SYSTEMATICS OF NEARCTIC *CALLOMYIA* (DIPTERA: PLATYPEZIDAE)

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PREFACE

This thesis is comprised of three chapters, one of which is an original manuscript that will be submitted for publication in a refereed journal.

Chapter 1.

This chapter is a general introduction and literature review of Platypezidae systematics focused on the subfamily Callomyiinae and the genus *Callomyia*.

Chapter 2.

This chapter is a manuscript in preparation for submission to the journal *Zootaxa*:

Cumming, H.J. and Wheeler T.A. Nearctic revision and phylogeny of the genus *Callomyia* Meigen (Diptera: Platypezidae).

Disclaimer: In accordance with Article 8.2 of the International Code of Zoological Nomenclature, new species names and taxonomic decisions proposed in this thesis are not to be considered published under the Code until they have been published in the primary literature.

Chapter 3.

This chapter is a general conclusion.

CONTRIBUTION OF AUTHORS

Heather Jean Cumming designed and executed the research in the manuscript and conducted all specimen-based work, field work, data collection and writing. Terry A. Wheeler was responsible for the supervision of the thesis research, editing of the manuscript, and providing lab facilities, equipment and research funding.

ABSTRACT

A Nearctic revision and phylogenetic analysis of the world species of the genus *Callomyia* Meigen (Diptera: Platypezidae) was undertaken. A total of ten species are recognized from the Nearctic Region (*C. argentea* Cumming **sp. nov.**, *C. arnaudi* Cumming **sp. nov.**, *C. bertae* Kessel, *C. browni* Cumming **sp. nov.**, *C. calla* Kessel, *C. corvina* Kessel, *C. gilloglyorum* Kessel, *C. proxima* Johnson, *C. velutina* Johnson, and *C. venusta* Snow), including three new species and three new synonyms. Delimitation of species was based primarily on morphological data, however, molecular sequence data (DNA barcodes) were used wherever possible to help determine species boundaries and associate sexes. Species descriptions, diagnoses, and illustrations of distributions, habitus, male terminalia and additional important diagnostic characters are presented. A key to the Nearctic species for both sexes is also provided. The phylogenetic analysis used 32 morphological characters, 28 adult and four larval characters, and supported the monophyly of *Callomyia*. It also revealed that the Nearctic species do not form a monophyletic group and are distributed within at least three major clades. Close relationships were found between some of the Nearctic and Palaearctic species, but no Holarctic species were discovered.

RÉSUMÉ

Une révision Néarctique et une analyse phylogénique des espèces mondiales du genre *Callomyia* Meigen (Diptère: Platypezidae) ont été entrepris. Dix espèces sont reconnues dans la région du Néarctique (*C. argentea* Cumming **sp. nov.**, *C. arnaudi* Cumming **sp. nov.**, *C. bertae* Kessel, *C. browni* Cumming **sp. nov.**, *C. calla* Kessel, *C. corvina* Kessel, *C. gilloglyorum* Kessel, *C. proxima* Johnson, *C. velutina* Johnson, et *C. venusta* Snow), dont trois nouvelles espèces et trois nouveaux synonymes. La délimitation des espèces est principalement basée sur des données morphologiques. Toutefois, des données de séquences moléculaires (codes-barres d'ADN) ont été utilisés, lorsque possible, afin d'aider à séparer les espèces et à associer les sexes. Des descriptions d'espèces, diagnostiques, ainsi que des illustrations de leurs distributions géographiques, des espèces à part entière, des parties génitale des mâles et des caractères diagnostiques additionnels important sont présentées. Une clé d'identification des espèces Néarctiques pour chaque sexe est aussi fournit. L'analyse phylogénétique incluant 32 caractères morphologiques, 28 caractères pour le stade adulte et quatre pour le stade larvaire, supporte la monophile de *Callomyia*. Cette analyse révèle d'ailleurs que les espèces Néarctique ne forment pas un group monophylétique. Elles sont plutôt distribuées en au moins trois clades important. Des relations rapprochées entre quelques espèces Néarctique et Paléarctique ont été trouvé, mais aucune espèce Holarctique n'a été découverte.

CHAPTER 1. GENERAL INTRODUCTION AND LITERATURE REVIEW

Significance of Diptera

The insect order Diptera (the true flies) is one of the most species rich groups of organisms, making up 10-15% of known animal species (Yeates et al. 2007). Diptera are one of the four megadiverse insect orders, containing 153 000 described species, and with many species awaiting description, the actual number of extant species is probably much larger (Brown 2005; Woodley et al. 2009; Pape et al. 2011). According to Hammond (1992), most species of flies have not been collected and still await discovery, and if all were known, the group could number a million or more species. Because there are still so many species to be discovered and described, Diptera is one of the true frontiers of systematic research (Brown 2010).

The direct relevance of flies to humanity is undeniable. Many species negatively impact humans by being disease vectors or plant pests, while others have positive impacts as they are important in pollination of plants, decomposition of plant and animal material, biological control, and medical or forensic use (Brown 2010). Although the economic importance of flies has been well studied and continues to be an important area of research, we are only beginning to understand the diversity and evolutionary relationships of the majority of Diptera taxa, as well as the function of most Diptera species in ecosystem processes.

Many Diptera families (e.g., Cecidomyiidae, Mycetophilidae, Sciaridae, Rhagionidae, Phoridae, Lauxaniidae, Anthomyiidae) are significant components of forest ecosystems in terms of both abundance and species richness, because they comprise some of the major components of forest food webs, including forest decomposition (Marshall 2012). Despite their significance in these complex ecosystems, there remains a lack of knowledge about the biodiversity and ecological relevance of many of these forest-inhabiting Diptera taxa (Lévesque-Beaudin & Wheeler 2011).

Biology of the Platypezidae

One family that is almost exclusively associated with forest habitats is the Platypezidae, or flat-footed flies. The Platypezidae are small to medium sized flies (1.4–10.0 mm long) that are found worldwide on all continents except Antarctica (Collin 1931; Kessel & Clopton 1970; Smith 1980; Kessel 1987; Chandler 1994; Chandler & Shatalkin 1998; Chandler 2010). They occur associated with fungi in damp forests, as all known larvae are fungivorous (Chandler & Shatalkin 1998). Larvae develop in the fruiting bodies of various fungi that mainly grow on wood and therefore they play a role in the decomposition of forest ecosystems (Chandler 2010). The larvae are typically monophagous or oligophagous, developing in a single fungus species or a few related species or genera, particularly in the fungus subclass Homobasidiomycetes (Chandler 1991). Although some information about platypezid larval biology has been documented in the literature (e.g., Chandler 1991; Chandler & Shatalkin 1998), the immature stages of many platypezid species are still unknown and rearing records for the group as a whole, remain spotty (Chandler 2001). The seasonal occurrence of species is largely dependent on the availability of host fungi and as a result individuals are often found in the fall when fungus fruiting bodies are most abundant and diverse (Chandler 2001). Adults are frequently observed running about erratically on broad leaves of trees or shrubs, usually where filtered sunshine occurs. This behavior is thought to be associated with feeding on honeydew (Chandler & Shatalkin 1998). Copulation occurs through aerial mating swarms, in which females are attracted to swarms of dancing males where aerial coupling takes place (Kessel 1987). These swarms have been observed in forest openings.

Although the Platypezidae form an important component of forest ecosystems, much taxonomic work is needed on this family, particularly outside of the Palaearcrtic Region. Sound taxonomic work, including stable classifications, will provide the essential basis for future biodiversity, ecological, and behavioral studies on this family, as well as studies pertaining to forest habitats in general.

Platypezidae classification

The family Platypezidae is easily recognized by enlarged or flattened hind tarsi (found in both sexes but generally more pronounced in females), a large cell cu*p* on the wing, and holoptic eyes in males (Chandler 2001). In general platypezids are black, grey, orange or yellow in colour, often with unique patterns that in some species include blue or silver-grey markings.

Sexual dimorphism in colour is found in many species of this family, with males usually being darker than females (Chandler & Shatalkin 1998).

Platypezidae belong in the lower Cyclorrhapha, also referred to as the Aschiza, and is considered to be one of the most generalized (i.e., possessing numerous plesiomorphic characters) families within this group (Hennig 1976; McAlpine 1989; Chandler 2001). There are many competing hypotheses about the phylogenetic relationships of the families that belong in the lower Cyclorrhapha, and therefore the placement of Platypezidae within this group is ambiguous. Cumming et al. (1995) placed this family as the sister group to the Lonchopteridae, Phoroidea (i.e., Phoridae including Sciadocerinae, and Ironomyiidae) and Eumuscomorpha (Syrphidae, Pipunculidae and Schizophora), based on the absence of both a thumb-like condyle on the pedicel of the antenna and pupal respiratory organs that project through the puparium, which are synapomorphies of the Lonchopteridae + Phoroidea + Eumuscomorpha. Zatwarnicki (1996) generally agreed with this placement of Platypezidae (plus Opetiidae), but excluded the Lonchopteridae. Disney (1994) considered the Platypezidae to be basal only to the Phoroidea (including the Lonchopteridae), based on the absence of the characteristic thumb-like condyle on the pedicel of the antenna and holoptic rather than dichoptic eyes in males, even though the apomorphic states also occur within the Eumuscomorpha (Cumming et al. 1995; Sinclair & Cumming 2006). Molecular phylogenetic studies place the Platypezidae (usually with Opetiidae) as the sister group to the Phoroidea (sometimes including Lonchopteridae) based on DNA sequence analysis of 28S rDNA, the nuclear protein coding gene CAD, and four other nuclear genes (aats1, EF-1α, pgd, tpi) (Collins & Wiegmann, 2002a, 2002b; Moulton & Wiegmann 2004, 2007; Wiegmann et al. 2011). The relationships of the Platypezidae to the remaining lineages of the lower Cyclorrhapha remain complicated and unresolved. Because the family is one of the most generalized in the lower Cyclorrhapha, it is probable that it, along with Opetiidae, might be placed near the base of the Cyclorrhapha. However, this is only shown in the cladogram of Cumming et al. (1995). All other hypotheses on the relationships of the Platypezidae, including the recent large scale analysis of relationships by Wiegmann et al. (2011), indicate that the Platypezidae and Opetiidae are farther removed from the base of the Cyclorrhapha.

Platypezidae currently contains approximately 250 described species worldwide, classified in roughly 20 genera, depending on the classification followed (Chandler 2001). There are four subfamilies included within the family, namely Microsaniinae, Melanderomyiinae, Platypezinae, and Callomyiinae (formerly referred to as the Platypezininae) (Chandler 2001). The first two subfamilies listed are monogeneric, whereas the latter two are much more diverse, containing many genera and species (Chandler 2010). The family appears to be most diverse in the Holarctic Region, as most genera occur only or mainly in this region, and the Nearctic fauna is relatively large with about 75 described species (Kessel 1987; Chandler 1991; Chandler & Shatalkin 1998). The Neotropical fauna is the least well known, with only 14 described species in six genera (Collin 1931; Chandler 2010).

The family is best known in the Palaearcrtic Region, particularly from Europe because of Chandler's (2001) monograph on the European Platypezidae. Shatalkin (1980b, 1981, 1985, 1992) described species of platypezids from the Far East of Russia, which added to the knowledge of the Palaearctic fauna outside of Europe. The most recent platypezid work from this region has been several faunistic studies, primarily from the Czech Republic and Slovakia (Vaňhara 1986, 1995; Tkoč & Vaňhara 2006; Roháček & Ševčik 2007, 2011; Tkoč 2011; Tkoč et al. 2012). Some of these studies (e.g., Tkoč 2011) include rearing records and information on larval biology.

The earliest taxonomic works on the Nearctic Platypezidae were by Snow (1894, 1895) and Johnson (1908, 1910, 1916, 1923). Kessel and his co-authors (e.g., Kessel 1948, 1961a; Kessel & Pearce 1966; Kessel & Kirby 1968; Kessel & Maggioncalda 1968; Kessel 1970, 1987) subsequently studied the Nearctic fauna, describing many genera and species from this region. Despite Kessel's efforts, the Nearctic fauna is poorly known in comparison to the Palaearctic fauna and still needs considerable work. The generic and species concepts need to be tested and re-evaluated, reliable keys to species need to be provided, and there have been no phylogenetic analyses of relationships.

Chandler (2001) presented the most comprehensive classification of the Platypezidae. He found that the family is monophyletic on the basis of uniserial acrostichal setae (lost in Platypezinae), compression of the hind leg (not evident in Melanderomyiinae), and wing with M_{1+2} forking beyond crossvein dm-cu (with the fork lost in some genera). He also proposed the following phylogenetic relationships between the subfamilies: Microsaniinae + Melanderomyiinae as the sister group to Callomyiinae + Platypezinae, and indicated that the Callomyiinae and the other large subfamily Platypezinae form a monophyletic group. The monophyly of this latter lineage is based on only one synapomorphy: the female mid and hind tarsi bearing depressed, less sclerotized areas devoid of setulae, termed ‘soles’. In Callomyiinae, these soles are depressed areas devoid of setulae, whereas in Platypezinae, they are larger well-defined excavations with densely fine-haired membranous interiors (Chandler 2001). In general, the Callomyiinae are distinguished from the Platypezinae by their retention of plesiomorphic characters, particularly a single row of acrostichal setae and a single row of dorsocentral setae on each side of the scutum (Chandler and Shatalkin 1998).

The subfamily Callomyiinae

Chandler (2001) proposed Callomyiinae as a monophyletic clade based on the following apomorphies: presence of uniformly dark setulae on the hind tibia and tarsus; male with prominent posteroventral seta (‘oxhorn’ or ‘safety-pin’ seta) near base of the fore femur (erect basally then bent to run parallel with the femur and fit into a corresponding anteroventral notch on the apical half of the mid femur); male with a strong posteroventral seta near the base of the hind femur; larva with a ground plan of eight processes per segment. However, two other studies: Rotheray et al. (2004) based on larval and pupal characters, and Tkoč et al. (2010) based on a preliminary molecular analysis of four mitochondrial markers, suggest the subfamily is paraphyletic in relation to the Platypezinae.

The Callomyiinae contains six genera worldwide, namely *Agathomyia* Verrall (Nearctic, Neotropical, Palaearctic, Oriental and Australasian), *Bertamyia* Kessel (Nearctic, Neotropical and Afrotropical), *Callomyia* Meigen (Nearctic, Palaearctic and Oriental), *Chydaeopeza* Shatalkin (Palaearctic), *Grossoseta* Kessel & Kirby (Nearctic), and *Platypezina* Wahlgren (Nearctic and Palaearctic) (Chandler 2001). Chandler (2001) analyzed the phylogenetic relationships of these six genera and considered each genus to be monophyletic, even though some were not supported by any synapomorphies. He proposed that *Platypezina* and *Grossoseta* are closely related (based on the retention of many plesiomorphic characters and the presence of a long coiled phallus, found in both genera) and the sister group to the remaining four genera. *Callomyia*, *Agathomyia*, *Chydaeopeza*, and *Bertamyia* together form a monophyletic group characterized by several synapomorphies, such as wing vein M_{1+2} unbranched, pterostigma absent, head setation reduced, and phallus short and wide, forming a hook apically (Chandler

2001). It is unclear whether *Agathomyia*, from which *Chydaeopeza* and *Bertamyia* were split, forms a monophyletic genus without them (Chandler 2010). *Callomyia* was placed as the sister group to *Agathomyia*, *Chydaeopeza* and *Bertamyia* on the basis of having two apical spurs on the midtibia, instead of only one.

Although Chandler (2001) analyzed the phylogenetic relationships of the Callomyiinae, additional phylogenetic work is needed because there are conflicting studies that suggest the subfamily is paraphyletic (Rotheray et al. 2004; Tkoč et al. 2010). In addition, several included genera are not supported by synapomorphies and may not be monophyletic. Therefore, a new comprehensive phylogenetic analysis of this subfamily is necessary to resolve these problems.

The genus *Callomyia* Meigen

The genus *Callomyia* currently contains 21 described species that are distributed mainly in the Holarctic Region, except for two species from the Oriental Region. Currently there are ten Nearctic species (Kessel & Buegler 1972), five species from Europe (Chandler 2001), four species from Siberia and the Far East of Russia (Shatalkin 1980, 1982, 1992), one species from Nepal (Kessel 1966), and one recently described species from Yunnan, China (Tkoč 2012).

Members of this genus are relatively small in size (2.9–4.8 mm long). They are typically dark brown to velvety black, often exhibiting distinct colour patterns of metallic bluish-white, silver-blue, silver-grey, and yellow to orange. Like many other species of Playpezidae, they exhibit pronounced sexual differences in colour, with males being darker than females. *Callomyia* appears to be monophyletic based on the setulose first longitudinal vein (R_1) and the uniquely shaped larvae that have a double pair of marginal, intricately patterned, processes on each segment (Kessel 1961b; Kessel & Buegler 1972; Krivosheina 2008b). The larvae of other genera of Platypezidae have only a single pair of simple marginal processes on each segment. The metathoracic segment and first abdominal segment are also fused in *Callomyia* larvae, unlike other platypezid larvae (Chandler 2001). The monophyly of the genus is also supported by Tkoč et al.'s (2010) preliminary molecular analysis of the family.

Species of *Callomyia* seem to occur in darks woods and can be found where filtered sunlight penetrates the forest (Kessel & Kessel 1962; Kessel & Buelger 1972). They do not run around in a jerky manner on the horizontal surfaces of leaves as is characteristic of most other platypezid species, but instead are usually observed slowly walking on leaves. They have also been seen hovering in the air where they appear almost motionless, greatly resembling spiders awaiting their prey (Kessel & Buelger 1972). The known larvae of *Callomyia* are mycophagous, like all other platypezid larvae, and develop on Basidiomycota fungi that grow on decaying wood (Kessel & Clopton 1969; Chandler 1991; Krivosheina 2008b; Tkoč et al. 2012). *Callomyia* larvae are surface feeders on fungi, feeding on moist mycelium encrusted substrates (Chandler & Shatalkin 1998; Chandler 2001; Krivosheina 2008a). Only a few species of this genus are known from the immature stages and little is known about their host associations, with the majority of information coming from European studies. Kessel (1961b) recorded and described the larvae and puparia of *Callomyia gilloglyorum* Kessel, the only immatures known from the Nearctic Region. The larvae of this species were found on white mycelia under the bark of a fallen pine tree (*Pinus* sp.). Unfortunately, the fungus species was not identified so nothing more is known about the host association of *C. gilloglyorum*. A few Palaearctic species of *Callomyia* are known from the immature stages. The larvae of *C. admirabilis* Shatalkin, *C. amoena* Meigen and *C. speciosa* Meigen have been found on mycelia on decaying trunks or branches of deciduous trees lying on the ground (Lundbeck 1927; Krivosheina & Mamaev 1967; Krivosheina 2008b). *Callomyia krivosheinae* Shatalkin larvae were discovered developing under the bark of a cedar stump, in white mould (Krivosheina 2008b). The larvae of an unidentified European species of *Callomyia* were found on the fruiting body of *Corticium,* an encrusting fungus on fallen trunks and branches (Lundbeck 1927; Chandler & Shatalkin 1998).

The earliest taxonomic work on the genus *Callomyia* was by Meigen (1804, 1824), in the Palaearcrtic Region. He described the type species, *C. elegans* Meigen (1804), on which the genus was based. Subsequently, Meigen (1824) described two additional species, *C. amoena* and *C. speciosa*. Zetterstedt (1838) described the new species *C. dives* Zetterstedt, from Europe. Chandler (1974) revised the four previous Palaearctic species mentioned, illustrating the male terminalia of all four species and providing a key to species. Chandler (1976) described the new species *C. saibhira* Chandler, from females only, and then associated and described the male of this species in his European monograph (Chandler 2001). In this work he also redescribed each of the five European species and provided a key to species for both sexes. Shatalkin (1980a, 1982, 1992) described four new species of *Callomyia* (i.e., *C. admirabilis*, *C. dorsimaculata* Shatalkin, *C. krivosheinae*, and *C. sonora* Shatalkin) from the Far East of Russia and the Amur

Region. Shatalkin (1982) originally described *C. dorsimaculata* from males only, as the females were unknown, but he later (1985) associated and described the female of this species. All of the Palaearctic species of *Callomyia* are known from both sexes and the male terminalia of every species, except *C. sonora*, have been described and illustrated. In addition, Krivosheina (2008b) described the larvae and puparia of *C. admirabilis*, *C. amoena*, *C. krivosheinae*, and *C. speciosa*, and provided a key to the immature stages of these species.

In the Oriental Region, Kessel (1966) described the new species *C. coei* Kessel, from Nepal and Tkoč (2012) described the new species *C. triangulata* Tkoč, from south China. Both of these species are known from females only.

The first taxonomic work on *Callomyia* in the Nearctic Region was by Snow (1894), who described *C. venusta* Snow from New Mexico. This paper was the first record of the genus from North America. Johnson (1916) subsequently described two additional new species, *C. proxima* Johnson and *C. velutina* Johnson, from eastern North America. Kessel (1948, 1961a, 1961b) described six new species (i.e., *C. bertae* Kessel, *C. calla* Kessel, *C. clara* Kessel, *C. cleta* Kessel, *C. corvina* Kessel, and *C. gilloglyorum*) from western North America but did not include a species key. The last regional Nearctic revision of *Callomyia* was by Kessel & Buegler (1972), which included a description of a new widespread species, *C. liardia* Kessel & Buegler. All of the Nearctic species of *Callomyia* were treated in this last revision, including a key to the species for both sexes.

Despite these earlier studies and Kessel & Buegler's (1972) later revision, there still appear to be many taxonomic problems within Nearctic *Callomyia*. The Nearctic species concepts are based primarily on adult colour with little supporting morphological information. Snow (1894) and Johnson (1916) described species from very few specimens and based their species descriptions completely on colour. Kessel (1948, 1961a, 1961b) expanded these species concepts but also based his species descriptions primarily on colour. Although Kessel & Buegler (1972) attempted to incorporate features of the male terminalia into a number of their Nearctic species concepts, they appear to have dissected relatively few males. In addition, their illustrations of the male terminalia are simplistic and often inaccurate, making them hard to understand. Their key to the Nearctic species of *Callomyia* is based entirely on colour and is very difficult to interpret. This is because many of the species differ only slightly in colour and appear to show more colour variation within species than is stated in their revision. Also, eight of the 10

Nearctic species were described from one sex only, with five species known only from males and three species known only from females. This is probably due to the prevalence of sexual dimorphism found in this group, making it difficult to associate the sexes of these species. Because so many of the Nearctic species are known from one sex only, it is probable that there are a number of synonyms within the described Nearctic species of *Callomyia*. In addition, species of *Callomyia*, like many other Platypezidae, are rarely collected and are poorly represented in collections. Most of the Nearctic specimens available for study were collected over many years by a single collector (E.L. Kessel), and many species are known from few specimens. This makes it difficult to assess intraspecific variation, and is also a challenge in obtaining fresh material for molecular analysis.

Objectives

Given the taxonomic problems within Nearctic *Callomyia*, the purpose of this thesis was to revise the Nearctic species of *Callomyia*.

All species known prior to this work and new species recognized here are described and diagnosed, with the habitus, male terminalia, and distributions illustrated. Existing species concepts are tested and expanded, using both colour and additional morphological characters, especially male terminalia. Molecular sequence data (DNA barcodes) are also used to delimit species and associate sexes, wherever possible. New information on species limits and characters will be used to produce a revised key to the Nearctic species.

In addition, the phylogenetic relationships between the world species of *Callomyia* are reconstructed to test the monophyly of the genus and propose a hypothesis on relationships between the species, particularly with respect to the placement of the Nearctic species.

REFERENCES

Brown, B.V. (2005) Malaise trap catches and the crisis in Neotropical Dipterology. *American Entomologist*, 51, 180–183.

Brown, B.V. (2009) Introduction. *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, Volume 1, NRC Research Press, Ottawa, Ontario, Canada, pp. 1–7.

Chandler, P.J. (1974) Additions and corrections to the British list of Platypezidae (Diptera), incorporating a revision of the Palaearctic species of *Callomyia* Meigen. *Proceedings and Transactions of the British Entomological Society*, 7, 1–32.

Chandler, P.J. (1976) A new species of *Callomyia* Meigen (Diptera: Platypezidae) from Bulgaria. *Entomologist's Gazette*, 27, 257–261.

Chandler, P.J. (1991) Platypezidae. *In*: Soos, A. & Papp, L. (Eds.), *Catalogue of Palaearctic Diptera, Volume 7, Dolichopodidae–Platypezidae*. Elsevier Science Publishing, pp. 205–217.

Chandler, P.J. (1994) The Oriental and Australasian species of Platypezidae (Diptera). *Invertebrate Taxonomy*, 8, 351–434.

Chandler, P.J. (2001) The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica*, 36, 1–276.

Chandler, P.J. (2010) Platypezidae (flat-footed flies). *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, Volume 2, NRC Research Press, Ottawa, Ontario, Canada, pp. 715–719.

Chandler, P.J. & Shatalkin, A.I. (1998) Family Platypezidae. *In*: Papp, L. & Darvas, B. (Eds.), *Contributions to a Manual of Palaearctic Diptera, Volume 3, Higher Brachycera.* Science Herald, Budapest, pp. 27–49.

Collin, J.E. (1931) Platypezidae, Pipunculidae. *Diptera of Patagonia and South Chile*, 6, 49–61.

Collins, K.P & Wiegmann, B.M. (2002a) Phylogenetic relationships and placement of the Empidoidea (Diptera: Brachycera) based on 28S rDNA and EF-1α sequences. *Insect Systematics and Evolution*, 3, 422-444.

Collins, K.P. & Wiegmann, B.M. (2002b) Phylogenetic relationships of the lower Cyclorrhapha (Diptera: Brachycera) based on 28S rDNA sequences. *Insect Systematics and Evolution*, 33, 445–456.

Cumming, J.M., Sinclair B.J. & Wood, D.M. (1995) Homology and phylogenetic implications of male terminalia in Diptera-Eremoneura. *Entomologica Scandinavica*, 26, 121–151.

Disney, R.H.L. (1994) Continuing the debate relating to phylogenetic reconstruction of the Phoridae (Diptera). *Giornale Italiano di Entomologia*, 7, 103–117.

Hammond, P. (1992) Species inventory. *In*: Groombridge, B. (Ed.), *Global Biodiveristy*: *Status of the Earth's Living Resources*. Chapman & Hall, London, pp. 17–39.

Hennig, W. (1976) Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). *Stuttgarter Beiträge zur Naturkunde* (A), 283, 1–63.

Johnson, C.W. (1908) A note on *Calotarsa*, and description of two new species of *Calimyia*. *Psyche*, 15, 59.

Johnson, C.W. (1910) A revision of the species of *Agathomyia* of the Eastern United States. *Psyche*, 17, 7–8.

Johnson, C.W. (1916) Further studies on the Platypezidae. *Psyche*, 23, 27–33.

Johnson, C.W. (1923) A review of the Platypezidae of eastern North America. *Occasional Papers of the Boston Society of Natural History*, 5, 51–58.

Kessel, E.L. (1948) New species of *Callomyia* from California (Diptera: Clythiidae). *The Wasmann Collector*, 7, 140–148.

Kessel, E.L. (1961a) New species of flat-footed flies from North America (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 19, 191–227.

Kessel, E.L. (1961b) The immature stages of *Callomyia*, with the description of a new species of this genus (Diptera: Platypezidae). *Occasional Papers of the California Academy of Sciences*, 30, 1–10.

Kessel, E.L. (1966) Diptera from Nepal, new species of *Platypeza* and *Callomyia* (Family Platypezidae). *Bulletin of the British Museum (Natural History), Entomology*, 17, 453–455.

Kessel, E.L. (1970) *Bertamyia*, a new genus of Platypezininae (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 28, 185–190.

Kessel, E.L. (1987) Platypezidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Coords.), *Manual of Nearctic Diptera*, Volume 2. Agriculture Canada Monograph, 28, pp. 681–688.

Kessel, E.L. & Buegler, M.E. (1972) A review of the genus *Callomyia* in North America, with the description of a new species (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 30, 241–278.

Kessel, E.L. & Clopton, J.R. (1969) The Platypezidae of the Oriental Zoogeographic Region and Islands to the east, with descriptions of four new species (Diptera). *The Wasmann Journal of Biology*, 27, 25–73.

Kessel, E.L. & Clopton, J.R. (1970) The Platypezidae of the Ethiopian zoogeographic region, with descriptions of new species and a new genus (Diptera). *The Wasmann Journal of Biology*, 28, 47–167.

Kessel, E.L. & Kessel, B.B. (1962) Mating behaviour and activity – rest periodicity in *Protoclythia californica* (Diptera: Platypezidae). *Proceedings of the California Academy of Sciences*, (4) 32, 57–78.

Kessel, E.L. & Maggioncalda, E.A. (1968) A revision of the genera of Platypezidae, with the descriptions of five new genera and considerations of phylogeny, circumversion and hypopygia (Diptera). *The Wasmann Journal of Biology*, 26, 33–106.

Kessel, E.L. & Pearce, M.J. (1966) The genus *Agathomyia* in the Americas south of the United States (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 24, 261–278.

Krivosheina, N.P. (2008a) Macromycete fruit bodies as a habitat for Dipterans (Insecta, Diptera). *Entomological Review*, 88, 778–792.

Krivosheina, N.P. (2008b) On biology of xylobiont platypezid larvae of the genus *Callomyia* (Diptera, Platypezidae). *Entomological Review*, 88, 973–982.

Krivosheina, N.P. & Mamayev, B.M. (1967) [Key for the identification of larvae of wood-inhabiting Diptera]. Nauka, Moscow. 367 pp. (in Russian).

Lévesque-Beaudin, V. & Wheeler, T.A. (2011) Spatial scale and nested patterns of beta-diversity in temperate forest Diptera. *Insect Conservation and Diversity*, 4, 284–296.

Lundbeck, W. (1927) Diptera Danica. Genera and species of flies hitherto found in Denmark. Volume 7, Platypezidae and Tachinidae. Gad, Copenhagen, pp. 1–39.

Marshall, S.A. (2012) *Flies: the natural history and diversity of Diptera.* Firefly Books Ltd., Richmond Hill, Ontario, 616 pp.

McAlpine, J.F. (1989) Phylogeny and classification of the Muscomorpha. *In*: McAlpine, J.F. & Wood, D.M. (Coords.), *Manual of Nearctic Diptera*, Volume 3. Agriculture Canada Monograph, 32, 1397–1518.

Meigen, J.W. (1804) *Klassifikazion und Beschreibung der europäischen zweiflügeligen Insekten. (Diptera Linn.)*. Erster Band. Abt. I. pp. i–xxviii + 1–152, pls. 1–8; Abt. II, pp. i–vi + 153–314, pls. 9–15. Braunschweig.

Meigen, J.W. (1824) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten (Diptera Linn.)*. Volume 4. Dritter Theil. Schulz-Wundermann, Hamm, xii + 428 pp.

Moulton, J.K. & Wiegmann, B.M. (2004) Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution*, 31, 363–378.

Moulton, J.K. & Wiegmann, B.M. (2007) The phylogenetic relationships of flies in the superfamily Empidoidea (Insecta: Diptera). *Molecular Phylogenetics and Evolution*, 43, 701–713.

Pape, T., Blagoderov, V. & Mostovski, M.B. (2011) Order Diptera Linneaus, 1758. *In*: Zhang, Z.-Q., ed., Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 222-229.

Roháček, J. & Ševčik, J. (2007) Faunistic records from Czech Republic and Slovakia: Platypezidae. *Acta Zoologica Universitatis Comenianae*, 47, 1–256.

Roháček, J. & Ševčik, J. (2011) The fauna of Opetiidae and Platypezidae (Diptera) in the Gemer region (Central Slovakia). *Časopis Slezského Zemského Muzea, Série A – Vědy Přírodní* (Opava), 60, 41–47.

