

THE LARVAE OF THE SPATANGIDAE

By C. B. Rees, D.Sc.

The Scottish Marine Biological Association, Oceanographic Laboratory, Edinburgh

(Text-figs. 1-5)

INTRODUCTION

Mortensen (1927) has given an account of the distribution of the six species of Spatangidae which occur in British waters. Of these, four may be regarded as widespread and, in places, numerous: *Echinocardium cordatum* (Pennant), *E. flavescens* (O. Fr. Müller), *Spatangus purpureus* O. Fr. Müller, and *Brissopsis lyrifera* (Forbes). The fifth species, *Echinocardium pennatifidum* Norman, has been found on the south, west and north British coasts, and down to Durham on the east coast, though nowhere in large numbers. The sixth species, *Spatangus raschi* Lovén, is much more restricted, and is known only from fairly deep water off the west coast of Ireland and off the Shetland Islands.

Our knowledge of the larval forms of these species is not satisfactory. The larva of *Echinocardium cordatum* has been described by Mortensen (1898) and MacBride (1914). However, Thorson (1946) refers to the possibility that the larva of *E. flavescens* may be very similar to that of *E. cordatum*.

Chadwick (1914) described some young larvae which he assigned to *E. flavescens*, but Mortensen (1920) would not accept the certainty of this identification and gave *Brissopsis lyrifera* as a possible alternative. Despite the fact that Chadwick's drawings are poor (Mortensen, 1920, who saw the original material, pointed out that the post-oral arms are fenestrated, not simple as shown in the drawings), there is little doubt that Chadwick's identification was correct. It is a curious fact that Mortensen acknowledged seeing Chadwick's '*E. flavescens*' and gave *Brissopsis* as an alternative in the same paper (1920) in which he described the larva of *B. lyrifera*. As will be seen below, the larvae of the two species are, in fact, easily distinguishable even in very young stages. It has been accepted up to now that the larvae of *Echinocardium flavescens* are unknown (Mortensen, 1927; Thorson, 1946).

Young larvae described by Krohn (1853) were assigned by him to *Spatangus purpureus*. In this case, also, Mortensen (1913) questioned the identity. Mortensen (1913) has described the fully grown larva of *S. purpureus*, giving as its main characteristic the exceedingly long posterior process, but there is reason to believe (see below) that identification based on such a characteristic is unsatisfactory. The best account of *S. purpureus* larvae is given by Ohshima

(1921). Mortensen (1920) was unable to say how the younger larvae of *Spatangus* and *Brissopsis* may be distinguished.

The late larva of *B. lyrifera* was described by Mortensen (1920). He showed that it is easily distinguished from the late larvae of *Echinocardium cordatum* and *Spatangus* by the absence of postero-lateral arms. Mortensen (quoted by Thorson, 1946, p. 358) subsequently raised the possibility that there may be a still later stage than that described, in which the postero-lateral arms are more distinct. It may be said now that, even in larvae at the point of metamorphosis, no sign of a postero-lateral rod is present in the skeleton. The younger larvae have not been described.

Nothing is known of the development of *Echinocardium pennatifidum* and *Spatangus raschi*.

From the published descriptions, it is not possible to identify with any certainty most of the spatangid larvae which occur in plankton samples from British waters. A large proportion are usually in early stages of development which have not been adequately described. In most areas the larvae of *Echinocardium flavescens* and *E. pennatifidum* will present alternative possibilities even in the identification of later stages. *Spatangus raschi* is so much more restricted in its distribution that lack of knowledge of its larva is not so important.

The object of this report is to provide means of identifying the larvae of the four more common species from very young stages onwards. The first section is devoted to a more complete account of the general structure of the spatangid skeleton than appears to be available in the literature.

In view of the variation involved in the larvae it would be as well to specify the source and extent of the material on which the descriptions are based. Abundant larvae of *Echinocardium cordatum* and *E. flavescens* have been available in the samples collected by the Continuous Plankton Recorder in the plankton survey of the North Sea (Rae, 1952). Rather better preserved material has been obtained in Plankton Indicator samples from the north-east Scottish fishing grounds. *Spatangus purpureus* larvae have been much less abundant in both sets of samples; of the order of a hundred larvae have been identified. Approximately the same number of larvae of *Brissopsis lyrifera* have been identified, partly from samples taken from the Clyde (kindly provided by Dr D. T. Gauld) and partly from Recorder samples taken over the Continental Slope south-west of Ireland.

