On the Cœlomic Cilia and Circulation of the Body-Fluid in *Tomopteris helgolandica.*

By

Dr. Anton Meyer.

With 1 Figure in the Text.

A. INTRODUCTION.

The œcological significance of cilia and ciliary currents has been studied hitherto mainly so far as they are connected either with the epidermis or with the intestine. Epidermal cilia produce currents by which either the animal itself is moved or the surrounding medium is carried over the surface of the unmoved animal. In the latter case the ciliary currents serve for collecting substances, ordinary food and oxygen. It may be said, that the degree of specialisation of epidermal cilia generally indicates the degree of intimate dependence of the animal on its outside conditions (natural surroundings). (The cases where epidermal cilia are connected with sense organs are comparatively few.)

Intestinal cilia have a more limited significance: they never serve for movement of the animal nor for sensory functions, but are probably restricted to aiding the absorption of chymus and of oxygen by moving the content of the intestine. Since the ciliated intestinal surfaces are neither fully exposed to the outside conditions nor completely closed from the latter, we may express their position as semi-inside or internal.

Besides the epidermal and entodermal layers there is a third layer which builds up the architecture of many classes of animals and which resembles the first two layers in its epithelial character and in the possession of an extensive free surface; it is the cœlomic epithelium which surrounds the body cavity and is well developed in the Echinoderms, Chætognatha, Brachiopoda, Phoronidea, Bryozoa ectoprocta, Sipunculoidea, and Annelids. The cœlomic cavity indeed is thus the innermost part of these animals; it is the place of sexual reproduction, and holding an intermediate position between the nutritive organs on the one side and the muscular body wall which produces waste products, it becomes connected with both nutrition and excretion. The sexual products and excretory matters are carried out through the segmental organs; they represent a cœlomic derivative, the covering with cilia

of which is well known. The remaining parts of the cœlomic epithelium, however, show, in many cases, also a covering with cilia, which may be called cœlomic cilia in the strict sense.

The cœlomic cilia have escaped observation for a long time, and with exception of the Brachiopoda (Morse, 1901*) they have in no case been made the subject of closer examination. As will be seen from the following, the cœlomic cilia may attain a high level of physiological differentiation which is expressed in the regular arrangement and distribution, in the constancy of the direction of the effective stroke of all cilia in a given area, and in the co-ordination of the directions in neighbouring areas. The result of these is a circulation of the cœlomic body fluid which includes more or less the complete body cavity.

Before describing the cœlomic cilia and circulatory currents in a special case, it may be well to establish the positions of cœlomic cilia in relation to the epidermal and intestinal cilia and their œcological significance in the following scheme :—

CILIATED EPITHELIA.

Position in the general architecture of lower animals.	Œcological significance.
I. Outside (external)	Moving the animal (locomotion). Moving the surrounding medium and collecting :— 1. Food (nutrition). 2. Oxygen (respiration).
II. Semi-inside (internal)	Moving the content of the intestine (nutrition, respiration).
III. Fully-inside (inside)	Moving and circulating the cœlomic body fluid (circulation, etc.).

Cœlomic cilia in the Annelids were first specially examined by myself in *Tomopteris helgolandica* (*catharina*) in 1926 and later in full detail in another species from the Mediterranean (*T. elegans*), and also in various other classes (Bryozoa ectoprocta, Chætognatha, Polynoids) 1927.† The species common in the North Sea and the Channel, *T. helgolandica*, is somewhat different from the Mediterranean species ; therefore a special examination of *T. helgolandica* seemed necessary.

A few words on the general structure may be in place.

* Morse, E. S., 1901 : "Observations on Living Brachiopoda." Memoirs Boston Soc. of Nat. Hist., Vol. V.

† Die Segmentalorgane von *Tomopteris catharina* . . . ein Beitrag zur Theorie d. Segmentalorgane, Zeitschr. f. wiss. Zool., 1926.

Über Cölombewimperung u. cölomatische Kreislaufsysteme bei Wirbellosen, *ibid.*, 1927.

B. GENERAL REMARKS ON THE STRUCTURE OF TOMOPTERIS.

The Tomopterids are a family which is entirely restricted to pure planktonic life. Among the Annelid families they are a somewhat outstanding type; in external appearance they are noteworthy for the elongated shape of the parapodia, the fin-shape and purely glandular character of the cirri, the absence of bristles in the segments behind the mouth, also for the great length of a pair of tentacular cirri, for their transparency, and in some cases for the presence of a caudal region (Fig. 1, A). The transparency is due to the entire absence of pigment cells and to the thinness of the muscular layer and absence of connective tissues. The caudal region is a body region which does not reach full development; undoubtedly it is becoming vestigial and is in some species, e.g. *T. elegans*, fully suppressed and has phylogenetically disappeared.

