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The Significance of the Elongate, Rectangular Mesh Found in Capture Nets of Fine Particle Filter Feeding Trichoptera Larvae

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With 6 figures in the text

Abstract

Striking similarities exist in capture net mesh shapes of fine particle feeding Trichoptera larvae, even among genera in families that are not closely related phylogenetically. The capture nets of these fine particle feeders have elongate rectangular mesh openings. There are several important consequences associated with this type of mesh design.

The suborder Annulipalpia consists of some seven families of Trichoptera (Ross, 1967). With a few exceptions, their larvae are confined to flowing waters. Larvae of most Annulipalpia use capture nets spun with their silk glands for trapping drifting food particles.

Size and structure of capture nets of various species in the suborder vary considerably. Some larvae such as *Neureclipsis bimaculata* L. (Psychomyiidae) have no distinct capture net mesh openings and the nets consist of a number of layers of randomly arranged silk strands (BRICKENSTEIN, 1955). *Chimarra* spp. (Philopotamidae) spin sac-like nets with remarkably uniform mesh sizes (WILLIAMS & HYNES, 1973) while the meshes of *Wormaldia* spp. are somewhat more variable (NIELSEN, 1942). Capture nets of the Hydropsychidae have fairly regular mesh openings whose dimensions vary according to species and instar (SATTLER, 1958; KAISER, 1965; WILLIAMS & HYNES, 1973; and WALLACE, 1975 a).

The phylogenetic placements of *Chimarra* and *Wormaldia* (Philopotamidae) and *Macronema* (Hydropsychidae) are at opposite extremes of the Annulipalpia (Ross, 1967). Yet when the shapes and sizes of individual capture net mesh openings of various members of the Annulipalpia are compared some striking similarities exist between members of the above three genera. All three genera are small particle or microseston feeders (WILLIAMS & HYNES, 1973; SATTLER, 1963; WALLACE & SHERBERGER, 1974, and 1975; WALLACE 1975 b and WALLACE Unpubl. data). In this paper we discuss the biological significance of the narrow, elongate mesh com-

mon to capture nets of fine particle feeders at opposite systematic extremes of the Annulipalpia.

Materials and Methods

Larvae and their nets were preserved in 80% ETOH solution. Nets were mounted on slides in glycerine and mesh measurements made using a compound microscope equipped with a drawing tube in conjunction with a stage micrometer. Portions of the smaller meshed nets were cut and floated on aluminum studs. The studs were then removed from the alcohol and the nets spread flat and allowed to dry. These nets were then vapor coated with a thin conductive layer of palladium gold (40 : 60) alloy and examined with a Cambridge Stereoscan scanning electron microscope. Photographs were obtained from both compound and scanning electron microscopes with Polaroid P/N Type 55 film.

The Width/Length Ratio (W/L R) referred to throughout this paper is obtained by dividing the average width of a mesh opening by its average length. It should be mentioned that there is some disagreement in the literature on how the length and width of meshes in capture nets of the family Hydropsychidae are determined (KAISER, 1965; and SATTLER, 1965). We have used the longer dimension of the mesh opening as the length and the shorter dimension as the width throughout this article. The W/L R serves as a rapid means of visualizing the shape of individual mesh openings. Those with higher values approach a square shape while those with lower values have a very elongate rectangular shape.

Results and Discussion

Some individual capture net meshes of larval Hydropsychidae are shown in Fig. 1. ROSS (1956) and FLINT (1974) recognized four subfamilies of hydropsychids: Arctopsychinae, Diplectroninae, Hydropsychinae and Macronematinae. The first three subfamilies have meshes of somewhat similar shape but not size (Fig. 1 b—f). Studies of feeding habits of their larvae have indicated that they are somewhat omnivorous (e.g., SATTLER, 1958; WILLIAMS & HYNES, 1973; and WALLACE, 1975 a and 1975 b). The W/L R of individual meshes of these 3 subfamilies are generally between 0.5 and 0.79. But, in those belonging to the specialized group Macrone-matinae (ROSS, 1956), *Macronema* spp. are microseston feeders (SATTLER, 1963; WALLACE & SHERBERGER, 1974; and WALLACE (1975 b) with a W/L R of 0.125 or less.

