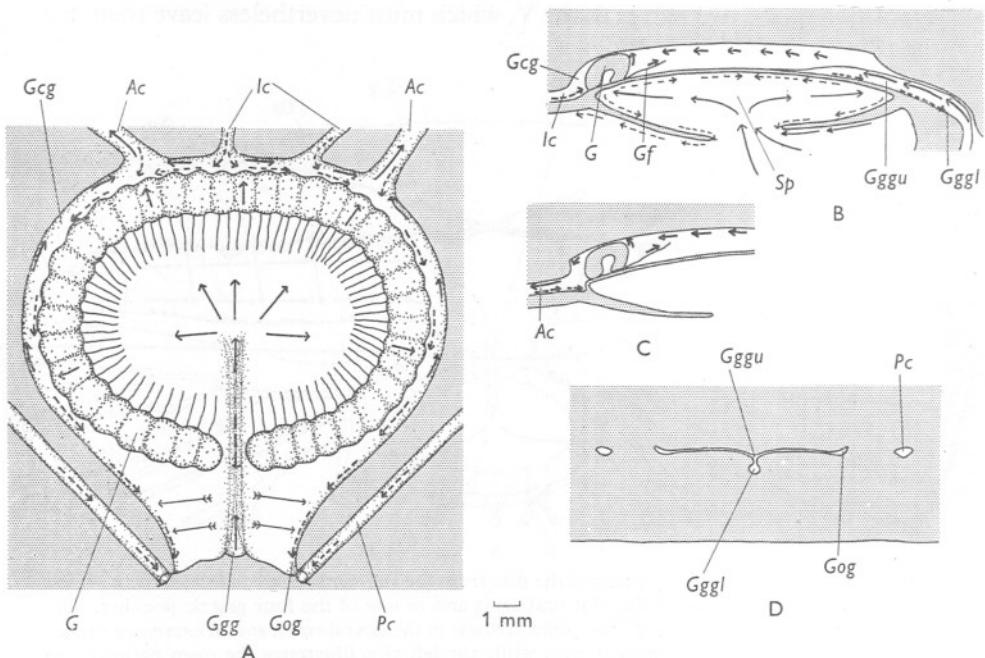

Fig. 4. *Aurelia:* A, diagrammatic view of a gastric pouch from above, with the ex-umbral surface and upper mesogloea removed; B, a radial section across the same pouch and the sub-genital pit below; C, a part section of the same pouch at the origin of an adradial canal; D, a section across the gastro-genital groove inward of the gonad. The solid arrows show ingoing currents, the broken arrows outgoing currents, the feathered arrows rejection reactions, and the thin arrows in B represent the water circulation in the sub-genital pit. *Ac*, adradial canal; *G*, gonad; *Gf*, gastric filament; *Gcg*, gastro-circular groove; *Ggg*, gastro-genital groove; *Gggl*, lower, and *Gggu*, upper, parts of the gastro-genital groove; *Gog*, gastro-oral groove; *Ic*, interradial canal; *Pc*, perradial canal; *Sp*, sub-genital pit.

superficially unless inert material is injected into the groove, when a rejection reaction occurs and material in the upper part of the groove may pass through to the lower part and be carried outwards (Fig. 4 B, D, *Gggl*). If much inert material is present in the groove a further rejection reaction may take place, the material being passed laterally to the origin of the oral arm basal tract, apparently by withdrawal of the sides of the groove from apposition with the roof (Fig. 4 A, feathered arrows).

Food material entering the gastric pouch by the gastro-genital groove is swept centrifugally by cilia on the roof of the pouch, and comes to rest against the gastric filaments. The cilia of the filaments beat distally, and function mechanically as a means of breaking up food masses. The separated particles pass up and over the gonads into the gastro-circular groove running round the gonads (Fig. 4 A, B, *Gcg*). Food materials travel along the roof of this groove, to the openings of the adradial canals, into which they pass. The floor of the groove is largely excretory, for indigestible matter from the interradial canals travels round it to the gastro-oral grooves (Fig. 4 A, *Gog*) along which it passes to the basal grooves of the oral arms (Fig. 3, right half). Thus the gastro-circular groove forms a further selection mechanism. Selection can also occur in the main body of the pouch, where the centripetally beating cilia on the floor can carry material to the lower part of the gastro-genital groove.

