

The Development of the Polychaete *Haploscoloplos fragilis*

By D. T. ANDERSON

(From the Zoology Department, University of Sydney, Australia)

SUMMARY

The eggs of *Haploscoloplos fragilis*, laid in gelatinous cocoons, develop as yolky trochophores which add 4 segments before hatching on the 6th day and two more during a pelagic phase before settling and the onset of feeding on the 10th day. The 6 (embryonic) segments bear a metatroch and 5 amphitrochs. The embryo also has an akrotrach, prototroch, telotroch, and neurotroch. All cilia disappear after settling, when the embryo shows resumption of segment formation. Anterior to the first trunk segment lie the prostomium and mouth region. The latter becomes subdivided by an annulus, but later fuses with the first trunk segment as the peristomium. All other segments become chaetigerous, the 5 embryonic being of thoracic type, the post-embryonic abdominal. At the posterior end of the body lies the pygidium, with the segment-forming growth zone immediately in front of it.

The development of trunk segments in two series, embryonic and post-embryonic, is characteristic of ariciids, as is the fusion of the first trunk segment with the mouth region to form the peristomium. It is possible that the mouth region incorporates at least one other cephalized segment.

Ariciid eggs vary in size among species. No direct relationship exists between egg size and pelagic development. The mode of oviposition also varies. Whether or not a pelagic phase occurs depends on the stage at which the embryo becomes free in the water, which is governed in turn by properties of the cocoon (e.g. jelly viscosity). A pelagic phase is always associated with enhanced ciliation, while in non-pelagic development ciliation is reduced. The basic ciliation (akrotrach, prototroch, metatroch, telotroch, and neurotroch) is usually supplemented by additional segmental bands.

CONTENTS

| | PAGE |
|--|------|
| INTRODUCTION | 257 |
| MATERIAL AND METHODS | 258 |
| THE EXTERNAL FEATURES OF DEVELOPMENT | 258 |
| The embryonic period | 258 |
| The post-embryonic period | 263 |
| DISCUSSION | 267 |
| The egg | 267 |
| Mode of oviposition | 267 |
| Pelagic phases in the life-history | 268 |
| Ciliation | 268 |
| Development of the head | 271 |
| REFERENCES | 272 |

INTRODUCTION

THE external features of development have been described for several species of ariciid polychaete, but little attempt has been made to assess the general pattern of development and its variations in the family. The present study of the development of *Haploscoloplos fragilis* Verrill and its comparison with the development of other species (*H. bustoris* (Horn &

Bookhout, 1950), *H. kerguelensis* (Okuda, 1946), *Scoloplos armiger* (Anderson, 1959), *Aricia foetida* (Salensky, 1883; Lo Bianco, 1899; Schaxel, 1912) and *Nainereis laevigata* (Okuda, 1946)) have brought to light certain hitherto undisclosed features of polychaete life histories.

MATERIAL AND METHODS

H. fragilis is common in sandy intertidal flats at Botany Bay on the New South Wales coast (Anderson, 1960). Eggs are laid in the late winter (July and August) in cylindrical gelatinous cocoons some 10 cm long and 3 to 4 mm broad, one end of the cocoon being anchored in the sand. A layer of sand-grains adheres to the surface of the cocoon. Embedded in the jelly are several thousand eggs in spirally wound longitudinal rows. The early phases of development are passed in the cocoon. Hatching occurs at 6 days and a brief post-hatching pelagic phase is followed by settling and burrowing.

Cocoons were maintained in bowls of sea-water at 17° C. After hatching, the embryos were provided with beach-sand in which they burrowed after settling, feeding on diatoms and other organic material. Drawings of living embryos were made with the aid of a camera lucida. Phase-contrast microscopy was used to elucidate ciliation.

EXTERNAL FEATURES OF DEVELOPMENT

The embryonic period

The unfertilized egg of *H. fragilis* (fig. 1, A) is opaque, spherical, 150 μ in diameter, greenish brown to orange by reflected light, brown by transmitted light, and covered by a transparent egg membrane 2 μ thick. At fertilization the membrane becomes raised from the egg surface. After spiral cleavage and gastrulation it forms the embryonic cuticle.

Early on the 2nd day, prototrochal cilia (*p*) appear as a broad band on each side of the anterior half (fig. 1, B) and the embryo begins to elongate. Towards the end of the same day a telotroch (*t*) arises as a narrow band of longer cilia near the posterior end (fig. 1, C). The increase in length of the embryo results from activity of a growth zone in front of the telotroch. Behind the telotroch lies a terminal post-segmental pygidium.

