Relations between Metachronism and the Direction of Ciliary Beat in Metazoa

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With one plate (fig. 2)

SUMMARY

In various ciliated epithelia one can distinguish either symplectic, antiplectic, dexioplectic, or laeoplectic metachronal waves, according to whether the effective beat of their cilia is with, against, to the right of, or to the left of, the direction of movement of the waves. In a given epithelium the relation between the direction of the waves and the direction of beat is constant.

Symplectic waves are probably associated with the transport of large particles, or viscous masses of mucus; antiplectic and diaplectic waves are better suited for creating water currents. It is unusual to find both dexioplectic and laeoplectic waves in the same animal; indeed, it is the rule for only one of these two types of metachronism to occur throughout a given systematic group. Dexioplectic waves are found in Protochordata, primitive Spiralia, the velum of Eulamellibranchiata, Phoronidea, Brachiopoda, Bdelloidea, and Melicertida; laeoplectic waves are found in *Chaetopterus*, Mollusca generally, Bryozoa, and Ploima. The incidence of dexioplectic and laeoplectic metachronism is not influenced by morphological reversals of symmetry such as the *situs inversus*. The relation between the direction of beat and the direction of the waves is therefore probably determined by cytological or stereochemical factors, rather than by gross morphology.

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INTRODUCTION, INCLUDING DEFINITIONS OF TERMS USED

IN most ciliated epithelia the cilia are arranged in rows, in two directions which are at right angles to one another. One of these directions approximates to the direction in which the cilia beat. The rows which run in this direction may therefore be called orthoplectic rows, and those which run in the other direction, diaplectic rows. In one of these two directions the cilia of a given row often beat synchronously, but in the other direction each cilium beats immediately after its neighbour, producing metachronal waves.

In the best-known examples of ciliary metachronism the waves move along the orthoplectic rows of cilia, travelling either in the same direction as the effective beat (these may be termed symplectic waves) or in the opposite direction (antiplectic waves). In many animals, however, the waves move along the diaplectic rows, and the effective beat may then be either to the right or to the left of the direction of movement of the waves, which may therefore be termed dexioplectic or laeoplectic waves.

It is well known, from observations on orthoplectic waves, that the relation between the direction of metachronism and the direction of beat is constant in a given epithelium. This constant relation is maintained even when the usual direction of beat is reversed, whether teratologically as in the gills of *Mytilus* (Atkins, 1930), surgically as in the epithelium of the frog's mouth (Brücke, 1916), in response to chemical stimulation, as in the labial cilia of *Metridium* (Parker, 1905), or voluntarily as in the ctenophores responding to mechanical stimuli (Fedele, 1925), and in the enteropneust, *Saccoglossus cambrensis*, when it reverses the beat of the trunk cilia. Thus in a variety of epithelia, showing both symplectic and antiplectic waves, whenever the ciliary beat is reversed the direction of movement of the waves is reversed too. There seems to be some link between the direction of the effective beat and the direction of movement of the waves.

The constancy of this link would be less surprising were it always to have adaptive value, but though there are functional differences between symplectic and antiplectic metachronism, there are no such differences between dexio- and laeoplectic metachronism. The incidence of one or the other of the two types of diaplectic metachronism must therefore, in general, have purely phylogenetic significance.

SYMPLECTIC AND ANTIPLECTIC METACHRONISM

Symplectic metachronism is particularly well known from early observations on the cilia of the frog's gullet and from the analogy of wind passing over a field of corn. Nevertheless, it occurs comparatively infrequently, and was not observed during the present survey, which mainly involved marine animals. This type of metachronal co-ordination requires the cilia to be bunched together during their effective stroke (fig. 1), an arrangement which would be well adapted for the transport of large particles or viscous masses

of mucus. If a cilium should be checked by contact with a large particle, its neighbours, following behind it, would immediately catch up with it and help it to move the particle along.

This arrangement would not be the most efficient way of causing a current in a fluid medium of low viscosity, since each cilium would push water already set in motion by the one behind. Antiplectic metachronism, which may be seen in a variety of animals (table 1, see p. 517), does this more efficiently, since it leads to the cilia, which are performing their effective stroke, being spaced out like the blades of a paddle wheel, whilst those which are recovering present the least possible resistance to water flow by being bunched together
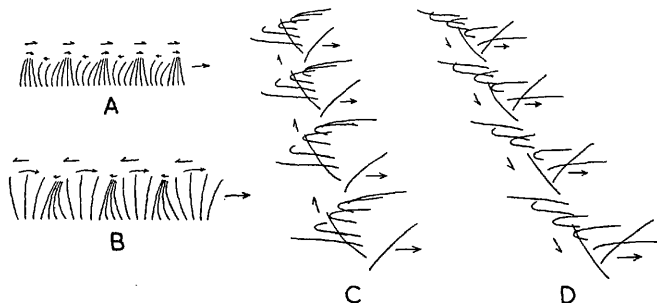

FIG. 1. Diagrams to illustrate the arrangement of cilia which are subject to the four main types of metachronal co-ordination. Each diagram represents a row of cilia the effective stroke of which is to the right and approximately in the plane of the paper (the diaplectic rows *C* and *D* are tilted to give a stereoscopic view along them). In this, and in subsequent figures, the direction of movement of metachronal waves is shown by single-barbed arrows, and the direction of effective beat by complete arrows. A, symplectic metachronism, in which the cilia performing the effective stroke are bunched together; B, antiplectic metachronism, in which the cilia performing the effective stroke are spread out; C, dexioplectic, and D, laeoplectic metachronism.

(fig. 1). This consideration raises the question whether the reversal of the effective beat in, for instance, Ctenophora, inevitably follows reversal of metachronism, without any other change taking place. In many ciliated epithelia, however, it can be seen clearly that the flexural characteristics of the cilia are of major importance in determining the direction of beat.

DIAPLECTIC METACHRONISM

For the sake of clarity, diagrams of the two types of diaplectic metachronism are given in fig. 1. Diaplectic waves are better illustrated in Dr. D. P. Wilson's photographs (fig. 2) which greatly aid analysis of their form. The ciliated girdles of larvae (fig. 4) and the lateral belts of cilia, which fringe branchial and lophophoral filaments and gill slits in a variety of adult animals, provide familiar examples of this type of metachronism, which is therefore found

generally, but not exclusively, wherever narrow belts of cilia are elongated transversely to the direction of beat. The cilia are often large, and the metachronal waves particularly conspicuous.

