The identity of *Neocnemodon calcarata* (Loew) (Diptera: Syrphidae), a specialized flower fly predator of Woolly Apple Aphid

[Die Identität von *Neocnemodon calcarata* (Loew) (Diptera: Syrphidae), einer Schwebfliege, die als Prädator auf die Wollige Apfellaus spezialisiert ist]

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Abstract

The names and identities of the specialized flower fly predators of the Woolly Apple Aphid, *Eriosoma lanigerum* (Hausmann, 1802) are fixed. These predators, *Neocnemodon calcarata* (Loew, 1866) and *Neocnemodon vitripennis* (Meigen, 1822), are important biological control agents as they prey on both arboreal and root colonies of the aphid. A lectotype is designated for *Pipiza calcarata* Loew, 1866, and type notes of *N. calcarata* and *N. vitripennis* are provided.

Key words: *Eriosoma lanigerum*, *Malus domestica*, Aphididae, biological control agent

Zusammenfassung

Die Namen und Identitäten der in ihren prädatorischen Aktivitäten auf die Wollige Apfelblattlaus, *Eriosoma lanigerum* (Hausmann, 1802) spezialisierten Schwebfliegenarten werden geklärt. Die beiden Schwebfliegenarten *Neocnemodon calcarata* (Loew, 1866) und *N. vitripennis* (Meigen, 1822), erweisen sich als wichtige Gegenspieler der Wolligen Apfelblattlaus, da sie sowohl Baum- als auch Wurzelkolonien des Schädlings erbeuten. Für *Pipiza calcarata* Loew, 1866, wurde ein Lectotypus festgelegt und zu den Typen von *N. calcarata* und *N. vitripennis* werden Informationen gegeben.

Stichwörter: *Eriosoma lanigerum*, *Malus domestica*, Aphididae, natürlicher Gegenspieler zur biologischen Schädlingsbekämpfung

Introduction

Flower flies of the subfamily Pipizinae (Diptera: Syrphidae) include species with larvae that prey on woolly aphids (Hemiptera: Aphididae: Eriosomatinae) and other sternorrhynchan hemipterans that produce waxy exudates, including Adelgidae, Phylloxeridae, and Psyllidae (Rojo et al. 2003; Mengual et al. 2015). Encompassing eight genera and ca. 180 species, Pipizinae are dark pigmented (presumed non-mimetic) syrphids with a cosmopolitan distribution, excluding the Afrotropical Region. The monophyletic Pipizinae is sister to the species-rich Syrphinae, whose clade encompasses mainly predatory larvae that feed on hemipterans. The mainly saprophagous Eristalinae is a paraphyletic grade to this group (Pipizinae + Syrphinae), and the whole taxon is sister to the myrmecophagous Microdontinae (Mengual et al. 2015; Young et al. 2016; Pauli et al. 2018; Moran et al. 2021). Within the Holarctic Region Pipizinae exhibits the greatest species diversity, and includes ca. 35 species in the genus

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Neocnemodon Goffe, 1944. In North America and Europe, respectively, *Neocnemodon calcarata* (Loew, 1866) and *Neocnemodon vitripennis* (Meigen, 1822) are notable as specialist predators of the economically important Woolly Apple Aphid (WAA), *Eriosoma lanigerum* (Hausmann, 1802) (Hemiptera: Aphididae: Eriosomatinae).

WAA is a cosmopolitan pest of apple trees, *Malus domestica* Borkhausen, 1803 (Baker 1915), colonizing both the roots and arboreal parts of the plant (Brown et al. 1991). In 2000, a major and widespread outbreak of WAA occurred in many orchards in the Mid-Atlantic region of the U.S.A., likely in response to cancellation of the registration of methyl parathion in 1999. Previously, methyl parathion had been widely used in commercial apple production, due to its broad-spectrum activity against many orchard pests, including WAA. During the outbreak in 2000, JCB observed many WAA colonies being predated by syrphid larvae, and raised some of these larvae to the adult stage. Subsequently, JCB learned that FCT was located in Washington, D.C., close to his workplace in northwestern Virginia, and was delighted that FCT was very interested in the findings and specimens. FCT quickly identified one of the most common species attacking the aphids as *Neocnemodon calcarata* (but see below), which piqued his interest further, given his counsel that it was a member of the Pipizinae, which in his opinion at that time, needed further research and taxonomic revision.

Shortly after FCT became involved with our work, BDS joined JCB's laboratory as a Masters student, and was tasked with working on *N. calcarata* and its role as a WAA biocontrol agent. FCT gave generously of his time and expertise to assist us with various aspects of the project, for which we are eternally grateful. We learned that *N. calcarata* appeared to be a specialized predator of WAA in the apple ecosystem (Short & Bergh 2004) and, along with the specialized WAA parasitoid, *Aphelinus mali* Haldeman, 1851 (Hymenoptera: Aphelinidae), is a key member of a guild of WAA natural enemies (Bergh & Stallings 2016). Marked differences in the exochorionic sculpturing of eggs of the three most common syrphid predators of WAA, *N. calcarata*, *Eupeodes americanus* (Wiedemann, 1830), and *Syrphus rectus* Osten-Sacken, 1875, enabled reliable differentiation among them in the field and laboratory (Short & Bergh 2005). Various aspects of *N. calcarata* biology and ecology were investigated, including its host preference and voracity (Short & Bergh 2004), developmental rate (Bergh & Short 2008), and its seasonal phenology and abundance (Bergh & Short 2008, Gresham et al. 2013). Following a major outbreak of WAA in New Zealand in 2009, Plant and Food Research New Zealand became keenly interested in the possibility of releasing *N. calcarata* in their apple orchards, leading to work on aspects of the reproductive biology of the fly in relation to the potential to rear it in quarantine for host range testing in New Zealand (Gresham et al. 2013).

