

Evolution of feeding and case-making behavior in Trichoptera

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Abstract. A phylogeny of the families of Trichoptera is reviewed to provide a basis for understanding the probable evolution of feeding tactics and case or retreat constructions by larvae. At least 48 hierarchically inclusive homologues are known, mostly from larval, pupal, and adult morphology. Their resulting phylogeny indicates that Rhyacophilidae, Hydrobiosidae, Glossosomatidae, and Hydroptilidae are more closely related to Philopotamidae, Hydropsychidae, and their allies than to Limnephilidae, Leptoceridae, and their allies. This phylogeny implies that the ancestral caddisfly larva was probably a tube-dwelling detritivore, inhabiting humus and detrital mats near the shores of lentic or lotic-depositional habitats. This ancestor evolved into a tube-case-making detritivore and scraper in the ancestor of Integripalpia and into a retreat-making collector-gatherer in the ancestor of Annulipalpia. All other larval feeding and case-making tactics evolved from these ancestral habits.

Key words: *feeding behavior, case-making behavior, trichopteran evolution, trophic relationships, retreat-making behavior.*

A comparative (phylogenetic) understanding of the behavior of benthic animals often helps provide valuable predictions for yet-unobserved phenomena in particular species (e.g., Resh et al. 1976). For the purpose of reconstructing phylogenies, however, so little is known about behavioral characters in many groups that such features are usually not as useful as others such as morphological ones. (Some notable exceptions to this general tendency, however, are McKittrick's [1964] phylogeny of cockroaches based largely on reproductive behavior and Lloyd's [1966] phylogeny of fireflies based on flashing behavior.)

Thus, it is often only after phylogenies have been developed on the basis of clearly unique homologues (=synapomorphies, each at its appropriate hierarchical level; e.g., Ruppert 1982, Wiley 1981) in morphology that the evolution of feeding behavior and similarly puzzling characters can best be understood. A recent reinterpretation by Weaver (1983, 1984) of trichopteran phylogeny permits a fresh perspective on the evolutionary history of feeding tactics and case- and retreat-making habits in caddisflies.

Evolution and Classification of Trichoptera

Three contemporary phylogenetic reconstructions of Trichoptera by Ross, Schmid, and Weaver are compared in Figure 1. Ross's phylogeny (1956, 1964, 1967) differs from the others by having the members of Rhyacophiloidea paraphyletic in Integripalpia. (Paraphyletic groups are those which exclude selected descendant lineages; they have only minimal predictive usefulness, they have arbitrary taxonomic limits, and they confuse the scientific information storage and retrieval system [Morse 1981].) The sequence of ancestral lines leading successively to his rhyacophiloid families Rhyacophilidae-Glossosomatidae-Hydroptilidae and then Limnephiloidea was based almost entirely on the supposition of a transformation series in larval case-making behavior. Ross hypothesized that the primitive caddis larva was philopotamid-like in making a tube net of silk. This character was inherited by the ancestor of Annulipalpia, but was lost in the ancestor of Integripalpia which became free-living. The integripalpiian descendants successively evolved from a relatively "simple" free-living

