

The structure of the pretarsus in the third instar larvae of the Chrysopidae

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Summary

The trumpet-shaped empodium is characteristic of the larvae of the Chrysopidae but previous descriptions of the organ are vague and contradictory. In this study, the empodium has been examined in eleven species of Chrysopinae and one species of *Nothochrysa*.

In the third instar larva, the empodium consists of a strongly-sclerotized tube. The distal end is dilated and covered by an unsclerotized integument, the inner surface of which bears a concave, strongly-sclerotized plate. This bilaminar structure appears to operate as a flexible diaphragm, activated by pressure changes within the lumen of the empodium. Adhesion is achieved by suction between the diaphragm and the substrate. Small changes in pressure within the lumen of the pretarsus may be transmitted to the empodium and the bilaminar plate through a transverse septum in the pretarsus. The application of the empodium to the substrate and the changes in pressure within the pretarsus appear to be integrated into the musculo-elastic mechanism responsible for retracting and extending the tarsal claws.

The fine setae on the distal end of the empodium, observed by previous authors, are not substantiated and are attributed to the misinterpretation of superimposed structures viewed by transmission light microscopy.

The planipennian larval limb is typified by the presence of a single tarsal segment terminating in a pretarsus usually bearing two claws and between which a single median process, the empodium, may be developed. The empodium is conical in the first instar Mantispid and first instar Hemerobiid larvae and in all the instars of the Psychopsidae.

In the Chrysopidae, the empodium is characteristically trumpet-shaped in all the larval instars. The empodium's contribution to adhesion was demonstrated by excising the empodia from two third-instar *Nineta flava* (SCOPOLI) larvae, which had previously demonstrated their ability to walk on a glass plate. Neither larva appeared to show distress and each continued to be active on a paper-tissue substrate. However, when each larva was replaced on the glass surface, it was unable to adhere to the plate and was immobile, although continuing to perform futile locomotory limb actions.

The empodium's contribution is not restricted to locomotion. The ability to capture and retain active prey without being dislodged and to exploit enclosed prey, such as leaf-mining larvae and pupae in cocoons, both demand that the larva be efficiently anchored to the substrate.

Whilst the empodium has attracted the attention of insect morphologists, descriptions of the organ are conflicting or inconclusive. SMITH (1922) reported that "it is usually stated that they [the empodia] adhere by suction, but the absence of strong musculature and the irregular border of the arolium appear to be against this view. Furthermore, no trace of any secretion could be seen by repeated observations". WITHYCOMBE (1925) gave more detail: "the trumpet form of empodium . . . is a very sensitive organ, as well as being adhesive. The base of the stalk is freely hinged to a point between the tarsal claws, and up this stalk passes what appears to be a nerve fibril. Distally the empodium becomes cup-shaped. Inside, the cup is seen to be set with many minute hairs, which are probably tubular and emit a sticky fluid. I am also inclined to think that some or all of the hairs are tactile". KILLINGTON (1936)

repeated WITHYCOMBE's view and added that the empodium is "not always applied to the surface upon which the larva is walking and is undoubtedly an important tactile organ". PRINCIPI (1940) illustrated the empodium of *Chrysopa septempunctata* WESMAEL and described the structure as an adhesive organ. Her figures do not show the detailed structures described by WITHYCOMBE. DEWITZ (1884) considered that the empodium produced a secretion although this has never been substantiated.

In this study, the empodia in eleven species of British Chrysopinae and of *Nothochrysa capitata* (FABRICIUS) have been examined. The structure is consistent in all the material examined but differs in several important aspects from that described by WITHYCOMBE and KILLINGTON.

WITHYCOMBE's observations must therefore be satisfactorily explained and the structure and function re-appraised.

Larvae were killed by immersion in very warm water (approximately 80°C) and stored initially in Paml's fluid for about 30 days, then transferred to an ethanol/glycerol mixture for permanent storage. Paml's fluid was prepared according to MAHONEY (1966). Material was prepared for paraffin wax sectioning and cut to 9 micron serial sections on a standard microtome. The sections were stained with One-stage Mallory's prepared according to HUMASON (1962). Individual larvae were prepared by air-, vacuum- and freeze-drying techniques and mounted on aluminium specimen stubs, using PVA adhesive, and were coated with gold in a Pearce-Edwards S150 Sputter Coater prior to examination in an Cambridge Instruments S150 "Stereoscan" Scanning Electron Microscope.

In the Chrysopid larva, the pretarsus appears to be of the typical endapterygote structure described by SNODGRASS (1935). The soft integument forming the base of the pretarsus bears two lateral claws, the unguis. Each claw articulates dorsally with the unguifer, a median process on the tarsus. The unguitractor is a ventral, triangular plate, extended at its distal end into a median peg which projects between two distal sclerites, the planta. The proximal end of the unguitractor is attached to the tendon-like, pretarsal, depressor-muscle apodeme. The pretarsus is supported laterally by the sub-triangular auxilia. The distal surface of the pretarsus is completed by a lobe of integument, the arolium, from which the empodium arises. The dorso-frontal lobe of the arolium is sclerotized between the claws and there are sclerotized strips on the lateral walls of the arolium, between the proximal end of the empodium and the lateral ends of the planta. The external appearance of the pretarsus is illustrated (figs. 1–3).