The Canals

It must be noted that the details of currents given in this paper may not apply to all specimens of *Aurelia*, since structural variation is not uncommon (Browne, 1901). This is especially true of the canals, and slight differences in the method of branching of the perradial and interradial canals can be found in practically every specimen; in some cases there may exist anastamoses between the adradials and the side branches of the other canals, which may by-pass the normal circulation.

The cilia on the roof and sides of the adradial canals beat centrifugally, and convey food from the gastric pouches to the marginal canals (Fig. 1, left half). The cilia lining the floor of the adradial canals beat in the opposite direction, and indigestible particles that have penetrated this far may be carried back to the gastro-circular groove (Fig. 4 A). Water and particles entering the marginal canal from the adradial canals pass round on either side of the adradials to the side and main branches of the perradial and interradial canals along which they travel towards the centre of the disc (Fig. 1, left half). The interradial canals open into the gastro-circular grooves, and particles are transferred to the floor tract of the latter, while the perradial canals communicate directly with the bases of the oral arm grooves (Fig. 3, right half).

So far, only one current has been detected in the interradial and perradial canals. These canals are flattened horizontally, while the adradials, which carry two currents, one above the other, have their greatest dimension vertically. In all canals the circulation seems to be assisted by the muscular pulsations of the umbrella, the walls of the canals expanding and contracting with the coronal muscles.

THE CILIARY CURRENTS OF THE LARVAL STAGES

The direction of beat of the cilia remains fairly constant through the successive larval stages to the adult. For example, the locomotion of the planula is effected by cilia which beat orally (Fig. 5 A); after settlement on the aboral end, the same direction of beat now serves to accumulate food particles near the mouth (Fig. 5 B). A similar direction is maintained on the developing tentacles, which can, however, vary the ultimate direction of the particles collected by changing their posture. After strobilation the orally directed current of the scyphistoma becomes the centrifugal current of the exumbral surface of the ephyra, while the orally directed current near the mouth of the scyphistoma is represented by similarly directed currents on and near the manubrium of the ephyra (cf. Gemmill, 1920). The other external currents of the ephyra are centrifugal.
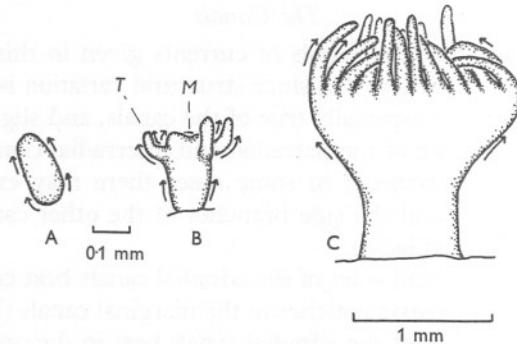

Fig. 5. *Aurelia:* A, planula, B, early scyphistoma, and C, later scyphistoma stages, showing external currents. *M*, mouth; *T*, tentacle.

The internal currents of the early ephyra are simple and adapted to the wide open gastric cavity and absence of a marginal canal (Fig. 6 A). The cilia on the roof of the gastric cavity beat centrifugally, and those on the floor centripetally, but much swirling is caused by the gastric filaments and by the muscular contractions of the animal. The more complicated canal system and circulation of the later stages develops with the expansion of the area of the

Legend to Fig. 6.

