METAMORPHOSIS FROM THE VIEWPOINT OF ANIMAL PHYLOGENY

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METAMORPHOSIS FROM THE VIEWPOINT OF ANIMAL PHYLOGENY[1)]

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The life-history of animals becomes quite complicated by the occurrence of the phenomena, metagenesis and heterogony. Metagenesis is very common in some marine animals such as Coelenterata, Salpians, etc. In these groups one of the generations (sexual or asexual)is generally better developed than the other, and the phylogeny of this group is mainly based on the morphology and embryology of the superior phase with the inferior one taken into consideration. In the Hydrozoa, however, these two phases, polyps and medusae, are respectively differentiated in detail. Moreover, the trends of differentiation in these phases do not coincide with each other. Therefore, it is very difficult for the present to establish a unitary system for the Hydrozoa. Heterogony occurs in some parasites, insects and small fresh-water animals. This phenomenon seems to be caused to make possible the taking of ample nutrition in the larval stage or to enable the endurance of severities of environmental conditions; it does not correlate with animal phylogeny.

In the course of animal development there are known two types; one direct development and the other indirect development or with metamorphosis. Most of the marine animals have one or several larval stages, therefore metamorphosis generally occurs in these animals; e.g. in Coelenterata, Platyhelminthes, Nemertini, Polychaeta, Mollusca and Echinodermata. These animals have each larval forms specific to their own respective groups. These larvae are of special importance in the consideration of phylogenetic problems. Of course, these larvae themselves do not indicate the ancestral forms, as was formerly believed, but the phylogenetic significance lies in the presence of common or similar larval forms in the animals phylogenetically closely allied. In other words, the trochophora does not illustrate the ancestral forms of Polycheata and Mollusca but these animal groups have some phylogenetic relations with each other in having the similar

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larval forms which seem to have resulted from some adaptation. These larvae undergo metamorphosis before growing to the adult stage. From the phylogenetical viewpoint much importance must be attached to the further process of metamorphosis in these larvae, as a result of which the animal groups are sometimes divided into classes, orders and families. For instance, the classification of Crustacea is established on the basis of further development of the nauplius, the common larval form of all of them.

In the marine invertebrates the larvae assume sundry modes of life after metamorphosis; some remain pelagic throughout their whole life, some sink to the bottom, entering into a sluggish life, some attach to some substrata such as rocks and sea-algae, ending in sessile life and some seek their hosts, exhibiting parasitic life. Out of these animal groups, sessile and parasitic forms illustrate more or less a retrograde development during metamorphosis because of the change from an active free swimming life into an inactive stationary one. Of course, there appear in these animals some new organs during metamorphosis. But such organs are mostly due to environmental adaptation and have no significance from the viewpoint of phylogeny. On the other hand, most of the neurolocomotor and nutritive organs have a tendency to become degenerated and sometimes have completely disappeared in the adult, especially in the parasitic forms. Such being the case, it is quite difficult to follow the phylogenetic data concerning the post-larval development of these groups. For instance, the ascidians give rise to ascidian tadpoles in which the notochord, nerve system etc. gradually degenerate after attaining sessile life (Hirai, 1951). In such animals the process of metamorphosis is not extensive but retrogressive to adapt to a new life, so it is far from having any role in the phylogeny.

There are rather many marine animals which are sedentary and sluggish in locomotion. Representatives of them are Platyhelminthes, Nemertini, Mollusca and Echinodermata. Among them the two phyla, marine Platyhelminthes and Nemertini are not only alike in the possession of the larva, protrochula, but also there are observable morphological and œcological similarities in them. According to Iwata (1960) the life-history of the Nemerteans is different according to the orders. Species belonging to the Palaeonemertea, Hoplonemenrtea and Bdellomorpha exhibit direct development, without going through any metamorphosis, whereas those belonging to the Heteronemertea have larval forms which are divided into the following three kinds, pilidium, Desor's larva and the intermediate one newly described by Iwata. In the Heteronemertea amnion invaginations always occur in these larvae and then the second larvae are formed. Among the three former orders the genus *Cephalothrix* alone is exceptional and has a special larval form. From this fact Iwata, taking into consideration morphological differences of tissue of that genus from the rest, proposes the institution of a new order,