A functional advantage of diaplectic metachronism is that it allows large, strongly flexural cilia to operate freely, without striking their neighbours, since the beat is synchronized throughout each orthoplectic row. Cilia out of phase in the direction of beat must either move with a small amplitude or be widely spaced (as in ctenophores). Another result of this extra freedom is that cilia showing diaplectic metachronism may undergo fusion between adjacent individuals not only within the diaplectic rows, as in the undulating membranes of many ciliates, but alternatively, within the orthoplectic rows, as in the compound cilia of the nudibranch velum (Carter, 1928). On the other hand, fusion of cilia showing orthoplectic metachronism is only possible within the diaplectic rows, as in the swimming plates of ctenophores.

Since it would be inefficient to have cilia of more than a certain size beating in crowded orthoplectic rows, and therefore moving in water already set in motion by their neighbours, the number of cilia in each orthoplectic row is often small, or unity (fig. 7, p. 512). The narrow diaplectic belts, which result from such an arrangement, often occur repeatedly, at intervals, in a manner which may or may not be related to metamerism of the animal (e.g. figs. 5, A and 6, D, pp. 509 and 511).

The direction of rotation of certain ciliated larvae indicates that the beat of the cilia is not always exactly at right angles to the direction of movement of the metachronal waves. Most larvae with diaplectic ciliary girdles rotate constantly in one direction, and this is generally opposite to the direction of movement of the waves. The speed of rotation is usually much less than the speed of the waves, but larvae of a spherical or saucer-like form, with little resistance to rotation, rotate at a speed nearly as great as that of the waves, which suggests that the waves are responsible for the rotation. This is to be expected (Burdon-Jones, 1952), for each group of cilia on the recovery stroke

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FIG. 2 (plate). A, tornaria larva of *Glossobalanus sarniensis*, viewed abapically (with the telotroch beating towards the observer). The metachronal waves, being dexioplectic, appear, from this viewpoint, to move clockwise. The prominent cilia, which form the crests of the waves, are those performing their effective stroke. Immediately clockwise from these, in the troughs of the waves, the cilia are extended away from the observer, at the beginning of the effective stroke. Immediately anticlockwise from the crests of the waves are cilia at the end of the effective stroke. These do not lie flat, so do not form troughs. Further anticlockwise, between these and the troughs, are cilia on the recovery stroke, which reflect light strongly, presumably because they are strongly flexed.

B, the same, viewed ventrolaterally, with the telotrochal waves of the near side moving from left to right of the observer. In this view the crests of the waves are formed by the cilia at the beginning of the effective stroke. Immediately to the left of these the cilia are performing the effective stroke, the rapidity of which is reflected in the steepness of this part of the waves. To the left of the troughs lie the cilia which are on the recovery stroke. The oblique arrangement of these cilia, as the animal moves through the water, is probably responsible for its rotation.

(Photographed by Dr. D. P. Wilson, by electronic flash.)
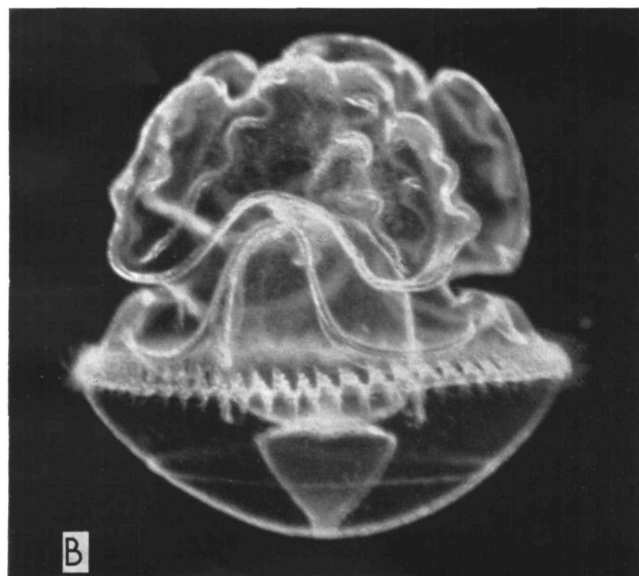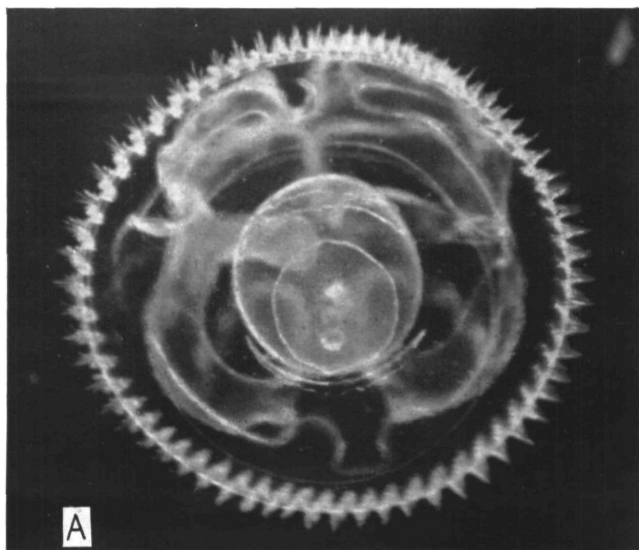
1 mm.