Fig. 6. *Aurelia:* A, an early ephyra, the currents of which were reported by Gemmill (1920); B, a slightly older ephyra than A, showing the origin of the marginal canal; C, 10 mm. stage, with marginal tentacle and velarium developing; D, a slightly larger view of an adradius of the specimen in C, but from the ex-umbral aspect; E, 15–20 mm stage, with oral arms and gastric pouch. All except D from the sub-umbrellar surface. *Ac*, adradial canal; *Bg*, basal tract; *Gf*, gastric filament; *Gcg*, gastro-circular groove; *Ggg*, gastro-genital groove; *Gog*, gastro-oral groove; *Gp*, gastric pouch; *Gprg*, gastric pouch ring groove; *Ic*, interradial canal; *L*, lappet; *Lt*, lateral tract; *Mc*, marginal canal; *Mn*, manubrium; *Mt*, marginal tentacle; *Pc*, perradial canal; *Pt*, primary tentacle; *R*, rhopalium; *V*, velarium.
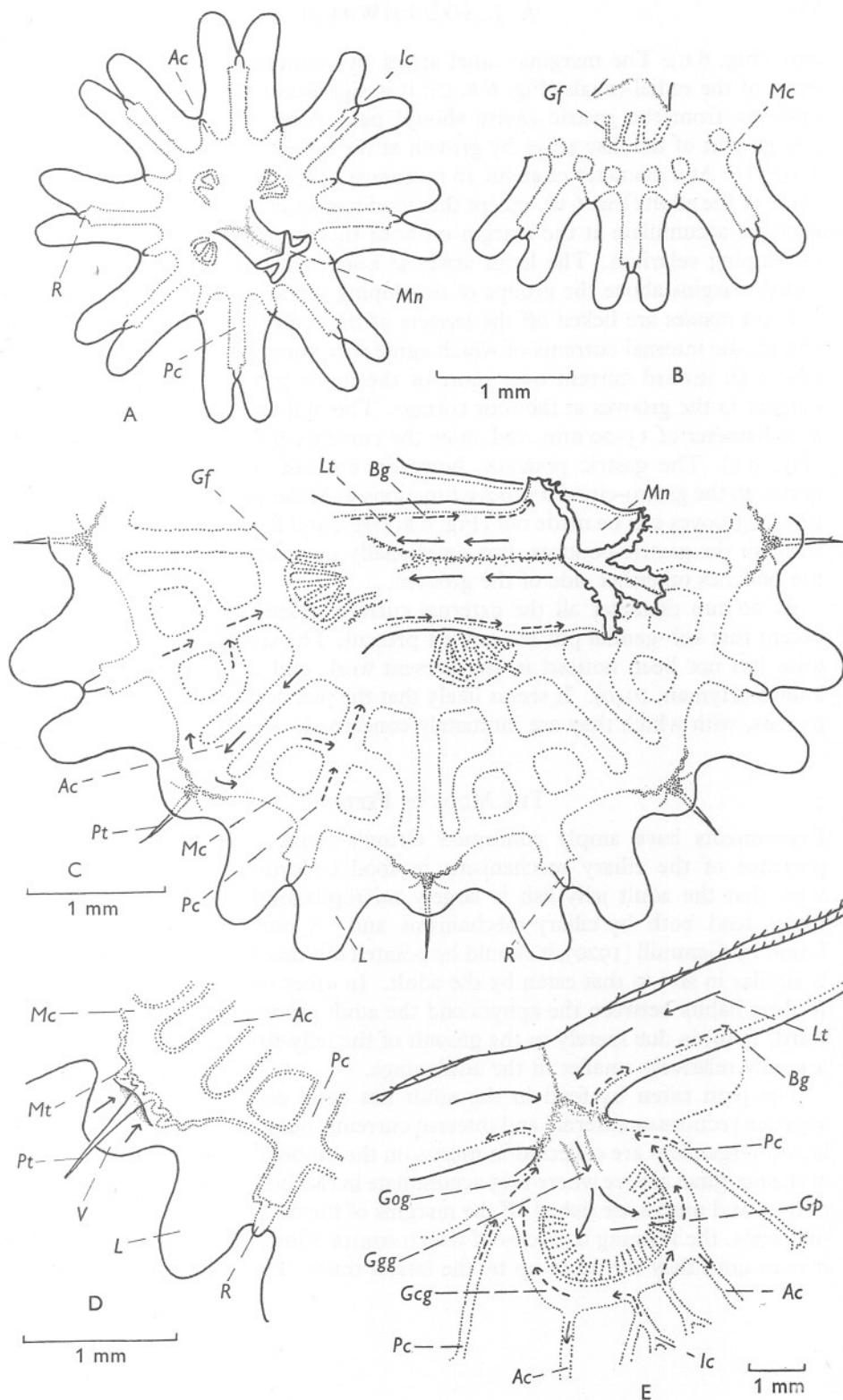
Fig. 6.

