

CYPRILEPAS HOLMI WILLS 1962,
A PEDUNCULATE CIRRIPEDE FROM THE
UPPER SILURIAN OF OESEL, ESTHONIA

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ABSTRACT. An account is given of about fifty examples of a pedunculate cirripepe, *Cyprilepas holmi* Wills 1962, some still attached to the chitinous skin of *Eurypterus fischeri* Eichw. The bivalve chitinous shell and attachment peduncle of the cirripepe are described. Comparison is made with the *Cypris*-larva and early post-larval stages of the present-day *Lepas*.

BIOLOGISTS and ecologists, as well as palaeontologists, may be interested in the discovery of what appears to be a pedunculate cirripepe in rocks as ancient as the Silurian; and to find that this sessile animal had a bivalve chitinous shell not unlike that of the *Cypris*-larva invariably present in all cirripedes. Because of this resemblance to the *Cypris*-larva, the fossil has been named *Cyprilepas holmi* (Wills 1962, p. 567), the specific name being in honour of Gerhard Holm, who in his classic paper (1898) on *Eurypterus fischeri* Eichw. figured one on his pl. 4, fig. 22 as 'Kiemenblätter?', zwei zusammenhaftende' of *Eurypterus*, although on p. 39 he rejected this ascription.

Discovery and mode of occurrence. While engaged in etching out the chitinous skins of *E. fischeri* from the silty Upper Silurian limestone of Oesel, Esthonia, I cut one specimen (E10) longitudinally into two parts (R. and L.) before treatment with acid. As etching proceeded I noticed about ten of the small objects which form the subject of this paper waving about in the acid. All were clustered round the first bit of *Eurypterus* to appear (Pl. 22, figs. 1, 2). The majority lay round its edges, but a few were on its flattened surface (Pl. 22, fig. 3). Most of them floated free as the etching proceeded, but in one or two cases I had to prise them off with a fine needle. Ultimately I extracted more than fifty from the two halves of the specimen, and a number can still be observed attached to various appendages now in the final mount, BU 739, and on two leg-joints mounted as BU 748. A few were seen when etching another specimen. As noted above, Holm also isolated one example from the same locality.

As the etching of E10 proceeded it became clear that this specimen of *Eurypterus* was a moulted skin that had lain ventral side up on the sea-bed, and had then been partially covered by calcareous silt. Gentle currents had carried away the metastoma, and displaced and broken up the greater part of the last two appendages, bits of which were found well away from the body. Since all the shells were attached to upward-stretching parts of the appendages or to the drifted bits, it seems certain that these parts were exposed above the layer of silt and were solid objects to which the floating larvae of this sessile organism could anchor themselves.

Morphology. The fossils consist of a chitinous bivalve shell, not unlike a small *Isaura* [*Estheria*] or a *Cypris*, and a cylindrical chitinous attachment-stalk, both now flattened.

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By analogy with modern pedunculate cirripedes these two parts may be regarded as the capitulum and peduncle respectively, joined at the anterior end of the shell. The combined length of shell and stalk varies from about 2.2 mm. to 4.8 mm. (Pl. 22, figs. 4-9).

(a) The *shell*. The two valves of the shell are always squashed flat with some distortion and folding. Between the two valves there is usually a small amount of silt, but in no case have I observed any evidence of a cavity such as would be expected if the fossil, prior to acid etching, had had calcareous plates comparable to those that reinforce the very tenuous chitin of the bivalve outer-skin of a post-larval present-day *Lepas*. Usually the valves lie fairly symmetrically one above the other, and often it appears as if one is larger than the other, as in ostracods (Pl. 22, figs. 5, 6). In this condition most are roughly oval, approximately two-thirds as wide as long; but the smaller ones have almost circular outlines. The length of the shell, apart from the stalk, varies from 1.4 to 3.0 mm. In a few cases the compression has opened the two valves at the posterior end (Pl. 22, figs. 7, 8). The hinge appears to occupy the full length of the carinal side and to extend part-way across the rather blunt anterior end to the points where the free edges of the two valves merge on either side into the skin of the stalk. The edges of the shells are slightly thickened. The valves have been crushed irregularly, but show no growth-lines at all.

The chitin of a single valve appears structureless at low magnifications, but under a high power it displays a faint meandering mesh-pattern (Pl. 22, fig. 11). On three specimens, however, there is a definite hexagonal patterning visible on the chitin (Pl. 22,

EXPLANATION OF PLATE 22

Cyprilepas and *Lepas*.

