

A RARELY SEEN TAXONOMIC REVISION WITH IMMENSE VALUE FOR 41 YEARS: REFLECTIONS ON THE 1981 MONOGRAPH OF *TRICHONTA* WINNERTZ, 1864 (DIPTERA, MYCETOPHILIDAE) BY RAYMOND GAGNÉ, WITH AN INTEGRATIVE REVISION OF THE *TRICHONTA VULCANI* (DZIEDZICKI, 1889) SPECIES COMPLEX

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Abstract.—We celebrate Raymond J. Gagné for his contributions to taxonomy of the Mycetophilidae (Diptera), specifically for his forty-one-years-old monograph of Holarctic *Trichonta* Winnertz, 1864 that is still the primary source used for species identification in the genus. We briefly reflect on his monograph's impact and demonstrate by use of recent DNA barcode data extracted from BOLD Systems (BOLD) that the model for the distribution of Holarctic Mycetophilidae that Gagné presented in the monograph still holds up to scrutiny. To demonstrate the refined species concept now being applied by use of an integrative taxonomic approach that includes DNA barcodes, we revise a small, but distinct, species complex that Gagné recognized as one morphologically defined species and used as an example of an old pan-Holarctic taxon, *Trichonta vulcani* (Dziedzicki, 1889). We find the *Trichonta vulcani* species complex (sensu Kallweit 1998) to consist of at least six species in

the Holarctic Region of which three are being described as new to science: *Trichonta japonica* Kurina, new species (East Palearctic), *Trichonta neovulcani* Kjaerandsen, new species (East Nearctic), *Trichonta raymondgagnei* Kjaerandsen, new species (Holarctic), *Trichonta trifida* Lundstrom, 1909 (wide Palearctic), *Trichonta tristis* (Strobl, 1898) (wide Palearctic), and *Trichonta vulcani* (Dziedzicki, 1889) (wide Palearctic). All six species are distinctly separated by DNA barcodes that correspond well to minor, but constant, differences in their male terminalia. However, one of the widespread species, *Trichonta trifida*, displays some genetic and morphological differentiation between western and eastern Palaearctic populations. We presently consider these populations conspecific pending broader sampling. We further propose a replacement name *Trichonta nepalensis* Kjaerandsen, new name for *Trichonta superba* Gagné, 1981, a junior primary homonym of *Trichonta superba* Ostroverkhova, 1979, the latter being a junior secondary synonym of *Trichonta tristis* (Strobl, 1898).

Key Words: nomen novum, morphological description, DNA barcoding, Holarctic zoogeography

DOI: 10.4289/0013-8797.124.3.??

Forty-one years ago, Raymond J. Gagné revised the entire Holarctic fauna of the fungus gnat genus *Trichonta* Winnertz, 1864 in a concise monograph (Gagné 1981). Gagné examined some 4500 specimens of the genus from 21 scientific collections in North America and Europe. He recognized 67 named species and described another 34 species as new to science. This outstanding work set the standard for and is still the primary source used for identification of species of *Trichonta*. As outlined in the introduction of that publication, Gagné emphasized the importance of such revisionary works covering all the species of a larger geographic area over local species lists and minor stepwise upgrades. Unfortunately, 41 years on, only a handful of species rich fungus gnat genera, like *Trichonta*, have in this rigorous way been revised on a larger regional or world basis (see Kjaerandsen 2022). Still, 22 new species of *Trichonta* have been described stepwise after the 1981 revision, mostly from Russia (Braginia 1994; Zaitzev 1988, 1997, 1999, 2003; Zaitzev and Menzel 1996) and China (Wu and Yang 1992, Wu et al. 1995, Yang and Wu 1996, Wu et al. 2007), but also two new species from Europe (Chandler 1992, Chandler and Ribeiro 1995). Outside the Holarctic Region, the genus continues to be as poorly known as it was in 1981. Despite numerous undescribed species from the other continents we have examined in museum collections, only 14 species have been described from South America (11), Africa (1), and Australia (2). In all

about 140 species are currently placed in the genus *Trichonta* (Evenhuis and Pape 2021, Fungus Gnats Online Authors 2022). The genus *Trichonta* is classified in the tribe Mycetophilini that, together with the tribe Exechiini, make up the subfamily Mycetophilinae (Mycetophilidae) (e.g., Rindal and Sølvi 2006).

In the first part of the monograph, Gagné (1981) dealt with zoogeographical patterns analyzed on the basis of distribution data, specifically for the species in the Holarctic Region and more generally in the world. He compared the data on *Trichonta* with distribution patterns from the few other genera of fungus gnats (Mycetophilidae and Ditomyiidae) revised at the time and hypothesized a general model for the geographical distribution of Mycetophilidae in the Holarctic Region.

Here we reflect on the impact of Gagné's monograph on subsequent work on *Trichonta* and briefly re-examine his new distribution model by use of recent DNA barcoding data that we extracted from Barcode of Life Data Systems (BOLD). To demonstrate the usefulness of the integrative taxonomic approach applied here, which led to a refined species concept for *Trichonta*, we revise a small, but distinct, species complex (our *T. vulcani* complex) that Gagné recognized as a single, morphologically defined species exhibiting the old pan-Holarctic pattern of distribution (*T. vulcani* (Dziedzicki, 1889)).

MATERIALS AND METHODS

Distributional data of DNA barcoded specimens and their Barcode Index Numbers (BINs) representing Holarctic Mycetophilidae including the genus *Trichonta*, were extracted from the public data portal of Barcode of Life online database BOLD Systems (BOLD) and divided into three biogeographical regions, the Palearctic, the Eastern Nearctic and the Western Nearctic Regions (see Gagné 1981). The latter two regions were separated along the Great Continental Divide by use of the polygon selection tool on BOLD, which can be regarded as a fairly accurate, although not perfect, approximation.

Specimens studied here originate from all the major museum collections of fungus gnats in Norway, Sweden, Finland, Estonia, and the European part of Russia (see below). Also, we borrowed material of central and eastern Russian provenance from the same and a few additional institutions as well as Canadian vouchers for DNA barcodes from the Centre for Biodiversity Genomics. The following abbreviations for institutions are used here:

CBG–BIOUG—Canada, University of Guelph, Centre for Biodiversity Genomics.

FRIP—Russia, Petrozavodsk, Forest Research Institute, Russian Academy of Sciences.

IPEE—Russia, Moscow, Severtsov Institute of Ecological and Evolutionary Problems.

IZBE—Estonia, Tartu, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences (former Institute of Zoology and Botany).

LMM—Finland, Regional Museum of Lapland, Rovaniemi.

MZH—Finland, Helsinki, Finnish Museum of Natural History.

TMU—Norway, Tromsø, UiT—The Arctic University of Norway, Tromsø University Museum (The Arctic University Museum of Norway).

NHRS—Sweden, Stockholm, The Swedish Museum of Natural History.

ZISP—Russia, St. Petersburg, Zoological Institute, Russian Academy of Sciences.

ZMUM—Russia, Moscow, Zoological Museum of Moscow University.

Most studied specimens originate from ethanol samples taken by various insect traps, mostly Malaise traps but also window traps, light traps and by sweepnetting. Specimens, especially those representing types and barcode vouchers were dried by baths in Hexamethyldisilazane (chemical formula: $[(\text{CH}_3)_3\text{Si}]_2\text{NH}$), acronym: HMDS, see Brown 1993) and then pinned. Male terminalia were detached when needed, cleared in hot lactic acid by short pulse-heating in a microwave oven, before being transferred to glycerin in excavated slides for microscope imaging. The dissection of the terminalia for imaging of details of its parts is partly a destructive procedure resulting in fragmented specimens, but all parts were preserved and stored in glycerin in sealed microtubes on the pin together with the rest of the specimen.

Images of specimens and their terminalia were captured with Leica M205C stereomicroscopes by use of the Leica Application Suite (LAS X) software. Z-stacked image series were processed into extended focus images by the Helicon Focus software enabling some manual editing of layers for increased visibility of specific characters. Extended focus images were further processed with Adobe Photoshop to adjust levels and contrast, reduce shadows and clean up the background. Individual images were then processed by the Topaz Sharpen AI software to remove blur and suppress noise for enhanced sharpness. Finally, individual images were arranged into species plates, with identical angles of view for each species to ease comparison among the species.

Morphological terminology generally follows Söli (1997) with updates on wing venation in Söli (2017). Specific terms for branches and lobes of the male gonostylus are those suggested for Exechiini by Kjærandsen (2006). These terms do not necessarily denote homologies in both tribes, pending further studies into the gonostylar evolution within Mycetophilini.

Due to the COVID-19 pandemic raging in 2020–2022, this work, including the writing of the manuscript, was carried out using Microsoft TEAMS, a digital platform enabling the authors to tightly collaborate as a Nordic-Baltic taxonomic research team by sharing and discussing images and documents on a daily basis.

RESULTS AND DISCUSSION

Reflections on the 1981 *Trichonta* Revision by Raymond J. Gagné

Comprehensive studies comprising all the species of a taxon worldwide or from a large geographical range are termed taxonomic revisions or monographs. Raymond J. Gagné published two taxonomic revisions addressing genera of the family Mycetophilidae before he moved on to become a world authority of gall midges (Cecidomyiidae). His first mycetophilid revision covered the Nearctic species of the genus *Phronia* Winnertz, 1864 (Gagné 1975). Here we will focus on his second contribution to Mycetophilidae, his monograph of Holarctic *Trichonta* (Gagné 1981). Both these works have a substantial impact on similar, subsequent efforts by enabling investigators to correctly identify species using morphological indicators. This holds specifically true for the monograph on *Trichonta* with its Holarctic coverage. Gagné's illustrations of terminalia (= genitalic structures) were clear and concise although sometimes difficult to interpret due to restricted angles of view of the very complex, three-dimensional structures. Monographs of similarly broad scope have only been published for the genus *Sciophila* Meigen, 1818 by Zaitzev (1982) and for the genus *Mycomya* Rondani, 1856 by Väisänen (1984). Insofar Gagné's paper on *Trichonta* may be seen as an important contribution to a trend in the early 1980s that, although short-lived, was groundbreaking for revisionary work on Mycetophilidae. Interestingly, this trend coincides with the more general observation that there was a peak in the number of taxonomic revisions around 1990, before a dramatic and rapid decrease in revisionary taxonomy similar to levels seen in the 1950s (Kjærandsen 2022). As taxonomists who have used his monograph of *Trichonta* extensively for several decades, we are truly grateful for Gagné's tenacity, farsightedness, and accuracy.

