The identity of *Dactylocladius commensalis* (Diptera: Chironomidae) revealed

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Abstract

The chironomid species commensal on Blephariceridae described as *Dactylocladius commensalis* Tonnoir, 1923 from New Zealand has remained enigmatic since its first discovery. The taxon has not been restudied despite the apparent strong commensal/phoretic affinity of the aquatic immature stages with species of the common blepharicerid genus *Neocurupira* Lamb, 1913, especially species belonging to the *hudsoni* complex in which occurrence can reach 100% of all populations. The genus *Dactylocladius* Kieffer, 1906 is no longer meaningful because the type species is lost and of uncertain identity and is treated as a nomen dubium. Here the species is recognised from recently collected material by the congruence of morphology of all life history stages to the original description, and the tight association with torrenticole blepharicerid larvae. Phylogenetic analyses suggest that it is close to certain austral Orthocladiinae, namely *Kaniwhaniwhanus* Boothroyd, 1999, *Botryocladius* Cranston & Edward, 1999, *Pirara* Boothroyd & Cranston, 1995, and especially *Naonella* Boothroyd, 1994. A new genus, *Tonnoirocladius* gen. n. is established for the species *Tonnoirocladius commensalis* (Tonnoir) (comb. n.), since it differs substantially from the putative sister genus, the New Zealand *Naonella*.

Keywords: Chironomidae, Orthocladiinae, New Zealand, Blephariceridae, commensalism, phoresy

Introduction

Commensalism involving chironomid larvae and other aquatic insects is very common and globally widespread; evidently at least some cases involve ectoparasitism. Host organisms include Odonata, Ephemeroptera, Megaloptera and Hemiptera and fish (Tokeshi 1993; Roque et al. 2004). Dipteran hosts are unusual and the description by Tonnoir (1923) of a commensal chironomid, *Dactylocladius commensalis* Tonnoir, on New Zealand larval Blephariceridae remains a rare observation. Since the first report and description, our understanding of *Dactylocladius* Kieffer has altered (to nomina dubia in the absence of a genotype) and the identity and relationships of this commensal taxon has never been clear. With recent material collected by Peter Zwick and Greg Courtney, and in the light of recent descriptions of some ‘more obscure’ southern hemisphere genera of Orthocladiinae.
(e.g. *Kaniwhaniwhanus* Boothroyd, 1999; *Naonella* Boothroyd, 1994; *Botryocladius* Cranston & Edward, 1999; *Pirara* Boothroyd & Cranston, 1995) it is timely to redescribe the species and seek features to allow assessment of its relationships, and thus its generic placement. Morphological and preliminary molecular analyses have been undertaken to this end.

**Material and methods**

Specimens were removed from larval Blephariceridae either by the collector (P. Zwick or G. W. Courtney), or by the author, or found in vials in which Blephariceridae had been stored. The freshest specimens were transferred to high-strength isopropanol for DNA extraction and molecular sequencing. Microscope slides were prepared using either Euparal mountant after clearing and neutralising or Hoyers mountant, subsequently ringed, both for larvae, pupae and pharate adults (i.e. developed, retained within their pupal exuviae). No free adults have been studied—all adult descriptions are based on pharates and thus limited in ability to interpret some features. Standard terminology following Sæther (1980) and Cranston (1994) is used.

The following acronyms are used for the institutions where material is located:

- **ANIC** Australian National Insect Collection, CSIRO Entomology, Australia
- **BMNH** Entomology Department, The Natural History Museum, Cromwell Road, London, UK
- **NZAC** New Zealand Arthropod Collection, Entomology Division, Landcare Research New Zealand Ltd., Private Bag 92170, Auckland, New Zealand
- **ZSM** Zoologische Staatssammlung, Munich, Germany

**Taxonomy**

*Tonnoirocladius* Cranston, gen. n. (Figures 1–16)

*Type species.* *Dactylocladius commensalis* Tonnoir, 1923, by monotypy and present designation.

*Etymology.* From *Tonnoir* – the Belgian-born, antipodean-adopted Dipterist André Léon Tonnoir, discoverer of this unusual taxon, and – *cladius*, a branch, as in clade.