disc (Fig. 6 c). The marginal canal arises by connexion between the outer parts of the radial canals (Fig. 6 B, C): it is significant that the main outward currents from the gastric cavity should pass along the adradial canals, as a large part of the disc arises by growth at the adradial margins, between the rhopalia. At a diameter of about 10 mm most of the ciliary currents resemble those of the adult (Fig. 6 c), except that food masses collected by the umbrellar surfaces accumulate at the margin on both the rhopalial lappets and on the developing velarium. The latter arises as a series of small lappets at the adradial margins above the groups of developing tentacles (Fig. 6 D).

Food masses are licked off the lappets of the ephyra by the mobile manubrium, the internal currents of which agree with those of the oral arms of the adult: an inward current over most of the inner surfaces, and an outward current in the grooves at the four corners. The oral arms are fully developed at a diameter of 15–20 mm, and show the currents and reactions of the adult (Fig. 6 E). The gastric pouches, however, are not complete at this stage, although the gastro-circular groove functions as in the adult. Incipient gastrogenital grooves can be made out (Fig. 6 E, *Ggg*), and food usually passes down them to the gastric pouches, but occasionally material may be seen to enter the pouches on either side of the grooves.

At 20 mm diameter all the external currents resemble those of the adult, except that sub-genital pits are not yet present. The stage at which these pits arise has not been noticed in the present work, and does not appear to be known (Hyman, 1940). It seems likely that the pits develop together with the gonads, with which they are intimately concerned.

THE MODE OF FEEDING

Experiments have amply confirmed Orton's (1922) evidence of the importance of the ciliary mechanisms in food collection and reinforced the view that the adult jelly-fish is largely microphagous. Although the larval stages feed both by ciliary mechanisms and by muscular macrophagy as found by Gemmill (1920), it should be pointed out that the food they consume is similar in size to that eaten by the adult. In other words, the difference in feeding habits between the ephyra and the adult reported previously (Southward, 1949) is due merely to the growth of the jelly-fish: the food organisms are only relatively smaller in the adult stage.

The path taken by food in the adult has been described already in the separate sections on external and internal currents, but may be briefly recapitulated. Organisms are collected in mucus on the umbrellar surfaces and passed to the marginal groove where they accumulate in the food-pouches. The masses of food and mucus are licked off the margins of the umbrella by the tips of the oral arms, the fringing tentacles of which contract inwards and hold the food masses until they are taken up by the lateral tracts. The food is passed along

the lateral tracts to the gastro-genital grooves, by way of which it enters the gastric pouches. After being separated by the gastric filaments the food particles are distributed along the canals. Digestion has not yet been studied in *Aurelia*, but it seems possible that, as in *Cassiopeia* (Smith, 1936), the gastric filaments can produce some extracellular enzymes.

The collection of food can be observed directly by placing *Aurelia* in a suspension of plankton organisms: indirectly, the type of food being collected can be determined by examination of the mucous masses in the food pouches. The ex-umbrellar surface plays least part in the process of food collection, since large copepods and other organisms are swept off during pulsation of the bell. The main collecting takes place on the sub-umbrellar surfaces, on the oral arms and at the margin of the umbrella, the action of swimming causing a current of water to pass over these parts.

A specimen 10 cm in diameter cleared all the coarse plankton from 700 ml. of water in less than an hour, but much larger volumes of sea water should be passed over the external surfaces in nature. *Aurelia* easily picks up small copepods (e.g. *Tigriopus*) on the external surfaces, and at 15° C these can reach the food pouches within 10 min, the oral arms in 12 min and the gastric filaments in 50 min. Material picked up by the oral arms directly reaches the gastric pouches more quickly, sometimes within 10 min.