Rotheray, G.E., Chandler, P.J. & Gilbert, F. (2004) Final stage larvae and puparia of Platypezidae (Diptera). *Insect Systematics and Evolution*, 35, 79–106.

Shatalkin, A.I. (1980a) [New species of Platypezidae (Diptera) from Middle Amur Territory]. *Éntomologicheskoye Obozrenie*, 59, 660–665 (in Russian, English summary).

Shatalkin, A.I. (1980b) [Three new species of flies (Diptera, Platypezidae) from Amur district]. *Zoologicheskii Zhurnal*, 59, 1746–1748 (in Russian).

Shatalkin, A.I. (1981) [New species of flat-footed flies (Diptera, Platypezidae) in the entomofauna of the USSR]. *Byulleten moskovskoe Obshchestvo Ispytatelej Prirody, Biologicheskii*, 86, 57–61 (in Russian).

Shatalkin, A.I. (1982) [New species of flat-footed flies (Diptera, Platypezidae) from Siberia and the far east]. [*Helminths, Mites and Insects. New and Little-Known Species of the Siberian Fauna*], 16, 68–75 (in Russian).

Shatalkin, A.I. (1985) [A revision of the flat-footed flies (Diptera, Platypezidae) of USSR]. *Archives of Zoological Museum, Moscow State University*, 23, 69–136 (in Russian).

Shatalkin, A.I. (1992) New and little-known Palaearctic species of Platypezidae, Psilidae and Lauxaniidae (Diptera). *Russian Entomological Journal*, 1, 59–74.

Sinclair, B.J. & Cumming, J.M. (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa*, 1180, 1–172.

Smith, K.G.V. (1980) 36. Family Platypezidae. *In* Crosskey, R.W. (Ed.), *Catalogue of the Diptera of the Afrotropical Region*. British Museum (Natural History), London, pp. 480–482.

Snow, W.A. (1894) American Platypezidae. *Kansas University Quarterly*, 3, 143–152.

Snow, W.A. (1895) American Platypezidae. *Kansas University Quarterly*, 3, 206–207.

Tkoč, M. (2011) New records of *Polyporivora picta* (Meigen, 1830) from the Czech Republic and Greece with notes on its larval biology and distribution in Europe (Diptera: Platypezidae). *Časopis Slezského Zemského Muzea, Série A – Vědy Přírodní* (Opava), 60, 263–267.

Tkoč, M. (2012) A new species of the flat-footed fly genus *Callomyia* (Diptera: Platypezidae) from South China. *Acta Entomologica Musei Nationalis Pragae*, 52, 289–296.

Tkoč, M., Vaňhara, J. & Tóthová, A. (2010) Phylogeny of flat-footed flies (Diptera, Platypezidae) based on mitochondrial gene analyses. Unpublished poster and handout presented at 7th International Congress of Dipterology, San Jose, Costa Rica, August 2010.

Tkoč, M., Mocek, B. & Barták, M. (2012) New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Slovakia. *Klapalekiana*, 48, 269–274.

Tkoč, M. & Vaňhara, J. (2006) Faunistic Records: Diptera, Platypezidae, *Lindneromyia hungarica* Chandler, 2001. *Entomofauna Carpathica*, 18, 36.

Vaňhara, J. (1986) The flat-footed flies (Opetiidae and Platypezidae, Diptera) in a lowland forest. *Dipterologica Bohemoslovaca*, 4, 79–84.

Vaňhara, J. (1995) Recent distribution of flat-footed flies (Diptera: Opetiidae and Platypezidae) in Czech and Slovak Republics with a revised check list and species quality indexing. *Časopis Slezského Zemského Muzea, Série A – Vědy Přírodní* (Opava), 44, 43–61.

Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.-W., Lambkin, C., Bertone, M.A., Cassel, B.K., Bayless, K.M., Heimberge, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair, B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S.N., Schmidt-Ott, U., Kampmeier, G.E., Thompson, F.C., Grimaldi, D.A., Beckenbach, A.T., Courtney, G.W., Friedrich, M., Meier, R. & Yeates, D.K. (2011) Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 5690–5695.

Woodley, N.E., Borkent, A. & Wheeler, T.A. (2009) Phylogeny of the Diptera. *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, Volume 1, NRC Research Press, Ottawa, Ontario, Canada, pp. 79–94.

Yeates, D.K., Wiegmann, B.M., Courtney, G.W., Meier, R., Lambkin, C. & Pape, T. (2007) Phylogeny and systematics of Diptera: Two decades of progress and prospects. *Zootaxa*, 1668, 565–590.

Zatwarnicki, T. (1996) A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus*, 7, 103–175.

Zetterstedt, J.W. (1838) Dipterologia Scandinaviae – Sectio Tertia: Diptera, pp. 477–868. *Insecta Lapponica*, Lipsiae. vi + 1140 pp.

CONNECTING STATEMENT

Systematic studies on the immensely diverse order Diptera comprise an important area of research, as the group is rich in undescribed species and little is known about the diversity and evolutionary relationships of many of the included taxa. Taxonomic revisions of genera are fundamental to this area of research because they provide an understanding of the diversity within a given genus through species delimitation and comprehensive species identification tools. When a phylogenetic hypothesis of species relationships is included in a revision, the evolutionary history of the species is elucidated, allowing inferences to be made on biogeographic and ecological patterns pertaining to the group. There have been very few comprehensive Nearctic revisions of genera within the flat-footed fly family Platypezidae. The genus *Callomyia* was selected for study in the Nearctic Region because it exhibits many taxonomic problems within the region, compared to the better known Palaearctic members of the genus. In the next chapter, a Nearctic revision of the genus *Callomyia*, in conjunction with a phylogenetic analysis of the world species, provides a stable classification of the group on a worldwide basis. Sound systematic work on this genus, including proper identification tools, provides the essential foundation for future biodiversity, ecological, and behavioral studies involving *Callomyia* species in the Nearctic Region.

CHAPTER 2. NEARCTIC REVISION AND PHYLOGENY OF THE GENUS *CALLOMYIA* MEIGEN (DIPTERA: PLATYPEZIDAE)

ABSTRACT

The Nearctic fauna of the genus *Callomyia* Meigen is revised and a phylogeny of the world species, based on morphological characters, is presented. In this study, morphological data are used primarily to delimit species, combined with molecular sequence data (DNA barcodes) wherever possible, to help determine species boundaries and associate sexes. Species descriptions, diagnoses, and distribution maps are presented, along with illustrations of habitus, male terminalia, and additional important diagnostic characters. A key to the Nearctic species for both sexes is provided.

A total of ten species are recorded from the Nearctic Region including three new species: *C. argentea* Cumming **sp. nov.**, *C. arnaudi* Cumming **sp. nov.**, *C. bertae* Kessel, *C. browni* Cumming **sp. nov.**, *C. calla* Kessel, *C. corvina* Kessel, *C. gilloglyorum* Kessel, *C. proxima* Johnson, *C. velutina* Johnson, and *C. venusta* Snow. The female of *C. velutina* is recognized and described, and three new synonymies are proposed: *C. cleta* Kessel is a junior synonym of *C. calla* **syn. nov.**; *C. clara* Kessel is a junior synonym of *C. corvina* **syn. nov.**; and *C. liardia* Kessel & Buegler is a junior synonym of *C. proxima* **syn. nov.** Phylogenetic relationships within the genus are reconstructed. The genus is monophyletic based primarily on the setulose R_1 wing vein, female antennal size and three larval characters. The Nearctic species do not form a monophyletic group with respect to the Old World species.

Keywords: flat-footed flies, taxonomy, morphology, DNA barcodes, phylogenetic analysis, distribution, North America.

INTRODUCTION

The genus *Callomyia* Meigen (Diptera: Platypezidae) currently contains 21 described species that are distributed mainly in the Holarctic Region, except for two species from the Oriental Region. Currently there are ten Nearctic species (Kessel & Buegler 1972), five species from Europe (Chandler 2001), four species from Siberia and the Far East of Russia (Shatalkin 1980, 1982, 1992), one species from Nepal (Kessel 1966), and one recently described species from Yunnan, China (Tkoč 2012).

Members of this genus are relatively small sized flies (although average for Platypezidae), ranging in body length from 2.9–4.8 mm. They are typically dark brown to velvety black, displaying distinctive thoracic and abdominal colour patterns of metallic bluish-white, silver-blue, silver-grey, and yellow to orange (Fig. 1). Like many other species of Playpezidae, they exhibit pronounced sexual differences in colour, with males generally being much darker than females (Chandler 2001).

Callomyia belongs in the subfamily Callomyiinae, which contains six genera worldwide (Chandler & Shatalkin 1998). Within this subfamily, the genus appears to be monophyletic based on the following apomorphic characters: wing with setulose R_1 vein (Fig. 2) that is present in both sexes, larvae with the metathoracic and first abdominal segment fused and a double pair of uniquely plumose marginal processes on each segment (Fig. 3) (Chandler 2001). Additional characters that separate this genus from other platypezids are in the generic diagonis below.

The first taxonomic publication on *Callomyia*, and the first record of the genus, in the Nearctic Region was a description of a new species, *C. venusta* Snow, from New Mexico by Snow (1894). Johnson (1916) subsequently described two additional species from eastern North America. Kessel (1948, 1961a, 1961b) described six new species from western North America but did not include a species key. The last regional Nearctic revision of *Callomyia* was by Kessel & Buegler (1972), which included a description of a new widespread species. All of the Nearctic species of *Callomyia* were treated in that revision, including a key to the species for both sexes.

Despite these earlier studies, including Kessel & Buegler's (1972) revision, there are still many taxonomic problems within Nearctic *Callomyia*. The Nearctic species concepts are based primarily on adult colour with little supporting morphological information. Snow (1894) and Johnson (1916) described species from very few specimens and based their species descriptions completely on colour. Kessel (1948, 1961a, 1961b) expanded these species concepts only slightly and still based his descriptions largely on colour. Although Kessel & Buegler (1972) attempted to incorporate features of the male terminalia into some of their species concepts, it appears that they did not use this character system to determine species identities or delimit species boundaries. For example, their key to species was based entirely on colour and is difficult to interpret because many of the species appear to exhibit more intraspecific colour variation than indicated in their revision. Kessel & Buegler's (1972) inability to correlate colour variation with additional morphological variation (both intra and interspecifically) within Nearctic *Callomyia*, appears to have led to many inaccuracies in the taxonomy of this group.

Eight of the ten currently recognized Nearctic species were described from one sex only (five species only from males; three species only from females). This is probably due to the prevalence of sexual dimorphism in this group, making it difficult to associate the sexes of these species. Given that so many of these species are known from a single sex, it is reasonable to assume that there are a number of potential synonyms within the recognized Nearctic species of *Callomyia*.

Furthermore, species of *Callomyia*, like many other Platypezidae, are rarely collected and are poorly represented in collections. Most of the Nearctic specimens available for study were collected over many years by a single collector (E.L. Kessel), and many species are known from few specimens. This makes it difficult to assess intraspecific variation, and is also a challenge in obtaining fresh material for molecular analysis.

In view of these taxonomic problems, the purpose of this paper is to revise the Nearctic species of *Callomyia*. This will be accomplished by expanding and testing current species concepts, using both colour and additional morphological characters, in combination with molecular sequence data (DNA barcodes) wherever possible. All valid species will be redescribed, their geographic distribution mapped, and important diagnostic characters illustrated. A key to the Nearctic species will also be provided. In addition, a phylogenetic analysis of the world species of *Calloymia* will be conducted to confirm the monophyly of the genus and determine species relationships.

MATERIALS AND METHODS

Specimens of *Callomyia* were borrowed for study from the following institutions (including acronyms used in text): American Museum of Natural History, New York, NY, USA (AMNH); California Academy of Sciences, San Francisco, CA, USA (CAS); Canadian National Collection of Insects, Ottawa, ON, Canada (CNC); California State Collection of Arthropods, Sacramento, CA, USA (CSCA); Cornell University Insect Collection, Ithaca, NY, USA (CUIC); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); Natural History Museum of Los Angeles County, Los Angeles, CA, USA (LACM); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM); Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ); National Museum, Kunratice, Prague, Czech Republic (NMPC); University of Kansas National History Museum, Snow Entomological Museum, Lawrence, KS, USA (SEMC); National Museum of Natural History, Washington DC, USA (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK); Zoological Museum, Moscow State University, Moscow, Russia (ZMMU); Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMUC).

Label data for holotypes, lectotypes, and allotypes are cited verbatim and listed from the top downward. Data from each label are listed within quotation marks and a change in label is represented by a semicolon. Line breaks on labels are indicated with a slash (/) and additional information is given in square brackets. Label data for other specimens, including secondary types, are abridged and listed alphabetically (sorted by country, state/province).

Morphological terminology, including male terminalia, follows Cumming & Wood (2009). Male and female terminalia were removed from the specimen and cleared in hot 85% lactic acid. The lactic acid was heated in a microwave for three to four 15 second intervals, with each interval followed by a one to two minute cooling period. Cleared terminalia were placed in glycerin on a depression slide for examination and then stored in glycerin in gentialia vials that were pinned below the original specimen. Male terminalia were drawn with a Leica DMLB compound microscope equipped with a drawing tube. The genitalic figure is oriented with the anatomically dorsal parts directed towards the top of the page and the anatomically ventral parts directed towards the bottom of the page, following the platypezid figures in Sinclair and Cumming (2006, figs. 355–357).

Most photographs were taken with an INFINITY USB 2.0 camera attached to a Leica MZ125 dissecting microscope, using the Infinity Capture imaging software, and the resulting layers stacked using CombineZP. Additional photographs were taken with a Leica DFC 425C camera attached to a Leica dissecting microscope, using Leica Application Software (LAS), and the resulting layers stacked using Zerene Stacker (version 1.04Build T201303012035).

To provide additional evidence for species identity, especially in the case of sexually dimorphic species, 21 *Callomyia* specimens were submitted for barcoding to the Biodiversity Institute of Ontario in Guelph, ON, Canada. Specimens up to 30 years old were selected for submission. To obtain DNA barcodes (658 base pairs from the 5′ end of COI), a single leg was removed from each specimen and the DNA was extracted, amplified, purified and sequenced following the protocols given by Hajibabaei et al. (2005). The primers used in this study were: LCO1490 (hebF; 5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (hebR; 5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al.1994). COI sequence data were analyzed using a Neighbour-joining tree created in the Barcode of Life Data Systems (BOLD) (Ratnasingham & Hebert 2007). When building the Neighbour-joining tree, the BOLD Aligner (Amino Acid based HMM) was selected to align sequences using only specimens that produced a sequence length of ≥ 600 bp. This included 17 of the 21 sequenced *Callomyia* specimens and two outgroup specimens (Table 1). The remaining four specimens of *Callomyia* produced short sequence lengths (≤ 164 bp) and were not analyzed for study. The Neighbour-joining method was used to identify COI sequences that clustered together in the tree. COI sequences that clustered together with <2% genetic divergence were considered to belong to the same species (Hebert et al. 2003). These barcode sequences, along with additional data, including images of specimens, can be accessed through the Barcode of Life Data Systems (http://www.barcodinglife.org/) in the public project 'Callomyia Platypezidae [CNCPC]'. All successful COI sequences were also deposited in GenBank (Table 1).

Thirty-two characters were included in the phylogenetic analysis, including 18 binary and 14 multistate characters (see character list under "Phylogenetic analysis of *Callomyia* species relationships"). All characters, including multistate characters, were equally weighted and treated as unordered. Characters were scored for 19 ingroup taxa and four outgroup taxa. Ingroup taxa consisted of all of the world species of *Callomyia*, except *Callomyia coei* Kessel and *Callomyia triangulata* Tkoč, which were examined but not included in the analysis. These two species were excluded because they are only known from females and the analysis was largely based on male characters, which would have resulted in many missing character states. The four outgroup taxa selected for the analysis were single exemplar species from the platypezid subfamilies Melanderomyiinae (*Melanderomyia kahli* Kessel) and Callomyiinae (*Grossoseta johnsoni* (Kessel), *Agathomyia antennata* (Zetterstedt), and *Bertamyia notata* (Loew)). Character polarity was determined by rooting the tree with the four outgroups, which together were constrained to be paraphyletic in relation to the ingroup. Parsimony analysis of the character state matrix (Table 2) was performed using PAUP* version 4.0b10 (Swofford 2002). A heuristic search with stepwise addition was conducted to find the most parsimonious trees using random addition sequence of taxa, tree-bisection-reconnection (TBR) branch swapping, and 1000 random replications. Once the heuristic search was completed, the trees were condensed by collapsing branches if the minimum branch length was equal to zero. *A posteriori* character weighting was implemented using successive approximations according to the rescaled consistency index (RC). Tree statistics such as consistency index (CI), retention index (RI), and rescaled consistency index (RC) were used to assess the fit of data to the cladograms. Bremer support (Br) values (Bremer 1994) were determined for the branches supported in all of the equally parsimonious trees using TreeRot version 2c (Sorenson 1999). Character state distribution was examined using MacClade version 4 (Maddison & Maddison 2003).

SYSTEMATICS

Callomyia Meigen

Cleona Meigen, 1800: 30. Type species: *Callomyia elegans* Meigen (Coquillett, 1910: 525). Suppressed by International Commission of Zoological Nomenclature, 1963: 339.

Callomyia Meigen, 1804: 311. Type species: *Callomyia elegans* Meigen (monotypy).

Heteroneura Fallén, 1810: 7, 25. Type species: *Heteroneura leptiformis* Fallén, 1810 (= *Callomyia elegans* Meigen, 1804).

Callomyza Fallén, 1815: 6, unjustified emendation.

Callimyia Agassiz, 1846: 59, unjustified emendation.

Callimyza Agassiz, 1846: 59, unjustified emendation.
Calomyia Roser, 1840: 55, unjustified emendation.

Diagnosis.

This genus and the other genera of Callomyiinae (*Agathomyia* Verrall, *Bertamyia* Kessel, *Chydaeopeza* Shatalkin, *Grossoseta* Kessel & Kirby, *Platypezina* Wahlgren), are distinguished from the large subfamily Platypezinae by the following characters: uniserial median row of acrostichal setae (versus acrostichals absent); hind tarsomere 1 elongate, at least as long as tarsomeres 2−4 combined; soles on hind tarsus much less developed and unflattened; body more elongate and slender; male with strong posteroventral seta ('oxhorn' or 'safety-pin' seta) at base of forefemur (absent in *Platypezina*); male with posteroventral seta at base of hind femur (absent in *Bertamyia* and positioned ventrally in *Platypezina*); larva with ground plan of eight processes per segment (versus ground plan of six processes per segment) (Kessel & Buegler 1972; Chandler & Shatalkin 1998; Chandler 2001; Chandler 2010).

The most obvious distinguishing adult characteristic of *Callomyia* is wing vein R_1 bearing a dorsal series of short setulae along most of its length (Fig. 2) (Kessel & Buegler 1972). *Callomyia admirabilis* Shatalkin lacks this character, but belongs in *Callomyia* on the basis of other diagnostic features of the larva and male terminalia (Shatalkin 1980; Chandler 2001). *Callomyia* is also characterized by the following unique larval features: body oval and dorsoventrally flattened; metathoracic and first abdominal segments fused; plumose marginal processes duplicated on each segment, with four processes on each side of the anterior dorsal segment (segment 2), the fused segment (segments 3+4), and the posterior dorsal segment (segment 11) (Fig. 3) (Chandler 2001).

Callomyia also differs from *Grossoseta* and *Platypezina* by having wing vein M_{1+2} unbranched (Fig. 2) (Kessel & Maggioncalda 1968). Furthermore, the phallus of *Callomyia* is short, wide and laterally compressed, with two parallel apically hooked sclerites (e.g., Fig. 55), whereas the phallus of *Grossoseta* and *Platypezina* is long and coiled (Chandler 2001).

Callomyia, *Agathomyia*, *Chydaeopeza*, and *Bertamyia* are characterized together by the following features: wing vein M_{1+2} unbranched, pterostigma mainly absent, head setation reduced, phallus short and apically hooked (Chandler 2001). However, *Callomyia* differs from these three genera (in addition to the setulose R_1 vein and diagnostic larval characters mentioned above) by having two apical spurs (anteroventral and posteroventral) on the midtibia, instead of usually only one (posteroventral spur) (Chandler 2001). In addition, the posteroventral seta at the base of the hind femur is apically tapered in *Callomyia*, but is blunt in *Agathomyia* and absent in *Bertamyia*. The postsutural supra-alar seta on the thorax, which is present in *Callomyia*, is also absent in *Bertamyia* (Kessel 1987).

Description.

Male. Body length 3.35–4.8 mm. Head holoptic with eyes bare, facets enlarged dorsally. Ocelli on raised tubercle, with 2 pairs of ocellar setae, anterior pair longer. One pair of paravertical setae and row of shorter postocular setae; postgena and posterior portion of gena with numerous long setae; anterior portion of gena and face bare; frons with pair of short frontal setae. Mouthparts short; palpus narrow. Antenna with scape and pedicel short, subequal to or shorter than length of first flagellomere; scape with preapical seta; pedicel with circlet of small to long setae, dorsal setae longest; first flagellomere short-oval (Fig. 41) to elongate-conical (Fig. 42); arista long, terminal, with 2 short basal aristomeres.

Thorax dark brown to velvety black often with silver-grey or silver-blue dusting (formed by tomentum), and silver-grey, silver-blue or metallic bluish-white markings on mesonotum and/or pleura. Proepisternum with 2–4 upper setae and 1 lower seta. Postpronotal lobe with 2–3 setae. Scutum with 6–10 acrostichal setae; 9–14 dorsocentral setae, posterior 3–4 longest; 4–5 presutural intra-alar setae in transverse row (posthumerals); 2–3 presutural intra-alar setae (posterior seta longest); 2–3 postsutural intra-alar setae; 5–8 notopleural setae, anterior seta and posterior 2 setae longest; 1 postsutural supra-alar seta; 1 postalar seta. Scutellum with lateral and apical pair of setae, apical pair longest.

Legs pale yellow to dark brown, hind leg and apical tarsomeres usually darker. Foreleg: coxa with several long setae on anterior and apical surface; femur with strong posteroventral (oxhorn) seta near base, longer than posteroventral row of setae, posterodorsal surface with long setae; tibia with anterior and posterior preapical setae, tarsomere 1 with long posteroventral hair-like setae. Midleg: coxa with several long setae on anterior and apical surface; femur with anteroventral notch at apical quarter, one anteroventral preapical seta; tibia with long median dorsal seta (Fig. 50) and shorter median anterodorsal seta sometimes present above it (Fig. 49), short anterodorsal and posterodorsal preapical setae present, two ventral apical spurs present with posteroventral spur longest. Hind leg: coxa with several long setae on lateral and apical surface; femur with row of long dorsal setae and row of shorter anteroventral setae, distinct apically tapered posteroventral seta at base (Figs 53, 54); tibia clavate with several strong anterodorsal setae; tarsomere 1 broadly cylindrical and slightly compressed (slightly narrower, subequal or slightly broader than apical width of tibia), with several strong short ventral setae; tarsomeres 2–5 narrower than tarsomere 1.

Wing hyaline (Fig. 47) to yellowish-brown tinted (Fig. 48) with cell sc usually more opaque; membrane uniformly covered with microtrichia, sparse on basal cells (c, br, bm, cu*p*). Vein R_1 with dorsal series of 9–19 short setulae beneath expanded portion of cell sc (setulae absent in *C. admirabilis*); plane of crossvein r–m approximately level with middle of cell c; M_{1+2} unbranched; crossvein dm–cu longer than its distance from wing margin along CuA_1; cell cu*p* elongate and tapered apically, 2 to 3X length of A_1+CuA_2. Halter yellow to dark brown with stem darker in some species.

Abdomen dark brown to velvety black in most species (mainly yellow in *C. browni* **sp. nov.**), with distinctive patterns of metallic bluish-white, silver-blue, silver-grey, brownish-yellow or yellow markings of variable extent in each species. Setae dark, long and thin on tergites 1–3, strong on tergite 6.

Terminalia yellow to grey with surstylus brown to black. Epandrium with strong ventroapical setae; ventral lobe minute, short or moderately long; apical process short to elongate and broad, rounded or pointed at apex. Surstylus broadly lamellate with narrow ventral process (Fig. 56), bifid with outer and inner process (Fig. 57), or molar-like with 2 large cusps (Fig. 55). Hypandrium rectangular with strong ventral setae; moderately long to elongate slender apical process; process trifid (Fig. 56), bifid (Fig. 57) or simple (Fig. 60), usually with preapical setae. Postgonite very long and narrow to long and wide; apex pointed, rounded or truncate. Phallus wide, short, laterally compressed, curved ventrally, sharp or bluntly hooked at apex. Cercus and hypoproct fleshy and thinly sclerotized, setulose.

Female. Body length 2.9–4.6 mm. Head dichoptic with eyes virtually bare, facets of equal size. Ocelli on slightly raised tubercle, with 2 pairs of ocellar setae, anterior pair elongate. One pair of lateroclinate orbital setae; one pair of long lateroclinate outer vertical setae; one pair of long paravertical setae and row of shorter postocular setae; postgena and posterior portion of gena with numerous long setae; anterior portion of gena and face bare; frons with 1–2 pairs of short frontal setae. Mouthparts short; palpus slightly broadened apically. Antenna with scape and pedicel short, subequal to or shorter than length of first flagellomere; scape with preapical seta; pedicel with circlet of small to long setae; first flagellomere short-oval (Fig. 43) to subtriangular (Fig. 44), elongate-conical in *C. dives* Zetterstedt; arista long, terminal, with 2 short basal aristomeres.

Thorax pale yellow to brownish-yellow, silver-grey, or brown to velvety black, often with silver-white, silver-grey or silver-blue dusting (formed by tomentum); usually with silver-blue or metallic bluish-white markings on mesonotum and/or pleura. Chaetotaxy as in male, except dorsocentral setae with posterior 2–3 longest, 2–4 presutural intra-alar setae and 5–6 notopleural setae.

Legs pale yellow to brown, hind leg and apical tarsomeres usually darker. Foreleg: coxa with several long setae on anterior and apical surface; femur without strong posteroventral (oxhorn) seta near base, posteroventral row of setae short, posterodorsal surface with short setae; tibia with short anterior and posterior preapical setae, tarsomere 1 with posteroventral hair-like setae. Midleg: coxa with several long setae on anterior and apical surface; femur without anteroventral notch at apical quarter, anteroventral preapical seta weak; tibia with short (Fig. 52) to long (Fig. 51) median dorsal seta present in most species, preapical setae indistinct, two ventral apical spurs present with posteroventral spur longest. Hind leg: coxa with several long setae on anterior and apical surface; femur with short to long setae on dorsal surface and row of short anteroventral setae (apical seta longest), without distinct apically tapered posteroventral seta at base; tibia slightly clavate with short to long anterodorsal setae; tarsomere 1 cylindrical and slightly compressed (subequal or slightly narrower than apical width of tibia), with several strong short ventral setae; tarsomeres 2–5 subequal to width of tarsomere 1.

Wing hyaline to yellow tinted (apical half yellowish-brown tinted in *C. sonora* Shatalkin), with cell sc usually more opaque; membrane uniformly covered with microtrichia, sparse on basal cells. Venation as in male. Halter pale yellow to brown.

Abdomen with distinctive pattern in each species of contrasting black and yellow, orange, silver-grey, silver-blue, silver-yellow, or silver-white markings (abdomen mainly yellow in *C. calla* Kessel). Setae dark, long and thin on tergites 1–2, stronger on segments 5–7; sternite 6 with 2–3 pairs of stout medial setae (anterior pair more closely approximated).

Terminalia pale yellow to dark brown, silver-grey, or metallic bluish-white. Segment 8 short and broad, setulose. Proctiger with epiproct pointed; hypoproct broad, flat and rounded posteriorly; cercus oval. Spermathecae spherical, pigmented.

Immatures.

The larvae (Fig. 3) and puparia of *Callomyia* (puparium identical in shape to full-grown larva) are distinct from other platypezid genera. They differ by having a broad oval and dorsoventrally flattened body that has 9 segments visible in dorsal view (instead of 10 in all other platypezid genera (Chandler & Shatalkin 1998)), due to fusion of the metathoracic and first abdominal segments (3+4). Each segment has intricately shaped marginal processes that are arranged as follows: segment 2, 3+4, and 11 with four processes on each side, and the intervening segments with two processes on each side. These processes are elongate and pointed, and have lateral projections that give them a plumose appearance (Kessel 1961b; Chandler 2001; Krivosheina 2008b). All known larvae (length 2–5 mm) are white initially, becoming pale grey to dark grey upon maturity (Kessel 1961b; Chandler 2001).

The species of *Callomyia* that are known from the immature stages are *C. admirabilis*, *C. amoena* Meigen, *C. dives* (M. Tkoč pers. comm.), *C. gilloglyorum* Kessel, *C. krivosheinae* Shatalkin, and *C. speciosa* Meigen (see Kessel 1961b; Kessel et al. 1973; Chandler & Shatalkin 1998, Chandler 2001, Krivosheina 2008b).

Biology.

The known larvae of *Callomyia* are mycophagous, like all other platypezid larvae, and develop on Basidiomycota fungi that grow on decaying wood (Kessel & Clopton 1969; Chandler 1991; Krivosheina 2008b; Tkoč et al. 2012). *Callomyia* larvae are surface feeders on fungi, feeding on moist mycelium encrusted substrates (Chandler & Shatalkin 1998; Chandler 2001; Krivosheina 2008a). Only a few species of this genus are known from the immature stages and little is known about their host associations, with the majority of information coming from European studies. Kessel (1961b) recorded and described the immature stages and biology of *C. gilloglyorum*, the only known immatures of Nearctic *Callomyia*. The larvae were found on white mycelia under the bark of a fallen pine tree (*Pinus* sp.). Unfortunately, the fungus species was not identified so nothing more is known about the host association. A few Palaearctic species of

Callomyia are known from the immature stages. The larvae of *C. admirabilis*, *C. amoena* and *C. speciosa* have been found on mycelia on decaying trunks or branches of deciduous trees lying on the ground (Lundbeck 1927; Krivosheina & Mamaev 1967; Krivosheina 2008b). *Callomyia krivosheinae* larvae were discovered developing under the bark of a cedar stump, in white mould (Krivosheina 2008b). The larvae of an unidentified European species of *Callomyia* were found on the fruiting body of *Corticium,* an encrusting fungus on fallen trunks and branches (Lundbeck 1927; Chandler & Shatalkin 1998).

The life cycles of *Callomyia* species are unknown. Larvae of *C. gilloglyorum* were collected on 1 May 1954, and adults emerged on 15 August, 1 November and 9 November of that year (Kessel 1961b). These records appear to indicate a long developmental time for the immature stages of this species.

Adults of *Callomyia* occur in shaded woods and can be found where filtered sunlight penetrates the forest (Kessel & Kessel 1962; Kessel & Buelger 1972). Like other platypezids, they have been observed in damp wooded areas on understory vegetation close to streams or rivers (Kessel 1987; Tkoč et al. 2012).

Adults of this genus do not run around erratically on broad leaves, a behavior typically displayed by most other platypezids (especially in the subfamily Platypezinae), but instead walk slowly on leaves, evidently feeding on honeydew and other surface deposits (Chandler & Shatalkin 1998; Chandler 2001). Adults have also been observed hovering in the air, appearing almost motionless (Kessel & Buelger 1972). Like all other platypezids observed, males of *Callomyia* species form aerial mating swarms, usually under trees, often using a clearing in the forest canopy as a marker, where they 'dance' to attract females (Kessel & Buegler 1972; Kessel 1987; Chandler 1991).

