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Construction behavior for new pupal cases by case-making caddis larvae: Further comment. (Trichoptera: Integripalpia).

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Abstract. Evidence is discussed pertaining to a proposal by MALICKY that final-instar larvae in some species of the Limnephilidae construct a new and different case for pupation. Intraspecific variation among examples cited in support of this view raises the question whether the behavior described in the Limnephilidae is comparable with pupation behavior in *Yphria* (Phryganeidae) and *Phryganopsyche* (Phryganopsychidae), where intraspecific variation has not been observed, and where larvae do construct a new case of fundamentally different architecture for pupation – an unusual aspect of behavior in the Integripalpia. Comment is also made on the opinion offered by MALICKY that cases, nets, and other structures built by caddis larvae are not suitable evidence for behavior in Trichoptera.

A short article by MALICKY (Braueria 27; 2000) concerning larval and pupal cases of case-making Trichoptera prompts my return to some earlier observations and inferences. At issue is my view, stated most recently in 1998, that in a very few species of the Integripalpia, larvae construct an entirely new and architecturally different case for pupation at the end of the final larval instar. MALICKY cites several examples from the Limnephilidae in support of his view that this behavior is not at all unusual.

My observations concern two species: *Yphria californica* (Phryganeidae), and *Phryganopsyche latipennis* (Phryganopsychidae). The salient points are summarized here.

Yphria californica (BANKS) (WIGGINS 1962, 1998).

This is the sole extant species in the subfamily Yphriinae of the Phryganeidae. The larval case is slightly curved and composed of fragments of rocks and twigs (Figure 1, left). Rock fragments are concentrated in a V-shaped conformation on the ventral concave surface, and tapered posteroventrally from the anterior edge. The wall of the larval case is relatively thick and rigid, and is resistant to compression.

The pupal case (Figure 1, right) is a straight-sided cylinder constructed mainly of flakes of biotite (mica) and fragments of quartz, mixed with small bits of bark. Each end of the pupal case is enclosed by a loosely constructed bulbous covering of fine rock fragments held together with silk, with some meshed spaces between the fragments which would permit water to circulate through the pupal case. Beneath the bulbous enclosure, a stout meshwork of silk closes the anterior end of the case, but a similar meshwork is lacking from the posterior end. The wall of the pupal case is thin and flexible, offering little resistance to compression.

Pupal cases in *Yphria* are buried in sandy sediments of small mountain streams in California and Oregon, and in sorting through these sediments I found many empty larval cases as well as pupal cases. Whether the pupal case is constructed as an adjunct to the larval case and then cut free, or is constructed by the larva after it has vacated the larval case, I do not know. Protected from predators by burrowing in the sediment, it is certainly possible that larvae would free themselves of the larval case while constructing a new pupal case; indeed of all phryganeids that I have encountered, larvae of *Yphria* are the most inclined to vacate their cases on the slightest provocation. My collections revealed no examples of the two case types joined together, as would be expected from a gradual structural transition from one to the other.

My interpretation of these observations is that, leaving aside modifications of the pupal case for closure during metamorphosis, the larval and pupal cases are fundamentally different in architecture. They also differ markedly in selection of materials, and the transition is made at the close of the final larval instar.

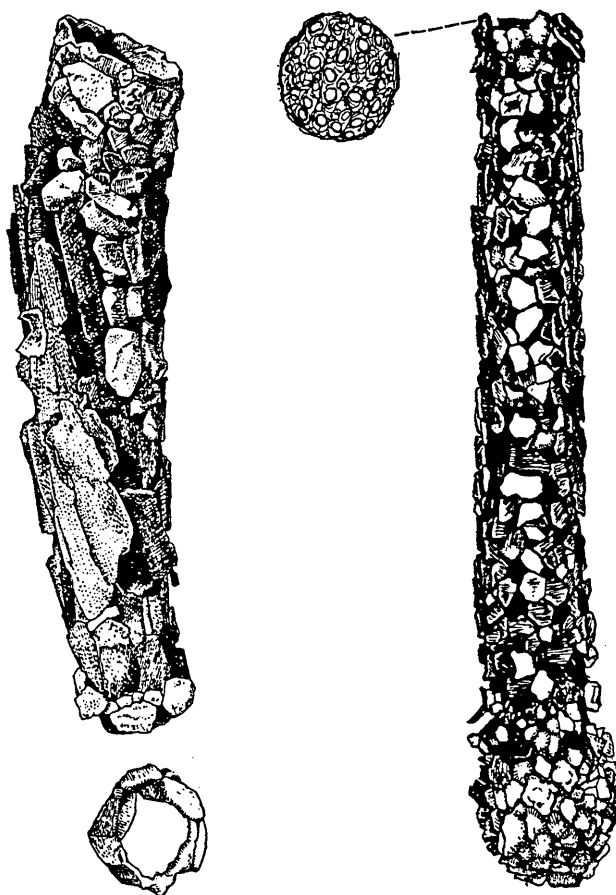


Fig. 1. Larval case (left) and pupal case (right) of *Yphria californica* (BANKS). (From WIGGINS 1998).