Meanwhile, FCT proceeded to develop a manuscript designating a lectotype for *Pipiza calcarata* (=*Neocnemodon calcarata*). However, despite our combined efforts over a number of years, it was never published, and he once sardonically described it as "one of the many piles of guilt littering the floor of my office". Subsequent to FCT's work on the paper, taxonomic revisions of the Pipizinae by Vujić et al. (2013), Mengual et al. (2015), and Skevington et al. (2019) have established *Neocnemodon* as a separate genus, and not, as was used by FCT, a subgenus of *Heringia* Rondani, 1856. The following is a revised version of FCT's original manuscript, reflecting the current taxonomic paradigm. It includes his methods and descriptions, our updated drawings of the male genitalia of *N. calcarata*, photographs of the male and female flies, and sequencing of its genetic barcode (5′-end of the mitochondrial cytochrome *c* oxidase subunit I gene). Per FCT's explicit instructions during the development of the original manuscript, his name appears last in the list of authors.

Material and methods

Terminology follows Thompson (1999) and Skevington (2019), the abbreviations found in the synonymies follow Thompson & Thompson (2007), and the use of the asterisk in the distribution statement refers to verified records found in the material examined section. In the synonymies, all citations to the various names are included. Many of the earlier ones may be based on misidentifications or broader species concepts. However, regardless of their taxonomic status, these earlier citations are of value, as they document historical information that may be verified by vouchers. For example, we know today that Schiner (1861) broadly interpreted the species *vitripennis*, as there are vouchers in the museum in Vienna with his determination label. For Schiner, *vitripennis* was equivalent to the present concept of the genus *Neocnemodon* [see Thompson & Torp (1986: 237) on Schiner's broad interpretation of other species, such as *Sphegina clunipes* (Fallén, 1816)]. Also, *calcarata* was more broadly interpreted by earlier workers. Three vouchers in the USNM collection, labeled as *calcarata* by Shannon and Curran, are specimens of *Neocnemodon coxalis* (Curran, 1921). The modern classification of *Neocnemodon* (as *Heringia*) only began when the importance of the species for the biological control of aphids was recognized (Delucchi & Pschorn-Walcher 1955; Pschorn-Walcher & Zwölfer 1956; Delucchi et al. 1957).

Adult male and female *N. calcarata* were reared from larvae collected in Winchester, Virginia, and photographed with a Canon EOS 6D digital SLR with a MP-E 65 mm lens. Specimens preserved in 100 % ethanol were dried and their DNA extracted with a Qiagen DNeasy kit. The primers, LCO1490 (forward) and HCO2198 (reverse), were used to amplify a 600 bp region of the mitochondrial cytochrome *c* oxidase subunit I gene, a region which is commonly used as a species barcode for rapid identification and taxonomy (Hebert et al. 2003). DNA was sequenced according to methods described in Means & Marek (2017).

Taxonomy section

The following characters will separate the presumed sister species, *N. calcarata* and *N. vitripennis*, from all other flower flies. They are broken up into characters that separate the group (tribe Pipizinae) from other Syrphidae, the genus *Neocnemodon* from other pipizines, and these sister species from other *Neocnemodon* species. *Neocnemodon calcarata* is described in full and a diagnosis is provided to separate *calcarata* from its putative sister, *vitripennis*. Note that *N. vitripennis i*s restricted to the Old World, while *N. calcarata* is a New World species.

Tribe Pipizinae is characterized by: 1) eyes pilose; 2) face pilose; 3) oral margin simple, not medially notched; 4) face simple, concave, without tubercle; 5) crossvein r-m basal, at basal 1/4 of cell dm; 6) postpronotum pilose; and 7) metasternum reduced and bare. Genus *Neocnemodon* is characterized by: 1) anepisternum bare on flattened anterior portion; 2) katepimeron pilose; 3) vein Sc ending beyond crossvein r-m; 4) cell r_{4+5} acute apically; 5) vein M_1 progressive apically, joining vein R_{4+5} at acute angle; and 6) postpedicel short, at most 1.5 times as long as broad.

The genera *Heringia* and *Neocnemodon* are readily separated by the length of the postpedicel and the presence of a spur in the metatrochanter in the males of the latter. The genus *Heringia* was established by Rondani (1856: 53) with *Pipiza heringi* Zetterstedt, 1843 as its type species by original designation. The name *Neocnemodon* (Goffe 1944: 128) is a replacement name for *Cnemodon* Egger (1865: 573), a junior homonym of *Cnemodon* Schoenherr, 1823 (Coleoptera: Curculionidae). *Cnemodon* was established for two new species, of which Goffe (1944: 128) subsequently selected *Cnemodon latitarsis* Egger, 1865 as the type species.