Serial sections were stained to differentiate areas of sclerotized and simple integument (figs. 4–6). The sclerotized dorso-frontal lobe of the arolium appears to represent the junction of the arolium and a partially-sclerotized internal fold; the fold is ventrally unsclerotized. The fold is bi-lobed and projects distally to transversally double upon itself before joining the ventral integument of the arolium. Between the distal end of the planta and the junction of the internal fold, the ventral integument projects laterally beneath the ventral edge of each claw, forming a group of three papillae (fig. 5; p). The papillae appear uniform and can be distinguished from setae by their staining characteristics and by the absence of articular bases.

The internal fold divides the pretarsal lumen into two chambers. The distinctive empodium is a strongly-sclerotized tube projecting from the distal aroliar integument. The lumen of the distal aroliar chamber is continuous with the lumen of the empodium. The external dorsal surface of the empodium appears to be corrugated and is usually flanged at the 'shoulder' of the dilated distal end. This ribbed appearance is consistent irrespective of the treatment of the material and appears to represent the true surface nature. The distal end of the empodium is dilated to form an ovoid cone which terminates in a transversely-folded pad (fig. 5; el.). The pad is a bilaminar structure with an outer surface of flexible unsclerotized integument and an inner concave, strongly-sclerotized plate. The pad is ventrally attached to the ovoid rim of the empodium by a narrow strip of integument. A wider band of integument attaches the dorsal side of the pad to the dorsal rim. In dried material, the differential contraction of soft and rigid layers results in the complex folding of the pad and a distinctive ribbed appearance to the ventral lip. Due to the distortion of the structures caused by drying, precise measurements of

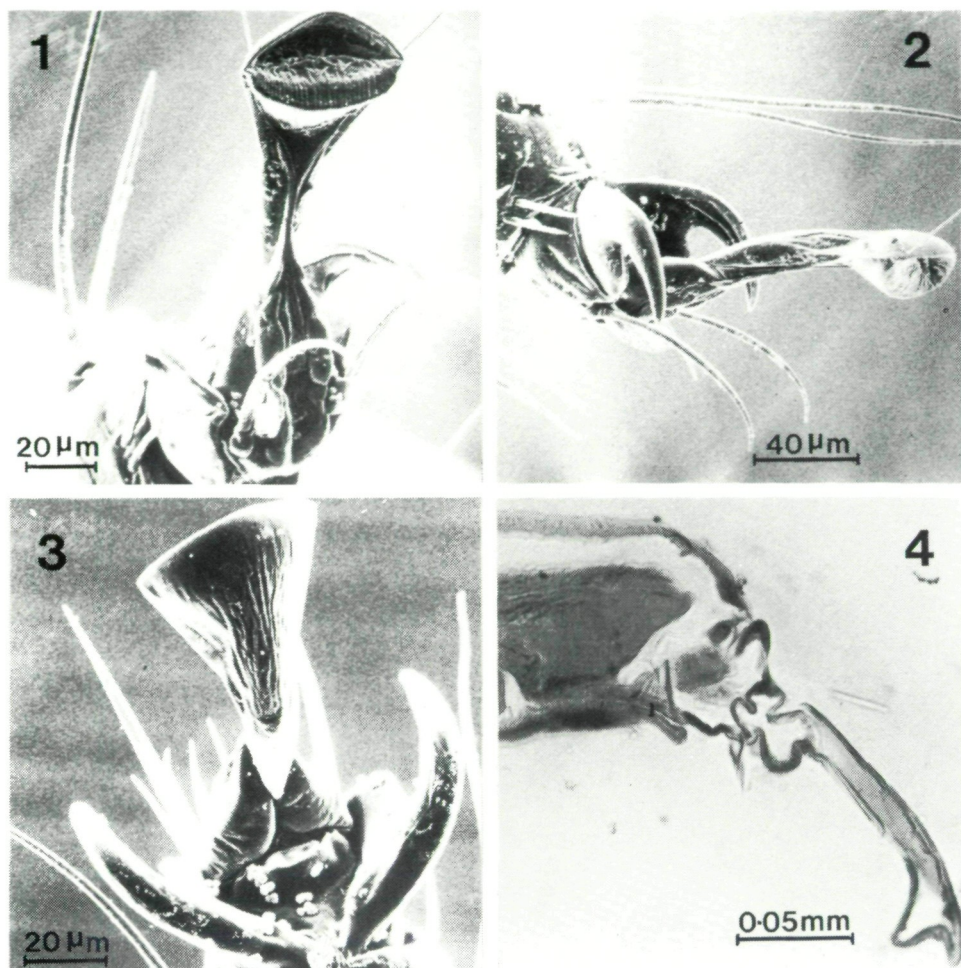


Fig. 1–3: *Chrysopa ventralis* CURTIS, pretarsus of right fore-limb of the third instar larva:

- (1) ventral aspect;
- (2) lateral aspect;
- (3) dorsal aspect;

Fig. 4: *Nineta flava* (SCOPOLI), pretarsus of right hind-limb of the third instar larva, median longitudinal section.

the pretarsus, particularly of the cross-sectional area of the distal empodium have not been possible.