Key to males of *Callomyia* species in North America

1. Abdomen with yellow or brownish-yellow markings, silver-blue markings if present restricted to tergite 5 ... 2

\- Abdomen dark brown to black, without yellow or brownish-yellow markings, usually with silver-grey, silver bluish-grey, silver-blue or metallic bluish-white markings ... 4

2. Yellow markings on abdomen more brownish-yellow (Figs 9, 19); tergite 5 without silver-blue markings; hind tarsomere 1 long and narrow, slightly narrower than apical width of hind tibia; hypandrial process with long finger-like basoventral lobe (Fig. 59) ... *C. calla* Kessel

\- Yellow markings on abdomen yellow to bright yellow (Figs 7, 14, 18, 24); tergite 5 usually with lateral to anterolateral silver-blue markings (Figs 7, 14); hind tarsomere 1 thicker, subequal to or slightly broader than apical width of hind tibia; hypandrial process with shorter basoventral lobe (Figs 58, 64) ... 3

3. Lemon yellow markings on abdominal tergites 1–4 (Figs 7, 18); sternite 8 yellow; hind tarsomere 1 length approximately 2X width, slightly broader than apical width of hind tibia; molar-like surstylus in posterior view with ventral inner cusp broadly truncate medially (Fig. 66) ... *C. browni* Cumming **sp. nov.**

\- Yellow markings only on abdominal tergites 1–3 (Figs 14, 24), sometimes only on tergites 1–2; sternite 8 brown to grey; hind tarsomere 1 length approximately 2.5X width, subequal to apical width of hind tibia; molar-like surstylus in posterior view with ventral inner cusp more narrowly truncate medially (Fig. 69) ... *C. venusta* Snow

4. Thorax partially dark brown to black with metallic bluish-white or silver-blue markings on lateral portion of presutural scutum and most of postsutural scutum (Figs 5, 8, 16, 17); abdominal markings more blue, either metallic bluish-white or silver-blue (Figs 5, 6, 8) ... 5

\- Thorax mainly dark brown to black, sometimes with silver-grey dusting on scutum (Figs 15, 20–23); abdominal markings more silvery, either silver-grey or silver bluish-grey (Figs 4, 10–13) (sometimes indistinct) ... 6

5. Metallic bluish-white markings on abdominal tergites 1–4 and 6 (Figs 5, 6); legs mainly brown (Fig. 5); halter dark brown; surstylus broadly lamellate with narrow ventral process, hypandrial process trifid (Fig. 56) ... *C. arnaudi* Cumming **sp. nov.**

- Silver-blue markings only on abdominal tergites 1–4 (Fig. 8); legs mainly pale yellow with hind leg darker (Figs 8, 17); halter yellowish-orange; surstylus bifid with long outer and inner processes, hypandrial process bifid (Fig. 57) ... *C. bertae* Kessel

6. Abdomen primarily dark brown to black with silver-grey markings (when present) restricted to tergites 1 and 2 or tergites 3 and 4 (Figs 12, 13) ... 7

- Abdomen partially dark brown to black with more extensive silver-grey or silver bluish-grey markings on at least tergites 1–5 (Figs 4, 10, 11) ... 8

7. Midtibia with median anterodorsal seta usually present above median dorsal seta (Fig. 49); abdomen usually with posterolateral to posteroventral silver-grey markings on tergites 3 and 4 (Fig. 12); surstylus bifid with long outer and inner processes, hypandrial process bifid (Fig. 62) ... *C. proxima* Johnson

- Midtibia with median anterodorsal seta absent, only median dorsal seta present (Fig. 50); abdomen with lateral silver-grey dusting on tergites 1 and 2 (rarely absent), sometimes extending to tergites 3 and 4 (Fig. 13); surstylus molar-like, hypandrial process trifid (Fig. 63) ... *C. velutina* Johnson

8. Wing clear (Fig. 47); base of hind femur with strong stout posteroventral seta (Fig. 53); surstylus molar-like (Fig. 55) ... *C. argentea* Cumming **sp. nov.**

- Wing yellowish-brown tinted (Fig. 48); base of hind femur with long thin posteroventral seta (Fig. 54); surstylus broadly lamellate with narrow ventral process (Figs 60, 61) ... 9

9. Halter brown to dark brown; silver markings on abdomen silver-grey (Fig. 11); antenna with first flagellomere elongate-conical (Fig. 42); scutum with 7–8 notopleural setae; midtibia with median anterodorsal seta absent, only median dorsal seta present (see Fig. 50); hypandrial process trifid, with 2 apical projections and 1 basoventral lobe (Fig. 61); epandrial apical process elongate and pointed (Fig. 61); epandrial ventral lobe short and broad (Fig. 61) ... *C. gilloglyorum* Kessel

- Halter orange; silver markings on abdomen more silver bluish-grey (Fig. 10); antenna with first flagellomere short-oval (see Fig. 41); scutum with 6 notopleural setae; midtibia with median anterodorsal seta usually present above median dorsal seta (see Fig. 49); hypandrial process simple, without projections (Fig. 60); epandrial apical process short and broad (Fig. 60); epandrial ventral lobe long and narrow, curved posteriorly (Fig. 60) ... *C. corvina* Kessel

Key to females of *Callomyia* species in North America

This key does not include *C. argentea*, *C. bertae* and *C. browni*, as females of these species are unknown.

1. Antenna with first flagellomere subtriangular (Fig. 44); abdomen with alternate black and silver-grey markings (Fig. 37) ... *C. gilloglyorum* Kessel

\- Antenna with first flagellomere short-oval (Fig. 43); abdomen with yellow, pale orange, metallic bluish-white and/or silver-blue markings (Figs 33, 35, 36, 38–40) ... 2

2. Abdomen entirely yellow (sometimes more brownish-yellow or brownish-orange) (Figs 27, 35) ... *C. calla* Kessel

\- Abdomen darker, never entirely one colour, with yellow, pale orange, metallic bluish-white and/or silver-blue markings (Figs 33, 36, 38–40) ... 3

3. Thorax mainly silver-blue dusted with black median dorsal stripe on scutum (Figs 28, 36) ... *C. corvina* Kessel

\- Thorax mainly brown to black with metallic bluish-white or silver-blue markings on lateral portion of presutural scutum, notopleuron and most of postsutural scutum (Figs 25, 30–32, 33, 38–40) ... 4

4. Abdominal tergites 1 and 2 pale orange with silver-white dusting, tergite 6 metallic bluish-white (Fig. 33); halter pale orange; legs mainly brown (Fig. 25) ... *C. arnaudi* Cumming **sp. nov.**

- Abdominal tergites 1, 2 and sometimes 3 yellow, tergite 5 or 6 silver-blue (Figs 38–40); halter yellow; legs mainly yellow to yellowish-brown with hind leg darker (Figs 30–32) ... 5

5. Abdomen with only tergites 1 and 2 yellow (both interrupted by median dorsal dark band) (Fig. 38); tergite 5 black and tergite 6 silver-blue; midtibia with long median dorsal seta (Fig. 51) ... *C. proxima* Johnson

- Abdomen with tergites 1–3 entirely yellow (Figs 39, 40); tergite 5 silver-blue and tergite 6 black; midtibia with median dorsal seta short (Fig. 52) or absent ... 6

6. Abdomen with silver-blue on tergite 5 interrupted by median dorsal dark band (Fig. 39) (sometimes partially interrupted); scutum with 2–3 presutural intra-alar setae, 3 at least on one side (Fig. 45); midtibia usually with short median dorsal seta (Fig. 52) ... *C. velutina* Johnson

- Abdomen with tergite 5 entirely silver-blue (Fig. 40); scutum with only 2 presutural intra-alar setae (Fig. 46); midtibia with median dorsal seta absent ... *C. venusta* Snow

Species descriptions

Callomyia argentea Cumming sp. nov.

(Figs 4, 15, 47, 53, 55, 65, 70)

Diagnosis.

This western Nearctic species is characterized by silver-grey markings on abdominal tergites 1−5 and male terminalia with a molar-like surstylus. *Callomyia argentea* is similar in appearance to the western Nearctic species *C. corvina* and *C. gilloglyorum* because of its similar abdominal colour pattern, but can be distinguished from these species by its molar-like surstylus (versus broadly lamellate surstylus), hyaline wings (versus yellowish-brown tinted wings), and stronger stouter posteroventral seta on the base of the hind femur. *Callomyia argentea* has similar male terminalia to *C. velutina* from eastern and western North America, but its terminalia differ by a ventral inner surstylus cusp that is more extended and rounded in lateral view and truncate in posterior view (versus more pointed in lateral view and narrowly truncate in posterior view), a postgonite that is truncate apically (versus rounded apically), and a phallus that is gradually hooked towards the apex (versus a sharp extended hook apically).

Description.

Male. (Figs 4, 15) Body length 3.7–4.2 mm. Head dark silver-grey; mouthparts brownish-yellow to brown with palpus brown to dark brown; antenna with scape, pedicel, first flagellomere and arista dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax mainly dark brown to black, velvety black in some specimens; notopleuron and supra-alar area of scutum silver-grey dusted in some specimens; propleuron, mesopleuron and metapleuron mainly silver-grey dusted; mediotergite and laterotergite silver-grey dusted. Scutum with 6 notopleural setae.

Legs light brown to brown, hind leg darker with tibia and tarsomeres dark brown. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with strong stout posteroventral seta (Fig. 53). Hind tarsomere 1 slightly expanded, subequal to apical width of hind tibia, length approximately 2.5X width.

Wing hyaline (Fig. 47) with cell sc faintly yellow, whitish in some specimens. Halter with stem brown; knob orange, yellow in some specimens.

Abdomen dark brown to black with lateral silver-grey markings on tergites 1 and 2; ventrolateral silver-grey markings on tergites 3–5; tergite 6 silver-grey dusted; tergite 7 entirely grey; sternites light brown, sternite 8 grey.

Terminalia (Figs 55, 65) with epandrium grey; surstylus black; hypandrium brown; hypandrial process and cercus brownish-yellow. Epandrium with short broad ventral lobe, rounded at apex; apical process moderately long, pointed at apex. Surstylus molar-like, with 2 large cusps moderately excavated in between; dorsal outer cusp broadly rounded in lateral view; ventral inner cusp narrow and extended, rounded at apex in lateral view, truncate and minutely serrate medially in posterior view (Fig. 65). Hypandrium with moderately long apical process; process trifid, with 2 short apical projections and short broad triangular basoventral lobe. Postgonite long, slightly expanded apically, truncate at apex. Phallus gradually hooked towards apex. Cercus short.

Female. Unknown.

Type material.

HOLOTYPE, ♂ labelled: “SilverLake/ MonoCo. Cal./ VI.19.61”; “T 86°/ 12:45/ FC 50/ RH24%/ E7200”; “ E.L. Kessel/ Collector”; “Callomyia/ velutina/ Johnson/ Det.Kessel”; “HOLOTYPE ♂/ *Callomyia argentea*/ H.J. Cumming [red label]” [dissected] (CAS). **PARATYPES: CANADA: BRITISH COLUMBIA:** Kleanza Creek Province Camp Ground, Highway 16, 31.vii.1962, E. L. Kessel (1 ♂, CAS); **USA: CALIFORNIA:** Donner Summit, 2227m, 16.viii.1999, 39°20.55’N120°20.44’W, sweep vegetation, J. Savage (1 ♂, LEM); Mono County, Silver Lake, 19.vi.1961, E. L. Kessel (1 ♂, CAS); **OREGON:** Lake County, Drews Creek at Highway 66, 21.ix.1963, E. L. Kessel (1 ♂, CAS); Umatilla County, Woodward Forest Camp, Highway 204, 25.viii.1962, E. L. Kessel (2 ♂, CAS).

Geographical distribution and seasonal occurrence (Fig. 70).

Callomyia argentea is currently known from western North America (British Columbia, Oregon and California). Adults have been collected from late June to late September.

Etymology.

This species name is derived from the Latin *argentea* for silvery, in reference to this species’ similar appearance to *C. velutina*, but with more silver on the abdomen.

Callomyia arnaudi Cumming sp. nov.

(Figs 5, 6, 16, 23, 33, 56, 71)

Diagnosis.

This southwestern Nearctic species is characterized by striking metallic bluish-white colour on the thorax and abdomen, and male terminalia with a broadly lamellate surstylus. The male is similar to the southwestern Nearctic species *C. bertae*, except for differences in colour and terminalia that are indicated in the key to species. *Callomyia arnaudi* has similar male terminalia to the western Nearctic species *C. gilloglyorum*, but the ventral process of the broadly lamellate surstylus is shorter in *C. arnaudi*, as well as the apical projections and basoventral lobe of the hypandrial process. The female of *C. arnaudi* is similar to *C. velutina*, from eastern and western North America, because of its similar thoracic and abdominal colour pattern, but can be distinguished from this species by differences in colour (metallic bluish-white versus silver-blue, and pale orange on tergites 1 and 2 versus yellow on tergites 1–3). Also, the coloured abdominal segment interrupted by a median dorsal dark band occurs on tergite 4 in *C. arnaudi* as opposed to tergite 5 in *C. velutina*.

Description.

Male. (Figs 5, 6, 16) Body length 3.35 mm. Head metallic bluish-white; mouthparts including palpus brownish-yellow; antenna with scape, pedicel, first flagellomere and arista dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax dark brown to black with metallic bluish-white markings on lateral portion of presutural scutum, notopleuron, posterior portion of postsutural scutum, postalar callus, propleuron, mesopleuron, metapleuron, mediotergite and laterotergite; dark portion of presutural scutum silver-grey dusted. Scutum with 6 notopleural setae.

Legs brown with base of tibiae brownish-yellow; coxae metallic bluish-white dusted. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with long thin posteroventral seta (as in Fig. 54). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing hyaline with cell sc faintly yellow. Halter dark brown.

Abdomen dark brown to black with lateral metallic bluish-white markings on tergites 1, 2 and 6; ventrolateral metallic bluish-white markings on tergites 3 and 4; sternites metallic bluish-white dusted, sternite 8 metallic bluish-white.

Terminalia (Fig. 56) with epandrium metallic bluish-white; surstylus and hypandrium brown; cercus brownish-yellow. Epandrium with short tooth-like ventral lobe, pointed at apex; apical process elongate, pointed at apex. Surstylus broadly lamellate with narrow ventral process; dorsal lobe broad with rounded apex; ventral process moderately long, slightly curved dorsally. Hypandrium with elongate slender apical process; process trifid, with 2 moderately long narrow apical projections and short narrow basoventral lobe. Postgonite very long and narrow, tapered towards apex. Phallus sharply hooked at apex. Cercus short.

Female. (Figs 25, 33) Body length 3.0–3.2 mm. Head metallic bluish-white with dorsolateral portion of occiput bordering vertex reddish-brown; mouthparts brownish-yellow with palpus pale yellow; antenna with scape, pedicel, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (as in Fig. 43).

Thorax brown and silver-grey dusted, with metallic bluish-white markings on postpronotal lobe, lateral portion of presutural scutum, notopleuron, posterior portion of postsutural scutum, postalar callus, propleuron, mesopleuron, metapleuron, mediotergite and laterotergite; scutellum dark brown to black. Scutum with 2 presutural intra-alar setae.

Legs brown with trochanters, base and apex of femora, and base of tibiae brownish-yellow; coxae metallic bluish-white dusted. Midtibia with median dorsal seta absent.

Wing hyaline. Halter pale orange.

Abdomen dark brown to black with tergites 1 and 2 entirely pale orange and silver-white dusted; tergite 4 metallic bluish-white, interrupted by median dorsal dark band; tergites 6 and 7 entirely metallic bluish-white; sternites pale orange to light brown.

Terminalia with segment 8 metallic bluish-white; epiproct, hypoproct and cercus metallic bluish-white.

Type material.

HOLOTYPE, ♂ labelled: “USA: NEW MEXICO/ McKinleyCo. 4mi./ S. Fort Wingate/ 8000’ 9-VII-1966/ P.H.Arnaud, Jr.”; “PAUL H. ARNAUD, JR./ COLLECTION/ Gift to California/ Academy of Sciences/ SanFrancisco,CALIF.”; “HOLOTYPE ♂/ *Callomyia arnaudi*/ H.J. Cumming [red label]” [dissected] (CAS). **PARATYPES: USA: NEW MEXICO:** same data as holotype (1 ♀, CAS); same data as holotype except 10.vii.1966 (1 ♀, CAS).

Geographical distribution and seasonal occurrence (Fig. 71).

Callomyia arnaudi is only known from the type series collected four miles south of Fort Wingate in McKinley County, New Mexico, in early July.

Etymology.

This species is named after Dr. Paul. H. Arnaud Jr. of the California Academy of Sciences, who collected the type specimens.

Remarks.

Callomyia arnaudi is closely related to the Nearctic species *C. gilloglyorum* and the Palaearctic species *C. dives* and *C. saibhira* Chandler, as shown in the strict consensus tree (Fig. 79). The male terminalia of *C. arnaudi* are most similar to the terminalia of *C. saibhira* (comparison based on description and figures of *C. saibhira* in Chandler (2001, figs 238−240). However, the thoracic and abdominal colour patterns and shape of the hypandrial process differ between these two species.

Callomyia bertae **Kessel**

(Figs 8, 17, 26, 34, 57, 71)

Callomyia bertae Kessel, 1961a: 193. Type locality: Pinos Altos Mountains, New Mexico, USA.

Diagnosis.

This southwestern Nearctic species is characterized by its silver-blue thoracic and abdominal markings and male terminalia with a bifid surstylus. *Callomyia bertae* is most similar in colour to the southwestern Nearctic species *C. arnaudi*, but can be distinguished from this species by a different pattern of silver-blue markings on the abdomen, paler legs and a paler halter colour, and differences in the male terminalia that are indicated in the key to species. The male terminalia of *C. bertae* are similar to those of *C. proxima* from eastern and western North America, but are yellow with a dark brown surstylus (versus brown to grey with a dark brown to black surstylus) and have a longer dorsal projection on the hypandrial process.

Redescription.

Male. (Figs 8, 17) Body length 3.5 mm. Head dark silver-grey; mouthparts including palpus brownish-yellow; antenna with scape, pedicel, first flagellomere and arista dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax dark brown to black with silver-blue markings on lateral portion of presutural scutum, notopleuron, most of postsutural scutum, and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey dusted. Scutum with 5 notopleural setae.

Legs pale yellow with fore and mid tarsomeres 4 and 5 dark brown, hind leg darker with tibia and tarsomeres dark brown. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with long thin posteroventral seta (as in Fig. 54). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing hyaline. Halter yellowish-orange.

Abdomen black with dorsolateral silver-blue markings on tergites 1 and 2; posterolateral silver-blue markings on tergites 3 and 4; tergite 7 entirely light brown; sternites pale yellowish-brown, sternite 8 light brown.

Terminalia (Fig. 57) yellow, except surstylus dark brown. Epandrium with minute ventral lobe, barely apparent; apical process short, broad at apex. Surstylus bifid with long outer and inner process, both rounded at apex; outer process broader and longer; inner process narrower and shorter. Hypandrium with moderately long apical process; process bifid, with 2 apical projections; dorsal projection narrow and long, ventral projection broad and short. Postgonite long and moderately wide, somewhat truncated and slightly pointed at apex. Phallus sharply hooked at apex. Cercus short.

Female. Unknown.

Type material.

HOLOTYPE, ♂ labelled: “Pinos Altos/ Mts.,Grant/ Co.,N.M./ 8-28-51”; “E.L.Kessel/ Collector”; “HOLOTYPE/ Callomyia/ bertae/ Kessel [red label]”; “California Academy/ of Sciences/ Type No. 6452” [dissected, first flagellomere and arista missing from antenna] (CAS).

Geographical distribution and seasonal occurrence (Fig. 71).

Callomyia bertae is only known from the holotype collected from the Pinos Altos Mountains in Grant County, New Mexico, in late August.

Remarks.

Callomyia bertae is closely related to the Nearctic species *C. proxima* and the Palaearctic species *C. dorsimaculata* Shatalkin, *C. elegans*, and *C. sonora*, as shown in the strict consensus tree (Fig. 79).

A series of female specimens from Durango, Mexico (Fig. 71) are possibly conspecific with the male of *C. bertae*, based on similarities in colour. These females (Figs 26, 34) have similar metallic bluish-white thoracic and abdominal colour patterns to the females of *C. arnaudi* (which is similar to *C. bertae* – see "Diagnosis" above), but abdominal tergite 4 is entirely metallic bluish-white and is not interrupted by a median dorsal dark band. In addition, these potential *C. bertae* females are larger in size than the females of *C. arnaudi*. These females are also similar in appearance to the females of *C. gilloglyorum* because of similar thoracic and abdominal colour patterns. However, the colour of these potential *C. bertae* females is more metallic bluish-white than silver-grey and abdominal tergites 2, 4 and 6 are complete and not interrupted by a median dorsal dark band.

***Callomyia browni* Cumming sp. nov.**

(Figs 7, 18, 58, 66, 71)

Diagnosis.

This southwestern Nearctic species is characterized by striking lemon yellow colour on the abdomen and halter, an expanded hind tarsomere 1 that is slightly broader than the apical width of the hind tibia, and male terminalia with a molar-like surstylus. *Callomyia browni* is most similar to the widespread Nearctic species *C. venusta*, but can be distinguished by its lemon yellow markings on abdominal tergites 1–4 (versus yellow markings only on tergites 1–3, or even further reduced), yellow colour on sternite 8 (versus brownish-grey colour), strong stout posteroventral seta on the base of the hind femur (versus a somewhat longer and thinner posteroventral seta), broader hind tarsomere 1, two large very widely excavated surstylus cusps (versus less widely excavated), and a ventral inner surstylus cusp that is broadly truncate in posterior view (versus more narrowly truncate).

Description.

Male. (Figs 7, 18) Body length 4.1 mm. Head brownish grey with silver-blue reflections; face brownish-yellow ventrally; gena and postgena brown; mouthparts including palpus yellow; antenna with scape and pedicel brownish-yellow, first flagellomere and arista brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax black with silver-blue to silver-brown markings on postpronotal lobe, lateral portion of presutural scutum, notopleuron, postalar callus, propleuron, mesopleuron and metapleuron; posterior portion of postsutural scutum silver-blue; mediotergite and laterotergite silver-brown. Scutum with 6 notopleural setae.

Legs pale yellow with fore and mid tarsomeres 4 and 5 yellowish-brown, hind leg darker with apex of femur, tibia and tarsomeres brown. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with strong stout posteroventral seta (as in Fig. 53). Hind tarsomere 1 expanded, slightly broader than apical width of hind tibia, length approximately 2X width.

Wing hyaline with cell sc bluish-white. Halter lemon yellow with base of stem brown.

Abdomen with tergites 1–3 entirely lemon yellow; tergite 4 pale yellow, interrupted by median dorsal brown band extending posteriolaterally; tergite 5 dark brown with anterolateral silver-blue marking; tergite 6 and 7 entirely dark brown; sternites white, sternite 8 pale yellow.

Terminalia (Figs 58, 66) with epandrium and hypandrium brown; surstylus dark brown; hypandrial process and cercus brownish-yellow. Epandrium with short broad ventral lobe, rounded at apex, slightly anteriorly directly; apical process moderately long, broad basally, pointed at apex. Surstylus molar-like, with 2 large cusps very widely excavated in between; dorsal outer cusp broadly rounded in lateral view; ventral inner cusp rounded in lateral view, broadly truncate and minutely serrate medially in posterior view (Fig. 66). Hypandrium with moderately long apical process; process trifid, with 2 minute apical projections and small basoventral lobe. Postgonite long and widened toward apex, somewhat truncated and pointed at apex. Phallus with sharp extended hook at apex. Cercus short.

Female. Unknown.

Type material.

HOLOTYPE, ♂ labelled: “USA : NM. Catron Co. 2.4km/ W Luna. 7-8.VII.1987/ B.V.Brown.yellow pans/ 2300m.oak/ pine/ juniper”; “LACM ENT 304317”; “HOLOTYPE ♂/ *Callomyia browni*/ H.J. Cumming [red label]” [dissected] (LACM).

Geographical distribution and seasonal occurrence (Fig. 71).

Callomyia browni is only known from the holotype collected 2.4 kilometers west of Luna in Catron County, New Mexico, in early July.

Etymology.

This species is named after Dr. Brian V. Brown of the Natural History Museum of Los Angeles County, who collected the unique holotype.

Callomyia calla Kessel

(Figs 2, 9, 19, 27, 35, 41, 59, 67, 72)

Callomyia calla Kessel, 1948: 141. Type locality: Marin County, California, USA.
Callomyia cleta Kessel, 1948: 144. Type locality: Marin County, California, USA. **syn. nov.**

Diagnosis.

This western Nearctic species is characterized by extensive yellow to brownish-yellow colour, particularly in the female. The female is mostly yellow (sometimes pale yellow or brownish-yellow, rarely brownish-orange) with abdominal tergites 1, 2 and 7 silver-white dusted. The male, which is darker, is distinguished by brownish-yellow markings on abdominal tergites 1–5 (sometimes silver-grey dusted), a strong stout posteroventral seta on the base of the hind femur, and terminalia characterized by a hypandrial process with an elongate finger-like basoventral lobe and a molar-like surstylus. The surstylus of *C. calla* can be distinguished from other Nearctic species with a molar-like surstylus (*C. argentea*, *C. browni*, *C. velutina*, and *C. venusta*) by having two large cusps that are deeply excavated and pointed in lateral view.

Redescription.

Male. (Figs 9, 19) Body length 4.0–4.25 mm. Head silver-grey; mouthparts including palpus brownish-yellow; antenna with scape and pedicel pale yellow, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (Fig. 41).

Thorax mainly dark brown with silver-grey dusting on notopleuron, supra-alar area of scutum, posterior portion of postsutural scutum, postalar callus, mediotergite and laterotergite; propleuron, mesopleuron and metapleuron silver-grey; postpronotal lobe yellowish-brown posteroventrally. Scutum with 6 notopleural setae.

Foreleg and midleg pale yellow to brownish-yellow with tarsomeres 3–5 brown, hind leg brown; coxae silver-grey dusted. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with strong stout posteroventral seta (as in Fig. 53). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing hyaline or faintly yellowish tinted, cell sc brownish-yellow in some specimens. Halter brownish-yellow to brown.

Abdomen dark brown to black with lateral brownish-yellow markings on tergites 1–5, brownish-yellow markings more ventrolateral in some specimens; lateral silver-grey dusting on tergites 1, 2, 4, 5, 6 and sometimes 7; sternites white to pale yellow, sternite 8 brown.

Terminalia (Figs 59, 67) brown to grey, surstylus darker; hypandrial process and cercus brownish-yellow. Epandrium with short narrow ventral lobe, rounded at apex; apical process short to moderately long, broad basally, pointed at apex. Surstylus molar-like, with 2 large cusps deeply excavated in between; dorsal outer cusp and ventral inner cusp pointed in lateral view; ventral inner cusp tapered medially in posterior view (Fig. 67). Hypandrium with moderately long apical process; process trifid, with 2 minute apical projections and elongate finger-like basoventral lobe. Postgonite long and moderately wide, truncate at apex. Phallus with sharp extended hook at apex. Cercus short.

Female. (Figs 27, 35) Body length 3.75–4.0 mm. Head silver-grey with postgena pale-yellow; mouthparts including palpus pale yellow to yellow; antenna with scape and pedicel pale yellow, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (as in Fig. 43).

Thorax pale yellow to brownish-yellow with silver-white dusting; scutum darker dorsally in some specimens. Scutum with 2–3 presutural intra-alar setae.

Legs pale yellow, hind leg darker with apex of femur, tibia and tarsomeres yellowish-brown. Midtibia with median dorsal seta absent.

Wing hyaline with cell sc faintly white in some specimens. Halter pale yellow to yellow.

Abdomen mainly yellow, brownish-yellow to brownish-orange in some specimens, with tergites 1, 2 and 7 entirely silver-white dusted; anterolateral silver-white dusting on tergites 4 and 5; sternites white to pale yellow.

Terminalia with segment 8 yellow, silver-white dusted; epiproct, hypoproct and cercus pale yellow to yellow.

Type material.

Callomyia calla Kessel, **HOLOTYPE**, ♂ labelled: "Mill Valley,/ Marin Co. Cal./ 10-22-45"; E.L. Kessel/ Collector"; "HOLOTYPE [red label]"; "Callomyia/ calla/ Kessel/ 5998 [on left hand edge] [pink label]"; "California Academy/ of Sciences/ Type No. 5998" [dissected] (CAS). **PARATYPES: USA: CALIFORNIA:** same data as holotype except 4.x.1945 (2 ♂, CAS), same except 5.x.1945 (2 ♂, CAS), same except 7.x.1945 (3 ♂, CAS; 1 ♂ CUIC), same except 14.x.1945 (2 ♂, CAS), same except 21.x.1945 (5 ♂, CAS), same except 24.x.1945 (4 ♂, CAS), same except 25.x.1945 (3 ♂, CAS), same except 1.xi.1945 (1 ♂, CAS; 1 ♂, CNC), same except 5.xi.1945 (1 ♂, CAS; 1 ♂, SEMC).

Callomyia cleta Kessel, **HOLOTYPE,** ♀ labelled: "Mill Valley,/ Marin Co. Cal./ 11-1-45"; "E.L. Kessel/ Collector"; "HOLOTYPE [red label]"; "Callomyia/ cleta/ Kessel/ 5999 [on left hand edge] [pink label]"; "California Academy/ of Sciences/ Type No. 5999" (CAS). **PARATYPES: USA: CALIFORNIA:** same data as holotype (1 ♀, CAS; 1 ♀, SEMC); same data as holotype except 7.x.1945 (1 ♀, CAS), same except 14.x.1945 (3 ♀, CAS), same except 21.x.1945 (4 ♀, CAS), same except 22.x.1945 (6 ♀, CAS), same except 23.x.1945 (1 ♀, CAS), same except 24.x.1945 (8 ♀, CAS; 1 ♀, CNC; 1 ♀, CUIC), same except 25.x.1945 (4 ♀, CAS), same except 4.xi.1945 (2 ♀, CAS), same except 5.xi.1945 (1 ♀, CAS).

Additional material examined.

