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Aquatic xylophagous Orthocladiinae – systematics and ecology

(Diptera, Chironomidae)

By P. S. Cranston and D. R. Oliver

Abstract

Wood-mining Orthocladiinae are reviewed. *Chaetocladius ligni*, the first xylophagous member of the genus, is described as new to science. *Symposiocladius* Cranston, erected for *lignicola* Kieffer, is synonymised with, and treated as a subgenus of, *Orthocladius* Wulp. Extensive morphological variation in *O. lignicola* is recognized and discussed. Observations on the biology of xylophagous chironomids are reviewed with suggestions for further study.

Introduction

Larval Chironomidae occur in the most diverse geographic and habitat ranges of any insect family, from high Arctic lakes, permanent montane snowfields and glaciers through temperate and tropical ecosystems to terrestrial mosses in the Antarctic. In many aquatic biotopes, chironomids may dominate in abundance and even biomass, despite their relatively small size. Studies on systematics and ecology of northern hemisphere Chironomidae have elucidated their importance in lake classification, both extant (e. g. Brundin, 1949; Saether, 1979; Wiederholm, 1976) and historic (e. g. Warwick, 1975), and allowed recognition that chironomid community structure is an integral part of environmental monitoring and assessment of lotic water quality.

A research area that has received rather less intensive study is the rôle of larval chironomids in the decomposition of aquatic immersed wood. Foremost amongst those examining invertebrates in such ecosystems is N. H. Anderson and his associates at Oregon State University. Their work has resulted in both research and review publications (e. g. Anderson et al., 1978; Dudley & Anderson, 1982) and the provision of specimens of wood-mining Chironomidae for systematic studies. This material reveals that taxonomic problems remain and there are still undescribed xylophagous species of ecological significance. We take this opportunity to describe a new species of wood-mining *Chaetocladius* Kieffer, to reassess the taxonomy of *Symposiocladius* Cranston, and to consider the range and diversity of xylophagous Chironomidae. We conclude with some observations on past studies and make suggestions for future research.

Methods and abbreviations

All new material examined is slide mounted in Canada Balsam or Euparal and deposited in the Canadian National Collection, Ottawa, Canada (CNC), unless otherwise stated. Abbreviations of other Institutes are as follows:

OSU – Oregon State University, Corvallis, Oregon, U.S.A.
BMNH – British Museum (Natural History), Cromwell Road, London, England.
MZBN – Museum of Zoology, Bergen, Norway.
USNM – United States National Museum, Washington, D. C., U.S.A.
ZSBS – Zoologische Staatssammlung, Munich, German Federal Republic.

Morphological terminology follows SAETHER (1980). Other abbreviations used in text: dc$_{1-4}$ – Pupal dorsocentral setae; Fe – Femur; L. – Larva; Le. – Larval exuviae; L. R. – Leg ratio = Length of tarsomere 1: Length of tibia; P. – Pupa; Pe. – Pupal exuviae; pc$_{1-3}$ – Pupal precorneal setae; Ta$_{1-5}$ – Tarsomeres; Ti – Tibia.

Chaetocladius (Chaetocladius) ligni spec. nov.

Adult male (n = 5):

Body length 2.8–3.4 mm, wing length 1.48–1.82 mm.

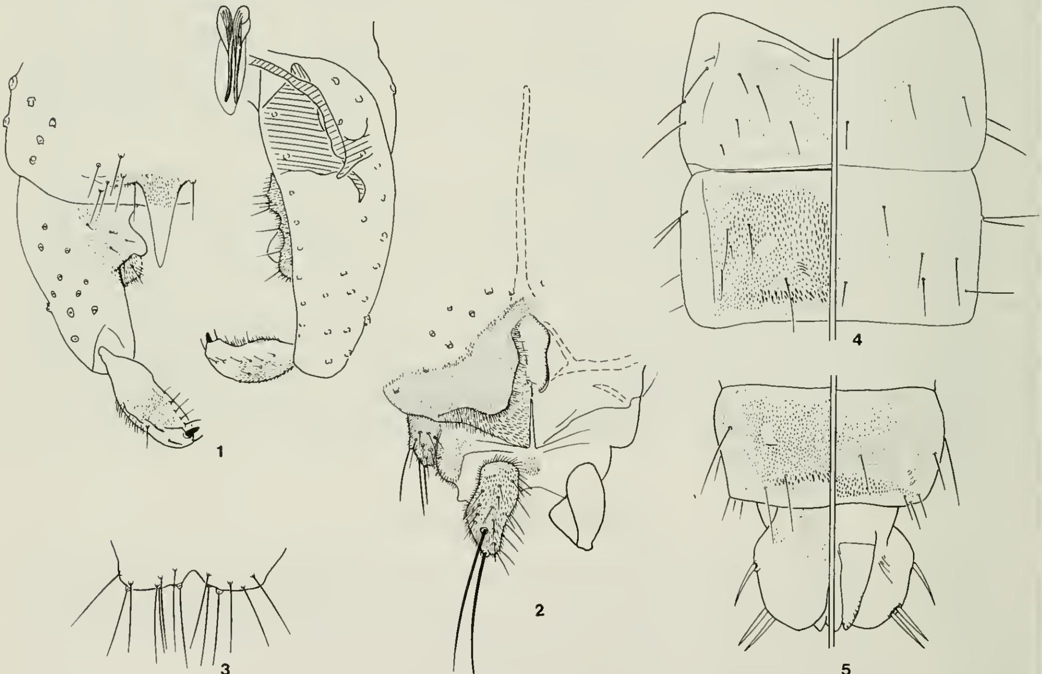
Antennal ratio 0.55–0.99, apical flagellomere 213–340 μm long. Head with 3–5 inner verticals continuous with 6–9 outer verticals and postorbitals; 7–10 clypeals; palp segment 4 shorter than 3rd and 5th segments, 5th segment longer than 3rd.

