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Micrasema longulum (Trichoptera: Brachycentridae) builds a special pupation chamber

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Larvae of the caddisfly suborder Integripalpia normally pupate in the last instar larval tube-case. Measurements of case structures show that larvae of *Micrasema longulum* differ in adding a long parallel-sided anterior section to their tube-cases, shortly before pupation. They pupate in the newly built section, discarding the slightly conical larval case. Literature data suggest that two additional species of *Micrasema* exhibit similar behaviour. Production of a special section of tube-case for pupation is reminiscent of the situation in the primitive suborders Annulipalpia and Spicipalpia which build a pupal case which is often the only construction during the entire life cycle. It is uncertain if the behaviour of *Micrasema* is atavistic, or if it developed independently.

Micrasema longulum (Trichoptera : Brachycentridae) construit un fourreau nymphal spécial

Mots-clés : Trichoptère, construction de fourrreau, étui, étui nymphal, trait atavistique.

Les larves de Trichoptères du sous-ordre des Integripalpia normalement se nymphosent dans le fourreau larvaire. Des mesures montrent que les larves de *Micrasema longulum* ajoutent une longue partie à parois parallèles à leurs fourreaux, peu avant la nymphose. La nymphose prend place dans la partie nouvellement construite; le fourreau larvaire conique est détaché. Selon la littérature, deux autres espèces de *Micrasema* semblent se comporter d'une manière semblable. Cette construction d'une partie spéciale de fourreau pour la nymphose rappelle la situation dans les sous-ordres primitifs, Annulipalpia et Spicipalpia, qui construisent un cocon nymphal représentant souvent la seule construction de ces larves. Nous ne savons pas si le comportement des *Micrasema* est atavistique ou s'il s'est développé de façon indépendante.

1. Introduction

Since the early days of the study of Trichoptera, their case building behaviour has attracted much attention. There are nevertheless gaps in our knowledge, sometimes even for common well-studied species, like *Micrasema longulum* McLachlan. In the Breitenbach near Schlitz, the study stream of the Limnologische Fluss-Station, this species is the only representative of the family Brachycentridae; it occurs usually in low numbers but was regularly contained in approximately monthly benthos samples taken in 1986-88. Samples taken in the middle of April 1988 contained strikingly long examples of the smooth brown silken cases. Although cases were up to almost 15 mm long, they contained fifth instar larvae of normal dimensions; their head capsule width agreed with last instar specimens in normally sized cases. Later samples contained only normally sized cases, mostly pupae.

Tube-case building caddisfly larvae are known to extend their cases at the anterior end as they grow, and to cut posterior tube sections that become too narrow for the larval body. Although not increasing its size at pupation, shortly before the attachment of the tube and actual pupation the present animals had nevertheless prolonged their cases much more strikingly than at any other time. The new extended part of the case was distinctly less conical than the original larval tube; in fact, it seemed to be parallel-sided. Excess tube length was

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subsequently cut at the rear end, and attached pupal cases were distinctly shorter than the prepupal ones; pupal cases were hardly conical. The length of tube cut before pupation seemed to be greater than portions cut off the tube at larval moults.

Apparently, larvae of *Micrasema longulum* build a new anterior section of case in which they pupate, a special pupation chamber, instead of remaining and pupating within their normal larval case; in fact, much or almost all of the original larval case seemed to be discarded. Evidence in support of this interpretation is presented.

2. Material and methods

Preserved specimens of *M. longulum* collected from the Breitenbach, a small clear foothill stream near Schlitz, Hesse, Germany, at about 230 m a.s.l., in 1986-88 were measured. Additional last instar larvae were collected on 1 April 1997 from the upper rhithral section of the Fulda river near Gersfeld-Rendelmühle, Rhön Mts, Hesse, Germany, at 458 m a.s.l. These specimens were kept alive in small cages with gauze windows in a channel with recirculating stream water, at 10-12°C and approximately ambient daylength. Cages were provided with some pebbles, with bits of *Fontinalis* moss, and fragments of decomposing softwood leaves. As far as possible, prepupal specimens were kept singly until near adult emergence. Their pupal cases and the length of tube cut were measured; the sex of the developing adults was also determined.