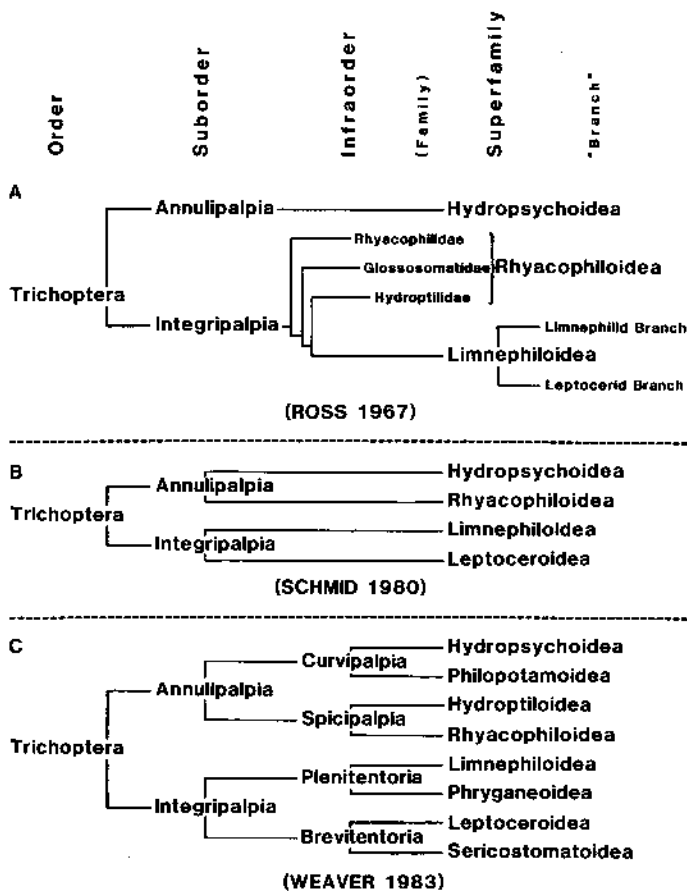


FIG. 1. Comparison of three contemporary phylogenetic reconstructions of Trichoptera.

larva (as in Rhyacophilidae), through steps of increasing complexity, to saddle-case-making (as in Glossosomatidae), to purse-case-making (as in Hydroptilidae), and finally to tube-case-making in Limnephiloidea. The simplicity of the individual behavioral steps in the case-making process (Ross 1964) leaves much room for erroneously inferring their homologous development, especially since the sister-group relationship of the saddle-case maker (Glossosomatidae) with the purse-case maker (ancestor of Hydroptilidae and Limnephiloidea) is not supported in Ross's scheme by any structural homologies.

The phylogeny proposed by Schmid (1980; Fig. 1B) conforms closely to the classic alignment of the suborders Annulipalpia and Integripalpia as first presented by Martynov (1924). There is little difference in the families that Ross and Schmid included in Hydropsychoi-

dea, Rhyacophiloidea, and the "tube-case" makers (Ross's Limnephiloidea, Schmid's Integripalpia) except that Schmid included Rhyacophiloidea as a monophyletic taxon in Martynov's Annulipalpia. Also, Schmid's Limnephiloidea and Leptoceroidea are comparable with Ross's limnephilid and leptocerid branches of Limnephiloidea. However, Schmid did not mention as many families as did Ross, and unfortunately he did not explicitly state the homologues supporting his phylogeny, making it difficult to comment on the logic of his interpretation.

Weaver's (1983, 1984; Fig. 1C) reconstruction of the phylogeny of Trichoptera, based on 48 unique, hierarchically nested homologues, agrees more with Schmid's than with Ross's concerning the members of Annulipalpia and Integripalpia. However, there are some refinements in the classification (Table 1), especially

TABLE 1. Higher classification of Trichoptera from phylogeny in Figure 2.

Order Trichoptera Kirby, 1813

Suborder Annulipalpia Martynov, 1924

Infraorder Curvipalpia Weaver, 1984 (=Hydropsychoidea of Schmid, 1980)

Superfamily Hydropsychoidea Curtis, 1835, sensu stricto

Superfamily Philopotamoidea Stephens, 1829

Infraorder Spicipalpia Weaver, 1984 (=Rhyacophiloidea of Schmid, 1980)

Superfamily Hydroptiloidea Stephens, 1836

Superfamily Rhyacophiloidea Stephens, 1836, sensu stricto

Suborder Integripalpia Martynov, 1924

Infraorder Plenitentoria Weaver, 1984 (=Limnephiloidea of Schmid, 1980)

Superfamily Limnephiloidea Kolenati, 1848, sensu stricto

Superfamily Phryganoidea Leach, 1815

Infraorder Brevitentoria Weaver, 1984 (=Leptoceroidea of Schmid, 1980)

Superfamily Leptoceroidea Leach, 1815, sensu stricto

Superfamily Sericostomatoidea Stephens, 1836

Brevitentoria incertae sedis: Family Tasimiidae Riek, 1968

with the addition of four infraorders replacing the superfamilies recognized by Schmid. This classification (Table 1) is slightly modified from that published earlier by Weaver (1983, 1984) in that the subordinal names Annulipalpia and Integripalpia are conserved here. The evolutionary relationships of families within these taxa are depicted in Figure 2; note that the relationships of several families, especially in Integripalpia, remain unresolved.

Feeding Behavior

Caddis larvae appear to use a variety of food-gathering tactics as great as, or greater than, any other order of aquatic insects (seven of nine principal tactics, table 6C in Merritt and Cummins 1984). Mackay and Wiggins (1979) suggested that much of this diversity is an expression of ecological opportunities made possible by the secretion of silk.

