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ABSTRACT

The relationships between *Gordius villoti* Rosa and *Allogamus auricollis* Pictet larvae are described. The horsehair worms and host life cycles have been investigated in laboratory and field conditions and aspects of their morphology and behaviour are discussed.

KEY WORDS: Nematomorpha; Trichoptera; *Allogamus*, Host-parasite interaction

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INTRODUCTION

Arthropods are well known as hosts of gordiids. Starting from the first observations of Aldrovandus (1623) several Myriapoda, Crustacea and Chelicerata have been reported as occasional hosts for these parasites, but nearly all insect orders are preferably associated with larvae or developmental stages of these worms (for a review, see Cappucci, 1976). The parasites are normally found inside the body cavity of arthropods (Bareth, 1974, 1975; Corallini Sorcetti & Moretti, 1987) but they have occasionally been reported also from the gut (Camerano, 1897) and gonads (Camerano, 1892) of other hosts.

Natural infection was believed to occur through the body wall of the host (Camerano, 1887, 1888, 1892, 1897; Villot, 1887, 1889, 1891; Dorier, 1965), but it has been demonstrated experimentally to occur only through feeding activity (Montgomery, 1904; May, 1919; Dorier, 1925; Cappucci, 1976). Apart from the classical descriptions (Rauther, 1905; Vejdovsky, 1886, 1894; Dorier, 1965; Jagersten, 1972), there are more recent data on the morphology and function of adult free-living animals (Swanson, 1970; Eakin & Brandenburger, 1974; Lanzavecchia *et al.*, 1977, 1979; Lora Lamia & Cotelli, 1977; Seymour, 1983) and on larval stages (Schepotieff, 1908; Hyman, 1951; Zapotosky, 1974). On the contrary, few studies have been conducted on the metamorphosis and the juvenile stages of the horsehair worms (Montgomery, 1904; Bareth, 1975; Andreeva, 1978). We report here both a massive presence of stages of development of *Gordius villoti* in the hemocelic cavity of *Allogamus auricollis* (Thricoptera, Limnephilidae) larvae and the possibility of using the breedings of both hosts and parasites to study the changes in the worm during its parasitic life and the relationship with the host's tissues.

MATERIALS AND METHODS

Swimming horsehair worms were collected close to the surface near the banks, whereas slower specimens were collected both among caddis fly cases and among roots, vegetable deposits and materials of industrial origin, such as tires, nylon fences etc. Caddis flies were mainly found underneath large stones and other underwater substrata, on the downstream side.

Allogamus auricollis larvae were kept in separate tanks at 17 °C and fed with *Tubifex* sp. and lettuce leaves. Adult gordian worms were kept in separate tanks in the same conditions, and mating, egg deposition and development were observed.

For transmission electron microscopy, specimens were fixed in glutaraldehyde 4% in cacodylate buffer 0.1 M, post-fixed in osmium tetroxide and embedded in epon-araldite resin. Thin sections were observed with a Jeol 100B electron microscope. Specimens for scanning electron microscopy were prepared according Ohtzuka *et. al.* (1981) and observed with a Cambridge Stereoscan 250 Mk2.

OBSERVATIONS

Collecting sites

During research on the quality of freshwater in the Bergamo province (Magnetti, unpublished data), from

September 1985 observations were made of the macrobentic fauna of the River Serio within a 30 km tract, in which the river is still torrent-like and the quality of the water is good (EBI 9) according to the Extended Biotic Index method (Woodiwiss, 1980). The collecting stations and the macrobentic populations are summarized in Figure 1 and Table I (see Ghetti, 1979).

Sample collection

In all collecting stations, numerous horsehair worms were found particularly among *Allogamus auricollis*. No morphometric analysis was carried out on caddis fly larvae and thus they cannot be assigned to any specific stage of development.

In winter 1985-86, in exactly the same collecting conditions, neither adult horsehair worms nor caddis fly larvae were found. The latter reappeared in April 1986 and were sampled until the second half of September when they started the pupal stage. Free-living gordiids were sampled again from August to late September. The size and colour of the collected specimens were uneven and the male/female ratio was nearly one to four.

In 1987 observations had to be stopped because of floods which altered the river flow rate dramatically and prevented regular sampling in the stations.

