

A CONTRIBUTION TO THE UNDERSTANDING OF EUROPEAN CORYNONEURINI, WITH THE DESCRIPTION OF THREE SPECIES NEW TO SCIENCE

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<https://zoobank.org/7F3C3C7E-ED8A-4373-9816-4298E5CED9A6>

Abstract

Northern European *Corynoneura* species with the combination of comparatively short extension of the hind tibia apex and a thick transverse sternapodeme are morphologically similar to species in *Thienemanniella*. Moreover, the generic placement of *Corynoneurella paludosa* Brundin has been debated. We present results from morphological and molecular analyses that clarify the taxonomy of *C. paludosa*. Consequently, we regard *Corynoneurella* as a junior synonym of *Corynoneura*, move *Corynoneurella paludosa* to *Corynoneura* and return *Corynoneurella afra* (Lehmann) to *Thienemanniella*. Our observations also conclude that *Corynoneurella paludosa* sensu Langton is morphologically different from *C. paludosa* (Brundin) and is best placed in *Thienemanniella* as *Thienemanniella langtoni* sp. n. *Corynoneura ferringtoni* sp. n. and *Corynoneura minimagna* sp. n. are described and diagnosed based on adult male morphology and DNA barcodes. We redescribe *Corynoneura minuscula* Brundin, discuss *Corynoneura magna* Brundin, and suggest a solution for the identity of *Corynoneura celeripes* Winnertz. Finally, we provide an identification key to adult males of Holarctic *Corynoneura* species with a short hind tibial extension.

Introduction

Species of the tribe Corynoneurini (Orthocladiinae), also known as the *Corynoneura*-group, are amongst the smallest within the Chironomidae (Diptera), with a typical wing length of 0.9-1.8 mm. The group is species rich and often numerous in all kinds of aquatic and semiaquatic habitats such as streams, creeks, ponds, lakes, bogs and fens, and are recorded from fresh and brackish waters (e.g. Andersen et al. 2013, Moller Pillot 2013). Corynoneurini species are challenging to identify morphologically due to their small size and limited number of diagnostic characters. For adults, it is usually necessary to examine a slide mounted

specimen with a cleared abdomen under a compound microscope to see both the external and internal characteristics. The morphology of associated life stages supports species as well as generic boundaries within the tribe (Andersen and Sæther 2005, Wiedenbrug and Trivinho-Strixino 2009). However, immature stages and female adults are unknown for many species and the generic diagnoses might change when more associated life stages are included.

Identification of Chironomidae species using DNA barcoding works very well in most cases given that there is a decent reference library for comparison (Ekrem et al. 2007, Lin et al. 2015, Gadawski et al. 2022). Thus, building a high-quality reference library of Chironomidae makes it possible to include taxonomically challenging taxa like the Corynoneurini in freshwater biomonitoring. Moreover, DNA barcode data has proven valuable in taxonomic studies where species boundaries were uncertain and has contributed to increased knowledge of species diversity for several groups within the Chironomidae as well as association of life stages (Stur and Spies 2011, Stur and Ekrem 2015, Lin et al. 2018, Stur and Ekrem 2020).

Species of the tribe Corynoneurini are characterized by having a wing with an apically fused costa where R1 and R2+3 form a thick clavus (Fig. 1) (Sæther and Kristoffersen 1996). The tribe comprises nine genera, *Corynoneura* Winnertz, 1846; *Corynoneurella* Brundin, 1949; *Ichthyocladus* Fittkau, 1974; *Notocladus* Harrison, 1997; *Onconeura* Andersen et Sæther, 2005; *Physoneura* Ferrington et Sæther, 1995; *Tempisquitoneura* Epler et de la Rosa, 1995; *Thienemanniella* Kieffer, 1911 and *Ubatubaneura* Wiedenbrug et Trivinho-Strixino, 2009 (Wiedenbrug and Trivinho-Strixino 2009, Ashe and O'Connor 2012,). Only species of the genera *Corynoneura*, *Thienemanniella* and *Corynoneurella* are reported from the Holarctic region.



Figure 1. *Corynoneura minimagna* sp. n., male adult. Scale bar = 1 mm.

As more *Corynoneurini* species are found and described the boundaries between the genera appear increasingly blurred. For instance, morphological traits in adult males such as microtrichia between the ommatidia or oral projections of the transverse sternapodeme, previously regarded as typical of members of the genus *Thienemanniella* (Cranston et al. 1989, Sæther et al. 2000), are now found in several *Corynoneura* species (*C. bodoquena* Wiedenbrug et al., 2012; *C. diogo*, Wiedenbrug et al. 2012; *C. tyrrhena* Moubayed-Breil, 2015; *C. sundukovi* Makarchenko et Makarchenko, 2010) (Makarchenko and Makarchenko 2010, Wiedenbrug et al. 2013, Moubayed-Breil 2015). On the other hand, *Thienemanniella partita* Schlee, 1968, a species which otherwise fits well the definition of *Thienemanniella*, seem to have bare eyes, as does *T. nipponica* Tokunaga, 1936 (Spies and Sæther 2004, Fu et al. 2010a, b, Fu et al. 2020). Currently, the main features to morphologically differentiate *Corynoneura* from *Thienemanniella* seem to be the presence of a keel at the fore trochanter (Schlee 1968, Wiedenbrug et al. 2013) and a relatively short clavus (Spies et al. 2022) in the adult. The presence of a pearl row on the wing-sheath of the

pupa (Coffman et al. 1986) (except for *Corynoneura franciscoi* Wiedenbrug, Lamas & Trivinho-Strixino, 2012), and a long four-segmented antennae in the larva (Andersen et al. 2013) define the genus in the immature stages.

Corynoneurella was established by Brundin (1949) who placed the genus between *Corynoneura* and *Thienemanniella*. He considered the non-elongated apex of the hind tibia to be sufficient to separate *Corynoneurella* from *Corynoneura*, even though the other characters fit well with the contemporary diagnosis of the latter genus. Brundin (1949) also stated that *Corynoneurella* might be considered a subgenus of *Corynoneura* in the future since *Corynoneura magna* Brundin, 1949 and *Corynoneura minuscula* Brundin, 1949 also have an atypical hind tibial apex. Schlee (1968) later transferred *Corynoneurella paludosa* to *Corynoneura* as all diagnostic characters fit his concept of that genus. Langton (1997) re-established the genus *Corynoneurella* based on a paratype male pupa he regarded to be conspecific with *Corynoneurella paludosa* and emended the diagnosis for *Corynoneurella* to include pupal characters. The genus was accepted

as valid by Fu et al. (2010a, 2010b) who transferred *Thienemanniella afra* Lehmann, 1981 to *Corynoneurella* mainly based on the pupal characters that fit the diagnosis of *Corynoneurella* sensu Langton (1997). In the world catalogue of Chironomidae, Ashe and O'Connor (2012) listed *Corynoneurella* as a valid genus with the species *Corynoneurella paludosa* and *Corynoneurella afra*.

Here we wish to contribute to the knowledge of the tribe Corynoneurini by clarifying the identity of *Corynoneurella paludosa* and related *Corynoneura* species. We selected *Corynoneura* species where adult males possess a well-developed thick transverse sternapodeme (Fig. 4G) as opposed to a thin transverse apodeme as seen in *Thienemanniella* (Cranston et al. 1989, fig. 9.88E, F) or missing as seen in other *Corynoneura* (Cranston et al. 1989, fig. 9.17G). In addition, these species have a hind tibia with a short apical extension, less than 0.7 times the tibial apex width (Fig. 3B). Through the examination of type material and the association of morphotypes with DNA barcodes, we argue for synonymizing *Corynoneurella* with *Corynoneura*, and describe three species new to science. We also provide a preliminary molecular phylogeny of selected species in *Corynoneura* and *Thienemanniella* to support our decisions.

Methods

Specimen sampling and morphology

Specimens were sampled as part of various projects and field campaigns in Europe with adult midges collected by sweep-nets, Malaise traps or emergence traps near a variety of freshwater habitats. In addition, nominal types and reference material from scientific collections were obtained as loans and compared with freshly collected specimens when possible. Institutional abbreviations: NHRS = Swedish Museum of Natural History, Entomology Collections, Stockholm, Sweden; NTNU-VM = NTNU University Museum, Trondheim, Norway; ZSM = SNSB - Zoologische Staatssammlung München, Munich, Germany (Bavarian State Collection of Zoology); LUOMUS = Finnish Museum of Natural History, Helsinki, Finland; ZFMK = Zoological Research Museum Alexander Koenig, Bonn, Germany; PHL = private collection Peter H. Langton, Northern Ireland.

The terminology used follows Sæther (1980). Tibia of hind leg = ti_3 . Measurements of the apex-extension of the hind tibia are according to Schlee (1968: 140, figs 131-133). Setation of apex of hind tibia (Schlee, 1968: 136, figs 111-113), (A = apical seta, S = long spur, s = short spur). Keel at the fore

trochanter of the adult according to Schlee (1968 figs 89, 90, 130) and in Figs 4E, 5, 6E, not as interpreted in Fu et al. (2010a, b) and Wiedenbrug et al. (2013).

All photographs except Fig. 1 were taken with a Leica DMC4500 digital camera fitted on a Leica DM6000B compound microscope using differential interference contrast. The software Leica Application Systems X was used to take z-stacked photographs that were assembled using the default settings, with subsequent polishing in Adobe Photoshop. Figure plates were made with Adobe Illustrator. The image in Fig. 1 was taken with a Leica DMC 5400 fitted on a Leica MZ16A stereo microscope using the same software.