With the Martynov-Schmid-Weaver ideas on family relationships in Trichoptera as a conceptual framework, it is possible now to reinterpret the evolution of caddis larval feeding habits and some other initially puzzling behavioral characters. This will be accomplished by hypothesizing for the ancestor of each monophyletic group its minimum common denominator or "minimum character state set" (Morse and White 1979); that is, the character or least-sum-of-characters found in the immediate descendants of each ancestor. For example, if character A is known in all descendants of some immediately common hypothetical ancestor,

then that ancestor probably had character A; if character A occurs in one descendant and B in another, the ancestor probably had some antecedent combination A-B; if the A-B combination occurs in one descendant and a different character C in another, the hypothesis with the greatest empirical content is that the ancestor had a combination A-C or B-C, but not A-B or A-B-C. If A or B are in the character complex of the next immediate ancestor, logical parsimony will decide in favor of A-C or B-C, respectively.

Occasionally, special difficulties are encountered when sister lineages have specialized behaviors which, if considered collectively as features of a highly varied repertoire in their immediate ancestor, defy common sense. Were ancient species more variable in their behavioral traits than are modern species? We think not. Thus, for problematic cases such as this, we consider the search for some third "common denominator" character as being compatible with the procedure summarized above. For example, it seems unlikely that a single species, such as the ancestor of Spicipalpia, could have been both a predator and a scraper. The structures and behaviors associated with each of these feeding tactics are so different as to seem mutually exclusive for a single species, judging from modern species. Alternatively, some third feeding tactic more likely was used by this ancestor, from which scraping and predation arose in different descendant lineages. The most likely candidate from among known modern tactics is collecting-gathering since it encoun-

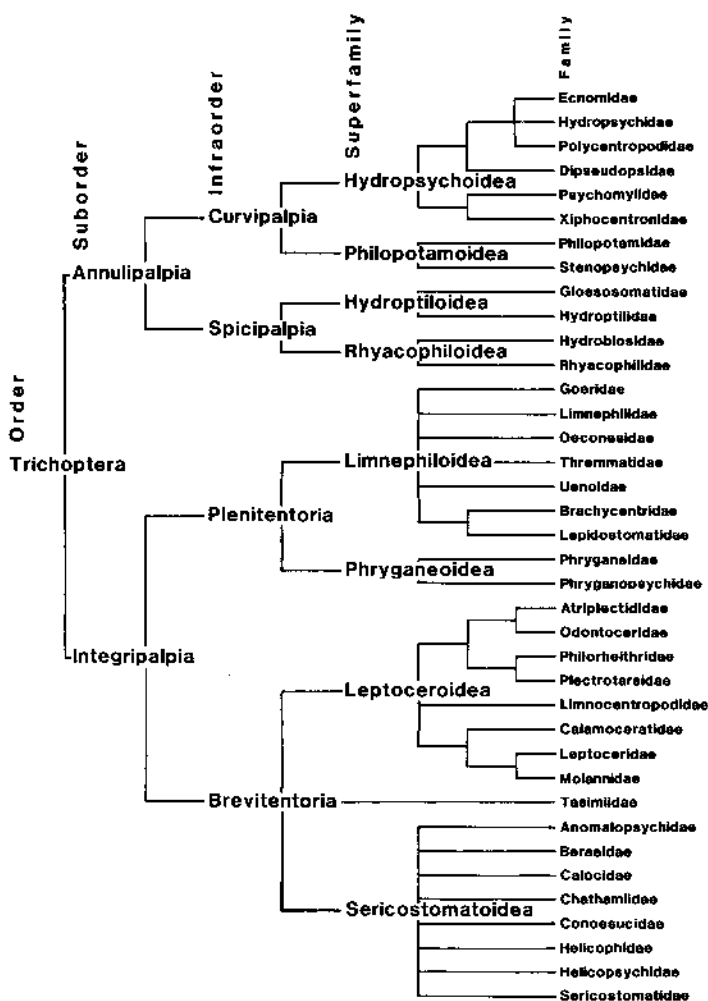


FIG. 2. Phylogenetic reconstruction of Trichoptera, modified from that of Weaver, 1983.

ters all the smaller food items of scrapers and predators, it seems to require the least morphological and behavioral specialization, and it is the tactic used by primitive lineages of most panorpoid insect orders. Merritt and Cummins (1984) considered collectors-gatherers as the group most generalized in their acquisition of food.