*Diagnosis*

The larva has SI bifid with weak inner branch, mentum with broad median tooth flanked by double sclerotised layers perhaps equating to ventromental plate(s), with dense beard of fine simple setae, mandible with large gap between innermost tooth and mola, with one of the anal tubules protruding antero-medially. The pupa lacks a thoracic horn and hooklets on tergite II, tergites III–VIII each with anterior transverse bands of spinules and posterior transverse band on conjunctiva of anteriorly-directed spines (not hooked), sternites IV–VI with transverse conjunctival bands of anteriorly-directed spines, anal lobe with three short, stout curved macrosetae, without fringe. The adult has bare eyes, 1–2 small hooked/scalpellate acrostichals in light oval area in mid-scutum, tibial spurs ‘flared’ with small to strong denticles, male with terminally pectinate claws, without anal point, virga or crista dorsalis, with rectangular inferior volsella.
Tonnoirocladius commensalis (Tonnoir, 1923) comb. n. (Figures 1 – 16)

Dactylocladius commensalis Tonnoir, 1923. Type-material not found, presumed lost.

Material

2L, 1L(P), 1Pe, 1P, 3Pf, 1Pm, 2Pm, NEW ZEALAND, South Island, nr Greymouth, trib. of Hokitika R, Feb 1972, P. Zwick, ex-Neocurupira hudsoni (ZSM).
8L, 2P, 1Pf, 3Pm, Westland, coast rd s. Paparoa N.P., Bakers Creek above crossing, 22.ix.2004, elev 5 m. asl., G. W. Courtney, ex-Neocurupira hudsoni (NZAC).
9L, 4Pf, 1Pm, Fjordland N.P. Hollyford River, 15.ix.2004, 490 m. asl., G. W. Courtney, ex-Neocurupira hudsoni (NZAC).

Larva

Fourth-instar larva medium-sized, 3.6 mm long, head capsule 360–400 μm. Dorsal surface of head with delimited frontoclypeal apomere (S3 on anterior margin of plate bearing S4, S5) and complete labral sclerite, with some anterolateral fragmentation.

Antenna (Figure 1) 5 segmented, apical 3 segments more or less subequal, segment 3 subequal to or slightly shorter than segment 4; blade bifid, inner branch a little shorter than outer, not extending to antennal apex; style slightly longer than 3rd segment, Lauterborn organs subequal to segment 3. Antennal ratio c 0.5. Ring organ at 1/4 of segment 1.

Labrum (Figure 2) with SI bifid, with inner branch very weak, outer branch stout; remaining S setae simple, SII and SIII thickened, SIV single, very short; chaetae short, simple; premandible stout, with weak indication of 2 apical teeth, no inner teeth and without
brush. Labral lamellae absent. Pecten epipharyngis of 3 unfused scales; with one pair of chaetulae laterales scale-like, other weakly pectinate. Ungula short and squat with few short and simple or pectinate chaetae. Basal sclerite spatulate.

Mentum (Figure 3) with median tooth broad and either simple and with crenulate anterior margin, or perhaps comprising four indistinctly separated shallow teeth with median pair smaller and slightly recessed; 4 pairs of lateral teeth, the outermost protruding anterior to its inner neighbours. Broad median mentum and first two pairs laterals paler than mid-brown lateral-most pair. Posterolateral mentum highly complex and may or may not include a 'conventional' ventromental plate, but comprises at least 2 sclerotised layers posterolateral to base of outermost

lateral tooth; with dense beard of fine simple setae extending from basal mentum to laterad of apex of outermost mental tooth. Setae submenti (and other central cephalic setae) stout.

Mandible (Figure 4) with outer margin smooth, inner margin unevenly rounded. Apical tooth much shorter than combined 3 inner teeth, scarcely protruding beyond line of inner teeth. Large gap between innermost tooth and mola. Seta subdentalis short. Seta interna narrow with few simple branches. Maxilla squat, bearing relatively elongate simple setae.

Body without any evidence of lateral setae. Anterior parapods separate, with crown of elongate, simple, yellow spines, slightly shorter highly pectinate yellow claws and simple shorter pale claws. Posterior parapods separate, with apical group of simple brown claws. Procercus very short, pale, as wide as high, without spurs, bearing laterally a short setae, and apically 4 medium-length anal setae. Anal tubules comprising one pair of elongate-oval tubules projecting posterolaterally from anal area posterior to parapods (as is conventional in Chironomidae); second pair modified such that one protrudes antero-ventrally between posterior parapods and its paired partner apparently arises from a common base and extends in a more postero-ventral position. In contrast to Tonnoir (1923, Figure 10), all anal tubules are subequal in length.