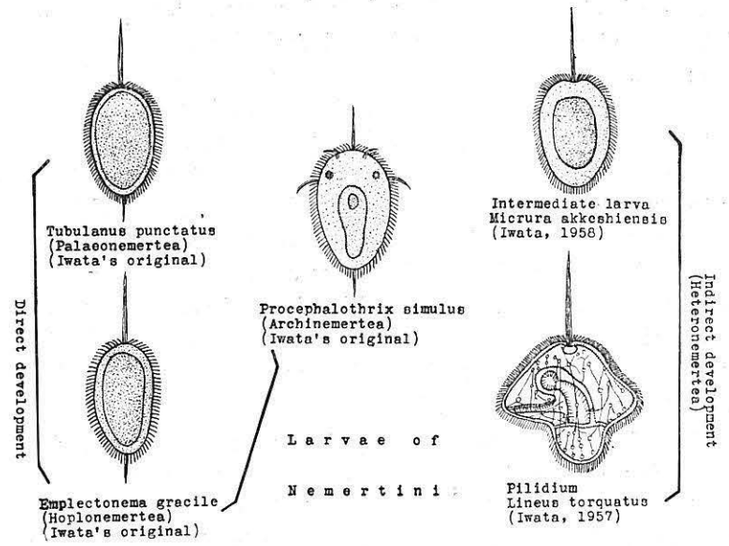

Fig. 1.

Archinemertea, for the Cephalotrichidae at the suggestion of the present writer. The order Bdellomorpha has been united to the Hoplonemertea on the basis of morphological and embryological observations. In the marine Polyclada, parallelism is observed. In this group one can find two types of development, one direct and the other indirect (Kato, 1940). In the Polyclada Müller's larva and Goette's larva are known; the former belongs to *Planocera* and the latter to *Stylochus*. Polyclads belonging to the families Leptoplanidae and Diplosolenidae make direct development, i.e., the embryos hatch as adult-like larvae.

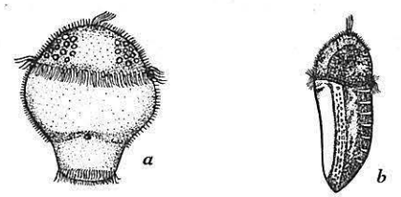

Fig. 2. Trochophorae in metamorphosis.
a. Epimenia verrucosa (Baba, 1941)
b. Cryptochiton stelleri (Okuda, 1947)

In the Mollusca there are reported two types of larvae, the trochophora and the further developed veliger. It is very interesting that the primitive groups, Solenogastres and Loricata, have only a primitive trochophora which directly transforms into the adult without formation of any veliger (e.g., cf. Baba, 1940 and Okuda, 1947). Though the trochophora is seen in some primitive Prosobranchia and Lamellibranchia, it is rather rare in the higher Mollusca. Veliger larvae are widely distributed in the phylum.

In the Echinodermata the four following larval forms are well-known: echinopluteus, ophiopluteus, bipinnaria and auricularia. These are specific for the classes: Echinoidea, Ophiuroidea, Asteroidea and Holothuroidea respectively. It is remarkable that several classes are characterized by their larval forms, all of which themselves are similarly formed in general plan. After the partial death of these larvae, young adult forms survive. It seems that it would be very interesting to study the arrangement of ossicles in these young adult echinoderms from the phylogenetic viewpoint. Doliolaria is generally reported as a larval form of the Holothuroidea, but similar forms are observed in other classes, and moreover, it resembles the larva of the Crinoidea and also somewhat the trochophora widely distributed in the Protostomia. Occurrence of similar types in two animal groups phylogenetically so different seems to be attributable to the phenomenon of convergence in marine life.

The life modes of Polychaeta are very divergent; some are pelagic, some sedentary swimming, some sedentary creeping, some burrowing in sand, some inhabiting a tube buried in sand and some attached to substrata and wholly sessile. The larva common to the group is trochophora which is divided into two types, protrochophora and metatrochophora according to stage. Protrochophorae of Polychaeta are in general structure very similar to each other and it is rather hard to identify the adult worms by these larvae, though characters specific for adults are more or less distinguishable upon detailed observation.