CANADA: BRITISH COLUMBIA: Cameron Lake, Vancouver Island, 10.x.1961, E. L. Kessel (1 ♀, CAS); Cultus Lake Provincial Park, 6.ix.1960, E. L. Kessel (1 ♂, CAS); Emory Creek Provincial Camp, 8.ix.1961, E. L. Kessel (1 ♂, CAS); Kleanza Creek, 12 miles E. of

Terrace, 13.viii.1965, E. L. Kessel (1 ♀, CAS); Robson, 4.viii.1950, H. R. Foxlee (1 ♂, CNC), same except 30.vii.1947 (1 ♂, CNC); Saint Mary's, 12.vii.1926, A. A. Dennys (1 ♀, CNC); Vancouver Island, 2.3 km from Lake Cowichan, 19-28.vii.1985, I. M. Smith (1 ♀, CNC); **USA: ALASKA:** Haines, 20.vii.1962, E. L. Kessel (1 ♂, CAS); **CALIFORNIA:** Alpine County, Grover Hot Springs State Park, 1.x.1960, E. L. Kessel (2 ♂, CAS); Amador County, 4 mi. E. of Volcano, 2.x.1960, E. L. Kessel (7 ♀, 4 ♂, CAS); Del Norte County, Idlewild, 11.ix.1961, E. L. Kessel (1 ♂, CAS); El Dorado County, Eagle Falls Camp, Lake Tahoe, 18.ix.1960, E. L. Kessel (1 ♂, CAS); El Dorado County, 45 mile Camp, Highway 50, 17.ix.1960, E. L. Kessel (1 ♀, CAS); Humboldt County, Grizzly Creek State Park, 23.ix.1960, E. L. Kessel (2 ♀, CAS), same except 12.ix.1961 (2 ♂, CAS); Lake County, Adams Springs, 22.xi.1959, E. L. Kessel (1 ♀, CAS); Marin County, Inverness, 1.x.1949, E. L. Kessel (1 ♂, CAS); Marin County, Lily Pond Alpine Lake, 18.ix-27.x.1970, D. D. Munroe (1 ♂, CNC); same except 1500', 13.ix-27.x.1970 (1 ♀, CNC), same except 7.x.1970 (1 ♀, CNC), same except 30.x.1970 (3 ♀, CNC), same except 15.xii.1970 (2 ♀, CNC); Mariposa County, 11 mile Creek, Yosemite National Park, 22.x.1960, E. L. Kessel (1 ♀, CAS); Mendocino County, Pieta Creek and Highway 101, 6.x.1963, E. L. Kessel (1 ♀, CAS); Mendocino County, Standish Hickey State Park, 13.x.1963, E. L. Kessel (1 ♀, CAS); Nevada County, White Cloud Forest Camp, 19.x.1962, E. L. Kessel (3 ♀, CAS); Plumas County, Greenville, 27.ix.1959, E. L. Kessel (5 ♂, CAS), same except 2.x.1959 (5 ♀, 2 ♂, CAS), same except 9.x.1959 (1 ♀, 2 ♂, CAS); Riverside County, Fuller Mill Camp Ground, 14.vi.1961, E. L. Kessel (1 ♂, CAS); Santa Clara County, Standford University, 23.x.1905, J. M. Aldrich (1 ♀, USNM), same except 26.xi.1953, P. H. Arnaud (1 ♀, CAS); Shasta County, Castle Crags State Park, 22.ix.1963, E. L. Kessel (1 ♀, 1 ♂, CAS), same except 26.ix.1963 (2 ♀, 1 ♂, CAS); Siskiyou County, 4 mi. N. of Dunsmuir, 22.ix.1963, E. L. Kessel (2 ♀, 2 ♂, CAS), same except 26.ix.1963 (1 ♀, CAS); Siskiyou County, Happy Camp, 24.x.1959, E. L. Kessel (1 ♂, CAS); Tehama County, Potato Patch Camp Ground, Hwy. 36, 16.x.1959, E. L. Kessel (1 ♀, CAS); Trinity County, Rush Creek Camp Ground, 30.x.1959, E. L. Kessel (1 ♂, CAS); Tuolumne County, 2.x.1930, A. C. Browne (1 ♂, CSCA); Yuba County, Celestial Valley, Hwy. 49, 20.x.1962, E. L. Kessel (1 ♀, CAS); **IDAHO:** Bonner County, Indian Creek State Park, 11 miles N. of Coolin, 3.ix.1962, E. L. Kessel (1 ♀, CAS); Chatcolet, 1.viii.1915, A. L. Melander (1 ♀, USNM); Moscow Mountain, 26.viii.1916, A. L. Melander (1 ♀, USNM), same except 25.vi.1920, R. C. Shannon (1 ♂, USNM), same except 25.vii.1920 (1 ♂, USMN); Priest L., 3.ix.1919, A. L. Melander (1 ♀, USNM); Priest L., Lookout Mountain, 20.viii.1919, A. L. Melander (1 ♀, USNM); **MONTANA:** Sanders County, Bull River Forest Camp, 31.viii.1964, E. L. Kessel (1 ♀, 1 ♂, CAS); **OREGON:** Benton County, Alsea falls area, Fall Crk. jct. trail 6, 11-31.x.2012, Malaise trap, S. Fitzgerald (1 ♀, CNC); Hood Mountain, Hood Rapids, 29.vii.1921, A. L. Melander (1 ♂, USNM); Hood River County, Parkdale, 8.viii.1962, E. L. Kessel (3 ♂, CAS); Lane County, Limberlost FC, Hwy. 126, 6.ix.1962, E. L. Kessel (1 ♀, CAS); Lane County, McKenzie Bridge, E. L. Kessel, 9.viii.1962 (1 ♂, CAS), same except 22.viii.1962 (1 ♀, 1 ♂, CAS); McMinnville, 6.ix.1946, K. M. Fender (1 ♀, 1 ♂, CAS); Paradise Forest Camp and Highway 126, 6.ix.1962, E. L. Kessel (17 ♀, 3 ♂, CAS), same except 7.ix.1962 (4 ♀, CAS); Peavine Ridge near McMinnville, 31.viii.1953, K. M. Fender (1 ♂, CAS), same except 14.ix.1955 (1 ♂, CAS); Union County, Hwy. 204, 19 mi. N.W. of Elgin, 26.viii.1962, E. L. Kessel (2 ♂, CAS); **WASHINGTON:** Asotin County, Field Spring State Park, 29.viii.1962, E. L. Kessel (5 ♀, 2 ♂, CAS); Chehalis, 11.viii.1925, A. L. Melander (1 ♂, USNM); Cowlitz County, Seaquest State Park, 9.ix.1961, E. L. Kessel (1 ♀, CAS); Larrabee State Park, 6.ix.1959, E. L. Kessel (1 ♀, CAS); Orcasis above Mountain Lake, 18.viii.1925, A. L. Melander (1 ♂, USNM); Pend Orielle County, 1 mi. N. of Pend Orielle State Park, 4.ix.1962, E. L. Kessel (1 ♀, 1 ♂, CAS); Mt. Rainier, Longmire, 26.viii.1921, A.L. Melander (1 ♀, USNM).

Geographical distribution and seasonal occurrence (Fig. 72).

Callomyia calla is a western North American species currently known from Alaska, British Columbia, Washington, Idaho, Montana, Oregon and California. Adults have been collected from mid-June to late November.

Remarks.

Callomyia calla and *Callomyia cleta* were described from one sex only (*C. calla* from males and *C. cleta* from females) by Kessel (1948). Both species (with holotypes examined) are considered to be conspecific because they have been collected together from multiple localities, including the type locality. In addition, these two nominal species have more extensive yellowish markings than other Nearctic *Callomyia* species collected within the same geographic range.

The names *C. calla* Kessel and *C. cleta* Kessel are now considered subjective synonyms and were published together in the same work by Kessel (1948). As First Reviser (Article 24.2.2

of ICZN 1999) the name *C. calla* Kessel is herein selected as having precedence over *C. cleta* Kessel.

Callomyia corvina **Kessel**

(Figs 10, 20, 28, 36, 48, 54, 60, 73)

Callomyia corvina Kessel, 1948: 140. Type locality: Marin County, California, USA.
Callomyia clara Kessel, 1948: 146. Type locality: Marin County, California, USA. **syn. nov.**

Diagnosis.

This western Nearctic species is characterized by its thoracic and abdominal colour patterns and male terminalia with a broadly lamellate surstylus and simple hypandrial process without projections. The female is distinguished by its distinctive thoracic colour pattern that is mainly silver-blue dusted with a black median dorsal stripe on the scutum and by its abdominal silver-yellow or silver-blue markings on tergites 1−4 and 6. The male is distinguished by its abdominal silver bluish-grey markings on tergites 1–5 and sometimes 6, yellowish-brown tinted wing, and features of the terminalia mentioned above. The male of *C. corvina* is similar to the western Nearctic species *C. gilloglyorum*, but differs in colour, terminalia, shape of the first flagellomere, and setae on the notopleuron and midtibia, as indicated in the key to species.

Redescription.

Male. (Figs 10, 20) Body length 4.0–4.2 mm. Head dark silver-grey; mouthparts brownish-yellow with palpus pale yellow; antenna with scape, pedicel, first flagellomere and arista dark grey to dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax mainly dark brown to black with indistinct silver-grey dusting on lateral portion of presutural scutum, notopleuron, supra-alar area of scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey; postpronotal lobe yellowish-brown posteroventrally. Scutum with 6 notopleural setae.

Legs yellowish-brown to brown with tarsomeres 4 and 5 dark brown, hind leg with apex of femur and base of tibia brownish-yellow; coxae silver-grey dusted. Midtibia with median anterodorsal seta present in most specimens, median dorsal seta present (as in Fig. 49); base of hind femur with long thin posteroventral seta (Fig. 54). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing yellowish-brown tinted (Fig. 48). Halter orange with base of stem brown.

Abdomen black to velvety black with lateral dark silver bluish-grey markings on tergites 1–4; ventrolateral dark silver bluish-grey marking on tergite 5; ventrolateral silver-grey marking on tergite 6; tergite 7 entirely brown to grey; sternites light brown, sternite 8 brown to grey.

Terminalia (Fig. 60) with epandrium and hypandrium grey; surstylus brown; hypandrial process and cercus brownish-yellow. Epandrium with moderately long narrow ventral lobe, curved posteriorly, blunt at apex; apical process short, broad at apex. Surstylus broadly lamellate with narrow ventral process; dorsal lobe lengthened with slightly truncate apex; ventral process moderately long, straight. Hypandrium with elongate slender apical process; process simple and pointed at apex, without apical projections and basoventral lobe. Postgonite long, slightly expanded apically, truncate at apex. Phallus slightly curved towards apex, without sharp hook. Cercus short.

Female. (Figs 28, 36) Body length 2.9–3.85 mm. Head silver-blue with coppery reflections on occiput and gena in some specimens, postgena pale-yellow in some specimens; mouthparts including palpus pale yellow to yellow; antenna with scape and pedicel brown to brownish-yellow, pale yellow apically, first flagellomere and arista entirely brown. Antenna with first flagellomere short-oval (as in Fig. 43).

Thorax mainly silver-blue dusted; postpronotal lobe brownish-yellow; scutum with median dorsal stripe and supra-alar area black; scutellum mostly black, brownish-yellow basolaterally. Scutum with 2–4 presutural intra-alar setae.

Foreleg and midleg pale yellow to yellow with tarsomeres yellowish-brown in most specimens; hind leg darker with apex of femur, tibia and tarsomeres yellowish-brown to brown. Midtibia with short median dorsal seta present in most specimens (as in Fig. 52).

Wing hyaline with cell sc bluish-white in some specimens. Halter pale yellow to yellowish-orange.

Abdomen dark brown to black with tergites 1, 2 and 6 entirely silver-yellow or silver-blue; posterior silver-yellow or silver-blue markings on tergites 3 and 4, marking on tergite 4 interrupted by median dorsal dark band in most specimens; sternites pale yellow to pale orange.

Terminalia with segment 8 brown; epiproct brown, hypoproct and cercus yellow to yellowish-brown.

Type material.

Callomyia corvina Kessel, **HOLOTYPE**, ♂ labelled: "Mill Valley,/ Marin Co. Cal./ 10-5-45"; "E.L. Kessel/ Collector"; "HOLOTYPE [red label]"; "Callomyia/ corvina/ Kessel/ 5997 [on left hand edge] [pink label]"; "California Academy/ of Sciences/ Type No. 5997" [dissected] (CAS). **PARATYPE: USA: CALIFORNIA:** same data as holotype except 25.x.1945 (1 ♂, CAS).

Callomyia clara Kessel, **HOLOTYPE**, ♀ labelled: "Mill Valley,/ Marin Co. Cal./ 11-5-45"; "E.L. Kessel/ Collector"; "HOLOTYPE [red label]"; "Callomyia/ clara/ Kessel/ 6000 [on left hand edge] [pink label]"; "California Academy/ of Sciences/ Type No. 6000" (CAS).

Additional material examined.

USA: CALIFORNIA: Amador County, 4 mi. E. of Volcano, 2.x.1960, E. L. Kessel (1 ♂, CAS); El Dorado County, Eagle Falls, 18.ix.1960, E. L. Kessel (1 ♂, CAS); Humboldt County, Grizzly Creek Redwoods State Park, 23.ix.1960, E. L. Kessel (1 ♀, CAS); Los Angeles County, Pasadena, 2.xi.1949, E. L. Kessel (1 ♀, CAS); Los Angeles County, Topanga Cyn., 34.08N118.59W, 6-20.xii.1993, malaise trap, B. Brown & G. Hendler (1 ♀, LACM); Los Angeles County, 9 km N. La Canada, 34.25N118.19W, 16-30.xi.1994, malaise trap 900 m, B. Brown (1 ♀, LACM), same except 30.xi-14.xii.1994 (1 ♀, LACM); Marshfield, 14.ix.1934, A.L. Melander (1 ♀, USNM); Monterey County, Nacimiento Canyon Camp, 9.x.1960, E. L. Kessel (1 ♀, CAS); Riverside County, El Cariso Camp Ground, 1.iv.1961, E. L. Kessel (1 ♂, CAS); Riverside County, Upper San Juan Forest Camp, 6.xii.1961, E. L. Kessel (1 ♀, CAS); Riverside County, Upper San Juan Camp Ground, 1.iv.1961, E. L. Kessel (1 ♀, 1 ♂, CAS); San Bernardino County, Thurman Flats, 22.x.1965, P. H. Arnaud Jr. (1 ♂, CAS); Shasta County, Castle Creek, 18.x.1959, E. L. Kessel (1 ♂, CAS); Stanislaus County, Del Puerto Canyon, Frank Raines Park, 1120', 3.iv.1970, P. H. Arnaud Jr. (1 ♂, CAS), same except 335 m, 5.iv.1970 (1 ♀, CAS); **IDAHO:** Moscow Mountain, 9.vii.1920, A. L. Melander (1 ♀, USNM); **OREGON:** Lane County, Limberlost Forest Camp, Hwy. 126, 6.ix.1962, E. L. Kessel (1 ♂, CAS); **WASHINGTON:** Mt. Rainier, Longmire, 20.vii.1922, A.L. Melander (1 ♀, USNM).

Geographical distribution and seasonal occurrence (Fig. 73).

Callomyia corvina is currently known from western USA (Washington, Idaho, Oregon and California). Adults have been collected from early April, July and September to mid-December.

Remarks.

Callomyia corvina is most closely related to the widespread Palaearctic species *C. speciosa*, as shown in the strict consensus tree (Fig. 79). These two species have similar male terminalia and female abdominal colour pattern. However, the male terminalia of *C. corvina* have a broadly lamellate surstylus with a longer and thinner ventral process and a wider hypandrial process. The female abdominal markings of *C. corvina* differ by the silvery yellow or blue colour on tergite 4 being interrupted by a median dorsal dark band, which is uninterrupted in *C. speciosa*.

Callomyia corvina and *Callomyia clara* were described from one sex only by Kessel (1948) with *C. corvina* described from males and *C. clara* described from a female. Both species (with holotypes examined) are considered to be conspecific because they have been collected from many of the same localities, including the type locality, at or around the same time.

The names *C. corvina* Kessel and *C. clara* Kessel are now considered subjective synonyms and were published together in the same work by Kessel (1948). As First Reviser (Article 24.2.2 of ICZN 1999) the name *C. corvina* Kessel is herein selected as having precedence over *C. clara* Kessel.

***Callomyia gilloglyorum* Kessel**

(Figs 3, 11, 21, 29, 37, 42, 44, 61, 74)

Callomyia gilloglyorum Kessel, 1961b: 4. Type locality: Alameda County, California, USA.

Diagnosis.

This western Nearctic species is characterized by contrasting black and silver-grey abdominal colour, an elongate conical first flagellomere in the male and subtriangular first flagellomere in the female, 7–8 notopleural setae on the male scutum, male with yellowish-brown tinted wing, and male terminalia with a broadly lamellate surstylus and a trifid hypandrial process. The male is similar to the western Nearctic species *C. corvina*, but differs in colour, terminalia, shape of the first flagellomere, and setae on the notopleuron and midtibia, as indicated in the key to species. The male of *C. gilloglyorum* also has very similar terminalia to the southwestern Nearctic species *C. arnaudi*, but differs by a longer ventral process on the broadly lamellate surstylus and longer projections on the hypandrial process.

Redescription.

Male. (Figs 11, 21) Body length 3.8–4.1 mm. Head silver-grey; mouthparts including palpus brownish-yellow; antenna with scape, pedicel, first flagellomere and arista dark brown. Antenna with first flagellomere elongate-conical (Fig. 42).

Thorax mainly dark brown to black with indistinct silver-grey dusting on lateral portion of presutural scutum, notopleuron, supra-alar area of scutum and posterolateral portion of postsutural scutum; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey; postpronotal lobe yellowish-brown posteroventrally. Scutum with 7–8 notopleural setae.

Legs yellowish-brown to brown with trochanter, base and apex of femur, and base of tibiae yellow; tarsomeres 3–5 dark brown; coxae silver-grey dusted. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig 50); base of hind femur with long thin posteroventral seta (as in Fig. 54). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing yellowish-brown tinted (as in Fig. 48). Halter with stem brown, knob dark brown.

Abdomen dark brown to black with lateral to ventrolateral silver-grey markings on tergites 1, 2 and 4; ventrolateral silver-grey markings on tergites 3 and 5; posteroventral silver-grey dusting on tergite 6 in most specimens; tergite 7 entirely brown to grey; sternites light brown, sternite 8 brown to grey.

Terminalia (Fig. 61) with epandrium and hypandrium grey; surstylus and hypandrial process brown; cercus brownish-yellow. Epandrium with short broad ventral lobe, rounded at apex; apical process elongate, narrow, pointed at apex. Surstylus broadly lamellate with narrow ventral process; dorsal lobe lengthened with rounded apex; ventral process elongate, moderately curved dorsally. Hypandrium with elongate slender apical process; process trifid, with 2 very long narrow apical projections and long narrow basoventral lobe. Postgonite very long and narrow, rounded at apex. Phallus sharply hooked at apex. Cercus short.

Female. (Figs 29, 37) Body length 2.9–3.5 mm. Head silver-grey with vertex, occiput and face silver-brown to reddish-brown in some specimens; mouthparts brownish-yellow with palpus pale yellow; antenna with scape and pedicel yellowish-brown, first flagellomere and arista brown to dark brown. Antenna with first flagellomere subtriangular (Fig. 44).

Thorax mainly silver-grey; scutum brown dorsally; scutellum darker medially in some specimens. Scutum with 2–3 presutural intra-alar setae.

Legs brownish-yellow with tarsomeres 3–5 brown to dark brown; coxae silver-grey dusted in most specimens. Midtibia with short median dorsal seta present in most specimens (as in Fig. 52).

Wing hyaline. Halter brownish-yellow to brownish-orange.

Abdomen dark brown to black with tergites 1, 2, 4, 6 and 7 silver-grey, tergites 2, 4 and 6 interrupted by a median dorsal dark band in some specimens; tergites 3 and 5 with posterior silver-grey dusting in some specimens; sternites pale yellow, silver-grey dusted in some specimens.

Terminalia with segment 8 silver-grey; epiproct, hypoproct and cercus brownish-yellow, silver-grey in some specimens.

Type material.

HOLOTYPE, ♂ labelled: “Oakland/ Alameda/ Co. Cal.”; “J. Gillogly/ Collector”; “Larvae/ V.1.54/ Emerged/ XI.9.54”; “HOLOTYPE/ Callomyia/ gillogly-/ orumKessel [red label]”; “California Academy/ of Sciences/ Type No. 6446” (CAS). **ALLOTYPE,** ♀ labelled: “Oakland/ Alameda/ Co. Cal.”; “J. Gillogly/ Collector”; “Larvae/ V.1.54/ Emerged/ VIII.15.54”; “ALLOTYPE/ Callomyia/ gillogly-/ orumKessel [red label]”; “Collection of the/ CALIFORNIA ACADEMY/ OF SCIENCES, San/ Francisco, California” (CAS). **PARATYPES: USA: CALIFORNIA:** same data as holotype (3 ♀, 2 ♂, CAS); same data as holotype except emerged 1.xi.1954 (1 ♂, CAS).

Additional material examined.

CANADA: BRITISH COLUMBIA: King Salmon Lake, 15.vii.1960, W. W. Moss (1 ♀, CNC); Manning Provincial Park, small creek vic. Manning Park Lodge, 5.viii.1986, P. H. Arnaud Jr. (1 ♂, CAS); **USA: ALASKA:** Spenard, 17.viii.1959, E. L. Kessel (1 ♂, CAS); **CALIFORNIA:** Humboldt County, Prarie Creek, 4.xi.1960, E. L. Kessel (1 ♂, CAS); Marin County, Inverness, 14-29.xii.1963, P. H. Arnaud Jr. (1 ♀, CAS); Sacramento County (1 ♂, USNM); Stanislaus County, Del Puerto Canyon, Frank Raines Park, 1120', 3.iv.1970, P. H. Arnaud Jr. (1 ♀, CAS); Tulare County, ½ mi. S.E. Ash Mt., Seq. N. Park HQ, 10.iii.1984 (1 ♂, CSCA); **MONTANA:** Sanders County, Bull River Forest Camp, 31.viii.1964, E. L. Kessel (1 ♀, CAS); **OREGON:** Lane County, Paradise Forest Camp, Hwy. 126, 6.ix.1962, E. L. Kessel (1 ♀, CAS); Wallowa County, Arrow Forest Camp, Lostine River, 27.viii.1962, E. L. Kessel (1 ♂, CAS).

Geographical distribution and seasonal occurrence (Fig. 74).

Callomyia gilloglyorum is a western North American species currently known from Alaska, British Columbia, Montana, Oregon and California. Larvae have been collected in early May, from which adults emerged in mid-August and early November. Adults have also been collected from early March to early April and July to late December.

Remarks.

Callomyia gilloglyorum is most closely related to the widespread Palaearctic species *C. dives*, as alluded to by Chandler (2001) and shown in the strict consensus tree (Fig. 79). These two species have similar male terminalia and abdominal colour patterns. The male terminalia of *C. gilloglyorum* differ from the latter species by having a longer ventral process on the broadly lamellate surstylus, longer apical projections and a shorter basoventral lobe on the hypandrial process, and a narrower postgonite. The male terminalia of *C. gilloglyorum* are also similar to those of the Palaearctic species *C. saibhira* (based on figures 238−240 in Chandler (2001)). Both the male and female abdominal colour patterns are similar to *C. dives*, however the black and silver-grey colour is duller, with *C. dives* having more striking silver and velvety black colour.

Callomyia gilloglyorum is the only North American species of *Callomyia* for which the immature stages are known (Fig. 3). Larvae were reared from white mycelia (fungus species not identified) under the bark of a fallen pine tree (*Pinus* sp.) (Kessel 1961b). The reared larvae took four to seven months to emerge as adults in the laboratory, possibly indicating a long developmental time in nature. However, seasonal records for adults collected from early March to early April and July to late December suggest shorter immature developmental times with multiple generations per year. Also, the early March and late December seasonal records, both from California, may indicate that adults of this species overwinter.

Callomyia proxima **Johnson**

(Figs 12, 22, 30, 38, 49, 51, 62, 75)

Callomyia proxima Johnson, 1916: 32. Type locality: Mt. Washington, New Hampshire, USA.
Callomyia liardia Kessel & Buegler, 1972: 262. Type locality: Liard Hot Springs, British Columbia, Canada. **syn. nov.**

Diagnosis.

This apparently disjunct eastern and western Nearctic species is characterized by its abdominal colour patterns, midtibial setae, and male terminalia with a bifid surstylus that has long outer and inner processes and a bifid hypandrial process. The female is distinguished by a long median dorsal seta on the midtibia and a distinctive abdominal colour pattern (yellow on tergites 1 and 2, silver-yellow or silver-blue on posterior portion of tergites 3 and 4 – all interrupted by a median dorsal dark band – and tergite 6 entirely silver-blue). The male is distinguished by a median anterodorsal seta that is usually present above a median dorsal seta on the midtibia, a dark brown to velvety black abdomen usually with posterolateral or posteroventral silver-grey markings on tergites 3 and 4, and features of the terminalia mentioned above. The male of *C. proxima* is similar to *C. velutina* from eastern and western North America, but differs by the silver-grey abdominal markings, a median anterodorsal seta on the midtibia, and terminalia, as indicated in the key to species. The male terminalia of *C. proxima* are also very similar to the southwestern Nearctic species *C. bertae*, with differences indicated under the diagnosis of that species.

Redescription.

Male. (Figs 12, 22) Body length 3.4–4.1 mm. Head silver-black; mouthparts including palpus brownish-yellow; antenna with scape, pedicel, first flagellomere and arista dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax mainly velvety black, dark brown in some specimens; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey dusted. Scutum with 6 notopleural setae.

Foreleg and midleg light brown, hind leg dark brown, apex of femur and base of tibiae brownish-yellow. Midtibia with median anterodorsal seta present in most specimens, median dorsal seta present (Fig. 49); base of hind femur with long thin posteroventral seta (as in Fig. 54). Hind tarsomere 1 long, slightly narrower than apical width of hind tibia, length approximately 3X width.

Wing hyaline with cell sc faintly yellow, whitish in some specimens. Halter with stem brown to dark brown, knob yellow to orange.

Abdomen mainly dark brown to velvety black with posterolateral to posteroventral silver-grey markings on tergites 3 and 4 in most specimens; tergite 7 entirely brown to grey; sternites light brown, sternite 8 brown to grey.

Terminalia (Fig. 62) with epandrium grey; surstylus dark brown to black; hypandrium and cercus brown. Epandrium with minute ventral lobe, barely apparent; apical process short, broad at apex. Surstylus bifid, with long outer and inner process, both rounded at apex; outer process broader and longer; inner process narrower and shorter. Hypandrium with moderately long apical process; process bifid, with 2 short apical projections; dorsal projection narrow and longer, ventral projection broad and shorter. Postgonite long and moderately wide, somewhat truncated and slightly pointed at apex. Phallus sharply hooked at apex. Cercus short.

Female. (Figs 30, 38) Body length 3.35–3.85 mm. Head silver-blue with occiput silver-black; mouthparts brownish-yellow with palpus yellow to orange; antenna with scape and pedicel brown, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (as in Fig. 43).

Thorax black to velvety black with silver-blue markings on entire lateral portion of presutural scutum, notopleuron, most of postsutural scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-blue dusted; postpronotal lobe and supra-alar area of scutum brownish-yellow. Scutum with 2–3 presutural intra-alar setae.

Foreleg and midleg yellow to yellowish-brown with tarsomeres 3–5 brown to dark brown; hind leg darker with apex of femur, tibia and tarsomeres dark brown. Midtibia with long median dorsal seta present (Fig. 51).

Wing hyaline with cell sc bluish-white in some specimens. Halter yellow.

Abdomen dark brown to black with tergites 1 and 2 yellow, both interrupted by median dorsal dark band; posterior silver-yellow or silver-blue markings on tergites 3 and 4, both interrupted by median dorsal dark band; tergite 6 entirely silver-blue; sternites white to pale yellow.

Terminalia with segment 8 and epiproct yellowish-brown to brown, silver-grey dusted; hypoproct and cercus brownish-yellow.

Type material.

Callomyia proxima Johnson, **LECTOTYPE** (designated by Kessel & Buegler 1972), ♀ labelled: "Mt Washington/ betw. 2 & 3 mile [hand written] N H [New Hampshire]/ VII.16.1915 [hand written]"; "Paratype/ No. [red label]"; "C.W. Johnson/ Collector"; "M.C.Z./ Paratype/ 26892 [red label]"; "MCZ ENT/ 00304201 (MCZ). **PARALECTOTYPE: USA: NEW HAMPSHIRE:** Mount Washington, 2-3 mi. post Carriage Road, 16.vii.1915, C. W. Johnson (1 ♀, MCZ).

Callomyia liardia Kessel & Buegler, **HOLOTYPE**, ♂ labelled: "Liard Hot/ Sprs.. B.C./ VII.26.62/ E.L.Kessel"; "HOLOTYPE/ Callomyia/ liardia/ Kessel &/ Buegler [pink label]"; "California Academy/ of Sciences/ Type No. 11265" [dissected] (CAS). **PARATYPES: CANADA: BRITISH COLUMBIA:** same data as holotype (1 ♂, CAS); Kleanza Creek, 12 mi. E. of Terrace, 13.viii.1965, E. L. Kessel (1 ♂, CAS); Liard Hot Springs, Mile Post 496, Alaska Hwy, 8.viii.1959, E. L. Kessel (1 ♂, CAS); **USA: ALASKA:** 27 miles S. of Livengood, 28.vi.1962, E. L. Kessel (2 ♂, CAS); Mile Post 1231, E. of Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (1 ♂, CAS); Mile Post 1277, E. of Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (1 ♂, CAS); Peters Creek Camp Ground, 1.vii.1962, E. L. Kessel (1 ♂, CAS); Richardson Highway, 21 miles N. of Delta Junction, 29.vi.1962, E. L. Kessel (1 ♂, CAS); Salcha River Camp Ground, 28.vi.1962, E. L. Kessel (1 ♂, CAS); Spenard, 24.viii.1957, E. L. Kessel (1 ♂, CAS), same except 25.viii.1957 (1 ♂, CAS), same except 17.viii.1959 (1 ♂, CAS), same except 25.viii.1959 (1 ♂, CAS), same except 26.viii.1959 (1 ♂, CAS); 9 mi. E. of Valdez, 12.vii.1962, E. L. Kessel (1 ♂, CAS).

Additional material examined.

CANADA: BRITISH COLUMBIA: Kleanza Creek, 12 mi. E. of Terrace, 14.viii.1965, E. L. Kessel (4 ♀, CAS); Liard Hot Springs, Mile Post 496, Alaska Hwy, 2.ix.1957, E. L. Kessel (1 ♂, CAS), same except 8.viii.1959 (2 ♀, CAS); Liard Hot Springs, 26.vii.1962, E. L. Kessel (1 ♂, CAS); Mile Post 104, Alaska Highway, 5.viii.1957, E. L. Kessel (3 ♀, 3 ♂, CAS), same except 5.viii.1959 (4 ♂, CAS); Mile Post 350, Alaska Highway, 6.viii.1957, E. L. Kessel (1 ♀, CAS); Mount Thornhill, near Terrace, 30.vii.1960, W. R. Richards (2 ♂, CNC); Whiskers Province Camp Ground, Hart Hwy., 29.vii.1962, E. L. Kessel (1 ♂, CAS); **ONTARIO:** Bruce Peninsula NP, Cameron Lake Road, 4.vii.1998, 45°12.5N81°33.5W, K. N. Barber, sweep veg./grasses, mixed forest (1 ♂, DEBU); Bruce Peninsula NP, Bruce Trail nr. Crane Lake, 29.viii.1999, S. A. Marshall (1 ♂, DEBU); Bruce Peninsula NP, Dunks Bay, 20.vii.1996, S. A. Marshall (1 ♂, DEBU), same except 27.vii.1997 (1 ♂, DEBU), same except 4.vii.1998, 45°14'N81°38'W, DEBU 00075059 (1 ♀, 5 ♂, DEBU), same except 1-2.viii.1999 (1 ♀, DEBU); Crow Lake, Marmora area, 18.viii.1959, L. K. Smith (1 ♀, CNC); **QUEBEC:** Gatineau Park, King Mountain/Black Lake Trail, 29.viii.2012, 45°29'20"N75°51'53"W, H. J. Cumming, JSS26016 (1 ♂, LEM); Gatineau Park, Waterfall Trail, 3.ix.2012, 45°28'42"N75°51'06"W, H. J. Cumming & S. H. Cumming, JSS26018, JSS26017 (1 ♀, 1 ♂, LEM), same except 24.viii.2013, J. M. Cumming (1 ♀, CNC); Old Chelsea, 31.viii.1958, J. R. Vockeroth (1 ♀, CNC); Old Chelsea, Summit King Mountain, 1150', Gatineau Park, 9.viii.1985, J. R. Vockeroth, CNC DIPTERA 192199 (1 ♀, CNC); **USA: ALASKA:** Anchorage, 19.vii.1921, J. M. Aldrich (1 ♀, 3 ♂, USNM), same except 21.vii.1921 (5 ♂, USNM), same except 20.vii.1951, R. S. Bigelow (2 ♀, CNC); 6 mi. W. of Circle city, 23.vi.1962, E. L. Kessel (1 ♂, CAS); Haines, 11.viii.1959, E. L. Kessel (1 ♀, CAS); Johnson Lake, 16 mi. S. of Soldatna, 5.vii.1962, E. L. Kessel (1 ♂, CAS); 4 mi. S. of Livengood, 27.vi.1962, E. L. Kessel (1 ♂, CAS); 27 miles S. of Livengood, 28.vi.1962, E. L. Kessel (1 ♂, CAS); Mile Post 1231, E. of Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (3 ♀, 1 ♂, CAS); Mile Post 1277, E. of Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (2 ♂, CAS); Mosquito Lake, 27 miles N. of Haines, 17.vii.1962, E. L. Kessel (1 ♂, CAS); Richardson Highway, 21 miles N. of Delta Junction, 29.vi.1962, E. L. Kessel (3 ♂, CAS); Soldatna, 5.vii.1962, E. L. Kessel (1 ♂, CAS); Spenard, 24.viii.1957, E. L. Kessel (1 ♂, CAS), same except 17.viii.1959 (2 ♀, 8 ♂, CAS), same except 19.viii.1959 (2 ♂, CAS), same except 7.vii.1962, E. L. Kessel (2 ♂, CAS); 9 mi. E. of Valdez, 12.vii.1962, E. L. Kessel (1 ♀, 1 ♂, CAS); Wasilla, 10.viii.1959, E. L. Kessel (1 ♂, CAS); **MASSACHUSETTS:** Chester, 5.viii.1914, C. W. Johnson (1 ♂, MCZ, paratype of *C. velutina*); **NEW HAMPSHIRE:** Bretton Woods, 1.vii.1936, A. L. Melander (1 ♀, USNM); Mount Washington, 6.vii.1914, C. W. Johnson (1 ♂, MCZ, paratype of *C. velutina*), same except betw. 1 & 2 mile, 24.vii.1915 (1 ♂, MCZ, paratype of *C. velutina*); Mount Washington, Raymond Path, 28.vii.1915, C. W. Johnson (1 ♂, MCZ, paratype of *C. velutina*); **NEW YORK:** Ithaca, vi, R. C. Shannon (1 ♂, USNM); St. Lawrence County, Cranberry L., 25.vi.1963, W. W. Wirth, swamp (1 ♂, USNM); Trumansburg, 19.vii.1983, D. Grimaldi (1 ♂, AMNH); **NORTH CAROLINA:** Macon County, Wayah Gap, 3500', 10.viii.1957, J. G. Chillcott (1 ♀, CNC); **UTAH:** Cache County, W. Hodges Canyon, 14-18.vii.1978, Hanson & Knowlton (1 ♀, LACM); **WEST VIRGINIA:** Pocahontas County, Island Cpg, E. fork Greenbriar, 1.vii.1982, Mathis & Flint (1 ♂, USMN).