Species *N. calcarata* and *N. vitripennis* are characterized in the male by: 1) mesocoxa with long ventral process (Fig. 3); 2) metatrochanter with a long, slender, apically expanded process (Fig. 2); 3) sterna 3 and 4 simple, without carinae; and 4) wing partially bare basomedially. Also, the probasitarsomeres of both species are identical but differ from other *Neocnemodon* species [see figures in Verlinden (1994: 109) and van Veen (2004: 122)]. Females of *Neocnemodon* species are inseparable by morphological features. In their review of the Palaearctic species of *Heringia* (including *Neocnemodon*), Claussen et al. (1964) divided *Neocnemodon* into two species groups. Both *calcarata* and *vitripennis* belong to the *latitarsis* group.

Neocnemodon calcarata (Loew)

(Figs 1–4, 6)

Common name: Opaque Spikeleg (Skevington et al. 2019).

***Pipiza calcarata* Loew, 1866**: 154 [also 1872: 28, species #6]. Type-locality: New York. Lectotype ♂, MCZ here designated. Osten-Sacken 1875: 43, 1878: 120 (catalog citations); Williston 1887: 24 (translation original description); Smith 1890: 383 (New Jersey); Johnson 1900: 658 (New Jersey), 1910a: 764 (New Jersey); Aldrich 1905: 350 (catalog citation); Jones 1907: 239 (descr.); Kertész 1910: 15 (syn.); Metcalf 1913: 81 (cit.), 1921: 210 (MG*); Winn & Beaulieu 1915: 133 (Quebec); Banks et al. 1916: 178 (Va., D.C., Md.); Britton 1920: 185 (Connecticut); Curran 1921a: 363 (A* descr., distr.), Fluke 1922: 224 (descr. note, Wisconsin).

***Cnemodon calcarata* (Loew, 1866)** of: Curran 1921: 363, figs. 4–6, 8, 49 (key ref., description), 1926: 157 (New York), 1934b: 3 (New Hampshire, Slosson Coll.); Wehr 1924: 140 (Nebraska); Johnson 1925a: 162 (Maine); Johannsen 1928: 793 (New York); Petch & Maltais 1932: 45 (Quebec); Brown 1934: 247 (Ontario); Brimley 1938: 349 (North Carolina); Strickland 1938: 201 (?Alta.); Telford 1939: 40 (Minnesota); Procter 1946: 388 (Maine); Foxlee 1956: 36 (British Columbia).

***Neocnemodon calcaratus* (Loew, 1866)** of: Wirth et al. 1965: 581 (cat. cit.); Cole 1969: 309 (distr. western N.A.); Boyes & van Brink 1972: 324 (chromosomes*, British Columbia, Quebec); Telford 1975: 10 (Washington, Idaho).

***Pipiza radicum* Walsh & Riley, 1869**: 83. Type-locality: Illinois, near Cobden and at Du Quoin. Syntypes destroyed (see below). Osten-Sacken 1878: 120 (catalog citation, ?= *femoralis* Loew, 1866); Johnson 1900: 658 (New Jersey), 1910a: 764 (New Jersey); Coquillett 1904: 200 (taxonomic notes, synonymy, types); Kertész 1910: 21 (cat. cit.); Metcalf 1913: 82 (Ohio), 1916a: 99 (N.C.); Winn & Beaulieu 1915: 133 (Quebec); Davidson 1916: 456 (econ. import., prey *Eriosoma lanigerum* and *Phylloxera vitifoliae* (Fitch, 1855)); Britton 1920: 185 (Connecticut); Curran 1921: 356 (considered a synonym of *salax* Loew, 1866); Fluke 1922: 225 (Wisconsin); Knowlton 1931: 156 (Utah); Jaques 1937: 386 (Iowa); Brimley 1938: 349 (North Carolina); Heiss 1938: 69 (immature stages).

***Pipiza pistica* Williston, 1887** (unverified) of: Johnson 1900: 658 (New Jersey); Snow 1895: 227 (New Mexico); Chagnon 1901a: 44 (20) (description, key reference), 1901b: 8 (Quebec); Aldrich 1905: 350 (cat. cit.); Jones 1907: 239 (descr. note, Colo.); Tucker 1907: 98 (Colorado); Graenicher 1909: 24 (flower *Solidago canadensis*), 1910: 36, 1911: 68, 1913: 180 (Wisconsin); Kertész 1910: 311 (syn.); Banks et al. 1916: 179 (flower *Sedum ternatum*) Virginia, Maryland); Nicolay 1919: 278 (New Jersey); Jones 1922: 19 (Colorado); Hallock & Parker 1926: 10 (New Jersey); Robertson 1928: 173 (Illinois, flower *Rosa setigera*).

***Pipiza pisticoides* Williston, 1887** of: Metcalf 1913: 81 (H* Ohio), 1916b: 224 (AH* L* P* HSP* biol., descr. (L P A) prey (*Schizoneura lanigera* Gillette, 1908) Maine), 1916a: 99

(North Carolina), 1921: 209 (MG*); Holdsworth 1970: 532 (in *Eriosoma lanigerum* colonies, Ohio).

***Neocnemodon calcarata* (Loew, 1866)** of: Skevington et al. 2019: 306 (description, notes).

Description

Length (7): 5.6–7.2 (6.4) mm, body; 4.8–5.7 (5.2) mm, wing.

MALE. **Head**: Black; face shiny except very narrowly white pollinose laterally along eye margin, black pilose; gena sparsely gray pollinose, black pilose; lunule shiny, slightly orange laterally; frontal triangle shiny except dorsal 1/3 black pollinose, black pilose; eye contiguity long, as long as vertical triangle; eye white pilose; vertical triangle equilateral, black pollinose, brownish-yellow pilose; occiput white pollinose and pilose on ventral 2/3, black pollinose and pilose dorsally. Antenna: scape and pedicel brownish orange, black pilose; postpedical elongate oval, brownish black except yellow basoventral 1/3; arista yellowish basally becoming brown apically.