Molecular analyses

Three legs from each of 209 individual specimens belonging to 32 species were sampled and shipped to the Centre for Biodiversity Genomics (CBG) at the University of Guelph for molecular analysis as part of the International Barcode of Life initiative. In addition, eight Canadian specimens provided by CBG were included and DNA barcoded. Metadata from all specimens, except the German specimens of *C. ferringtoni* sp. n., is available in the dataset DS-CORYTHIE (DOI: <https://dx.doi.org/10.5883/DS-CORYTHIE>) in the Barcode of Life Data Systems database (<https://boldsystems.org>). DNA extractions followed an in-house silica membrane-based protocol at the Canadian Centre for DNA Barcoding. PCR of the 658 bp Cytochrome c oxidase subunit 1 (COI) barcode fragment was performed on all specimens and used a cocktail (C_LepFolF/C_LepFolR) of the established LepF1/LepR1 and Folmer primers (Hernández-Triana et al. 2014). PCR of 18S was performed on a subset of specimens aiming to represent all barcode clusters in the dataset and used the primers 18S_ai and 18S_bi amplifying an approximately 1000bp long fragment of the nuclear small ribosomal unit (Whiting et al. 1997). Both fragments were sequenced bi-directionally using Applied Biosystems Big Dye termination on ABI 3730XL sequencers.

Sequence contigs were aligned using the Muscle algorithm in MEGA 11 (Tamura et al. 2021) with gap opening costs = -200 and gap extension costs = -50. Alignment of COI was trivial as there were no indels. For 18S, the alignment had no indels for the in-group, while three gaps were inserted in the alignment to accommodate the chosen outgroup taxon *Psectrocladius limbatellus*. The software Mesquite 3.70 (Maddison and Maddison 2021) was used to manipulate taxon names and conca-

tenate alignments of COI and 18S sequences. Substitution models for the four potential partitions 1st position COI, 2nd position COI, 3rd position COI and 18S were tested using PartitionFinder2.0 (Lanfear et al. 2017). The resulting two partitions (1) 3rd position COI and (2) 1st position COI, 2nd position COI and 18S received the best BIC scores for the models TRN+I+G (1) and TIM+I+G (2) respectively.

Phylogenetic analyses were conducted with MrBayes 3.2 (Ronquist et al. 2012) implementing the partitions above and the GTR+I+G model (considered to be the closest available model to the TRN and TIM substitution models) as well as the alternative ‘model jumping’ option in separate runs. All analyses were done with 10 000 000 generations with sampling every 1000 with all parameters and branch lengths unlinked and a burn-in of 10%. Resulting probabilities and other output were examined using Tracer 1.7.2 (Rambaut et al. 2014) to evaluate convergence. Trees were inspected and figures generated using FigTree 1.4.4 (Rambaut 2016).

Results

The phylogenetic consensus trees from the Bayesian analyses all returned a well-supported monophyletic *Thienemanniella* embedded in *Corynoneura* (Fig. 2). However, many of the more basal branches have low posterior probabilities, indicating that the presented relationships between *Thienemanniella* and groups of *Corynoneura* largely are unsupported. Two exceptions are the *scutellata*-group containing *C. arctica*, *C. edwardsi*, *C. scutellata* and three interim species, and the *lobata*-group containing *C. lobata* and six interim species. The *Corynoneura* species that have short hind tibial extensions and thick transverse sternapodemes (*C. ferringtoni* sp. n., *C. minimagna* sp. n., *C. minuscula*, *Corynoneurella paludosa*) do not constitute a monophyletic unit, and there is no molecular evidence that *Corynoneurella paludosa* should be considered a separate taxon at the genus-level.

Corynoneura celeripes Winnertz, 1852

Corynoneura celeripes Winnertz sensu Brundin, 1949:833; Schlee, 1968:18; Fu et al., 2009: 37; Fu et al., 2017: 70; nec sensu Pinder 1978; nec sensu Langton & Pinder, 2007.

Material examined: Two adult males (NHRS-BYWS 000002988 and NHRS-BYWS 000002989, both A288). Sweden, Väjö municipality, lake In-naren, 1947 coll. Brundin NHRS.

One male on microscopy slide (NHRS-BY-WS000002199, B25), Sweden, Dalarna, peat bog near Ludvika, leg. L. Brundin, 05.vi.1946.

Diagnostic characters. *Corynoneura celeripes* adult males can be distinguished from other congeners by having a moderately short apical extension on the hind tibia; inferior volsella moderately large, almost triangular, situated at about mid length of gonocoxite; transverse sternapodeme anterior margin straight, thick; phallapodeme short, knife-shaped, joining sternapodeme at caudal curve.

Remarks

During our work with *Corynoneura celeripes* Winnertz, it became obvious that there are two main conceptions of this species in the literature. One following the opinions of Brundin (1949) and Schlee (1968), and one following Pinder (1978) and Langton and Pinder (2007). The latter is probably based on the opinion of Edwards (1924). Unfortunately, Winnertz’ type specimens appear to be lost as they likely were part of the insect collection at the Zoological Museum in Bonn that was lost during the Second World War (Hirvenoja and Hirvenoja 1988). According to Horn and Kahle (1935-1937), most of Winnertz’ Diptera material was deposited in Bonn.

The original description of *C. celeripes* is based on two females “aus hiesiger Gegend” [from the vicinity] and is almost exclusively based on colour and colour patterns. On the same page, Winnertz (1852) also describes the much darker *C. atra* based on two adult males collected at the same time and place, indicating that this might be the male of *C. celeripes*. Edwards (1924) confirms this synonymy with male and female adult specimens reared from pond water that agree with Winnertz’ description but also writes “As this species has no antennal rosette it may not be Winnertz’s *C. celeripes*, ...”. We have adult male specimens that confirm well with Edwards’ description as well as with the characters and drawings presented by Pinder (1997) and Langton and Pinder (2007), where females associated with DNA barcodes have strongly pigmented distal half of the costa (BIN BOLD:ACX7382). As this is a character that Winnertz almost certainly would have detected but described the wings of his *C. celeripes* as shimmering whitish, we find it unlikely that Edwards described specimens of the same species as Winnertz. Adult males of *Corynoneura celeripes* sensu Edwards have strongly elongated apices of the hind tibia and the species is therefore not further treated in the present work.

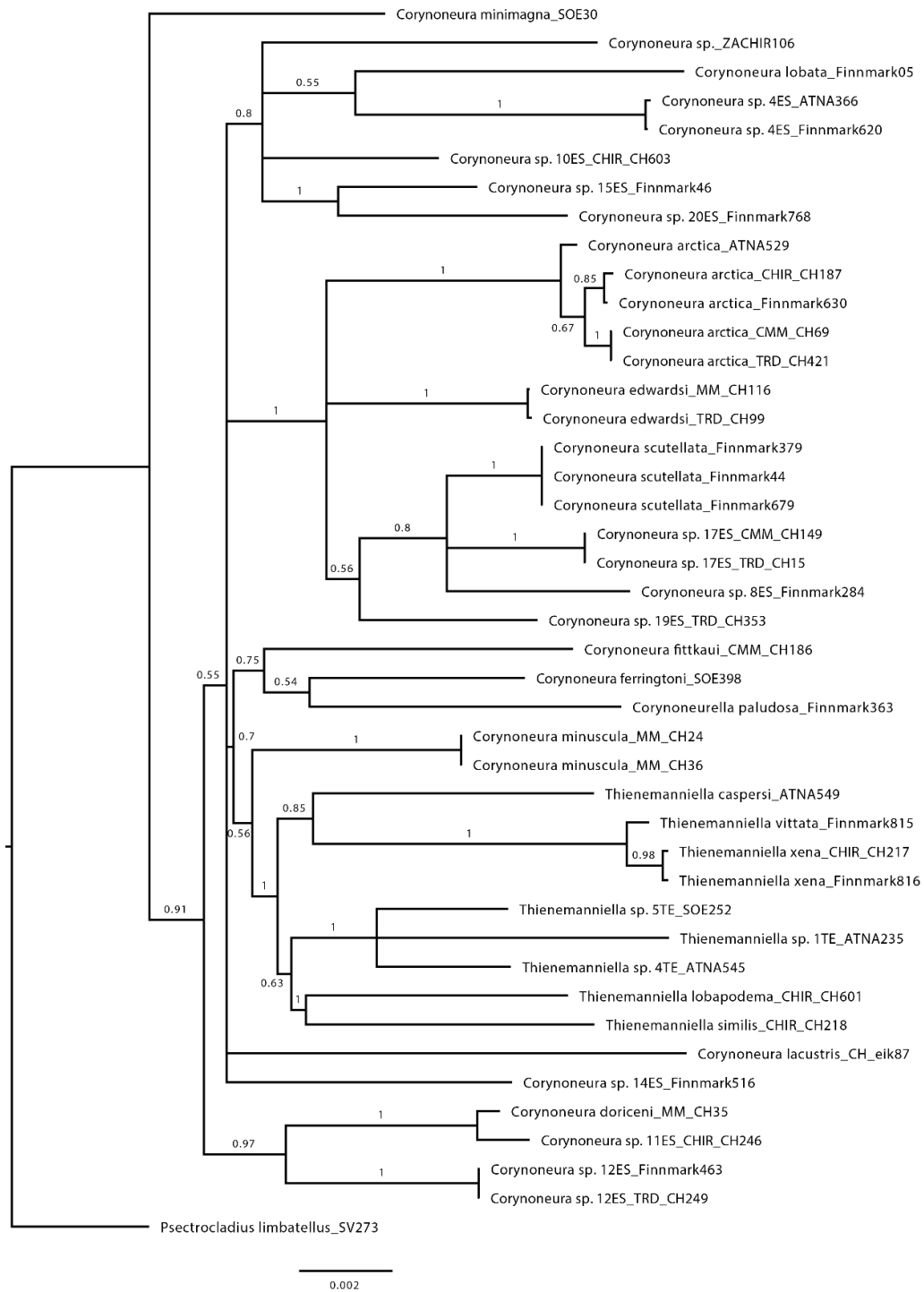


Figure 2. Phylogenetic tree generated using partial COI and 18S sequence data for selected Corynoneurini. Results from Bayesian analysis using 10 million generations and the GTR+I+G substitution model. Posterior probabilities above 50% on branches.