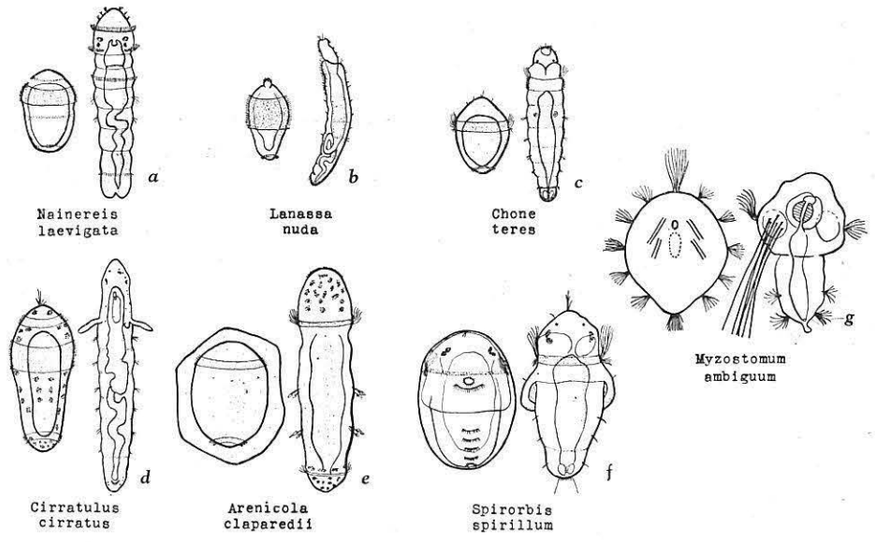

Fig. 3. Larval types of Polychaeta; Protrochophora and Metatrochophora. a-f (Okuda, 1946), g (Kato, 1952)

Metatrochophorae of this animal group are peculiar to the adult worms and highly valuable for identification of their family groups. Mitraria larva is specific to the Maldanidae. The metatrochophora of the Spionidae and Myzostomidae is characterized by the possession of long and stout bristles. Generally in the swimming forms the episphere undergoes remarkable changes, being gradually equipped with antennae, cirri and tentacles, while in the sedentary burrowing forms the head remains simple but the hyposphere, i.e. trunk, is gradually furnished with long cirri, branchial cirri etc. The early process of metamorphosis in the Polychaeta is seen in the metatrochophora as shown in the figures here given (Fig. 3). The protrochophorae of sessile polychaetes are often similar to those of swimming forms but metatrochophorae are characterized in having branchial rudiments in the head region as shown in the Sabellidae. The protrochophora of *Spirorbis* belonging to the Serpulidae has a rudiment of coller-membrane just posterior to the equatorial region, which gradually swells out in later stage. This metatrochophora is characterized in having the rudiments of branchial crown and operculum. In the classification of polychaetes the metamorphosis is a valuable indication of the familial position. The protrochophora of the Myzostomidae is something like an atrochous larva; its metatrochophora is characterized by the possession of a pair of remarkable bristles and a well-developed proboscis. In the further developed stages one can see a few segments (Kato, 1951). After having atached to the host the larva metamorphoses into a peculiar flattened and elliptical form, having a row of side organs and marginal cirri. The metamorphosis of this epizoic worm shows a convergency with that of epizoic Ctenophora, *Ctenoplana* and *Coeloplana*.

In the Coelenterata the class Scyphozoa is characterized by their well developed pelagic forms, Scyphomedusae. The Scyphozoa is divided into two groups: Scyphostomidae and Ephyridae. The first group includes two orders: Cubomedusae and Stauromedusae. These members have four radial pockets as seen in the scyphistoma and seem to have no ephyra. The second group covers three orders: Coronatae, Semaeostomae and Rhizostomae. The animals belonging to these orders coincide with each other in their developmental process in having the three following stages, viz., planula, scyphopolyp and ephyra. Their planulae and scyphopolyps are generally similar, and young ephyrae of them are also nearly the same in general plan. But the further metamorphosis of the ephyrae is remarkable; these groups can be phylogenetically arranged according to their metamorphosing processes.

The ephyra just detached from the scyphopolyp has a cruciform mouth in the central part, eight paired ephyral lappets, each pair having a sensory organ, a large central stomach cavity and eight radial pockets. Of course, the metamorphosis of the ephyra occurs in several portions of the body, e.g. subdivision of marginal lappets and increase of gastral filaments occur, but the main transformation

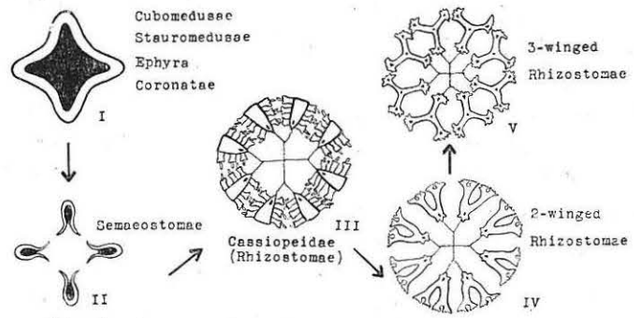

Fig. 4. Cross sections of oral parts of Scyphomedusae.

lies in the change of the manubrium and canal system.