One long prepupal case was split longitudinally into several strips with a razor blade and examined microscopically.

3. Results

Overall case structure and changes with instar observed in the present study agreed generally with descriptions in the literature, e.g., Décamps (1970), Bohle (1974), Chapin (1978), Sedlak (1980, from translation by Waringer) or Waringer & Graf (1997). There were no differences in size or shape between specimens from the two streams.

3. 1. Case material

24 larvae which, by their head width (Table 1), were 1st to 3rd instar larvae, had sand-covered posterior case sections; one of the two 4th instar larvae also had some sand, but on only 2 % of the case length. All other cases were made entirely of silk. Spinning was not observed; a finished case showed structures in agreement with the description by Bohle (1974). They were the same over the entire case length, case building mode does not seem to change during the last instar.

3.2. Shape of case openings

The front opening of all larval cases was circular. Occasional specimens that had been preserved at a moult had originally had the front end of their tubes attached to some *Fontinalis* leaves ; the front itself was closed by a dome-shaped lid of a lace-like structure on which individual silk strands were remarkably thicker than others, almost like little ribs. The posterior opening of 3rd instar cases was circular, smooth-edged, without projections, while 4th and 5th instar cases had rear openings in the form of a clover-leaf.

Table 1. *Micrasema longulum*, larval head width (HCW, in mm), case material and shape of the posterior case opening, partly after Bohle (1974).

Tableau 1. *Micrasema longulum*, largeur de tête larvaire (HCW, en mm), matériel d'étui et forme d'aperture postérieure d'étui, en partie après Bohle (1974).

Instar	HCW, mean ± s.d. [Range]	n	Case material	Posterior opening
L1	0.24 ± 0	4	Sand (mean 63%) & Silk	Irregular
L2	0.265 ± 0.005 [0.26-0.27]	6	Sand (mean 55%) & Silk	Circular
L3	0.35 ± 0.020 [0.30-0.38]	21	Sand (mean 28%) & Silk	Trilobed
L4	0.47 ± 0.03 [0.42-0.52]	32	Silk	Trilobed
L5	0.65 ± 0.05 [0.56-0.72]	58	Silk	Trilobed
Prepupa			Silk	Trilobed
Pupa			Silk	Multiporous

3.3. Case length and diameter

Case length varied continuously from 2.3 to 14.9 mm, groups or instars could not be distinguished. The longest cases observed were prepupal larval cases; the longest pupal case measured only 10.8 mm, most were much shorter (mean ± s.d. = 7.38 ± 1.28).

In contrast, specimens could be assigned to instar not only by their head width but also by the diameter of their case at the front and rear ends; differences in diameter between adjacent larval instars were significant to very highly significant (Tab. 2). The front diameters of last instar and pupal cases did not differ significantly, while their rear diameters differed very highly significantly. The front and rear diameters of pupae, although similar, differed also highly significantly (T-test, SPPS for WINDOWS).

3.4. Shape of tube case

Larval and pupal cases looked different, pupal cases appearing much less conical than larval cases. The data in Table 2 show that, across all larval instars and irrespective of case length, the larval front opening is 2.02 ±0.23 times wider than the rear opening (means ± s.d.); if only last instar larvae are considered, the relation is even slightly more uniform, the front opening being 2.06 ±0.18 larger. In contrast, the pupal anterior case opening is only 1.19±0.06 times wider than the rear opening. The angle at which the tube walls actually diverge therefore depends solely on tube length, which increases during larval growth. Consequently, Fig. 1 shows a distinctly negative relation between the angle and the larval case length; the angle drops from a maximum of 6° to 2°. Measurements of terminal diameters and length indicate divergence of pupal case walls at angles between 2.3° and 0.5°, a trend with tube length is possible but not pronounced.

3.5. Portion of case cut at pupation

Bohle (1974) observed that the first instar repeatedly cuts portions of the larval case but noticed a different behaviour when the first instar larva cuts the tube end before the moult. He emphasized that the same behaviour is repeated in subsequent instars, each of which cut their case only once, before a moult. His precise illustration of the lengths of tube cut before moults provides the basis for data on instars 1-3 in Table 3. The length cut by the fourth instar was recor-

Table 2. Case dimensions (mm ; mean ± s.d.) of different larval instars and of pupae of *Micrasema longulum*.