Examination of the mucous masses in the food pouches of freshly captured specimens usually shows plankton typical of the place of capture. Thus, the food pouches of *Aurelia* from Port Erin Bay in early June showed principally copepods, which were then present in great abundance in the sea. Specimens from the River Mersey had large amounts of detritus (probably silt and sewage), in addition to diatoms, ciliates, flagellates and some crustacean eggs, in the food pouches. The pouches of further specimens from a tide pool near the mouth of the Mersey estuary contained, in addition to large amounts of detritus, many *Noctiluca* and some balanoid cyprids, both common in the local plankton at the time. Other specimens kept in tanks at Port Erin had collected plankton typical of the local sea-water supply, namely diatoms, algal fragments, polychaete larvae and harpacticid copepods. *Aurelia* placed in pure cultures of the diatom *Nitzschia* or the copepod *Tigriopus* rapidly accumulated these organisms in the food pouches, and later, in the gastric pouches.

The evidence for plankton feeding, and microphagy in general, is thus very strong. Attempts to show macrophagy in the adult have always failed, as food particles above 5 mm diameter are always dropped or rejected from the margin or the oral arm grooves. A further limitation of the size of food masses is imposed by the narrowness of the gastro-genital grooves. Although, theoretically, the mouth communicates with a gastric pouch by the whole width of the tract between the two gastro-oral grooves (Fig. 4 A), in practice food enters a pouch only along the gastro-genital grooves.

Selection mechanisms play an important part in the feeding processes of

microphagous animals, and *Aurelia* shows such mechanisms at several stages in the food path. The tentacles may accept or reject according to their position relative to the marginal groove, and their degree of contraction, but the oral arms constitute the major selective device outside the gastric pouches. As Henschel (1935) showed, the arms have a well-marked chemical sense, and respond to proteins and nitrogenous substances, but not to carbohydrates or inorganic particles. The reaction to food masses, plankton, or mussel extract is seen first as a contraction of the fringe of capitate tentacles (which bear batteries of nematocysts), and the material is then taken up by the lateral tract. Materials such as carmine, graphite or starch grains cause little or no contraction of these tentacles and are not usually taken up by the lateral tract. If such indigestible particles are taken up by the lateral tract (possibly as a result of the presence of unseen food organisms in the water) they are later rejected before reaching the gastric pouches, by a lateral movement in the tract (Fig. 3, right half). This rejection reaction can often be halted, and the material caused to be taken up again, by stimulation with proteins (e.g. egg albumen), and if the stimulus is sufficiently strong the indigestible material may pass to the gastric pouches. On the other hand, further addition of much indigestible material to the lateral tract may cause the arm to reject the whole contents of the tract, including any food masses that may be present.

In the absence of obvious structural features, such as the grooves in the throat of the anemone *Metridium* (Elmhirst, 1925; but cf. Parker & Marks, 1928), it might be thought that the rejection reaction shown by the oral arms of *Aurelia* was due to a change in direction of beat of the cilia. Unfortunately it has not been possible to see the direction of beat of a cilium directly *in situ* in the arm, and it is difficult to expose a single inner surface without damaging the cilia. However, it is possible that the 'reversal' is only apparent. Thus, the normal ingoing current of the lateral tract creates its own 'canals' by apposition of the sides of the groove around the food or other particles; relaxation of the muscle fibres partly responsible for this apposition would allow these canals to communicate with the exterior, and the rejection might merely result from the material taking the easier path to the exterior. Further investigation of the rejection reaction is necessary before this theory can be accepted.

The other selection mechanisms occur in the gastric pouches and in the adradial canals. That described for the gastro-genital groove (p. 206) is probably of chemical nature like the oral arm reaction, but the remainder may be mechanical, serving to sort out the heavier, and therefore presumably inorganic particles from the food.

Although scattered batteries of nematocysts are present on the ex-umbrellar surface of *Aurelia*, they appear to play little part in food capture in the adult; their penetrating powers, assessed on human epidermis, are much poorer than those of other semaeostome medusae. In the ephyra, however, the

nematocysts help to hold captured organisms on the lappets (Gemmill, 1921) until they can be licked off by the manubrium. The smallest ephyra stage (Fig. 6 A) has been seen to hold and later ingest in this way as many as six nauplii of *Balanus balanoides*, almost simultaneously: at the same time, masses of smaller organisms collected by the ciliary currents were also eaten. Ephyrae of up to 10 mm diameter were found feeding on the newly hatched plaice larvae in the fish-hatchery at Port Erin, and one specimen accepted up to three larvae, one after the other, in the same way that the earlier stage dealt with nauplii. In these stages the manubrium showed marked selection mechanisms, and, like the oral arms of the adult, rejected indigestible particles.