It is regretted that, for various reasons, so few measurements are given. Few as these are, however, they serve a more definite function than words such as long, short, longer, shorter, which are frequent in descriptions.

The descriptions are based entirely on the skeletal parts which may be seen clearly by immersing the larvae, if necessary, in hypochlorite solution; a 'domestic bleach' is very suitable for this purpose.

GENERAL ACCOUNT OF THE SPATANGID SKELETON

Fig. 1 gives in diagrammatic fashion the essential structure of the body skeleton of an early larva (A) and of a fully developed larva (B). Corresponding plans of the skeleton are given in the adjoining figures *a* and *b*. Characteristic of spatangid larvae is an unpaired posterior arm¹ arising from the posterior transverse rod.

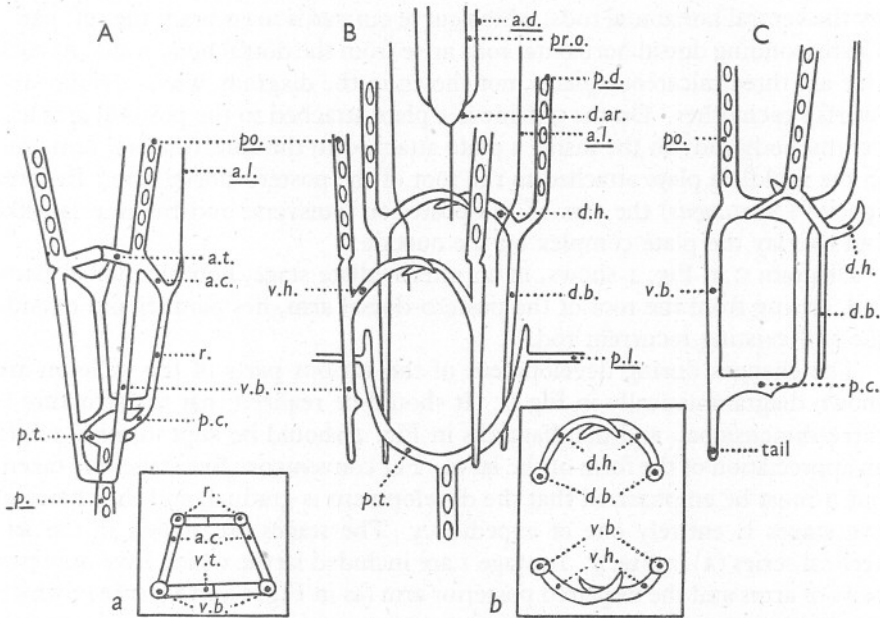


Fig. 1. Diagram of the general structure of the body skeleton of spatangid larvae. The young stage is shown in A and the late stage in B; corresponding plan views are shown in *a* and *b*. C shows part of the intermediate stage. Abbreviations applying to arm rods are underlined. All abbreviations, except for *po.*, postoral, and *pr.o.*, preoral, are composite: *a.*, anterior; *ar.*, arch; *b.*, body; *c.*, connexion; *d.*, dorsal; *h.*, horizontal; *l.*, lateral; *p.*, posterior; *r.*, recurrent; *t.*, transverse; *v.*, ventral. The term 'rod' should be added where appropriate.

In the young larva the body skeleton is box-like with the fenestrated postoral arms arising from the two anterior ventral corners and the simple antero-lateral arms from the two anterior dorsal corners. The box is made up of two side pieces, each piece consisting of a ventral body rod and a recurrent rod, joined by an anterior and a posterior connexion. The two side pieces are connected in the median plane by three projections, of which the anterior transverse rod is the most distinct and persistent. The connexion at the posterior end of the body rod is not firm and gives way early in development.

¹ Throughout this account the term 'arm' refers to the skeletal arm rods, as distinct from other rods (see Fig. 1).

When present it is convenient to recognize a 'tail' in the body rod, that part posterior to the posterior connexion.

The late larva is very much larger and the rigid box of the young larva becomes transformed to cope with the increase in size. The skeleton is still box-like, but the anterior and posterior connexions have disappeared and the recurrent rod is replaced by the dorsal body rod which is part of the root of the fenestrated postero-dorsal arm. The anterior transverse rods are replaced by the ventral horizontal rods, which curve outwards to embrace the soft parts. Corresponding dorsal horizontal rods arise from the dorsal body rods. At each side are three calcareous plates, not shown in the diagram, which overlay and overlap each other. On the outside is a plate attached to the postoral arm and ventral body rod, on the inside a plate attached to the antero-lateral arm, and in the middle a plate attached to the root of the postero-dorsal arm. In some species (*Spatangus*) the tips of the posterior transverse rod become fan-like and overlay the plate complex on the outside.

