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THE IMMATURE STAGES OF THE EUCHARIDAE.

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The immature stages of the Eucharidae are of special interest because of the high degree of specialization which they have attained to enable them first to reach the host stages upon which they are to develop and then to continue their development upon or within them. Their form and habits show a close relationship to the Perilampidae, to which the adults are linked taxonomically. During the past twenty years the writer has had the opportunity of examining one or more of the immature stages of 12 species, representing 8 genera,[1] and these, with the forms described by other authors, provide a basis for a brief comparative study.

The Egg.

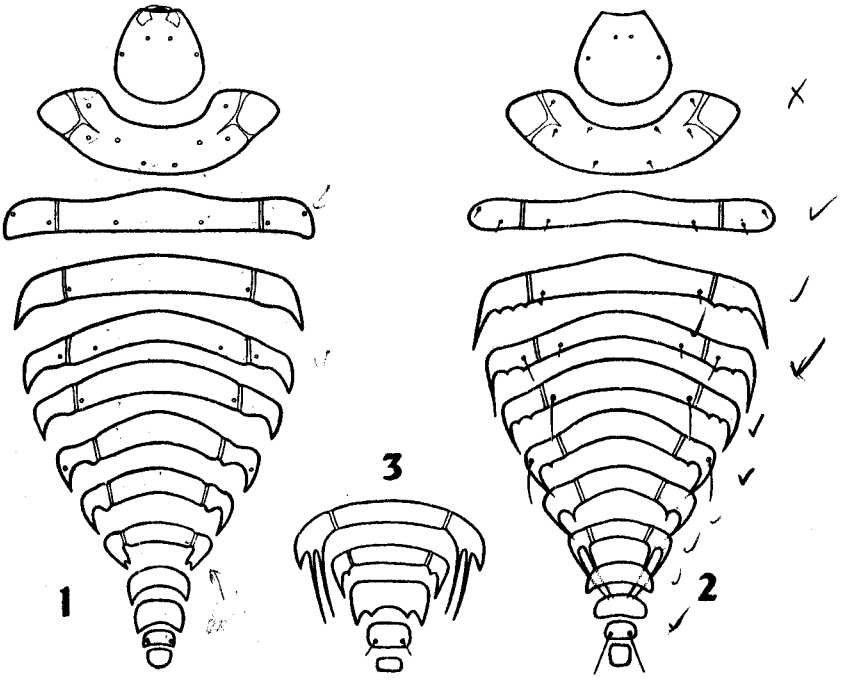
The eggs of the Eucharidae are all of the stalked type, with the stalk at the anterior end. The range in size is not so great as might be expected from the difference in size of the adult females of the various species. Several species of *Eucharis* and *Kapala*, which are of large size, deposit eggs measuring 0.18 mm. in length, while the smallest egg thus far observed is that of *Kapala* sp., which is 0.12 mm. long. In lateral outline the egg body is distinctly more convex on what is believed to be the dorsum than on the venter. The stalk ranges in length from less than one-fourth that of the main body in *Parapsilogaster montanus* Gir. (Ishii, 1932) to twice its length in *Psilogaster antennatus* Gahan. Egg clusters found by W. A. McCubbin and A. S. Mills in the buds of *Serjania diversiflora* at Barceloneta, Puerto Rico, which were almost certainly those of a Eucharid, showed the stalk to be three times the length of the egg body. In all species the stalk remains quite turgid after deposition of the egg.

[1] Acknowledgments are extended to A. B. Gahan for determinations and for descriptions of those species which are new (Proc. U. S. Nat. Mus. 88 : 425–458, 1940).

THE FIRST INSTAR.

In the earlier attempts to study the characters of eucharid planidia the specimens used were either freshly killed or slide-mounted individuals which had only recently hatched and were not appreciably distended by feeding. The small size of these larvae and their heavily sclerotized segmental bands, combined with the tendency of each segment to telescope into the one preceding it, made it extremely difficult to observe the detailed morphological characters, or even to determine the exact number of segments. It was found later that the exuviae were perfectly adapted for this purpose. In all species except *Stilbula tenuicornis* (Ashm.) the exuviae are found adhering to the venter of the second and third instars. They lie perfectly flat, with at least the first seven segmental bands widely separated, so that they can be detached and mounted directly in balsam. The head is detached from the remainder of the exuviae and remains attached by the mandibles to the skin of the host.