During the 3rd day (fig. 1, D) an anterior prototrochal region is demarcated by an annulus from a narrow trunk, and at the anterior end of the trunk a pair of lateral grooves marks the posterior border of a metatrochal or first trunk segment (*mes*) on which a further circlet of cilia, the metatroch (*me*), is formed. The embryo does not normally move through the jelly of the cocoon

FIG. 1. A, unfertilized egg. B, early 2-day embryo, dorsal view. C, later 2-day embryo, dorsal view. D, early 3-day embryo, dorsal view. E, early 4-day embryo, dorsal view. F, early 5-day embryo, dorsal view. G, early 6-day embryo, dorsal view. H, early 7-day embryo, dorsal view. I, early 8-day embryo, dorsal view. *a*, anus; *ak*, akrotroch; *am 1*, *am 2*, *am 3*, amphitrochs of chaetigers 1, 2 and 3; *ann*, post-prostomial annulus; *ch 1*, *ch 2*, *ch 3*, chaetiger 1, 2, 3; *e*, eye; *me*, metatroch; *mes*, metatrochal segment; *mr*, mouth region; *p*, prototroch; *pro*, prostomium; *py*, pygidium; *t*, telotroch.

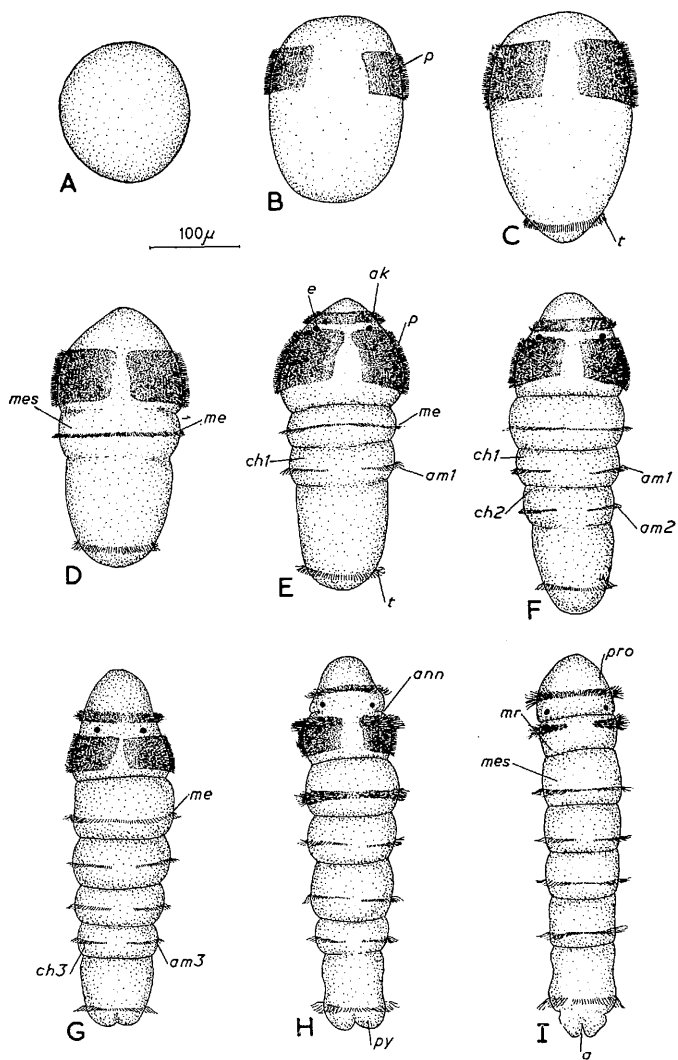


FIG. 1

at this stage, but if artificially released from the cocoon is able to glide by ciliary action through the water.

On the 4th day, as the trunk continues to grow (fig. 3, A, p. 264) the annulus at the posterior margin of the metatrochal segment is completed and a further pair of lateral grooves appears at the boundary of the second trunk segment (*ch 1*, fig. 1, E). An amphitroch, a pair of narrow half-circles of cilia, develops rapidly on this segment. At the same time the ciliation of the embryo is augmented by an akrotroch (*ak*), a circlet of cilia in front of the prototroch, and a neurotroch (*n*, fig. 2, A), a narrow mid-ventral band of cilia extending from the anterior border of the metatrochal segment to the telotroch. Slow ciliary gliding through the jelly of the cocoon now begins, and if released into the water, the embryo glides rapidly. Progress in the cocoon is greatly impeded by the viscous jelly. It is probably significant that the viscosity of the jelly lessens, so that the cocoon gradually liquifies, towards the time of hatching (see discussion, p. 271).

Muscular movements of the embryo also begin on the 4th day, with irregular elongation and contraction and lateral bending as far back as the anterior margin of the second trunk segment. A pair of dark-brown eye-spots (*e*) appears at the same time at the antero-lateral margins of the prototroch.

On the 5th and 6th days (fig. 1, F, G) two further trunk segments (*ch 2*, *ch 3*) are successively delimited. Each rapidly gains an amphitroch and takes part in the slow elongation-contraction movements of the embryo. On the 6th day the pre-pygidial growth zone becomes dormant (fig. 3, A), growth temporarily ceases, and the embryo hatches from the cocoon. During the next 4 days, as the tissues of the embryo differentiate towards their functional condition, no further segments are added to the trunk (figs. 1, G, H; 2, A; 3, A).

