

Trichoptera Phylogeny, Adaptations, and Biogeography Through Geologic Time

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Abstract

Trichoptera are a well-studied group of aquatic insects that are recognized by both entomologists and limnologists, for their especially peculiar habit of building nets and cases. The phylogeny of the order is a point of controversy with systematists. However, the knowledge of their biogeography and their water quality and temperature tolerance provides great promise for the study of past aquatic environments and predictions of future climate change.

Introduction

Trichoptera have long been favorites of naturalist and limnologists because of their case making abilities and ability to be used as water quality indications at least since the time of Aristotle (Weaver and Morse 1986). Trichoptera are a cosmopolitan, holometabolous insect whose larvae are aquatic. Trichoptera comprise the most diverse insect order whose members are exclusively aquatic (with a few exceptions). The larval stages have adapted to lakes, rivers, wetlands, and streams around the world and have been particularly successful in subdividing resources within these habitats (Merritt and Cummins 1996). Trichoptera are primarily detritivores and are very important members of freshwater food webs (Resh and Rosenberg 1984).

There have been 12,000 Trichoptera species from 45 families and 600 genera described. It has been estimated that the order may contain as many as 50,000 species

(Holzenthal et al 1997-2005). The three suborders that are currently recognized are largely characterized in the way silk is used, whether to produce nets or tubes or as adhesive to make various types of cases. Some are free-living, however, they still put down a strand of silk as they move about the substrate, much like the larvae of Lepidoptera (Ross 1964).

Trichoptera are important in the trophic dynamics and energy flow in aquatic ecosystems. Unlike many of the aquatic Diptera, they are generally not considered pests. The larvae are useful as biological indicators for assessing water quality. Extensive knowledge of trichopteran past dispersal, habits, and life cycle adaptations has made them very suitable for this. Because of this past dispersal larval sclerites and cases have been used in paleolimnological studies to assess climate change (Solem and Birks 2002).

Morphological Analysis and Phylogeny

The Trichoptera are a specialized member of the Neuropteroid orders (Neuroptera, Lepidoptera, Trichoptera). Therefore any characteristics, which they possess, that have a history in the Neuropteroid and more primitive orders, should be considered to be primitive within the Trichoptera (Ross 1967). Many of these primitive features can be seen in the sister group relationship between Trichoptera and Lepidoptera. This relationship is one of the most strongly supported in entomology (Kjer et al 2001).

The very close morphological agreement of adult Trichoptera and Lepidoptera substantiates the phylogenetic placement of the groups (Ross 1967). A comparison of primal and derived characteristics in primitive Trichoptera and Lepidoptera gives insight into what the primeval Trichoptera may have been like. In all adult Lepidoptera, the median ocellus is lost, the praescutum is not delineated laterally, the media of the front wing has only three branches, and the female tenth segment has no cerci. These represent reductions in the condition found in primitive Trichoptera. In Trichoptera the larval antenna is represented by only one or two apical papillae where there are two or three distinct segments in Lepidoptera. Also, the larval spiracles are absent in the Trichoptera (Ross 1967). This points to the conclusion that these two orders must have arisen from a

common ancestor in which all of these characteristics were present. In all probability, the adult of the ancestor would have been much like a trichopteran and the larvae much like a lepidopteran. In the lineage that led to the Trichoptera, the larvae became highly modified for an aquatic existence; however, they probably retained the ancestral diet of fine and coarse particulate organic matter (Weaver and Morse 1986). The adults changed very little. Conversely, in the lineage leading to the Lepidoptera the adults lost many characteristics but the larvae remained relatively unchanged (Ross 1967) except for feeding specialization: shredding live plant material (Weaver and Morse 1986).

The sister group of Lepidoptera and Trichoptera comprises the Amphiesmenoptera. Within the Trichoptera, it is now accepted that the order contains two monophyletic suborders: Annulipalpia and Integripalpia with a third suborder Spicripalpia, whose monophyly is ambiguous (Kjer et al 2001).

Annulipalpians larvae make fixed retreats from which they spin a silken net or capture invertebrate prey (Kjer et al 2001). In this family group the apical segment of each adult palp is annulated, the adult supratentorium is lacking, the wings have a crossvein *m*, the female tenth segment has distinct cerci, and the larval anal hooks are large, slender, and sickle-shaped (Ross 1967).