THE CURRENTS AND REPRODUCTION

As is well known (Agassiz, 1860; Hargitt & Hargitt, 1910), the gametes of *Aurelia* issue from the gonads and gastric pouches along the oral arms; the eggs, which are already fertilized, become enclosed in pockets of the inner, endodermal, surfaces of the oral arms, near the margins of the grooves, where they develop to the planula stage. Goodey (1908, 1909) believed that the eggs and sperm left the gastric pouches by way of the gastro-genital grooves ('gonadial grooves'), and was able to show their presence in this channel in preserved and sectioned material. However, in the course of the present work it was frequently observed that mature female *Aurelia*, after handling, passed eggs and planulae round the canals, and their presence in any part of the system is not remarkable. Widmark (1913) observed the passage of gametes along the gastro-oral arm grooves ('eck-canalen'). During the present study only four specimens have been seen to spawn, two males and two females, but in all the gametes likewise issued along the gastro-oral arm grooves (Fig. 3, left half). In the males the bulk of the sperm was passed to the basal grooves of the oral arms, in which it travelled to the tips of the arms, where it was ejected in mucous masses. The females differed in that the eggs travelled only a short distance in the basal grooves, and were quickly passed to the lateral tracts, in which they moved laterally, quite like rejected material, to the margins of the grooves.

Internal fertilization is presumably effected by the females picking up the sperm masses ejected by the males, and passing them to the gastric pouches in the normal feeding currents. Sperm masses were, in fact, found in the marginal food pouches of a female kept in the same tank as a spawning male. The process is probably assisted by the shoaling that frequently occurs during the breeding period (Agassiz, 1860; Southward, 1954).

COMPARISON WITH OTHER JELLY-FISH

In its restriction to a largely microphagous habit, and in its reliance upon ciliary mechanisms for food transport and internal circulation, *Aurelia* resembles the rhizostome medusa *Cassiopeia* (Smith, 1936). However, studies

of other semaeostome and rhizostome mudusae, not completed, show that the two groups have many common features of physiology. Thus, the centrifugal currents of the ex-umbrellar and sub-umbrellar surfaces of *Aurelia* are present, slightly modified, in *Cassiopeia* and apparently in the semaeostomes *Chrysaora* and *Cyanea*, but in these species the currents play little part, if any, in food collection. In all these species, and in *Rhizostoma* as well, the inner surfaces of the oral arms show similar currents and functions: an outgoing current in the base of the groove (in rhizostomes that part of the oral arm canal nearest the sub-umbrellar surface) and an ingoing current, often capable of rejection, on the remaining surfaces.
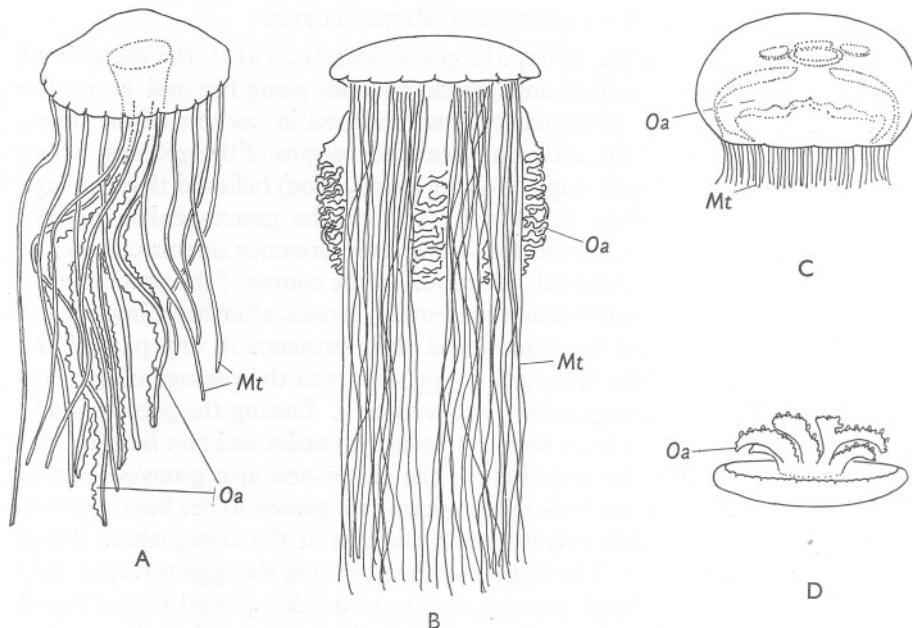