Taxonomy differs fundamentally from many other fields of biology in that its results may have a long-lasting impact—they are used and cited several decades or even centuries after being published. It is also an image-accentuated field of science where high-quality illustrations or photographs play an essential role in disseminating crucial information

regarding phenomena of high complexity. The more comprehensive the treatment and more accurate the included text and illustrations, the longer the taxonomic impact. This is documented by citations to the work, which, on the whole might be low in frequency, but regular and consistent over the life of the work. However, citation frequency of taxonomic papers would be much higher, if editors required that authors cite taxon hypotheses, particularly species, in secondary literature (see Engel et al. 2021). As we ourselves have experienced, it is almost impossible today to receive funding for taxonomic revisions, especially those that tackle species-rich genera and involve a considerable amount of basic, descriptive work. Such works, which require skills and practical experiences that take decades to acquire, are the backbone of reliability and advance in taxonomy and, for other biological disciplines, the source of high-quality interpretation of scientific names.

Gagné's Model for the Distribution of Holarctic Mycetophilidae Revisited Using BINs from BOLD

Gagné's (1981) model for patterns of geographical distribution in Holarctic Mycetophilidae builds on three observations, as follows:

- (1) There is a high proportion of Holarctic species and a near equal proportion of species found either in the Palearctic or the Nearctic Regions.
- (2) Most of the species groups that are recognized as natural contain both Holarctic as well as regionally restricted species.
- (3) The European fauna shares more species with the eastern Nearctic than with the western Nearctic fauna.

Based on these observations, Gagné hypothesized plesiomorphic relationships in amphipolar and Holarctic faunas, and suggested that an old Eocene connection via the hypothesized North Atlantic land bridges would explain more of the observed distribution patterns of Holarctic Mycetophilidae than more recent connections via the Bering land bridge. This Western Palearctic/Eastern Nearctic (WP—EN) connection would imply that some of today's Holarctic species date to at least 20 million, likely some 50 million years back in time (see Sanmartin et al. 2001). This supposition Gagné (1981) was strengthened by referring to fungus gnats (and gall midges) in Tertiary amber that are generally similar to extant species.

In 1981, the body of distributional data available for fungus gnats was scarce, and reliable revisionary works containing such data were few. In other words, Gagné (1981) had to derive most of his conclusions from his own data. His model must, therefore, be regarded

as both ambitious and novel. Only three years later, Väisänen (1984), although clearly inspired by Gagné's work, opposed the distribution model when he revised the large genus *Mycomya* with 165 species in the Holarctic Region. Väisänen (1984) found only two species with the Eastern Nearctic and European distribution pattern and suggested that missing distributional data and anthropogenic dispersal could explain the pattern found by Gagné.

Does the distribution model stand up to scrutiny today and can it be refined and improved? While revisionary works providing detailed distribution data are still almost as scarce as then, an entirely new and rich source of data has become available as DNA barcodes assembled through the Barcode of Life Database (BOLD Systems or BOLD). This database now contains well over a million submissions of DNA barcodes of Sciarioidea (the superfamily that includes Mycetophilidae) worldwide, which are publicly available for open access to downloads and analyses, with identifications of taxa found in the Holarctic Region resolved to either generic level (Nearctic barcodes) or specific level (Palearctic barcodes) (see Kjærandsen 2022). The entire dataset (extraction date, 26 February 2022) specified for the four major Holarctic subregions, Western Nearctic (WN), Eastern Nearctic (EN), Eastern Palearctic (EP), and Western Palearctic (WP) (see Sanmartin et al. 2001), comprised 9930/26011/549/7919 sequences and 706/1066/159/1013 BINs, respectively.

Although a deeper analysis of the zoogeographical patterns underlying the distribution of Mycetophilidae in the Holarctic Region is beyond the scope of this paper, it is interesting to note that the pattern involving old Atlantic intercontinental connections (WP—EN) is clearly reflected in modern DNA barcode data (Fig. 1). This finding is somewhat contrary to that of Burdikova et al. (2019), that the Exechiini, the sister-tribe to the Mycetophilini, underwent a rapid radiation in the Neogene. Actually, all the three distribution patterns proposed by Gagné (1981) are well supported by barcoding data when BINs are used as proxies for species (Fig. 1):

- (1) There are nearly equal ratios of endemic Nearctic and Palearctic BINs both in *Trichonta* (appropriately 37% and 42%, respectively) and Mycetophilidae (48% and 40%), though the share of BINs with Holarctic distribution is significantly lower (19% in *Trichonta* and 12% in Mycetophilidae) than the about 40% of Holarctic species estimated by Gagné (1981) for *Trichonta* and *Phronia*.
- (2) The *Trichonta vulcani* complex has one Holarctic species, two to three exclusively Nearctic species, and four exclusively Palearctic species.

(3) There is a clearly closer affinity between Eastern Nearctic and Palearctic BINs in both *Trichonta* (9%) and Mycetophilidae (4%), compared to each 1% between Western Nearctic and Palearctic *Trichonta* and Mycetophilidae.

The latter finding may be partly due to an area-size effect as the Western Nearctic Region is much smaller than the Eastern Nearctic Region, especially in northern Canada from where the majority of available barcode sequences originates. However, the skewness of BINs distribution shared by the two Nearctic subregions is much lower than that of the available sequences. The similarity might be slightly higher if the Palearctic BINs considered in the analyses were all from western Europe as in the case of Gagné's (1981) data. Our reason here (Fig. 1) to refrain from subdividing the Palearctic Region is that the sampling coverage in the Eastern Palearctic Region is very weak (see above).

The lower-than-expected ratio of Holarctic species is worth a note here. In Mycetophilidae, there may be many fewer true circumpolar taxa than was earlier thought, although a lower proportion was already noted by Kjærandsen et al. (2007) regarding the Swedish fauna: 25% in Mycetophilidae and 38% in Mycetophilini. It is likely that minor morphological differences between North American and European specimens were overlooked in the past, considering that many species with tentatively Holarctic distribution are in need of thorough revision using the integrative approach. Data now available might also indicate a substantial amount of speciation events underway, with BIN splits not yet being reflected in morphological segregation (see Kjærandsen 2022 for a discussion). As an example, the barcoded Japanese specimen of *Trichonta trifida* is split into a separate BIN on BOLD (see Fig. 6) while the morphological segregation is considered too small to regard it as a separate species. Further, Canadian specimens of *Trichonta raymondgagnei*, new species form an isolated cluster within its assigned BIN with the barcoding gap being too small to regard this subset as a distinct species (see Fig. 6).

Revision of the *Trichonta vulcani* Dziedzicki Species Complex

When Lundström (1909) described *Trichonta trifida* Lundstrom, he was the first to correctly place species belonging to this species complex in the genus *Trichonta*. He made no mention of and might not have been aware of its close relationship to *Phronia vulcani* Dziedzicki, 1889. Likewise, Ostroverkhova (1970), when describing *Phronia setigera* Ostroverkhova, did not realize the connection either, until later when she considered *P. setigera* a synonym of *P. vulcani* in her book about Siberian fungus gnats (Ostroverkhova

1979). In a revision of Nearctic *Phronia*, Gagné (1975) moved *Phronia vulcani* to *Trichonta*. The species has later been treated in a wide sense to include *Trichonta trifida*, *Phronia setigera*, and *Phronia appropinquata* Strobl, 1900 as junior synonyms. Gagné (1981) did not study any of the type specimens when he synonymized *Trichonta trifida* and *Trichonta setigera*—again, being unaware of the synonymy already proposed by Ostroverkhova (1979)—with *Trichonta vulcani*, and wrote that they were conspecific based on the published illustrations accompanying the original descriptions. Ostroverkhova (1979) had also described another, similar species, *Trichonta superba* Ostroverkhova, 1979, also overlooked by Gagné, that Kallweit (1998) synonymized with *Trichonta tristis* (Strobl, 1898), yet another species described as *Phronia* and overlooked by Gagné. This was the second species of the complex that was clearly distinct from, yet quite closely related to, *Trichonta vulcani*. When building the Nordic reference library of DNA barcoded fungus gnats from 2014 forward (see Kjærandsen and Sjøli 2020, Kjærandsen 2022), it became clear that even more species were involved in this species complex. Kjærandsen and Sjøli (2020) recognized four species from Norway, including *Trichonta trifida*, which was reinstated as a valid species in addition to *Trichonta vulcani* and *Trichonta tristis*. Kjærandsen and Sjøli (2020) further realized that the species that Gagné illustrated to represent *Trichonta vulcani* most likely belonged to yet another, unnamed species. Here we take the opportunity to name this species in honor of Raymond J. Gagné and have assembled what we could find of material belonging to this species complex for a Holarctic revision. One of two species recorded from Japan is described as a second new species and a loan of DNA barcoded specimens from Canada revealed yet another new species.

Diagnostic characters of the imago.—Species of the *Trichonta vulcani* species complex (Fig. 2) are easily separated from other *Trichonta* species by the long petiole of the posterior fork (of veins $M_4 + CuA$), forking distinctly distal to the anterior fork (of vein M) (Fig. 4), opposite of what is seen in all other *Trichonta*, where the posterior fork divides distinctly proximal to the anterior fork (Fig. 3). This gave rise to confusion with and sometimes placement of these species in the similar genus *Phronia*, but in *Phronia* the posterior fork petiole is normally much longer and forking even more distal (Fig. 5). The two genera can further be separated by the subcostal vein which ends in the Radial stem in *Trichonta* (Figs. 3, 4) while it ends free in *Phronia* (Fig. 5). Gagné (1981) further mentioned the presence of a posterodorsal seta on the hind coxa as a diagnostic character to separate *Trichonta vulcani sensu lato* from *Phronia*. All species of the *Trichonta vulcani* species complex treated here have this seta present.

DNA barcodes and BIN registry.—Altogether 40 specimens belonging to the *Trichonta vulcani* species complex have been successfully barcoded. These are divided into seven different BINs representing the six species described here (Fig. 6) plus one BIN (BOLD:ACJ0107) that consists of three females only and hence are not described pending associated males. Three of the barcodes, representing two species, are based on samples of larvae.

General characteristics of males.—The male terminalia of species belonging to the *Trichonta vulcani* species complex all have a similar, characteristic construction which is diagnostic for the group. The genitalia are quite large in comparison to the body size (especially in *T. tristis*) and the gonostylus (Figs. 8–10) is very elaborate with literally an “eruption” of branches and lobes, likely the basis for the species epithet “*vulcani*.” Tergite 9 (Fig. 7) is divided into two short, ovate sclerites with rather few setae. The cerci (Fig. 7) are medium long, narrowly ovate with a slight difference in the outline between species. The gonocoxites (Fig. 8) are fused into a synsclerite, closed ventrally and open dorsally. The ventromedial margin of the gonocoxites (Fig. 8) is reinforced to form a sclerotized fold with two soft peaks, possibly being homologous with the hypandrial lobe developed in many species of the tribe Exechiini. The detailed outline of this fold is characteristic for each species. Between this structure and the aedeagal apparatus there is a thin phragma (see Fig. 57) that is reticulated in some species. The aedeagal apparatus (Fig. 11) is short and lyre-shaped with only minor differences between the species. The gonostyli (Figs. 9, 10) are large, consisting of a ventral, dorsal, internal and anterior branch. The ventral branch of the gonostylus (Figs. 8–10) is trifurcate (hence the species epithet “*trifida*”) with the middle lobe forming a characteristic, narrow aristate lobe, glabrate except with a short spine apically. The dorsal branch of the gonostylus (Figs. 9, 10) is inconspicuous and difficult to characterize. The internal branch of the gonostylus (Figs. 9, 10) consists of two large, inflatable and striated cushions. The anterior branch of the gonostylus (Figs. 9, 10) is dilated with fan-shaped rows of strong setae, like typically seen in many species of both *Trichonta* and *Phronia*.