Fig. 2

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is arranged so that it presents an oblique (though of course incomplete) surface to the water through which the larva is moving (fig. 2, B). In many molluscs, however, the veligers rotate constantly in the same direction as that in which the waves move, which suggests that the beat of their cilia is somewhat oblique. It should be noted, too, that the lateral cilia of the lamellibranch ctenidia have obliquely arranged basal granules (Atkins, 1938).
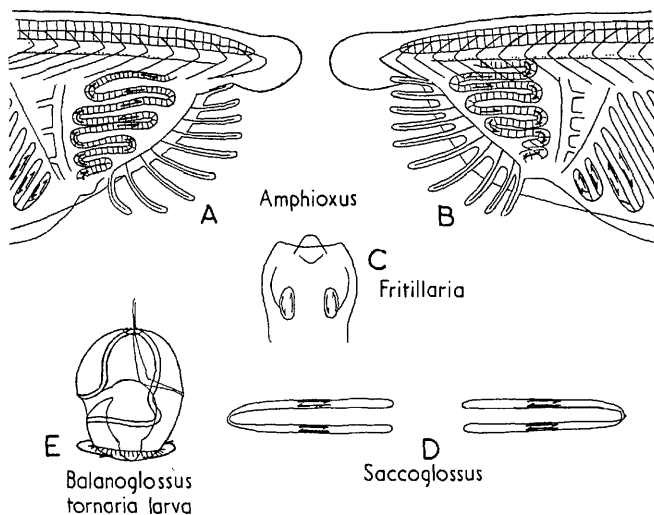

FIG. 3. Directions of movement of dexioplectic metachronal waves in Protochordata. A, anterior end of *Amphioxus*, from right side, showing waves of wheel organ and gill slits; B, the same, from left side; C, gill slits of *Fritillaria*, viewed ventrally (with cilia beating towards observer), after Fol; D, gill slits of *Saccoglossus*, viewed from inside pharynx (with cilia beating away from observer); E, tornaria of *Balanoglossus*, showing waves of telotroch.

PRELIMINARY SURVEY OF THE DISTRIBUTION OF DEXIOPLECTIC AND LAEOPLECTIC METACHRONISM IN METAZOA

Many of the following observations relate to planktonic larvae (e.g. fig. 4), which were reared from spawn or from artificial fertilizations, or which were identified from the plankton at Naples or at Bangor.

Protochordata (table 2, p. 517)

Wherever diaplectic waves occur in this group they invariably beat to the right. The waves produced by the cilia bordering the gill slits therefore move in what appears, from outside, to be an anticlockwise direction on both sides

of the body (e.g. fig. 3, C). This bilaterally asymmetrical movement previously seemed difficult to explain (Knight-Jones and Millar, 1949), but it is of a sort found, as a rule, wherever diaplectic metachronism occurs. Similarly, the

A   B   Müller's larva of polyclad   C   pilidium larva   H   echinopluteus
Müller's larva of polyclad
(Thysanozoon)   of nemertine

D   E   veligers of   J
trochophore of   eulamellibranch   K
polychaete (Pomatoceros)   and gastropod   cyphonautes larva
(Clio)   of bryozoan

F   G   L
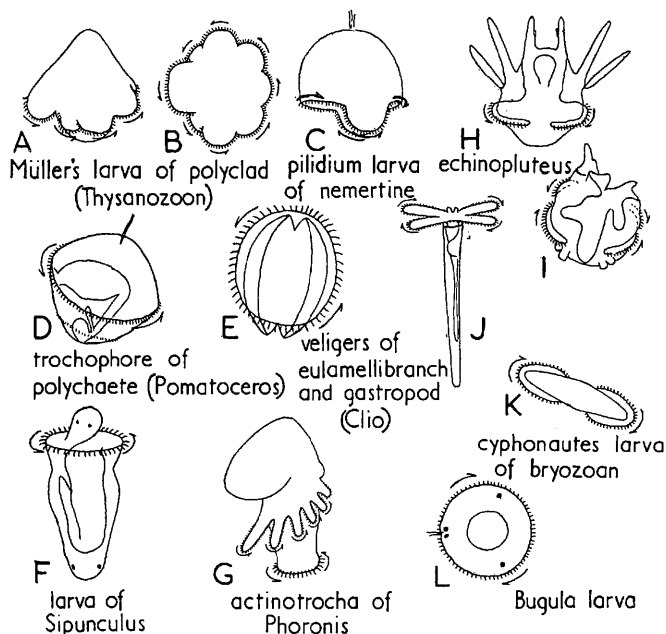larva of   actinotrocha of   Bugula larva
Sipunculus   Phoronis

Fig. 4. Movement of diaplectic metachronal waves round the ciliated girdles of some marine invertebrate larvae. The cilia of all beat posteriorly or abapically (directly or obliquely away from the observer in all these figures except A and C). In A to G the waves are dexioplectic; in H and I the waves move bilaterally symmetrically, being dexioplectic on one side and laeoplectic on the other; in J to L the waves are laeoplectic. A, Müller's larva of *Thysanozoon*, from left side; B, the same, viewed apically; C, pilidium larva of nemertine, from left side; D, trochophore of *Pomatoceros*, apico-lateral view, from left side; E, veliger of eulamellibranch, viewed apically; F, larva of *Sipunculus*, apico-lateral view, from right side; G, actinotroch of *Phoronis*, from left side; H, echinopluteus, viewed ventrally; I, echinopluteus about to meta-morphose, apico-lateral view, from right side; J, veliger of the pteropod, *Clio* (*Creseis*) *acicula*, viewed apico-ventrally; K, cyphonautes larva of bryozoan, viewed apically; L, larva of *Bugula*, viewed apically.

waves of the wheel organ in *Amphioxus* travel dorsally on the right side and ventrally on the left (fig. 3, A and B), the beat of the cilia being in a generally posterior direction, at right angles to the winding course of the ciliated tract. The waves of the telotroch in larval Enteropneusta (fig. 2) are also dexioplectic.

Echinodermata

The echinopluteus (fig. 4, D), with its powerfully ciliated epaulettes, is the only animal observed which has achieved a symmetrical arrangement of diaplectic metachronism, by having dexioplectic waves on one side and laeoplectic waves on the other. This arrangement of opposing waves must counter
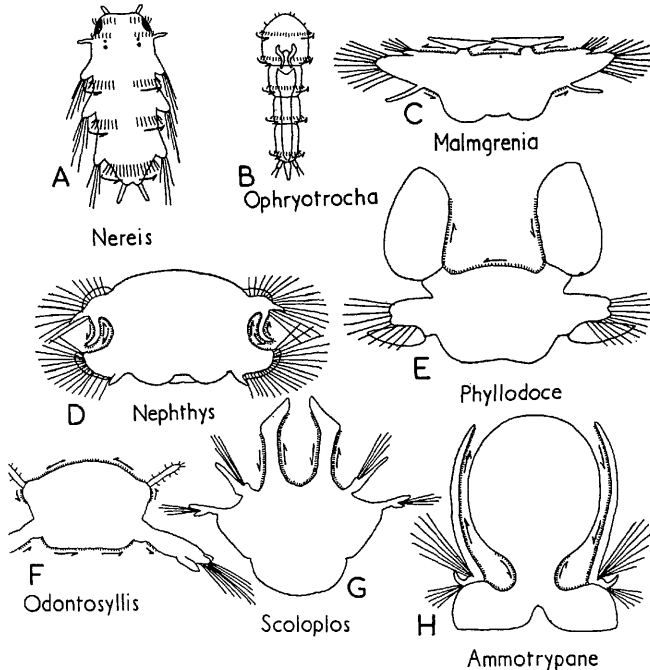