Just before hatching, several rows of cilia at the anterior end of the prototroch increase in length (fig. 1, H), while the prototroch as a whole lessens in area. A pair of lateral grooves appearing between the anterior border of the prototroch and the akrotroch also marks off the eye-bearing prostomium from the mouth region (*mr*), the latter including the prototroch and the ventral mouth.

On escaping from the jelly, the embryo (fig. 1, H) moves for a short time by ciliary gliding on the substratum close to the cocoon. It then becomes negatively geotropic and swims by means of its cilia towards the water surface. This behaviour persists for one to several hours. No photic response is involved, although the eyes are well developed, since no orientation towards a uni-directional light source is detectable in the pelagic embryo. In swimming,

FIG. 2. A, early 8-day embryo, lateral view. B, early 9-day embryo, dorsal view. C, early 10-day embryo, dorsal view. D, 14-day pre-adult, dorsal view. E, 22-day pre-adult, dorsal view. *a*, anus; *add*, additional annulus on mouth region; *ak*, akrotroch; *am 1*, *am 2*, *am 3*, &c., amphitrochs of chaetigers 1, 2, 3, &c.; *amm*, post-prostomial annulus; *ch 1*, *ch 2*, *ch 3*, &c., chaetiger 1, 2, 3, &c.; *cha*, chaeta; *cil*, cilia; *f*, food; *gz*, growth zone; *int*, intestine; *m*, mouth; *me*, metatroch; *mes*, metatrochal segment; *mr*, mouth region; *n*, neurotroch; *oes*, oesophagus; *p*, prototroch; *pra*, proboscis apparatus; *pro*, prostomium; *py*, pygidium; *st*, stomach; *t*, telotroch.

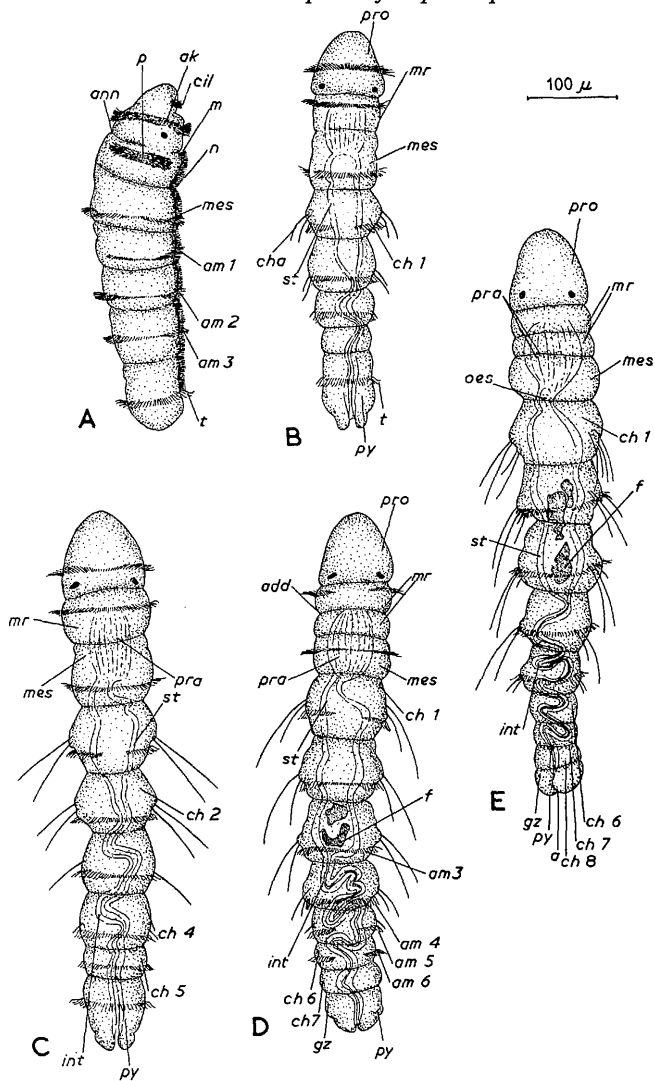


FIG. 2

the body is held straight and the circlets of cilia beat in anticlockwise metachronal rhythm, diagonally backwards, so that the embryo pursues a straight course through the water, rotating on its long axis. The neurotrochal cilia, which beat directly backwards, assist in driving the embryo along.

Soon the embryo loses its negative geotropism and begins to swim at random through the water. Then, with cilia still beating, it bends itself in a half circle either to right or left, and spirals slowly to the bottom under its own weight. Once contact is made, a thigmotactic response results in ciliary gliding between the sand-grains, with some muscular bending and elongation and contraction of the body as far back as the 4th trunk segment (*ch 3*). Settling and the events which follow are not affected by the nature of the substratum. Embryos settling on sand from their natural habitat and embryos settling on clean glass showed no differences in behaviour or subsequent development.

Once the bottom-living habit is established, histo-differentiation begins. The cilia of the various ciliary bands act in unison in alternating irregular periods of metachronal activity and rest, indicating that they are under nervous control. The trunk segments become more clearly defined, the outer parts of the embryo more transparent, and muscular movements more vigorous. The embryo is, however, far from adopting the adult mode of life. The cilia of the various trochs increase in size and activity and the embryo continues to make frequent excursions through the water. Chaetae are still undeveloped, burrowing by peristalsis does not occur, and the negative phototactic response which results in burrowing in later stages of development is not yet established.