Females.—Gagné (1981) illustrated the female terminalia for 19 *Trichonta* species and demonstrated that they have good diagnostic characters, probably enabling separation of many if not most of the species. He did not mention, however, how females were associated with males, which can be a challenging and risky task absent genetic data. Gagné illustrated a female from Iowa, USA to represent *Trichonta vulcani*, but it is unclear now to which species in the complex this specimen actually belongs. As very few females belonging to the

Trichonta vulcani species complex so far have been DNA barcoded, and safe associations of the sexes thus are difficult, we refrain from describing females here pending more barcode associations.

Immature stages.—As concluded by Gagné (1981) little is known about the biology of *Trichonta* in general. The larvae of two species, *Trichonta falcata* Lundström, 1911 and *Trichonta vitta* (Meigen, 1830), were described and illustrated in detail by Madwar (1937). In some cases, larvae feed within the substance of a fungus, such as *Trichonta venosa* (Staeger, 1840) which was reared from larvae living in puff-balls (*Lycoperdon* Tourn. ex L.) (Edwards 1925). Most species with known larval associations have been recorded on fungi encrusting dead wood (Jakovlev 2011). Recent observations of larvae from rotting wood and numerous records of adult *Trichonta* obtained with emergence traps set up on fallen trunks, branches and stumps (Jakovlev unpubl.) suggest that some species live both on resupinate fruiting bodies and on fungal mycelium. Here we confirm the latter with new records of larvae of *Trichonta raymondgagnei*, new species and *T. trifida* from under bark of rotting logs and stumps of birch (*Betula*) (Betulaceae). On October 4, 2020, two larvae were collected under the bark of on an overgrown, decaying stub of birch covered with mosses in Tromsø, Norway. These larvae were filmed alive before being sampled and submitted for DNA barcoding. The sequence from one of them matched *T. raymondgagnei*, meaning that they aligned with already sequenced males within the same BIN on BOLD (Fig. 6) while the other failed to give a sequence. A short video of the larva moving and grazing on the bark can be viewed here: <https://www.facebook.com/100001790498293/videos/3337134713022846/>. The next year, on September 26, 2021, an aggregation of very similar larvae belonging to the *Trichonta vulcani* species complex was found on a lying, decaying log of birch at another locality in Tromsø. One of these larvae, also matching *T. raymondgagnei* by barcoding (Fig. 6), was photographed (Fig. 12) and filmed alive, a short video of it moving and grazing on the bark can be viewed here: <https://www.facebook.com/100001790498293/videos/592213951910355/>. Another larva submitted for barcoding from the same log of birch matched with *T. trifida* (Fig. 6) demonstrating that several species can live together in the same microhabitat.

These new records and filmed observations document beyond doubt that larvae of the *Trichonta vulcani* species complex live under bark of decaying logs and stumps of deciduous trees (birch) where they graze on mycelium either under the bark or on the log itself. These larvae were always covered with a nearly flat sheet of dry mucilage constructed from the detritus on which the larvae were feeding. According to Madwar (1937) those *Trichonta*

larvae that are found on the surface of bark-growing fungi have the same kind of covering sheet, while those living within the substance of fungi for obvious reasons lack such a covering sheet. This is similar biology to what is known for species in the genus *Phronia*, whose larvae live under bark of decaying wood, often on the surface of fungi encrusting damp rotten wood, and often also have a covering sheet. In the case of *Phronia*, however, the larvae are distinctly shortened and thickened, and those that have a covering sheet make a hard, conical case of it, distinctly different from those found on *Trichonta* larvae.

Diversity and distribution.—The *Trichonta vulcani* species complex as presently defined consists of six recognized species with a wide Holarctic distribution. The BOLD archive of DNA barcodes indicates the existence of one more species, but this is represented with three females only. Four of the species occur in the Western Palearctic, five in the Eastern Palearctic, one in the Western Nearctic and two (possibly three) in the Eastern Nearctic.

Trichonta vulcani (Dziedzicki, 1889), *sensu stricto*
(Figs. 13–22)

Phronia vulcani Dziedzicki, 1889: 490

Phronia appropinquata Strobl, 1900: 177 – synonymy by Kallweit (1998)

Phronia setigera Ostroverkhova, 1970: 455 – synonymy by Ostroverkhova (1979: 258) and again by Gagné (1981: 29)

Trichonta vulcani (Dziedzicki, 1889) – new genus combination by Gagné (1975: 301)

Differential diagnosis.—The species is most easily recognized by the smoothly undulating ventromedial margin of the gonocoxite (Figs. 14, 19) where the central suture is longer than the extension of the two peaks beyond the midpoint termination as seen in ventral view. In *T. tristis* and *T. neovulcani*, new species the peaks are higher, in *T. trifida* and *T. raymondgagnei*, new species they are lower and not smoothed in the same way. In *T. japonica*, new species, the undulation is small and the peaks are almost merging medially. The setose, distal lobe of the ventral branch of the gonostylus is somewhat subrectangular in ventral view (Fig. 14); the glabrate medial lobe is parallel-sided and ending in a strong, angled spine (Figs. 14, 20); the mesial, small lobe is bold and has an apical spine and four strong setae (Figs. 14, 20). The anterior branch of the gonostylus is triangular in mesial view, with a broad row of small setae along the mesial, anterior edge (Fig. 22). The aedeagal

apparatus has narrow, blunt parameres and tiny horns medially (Fig. 18). The cerci are narrow, without distinct excavation mesially (Fig. 17).

DNA barcode BIN registry.—Uniquely assigned to the BIN BOLD:ADL1998 (Fig. 6). The BIN currently has 4 barcode compliant members from Norway, 3.37% distant from the nearest neighbor, *Trichonta neovulcani* in BOLD:ACI6835.

Species identity and remarks.—The original description of *Phronia vulcani* was accompanied with detailed illustrations of the male terminalia (Dziedzicki 1889) clearly conforming with our strict interpretation here. The species continued to be treated as belonging to the genus *Phronia* by Johannsen (1909) and Landrock (1940) until Gagné (1975), in a revision of Nearctic *Phronia*, moved it to *Trichonta*. The species has later been treated in a wide sense to include the species *Trichonta trifida*, *Phronia setigera* and *Phronia appropinquata* as junior synonyms. The synonymy with *Phronia setigera* was first suggested with a question mark by Gagné (1975) and later confirmed by Ostroverkhova (1979) and Gagné (1981). The illustration provided by Ostroverkhova (1970) is poor and impossible to relate to any of the species other than that it seems to belong to the *vulcani* complex while the illustrations provided by Ostroverkhova (1979) and Zaitzev (2003) to represent *T. vulcani* may rather refer to either *T. trifida* or *T. raymondgagnei*.

Voucher material.—NORWAY: Agder (AAY), Birkenes, Birkeland, Nordåsvegen, 58°20'00"N 008°14'24"E, 74 masl, Light trap (LT1), 1 Jul–31 Aug 2019 (Leg. S. Svendsen) — TSZD-JKJ-108381 (TMU, pinned male); Agder (VAY), Kristiansand, Nedre Jegersbergvann, 58°10'09"N 008°00'00"E, 21, MT 3, at lake, 4–21 Jun 2019 (Leg. K. Berggren) — TSZD-JKJ-111174 (TMU, pinned male); Finnmark (FV), Alta, Gargialia, 69°48'21"N 023°29'40"E, 211, Malaise trap (MT 6), 29 Jul–29 Sep 2017 (Leg. J. Kjærandsen and M. T. Dahl) — TSZD-JKJ-103597 (TMU, pinned male); Nordland (NSI), Grane, Stormobekken, 65°35'42"N 013°24'11"E, Malaise trap (MT 3), 29 May–31 Jul 2018 (Leg. J. Kjærandsen, J. P. Lindemann and P. Dominiak) — TSZD-JKJ-105713 (TMU, pinned male), TSZD-JKJ-106532 (TMU, pinned male); SWEDEN: SÖ, Haninge, Tyresta, Urskogsslingan, granskog, 59°10'33"N 018°14'51"E, Malaise trap (trap id. 4-89), 21 Jul–4 Aug 2003 (Leg. Swedish Malaise Trap Project) — TSZD-JKJ-208262 (NHRS, slide mounted male in Canada Balsam). FINLAND: Äänekoski, Kylmähauta, 62.5193N 25.6825E, sweep net, 16 Jun 2003 (Leg. J. Penttinen) — NVO.JP-Myc-316 (LMM, male in ethanol); Espoo, Kolmperä, 60.25N 24.53E, 22 Jul 1962 (Leg. W. Hackman) — (MZH, 2 males in ethanol); Helsinki, Villinki, 60.16N 25.11E, 7 Jun 1964 (Leg. O. Ranin) — (MZH, 1 male in ethanol); Pielisjärvi, Koli, 63.12N 29.87E 5 Jul 1965 (Leg. R. Tuomikoski) — (MZH, 3 males in ethanol). RUSSIA:

Altai Reg., Teletskoe Lake, near Artybash, 22-24 Jun 1981 (Leg. A. Zaitzev) (IPEE, pinned male, terminalia in glycerol); Karelia, Kivach Nat. Res., 62.27N 33.99E, Malaise trap, 24 Aug-25 Sept 1989 (Leg. A. Polevoi) (FRIP, pinned male, terminalia in glycerol); Karelia, 1 km NW of Pinguba, 61.8746N 34.5413E, Malaise trap, 12-26 Jun 2012 (Leg. A. Polevoi) (FRIP, pinned male, terminalia in glycerol); Leningrad Reg., 1 km SE of Gimreka, 61.1512N 35.6398, Malaise trap, 23 Apr-25 May 2008, (Leg. A. Polevoi) (FRIP, pinned male, terminalia in glycerol); Murmansk Reg., Pasvik Nat. Res., Kalkupya Mt., 69.2871N 29.3521E, Malaise trap, 20 Jul-11 Oct 2007 (Leg. A. Bulychev) (FRIP, pinned male, terminalia in glycerol). ESTONIA: Võru District, Haanja, Suur-Munamägi, 57.7137N 27.0598E, sweepnet, 3 Sep 1995 (Leg. O. Kurina) – IZBE0227766 (IZBE, pinned male); Rapla District, Märjamaa, Märjamaa järta, 58.9000N 24.4667E, sweepnet, 27 May 2006 (Leg. O. Kurina) – IZBE0227767 (IZBE, pinned male); Tartu District, Palupõhja, Kaha, 58.4318N 26.2413E, Malaise trap, 4 Aug-18 Aug 2009 (Leg. V. Soon) – IZBE0250815 (IZBE, male in ethyl alcohol); Ida-Virumaa District, Muraka Nature Reserve, 59.0894N 27.155E, window trap, 30 Apr-14 May 2015 (Leg. I. Süda) – IZBE0252073 (IZBE, male in ethyl alcohol); Põlva District, Ihamaru Nature Reserve, 58.0977N 26.9258E, window trap, 27 Apr-13 May 2015 (Leg. I. Süda) – IZBE0252074 (IZBE, 5 males in ethyl alcohol).