FIG. 5. Movement of the dexioplectic metachronal waves shown by the segmentally arranged transverse ciliated tracts of polychaetes: A and B, larvae of *Nereis pelagica* and *Ophryotrocha puerilis*, in dorsal view. The remaining figures represent transverse sections, viewed anteriorly, with the cilia beating away from the observer: C, *Malmgrenia castanea*; D, *Nephthys caeca*; E, *Phyllodoce mucosa*; F, *Odontosyllis gibba*; G, *Scoloplos armiger*; H, *Ammotrypane aulogaster*.

the tendency for the whole body to rotate, which is shown by many larvae with waves which encircle the body always in the same direction. Perhaps rotation would hamper feeding or some other activity of the echinopluteus.

Turbellaria (table 3, p. 518)

Dexioplectic waves are found on the ciliated lobes of polyclad larvae (fig. 4, B), as originally figured by Müller (1850).

Nemertini

Dexioplectic waves travel round the marginal lappets of pilidium larvae (fig. 4, c).

Sipunculoidea

Dexioplectic waves travel round the ciliated girdle in larvae of *Sipunculus nudus* (fig. 4, F).

Archiannelida

Dexioplectic waves travel round the head of *Dinophilus taeniatus*. The small cilia, which beat posteriorly, were difficult to observe in active entire animals, but they were easily examined in a head which had been partially severed from the remainder of the body.

Polychaeta (table 3, p. 518)

Dexioplectic waves were observed in 56 out of 57 identified larvae and adults, which showed diaplectic metachronism, and in many unidentified larvae. As Segrove (1938) remarked, the ciliated girdles of larval polychaetes have their counterparts in the segmental transverse bands of many adults (fig. 5). These adult cilia are probably respiratory in function and generally beat posteriorly. Many polychaetes have longitudinal rows of cilia along the sides of the body (fig. 6, A and B). In some forms, such as *Syllis prolifera* and *Phyllodoce maculata*, these cilia beat ventrally, so the dexioplectic waves move anteriorly on the right side and posteriorly on the left; but in others, such as *Scalisetosus pellucidus* and *Sabellaria alveolata*, they beat dorsally, so the waves move posteriorly on the right side and anteriorly on the left. Several sedentary polychaetes, such as *Stylarioides eruca* (fig. 6, c and D), *Flabelligera affinis*, *Ampharete grubei*, and *Sabellaria alveolata*, have branchiae with cilia which are arranged in transverse bands and which drive currents distally, and dexioplectic waves which follow each band in a partial or complete circuit of the branchia.

An apparent example of reversal of cilia was observed in *Microspio mecznikowianus*, which lives in sandy mud at Naples. When this form is left undisturbed its branchial cilia beat anteriorly, so their functions probably include the expulsion of waste products, as in many tubicolous forms. But when *Microspio* is agitated these cilia beat posteriorly, as in other Spionidae, drawing fresh water into the tube to meet increased oxygen requirements. Whenever the ciliary current reverses, the metachronal waves also travel in the reverse direction, but close examination of the inner surfaces of the branchiae shows that there are two closely adjacent rows of cilia on each, only one of which is active at a time. The cilia of the row which is active beat over the top of those of the other row, which lie flat, at the beginning of the effective stroke, as resting cilia usually do (Gray, 1928). The metachronal waves of the active cilia are always dexioplectic, those of the two adjacent rows travelling in opposite directions (fig. 7).

The only polychaetes observed with laeoplectic waves were larvae of *Chaetopterus variopedatus*. Adult Chaetopteridae have small cilia, which do not show clearly diaplectic metachronism.

Mollusca (table 4, p. 518)

The lateral cilia of the ctenidia show laeoplectic waves in all classes, except in Cephalopoda, which have unciliated muscular ctenidia expanding and contracting like lungs, and in Scaphopoda, which lack ctenidia. The lateral cilia
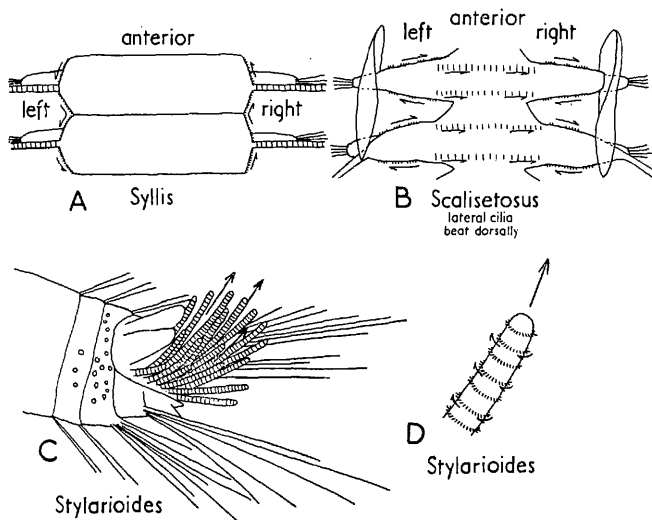

FIG. 6. Further examples of the dexioplectic metachronal waves of polychaetes. A, two segments of *Syllis prolifera*, viewed dorsally, with the longitudinal ciliated tracts of each side beating away from the observer; B, two segments of *Scalisetosus pellucidus*, viewed dorsally, with the longitudinal ciliated tracts of each side beating towards the observer, and the transverse tracts of the dorsal surface beating posteriorly (towards the bottom of the figure); C, anterior end of *Stylarioides eruca*, viewed dorso-laterally from the right side, showing the currents produced by the branchial cilia, which beat distally; D, distal end of a branchia from *Stylarioides,* showing the encircling rings of cilia, the current produced, and the direction of the metachronal waves.