Detailed studies have been made of the first exuviae of *Eucharis scutellaris* Gahan (Fig. 1) and *Chalcura deprivata* (Walk.) (Fig. 2), and the general characters found in these two



occur also in all other species examined. The number of segments in each case has been found to be greater than previously believed. Following the head there are twelve segments represented by sclerotized bands, the last of which is only lightly sclerotized and represents the segment comprising the caudal sucker. The lesser number recorded in other species is probably due to an inability to distinguish the minute telescoped posterior abdominal segments, particularly the last five.

The head capsule is of the form shown in the illustration and is heavily sclerotized dorsally and laterally. It bears two pairs of minute sensory setae dorsally. The mandibles are heavy and comma-shaped.

The first segmental band is much larger than those following, with its ends markedly curved cephalad. The succeeding bands are almost straight, with a progressively greater curve caudad on those to the sixth abdominal segment. Pleural plates are present on the bands of the thoracic and first five abdominal segments. The plates of the first thoracic segment are quadrangular in outline and represent the lateroposterior portions of the band, while on the following segments they comprise the entire lateral portions of the band. The line of demarcation between the pleural and dorsal plates is faint and can be seen in the exuviae but not in living or mounted planidia. In *Eucharis scutellaris* the lateroposterior portion of each plate of the third thoracic to the fifth abdominal segments, inclusive, is produced into a sharply pointed, posteriorly directed process which on the posterior segments is almost spine-like. On the inner posterior margin of the plates there is a broadly rounded "tooth" which becomes more pronounced on the successive segments and on the fifth of the abdomen it is much enlarged, almost equal in length to the terminal process, and is united with it for the greater portion of its length.

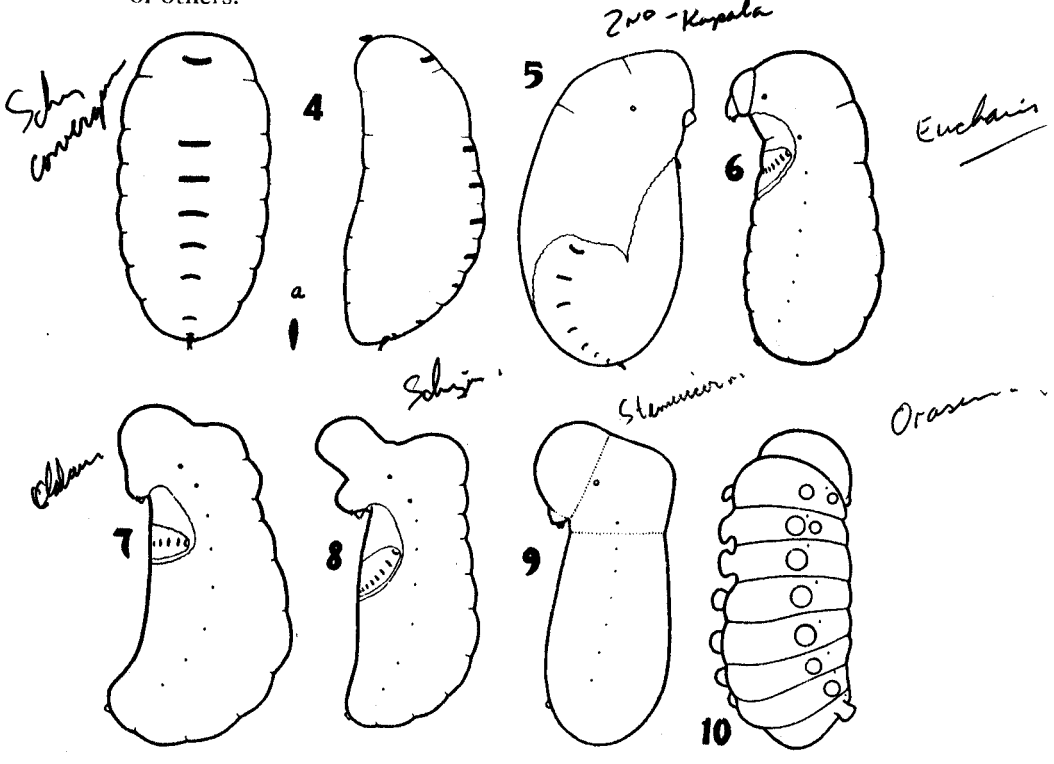
Except on the first two thoracic segments, the pleural plates of *Chalcura deprivata* have the lateroposterior areas produced into long curved processes which are distinctly spinelike. Those of the third thoracic and the first four abdominal segments are one to one and one-half times the length of the plate itself. The posterior margin of the plate of the third thoracic segment has three small teeth, while there are only two on each of the following two segments. The third, fourth, and fifth abdominal segments have each a single sharp tooth at the inner posterior margin of the plate, the one on the fifth segment being spinelike and equal in length to the terminal process and forming with it a pair of parallel spines four times the length of the plate itself. In *Parapsilogaster laeviceps* Gahan (Fig. 3) the terminal portion of the plate of this fifth abdominal segment is curved posteriorly and a pair of spines, five times the length of the plate, arise from the middle of the posterior margin. The inner tooth of the