Thorax with 7–9 lateral antepronotals, 13–18 uni– to partly biserial dorsocentrals, 5–8 uniserial posterior prealars, 6–10 uniserial scutellars.

Wing with obtuse anal lobe, brachiolum with 1 setae, R with 5–21 setae, R$_1$ with 5–9 setae, R$_{4+5}$ with 12–21 setae; 5–8 squamals.

Legs with pseudospurs on tarsomere 1 and 2 of mid and hind legs; tarsomere 1 of mid leg with 0 sensilla chaetica, hind leg with 0–3 sensilla chaetica on apical one-quarter and sometimes also on middle third; pulvilli small. Fore leg ratio, 0.71–0.76; mid leg ratio, 0.42–0.47; hind leg ratio, 0.55–0.58.

Hypopygium (Fig. 1) with long, narrow anal point. Virga consisting of cluster of long, dark spines. Gonocoxite with dorsal part of inferior volsella narrow, bare, apically rounded and slightly curved posteriorly; ventral part variable in shape, usually rounded, sometimes almost absent. Gonostylus with rounded outer corner and low, broad, crista dorsalis.



Figs. 1–5. *Chaetocladius ligni* spec. nov. Adult male, – 1 Hypopygium . Adult female, – 2 genitalia, – 3 tergite IX. Male pupa, – 4 segments I and II, left tergites, right sternites, – 5 segments VIII and anal end, left dorsal, right ventral.

Adult female (n = 2):

As male, except, wing length 1.66–1.82 mm.

Antenna with 5 flagellomeres, apical flagellomere with strong apical seta. Head with 11–12 temporals, 10–13 clypeals.

Thorax with 9–12 lateral antepronotals, 26–33 dorsocentrals, 8–9 posterior prealars, 9 scutellars.

Wing with obtuse (almost right-angled) anal lobe; R with 18–20 setae, R_1 with 12–16 setae, R_{4+5} with 29–30 setae; 6–9 squamals.

Legs. Tarsomere 1 of mid leg with 27 (n = 1) sensilla chaetica on distal two-thirds, hind leg with 29–32 sensilla chaetica on distal two-thirds. Fore leg ratio, 0.74–0.75; mid leg ratio, 0.41–0.45; hind leg ratio, 0.56.

Genitalia (Fig. 2) very similar to those illustrated for the genus by Sæther (1977, fig. 54 A–C) except concavity of distal margin of tergite IX deeper (Fig. 3). Also 2 long, strong setae arise from each cercus.

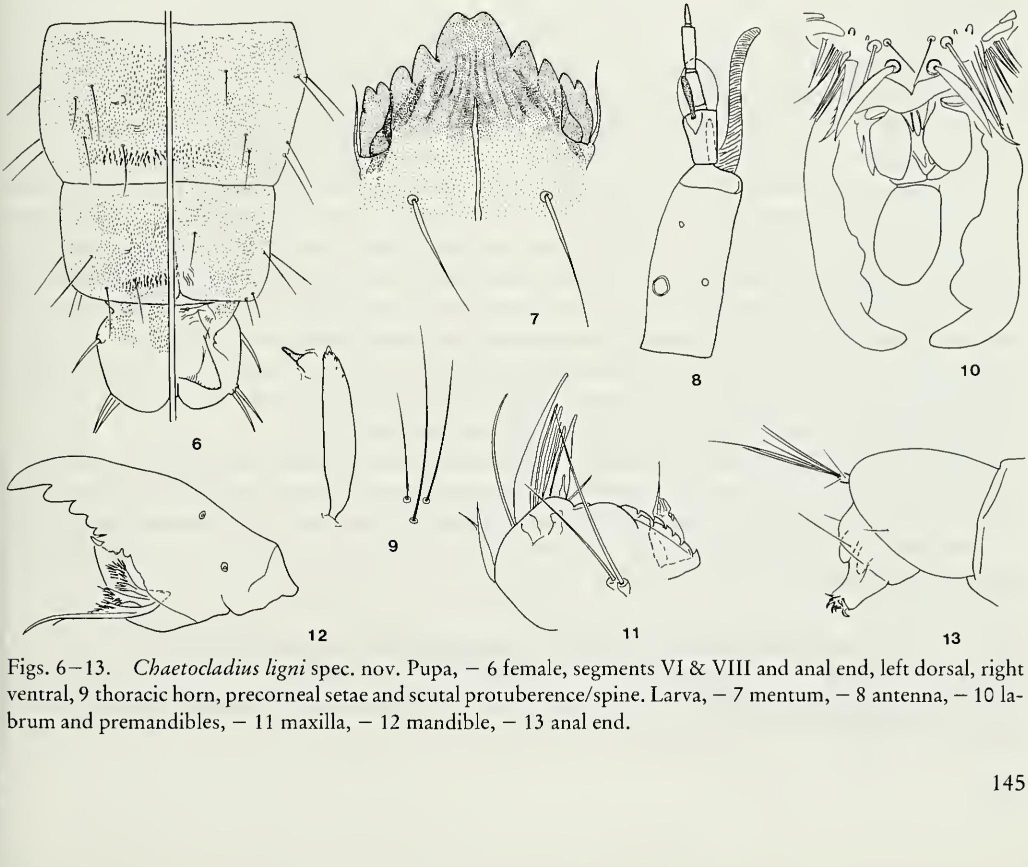
Pupa (n = 12):