Diagram C in Fig. 1 shows, in an intermediate stage, how the dorsal body rod, arising from the root of the postero-dorsal arm, lies parallel and outside the still existing recurrent rod.

The changes during development of the various parts of the skeleton are shown diagrammatically in Fig. 2. It should be realized that the structure is three-dimensional, and the diagrams in Fig. 1 should be kept in mind to aid an appreciation of the form of the larva. For convenience five stages are taken, but it must be emphasized that the development is gradual, and the choice of five stages is entirely one of expediency. The stages are shown in the left vertical series (A) in Fig. 2. In stage 1 are included larvae which have only two pairs of arms and the unpaired posterior arm (as in Fig. 1), and larvae in which the development of the third pair of arms, the postero-dorsal, has commenced. Stages 2-5 are shown in the diagrams of Fig. 2A only by the dorsal arch and its associated arms. The disposition of the dorsal arch in the complete larva is illustrated in Fig. 1B. In stage 2 larvae the dorsal arch and the beginnings of the pre-oral arms are present. In stage 3 larvae there are the rudiments of the antero-dorsal arms. In stage 4 the antero-dorsal arms are half-developed and stage 5 is the final stage.

The root of the postero-dorsal arm in stage 1 is a three-rayed star (Fig. 2B). By stage 2 one of the star rays has increased in size and become the dorsal body rod with a short branch, the dorsal horizontal rod. In later stages the dorsal horizontal branch increases greatly in size. The remaining two rays of the star elongate slightly, curve and coalesce to form the circumference of a calcareous plate which is developed by stage 5.

The posterior transverse rod bearing the posterior arm is three-rayed in stage 1 (Fig. 2C). Two rays elongate by stage 2 and by stage 3 the elongated rays have the rudiments of the postero-lateral arms, which increase greatly through stage 4 to their full length in stage 5.