During the 8th day (figs. 1, 1; 2, A) the prostomium becomes fully delimited and develops, in addition to its akrotrich, a more anterior short transverse ventral band of cilia (*cil*). The mouth region decreases in size as the prototroch becomes reduced to its two half-circles of longer cilia. All other cilia increase slightly in length and show spasmodic bursts of vigorous activity in unison, usually resulting in swimming. The main movement, however, is ciliary gliding between sand-grains. The muscular elongation and contraction which accompanies this does not assist forward progression, since the embryo, lacking chaetae, is unable to establish fixed points of contact with the substratum.

On the 9th day the first chaetae appear in rapid succession as two notopodial pairs on chaetigers 1 and 2 and a single notopodial pair on chaetiger 3 (table 1). The metatrochal segment remains without chaetae throughout development. Protrusion of the proboscis also begins on the 9th day, and this, together with the presence of the chaetae, makes it possible for the embryo to crawl over the surface of the sand-grains by muscular as well as ciliary action. Muscular crawling occurs in essentially the adult manner, by peristalsis, but is assisted by rhythmic protrusion, adhesion, and withdrawal of the proboscis. This does not occur in the adult as a locomotory activity.

Delineation of segments also recommences on the 9th day (fig. 3, A).

Within the persistent undifferentiated zone between the 4th trunk segment and the telotroch, the 5th trunk segment is demarcated, following a delay of 4 days since its components were laid down by the prepygidial growth zone.

TABLE I
Summary of development of chaetae in *H. fragilis*

| Day: | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 22 | 24 | 29 |
|-----------|---|---|----|----|----|----|----|----|----|----|
| Segment 1 | o | o | o | o | o | o | o | o | o | o |
| | o | o | o | o | o | o | o | o | o | o |
| " 2 | o | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
| | o | o | o | 1 | 1 | 2 | 2 | 2 | 2 | 3 |
| " 3 | o | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
| | o | o | o | o | 1 | 1 | 2 | 2 | 2 | 3 |
| " 4 | o | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
| | o | o | o | o | o | o | 1 | 1 | 2 | 2 |
| " 5 | o | o | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 3 |
| | o | o | o | o | o | o | o | 1 | 1 | 1 |
| " 6 | o | o | o | o | o | o | 1 | 2 | 2 | 2 |
| | o | o | o | o | o | o | o | o | o | 1 |
| " 7 | o | o | o | o | o | o | o | o | o | 1 |
| | o | o | o | o | o | o | o | o | o | o |
| " 8 | o | o | o | o | o | o | o | o | o | o |
| | o | o | o | o | o | o | o | o | o | o |
| " 9 | o | o | o | o | o | o | o | o | o | o |
| | o | o | o | o | o | o | o | o | o | o |
| " 10 | o | o | o | o | o | o | o | o | o | o |
| | o | o | o | o | o | o | o | o | o | o |

The post-embryonic period

On the 10th day, although there is no decrease in ciliation, changes occur which make it possible to define subsequent development as post-embryonic and to term the developing organism a pre-adult (fig. 2, c). Feeding begins, the prepygidial growth zone (*gz*) becomes active once more, adult external features become more obvious, neurotrochal gliding ceases, peristaltic burrowing carries the embryo down into the sand, and swimming excursions become very infrequent. The last of the trunk segments laid down by the growth zone during the embryonic (lecithotrophic) period is demarcated on the 10th day (fig. 3, A) as the 6th trunk segment (chaetiger 5) after a delay of 4 days since its formation. Both it and chaetiger 4 develop amphitrochs. All remaining segments are formed after resumption of growth-zone activity and can be defined as post-embryonic. It will be seen below that the two series of segments differ not only in the time relations of their formation but also in their development. The transition from one mode of segment formation to the other is marked by a delay in growth of the last embryonic segment and also by a transient amphitroch (*am* δ , fig. 2, D), typical of the embryonic chaetigers, on the first post-embryonic segment (*ch* δ). The embryonic segments are