**Pupa**

Frontal apotome (Figure 5) with weak frontal setae (30 – 35 μm long) lying between pedicel sheaths just anterior to slightly raised contiguous tubercles, pedicel sheaths lack pearls; frons with transverse creases. Ocular seta strong.

Thorax (Figure 6) weakly rugulose dorsally and anteriorly; 2 dorsal antepronotals, 0 laterals; 3 well developed, fine precorneals, subequal in length, sometimes with short, fine asymmetrical 4th precorneal; dc₁ and dc₂ close, distant from closely approximated dc₃ and dc₄. Prealar seta may be present. Thoracic horn absent.

Abdomen (Figures 7 –10) with tergites I and II bare, or with minor fine spinulation anteromedially on II, III – VII with broad and deep anterior transverse band of fine spinules,
smaller (ca. <5 μm) and clustered anteriorly, longer (ca. >5 μm) and more separate posteriorly; V–VIII with posterior transverse band of spines, few and small on V, increasing in size and width tending toward tubercles and becoming multiserial on more posterior tergites; conjunctives III–VI with multiserial transverse band of long, slender, anterior-directed spines, up to 30 μm long. Sternites (Figure 10) I–III without spinules or spinulation, anterior V–VIII with spinulation pattern corresponding with but mostly stronger than on corresponding tergites, (V) VI–VIII with transverse row of spinules; conjunctives IV–VI with anteriorly-directed, long, fine spines, as on tergal conjunctives. Pedes spurii A and B absent. Apophyses absent.

Setation: segment 1 with 5D, IV, 2L setae; segments II–VII with 5D, 5V and 3L setae, L1 and L2 closely approximated; segment VIII with 2D, 2V, 1L. All L setae simple and fine.

Anal lobe rounded, with crenulate margin and median circular patch of fine spinules, with 3 short stout macrosetae. Male genital sheaths long and extending well beyond anal lobe and macrosetae (Figure 7), female genital sheaths not extending as far as apex of anal lobe (Figure 8).

**Adult male (pharate specimens only)**

Small, body length c. 3.4 mm, wing (sheath) length 0.9 – 1.0 mm. Antenna with 13 flagello-meres, 2nd and 3rd near globular, successive segments becoming increasingly elongate, with sparse but complete plume extending to apex, lacking strong subapical seta; groove extending from flagellomere 3 to 13; 1 sensilla chaetica on flagellomere 3 and several sub-apical on 13. A.R. 0.22.

Head with eye bare, with microtrichia close to mesal margin of ommatidia, without dorsomedial extension. Temporal setation restricted to 6–7 more or less uniserial postorbitals. Clypeus quadrate, moderately setose. Palps with 5 segments, each consecutive segment longer than previous. Third segment without pit or sensilla chaetica.

Thorax medium brown. Antepronotum well developed, lobes not medially narrowed, in contact medially. Thoracic setation: 2–3 lateral antepronotals; 1–2 small hooked/scalpellate acrostichals in light oval area in mid-scutum; 9 uniserial dorsocentrals arising from pale oval areas that may encompass more than 1 seta; 3–4 prealars; 7–9 uniserial scutellars. Lateral thorax without setae.

Wing membrane with fine punctation, without macrotrichia. R$_{4+5}$ ending above M$_{3+4}$. Brachiolum with 1 seta, R with 5–6, remaining veins without setae. Squama with 10 setae. Anal lobe rounded, not produced. Costa with slight extension; FCu distal to r-m (ratios incalculable) Cu$_1$ straight.

Leg ratios incalculable, fore tibial spur moderately long, shorter than tibial apex, medium tibia with two short subequal spurs; spurs of fore- and mid-legs basally with flared denticles; hind tibia with shorter spur more than half length of longer spur, each with strongly divergent denticles; comb irregularly biserial; pseudospurs absent. Sensilla chaetica apparently absent. Pulvilli well-developed, half length of terminally-pectinate claws.