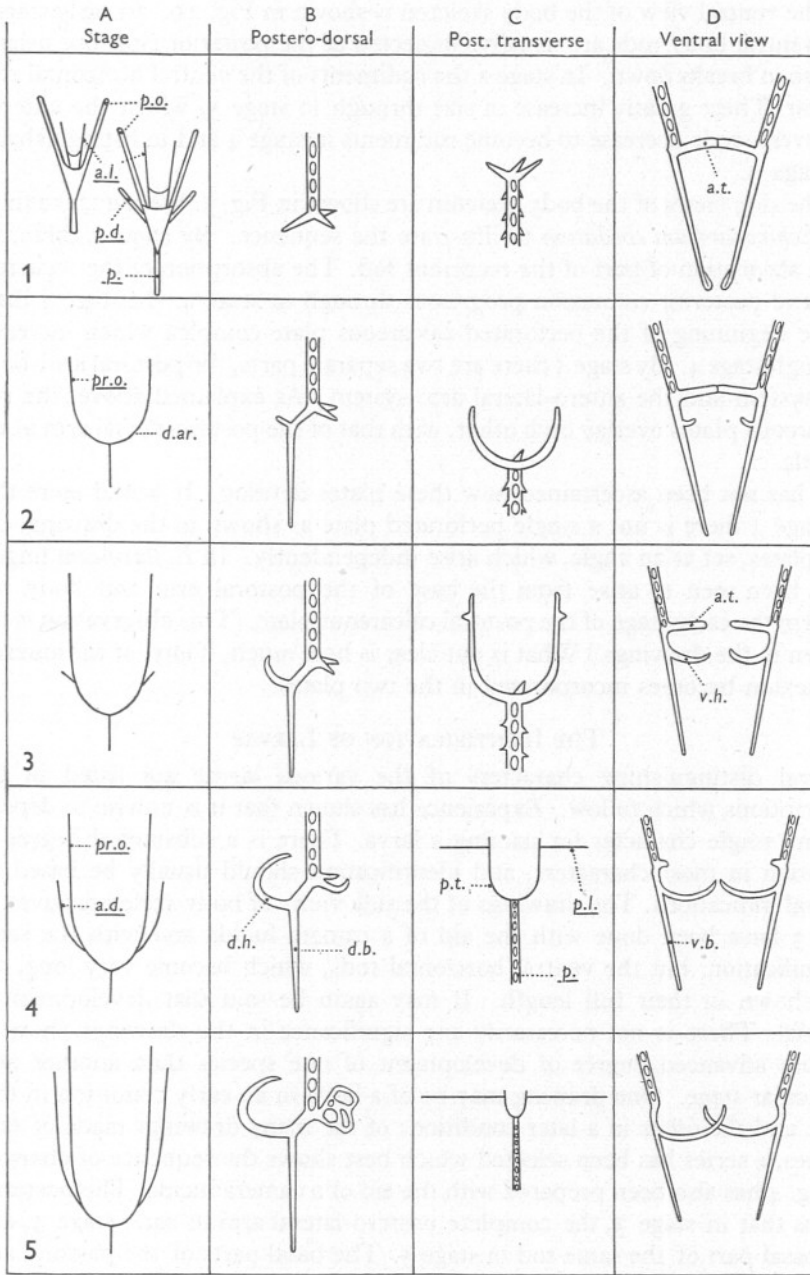


Fig. 2. Showing diagrammatically in vertical series the development, through five stages (A), of the postero-dorsal arm rod (B), the posterior transverse rod (C) and the body skeleton as seen in ventral view (D). Abbreviations as in Fig. 1.

The ventral view of the body skeleton is shown in Fig. 2D. In early stage 1 the ventral body rods are usually connected at the posterior end, but usually this soon breaks down. In stage 2 the rudiments of the ventral horizontal rods appear. These greatly increase in size through to stage 5, whilst the anterior transverse rods decrease to become rudiments in stage 4 and indistinguishable in stage 5.

The side views of the body skeleton are shown in Fig. 3. We may take those for *Echinocardium cordatum* to illustrate the sequence. By stage 2 there has been absorption of part of the recurrent rod. The absorption of the recurrent rod and posterior connexion progresses through to stage 4. In stage 3 there is the beginning of the perforated calcareous plate complex which increases through stage 4. By stage 5 there are two separate parts, the postoral arm-body rod system and the antero-lateral arm system. As explained above, the two calcareous plates overlay each other, with that of the postero-dorsal arm in the middle.

It has not been ascertained how these plates develop. It would seem that in stage 4 there is not a single perforated plate as shown in the drawing, but two plates, set at an angle, which arise independently. In *E. flavescens* fingers have been seen to arise from the base of the postoral arm and body rod to form the early stage of the postoral calcareous plate. (This observation is not shown in the drawings.) What is not clear is how much, if any, of the anterior connexion becomes incorporated in the two plates.

THE IDENTIFICATION OF LARVAE

Several distinguishing characters of the various larvae are listed in the descriptions which follow. Experience has shown that it is unwise to depend on any single character for naming a larva. There is a substantial degree of variation in most characters, and identification should usually be based on several indications. The drawings of the side views of body skeletons given in Fig. 3 have been done with the aid of a camera lucida and with the same magnification, but the ventral horizontal rods, which become very long, are not shown in their full length. It may again be said that development is gradual. There is not necessarily any significance in the drawings showing a more advanced degree of development of one species than another at a particular stage. One drawing may be of a larva in an early condition in that stage and the other in a later condition; of the many drawings made of each species, a series has been selected which best shows the sequence of changes.

Fig. 4 has also been prepared with the aid of a camera lucida. The posterior arm is that in stage 3, the complete postero-lateral arm in early stage 4, and the basal part of the same rod in stage 5. The basal parts of the postoral and postero-dorsal arms are in stage 2, but the length of the unfenestrated part, which is the feature illustrated, remains more or less the same throughout the development of a larva and is independent of stage of development.