The families comprising the Annulipalpia can be arranged in a

phylogenetic sequence on the basis of a successive loss of primitive characteristics combined with the acquisition of a few specialized traits. The most primitive of the annulipalpi branch includes the Stenopsychidae and Philopotamidae, which have an elongate larval head and have retained the ocelli and primitive condition of the apodemes of the eighth and nine female segments (Ross 1967). This ancestor kept the feeding specialization developed in the late Permian or early Triassic of eating fine particulate organic matter or FPOM (Weaver and Morse 1986).

The more specialized branch gave rise to an ancestor in which the ocelli were lost and the apical segment of the maxillary palps became divided into distinctive sub-segments separated by pieces of membrane. In other branches the mesopraescutum remained fully formed, the female eighth and ninth segments retained well-developed internal apodemes, and the larval ligulae became elongate and pointed. This line gave rise to the Xiphcentronidae and the Psychomyiidae (Ross 1967).

Integripalpi larvae make portable tube cases from which they feed in any number of manners, most commonly as shredders or predators but also as scrapers, filterers, herbivores, or others (Kjer et al 2001). This case-making ability is an important taxonomic feature as well as having evolutionary significance. When Integripalpi larvae are removed from its case, many of them immediately burrow

into the substrate and fortify this burrow with silken secretions forming a provincial case. This suggests that tube-case-making resulted from tactile demands inherited from soil dwelling ancestors. The retreat case-making of the Annulipalpia may have resulted from the same demands (Weaver and Morse 1986). In this family group, the apical segment is not annulated; the adult supratetorium is presenting many groups, the wings have lost the crossvein *m*; the female has no obvious cerci; the larval hind legs project sideways, and the larval anal hooks are short and very stout (Ross 1967).

Integripalpia appear to be represented by two major branches: the limnephilid and letocerid. In the limnephilid branch the supratetorium was retained, the M4 vein was lost in the male front wing, and the larval posterior suture of the pronotum was considerably anterior to the hind margin. In the leptocerid branch the adult lost the ocelli, the supratetorium was reduced to a stub, the M4 vein was retained in the males, and the larval posterior suture of the pronotum was close to the posterior margin (Ross 1967).

The position of the pronotal suture of the leptocerid branch is virtually identical to its position in all non-Integripalpia; therefore, the anterior position of this suture in the limnephilid branch appears to be a specialized change binding the limnephilid as a monophyletic group. This is strengthened by two other additive specializations. First, in all but the Limnocentropodidae the

adult labrum is elongate, the apical portion is set as a narrower piece. Secondly, in all but the Limnocoentropodidae and the Brachycentridae the larvae have a prosternal horn arising between the front legs (Ross 1967).

Spicipalpia included the free-living predaceous larval groups (Rhyacophiloidae and Hydrobiosidae), the purse-case makers (Hydroptilidae), which feed by piercing algae cells or by gathering fine detritus; and the saddle-case makers (Glossosomatidae), which are specialized for scraping periphyton from the upper surfaces of stones (Kjer et al 2001).

This suborder preserves a remarkable number of primitive characteristics and is probably the most ancient branch of Trichoptera. Some larvae are free-living (however, they still leave a strand of silk on the substrate when they move). The Glossosomatidae represent the next step in specialization. Their larvae build saddle-like cases and have highly modified anal legs and hooks. Glossosomatidae also developed a scraper strategy, scraping algae from the surfaces of the substrate (Weaver and Morse 1986). In the third Spicipalpia, the Hydroptilidae, the anal legs became shorter, the apical hooks became directed laterally and situated some distance dorsally up the segment, and the larval antennae became reduced to a single rod (Ross 1967).