Figs. 1-12. *Cyprilepas holmi* Wills, attached to or associated with *Eurypterus fischeri* Eichw., Upper Silurian, Oesel, Esthonia.

- 1, 2. Two views of a single specimen attached to an edge of a segment of an appendage of *E. fischeri* (black), moving about in the etching acid which was disturbed between successive exposures, thus altering the posture of the shell.
3. Two segments of an appendage of *E. fischeri* with four specimens of *Cyprilepas* (outlined in ink) held virtually in their original positions by 'Durofix' which is itself blurred by adherent silt-particles. BU 748.
- 4-6. Young examples, two possibly showing the attachment-disc (*di*). BU 744, 750, 749 (paratypes).
- 7-9. Larger examples showing the two valves of the shell and variations in the stalk as it is preserved. BU 745, 746 (paratypes), and 743 (holotype).
10. Hexagonal patterning on part of the shell of the holotype (BU 743). Cf. fig. 14.
11. Linear markings on a single valve of the shell. BU 747.
12. ? Papillae seen through the double skin of the stalk (BU 745). Cf. fig. 15.

Figs. 13-15. *Lepas australis* Darwin. Australian and New Zealand waters. Recent.

13. Late *Cypris*-larva showing rudiments of the calcareous plates (*sc*, scutum; *te*, tergum; *ca*, carina) together with the hair-clad stalk (*ha*) of the future post-larval animal, all within the chitinous bivalve shell (*sh*) of the *Cypris*-larva with its attachment-disc (*di*). Cirri (*ci*).
14. Part of the chitinous shell of a *Cypris*-larva at the stage seen in fig. 13, after decalcification, showing the impress of the hexagonal patterning on one of the calcareous plates. Cf. fig. 10.
15. A detached post-larval individual after the first post-attachment moult and the loss of the *Cypris*-like shell; *pa*, papillate stalk (cf. fig. 12); other lettering as in fig. 13.

fig. 10). The significance of this as evidence for the original existence of calcareous plates within the shell is discussed below.

(b) The *peduncle*, now compressed, was a cylindrical structure opening out from the body of the capitulum at the anterior end of the hinge. In some cases it can be seen that its sides are continuations of the two valves. At the distal end where it was attached to the *Eurypterus*, there is either a sucker-like disc (Pl. 22, fig. 6) or a sharp point (Pl. 22, figs. 5, 7). The latter is probably due to fracture, but the disc has only been seen in two or three cases. The stalk may be a simple tapered tube (Pl. 22, figs. 5, 8), but more usually is divided into from two to four parts by transverse bands that appear to be either thickenings or, more probably, folds of the skin. The bands are usually obscured by silt. Their number bears no obvious relationship to the length of the stalk. I incline to the view that they functioned to give flexibility and perhaps muscle attachments in what must have been an organ capable of retraction and of bending.

The texture of the chitin of the stalk is sometimes distinctive. It then appears to be ornamented by transverse rows of drop-like markings which are probably minute papillae on the two superimposed layers of skin (Pl. 22, fig. 12).

The ratio of stalk-length to shell-length lies between 2 and 3, but it varies irregularly—in some cases, no doubt, because the stalk is incomplete.

Affinities. Modern bivalve shells that are sessile belong either to the Mollusca, Brachiopoda, or Crustacea. Only the last (in the pedunculate Cirripedia, such as the Lepadidae) presents any points of similarity to *Cyprilepas*.

For purposes of comparison, I obtained through the kindness of Dr. B. Patel of the Menai Straits Marine Biology Station and of Dr. T. M. Skerman of the New Zealand Oceanographic Institute, both *Cypris*-larvae and young adults of *Lepas*. In these one can recognize the growth stages described by Calman (1909).

Every Cirripede begins as a *Nauplius*-larva and then passes through a *Cypris*-larva stage. In the latter the animal is enclosed within a bivalve chitinous shell. At first the larva is free: later it attaches itself to some object by a disc secreted by its *two* antennules. In the later development of the *Cypris*-larva (Pl. 22, fig. 13) there appears *inside* the chitinous *Cypris*-like shell, a single hair-clad stalk (the pair of antennules is no longer visible) connecting the disc (external to the shell) to the capitulum which displays rudiments of five calcareous plates (*ca*, *sc*, *te*). The plates are milky-white structures exhibiting a conspicuous hexagonal surface-patterning.