Geographical distribution and seasonal occurrence (Fig. 75).

Callomyia proxima is currently distributed in both western North America (Alaska, British Columbia and Utah) and eastern North America (Ontario, Quebec, New York, New Hampshire, Massachusetts, West Virginia and North Carolina). Adults have been collected from late June to early September.

Remarks.

Callomyia proxima is closely related to the Nearctic species *C. bertae* and the Palaearctic species *C. dorsimaculata*, *C. elegans*, and *C. sonora*, as shown in the strict consensus tree (Fig. 79). Within this clade, *C. proxima* is most similar to *C. elegans* because of similar male terminalia, setae on the midtibia, and thoracic and abdominal colour patterns. However, it is more robust than *C. elegans* and its male terminalia differ by having a wider ventral projection on the hypandrial process and a shorter and wider postgonite.

Two female specimens of *C. proxima* yielded COI barcode sequences (CNC DIPTERA 192199 and JSS26018) and two male specimens, initially identified as *C. liardia*, also yielded barcodes (JSS26016 and JSS26017) (Table 1). In the Neighbour-joining tree (Fig. 78), these four specimens clustered closely together (<2% genetic divergence), suggesting that *C. proxima* and *C. liardia* are conspecific. A third male specimen of *C. liardia* yielded a barcode (DEBU 00075059) (Table 1) and also clustered with the four specimens mentioned above, but had >2% genetic divergence from these specimens. Although this specimen has a greater genetic divergence from the others, it appears to be morphologically identical to *C. liardia* (= *C. proxima*). Only 620 bp of COI could be sequenced for that specimen (658 bp were sequenced from the others), which could explain its position slightly outside the *C. proxima/ C. liardia* cluster. Further barcode sequence data are required to resolve any potential species boundary problems within the *C. proxima* cluster.

Callomyia proxima was described from females only by Johnson (1916) and Kessel & Buegler (1972) later described *Callomyia liardia* from males only. Both species (with lectotype and holotype examined respectively) are considered to be conspecific because they have been collected together from multiple localities, including both type localities. In addition, DNA barcode data from these two nominal species supports the new synonymy proposed.

Kessel & Buegler (1972) considered four of the seven paratypes of *C. velutina* to be conspecific with *C. liardia* (= *C. proxima*). Three of these four paratypes are listed under "Type Material" of *C. velutina* and have been added to "Additional material examined" of *C. proxima*, above. The fourth paratype was not examined. Another paratype of *C. velutina* (from New Hampshire, Mount Washington, Raymond Path) was also discovered to be conspecific with *C. proxima* and is listed under "Type Material" of *C. velutina*.

***Callomyia velutina* Johnson**

(Figs 13, 23, 31, 39, 45, 50, 52, 63, 68, 76)

Callomyia velutina Johnson, 1916: 32. Type locality: Mt. Washington, New Hampshire, USA.

Diagnosis.

This apparently disjunct eastern and western Nearctic species is characterized by its abdominal colour patterns and male terminalia with a molar-like surstylus, apically rounded postgonite, and trifid hypandrial process. The female of *C. velutina* is very similar to the widespread Nearctic species *C. venusta* because of its similar thoracic and abdominal colour patterns, but differs by an extra presutural intra-alar seta on the scutum and a silver-blue marking on tergite 5 that is interrupted by a median dorsal dark band (versus tergite 5 entirely silver-blue). The male of this species is similar to *C. proxima* from eastern and western North America, but differs by its lateral silver-grey dusting on abdominal tergites 1 and 2 (versus more distinct posterolateral to posteroventral silver-grey markings only on tergites 3 and 4) and terminalia with a molar-like surstylus and trifid hypandrial process (versus bifid surstylus and bifid hypandrial process). *Callomyia velutina* has male terminalia that are most similar to the Nearctic species *C. argentea* and *C. venusta*, but its terminalia differ primarily from these species by an apically rounded (versus apically truncate) postgonite.

Redescription.

Male. (Figs 13, 23) Body length 3.6–4.5 mm. Head silver-grey with coppery reflections on gena and postgena; mouthparts brownish-yellow to light brown with palpus brown; antenna with scape, pedicel, first flagellomere and arista brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax mainly dark brown to black with indistinct silver-grey dusting on notopleuron, supra-alar area of scutum, posterior portion of postsutural scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey; postpronotal lobe yellowish-brown posteroventrally. Scutum with 6 notopleural setae.

Legs brown, hind leg darker with tibia and tarsomeres dark brown; apex of femur and base of tibiae brownish-yellow; coxae silver-grey dusted in most specimens. Midtibia with median anterodorsal seta absent, median dorsal seta present (Fig. 50); base of hind femur with long thin posteroventral seta (as in Fig. 54). Hind tarsomere 1 slightly expanded, subequal to apical width of hind tibia, length approximately 2.5X width.

Wing hyaline with cell sc faintly yellow. Halter with stem brown; knob orange, yellow in some specimens.

Abdomen mainly dark brown to black with lateral silver-grey dusting on tergites 1 and 2; ventrolateral silver-grey dusting on tergites 3 and 4 in some specimens; tergite 7 entirely silver-grey dusted; sternites light brown, sternite 8 brown to grey.

Terminalia (Figs 63, 68) brown to grey, surstylus darker; hypandrial process and cercus brownish-yellow. Epandrium with short tooth-like ventral lobe, pointed at apex, slightly anteriorly directed; apical process short to moderately long, pointed at apex. Surstylus molar-like, with 2 large cusps moderately excavated in between; dorsal outer cusp broadly rounded in lateral view; ventral inner cusp slightly pointed in lateral view, narrowly truncate and minutely serrate medially in posterior view (Fig. 68). Hypandrium with moderately long apical process; process trifid, with 2 short apical projections and short stout rounded basoventral lobe. Postgonite long and moderately wide, rounded at apex. Phallus with sharp extended hook at apex. Cercus short.

Female. (Figs 31, 39) Body length 3.3–4.25 mm. Head silver-blue with occiput silver-grey to silver-brown; mouthparts including palpus pale yellow to brownish-yellow; antenna with scape and pedicel brown, pale yellow apically, first flagellomere and arista entirely brown. Antenna with first flagellomere short-oval (as in Fig. 43).

Thorax mainly black to velvety black with silver-blue markings on postpronotal lobe, entire lateral portion of presutural scutum, notopleuron, most of postsutural scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-blue dusted; postpronotal lobe posteroventrally, supra-alar area of scutum, postalar callus anteriorly and anepimeron pale yellow to yellowish-brown. Scutum with 2–3 presutural intra-alar setae, usually 3 at least on one side (Fig. 45).

Foreleg and midleg pale yellow to yellowish brown with tarsomeres 3–5 brown; hind leg darker with apex of femur, tibia and tarsomeres dark brown; coxae silver-blue dusted in most specimens. Midtibia with short median dorsal seta present in most specimens (Fig. 52).

Wing hyaline with cell sc bluish-white in some specimens. Halter yellow.

Abdomen dark brown to black with tergites 1–3 yellow; lateral silver-white markings or dusting on tergites 1 and 2; tergite 4 dark brown to black, brownish-yellow in a few specimens; tergite 5 silver-blue, interrupted by median dorsal dark band (partially interrupted in some specimens); sternites white to light brown.

Terminalia with segment 8 and epiproct yellowish-brown to brown, silver-grey dusted; hypoproct and cercus yellow to brownish-yellow.

Type material.

HOLOTYPE, ♂ labelled: “Mt Washington/ Betw. 1 & 2 m [hand written] N H [New Hampshire]/ VII.24.1915 [hand written]”; “HOLOTYPE/ No. [red label]”; “C.W. Johnson/ Collector”; “MCZ-ENT/ 00304204” (MCZ). **PARATYPES: USA: MASSACHUSETTS:** Chester, 5.viii.1914, C. W. Johnson (1 ♂, MCZ) (paratype of *C. velutina*, but conspecific with *C. proxima* – see “Remarks”); **NEW HAMPSHIRE:** Bretton Woods, 28.vi.1913, C. W. Johnson (1 ♂, MCZ); Mount Washington, 6.vii.1914, C. W. Johnson (1 ♂, MCZ), same except betw. 1 & 2 mile, 24.vii.1915 (1 ♂, MCZ) (both paratypes of *C. velutina*, but conspecific with *C. proxima* – see “Remarks”); Mount Washington, Raymond Path, 8.vii.1914, C. W. Johnson (1 ♂, MCZ); Mount Washington, Raymond Path, 28.vii.1915, C. W. Johnson (1 ♂, MCZ) (paratype of *C. velutina*, but conspecific with *C. proxima* – see “Remarks”).

Additional material examined.

CANADA: ALBERTA: Bilby, 1.vii.1924, O. Bryant (1 ♂, USNM); Fort Vermilion, 23.viii.1961, E. L. Kessel (1 ♀, CAS); Little Smokey River and Highway 43, 11.vi.1962, E. L. Kessel (1 ♂, CAS); **BRITISH COLUMBIA:** Cultus Lake Provincal Park, 6.ix.1960, E. L. Kessel (1 ♂, CNC); Kleanza Creek Province Camp Ground, Highway 16, 31.vii.1962, E. L. Kessel (1 ♂, CAS); Kleanza Creek, 12 mi. E. of Terrace, 14.viii.1965, E. L. Kessel (2 ♀, 3 ♂, CAS); Liard Hot Springs, 14.vii.1962, E. L. Kessel (1 ♀, CAS), same except 26.vii.1962 (1 ♀, CAS); Liard Hot Springs, Mile Post 496 Alaska Highway, 1500’, 9-10.vii.1959, R. E. Leech (1 ♂, CNC), same except 2.ix.1957, E. L. Kessel (1 ♀, 1 ♂, CAS); Liard River, 8.viii.1959, E. L. Kessel (1 ♀, CAS); Mile Post 104, Alaska Highway, 5.viii.1957, E. L. Kessel (3 ♀, 5 ♂, CAS), same except 5.viii.1959 (2 ♂, CAS); Mile Post 236, Alaska Highway, 13.vi.1962, E. L. Kessel (1 ♂, CAS); Mile Post 305, Alaska Highway, 6.viii.1957, E. L. Kessel (2 ♀, CAS), same except 6.viii.1959 (3 ♀, CAS); Mount Thornhill near Terrace, 29.vii.1960, W. R. Richards (1 ♀, CNC); Prince Rupert, 1.viii.1962, E. L. Kessel (1 ♂, CAS); Smithers, Highway 16, 30.vii.1962, E. L. Kessel (1 ♂, CAS); Vancouver, 13.ix.1932, H. B. Leech (1 ♀, CNC); **NOVA SCOTIA:** CBHNt. Pk. North Mt. PG765864, 1.vii.1984, dry spruce birch forest, H. J. Teskey, CNC DIPTERA 192200 (1 ♀, CNC); **ONTARIO:** Algonquin Provincial Park, Swan Lake Research Stn., Scott Lake, south end wet Hemlock Zone, 15.vi.1995, S. A. Marshall, JSS19226 (1 ♂, DEBU); Thunder Bay Distr., Pukaskwa N.P., Coastal Trail Playter Harbour, White River, sweep, 21.vii.2001, M. Buck, JSS25814 (1 ♀, DEBU); **YUKON TERRITORY:** Dawson City, 18.vi.1962, E. L. Kessel (3 ♀, 4 ♂, CAS; 1 ♂, CNC); Mile Post 102, Klondike Highway, 18.vi.1962, E. L. Kessel (4 ♀, 5 ♂, CAS; 1 ♂, CNC); **USA: ALASKA:** Anchorage, 19.vii.1921, J. M. Aldrich (2 ♂, USNM), same except 20.vii.1921 (1 ♂, USNM), same except 21.vii.1921 (2 ♀, 1 ♂, USNM); Chatanika River Camp Ground, 21.vi.1962, E. L. Kessel (2 ♂, CAS); Chickaloon River and Glenn Highway, 30.vi.1962, E. L. Kessel (1 ♀, 8 ♂, CAS), same except 1.vii.1962 (4 ♂, CAS); 20 mi. W. of Circle City, 23.vi.1962, E. L. Kessel (1 ♂, CAS); Clearwater, Alcan Camp Ground, 19.vi.1962, E. L. Kessel (1 ♀, CAS); Haines, 11.viii.1959, E. L. Kessel (1 ♀, CAS); Johnson Lake, 16 mi. S. of Soldatna, 5.vii.1962, E. L. Kessel (1 ♀, CAS); King Salmon, viii.1960, M. R. Wheeler & L. Throckmorton (1 ♀, CAS); 4 mi. S. of Livengood, 26.vi.1962, E. L. Kessel (1 ♂, CAS), same except 27.vi.1962 (1 ♀, 4 ♂, CAS); Matanuska River Camp Ground, 1.vii.1962, E. L. Kessel (2 ♂, CAS), same except 10.vii.1962 (2 ♂, CAS); Mile Post 90, 5 mi. E. of Soldatna, 5.vii.1962, E. L. Kessel (1 ♂, CAS); Mile Post 44 on Sterling Highway, 2.vii.1962, E. L. Kessel (2 ♀, 2 ♂, CAS); Mile Post 1231, E. Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (3 ♀, CAS); Moon Lake, Alaska Hwy. DC-1331, 8.vii.1978, P. H. Arnaud Jr. (1 ♀, CAS); Moose Creek Camp Ground, 1.vii.1962, E. L. Kessel (1 ♂, CAS); Peters Creek Camp Ground, 1.vii.1962, E. L. Kessel (1 ♀, CAS); Richardson Highway, 21 mi. N. of Delta Junction, 29.vi.1962, E. L. Kessel (11 ♂, CAS); same except 27 miles N. of Delta Junction (9 ♀, CAS); Salcha River Camp Ground, 20.vi.1962, E. L. Kessel (5 ♂, CAS), same except 29.vi.1962 (1 ♀, 10 ♂, CAS); Shaw Creek, 289 mi. Rich Highway, 11.vii.1951, Mason and McGillis (1 ♀, 1 ♂, CNC); Soldatna, 5.vii.1962, E. L. Kessel (1 ♂, CAS); 16 mi. S. of Soldatna, 3.vii.1962, E. L. Kessel (1 ♀, 5 ♂, CAS); Spenard, 25.viii.1957, E. L. Kessel (1 ♂, CAS), same except 16.viii.1959 (1 ♂, CAS), same except 17.viii.1959 (3 ♀, CAS), same except 7.vii.1962 (1 ♂, CAS); 9 mi. E. Valdez, 11.vii.1962, E. L. Kessel (1 ♀, 1 ♂, CAS); same except 12.vii.1962 (2 ♀, 5 ♂, CAS); **CALIFORNIA:** Eldorado County, Fallen Leaf, 13.vii.1961, J. G. Chillcott (1 ♀, CNC); **NEVADA:** Ormsby County, 1 mi. E. Lake Tahoe, 20.vii.1950, C. P. Alexander (1 ♀, CAS); **NEW HAMPSHIRE:** Franconia, collection of Mrs. A. T. Slosson (1 ♀, AMNH; 1 ♀, USNM); **NEW YORK:** Adirondacks, Avalanche Trail, 30.vii.1929, A. L. Melander (1 ♀, USNM).

Geographical distribution and seasonal occurrence (Fig. 76).

Callomyia velutina is currently distributed in both western North America (Alaska, Yukon Territory, British Columbia, Alberta, California and Nevada) and eastern North America (Ontario, Nova Scotia, New York and New Hampshire). Adults have been collected from early June to early September.

Remarks.

The female of *C. velutina* is very similar to the female of the widespread Palaearctic species *C. amoena*, particularly in thoracic and abdominal colour patterns. However, the males of these two species differ in features of the terminalia, as well as in abdominal colour pattern.

One male specimen of this species yielded a barcode (JSS19226) and two female specimens, initially identified as *C. venusta*, also yielded barcodes (CNC DIPTERA 192200 and JSS25814) (Table 1). Until now, the female of *C. velutina* was unknown and was hidden within females of *C. venusta*. This barcode data revealed these cryptic females of *C. velutina* because they clustered closely together with the *C. velutina* male (<2% genetic divergence) in the Neighbour-joining tree (Fig. 78). Upon further inspection of these cryptic females, subtle morphological differences were found that distinguish females of *C. velutina* from those of *C. venusta*, which are indicated in the "Diagnosis" of *C. velutina* above.

Kessel & Buegler (1972) considered four of the seven paratypes of *C. velutina* to be conspecific with their new species *C. liardia* (= *C. proxima*). An additional paratype of *C. velutina* was also discovered to be conspecific with *C. proxima* (see "Remarks" under *C. proxima*). These records have been added to the "Additional material examined" of *C. proxima*.

***Callomyia venusta* Snow**

(Figs 1, 14, 24, 32, 40, 43, 46, 64, 69, 77)

Callomyia venusta Snow, 1894: 151. Type locality: Magdalena Mountains, New Mexico, USA.

Diagnosis.

This widespread Nearctic species is characterized by yellow and silver-blue markings on the abdomen (reduced in some males) and male terminalia with a molar-like surstylus and apically truncate postgonite. The male of *C. venusta* is most similar to the southwestern Nearctic species *C. browni*, but differs in abdominal colour, posteroventral seta somewhat longer and thinner on the base of the hind femur, width of hind tarsomere 1, and the terminalia, as indicated in the key to species. The male of this species also has similar terminalia to *C. velutina* from eastern and western North America, but the postgonite is truncate and slightly pointed apically (versus rounded apically). The female of *C. venusta* is very similar to *C. velutina* because of similar thoracic and abdominal markings. However, *C. venusta* can be distinguished from *C. velutina* by a complete silver-blue marking on abdominal tergite 5 (versus a silver-blue marking that is interrupted by a median dorsal dark band) and one less presutural intra-alar seta on the scutum.

Redescription.

Male. (Figs 14, 24) Body length 4.0–4.8 mm. Head silver-blue to silver-grey, occiput dark silver-grey; mouthparts including palpus brownish-yellow to brown; antenna with scape, pedicel, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (as in Fig. 41).

Thorax dark brown to velvety black with silver-grey dusting on postpronotal lobe, presutural scutum and supra-alar area of scutum; silver-grey to silver-blue markings usually on lateral portion of presutural scutum, notopleuron, posterior portion of postsutural scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-grey; postpronotal lobe yellowish-brown posteroventrally. Scutum with 6 notopleural setae.

Legs yellowish-brown to dark brown, hind leg darker with apex of femur, tibia and tarsomeres dark brown; apex of femur and base of tibiae brownish-yellow; coxae silver-grey dusted in most specimens. Midtibia with median anterodorsal seta absent, median dorsal seta present (as in Fig. 50); base of hind femur with strong stout posteroventral seta (as in Fig. 53). Hind tarsomere 1 slightly expanded, subequal to apical width of hind tibia, length approximately 2.5X width.

Wing hyaline with cell sc yellowish-brown in most specimens. Halter yellow with base of stem brown.

Abdomen dark brown to black with tergites 1–3 yellow, yellow reduced in some specimens (only on tergites 1 and 2, or only 2); lateral silver-white dusting on tergites 1 and 2;

lateral to anterolateral silver-blue marking on tergite 5, marking silver-grey or absent in some specimens; posterior silver-grey dusting on tergite 6 in some specimens; tergite 7 entirely brown to grey; sternites pale yellow to light brown, sternite 8 brown to grey.

Terminalia (Figs 64, 69) brown to grey, surstylus darker; hypandrial process and cercus brownish-yellow. Epandrium with short broad ventral lobe, rounded at apex, anteriorly directed; apical process moderately long, broad basally, pointed at apex. Surstylus molar-like, with 2 large cusps widely excavated in between; dorsal outer cusp broadly rounded in lateral view; ventral inner cusp slightly rounded in lateral view, truncate and minutely serrate medially in posterior view (Fig. 69). Hypandrium with moderately long apical process; process trifid, with 2 short apical projections and short stout rounded basoventral lobe. Postgonite long and wide, somewhat truncated and pointed at apex. Phallus with sharp extended hook at apex. Cercus short.

Female. (Figs 1, 32, 40) Body length 3.25–4.25 mm. Head silver-blue with occiput silver-grey to silver-brown; mouthparts including palpus pale yellow to brownish-yellow; antenna with scape and pedicel yellowish-brown to brown, first flagellomere and arista brown to dark brown. Antenna with first flagellomere short-oval (Fig. 43).

Thorax mainly black to velvety black with silver-blue markings on postpronotal lobe, entire lateral portion of presutural scutum, notopleuron, most of postsutural scutum and postalar callus; propleuron, mesopleuron, metapleuron, mediotergite and laterotergite silver-blue dusted; postpronotal lobe posteroventrally, supra-alar area of scutum, postalar callus anteriorly and posterior margin of anepimeron pale yellow to yellowish-brown. Scutum with 2 presutural intra-alar setae (Fig. 46).

Foreleg and midleg pale yellow to yellowish-brown with tarsomeres 2–5 brown; hind leg darker with apex of femur, tibia and tarsomeres dark brown; coxae silver-blue dusted in most specimens. Midtibia with median dorsal seta absent.

Wing hyaline with cell sc yellowish-white in some specimens. Halter yellow.

Abdomen dark brown to black with tergites 1–3 yellow; lateral silver-white markings or dusting on tergites 1 and 2; tergite 4 usually dark brown to black, yellow or silver-blue in a few specimens; tergite 5 entirely silver-blue; sternites white to light brown.

Terminalia with segment 8 and epiproct brown to dark brown, silver-grey dusted; hypoproct and cercus brownish-yellow.

Type material.

LECTOTYPE (designated by Kessel & Buegler 1972), ♂ labelled: "Magdelena./ New Mexico"; "Type."; "Callomyia/venusta/Snow" [handwritten on thick red label]; "Callomyia/ venusta/ Snow/ Det. Kessel"; "LECTOTYPE/ Callomyia/ venusta Snow/ labeled by PHArnaud I-1979/ Designated by Kessel/ + Buegler (1973) 1972 [handwritten on pinkish hand-coloured label]" (SEMC). **PARALECTOTYPES: USA: NEW MEXICO:** Hop Canyon, Magdalena Mountains, viii.1894, W. A. Snow (2 ♀, 1 ♂, SEMC).

Additional material examined.

CANADA: ALBERTA: Banff, Johnston Canyon, 4700', 18.vii.1962, K. C. Herrmann (1 ♀, 1 ♂, CNC), same except W. R. M. Mason (1 ♀, CNC), same except 6.viii.1962, malaise trap, W. R. M. Mason (1 ♀, CNC); Cypress Hills, Bear Creek Trail, 15.vii.1980, S. A. Marshall (1 ♀, DEBU); Waterton Lakes Nat. Pk., 7-12.vii.1980, H. J. Teskey, CNC DIPTERA 192201 (1 ♀, CNC); **BRITISH COLUMBIA:** Canadian Customs, Haines Highway, 21.vii.1962, E. L. Kessel (1 ♀, CAS); Fernie Provincial Camp Ground, 9.viii.1963, E. L. Kessel (1 ♂, CAS); Glacier National Park, ca. 1.6 km N. Glacier, 14.vii.1974, Paul H. Arnaud Jr. (1 ♀, CAS); Kleanza Creek, 14 miles E. of Terrace, 17.vi.1960, J. G. Chillcott (1 ♀, CNC); Liard Hot Springs, Mile Post 496, 8.viii.1959, E. L. Kessel (1 ♂, CAS); Mile Post 104, Alaska Highway, 5.viii.1957, E. L. Kessel (1 ♂, CAS), same except 5.viii.1959, E. L. Kessel (1 ♂, CAS); Richter Pass Rd., 7 mi. W. Osoyoos, 2.vi.1958, H. & A. Howden (1 ♀, CNC); Robson, 31.v.1947, H. R. Foxlee (1 ♀, CNC), same except 6.vi.1947 (1 ♀, CNC), same except 1.vi.1952 (1 ♀, CNC); Terrace, 24.vii.1960, W. R. Richards (1 ♀, CNC); Vancouver Is., 2.3 km from Lk. Cowichan, 19-28 vii.1985, I. M. Smith (1 ♂, CNC); Whiskers Province Park, 2.ix.1959, E. L. Kessel (1 ♀, CAS), same except 3.ix.1959 (1 ♀, CAS); **NEW BRUNSWICK:** Barber D., 24.vi.1914, J. D. Tothill (1 ♀, CNC); **QUEBEC:** James Bay Rte. km 133.7, 50°29'52N, 77°25'11W, black spruce/Sphagnum, yellow pans, 7-16.vii.2001, M. & B. Buck, JSS25815 (1 ♀, DEBU); Laniel, 18.vi.1944, A. R. Brooks (1 ♀, CNC); **YUKON TERRITORY:** Alaska Highway and Morly River, 24.vii.1962, E. L. Kessel (1 ♂, CAS); Dawson City, 18.vi.1962, E. L. Kessel (1 ♀, CAS); Mayo, 12.vi.1962, E. L. Kessel (1 ♀, CAS); Mile Post 102, Klondike Highway, 18.vi.1962, E. L. Kessel (1 ♀, CAS); **USA: ALASKA:** Bedrock Creek Camp Ground, 24.vi.1962, E. L. Kessel (1 ♀, CAS); Chatanika River Camp Ground, 21.vi.1962, E. L. Kessel (1 ♀, CAS); Chickaloon

River and Glenn Highway, 1.vii.1962, E. L. Kessel (1 ♀, CAS); Clearwater, Alcan Camp Ground, 19.vi.1962, E. L. Kessel (1 ♂, CAS); Haines, 11.viii.1959, E. L. Kessel (1 ♀, 4 ♂, CAS); same except 20.vii.1962 (3 ♀, CAS), same except 21.vii.1962 (2 ♀, CAS); Hyder, Camp Run-A-Muck, 5.viii.1996, 01604, Arnaud Flight Trap, P. H. Arnaud Jr. & M. M. Arnaud (2 ♀, CAS); 4 mi. S. of Livengood, 26.vi.1962, E. L. Kessel (2 ♀, CAS), same except 27.vi.1962 (3 ♀, 3 ♂, CAS); Mile 290, Richard Highway, 19.vi.1951, W. R. M. Mason (1 ♀, CNC); Mile Post 1254, East of Tetlin Junction, Alaska Highway, 14.vii.1962, E. L. Kessel (1 ♀, CAS); Moon Lake Camp Ground, 19.vi.1962, E. L. Kessel (1 ♂, CAS); Moose Creek, 1.vii.1962, E. L. Kessel (1 ♀, CAS); Mosquito Lake, 27 miles N. of Haines, 16.vii.1962, E. L. Kessel (2 ♀, 2 ♂, CAS), same except 17.vii.1962 (2 ♂, CAS); Richardson Highway, 27 miles N. of Delta Junction, 29.vi.1962, E. L. Kessel (1 ♀, 1 ♂, CAS); Seward, 26.vii.1921 (1 ♂, USNM); Seward Highway, 41 miles N. of Seward, 2.vii.1962, E. L. Kessel (1 ♂, CAS); Spenard, 17.viii.1959, E. L. Kessel (1 ♀, CAS); 9 miles E. of Valdez, 11.vii.1962, E. L. Kessel (7 ♀, 3 ♂, CAS), same except 12.vii.1962 (8 ♀, 3 ♂, CAS); **ARIZONA:** Cochise County, Pinery Center, 11.viii.1964, E. L. Kessel (1 ♀, CAS); Coconino County, Oak Creek Canyon, 8.viii.1964, E. L. Kessel (1 ♂, CAS); White Mountains, Coulter Ranch, 28.vi.1947, J. L. Sperry (1 ♂, USNM); **COLORADO:** Chaffee County, 2 miles E. of Garfield, 20.viii.1964, E. L. Kessel (1 ♀, CAS); 9 mi. N. Dillon Summit County, Blue River FC, 24.viii.1964, E. L. Kessel (1 ♀, CAS); Doolittle Ranch, Mt. Evans, 9000', 23.vii.1961, S. M. Clarke (1 ♂, CNC); Gilpin County, 3 mi. W. Rollinsville, 7.viii.1973, D. D. Wilder (1 ♂, CAS); Jefferson County, 6 mi. N.W. of Conifer, 22.viii.1964, E. L. Kessel (5 ♂, CAS); Lake County, 4 mi. W. of Twins Lakes, 22.viii.1964, E. L. Kessel (1 ♂, CAS); Peaceful Valley, viii.1926 (1 ♂, USNM); Pitkin County, 4 mi. E. of Aspen, 23.viii.1964, E. L. Kessel (1 ♂, CAS); Rio Grande County, 8000' South Fork, 20.vi.1972, malaise trap, W. W. Wirth (1 ♀, USNM); **IDAHO:** Kootenia County, Hwy 97, St. Joe National Forest, Forestry Rd. 438, 600 m N47°36.392' W116°40.099', tribs Beauty Ck., 19.vi.2014, B. J. Sinclair (1 ♂, CNC); Moscow Mt., 17.vi.1918, A. L. Melander (1 ♀, USNM); Priest Lake, 4 mi. Camp, viii.1920, A. L. Melander (1 ♀, USNM); Waha, 30.v.1924, A. L. Melander (1 ♀, USNM); **MAINE:** Mt. Katahdin, 10.vii.1959, H. C. Huckett (1 ♀, CNC); **MONTANA:** Sanders County, 9 mi. E. of Paradise, 31.viii.1962, E. L. Kessel (1 ♀, CAS); **NEW MEXICO:** Grant County, Pinos Altos Mountains, 28.viii.1951, E. L. Kessel (1 ♀, CAS); **NEW YORK:** Adirondacks, Avalanche Trail, 30.vii.1929, A. L. Melander (2 ♀, USNM); Chittenango, 7.ix.1970, D. J. Peckham (4 ♂, USNM); West Ridge McLean Resevoir, 22.viii.1924, collector unknown (1 ♀, CUIC); **UTAH:** Cache County, Logan Cyn., Bunchgrass Creek, 19-23.vii.1986, Hanson & Knowlton (1 ♀, LACM); Cache County, Logan Cyn., Twin Creek, 1-6.vii.1979, W. J. Hanson (1 ♀, LACM), same except 23-30.viii.1979 (1 ♂, LACM), same except 1-8.vii.1988 (1 ♀, LACM); Cache County, Logan Cyn., Tony Gr., 27.vi-6.vii.1987, N. Youssef (1 ♀, 1 ♂, LACM); Cache County, Tony Grove Creek, 1-6.viii.1990, W. J. Hanson (1 ♂, LACM), same except 8-15.vii.1994 (1 ♂, LACM); Summit County, Bear River R.S. 3 mi. S.E., 5-12.viii.1971, malaise trap, Hanson & Knowlton (1 ♀, LACM); Uinta Mountains, Cub Creek, 17.vii.1952, G. F. Knowlton & G. E. Bohart (2 ♀, LACM); **WASHINGTON:** Chimacum, 23.viii.1910, A. L. Melander (1 ♂, USNM); Friday Harbor, 25.vi.1909 A. L. Melander (1 ♀, USNM); Olympic National Park, Boulder Lake, 21.vii.1953, K. M. Fender (1 ♂, CAS); **WYOMING:** Grand Teton N.P., Jackson Lake Village, 23.vii.1971, G. C. Steyskal (1 ♀, USNM); **MEXICO:** Durango, 3 mi. E. El Salto, 8200’, 1.vii.1964, J. F. McAlpine (1 ♀, CNC); Durango, 10 mi. W. El Salto, 9000’, 8.vi.1964, J. F. McAlpine (2 ♂, CNC), same except 14.vi.1964, H. F. Howden (1 ♀, CNC), same except 19.vi.1964 (3 ♀, CNC), same except 21.vi.1964 (1 ♀, CNC), same except 30.vi.1964, R. M. Mason (1 ♀, CNC), same except 1.vii.1964 (1 ♀, CNC); Durango, 14 mi. S.W. El Salto, 8000’, 26.vi.1964, J. F. McAlpine (1 ♂, CNC).

