The Larval Retreat and Food of *Arctopsyche;* with Phylogenetic Notes on Feeding Adaptations in Hydropsychidae Larvae (Trichoptera)[1]

J. BRUCE WALLACE

Department of Entomology, University of Georgia, Athens 30602

ABSTRACT

Arctopsyche larvae generally construct somewhat cornucopia-shaped dwellings at the top and sides of large rocks in swift mountain streams and spin a capture net across a U-shaped frame at the anterior end of the larval abode. There is an increase in net mesh size in successive larval instars. The individual meshes of mature larval capture nets are the largest found to date in the Hydropsychidae. Based on larval foregut con-tents, 2nd instars are about 50% plant detritivores and 50% predators. In the last 2 instars foregut contents consisted of ca. 90% insect fragments and 10% plant material. The structure of the nets and larval abodes supports the placement of the Arctopsychinae as primitive Hydropsychidae. In the evolution of hydropsychid larvae there is a tendency toward more complicated larval feed-ing structures and smaller capture net mesh sizes.

Ross (1956) recognized 4 distinct subfamilies of Hydropsychidae: Arctopsychinae, Diplectroninae, Hydropsychinae and Macronematinae, which are listed in order of increasing specialization. The lar-vae of Hydropsychidae use silken nets to capture drifting food in streams. The following have pub-lished details of net structures and biology: Hydro-psychinae: Sattler (1955, 1958), Kaiser (1965), Schuhmacher (1970), Williams and Hynes (1973); Diplectroninae: Sattler (1963a); and Macronemati-nae: Sattler and Kracht (1963), Sattler (1963b, 1968), Wallace and Sherberger (in press a, in press b).

In this paper the larval retreat and net of *Arcto-psyche* is described. *Arctopsyche* and the related genus *Parapsyche* have been placed in a separate family, Arctopsychidae, by a number of authors (e.g., Milne and Milne 1938, Ulmer 1957, Lepneva 1964 and Schmid 1968). However, Flint (1961) and Smith (1968) followed the placement of Ross (1956) in according only subfamily status to the group. As noted by Flint (1961), the large gula, which sepa-rates the genae ventrally over their entire length, is the only distinctive morphological structure limited to larval arctopsychines. For this and other reasons cited later in this paper, the subfamily classification is followed here.

MATERIALS AND METHODS

For the most part I discuss *Arctopsyche irrorata* Banks, from North Carolina and northern Georgia, but I also consider some larvae and retreats of *Arctopsyche grandis* (Banks) from western North America.

Larvae with their nets and retreats intact were removed from the sides and tops of rocks in swift mountain streams. *Arctopsyche irrorata* larvae are limited to medium and large streams at higher eleva-tions in the southern portion of this range (Gordon and Wallace, in press) and are generally found in the areas of swiftest stream currents (Flint 1961). Orientation of the larval retreats relative to current direction was noted at the time of collection. Stream velocity was measured with a rubber bag current meter (Gessner 1955).

Larvae and their retreats were preserved in an 80% ethanol solution to determine net and retreat construction details. Larval instar was determined by measuring the width of the head capsule at the level of the eyes. Nets were carefully cut away from the retreats and mounted on slides in glycerine. Net mesh measurements were made with a drawing tube and a stage micrometer. Averages of mesh opening sizes were based on the average size of a minimum of 15 openings for nets of at least 2 individuals of each (2–5) instar selected at random. The few, very large, irregular meshes at the edge of the net were not included in the measurements.