Length, 2.9–3.7 mm.

Frontal apotome with small frontal seta on small cephalic tubercle.

Thoracic horn cylindrical with spinose apex (Fig. 9), 112–165 μm long. Narrow, pointed to bluntly rounded tubercle on scutum dorsomedial to base of thoracic horn (Fig. 9).

Tergites II–VIII covered with coarse spinules grading into posterior spine band; sternites with weak shagreen on II becoming more extensive and stronger on successive posterior sternites; posterior margin of sternite VIII straight with spines (♂) or bilobed without spines (♀) (Figs. 4–6). All L-setae hair-like. Anal lobe broad with outer margin up-curved; megasetae about 10× as long as wide, with middle megaseta located close to posterior megaseta (Figs. 5, 6).



Figs. 6–13. *Chaetocladius ligni* spec. nov. Pupa, – 6 female, segments VI & VIII and anal end, left dorsal, right ventral, 9 thoracic horn, precorneal setae and scutal protuberence/spine. Larva, – 7 mentum, – 8 antenna, – 10 labrum and premandibles, – 11 maxilla, – 12 mandible, – 13 anal end.

Larva, Fourth instar (n = 15):

Antenna (Fig. 8) five-segmented with segments consecutively shorter or segments 3 and 4 subequal; antennal blade ending at level of segment 5; Lauterborn's organs large, subequal in length to segment 3. Antennal ratio, 1.06–1.43 (n = 13).

Labrum (Fig. 10) with anterior part folded under frontoclypeus; SI smooth, lamelliform, S II and S III smooth, S IV consisting of 2 simple pegs; labral lamellae absent; labral chaetae and spinulae smooth with chaeta media serrate on one margin; pecten epipharyngis consisting of 3 small spines; median pair of chaetulae laterales large, rectangularly rounded, covering rest of chaetulae; chaetulae basales with bifid apex; basal sclerite large.

Premandible with 1 apical tooth and low-rounded accessory tooth; brush weak.

Mandible (Fig. 12) 144–166 μm (n = 11) long with short apical tooth and 4 inner teeth; seta interna with 5 serrate branches and 1 long smooth to serrate branch.

Mentum (Fig. 7) with long apically bifid median tooth and 4 pairs of shorter lateral teeth; lateral notch present at level of base of 4th lateral tooth; ventromental plates small.

Maxilla (Fig. 11) with weak pecten galearis.

Abdomen (Fig. 13) with preanal segment curved over remaining posterior segments; procercus with 6 anal setae, directed posteriorly.

Type-material: Holotype ♂ slide-mounted in Canada Balsam: U.S.A., Oregon: Benton County, Berry Creek, 15.X.1984 (mass reared from immersed wood) (N. H. Anderson) (CNC No. 19701). Paratypes: U.S.A., Oregon: same locality as holotype, 12.X.1982–12.XI.1984 (mass reared from immersed wood) (N. H. Anderson) (1 ♀, 2 ♂ P. with associated Le., 1 ♀ P., 11 Pe., 20L.); Crook County, Allen Creek, 26.VIII.1978 (T. Dudley) (1 ♀ P.), Ochoco Creek, IX.1978 (T. Dudley) (1 ♂); Lake County, Mack Creek, 7.VII.–28.IX.1982 (mass reared from immersed wood) (N. H. Anderson) (2 ♂♂, 1 ♂ with associated Pe., 1 ♀, 1 P., 2 L.) (BMNH, CNC, MZBN, USNM, ZSBS).

Remarks:

Adult males of *C. ligni* are similar to those of *C. melaleucus* (Meigen) (Edwards, 1929; Pinder, 1978), differing by having a lower antennal ratio and a smaller inferior volsella. The presence of two long cercal setae will distinguish the adult females from all other *Chaetocladius* including *C. melaleucus* (see Goetghebuer, 1942). Also the immature stages do not equate with the adult male resemblance (see Pinder & Armitage, 1985, for detailed descriptions of the immature stages of *C. melaleucus).*

The distinctive scutal tubercle is not known to occur on other *Chaetocladius* pupa except on a single pupal exuviae mass reared from immersed wood (Québec, Gatineau Park, stream nr. Beech Grove, 5.VI.1985, P. S. Cranston & M. E. Dillon). This exuviae, otherwise similar to *C. ligni,* has an almost smooth thoracic horn and short (c. 3× as long as wide), thorn-like megasetae. An adult male obtained, at a later date, from the same rearing container cannot be distinguished from *C. ligni.* At present, it is not possible to determine if the pupal differences are due to variation because of the absence of larvae and positive association of the two life history stages. Therefore, eastern specimens, including an adult male from New Hampshire (White Mountain National Forest, Ammonoosuc River, 26.V.1981, D. R. Oliver & M. E. Roussel) are not included in the type series of *C. ligni.*

The larva differs from the generic diagnosis of Cranston et al. (1983) plus the addition by Pinder and Armitage (1985). SI is simple not serrated, plumose or branched, the premandible has 1 tooth apically, not 2, the basal sclerite is large, and the preanal segment is curved over the posterior segments. Furthermore, the mentum has only 4 lateral teeth although the lateral notch may be the remains of the notch between the 4th and 5th lateral teeth.