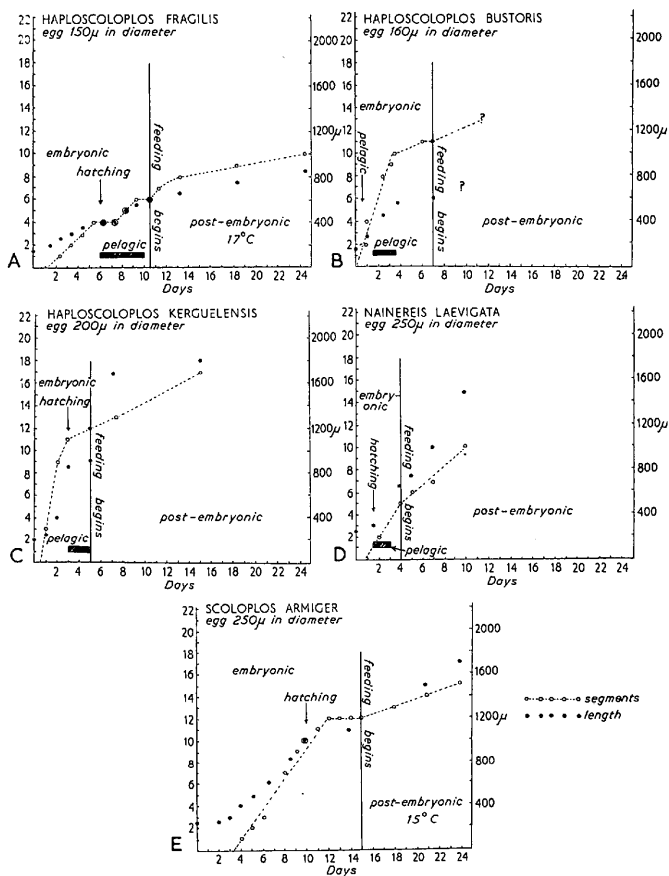


FIG. 3. External delineation of trunk segments and increase in length in developing arciids. A, *H. fragilis*. B, *H. bustorius* (from data of Horn & Bookhout, 1950). C, *H. kerguelensis* (from data of Okuda, 1946). D, *Nainereis laevigata* (from data of Okuda, 1946). E, *S. armiger* (from data of Anderson, 1959). Ordinates: on the left, number of segments; on the right, length.

formed from material already present in the fertilized egg, the post-embryonic from material acquired through active feeding.

With the onset of post-embryonic life, overall growth slowly continues and the pre-adult (so called because its proboscis is a temporary structure replaced

in the adult by a more complex proboscis) increases both in length and bulk. For the first 4 weeks of post-embryonic life the rate of increase is more or less constant. The rate at which the post-embryonic segments are formed is also constant, but differs from that obtaining during the embryonic period (fig. 3, A). The first post-embryonic segment, chaetiger 6, is delimited on the 12th day, the second on the 14th, &c. Each segment is externally delineated as soon as the material for it has been produced by the growth zone, although its subsequent development proceeds very slowly. The embryonic segments, in contrast, are slow to delineate, so that a long undemarcated zone characterizes the embryonic period; but once delineated they develop rapidly to a functional peristaltic condition. The latter is not attained by the post-embryonic segments, which thus resemble the abdominal segments of the adult and can be taken as representing the abdomen of the pre-adult. The actively peristaltic embryonic segments with their well-developed chaetae are of recognizably thoracic type. The adult, however, has 16 thoracic chaetigers. As in all ariciids, the early abdominal segments of *H. fragilis* transform to thoracic type as further segments are added to the body.

Each of the 4 components of the pre-adult body, head, thorax, abdomen, and pygidium, undergoes changes during the first 4 weeks of pre-adult life.

The head. In the adult, the head comprises the prostomium and peristomium, the latter a compound structure incorporating the mouth region and metatrochal segment of the embryo. The prostomium, once delimited, undergoes little change other than increase in size. The anterior ventral band of cilia (*cil*, fig. 2, A) is soon lost. The akrotrach persists in the pre-adult for 2 days and is then resorbed. On the mouth region, the prototroch persists until the 18th day. The neurotroch is resorbed with it (table 2) and thereafter no ciliary gliding occurs.

A more important event in the mouth region is the formation of an additional annulus (*add*, fig. 2, D), dividing the mouth region into anterior and posterior parts. The significance of this annulus, which persists through early pre-adult life, is mentioned in the discussion (p. 271).

On the metatrochal segment, the metatroch, like the prototroch, is resorbed by the 18th day. The segment then gradually fuses with the mouth region.

The thorax. By the time the first 5 chaetigers (the 2nd to 6th embryonic segments) are clearly outlined (fig. 2, c), the chaetae of the first 3 are long and a single pair of notopodial chaetae has begun to develop on the 4th. Subsequent elaboration of the thoracic segments takes place from before backwards, the first 3 showing rapid succession, the 4th and 5th being delayed in accordance with the lag in their initial development. The number of chaetae on the segments gradually increases (table 1), the notopodial being dorso-lateral and the neuropodial laterally placed. All are of the simple serrate type. The amphitrochs of the thoracic segments become less conspicuous after the 12th day but are not finally resorbed until the 24th or 25th (table 2), by which time metamorphosis is complete.

The abdomen. The post-embryonic segments, chaetiger 6, &c., which make up the abdomen of the pre-adult, show little change during early pre-adult life.

The pygidium. The pre-pygidial growth zone retains its simple cylindrical form in the pre-adult, but behind it the telotroch, well developed at the beginning of pre-adult life, is soon resorbed (table 2), so that the growth zone and pygidium become externally confluent. At the same time, the lateral regions of the pygidium enlarge as two lobes, leaving a median groove in which the anus, formed towards the end of the embryonic period, gradually migrates to a dorsal position.