fourth abdominal segment is also equal in length to the outer one. This species is distinctive also in having pleural plates on the sixth abdominal segment and in the enlargement and projection posteriorly of the lateral portions of the band of the seventh segment. Ishii describes and figures the planidium of *Kapala foveatella* Gir., which is stated to have a long bladelike "appendage" at each posterior-ventral corner of the band of the fifth abdominal segment, which extends beyond the end of the abdomen. These "appendages" are very evidently extensions of the pleural plates similar to, though more highly developed than, those of *P. laeviceps* and *C. deprivata*. The planidium of *Schizaspidia antennata* Gahan has the pleural plates of this segment produced into heavy, curved, spinelike structures one-third the length of the entire body. In mounted specimens they project ventrally almost at right angles to the body axis. Exuviae were not available for a detailed examination of this structure. In the planidia of the various species which have been examined the pleural plates of the fifth abdominal segment show a much greater variation in form that those of any other segment.

The sclerotized bands of the planidium of *Stilbula cyniformis* (Rossi) figured by Parker and Thompson (1925) lack the pleural plates of the first four segments. In cast skins these plates have a tendency to curl inwards, rendering them invisible or indistinct.

The sensory setae and spines of the body occur upon the segmental bands. In *Eucharis scutellaris*, *Kapala terminalis* Ashm., *Parapsilogaster laeviceps* and *Chalcura deprivata* there are four pairs of setae on the dorsal plate of the first thoracic segment and one pair on each of the four following segments and on the eighth abdominal segment. The pleural plates of the second thoracic segment bear each two setae and those of the first and third abdominal segments only one. The setae of the first four body segments are usually minute, while those of the second and third abdominal segments may be nearly twice the length of the band itself, as in *C. deprivata*. In this species and *Stilbula manipurensis* Clausen the caudal spines on the eighth abdominal segment are twice the length of the band, whereas in *P. laeviceps* they are only half its length. The positions of the spines and setae on the segmental bands, as shown in figures 1 and 2, may vary slightly between species, but their number is consistent in all species of which series of exuviae have been available for examination. Wheeler and Wheeler (1937) mention and figure a single pair of setae, approximately equal to the bands in length, at the posterior dorsal margin, near the median line, of each thoracic band of *Orasema costaricensis* W. & W. and *O. sixaolae* W. & W.

The existence of an open tracheal system in eucharid planidia is still open to question. In the description of *Stilbula manipurensis* (Clausen, 1928) it was stated that a single pair of spiracles is present at the anterior lateral margin of the plate of the first thoracic segment. It is now believed that this is erroneous, and the minute "openings" observed were more probably the bases of setae which had been broken off. Neither Ishii nor Wheeler and Wheeler, in their descriptions of the planidia of a series of species, mention the presence of spiracles. In the related Perilampidae a single pair is said to occur dorsolaterally at the anterior margin of the second band of some species and on the intersegmental membrane in the pleural area of others.



The late first instar larva bears little resemblance to that which has just emerged from the egg. The body is enormously distended, being one thousand or more times as large as before. The dorsal and lateral views of *Schizaspidia convergens* (Walk.) are shown in figure 4 and, for comparison, an unfed planidium, drawn to the same scale, is represented at *a*. This is unquestionably a first instar larva rather than a second, as a close

examination showed the mouthparts in motion and one individual reattached itself to the host and resumed feeding. The intersegmental membranes are stretched so widely that the sclerotized bands, which previously had completely enclosed the dorsum and sides of the body, are now only small darkened markings on the median dorsal line and extend over only one-fifth the body width. The greatest separation occurs between the first and second bands and there is here an apparent segment which lacks a band. The bands of the five posterior abdominal segments show little or no separation and this minute conelike portion of the body projects caudad from the dorsum of the greatly distended intersegmental area between the fourth and fifth abdominal segments. The head, now very small in relation to the remainder of the body, is situated slightly ventrad of the hemispherical first thoracic segment.