Geographical distribution and seasonal occurrence (Fig. 77).

Callomyia venusta is a widespread North American species that ranges from Alaska to New Brunswick south to Mexico. Adults have been collected from late May to early September.

Remarks.

This species exhibits variation in abdominal colour and male terminalia. Some male specimens, with diagnostic morphological features characteristic of *C. venusta*, have reduced yellow markings on the abdomen (yellow only on tergites 1 and 2 instead of tergites 1–3) and reduced silver-blue on tergite 5 (marking sometimes completely absent). A few female specimens also have abdominal tergite 4 yellow instead of dark brown to black. In addition, an eastern series of four male specimens from Chittenango, New York show some variation in the hypandrial process of the terminalia. These specimens are the only male representatives of *C. venusta* from eastern North America (all other eastern specimens are females). Three of these males have a reduced basoventral lobe on the hypandrial process, whereas the fourth male, which was collected on the same day as the others, has the same sized basoventral lobe as more western male specimens of *C. venusta*. Additional collecting of eastern *C. venusta* males is required to determine the extent of variation in the terminalia and whether it represents intra or interspecific variation. Fresh material from both eastern and western populations would also be useful to obtain DNA barcode data, which could help determine if *C. venusta* is a single species or perhaps a species complex.

Two female specimens of *C. venusta* yielded COI barcode sequences (CNC DIPTERA 192201 and JSS25815) (Table 1). These two specimens clustered closely together with <2% genetic divergence in the Neighbour-joining tree (Fig. 78). Two additional female specimens that were initially identified as *C. venusta*, also yielded barcodes. These females clustered with a male specimen of *C. velutina* and are now considered to be females of *C. velutina*, see "Remarks" under *C. velutina*.

Phylogenetic analysis of *Callomyia* species relationships

The phylogenetic analysis was based on 19 species of *Callomyia*, including all described species except the Oriental species, *C. coei* and *C. triangulata* (see Material and Methods), and four platypezid outgroups. Morphological characters and character states are listed below and character state matrix is in Table 2.

Head

1. *Male first flagellomere size.* Large or extended (0); small or short (1).
2. *Female first flagellomere size*. Large or extended (0); small or short (1).
3. *Male first flagellomere shape*. Disc-like (0); oval (1); subtriangular (2); elongate-conical (3).
4. *Female first flagellomere shape*. Disc-like (0); oval (1); subtriangular (2); elongate-conical (3).

Thorax

5. *Postsutural supra-alar seta*. Present (0); absent (1).
6. *Male notopleural setae*. ≤ 4 setae (0); 5−6 setae (1); ≥ 7 setae (2).

Legs

7. *Female mid and hind tarsal 'soles'*. Absent (0); present (1).
8. *Midtibial anteroventral and posteroventral apical spurs*. Only posteroventral spur present (0); both spurs present (1).
9. *Male midtibial median anterodorsal and dorsal setae*. Absent (0); dorsal seta present, anterodorsal seta absent (1); anterodorsal and dorsal setae present (2).
10. *Female midtibial median dorsal seta*. Dorsal seta short or absent (0); dorsal seta long (1).
11. *Male hind femoral median posteroventral seta*. Absent (0); present (1).
12. *Male hind femoral basal posteroventral seta*. Absent (0); long thin and apically tapered (1); strong stout and apically tapered (2); strong stout and blunt (3).

Wing

13. *Vein* M_{1+2}. Branched (0); unbranched (1).
14. *Vein* R_1. Bare (0); setulose (1).
15. *Microtrichia*. Present on entire wing (0); reduced on wing and absent on costal cells (1).
16. *Wings tinted*. Present in both sexes on entire wing (0); present in both sexes apically (1); absent in females (2); absent in both sexes (3).

Male terminalia

17. *Surstylus*. Single lobed (0); double lobed (1).
18. *Surstylus shape*. Rectangular or triangular (0); molar-like (1); bifid (2); broadly lamellate (3).
19. *Surstylus ventral process*. Absent (0); moderately long (1); elongate (2).
20. *Surstylus ventral inner cusp*. Absent (0); tapered medially (1); narrowly truncate (2); moderately to broadly truncate (3).
21. *Apical process of epandrium*. Absent (0); short (1); elongate (2).
22. *Ventral lobe of epandrium*. Absent (0); minute (1); short (2); long (3).
23. *Postgonite length*. Short (0); long (1).
24. *Postgonite apex*. Rounded or tapered (0); truncate (1); fanned (2).
25. *Phallus*. Tubular (0); laterally compressed and blunt at apex (1); laterally compressed and hooked at apex (2).

26. *Hypandrial process length*. Short (0); long (1).
27. *Hypandrial process shape*. simple (0); bifid (1); trifid (2).
28. *Trifid hypandrial process apical projections and basoventral lobe*. Absent (0); short apical projections, short basoventral lobe (1); short apical projections, long basoventral lobe (2); long apical projections, short basoventral lobe (3); long apical projections, long basoventral lobe (4).

Larva

29. *Lateral processes*. Six or fewer processes per segment (0); eight processes per segment (1).
30. *Body shape*. Cylindrical and not flattened (0); oval and dorsoventrally flattened (1).
31. *Fusion of body segments*. Metathoracic and first abdominal segments not fused (0); metathoracic and first abdominal segments fused (1).
32. *Marginal processes*. Not duplicated on each segment (0); duplicated on each segment (1).

Results of phylogenetic analysis.

The parsimony analysis of the character state matrix (Table 2) resulted in 136 most parsimonious trees (length = 88, CI = 0.64, RI = 0.73, RC = 0.46). The strict consensus tree of the 136 most parsimonious trees (Fig. 79) is illustrated with tree support values (Bremer supports) above the branches. *A posteriori* character weighting using successive approximations according to the rescaled consistency index (RC) produced 32 trees from the 136 most parsimonious trees. One of these 32 trees (Fig. 80) was selected to show character state distribution.

The phylogenetic analysis confirmed the monophly of *Callomyia*, as indicated by a high Bremer support (Br = 5) shown in the strict consensus tree (Fig. 79). Thirteen character states support the monophyly of the group (Fig. 80), four of which are uniquely derived (female antennal size (2.1) and three larval characters (30.1, 31.1, 32.1)) and nine are homoplasious. The setulose R_1 wing vein (14.1) is a synapomorphy of *Callomyia*, however it shows homoplasy within the genus because of loss of this character state in *C. admirabilis*. Although the three larval character states appear synapomorphic for *Callomyia*, exact placement of these states on the cladogram is equivocal due to missing data, as only six species of *Callomyia* are known from the larval stage (see Table 2).

Within *Callomyia* there are two distinct clades (Fig. 79), based primarily on characters of the male terminalia, especially the shape of the surstylus. The first major clade (*C. bertae* + *C. proxima* + *C. dorsimaculata* + *C. elegans* + *C. sonora*) is supported by a uniquely shaped bifid surstylus (18.2) and a minute ventral lobe of the epandrium (22.1) (Fig. 80). The second major clade is supported, in part, by a molar-like shaped surstylus (18.1) and a trifid shaped hypandrial process (27.2). Included within this large clade is another monophyletic group that is defined primarily on the basis of a broadly lamellate shaped surstylus (18.3).

The phylogenetic analysis also reveals that the Nearctic species of *Callomyia* do not form a monophyletic group and are distributed within at least three *Callomyia* clades, as shown in the strict consensus tree (Fig. 79). Some Nearctic and Palaearctic species are closely related (e.g., *C. gilloglyorum* and *C. dives*; *C. corvina* and *C. speciosa*), while other species from these two regions (e.g., *C. proxima* and *C. elegans*) appear related but are not as fully resolved in the strict consensus tree. Although these Nearctic and Palaearctic species pairs are very similar, consistent morphological differences that indicate they are distinct species. This suggests that there are no Holarctic species within *Callomyia*, which is also supported by the DNA barcode data (Fig. 78).

DISCUSSION

Ten species of *Callomyia* are now known from the Nearctic Region. However, the total number of Nearctic species has not changed since Kessel and Buegler's (1972) revision of the group, because three species have now been synonymized (*C. cleta* = *C. calla*, *C. clara* = *C. corvina*, *C. liardia* = *C. proxima*) and three new species have been described (*C. argentea* **sp. nov.**, *C. arnaudi* **sp. nov.**, and *C. browni* **sp. nov.**). In addition, the cryptic female of *C. velutina* was discovered, which was previously concealed among similarly coloured females of *C. venusta*.

Previous species concepts of Nearctic *Callomyia* were based almost entirely on adult colour, although little attempt was made to understand the limits of colour variation (either intra and interspecifically). This is because few, if any additional morphological characters (including male terminalia) were used in combination with colour to determine species boundaries within the group. In this revision, additional morphological characters (i.e., antennal shape, setation, features of the legs, and male terminalia) were used, in combination with colour, to expand and test the species concepts. Chandler (1994) found that differences in the male terminalia of Platypezidae are the most conclusive means for establishing species limits. This appears to be the case in Nearctic *Callomyia*, as the male terminalia are diagnostic for all of the species. The male terminalia, along with other structural characters used in both males and females (i.e., shape of the first flagellomere, length of hind tarsomere 1, setae on the thorax, and setae on the legs) helped determine the limits of colour variation within and between the species. Once colour variation was better understood, it became useful for delimiting many of the species and this is reflected in the key to species for each sex.

Three species of Nearctic *Callomyia* (*C. argentea* **sp. nov.**, *C. bertae*, and *C. browni* **sp. nov.**) are currently known from males only. Species of this genus are rarely collected in the Nearctic Region, which has resulted in some species being known from a single or very few specimens (e.g., species listed above). Because of limited collecting records, in addition to the presence of sexual dimorphism and a lack of rearing events (Chandler 1974), associating the sexes of Nearctic species has been difficult. Despite these constraints, six species that were known from a single sex have now been associated and synonymized. This is based on evidence from collecting series (same locality and date) and some DNA barcode data. Nevertheless, further collecting of the Nearctic species is required to at least discover the missing females of the three species known only from males and to provide fresh material for additional DNA barcoding. In addition, discovery of the immature stages of Nearctic species other than *C. gilloglyorum*, will add to our knowledge of larval morphology and fungal host-associations, and if reared will also assist with the association of sexes.

Only a small amount of DNA barcode data (17 specimens of *Callomyia*) was available for this revision. These specimens were analyzed in a Neighbour-joining tree (Fig. 78) with two outgroup specimens. Within this tree, the 17 specimens formed six species clusters, based on <2% genetic divergence, although one male specimen of *C. liardia* (= *C. proxima*) had a slightly greater genetic divergence than the remainder of the *C. proxima*/ *C. liardia* cluster (see "Remarks" under *C. proxima*). This preliminary barcode data supported the synonymy of *C. liardia* and *C. proxima* and helped reveal the identity of the female of *C. velutina*, which was previously confused with the female of *C. venusta*. In addition, specimens of three Palaearctic species (*C. amoena*, *C. dives*, and *C. speciosa*) were analyzed in the Neighbour-joining tree. These Palaearctic species each formed their own individual clusters, which remained separate (>2% genetic divergence) from the Nearctic species analyzed (e.g., *C. amoena* and *C. velutina*).

The Holarctic and Oriental distribution of *Callomyia*, along with its placement in the Platypezidae (a lower Cyclorrhaphan family), suggests a Laurasian lineage of late Mesozoic or early Tertiary age. This agrees with the fossil record of Platypezidae, which is known as far back as the Upper Cretaceous (Grimaldi & Cumming 1999), and is consistent with patterns shown in other Northen Hemisphere Diptera groups of similar age (Sinclair et al. 2011; Saigusa 2012). An evolutionary history of the genus throughout the Tertiary would have provided ample opportunity for faunal interchange between the Old and New World. This would explain the close relationships found between many of the Nearctic and Palaearctic species of *Callomyia* (Fig. 79). The resolved sister-group relationship between *C. gilloglyorum* and *C. dives*, from western Nearctic and widespread Palaearctic respectively, likely suggests a Tertiary connection across Beringia (Savage & Wheeler 1999). The other resolved sister-group relationship between *C. corvina* and *C. speciosa*, from western Nearctic and western Palaearctic respectively, is an unusual pattern for sister groups of Tertiary age because it is usually found in relationships that date from the Cretaceous (Sanmartin et al. 2001). It is likely that the geographic distributions of these two species are poorly represented due to limited collecting events, which will require further collecting in the eastern Palaearctic and eastern Nearctic to determine whether a Berginian or north Atlantic connection was involved. Greater resolution in the terminal branches of the phylogeny is required to determine further sister-group relationships between the Nearctic and Palaearctic species, which may help uncover additional zoogeographic connections within *Callomyia*.

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REFERENCES

Agassiz, L. (1846) *Nomenclatoris zoologici index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus*. [= Fasc. XII]. “1847”. Jent & Gassman, Solothurn. viii + 393 pp.

Bremer, K. (1994) Branch support and tree stability. *Cladistics*, 10, 295–304.

Chandler, P.J. (1974) Additions and corrections to the British list of Platypezidae (Diptera), incorporating a revision of the Palaearctic species of *Callomyia* Meigen. *Proceedings and Transactions of the British Entomological Society*, 7, 1–32.

Chandler, P.J. (1991) Platypezidae. *In*: Soos, A. & Papp, L. (Eds.), *Catalogue of Palaearctic Diptera, Volume 7, Dolichopodidae–Platypezidae*. Elsevier Science Publishing, pp. 205–217.

Chandler, P.J. (1994) The Oriental and Australasian species of Platypezidae (Diptera). *Invertebrate Taxonomy*, 8, 351–434.

Chandler, P.J. (2001) The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica*, 36, 1–276.

Chandler, P.J. (2010) Platypezidae (flat-footed flies). *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, Volume 2, NRC Research Press, Ottawa, Ontario, Canada, pp. 715–719.

Chandler, P.J. & Shatalkin, A.I. (1998) Family Platypezidae. *In*: Papp, L. & Darvas, B. (Eds.), *Contributions to a Manual of Palaearctic Diptera, Volume 3, Higher Brachycera.* Science Herald, Budapest, pp. 27–49.

Coquillett, D.W. (1910) The type-species of the North American genera of Diptera. *Proceedings of the United States National Museum*, 37, 499–647.

Cumming, J.M., & Wood, D.M. (2009) Adult morphology and terminology. *In*: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*, Volume 1, NRC Research Press, Ottawa, Ontario, Canada, pp. 9–50.

Fallén, C.F. (1810) *Specim. entomolog. novam Diptera disponendi methodum exhibens*. Berlingianis, Lund. 26 pp.,1 pl.

Fallén, C.F. (1815) *Platypezidae et Bombyliarii Sveciae.* Lund. 12 pp.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplifcation of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Grimaldi, D. & Cumming, J. (1999) Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History*, 239, 1–124.

Hajibabaei, M., deWaard, J.R., Ivanova, N.V., Ratnasingham, S., Dooh, R.T., Kirk, S.L., Mackie, P.M. & Hebert, P.D.N. (2005) Critical factors for assembling a high volume of DNA barcodes. *Philosophical Transactions of the Royal Society, B*, 360, 1959–1967.

Hebert, P.D.N., Ratnasingham, S. & de Waard, J.R. (2003) Barcoding animal life: cytochrome c oxidase subunit 1 divergence among closely related species. *Proceedings of the Royal Society, B*, 270, S96–S99.

International Commission on Zoological Nomenclature (1963) Opinion 678. The suppression under the plenary powers of the pamphlet published by Meigen, 1800. *Bulletin of Zoological Nomenclature*, 20, 339–342.

International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London. xxix + 306 pp.

Johnson, C.W. (1916) Further studies on the Platypezidae. *Psyche*, 23, 27–33.

Kessel, E.L. (1948) New species of *Callomyia* from California (Diptera: Clythiidae). *The Wasmann Collector*, 7, 140–148.

Kessel, E.L. (1961a) New species of flat-footed flies from North America (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 19, 191–227.

Kessel, E.L. (1961b) The immature stages of *Callomyia*, with the description of a new species of this genus (Diptera: Platypezidae). *Occasional Papers of the California Academy of Sciences*, 30, 1–10.

Kessel, E.L. (1966) Diptera from Nepal, new species of *Platypeza* and *Callomyia* (Family Platypezidae). *Bulletin of the British Museum (Natural History), Entomology*, 17, 453–455.

Kessel, E.L. (1987) Platypezidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Coords.), *Manual of Nearctic Diptera*, Volume 2. Agriculture Canada Monograph, 28, pp. 681–688.

Kessel, E.L. & Buegler, M.E. (1972) A review of the genus *Callomyia* in North America, with the description of a new species (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 30, 241–278.

Kessel, E.L., Buegler, M.E. & Keyes, P.M. (1973) A survey of the known larvae and puparia of Platypezidae, with a key to ten genera based on immature stages (Diptera). *The Wasmann Journal of Biology*, 31, 233–261.

Kessel, E.L. & Clopton, J.R. (1969) The Platypezidae of the Oriental Zoogeographic Region and Islands to the east, with descriptions of four new species (Diptera). *The Wasmann Journal of Biology*, 27, 25–73.

Kessel, E.L. & Kessel, B.B. (1962) Mating behaviour and activity – rest periodicity in *Protoclythia californica* (Diptera: Platypezidae). *Proceedings of the California Academy of Sciences*, (4) 32, 57–78.

Kessel, E.L. & Maggioncalda, E.A. (1968) A revision of the genera of Platypezidae, with the descriptions of five new genera and considerations of phylogeny, circumversion and hypopygia (Diptera). *The Wasmann Journal of Biology*, 26, 33–106.

Krivosheina, N.P. (2008a) Macromycete fruit bodies as a habitat for Dipterans (Insecta, Diptera). *Entomological Review*, 88, 778–792.

Krivosheina, N.P. (2008b) On Biology of xylobiont platypezid larvae of the genus *Callomyia* (Diptera, Platypezidae). *Entomological Review*, 88, 973–982.

Krivosheina, N.P. & Mamayev, B.M. (1967) [Key for the identification of larvae of wood-inhabiting Diptera]. Nauka, Moscow. 367 pp. (in Russian).

Lundbeck, W. (1927) Diptera Danica. Genera and species of flies hitherto found in Denmark. Volume 7, Platypezidae and Tachinidae. Gad, Copenhagen, pp. 1–39.

Maddison, W.P. & Maddison, D.R. (2003) *MacClade 4: Analysis of phylogeny and character evolution. Version 4.06.* Sinauer Associates, Sunderland, Massachusetts.

Meigen, J.W. (1800) *Nouvelle classification des mouches à deux ailes (Diptera L.) d'après un plan tout nouveau. Par J.G. Meigen.* Fuchs, Paris. 40 pp.

Meigen, J.W. (1804) *Klassifikazion und Beschreibung der europäischen zweiflügeligen Insekten. (Diptera Linn.)*. Erster Band. Abt. I. pp. i–xxviii + 1–152, pls. 1–8; Abt. II, pp. i–vi + 153–314, pls. 9–15. Braunschweig.

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364.

Roser, C. von. (1840) Erster Nachtrag zu dem in Jahre 1834 bekannt gemachten Verzeichnisse in Württemberg vorkommender zweiflügliger Insekten. *Correspondenzblatt de Königlich Württembergischen Landwirtschaftlichen Vereins* 37 [5 n. ser., 17] (1), 49–64.

Saigusa, T. (2012) A new Asio-Nearctic subgenus of *Rhamphomyia* (Diptera: Empididae: Empidinae). *The Canadian Entomologist*, 144, 291–322.

Sanmartin, I., Enghoff, H. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, 73, 345–390.

Savage, J. & Wheeler, T.A. (1999) Systematics of *Cetema* Hendel (Diptera: Chloropidae): revision of the Nearctic species and phylogeny and zoogeography of the Holarctic fauna. *Entomologica Scandinavica*, 30, 249–262.

Shatalkin, A.I. (1980) [New species of Platypezidae (Diptera) from Middle Amur Territory]. *Éntomologicheskoye Obozrenie*, 59, 660–665 (in Russian, English summary).

Shatalkin, A.I. (1982) [New species of flat-footed flies (Diptera, Platypezidae) from Siberia and the far east]. [*Helminths, Mites and Insects. New and Little-Known Species of the Siberian Fauna*], 16, 68–75 (in Russian).

Shatalkin, A.I. (1992) New and little-known Palaearctic species of Platypezidae, Psilidae and Lauxaniidae (Diptera). *Russian Entomological Journal*, 1, 59–74.

Sinclair, B.J. & Cumming, J.M. (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa*, 1180, 1–172.

Sinclair, B.J., Brooks, S.E., Cumming, J.M. & Coovert, G.A. (2011) Revision of the Nearctic species of *Heleodromia* (Diptera: Empidoidea: Brachystomatidae). *The Canadian Entomologist*, 143, 629–651.

Snow, W.A. (1894) American Platypezidae. *Kansas University Quarterly*, 3, 143–152.

Sorenson, M.D. (1999) *TreeRot, Version 2*. Boston University, Boston, Massachusetts.

Swofford, D.L. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10.* Sinauer Associates, Sunderland, Massachusetts.

Tkoč, M. (2012) A new species of the flat-footed fly genus *Callomyia* (Diptera: Platypezidae) from South China. *Acta Entomologica Musei Nationalis Pragae*, 52, 289–296.

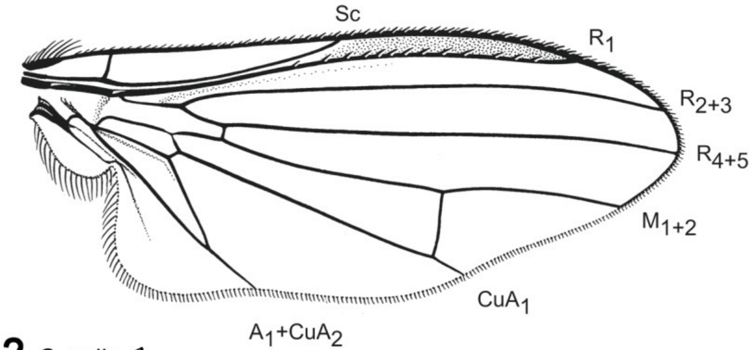
Tkoč, M., Mocek, B. & Barták, M. (2012) New records of the flat-footed flies (Diptera: Platypezidae) from the Czech Republic and Slovakia. *Klapalekiana*, 48, 269–274.

Table 1. Voucher information for *Callomyia* specimens submitted for barcoding, including geographic locality, institution housing the specimen (in parentheses), unique voucher number and GenBank number. Nearctic species names as used by Kessel & Buegler (1972).

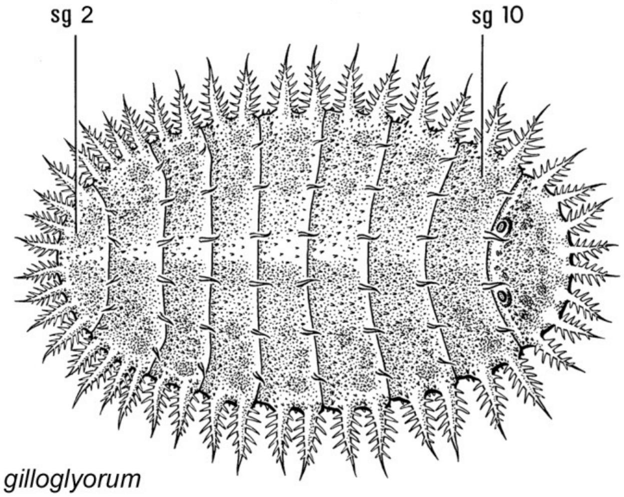
Species, sex	**Locality**	**Voucher**	**GenBank**
Callomyia amoena ♂	Germany: Nordrhein-Westfalen (CNC)	CNC DIPTERA 192202	KM438940
Callomyia amoena ♂	France: Lorraine (CNC)	CNC DIPTERA 192203	KM438939
Callomyia amoena ♀	Germany: Nordrhein-Westfalen (CNC)	CNC DIPTERA 192204	KM438941
Callomyia dives ♂	Spain: Canary Islands (ZMUC)	JSS26019	KM438942
Callomyia liardia ♂	Canada: Ontario (DEBU)	DEBU 00075059	KM438944
Callomyia liardia ♂	Canada: Quebec (LEM)	JSS26016	KM4389445
Callomyia liardia ♂	Canada: Quebec (LEM)	JSS26017	KM438943
Callomyia proxima ♀	Canada: Quebec (CNC)	CNC DIPTERA 192199	KM438947
Callomyia proxima ♀	Canada: Quebec (LEM)	JSS26018	KM438946
Callomyia speciosa ♀	Spain: Segovia (CNC)	CNC DIPTERA 192205	KM438948
Callomyia speciosa ♂	Germany: Bayern (CUIC)	CNC DIPTERA 192207	KM438949
Callomyia speciosa ♀	Germany: Bayern (CUIC)	CNC DIPTERA 192208	KM438950
Callomyia velutina ♂	Canada: Ontario (DEBU)	JSS19226	KM438951
Callomyia venusta ♀	Canada: Nova Scotia (CNC)	CNC DIPTERA 192200	KM438954
Callomyia venusta ♀	Canada: Ontario (DEBU)	JSS25814	KM438955
Callomyia venusta ♀	Canada: Alberta (CNC)	CNC DIPTERA 192201	KM438952
Callomyia venusta ♀	Canada: Quebec (DEBU)	JSS25815	KM438953
Agathomyia sp. ♀	Canada: Quebec (LEM)	JSS20530	KM438937
Bertamyia notata ♀	Canada: Ontario (CNC)	CNC DIPTERA 197610	KM438938

Table 2. Character state matrix used for *Callomyia* phylogenetic analysis (characters 1–32). Outgroup taxa are listed at beginning of table. Missing character states are indicated by a "?".