DISCUSSION

The main interest of this study lies in the opportunity it provides for comparative discussion of the life-histories of the Ariciidae. A wide range of variation occurs within the 6 species (including *H. fragilis*) whose development is known. Comparison is made below of their eggs, modes of oviposition, pelagic phases, and ciliation. The question of the composition of the head is briefly raised as a result of the discovery of new facts pertaining to it.

The egg

The eggs of ariciids vary both in size and colour among species:

H. fragilis (this paper, p. 258)

150 μ diameter, greenish brown-orange

H. bustoris (Horn & Bookhout, 1950)

160 μ diameter, cream

H. kerguelensis (Okuda, 1946)

200 μ diameter, brown

S. armiger (Anderson, 1959)

250 μ diameter, orange

N. laevigata (Okuda, 1946)

250 μ diameter, creamy yellow

A. foetida (Salensky, 1883)

? dull green-yellowish brown

In the generally accepted view, a polychaete egg greater than 160 μ in diameter undergoes non-pelagic development (Newell, 1951). This would imply a direct effect of egg size on subsequent events. The ariciids, however, do not confirm this. Although 4 of the 6 species above follow the rule, both *H. kerguelensis* and *N. laevigata*, in spite of their egg size, retain pelagic phases. The occurrence or absence of a pelagic phase in ariciid development depends on more complex factors than the dimensions of the egg.

Mode of oviposition

Among the factors associated with ariciid development, mode of oviposition appears at first sight to be unimportant. As the following table shows, mode

of oviposition varies within genera and a pelagic phase may or may not follow deposition in a similar spawn:

| | Oviposition | Pelagic phase |
|------------------------|-----------------------------------|---------------|
| <i>H. fragilis</i> | in cylindrical gelatinous cocoons | occurs |
| <i>H. bustoris</i> | freely into water | „ |
| <i>H. kerguelensis</i> | in pear-shaped gelatinous cocoons | „ |
| <i>S. armiger</i> | in pear-shaped gelatinous cocoons | omitted |
| <i>N. laevigata</i> | in small jelly masses | occurs |
| <i>A. foetida</i> | in cylindrical gelatinous cocoons | omitted |

Thorson's (1946) statement that there is no relation in polychaetes between the manner in which the eggs are spawned and the subsequent pattern of the life-history thus appears to be applicable to ariciids. Closer examination, however, reveals that this is not so. The nature of the spawn must be taken into account in explaining differences in the development of different species.

Pelagic phases in the life-history

The occurrence or omission of a pelagic phase constitutes a major difference in development among ariciids. The pelagic phase where it occurs also varies among species both in onset and duration.

| | Hatches | Becomes pelagic | Remains pelagic |
|------------------------|---------------|-----------------|-----------------|
| <i>H. fragilis</i> | at 6 days | at 6 days | 4 days |
| <i>H. bustoris</i> | (laid freely) | on the 1st day | 3½ days |
| <i>H. kerguelensis</i> | at 3 days | at 3 days | 3 days |
| <i>S. armiger</i> | at 10 days | — | — |
| <i>N. laevigata</i> | at 1½ days | at 1½ days | 1½ days |
| <i>A. foetida</i> | at 6 days | — | — |

The only species whose eggs are laid freely, *H. bustoris*, becomes pelagic as a lecithotrophic trochophore. Other species reach a similar developmental stage on the 2nd day (compare fig. 1, B, p. 259), but are held within the jelly of the cocoon. If artificially released they are capable of ciliary gliding, and in *H. fragilis* and *H. kerguelensis* of swimming, so that the delay in escaping from the cocoon in natural conditions depends on properties of the cocoon jelly. The importance of this as a determinant of the subsequent course of development will be demonstrated below.

Ciliation

Whether or not the early stages of developing ariciids become pelagic once free in the water depends on the degree of elaboration of their ciliated bands. These may be divided into a basic series common to all species and a number of additional bands varying in arrangement among species.

The basic ciliation comprises an akrotrich, prototroch, metatroch, telotroch, and neurotroch. The prototroch always appears first, at the trochophore stage, but more important than this, the time of appearance of all bands is

related to the time at which the pelagic phase of the species begins, irrespective of egg size. In order of first appearance of their basic ciliation, the 6 species under consideration arrange themselves as follows: *H. bustoris*, *N. laevigata*, *H. kerguelensis*, *H. fragilis*, *S. armiger*, *A. foetida*.