After the first moult the *Cypris*-like shell disappears and a miniature adult (Pl. 22, fig. 15) now has its soft parts contained within two valves of tenuous chitin lined by five calcareous plates arranged in two pairs with the fifth or carinal plate along the hinge. The outside of the plates has the same hexagonal patterning as in the larva. The covering of very tenuous chitin thickens somewhat in the sutural strips between the plates. This whole structure is the capitulum. Its chitin is continued into a strong papillate peduncle.

The shells of the *Cypris*-larva of *Lepas* are all about the same size, *c.* 1.6 mm. in length. The youngest post-larval individual that I have seen has a total length of 1.8 mm., of which 1.3 mm. is shell. The smallest known *Cyprilepas* has a total length of 2.2 mm., of which 1.3 mm. is shell. These figures suggest that all the known specimens of *Cyprilepas* were early post-larval individuals.

In order to get a true comparison of the young *Lepas* with the fossils which had been extracted by an acid etch, and consequently must have lost any calcareous plates that may have been present originally, one *Cypris*-larva at the stage represented by Plate 22, fig. 13, and several very small post-larval individuals like the one shown on Plate 22, fig. 15, were treated with acid to remove the calcareous plates; and the soft parts, including as much of the lining of the valves as possible, were dissected away. A very tenuous film of chitin remained, which shows:

(a) *in the larva*, a very distinct patterning of hexagons (Pl. 22, fig. 14) representing the impress of the ends of the prismatic columns that formed the rudimentary calcareous plates, but no growth-lines to define the limits of the plates;

(b) *in the post-larval individuals*, a similar hexagonal patterning is to be seen, but only on certain small areas of each plate. The outlines of the plates, however, are clearly indicated by narrow growth-lines conspicuous round their edges where the plate adjoined a sutural strip. Earlier growth-lines, where seen, are extremely narrow.

There is a remarkable resemblance between the hexagonal patterning on the inside of the decalcified chitin of *Lepas* and the admittedly less-distinctly hexagonal markings seen on three specimens of *Cyprilepas*, noted above in the description of the shell. It remains a matter of speculation whether the latter can be accepted as valid evidence of the original presence of a calcareous plate or plates within its shell; but the complete absence from the shell of any growth-lines or thickened sutural strips, makes it certain that there were not five plates as in *Lepas*. If there were plates at all, there were two, one lining the inside of each chitinous valve, and perhaps leaving their impress only on certain parts of it, as was noted in the post-larval *Lepas*.

The peduncle seen within the *Cypris*-larva shell of *Lepas* is clad with hairs (Pl. 22, fig. 13*ha*), but after the first moult it is covered with papillae (Pl. 22, fig. 15*pa*). The markings seen on some of the stalks of *Cyprilepas* (Pl. 22, fig. 12) probably represent papillae, but in no case has it been possible to find only a single layer of chitin on which to check this point. All that can be claimed is that the peduncle skin structure in the fossil resembles that of the post-larval rather than that of the larval state in *Lepas*.

The attachment-disc of *Lepas* is conspicuous in the advanced *Cypris*-larva. As growth proceeds it becomes obscured by the stalk, and fully adherent to the supporting object. In line with this is the observation that in the fossils it is on the smaller individuals that the disc can be recognized with some certainty (Pl. 22, figs. 4, 6).

CONCLUSIONS

1. The capitulum of *Cyprilepas* consisted of a bivalve chitinous shell resembling that of a *Cypris*-larva of a cirripede, but equally like that of an adult entomostracan, such as *Isaura* [*Estheria*] or *Cypris*. This chitinous shell may have been reinforced by a lining of calcareous matter possessing a prismatic texture which produced a hexagonal patterning on the chitin that has occasionally been preserved. There is no evidence that such calcareous matter, if it existed, formed five independent plates, like those in Recent pedunculate lepadid cirripedes.

2. The peduncle of *Cyprilepas* resembles that found in early post-larval stages of *Lepas* in having a thick papillate chitinous sheath. The constrictions usually seen in it in the fossils are not matched in any of the small adults of *Lepas* that I have examined.

3. The size of the whole organism and the possession of a papillate peduncle show that *Cyprilepas* was an early post-larval stage of a lepadomorph pedunculate cirripepe, differing from young post-larval Lepadidae in the absence of the five calcareous plates forming the capitulum of the latter, and from Scalpellidae in the absence of numerous plates from the capitulum and of calcareous scales from the peduncle.

