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## 25 Symbiotic associations between Chironomidae (Diptera) and Ephemeroptera

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*An updated list of all known chironomid-mayfly associations is presented. New unpublished, recently published and other associations not reported in Arvy and Peters (1976) are discussed, particularly those from the Nearctic. Sixty different chironomid mayfly associations involving 24-26 chironomid species are currently known worldwide.*

*Nearctic chironomid species and/or associations reported for the first time include: Nanocladius (Plecopteracoluthus) sp. #1, parasitic on Ephemera guttulata; N. (P.) sp. #2 (= Symbiocladius sp. of Mayo 1969), parasitic on Thraulodes speciosus, Choroterpes sp. and Leucrocuta sp.; Epoicocladius sp. #4, a commensal on Hexagenia sp.; and four orthoclad species that are facultative commensals on Drunella walkeri.*

*Nearctic ephemerid mayfly nymphs are hosts for larvae of five species of symbiotic Orthoclaadiinae. Four of these midge species may be present in a single stream and individual nymphs of Ephemera guttulata may harbour as many as three species at once. Interspecific competition between symbiotic midges on ephemerid nymphs appears to be minimized by their host specificity and/or by the different attachment site preferences and feeding habits of each species on their hosts.*

*The discovery of parasitic species of Epoicocladius and Nanocladius (Plecopteracoluthus) indicate that at least some parasitic Orthoclaadiinae may have evolved from commensal ancestors.*

### **Introduction**

Species of Chironomidae exhibit a wide range of habits and microhabitat preferences including some taxa that live in close association with other aquatic animals such as sponges, bryozoans, snails, molluscs, insects and even fish (Freihofer

and Neil 1967; Steffan 1967; Fittkau 1974). Insect hosts of larval chironomids include: Ephemeroptera (Table 1), Plecoptera (Bottorff and Knight 1987), Odonata (Dudgeon 1989; Hawking and Watson 1990), Hemiptera (Roback 1977; Bottorff and Knight 1987), Megaloptera (Gotceitas and Mackay 1980; de la Rosa 1992), Trichoptera (Dratnal 1979) and other Diptera (Tonnoir 1923).

Reports of symbiotic associations between chironomid larvae and mayfly nymphs have steadily accumulated since Claassen's (1922) description of parasitism by *Symbiocladius equitans* larvae on *Rhithrogena* sp. nymphs. Arvy and Peters (1976) listed 23 chironomid-mayfly symbioses involving nine species of Chironomidae in their compilation of all known mayfly endo- and ectosymbionts. Nymphs of three species of Ephemeridae were known to host commensal larvae of two species of *Epoicocladius* in the Holarctic. The larvae of five species of *Symbiocladius* were reported to parasitize nymphs of a variety of heptageniid taxa in the Holarctic and rheophilic leptophlebiid nymphs in Australia and the Neotropics. In addition, larvae and pupae of a species thought to belong to *Symbiocladius* were noted on *Thraulodes speciosus* nymphs in the Nearctic (Mayo 1969) and an undetermined chironomid larva had been observed on heptageniid nymphs in the Afrotropics (Germain and Grenier 1967).

Since 1976, several reports and descriptions of new chironomid species found on mayfly nymphs (e.g., Epler 1986; Matena and Soldán 1986; Jacobsen 1992) and new host records for existing taxa (e.g., Wiens et al. 1975; Soldán 1978) have been published. In addition, I have found a new parasitic chironomid species, several new host records for currently described species and a series of facultative commensal associations involving a single host during recent collecting trips in North America. These new species and records represent a considerable expansion of Arvy and Peters' (1976) listings.

In this paper I present an updated list of chironomid-mayfly symbiotic associations worldwide and review and discuss associations not reported in Arvy and Peters (1976), especially those from the Nearctic.