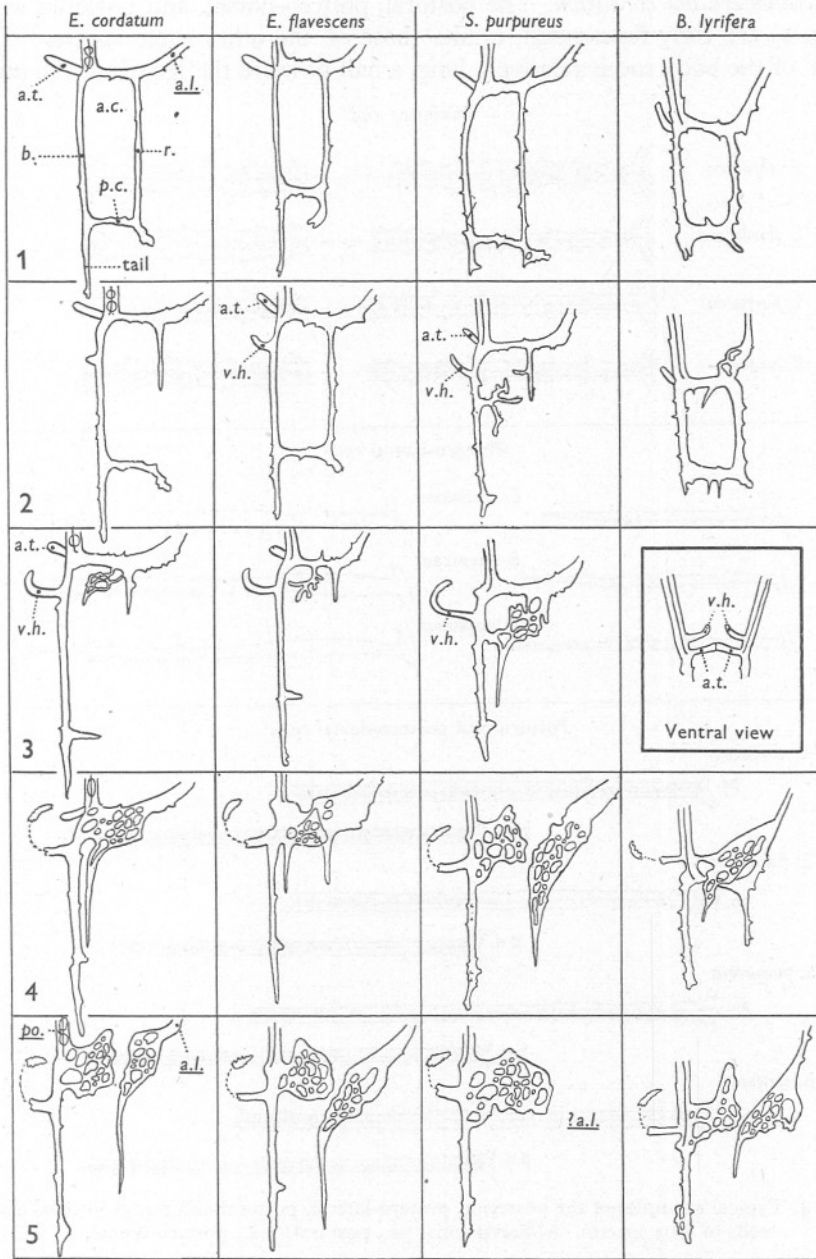


Fig. 3. The development, through five stages, of the body skeleton of four species, as seen in side view. A diagrammatic ventral view only is given for stage 3 of *B. lyrifera*. Abbreviations as in Fig. 1.

Echinocardium cordatum. The postoral, postero-dorsal, and posterior arms (Fig. 1) are fully fenestrated, unlike those of the other three species. The 'tail' of the body rod is relatively long, a half or more the length of the main