Brundin (1949) recorded *C. celeripes* from several lakes in Sweden, and keyed and figured the hypopygium. He did not describe the coloration in his specimens, but his drawing of the hypopygium resembles those of Edwards in having an obvious inferior volsella curved into a posteriorly pointed apex. The inner margin of the gonostylus, however, is straight in Brundin's drawing (Brundin 1949, fig. 205), while strongly curved in Edwards' drawing (Edwards 1924, fig. 10). We find it likely that Brundin described specimens of *C. celeripes* Winnertz although it is unlikely that he saw type material. Schlee (1968) mentioned *Corynoneura celeripes* as a species in *Corynoneura* with thick transverse sternapodeme and hind tibia with relatively short apex-extension. Schlee (1968) adopted Brundin's concept of the species and examined specimens from Brundin sample no. A288. He described the male adult hind tibia as very little widened and prolonged, with an extension shorter as in *C. edwardsi* Brundin, 1949. Brundin (1949: 833), on the other hand, referred to the hind tibia of *C. celeripes* as moderately strongly prolonged, more prolonged than in *C. minuscula* and *C. magna*. We had the opportunity to examine two adult males from Brundin's sample A288, and although in rather poor condition, the rather short extension of the hind tibia apex is clear (Fig. 3B), as is the posteriorly pointed inferior volsella (Fig. 3A) and the lack of a developed antennal rosette (Fig. 3C). Our examination could also confirm that Schlee's interpretation of the sternapodemes and phallapodemes is correct (Schlee 1968, figs 50-51). Thus, *C. celeripes* sensu Brundin falls within the boundaries of the *Corynoneura* species treated here. Unfortunately, we have not had access to other specimens that belong to *C. celeripes* sensu Brundin and have therefore nothing to add

to Schlee's (1968) detailed description of the species. Brundin (1949) reported the distribution of *C. celeripes* to include Sweden, Finland, England, the Netherlands, Belgium, France, Germany, Austria and the USA, but in light of our current knowledge about the diversity in *Corynoneura*, all these records are questionable. The current public records of this species in BOLD are likely misidentified.

***Corynoneura ferringtoni* sp. n.**

<https://zoobank.org/C2B073A3-6FD0-4DE1-B603-489E05FF9959>

Type material. Holotype: Male adult (NTNU-VM 202004), Norway, Telemark, Drangedal, Sannes-Langen, lakeshore and bog, 59.04388°N, 9.30952°E, 66 m asl, leg. Elisabeth Stur & Patrycja Dominiak, 17.vi.2020, [BOLD ID: MM-CH210]. Paratypes: One male adult (NTNU-VM 145171), Norway, Trøndelag, Røros, Sølendet, kilde C3, 62.691°N, 11.833°E, 780 m asl, leg. T. Ekrem & E. Stur, 11.vi.2006 [BOLD ID: SOE398]. One male adult (NTNU-VM 145170), Norway, Trøndelag, Røros, Sølendet, kildebekk B2 62.689°N, 11.832°E, 785 m, leg. O. Hanssen, 22.VI.2012 [BOLD ID: SOE440]. One male adult (NTNU-VM 124583), Norway, Trøndelag, Røros, Sølendet, Kilde C-1, 62.691°N, 11.833°E, 788 m asl, leg. Aagaard et al., 10.vii.2005 [BOLD ID: SOE35]. Three male adults (ZFMK) Germany, Baden-Württemberg, Nationalpark Schwarzwald, Pfälzer Grube Quelle n° 816 on top, emergence trap, leg. R. Gerecke & S. Wiedenbrug, 13.vi.2016 [BOLD ID: ZFMK-TIS-2.598.342, ZFMK-TIS-2.598.343] and 5.vii.2017 [BOLD ID: ZFMK-TIS-2598404]. Two male adults (ZSM) Germany, Bayern, Allgäu, Oberstdorf, Engelkopf, 1210 m asl, 47.39500°N, 10.21617°E, 13.-29.v.2015, leg. Doczkal & Volgt, [BOLD ID: CCDB24183-E11, CCDB24183-E10].

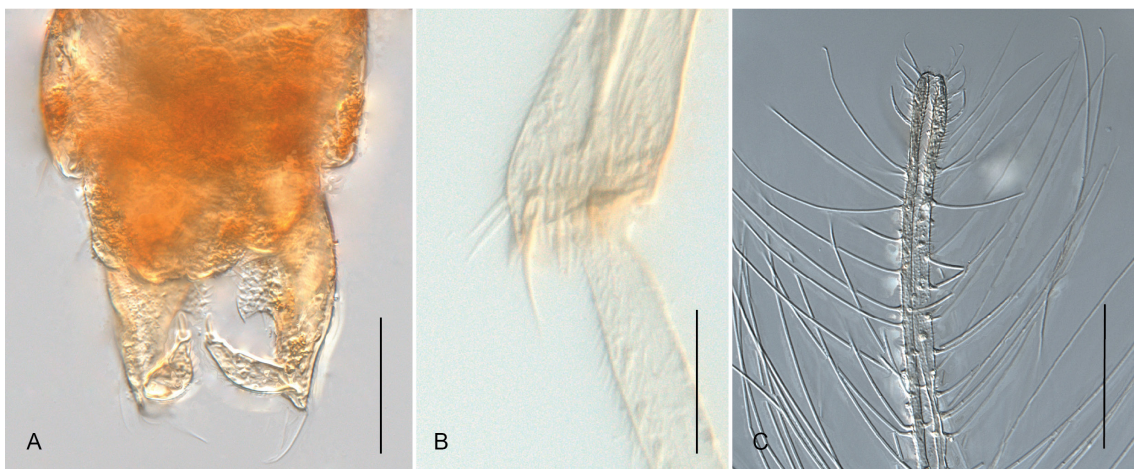


Figure 3. *Corynoneura celeripes* Winnertz sensu Brundin, male adult. A: Hypopygium (NHRS-BYWS000002199), B: Hind tibial apex (NHRS-BYWS000002199), C: Antennal apex (NHRS-BYWS000002989). Scale bars: A, C = 50 μ m; B = 30 μ m)

Other material examined (Private collection Nicola Reiff): One male adult Austria, Ennstaler Alpen, Tamischbach, Quellhorizont S Ischbauernkopf, rechts, 47.63660°N, 14.70691°E, 955 m asl, 23.vii.2016, leg. H. Haseke & C. Remschak. One male adult Austria, Nationalpark Gesäuse, Einzugsgebiet Mühlbach, Moos- Algenquelle beim Hochsitz 47.63953°N, 14.66209°E, 845 m asl, 01.viii.2014, leg. H. Haseke & C. Remschak.

Etymology. The species is named in honour of our colleague and friend Leonard C. Ferrington, Jr., for his long-standing contributions to Chironomidae research.

Diagnostic characters. *Corynoneura ferringtoni* adult males can be differentiated from other *Corynoneura* species by having a very short apical extension on the hind tibia; superior volsella broadly triangular; inferior volsella small, almost