Distribution.—Widespread Palaearctic, from Western Europe east to Altai Region of Russia, north to Finnmark in Norway.

Occurrence and habitat.—Rather few records have been confirmed to belong to this species in its new, strict sense. It has been more widely reported previously by its *sensu lato* interpretation. It has been collected both with Malaise traps and light traps. It is known from a range of habitats in the Nordic Region, from southern, old-growth mixed forests, to aspen dominated and mixed taiga forests and oroarctic birch forests.

Biology.—Unknown, but larvae suspected to live under bark of decaying wood like for *Trichonta trifida* and *Trichonta raymondgagnei*.

***Trichonta neovulcani* Kjaerandsen, new species**

<http://zoobank.org/9DD5D208-08F7-4625-B9F8-51784D623B84>

(Figs. 23, 33)

Differential diagnosis.—This species is separated from the most closely related species, *T. vulcani*, by having a larger and deeper undulating ventromedial margin of the gonocoxites where the central suture is shorter than the extension of the two peaks beyond the midpoint

termination as seen in ventral view (Figs. 25, 30). The gonocoxal synsclerite is relatively longer than in the other species of the complex (Figs. 24–26), except for *T. tristis* and *T. japonica*. The glabrate medial lobe of the ventral branch of the gonostylus is parallel sided, but distinctly bent subapically before ending in a strong spine (Figs. 24, 25, 31, 32) and the mesial, small lobe is bold and has a lanceolate apical spine and three strong setae (Figs. 31, 32). The anterior branch of the gonostylus is fan-shaped in mesial view, with a broad row of small setae along the inner, anterior edge and broad, lanceolate setae along the apical margin (Fig. 33). The aedeagal apparatus has medium broad, blunt parameres and blunt horns medially (Fig. 29). The cerci are distinctly broadened medially, with shallow excavation mesially (Fig. 28).

DNA barcode BIN registry.—The species is uniquely assigned to the BIN BOLD:ACI6835 (Fig. 6). The BIN currently has 4 barcode compliant members from Canada, 3.37% distant from the nearest neighbor, *Trichonta vulcani* in BOLD:ADL1998.

Description.—(holotype, Fig. 23, in rather poor condition with broken antennae and only one entire fore leg and half of one mid leg and half of one hind leg intact, terminalia detached and cleared). Coloration uniformly yellowish brown (somewhat paled after years in ethanol) on head, body and terminalia; setation pale. Antenna pale yellowish brown, legs yellow. Halter pale yellow. Three ocelli present, lateral ocellus touching eye margin. Mid-cranial suture entire from middle ocellus to posterior margin of head. Face quadrangular, clypeus subquadrangular, shorter than face. Palp normally drop-shaped, short, apical segment lost. Second antennal flagellomere about 1.5 times as long as wide. Scutum evenly covered with pale, small setae and dorsocentral row of larger setae. Scutellum with one row of small setae and four larger bristles. Wing densely covered with microtrichia. Wing length 2.75 mm. Costa, C, slightly produced beyond apex of R₅. Sc bare, long, length from h 0.45 of R stem, ending in R. Radial sector and forks setose on dorsal side. Furcation point of posterior fork distal of that of anterior fork, ratio of M₁ to M₄ 1.9. CuP weak, reaching halfway to wing margin. Anepisternum with three setae, laterotergite hairy, mediotergite bare. Length ratio of 1st tarsomere:fore tibia 0.71.

Male terminalia: Tergite 9 divided into two subcircular sclerites, each with a few setae of variable size (Fig. 28). Cerci long ovate, distinctly broadened medially, with shallow excavation mesially (Fig. 28). Gonocoxites fused into a long synsclerite, closed ventrally and open dorsally. Ventromedial margin of gonocoxites reinforced to form an undulating sclerotized fold with two soft peaks where the central suture is shorter than the extension of the two peaks beyond the midpoint termination as seen in ventral view (Figs. 25, 30).

Phragma between this structure and aedeagal apparatus reticulated (Fig. 27). Aedeagal apparatus lyre shaped, with medium broad, blunt parameres and blunt, small horns medially (Fig. 29). Ventral branch of gonostylus with setose, distal lobe, subrectangular in ventral view (Figs. 25, 31); glabrate medial lobe parallel-sided but distinctly bent subapically before ending in a strong spine (Figs. 24, 25, 31, 32); mesial, small lobe bold, with lanceolate apical spine and three strong setae (Figs. 31, 32). Dorsal branch of gonostylus forming two small, setose sclerites (Figs. 32, 33). Dorsointernal branch forming two large, inflatable and striated cushions. Ovate, glabrate sclerite ventral of the dorsointernal lobe possibly representing medial branch of gonostylus. Anterior branch of gonostylus fan-shaped in mesial view, with broad row of small setae along inner, anterior edge and broad, lanceolate setae along apical margin (Fig. 33).

Holotype.—CANADA: Newfoundland and Labrador, Gros Morne National Park, James Callaghan Trail, 49.5686N 57.8302W, 39 masl, two Malaise traps at mature conifer stand with balsam fir and wind damage, 29 May—09 Jun 2013 (Leg. R. Reid) — male, BIOUG09479-A09 (CBG–BIOUG, HMDS-dried and pinned with terminalia in glycerin vial on the pin).

Paratypes.—CANADA: Newfoundland and Labrador, Terra Nova National Park, Blue Hill Road, 48.598N 53.9702W, 127 masl, two Malaise traps at old balsam fir site with mixed wood, dog berry saplings, birch and mountain ash, 11—25 Jun 2013 (Leg. E. Perry) — male, BIOUG12142-A02 (CBG–BIOUG, HMDS-dried and pinned). CANADA, Alberta, Jasper National Park, Miette Hotsprings, 53.124N 117.775W, 1439 masl intercept trap at valley bed with creek, rocky and mossy along ridge, 17—25 Jul 2012 (Leg. BIOBus 2012) — male, BIOUG06615-A02 (CBG–BIOUG, HMDS-dried and pinned with terminalia in glycerin vial on the pin).

Additional material.—CANADA: Ontario, Pukaskwa National Park, Heron Bay near Park Office, 48.601N 86.2893W, 13—27 May 2013, (Leg. C. Harpur) — female associated by BIN registry, BIOUG08594-E08 (CBG–BIOUG, HMDS-dried and pinned).

Etymology.—The species epithet refers its close relationship to *Trichonta vulcani* with the prefix *neo-* denoting both “new” and “modified” as well as originating from the New World.

Distribution.—Recorded from Alberta, Ontario and Newfoundland in Canada.

Occurrence and habitat.—So far, known only from the four DNA barcoded specimens. Collecting localities in four different Canadian national parks indicate association with old-growth (mixed) coniferous taiga forests, and with balsam fir at two of the localities.

Biology.—Unknown, but larvae suspected to live under bark of decaying wood like for *Trichonta trifida* and *Trichonta raymondgagnei*.

Trichonta trifida Lundstrom, 1909

(Figs. 34–53)

Trichonta trifida Lundström, 1909: 32 – reinstated as separate from *Trichonta vulcani* by Kjærandsen and Søli (2020)

Differential diagnosis.—This species is most easily recognized by the ventromedial margin of the gonocoxite forming a very shallow undulation with two small, subtriangular peaks and ending in oblique angled sides (Figs. 35, 40). The male terminalia (Figs. 34, 35) is small and short compared to other species, except *Trichonta raymondgagnei*. The setose distal lobe of the ventral branch of the gonostylus is small and rounded in ventral view (Figs. 35, 41); the glabrate medial lobe tapers, usually with a sharp angle change mediomesally, ending in an acute tip with a small spine (Figs. 35, 41, 42); the mesial, small lobe is less bold and has a less strong, lanceolate apical spine and four strong setae (Figs. 35, 41, 42). The anterior branch of the gonostylus is semicircular in mesial view, without any narrow row of smaller setae along the inner, anterior edge (Fig. 43). The aedeagal apparatus has broad, blunt parameres and medium sized, blunt horns medially (Fig. 39). The cerci are evenly broad basally, then narrowing with a shallow excavation mesially (Fig. 38).

DNA barcode BIN registry.—So far, assigned to two BINs on BOLD: BOLD:ADO7293 and BOLD:AEN8945 (Fig. 6). BOLD:ADO7293 currently has 6 barcode compliant members from Norway (5) and Far East Russia (1), 2.88 % distant from the singleton from Hokkaido, Japan in BOLD:AEN8945. Attempts to sequences two additional submitted specimens from Hokkaido failed. *Trichonta raymondgagnei* in BOLD:ACI8376 is their closest neighbor, 6.77% different from BOLD:ADO7293 and 6.12% different from BOLD:AEN8945, respectively. The recently sequenced larva is pending BIN assignment and may end up in yet another BIN being 3.52% different from other Norwegian males in BOLD:AEN8945 and 3.82% different from the male from Hokkaido, Japan in BOLD:AEN8945.