Thorax: Black except postpronotum brownish orange; postpronotum black pilose; scutum dull brownish-black pollinose, white pilose except black pilose adjacent to postpronotum, dorsal to wing, medially on post alar callus and marginally on scutellum; pleuron sparsely gray pollinose except shiny area anteromedially on katepisternum, pale pilose; calypter brown; plumula brownish basally, white apically; halter orange, except capitilum brownish-orange. **Wing**: hyaline, microtrichose except bare as follows: cell h, basal 1/3 cell c, basal 1/2

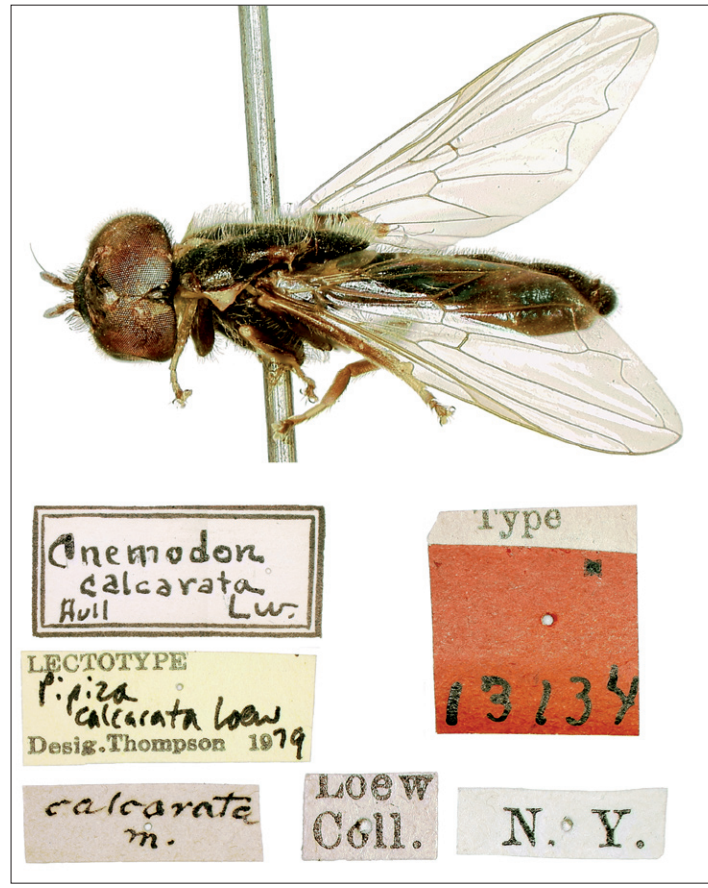

Fig. 1: *Neocnemodon calcarata* (Loew), lectotype male with labels.

cell r_1, basal 2/3 cell r_{2+3}, anterobasal 1/4 cell cua and narrowly basomedially on alula. **Legs**: Coxa black, gray pollinose, black and white pilose; mesocoxa with long narrow ventral prong on anteromesial corner; trochanter black, gray pollinose, black and white pilose; metatrochanter with long basoventral prong only slightly expanded apically; femora black except yellow on apices, mainly black pilose, with white pile basally and dorsally; tibiae orange basally and apically, black medially, black pilose on dark areas, pale pilose on pale areas; mesotibia expanded slightly posteromedially; pro- and mesotarsi orange; metatarsus brownish-black except orange middle two tarsomeres and on apex of basitarsomere, black pilose.

Abdomen: Black; tergum 1 black pollinose, black pilose except white pilose laterally; tergum 2 dull black pollinose, black pilose except for triangular patch of white pile on medial 1/2 and white pilose laterally; tergum 3 black pollinose except shiny laterally and in form of large mediolateral macula, short black pilose on dull areas, white pilose on shiny areas; tergum 4 black pollinose on basomedial 3/4, lateral and apical margins broadly shiny, short black pilose on dull areas, long white pilose on shiny areas except basolateral 1/5 and apicolateral corner black pilose; sterna shiny except sparsely gray pollinose on sternum 1, black pilose; male genitalia black pilose.

Variation. The eye pile ranges from white to brown to almost black; the thoracic pile ranges from white to yellow to brown; and the metatarsus from having yellow middle tarsomeres (2-3) to being entirely dark. The above description is based on the lectotype of *calcarata*. The type and the reared specimens from Virginia agree well. The holotype of *Cnemodon elongata* Curran, 1921 and many other specimens are darker. Variation in leg color within species is interpreted as seasonal variation.

Distribution. British Columbia to Quebec, south to Kansas and Virginia (Skevington et al, 2019).