Slides for gut analysis were prepared using the Millipore Filter technique (Cummins 1973). Only the contents of the proventriculi were examined, since the sclerous spiculi in the posterior of the proven-triculus (Harris[2]) possibly alter the size of food particles passing to the mid- and hindgut. However, rather than separate the plant and animal material (Cummins 1973), all the contents of the foregut were filtered and allowed to accumulate on the membrane filter. I determined the plant or animal origin of each large fragment and outlined it on paper with the aid of a drawing tube and compound microscope. A stage micrometer and drawing tube were used to draw the area of a 1 mm² on paper at the magnifi-cation (60×) at which the food particles were sketched. The particle outlines and the 1-mm² area were then photocopied and their outlines carefully cut out and weighed on a Mettler H-16 balance. The weight of the 1-mm² area outlined with the drawing tube served as a standard for estimating average sur-face area of the outlined particles. Although such sketches are unidimensional and show only area, not depth, of the individual particles, the technique does allow a reasonably accurate estimate of individual particle size. I weighed several equal sized pieces of copy paper of the same area and the greatest vari-ation in paper weight was 3.5%.

[2] Harris, T. 1971. A morphological and evolutionary study of the proventriculi of Hydropsychidae (Trichoptera). Unpubl. Ph.D. Thesis, Univ. Ga., Athens. 91 pp.
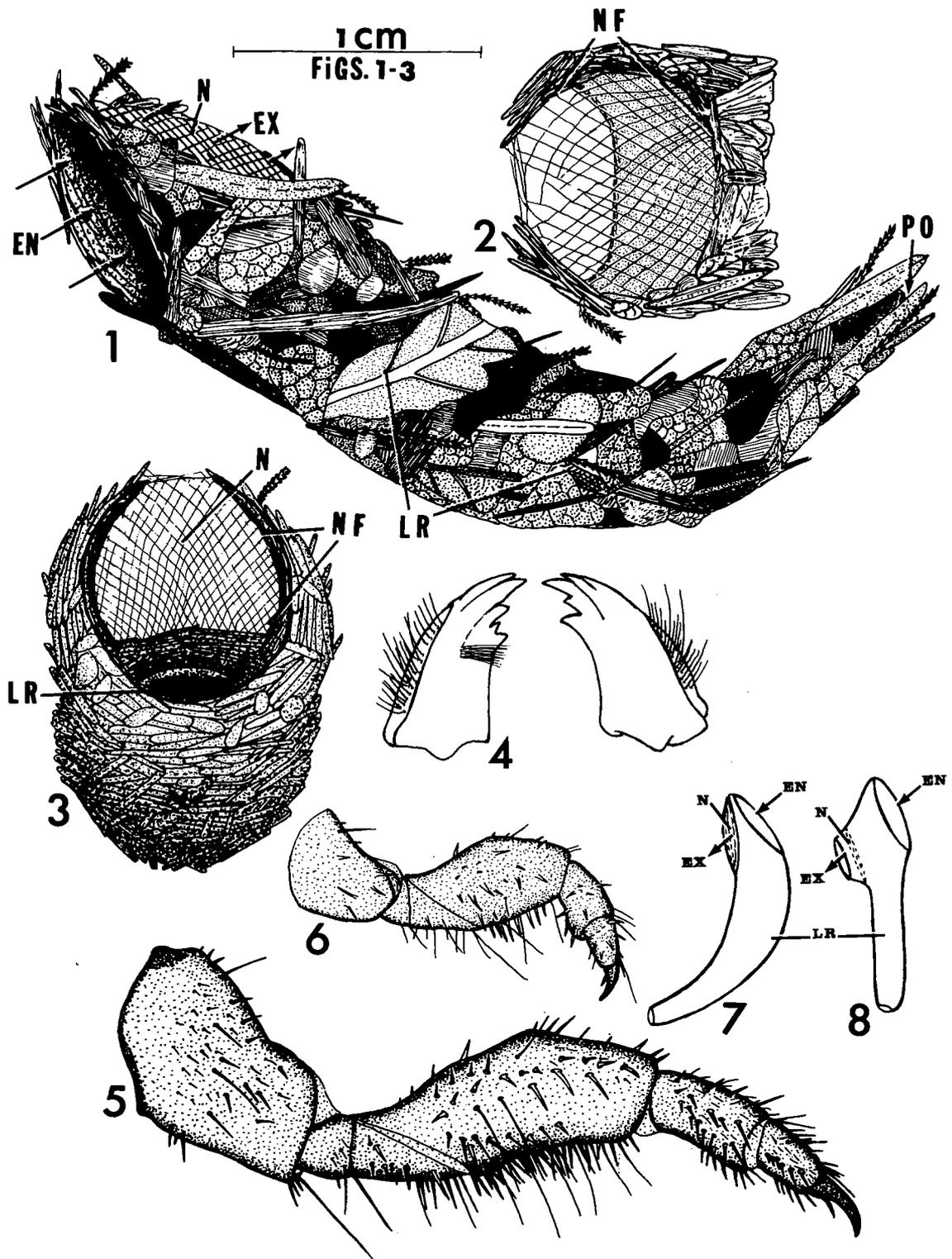
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Fig. 1–6.—*Arctopsyche irrorata*. 1, larval retreat and net of mature larva, lateral view; 2, anterior end of the larval retreat showing the location of the feeding net, posterodorsal view; 3, frontal view of the anterior opening of the retreat as it faces directly into the current; 4, mandibles of mature larva, dorsal view; 5, left leg of mature larva, anterior view; note the short stout setae on the trochanter, femur, tibia, and tarsus; and 6, same of second instar larva.