The additional ciliated bands are segmental bands lying behind the metatroch of the achaetous first trunk segment. Their development is closely linked with that of the basic ciliation, but also with the mode of formation of the trunk segments. All ariciids develop a number of embryonic segments in rapid succession; then, after a pause during which differentiation is completed, they begin to feed and to add post-embryonic segments at a slower rate (fig. 3, A-E). They show no adaptations to plankton feeding, and a pelagic phase where it occurs always lies within the embryonic period, settling being an essential preliminary to the benthic feeding of post-embryonic life. The additional ciliated bands are therefore found only on the embryonic segments.

| | No. of embryonic trunk segments | No. of segmental bands additional to metatroch | Settling |
|------------------------|---------------------------------|--|----------|
| <i>H. fragilis</i> | 6 in 9 days | 6 amphitrochs | 10th day |
| <i>H. bustoris</i> | 10 in 4 days | 7 gastrotrochs | 4th day |
| <i>H. kerguelensis</i> | 11 in 3 days | 9 amphitrochs | 5th day |
| <i>S. armiger</i> | 12 in 12 days | 3 gastrotrochs | — |
| <i>N. laevigata</i> | 3 in 3 days | none | 3rd day |
| <i>A. foetida</i> | ? | 3 gastrotrochs | — |

H. bustoris lies closest to the primitive polychaete condition. Although the pelagic phase is lecithotrophic, the freely spawned eggs become pelagic at the trochophore stage with a full basic ciliation. Owing to the availability of building material from the egg, the number of trunk segments formed during the pelagic phase is greater than the primitive polychaete number of 3 or 4 (see table above and fig. 3, B) but almost all of them develop additional segmental trochs. Presumably advantages are gained from the retention of a pelagic phase (e.g. distribution) and selection has favoured the precocious development of cilia even though other factors (e.g. a large egg) weigh against it.

In species whose eggs are spawned in jelly, there are two main evolutionary innovations—the jelly itself and in most cases a larger egg. The latter, as has already been pointed out, does not determine directly the presence or absence of a pelagic phase. *N. laevigata* has a pelagic phase, *S. armiger* does not. However, *N. laevigata* escapes from the jelly mass as an immediate post-trochophore with a fully developed basic ciliation. *S. armiger* escapes from its elaborate cocoon only after 10 days, by which time its cilia are largely resorbed. In this species the basic ciliation is not completed until the end of the 4th day. The difference between the two can be explained if it is assumed that in their common ancestors the post-trochophore stage resembled that of *H. bustoris*, but that the properties of the introduced cocoon in *S. armiger*

were such as to prevent escape until the normal benthic stage had been reached. The pelagic phase being thus eliminated from the life-history, reduction in early ciliation has occurred as a corollary. The vestigial nature of additional ciliated bands of *S. armiger*, which comprise only 3 small transient gastrotrachs, confirms this. Non-pelagic development and reduced ciliation in *A. foetida* can presumably be explained in the same way. In *N. laevigata*, in contrast, in spite of an equally large egg, early escape from the simple jelly mass is associated with persistence of a pelagic phase and precociously developed cilia. The apparently anomalous absence of additional segmental trochs in this species is linked with the slow rate of delineation of the trunk segments (fig. 3, D). Growth of the trunk is not accompanied by segment delineation and the formation of additional segmental bands which would keep the embryo afloat. Settling therefore occurs early and as a corollary the embryo shows abolition of the segmental trochs.

H. kerguelensis, although it is restricted by the jelly of its cocoon for 3 days and shows some associated delay in establishing its basic ciliation, escapes at a time when pelagic activity is possible. Comparison with *H. bustoris* (fig. 3, B, C) shows that its pelagic life would be extremely brief if its cilia followed the same sequence of gain and loss as those of the latter species. Once more selection appears to have favoured maintenance of a pelagic phase, for the cilia of *H. kerguelensis* become more strongly developed than those of *H. bustoris*, 9 gastrotrachs developing before pelagic life begins. As a result, it remains pelagic for 2 days.

H. fragilis has an egg more or less equal in size to that of *H. bustoris* and a trochophore which can swim if artificially released; yet the embryo of this species does not hatch for 6 days. The delay can be ascribed partly to a slow rate of development (compare fig. 3, A, B) but also to the fact that the cocoon is more retentive than those of *N. laevigata* and *H. kerguelensis*. The basic ciliated bands are slow to develop, as in *S. armiger* and *A. foetida*, presumably due to the selective action of the cocoon environment; but escape still occurs at a time when the embryo has, relatively to its size, a ciliation sufficient for pelagic activity. As in *H. kerguelensis*, selection in the post-hatching stages of development appears to have been towards retention and elaboration of the cilia, prolonging pelagic life for a further 4 days. The 5 amphitrochs which develop on the embryonic segments confirm this. When settling occurs at 10 days, however, the cilia are still fully developed, being finally resorbed only on the 24th day. The explanation of early settling is to be found in the food requirement of the developing organism, which has utilized its yolk reserves by 10 days and has no special apparatus for plankton feeding; but this does not account for the extraordinary persistence of the ciliated bands after settling. Why they should be retained in *H. fragilis* when in other species they are rapidly lost once benthic life begins remains a mystery.

In general it can be concluded that in species whose embryo becomes free in the water at a stage sufficiently ciliated to be pelagic, natural selection has favoured retention and elaboration of cilia and a pelagic phase is maintained

irrespective of egg size. Where the properties of the gelatinous cocoon have been such as to preclude escape before the onset of metamorphosis, the resulting elimination of the pelagic phase has led to reduction of the ciliated bands. The occurrence or absence of a pelagic phase in ariciid development thus depends in part on the properties of the cocoon, i.e. on mode of oviposition, the most important property being probably the viscosity of the jelly. A detailed study of changes in jelly viscosity in the cocoons of different species between oviposition and hatching would be of particular interest.