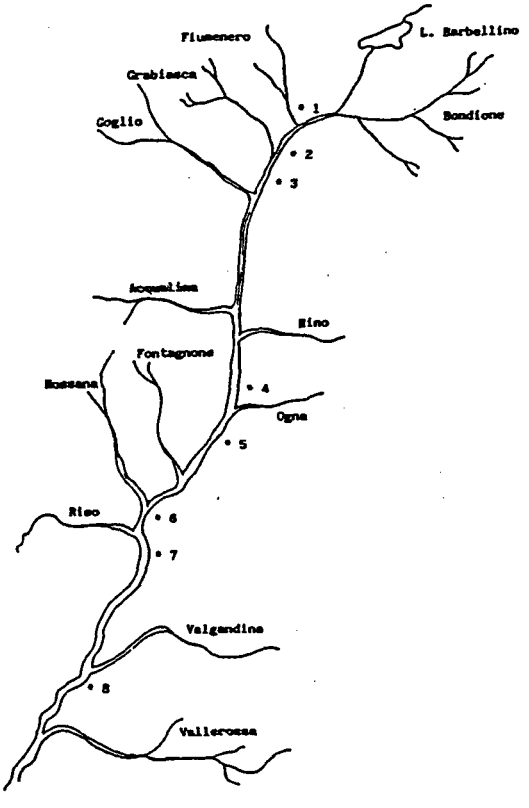


Fig. 1 - Schematic represention of the tract of the Serio River; the collecting stations are indicated (1-8).

Species determination

The identification of caddis fly larvae as *Allogamus auricollis* Pictet 1834 was kindly done by Prof. G.P. Moretti. Horsehair worms were identified using both free-living specimens from the collecting sites and specimens collected in tanks immediately after the outburst from cultured caddis flies. All observed specimens had a smooth cuticle with flat areoles and the males had a caudal end divided into two roundish lobes and provided by a post cloacal crescent. They can thus be assigned to the *Gordius* Linnaeus genus. The specimens had a black or dark brown cephalic collar, two dark longitudinal bands along the length of the body on opposite lateral sides and pale oval spots arranged with the major axis perpendicular to the worm body length, and were thus identified as *Gordius villoti* Rosa 1882.

Infestation

A sub-sample accounting for 30% of caddis fly larvae collected monthly was dissected to detect the parasite. The remainder were kept in tanks so as to allow possible parasites to develop further. Each time they were sampled, caddis flies showed a consistent percentage of horsehair worm infestation in all observed stations. Table II shows the data collected in 1986.

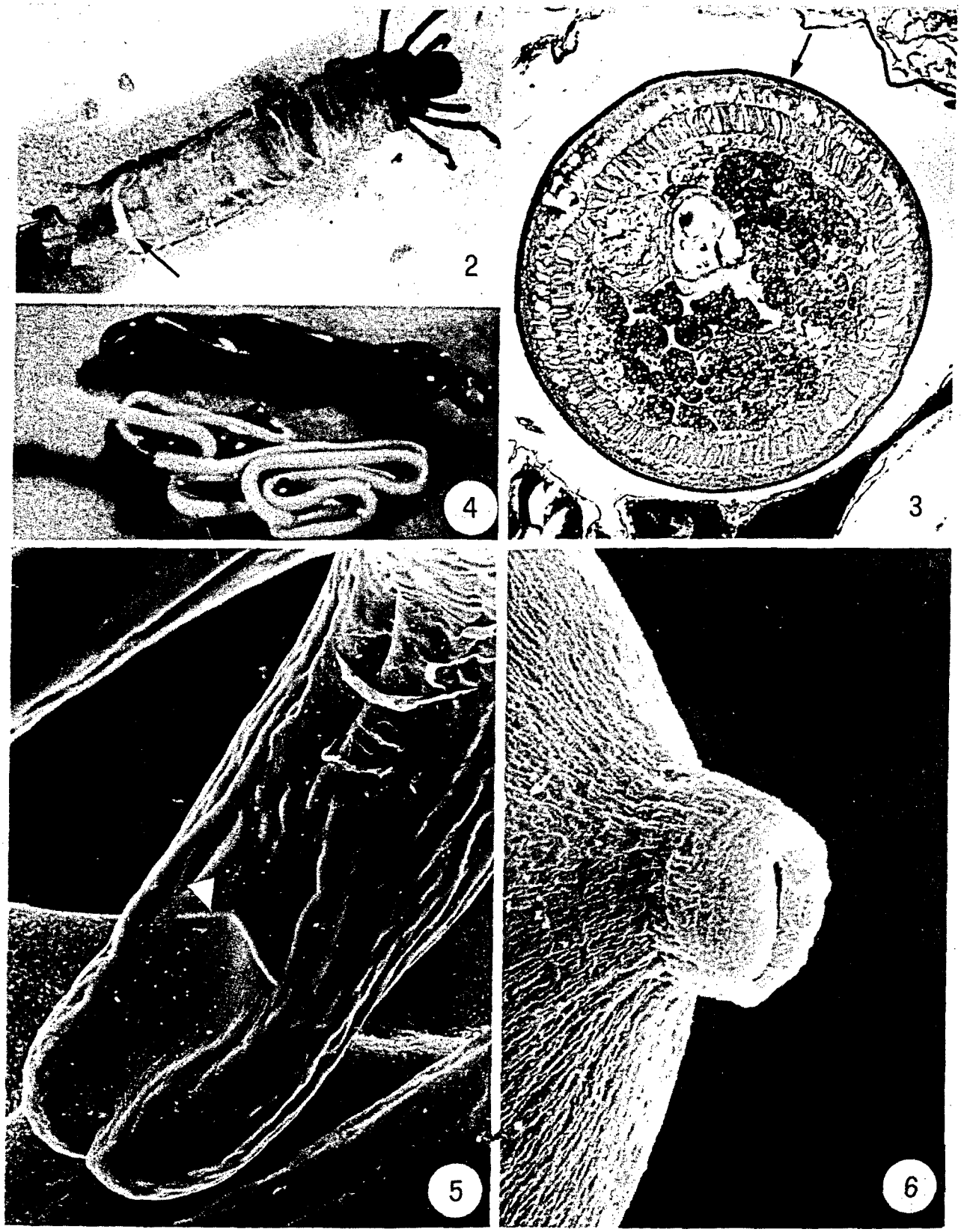
It was usually necessary to dissect the larvae in order to detect small-size horsehair worms. In summer the number of caddis fly larvae showing the parasite in transparence through the abdominal integument increased (Fig. 2).