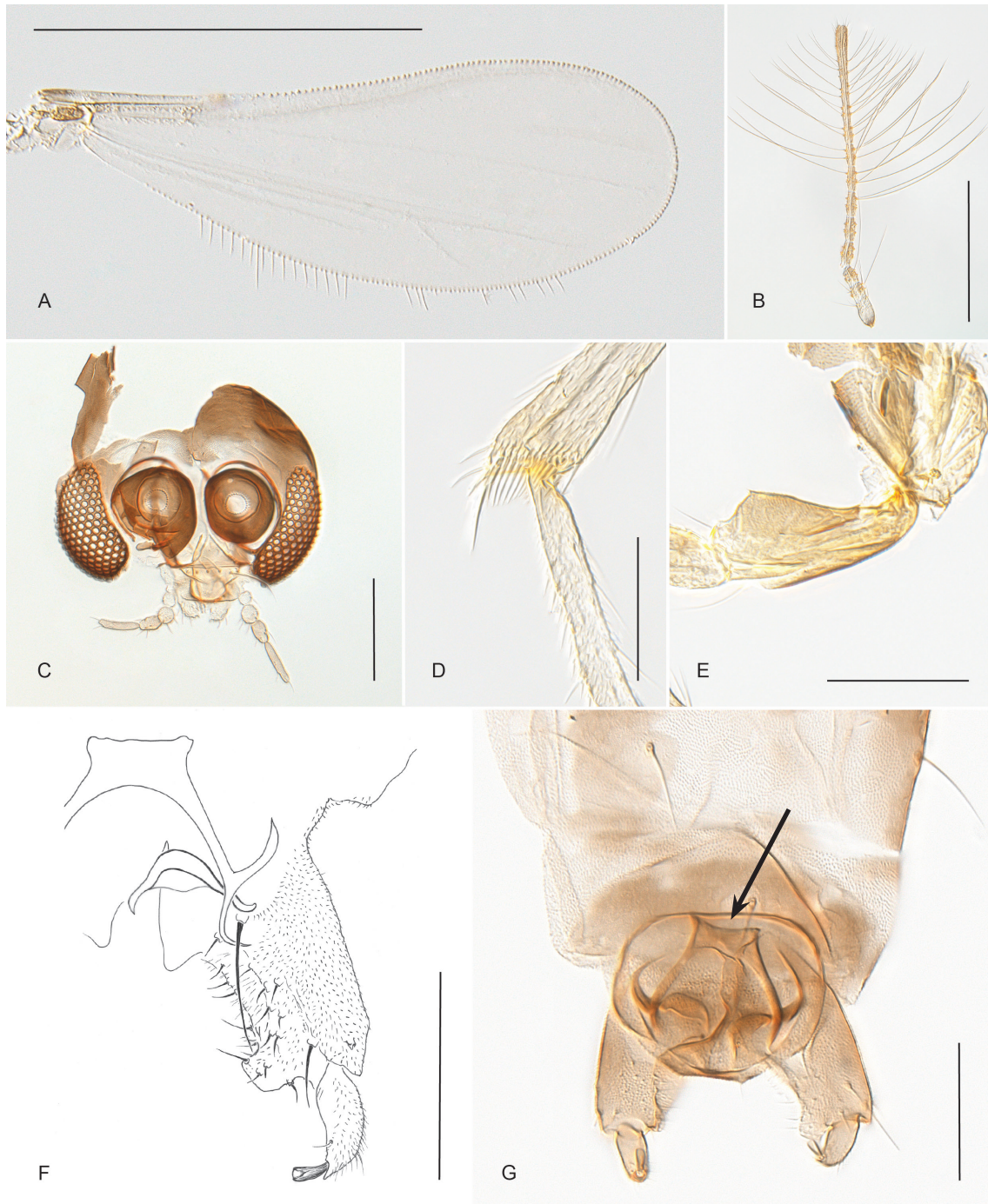


Figure 4. *Corynoneura ferringtoni* sp. n., male adult. A: Wing (NTNU-VM 145171); B: Flagellomeres (NTNU-VM 145171); C: Head (NTNU-VM 145171); D: Apex of hind tibia (NTNU-VM 124583); E: Fore trochanter (NTNU-VM 145171); F: Hypopygium (NTNU-VM 202004), G: Hypopygium (NTNU-VM 145171). Scale bars: A = 500 μ m; B = 200 μ m; C = 100 μ m; D-G = 50 μ m. Arrow pointing to the thick transverse sternapodeme.

square, situated distally at inner margin of gonocoxite; transverse sternapodeme anterior margin almost straight, thick, with oral extensions; phallapodeme short with curved, well-sclerotized anterior margin, joining sternapodeme at caudal curve.

Male adult (n = 3)

Colour. Head brown; thorax light brown, scutum, scutellum and postnotum dark brown; halteres white; abdominal tergites light brown, with white rectangular patch at tergite VII; legs light brown.

Head (Fig. 4C). AR = 0.65 - 0.69; antenna (Fig. 4B) with 9 flagellomeres (2); apical flagellomere 170 - 190 μm ; flagellomeres with more than one row of setae each; antennal tip slightly enlarged with a median small concavity, with short setae distributed on the apical fourth of the terminal flagellomere.

Thorax. See Table 1.

Wing (Fig. 4A). Wing length 0.77 - 0.79 mm; wing width/wing length 0.38 - 0.40; clavus/wing length 0.24 - 0.25.

Legs (Figs 4D, E). LR₁ 0.47 - 0.48 (2); Ti₃ with apical seta slightly curved (Fig. 4D); Ti₃ scale length/apical width 0.42 - 0.47.

Abdominal setation: TIII - TV 1, TVI - TVII 3 and TVIII 1.

Hypopygium (Figs 4F, G). Tergite IX with 4-6 setae; laterosternite with 1-2 setae; superior volsella conspicuously broadly triangular; inferior volsella small and almost square, situated distally at gonocoxite inner margin; sternapodeme thick, 25 μm wide with anterior extensions; phallapodeme anterior margin sclerotized, curved, joined with ster-

napodeme at caudal curve; gonostylus short, crista dorsalis absent (Fig. 4F).

Measurements and other characters in Table 1. Female, pupa and larva not known.

Remarks

The presence of a slightly enlarged antennal tip with a median small concavity, short setae distributed on the apical fourth of the terminal flagellomere, a comparatively short lateral sternapodeme and short phallapodeme are characters that indicate a morphological proximity of *C. ferringtoni* with *C. fittkai*, *C. celeripes*, *C. paludosa* and *C. makarchenkorum*. The shape and placement of the superior and inferior volsellae of the hypopygium separates *C. ferringtoni* from these species. Distribution: Barcoded records in BIN BOLD:AAI0860 are available from Norway and Germany. In addition, we have seen material from Austria (not DNA barcoded) that fits the diagnosis of *C. ferringtoni*, but these are not considered as part of the type material.

Corynoneura magna Brundin, 1949

Material examined. Holotype: Male adult, remains on microscopy slide (NHRS-BY-WS000002205, A63 or A6J) Sweden, Jönköping (Småland), Vetlanda, Lake Skären, leg. L. Brundin, 07.vi.1946.

According to Brundin (1949) the wing length of *C. magna* is 1.8 mm and the species has an AR between 0.8 and 1.0. The apex of the hind tibia resembles *C. minuscula*. The antennal apex, however, is pointed without a rosette, and not concave as in *C. minuscula*. The type material of *C. magna* is one single male with an abdomen separated



Figure 5. *Corynoneura magna* Brundin, 1949, holotype (NHRS-BYWS000002205, A63 or A6J). Fore trochanter. Arrow pointing to the stepwise structural transition of the keel in the distal end. Scale bar = 50 μm .

from the thorax, and a missing hypopygium. The holotype of *C. magna* has a fore trochanter with keel, and bare eyes (Fig. 5). Distribution: Sweden and Finland (Ashe and O'Connor 2012, Tuiskunen and Lindeberg 1986).

***Corynoneura minimagna* sp. n.**

<https://zoobank.org/1626ADF6-F4A7-4F62-A17D-D6B91A9A3B6E>

Holotype: Male adult (NTNU-VM 124528), Norway, Trøndelag, Røros, Sølendet, spring C-1, 62.691°N, 11.833°E, 788 m asl, 04.-10.vii.2005, leg. Aagaard et al. [BOLD ID: SOE30]. Paratypes: Four male adults (NTNU-VM 124550, NTNU-VM 124572, NTNU-VM 124594, NTNU-VM 280870) as holotype [BOLD ID: SOE32, SOE34, SOE36, not in BOLD].

Etymology. The species is named “minimagna” for its superficial resemblance to, but much smaller size than, *C. magna* (almost half the wing length).

Diagnostic characters. *Corynoneura minimagna* can be differentiated from other *Corynoneura* species by having a weak extension of the hind tibia; superior volsella rounded, weak, barely recognizable; inferior volsella a well-developed rounded lobe situated on posterior part of gonocoxite inner margin; transverse sternapodeme thick; phallapodeme with a curved sclerotized anterior margin joined with sternapodeme at caudal curve.

Male adult (n = 4)

Colour. Head brown; thorax light brown; halteres whitish; abdominal tergites light brown, with white rectangular patch at tergite VII; legs light brown.

Head (Figs 6B, C). AR = 0.47 - 0.79; antenna (Fig. 6D) with 10-12 flagellomeres, apical flagellomere 165 - 245µm; flagellomeres with more than one row of setae each; antennal tip tapering, with short setae distributed on the apical fourth of the flagellomere.

Thorax (Fig. 6F). See Table 1.

Wing (Fig. 6A). Wing length 0.95 - 1.03 mm; wing width/wing length 0.32 - 0.35; clavus/wing length 0.31 - 0.33.

Legs. LR₁ 0.53-0.57; Ti₃ with apical seta slightly curved (Fig. 6H); Ti₃ scale length/ apical width 0.42 - 0.53.

Abdominal setation (1): TII - TIV 1, TV - TVII 3, TVIII 1; SIII - SVI 2, SVII - SVIII 1.

Hypopygium (Figs 6G, I, J). Tergite IX with 6-10 setae, with concavity on median margin; laterosternite with one seta; superior volsella weakly

developed, wide and rounded; inferior volsella a well-developed lobe on posterior part of gonocoxite; sternapodeme thick, 27 µm wide, caudal extensions barely developed; phallapodeme anterior margin curved and sclerotized, joins with sternapodeme on caudal curve; gonostylus curved, crista dorsalis absent.

Measurements and other characters in Table 1. Female, pupa and larva not known.

Remarks

The tapering antennal tip, with short setae distributed on the apical fourth of the flagellomere combined the relative long lateral sternapodeme indicate a morphological proximity of *C. minimagna* to *C. disinflata* and *C. capitanea*. *Corynoneura minimagna* can be separated from these species by the shape and placement of the superior and inferior volsellae of the hypopygium. Distribution: So far only recorded from Norway.

***Corynoneura minuscula* Brundin, 1949**

Corynoneura minuscula Brundin, 1949: 698.

Corynoneura aurora Makarchenko et Makarchenko, 2010: 356, syn. n.

Material examined: Syntypes: Three male adults (two on microscopy slide, one in EtOH) (NHRS-BYWS000002202), Sweden, Kronoberg (Småland), Växjö, Lake Växjösjön, leg. L. Brundin, 29.vii.1946. One male adult abdomen on microscopy slide (NHRS-BYWS000002199, B25), Sweden, Dalarna, peat bog near Ludvika, leg. L. Brundin, 05.vi.1946. Other material: Two male adults, Germany, Baden-Württemberg, Bodensee-Gebiet, Buchenseen, leg. F. Reiss, 18.vi.1962. One male adult, Germany, Bavaria, Großer Ostersee bei Lauterbacher Mühle, leg. Burmeister, 30.viii.1981. Two male adults, Germany, Bavaria, am Gröben-see, Osterseen, leg. F. Reiss, 12.ix.1981. One male adult (NTNU-VM 201818), Norway, Telemark, Drangedal, Sannes-Langen, lakeshore and bog, 59.04388°N, 9.30952°E, 66 m asl., leg. Elisabeth Stur & Patrycja Dominiak, 19.viii.2019 [BOLD ID: MM-CH24]. One male adult (NTNU-VM 201830) Norway, Telemark, Drangedal, Haugstjenn ved FV 38, 59.09381°N, 8.95910°E, 90 m asl., Elisabeth Stur & Patrycja Dominiak, leg. 19.viii.2019 [BOLD ID: MM-CH36].