Material examined (27). **U.S.A.**: **Connecticut**: Stamford, Bartlett Tree Research Laboratory, 10 May 1930, S. W. Bromley (1 ♂, USNM). **District of Columbia, Washington**: 13.vi.1913, R. C. Shannon (1 ♂, USNM). **Idaho**: Lake Waha, 14.vi.1930 (1 ♂, USNM). **Indiana**: Lafayette, 24.vi, J. M. Aldrich (1 ♂, USNM); 6.viii.1917, J. M. Aldrich (1 ♂, USNM). **Maryland**: Hancock, viii.1915, F. R. Cole (1 ♂, USNM). **New Jersey**: Wenonah, 10.vii.1910 (1 ♂, USNM). **New York**: Lectotype ♂, here designated (1 ♂ lectotype, MCZ); Auburn, 16.viii.1969, D. J. Peckham (3 ♂, USNM); 6.viii.1970, D. J. Peckham (1 ♂, USNM); Long Island, Cold Springs, 5.vii.1931, C. H. Curran (1 ♂, USNM). **Pennsylvania**: Broomall, 24.viii.1910 (1 ♂, USNM); Lehigh Gap, 1.vii.1903 (1 ♂, USNM); Castle Rock, 30.vi.1910 (1 ♂, USNM). **Virginia**: Clarke Co., Shenandoah River, 3.ix.1923, J. M. Aldrich (2 ♂, USNM); Fairfax Co., Great Falls, 20.viii.1916 (1 ♂, USNM); Winchester (2 ♂, USNM), 27.vi.2000, J,C. Bergh (1 ♀, USNM), 29.vi.2000, J.C. Bergh (1 ♂, USNM). Texas, Paris, 1904, C. T. Brues (1 ♂, USNM). **West Virginia**: Kanawha Station, 27.vi.1918, S. A. Rohwer (1 ♂, USNM).

Names and types

Pipiza calcarata. Loew (1866) described *calcarata* from an unspecified number of males collected by Osten-Sacken in New York. In the collection of the Museum of Comparative Zoology today there is a single male with the appropriate labels (Fig. 1), which is here designated lectotype to fix the concept of the name and to ensure universal and consistent interpretation of the same.

Pipiza radicum. Walsh & Riley (1869) were the first to rear the "Root-louse *Syrphus*-fly", the common name they gave to the syrphid predator of WAA. Scientifically, they named the species *radicum* and provided descriptions of the adult female and the immature stages. The female was reared by Walsh from larvae found in Du Quoin, Illinois. This female, and all associated immature specimens, have been subsequently lost (Coquillett 1904). For no-

Fig. 2: *Neocnemodon calcarata* (Loew), male, ventral view of metaleg and base of abdomen. Sterna 1 and 2 eliminated to highlight trochanter process.

Fig. 3: *Neocnemodon calcarata* (Loew), male, ventral view of thorax and meso- and metalegs, showing processes on mesocoxa.

menclatural purposes, we restrict the name to the specimen from which the illustration of the female was made. Osten-Sacken in his catalog (1878: 120) noted that this species was "apparently the same as *femoralis* Loew". In this, he was followed by Williston (1887: 26), who merely listed it as a dubious synonym of *femoralis*. Coquillett (1904) re-examined the issue and concluded, however, that this species was the same as the one described in 1887 by Williston as *Pipiza pistica*. Coquillett based his decision on examination of the Williston types of *pistica* and a voucher from the rearing work done by earlier USDA workers (see Comstock 1880: 259). Therefore, he resurrected the name *radicum* as the valid name. Curran (1921: 355) later considered these two names (*Pipiza radicum* and *Pipiza pistica*) to be synonyms of *Heringia* (sensu stricto) *salax* (Loew, 1866). Curran's synonymy has led some authors (Rojo et al. 2003: 115) to incorrectly cite *H. salax* as a predator of WAA. *Pipiza radicum*, synonymized with *pistica* by Coquillett, is now considered a synonym of *Heringia salax*.

Pipiza pistica. Williston (1887) described this species from two females collected in New Haven, Connecticut. Both syntypes are in good condition, and in the USNM. These specimens appear to be *Heringia* (sensu stricto) *salax* as noted by Curran. Curran (1921: 347) noted that *Heringia* sensu stricto can be separated from *Neocnemodon* in the female by the mesotibia being slender (*Heringia*), not slightly rounded anteriorly (*Neocnemodon*) and postpedicel being elongate (*Heringia*), not "shorter and more roundish" (*Neocnemodon*). Our reared and associated females of *calcarata* do have the mesotibia slightly rounded anteriorly, moderately carinate dorsally, and with shorter pile than the slender, non-carinate and long pilose mesotibia of the syntypes of *Pipiza pistica*. Hence, I (FCT) accept Curran's placement of *pistica* as a synonym of *Heringia salax*.

Due to the nomenclatural and taxonomic confusion over these two species, *salax* and *calcarata*, earlier references to either need to be re-evaluated.

Pipiza pisticoides. Williston (1887) described this species from a single female taken near the base of Mount Washington on August 1st. He compared it to his *pistica*, but believed it to