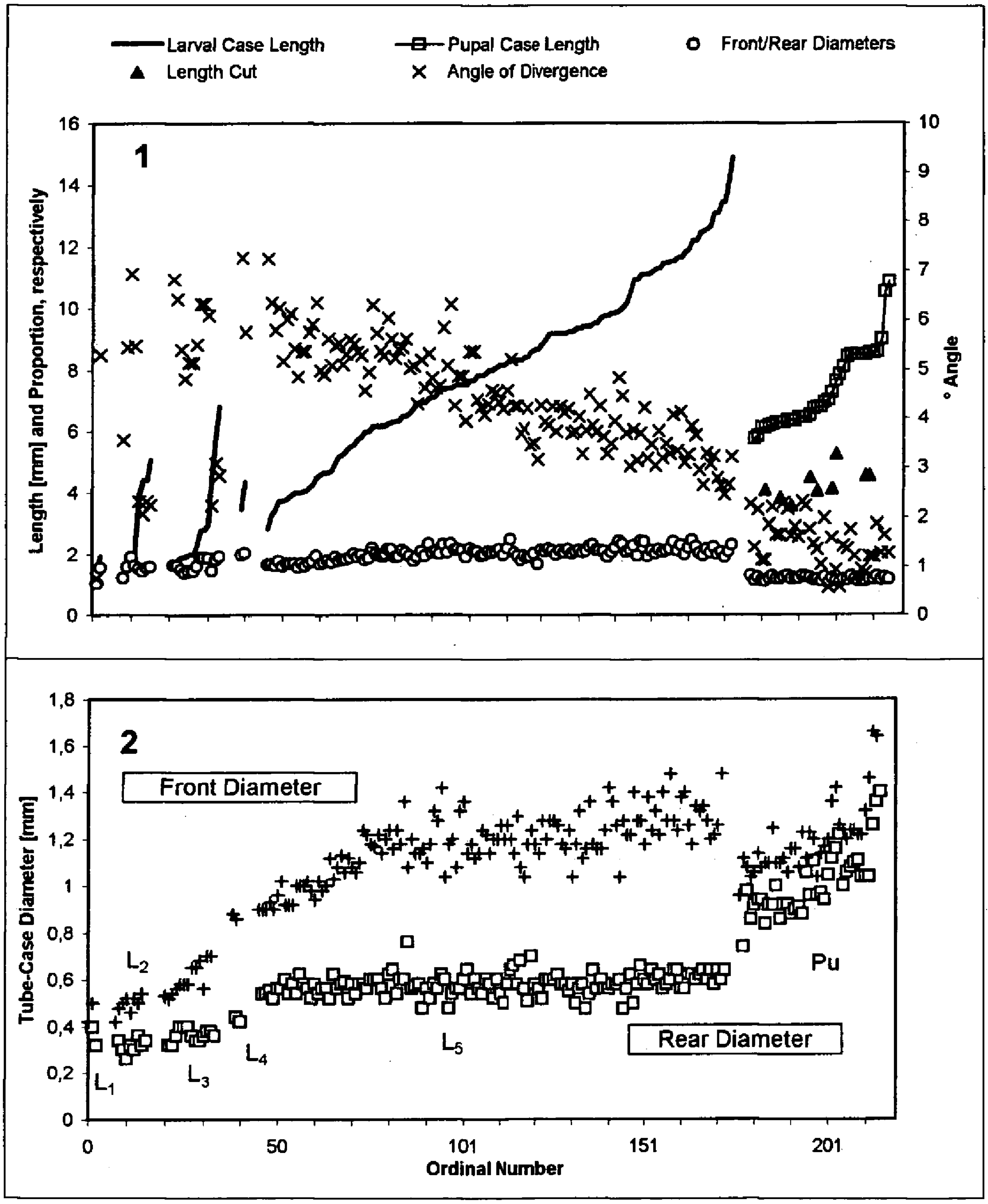
Tableau 2. Mesures d'étuis (mm ; moyen ± s.d.) des stades larvaires différents et des pupes de *Micrasema longulum*.