	1	1111111112	2222222223	33
	1234567890	1234567890	1234567890	12
Melanderomyia kahli	0000000000	0010000000	0002000000	00
Grossoseta johnsoni	1022001111	1100001101	00000000??	??
Bertamyia notata	0033101000	0010130000	0211211010	00
Agathomyia antennata	0033011011	0310120000	2300111010	00
Callomyia argentea	1?1?01111?	0211131103	1211212l??	??
Callomyia arnaudi	1111011110	0111131310	22102123??	??
Callomyia bertae	1?1?01111?	0111131200	11112110??	??
Callomyia browni	1?1?01111?	0211131103	12112121??	??
Callomyia calla	1111011110	0211131101	12112122??	??
Callomyia corvina	1111011120	0111121310	13112100??	??
Callomyia gilloglyorum	1132021110	0111121320	2210212411	11
Callomyia proxima	1111011121	0111131200	11112110??	??
Callomyia velutina	1111011110	0111131102	12102121??	??
Callomyia venusta	1111011110	0211131103	12112121??	??
Callomyia admirabilis	1111011121	0110131320	1211212111	11
Callomyia amoena	1111011111	0211121310	1211212111	11
Callomyia dives	1132011121	0111121320	2210212411	11
Callomyia dorsimaculata	1?1?011110	0211131200	11112110??	??
Callomyia elegans	1111011121	0211131200	11112110??	??
Callomyia krivosheinae	?1?10?11?0	0?11131310	1211212111	11
Callomyia saibhira	111101111?	0?11131310	22102124??	??
Callomyia sonora	1111011121	0211111200	11112110??	??
Callomyia speciosa	1111011121	0211131310	1311210011	11

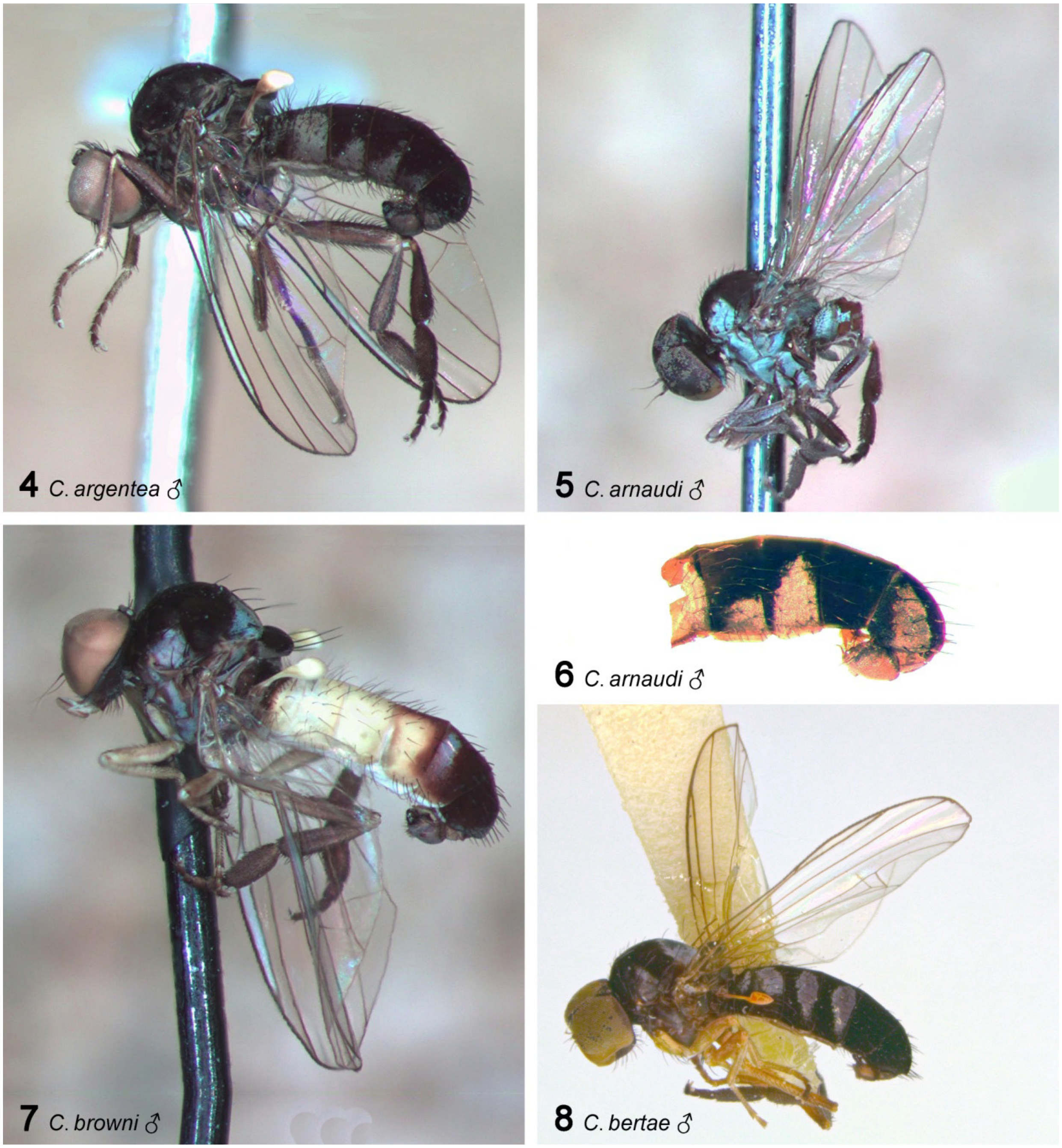


2 *C. calla* ♂

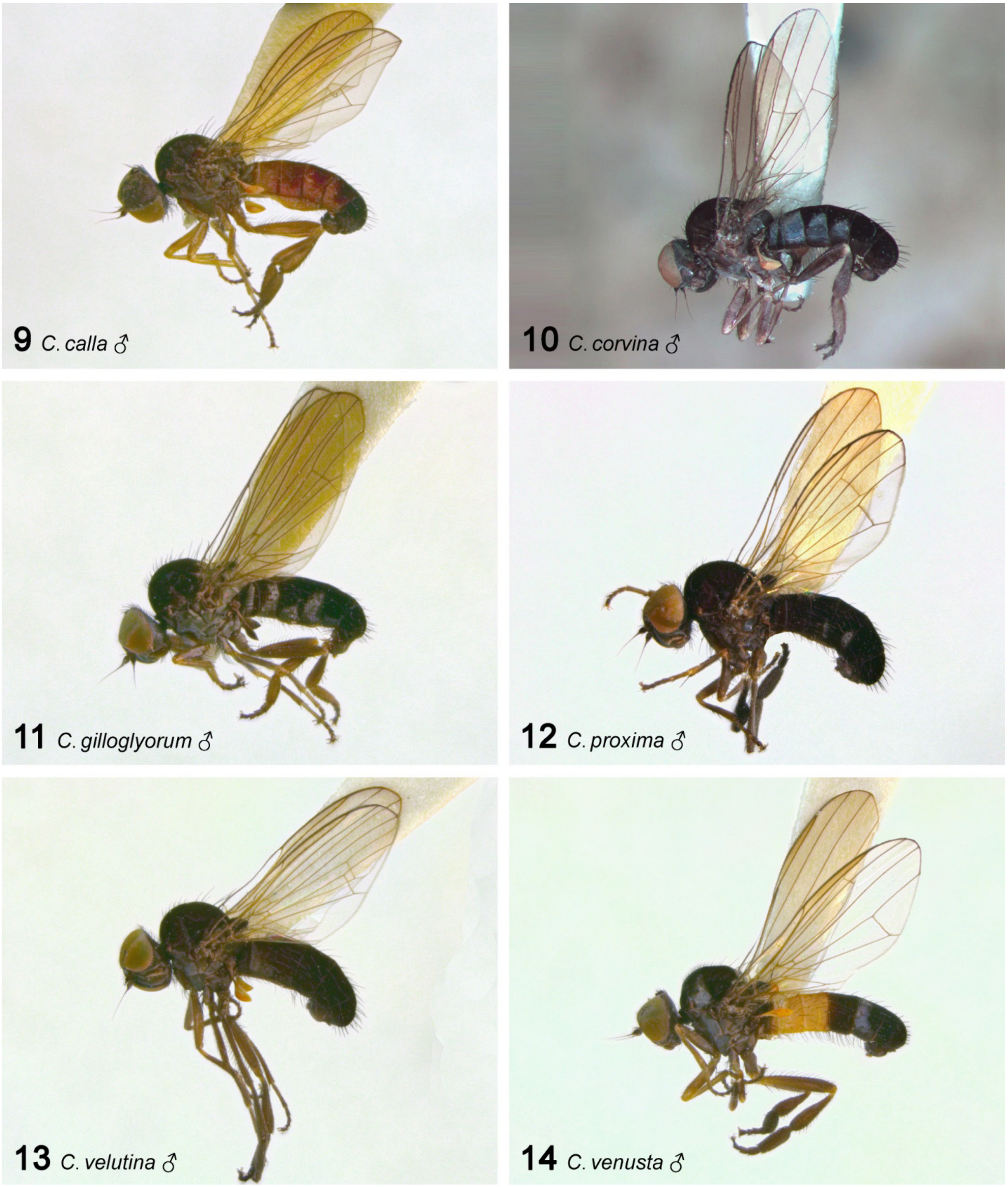


3 *C. gilloglyorum*

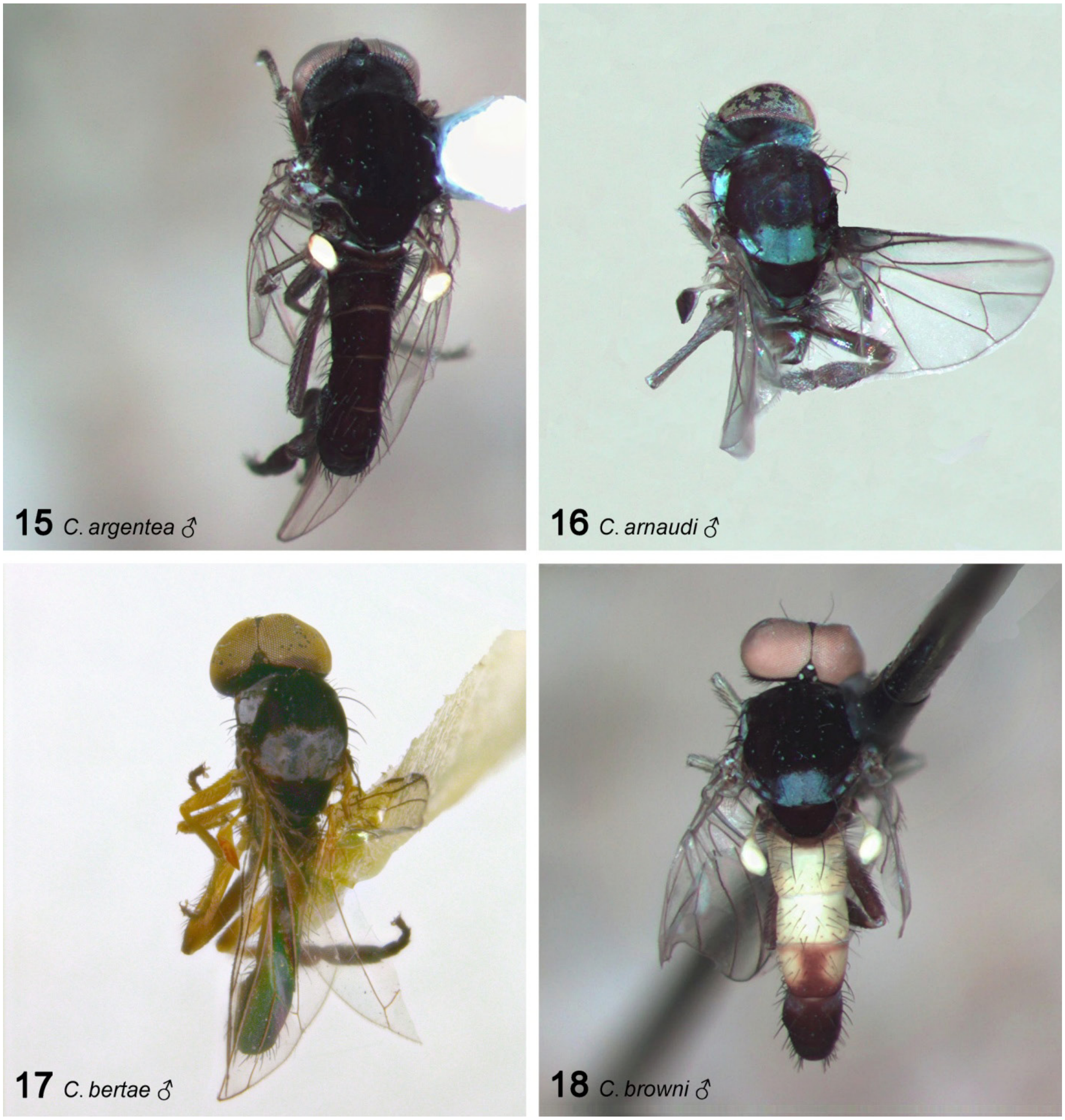
Figure 1. *Callomyia venusta*, female on leaf (photograph by Andrew Young). **Figure 2.** *Callomyia calla*, male wing (from Kessel 1987, fig. 50.4). **Figure 3.** *Callomyia gilloglyorum*, larva (from Kessel 1987, fig. 50.32). Abbreviations: A_1+CuA_2 – anal vein and second branch of anterior cubital vein; CuA_1 – first branch of anterior cubital vein; M_{1+2} – first branch of media; R_1 – first branch of radius; R_{2+3} – second branch of radius; R_{4+5} – third branch of radius; Sc – subcosta; sg – segment.



Figures 4–8. *Callomyia* males, lateral view. **4.** *C. argentea*. **5.** *C. arnaudi* (abdomen removed). **6.** *C. arnaudi* abdomen in glycerin (coloured markings more metallic bluish-white than depicted). **7.** *C. browni*. **8.** *C. bertae*.

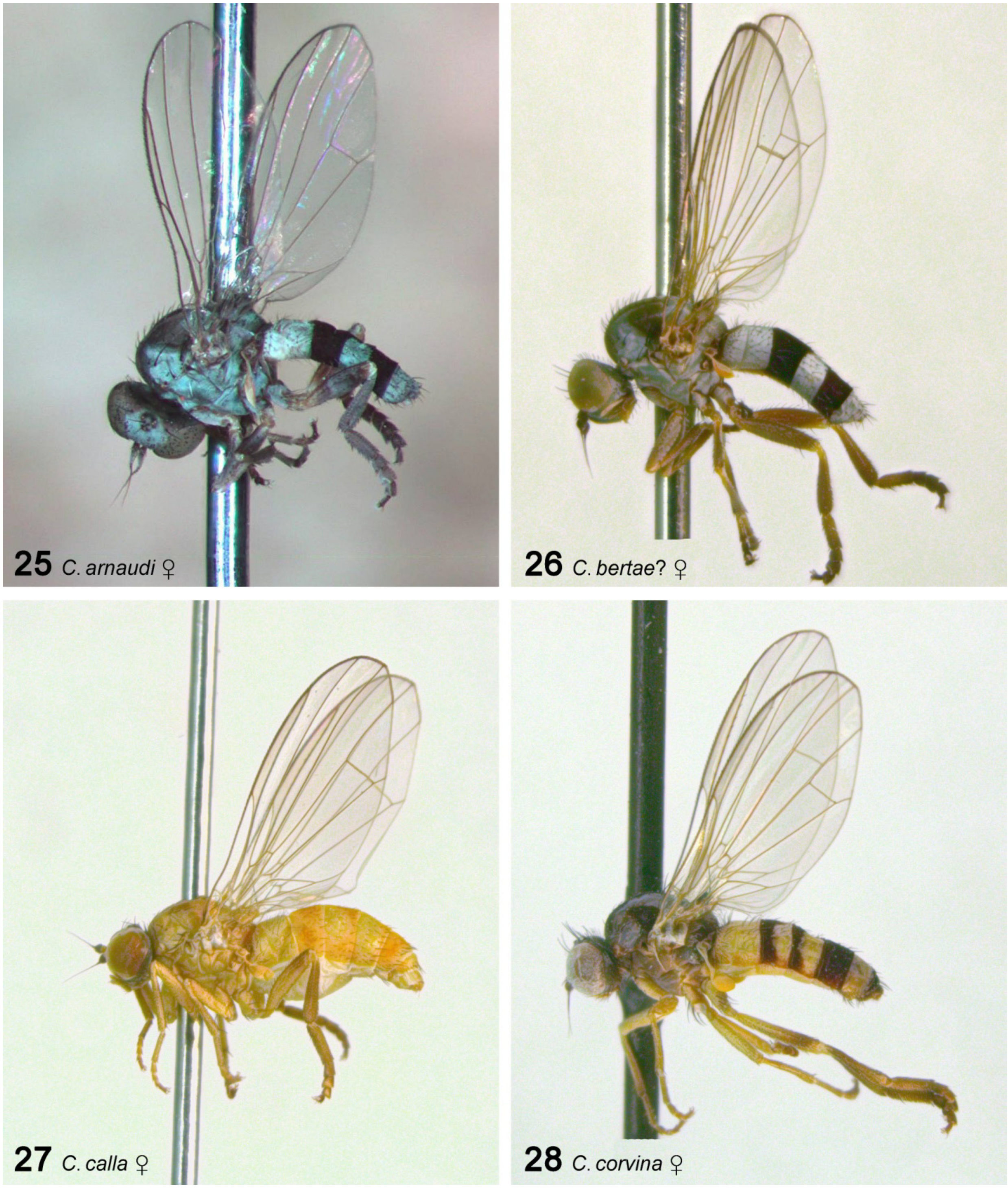


Figures 9−14. *Callomyia* males, lateral view. **9.** *C. calla*. **10.** *C. corvina*. **11.** *C. gilloglyorum*. **12.** *C. proxima*. **13.** *C. velutina*. **14.** *C. venusta*.

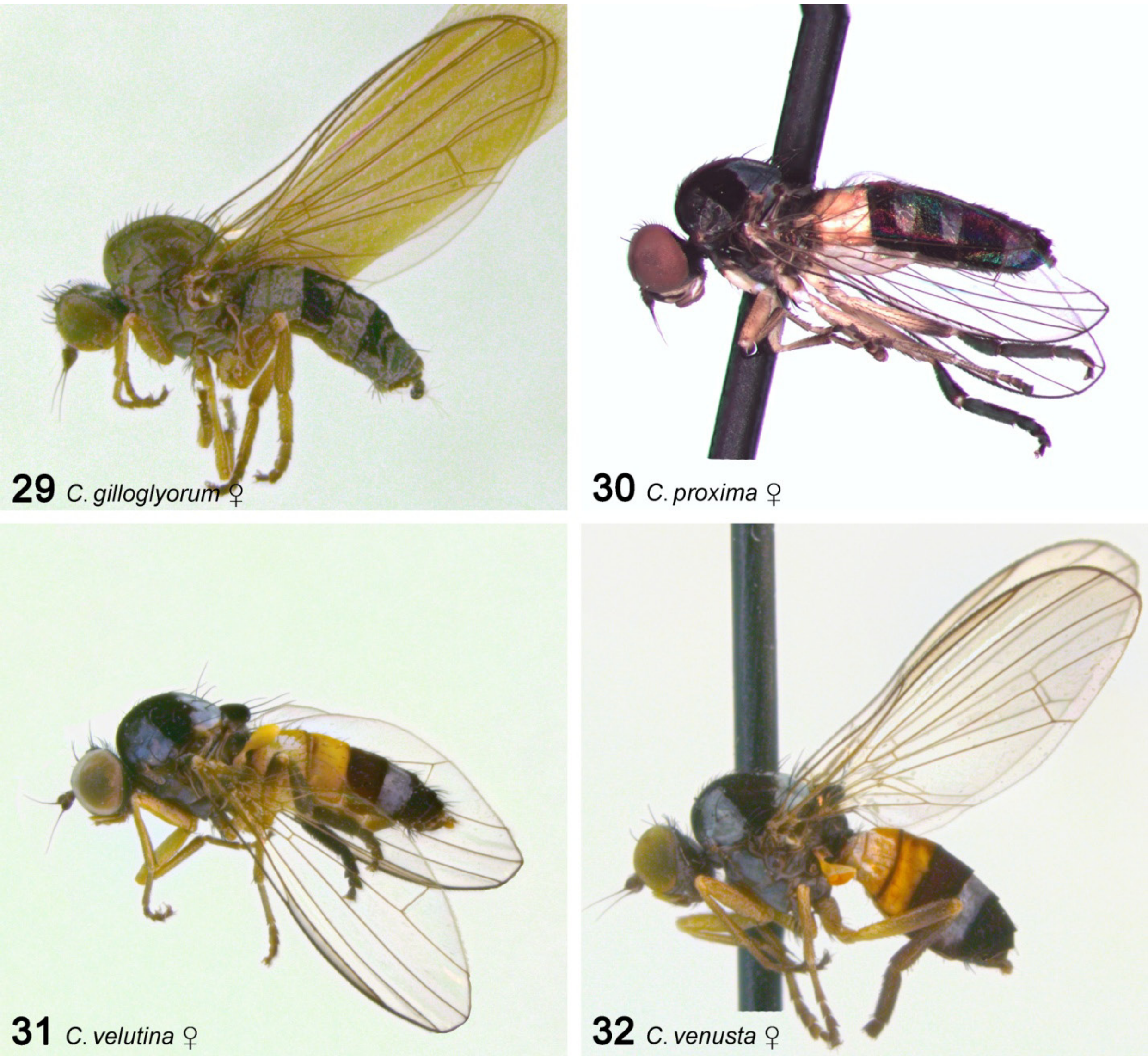


Figures 15−18. *Callomyia* males, dorsal view. **15.** *C. argentea*. **16.** *C. arnaudi* (abdomen removed). **17.** *C. bertae*. **18.** *C. browni*.

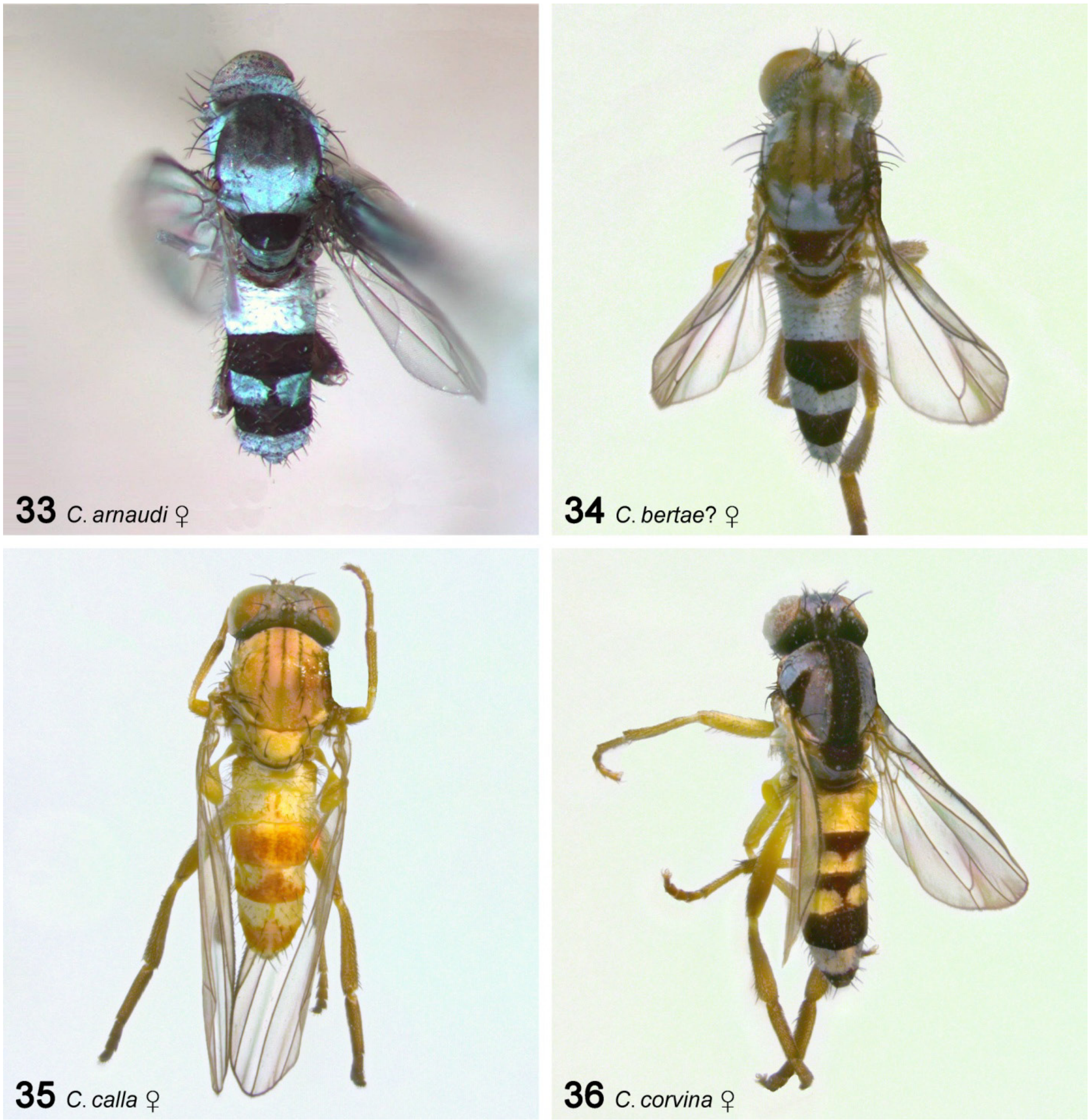
Figures 19−24. *Callomyia* males, dorsal view. **19.** *C. calla*. **20.** *C. corvina*. **21.** *C. gilloglyorum*. **22.** *C. proxima*. **23.** *C. velutina*. **24.** *C. venusta*.



Figures 25‒28. *Callomyia* females, lateral view. **25.** *C. arnaudi*. **26.** Possible *C. bertae* female. **27.** *C. calla*. **28.** *C. corvina*.

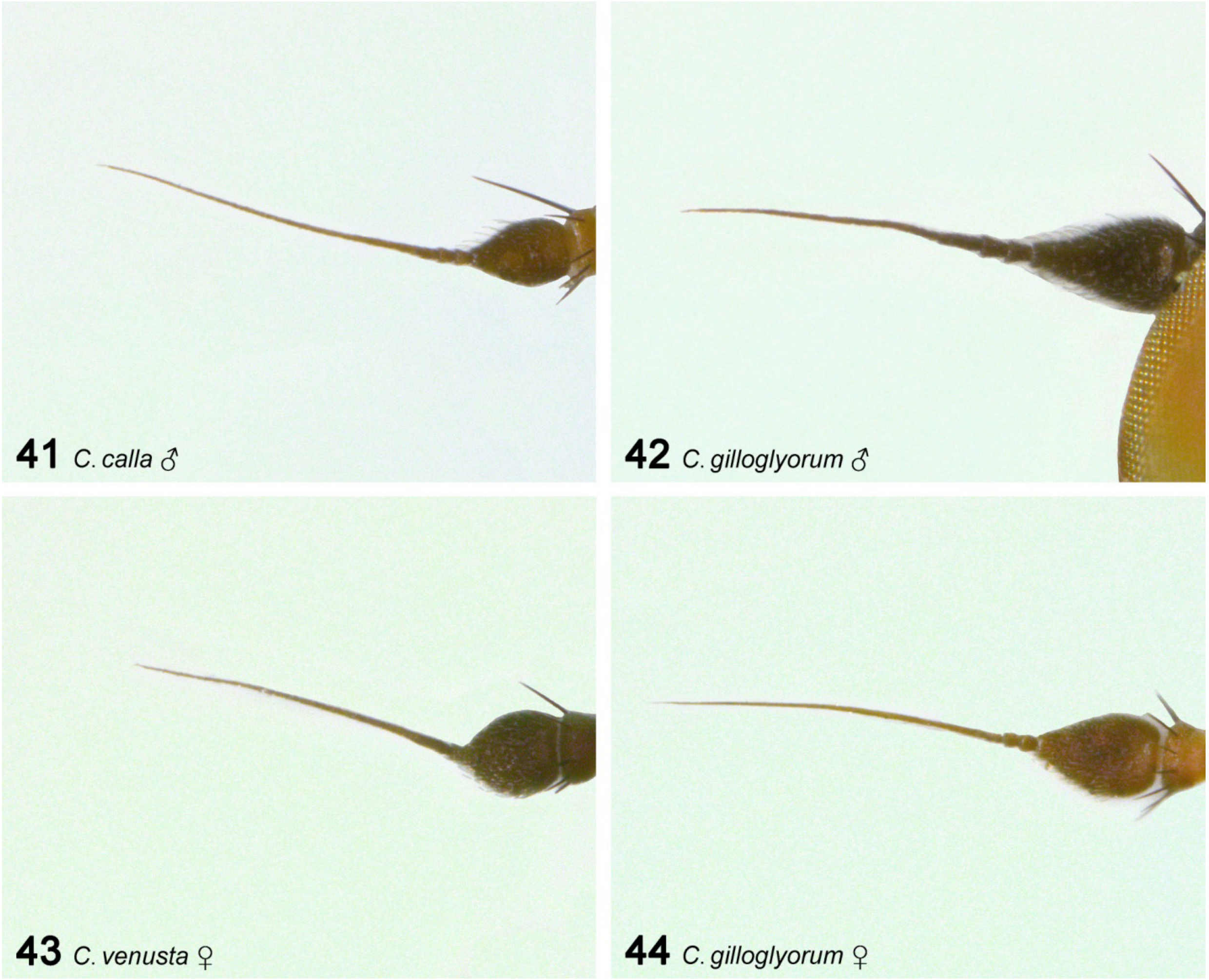


Figures 29−32. *Callomyia* females, lateral view. **29.** *C. gilloglyorum*. **30.** *C. proxima*. **31.** *C. velutina*. **32.** *C. venusta*.

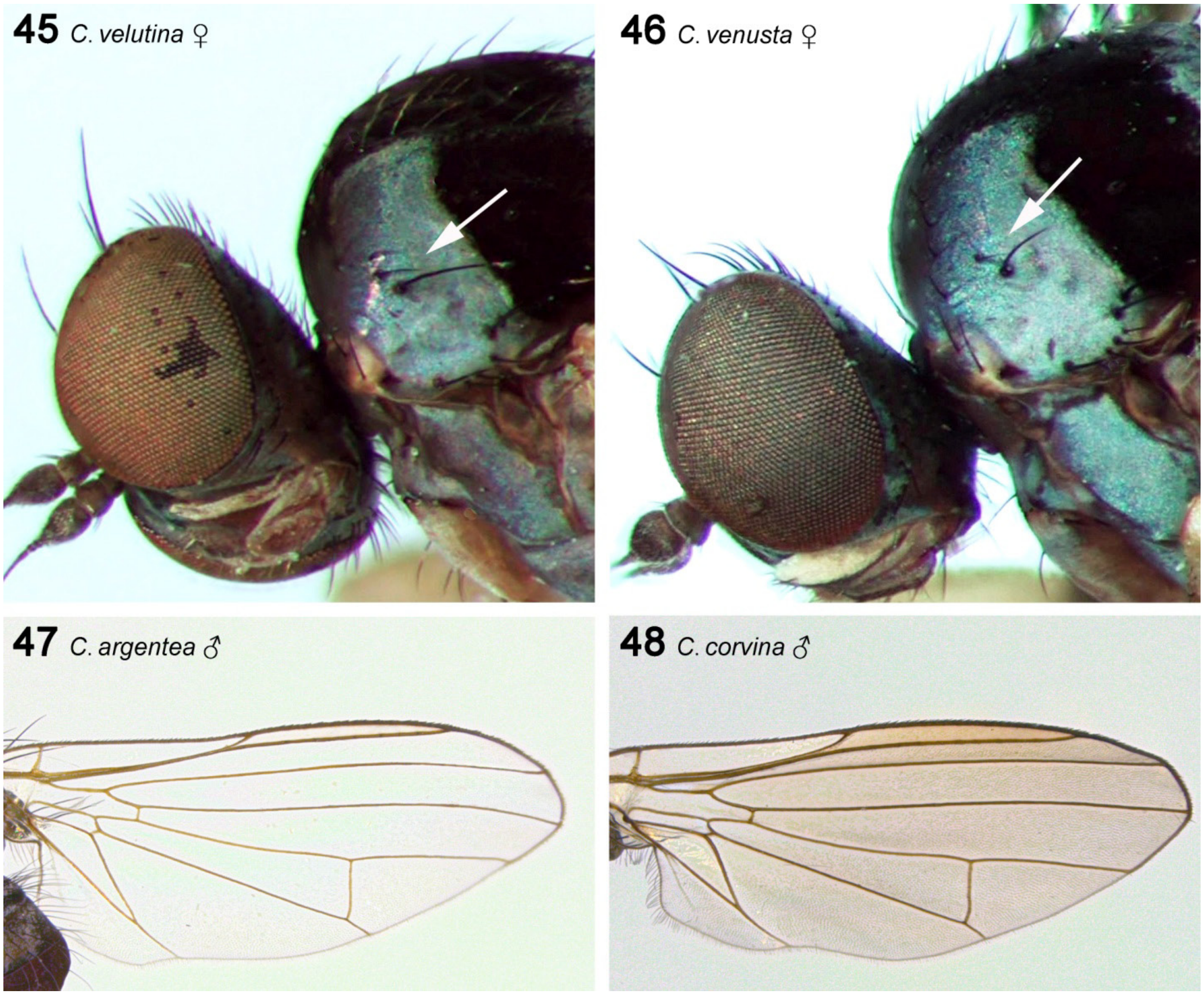


Figures 33–36. *Callomyia* females, dorsal view. **33.** *C. arnaudi*. **34.** Possible *C. bertae* female. **35.** *C. calla*. **36.** *C. corvina*.

Figures 37−40. *Callomyia* females, dorsal view. **37.** *C. gilloglyorum*. **38.** *C. proxima*. **39.** *C. velutina*. **40.** *C. venusta*.