Phryganopsyche latipennis (BANKS) (WIGGINS 1959, 1984; WIGGINS and GALL 1993).

Phryganopsyche, the sole extant genus of the Phryganopsychidae, occurs in Japan and S.E. Asia. The larval case (Figure 2, left), unlike any others known in the Integripalpia, is a flexible crude tube of detrital materials placed irregularly, and 2-3 times longer than its larval architect. The larval cases have so little structural rigidity that they even bend under their own weight when picked up. Similar construction is known in no other caddisfly.

The pupal case (Figure 2 right) is about the same length as the fully grown larva, and is constructed of pieces of detrital materials arranged transversely. The pupal cases are rigid, evidently because the pieces are firmly fixed to each other with silk. The pupal case is distinguished from others in the Integripalpia because no apical perforations are evident, although water must penetrate into the pupal case; and the loose weave of the inner silken cocoon undoubtedly allows some water to circulate through the case to provide oxygen for the developing pupa.

A strong contrast in architecture between the larval and pupal cases in *Phryganopsyche* is clearly evident. I am advised by workers in Japan who have collected these larvae and pupae in numbers that the pupal case is constructed as an adjunct to the larval case at the close of the final larval instar, and then severed before being closed off.

Discussion. 1. Construction of an enclosure for the metamorphosing pupa is a point of some phyletic significance in the Trichoptera. Most larvae in the Annulipalpia abandon their larval retreat and construct an entirely new domed enclosure for metamorphosis. (Buried tubes of the Dipseudopsidae are a specialized exception.) In most case-making Integripalpia, larvae do not construct a new enclosure for metamorphosis but pupate within the same larval case. This is a significant behavioral distinction of the Integripalpia, and therefore

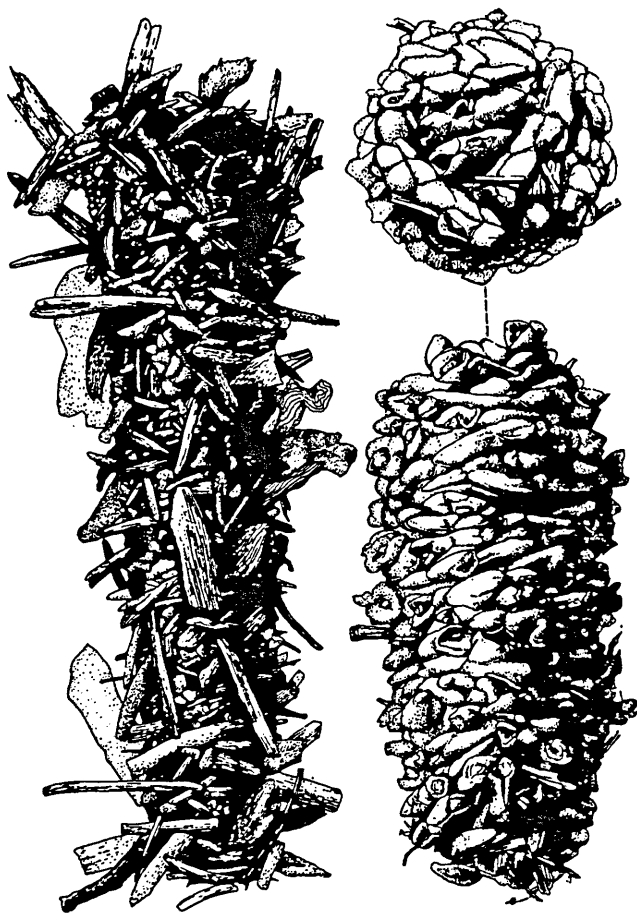


Fig. 2. Larval case (left) and pupal case (right) of *Phryganopsyche latipennis* (BANKS). (From WIGGINS and GALL 1993).

species departing from the normal behavior are noteworthy. The exceptions in *Yphria* and *Phryganopsyche* are especially interesting because *Yphria* is clearly the most primitive extant genus in the Phryganeidae, and because that family and the Phryganopsychidae are widely held to be among the most primitive case-making families (e.g. GALL 1997). I speculated (1998: 31) that these examples might represent retention in a few taxa of ancient relict behavior that has been lost among the Integripalpia generally, although not that this was necessarily evidence of monophyletic relationship. [The (mis) quotation to that effect in MALICKY'S article reads better in its original form: "This behavior in *Yphria* and *Phryganopsyche* could be interpreted as a relict condition from the common ancestry of the Annulipalpia and Integripalpia (see FRANIA and WIGGINS, 1997: figure 28)."]