Orthocladius Wulp subgenus Symposiocladius Cranston stat. nov.

Orthocladius Wulp, 1874: 132. Type-species: *Tipula stercoraria* DeGeer, 1776: 388 sensu Wulp (misident.) (des. Coquillett, 1910: 581) = *Chironomus oblidens* Walker, 1856.

Symposiocladius CRANSTON, 1982: 419. Type-species: *Orthocladius lignicola* Kieffer in POTTHAST, 1915: 273 (orig. des.). Syn. nov.

Symposiocladius was erected for the xylophagous *Orthocladius lignicola* Kieffer, a species with a highly distinctive larva, but closely resembling *Orthocladius (Orthocladius)* in pupa and adult (CRANSTON, 1982). The major reason given for the erection of a new genus was the presence of the larval abdominal l_4 seta developed as a setal brush, which Cranston described as an unique inside parallelism/underlying synapomorphy for the lineage *Synorthocladius* to *Cricotopus* (i. e., excluding *Orthocladius).* Two recent discoveries expose the fallacy of this reasoning: *Orthocladius annectens* Saether has previously unrecognized larval setal tufts and, since there is no doubt that *annectens* is truly an *Orthocladius*, setal tufts do occur in the *Orthocladius* lineage. Furthermore, *lignicola* larvae with only simple abdominal l_4 setae are now known (see below). The case well illustrates the erroneous nature of phylogenetic reasoning based upon ambiguous characters, particularly the use of non-unique derived character states ("underlying synapomorphies").

However, since the larva is highly distinctive and the pupa and female can be distinguished from other subgenera of *Orthocladius*, *Symposiocladius* can be retained as a subgenus of *Orthocladius* s. l. until the phylogeny is assessed and the ranking of other taxa presently given generic status, such as *Stackelbergina* Shilova and Zelentzov, is resolved.

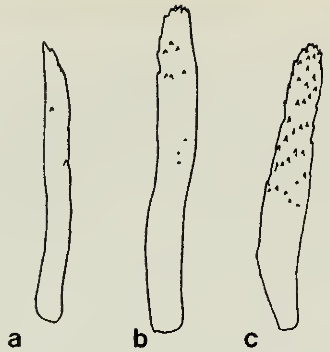
Orthocladius (Symposiocladius) lignicola Kieffer

Orthocladius lignicola Kieffer in POTTHAST, 1915: 273; CRANSTON, 1982: 421. Type-locality: West Germany, Sauerland, Haspersperre. Lectotype pupa examined CRANSTON, 1982: 421 (ZSBS).

CRANSTON (1982) described all stages of *O. lignicola* – "typical" *lignicola* in this discussion refers to this description. All specimens are closely associated as larvae with wood immersed in running water. Localities referred to in the discussion are cited in detail below.

In Berry Creek, *O. (Symposiocladius)* larvae (n = 100+) virtually always have a simple, or at most 2 branched abdominal l_4 seta and have more or less fused lateral mental teeth (Fig. 15 a) but otherwise resemble typical *lignicola*, with all measurements falling into the lower end of the range cited (CRANSTON, 1982: 426). This larval type ("A") is associated with pupae (type "A") lacking frontal setae, with a weakly spinose thoracic horn (Fig. 14 a) 200–280 μm long (n = 40), and with a blunt spinose apex to the anal lobe (Fig. 16 a). Adult males from Berry Creek fall towards the small end of the ranges cited by SOPONIS (1977: table ZZ, as *tryoni)* except for the terminal antennal flagellomere (450–550 μm long) and antennal ratio (0.98–1.18, n = 9) which fall at or below the cited range. Females cannot be distinguished from typical *lignicola* (CRANSTON, 1982: 421). Despite the apparent identity of the genitalia of both sexes, the low male antennal ratio, simple larval l_4 seta, absence of pupal frontal setae and differences in pupal anal lobe conventionally would indicate specific distinction. However, from Berry Creek we have seen a single *O. (Symposiocladius)* larva with fused lateral mental teeth, but with abdominal l_4 setal tufts with 6–8 branches about 80 μm long (typical *lignicola* have 20+ branches, up to 160 μm long) and one typical *lignicola* pupa with pharate adult (terminal flagellomere 620 μm long, antennal ratio 1.4). Furthermore a single prepupal larva of type "A" from Yukon contains a pupa with typical *lignicola* curved spinose apex to the anal lobe, but the frontal setae and thoracic horn cannot be seen.