Fig. 7, 8.—7, diagrammatic scheme of *Arctopsyche* spp. retreat and capture net; and 8, same of a *Diplectrona* and *Hydropsyche* type (latter after Sattler 1963a, 1963b). Abbreviations used in figures: EN, entrance for inflowing water; EX, exit for outflowing water; LR, larval retreat; N, capture net; NF, net frame or support; and PO, posterior opening of the larval retreat. Arrows in Fig. 1, 7 and 8 indicate the current direction.
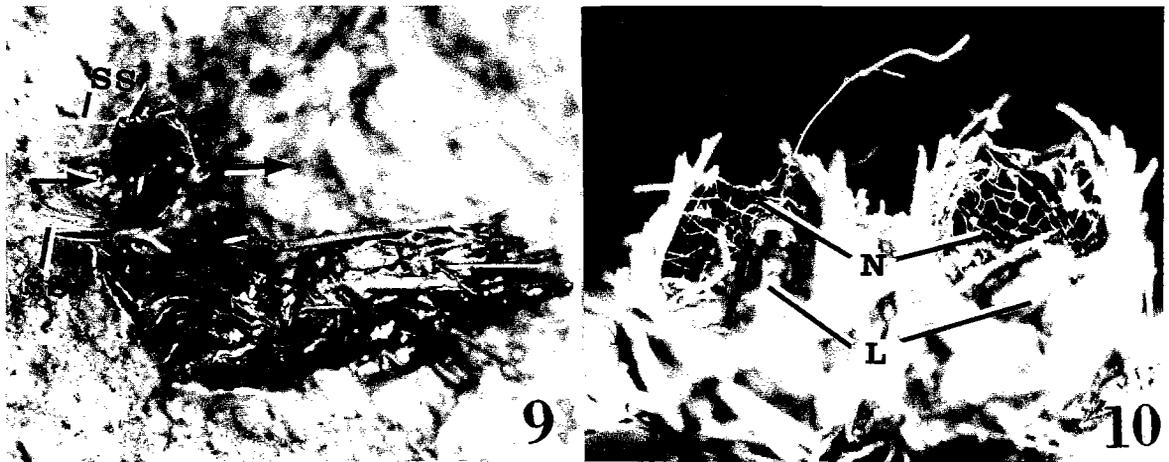
FIG. 9, 10.—*Arctopsyche irrorata*. 9, photograph of larval retreat, lateral view, of mature larva attached to the side of a large rock. Note heavy combined strands of silk (SS) anchoring anterior end of retreat to rock. Arrows indicate current direction; and 10, anterior view of two adjacent larval retreats. Note the larvae (L) in feeding position facing the capture net (N).