Fig. 7. Diagrammatic sketches of A, *Chrysaora*, B, *Cyanea*, C, *Aurelia* (in swimming position), and D, *Cassiopeia* (in attached posture), all in side view to show the relative proportions of the marginal tentacles (*Mt*) and the oral arms (*Oa*). A, C and D to the same scale, about ⅓ natural size; B, approximately one-half the scale of the rest.

Internally the species so far studied have a centrifugal current on the roof of the gastric pouches or gastric cavities, and a centripetal current on the floor. *Cyanea* and *Chrysaora*, however, differ from the rest in their lack of a marginal canal or plexus, and hence show no regular circulation in the radial canals (Widmark, 1911): in this they resemble the ephyra of *Aurelia*, in which the circulation is also partly ciliary and partly muscular. These two species differ from the adult *Aurelia* and the rhizostomes in possessing a wide central gastric cavity communicating freely with the oral arms, and might be said to be less

specialized. However, they diverge widely from the possibly ancestral ephyral type in another direction, for the oral arms and marginal tentacles are greatly elongated—specializations apparently directed towards a drift-net habit of feeding (Fig. 7).

If *Chrysaora* (Fig. 7 A) is the least specialized of these species (cf. Agassiz, 1860), *Aurelia* can be regarded as an intermediate stage in the direction of the rhizostomes, by reduction of the marginal tentacles and by the greater reliance placed on ciliary currents for food collection: the rhizostomes themselves have no tentacles, and the oral arms alone gather food. The final development of this trend may perhaps be found in *Cassiopeia*, which is sessile and employs the pulsations of the bell to pass water over the oral arms (Fig. 7 D). On the other hand, *Cyanea* shows greater adaptation than *Chrysaora* for the drift-net type of feeding; the enlarged frills of the oral arms (Fig. 7 B) must be necessary to cope with the increased number and catching area of the tentacles, to ensure that organisms captured are transferred to the arms.

SUMMARY

The jelly-fish *Aurelia aurita* possesses external and internal ciliary currents that play a large part in food collection and in the transport of food, reproductive products and excretory matter.

Adults feed on relatively small organisms, which are collected in mucus on all external surfaces and eventually passed to the inner surfaces of the oral arms.

The inner surfaces of the oral arms bear two ciliated tracts which operate simultaneously in opposite directions. The lateral tract carries food materials proximally towards the gastric pouches, but is capable of rejecting inedible matter. The basal tract carries excretory matter distally, away from the gastric pouches and canals to the exterior.

Rejection reactions are also found in the gastric pouches and radial canals, parts of which have currents moving in opposite directions on the roof and on the floor. These opposing currents appear to be derived from the system in the ephyra stage, where the circulation in the wide gastric cavity and blind-ending

canals is maintained partly by centripetal currents on the floor and centrifugal currents on the roof.

The directions of the main currents remain constant throughout the larval stages to the adult, although slight variations are introduced by morphological changes. The currents also remain the same during spawning, when the eggs and sperm leave the gastric pouches by the normal excretory path.

Many of the ciliary currents found in *Aurelia* are present in other semaeostome and rhizostome medusae, but only in *Aurelia* do the umbrella surfaces and currents play a large part in food collection. Some of the major morphological differences in the Scyphomedusae can be related to the different feeding habits of the various species.

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