beat towards the dorsal surface of the ctenidium, drawing water up between the lamellae (fig. 8, B and F). In most lamellibranchs the lamellae are drawn out into filaments, which are kinked to form a V on each side of the ctenidial axis. Since the lateral cilia always beat into the space enclosed by each V, the laeoplectic waves always appear to move as a pencil moves in writing a W, irrespective of whether the observer is viewing the anterior or the posterior surfaces of the filaments (fig. 8, G). The knowledge that the waves are

laeoplectic helps the study of ctenidial ontogenesis. In small post-larvae it is not easy to see which way the cilia of the first gill filaments are beating, but the distinct diaplectic waves, which are characteristic of the lateral cilia, can easily be seen through the transparent shells (fig. 8, H and I). On the justifiable
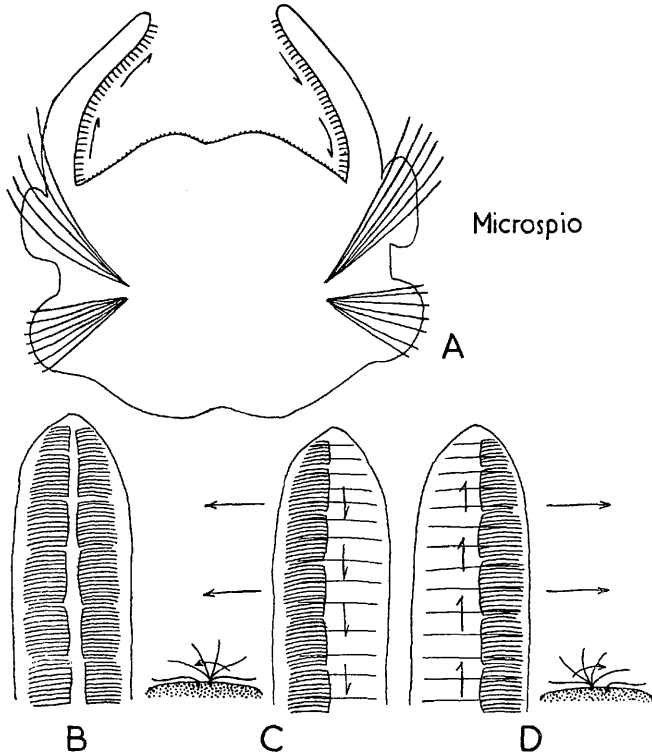

FIG. 7. A, transverse section of *Microspio mecznikowianus* showing movement of waves when the dexioplectic cilia of the branchiae are beating away from the observer; B, inner surface of a branchia showing the two rows of cilia, immobilized in the initial position of the effective stroke; C, branchia in section and in surface view showing the left-hand row of cilia still motionless and the right-hand row beating with dexioplectic metachronism (the beating cilia are indistinguishable individually in surface view); D, the same, but with the other row of cilia active.

assumption that these waves are laeoplectic it can be deduced that the cilia are beating away from the observer towards the midline, and hence that it must be the inner demibranchs which are developing first, as is known to be

the general rule in lamellibranchs. It would be interesting to apply such observations to *Xylophaga* and the Teredinidae, adults of which lack the inner demibranch (Purchon, 1941), though the characteristic opacity of the larval shell in these families would no doubt prove to be an obstacle.
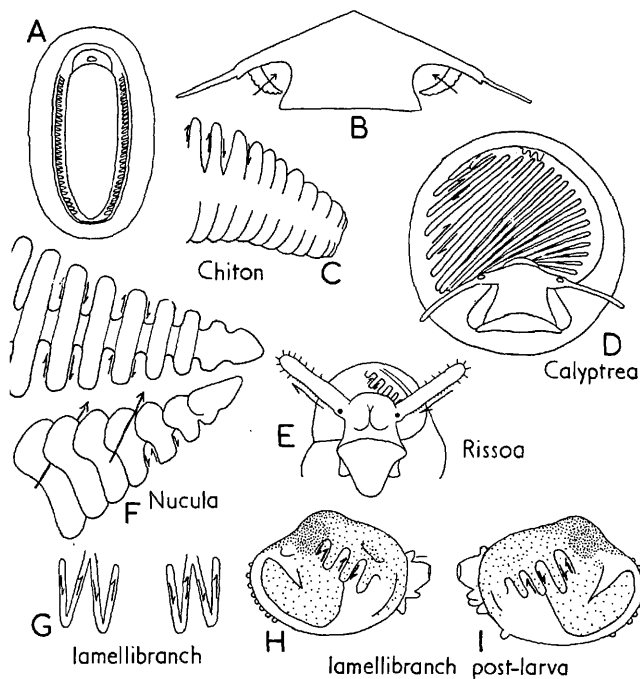

FIG. 8. Laeoplectic metachronism in some adult and post-larval Mollusca. A, *Chiton olivaceus* viewed ventrally, to show positions of ctenidia; B, *Chiton* in transverse section, to show movement of water currents drawn through the ctenidia by the lateral cilia; C, a ctenidium of *Chiton* viewed ventrally, showing the laeoplectic metachronal waves of the lateral cilia, which are beating away from the observer; D, *Calyptrea chinensis* viewed antero-ventrally, showing the greatly enlarged ctenidium and the waves of its lateral cilia, which beat away from the observer; E, *Rissoa soluta* viewed antero-ventrally, showing the waves produced by the cilia on the ctenidium and on the ventral surface of each tentacle, as they beat away from the observer; F, posterior ends of the paired ctenidia in *Nucula nitida*, viewed ventrally and from slightly to the left of the mid-line, showing waves produced by the lateral cilia, and currents produced by the lateral cilia of the right (lower) ctenidium (on the left ctenidium these cilia are beating directly away from the observer); G, diagrammatic cross-section of the ctenidia in a lamellibranch such as *Chlamys*, showing the movement of the waves produced by the lateral cilia, which presents a similar picture in both anterior and posterior views of the filaments; H, a eulamellibranch post-larva, from the left side, showing the movement of the waves produced by the lateral cilia of the rudimentary gill filaments; I, the same from the right side, to show that this movement is bilaterally asymmetrical.