RESULTS AND DISCUSSION

Arctopsyche irrorata is a univoltine species in the southern Appalachians. Adults emerge in late April and May. The early instars begin to appear in the streams in July. By early October most of the larvae are in the final instar and in late October only mature larvae are found. The species overwinter as mature larvae. Although stream temperatures may drop to 1°C during the winter all larvae had food in their guts during this period, indicating that the larvae feed throughout the winter. Two mature larvae collected on 15 April, 1971, contained no food, since most larvae were pupating at this time and it is likely that these 2 larvae with empty guts were at the stage of larval-pupal apolysis. The first pupae of *A. irrorata* are generally found in early April. The larvae of *A. irrorata* may spin the pupal cocoon in the posterior part of the larval retreat. The old larval capture net at the anterior end of the retreat generally accumulates deposits of inorganic and organic particles during the pupal stage.

Larval retreats are constructed of several layers of such plant detritus as large leaf fragments bound together by silk. Rarely, retreats are constructed in aquatic moss. The retreats are generally somewhat cornucopia-shaped with the large opening facing into the current (Fig. 1, 2, 3, and 9) at a slight angle. Heavy strands of silk secure the anterior end of the retreat to the rock substrate in the swift current (Fig. 9). Maximum velocity recorded for streams inhabited by *A. irrorata* was 176 cm/s; however, the velocities adjacent to the larval retreats were in the range of 50–127 cm/s. That portion of the downstream side of the retreat's anterior opening is fashioned into a U-shaped net frame composed of plant detritus (Fig. 2 and 3, NF). Across this frame the larva spins its capture net. Since most of the posterior three quarters of the tubular retreat housing the larva is not in direct line with the current (Fig. 1 and 9), most of

the water that enters the anterior opening passes directly through the capture net rather than being funneled through the entire apparatus (Fig. 1 and 3). Larvae in the field were oriented in the retreats with the mouthparts and forelegs projecting toward the U-shaped net (Fig. 10). Thus, depending on how the frame faces the current (e.g., at the top or side of the retreat) the larvae may be ventral side up (Fig. 10) or on their side when feeding. The narrower, posterior end of the larval retreat is not closed, so some water flows through the retreat over the larval gills and flushes out waste. Frequently the nets of several larvae may be contiguous, each facing directly into the current (e.g., Fig. 10).

As larval growth proceeds, the nets of the preceding instar are covered with plant debris which is attached by numerous strands of silk, and the retreats are enlarged anteriorly and a new net frame and net is constructed. The retreats of the 2nd instars vary from 6.5–15 mm long with the diameter of the anterior opening ranging from 2.2–2.8 mm. Retreats of 5th instar specimens were 22–48 mm long with an anterior opening diameter of 8–11 mm. In mature, 5th instar, larval retreats it is difficult to distinguish the nets of earlier instars due to the debris and many irregular silk strands added to the retreat. The silk strands holding the posterior portion of mature larval retreats together are ca. 8.5μ in diam whereas those at the anterior end of the retreat are 28.8μ in diam. This is the same variation found in the diameter of silk strands in the nets spun by 2nd and mature 5th instars, respectively (Table 1), suggesting that the posterior part of the mature larva's retreat is simply the retained retreat of earlier instars.

Table 1 shows the change in mesh size of the nets of larval instars 2–5. Kaiser (1965), Schuhmacher (1970), and Williams and Hynes (1973) have also noted increasing mesh sizes with later instars in the Hydropsychinae. Kaiser (1965) suggested mesh di-

Table 1.—Feeding net mesh dimensions of *Arctopsyche irrorata* larvae in the Tallulah River, Towns Co., Georgia, on 9 Sept., 1973.

Larval* instar	Silk strand diam (μ)	$\bar{X}$-Length of mesh (μ)	$\bar{X}$-Width of mesh (μ)	Max size of mesh (μ^2)	Min size of mesh (μ^2)	Avg mesh opening size (μ^2)
2	8.5	135.3	87.2	19,425	9,278	11,798
3	9.9	238.4	122.6	35,668	25,410	29,250
4	17.7	378.5	180.5	127,971	43,440	69,683
5	28.8	534.3	403.7	283,000	115,187	216,010

* No first instar nets were recovered.

mensions are determined by the distances between the maxillary palps, silk gland opening and sub-mentum.