In Mack Creek only typical *lignicola* larvae have been found (n = 25). Pupal exuviae derived from mass rearing from colonised immersed wood (not directly associated) all have a curved, spinose anal lobe apex typical of *lignicola*, a rather densely spinose cigar-shaped thoracic horn (Fig. 14 c), length 165–201 μm, but lack frontal setae (n = 17). This pupal type is associated with typical *lignicola* larvae associated with prepupae and a pupa from Starvation Creek. Mass rearings from immersed wood from Mack Creek give rise to males with a relatively long apical flagellomere (c. 600–650 μm) but rather



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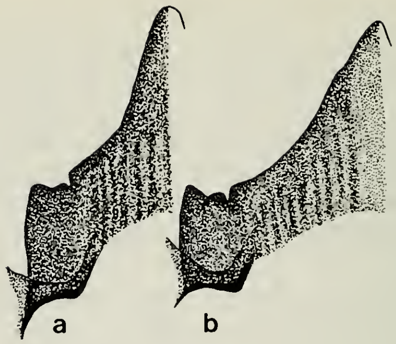

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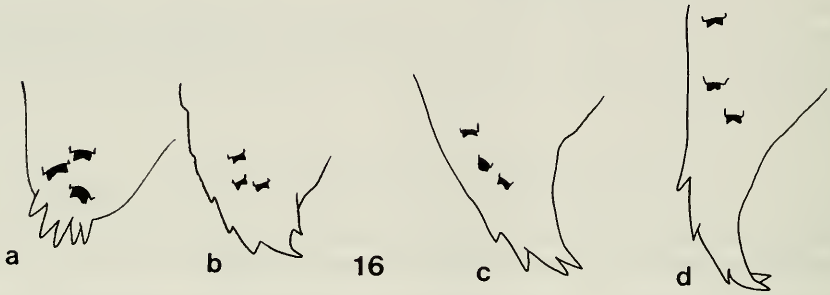

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Figs. 14–16. *Orthocladius (Symposiocladius) lignicola* Kieffer. Pupa, – 14 thoracic horn (a – Berry Creek, b – Beech Grove, c – Mack Creck), – 16 apex of anal lobe (a – Berry Creek, b and c – Beech Grove, d – Mack Creek). Larva, – 15 mentum (a – Berry Creek, b – Beech Grove).

low antennal ratio (1.2–1.3). This Mack Creek pupal type also occurs in Flynn Creek, together with type "A" pupae. Both typical *lignicola* and type "A" larvae were present, but no associations are available.

Re-examination of most of the material studied by Cranston (1982) confirmed that none of these "aberrant" types mentioned above were present, unrecognized, and showed that frontal setae (omitted from the description) were invariably present in earlier examined Nearctic and Palaearctic specimens. However, the low antennal ratio (relative to the mean value) cited by Soponis (1977: table ZZ) suggests that some adults associated with the larval types above are included, since adults associated with typical *lignicola* larvae and pupae tend to have an antennal ratio of at least 1.5.

In order to resolve the status of the specimens discussed above, immersed wood, mostly *Alnus* sp., known to contain *O. (Symposiocladius)* larvae was collected in mid-June and again in mid-July from a stream in Gatineau Park near Beech Grove. This was kept in an oxygenated aquarium cooled to approximately 12°C and emergent adults, cast skins and pharate adults were collected at intervals over the ensuing four months. Individual rearings were not possible since *lignicola* larvae are easily damaged in handling and die very readily. However, some larval/pupal and pupal/adult associations were made through failed emergence at the aquarium water surface. All larvae examined ($n = 29$) are typical *lignicola,* with well developed setal tufts, although the lateral mental teeth division is somewhat variably developed (Fig. 15b). Most pupae ($n = 38$ of 40) have frontal setae, a moderately spinose thoracic horn 220–275 μm long (Fig. 14b) and an anal lobe intermediate (Figs. 16b–c) between that of type "A" and typical *lignicola* (Figs. 16a, 16d). One pupa, otherwise similar to this, has only 1 scar of a frontal seta on one side of the frons, with no trace on the other side. One pupa has no trace of frontal setae, a weakly spinose thoracic horn 160 μm long and a blunt spinose apex to the anal lobe, closely resembling pupal type "A". The pharate adult within this pupa has an apical flagellomere length 415 μm and antennal ratio of 1.13. Adult males associated with the dominant pupal type in this mass rearing could not be distinguished from typical *lignicola*, having an apical flagellomere 540–640 μm long and antennal ratio of 1.4–1.6 (n = 10). Adult females cannot be distinguished from typical *lignicola*.

Clearly, from the evidence above, it is impossible to recognize separate species which can be confirmed from all life history stages. The adult males could be divided into those with an antennal ratio below 1.2 and a relatively short apical flagellomere (for example, below 550 μm) and those with a higher antennal ratio and longer apical flagellomere, but there is virtually continuous variation in these characters. There is remarkably little variation in both absolute size and wing length in all specimens examined, with the range less than 10% each side of the mean, thus it is unlikely that the increased length of the apical flagellomere and antennal ratio is explained by allometry. Although the low antennal ratio male is apparently associated with the type "A" larva and pupa, this is not exclusively so. The highest values of antennal ratio and apical flagellomere length are found in association with typical *lignicola* larvae and pupae in Nearctic and Palaearctic populations. Intermediate values of antennal ratio and apical flagellomere length are found in Mack and Flynn Creek and Québec populations which have typical *lignicola* larvae but at least 3 different combinations of pupal characters. However, there is no detectable correlation between pupal characters of the anal lobe, frontal setae and thoracic horn and the complex tergal and sternal spine patterns, pedes spurii A and B and thoracic setation. Adult females, increasingly recognised as valuable in the detection of cryptic species, are relatively invariate and indicate a single species.