By this method of reasoning, therefore, we infer the following evolutionary developments for feeding tactics in Trichoptera (Fig. 3): Resembling its mecopterous-dipterous predecessors, the browsing, detritivorous, eruciform larva of the amphiesmenopteran ancestor (of Trichoptera and Lepidoptera) (1) became specialized in the lepidopteran ancestor for shredding living plant tissue. (2) The trichopteran

ancestor retained its diet of deposits of fine and coarse particles of organic matter, preferring a moist to saturated environment in the microbially rich humus soils or detrital mats along the shores of late Permian or early Triassic aquatic environments such as littoral regions, slowly moving waterways, or marshes. (3) The integripalpien ancestor kept this general detritivory and added a scraping tactic for ingesting attached algae while (4) the annulipalpien ancestor became specialized for only deposits of fine particulate organic matter (FPOM). (5) Integripalpien descendants Plenitentoria and Brevitentoria retained their ancestor's feeding habits, but (6) Phryganezoidea switched to living plants and animals. (7) The ancestor of Spicipalpia continued to gather deposits of FPOM

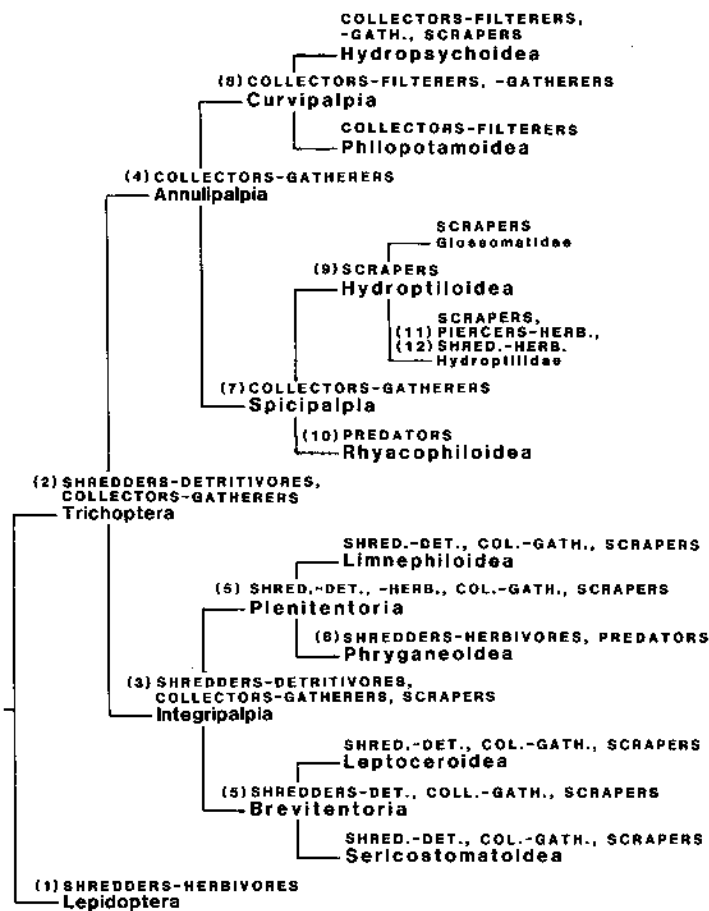


FIG. 3. Evolution of feeding strategies in Trichoptera.

while (8) that of Curvipalpia not only collected it from the substrate, but also specialized to filter suspended FPOM from the water with silken nets and, in its ancestral manner, then gathered it from the nets. (9) Interestingly, as mentioned above, the probable collector-gatherer ancestor of Spicripalpia evolved into one line (Hydroptiloidea) adapted to scraping algae and associated detritus from the upper surfaces of large, solid substrates while (10) another descendant (Rhyacophiloidea) became adapted for preying on small animals on all surfaces of these substrates. The glossosomatid and hydroptilid descendants of the Hydroptiloidea ancestor retained the scraping habit, but later (11) the ancestor of the Hydroptilini + Orthotrichiini (Marshall 1979) evolved, from the scraper strategy, the habit of moving out along strands of filamentous algae to pierce algal cells and suck their contents. Also, the

hydroptilids *Dibusa angata* Ross and the ancestor of Ptilocolepinae (12) independently evolved shredding behavior for red algae and bryophytes, respectively (Marshall 1979). Predatory behavior in species of *Orthotrichia*, *Hydropsyche*, *Polycentropus*, and *Oecetis* or filtering behavior in those of *Brachycentrus* or shredder-herbivory behavior in those of *Micrasema*, *Anisocentropus*, and *Triaenodes* evolved independently from the tactics implied by this phylogeny to have occurred in the ancestors at the superfamily levels. Thus, we infer that all of the principal feeding habits of Trichoptera evolved directly or indirectly from benthic detritivory.