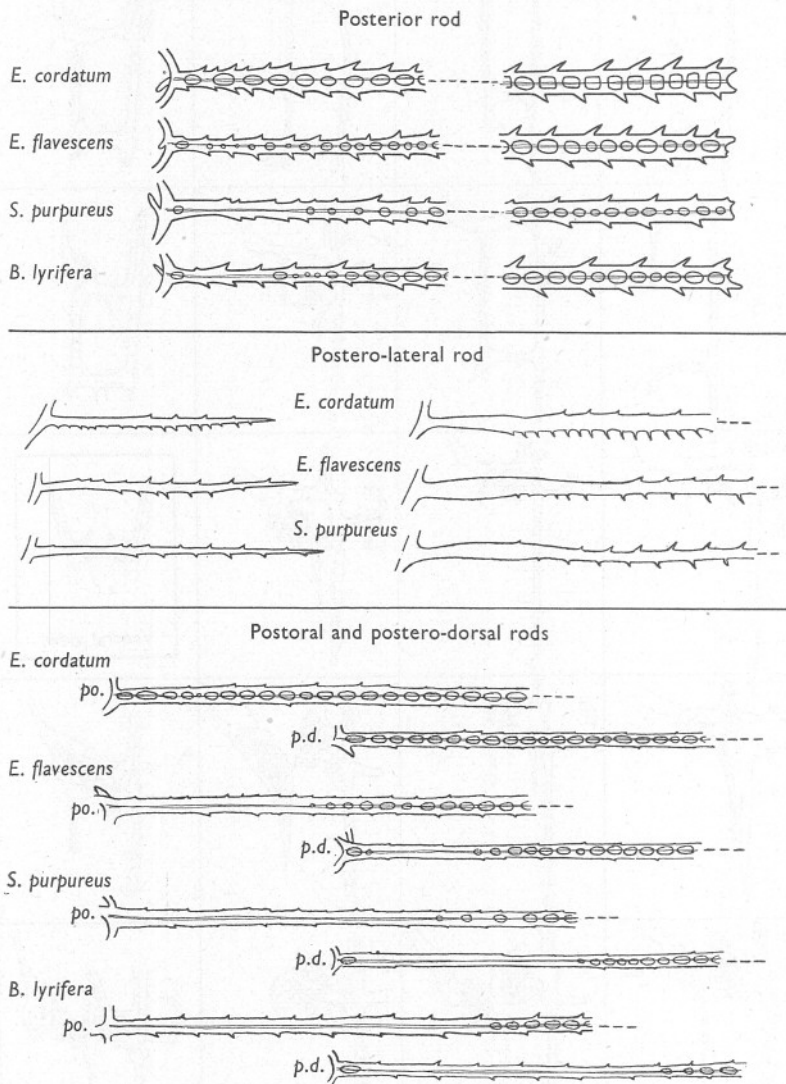


Fig. 4. Typical examples of the posterior, postero-lateral, postoral and postero-dorsal arm rods of four species. Abbreviations: *po.*, postoral; *p.d.*, postero-dorsal.

body rod. The earliest development of the calcareous plates is off the anterior connexion. The ventral horizontal rod is situated some distance posterior to the base of the postoral arm (and the anterior transverse rod). In the last

stage, the support for the posterior edge of the calcareous plate of the postoral arm is markedly anterior to the place of origin of the ventral horizontal rod. The postero-lateral arm is very spiny; there are approximately twice as many spines on the posterior edge as on the anterior.

Echinocardium flavescens. The posterior arm is, with rare exceptions, fully fenestrated. The fenestrations in the proximal part may be fairly large or very small; rarely a section may appear to be unfenestrated. The proximal part of the postoral arm is unfenestrated to a variable degree (Fig. 5), the great majority (forty-seven out of fifty measurements) to a length of 0.10–0.17 mm.

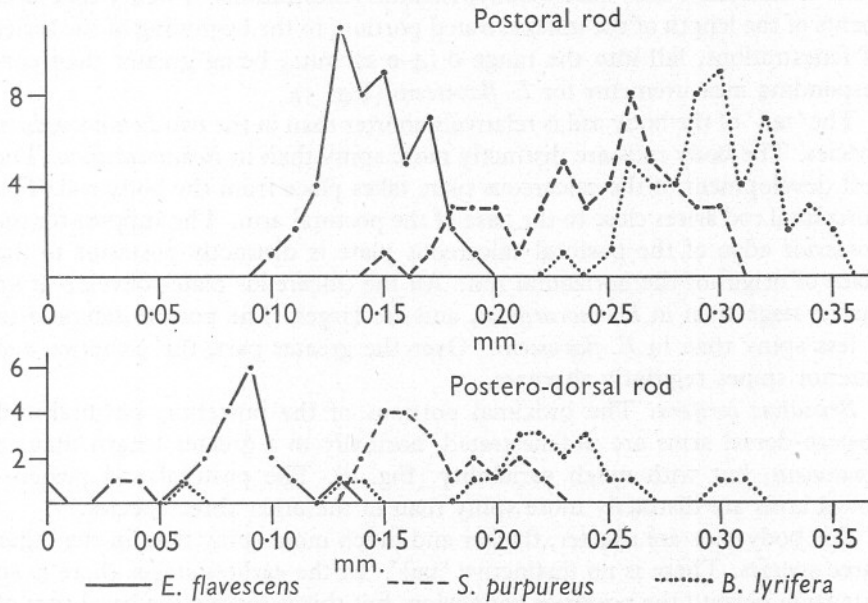


Fig. 5. Length-frequency distribution of the unfenestrated portion of the postoral arm (fifty measurements in each species) and the postero-dorsal arm (twenty measurements in each species) of *Echinocardium flavescens*, *Spatangus purpureus* and *Brissopsis lyrifera*.

inclusive. The proximal part of the postero-dorsal is unfenestrated, apart from a single basal fenestration. Along the unfenestrated part there may occasionally be an isolated fenestration. The length of the unfenestrated part, from the base of the arm to the beginning of the regular series of fenestrations, is variable (Fig. 5), twenty measurements falling into the range 0–0.13 mm.