There may well be other families in the Integripalpia in which larvae construct a new and architecturally different case for pupation. A fundamental issue, however, is the time of their derivation; obviously, the question of relict behavior assumes greater relevance for taxa of more ancient origin.

Examples illustrated by MALICKY (2000) of larval and pupal cases in the Limnephilidae show behavior common in that family: materials of the pupal case may be changed during the course of the final instar. However, in the examples given, intraspecific variation in the changes in timing and materials figures prominently. No variation of this sort is evident in *Yphria* or *Phryganopsyche*. If one adheres to MALICKY'S (2000) admonition that "...behavioral characters to be analyzed are the details of behavior such as *inherited motions and programmes* (italics mine) performed by the animals themselves", comparison between variable behavior in Limnephilidae and invariant behavior in other families is inappropriate. Moreover, changes in the architecture of the pupal case during the final instar in Limnephilidae

are marginal compared to changes in *Yphria* and *Phryganopsyche* (see Figures 1 and 2).

Homology for intraspecifically variable behavior in the behavior in some species of the Limnephilidae (MALICKY 2000) seems more likely to lie with the adaptive pattern exemplified in the North American limnephilid *Hesperophylax magnus* studied by MOLLES and NISLOW (1991). Their study demonstrated that, in streams with predatory fish, stoneflies, and dragonflies, final-instar larvae of *H. magnus* build cases of higher resistance to crushing and higher mineral content. In streams lacking these predators, final-instar *H. magnus* larvae build weaker cases of lower mineral content. Moreover, *H. magnus* larvae from populations building weaker cases under natural conditions build stronger cases under laboratory conditions in the presence of a predacious stonefly. Although preparation for pupation was evidently not considered in this study, only final-instar larvae were involved. The fundamental point of similarity, and possibly homology, among genera of the Limnephilidae, is that a change in the mineral content of the case is shown to be an adaptive intraspecific variable in construction behavior of the Limnephilidae.

Construction of a special pupation chamber in *Micrasema* of the case-making family Brachycentridae has been studied by ZWICK (1998). The evidence shows that a new pupal case is constructed at the close of the final larval instar, but there is no evidence of intraspecific variation and little change in materials. The architectural change is confined to replacement of a slightly curved larval case by a parallel-sided pupal case.

Whether pupation behavior in *Micrasema* is homologous with the Limnephilidae or with *Yphria*, or with neither one, is an open question. Case-making behavior in *Phryganopsyche* is so distinctive that it could be wholly independent in origin. But what is clear is that in both *Yphria* and *Phryganopsyche* pupation in a new case of fundamentally different architecture from the larval case is anomalous with the Integripalpia overall; and for both taxa there is independent evidence for a relatively ancient origin among case-making Trichoptera.

Is pupation behavior in *Yphria* and *Phryganopsyche* adaptive? There can be little doubt that this behavior was adaptive when initiated – and that at least for *Phryganopsyche*, it continues to be so. The central issue, however, is that because of the putative relict status of both genera, their unusual pupation behavior may be relict as well. The reasoning here reveals congruence of unusual pupation behavior in the Integripalpia, similar in principle to the Annulipalpia, with independent phylogenetic evidence that the Phryganeidae and Phryganopsychidae are relatively ancient families of the Integripalpia (e.g. FRANIA and WIGGINS, 1997). Congruence of independent lines of evidence, as here, is a powerful asset in phylogenetic reasoning.

In the Limnephilidae, I doubt that pupation behavior is comparable with the Phryganeidae and Phryganopsychidae because it seems more likely to be part of a continuum of case alterations in the final instar – which experimental evidence shows to be at least in part variable responses to ecological conditions.

2. In presenting his view that inherited motions and programs of the animals are the real behavioral characters to be analyzed, MALICKY offers further the opinion that cases, nets, and the like are not suitable evidence of behavior.

I suspect that a sizeable proportion of behaviorists would be surprised at this restrictive view of behavior. HANSELL, for example, has written an entire book (1984), *Animal Architecture and Building Behaviour*, in which he discusses an abundance of information (much of it from his own work on Trichoptera) derived from the structures built by insects as evidence bearing on the evolution of behavior. Another behaviorist, WENZEL, considers (1992)... "architectural constructs as a class of behavioral characters, or at least surrogates of behavioral characters, for which variation is measured more easily, and perhaps interpreted more easily, than most..."