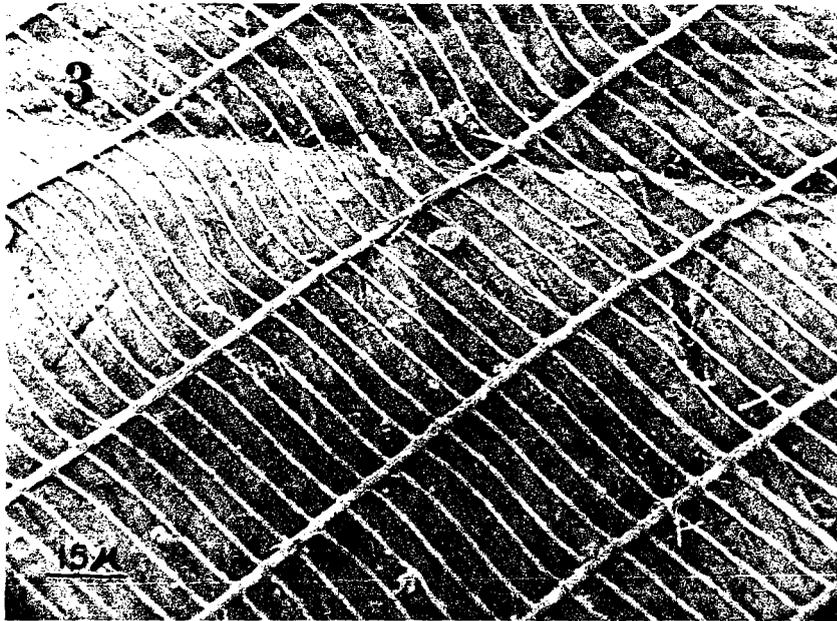
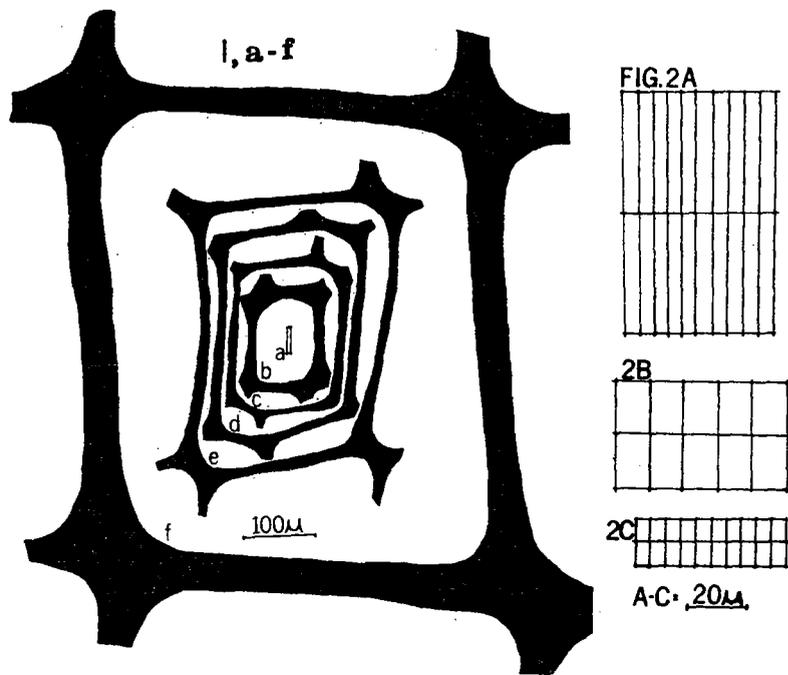
In both *Macronema carolina* BANKS and *M. zebratum* HAGEN (Figs. 1 a and 2 A) the individual mesh opening sizes are $5 \times 40 \mu$, or have an opening of $200 \mu^2$ (WALLACE & SHERBERGER, 1974; and WALLACE 1975 b). Their W/L R is 0.125. Using a W/L R of 0.6172, which is near the middle range of that found in other hydropsychids, the hypothetical mesh opening of a $200 \mu^2$ net is ca. 11.11 by 18μ (Fig. rot, fig. 2 B). The smallest particle that could be expected to be retained by a capture net having the above mesh size would be slightly larger than 11.11 microns. In the