Usually, there was only one horsehair worm per caddis fly, but superinfestation was not rare (Table II) and up to a maximum of seven worms were found per host. After the second half of September, 80% of the collected caddis flies were in the pupal case and had no parasites. As a consequence, the remaining larvae (20%) showed an apparent increase in the infestation percentage (up to 60%). Obviously, only healthy caddis fly larvae reached the pupal and adult state and thus, during this period, there is an enrichment of the parasitized specimens in the population.

Parasite morphology and behaviour

The horsehair worms extracted from the host were highly variable in size (1 mm to > 10 cm) and colour (from white to black). We were no able to detect earlier development stages of the parasite.

The size of the parasite increased during summer and reached that of free adult worms in August-September. The majority of the observed specimens started swimming immediately after being extracted from the host and only the smallest specimens were motionless. Whatever the size, the parasite was always free in the host's body cavity and never appeared to be in contact with host's tissues. This was evident from



Figs. 2-6 – 2. The presence of the parasite (arrow) is seldom directly visible in a case-free caddis fly. 3. Cross section of parasite inside host. The stocking is PAS positive (arrow) and the germ cells fill up the body cavity of the parasite. × 200. 4. Two horsehair worms extracted from one host. 5. Scanning electron micrograph of the stocking covering the caudal lobes and the post-cloacal crescent (arrowhead) of a young male. × 190. 6. At scanning electron microscopy it is clearly visible that the stocking forms a hollow peduncle at the front. × 1500.

TABLE I - *Number of specimens belonging to eleven different taxa found in the macrobentic population of the eight stations studied during the September 1985 samplings.*

		1	2	3	4	5	6	7	8
PLECOPTERA	Perla	2	18	6					
	Nemoura	4							
	Protonemura	30	34	9	3	78	102	64	32
	Leuctra	2	22	150	37	63	78	11	12
TRICHOPTERA	Rhyacophillidae	6	7			3	13	12	10
	Limnephilidae	175	62	214	49	138	241	140	271
EPHEMEROPTERA	Rhithrogena	5	32	62		21	10	3	
	Ecdyonurus	4	6	13	2	16	35		34
	Baetis	11	280	600	5	400	200	33	300
DIPTERA	Limonlidae	5	6	12		9		9	2
	Chironomidae	2	5	10		5	200	43	150
	Crenobia	45							
	Gordius	50	8	20	30	30	30	20	150

TABLE II - *For each collecting station (1-8) number of sampled caddis flies (CF) and parasitized caddis flies (PCF), percentage of infestation (%), number of horsehair worms at parasitic (P) and parasite host ratio (P/PCF) are indicated.*

	CF	PCF	%	P	P/PCF
1	100	9	9.0	9	1
2	58	5	8.6	5	1
3	200	36	18.0	45	1.25
4	55	3	5.4	3	1
5	120	7	5.8	9	1.28
6	200	40	20.0	40	1
7	300	16	5.3	26	1.63
8	304	62	20.3	62	1

the ease with which the worm could be extracted from the cavity and from histological sections (Fig. 3). The grown parasite is usually wound up on itself and around the host's silk glands, and it may be difficult to distinguish the glands from the parasite. In cases of superinfestation the development of different horsehair worms proceeds evenly, although considerable differences are sometimes observed in both size and cuticle pigmentation (Fig. 4).