Figures 17–18. New Zealand, South Island, blepharicerid / Tonnoirocladius locations. (17) Upper Otira River. (18) Holyford River (17, 18 copyright G. W. Courtney; reproduced with permission).
Tergites unicolorous, with scattered long setae, becoming sparser on each successively more posterior segment.

Genitalia (Figure 11). Tergite IX with few anterolateral long setae, without medial or apical setae; without anal point. Sternapodeme rounded, with very weak oral projections placed very lateral; phallapodeme weak. Hypopygium without virga; superior volsella absent; inferior volsella rectangular, with rounded hyaline distomedial corner, not obviously projecting. Gonostylus simple, with megaseta and without crista dorsalis.

Adult female (pharate specimens only), as male except

Antenna 5-segmented, AR 0.68. Clypeus broader than long. claws simple, pointed.

Tergite IX broad, undivided, evenly but sparsely setose; gonocoxite IX quite strongly protruding, with 6–7 long, 4–6 short setae. Gonapophysis VIII apparently undivided, with large ventrolateral lobe obscuring any sign of dorsomesal lobe; apodeme lobe broad and dark. Two pale, oval seminal capsules, without microtrichia or neck, with highly convoluted spermathecal ducts ending in common bulb prior to common opening on spermathecal eminence; labia hyaline, bare. Tergite X and cerci moderately developed, cerci quite setose.

Taxonomic discussion

The genus *Dactylocladius* Kieffer, 1906 was erected as a subgenus of the well established *Orthocladius* Wulp, 1874, with *Orthocladius kervillei* Kieffer, 1899 designated subsequently as type: given the seeming loss (or non-retention) of *O. kervillei*, the name is regarded as a nomen dubium (see Ashe 1983 for details). However, for a protracted period the genus (or as subgenus) was used for a variety of small dark non-descript orthoclads that now are allocated to a diversity of genera. Thus, the original generic allocation gives few clues as to the true (modern) identity, although Tonnoir’s original description was excellent in providing details of all life history stages. The original material has not been found, including by personal search of the collections of the Cawthron Institute, Nelson, and the Australian National Insect Collection, Canberra, nor are they in the New Zealand Arthropod Collection (Crosby 1999). In his study of the New Zealand Chironomidae, Freeman, while not specifically mentioning types, noted for the species that “such material as I have seen is in too poor a condition for me to offer redescriptions” (Freeman 1959, p. 418). Despite this, Freeman transferred the species to *Orthocladius*. Notwithstanding the lack of historic material, there is no doubt on biological or morphological reasons that we have the same species as Tonnoir described from similar locations and host blepharicerids (Tonnoir 1923).

Seeking a modern identity, the adult male can be keyed to *Chaetocladius* Kieffer, 1911 in Cranston et al. (1989), based on the bare wing and eye, and the presence of divergent lateral spines on the shaft of the mid- and hind leg spurs. *Chaetocladius* is a homogeneous grouping, but all included species share the following (putative) phylogenetically-informative character states (in contrast to *Tonnoirocladius*): the distinct anterpronotal setae start at the antepronotum (rather than being scalpellate and restricted to a mid-scutal pale area) and the anal point and virga are distinct (both are absent in *Tonnoirocladius*). Although the “flared” tibial spur structure is keyed as if unique to *Chaetocladius*, it occurs also in *Tokunagaia* Sæther, 1973 and to some extent in *Bryophaeocladus* Thienemann, 1934 and *Eukiefferiella* Thienemann, 1926 and in the austral genera *Botryocladus* and *Kaniwhaniwhanus*. Ignoring this feature, the taxon keys to *Eukiefferiella* if the pulvilli are considered weak, or *Psectrocladius* Kieffer, 1906 if considered long, but on all other features a relationship
to *Psectrocladius* is unrealistic. Although the female can be keyed to *Eukiefferiella* in Sæther (1977), this involves much ambiguity and internally incompatible, multichoice couplets.

The pupa keys readily and unambiguously to *Metriocnemus* Wulp, 1874 in Coffmann et al. (1986), to which it bears a superficial resemblance in lacking a thoracic horn, lacking any hooklets on tergites and in the anal lobe structure. However, no *Metriocnemus* have such strong conjunctival spines and the spinulation and spine bands of the tergites and sternites disagree in structure or distribution with any *Metriocnemus*.