200 μ^2 mesh net actually spun by *Macronema* (Figs. 1 a and 2 A) the minimum particle size that could be expected to be retained by the net would be slightly larger than 5.0 μ . Thus the narrow elongate meshes spun by *Macronema* (Fig. 2 A) are capable of capturing particles about twice as small as the mesh opening size shown in Fig. 2 B.

Again, assuming a hypothetical W/L R of 0.617 the mesh that would be required to capture particles in the 5.0 μ range is shown in Fig. 2 C, having mesh dimensions of ca. 5 \times 8.1 μ . However, there are two definite drawbacks associated with this design. First, the total length of silk strands required to spin an equal sized area of net using the meshes shown in Figs. 2 A and 2 C is less using the mesh size shown in Fig. 2 A. For example, to spin a small net area of ca. 8,000 μ^2 (50 \times 160 μ), using the mesh shown in Fig. 2 C, would require 11 strands each 160 μ in length and 19.75 strands of 50 μ in length or a total silk length of 2747.5 μ . Conversely, using the mesh spun by *Macronema* (Fig. 2 A) a net area of 8,000 μ^2 could be spun using 11 strands, each 160 μ in length and 5 strands, each 50 μ in length or a total silk length of 2010 μ . Thus the net spun by *Macronema* (Figs. 2 A and 3) uses ca. 26.8% less silk than the hypothetical net shown in Fig. 2 C.

The second drawback of the mesh shown in Fig. 2 C is that the number of meshes that would be required to complete a net is much more than that required for Fig. 2 A. In the hypothetical example given above for silk strand length, 40 meshes would be required for spinning 8,000 μ^2 of net area using the meshes shown in Fig. 2 A; whereas, 197.5 meshes would be required for spinning an 8,000 μ^2 net area using the mesh size shown in Fig. 2 C. Therefore considerably fewer spinning movements would be required with the mesh design actually used by *Macronema* (Fig. 2 A).

As mentioned in the introduction, the elongate rectangular mesh pattern is not restricted to *Macronema* in the Hydropsychidae. This mesh pattern is also exhibited in fine particle feeders in philopotamid genera that have been studied. For example, WILLIAMS & HYNES (1973) reported the larval capture net mesh openings of *Chimarra aterrima* HAGEN as being 6 \times 70 μ . Thus *C. aterrima* has a W/L R of ca. 0.086. Portion of a capture net of *Chimarra socia* HAGEN from Richmond County, Georgia, is shown in Fig. 4. Most of the net meshes are between 0.8 and 1.0 μ in width and 5 to 10 μ in length. However, the majority of the meshes are ca. 0.8 to 1.0 μ in width and 9 μ in length or with a W/L R of 0.088 to 0.111. There are a number of diagonal strands that apparently reinforce the net (Fig. 4, DS). A small portion near the anterior end of this sac-like net had meshes with openings of ca. 1 \times 1 μ (Fig. 5). We do not now



Figs. 1—3. 1, some typical capture net meshes of mature Hydropsychidae larvae, all drawn to the same scale; a, *Macronema carolina* BANKS; b, *Hydropsyche orris* Ross; c, *Diplectrona metaque* Ross; d, *Diplectrona modesta* BANKS; e, *Parapsyche cardis* Ross; and f, *Arctopsyche irrorata* BANKS. 2 A, mesh design