In small specimens and, even more so, in growing worms a few centimetres long, a thin translucent coat can be observed at both ends. At the scanning electron microscope, this coat appears as a continuous «stocking» throughout the worm's length (Fig. 5). In histologic sections (Fig. 3) the stocking was PAS positive.

At the fore end, the stocking covers the worm's terminal part ending in a hollow peduncle (Fig. 6) containing the remnants of the larval cephalic armouring (Figs. 7, 8 and 9). Even the shortest specimens have a perfectly formed digestive tube, while the nervous and muscular systems are still differentiating (Figs. 10, 11). Sexual dimorphism is externally recognizable in specimens over 1 cm long: the males have two caudal lobes that are detectable under the stocking. The two sexes can be identified on the morphology of the gonads (Figs. 11, 12) in histologic sections of shorter specimens.

The sex ratio is one to one, considering all specimens extracted from hosts and during August/September it is frequent to see horsehair worms actively moving inside the host.

Host morphology and behaviour

Each caddis fly larva was checked before dissection for outer structural or behavioural signals of parasitical presence. Caddis flies hosting small size parasites are in no way distinguishable from healthy specimens. When the size or number of parasites is large, caddis flies are less active and mobile and are therefore easily distinguishable in the sample. When observed out of the case, they often display one or more pigmented areas arranged dorso-laterally on the abdominal segments. These areas were interpreted as the sites of parasitic

penetration through the surface (Meissner, 1856; Cappucci, 1976; Andreeva, 1978). However, this does not appear to be the case because we found numerous parasitized specimens lacking this pigmented area, and specimens showing a pigmented area but no parasites during dissection.

Parasitized specimens become increasingly less active during summer, both in tanks and in natural surroundings. Finally they abandon their protection and show in transparence the horsehair worm which has begun its endless sinusoid movement. The parasitized larva is then attacked by other caddis flies which tear its integument and free the horsehair worm starts which its free life condition.

Biological cycle of the parasite

The outburst of the adult horsehair worm from cultured caddis fly larvae takes place from end-August to end-September; this period coincides perfectly with the period when adult horsehair worms are found in the River Serio.

The free horsehair worm is ignored by caddis flies and starts swimming freely, coming into contact with other conspecific gordiids, with which it can form more or less voluminous knots.

The movement capacity of these worms, particularly soon after the outburst, is higher than usually believed and can continue for several days. This behaviour will be described in detail elsewhere (work in progress).

Mating takes place in the knots as previously described (Villot, 1881, 1887; Wesenberg-Lund, 1939; Dorier, 1965; Cappucci, 1976), but also between specimens not grouped into knots as can be easily observed in tanks.

Egg deposition begins about 15 days after the earliest emerging of horsehair worms from hosts. Isolated worms have been observed during the deposition of a string of eggs that is as long as the whole female body. Deposition lasts about 48 hours. Considering the average egg diameter (30 μm) and the volume taken up by the entire string, the number of eggs laid can be calculated as roundabout 4 million (Fig. 13).

After deposition, the gordian knots contain a large mass of eggs surrounded only by closely interlaced females. The males remain at the periphery of the knot, and can therefore be easily isolated, or they swim freely. This condition may account for the unusual sex ratio of the free living sampled gordiids.

Free horsehair worms collected at the beginning of October are practically without germinal elements (Fig. 16), whereas germinal elements fill the entire cavity in specimens inside the host (Fig. 3), or sampled in previous periods (Fig. 17). This observation confirms that mating takes place in the same period also in natural surroundings.

Within a fortnight, the eggs start to hatch and hatching continues for a few weeks. A change in colour from white to brown indicates that the eggs have reached maturity. The larva is already highly mobile inside the egg and it frees itself by piercing the envelope with its cephalic armouring (Figs. 14, 15 and 18).

DISCUSSION

A host-parasite association between caddis fly larvae and developing stages of various horsehair worms has already been reported for North American freshwaters (Cappucci, 1976) and more recently for Italy (Scarì *et al.*, 1986; Corallini Sorcetti & Moretti, 1987; Valvassori *et al.*, in press).