The Hydroptilidae are a real enigma. The last instar makes either a purse case or a tube case, and its anal segment is much like the Integripalpia or tube-case makers. But all of the early instars are minute, free-living larvae that do no spinning, feed on algal threads, and hardly grow. This group moved away from the scraper strategy and developed a piercer strategy to suck the contents from these algae strands. The hydroptilids *Dibusa angata* and the ancestor of Ptilocolepinae independently evolved shredding behavior for red algae and bryophytes respectively, again moving away from the scraping behavior of Glossosomatidae (Weaver and Morse 1986). Almost all of the growth is in the final instar. In the early instars, the hind legs are relatively long and extended downward and have long, slender anal claws. All these traits are reminiscent of the Rhyacophiloidae or Annulipalpia. It appears that these characteristics of the early larvae of Hydroptilidae represent a peculiar reversal of evolution associated with Trichopteran life history (Ross 1967).

There has been considerable debate about the basal relationships of the Trichoptera. This has led to many different hypotheses about the evolutionary history of the group and confusion in the use of taxonomic categories (Holzenthal et al 1997-2005). In general the three major groups in the foregoing discussion are recognized mostly from the larval adaptations discussed. However, the relative relationships among the families of Spicipalpia remains the

central factor in resolving the basal relationships of Trichoptera.

One of the more interesting debates surrounding the phylogeny of Trichoptera is the idea that Hydroptilidae and Glossosomatidae (Spicipalpia) are sibling taxa allied to the Integripalpia, and the Rhyacophiloidae and Hydrobiosidae are sibling taxa allied to the Annulipalpia (Ivanov 2002). This challenges the monophyly of the Spicipalpia and shows that its apomorphies are plesiomorphic (Holzenthal et al 1997-2005).

With the advances in molecular biology the most recent analysis was done using a molecular data set from several gene fragments, including mitochondrial and nuclear DNA. This analysis also included morphological characteristics used in most cladograms. Forty-three of forty-five families were included in this study (Kjer et al 2001). In this analysis Annulipalpia and Integripalpia were monophyletic and Spicipalpia was most closely related to the Integripalpia. These results reject the idea of the separation of Spicipalpia as proposed by Ivanov.

Adaptations

The movement of trichopteran larvae and pupa back into the water had the influence of severe new selection pressures. Features common to most caddisflies give abundant evidence of the adaptations used to adjust to this new environment. The larvae lost its

spiracles and relied upon cutaneous respiration. The pupa evolved a set of dorsal plates armed with stout hooks, retained primitive strong mandibles to escape the cocoon, and the adult evolved a distinct tongue for imbibing fluids. The common ancestor would have had to possess all of these adaptations (Ross 1967).

The most striking adaptations of trichopterans are in the larvae and this part of the life cycle will be concentrated on. These adaptations are concerned with respiration, food gathering, swimming, and of course the remarkable net or case construction for which they are best known (Merritt and Cummins 1996). The case-making habits of trichopterans are quite diverse and can be a basis for dividing the order (Ross 1964) as has been discussed.

Other than the free-living Rhyacophiloidae, trichopterans make various types of cases and nets, often distinctive of the genus or family. These "homes" fall into three general categories: nets or retreats, tube cases in which only the front end is open, and saddle or purse cases in which both ends are open (Ross 1967).

The nets of the various types of retreat makers are all modified from an open-ended tunnel in which the larva can move back and forth rapidly. The larva feeds and completes its growth in these nets. When they are fully grown they will leave the nets and seek a sheltered spot to build a cocoon (Ross 1967). Most of these families

(Philopotamidae, Psychomyiidae, Ecnomidae, Xiphocentronidae, Polycentropodidae, and Hydropsychidae) are sedentary and construct fixed retreats to strain food particles from the surface (Merritt and Cummins 1996). Most rely on currents of running water to carry food to their retreats, although some do live along the shoreline of lakes. For example, Philopotamidae live in elongate, fine-meshed nets in reduced currents on the underside of rocks where they filter particles smaller than those filtered by other Trichoptera. The specialized membranous labrum clears accumulated particles from the net (Merritt and Cummins 1996).

Hydropsychidae construct retreats of organic and mineral fragments with a silken sieve placed adjacent to the entrance of the net to filter particles from the surface. Mesh size of the filter varies depending on the food source (some feed on other insects, while others ingest fine organic matter). One of the more interesting adaptations of Hydropsychidae is in the genus *Hydropsyche*. The larvae of this genus produce sound by rubbing their femur across ridges on the underside of the head. This sound is thought to be a defensive behavior to protect their retreat against other hydroptychids, but it's not known if it extends to general predators (Merritt and Cummins 1996).