Development of the head

In every species of ariciid so far examined, the delineation of the first trunk segment also results in demarcation of an anterior prototrochal region. The posterior half of this bears the prototroch and the mouth. The anterior half enlarges, a pair of dorso-lateral eye-spots appears in front of the anterior margin of the prototroch, and an annulus formed just behind the eyes then delimits an anterior akrotrich-bearing prostomium from a posterior prototroch-bearing mouth region.

The prostomium, which was shown by Anderson (1959) to be a pre-segmental body unit, undergoes little further change other than increase in size and loss of the akrotrich. In *N. laevigata* and *H. kerguelensis* the eyes regress during early pre-adult life but in other species they persist into the adult.

The mouth region, conversely, decreases in size as the prototroch regresses, while ventrally in front of and behind the mouth superficial folds develop as the upper and lower lips. Anderson (1959) adduced reasons for regarding the mouth region, as well as the prostomium, as a pre-segmental structure. In connexion with this, further events which take place in the mouth region of *H. fragilis* and also in *H. kerguelensis* are of interest. In *S. armiger* (Anderson, 1959) it was shown that 3 pairs of mesodermal somites initially invade the mouth region while it is still part of the prototrochal region, but that they do not induce a corresponding segmentation in the ectoderm of this region. Furthermore, no ventral nerve ganglia are associated with them, the first ganglion of the ventral nerve-cord lying in the metatrochal segment and subsequently migrating back to fuse with that of chaetiger 1. For these and other reasons, it was decided that the mouth-region somites of *S. armiger* could not be regarded as the somites of cephalized segments and that the polychaete head bore no obvious correspondence to the onychophoranarthropod head. In *H. fragilis* (p. 265) and *H. kerguelensis*, however, an additional annulus arises on the mouth region after it has been delimited from both the prostomium and the metatrochal (first trunk) segment, dividing the mouth region into anterior (mouth-bearing) and posterior parts. In external appearance the latter resembles an achaetous segment. The question therefore arises, does it correspond to any of one or more pairs of somites which invade the mouth region in either of these species, and does it show any signs of developing an ectodermal segmental ganglion as the first ganglion of the ventral

nerve-cord? If so, i.e. if it can be recognized as a cephalized segment, Anderson's (1959) view that the mouth region in ariciids and other polychaetes is definably presegmental will have to be revised, since it becomes possible that cephalization may have embryological consequences which lead to the segments concerned being recognizable only by the existence of a pair of mesodermal somites. Such a change of viewpoint would have considerable importance in the interpretation of segmental composition in metamericly segmented animals. It is hoped shortly to carry out the detailed embryological study which will confirm or deny this hypothesis.

Whether or not the mouth region becomes subdivided, the subsequent history of the adult peristomium is similar in all ariciids studied. The peristomium arises by fusion of the achaetous metatrochal segment with the mouth region. There are thus no grounds for denying that the peristomium in ariciids is a complex structure including at least one cephalized trunk segment in its composition.

I wish to express my thanks to Miss I. Bennett for advice on the collection of material, to Prof. P. D. F. Murray and Dr. L. C. Birch for valuable discussion, to Dr. L. E. R. Picken for his critical appraisal of the manuscript, and to the University Grants Committee of the University of Sydney for financial aid.

REFERENCES

- ANDERSON, D. T., 1959. 'The embryology of the polychaete *Scoloplos armiger*.' Quart. J. micr. Sc., **100**, 89.
- 1960. 'Ariciid polychaetes in Australia.' In the press.
- HORN, E. C., & BOOKHOUT, C. G., 1950. 'The early development of *Haploscoloplos bustoris*.' J. Elishah Mitchell sci. Soc., **66**, 1.
- LO BIANCO, S., 1899. 'Notizie biologiche riguardante specialmente il periodo di maturita sessuale degli animale del Golfo di Napoli.' Mitt. zool. Stat. Neapel, **13**, 448.
- NEWELL, G. E., 1951. 'The life history of *Cllymenella torquata* (Maldanidae).' Proc. zool. Soc. Lond., **21**, 561.
- OKUDA, S., 1946. 'Studies on the Development of Annelida Polychaeta. I.' J. Fac. Sci. Hokkaido Imp. Univ., **9**, 115.
- SALENSKY, W., 1883. 'Étude sur le développement des Annélides. Première partie. III. (i) *Pileolaria*, (ii) *Aricia*, (iii) *Terebella*.' Arch. Biol. Paris, **4**, 188.
- SCHAXEL, J., 1912. 'Versuch einer cytologischen Analysis der Entwicklungsvorgange. Teil I. Die Geschlechtzellbildung und die normale Entwicklung von *Aricia foetida* Clap.' Zool. Jb. Abt. Anat. u. Ont., **34**, 381.
- THORSON, G., 1946. 'Reproduction and larval development of Danish marine bottom invertebrates.' Medd. Komm. Havundersog., Abh. (Plankton), **4**, 1.