The 'tail' of the body rod, relative to the full length of the body rod, is as long as that of *E. cordatum*. The earliest development of the calcareous plates is off the anterior connexion. The ventral horizontal rod is situated nearer to the base of the postoral arm than in *E. cordatum*, and the support for the posterior edge of the postoral calcareous plate is more or less at the same level as the ventral horizontal rod, or very slightly anterior. The postero-lateral arm

is not so spiny as in *E. cordatum*; over the greater part the spines on the posterior and anterior edges regularly alternate.

Spatangus purpureus. The proximal part of the posterior arm is unfenestrated to a variable length, but commonly about 0.1 mm., apart from a single basal fenestration. In occasional larvae the variation in degree of fenestration may overlap that of *Echinocardium flavescens*. The postoral arm is unfenestrated to a length substantially greater than in *E. flavescens*, forty-eight out of fifty measurements falling into the range 0.18–0.3 mm. inclusive (Fig. 5). The proximal part of the postero-dorsal arm is unfenestrated except for a single basal fenestration and, occasionally, isolated fenestrations. Twenty measurements of the length of the unfenestrated portion, to the beginning of the series of fenestrations, fall into the range 0.14–0.22 mm., being greater than corresponding measurements for *E. flavescens* (Fig. 5).

The 'tail' of the body rod is relatively shorter than in the two *Echinocardium* species. The body rods are distinctly more spiny than in *Echinocardium*. The first development of the calcareous plate takes place from the body rod. The horizontal rod arises close to the base of the postoral arm. The support for the posterior edge of the postoral calcareous plate is distinctly posterior to the place of origin of the horizontal rod. All the calcareous plates develop at an earlier stage than in *Echinocardium*, and are larger. The postero-lateral arm is less spiny than in *E. flavescens*. Over the greater part, the posterior and anterior spines regularly alternate.

Brissopsis lyrifera. The proximal portions of the posterior, postoral and postero-dorsal arms are unfenestrated, normally to a greater length than in *Spatangus*, but with much variability (Fig. 5). The postoral and postero-dorsal arms are distinctly more spiny than in the other three species.

The body rods are shorter, thicker and much more spiny than in the other three species. There is no distinctive 'tail'. In the earliest stages there is an extension beyond the posterior connexion, but this is merely the basal part of the connexion which meets its partner in the median line.

The earliest development of the calcareous plates takes place off the basal part of the antero-lateral arms. The ventral horizontal rod emerges off the postoral arm proper, and anterior to the base of the arm (and anterior transverse rod). There is no postero-lateral arm even in the last stage.

DISCUSSION

To my knowledge, the most satisfactory account of a spatangoid skeleton is that by Ohshima (1921) of the larva of *Spatangus purpureus*. Some developmental stages were, however, not available to him, so his account is incomplete and significantly in error. He was unable to recognize that the anterior transverse rod is replaced during development by the ventral horizontal rod. Krohn (1853) gave a ventral view of a larva, corresponding to stage 3 in

Fig. 2, in which both transverse and horizontal rods are present, but did not comment on this. Ohshima (1921) judged that Krohn's drawing was either a misrepresentation or of an abnormal larva. It is, on the contrary, a normal stage of development.

I have not followed the development of the only clypeastroid known in British waters, *Echinocyamus pusillus* (O. Fr. Müller), in any detail, since there is no difficulty in identifying the larva. It is certain, however, that the same replacement of the transverse rod by the horizontal rod occurs, though this was not appreciated by Théel (1892), who described the larva in great detail. Onoda (1938) described the replacement as occurring in the larvae of *Echinarachnius brevis* Ikeda and *Astriclypeus manni* Verrill. Mortensen (1921, p. 231), on the other hand, refers only to the reduplication of the ventral transverse rod in clypeastroids. Later, he described a replacement as occurring in *Fibularia craniolis* (Leske) but called it 'a curious feature' (Mortensen, 1937). Despite this, it is probable that the replacement is a normal feature in clypeastroid larvae, as well as in spatangoid larvae.

Mortensen (1921, p. 202) pointed out that spatangoid larvae may be divided into two groups, one group containing species with postero-lateral arms and the other group those species without. This grouping has the disadvantage that young larvae (and of several spatangoid species only the young larvae have been described) cannot be assigned to a group, for the postero-lateral arm, if present in a species, is rather a late development. A review of the literature on spatangoid larvae suggests that the same grouping will result if the presence or absence of a 'tail' to the body rod is taken as the dividing character; this character would allow the division of very young larvae.