The massive presence of adult horsehair worms and their larval stages in *A. auricollis* reported here suggest that some factors may have altered a relationship, which is normally so infrequent as not to be detectable, despite the extensive analysis carried out on the River Serio (Marchetti, 1968) and other more recent routine samplings (A. Valle & P. Magnetti, unpublished data). An indirect confirmation of this may derive from parallel findings of such a relationship in the rivers Adda and Brembo (our unpublished data).

The uneven amount of specimens in different stations is partially attributable to the varying water flow rate. This could also be the cause of different infestation rates. The latter tend to be greater in downstream stations, where the current is definitely slower. In faster currents insufficiently swimming horsehair worm larvae can be easily carried to calmer water.

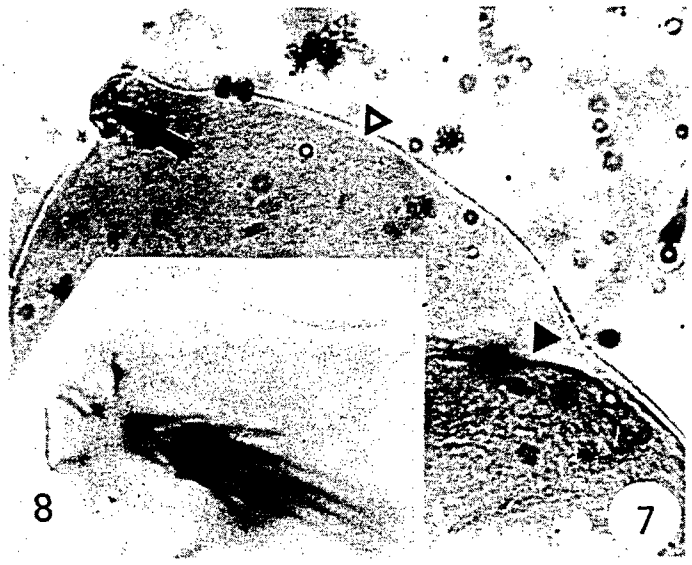
Whatever the penetration of the parasite into the host, the earliest stages of development observed are always in the hemocoelic cavity. The parasite does not appear to be connected with the host's tissues and are already covered in the stocking which shrouds them until development is complete, sometimes adhering to newly emerged specimens as torn shreds. Considering the position of the remnant of the cephalic armouring we can hypothesize that the stocking does not derive directly from the larval integument and may be formed either by the host or the parasite itself.

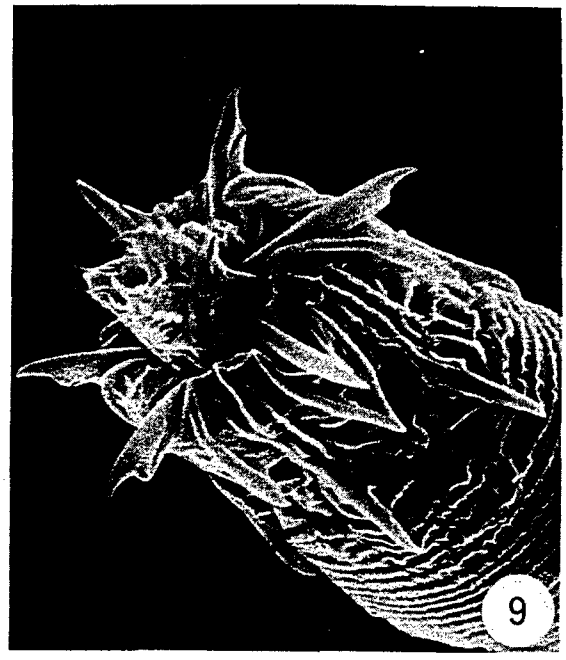
The presence of differently grown horsehair worms inside one caddis fly larva suggests that several parasites penetrate the same host in succession.