Diagnostic characters

Corynoneura minuscula can be differentiated from other *Corynoneura* species with short apical extension on the hind tibia by the following character combination: Superior volsella small, rounded lobe; inferior volsella well-developed and knob-

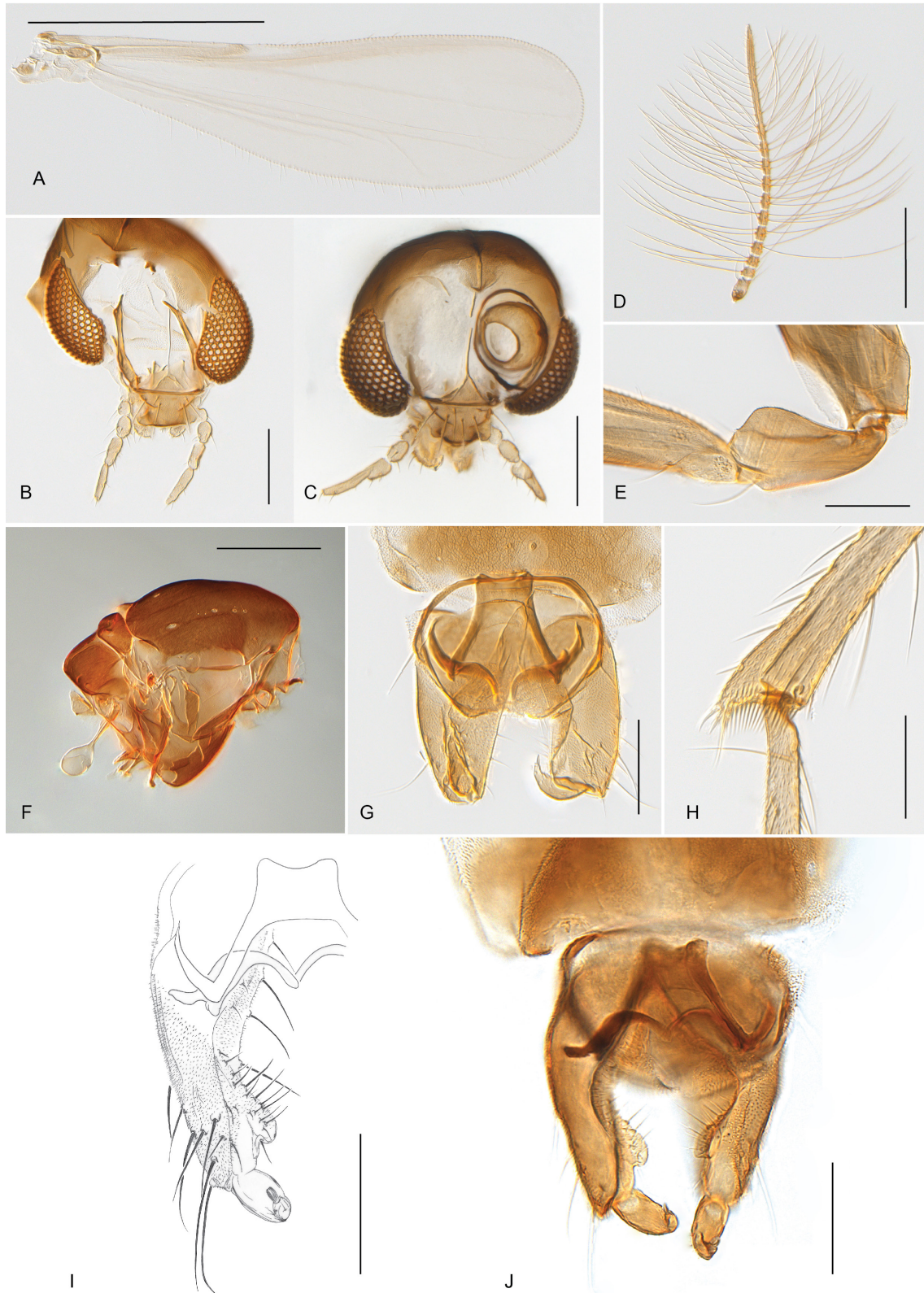


Figure 6. *Corynoneura minimagna* sp. n., male adult. A. Wing (NTNU-VM 124572); B. Head with normal palp (NTNU-VM 124594); C. Head with aberrant palp (NTNU-VM 124550); D. Flagellomeres (NTNU-VM 124572); E. Fore trochanter (NTNU-VM 124528); F. Thorax (NTNU-VM 280870); G. Hypopygium (NTNU-VM 124528); H. Apex of hind tibia (NTNU-VM 124528); I. Hypopygium (NTNU-VM 280870); J. Hypopygium (NTNU-VM 280870). Scale bars: A = 500 µm; D, F = 200 µm; B, C = 100 µm; E, G, H, I, J = 50 µm.

like with hyaline margin, placed at inner margin of gonocoxite at about half length; transverse sternapodeme u-shaped, thick; phallapodeme short with anterior margin sclerotized and rounded.

Male adult (n = 5)

Colour. Head dark brown; thorax brown, scutum, scutellum and postnotum dark brown; halteres white; abdominal tergites dark brown, with light brown rectangular patch at tergite VII; legs light brown.

Head (Figs 7C, F, G). AR = 0.51 - 0.79; antenna (Fig. 7B) with 10 - 12 flagellomeres, apical flagellomere 155 - 190 μm ; flagellomeres with more than one row of setae each; antennal tip slightly enlarged and tapering distally, with short setae distributed on the apical fourth of the flagellomere.

Thorax. See Table 1.

Wing. Wing length 0.73 - 0.88 mm (4); wing width/wing length 0.37 - 0.38 (4); clavus/wing length 0.25 - 0.29 (4).

Legs (Figs 7B, E). LR₁ 0.54 - 0.60; Ti₃ apical seta slightly curved (Fig. 7D); Ti₃ scale length/apical width 0.46 - 0.54. (Fig. 7B)

Abdominal setation: TII - TV 1, TVI - TVII 3, TVIII 1.

Hypopygium (Figs 7H, I, J). Tergite IX with 4 setae; laterosternite with 2 setae; superior volsella small, rounded lobe; inferior volsella well-developed, rounded knoblike with hyaline margin, situated at half length of the gonocoxite inner margin; transverse sternapodeme thick, 15 - 25 μm wide; phallapodeme short with rounded and sclerotized anterior margin, joined with sternapodeme at its caudal extension (Fig. 7H); gonostylus widened medially with rounded posterior margin, crista dorsalis absent (Figs 7H, I, J).

Measurements and other characters in Table 1.

Remarks

Schlee (1968) defined *C. minuscula* based on material from Germany (Brandenburg, coll. Mothes). He illustrated the apodemes and refers to Brundin's (1949) drawing of the hypopygium. In Schlee (1968), *C. minuscula* keys close to *C. fittkai* separated by the long inner setae on the superior volsella in *C. fittkai* and the shape of the gonocoxite inner margin. Fu et al. (2010b) transferred *C. minuscula* to *Thienemanniella* without further explanation. The most likely reason is that they erroneously coded this species with hairy eyes in their taxon-character matrix used in the phylogenetic analysis (Fu et al. 2010: 38). Following Fu et

al. (2010b), Ashe and O'Connor (2012) listed *C. minuscula* within the genus *Thienemanniella*.

Makarchenko and Makarchenko (2010) described *C. aurora* based on material they previously identified as *Corynoneura* cf. *minuscula*. Since *Corynoneura minuscula* was transferred to *Thienemanniella* by Fu et al. (2010b), Makarchenko and Makarchenko (2010) described their material as species new to science. They mentioned, however, the necessity of examining Brundin's type material of *Corynoneura minuscula* to confirm whether they are conspecific. Moller Pilot (2013): 53) recognized that *C. minuscula* has bare eyes and considered *C. aurora* Makarchenko et Makarchenko, 2010 a possible synonym of *C. minuscula*. We have seen Brundin's syntypes of *Corynoneura minuscula* and can confirm that the eyes are overall bare, except for some small microtrichia at the margin. Moreover, a superior volsella is present, and the fore trochanter has a keel. We thus consider *C. aurora* Makarchenko et Makarchenko a synonym of *C. minuscula* Brundin. Distribution: Records on BOLD belonging to BIN BOLD:ADA5504 are collected in Sweden, Finland and Norway. Non-barcoded records additionally from Russia and Germany. According to Ashe and O'Connor (2012) the species is also recorded from Canada, Austria, France and Spain.

Corynoneura paludosa (Brundin, 1949)

Corynoneurella paludosa Brundin, 1949: 830

Corynoneura paludosa (Brundin), Schlee, 1968: 48

Material examined. Syntype: One male adult on microscopy slide (NHRS-BYWS000002197, B34, BRD282), Sweden, Jämtland, Kålarne, Öster-Vontjärn, leg. L. Brundin, 12.vi.1946.

Other material: Two males on microscopy slide (NHRS-BYWS000002196, BRD281), Finland, Kemin Lappi (Lapponia kemensis pars occidentalis), Pohjoinen-Sodankylä, Posolampi (pond Poso), leg. M. Hirvenoja, 01.vii.1961. Six male adults (NTNU-VM 136459, NTNU-VM 200419, NTNU-VM 200420, NTNU-VM 235343, NTNU-VM 235344, NTNU-VM 235345), Norway, Finnmark, Porsanger, Fen near Gaggavann, sweep net, 70.42284°N, 26.73690°E, 106 m asl, leg. T. Ekrem & E. Stur, 17.vi.2010 [BOLD ID: Finnmark363, Finnmark855, Finnmark856]. Two male adults (NTNU-VM 229667, NTNU-VM 229668), Norway, Møre og Romsdal, Trollheimen, Folddalen, Gråhaugfjellet, sweep net, 62.91223°N, 9.11036°E, leg. T. Ekrem, 09.viii.2021 [BOLD ID: NO137, NO138].