## **Results and Discussion**

### *Distribution of Associations*

Ephemeroptera nymphs serve as hosts for more chironomid species and associations than any other insect order. Approximately 56 different chironomid larva-mayfly nymph associations involving 24-26 chironomid species are known at the present time (Table 1). For comparison, nymphs of Plecoptera, the next most "utilized" insect order, have been observed to host 10-11 chironomid species (4-5 obligate) that form 19-20 associations that I am aware of (e.g., Dossdall and Mason 1981; Dossdall et al. 1986; Bottorff and Knight 1987; Roback and Coffman 1987;

also Jacobsen personal observation). Most new symbiotic chironomid species and associations on mayflies have come from the Holarctic (Table 2), presumably reflecting the intensity of collecting and research on Chironomidae and Ephemeroptera in this region. With the exception of six facultative associations and three associations in which the identity of the larvae and its relationship with its host are unknown, the majority of chironomid-mayfly symbioses involve larvae from three orthoclad genera (*Epoicocladius*, *Nanocladius* (*Plecopteracoluthus*) and *Symbiocladius*) in obligate relationships with nymphs of species of Ephemeridae, Heptageniidae or Leptophlebiidae (Table 3).

### *Obligate Associations*

Ephemerid nymphs in the Northern Hemisphere have yielded the most new obligate symbiotic chironomid species and associations since 1976 and currently support the most known symbiotic chironomid taxa (7-9 species). Increases in known ephemerid-associated species are attributable to recent taxonomic clarification of existing species and records of *Epoicocladius* (Jacobsen 1992) as well as the discoveries of new species. Aside from an undescribed species of *Nanocladius* (*Plecopteracoluthus*) discussed below, all chironomid species associated with ephemerid nymphs belong to the genus *Epoicocladius*.

Until recently, two species of *Epoicocladius* were generally recognized as associated with burrowing mayflies (e.g., Cranston et al. 1983, 1989): a species reported from *Litobrancha recurvata* nymphs in the Nearctic (Johannsen 1937); and *E. ephemerae* (Kieffer), a well-documented European species from *Ephemera* spp. that was believed to be a junior synonym of a Nearctic species, *E. flavens* (Malloch), known only from the imagines. However, Saether (1967) mentioned that an *Epoicocladius* larva illustrated by Chernovskii (1949, as *Smittia ephemerae*) differed from European larvae of this species and could actually represent an additional species in Europe. Matena and Soldán (1986) described species of *Epoicocladius* collected from *Ephemera* spp. nymphs in Asia and North America that clearly differed from *E. ephemerae* and Johannsen's *Spaniotoma* sp. E. In addition, Soldán (1988) reported a new host for *E. ephemerae* in a study of the distribution of this species in Czechoslovakia.

In the Nearctic, nymphs of the Ephemeridae are hosts for larvae of three obligate commensal and two obligate parasitic species of orthoclad midges. Each of the Nearctic ephemerid genera support a different commensal species of *Epoicocladius* (Jacobsen 1992). Larvae of *E. sp. #2* (= *Spaniotoma* sp. E, Johannsen (1937)) cling to hairs on the thorax and hind tibiae of *Litobrancha recurvata* nymphs. Larvae of *E. sp. #3* live on the abdomen of *Ephemera* spp. nymphs. Finally, recent collections from the Mississippi River confirm Epler's (1992) circumstantial evidence for *Hexagenia* sp. being the host for larvae of a species

**Table 1. Symbiotic associations between ephemeropteran nymphs and chironomid larvae.**

Ephemeropteran host	Chironomid species	Relationship	References
Palaeartic - Europe			
Ephemeridae:			
<i>Ephemera danica</i>	<i>Epoicocladius ephemerae</i>	commensal	as <i>Camptocladius ephemerae</i> : Edwards (1929); as <i>Hydrobaenus ephemerae</i> : Gillies (1951); Henson (1955, 1956, 1957); Beales & Henson (1956); as <i>Epoicocladius ephemerae</i> : Svensson (1976, 1979); as <i>Epoicocladius flavens</i> : Svensson (1980); Tokeshi (1986, 1988); Soldán (1988)
<i>E. lineata</i>	<i>E. ephemerae</i>	commensal	as <i>Epoicocladius flavens</i> : Soldán (1988)
<i>E. vulgata</i>	<i>E. ephemerae</i>	commensal	as <i>Camptocladius ephemerae</i> : Súlc & Zavrel (1924); as <i>Smittia ephemerae</i> : Pagast (1931); as "Chironomiden-Larven": Wesenberg-Lund (1943); as <i>Epoicocladius ephemerae</i> : Sæther (1967); Svensson (1976); as <i>Epoicocladius flavens</i> : Soldán (1988)
	<i>E. sp.</i>	commensal	as <i>Smittia ephemerae</i> : Chernovskii (1949, 1961); see also Sæther (1967)
Heptageniidae:			
<i>Ecdyonurus affinis</i>			
<i>E. dispar</i>			
<i>E. fluminum</i>			
<i>E. forcipula</i>			
<i>E. lateralis</i>			