Some gastropods, for instance *Rissoa soluta* (fig. 8, E), have tracts of cilia on the tentacles, which show laeoplectic waves.

The velum of larval Mollusca usually shows clearly diaplectic waves, which are laeoplectic in most molluscs, but dexioplectic in Eulamellibranchiata. These waves were clearly laeoplectic in gastropod larvae of 29 identified species, representing all orders except pulmonates, and in many other gastropod larvae which could not be identified.
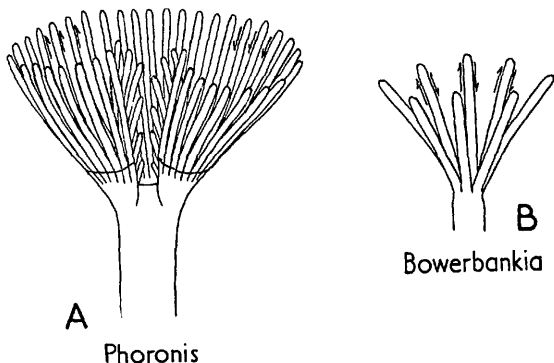

A
Phoronis

B
Bowerbankia

Fig. 9. Lophophores of A, *Phoronis*, with dexioplectic waves shown by the lateral cilia of the filaments, and B, the bryozoan *Bowerbankia*, with laeoplectic waves. In these forms the lateral cilia beat outwards.

Larvae of *Lepidochitona cinereus*, like those of most molluscs, rotate in what appears in apical view to be a clockwise direction. Their movement is unusually rapid, each rotation taking about 3 seconds. Their prototrochal waves are almost certainly laeoplectic, for they travel in the same direction as that of rotation, but at an even greater speed, moving through a complete circle in less than 2 seconds.

Larval oysters and mussels have laeoplectic metachronism on the velum. This agrees with the latest classification uniting these in the Anisomyaria, a group equivalent to the Eulamellibranchiata, veligers of which have clearly dexioplectic waves. No metachronal waves could be distinguished in trochophores of *Dentalium* or in veligers of the anisomyarian genera *Lima* and *Anomia*. Identification of larvae of Anisomyaria is considerably aided by observations of the velar waves and of the directions of rotation of the larvae (Knight-Jones, 1954).

Phoronidea (table 5, see p. 519)

Dexioplectic waves are produced by the ciliated girdles of actinotroch larvae (fig. 4) and by the lateral cilia of the adult tentacles (fig. 9).

Brachiopoda—Testicardines

Mr. Gareth Owen and Dr. R. B. Pike kindly sent living brachiopods from Scotland. Careful observation distinguished dexioplectic waves amongst the lateral cilia on the lophophore of *Terebratulina retusa*. The beat of these cilia was at right angles to the filaments, and from the inside towards the outside of the lophophoral loops. They were therefore important in causing a circulation of water, with incurrent lateral streams and an excurrent median stream, similar to that described by Richards (1952) in *Neothyris*, and by Orton (1914) in *Crania*. Richards did not observe any special activity of the lateral cilia.

Brachiopoda—Ecardines

Diaplectic metachronism could not be distinguished in larvae or adults of *Lingula* (Purchon, 1953) or in adults of *Crania anomala*.

Bryozoa (table 5, p. 519)

Laeoplectic waves are produced by the larval girdles (fig. 3) and by the lateral cilia of adult tentacles (fig. 8).

No metachronal waves could be distinguished in either larvae or adults of Endoprocta.

Rotifera (table 6, p. 520)

Dexioplectic waves are characteristic of the Bdelloidea and Melicertida (= Flosculariacea, Harring, 1913), laeoplectic waves of the Ploima (p. 516).

CONCLUSIONS OF SYSTEMATIC INTEREST

The results of the foregoing survey are summarized in table 7 (p. 520). In view of the facts that *Chaetopterus* is one of the most specialized of the polychaetes, and that the Mollusca form one of the most specialized groups of the Spiralia (groups showing spiral cleavage), it is highly probable that the primitive direction of diaplectic metachronism in the Spiralia was dexioplectic. Clearly this direction is reversed by mutation only at rare intervals.

The waves on the velum of eulamellibranch larvae probably represent a secondary reversion to the dexioplectic type for three reasons. First, laeoplectic metachronism is of general occurrence in Mollusca, being found in Amphineura, Gastropoda, and Lamellibranchiata. Secondly, the Anisomyaria, which have larvae with laeoplectic waves, have primitive features, including a larval hinge like the *Nucula* hinge, whilst the Eulamellibranchiata, on the other hand, form a compact and highly evolved group. Thirdly, the Eulamellibranchiata themselves show laeoplectic waves on their ctenidia, and the combination, in a single animal, of the two types of diaplectic metachronism, is a rare feature and so probably a secondary one. Although the most primitive groups of the Spiralia have dexioplectic waves, it therefore seems probable that the Precambrian ancestor of all the molluscs had already changed to

laeoplectic waves, and that since then the veligers of eulamellibranchs have changed back again.

The current division of the Rotifera into Digononta and Monogononta (table 6, p. 520), seems unsound, because it unites the Melicertida with the Ploima and divides them from the Bdelloidea. The question whether the gonads are paired or single is of doubtful systematic importance, since reduction may easily have occurred more than once in the evolution of these minute forms. The direction of diaplectic metachronism seems a more reliable guide to affinity, since it is of no adaptive importance and is probably bound up with intimate cell structure (p. 517). The Bdelloidea and Melicertida somewhat
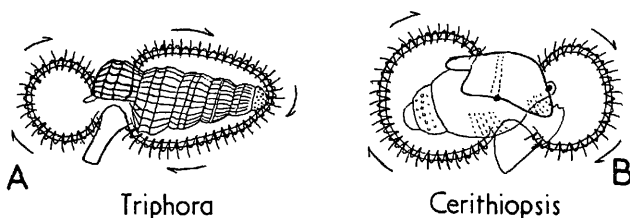

Fig. 10. Movement of metachronal waves in veligers, A of the *situs inversus* species of gastropod, *Triphora perversa*, and B of the normal species, *Cerithiopsis tubercularis*.

resemble each other in the form of the corona and mastax, so if further observations confirm the grouping set out in table 6, the Bdelloidea and Melicertida might well be linked as sub-orders of the Dexioplectica, a new order of rotifers, the members of which show dexioplectic metachronism. The remaining rotifers, which show either laeoplectic metachronism, or extreme reduction or modification of the ciliary apparatus, would fall into the three orders—Ploima, Seisonidea, and Collothecacea.