Case-making and Retreat-making Behaviors

Various mobile and sedentary habits and case- or retreat-making behaviors clearly play an im-

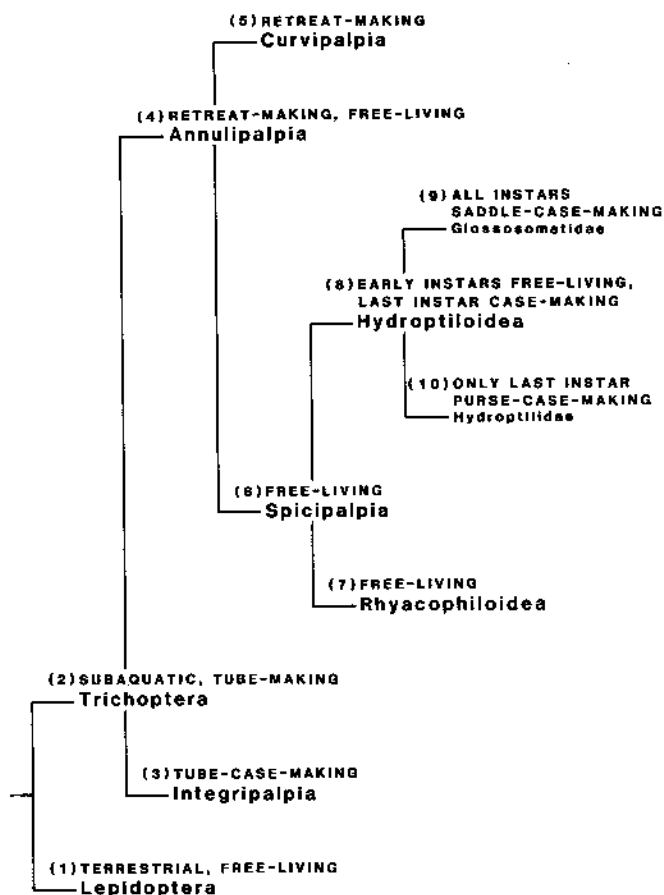


FIG. 4. Evolution of case- and retreat-making in Trichoptera.

portant part in feeding activities and should be viewed along with them. Case-making habits of Trichoptera have long been a source of fascination for naturalists (Hickin 1967), at least since the time of Aristotle (Lepneva 1964:130), and have been studied in detail for particular species by more than 40 scientists (Rowlands 1985) during the 1900s.

Hanna (1960) and Tomaszewski (1973, 1981) observed that when tube-case-making larvae are removed from their cases, many of them immediately dig into the substrate and fortify their burrows with silken secretions, forming a rough tube or provisional case. Tomaszewski (1981) suggested that this behavior provides evidence that tube-case-making resulted from tactile demands inherited from soil-dwelling ancestors. Retreat-making may have resulted from the same demands. Hanna (1960) and especially Milne and Milne (1939) have presented syn-

opses of case and retreat evolution which conform very closely with that implied by the Martynov-Schmid-Weaver phylogeny. Figure 4 shows that, like the free-living terrestrial amphipsecteran ancestor of Trichoptera and Lepidoptera, (1) the larva of the ancestral lepidopteran made no silk covering before pupation; it lived exposed on, or protected in, its host plant tissue. (2) The ancestral humus- and detritus-mat-dwelling caddis larva lived in a long, stationary hyporheic tube, prevented from collapse by silken secretions, perhaps similar to the tubes of Dipseudopsidae (e.g., *Phylocentropus*, Wiggins 1977, fig. 15.4D). (3) By severing the tube posteriorly as modern case-making larvae now normally do to separate their initial "provisional case" from their later "definitive case" (Hanna 1960), the first integripalpien larva was able to carry its protective covering about while taking advantage of rich detritus and at-