Table 1. (continued)

<i>E. subalpinus</i>			
<i>E. submontanus</i>			
<i>E. starmachi</i>	<i>Symbiocladus</i>	parasitic	Codreanu (1939); Fontaine (1964); Arvy & Peters (1976); Soldán (1978)
<i>E. torrentis</i>	<i>rhithrogenae</i>		
<i>E. venosus</i>			
<i>Heptagenia sulphurea</i>			
<i>Rhithrogena alpestris</i>			
<i>R. diaphana</i>			
<i>R. ferruginea</i>			
<i>R. hybrida</i>			
<i>R. iridina</i>			
<i>R. semicolorata</i>			
Leptophlebiidae:			
<i>Habroleptoides modesta</i>	<i>S. rhithrogenae</i>	parasitic	Soldán (1978)
Palaeartic - Asia			
Ephemeridae:			
<i>E. orientalis</i>	<i>Epoicocladus</i> sp.	commensal	Matena & Soldán (1986)
Heptageniidae:			
<i>Ecdyonurus</i> sp.	<i>Symbiocladus</i> sp.	parasitic	Üeno (1930)
<i>Epeorus latifolium</i>	<i>S.</i> sp.	parasitic	Matena & Soldán (1982)
<i>Rhithrogena</i> cf. <i>tianshanica</i>	<i>S.</i> sp.	parasitic	Matena & Soldán (1982)
Oriental			
Ephemeridae:			
<i>Ephemera</i> sp.	<i>Epoicocladus</i> sp.	commensal	Matena & Soldán (1986)
Afrotropical			
Heptageniidae spp.	"Chironomidae sp."	undetermined	Germain & Grenier (1967)

Table 1. (continued)

Australia

Leptophlebiidae:

<i>Atalophlebioides</i> sp.	<i>S. (Acletius) aurifodinae</i>	parasitic	Riek (1974); Hynes (1976)
<i>Atalonella</i> sp.	<i>S. sp.</i>	parasitic	Riek (1974)
<i>Australophlebioides</i> sp.	<i>S. sp.</i>	parasitic	Peters & Campbell (1991)

Nearctic

Ephemerellidae:

<i>Drunella flavilinea</i>	undetermined	undetermined	Needham et al. (1935)
<i>D. walkeri</i>	<i>Cricotopus bicinctus</i>	fac. commensal	Jacobsen, pers. obs.
	<i>C. sp.</i>	fac. commensal	Jacobsen, pers. obs.
	<i>Synorthocladius</i> sp.	fac. commensal	Jacobsen, pers. obs.
	<i>Thienemanniella</i> sp.	fac. commensal	Jacobsen, pers. obs.

Ephemeridae:

<i>Ephemera guttulata</i>	<i>Epoicocladius</i> sp. #1	parasitic	Jacobsen (1992)
	<i>E. sp.</i> #3	commensal	Roback (1953); Jacobsen (1992)
	<i>Nanocladius (Plecoptera-coluthus)</i> sp. #1	parasitic	Jacobsen, pers. obs.
<i>E. simulans</i>	<i>E. sp.</i> #3	commensal	Matena & Soldán (1986); Jacobsen (1992)
<i>E. varia</i>	<i>E. sp.</i> #3	commensal	Jacobsen (1992)
<i>Hexagenia</i> sp.	<i>E. sp.</i> #4	commensal	Epler (1992); Jacobsen (1992 & pers. obs.)
<i>Litobrancha recurvata</i>	<i>E. sp.</i> #2	commensal	Johannsen (1937, as " <i>Spaniotoma (Smittia)</i> sp. E. Group <i>Epoicocladius</i> "); Jacobsen (1992)

Table 1. (continued)