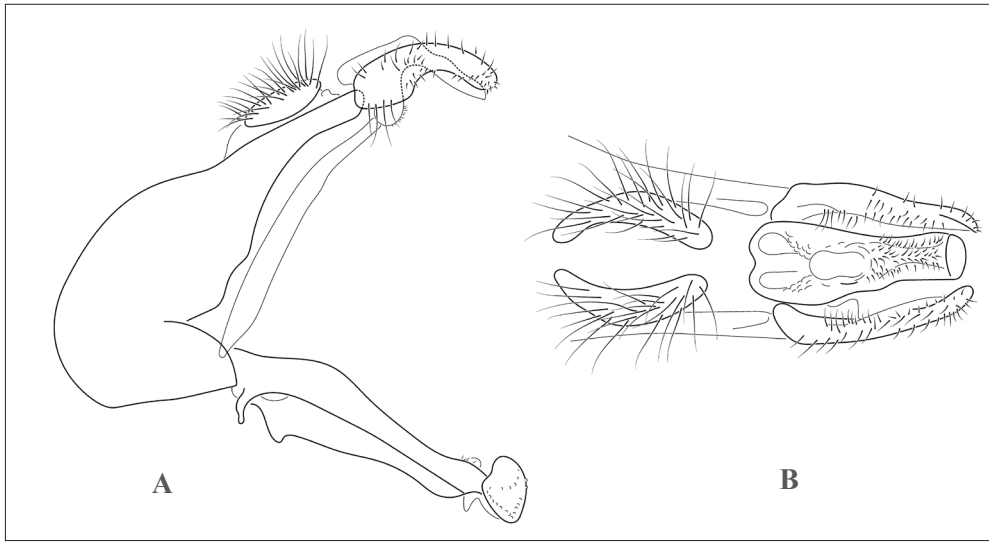

Fig. 4 A, B: *Neocnemodon calcarata* (LOEW), male genitalia. – **A**: Epandrium and hypandrium, lateral view; – **B**: Apical part of epandrium, subepandrial sclerite, surstyli and cerci, dorsal view.

be distinct as 1) the postpedicel was orbicular, as broad as long [*pistica* has a more elongate postpedicel]; 2) "the pile throughout is shorter [and] on the abdomen scarcely discernible"; and 3) "the size is also distinctly smaller". This holotype is now in poor condition in the USNM, but there is an additional female from the WILLISTON Collection with the same labels. While the taxonomy of females is not well known, these specimens clearly represent a species distinct from *pistica* as noted by WILLISTON. Currently *pisticoides* is interpreted as a different species whose male has the abdominal sternum 3 carinate apically (CURRAN 1921: 368; SKEVINGTON et al. 2019).

METCALF (1916) used the name *pisticoides* for a natural enemy of WAA in the Orono, Maine, area. He contrasted material collected in Ohio and one specimen reared from a pupar-

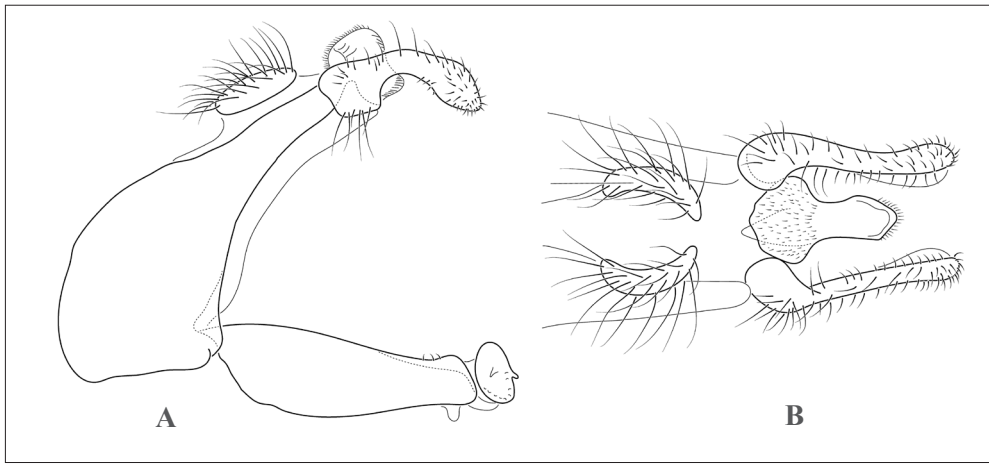

Fig. 5 A, B: *Neocnemodon vitripennis* (MEIGEN), male genitalia. – **A**: Epandrium and hypandrium, lateral view; – **B**: Apical part of epandrium, subepandrial sclerite, surstyli and cerci, dorsal view.

ium found among "*Schizoneura americana* on Elm" with his Maine material. He noted slight differences in antennal size and ratio, pilosity, and length of dm-cu crossvein. He therefore considered the Ohio specimens to refer to *radicum* and the Maine specimens to refer to *pisticoides*. Unfortunately, none of Metcalf's specimens have been found. However, Metcalf's measurements fall within the variation we have found for *calcarata* and his figure matches our females of *calcarata*, not the type of *pisticoides*.

Cnemodon elongata. Curran (1921) described this valid species from two males collected in Ontario. The holotype is in the California Academy of Sciences, is in good condition and has the following labels: "Type" [Curran's handwriting], "Orilla, Ont.," "22.6.14" 398 [Curran's handwriting], "H. Curran," "Cnemodon / elongata / Curran" [Curran's handwriting], "Type" [red] and "California Academy / of Sciences / Type no. 854." Skevington et al. (2019) illustrate some of the differences between *elongata* and *calcarata*.

Notes. Morphological molecular evidence from Vujić et al. (2013) and the phylogeny of pipizine syrphids by Mengual et al. (2015) have shown that species of *Neocnemodon*, including *vitripennis*, are sister to *Pipizella* and not *Heringia*, so *Neocnemodon* is a valid separate genus and not a subgenus of *Heringia*. Although *calcarata* was not included as an exemplar in the Mengual et al. (2015) phylogeny, presence of the apomorphic process on the mesocoxa (spike) clearly indicates that *calcarata* belongs to *Neocnemodon*.