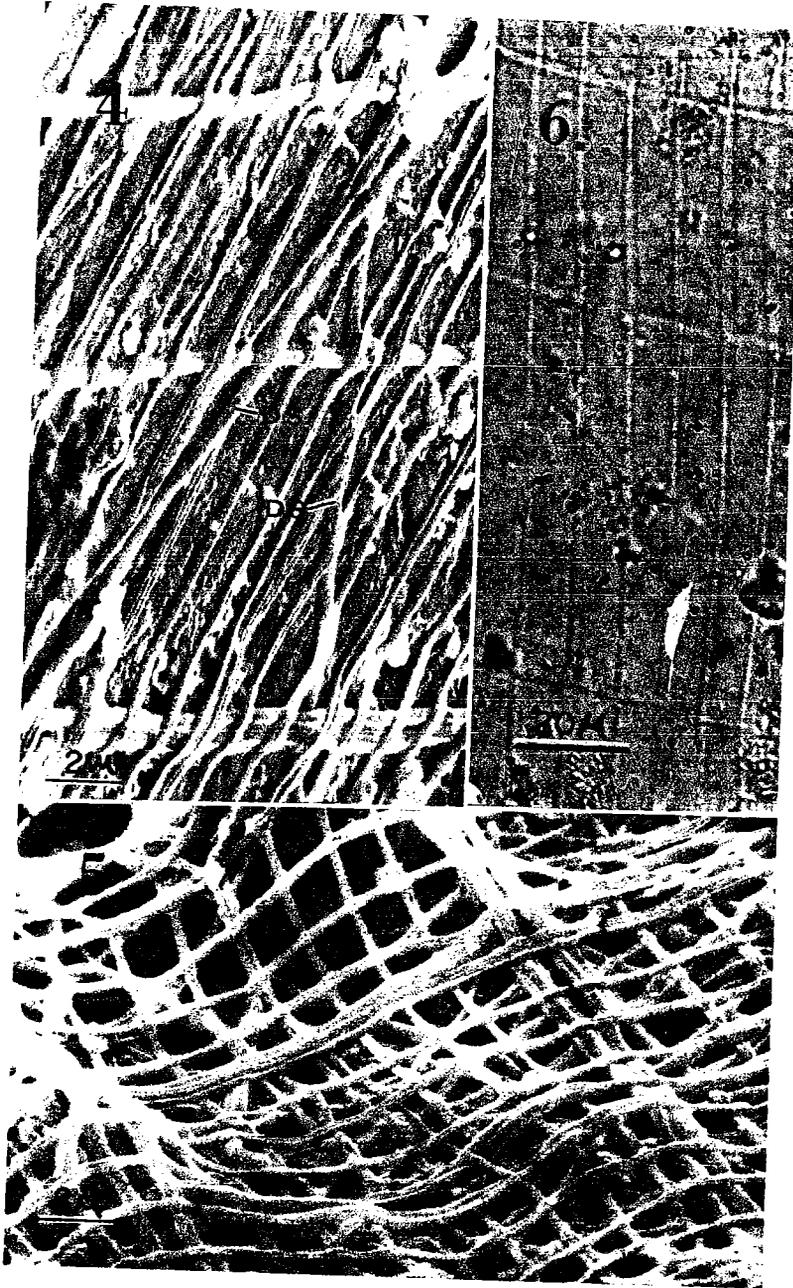
have an explanation for these unusually small meshes in this area of the *C. socia* capture net.

Nets of another philopotamid, *Wormaldia* spp. (Fig. 6), have rectangular meshes but they tend to be quite variable in size. Most of the mesh opening sizes of *Wormaldia* are between $9 \times 80 \mu$ and $9 \times 40 \mu$ (W/LR = 0.1125 and 0.225, respectively). However, meshes of both longer and shorter length are present. The sac-like *Wormaldia* net is actually composed of several individual layers of variable, rectangular mesh, which when fitted together, make a very fine meshed sieve.