Species identity and remarks.—We studied the holotype of *T. trifida* stored at MZH and bearing two labels: (1): “Finland, Karislojo, R. Frey leg.”, and (2): “Mus. Zool. H:fors. Spec.typ. No 4240. *Trichonta trifida* Lundstr.”— GAS.3038 (MZH, pinned male with a slide of terminalia on the same pin). The terminalia are mounted in Canada balsam, but not

sufficiently dissected to see diagnostic characters and to reliably associate the specimen. Nevertheless, the original illustration of Lundström (1909) of the male terminalia in ventral view provide enough details to recognize the species as different from *T. vulcani*. Its synonymy with *T. vulcani* was based on a somewhat broader morphological species concept prior to DNA barcoding. Kjærandsen and Søli (2020), however, correctly realized, with support from DNA barcodes, that the species needed to be reinstated in accordance with differences in the fine details of the male terminalia of these species as further outlined here. The combination of morphological details and DNA barcoding revealing a 6.12% distance to its nearest neighbor, *Trichonta raymondgagnei*, leaves little doubt about the identity of *T. trifida* as a separate species. A question remains whether it may eventually deserve to be split even further into several semicryptic species. A single, more strongly deviating but poorly preserved specimen from Altai is not included here, pending additional material and DNA barcode data from this region. Despite the genetic segregation of Far East Russian populations, and an even stronger segregation of the populations from Hokkaido, Japan, assigned to another BIN on BOLD, we find very little corresponding morphological variation in these eastern specimens (compare Figs. 34–43 with Figs. 44–53). At best there are minor differences in details of the aedeagal apparatus, ventromedial margin of the gonocoxite and details of the anterior branch of the gonostylus. The sequenced larva from Norway (Fig. 6) further complicates the issue as it is as different from Norwegian adults as it is from eastern Palearctic specimens, either indicating that yet another species is overlooked in the Nordic Region or that it actually is substantial genetic variation within *T. trifida* that is not strictly following a geographical cline from east to west.

Voucher material.—NORWAY: Finnmark (FØ), Sør-Varanger, Sametielva W Lundhytta, Pasvik, 69°27'00"N 29°42'26"E, 69, Malaise trap (MT 3), 17 Jun-24 Jul 2017 (Leg. J. Kjærandsen and M. T. Dahl) — TSZD-JKJ-103297 (TMU, pinned male); Nordland (NSI), Grane, Stormobekken, 65°35'42"N 013°24'11"E, sweep net around MT3, 29 May 2018 (Leg. J. Kjærandsen) — TSZD-JKJ-104402 (TMU, pinned male), TSZD-JKJ-104692 (TMU, pinned male); Malaise trap (MT 3), 29 May-31 Jul 2018 (Leg. J. Kjærandsen, J. P. Lindemann and P. Dominiak) — TSZD-JKJ-106531 (TMU, pinned male with terminalia in glycerine); Danielåsen, 65°34'12"N 013°42'02"E, Malaise trap in oldgrowth pine forest, 25 Jun-31 Jul 2020 (Leg. Jostein Lorås) — TSZD-JKJ-111280 (TMU, pinned male); Oppland, Sel, Sjøa NR, 61°45'13"N 9°17'09"E, 450 masl, sweep net along river E border, 31 Jul 2020 (Leg. J. Kjærandsen) — TSZD-JKJ-111235 (TMU, pinned male); Troms (TRY), Sandnes, Tromsøya, 69°41'33"N 018°55'54"E, 27 masl, picked from under bark of decaying log of

birch, 26 Sep 2021 (Leg. J. Kjærandsen) — TSZD-JKJ-112285 (TMU, barcoded larva in ethanol); Vestfold (VE), Larvik, Brånakollane NR, 59.1833N 10.05E, sweepnet, 19 May 2005 (Leg. O. Kurina) – IZBE0227765 (IZBE, pinned male). SWEDEN: Torne Lappmark (TO), Kiruna, Abisko, 68°21'01"N 018°49'50"E, window trap, 23-30 Jun 1976 (Leg. K. Müller) — TSZD-JKJ-236832 (TMU, male in ethanol). FINLAND: Vihti, Vihtijärvi, 5 Jun 1964, R.Tuomikoski leg. (MZH, 1 male in ethanol with terminalia in glycerin vial); Ilomantsi, Pirhu, 3-6.06.1994, A.Polevoi leg. (FRIP); Hämeenlinna, Evo, Lapinjärvi, 61.2384N 25.0878E, Trunk emergence trap in burnt clear-cut over decaying spruce log, 26 Jul – 27 Sep 2005 (Leg. J. Jakovlev) — GAS.1402 (MZH, 1 male in ethanol with terminalia in glycerin vial); Lapeenranta, Lake Saimaa, Pappilaniemi 61°9'18"N 28°4'39"E sweep net, 20 Jun 2004 (Leg. C. and M. Jaschhof — GAS.1400 (MZH, 1 male in ethanol with terminalia in glycerin vial); Sotkamo, Hiidenportti, Urpovaara 63.8866N 29.0732E sweep net, 11 Jul 2004 (Leg. C. and M. Jaschhof — GAS.1401 (MZH, 1 male in ethanol with terminalia in glycerin vial). ESTONIA: Pärnu District, Nigula Nature Reserve, Lagundpeaksi 58.0028N 24.6676E, sweepnet, 22 Aug 1991 (Leg. O. Kurina) – IZBE0228737 (IZBE, pinned male); Tartu District, Palupõhja, Kaha, 58.4318N 26.2413E, Malaise trap, 21 June-29 June 2009 (Leg. V. Soon) – IZBE0250268 (IZBE, male in ethyl alcohol). RUSSIA: Altai Reg., Teletskoe Lake, near Artybash, 11 Jul 1981 (Leg. A.Zaitzev) (IPEE, pinned male, terminalia in glycerol); Karelia, 1 km NW of Pinguba, 61.8746N 34.5413E, Malaise trap, 12-26 Jun 2012 (Leg. A. Polevoi) (FRIP, pinned male, terminalia in glycerol); Sakhalin Island, Nevelskii District, 10 Sept 1986, (Leg. A.Zaitzev leg) (IPEE, pinned male, terminalia in glycerol); Sakhalin Isl., Naiba River, 7 km upstream from Bykov, 13 Aug 1991 (Leg. V. Blagoderov) (IPEE, pinned male, terminalia in glycerol); Sakhalin Isl., Naiba River, 12 km upstream from Bykov, 16 Aug 1991 (Leg. V. Blagoderov) (IPEE, pinned male, terminalia in glycerol); Primorsky Krai, Anisimovka, 43.1319N 132.8003E, 414 masl, sweepnet, 9 May 2019 (Leg. O. Kurina) – IZBE0252077 (IZBE, male in ethyl alcohol); Primorsky Krai, 8 km W of Kaymanovka, Ussuriyskiy NR, 43.6344N 132.2922E, 130 masl, sweepnet, 13 May 2019 (Leg. O. Kurina) – IZBE0252076 (IZBE, 2 males in ethyl alcohol); Primorsky Krai, Gorno-Taezhnoe, 43.6961N 132.1378E, 85masl, sweepnet, 14 May 2019 (Leg. O. Kurina) – IZBE0251608 (IZBE, 1 male in ethyl alcohol), IZBE0252075 (IZBE, 10 males in ethyl alcohol); Primorsky Krai, Gorno-Taezhnoe, 43.6994N 132.1514E, 127 masl, sweepnet, 15 May 2019 (Leg. O. Kurina) – IZBE0253776 (IZBE, 1 male in ethyl alcohol). JAPAN: Hokkaido Prefecture, Eniwa-shi, No-named trib. to Ichankoppe-zawa stream, 42°49'49"N 141°24'23"E, 240, 25 Jun 2003 (Leg. J. Kjærandsen) — TSZD-JKJ-111943 (TMU, pinned

male with terminalia in glycerine), TSZD-JKJ-112565 (TMU, male in ethanol), TSZD-JKJ-232950 (TMU, male in ethanol); Chitose-shi, Kokeno-domon Gallery beside Lake Shikotsu, 42°42'43"N 141°19'16"E, 279 masl, 2 Oct 2006 (Leg. J. Kjørandsen) — TSZD-JKJ-111942 (TMU, pinned male with terminalia in glycerin), TSZD-JKJ-232951 (TMU, male in ethanol), TSZD-JKJ-233163 (TMU, male in ethanol); Kushiro-shi, Middle reach of Ibeshibetsu River near Lake Akan, Akan-cho, 43°29'17"N 144°08'52"E, 448 masl, sweep net at site 3, 4 Oct 2006 (Leg. J. Kjørandsen) — TSZD-JKJ-112555 (TMU, pinned male), TSZD-JKJ-112566 (TMU, male terminalia in glycerin), TSZD-JKJ-233359 (TMU, male terminalia in glycerin); Kushiro-shi, Akan-cho, Middle reach of Ibeshibetsu River near Lake Akan, 43.4880N 144.1478E, 448 masl, sweepnet, 4 Oct 2006 (Leg. O. Kurina) – IZBE0252071 (IZBE, 1 male in ethyl alcohol); Kushiro-shi, Akan-cho, San-no-sawa near Lake Akan, 43.4916N 144.2122E, 597 masl, sweepnet, 4 Oct 2006 (Leg. O. Kurina) – IZBE0253777 (IZBE, 1 male in ethyl alcohol). GEORGIA: Imereti Region, Marelisi, 41.9466N 43.2841E, 448 masl, sweepnet, 20 May 2012 (Leg. O. Kurina) – (IZBE, male in ethyl alcohol). ROMANIA: Balan, Hasmas Mt., Galkut valley 46.6493N 25.8415E, 1050 masl, 23 Aug 2014 (Leg. L-P Kolcsar) – NVO. LMM-Myc-1363 (LMM, male in ethanol).

Distribution.—Widespread in Palearctic Region, so far documented from the Nordic Region, including Estonia and Russian Karelia, southward to Georgia, eastward to Sakhalin Island in Far East Russia and Hokkaido, Japan. Appears to have a restricted, northern distribution in Norway.

Occurrence and habitat.—Quite frequently encountered in different habitats from broadleaved forests to mixed, coniferous taiga forests.

Biology.— A single larva associated to this species through DNA barcodes (Fig. 6), was collected from a lying, decaying log of birch at Tromsø, Norway (69.4 deg. N) in late September (2021). In southern Finland adults have been collected with trunk emergence traps set up on burnt clear-cut decaying spruce logs burned seven years earlier and then colonized by fungal mycelium under loosing bark and bearing fruiting bodies of *Phellinus* sp. (?*Ph. nigrolimitatus* (Romell) Bourdot and Galzin) and unidentified resupinate corticioid fungi.

***Trichonta raymondgagnei* Kjaerandsen. new species**

<http://zoobank.org/CBCBB1F9-CE9F-4135-B566-8B207009445B>

(Figs. 54–70)

Differential diagnosis.—This species is most easily recognized by the ventromedial margin of the gonocoxite forming a very shallow undulation with the two small, smooth peaks situated widely apart and ending in near vertical sides (Figs. 55, 60). The male terminalia are small and short (Figs. 54, 55) compared to other species, except *Trichonta trifida*. The setose distal lobe of the ventral branch of the gonostylus is wide and rounded in ventral view (Figs. 55, 61); the glabrate medial lobe evenly tapers and ends in an acute tip with an angled stout spine (Figs. 55, 61, 63); the mesial, small lobe is less bold and has a less strong, lanceolate apical spine and three strong setae (Figs. 55, 61). The anterior branch of the gonostylus is broad, asymmetrically falcate in mesial view, with a single row of smaller setae along the inner, acute, anterior edge (Fig. 63). The aedeagal apparatus has medium broad, blunt parameres and broad, blunt horns medially (Fig. 59). The cerci are evenly broad basally, then narrowing with a shallow excavation mesially (Fig. 58).