Mesh sizes of mature *Arctopsyche* larval capture nets are much larger than those recorded for other Hydropsychidae (Table 2). The large net mesh size of *Arctopsyche* is possibly an adaptation to the swift currents where the larval retreats are found. Faster currents are known to carry larger particles (Ruttner 1966) and a large mesh size may prevent clogging. However, the smaller retreats and nets of 2nd and 3rd instars (Table 1) function adjacent to those of 4th and 5th instars; thus, it is probable that the large mesh sizes reflect the feeding habits of *Arctopsyche* rather than being an adaptation exclusively to water velocity.

Table 3 summarizes the food of *A. irrorata* instars 2–5. Based on food particle sizes, the foreguts of 2nd instars contained slightly more plant than insect material; those of 3rd instars consisted of ca. 75% insect remains (Table 3). The last 2 instars had ca. 90% insect parts in their foreguts (Table 3). There is also an increase in particle size of the foregut contents during successive instars; however, in addition

to being an indication of the increase in size of the capture-net's mesh between instars (Table 1), this could also be correlated with the size of the *Arctopsyche* larvae and their ability to ingest larger particle sizes in later instars. Two points that should be emphasized regarding the larvae studied to obtain the data in Table 3 are: First, in the 4th and 5th instar guts there were many more small particles of insects than plant remains. These small particles, not listed in Table 3, consisted largely of insect fragments, like bits of legs. For example, in Table 4 all except the smallest particle sizes were measured in the guts of *Arctopsyche grandis* larvae, thus lowering the average particle size. However, most of these small particles were animal rather than plant material, which slightly increased the percentage of animal material in the gut. The 2nd point is that much of the 7–10% plant detritus remains in the guts of the last 2 instars of *A. irrorata* (Table 3) may be from the guts of herbivorous insect prey.

Foreguts of six 5th instar *A. irrorata* were examined at the Coweeta Hydrologic Laboratory, Macon County, N.C. on 19 Dec., 1972; on 18 April, 1973, eight foreguts were examined. The relative portions

Table 2.—Comparison of the individual net mesh dimensions of several mature Hydropsychidae larvae.

Species	Location	Reference	Dimension
Arctopsychinae			
Arctopsyche irrorata Banks	Eastern N. America	This study	403 ×534 μ
Arctopsyche grandis (Banks)	Western N. America	This study	429 ×587 μ
Parapsyche cardis Ross	Eastern N. America	Wallace unpubl.	272 ×341 μ
Diplectroninae			
Diplectrona felix McLach.	Europe	Sattler 1963a	130 ×190 μ
Diplectrona modesta Banks	Eastern N. America	Wallace unpubl.	188 ×243 μ
Diplectrona metaque Ross	Eastern N. America	Wallace unpubl.	145 ×181 μ
Hydropsychinae			
Hydropsyche angustipennis Curtis	Europe	Kaiser 1965	112 ×205 μ
Hydropsyche incommoda Ross	Eastern N. America	Wallace unpubl.	150 ×260 μ
Hydropsyche orris Ross	Eastern N. America	Wallace unpubl.	63 ×137 μ
Hydropsyche pellucidula Curtis	Europe	Kaiser 1965	241 ×368 μ
Hydropsyche sparna Ross	Eastern N. America	Williams and Hynes 1973	190 ×300 μ
Cheumatopsyche (prob. *analis* Banks)	Eastern N. America	Wallace unpubl.	77 ×111 μ
Macronematinae			
Macronema ulmeri Banks	S. America	Sattler (1963b, 1968)	4 × 32 μ
Macronema carolina Banks	Eastern N. America	Wallace and Sherberger In press a	5 × 40 μ
Macronema zebratum Hagen	Eastern N. America	Wallace unpubl.	5 × 40 μ
Macronema transversum Banks	Eastern N. America	Wallace and Sherberger In press b	3.3× 28.6 μ

Table 3.—Larger food particles in the foreguts of *Arctopsyche irrorata* in the Tallulah River, Towns Co., Ga., on 9 Sept., 1973.