Indeed the elongated rectangular meshes are not even restricted to insects. SATTLER (1963) noted the striking resemblance of shapes between the capture net of *Macronema ulmeri* BANKS and the netlike filter membrane collecting structure in "the house" of the marine tunicate *Oikopleura* described by LOHMANN (1913). This outer "filter" has openings of about $19.8 \times 141.6 \mu$ according to the scale in Figure 28 of SATTLER (1963) or a W/L R of 0.140. SATTLER reported that he did not know if the similarity between net shapes in *Oikopleura* and *Macronema* was accidental. It is interesting that JØRGENSEN (1966) reports the inner food collecting membrane of *Oikopleura* sp. to be a net-like structure with meshes of ca. $0.1 \times 0.8 \mu$ or a W/L R of 0.125. These mesh opening designs of small particle feeders appear to be a remarkable case of convergent evolution.

In summary, since the elongate rectangular mesh appears in diverse groups of fine particle feeders it must be assumed that this shape offers some selective advantage. In Trichoptera, larval nets with mesh shapes as shown in Figs. 2 A, 3, 4 and 6 would be advantageous from several standpoints. With a given amount of silk expenditure the elongate rectangular mesh is the simplest means of obtaining a mesh that will capture minute particles. Trichopteran silk is quite similar to that from the related order Lepidoptera which is proteinaceous (RUDALL & KENCHINGTON, 1971). Reducing silk expenditure would therefore reduce some of the total protein requirements for larvae. The small diameter of the silk strands of fine particle feeders vs. the larger diameters of those species that feed on larger materials (cf. Figs. 1 a, vs. 1 b—f) would also be important in reducing the protein expenditure. Fewer spinning movements are required to construct a net that captures minute particles when the

of *Macronema carolina* and *Macronema zebratum* HAGEN, both have mesh opening sizes of ca. $200 \mu^2$ and a W/L R of 0.125; 2 B, hypothetical mesh of a $200 \mu^2$ mesh opening having a W/L R of 0.617, similar to that found in most hydropsychids; 2 C, hypothetical mesh of a net with a mesh small enough to catch $5 \mu^2$ particles and having a W/L R of 0.617. 3, a portion of the capture net of *Macronema zebratum* at ca. $1,000 \times$ (SEM).



Figs. 4—6. 4, a portion of the capture net of *Chimarra socia* from Richmond County, Georgia, (SEM at 5,000 \times). Note the elongate rectangular mesh with some diagonal strands (DS); 5, another section of the same net at 5,000 \times (SEM); 6, a portion of the capture net of *Wormaldia* sp. (at 400 \times). This photo of the *Wormaldia* net shows only 1 of several layers of net.

meshes are constructed as in Fig. 2 A, which would save on both time and energy that larvae devote to net construction.

Summary

The elongate rectangular mesh is the simplest means of obtaining a mesh that will capture small particles with a given amount of silk expenditure. Reduction in silk expenditure would result in lower protein requirements for the larvae. In addition, fewer spinning movements are required to construct a net that captures fine particles if the elongate rectangular mesh design is used. Evidence is cited that this mesh pattern is not restricted to insects but also occurs in marine tunicates. The mesh design appears to be a case of functional convergent evolution.

Zusammenfassung

Das rechteckige Gewebe mit einer verlängerten Achse ist die einfachste Art, ein Gewebe zu erhalten, das kleine Teilchen mit einer bestimmten Menge von Seidenfadenverbrauch fangen kann. Eine Herabsetzung des Seidenfadenverbrauches bringt einen niederen Eiweißbedarf für die Larven mit sich. Wenn der verlängerte rechteckige Gewebeerwurf benutzt wird, sind außerdem weniger Spinnbewegungen nötig, um ein Gewebe zu konstruieren, das feine Teilchen fängt. Beweise sind erbracht, daß diese Gewebemuster nicht nur bei Insekten, sondern auch im Meer bei Tunicata bestehen. Der Gewebeerwurf scheint ein Fall von funktionell konvergierender Entwicklung zu sein.

Acknowledgements

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Errata

Our recent study, using the scanning electron microscope, has shown that the net in Fig. 6 contains many very regular elongate rectangular meshes not visible at 400× magnification. The large strands in the photograph provide a frame over which these minute strands are laid. This correction does not change, but rather supports, the interpretation presented in this paper.