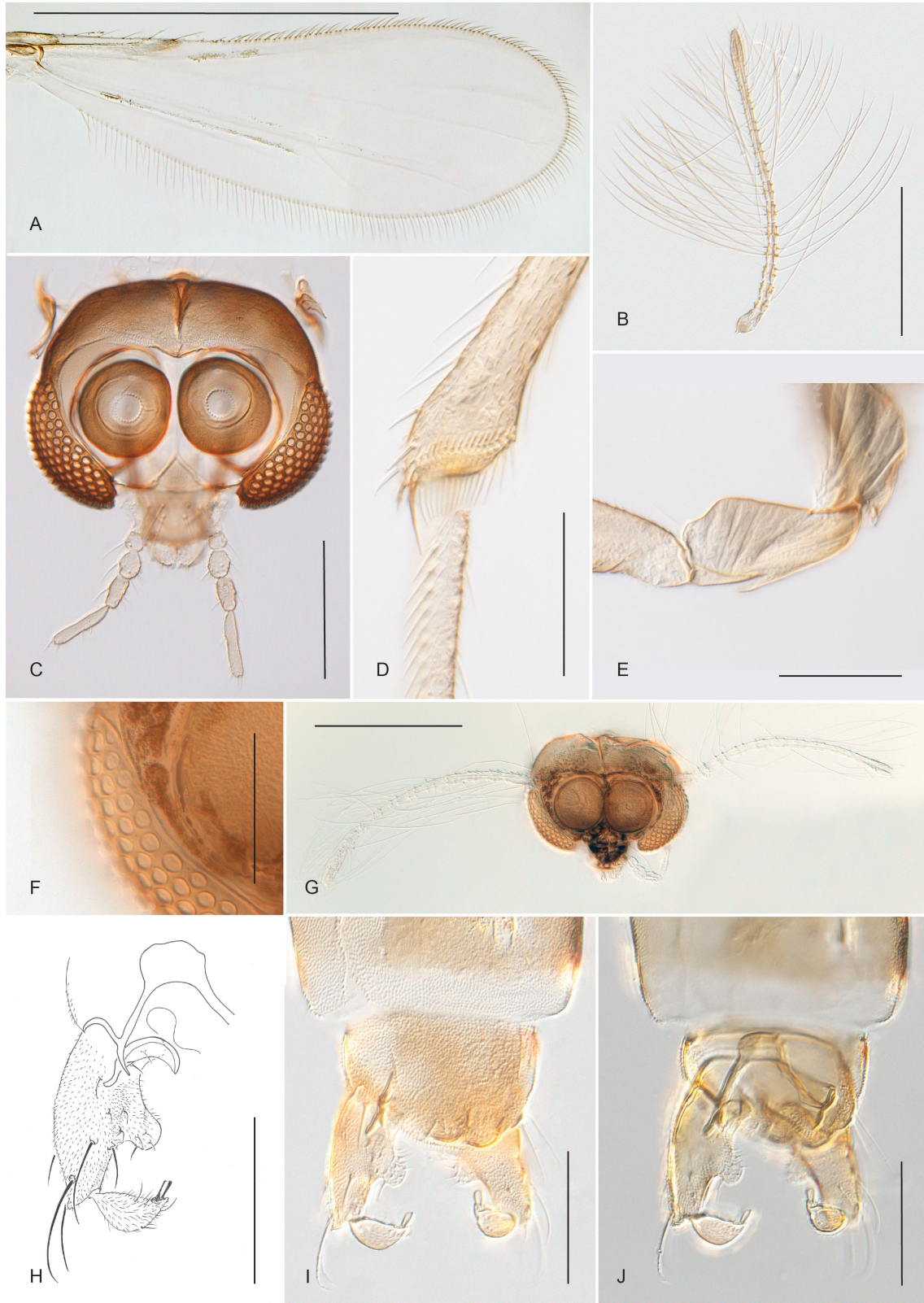


Figure 7. *Corynoneura minuscula*, male adult. A: Wing (NTNU-VM 201830); B: Flagellomeres (NTNU-VM 201830); C: Head (NTNU-VM 201830); D: Apex of hind tibia (NTNU-VM 201830); E: Trochanter (NTNU-VM 201830); F: Eye (syntype), G: Head with antennae (syntype); H-J Hypopygium (NTNU-VM 201830). Scale bars: A = 500 μ m; B, G = 200 μ m; C = 100 μ m; D-F, H-J = 50 μ m.

Diagnostic Characters. The male adult of *C. paludosa* can be differentiated from those of other *Corynoneura* species by the following character combination: apex of the hind tibia with very weak elongation; superior volsella well-developed, sclerotized; inferior volsella wide and rounded along the distal half of the gonocoxite; transverse sternapodeme thick; phallapodeme short with posterior margin convex and sclerotized; gonostylus thin, slightly curved.

Male adult (n = 4)

Colour. Head brown; thorax dark brown; halteres white; abdominal tergites brown, with white rectangular patch at tergite VII; legs brown.

Head (Fig. 8C). AR = 0.47 - 0.52. Antenna (Fig. 8B) with 12 flagellomeres, apical flagellomere 150 - 170 μm ; flagellomeres with more than one row of setae each; antennal apex enlarged with a median cavity, with short setae distributed on the apical fourth of the flagellomere (Fig. 8B).

Thorax. See Table 1.

Wing (Fig. 8A). Wing length 0.82 - 0.88 mm; wing width/wing length 0.35 - 0.43; clavus/wing length 0.29 - 0.31.

Legs (Figs 8D, E). LR₁ 0.49 - 0.5; Ti₃ with apical seta slightly curved (Fig. 8D); Ti₃ scale length/apical width 0.25 - 0.42.

Abdominal setation: TII - TV 1, TVI - TVII 3, TVIII 1 setae.

Hypopygium (Figs 8F, G). Tergite IX with 4-8 setae, two of them longer, situated at the posterior margin; laterosternite with 1-2 setae; superior volsella strongly sclerotized, well-developed, broadly triangular; inferior volsella rounded along posterior half of gonocoxite, with distal concave margin; sternapodeme thick, 18 - 28 μm wide; phallapodeme posterior margin convex and sclerotized, joined with sternapodeme at caudal extension; gonostylus thin, about the same width basally and medially, slightly tapering distally; crista dorsalis absent.

Measurements and other characteristics in Table 1. Female, pupa and larva not known.

Remarks

The mounted syntype of *Corynoneurella paludosa* has pubescent eyes, the antennal apex has a median cavity, a dorsal keel on the fore trochanter is present, and the apex of the hind tibia is only slightly extended (see also the drawing of the hypopygium of another syntype in Brundin 1949: 831, fig. 199). Despite the hypopygium of the studied syntype

being mounted laterally, the sclerotization of the posterior margin phallapodeme is clearly visible. The sclerotized superior volsella is visible and the gonostylus shows its distinct form as described and illustrated by Brundin (1949). In the literature, the eyes of *Corynoneura* are generally described as bare (e.g. Brundin 1956, Cranston et al. 1989, Goetghebuer 1932) and rarely as pubescent (Fu et al. 2017), and the character “bare eyes” is used in generic keys to differentiate *Corynoneura* from other Corynoneurini (e.g. Cranston et al. 1989, Sæther et al. 2000, Wiedenbrug and Trivinho-Strixino 2009). However, in our experience, specimens of other *Corynoneura* species (e.g. *C. gratias*, *C. arctica*) show sparsely distributed, short microtrichia between the ommatidia. Thus, we suspect that small microtrichia might have been overseen or not interpreted as conspicuous enough to be considered as pubescent in previous studies (Wiedenbrug and Trivinho-Strixino 2011). Moreover, the presence of a pearl row in the pupal wing sheaths of *C. paludosa* further support the placement in *Corynoneura* (Janne Raunio pers. com.)

The well sclerotized phallapodeme posterior margin observed in *Corynoneurella paludosa* (Fig. 8G) is a feature also present in several *Corynoneura* species from the Neotropical region, e.g., *Corynoneura esprañado* Wiedenbrug et al., 2012, and *C. humbertoi* Wiedenbrug et al., 2012. For these species, the immatures are known and fit the diagnosis of *Corynoneura*. In conclusion, we cannot find reliable morphological characters that warrant placement of *C. paludosa* in a genus outside of *Corynoneura*. Distribution: DNA barcoded specimens belonging to BIN BOLD:AAV3049 have been collected in Norway, Finland and Canada. In addition, we have Brundin’s type material from Sweden. Previous records from other regions should be compared against the current understanding of the species.

Thienemanniella langtoni sp. n.

Corynoneurella paludosa sensu Langton 1997, nec Brundin 1949

<https://zoobank.org/13CA9CD7-6AFF-4A0D-AD7E-DAE9A06E7BA8>

Etymology. The species is named in honour of Peter H. Langton for his many contributions to Chironomidae taxonomy.

Type material. Holotype: Pharate male (PHL), Spain, Pyrenees, Centre de Recerca d’Alta Muntanya (CRAM) de la Universidad de Barcelona (Vielha), 03.vii.1994, leg. P.H. Langton. Paratypes: 1 pharate male, 3 pupae as holotype.