Neocnemodon calcarata is most similar to *vitripennis* Meigen, but differs from that species as follows: 1) postpedicel longer (Figs 6, 7); 2) pro- and mesotibiae paler (Figs 6 A, B, 7 A–D); 3) mesotibia in male less dilated medially (Figs 6, 7); 4) metacoxa without apicolateral spur (Figs 2, 7); 5) metatrochanter in male with spur of different shape (Figs 2, 7); 6) male genitalia distinct with apical portion of surstyle of different shape as well as post anal hood (Figs 4 A, B, 5 A, B).

The COI barcode sequence of *N. calcarata* from Winchester, Virginia, has been deposited at the National Center for Biotechnology Information under the accession number ON155992.

Neocnemodon vitripennis (Meigen)

(Figs 5, 7)

Common name: Pale-haired Spikeleg.

***Pipiza vitripennis* Meigen, 1822**: 254. Type-locality: Austria [as Österreich]. Holotype ♂, NMW (see Thompson 1988: 204). Macquart 1829: 180 (description, northern France), 1834: 571 (description); Rossi 1848: 38 (Austria, flight period); Walker 1851: 272 (England); Schiner 1858: 309 (Austria), 1861: 264 (key reference, Austria), 1864: 111 (catalog citation); Rondani 1857: 182 (Italy); Heeger 1858: 295, pl. 1, figs. 1–6 (egg, larva, puparium) (biology, description of all stages, Austria); Neuhaus 1886: 123 (Germany, Berlin region); Kowarz 1885: 243 (similar to *latitarsis*).

***Cnemodon vitripennis* (Meigen, 1822)** of: Verrall 1901a: 177 (description, Great Britain, synonymy), 1901b: 28 (cat. cit.); Bezzi & Stein 1907: 14 (cat. cit.); Kertész 1910: 23 (cat. cit.); Drensky 1934: 112 (Bulgaria); Evenhuis 1958: 1, 1959: 238 (Netherlands, biol., prey (*Eriosoma lanigerum*); Stubbs & Falk 1983: 104, 207 (key reference, diagnosis, United Kingdom).

***Neocnemodon vitripennis* (Meigen, 1822)** of: Torp 1984: 145 (key ref., Denmark); Peck 1988: 85 (cat. cit.); Brădescu 1991: 12, 35 (Romania, key reference); Verlinden 1994: 109 (key ref, figures, Belgium); Vujić & Glumac 1994: 46 (Serbia).

***Heringia* (*Neocnemodon*) *vitripennis* (Meigen, 1822)** of: Vujić 1999: 139 (Serbia, key ref.); Stubbs & Falk 2002: 311 (United Kingdom, color habitus); van Veen 2004: 122 (key ref., figures, northwestern Europe).

Fig. 6 A–D: *Neocnemodon calcarata* (LOEW). – **A**: Female; – **B**: Male; – **C**: Mesotibia, male; – **D**: Antenna, male.

***Pipiza albohirta* WIEDEMANN, 1830**: 110. Type-locality: Unknown [as Vaterland?]. Lectotype ♂, NMW designated THOMPSON (1988: 204). Syn. by THOMPSON (1988: 204).

***Pipiza acuminata* LOEW, 1840a**: 30 [also 1840b: 564]. Type-locality: Poland, Poznan area [as Posener Gegend]. Holotype ♀ lost. SCHINER 1857: 309 (citation), 1861: 265 (citation); VERRALL 1870: 176 (Great Britain, with *vitripennis* of WALKER as synonym). Syn. by VERRALL (1901a: 181).