Instar/Stage	Rear diameter	Front diameter	Number examined
L_3	0.33 ± 0.02	0.49 ± 0.04	7
L_4	0.37 ± 0.01	0.64 ± 0.08	4
L_5	0.58 ± 0.04	1.20 ± 0.12	112
Pu	1.02 ± 0.02	1.21 ± 0.15	36

Table 3. Mean case length remaining and length cut at the end of larval instars of *Micrasema longulum* (data on instars 1-3 from Bohle 1974, his fig. 1). The length remaining in last instar larvae (L_5) is the length of the pupal case.

Tableau 3. Longueur moyenne d'étui qui reste et partie coupée à la fin des stades larvaires de *Micrasema longulum* (dates sur les stades 1-3 de Bohle 1974, sa fig. 1). La longueur qui reste au dernier stade correspond à la longueur d'étui nymphal.

Instar	Length remaining [mm]	Length cut [mm]	Percentage cut of original length
L_1	1.14	0.40	26
L_2	1.57	0.54	26
L_3	2.63	0.83	24
L_4	not recorded	not recorded	not recorded
L_5	7.38 ± 1.28	4.28 ± 0.49	37 ± 2.3



Figs. 1, 2. *Micrasema longulum*, dimensions of larval (instars L_1-L_5) and pupal (P) tube-cases, grouped by instar and sorted according to case length within each instar; abscissa of both figures identical.

Fig. 1 (top) : Tube-case lengths [mm], length of case cut before pupation [mm], angle at which case walls diverge (°), and relation between front and rear case diameters;

Fig. 2 (bottom) : Front and rear case diameters [mm].

Figs. 1, 2. *Micrasema longulum*, dimensions des étuis larvales (stades L_1-L_5) et nymphales (P), groupés par stade et arrangés suivant la longueur d'étui dans chaque stade ; l'abscisse est la même pour les deux figures.

Fig. 1 (en haut) : Longueurs d'étui [mm], partie d'étui coupée avant nymphose [mm], angle de divergence des parois d'étui (°) et proportion entre le diamètre antérieur et postérieur d'étui.

Fig. 2 (en bas) : Diamètres antérieurs et postérieurs d'étuis [mm].

ded neither by Bohle nor by me and remains unknown. The figure for the tube length cut by the 5th instar, before the pupal moult, was measured on 9 specimens from the Fulda river, kept in the laboratory.

3.6. Pupal cases

Pupal cases of *M. longulum* typically are erect little structures attached to stones or other supports by one or two strong, short bands of silk issuing from the edge of the narrow case end which is closed by a multiporous sieve membrane. Next to it, inside the case, lie the larval exuviae, then follows the posterior end of the pupa whose head rests under the erect slightly wider anterior end of the case which is covered by a slightly outward-bulging lid with a circular central pore.

3.7. Sexual differences

Female and male pupae are similar, but of different size. Although length ranges for males and females (6.3 - 8.4 and 8.5 - 10.8 mm, respectively) may seem to be separate from the very limited number (n = 14) of sexed pupae studied here, they probably overlap. The sexes do not differ in the size of front and rear case diameters, and consequently, the angle at which the tube walls diverge differs minimally between sexes, as a function of tube length.

3.8. Synopsis of changes of case size and shape

Figures 1 and 2 summarise the main facts :

1. Case length increases within each larval instar, and pupal cases are much shorter than the longest last instar cases;
2. Almost half of the original case length is cut at pupation;
3. The front diameter of case increases between instars and during each larval instar until a length of ca 8 mm is attained; then, increase levels off;
4. The rear diameter of the case increases between larval instars. It also varies within each instar; a vague correlation with case length seems to exist in early instars, but definitely not in the last instar;
5. In pupae, the rear and front diameters of the cases are less different than in larvae, and both increase with increasing case length;
6. The relation between front and rear diameters of a case is the same across all larval instars; in pupae the relation is different, but also constant.