Instar	Material	No. particles measured*	Avg particle size (μ^2)	Individual size range** of particles measured (μ^2)	Animal parts*** Plant parts
2	animal	28	17,678	5,407– 50,228	46.8%
	plant	38	14,789	4,755– 38,371	53.2%
3	animal	38	38,290	15,504–124,820	72.8%
	plant	29	18,759	10,945– 36,482	27.2%
4	animal	19	117,421	58,360–200,977	93.3%
	plant	6	26,833	19,652– 33,768	6.7%
5	animal	40	154,275	68,339–447,231	92.1%
	plant	15	35,200	17,133– 73,811	7.9%

* 5 larval guts were examined for all instars except for the fourth instar where only 2 larvae were collected on the above date.
** Includes only measurements of the larger particle sizes of each, plant and animal material; the range is based on the avg size of the largest and 3 smallest pieces measured except for the 4th instar where actual size of the smallest and largest particles are given.
*** Percent animal remains vs. plant based only on unidimensional size of particles and not on a weight basis.

of animal (89.3% and 90.8%, respectively) and plant (10.7% and 9.2%, respectively) material on each of the above 2 dates were similar to those of 5th instars from Georgia on 9 Sept., 1973 (Table 3). However, the average particle size of animal and plant material in the foreguts tends to increase from September to spring. The average animal particle size was 154,275 μ^2 in September vs. 414.321 μ^2 in spring; for plants 35,200 μ^2 in September vs. 80,953 μ^2 in spring. There was little seasonal variation in food of last instars, other than size of particles consumed. The size of the feeding net meshes during the winter and spring was the same as that given for 5th instars in Table 1.

The insect food items in the foreguts of *A. irrorata* consisted largely of fragments of Ephemeroptera and Plecoptera nymphs, Trichoptera larvae (including Hydropsychidae), Coleoptera (Elmidae larval and adult fragments), and Diptera (predominantly Chironomidae larvae with a few adult fragments). Several Chironomidae larvae are invariably associated with each detritus-laden larval retreat of *A. irrorata*. These dipterans live within the plant debris of the larval retreats.

A number of *Arctopsyche grandis* larvae and their nets and retreats from western North America were also examined. In collections from near Aspen, Col., on 18 Aug., 1973, and near Raymond, Col., on 22 Aug., 1973, 3rd, 4th, and 5th instars of *A. grandis* were found only on the tops and sides of large rocks in swiftly flowing mountain streams 3–9 m in width.

Retreat designs of these *A. grandis* larvae were identical to those of *A. irrorata* from eastern North America. Gut analysis of four 5th instar *A. grandis* from Raymond, Col., showed ca. 94% insect remains (Table 4). These remains consisted chiefly of immature Ephemeroptera, Plecoptera, Trichoptera and Diptera (Chironomidae). The average net mesh size of these mature larvae was 429×587μ (Table 2). A number of 4th instar *A. grandis* were found in a small spring seep ca. 1 m in width (8700 ft elev.) near Cuchara, Col., on 15 Aug., 1973. The Cuchara specimens constructed their nets and retreats on and between the underside of stones in a current of 20–30 cm/s. These 4th instars had net meshes of ca. 270×350μ and their foreguts contained ca. 70% animal material (Collembola, immature Ephemeroptera and Chironomidae) and ca. 30% plant detritus. S. D. Smith (personal communication) has also encountered some *A. grandis* in this type of habitat in Idaho. There is presently no explanation for this wide ecological tolerance shown by *A. grandis* larvae, but larvae fitting the present diagnosis of this species have considerable variations in head color patterns (Smith 1968). Mecom (1972) found *A. grandis* to be highly carnivorous during the early summer months and predominantly a detritus and diatom feeder during other seasons. However, he does not state how his food percentages were derived, whether by numerical or a size basis, or the larval instar of his specimens.

Table 4.—Food particle size in the foreguts of 5th-instar *Arctopsyche grandis* larvae near Raymond, Col., on 23 Aug., 1973.