Heptegeniidae:			
<i>Epeorus vitreus</i>	<i>Symbiocladius equitans</i>	parasitic	Roback (1953)
<i>E. nr. vitreus</i>	<i>S. chattahoocheensis</i>	parasitic	Caldwell (1984)
<i>Heptagenia maculipennis</i>	<i>S. equitans</i>	parasitic	Wiens et al. (1975)
<i>H. sp.</i>	<i>S. equitans</i>	parasitic	Wiens et al. (1975)
<i>Leucrocuta sp.</i>	<i>N. (P.) sp. #2</i>	parasitic	Jacobsen, pers. obs.
<i>Rhithrogena doddsi</i>	<i>S. equitans</i>	parasitic	Roback (1953)
<i>R. sp.</i>	<i>S. equitans</i>	parasitic	Wiens et al. (1975)
<i>R. sp.</i>	<i>S. equitans</i>	parasitic	Claasen (1922)
<i>Stenonema smithae</i>	<i>Rheotanytarsus sp.</i>	fac. commensal	White et al. (1980)
Leptophlebiidae:			
<i>Choroterpes sp.</i>	<i>N. (P.) sp. #2</i>	parasitic	Jacobsen, pers. obs.
<i>Thraulodes speciosus</i>	<i>N. (P.) sp. #2</i>	parasitic	as <i>Symbiocladius sp.</i> : Mayo (1969)
Tricorythidae:			
<i>Tricorythodes sp.</i>	<i>Rheotanytarsus sp.</i>	fac. commensal	Wilda (1987)
Neotropical			
Leptophlebiidae:			
<i>Meridialaris chiloensis</i>	<i>S. (A.) wygodzinskyi</i> (?)	parasitic	Pescador & Peters (1987)
<i>M. diguillina</i>	<i>S. (A.) sp.</i>	parasitic	Gonser (1990)
<i>M. irrarrazavali</i>	<i>S. (A.) wygodzinskyi</i> (?)	parasitic	Pescador & Peters (1987)
<i>M. laminata</i>	<i>S. (A.) wygodzinskyi</i> (?)	parasitic	Pescador & Peters (1987)
<i>M. sp.</i>	<i>S. (A.) wygodzinskyi</i>	parasitic	host as <i>Thraulodes sp.</i> : Roback (1965); Arvy & Peters (1976)
<i>Thraulodes sp.</i>	undetermined	undetermined	Mayo (1969)
<i>Traverella sp.</i>	<i>N. (P.) bubrachiatus</i>	commensal (?)	Epler (1986)

**Table 2.** Comparison of numbers of obligate symbiotic chironomid species and mayfly host associations presently known for each biogeographic region with those listed by Arvy and Peters (1976).

Region	Arvy and Peters (1976)		Currently known (August 1992)	
	No. chironomid spp.	No. associations	No. chironomid spp.	No. associations
Palearctic-Europe	2	13	3	22
Palearctic-Asia	1	1	3-4	4
Nearctic	3	6	8-9	17
Neotropical	1	1	3	6
Afrotropical	1	1	1	1
Oriental	0	0	1	1
Australian	1	2	1	3
Total	9	24	20-22	54

**Table 3.** Distribution of symbiotic species in three chironomid genera on three mayfly host families (number of associations are given in parentheses).

Chironomid genus	Ephemeropteran Family		
	Ephemeridae	Heptageniidae	Leptophlebiidae
<i>Epoicocladius</i> (6-8 spp.):			
parasitic (1 sp.)	1 (1)	0	0
commensal (5-7 spp.)	5-7 (10)	0	0
<i>Nanoocladius</i> (3 spp.):			
parasitic (2 sp.)	1 (1)	1 (1)	1 (2)
commensal (1 sp.)	0	0	1 (1)
<i>Symbiocladius</i> (7 spp.):			
parasitic (7 spp.)	0	5 (29-30)	3 (8)

tentatively designated as *E. sp. #4*, but which is likely to be *E. flavens* (Jacobsen 1992). Past reports of *Epoicocladius* larvae on *Hexagenia* (e.g., Cranston et al. 1983, 1989; Coffman et al. 1986) are presumably based upon Johannsen's (1937) description of *E. sp. #2* on *Litobrancha recurvata* (as *Hexagenia recurvata*).