DNA barcode BIN registry.—Uniquely assigned to the BIN BOLD:ACI8376 (Fig. 6). This BIN currently has 12 members (10 barcode compliant) from Norway and Canada, 2.58% distant from the nearest neighbor, an unidentified *Trichonta* from Canada represented by females only in BOLD:ACJ0107.

Description of imago.—(holotype, pinned, intact except left foreleg consumed for DNA barcoding). Coloration uniformly brown on head, body and terminalia except yellowish tinted humeral areas; setation pale except darker, large bristles. Antenna pale yellowish brown with yellow scape and pedicel, legs yellow with dark bristles. Halter yellow. Three ocelli present, lateral ocellus touching eye margin. Mid-cranial suture entire from frons to posterior margin of head. Face wide rectangular, clypeus semicircular, as long as face. Palp normally drop-shaped, apical segment approximately as long as fourth + third segment together. Second antennal flagellomere about 1.5 times as long as wide. Scutum evenly covered with pale, small setae and dorsocentral row of larger setae. Scutellum with one row of small setae and four larger bristles. Wing densely covered with microtrichia. Wing length 2.88 mm. C slightly produced beyond apex of R₅. Sc bare, long, length from h 0.44 of R stem, ending in R. Radial sector and forks setose on dorsal side. Furcation point of posterior fork distal of that of anterior fork, ratio of M₁ to M₄ 1.74. CuP weak, reaching halfway to wing margin. Anepisternum with three setae, laterotergite hairy, mediotergite bare. Length ratio of 1st tarsomere:fore tibia 0.94.

Male terminalia: Tergite 9 divided into two subcircular sclerites, each with a few setae of variable size (Fig. 58). Cerci long ovate, distinctly broadened medially, with shallow excavation mesially (Fig. 58). Gonocoxites fused into a synsclerite, closed ventrally (Fig. 55)

and open dorsally (Fig. 54). Ventromedial margin of gonocoxites reinforced to form an undulating sclerotized fold with the two small, smooth peaks situated widely apart and ending in near vertical sides (Figs. 55, 60). Phragma between this structure and aedeagal apparatus reticulated (Fig. 57). Aedeagal apparatus lyre shaped, with medium broad, blunt parameres and broad, blunt horns medially (Fig. 59). Ventral branch of gonostylus with setose distal lobe wide and rounded in ventral view (Figs. 55, 61); glabrate medial lobe evenly tapering and ending in an acute tip with an angled stout spine (Figs. 55, 61, 63); mesial, small lobe less bold with less strong, lanceolate apical spine and three strong setae (Figs. 55, 61). Anterior branch of gonostylus broad, asymmetrically falcate in mesial view, with single row of smaller setae along inner, acute, anterior edge (Fig. 63).

Description of larva.—Approximately 4.5 mm long (somewhat shrunken in ethanol) with brown chitinized head and 12 body segments. Head short cordiform (Figs. 64–66). Clypeal plate spatulate, widest at the level of antenna. Epicranial plates meet in thin strips before base of mouthparts ventrally and posterodorsally. Antenna large, globoid. Eye small, circular. Labrum globoid, hyaline, with five pairs of papillae. Details of mouthparts not discernible from undissected preparation. Prospiracle with three semicircular spiracular opening situated anterior to external scar (Fig. 67). Seven pairs of small abdominal spiracles, with central papilla and two spiracular openings (Fig. 68). Ten intersegmental locomotory pads with single row of chitinized hooks (Fig. 69), fourth to ninth pad with additional weak row of spinules and hooks (Fig. 70). The covering sheet (see Fig. 12) hard, constructed of brownish detritus, oblong and slightly curved to fit the shape of larval body, approximately 3.5 mm long, covering most of larval body.

Holotype.—NORWAY: Troms (TRY), Tromsø, Skjelhollet, Kvaløy, 69°46'05"N 018°51'05"E, window trap, 9 Aug-13 Sep 2015 (Leg. J. Kjærandsen) — TSZD-JKJ-104707 (TMU, pinned male).

Paratypes.—NORWAY: Nordland (NSI), Grane, Auster-Vefsna NR, Stilleelva W, 65°32'02"N 013°43'40"E, Malaise trap (MT 1), 30 Jul-5 Oct 2018 (Leg. J. Kjærandsen, J. P. Lindemann and P. Dominiak) — TSZD-JKJ-105559 (TMU, pinned male with terminalia in glycerin vial); Troms (TRI), Storfjord, Kavleelva, Skibotndalen, 69°18'53"N 020°23'44"E, 58 masl, 18 Aug-22 Sep 2019 (Leg. J. P. Lindemann) — TSZD-JKJ-111898 (TMU, pinned male with terminalia in glycerin vial); Finnmark (FV), Alta, Talvik, Vassbotndalen, 220 masl, Malaise trap along edge of small lake, 1-18 Aug 2021 (Leg. P. Dominiak) — TSZD-JKJ-112553 (TMU, pinned male), TSZD-JKJ-112554 MU, pinned male); Troms (TRY), Tromsø, Skjelhollet, Kvaløy, 69°46'05"N 018°51'05"E, window trap, 9 Aug-13 Sep 2015 (Leg. J.

Kjærandsen) — TSZD-JKJ-104706 (TMU, pinned male); Troms (TRY), Grønnåsen, Tromsøya, 69°41'03"N 018°57'43"E, 88, samples from overgrown, decaying stub of birch, 4 Oct 2020 (Leg. J. Kjærandsen) — TSZD-JKJ-111652 (TMU, pinned larva), TSZD-JKJ-111653 (TMU, barcoded, cleared larva in glycerin vial); Troms (TRY), Sandnes, Tromsøya, 69°41'33"N 018°55'54"E, 27 masl, picked from under bark of decaying log of birch, 26 Sep 2021 (Leg. J. Kjærandsen) — TSZD-JKJ-112287 (TMU, barcoded larva in ethanol); . FINLAND: Enontekiö, Pallas-Yllästunturi NP, Röyninkuru, 68.1482N 24.0750E, Malaise trap, 5 Jul-7 Aug 2013 (Leg. J. Salmela) — NVO.LMM-Myc-574 (LMM, male in ethanol, terminalia in glycerol). Hämeenlinna, Evo, Hautjärvi, 61.2042N 25.1426E, Malaise trap, 14 Jun – 9 Jul 2021 (Leg. J. Jakovlev) — MYC_JJ_2021_5 (BOLD Sample ID, MZH, male in ethanol, terminalia in glycerol). RUSSIA: Leningrad Reg., Purnoruchi, 11 km N of Grishino, 61.1924N 34,0396E, 11 Sept 2019 (Leg. A. Polevoi) (ZISP, pinned male, terminalia in glycerol); Karelia, Velikaya Guba, 4 km SW of Lipovitsy, 62.1051N 35.0255E, 23 Aug 2013, (Leg. A. Polevoi) (ZISP, pinned male, terminalia in glycerol); Karelia, Shoikapolda River, 62.5282N 37,3774E, 22 Aug 2006, (Leg. A. Polevoi) (ZISP, pinned male, terminalia in glycerol); Sakhalin Island, Nevelskii District, 2 Sept 1986, (Leg. A. Zaitzev leg) (ZMUM, pinned male, terminalia in glycerol).

Additional material.—RUSSIA: Kostroma Reg. 4 km N of Ugory, 29 Aug 1981, (Leg. A. Zaitzev) (IPEE, pinned male, terminalia in glycerol); Sakhalin Island, Nevelskii District, 16 Sept 1986 (Leg. A. Zaitzev) (IPEE, pinned male, terminalia in glycerol).

Etymology.—This species is named in honor of Raymond J. Gagné for his outstanding contributions to Mycetophilidae taxonomy, specifically the monograph of Holarctic *Trichonta* (Gagné 1981).

Distribution.—DNA barcoding reveals a wide Holarctic distribution across Canada (Yukon Territory, British Columbia, Alberta and Nova Scotia, these specimens were not studied by us, and the identification is based on the barcodes alone), through Far East Russia to Karelia and Leningrad Regions of Russia and the Nordic Region in Europe. This also appears to be the species illustrated by Gagné (1981) from Pennsylvania, USA under the name *Trichonta vulcani* (see Kjærandsen and Sjøli 2020).

Occurrence and habitat.—So far infrequently encountered in different habitats from oroarctic birch forests to mixed and old-growth coniferous taiga forests.

Biology.—Two larvae were associated to this species through DNA barcodes (Fig. 6). One was collected from under the bark of a decaying stump of birch overgrown with mosses in the beginning of October (2020) at Tromsø, Norway (69.4 deg. N). The other (Fig. 12) was

collected from a lying, decaying log of birch at another locality in Tromsø in late September (2021).

Trichonta tristis (Strobl, 1898)

(Figs. 71–80)

Phronia tristis Strobl, 1898: 287

Trichonta superba Ostroverkhova, 1979: 226 – synonymy by Kallweit (1998); nec *Trichonta superba* Gagné 1981: 27

Differential diagnosis.—This species is most easily recognized by the ventromedial margin of the gonocoxite forming two high, subtriangular peaks with a deep excavation in between (Figs. 72, 77). The male terminalia and gonostyli are exceptionally large (Figs. 71, 72) and the gonocoxital synsclerite is strikingly yellow in contrast to the otherwise brown body. The setose distal lobe of the ventral branch of the gonostylus is long subrectangular in ventral view (Fig. 72); the glabrate medial lobe gradually tapers and ends in a long, but less strong spine (Figs. 78–80); the mesial, small lobe is bold and has a strong, lanceolate apical spine and four strong setae (Figs. 72, 78). The anterior branch of the gonostylus is triangular in mesial view, with narrow row of small setae along the inner, anterior edge (Fig. 80). The aedeagal apparatus has narrow, acute parameres and large, pectinated horns medially (Fig. 76). The cerci are narrow, without any excavation mesially (Fig. 75).

DNA barcode BIN registry.—Uniquely assigned to the BIN BOLD:ADY2587 (Fig. 6). The BIN currently has 5 members (2 barcode compliant) from Norway, 9.76% distant from the nearest neighbor, *Trichonta trifida* in BOLD:ADO7293.

Species identity and remarks.—This species was not illustrated in the original description by Strobl (1898) and went under the radar as virtually unrecognized until Kallweit (1998) introduced it as the senior synonym of *Trichonta superba* Ostroverkhova, 1979. Zaitzev (2003) was the first to illustrate the species and confirmed the synonymy of Kallweit (1998). The crude illustration of *Trichonta superba* provided by Ostroverkhova (1979) is insufficient in details, but can be associated with *T. tristis* by the illustrated pectinate horns of the aedeagus (cf. Fig. 76). Gagné (1981) described a very different species from Nepal under the name *Trichonta superba* Gagné, 1981. This is in need of a replacement name, regardless of the status of *Trichonta superba* Ostroverkhova, 1979, its primary

homonym, and we propose here the name *Trichonta nepalensis* Kjaerandsen, new name for *Trichonta superba* Gagné, 1981.