Incomplete descriptions and illustrations of larvae of other species in this stage of development, particularly those of *Orasema viridis* Ashm. by Wheeler, *O. costaricensis* by Wheeler and Wheeler, and *Stilbula cyniformis* by Parker, indicate a comparable increase in size with a consequent equal separation of the segmental bands.

The Second Instar.

Larvae of this instar have been found only in *Stilbula tenuicornis* and *Kapala terminalis*. That of the first-named species (Clausen, 1923), is of nine distinct "segments," with the integument unsclerotized. The head is small and situated beneath the hemispherical first thoracic segment. The early second instar larva of *K. terminalis* (Fig. 5) is 1.0 mm. in length and indistinctly segmented, only two divisions of the thorax being visible, and there are no abdominal constrictions. The mandibles are minute and unsclerotized. The single pair of spiracles is situated near the anterior lateral margin of the second thoracic division.

Parker (1932) found the cast skin of the second instar of *Stilbula cyniformis*, from which he concluded that the body is oval in outline and without visible segmentation. Two pairs of spiracles were noted.

The Third Instar.

In the present study it has been possible to examine mature larvae of one or more species of *Stilbula*, *Schizaspidia*, *Eucharis*, *Chalcura*, and *Kapala*. That of *Stilbula tenuicornis* (Fig. 9) is 6.0 to 7.0 mm. in length, opaque glistening white in color, with visible segmental lines only between the head and thorax, between the first and the combined second and third thoracic segments, and between the thorax and the abdomen. The thorax is bent

ventrally so that the head is distinctly ventral and directed caudad. The abdomen is almost cylindrical, with a trace of intersegmental lines immediately after the molt which disappear quickly, and terminates in a small hemispherical button which is markedly ventral in position. The integument lacks sensory setae or spines and is thickly set with minute papillae. There are eight pairs of spiracles, rather than the single pair mentioned in the original description, of which the first, situated on the second thoracic division, is large, while the remainder are minute.

Parker has described and figured the larva of *S. cyniformis*,[2] which is similar to the above except that the head is much larger and does not lie so far beneath the thorax, the second thoracic division is not nearly so arched dorsally, the dermal papillae or tubercles occur only on the dorsum and sides, and the anal button is more terminal in position. The first two pairs of spiracles are much larger than those following.

The larva of *Schizaspidia convergens* (Fig. 8) is distinguished particularly by the marked dorsal projection of the first thoracic division. Nine abdominal segments, exclusive of the terminal button, are indicated by dorsal constrictions, while the ventral line is almost straight and lacks any trace of segmentation. The exuviae of the first instar adhere diagonally to the venter of the third and fourth abdominal segments.

The larva of *Chalcura deprivata* (Fig. 7) differs from that of *Schizaspidia convergens* only in a reduction in size of the thoracic divisions and a greater curvature in the posterior abdominal region, and the first exuviae lies transversely on the venter of the second and third abdominal segments. In this species and *S. convergens* there are indications that an additional pair of abdominal spiracles is present, but this could not be determined conclusively.

The third instar larva of *Eucharis scutellaris* (Fig. 6) is more nearly normal hymenopteriform than those previously discussed. Segmentation is distinct, though only ten body segments exclusive of the terminal button are indicated, and the first thoracic segment is relatively small and unmodified. There are

[2] Gahan has called attention to the great similarity of the adults of *S. tenuicornis* and *S. cyniformis* and indicates the possibility that the former may be merely a geographical race of the European species. Aside from the characters of the mature larva mentioned above, there are several differences in habit which distinguish them. *S. tenuicornis* oviposits only in the buds of trees, whereas *cyniformis* does so in the seed receptacles of a composite plant. The first instar larva of *tenuicornis* molts prior to transfer from the host larva to the pupa and consequently the exuviae are not found on the venter of the succeeding instars but remain attached to the larval exuviae of the host. In *cyniformis*, according to Parker, the successive exuviae are found upon the remains of the host pupa in the pleural area at the point where the larva had fed, indicating that the molt takes place after transfer to the pupa, rather than before.

nine pairs of spiracles, of which those of the mesothorax are much the largest.