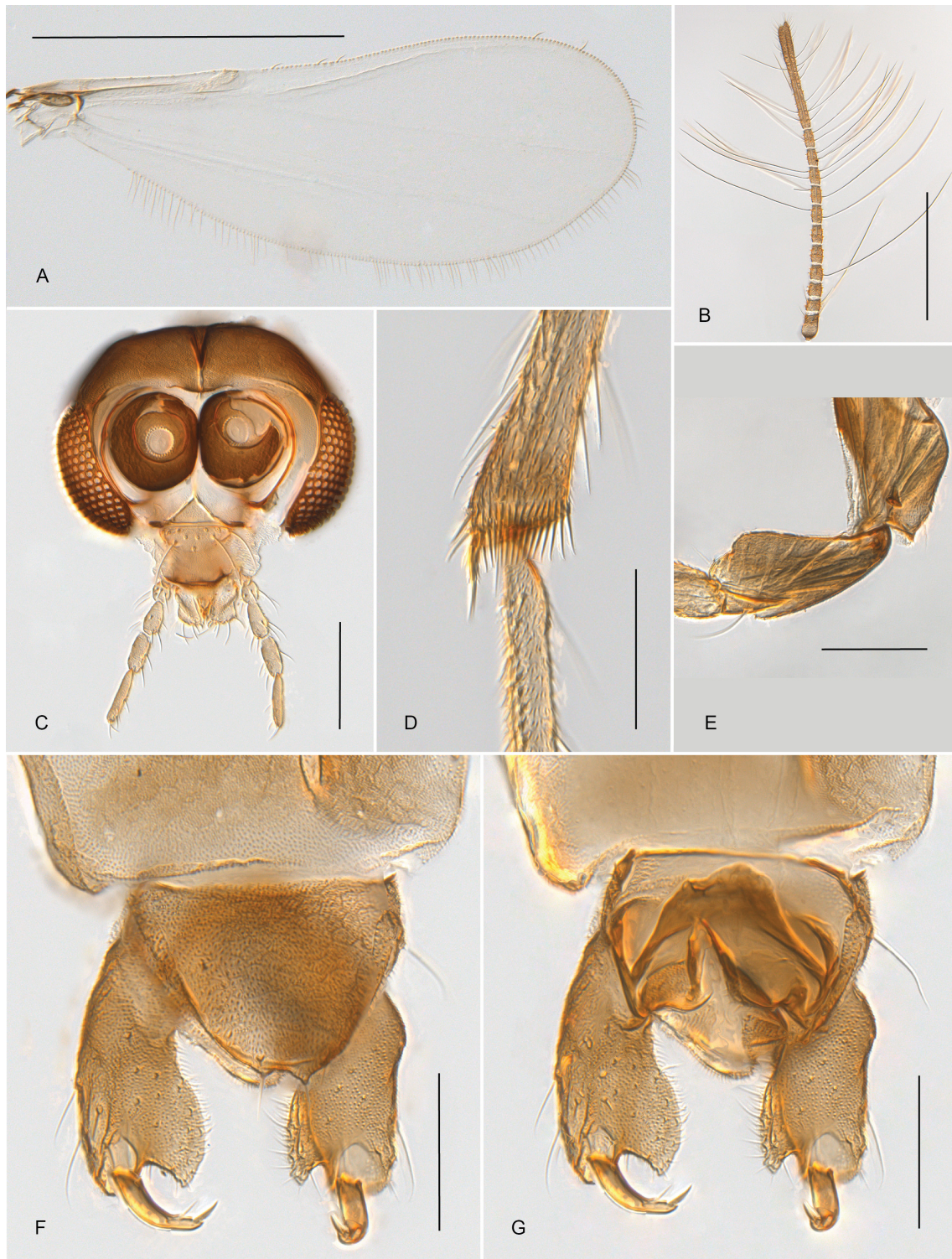


Figure 8. *Corynoneura paludosa* comb. n., male adult (NTNU-VM 136459). A: Wing; B: Flagellomeres; C: Head; D: Apex of hind tibia; E: Trochanter; F, G: Hypopygium. Scale bars: A = 500 μ m; B = 200 μ m; C = 100 μ m; D-G = 50 μ m.

Diagnostic characters. *Thienemanniella langtoni* can be separated from other congeners by combining characters of pupae and male adults: the latter having strongly pubescent eyes, fore trochanter with keel not having the stepwise abrupt structural transition in the distal end (as typically

seen in *Corynoneura*), straight transverse sternapodeme, superior volsella without microtrichia and setae, inferior volsella well-developed and placed distally on gonocoxite margin. The pupa separates from congeners in having a pearl row on the wing sheaths and long spinules on sternite II.

Table 1. Comparison of metric (in μm) and meristic characters of male adults of *Corynoneura*.

Character/Species	<i>C. paludosa</i> (n = 4)	<i>C. minuscula</i> (n = 5)	<i>C. ferringtoni</i> sp. n. (n = 3)	<i>C. minimagna</i> sp. n. (n = 4)	<i>C. celeripes</i> (n = 3)
Thorax length	530 (1)	420-465	425-450 (2)	540 (1)	~500
Abdomen length	750-770 (2)	-	680-830	-	~700
Wing length	820-880	730-780 (4)	770-790	950-1030	~800
AR	0.47-0.52	0.51-0.79	0.65-0.69 (2)	0.47-0.79	0.7(1)
Length apical flagellomere	260-280	155-190	170-190 (2)	165-245	210 (1)
flagellomeres	12	10-12	9	10-12	11 (1)
Clypeals	8-11	6 (3)	6-7 (2)	5 (1)	-
Palpomere 3	30-38	20-22	20 (1)	28 (1)	20 (1)
Palpomere 4	33-38	25-30	22 (1)	40 (1)	25 (1)
Palpomere 5	43-55	35-52	45 (1)	50 (1)	52 (1)
Dorsocentrals	5-6	4-5	4-5 (2)	4(1)	-
Prealars	2-3	2	2 (2)	2(1)	-
Scutellars	2	2	2 (2)	2(1)	-
Wing width/wing length	0.35-0.43	0.37-0.38 (4)	0.38-0.40	0.32-0.35	-
Clavus/Wing	0.29-0.31	0.25-0.29 (4)	0.24-0.25	0.31-0.33	-
LR ₁	0.49-0.56	0.54-0.60	0.47-0.48 (2)	0.53-0.57	0.53 (1)
Ti ₃ apex extension length/ Apex ti3 width	0.25-0.42	0.46-0.54	0.42-0.47 (2)	0.40-0.53	0.5-0.7 (2)
Apical setae on Ti ₃	curved	curved	curved	curved	curved
Setae on tergite IX	4-8	4	4-6	6-10	At least 4
Setae on laterosternite TIX	1-2	2	1-2	1	-
Gonocoxite length	85-100	75-77	67-75	102-115	87
Gonostylus length	28-48	20-25	25 (2)	35-45	35 (1)
Crista dorsalis	absent	absent	absent	absent	absent
Transverse stenapodeme	18-28	15-25	25	27	25 (1)

Remarks

Langton (1997) assigned these specimens from the Pyrenees to *Corynoneurella paludosa*, figured the male hypopygium and discussed the taxonomic placement based on adult male and pupal characters. His observations concluded that these specimens have characteristics that place them systematically between *Corynoneura* and *Thienemanniella*

and therefore re-erected the genus *Corynoneurella*. However, Langton's specimens do not match the diagnostic characters found in the examined syntype of *Corynoneurella paludosa* Brundin. Even though the inferior volsella and the gonostylus of *Corynoneurella paludosa* sensu Langton resemble the drawing of Brundin's *C. paludosa*, the superior volsella and the apodemes in these species are clearly different (Langton 1997, fig.

1). To avoid future confusion, we here designate a name for *Corynoneurella paludosa* sensu Langton (1997) and until further molecular and morphological evidence is present, place the species in *Thienemanniella*: The two pharate males have hairy eyes, but the microtrichia are relatively short just barely surpassing the ommatids (Fig. 9A). The trochanter of two examined pharate males is without the same type of keel seen in the *Corynoneurella* species in this paper (Fig. 9C), lacking the abrupt stepwise structural transition in the distal end (Fig. 5). The apex of the hind tibia is without extension (Fig. 9D), and the transverse sternapodeme is thin and wide with anterolateral projections (Langton 1997, fig. 1) as is typical for *Thienemanniella*. The ratio of the clavus length/wing length is not yet known since the available specimens were pharate males and pupae. The pupa has cylindrical macrosetae typical for *Thienemanniella*, but as typical for *Corynoneurella*, pearl rows are present in the wing sheaths (Fig. 9B). This character has, to our knowledge, not been recorded within *Thienemanniella* previously. Langton (1997) also mentions the presence of long spinules on sternite II in the pupa

which is another feature he considers typical for some *Corynoneurella* species. We expect the generic diagnoses to be emended as more immature stages of Corynoneurini species are described and therefore choose to tentatively place it in *Thienemanniella* until its placement is otherwise resolved.

As a consequence of the above-described misconception, the recorded distribution of *Corynoneurella paludosa* should be reconsidered. For example, Michiels (2004) reported *Corynoneurella paludosa* for the first time for Germany. We were able to study her material and can confirm that these specimens are not *Corynoneurella paludosa* sensu Brundin. Moreover, even though they resemble *Thienemanniella langtoni* sp. n., they are clearly different and probably belong to a species new to science that remains to be described.