Voucher material.—NORWAY: Nordland (NNØ), Narvik, Svadet, Henriksfjellet, 68°15'58"N 016°26'43"E, 150 masl, sweep netting along south side of Svadet, 2 Aug 2020 (Leg. J. Kjaerandsen) — TSZD-JKJ-111301 (TMU, pinned male); Nordland (NSI), Grane, Auster-Vefsna NR, Stilleelva W, 65°32'02"N 013°43'40"E, Malaise trap (MT 1), 28 May-30 Jul 2018 (Leg. J. Kjaerandsen, J. P. Lindemann and P. Dominiak) — TSZD-JKJ-105390 (TMU, pinned male), TSZD-JKJ-105391 (pinned male with terminalia in glycerin vial on the pin); Stormobekken, 65°35'42"N 013°24'11"E, sweep net, 31 May 2018 (Leg. J. Kjaerandsen) — TSZD-JKJ-104430 (TMU, pinned male); Hattfjelldal, Auster-Vefsna NR, Stilleelva E, 65°32'27"N 013°45'01"E, sweep net (Leg. J. Kjaerandsen) — TSZD-JKJ-104347 (TMU, pinned male), TSZD-JKJ-104348 (TMU, pinned male); Saltdal, Junkerdalsura NR, above Sagbenkhøla, 66°49'09"N 015°25'44"E, 330 masl, Malaise trap (MT 3), 30 May-24 Jul 2019 (Leg. J. Kjaerandsen, J. P. Lindemann and P. Dominiak) — TSZD-JKJ-107614 (TMU, pinned male); Rogaland (RI), Sauda, Vikaneset, Eikjehaugen, 59°34'06"N 006°17'00"E, 75, Malaise trap (MT 1), 20 Jun-10 Jul 2019 (Leg. Ø. Nyvold Larsen) — TSZD-JKJ-107994 (TMU, pinned female); Rogaland (RY), Sokndal, Skitmyr, 58°21'02"N 006°18'20"E, 22, 28 Jun-25 Jul 2019 (Leg. J. Birkeland) — TSZD-JKJ-107966 (TMU, pinned male), TSZD-JKJ-107973 (TMU, pinned male). FINLAND: Savukoski, Ainijärvi, 67.7622N 29.4367E, Malaise trap, 30 Jul – 28 Sep 2015 (Leg. J. Salmela) — NVO.LMM-Myc-1262 (LMM, male in ethanol); Hämeenlinna, Evo, Kotinen Strict Nature Reserve, 61°14'48"N 25°4'23"E, Malaise trap, 10 Sep – 3 Oct 2003 (Leg. J. Jakovlev) — GAS.1397 and GAS.1398 (MZH, 2 males in ethanol with terminalia in glycerin vial); Sipoo, Käsik-Solbacka, 60° 26,97993'N 25° 11,73226' E, Malaise trap, 13 May – 13Jun 2005 (Leg. J. Jakovlev) — GAS.1399 (MZH, 1 male in ethanol with terminalia in glycerin vial); Padasjoki, Vesijako Strict Nature Reserve 61°21'22"N 25°6'41"E, trunk emergence trap over decaying spruce log, 25 Aug – 11 Sep 2008 (Leg. J. Jakovlev) — GAS.1403 (MZH, 1 male in ethanol with terminalia in glycerin vial); Kuusamo, Juuma, Jäkälävuoma 66.26N 29.45E, 28 Jul 1966 (Leg. R. Tuomikoski) (MZH, 1 pinned male with terminalia in glycerin vial on the pin).

Distribution.—Widespread in the Palearctic Region, including Central Europe and the Nordic Region eastward through Krasnoyarskiy Kray and Altai Region, to Sakhalin Island in Far East Russia (Zaitzev 2003).

Occurrence and habitat.—Quite frequently encountered in different habitats from southern, broadleaved forests to mixed, coniferous taiga forests.

Biology.—In southern Finland adults have been collected with a trunk emergence trap over a decaying spruce log bearing fungal mycelia under loosing bark with fruiting bodies of *Antrodia xantha* (Fr.) Ryvarden. Otherwise unknown, but larvae suspected to live under bark of decaying wood like for *Trichonta trifida* and *Trichonta raymondgagnei*.

***Trichonta japonica* Kurina, new species**

<http://zoobank.org/F47BFE2D-BCA8-4BA9-AAD1-A896A2ECEDC3>

(Figs. 81–90)

Differential diagnosis.—This species is most easily recognized by the ventromedial margin of the gonocoxite forming a heavily convex sclerotized fold with a small apicomedial cavity (Fig. 82). The glabrate medial lobe of the gonostylus evenly tapers with a stout spine apically (Figs. 82, 84, 87); the mesial, small lobe of the gonostylus is fused with the basal part of the medial lobe and has a prominent strong seta posteriorly and two weaker setae more anteriorly (Figs. 84, 87). The internal branch of the gonostylus has an apically bifurcate finger-shaped lobe medially (Figs. 82, 87, 88). The dorsal branch of the gonostylus has two small lobes posteriorly, bearing apical spines, one of them hooked (Figs. 89, 90). The aedeagal apparatus is spearhead shaped, with elongated, convoluted parameres arched over the bipartite aedeagus (Figs. 81, 86). Tergite 9 is divided into two subcircular sclerites, each with setae of variable size spread over the whole surface (Fig. 85).

DNA barcode BIN registry.—The recently uploaded, single barcoded specimen (the holotype) is still pending BIN registry (Fig. 6). It is 10.4% different from the closest neighbor specimens of *Trichonta neovulcani* in BIN BOLD:ACI6835.

Description.—(holotype, terminalia detached, right foreleg missing beyond coxa, left fore and midlegs used for DNA barcoding). Coloration uniformly yellowish brown on body and terminalia except lighter humeral areas and dark brown head; setation pale except darker, large bristles. Antenna pale yellowish brown with lighter scape and pedicel, legs yellow, except hind coxa and apical parts of hind femur and hind tibia brownish, with dark bristles. Halter yellow. Three ocelli present, lateral ocellus almost touching eye margin. Mid-cranial suture entire from frons to posterior margin of head. Face quadrangular, clypeus semicircular, shorter than face. Apical segment of palpus widening apically, approximately as long as forth + third segment together. Second antennal flagellomere about 1.3 times as long as wide. Scutum evenly covered with pale, small setae and dorsocentral row of somewhat larger setae. Scutellum with small setae along marginal area and four larger marginal bristles. Wing

densely covered with microtrichia. Wing length 2.73 mm. C not produced beyond apex of R₅. Sc bare, long, length from h 0.54 of R stem, apical part vague, curved towards R. Radial sector and forks setose on dorsal side. Furcation point of posterior fork distal of that of anterior fork, ratio of M₁ to M₄ 1.70. CuP weak, reaching halfway to wing margin. Anepisternum with three strong setae at upper margin and with 5–6 weak setae on anterior half, laterotergite hairy, mediotergite bare.

Male terminalia: Tergite 9 divided into two subcircular sclerites, each with setae of variable size spread over whole surface. Cerci long ovate, somewhat broadened medially, with shallow excavation mesially (Fig. 85). Gonocoxites fused into a long synsclerite, closed ventrally and open dorsally. Ventromedial margin of gonocoxites reinforced to form a heavily convex sclerotized fold with a small apicomedial cavity (Fig. 82). Aedeagal apparatus spearhead shaped, with elongated, convoluted parameres arched over bipartite aedeagus, both prongs of which with spinelike apical parts (Fig. 86). Ventral branch of gonostylus with setose distal lobe, wide and rounded in ventral view (Fig. 87); glabrate medial lobe evenly tapering with a stout apical spine; mesial, small lobe discernible as dilatation (Fig. 87) of basal part of medial lobe, with a strong seta posteriorly and two weaker setae more anteriorly. Internal branch of gonostylus with an apically bifurcated finger-shaped lobe medially (Figs. 87, 88), well discernible from ventral and mesial views. Dorsal branch of gonostylus with two small lobes posteriorly, bearing apical spines, one of them hooked (Figs. 89, 90). Anterior branch of gonostylus fan-shaped in dorsal view, with broad row of setae along apical margin (Figs. 89, 90).

Holotype.—JAPAN: Kyūshū, Oita Pref., Oike, Yufuin Town near Mt. Kurotake, 33.1244N 131.2947E, 860 masl, sweeping, 29 Sep 2006 (Leg. O. Kurina) — male, IZBE0252072 (IZBE, mounted from ethyl alcohol and pinned with terminalia in glycerin vial on the pin).

Etymology.—The species is named after its occurrence in Japan.

Distribution.—Known only from Kyūshū Island in Japan.

Occurrence and habitat.—The holotype was collected from deciduous broad-leaved temperate forest in central Kyūshū, near Oike Spring.

Biology.—Unknown, but larvae are suspected to live under bark of decaying wood like those of *Trichonta trifida* and *T. raymondgagnei*.

The definitions for species belonging to the *Trichonta vulcani* complex are considerably narrowed here using an integrative taxonomic approach. The *Trichonta vulcani* complex, previously considered to be two species (sensu Kallweit 1998), is shown here to include at least six species, of which only one, *Trichonta japonica*, is a new discovery. DNA barcoding data give a clear picture of the species boundaries, although with some ambiguity regarding *Trichonta trifida* which currently is split into at least two BINs. This finding is only moderately supported by the slight morphological variation observed in *T. trifida*. A genetic distance of 2% segregation between far western and far eastern Palearctic populations of the same species was found earlier in nematoceros Diptera (see Kjærandsen (2019) for *Pachyneura fasciata* Zetterstedt, 1838 Pachyneuridae). Even so, the genetic distance separating Nearctic and Palearctic populations of *Trichonta raymondgagnei* is much less than 2%.

Will our results regarding the *T. vulcani* complex have a bearing on *Trichonta* in general? Our data (see above the zoogeographical discussion) indicate the contrary. The number of BINs of Holarctic *Trichonta* in relation to described species is still lower (95/126), a situation that is in stark contrast to Sciaroidea on BOLD in general, in which the number of BINs is 3.5 times larger than the number of described species (Kjærandsen 2022). At the same time, our experience with Nordic *Trichonta* suggests that there are a few more species complexes in need of revision, such as the *Trichonta atricauda* (Zetterstedt, 1852) complex, while the majority of species have already been correctly delimited and characterized by Gagné (1981). Without his rigorous revision, our integrative work would have been considerably more difficult.