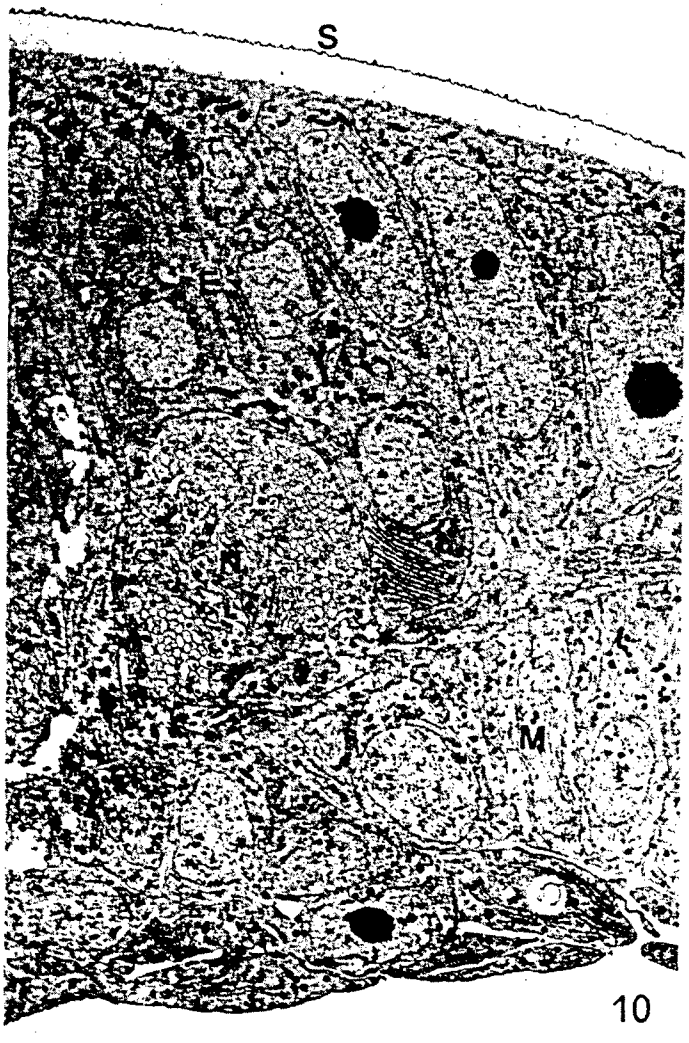
The reduced activity characterizing the parasitized larvae is clearly correlated to parasite burden. This kind of influence of the parasite on the host activity is a well studied phenomenon (Rau, 1983; Barnard, 1984) and is interpreted as the simplest way in which a host can be made more vulnerable to predators in order to permit the parasite to reach adult life condition.

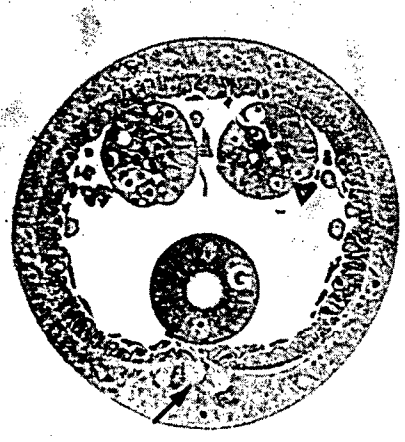
In order to clarify the various aspects of the host-parasite relationship which binds the two species, the significant larval development stages of Limnephilidae caddis fly must be considered in greater detail.

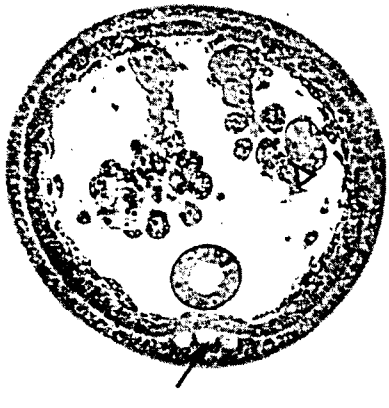
Hurjn & Wallace (1983) described the life cycle of the limnephilid *Goerita semata* in detail, stating that it takes place in about 22 months throughout 5 larval