The internal structure is noteworthy owing to the complete absence of transverse dissepiments. Another peculiarity is the absence of blood-vessels, which is connected with the reduced condition of retroperitoneal connective tissue and the conditions of planktonic life.

C. THE CŒLOMIC SYSTEM.

The cœlomic system includes the properties of the cœlom and the segmental organs.

The *cœlomic cavity* forms a continuous space on each side, both sides being separated by the dorsal and ventral mesentery of the gut; the cavity of the trunk region communicates widely with the cavities of the parapodia and so it shows parapodial and interparapodial sections. The mesenteries are wanting in the pharyngeal region, and the cœlomic cavity extends here forwards into the basal region of the head tentacles.

The content of the cœlomic cavity consists mainly of the sexual products, which are easily seen floating after separation from the gonads; the latter are situated in the cavities of the ventral and dorsal cirri of all segments behind the mouth. In the females a great number of oocytes become abortive and finally changed into numerous small plasmatic corpuscles. Those oocytes which develop into eggs are noteworthy through their considerable increase in size. True cœlomic corpuscles I have been unable to observe in *T. helgolandica* (but they are present in *T. planktonis* and *T. elegans*, although very rare). Statements of other authors, that there were a great number of true cœlomic corpuscles are wrong and are due to confusion with abortive oocytes or with spermatocytes.

It is also noteworthy that the secretion of the rosette-like organs (of both

categories) is discharged into the cœlomic cavity and is phosphorescent there. The rosette-like organs (rosettes and hyaline glands) are of mesodermal origin. Those of the second category (=rosettes) are, in young stages, situated in the basal region of the first and second parapodium (only) and are metamorphosed cœlomostomes, still showing in one species, *T. mariana*, their connection with solenocytes and retaining their original position in the basal region, where in the posterior segments (from the 6th onwards) the typical cœlomostomes and solenocytes are situated.

The connection of the cœlomic cavity with the exterior is established through the segmental organs, consisting of a spherical group of solenocytes, a small cœlomostome and a "nephridial" canal; the lumen of the latter can be expanded and contracted. In the females two pairs of large cœlomostomes are developed in the 4th and 5th segments; they are situated in a position which is not homologous with that of the ordinary cœlomostomes and represent a second set of cœlomostomes which is developed *later* in ontogeny as well as in phylogeny; they represent therefore secondary gonoducts.

The *cœlomic cilia* (Fig. 1, A, B) are represented as long ciliary rows; they occur in the trunk and in the parapodial cavities and also in the cavities of the cirri and of the head tentacles. The cœlomic epithelial layer is so thin that no cell boundaries are present, the nuclei are rare. There is generally one nucleus in the neighbourhood of each ciliary row.* The ciliary rows are arranged transverse to the longitudinal axis of the trunk and of the parapodia respectively. In the parapodia they occur on the opposite sides ventral and dorsal, but the first a little approximated to the posterior wall and the second to the anterior wall. The number of both sets is almost equal and mostly 4 to 6. In the trunk region the ciliary rows are more numerous on the ventral side; they are restricted to the interparapodial regions of the trunk and their number is usually 4 to 6. In the caudal region they are much more numerous, about 6 to 10, and are situated closely one behind the other.

The direction of the effective beat is the same in all the cilia of one row and it is also the same in all rows of one side. On the opposite sides (ventral and dorsal) the direction is opposite. The result of this antagonism is that the current of the cœlomic fluid is of a circulatory nature.

The *current* of the cœlomic fluid (Fig. 1, C) runs forward on the ventral side of the trunk, on the dorsal side backwards; in the parapodia it runs on the dorsal side outwards, on the ventral side inwards. The circulation of the parapodia is not confined to the same segment, but the greater part of the fluid which arrives ventrally in the base of the parapodium *enters*

* This can be made out with Fischer's solution of tannin-ferrous sulphate-alcohol fuchsin; it is necessary to let it act directly on the free cœlomic surface.