It is interesting to note that the *Trichonta vulcani* complex has a parallel in the species group around *Mycetophila ruficollis* Meigen, 1818. The *M. ruficollis* group consists of a number of generally similar species whose distinctions lie in minor details of the male terminalia, including differences in the shape of the ventromedial gonocoxal margin (see Jürgenstein et al. 2015). The function of this margin is unknown, but the fact is conspicuous that even in many other Mycetophilidae this part of the terminalia has specifically elaborate structures termed the hypandrial lobe (Söli 1997, Kjærandsen 2006).

Larvae of Mycetophilidae are very insufficiently known and thus largely ignored in the taxonomic exploration of the family, which is by and large focused on adult males. Larvae have been ignored partly due to the presumption that they lack morphological features diagnostic at the species level and partly because aggregation of several species in a single fungus or piece of decaying wood traditionally made associations with reared imagos difficult

to prove beyond doubt. DNA barcoding offers a new opportunity to reliably associate larvae with adults without the necessity to rear them. The larvae of two species, *Trichonta falcata* Lundstrom, 1911 and *Trichonta vitta* (Meigen, 1830), were described and illustrated in detail by Madwar (1937), which for Mycetophilidae must be regarded as outstanding. Here we describe the larvae of one of our new species and document a mode of life previously unknown in *Trichonta*: development under the bark of decaying wood. We think this is not the right place for describing the larval characters of *Trichonta* species in even more detail, but the fact that there are striking morphological differences (e.g., shape of head) compared to previously described *Trichonta* species, indicates that the larvae of Mycetophilidae may indeed have more species-specific morphological characters than previously thought.

ACKNOWLEDGMENTS

We are grateful to all the contributors of Sciarioidea specimens to the public Barcode of Life online database BOLD Systems (BOLD) and the staff at Centre for Biodiversity Genomics, University of Guelph, Canada for the loan of material from Canada. The help of Marina Krivosheina with the loan of specimens from IPEE collection is appreciated. Patrycja Dominiak is acknowledged for technical assistance in processing samples to BOLD and for drying and pinning voucher specimens. The work of JK was supported by UiT—The Arctic University of Norway, the Norwegian Biodiversity Information Centre (NBIC, projects nos. 45–14 and 27–17) and the Norwegian Barcode of Life initiative (NorBOL). The work of AP was carried out under state order to the Karelian Research Centre of the Russian Academy of Sciences (Forest Research Institute). The work of JS was supported by the Ministry of Environment, Finland (NORSCIID-project, VN/23830/2020).

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Figure Captions

Fig. 1. Venn diagram of Barcode Index Numbers (BINs) pulled from the public database on BOLD identified to the genus *Trichonta* (left) and the family Mycetophilidae (right). The BINs are divided between the Palearctic, Eastern Nearctic and Western Nearctic Regions (the latter two separated by the Great Continental Divide) and give numbers of endemic and shared BINs within and between each of the regions.

Fig. 2. Habitus photo of male *Trichonta trifida* Lundstom, 1909, specimen TSZD-JKJ-104402 in BIN BOLD:ADO7293 from Stormobekken in Nordland, Norway. HMDS dried specimen glued to a minuten.

Figs. 3–5. Wings of *Trichonta* and *Phronia* species. 3, *Trichonta venosa* (Staeger, 1840), representing a typical *Trichonta* wing. 4, *Trichonta vulcani* (Dziedzicki, 1889), typical for the species complex. 5, *Phronia basalis* Winnertz, 1864, representing a typical *Phronia* wing. Abbreviations: sc = endpoint of subcosta, a = furcation point of anterior fork (of vein M), b = furcation point of posterior fork (of vein M₄ + CuA).

Fig. 6. Subsection of ID-tree (Kimura-2-distance) obtained from BOLD with 40 sequences and BIN assignments for specimens belonging to the *Trichonta vulcani* species complex. The three associated larvae are marked with red color and text.

Figs. 7–11. Terminology of male terminalia of *Trichonta vulcani* (Dziedzicki, 1889), specimen TSZD-JKJ-103597 in BIN BOLD:ADL1998 from Gargialia in Finnmark, Norway. 7, Detached Tergite 9, Cerci and proctiger, in dorsal view. 8, Male terminalia in ventral view. 9, Detached gonostylus in mesial view. 10, Detached gonostylus in dorsal view. 11, Detached internal aedeagal apparatus with gonocoxal apodemes in dorsal view.

Fig. 12. Larva of *Trichonta raymondgagnei* Kjaerandsen new species, paratype, specimen TSZD-JKJ-112287 in BIN BOLD:ACI8376 from under the bark of a decaying log of birch in Tromsø, Norway, September 26, 2021.

Figs. 13–19. Male terminalia of *Trichonta vulcani* (Dziedzicki, 1889) *sensu stricto*, specimen TSZD-JKJ-103597 in BIN BOLD:ADL1998 from Gargialia in Finnmark, Norway. 13, Dorsal view. 14, Ventral view. 15, Lateral view. 16, Caudal view. 17, Tergite 9, proctiger and cerci, dorsal view. 18, Aedeagal apparatus, dorsal view. 19, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 20–22. Detached gonostylus of *Trichonta vulcani* (Dziedzicki, 1889) *sensu stricto*, specimen TSZD-JKJ-103597 in BIN BOLD:ADL1998 from Gargialia, Finnmark, Norway. 20, Ventral view. 21, Dorsal view. 22, Mesial view.

Fig. 23. Habitus photo of *Trichonta neovulcani* Kjaerandsen, new species in ethanol, holotype, specimen BIOUG09479-A09 in BIN BOLD:ACI6835 from Gros Morne National Park, Newfoundland, Canada. (CC-BY-NC-SA-4.0, CBG Photography Group, Centre for Biodiversity Genomics).

Figs. 24–30. Male terminalia of *Trichonta neovulcani* Kjaerandsen, new species, holotype, specimen BIOUG09479-A09 in BIN BOLD:ACI6835 from Gros Morne National Park, Newfoundland, Canada. 24, Dorsal view. 25, Ventral view. 26, Lateral view. 27, Caudal view. 28, Tergite 9, proctiger and cerci, dorsal view. 29, Aedeagal apparatus, dorsal view. 30, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 31–33. Detached gonostylus of *Trichonta neovulcani* Kjaerandsen new species, holotype, specimen BIOUG09479-A09 in BIN BOLD:ACI6835 from Gros Morne National Park, Newfoundland, Canada. 31, Ventral view. 32, Dorsal view. 33, Mesial view.

Figs. 34–40. Male terminalia of *Trichonta trifida* Lundström, 1909, specimen TSZD-JKJ-106531 in BIN BOLD:ADO7293 from Stormobekken, Nordland, Norway. 34, Dorsal view. 35, Ventral view. 36, Lateral view. 37, Caudal view. 38, Tergite 9, Proctiger and cerci, dorsal view. 39, Aedeagal apparatus, dorsal view. 40, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 41–43. Detached gonostylus of *Trichonta trifida* Lundstrom, 1909, specimen TSZD-JKJ-106531 in BIN BOLD:ADO7293 from Stormobekken, Nordland, Norway. 41, Ventral view. 42, Dorsal view. 43, Mesial view.

Figs. 44–50. Male terminalia of *Trichonta trifida* Lundstrom, 1909, specimen TSZD-JKJ-111943 in BIN BOLD:AEN8945 from Eniwa-shi, Hokkaido, Japan. 44, Dorsal view. 45, Ventral view. 46, Lateral view. 47, Caudal view. 48, Tergite 9, Proctiger and cerci, dorsal view. 49, Aedeagal apparatus, dorsal view. 50, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 51–53. Detached gonostylus of *Trichonta trifida* Lundstrom, 1909, specimen TSZD-JKJ-111943 in BIN BOLD:AEN8945 from Eniwa-shi, Hokkaido, Japan. 51, Ventral view. 52, Dorsal view. 53, Mesial view.

Figs. 54–60. Male terminalia of *Trichonta raymondgagnei* Kjaerandsen new species, paratype, specimen TSZD-JKJ-111898 in BIN BOLD:ACI8376 from Skibotndalen, Troms, Norway. 54, Dorsal view. 55, Ventral view. 56, Lateral view. 57, Caudal view. 58, Tergite 9, Proctiger and cerci, dorsal view. 59, Aedeagal apparatus, dorsal view. 60, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 61–63. Detached gonostylus of *Trichonta raymondgagnei* Kjaerandsen new species, paratype, specimen TSZD-JKJ-111898 in BIN BOLD:ACI8376 from Skibotndalen, Troms, Norway. 61, Ventral view. 62, Dorsal view. 63, Mesial view.

Figs. 64–70. Details of larva of *Trichonta raymondgagnei* Kjaerandsen new species, paratype, specimen TSZD-JKJ-111653 in BIN BOLD:ACI8376 from Tromsø, Troms, Norway. 64, Head, dorsal view. 65, Head, ventral view. 66, Head, frontal view. 67, Prospiracle (200%). 68, Spiracle on segment 6 (200%). 69, Single row of hooks on locomotory pad of segment 3. 70, Double row of hooks on locomotory pad of segment 9. Scalebar of 0,1 mm relates to all images, except 67 and 68 which is scaled to double size of the other.

Figs. 71–77. Male terminalia of *Trichonta tristis* (Strobl, 1898), specimen TSZD-JKJ-105391 in BIN BOLD:ADY2587 from Auster-Vefsna Nature Reserve, Nordland, Norway. 71, Dorsal view. 72, Ventral view. 73, Lateral view. 74, Caudal view. 75, Tergite 9 and cerci, Dorsal view. 76, Aedeagal apparatus, dorsal view. 77, Reinforced ventromedial margin of the gonocoxite, caudodorsal view.

Figs. 78–80. Detached gonostylus of *Trichonta tristis* (Strobl, 1898), specimen TSZD-JKJ-105391 in BIN BOLD:ADY2587 from Auster-Vefsna Nature Reserve, Nordland, Norway. 78, Ventral view. 79, Dorsal view. 80, Mesial view.

Figs. 81–86. Male terminalia of *Trichonta japonica* Kurina, new species, holotype, specimen IZBE0252072 in BIN BOLD:AEN9863 from Kyūshū, Japan. 81, Dorsal view, tergite 9 and cerci detached. 82, Ventral view. 83, Lateral view. 84, Dorsocaudal view. 85, Tergite 9, proctiger and cerci, dorsal view. 86, Aedeagal apparatus, dorsal view.

Figs. 87–90. Gonostylus of *Trichonta japonica* Kurina, new species, holotype, specimen IZBE0252072 in BIN BOLD:AEN9863 from Kyūshū, Japan. 87, Ventral view. 88, Mesial view. 89, Dorsal view. 90, Dorsal view, attached to gonocoxite.