Thienemanniella afra Lehmann, 1981

Thienemanniella afra was described by Lehmann (1981) based on males with associated pupae. The species was collected from a creek near Kisingani in the Democratic Republic of Congo. Fu and Sæther (2012) placed *Thienemanniella afra*

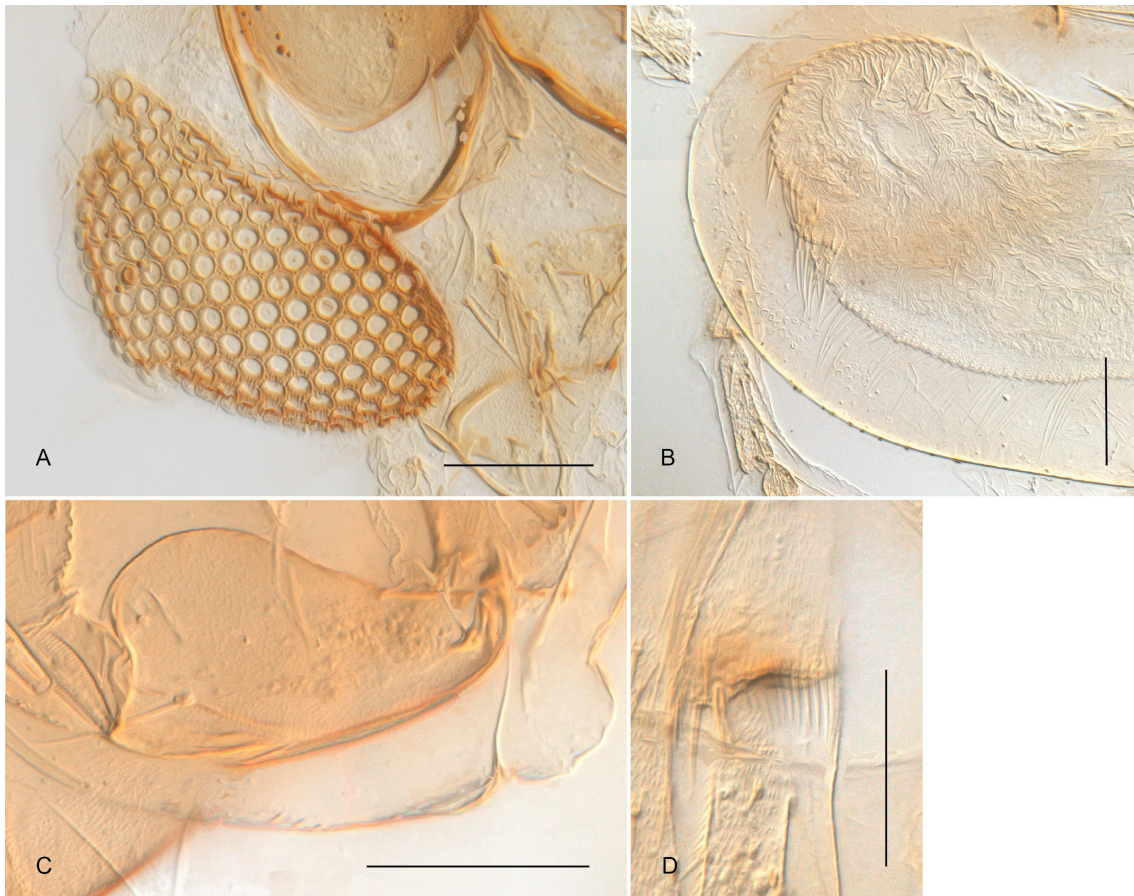


Figure 9. *Thienemanniella langtoni* sp. n., holotype, pharate male. A: Eye; B: wing sheath showing pearl row; C: Fore trochanter; D: Apex of hind tibia. Scale bars = 50 μ m.

Lehmann into *Corynoneurella*, suggesting that bare eyes in the adult male and missing pearl row in the pupa places the species in a position between *Thienemanniella* and *Corynoneura*, like *Corynoneurella paludosa* sensu Langton (1997). However, Fu et al. (2010b) mention several *Thienemanniella* species with bare eyes: *T. nipponica*, *T. flavescens*, *T. flaviscutella*, *T. okigrata*, *T. partita* and *T. togamijika*.

After examining the holo- and paratypes of *Thienemanniella afra* at the ZSM, we noted that the first trochanter does not have a dorsal keel. Based on this and the discussion above, we support Lehmann's original placement of the species and restore it to its original combination *Thienemanniella afra* until its generic assignment is otherwise revised.

Key to *Corynoneura* species with a short elongation of the hind tibial apex.

1. Antennal apex scarcely broadened, with or without small concavity, setae on antennal tip never arranged in form of a rosette; tibial apex of hind leg not elongated, half as long as tibial width or shorter; hind tibia with apical seta (A-seta) slightly curved; hypopygium with transverse sternapodeme present, straight, not pointed; phallapodeme joins posteriorly, or at posterior extension with sternapodeme (see Schlee 1968: 142 figs 151-152); phallapodeme slightly curved (Inner structures of *C. magna* not described by Brundin) 2

- Antennal apex usually without a small apical concavity with or without rosette; tibial apex of hind leg elongated more than half of the tibial width; apical seta (A-seta) curved or s-shaped; hypopygium with transverse sternapodeme straight, slightly curved, or absent - when absent, lateral sternapodeme meeting orally; phallapodeme joins either laterally, or posteriorly, or at posterior extension with sternapodeme (see Schlee 1968: 142 figs 151-153); phallapodeme long or short, and strongly or slightly curved not keyed

2. Wing length about 1.8 mm; AR between 0.8 and 1.0; inferior volsella as in Brundin (1949: 831, fig. 202) *C. magna* Brundin, 1949

- Wing length shorter than 1.8 mm; other combination of characters 3

3. Phallapodeme strongly sclerotized on convex posterior margin (Fig. 8G); inferior volsella wide, with base along distal half of gonocoxite; gonostylus comparatively thin, slightly curved (Figs 8F, G) *C. paludosa* Brundin, 1949

- Phallapodeme strongly sclerotized on anterior margin; inferior volsella considerably smaller with base along less than half of gonocoxite; gonostylus comparatively thin, straight or curved 4

4. Superior volsella short and triangular, bearing several long setae postero-median directed (Schlee 1968: 116, fig. 8) *C. fittkaui* Schlee, 1968

- Superior volsella without setae, not as above 5

5. Transverse sternapodeme thin with parallel sided margins; superior volsella long and narrow (Fu et Sæther 2012: 19, fig. 9) *C. disinflata* Fu et Sæther, 2012

- Transverse sternapodeme mostly thick, with at least posterior margin concave; superior volsella not as above 6

6. Antennal apex pointed; superior volsella triangular, small, restricted to oral ¼ of gonocoxite margin; inferior volsella small, placed caudally; gonostylus with well-developed megaseta (Fu et Sæther 2012: 12, fig. 5) *C. capitanea* Fu et Sæther, 2012

- Character combination not as above 7

7. Inferior volsella situated on distal end of inner margin of gonocoxite (Figs 4F, 6I) 8

- Inferior volsella not situated distally on inner margin of gonocoxite (Fig. 7H) 9

8. Antennal apex blunt with small concavity (Fig. 4B); superior volsella conspicuous and triangular; inferior volsella small, almost square in outline (Fig. 4F) *C. ferringtoni* sp. n.

- Antennal apex pointed (Fig. 6D); superior volsella indistinctive, flat, rounded; inferior volsella rounded, posteriorly pointed lobe (Fig. 6I) *C. minimagna* sp. n.

9. Inferior volsella small, placed at about ½ length of gonocoxite, rounded, knoblike with hyaline margin (Figs 7H-J), AR 0.5-0.8, wing length less than 0.9 mm *C. minuscula* Brundin, 1949

- Inferior volsella broader, placed in distal half of gonocoxite, albeit not far distally 10

10. AR 0.9-1.0, wing length about 1.4 mm, gonostylus curved (Krashenninikov 2012: 85 figs 1-3) *C. makarchenkorum* Krashenninikov, 2012

- AR 0.59-0.70, wing length about 0.9 mm (Schlee 1968), gonostylus with straight inner margin (Fig. 3A, Brundin 1949, fig. 205) *C. celeripes* Winnertz, 1852

Discussion

The generation of DNA barcodes from specimens and populations in the *Corynoneura*-group has revealed species-level diversity previously hidden behind similar morphology. The many interim names for species in this group in BOLD is an indication of this, as is the number of Barcode Index Numbers (BINs, Ratnasingham and Hebert (2013)) for this group in the database. Our findings for Europe, thus, is consistent with those of Silva and Wiedenbrug (2014) reported for neotropical taxa. It is perhaps not surprising that minute taxa such *Thienemanniella* and *Corynoneura* hold many undiscovered species as comparable results are found in other nematoceran families (e.g. Hebert et al. 2016, Kjørandsen 2022, Stur and Borkent 2014). However, as we show in this work and elsewhere (e.g. Anderson et al. 2013, Stur and Ekrem 2015), these undiscovered taxa are often not truly cryptic as small and consistent morphological differences usually can be found. Thus, integrative approaches in the analysis of species diversity, including morphological and molecular characters, certainly are useful in the quest to delineate taxonomic units at the species level (Silva and Wiedenbrug 2014).

From our results, it is apparent that as more species in the *Corynoneura*-group are discovered and described, the previous rather clear-cut generic boundaries become less distinct. As an example, Schlee (1968) used the presence of an elongated hind tibial apex in adult males as a synapomorphy for all *Corynoneura*, and shorter elongation to separate *C. paludosa*, *C. celeripes*, *C. minuscula* and *C. fittkai* from the remaining *Corynoneura*. The results from our phylogenetic analysis using COI and 18S data disagrees with this, albeit

many of the basal branches have low branch support (Fig. 2). There are, however, groups that appear more robust such as *Thienemanniella*, the *scutellata*-group and the *lobata*-group. Although taxon sampling and geographical representation needs to be improved considerably for a proper comparison, we observe that at least some of these relationships conflict with those presented by Schlee (1968) and Fu et al. (2009). Thus, the task to resolve the phylogeny of the *Corynoneura*-group remains open, and future molecular analyses should include multiple slow-evolving markers (such as 18S and CAD) to increase the robustness of phylogenetic groups above the species-level (Ekrem et al. 2010).

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