PROBABLE LOCATION OF THE FACTOR DETERMINING WHETHER DIAPLECTIC
METACHRONISM IS DEXIO- OR LAEOPLECTIC

Triphora perversa (fig. 10) is a gastropod showing complete *situs inversus* of the type which is known to be associated in certain pulmonates with reversed spiral cleavage. Its metachronal waves nevertheless travel round the velum in the same direction as in a normal gastropod. Similarly, *Spirorbis pagenstecheri* and *Spirorbis borealis* show contrasting morphological asymmetries, as a result of which they undergo dextral and sinistral coiling respectively, yet the direction of metachronism is the same in larvae of both species (table 3, p. 518).

Conversely, though metachronism is laeoplectic in gastropods and *Chaetopterus*, and dexioplectic in polyclads, nemertines, and most polychaetes, the direction of spiral cleavage is well known to be remarkably constant through-

out all groups of the Spiralia. Cleavage in *Chaetopterus* is in the usual direction (Mead, 1897).

It may be concluded that the asymmetry associated with diaplectic metachronism is independent of the familiar morphological asymmetries of animals. This independence is analogous with that shown by the spiralling of the sperm tail in *Limnaea*, which is in a constant direction in sperm from both normal and *situs inversus* individuals (Selman and Waddington, 1954). Evidently the direction of diaplectic metachronism is not determined by gross anatomy but probably by the micro-anatomy of the ciliated cells. It is likely to depend on some stereochemical peculiarity of the ciliary basal apparatus.

TABLE 1

Species observed

Examples of ciliated epithelia showing antiplectic metachronism

Swimming combs of Ctenophora	*Pleurobrachia pileus*
Antero-dorsal cilia of Turbellaria	*Dugesia tigrina*
	Crenobia alpina
Ventral groove in Serpulidae	*Pomatoceros triqueter*
	Spirorbis borealis
Tentacles and body in larval Chaetopteridae . .	*Chaetopterus variopedatus*
Food-collecting sulcus bordering velum in larval	
Gastropoda	*Nassarius incrassatus*
Frontal surface of ctenidium in Lamellibranchiata	*Cardium edule*
Collar and trunk epidermis of Enteropneusta . .	*Saccoglossus cambrensis*

TABLE 2

Protochordata in which dexioplectic metachronism was observed

HEMICHORDATA: *Saccoglossus cambrensis, S. horsti, Glossobalanus minutus*— lateral cilia of gill slits.
    Saccoglossus horsti, S. pusillus, and *Tornaria ritteri* (Ritter and Davis, 1904), *Balanoglossus clavigerus, Glossobalanus sarniensis* (Wilson, 1952)—larval telotroch.

UROCHORDATA:
    ASCIDIACEA: *Ascidia californica* (McGinitie, 1939), *Ascidiella aspersa, Ciona intestinalis, Perophora listeri, Diplosoma listerianum*—gill slits.
    THALIACEA: *Doliolum mulleri* (Fedele, 1923)—gill slits.
    LARVACEA: *Fritillaria urticans* (Fol, 1872)—gill slits.

CEPHALOCHORDATA: *Amphioxus lanceolatus* (Müller, 1842)—gill slits and wheel organ.

TABLE 3

Primitive Spiralia in which dexioplectic metachronism was observed

POLYCLADIDA: polyclad B* (Müller, 1850), *Thysanozoon brocchii.**

NEMERTINEA: Pilidium larvae* of several species.

SIPUNCULOIDEA: *Sipunculus nudus.**

ARCHIANNELIDA: *Dinophilus taeniatus.†*

POLYCHAETA ERRANTIA:
    APHRODITIDAE: *Harmothoë imbricata, Malmgrenia castanea,† Halosydne gelatinosa,† Scalisetosus pellucidus,† Acholoë astericola* (Davenport, 1952), *Sthenelais limicola,† Sthenelais boa.†*
    PHYLLODOCIDAE: *Phyllodoce maculata, Phyllodoce lamelligera,† Phyllodoce mucosa,† Eulalia viridis,* Eulalia marginata.**
    HESIONIDAE: *Kefersteinia cirrata,† Magalia perarmata.†*
    SYLLIDAE: *Syllis prolifera,† Eusyllis blomstrandi,† Odontosyllis gibba, Autolytus aurantiacus.†*
    NEREIDAE: *Nereis pelagica,* Nereis virens** (Burdon-Jones, 1953).
    NEPHTHYDIDAE: *Nephthys caeca,† Nephthys hombergi.†*
    EUNICIDAE: *Eunice vittata,† Staurocephalus rudolphii,† Ophryotrocha puerilis.*

POLYCHAETA SEDENTARIA:
    ARICIIDAE: *Nainereis laevigata,† Aricia cuvieri,† Scoloplos armiger.†*
    SPIONIDAE: *Nerine cirratulus, Nerine bonnieri,† Nerine foliosa,* Scolelepis fuliginosa, Microspio mecznikowianus, Prionospio malmgreni,* Polydora antennata, Polydora ciliata.*
    DISOMIDAE: *Poecilochaetus serpens.**
    PARAONIDAE: *Aricidea jeffreysii.†*
    CIRRATULIDAE: *Cirratulus cirratus** (Burdon-Jones, 1953).
    CHLORHAEMIDAE: *Flabelligera affinis,† Stylarioides eruca.†*
    OPHELIIDAE: *Ophelia bicornis** (Wilson, 1952), *Ammotrypane aulogaster.†*
    CAPITELLIDAE: *Capitella capitata,* Notomastus latericeus.†*
    ARENICOLIDAE: *Arenicola marina** (Howie, 1952).
    SABELLARIIDAE: *Sabellaria spinulosa,† Sabellaria alveolata.*
    AMPHICTENIDAE: *Pectinaria koreni.**
    AMPHARETIDAE: *Ampharete grubei.†*
    TEREBELLIDAE: *Polymnia nebulosa.**
    SABELLIDAE: *Dasychone lucullana.†*
    SERPULIDAE: *Salmacina dysteri,* Pomatoceros triqueter** (Burdon-Jones, 1953), *Spirorbis borealis,* Spirorbis pagenstecheri.**

Metachronism was laeoplectic in:
CHAETOPTERIDAE: *Chaetopterus variopedatus.**

    * Only larvae observed. † Only adults observed. The absence of an asterisk or a dagger indicates that metachronism was observed in both larvae and adults.