Polycentropodidae larvae construct shelters of several types. Sit and wait predators such as *Nyctiophylax* make a flattened tube of silk in depressions of rock or

logs. This allows them to wait in their tube until a prey species touches the silk, and they dart out to attack. *Neureclipsis* construct a funnel shaped filter net made of silk in slow currents and rest in the narrowed base (a single net may be 12 cm long). Larval *Phyloctropus* fashion branching tubes of silk and sand in loose sediments with the ends of the tubes protruding above the sediment surface. Water with food particles enters the upstream tube, passes through a filter of silk that retains the food particles and leaves the downstream tube (Merritt and Cummins 1996).

Psychomyiidae and Ecnomidae live in running water, however, they do not filter food from the current. These families graze on periphyton and FPOM around the ends of their retreats. Their retreats are made of fine sand and organic material with a silken lining and fastened to rocks or logs. Xiphocentronidae make a similar retreat (Merritt and Cummins 1996).

Larvae of the tube-case makers construct a tubular case, usually incorporating material from the substrate (from sand and twigs to mollusk shells). The larvae add to the case as they grow, cut off the excess narrow end, and spin a new perforated wall. Interestingly, in this cutting, the trichopteran uses a peculiar stretch-sensitive organ on the anal legs as a measuring tool. When fully grown, the larva seeks a sheltered spot to attach the case and begin pupation (Ross 1967). The families of this group include Phyganeidae, Brachycentridae,

Limnephilidae, Uenoidae, Leptostomatidae, Beraeidae, Sericostomatidae, Odontoceridae, Molannidae, Helicopsychidae, Calamoceratidae, and the Leptoceridae. The portable cases these families construct allow the larvae to move from place to place in search of food. Perhaps more importantly, respiratory dependence on natural currents is moderated as the larvae's undulating movements cause a current of water to move through the case bathing the gills. This has allowed the tube-case makers to exploit lentic habitats (Merritt and Cummins 1996).

The dominant family in the tube-case makers is the Limnephilidae with nearly 300 species and 50 genera in North America alone. This family's larvae are highly diverse in their case-making behavior, habitat and food. The subfamilies Dicosomoecinae, Limnepilinae, and Psuedostenophylacinae are detritavores or omnivores and have toothed mandibles. Larvae in the Apataniinae and Goerinae have specialized mandibles without teeth and feed mainly by scraping exposed rock for diatoms and fine particulate organic matter (FPOM). The Leptoceridae are biologically diverse and have a variety of habits; some are able to swim in their cases, and larvae in several genera are predacious; for example, feeding on sponges. Odontoceridae and Sericostomatidae larvae are primarily burrowers in loose sediment. Larval Brachycentridae are confined to running waters, some using their legs to filter the water for

food. Molannidae and Calamoceratidae are unusually cryptic, particularly *Heteroplectron* species using hollow twigs or pieces of bark for cases. Many of the Leptostomatidae are important components of the shredder community in cool streams. They construct cases of sand grains or silk in early instars, but later change to a four-sided case of leaf and bark pieces. Larvae of the Uenoidae live in running water and occur in aggregations of rock. Beraeidae live in water saturated muck. The most unusual larvae of the tube-case makers belong to the Helicopsychidae that construct cases coiled like the shell of a snail. Helicopsychidae graze on diatoms and FPOM from exposed rock in rivers and along the shores of lakes (Merritt and Cummins 1996).

The early larva of Glossosomatidae constructs a saddle-like case of stones with a central strap that is also made of stone built across its "belly". This rock case allows freshly aerated water to enter through the spaces between the stones and pebbles (Merritt and Cummins 1996). The head and legs protrude from one side of the case and the posterior end may protrude from the other (Ross 1967). These cases make their movements very sluggish (Ross 1964). The larva cuts the central strap and glues the dome-like portion of the case to the substrate to begin pupation (Ross 1967).