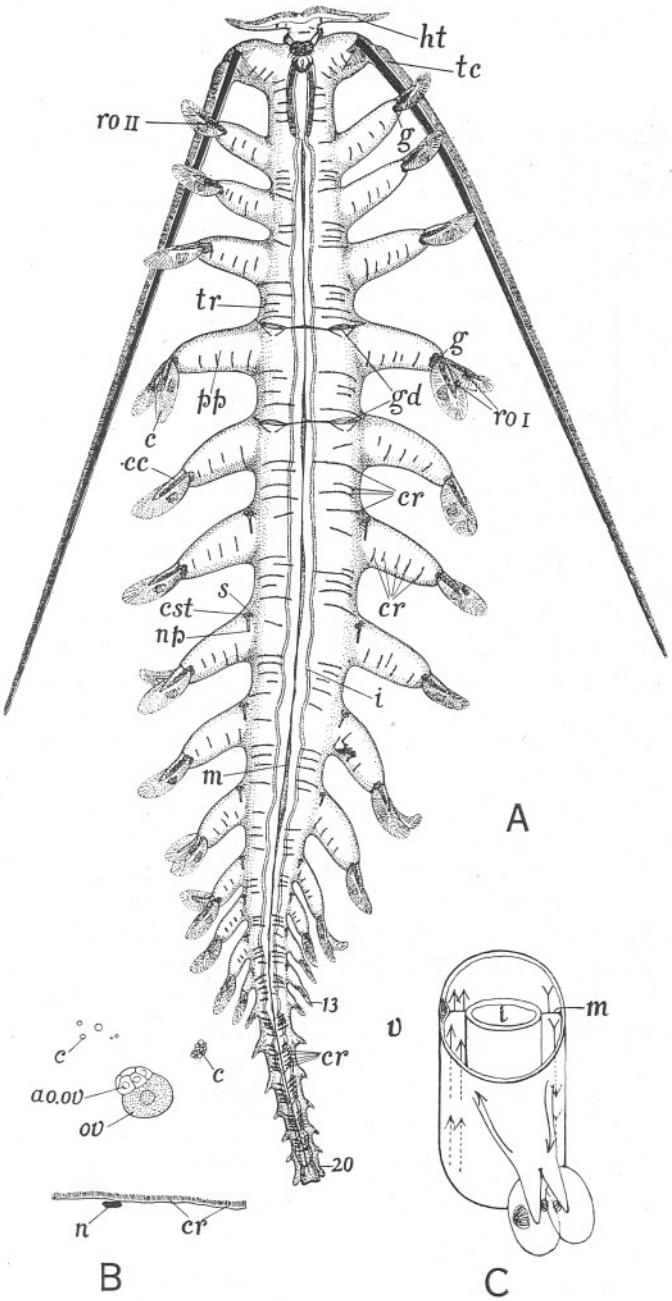

FIG. 1.—*Tomopteris helgolandica* ♀. (Watson Obj. 1, Oc. 2, working table. Reduced to one-half.) ht, head tentacles. tc, tentacular cirri (with a bristle). roI, rosette-like organs (phosphorescent) of first category (hyalin glands). roII, rosette-like organs (phosphorescent) of second category (rosettes). g, gonad. c, cirrus (=fin). cc, cirrus cavity. s, solenocytes. cst, cœlomostome. np, nephridiopore. gd, secondary gonoducts. cr, ciliary rows. i, intestine. m, mesentery. tr, trunk. pp, parapodium.

B, Content of the cœlomic fluid and ciliary row of *T. helgolandica* (Watson Obj. 3, Oc. 2, working table. Reduced to one-half.) c, corpuscles resulting from the abortive oocytes and also from the secretion of the rosette-like organs. ao. ov, abortive oocytes. ov, growing oocyte. cr, ciliary row with nucleus n.

C, scheme of the currents of the cœlomic fluid in *T. helgolandica* indicated by arrows. v, ventral. i, intestine. m, mesentery.

the trunk, and on the dorsal side fluid becomes drawn out from the trunk into the parapodium.

The directions of the circulation are more clear immediately above the ciliated surfaces than in the intermediate region, where the movement is slow and in its direction not constant, owing to the distance from the cilia and the viscosity of the fluid.

The cœlomic cilia in *T. helgolandica* are already present in young stages of nine parapodial segments* and the number of ciliary rows is almost fully established; but there also exists a small increase in the number during the progress of development and sexual maturity.

If we try to judge the general biological significance of cœlomic cilia and of the circulation produced by them we arrive at the following conclusions: (1) the cœlomic epithelium is phylogenetically of entero-cœlic (gono-cœlic) nature and therefore contains the possibility of development of cilia by inheritance from the cœlenteric ancestors; (2) cœlomic cilia are of œcological value especially in those animals where the blood-vessels are wanting and their functions are replaced by the cœlom; (3) the appearance of cœlomic cilia during individual life is not without connection with the development of the sexual products, and there exists also a relation of cœlomic cilia to the system of segmental organs which is clearly expressed in the addition of secondary components (secondary cœlomostomes and gonoducts) to the segmental organs; (4) the question whether in the primitive Annelid-ancestor circulation was carried out by cœlomic cilia or by true blood-vessels is not decided; until this question is solved from other arguments it remains undecided whether the occurrence of cœlomic cilia in the Annelids is a primitive (palingenetic) character or cenogenetic. From the physiological point of view it seems rather clear, that the occurrence of circulation by means of cœlomic cilia is more " primitive " than by means of contractile blood-vessels.

* These stages are still provided with a pair of bristle-bearing appendages (in front of the tentacular cirri) which are usually lost later.