TABLE 4

Mollusca

The lateral cilia of the ctenidia showed laeoplectic metachronism in:

AMPHINEURA: *Chiton olivaceus.*

GASTROPODA: *Fissurella nubecula, Rissoa parva, Rissoa soluta, Calyptraea chinensis.*

LAMELLIBRANCHIATA: *Nucula nitida, Mytilus edulis, Ostrea edulis* (Walne, 1952), *Lasaea rubra, Cardium edule, Chione fasciata, Cultellus pellucidus.*

The velar cilia showed laeoplectic metachronism in:

AMPHINEURA: *Lepidochitona cinereus.*

GASTROPODA:
PROSOBRANCHIATA: *Patella coerulea, Patina pellucida, Lacuna vincta, Littorina littorea, Rissoa soluta, Hydrobia ulvae, Crepidula fornicata, Trivia monacha, Cerithiopsis tubercularis, Triphora perversa, Balcis devians, Nassarius reticulatus, Nassarius incrassatus, Mangelia striolata, Nucella lapillus, Urosalpinx cinerea* (Hancock, 1953).
TECTIBRANCHIATA: *Philine aperta, Aplysia punctata* (Burdon-Jones, 1953), *Aplysia depilans.*
PTEROPODA: *Limacina inflata, Clio (Creseis) acicula.*
NUDIBRANCHIATA: *Limapontia depressa* and *Elysia viridis* (Burdon-Jones, 1953), *Acanthodoris pilosa, Adalaria proxima, Archidoris britannica, Idulia coronata, Facelina curta, Tergipes despectus* (Norris, 1952), *Cratena aurantia.*

LAMELLIBRANCHIATA:
ANISOMYARIA: *Ostrea edulis, Mytilus edulis, Mytilus galloprovincialis, Modiolaria marmorata.*

The velar cilia showed dexioplectic metachronism in:

EULAMELLIBRANCHIATA: *Kellia suborbicularis, Mysella bidentata, Montacuta ferruginosa,* several Tellinidae, *Abra prismatica, Spisula elliptica, Petricola lithophaga, Cardium edule, Cultellus pellucidus, Mya arenaria, Zirphaea crispata, Teredo pedicellata* (Isham, 1951), *Teredo navalis.*

No metachronal waves could be distinguished in trochophores of *Dentalium dentale* or in veligers of the anisomyarian forms *Lima hians* and *Anomia ephippium.*

TABLE 5

Dexioplectic metachronism is found in:

BRACHIOPODA TESTICARDINES: *Terebratulina retusa.**

PHORONIDEA: *Phoronis hippocrepia, Phoronis psammophila.*

Laeoplectic metachronism is found in:

BRYOZOA: Cyphonautes larvae of several species.
CTENOSTOMATA: *Alcyonidium gelatinosum, Alcyonidium hirsutum,** *Flustrella hispida, Bowerbankia imbricata, Zoobotryon pellucidum** (Cori, 1937).
CHEILOSTOMATA: *Bugula avicularia, Bugula plumosa, Bugula flabellata, Lepralia pallasiana.*
CYCLOSTOMATA: *Crisia cornuta.**
PHYLACTOLAEMATA: *Plumatella repens.**

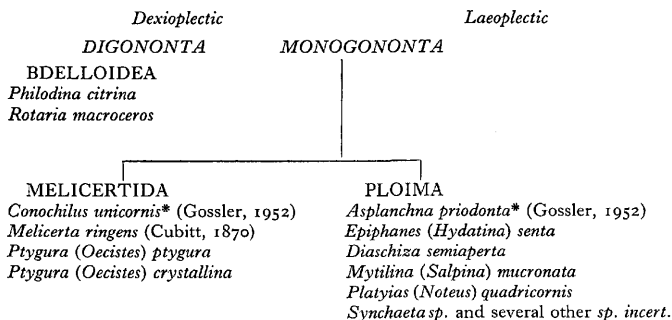Diaplectic metachronal waves could not be distinguished in:

BRACHIOPODA ECARDINES: *Crania anomala** (Pike, 1953), *Lingula sp.* (Purchon, 1953).

ENDOPROCTA: *Pedicellina cernuum, Loxosoma singulare.*

* Observations on adults only. In species not marked with an asterisk the cilia of the larval girdles were observed as well as the lateral cilia of the adult tentacles.

TABLE 6

In Rotifera, the metachronal waves of the trochal disk may be either dexioplectic (anticlockwise when viewed anteriorly) or laeoplectic (clockwise) as follows:

Dexioplectic		*Laeoplectic*
DIGONONTA	*MONOGONONTA*	

BDELLOIDEA
Philodina citrina
Rotaria macroceros

MELICERTIDA	PLOIMA
Conochilus unicornis* (Gossler, 1952)	*Asplanchna priodonta** (Gossler, 1952)
Melicerta ringens (Cubitt, 1870)	*Epiphanes (Hydatina) senta*
Ptygura (Oecistes) ptygura	*Diaschiza semiaperta*
Ptygura (Oecistes) crystallina	*Mytilina (Salpina) mucronata*
	Platyias (Noteus) quadricornis
	Synchaeta sp. and several other *sp. incert.*

No ciliary activity could be observed in *Collotheca (Floscularia) regalis*.

* Previous records (Gossler, 1950) of the reverse direction of metachronism in these species, were due to a correction having been applied for optical inversion (Gossler, 1952). No such correction should be applied.

TABLE 7

Dexioplectic	*Laeoplectic*
Platyhelminthes	
Nemertini	
Sipunculoidea	
Archiannelida	
Polychaeta generally $\longrightarrow$	Chaetopterus
Ancestral Spiralia? $\longrightarrow$	Mollusca generally
Eulamellibranch veligers $\swarrow$	
Phoronidea	Bryozoa
Brachiopoda	
Bdelloidea and Melicertida	Ploima
Protochordata	

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