4. Discussion

Larval silk production and case building are suggested homologous groundplan characters of the related orders, Lepidoptera and Trichoptera (e.g., Malicky 1973, Kristensen 1984, his synapomorphy XXI). At the same time, students agree that the various characteristic, sometimes elaborate, ways of retreat- and case-building among Trichoptera have developed independently in several different phyletic lines. Although the limits and interrelationships of these clades remain a matter of debate (e.g., Weaver & Morse 1986, Wiggins & Wichard 1989, Weaver 1992, Wiggins 1992, Morse 1997) there seems to be no doubt that the so-called tube-case-builders among the Trichoptera are a monophyletic unit, known as the Integripalpia (Frania & Wiggins 1997). The family Brachycentridae is an undoubted member of this taxon.

Genus *Micrasema* therefore exhibits Type 5 case building in the sense of Malicky (1973), with two basic elements: anterior extension of the tube (increasing both length and diameter) and cutting of the posterior end of the tubular larval case (Hanna 1960, Malicky 1973). Pupation occurs in the larval tube-case. Before pupation, the case may be modified in various ways, mainly relative to attachment structures and the construction of specific membranes sealing anterior and posterior ends of the tube. It is also often obvious that part of the larval case must be cut; for example, Klapálek (1893) measured the larval and pupal cases of a number of Trichoptera, most pupal cases being slightly shorter than the corresponding larval tube-cases. Hoffmann illustrated this nicely in *Lasiocephala basalis* (Kolenati) (1997, his figure 15).

For *Micrasema longulum,* Klapálek (1893) reported a very pronounced difference in length between the larval and pupal cases (up to 13 and 9 mm, respectively). He also noted that the pupal case is hardly curved and only little narrowed posteriorly and he further described the differences between the bulging anterior membrane with a few pores and the posterior membrane with the larger central opening. The anterior structure serves as an operculum that is easily detached and pushed open by the emerging pharate adult. How the changes in case structure occur was not explained; only for the exceptionally shaped case of *Molanna* were the parts of the case that are cut before pupation explicitly named.

Thienemann (1905) stated that very long larval tubes are generally cut at the rear end before pupation; otherwise the posterior pupal membrane is placed far inside the long larval tube. He observed that *M. longulum* first closes the anterior tube opening, then attaches the tube at the posterior end and finally closes it, before pupation. He also described the structure of the anterior and posterior membranes, mainly for *M. mini-*

mum, but did not mention if or how *Micrasema* cuts or otherwise changes the larval case. Subsequent descriptions of the tube-cases of *M. longulum* and its congeners (e.g., Hubault 1924, Décamps 1970, Lestage 1921, Tobias 1961) added information on the change of building material with larval instar, on the course of silk threads in the tube wall, on taxonomically useful structural details, etc.

Very substantial additions to case building and structure of Brachycentridae were only in the papers by Bohle (1972, 1974). For *M. longulum*, among many other details he (Bohle 1974) described the repeated cutting of the primordial cocoon and the single cutting of the rear part of the vertically attached cocoon at the end of each instar, in connection with larval moults. Bohle's attention focused on the early larval instars, excluding changes in the last larval instar and during pupation. His data on mean case length and the length cut at each moult (Table 3) suggest that a similar portion of the case length is cut each time during larval growth. However, a much greater portion is cut before pupation.

Lestage (1921) gave the largest posterior and anterior case diameters of *Micrasema* spp. as 0:5 - 0.9 and 1.00 - 1.08 mm, respectively, when 5 - 13 mm long; this agrees well with data in Table 2. The pupal case was said to be similar but smaller, because only the anterior tube section is retained. It is anteriorly closed by a membrane with normally many pores, but only 2 - 3 pores in *M. longulum*; in the present study, a single anterior opening was invariably observed.

The focus of the present study is on events in the last larval instars, limited material of earlier instars was only considered from comparison. Larvae in instar 2 and following are known to cut the case end only once, before moulting (Bohle 1974). Therefore, the increase of the posterior diameter of case with length of case occurring during larval instars 2 and 3 (Fig. 2) is probably illusion; actually, this is probably only an expression of size variation between specimens, not of a change within a given instar.

The fact that larval and pupal cases can be distinguished by their shapes leaves, by itself, no doubt that *Micrasema longulum* does not pupate in the larval case, but builds a special section of the tube-case that serves as pupation chamber. The pupal case is practically parallel-sided, despite the fact that measurements of terminal diameters and length suggest a minimal divergence of pupal case walls. The diameter at the very tube end is visibly a little smaller than the diameter immediately in front of it (see also Bohle, 1974), the divergence of case walls is merely appearance. Measurements a little in front of the tube may seem more appropriate but the exact point of measurement would be arbitrary. My interpretation that *M. longulum* builds a special pupal case, and discards most of the larval case, is in agreement with the sequence of events in the Breitenbach, where very long cases appeared only for a short period, immediately prior to pupation.