In the primitive Hydroptilidae, the larva makes a case that is shaped like a purse with the two

sides sewed together ventrally in a tight seam in its last instar (Ross 1967). This family is free living until then and very small. These cases are portable in most genera. The Tribe Leucotrichiini are sedentary, fixing flattened silk cases that resemble leech egg capsules to rocks in running waters. The genus *Dibusia* has a specific association with freshwater red algae, as this is their only food source, and they also construct their case of it in their final instar (Merritt and Cummins 1996).

Even in the larvae of Rhyacophiloidae the larvae leave a strand of silk when they move about although no net or case is made until just before pupation. At pupation it constructs a crude wall of rock fragments and constructs ovoid, closed cocoon of tough brown silk (Merritt and Cummins 1996, Ross 1967, Wiggins and Wichard 1989).

Analysis of the modes of trichopteran pupation does not show many special adaptations other than those common to the order (Ross 1967). There are two basic types of pupal enclosures and systems for water circulation. In one (Rhyacophiloidae, Hydrobiosidae, Glossosomatidae, and Hydroptilidae), the pupating larvae construct a closed cocoon of silk discrete from the pupal enclosure, usually made of small stones. Water currents bathe the external surface of the cocoon during metamorphosis. In the other (most families of Annulipalpia and Integripalpia), the larvae construct a pupal cell with open mesh or holes at each end to permit water currents to bathe the

surface of the pupa directly (Wiggins and Wichard 1989).

These two adaptations provide interesting insight into the Trichoptera-Lepidoptera linkage. Closed, ovoid, cocoons of parchment like silk occur in primitive lepidopterans. Therefore, cocoons of this type must be part of the ground plan for Trichoptera. On the other hand, the open pupal cells of Annulipalpia and Integripalpia would have been derived because of selection pressures in habitat. This adaptation, along with larval adaptations, allowed these groups to exploit warmer, slower flowing water, and lentic habitats (Wiggins and Wichard 1989).

The morphological adaptations in adults are not great. They involve chiefly oviposition, flight, feeding, and scent glands or pouches in the males.

Most ovipositional adaptations have to do with where the females will lay their eggs. In the Rhyacophiloidae, Xiphocentronidae, and some Philopotamidae the last three abdominal segments form a narrow extensile tube, and in some Trichoptera the tenth segment often has sensory papillae. Both modifications are likely used for probing or testing the substrate for oviposition. In several families, the middle legs are expanded, flattened, and fringed with hair to form oars that are used by the female to swim underwater to lay her eggs (Ross 1967).

Flight modifications are mainly associated with the speed of flight and with changes in body length. For example long narrow forewings are associated with rapid flight (Ross 1967).

Feeding adaptations involve chiefly the mandibles and the tongue. In several groups, the tongue is greatly enlarged and forms a proboscis (Ross 1967).

In many families, the males have highly developed scent glands and pouches. This is probably to insure mating under conditions of low population density (Ross 1967).

Geologic History and Paleodispersal

The Triassic was crucial for the subsequent evolution of Amphiesmenoptera because it was the probable time of major divergence. At that time, the family Nectrotauliidae included early Trichoptera and Lepidoptera. These ancestors did not yet acquire all the synapomorphies of these orders. Fossilized wings have determined this, as fossilized larvae are not yet available (Ivanov 2002).

The most representative collection of early Cenozoic Trichoptera are remnants found in the Baltic amber. The diversity known from this amber has more rich and abundant species than all other fossil deposits. Other abundant Trichoptera remains belong to Dominican amber and to lacustrine deposits with numerous Limnephilidae from the Miocene of

Europe and North America. The composition of the amber fauna shows that most families of Trichoptera have been developed in Late Mesozoic times. Contrarily, Lepidoptera had its major diversion to families in the early Cenozoic (Ivanov 2002).

The scarcity of Triassic Amphiesmenoptera remains indicate that these insects dwelled in habitats far from the sedimentation areas, such as, springs for Trichoptera or moist soil covered by mosses and liverworts for Lepidoptera. In any case, the first moths are known from the Jurassic indicating the establishment of the Trichoptera clade (Ivanov 2002).

Trichoptera are abundant and widespread on every continent except Antarctica (Ross 1967). In contrast to the widespread nature of the order as a whole, individual taxa within the order may occupy a very limited geographic area (Merritt and Cummins 1996). If the phylogeny has been worked out correctly, inferences concerning past dispersals can be made (Ross 1967).