The larva of *Brissopsis lyrifera* is a representative of the group without postero-lateral arms and without a 'tail' to the body rod. A particularly striking characteristic of the larva is the development of the ventral horizontal rod anterior to the transverse rod. In the larvae of *Echinocardium* and *Spatangus*, which are representative of the other group, the ventral horizontal rod develops posterior to the transverse rod.

The larvae of *Echinocardium* and *Spatangus* are very similar; the only difference observed which is likely to be of generic value is the mode of formation of the calcareous plate complex. More information about this process is required than is now available. That there is a basic difference is indicated by the position where the early development occurs, in the region of the anterior connexion in *Echinocardium*, off the body rods in *Spatangus*. It is noteworthy that *Brissopsis* differs from both *Echinocardium* and *Spatangus* in this respect also.

It is unfortunate that the larva of *Echinocardium pennatifidum* remains unknown, for it may prohibit certain identification of *E. cordatum* or *E. flavescens* in the plankton from some places. Arguing that the characters which are common to the larvae of the two latter species are generic characters, it is likely

that the larva of *E. pennatifidum* has postero-lateral arms and a 'tail' to the body rod, the ventral horizontal rod is posterior to the anterior transverse rod, and that the earliest development of the plate complex is in the region of the anterior connexion.

It is not unlikely that the larva of *E. pennatifidum* was present in my material. One of two types of larvae observed may, in fact, be of this species. A single larva observed had all features indicating *E. flavescens* except that the arms were fully fenestrated. This larva was probably outside the range of variation of either *E. cordatum* or *E. flavescens*, but it may have been a hybrid form rather than the unknown larva of *E. pennatifidum*. Several larvae suspected of being *E. cordatum* had postero-lateral arms which were more spiny than usual in undoubted *E. cordatum* larvae. In the main part of the arm in *E. cordatum*, the ratio of posterior spines to anterior spines is approximately 2:1; but in these particular larvae the ratio was greater than 3:1, due to more crowded spines in the posterior edge. These larvae may have been within the range of variation of *E. cordatum* larvae.

It has been usual to indicate the length of the arms, particularly of the posterior process, in describing echinoplutei. Little attention has been given to this point in the present investigation, partly because the available material has not been very suitable, and partly because it has appeared that too much attention to this may be misleading. To be really useful it is required to know the length at each stage and the variation in length. There is good reason for believing the variation in length is considerable. Mortensen (1927) says of *E. cordatum* that the posterior process is 'exceedingly variable in length, sometimes a mere short stump, sometimes as long as the postoral arms'. The larva of *Brissopsis* is described as having a short posterior process (Mortensen, 1920). This is true for larvae which I have seen which had been taken from the Clyde, but some undoubted *Brissopsis* larvae from south-west of Ireland had processes 2 mm. long, that is, longer than that given in Mortensen's (1913) drawing of the larva of *Spatangus purpureus*, whose process is said to be 'exceedingly long'. It would seem at least possible that the variation in the *Spatangus* process is also considerable. On the whole, the posterior process of *E. flavescens* appears to be longer than that of *E. cordatum*.

There is a difficulty in describing echinoplutei, in that the variations are on the whole considerable. The length of the processes and the extent of development of calcareous plates would seem in part determined by the environment. Hörstadius (1940) concluded, following an investigation of echinoid hybrids, that the amount of skeleton produced is increased by higher temperatures. Tennent (1929) pointed out that slight changes in the environmental medium may induce considerable changes in the character of the echinoderm larval skeleton. The length of the unfenestrated portion of the fenestrated arms is also very variable (Fig. 5). The position of the postoral calcareous plate in relation to the ventral horizontal rod, and the region of

early development of the plate complex should, however, prove to be good specific and generic characters.

SUMMARY

An account is given of the general structure of the body skeleton of the spatangid larva. A considerable change occurs in the skeleton as the larva increases in size, some parts being absorbed and new parts appearing. Of particular interest is the replacement of the anterior transverse rod by the ventral horizontal rod.

The skeletons of larvae, young stages to late stages, of *Echinocardium cordatum*, *E. flavescens*, *Spatangus purpureus* and *Brissopsis lyrifera* are described. The larvae of *Echinocardium* and *Spatangus* are, in essentials, very similar; that of *Brissopsis* differs greatly from them. A striking difference is that in *Brissopsis* the ventral horizontal rod arises from the postoral arm and anterior to the anterior transverse rod, in the other two genera it arises from the body rod posterior to the anterior transverse rod.

The replacement of the anterior transverse rod by a ventral horizontal rod is probably normal in clypeastroid larvae also.

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