The serial sections do not reveal any ducts, or associated glandular tissue, opening onto the distal surface of the empodium and an empodial secretion has not been substantiated.

Details of the preparation techniques used by WITHYCOMBE are not available. However, the examination of whole-mount preparations by transmitted light reveals that the corrugations on the upper surface of the empodium over-lie the ventrally-reflected distal ovoid ring. If several focal planes in a preparation are superimposed on a single drawing, the representation is similar to that depicted by WITHYCOMBE (1925). The single fibril, observed by WITHYCOMBE, appears very similar to the folding of the lateral flanges and the ventral

surface of the empodium observable in some preparations. It appears that the minute hairs observed by WITHYCOMBE are a misinterpretation of overlying surface corrugations and that the single nerve fibril was an artefact due to folding of the integument. WITHYCOMBE's results therefore reflect a difference in interpretation not in basic structure.

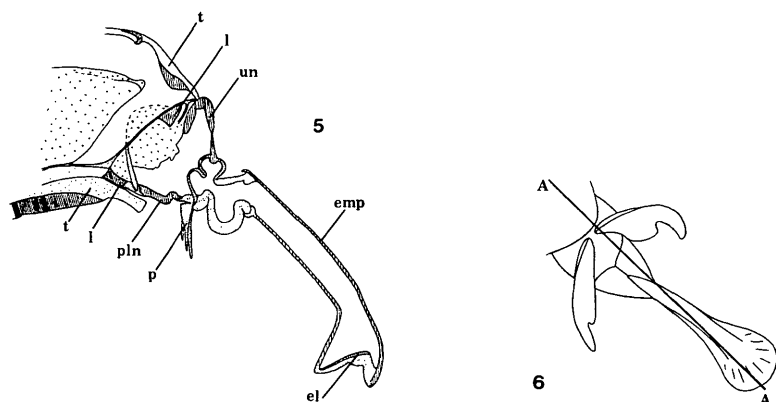


Fig. 5-6: *Nineta flava* (SCOPOLI), pretarsus of the right hind-limb of the third instar larva: (5) interpretation of the median longitudinal section of the pretarsus in fig. 4, in plane A-A' (fig. 6); (6) orientation A-A' of median longitudinal section fig. 5; el, bilaminar, 'elastic'; pad, emp, empodium; l, auxilia; p, papillae; pln, planta; t, tarsus; un, ungues.

The explanation of the operation of the empodium may lie in the bilaminar structure of the distal pad. The combination of an outer layer of unsclerotized integument and an inner layer of sclerotized cuticle imparts a degree of elasticity to the structure due to differential flexibility. A small increase in pressure within the lumen of the empodium will displace the pad outwards; when the pressure is equalised, the pad will recover its original position within the cone. If the cone of the empodium were applied to the substrate during this operation and sealed by the rim of soft integument, then the cone would function as an effective sucker. A further increase in lumen pressure would release and 'prime' the sucker for its next application.

The explanation requires a method of controlling small, precise changes in the pressure within the lumen. This may be achieved by the division of the pretarsal lumen into two chambers by the transverse fold or septum. The curved surface of the septum presents an increased surface area over which changes in the pressure within the tarsal-pretarsal cavity may be transmitted to the distal cavity of the pretarsus and the empodium.

The pretarsus is operated by a single depressor muscle which flexes, or retracts, the claws. The extension of the claws is achieved by the elasticity of the supporting basal components of the pretarsus. The same muscle/elasticity system may be responsible for the application of the empodium to the substrate. The function of the latero-ventral papillae is not readily apparent; they may improve the friction between the pretarsus and the substrate, preventing the limb from slipping about the applied empodium.

During normal locomotion an empodium need only provide short-duration suction 'pulses', corresponding to the application of the limb to the substrate, and not a sustained suction. However, when the larva is stationary, on a smooth surface, all the empodia are apparently applied continuously. Observations, using a smooth glass plate, suggest that the larva maintains a succession of small adjustments, during which, each limb is slightly extended and then slowly retracted with the empodium applied to the substrate. The tarsal claws and anal pseudopod contribute to adhesion and locomotion on normal substrates.

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Zeitschrift/Journal: [Monografien Entomologie Neuroptera](#)

Jahr/Year: 1984

Band/Volume: [MEN1](#)

Autor(en)/Author(s): Kirby Michael A.

Artikel/Article: [The structure of the pretarsus in the third instar larvae of the Chrysopidae. 261-265](#)