Evidence suggests that Trichoptera dispersals between Eurasia and North America can be grouped into four categories: Late Cretaceous-Paleocene, Eocene, Oligocene-Miocene, and the Pliocene-Pleistocene. During the Late Cretaceous-Paleocene, the early ancestral forms of primitive, diverse genera such as *Rhyacophila* (Rhyacophilidae) and *Sortoas* (Philopotamidae) spread throughout

Holarctica. These would have been cool-adapted forms. During the Eocene, warm climates moved north and the cool-adapted Trichoptera were restricted to mountainous areas. At this time, more warm-adapted genera moved in, such as, genera from the Hydropsychidae. During the Oligocene-Miocene, ecological conditions were very different and temperate deciduous forest dominated from New York to Alaska and from Siberia to Scotland. Many lineages associated with this ecosystem, such as the Glossosomatidae moved back and forth at this time. During the Miocene, the temperate deciduous became fragmented into widely separated units because of cooling temperature and have remained separate ever since. Each isolated population of trichopteran became the ancestral form of a cluster of closely related species. The Pliocene-Pleistocene saw a cooler period and many boreal species passed across the Bering Bridge. These dispersals are now represented by only one or two species in northeastern Asia, and one or two in western North America (Ross 1967).

The trichopteran fauna of North Africa is essentially European, part of the Mediterranean complex. The climatic oscillations of this region have led to the evolution of several distinct species in the Mountains of North Africa that are related to those of the Near East and Southern Europe. The fauna of Africa below the Sahara is quite different, tropical in nature, and

appears to be related to Asian fauna (Ross 1967).

In all of the trichopteran there is irrefutable evidence of only a single past dispersal between South America and Africa. This concerns the hydropsychid species *Leptonema tridens* (Ross 1967).

There are problems deciphering Trichoptera dispersal between North and South America in that the inter-American and circum-Caribbean area has been one of the world most prolific speciation hotbeds. However, the South American Protoptilinae appear to have come from a temperate North American lineage of the Glossosomatidae. It is highly probable that the connection and disconnection of land areas between the two American continents have produced the segregating and congregating factors responsible for the incredible amount of speciation (Ross 1967).

Trichopteran dispersal also suggests that there was a trans-Antarctic dispersal. That is to say, there was a land connection between Patagonia and Australia and New Zealand via Antarctica. For example in the genus *Smicridea* (Hydropsychidae), one of the subgenus occurs in Tasmania, the rest of the genus and certain ancestral types occur in Central and South America (Ross 1967).

The family Rhynchopsychidae contains only two known genera: *Rhynchopsyche* in Chile and *Kokiria* in New Zealand. The ancestor of

this family had to have had trans-Antarctic distribution (Ross 1967). Also, the Chilean species *Hudsonema flaminii* is most closely related to the Australian genus *Condocerus* (Holzenthal 1986).

New Directions in Paleo-research

Some of the new directions dealing with the evolution of Trichoptera involve paleoecology. Recently Hydroptilid cases have been collected in paleolimnology cores to interpret past aquatic environments. Fossil assemblages of the cases in Northern Europe point to rich vegetation in the littoral zone of these lakes (Bennike and Wiberg-Larson 2002).

Larval sclerites have also been used in this capacity (Bennike and Wiberg-Larson 2002). Fossil Trichoptera remains have been identified and quantified for the late-glacial and early-Holocene sediments from Kråkenes Lake in Western Norway. The sediment collected was deposited between 12,300 and 8850 year ago. This covers the Allerød Dryas and early-Holocene periods (Solem and Birks 2000). This study concentrated on the climate variation due to different glaciation periods and the associated Trichoptera reflected the geology.

Conclusion

The Trichoptera are a well-studied and well-represented group worldwide. Their relationship with the Lepidoptera is well documented, however, much work still needs to be done on the phylogenetic

relationship within the order, particularly in the suborder Spicipalpia. Because of their incredible biogeographical history and distribution and their well-known water quality tolerance there is the great promise for the use of fossilized remains in aquatic environments to monitor environmental change and predict climatic fluctuations, as well as monitor current conditions.

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