In each intensively sampled habitat more than one pupal type occurs, but this is not always correlated with the occurrence of more than a single type of larva or male. The variation evident in the Québec pupae, for example is not evident in larvae or adults. We conclude by suggesting that on present evidence *O. lignicola* is a single species and cannot yet be divided.

At present, it is not possible to explain the variation seen in *lignicola*, although several possibilities can be raised. There may be a clinal variation in the length of the apical antennal flagellomere and antennal ratio. The highest values for both are found in the easternmost populations examined in Québec and the lowest values in Oregon. Superimposed on this, there is some evidence that winter (Oregon) or spring (Québec) adults have a lower antennal ratio and shorter apical antennal flagellomere than adults emerging later. This must be analysed in more detail, with more individual associations of all life history stages and with control over the effect of rearing in laboratory cultures.

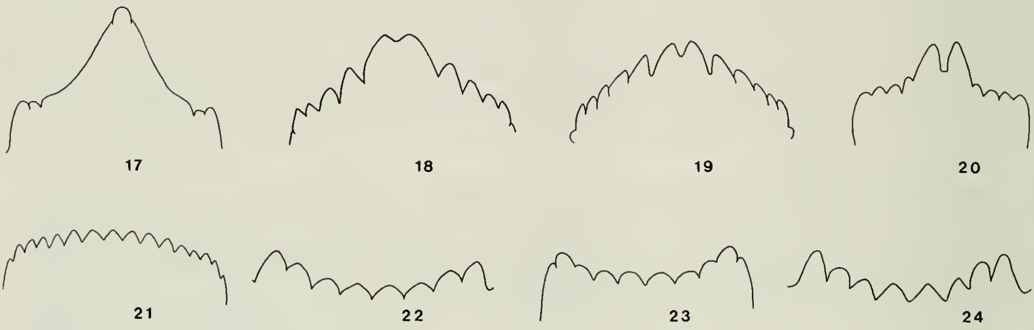
The apparently excessive variation in *O. lignicola*, in characters that are believed to be of specific importance in other taxa, might suggest a faulty species concept or inability to discriminate closely related species. However, recognition is growing that some taxa do show high variation in terms of traditional characters used in delimitation of chironomid species. For example, the hygropetric *Orthocladius (Eudactylocladius) fuscimanus* Kieffer and *O. (E.) dubitatus* Johannsen both show as much variation as does *O. lignicola*. In all cases the variation is demonstrated to be intraspecific through recognition of high variation present within a single population.

New material examined: CANADA, Yukon Territory: Alaska Highway, Watson Lake Campground, 60°07′ N, 128°48′ W, 23.V.1982 (E. Fuller) (1 prepupal L.); Québec: Pontiac County, Gatineau Park, 8 km N. Beech Grove, 45°35′N, 76°8′W, 18.V.1983 (D. R. Oliver & M. E. Roussel) (3 Pe.), 17.VI.1985 (mass reared from immersed wood) (P. S. Cranston and M. E. Dillon) (10♂♂, 8♀♀, 1♂ and 1♀ with associated Pe., 1 P. with associated Le., 44Pe., 29L., slide mounted, many more in spirit); Missisquoi County, 1 m. N. Abercorn, (reared ex *Acer*) 19.–27.VIII.1980 (A. Borkent) (3♂♂, 1♀ P. with associated Le., 9Pe.,). U.S.A., Oregon: Benton County, Berry Creek, 14.–28.VII.1982 (mass reared from immersed wood) (N. H. Anderson) (9♂♂, 1♂ with associated Pe., 10♀♀, 1♀P. with associated Le., 40Pe., 100+L); Lincoln County, Flynn Creek, 30.VII.–28.XII.1982 (mass reared from immersed wood) (N. H. Anderson) (2♂♂, 1♂P., 1♀P., 8Pe., 20+ L.); Lane County, Mack Creek, 7.VII.–28.IX.1982 (mass reared from immersed wood) (N. H. Anderson) (3♂♂, 17Pe., 20+ L.); Hood River

County, w. of Hood River, Starvation Creek, 27. VI. 1981 (A. Borkent) (1 Le. with associated prepupa, 5 L.). Some Berry, Flynn and Mack Creek specimens in collection of N. H. Anderson (OSU), remainder in CNC.

Discussion

A major impediment to the elucidation of the rôle of Chironomidae in aquatic wood decomposition, even in the best studied north temperate regions of the world, has been taxonomic. For example, Cranston (1982) traced the first discovery of a distinctive larva (called *"acutilabis")* to Konstantinov (1948), yet it was 30 years before its xylophagy was established, despite Thienemann's knowledge that the eventually associated pupa and adult belonged to a xylophage (hence the specific name *lignicola* given by Kieffer). Similarly, although the genus *Stenochironomus* Kieffer has been known to include wood-mining larvae since Zablotskii (1939), it was not until Borkent's (1984) monograph that its great taxonomic diversity and the wood-mining of its relatives was revealed.