The larva keys in Cranston et al. (1983) to *Paracladius* Hirvenoja, 1973, from which it differs in the shape of the outer mentum, the extent and density of the ventromental beard and the structure of the mandible.

Evidently the Holarctic keys to each life stage produce no consistent evidence for relationship, or even any phenetic resemblance. Thus, a data matrix has been constructed to assess the phylogenetic placement amongst a global set of Orthocladiinae genera. The data set was designed originally for testing relationships of *Parapsectrocladius* (Cranston 2000b) and expanded subsequently to investigate relationships amongst the “Brillia” group of genera (Cranston 2000a). To this matrix were added the austral taxa with phenetic resemblances, with morphology derived for *Naonella* from examination of specimens (Cranston collection) and from Boothroyd (1994, 2004), for *Kaniwhaniwhanus* from Boothroyd (1999), for *Botryocladius* from specimens and from Cranston and Edward (1999). Analysed under parsimony this matrix reveals a resolved clade (Figure 19) with *Tonnoirocladius* sister to *Naonella* with bootstrap support of 68%. This grouping forms an unresolved trichotomy with *Kaniwhaniwhanus* + *Pirara* and *Echinocladius*, with *Eukiefferiella* and *Tokunagaia* and *Cardiocladius* Kieffer, 1912 at successive nearest remove. Although molecular sampling for four genes (18s, 28s, CO1 and CAD) is incomplete for all genes and all candidate taxa, preliminary analysis indicates a close relationship between *Tonnoirocladius* and *Botryocladius* (Morse and Cranston unpublished). The question then arises as to how *Tonnoirocladius* differs from both species of *Naonella*, implicitly whether it deserves generic status. In the male, the principal difference lies in the shape of the inferior volsella that is characteristically “hooked” in both species of *Naonella*, and further, in *Naonella* the male claws are simple. *Naonella* adults do resemble *Tonnoirocladius* in lacking sensilla chaetica and having similarly formed and located acrostichals (pers. obs., contra Boothroyd 1994). The pupa of *Naonella* has frontals (pers. obs., contra Boothroyd 1994) and bears a general resemblance to *Tonnoirocladius* in lacking a thoracic horn, hooklets on tergite II, pedes spurii A and B, and having somewhat similar spinule patterns (including on the sternites), but has better developed anal macrosetae. However such a pupal type is common to several austral orthoclads (including some known by code names in Cranston 2000c) and phylogenetic inference from such

![Figure 19. Relationships of Tonnoirocladius estimated by maximum parsimony on datamatrix. Available at http://entomology.ucdavis.edu/chiropage/tonnoirocladius.pdf](http://entomology.ucdavis.edu/chiropage/tonnoirocladius.pdf)
resemblance is unwarranted. The larva of Naonella has setae beneath a distinctive ventromental plate of different construction to that of Tonnoirocladius.

Biology

According to Greg Courtney, who collected Neocurupira species for systematic studies, larval chironomids were phoretic on many specimens. Courtney observed that “nearly all associations appear to involve the Neocurupira hudsoni complex, although I occasionally found chironomids on other species of Neocurupira. I found no chironomids on Neocurupira chiltoni, Nothohoraia micrognathia and Peritheates spp. Levels of phoresy in some N. hudsoni populations (on instars 3 & 4) were probably close to 100%. The other extreme was 0%”.

Tonnoirocladius commensalis larvae were located either transversely (Figure 12) or sometimes wound around the ventral suckers (Figure 13). Late instar larvae could be found on small Neocurupira larvae (Figure 14), and several different instars of T. commensalis could co-occur on a single large host. Larvae could co-occur with pupae: pupae always were orientated transversely with their ventral surface appressed to the body of the host (Figure 15), with the ventral suckers providing lateral support (Figure 16). As with larvae, multiple specimens could be associated with one large blepharicerid larva: 3–4 were observed quite frequently.

Given Frutiger’s (2002) observations on the use by blepharicerid larvae of their ventral suckers to progress across the surface of rocks, the “load” of numerous commensal chironomid larvae and/or pupae surely must interfere with their locomotion and hydrodynamics in general.

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References