tached algae out on the benthic surface. Concurrently the anal legs and claws became specialized for grasping the interior of the case. Larvae of the ancestors of Limnephiloidea and Brevitentoria restricted the posterior end of their tube-case with a porous silk mesh, perhaps to discourage predatory ambush from the rear while allowing flow of oxygenated water (e.g., *Apatania*, Wiggins 1977, fig. 10.4C). (4) On the other hand, in Annulipalpia, extension of these ancestral, fixed tubes out onto exposed benthic surfaces such as rocks or logs resting on the bottom (superficially resembling the exposed tubes of subterranean termites) and then severance of the tubes from the bottom resulted in retreats like those of collector-gatherer Psychomyiidae and Xiphocentronidae larvae (e.g., Wiggins 1977, figs. 16.1E and 16.2D). Anal prolegs on this ancestral larva became longer and its claws larger to enhance intra-tube maneuvering. (5) The ancestral Curvipalpia larva oriented a broadened front end of its tube (e.g., *Dolophilodes*, Wiggins 1977, fig. 13.2F) into the stream current to capture drifting seston; the ancestral Hydropsychidae larva modified this upstream end specifically as a filter (e.g., *Hydropsyche*, Wiggins 1977, fig. 6.6G); (6) The Spicpalpia ancestral larva abandoned its retreat to adopt a foraging feeding strategy. (7) One descendant (ancestor of Rhyacophiloidea) became a roving predator (8) while another (ancestor of Hydroptiloidea), in its final instar, covered itself precociously (Ross 1964) with a prepupal case for protection from predation while grazing on periphyton. Unique features of this larval case in the ancestral hydroptiloid included the following: (a) two sheets of silk, each reinforced by cementing together various substrate particles; (b) lateral, marginal seams joining these sheets; (c) openings from which head and thoracic legs protrude at one end and anal claws at the other interchangeably. (9) In the scraping glossosomatid ancestor, the upper surface of this case was dome-shaped, retaining the form of the ancestral annulipalpiian pupal chamber, to which the lower sheet of material was added across the venter of the body, with smaller stones than employed on the upper surface (e.g., *Glossosoma*, Wiggins 1977, fig. 4.4B). This so-called "saddle case" began to be constructed by all larval instars. (10) In the Hydroptilidae ancestor, the two sheets became

nearly identical in size, shape, and composition, forming a so-called "purse case" (e.g., *Palaeagapetus*, Wiggins 1977, figs. 7.12B and G) and, in the Hydroptilini + Orthotrichiini ancestor (Marshall 1979), rotated to a vertical position for efficient movement among strands of algae as these were exploited for food (e.g., *Hydroptila*, Wiggins 1977, figs. 7.4B and C). Species in sister hydroptilid genera *Neotrichia* and *Mayatrichia* make more or less tubular cases in which the pair of seams is obscured (Wiggins 1977, figs. 7.7B and 7.8F).

Closing Remarks

The Martynov-Schmid-Weaver phylogeny implies that neither collecting-filtering (as in Philopotamidae) nor predation (as in Rhyacophilidae) were the ancestral larval feeding strategies in fast-flowing, cold-water, lotic-erosional habitats as Ross hypothesized; instead, the first caddisflies were detritivores in the lentic or lotic-depositional hydrosammon zone (probably cold). This observation predicts that, as the habits of more caddisfly larvae become known, detritivory probably will continue to be found generally throughout the order, particularly in less specialized early instars, while other feeding habits will be confined to isolated monophyletic groups. Furthermore, different groups exhibiting these other, superficially similar feeding habits will likely be found to have different structural and physiological adaptations for accomplishing them.

This phylogeny also implies that a free-living or net-spinning larva was not part of the groundplan of Trichoptera as Ross hypothesized, but that retreat-making and tube-case-making probably arose directly from a common ancestral tube-making behavior pattern; free-living, saddle-case-making, and purse-case-making behaviors arose independently, not as offshoots of a single, primitive transformation series leading to tube-case-making. Tube-case-making behavior probably evolved from a primitively larval activity; saddle- and purse-case-making from a pupation activity, precociously adapted for larval purposes. This observation predicts that detailed study of tube-case-making behavior will likely prove it to be fundamentally different from saddle- and purse-case-making.

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