Figs. 17–22. Larva, outline of anterior margin of mentum. – 17 *Orthocladius (Symposiocladius) lignicola* Kieffer, – 18 *Chaetocladius ligni* sp. nov., – 19 *Limnophyes* sp. ident., – 20 *Xylotopus par* (Coquillett), – 21 *Polypedilum (Polypedilum) fallax* (Johannsen), – 22 *Harrisius pallidus* Freeman, – 23 *Stenochironomus (Stenochironomus) hilaris* (Walker), – 24, *Xestochironomus subletti* Borkent.

There are several reasons for the relative paucity of taxonomic studies, including failure to include woody substrates in routine aquatic invertebrate surveillance, difficulties in sampling immersed wood and the fragile nature of many xylophagous larvae. However, there is no doubt that suitably located immersed wood of an appropriate age, especially *Alnus* spp., may have dense mixed populations of wood-mining Chironomidae, contributing substantially to the diversity and biomass of the aquatic biota. For example, Kaufman (1983) reported an annual standing biomass of 5000 mg/m^2 of *Xylotopus par* (Coquillett) and Anderson (in prep), a lower figure of 57 mg/m^2 from a mean of 618 *C. ligni* and *O. lignicola*/m^2. Sampling can pose difficulties and assessment of adult emergence from rearings from aquarium retained wood may avoid many problems. However this method, widely used by Anderson and his colleagues, only allows, at best, circumstantial larval/adult associations. Furthermore, wood held in the laboratory gives rise to adult emergence from both xylophages and insects using the wood surface as a substrate for other feeding methods. High pressure hosing of the wood after recovery from the aquatic habitat may remove many non-stenotopic invertebrates, but ambiguity remains. However, obligate wood feeders starve if removed from wood. Thus the optimum method to obtain associations of xylophagous larva, pupa and adult is to mass rear in natal wood, obtaining larval head capsules by recovery from mines that contain pupae whose identity can be established through pupal/adult associations either as pharate adults or through partial emergence.

Mass rearing, as discussed above, does not readily discriminate between obligate xylophages and other benthic insects associated in a less stenotopic manner with woody substrates. Discussions concerning xylophagy are handicapped by our still limited knowledge of the precise nature of associations with wood. A major criterion is the making of mines or galleys in wood, and/or the domination of the larval gut contents by wood. Even observations on gut contents may be ambiguous, since insects deriving epilignic nutrients (from superficial components on immersed wood) will ingest non-dietary wood fibres, particularly from extremely soft and decomposing woods. Analyses of xylophagous chironomid guts to establish the presence either of cellulases or a symbiont cellulose decomposer fauna, required to confirm stenoxylophagy, have been made only in *X. par* (Kaufman et al., 1986) and even this study failed to demonstrate cellulase activity of gut microflora. Therefore, our assessments of habit are of necessity somewhat circumstantial, but we present the following list and categories of xylophagous Chironomidae:

Taxa strongly suspected of being obligate xylophages, only found mining in immersed wood, and with guts consistently filled with wood fibres, include: Chironominae: *Stenochironomus (Stenochironomus), Harrisius* Freeman and *Xestochironomus* Sublette & Wirth species (Borkent, 1984); *Polypedilum (Polypedilum* Kieffer), including at least Nearctic *fallax* (Johannsen) (Johannsen, 1937, Roback, 1953); Orthocladiinae: *Chaetocladius ligni* sp. nov.; *Orthocladius (Symposiocladius) lignicola* Kieffer (Cranston, 1982); *Xylotopus par* (Coquillett) (Oliver, 1982; 1985).

Taxa which may be obligate xylophages but confirmation is lacking include: Chironominae: *Glyptotendipes (Phytotendipes) testaceus* Townes (reared from a water soaked log in Arkansas, Derreoux Creek, W. Pine Bluff, route 270, 12. III. 1972, H. Teskey, C. N. C.); other perhaps misidentified *Glyptotendipes,* including *gripekoveni* (Kieffer) from the Netherlands (Gripekoven, 1914) *glaucus* (Meigen) (= *pallens* [Meigen]) from England (Burtt, 1940) and *"dendrophila"* from the Soviet Union (Zvereva, 1950); Orthocladiinae: *Limnophyes* sp. indet. unreared from Oregon streams, perhaps associated with *L. pilicistulus* Saether adults emerged from laboratory mass rearings of immersed wood (N. H. Anderson).

Taxa with distinct associations with immersed wood, but either unsubstantiated as miners and/or having a wood diet: Chironominae: *Stelechomyia perpulchra* (Mitchell) from S. E. USA (Reiss, 1982); *Polypedilum (Polypedilum)* including palaearctic *pedestre* (Meigen); Orthocladiinae: *Brillia*, particularly *flavifrons* group species in Palearctic and Nearctic regions; Diamesinae: *Pagastia* larval type A of Oliver and Roussel, 1982 (Nearctic observations by Cranston).

Many other Chironomidae have been recorded from immersed woody substrates but the nature of the wood association is unclear. For example, many of the genera listed by Dudley and Anderson (1982) appear to be no more than casual visitors using the wood as either resting sites or for feeding. Our categories above reflect our knowledge of mining: we have too little evidence to consider the rôle of these epiphytic taxa in wood degradation.