Material	No. particles measured*	Avg particle size (μ^2)	Individual size range of particles measured (μ^2)**	Animal parts Plant parts***
animal	188	115,276	2,512–1,174,615	93.64%
plant	68	21,645	1,696– 92,358	6.36%

* 4 larval foreguts were examined.
** Includes measurements of the larger particle size (unidimensional) of each, plant and animal; the range is based on the average size of the 3 largest and 3 smallest pieces measured.
*** Percent plant vs. animal based only on unidimensional size of particles and not on a weight basis.

Arctopsyche larvae have 2 anatomical features that suggest they are primarily predaceous. The foreleg of 5th instars has stout spines on the anterior (inside) margin which are apparently an adaptation for seizing prey (Fig. 5). On the forelegs of the 2nd instars, which are ca. 50% detritivores (Table 3), the stout setae are only partially developed (Fig. 6). In the Hydropsychinae and Diplectroninae (*Hydropsyche* spp., *Cheumatopsyche* spp., *Potamyia* sp. and *Diplectrona* spp.) which I have examined, the larvae have either very few stout spines or they are absent completely and represented by smaller setae. In *Macronema* (Macronematinae) the forelegs have dense brushes of long setae (rather than spines) which are used for capturing microseston from their very fine mesh net (Sattler 1963b, 1968, Wallace and Sherberger in press a, b). The 2nd distinctive feature of *Arctopsyche* larvae that suggests their predaceous habits is the mandibular structure (Fig. 4). The mandibles are long and somewhat sickle-shaped with all teeth located apically. With the exception of *Parapsyche* spp. (Arctopsychinae), no other known North American hydropsychid larvae have this mandibular structure (cf. Fig. 282–290, Ross 1944).

Despite these differences, there is extensive evidence to indicate that arctopsychines do not warrant family status. Flint (1961) has reported that the only distinctive morphological structure of larval Arctopsychinae is the large gula which divides the genae over their entire length. This is perhaps reflected in the large net mesh sizes found in Arctopsychinae larvae (Table 2), since the length of the meshes in hydropsychid larvae is governed by the distance between the maxillary palps (Kaiser 1965). The manner in which the nets are spun, a figure-8 pattern, is identical to that found in the genus *Hydropsyche* (Sattler 1958). There is much more similarity between the nets of *Arctopsyche* spp. and *Hydropsyche* spp. than exist between the nets of *Hydropsyche* spp. and *Macronema* spp. (see Sattler 1958, 1968, and Wallace and Sherberger in press a, b). The overall design of the larval abode and feeding net of *Arctopsyche* is very similar to that found in *Hydropsyche* (Sattler 1963b) and *Diplectrona* (Sattler 1963a), with slight differences in the net arrangement (cf. Fig. 7 and 8). In many *Hydropsyche* and *Diplectrona* (Fig. 8) the capture net is spun across an enlarged anterior opening with the larval retreat, often constructed diagonally to the current, opening in front of the net (Fig. 8). In *Arctopsyche* the net is invariably an integral part of the anterior end of the larval retreat, with the dwelling's characteristic U-shaped bend (Fig. 1, 2, 3, 7, and 9) allowing most of the water entering the larval abode to be filtered through the capture net rather than being diverted through the larval retreat. The basic net and retreat designs shown in Fig. 7 and 8 emphasize the close relationships of *Arctopsyche* with the nets of other hydropsychid genera, i.e., *Diplectrona* and *Hydropsyche*.

In essence, in the evolution of hydropsychid larvae we see rather simple curved tube dwellings with very

large meshed capture nets (Table 2) in the primitive, largely predaceous *Arctopsyche*. Conversely, in the specialized genus *Macronema* there are complicated dwelling and feeding structures (Sattler 1963b, Wallace and Sherberger in press a, b) and their larvae have evolved very minute meshed capture nets (Table 2) for microseston feeding. Coincident morphological changes, especially for those structures used in feeding, have occurred in the larvae, enabling hydropsychids to adapt diverse feeding habits in habitats ranging from swift mountain streams to large lowland rivers.

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