Larvae of a large parasitic species of *Epoicocladius* (*E. sp. #1* in Table 1) grasp unsclerotized integument on the meso and metathorax of *Ephemera guttulata* nymphs with their mandibles and feed on the host's hemolymph. *E. guttulata* nymphs also serve as hosts for larvae and pupae of a large undescribed species of *Nanocladus* (*Plecopteracoluthus*). Larvae of this species, designated as *N. (P.) sp. #1* in Table 1, construct a silken tube on the dorsum of the nymph's abdomen behind the wing pads and between the gills. Pupation also occurs in this position with the head and thorax situated above the middle abdominal segments and directed posteriad. The lack of significant amounts of sediment or detritus in the gut of larvae and the presence of scars on the host suggest this species also feeds upon the host's hemolymph.

On the Allegheny Plateau in the eastern United States, it is not unusual to find as many as four of the above species in a single stream and individual nymphs of *Ephemera guttulata* may harbour up to a total of 17 larvae representing three species (*E. sp. #1*, *E. sp. #3* and *N. (P.) sp. #1*) at once. This is the first record of sympatric coexistence of symbiotic chironomid taxa on nymphs of a mayfly family and the first report of a mayfly nymph hosting more than one obligate chironomid species simultaneously. de la Rosa (1992) recently reported a similar instance of multiple chironomid species associated with Megaloptera in Costa Rican streams involving an obligate and two facultative commensal species. Interspecific competition between Nearctic symbiotic chironomids on ephemerid hosts appears to be minimized by their host specificity and/or by the different attachment site preferences and feeding habits of each species on their nymph hosts. The length of the host family's life cycle (generally two years for the Ephemeridae in the temperate Holarctic) may be influential in the development of host specificity (Svensson 1979) and therefore facilitate sympatric coexistence of symbiotic Chironomidae on Ephemeridae in the Nearctic.

Relatively few new species have been documented from nymphs of each of the families Heptageniidae and Leptophlebiidae since 1976. In the Palaearctic, Matena and Soldán (1982) reported a possible new species of *Symbiocladius* from two heptageniid species in Siberia. In addition, Soldán (1978) recorded seven new hosts for *S. rhithrogenae*, including a first record from a leptophlebiid species.

Hynes (1976) described the mature pupa and larva of a new species of *Symbiocladius*, *S. (Acletius) aurifodinae*, from nymphs of Atelophlebiinae in Australia. This is presumably the same species observed by Riek (1974) though Hynes does not mention this reference. Peters and Campbell (1991) also reported finding *Symbiocladius sp.* on nymphs of *Australophlebioides sp.*

Two new species of chironomids have been described from leptophlebiid and heptageniid nymphs in North America. *Symbiocladius chattahoocheensis*, a species closely related to *S. equitans*, parasitizes *Epeorus* sp. nymphs in Georgia (Caldwell 1984). *Nanocladius (Plecopteracoluthus) bubrachiatus*, the first species of *Nanocladius* recorded from mayfly nymphs, lives in apparent commensal association with *Traverella* sp. in Honduras (Epler 1986). Four host records for *Symbiocladius (Acletius)* sp. in South America are provided by Pescador and Peters (1987) and Gonser (1990).

I recently collected and reared a midge species associated with *Thraulodes speciosus* in Arizona that Mayo (1969) identified as *Symbiocladius* but which Hynes (1976) speculated to be a species of *Nanocladius (Plecopteracoluthus)*. This chironomid is indeed a new species of *Nanocladius (Plecopteracoluthus)*. Larvae and pupae were collected from *Choroterpes (C.)* sp. and *Leucrocota* sp. as well as from *Thraulodes speciosus*. The relatively small amounts of sediment found in the gut of larvae and the presence of scarring and gill damage on the nymphs suggest this species is parasitic on its hosts.

### *Facultative Associations*

Facultative or accidental associations of chironomid larvae on other aquatic animals are common and generally arise as a consequence of either drift or mutual habitat preferences that promote proximity to one another and the structural and behavioural features of the host that accommodate the tube-building requirements of the larva. Surprisingly, only two facultative associations have been reported between midges and mayflies, both of which involved filter-feeding larvae of *Rheotanytarsus* sp. that use the host as a substrate on which to anchor their feeding tubes (White et al. 1980; Wilda 1987).