The wood mining taxa listed above show no close phylogenetic relationships to one another, with the exception of internal relationships within the *Stenochironomus* complex. Thus several unrelated (or at least very distantly related) taxa have come to occupy aquatic woody microhabitats. Three subfamilies are represented: the Diamesinae, Orthocladiinae and Chironominae. Only within the *Stenochironomus* complex (Borkent, 1984) is there evidence of species formation in a monophyletic grouping probably following ancestral adoption of the wood mining habit (Borkent, 1984). In other taxa here considered the mining habit has been independently acquired. Phyletically close relatives of mining taxa tend to be rheophilic and, where known, appear to be Aufwuchs grazers. Taxa in which mining is probable, but not established with certainty, include some species that otherwise burrow in immersed leaves *(Brillia, Stelechomyia, Polypedilum).* Since there are examples of presumed wood mining in which the immersed wood is so soft that it is friable by hand, there may be little distinction between grazing on immersed leaf surfaces and on soft wood. In either case, the source of nutrition may be other than wood derived cellulose since the chironomid gut contents frequently contain algae and fungi in addition to wood fibre.

Given that wood mining Chironomidae are not related, are there morphological features (convergences) associated with the larval habit? One of the few characteristics that unite many miners, irrespective of subfamily, is the very flimsy body cuticle, which cannot support the flaccid larva outside the mine. This is particularly striking in *O. (Symposiocladius)* and *Stenochironomus,* less so in *Xylotopus,* and explains the fragility of the larva leading to larval death if extracted live from wood for rearing. Within the Orthocladiinae, structures of the wood miners' head capsule show some convergence, with the mental teeth characteristically elongate (Figs. 17–20) and heavily sclerotised relative to non-mining congeners or close relatives. Other similarities include the broadening and shortening of the mandible and the narrowing of the anterior labrum, with a folding of the anterior part beneath the frontoclypeus in such a way that it cannot be flattened readily for microscope examination. In *C. ligni, O. (S.) lignicola* and the undescribed mining *Limnophyes* species referred to above, the S I seta is simple compared to the condition in congeners, but there is little evidence of any further reduction in head capsule appendages such as the antenna, maxilla, and labral chaetae, or in the abdominal appendages (prolegs, procerci, and anal tubules). In contrast, the obligate wood miner *X. par* lacks these orthocladiine character state changes associated with the mining habit, with the exception of the lateral compression and strong folding of the labrum beneath the frontoclypeal apotome.

In contrast to the Orthocladiinae, mining Chironominae do not have an anteriorly projecting median part of the mentum (Figs. 21–24). *Stenochironomus* do indeed have a modified mentum, but this mentum is transverse with very reduced teeth. The very great reduction of the striae of the ventromental plates is also characteristic, is perhaps associated with a loss of silk making and is part of a transformation series that includes non-wood mining species. *Polypedilum* miners appear little different from non-mining congeners and neither does *Glyptotendipes testaceus* differ greatly from its non-(wood) mining relatives. The diamesine *Pagastia* (larval type A) has a most curiously modified mentum with the teeth obscured by lying ventral (and posterior) to a continuous ventromental plate (Oliver & Roussel, 1982, fig. 4). It is impossible to speculate on how this unusual structure may be related to feeding, let alone to wood mining.

Although much work remains to be done, some ecological generalisations can be made concerning wood-mining Chironomidae. Firstly, mining Chironomidae may be locally abundant but by no means all immersed wood contains larvae. In lotic systems, suitable wood must be anchored in the current, but not such that it becomes covered in sediment. Mining Orthocladiinae are not found in poorly oxygenated running waters, although at least in Britain, *O. (S.) lignicola* larvae can tolerate high organic loadings in fast current. In contrast to the situation in lotic systems, Orthocladiinae are much less common in lentic habitats, where Chironominae (notably *Stenochironomus)* dominate the wood-mining chironomids. Once again, immersed wood must be free from sediments for successful colonisation (A. Borkent, pers. comm.).

The quality and texture of wood is important in relation to the frequently observed differences in colonisation of different wood species. For example, it is a common observation that alder (*Alnus* spp.) in the Holarctic, and maple *(Acer)* in the Nearctic, are strongly preferred substrates for many miners. Unquantified observations in Britain show that in a stream known to support *O. lignicola,* freshly placed *Alnus* branches were colonised after five winter months and larvae were not found in any other immersed wood, ranging from oak *(Quercus)* to pine *(Pinus). O. lignicola* is most abundant in wood so recently immersed that a knife is required to excise larvae and is not found in soft wood. In contrast, *X. par* and *Pagastia* larval species A appear to be most abundant in wood friable enough to crumble by hand. However, faunal succession in relation to temporal changes in wood quality are little known at present. The rôle of chironomids in wood breakdown and their dietary use of apparently refractory wood and/or associated microbial flora are poorly understood and elucidation through further study is required.

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Dr. P. S. Cranston,
ANIC
CSIRO Entomology
Canberra, ACT 2601, Australia

Dr. D. R. Oliver,
Biosystematics Research Centre,
Agriculture Canada, Ottawa K1A 0C6, Canada

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