4. If *Cyprilepas* be accepted as a lepadomorph cirripepe, the range of that sub-order is extended from the Middle Carboniferous (*Praelepas jaworskii* Tschernischew) to the Upper Silurian (the Ordovician and Silurian machaeridians are now excluded from the cirripepes). The Lepadidae are not known before the Eocene.

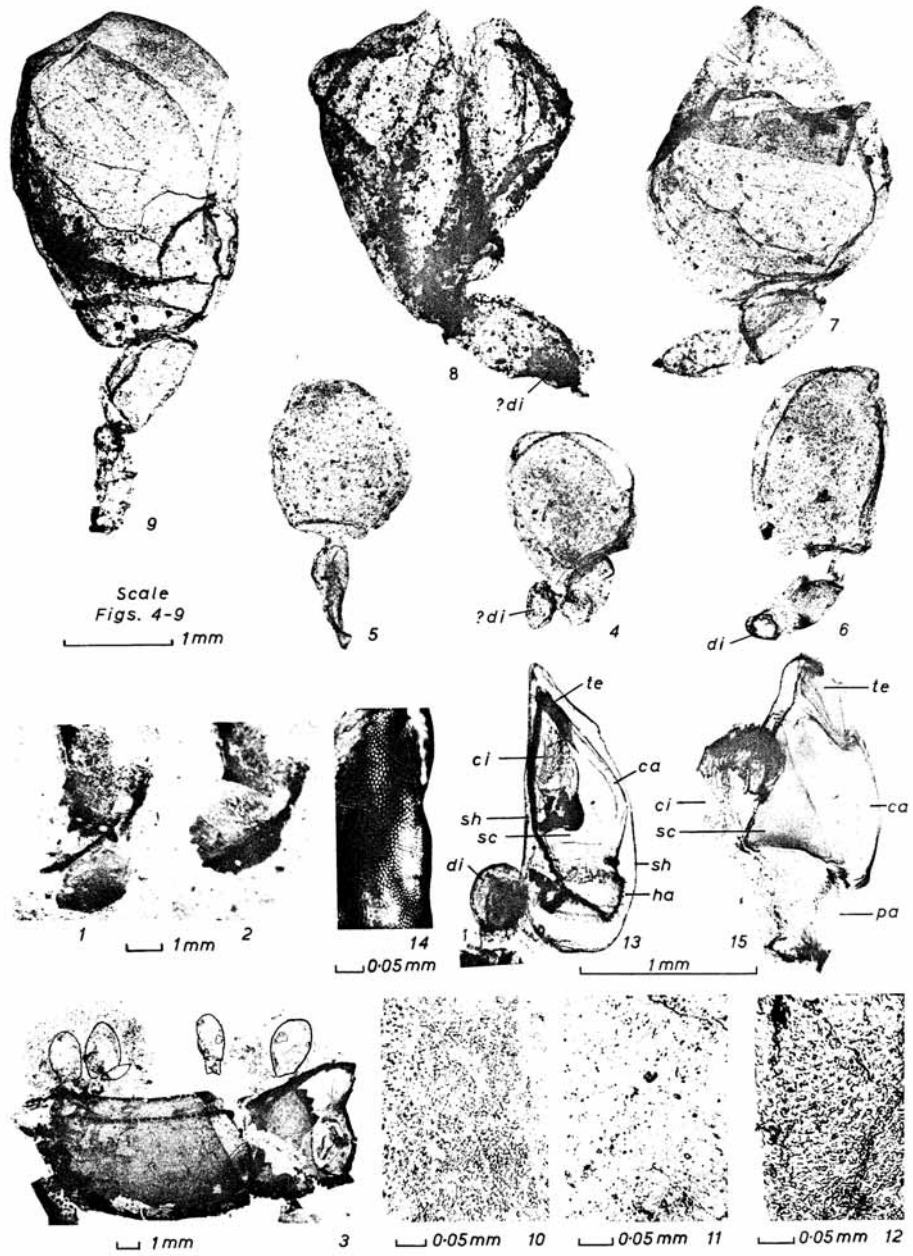
Specimens with the prefix BU are in the collection of types and figured specimens in the Department of Geology, University of Birmingham. Of the figured specimens, BU 743 on Plate 22, fig. 9, is the holotype; the others, BU 744-50, are paratypes.

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