From the literature it appears that although the behaviour of *M. longulum* is certainly not standard, it is also not unique. Thienemann (1905) mentioned the posterior pupal membrane is placed far inside the long larval tube if the tube is not cut before pupation (p. 498); however, the only example I found mentioned in the text is of *M. minimum* where Thienemann says the anterior (!) membrane is placed far inside the tube. If it were actually the posterior membrane which is placed far forward in the larval case, the situation might resemble *M. longulum*, except that the empty part of tube is not cut.

Ito (1995) mentioned that during the last larval instar of *Micrasema gelidum* McLachlan the tube-case changes from curved to straight. Her illustrations clearly show that, like in the present species, the pupal case has almost parallel sides and corresponds to only about the anterior two thirds of the late last instar case. A multiporous membrane on the slightly narrower posterior case end replaces the quadrilobed larval case foramen.

There is a detailed account of case shape and case development of *M. quadriloba* Martynov in Japan (Isobe et al. 1994). The smooth, apparently entirely silken case of *M. quadriloba* shows angular bends, except in the smallest (first instar) larvae. As instars II-IV extend their cases, a second subterminal bend develops. The posterior disc of the larval case has a single simple central foramen. Long cases with two bends occur only during short periods of the life cycle, immediately before moults (Isobe et al. 1994, their fig. 5). Before moulting, the larva cuts the end of its case at the posterior bend and closes the anterior end with a convex, porous opercle; this appears to be similar to what was noticed at larval moults of *M. longulum* in the Breitenbach.

In the last instar, the anterior prolongation of the case of *M. quadriloba* involves no second bend, so that a straight case remains when the last instar larva cuts the larval case at the single bend. Evidently, this straight case is then considerably extended before pupation, because the pupal case is figured as being longer than the entire larval case before cutting, and about twice as long as the straight section of the larval case. The posterior membrane of the pupal case is a multiporous sieve plate, like in *M. longulum*; there is no (pictorial !) information on the anterior membrane closing the case. Despite the rather different aspect of the angularly bent larval case, the situation seems to be very similar to what is here described for *M. longulum*; *M. quadriloba* does also seem to pupate in a specifically built tube section. Similar behaviour may occur in other Trichoptera, but remains presently unreported.

The building of a special pupation chamber by *Micrasema* is reminiscent of the situation encountered in other, primitive Trichoptera groups. Most Spicipalpia and Annulipalpia seem to maintain an ancestral condition in that a real case is built only by the last instar, almost exclusively for pupation. Earlier larval instars may not build at all, or build retreats or capture nets of various kinds. There are two exceptions to this, both in the Spicipalpia which are believed to comprise the most primitive extant families of Trichoptera (Frania & Wiggins 1997).

The glossomatid saddle-case-makers (Spicipalpia) build a new case for each of the larval instars and for the pupa; Bohle & Fischer (1983) suggest homology of these cases with pupal cases in, e.g., Rhyacophilidae; case building in Glossosomatidae appears as a kind of premature building of the pupal case. A similar interpretation may even more appropriately describe the situation in Hydroptilidae. The family is presently included in Spicipalpia, but its real affinities remain doubtful (Frania & Wiggins 1997, Morse 1997). Hydroptilid larvae build only in the last instar, but long before pupation; actually, the fifth instar spends most of its life in variably shaped portable or attached purse cases that are sealed before pupation (Klapálek 1893, Thienemann 1905).

Building of larval tube-cases in the Integripalpia is recognized as distinct from the building activities of the other taxa, and regarded as a groundplan character of the group (Frania & Wiggins 1997, Morse 1997); building of special pupal cases or tube-case portions was not previously reported. Whether the behaviour of *Micrasema longulum* has arisen independently, or whether it is an atavistic trait reminiscent of Annulipalpia and Spicipalpia will have to be decided in comparative studies.

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