The medusae belonging to the Coronatae retain most of the ephyral features; the manubrium remains four-sided, though lips are enlarged and the radial canals are represented by eight (4 perradial and 4 interradial) canals. In the Semaeostomae the ephyral cruciform lips are enlarged and develop to form four large oral arms. These oral arms have each a median furrow leading to the central mouth which connects with the stomach cavity. In the Rhizostomae the central mouth is generally closed by infolding of peripheral parts of the oral arms which become eight by bifurcation of four original ones, leaving numerous suctorial mouths on complicated peripheral crisps. The intermediate stage of the oral arms is seen in Semaeostome medusa *Aurosa* of which the four arms are bifurcated midway near the end. In the Cassiopeidae each oral arm has several side branches alternately disposed, which are divided again into a few terminal branches, forming crisps among which long appendages are found and many suctorial mouths open. In the Rhizostome family the median furrow of the Semaeostomae differentiates into a central axial canal of each arm and its many side branches repeating bifurcation. In Rhizostomae belonging to *Netrostoma* and *Stomolophus* the oral arms take a two-winged form. In most of the Rhizostomae, however, on account of upward shifting of the paired wings and formation of an axial wing, three-winged oral arms are formed. In the arms of this type one canal runs in the axis of each wing in addition to the axial canal. These three canals give rise to many abaxial branches which repeat again branching and lead to numerous suctorial mouths. The metamorphosis of the three winged medusae such as *Mastigias* (Uchida, 1926) from the ephyra to the adult covers all stages of Coronatae, Semaeostomae, Cassiopeidae and two-winged Rhizostomae.

As to the canal system, Scyphomedusan members can be arranged under several developmental scala. The young ephyrae of Semaeostomae and Rhizostomae are quite the same in form, the ephyrae being different from that of Coronatae in having eight adradial short diverticula. In the Pelagiidae the adradial

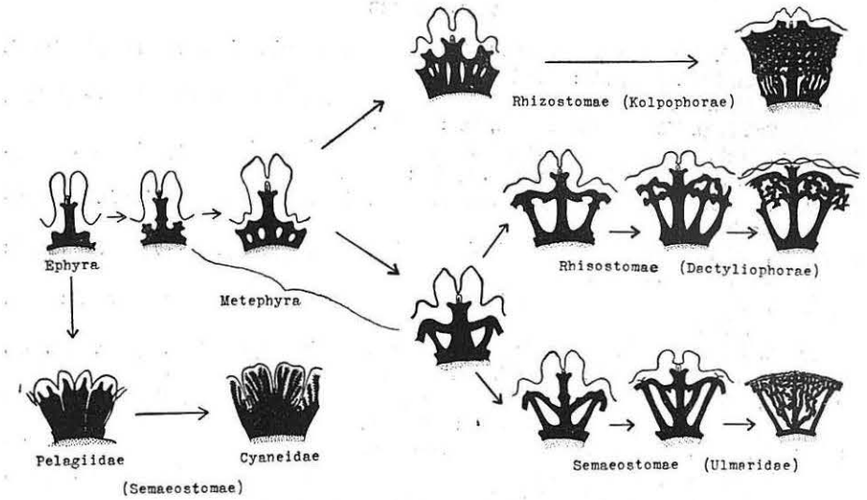

Fig. 5. Canal systems of the Ephyridae.

diverticula develop to adradial radial pockets (canals). Therefore, the Pelagiidae have 16 radial canals, the adradial ones giving rise further to several additional short abaxial branches, while the perradial and interradial canals remain as is in original form. In the Cyaneidae, 16 radial canals each give rise to a few radial branches which repeat branching and form a somewhat complicated canal system. On the other hand, as the metephyra is formed, the canal system of Ulmaridae and Dactyliophorae (Rhizostome) is to be furnished with the circular canal and to have each its own characteristic form as shown in the figure 5. The mode of formation of the canal system is somewhat similar in these two animal groups, but in the Ulmaridae, radial canals arising from the perradial and interradial ones construct the net-work there, whereas in the Dactyliophorae the net-work is only formed near the paripheral region, leaving the basal half of the main sixteen canals free from the net-work. In these two groups the canal system is formed by "Ausstülpung" of Stiasny. The canal system of Kolpophorae (Rhizostomae) is featured by possessing the complicated net-work of canal system formed by "Inselbildung" of Stiasny. The metamorphosis of the canal system will be followed in each scyphomedusa according to complication of the scala.

The life of these Scyphomedusae is always pelagic and a continuation of the life of the ephyra, so the metamorphosis has special significance from the viewpoint of their phylogeny.

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