I have recently observed a series of facultative associations in which host use is more similar to that exhibited by obligate commensal species in that the larvae feed directly off the host's body surface. Nymphs of *Drunella walkeri* in the Sinnemahoning River in Pennsylvania develop rich growths of diatoms and filamentous algae on their dorsal body surfaces. Larvae of four orthoclad species, which normally live apart from insects, construct and occupy tubes on these nymphs and, based upon their gut contents, apparently graze on the algae. Additional chironomid species will likely be found on *D. walkeri* nymphs and other *Drunella* spp. (see Needham et al. 1935:217) in future collecting.

### *The Nature of Associations*

The associations of only two chironomid-mayfly symbioses have been extensively investigated up to the present time. Codreanu (1939) examined the interrelationship between *S. rhithrogenae* and its heptageniid hosts in detail. Larvae

of *S. rhithrogenae* attach to nymphs as first instars, feed on the host's hemolymph and induce a cancer-like proliferation of blood cells within the host that may be beneficial to the larvae. Codreanu claimed that the size and maturity of the nymph selected influence larval development time, the size of the adult midge and even its sex. For example, attachment to large hosts accelerates larval development and tends to produce larger adult midges that are predominantly female. The duration of the host's nymphal life is relatively unaffected; however, mature nymphs are unable to metamorphose to adulthood.

Nearctic chironomid parasites of Ephemeroptera inflict visible damage to their hosts such as gill deformation (*N. (P.)* sp. #2) and conspicuous scarring (*E.* sp. #1, *N. (P.)* sp. #1) but do not appear to notably inhibit their development or emergence (Claassen 1922; Jacobsen personal observation). However, considering the large size of these parasitic larvae, infected mayflies are likely to suffer some loss of fitness from parasite-induced reductions in resources available for reproduction.

Svensson (1976, 1979) and Tokeshi (1986) investigated the life history and population ecology of *E. ephemerae* and observed several features of its commensalistic association with *Ephemera danica* that reveal its obligate nature including: (1) utilization of nymphs by all larval instars and pupae; (2) failure to observe free-living larvae; (3) the ability of disassociated larvae to actively locate and attach to new hosts; (4) the importance of *Ephemera*, particularly larger nymphs, for completion of the midge's life cycle; and (5) synchronization of the midge population's spring emergence with that of its host. Svensson (1976) suggested that the greater benefits gained by larvae maximizing time on large hosts (enhanced feeding, security) and perhaps facilitated transport of pupae out of the substrate would tend to promote synchronous emergence. Tokeshi (1986) observed constant densities in a population of *E. ephemerae* over a year and considered the security to larvae provided by appropriate sized nymphs to be the most tangible benefit to the midge in this association.

My observations on Nearctic chironomids associated with Ephemeridae indicate that emergence periods for parasitic species (*Epoicocladus* sp. #1, *Nanocladus (Plecopteracoluthus)* sp. #1) populations also coincide with those of their hosts. However, peak emergence of commensal species' populations precedes that of their hosts by several weeks, suggesting that the selective pressures shaping the life histories of these Nearctic commensal species may differ somewhat from those affecting *E. ephemerae*.

### *Evolution of Parasitism in Orthoclaadiinae*

In early reviews of relationships between symbiotic Chironomidae and their aquatic hosts, Edwards (1929) and Henson (1956) suggested that phoresy or

commensalism may represent intermediate stages in an evolutionary progression from free-living life strategies towards parasitism. However, Steffan (1965, 1968) argued that parasitism and phoresy or commensalism within the subfamily Orthocladiinae represent separate, independently derived life strategies within the Chironomidae. He suggested parasitic taxa evolved from either predacious or less intimately associated parasitic ancestors while commensal-phoretic species evolved separately from algal or sediment-detrital feeding ancestors. The discovery of parasitic species of *Epoicocladius* and *Nanocladius* (*Plecopteracoluthus*), both taxa whose larvae were previously believed to be entirely commensal, indicate that at least in two clades within the Orthocladiinae, parasitic species may have evolved from commensal ancestors.

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