In *Kapala terminalis* the thoracic segments are large and modified in much the same way as in *Schizaspidia convergens*. Larvae which are not fully fed have the posterior portion of the abdomen sharply curved ventrally and tapering gradually to the apical button. At maturity this distinctive body form becomes less conspicuous.

Brues (1919) gives a description of a single mature larva of *Psilogaster fasciiventris* Brues which was on the point of transforming to the pupal stage. He mentions a "large vesicular swelling" at the anterior end of the body, indicating a thoracic formation similar to that found in *Schizaspidia convergens*. The exuviae of the first instar was found adhering to the venter of the abdomen immediately behind the head.

The third instar of *Orasema* appears to have distinctive characters not present in the genera already discussed. In describing the immature stages of *O. viridis* Wheeler (1907) mentions the existence of a semipupal stage, separated by a molt from the third stage. The third instar larva has been referred to as "tuberculate" or "pustulate" because of the row of large, almost spherical tubercles on each side of the body just above the lateral margins. The advanced semipupa as figured by him may well be a fully fed third instar larva with the body greatly distended and the lateral tubercles consequently much reduced in relative size and appearing only as rounded elevations.

Wheeler and Wheeler describe the mature larva of *Orasema costaricensis* (Fig. 10), which is identical in general form with the pustulate larva mentioned above. The nine pairs of segmental pustules occur on a line immediately above the spiracles, and, in addition, the meso- and meta-thorax bear an additional pair below this line. The head is small and situated ventrally. The nine pairs of spiracles occur on the last two thoracic and the first seven abdominal segments. The described and figured semipupa appears to be a transient stage not separated by a molt from the mature larval stage.

The occurrence of the pustulate form of larva in *Orasema* and not in the genera previously discussed may be correlated with the habits of the host and the relationship between host and parasite. *Solenopsis* and *Pheidole*, the usual hosts of *Orasema*, produce naked pupae, and consequently these pupae, and the eucharid larvae of different stages of development which they bear, are accessible to the worker ants and are tended by them. *Odontomachus*, *Camponotus*, *Formica*, and *Myrmecia*, the hosts of the other eucharid genera and species discussed, pupate within cocoons, and because of this habit the third instar parasite larvae are never accessible to the worker ants.

The Pupa.

The pupae of the Eucharidae follow closely the general body form of the adults. The abdomen of the female is very large as a result of the great mass of developing eggs which it contains. In *Stilbula tenuicornis*, *Eucharis scutellaris*, and others, it is exceptionally long and is widest in the posterior region, whereas in *Orasema* it is nearly spherical. In the above two species and *O. viridis* the abdomen bears transverse ridges of uniform elevation intersegmentally on the dorsum and sides of the abdomen. The pupa of *Psilogaster fasciiventris* described by Brues has vesicular swellings over the entire body and the abdominal ridges are broken medially on the dorsum and bear conical "teeth" or projections at the ends of each portion. These are most highly developed on the anterior segments. *Schizaspidia convergens*, *Chalcura deprivata*, and *Kapala terminalis* have these projections limited to the lateral areas. *Orasema coloradensis* Wheeler, as described by Wheeler, has a series of prominent pustules evenly spaced over each abdominal ridge, while *O. costaricensis* has only a median dorsal row of pustules on the posterior thoracic and the petiolar regions.

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EXPLANATION OF FIGURES.

1. The head and segmental bands of the first larval exuviae of *Eucharis scutellaris* Gahan.
2. The same of *Chalcura deprivata* (Walk.).
3. The bands of the fifth to ninth abdominal segments of *Parapsilogaster laviceps* Gahan.
4. Dorsal and lateral views of the fully fed first instar of *Schizaspidia convergens* (Walk.), showing the wide separation of the segmental bands of the first seven body segments and (*a*) an unfed first instar drawn to the same scale.
5. The early second instar of *Kapala terminalis* Ashm., lateral view, with the first larval exuviae still enveloping the posterior portion of the body.
6. The third instar of *Eucharis scutellaris* Gahan.
7. The third instar of *Chalcura deprivata* (Walk.).
8. The third instar of *Schizaspidia convergens* (Walk.).
9. The third instar of *Stilbula tenuicornis* (Ashm.).
10. Dorsolateral view of the third instar larva of *Orasema costaricensis* W. & W., showing the tuberculate processes. (Redrawn, after Wheeler and Wheeler, 1937.)