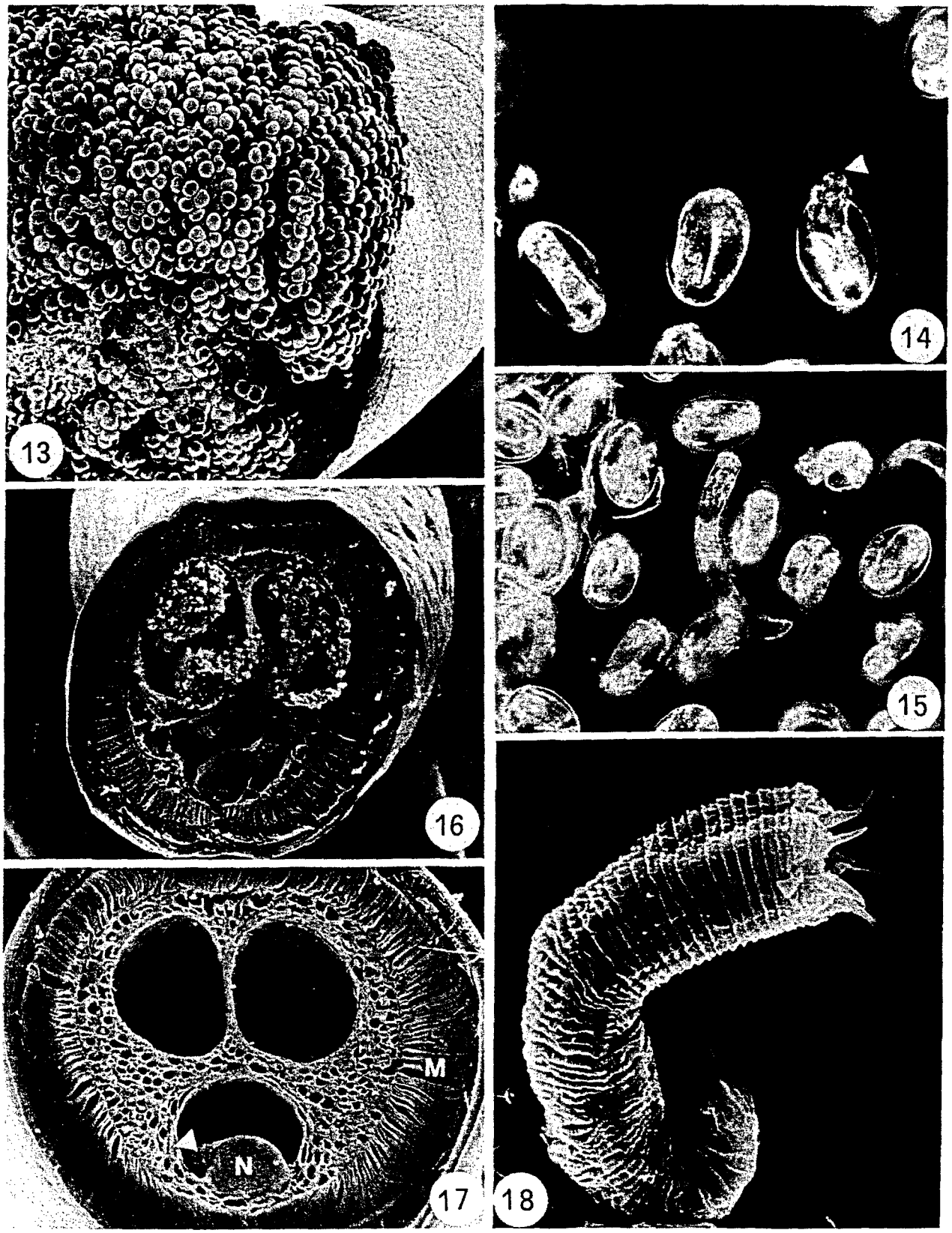








Figs. 7-12 – 7 and 8. Remnants of larval cephalic armouring are visible inside the peduncle of the stocking (Δ). Solid arrowhead indicates the fore end of the worm 7. × 380; 8. × 1100. 9. The structural details of larval armouring are clearly visible at scanning electron microscopy. × 2600. 10. Cross section of the parasite's body wall. Stocking (S), epithelium (E), developing nervous system (N) and muscular layer (M) are clearly distinguishable. × 4200. 11-12. Semithin cross sections of young male (11) and female (12) horsehair worms. At this stage of development, the nervous system is intraepithelial (arrows). Gut (G) and gonads (arrowheads) are clearly distinguishable. 11. × 250; 12. × 200.



Figs. 13-18 – 13. Scanning electron micrograph of eggs coming out of the sectioned female body during fixation. × 120. 14-15. Eggs and free larvae are clearly visible at dark field microscopy. The arrowhead indicates the cephalic crochets of a larva during hatching. 14. × 550; 15. × 300. 16-17. Scanning electron micrographs of cross sectioned gordiids. The difference in the presence of germ cells inside the body cavities is clearly visible. M = muscles; N = nervous system; Arrowhead = gut. × 200. 18. General aspect of the larva with retracted cephalic crochets armouring. × 2000.

stages. The first and the second instars are particularly short, thus the caddis fly development takes mainly place in stages III, IV and V. *Allogamus auricollis* is known to develop through 5 larval stages with a pupation case reaching 19 mm in length and 4.3 mm in width (Kiauta & Kiauta, 1979). These dimensions fit perfectly with those of our sample. This species is a typical autumn caddis fly and emergence takes place in August/December according to temperature (Kiauta & Kiauta, 1979; Moretti, 1983). The laid eggs develop in 10-30 days (Moretti, 1983).