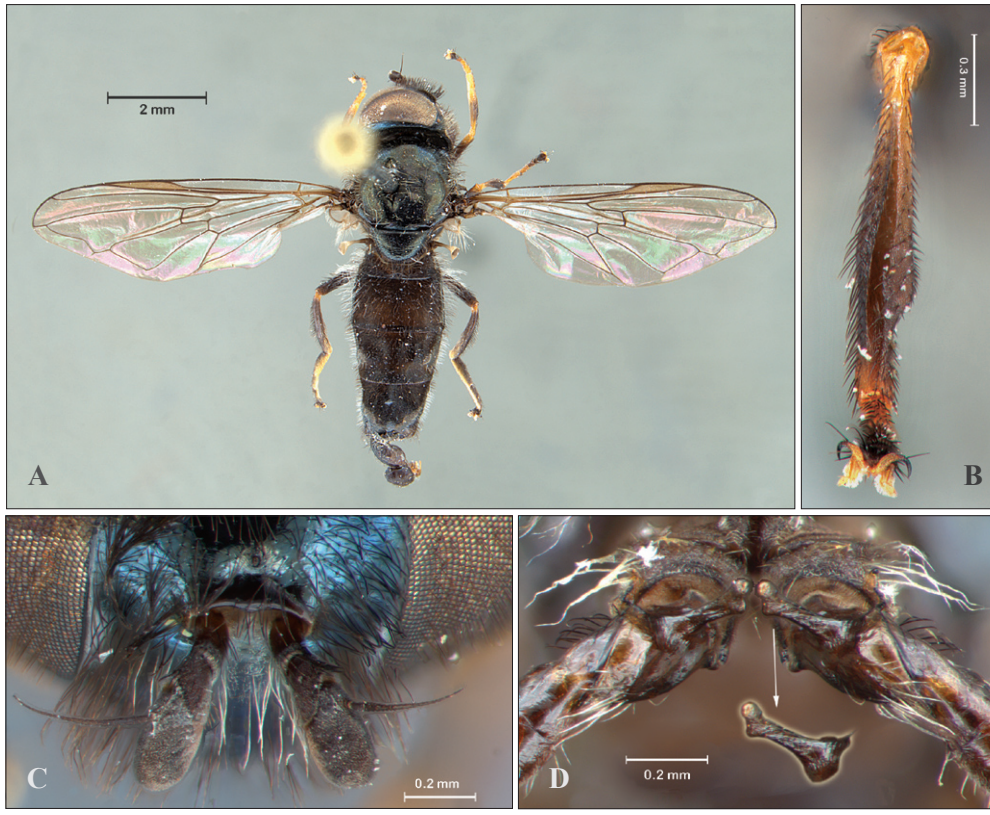

Fig. 7 A–D: *Neocnemodon vitripennis* (Meigen), CNC_Diptera149534. – **A**: Dorsal habitus; – **B**: Mesotibia; – **C**: Antenna; – **D**: Metatrochanter spurs (right one copied and highlighted to better recognision of its shape).

***Pipiza aphidiphaga* Costa, 1853**: 85. Type-locality: Italy, Naples. Palma 1864: 65 (Italy, Naples); Rondani 1868: 54 (note, syn. of *vitripennis*?). Syn. by Rondani (1868: 34).

***Cnemodon dreyfusiae* Delucchi & Pschorn-Walcher, 1955**: 502. Type-locality: Austria. Holotype ♂, NMW. Syn. by Collin (1960: 144).

As this species is virtually identical to *calcarata*, we forgo a formal description. A differential diagnosis is provided above to separate *vitripennis* from *calcarata*.

Names and types

Pipiza vitripennis. Meigen (1822) described *vitripennis* from a male (= holotype) collected in Austria and sent to him from Megerle under the manuscript name *Scava* [=*Scaeva*] *dubia*. Thompson (1988: 205) identified the holotype in the Vienna Museum (NMW), which is labeled "*vitripennis*, Coll. Winthem" "*C. dreyfusiae*, Pschorn, V. Delucchi det." "Lectotype, *Pipiza*, *vitripennis*, Meigen, Design. Thompson 1985" [yellow]. The type is very pale and has apparently been bleached by the sun.

Neocnemodon vitripennis was frequently misidentified and/or was treated as a broader species concept in the earlier literature. Delucchi & Pschorn-Walcher (1955) were the first to properly redefine the species. Unfortunately, as noted by Collin (1960: 145), and verified by Thompson (1988), they re-described the species as *dreyfusiae*.

Pipiza albohirta. Wiedemann (1830) described *albohirta* from a male from an unknown locality [as Vaterland?]. Thompson (1988: 204) found a male in the Vienna Museum (NMW) with the appropriate labels and designated it as lectotype. He identified the specimen as *vitripennis* Meigen.

Pipiza acuminata. Loew (1840) described *acuminata* from only a female collected in the area in and around Poznan, Poland [as Posener Gegend]. Verrall (1901a: 181) reviewed this name and placed it as a synonym of *vitripennis*. As the type is lost (see Verrall) and also based on a female, Verrall's synonymy is to be accepted.

Pipiza aphidiphaga. Costa (1853) described *aphidiphaga* from adults reared from larvae preying on aphids causing leaf galls on elm in the Naples region. Rondani (1868: 34) suggested that *aphidiphaga* should be considered a synonym of *vitripennis*. The types of Costa were deposited in the museum in Naples, but while the material did survive World War II, the insect collection was discarded recently (Thompson & Thompson 2007, in respect to the Rondani material, the same is true of Costa material). While the biological data suggest that *aphidiphaga* may be a synonym of another *Neocnemodon* species, we leave the name as a synonym of *vitripennis*, as that is where Rondani placed it. However, even if the types are found and their identities were determined, the name would remain a *nomen oblitum* as it has never been used as valid since its introduction.

Cnemodon dreyfusiae. Delucchi & Pschorn-Walcher (1955) based their species on a holotype male from Austria from the collection of Egger and determined by Egger as *vitripennis* Meigen. This type is in the Vienna Museum (NMW) and labeled as "Schiner, 1866" "Austria, Coll. Egger" "*vitripennis*, det. Egger" "Type" [red], and "*Cnemodon dreyfusiae* n. sp., det. Delucchi & Pschorn". For its taxonomy, see above under *vitripennis*.

Distribution. Southern Sweden to central France, Ireland eastward through northern and central Europe into Russia and through Siberia to the Pacific coast (Speight 2020).

Material examined. **AUSTRIA**: LT of *albohirta* & *vitripennis*, HT *dreyfusiae*. Austria [as Österreich]. Holotype ♂ (1 ♂, NMW). **NETHERLANDS**: Rhynauwen, 12.viii.1965, H. J. P. Lambeck (2 ♂, 2 ♀, USNM). **GERMANY**: Berlin, Finkenkrug, 16.vii.1905 (1 ♂, USNM).

Notes. *Neocnemodon vitripennis* is the common predator of the WAA in northern Europe (Evenhuis 1959).

According to Peck (1988: 84), this species is apparently absent from Central Asia, as she does not list Kazakhstan or any of the other countries of the former Soviet Middle Asia. Given the origin of apple there (Dzhangaliev 2003), a careful examination of the pests and their predators and parasites on the wild ancestor of apple would be an interesting contribution to resolving the puzzle of the apple microecosystem.

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