Since Trichoptera are extraordinarily well endowed with behavioral information embedded in their architectural constructs, I believe that students of this order should take maximum advantage of their good fortune. However narrowly one chooses to define behavior, the cases, retreats, and other structures made by caddis larvae are unquestionably an aspect of their motions and programs.

I suggest a balanced approach. Acquisition of comparative behavioral data on motions and programs is certainly to be encouraged; information of this sort is uncommon for Trichoptera at the present time, and is not easily assembled. By contrast, the products of construction behavior are readily accessible in Trichoptera. If, in due course, the two data bases should prove to be in conflict, there will be another issue to resolve. But if the two data bases derived from behavior should prove to be concordant, we could rejoice in the discovery of another source of congruence – which is the real foundation of phylogenetic reconstruction and of classification.

Furthermore, the products of construction behavior by caddis larvae connect directly to an outstanding palaeontological record reaching back in time for some 175 million years (e.g. SUKATCHEVA 1991). These constructs show a high level of congruence with morphological characters in supporting two of the major evolutionary lineages of Trichoptera – Annulipalpia (s.s.) and Integripalpia (s.s.) (e.g. FRANIA and WIGGINS 1997). Indeed, it would be a prediction from this broad congruence of phylogenetic information that behavior assessed from motions and programs would reveal patterns congruent with the lineages of Integripalpia (s.s.) and Annulipalpia (s.s.). But if it turns out that the two aspects of behavior really do lead to different interpretations, the only way to connect behavior based on motions and programs with the palaeontological record is to try to understand its relationship in living animals with the products of larval construction behavior.

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Reply to WIGGINS by H.MALICKY:

1. WIGGINS has demonstrated in a convincing manner that the larvae of *Yphria californica* and *Phryganopsyche latipennis* construct an entirely new case before pupation, made in a different construction style and of different material, and he concludes that this behaviour is of phylogenetic significance because these two species are phylogenetically significant for other reasons. *Micropterna taurica* (and *Micrasema longulum*) does exactly the same, without intraspecific variation. WIGGINS says now that this may be only adaptive, because limnephilids are not phylogenetically significant for other reasons. If I have correctly understood, this may be an example for a circular conclusion.

2. The study by MOLLES & NISLOW on *Hesperophylax magnus* deals with the cases of the 5th instar larvae only, and has nothing to do with pupal case construction.

3. Concerning the possibility of comparing cases, nets and the like for phylogenetic analysis, they are certainly useful, but the analysis must be made with the behaviour of the animals and not with the results. Similarities in shape, shared by *Ichthyosaurus*, shark, trout and dolphin are analogous, not homologous. I may only repeat what I had said at an earlier occasion to the opinion expressed by WIGGINS (Proc.6th Int.Symp.Trich.:349): "A coffee cup made of clay may be produced by different methods: turning on a potter's wheel; forming a cylinder with subsequent hollowing out; cutting plates which are bent and stuck together; pouring liquid clay into a mould. The resulting form of the cup will be exactly the same, but the specimens are analogous, not homologous." Obviously the term homology is used in a different meaning by different workers.



Corrigenda to:

Bibliographia Trichopterorum Volume 1, 1996. Pensoft, Sofia/Moscow/St.Petersburg.

It is now about 5 years since publication of vol.1. Several errors in that volume have been brought to my notice, but none in the past 3 years. Hence I list these below, for the benefit of users of the B.T. They will also be listed in volume 2.

Entry 0009, on p. 1, is not Anonymous, but by A.ADLMANSEDER.

Entry 0666, p. 37, should read ‚Bulg., bulg., fr.‘, not ‚Russ., russ., fr.‘. My apologies to Krassimir Kumanski.

Entry 1283, p. 71. Wang,S. 1963. Volume number is ‚12(3):55-66‘, not ‚3:55-66‘.

P. 564, column 3, 2nd entry – ‚*flavopunctata*, *Dolophilodes*‘ is out of alphabetical order.

P. 568, column 3, between ‚*maurus*, *Thya*‘ and ‚*mazamae*, *Psychoglypha*‘ the alphabetization of entries is scrambled. Also, ‚*maxima*, *Aethaloptera*‘ is entered twice, in separate places.

P. 590. The expansion of Schweiz.Z.Hydrobiol. should read ‚Hydrobiologie‘, not ‚Hydrologie‘.

If other errors are spotted please let me know, for listing in volume 2. My thanks to Krassimir Kumanski, Joe Waringer, and others for spotting these errors.

Andrew P. Nimmo