Since no detailed observations exist about the *A. auricollis* species, Hurjn and Wallace's descriptions of *Goerita semata* can be used. The latter is present in two cohorts of specimens at different stages of development at all times of year.

Extrapolating these data for *A. auricollis*, the development cycle may be possibly summarized as in Table III.

Caddis fly larvae which were sampled from April to August 1985 should belong to two different cohorts and include III, IV and V larval stage individuals. The absence of larvae observed in the stations in winter months may be explained by the migrations which these animals may do in the coldest period.

In Table III are summarized field and laboratory observations; free-living horsehair worms appear between August and September, mate and lay egg strings which can be found after a fortnight approximately.

Hatching starts after two weeks of deposition of the egg string as observed in laboratory, and is protracted for several weeks.

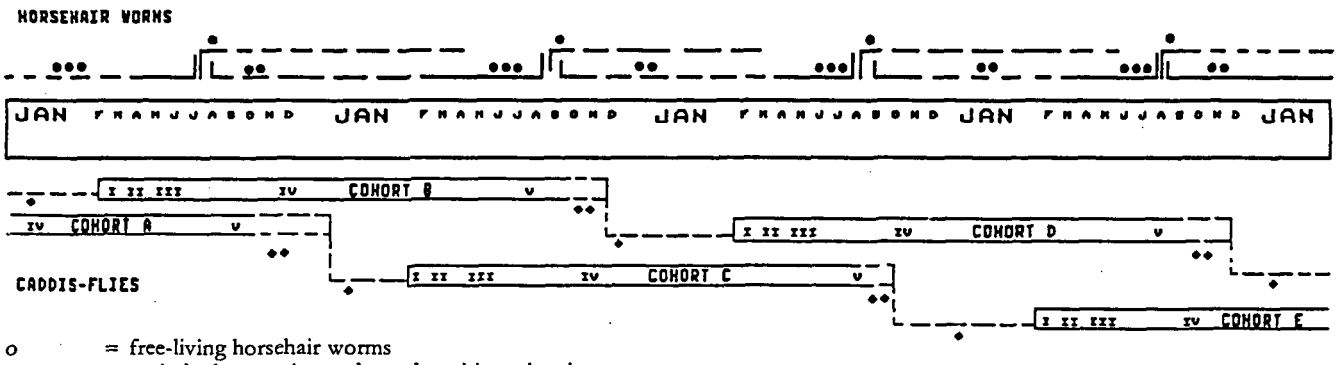
Survival of larvae has never been quantified with certainty and some authors (Dorier, 1925; Cappucci, 1976) hypothesize that larvae enkyst, and so can survive for a long time until penetration into a host.

These larvae could thus infest caddis flies belonging to the B cohort which are in an advanced development stage. They could also infest young larvae of the C cohort of the instars I and II, i.e. specimens hatched from eggs laid by the A cohort. Furthermore, caddis flies of the B cohort could already be infested since the autumn, which can explain why differently developed parasites are found in one host. Consequently, a horsehair worm larva penetrating a caddis fly of the B cohort must leave the host after about 10 months, as the latter has completed its larval condition. On the contrary, a horsehair worm which infests a specimen of the C cohort has the possibility of completing its development in about 22 months. Beside permanence inside the host, development can be influenced by the caddis fly's size, and by the feeding supply available.

The type of development, varying both in quality and in quantity, which young horsehair worms undergo can partially explain the great variety in sizes and colours characteristic of free specimens.

On the other hand, we have to consider that a 2-year life cycle has been reported only for *Allomia* spp. (Wiggins, 1977) and *Lepania cascada* (Wiggins, 1973, 1977) and a 2- to 3-year life cycle has been reported by Mutch & Pritchard (1984) for *Philocasca alba*. More generally a 2-year life cycle is considered unusual for members of the Limnephilidae family and for the Trichoptera in general (Wiggins, 1977). If we consider *Allogamus auricollis* as characterized by a 1-year life cycle, then the difficulty in collecting their larvae during winter months would be explained by a true absence and not by a migration along the stream during the coldest periods. On the other hand, the asynchronous development of different parasites inside the same host and the findings of free-living horsehair worms of different sizes and colours could be interpreted only assuming an enkystement of horsehair worm larvae that could thus penetrate a host in succession or in different periods of the year.

TABLE III - *Schematic representation of hypothetical life cycles of both* A. auricollis *and* Gordius. *The broken line indicates periods of undefined length.*



o = free-living horsehair worms
oo = period when mating and egg deposition take place
ooo = period when free or encysted larvae are present
◆ = period when caddis flies lay eggs
◆◆ = period when caddis flies in pupal stage are present

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