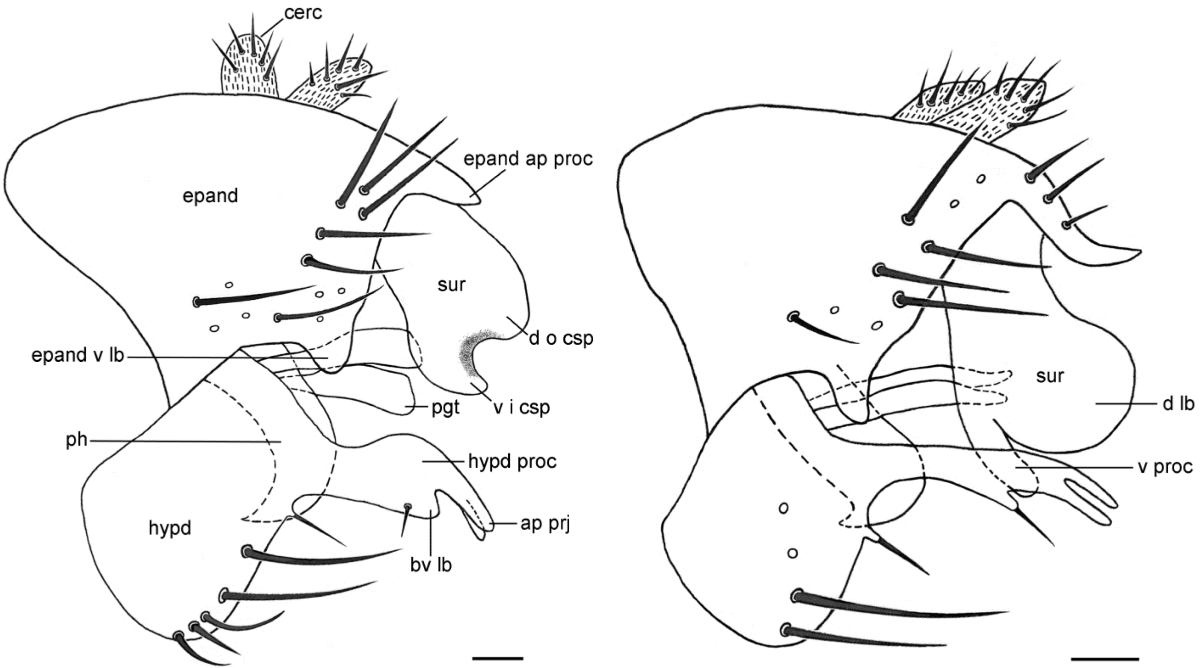


Figures 41−44. *Callomyia* antennae. **41.** *C. calla*, male antenna (first flagellomere short-oval). **42.** *C. gilloglyorum*, male antenna (first flagellomere elongate-conical). **43.** *C. venusta*, female antenna (first flagellomere short-oval). **44.** *C. gilloglyorum*, female antenna (first flagellomere subtriangular).

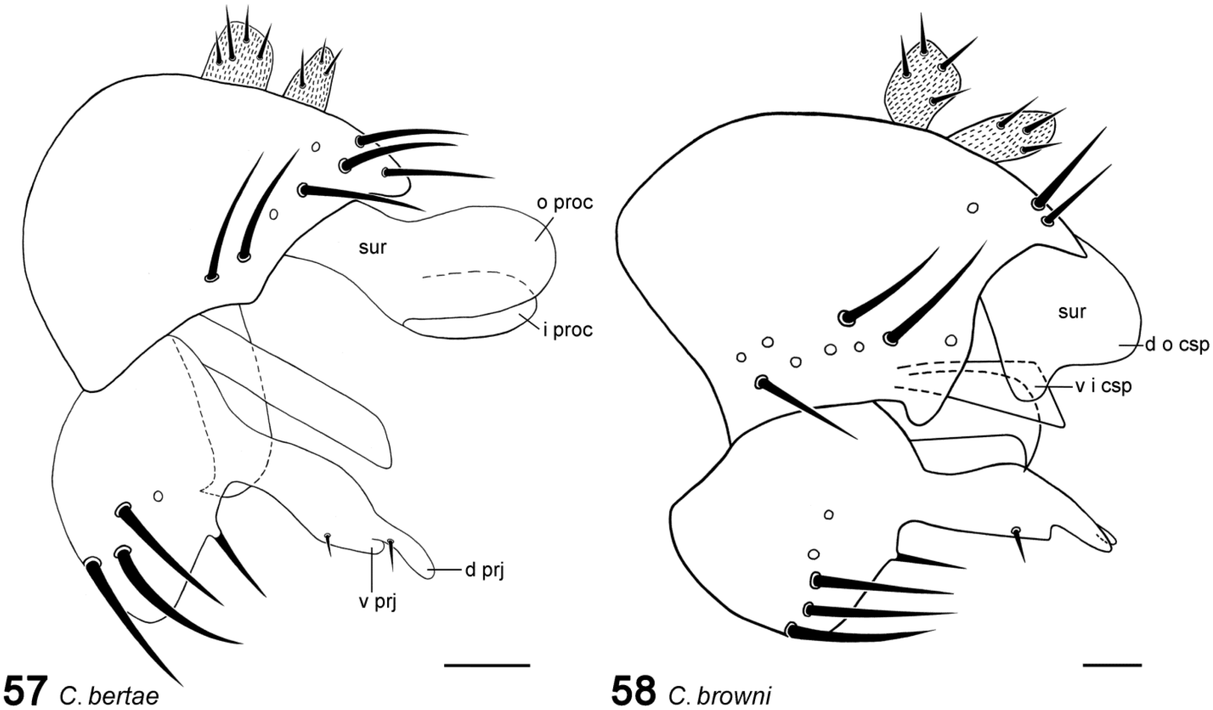


Figures 45−48. *Callomyia* thoracic bristles and wings. **45.** *C*. *velutina*, female (scutum with 3 presutural intra-alar setae). **46.** *C*. *venusta*, female (scutum with 2 presutural intra-alar setae). **47.** *C*. *argentea*, male wing. **48.** *C*. *corvina*, male wing.

Figures 49−54. *Callomyia* legs. **49.** *C. proxima*, male midleg (with tibial setae). **50.** *C. velutina*, male midleg (with tibial seta). **51.** *C. proxima*, female midleg (with tibial seta). **52.** *C. velutina*, female midleg (with tibial seta). **53.** *C. argentea*, male hind leg (with femoral seta). **54.** *C. corvina*, male hind leg (with femoral seta). Abbreviations: ad s – anterodorsal seta; d s – dorsal seta; pv s – posteroventral seta.

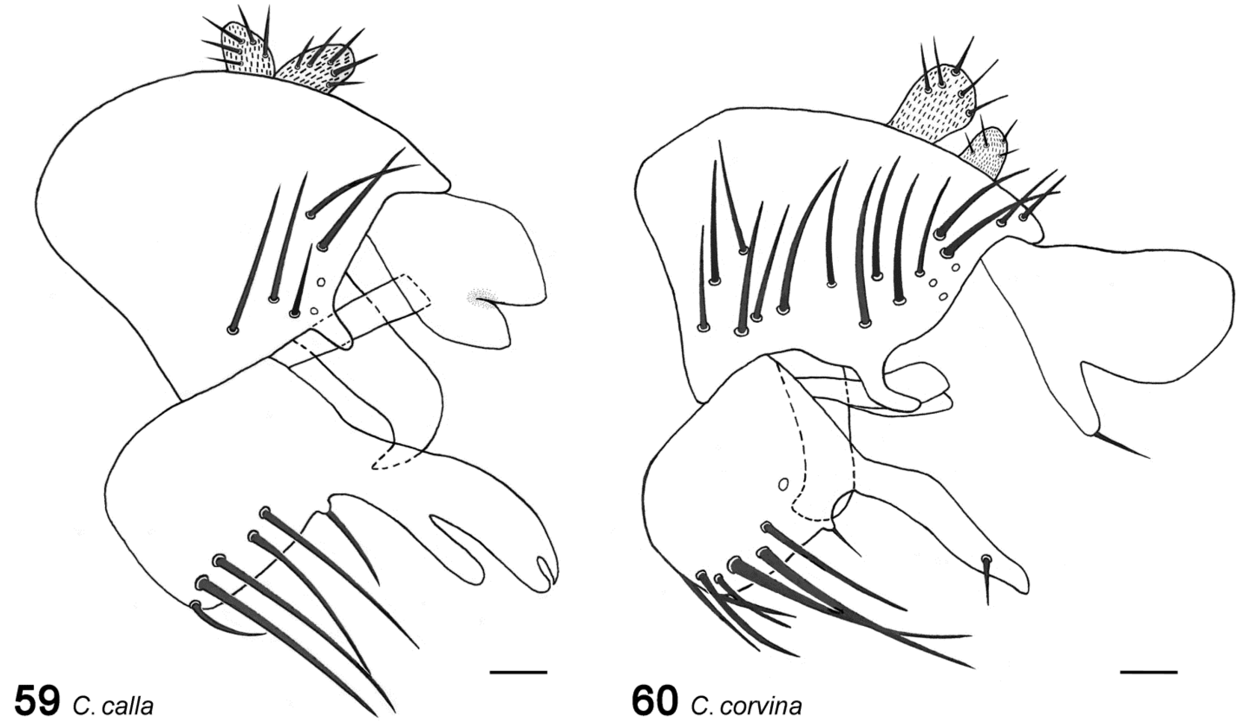


55 *C. argentea* **56** *C. arnaudi*

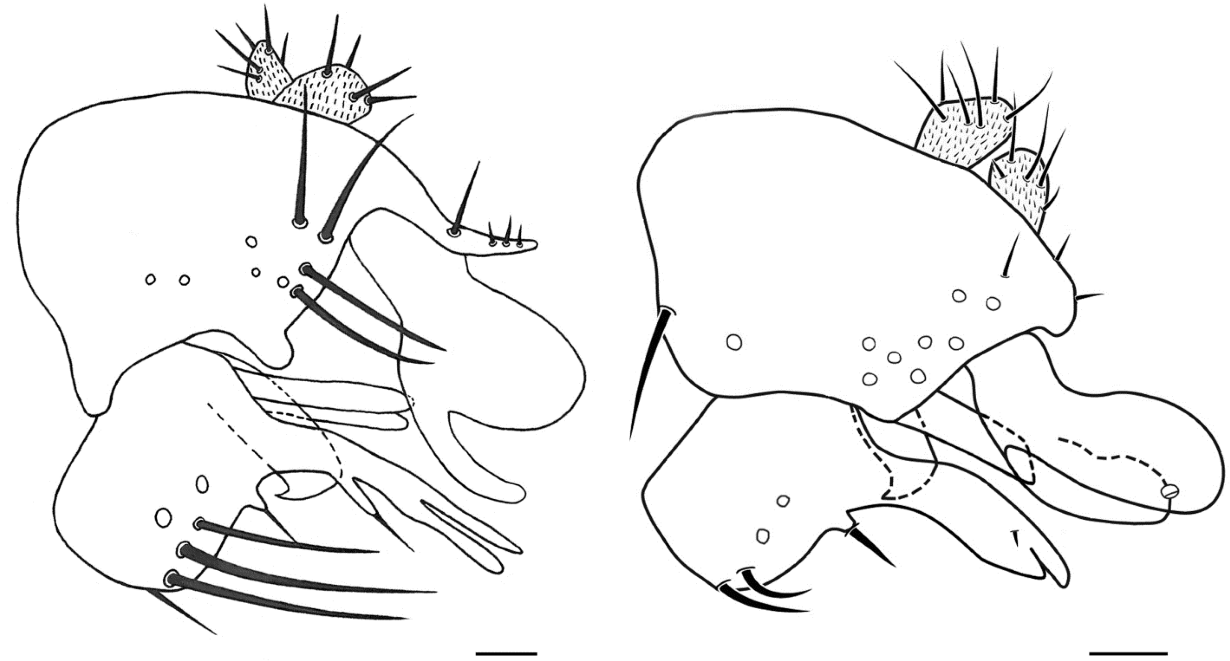


57 *C. bertae* **58** *C. browni*

Figures 55‒58. *Callomyia* male terminalia, lateral view. **55.** *C. argentea*. **56.** *C. arnaudi*. **57.** *C. bertae*. **58.** *C. browni*. Abbreviations: ap prj – apical projection; bv lb – basoventral lobe; cerc – cercus; d lb – dorsal lobe; d o csp – dorsal outer cusp; d prj – dorsal projection; epand – epandrium; epand ap proc – epandrial apical process; epand v lb – epandrial ventral lobe; hypd – hypandrium; hypd proc – hypandrial process; i proc – inner process; o proc – outer process; pgt – postgonite; ph – phallus; sur – surstylus; v i csp – ventral inner cusp; v prj – ventral projection; v proc – ventral process. Scale bar = 0.1 mm.

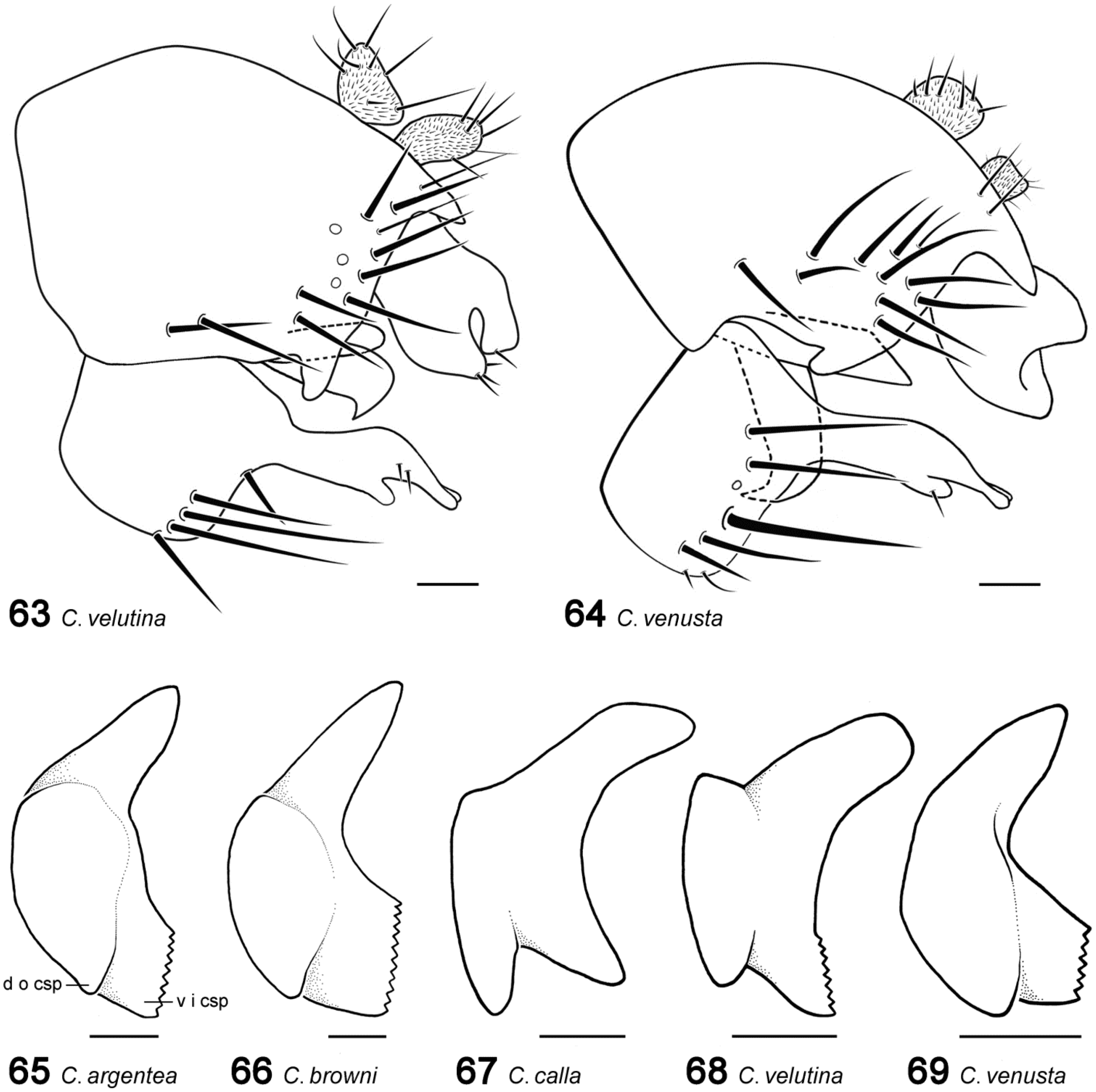


59 *C. calla* **60** *C. corvina*



61 *C. gilloglyorum* **62** *C. proxima*

Figures 59−62. *Callomyia* male terminalia, lateral view. **59.** *C. calla*. **60.** *C. corvina*. **61.** *C. gilloglyorum*. **62.** *C. proxima*. Scale bar = 0.1 mm.



Figures 63−69. *Callomyia* male terminalia, lateral view (63−64); surstyli, posterior view (65−69). **63.** *C. velutina*. **64.** *C. venusta*. **65.** *C. argentea*. **66.** *C. browni*. **67.** *C. calla*. **68.** *C. velutina*. **69.** *C. venusta*. Abbreviations: d o csp – dorsal outer cusp; v i csp – ventral inner cusp. Scale bar: Figs 63−64 = 0.1 mm; Figs 65−69 = 0.05 mm.

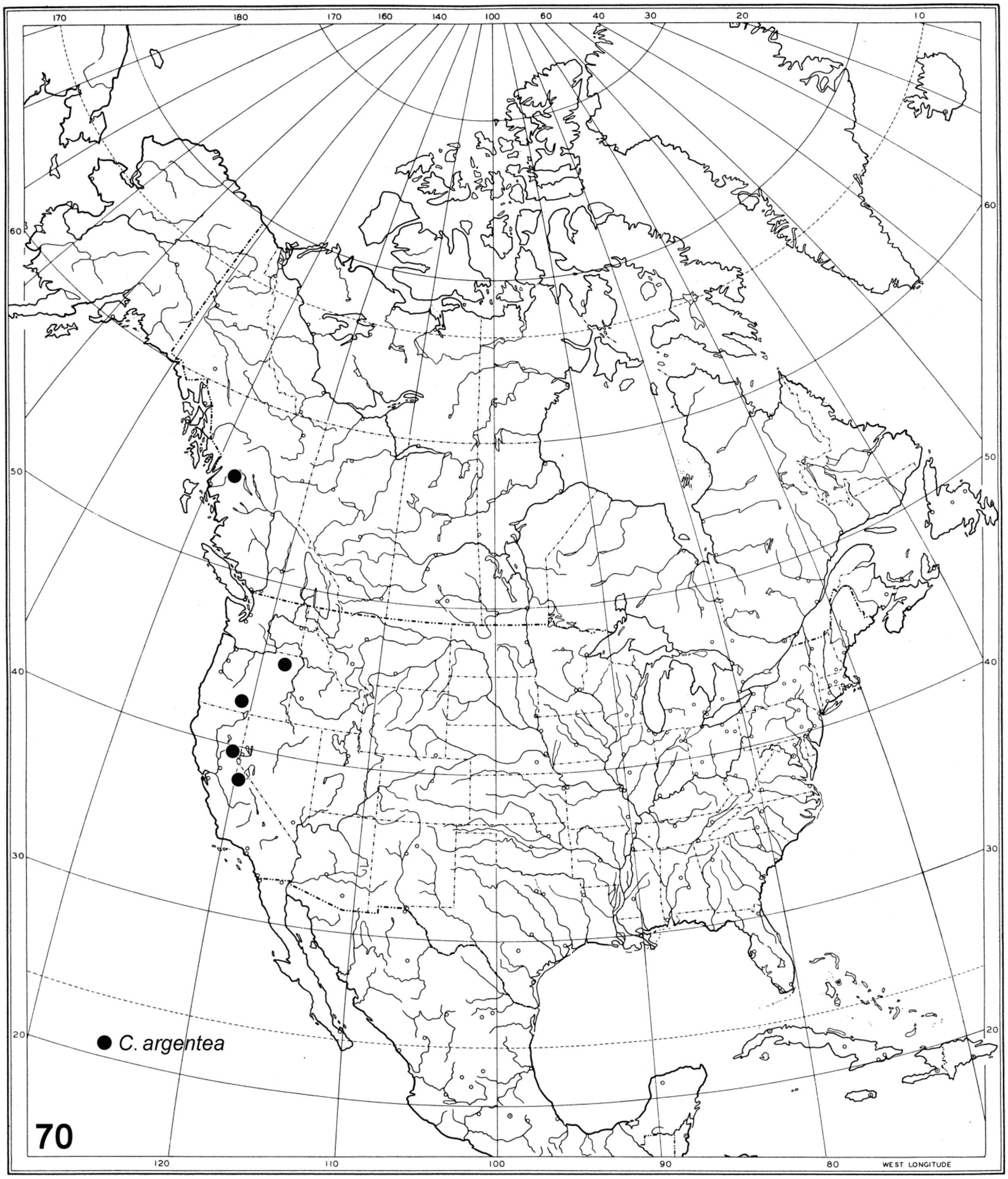


Figure 70. Known distribution of *C. argentea*.

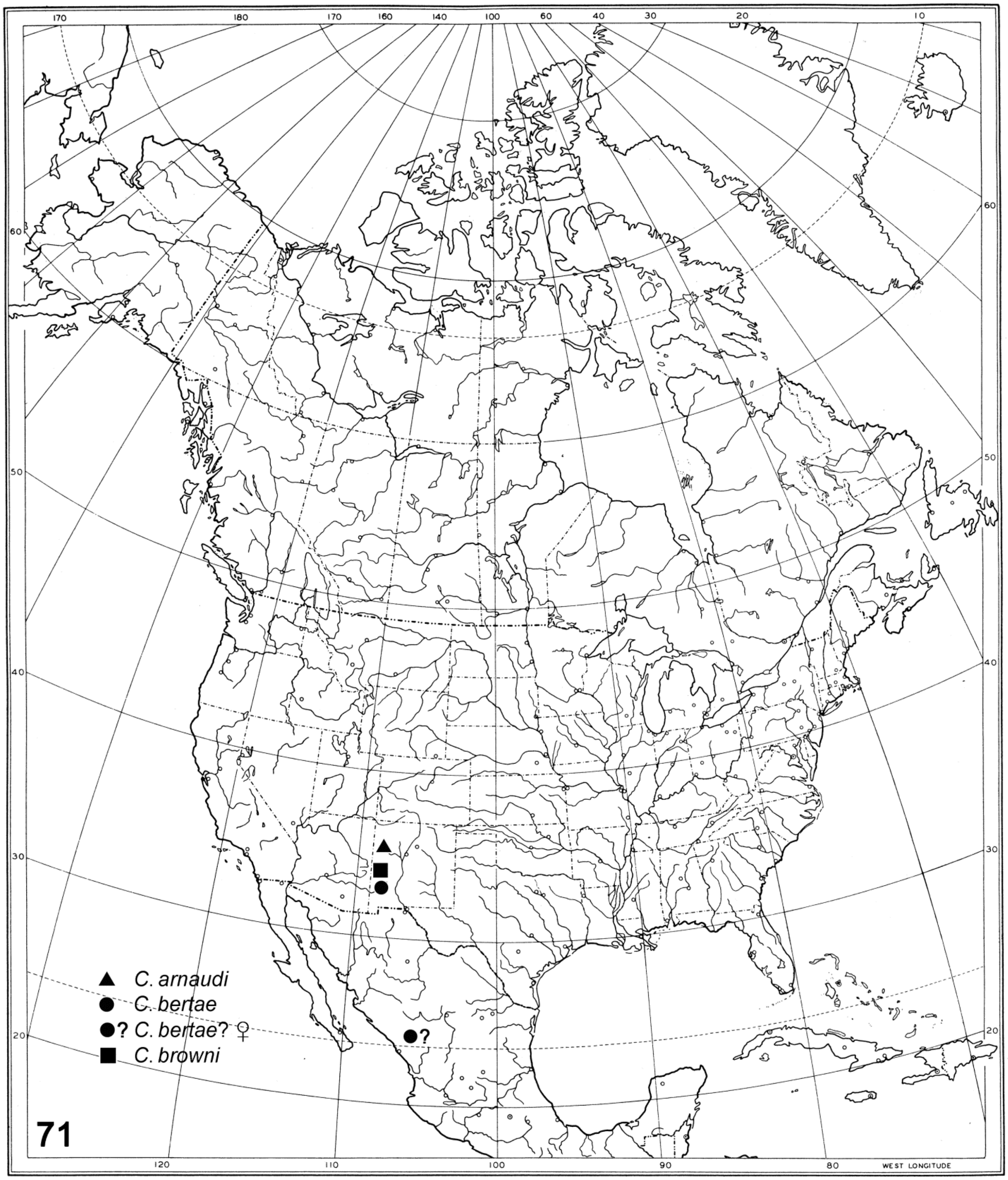


Figure 71. Known distribution of *C. arnaudi*, *C. bertae*, and *C. browni*.

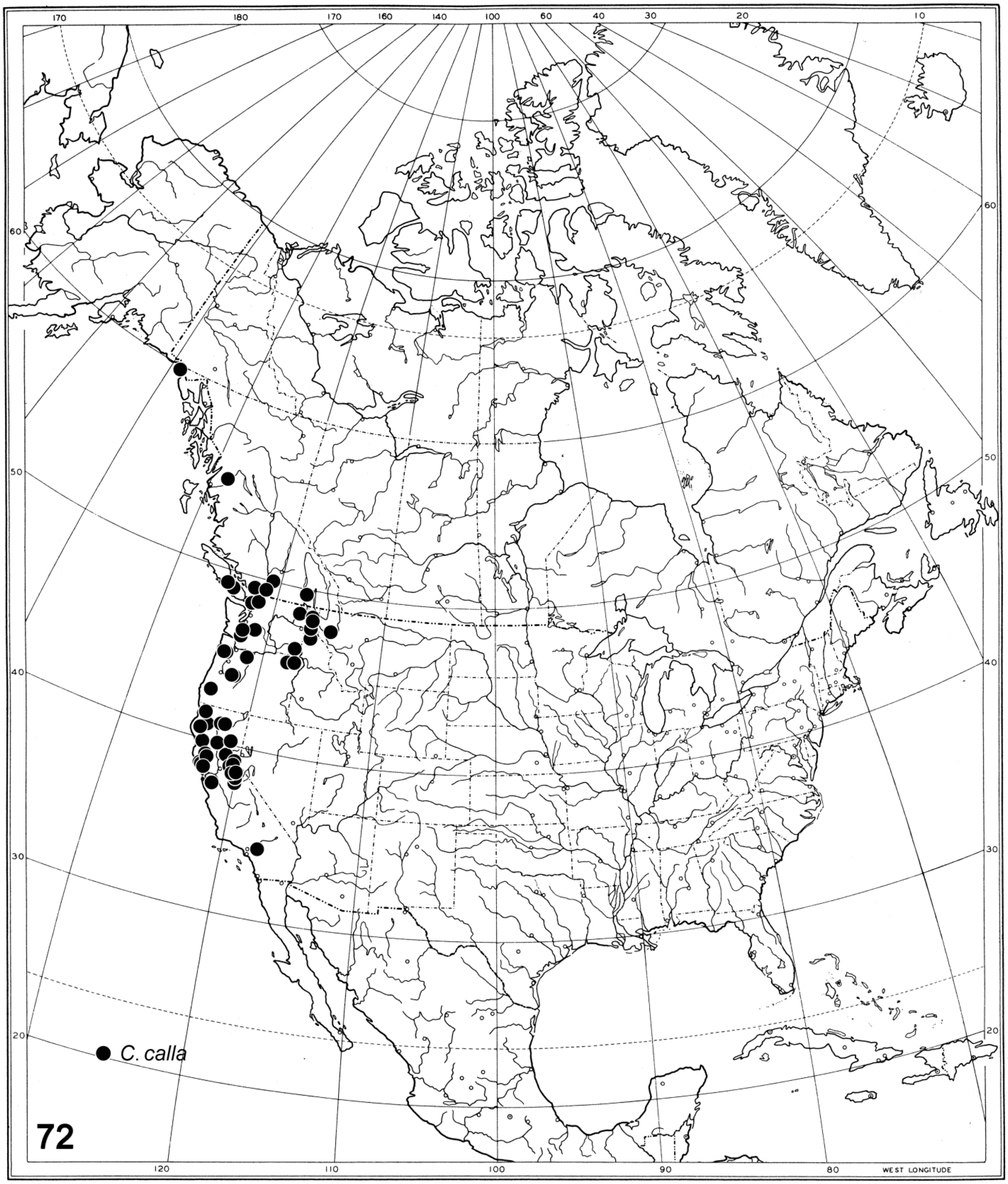


Figure 72. Known distribution of *C. calla*.

Figure 73. Known distribution of *C. corvina*.

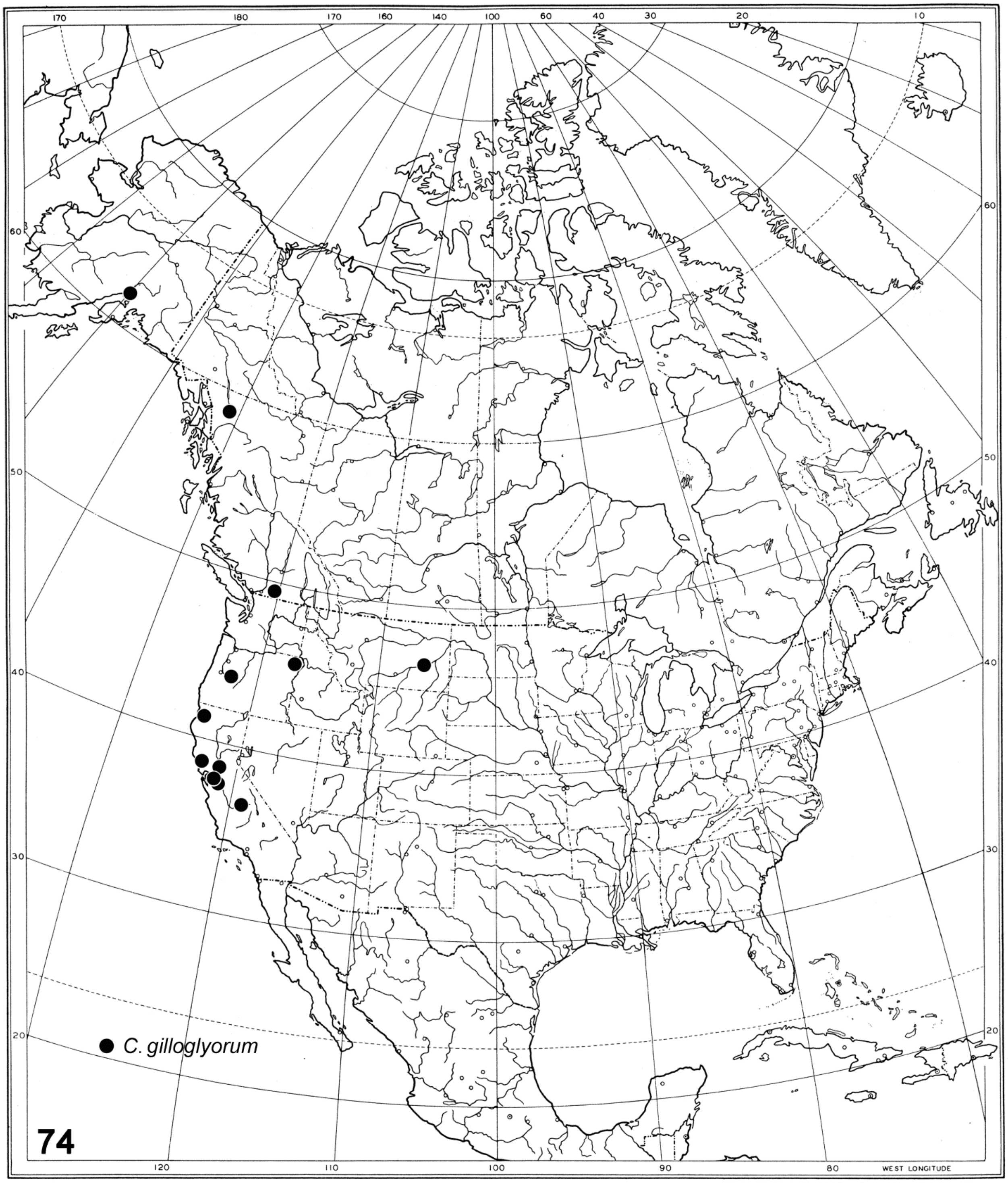


Figure 74. Known distribution of *C. gilloglyorum*.

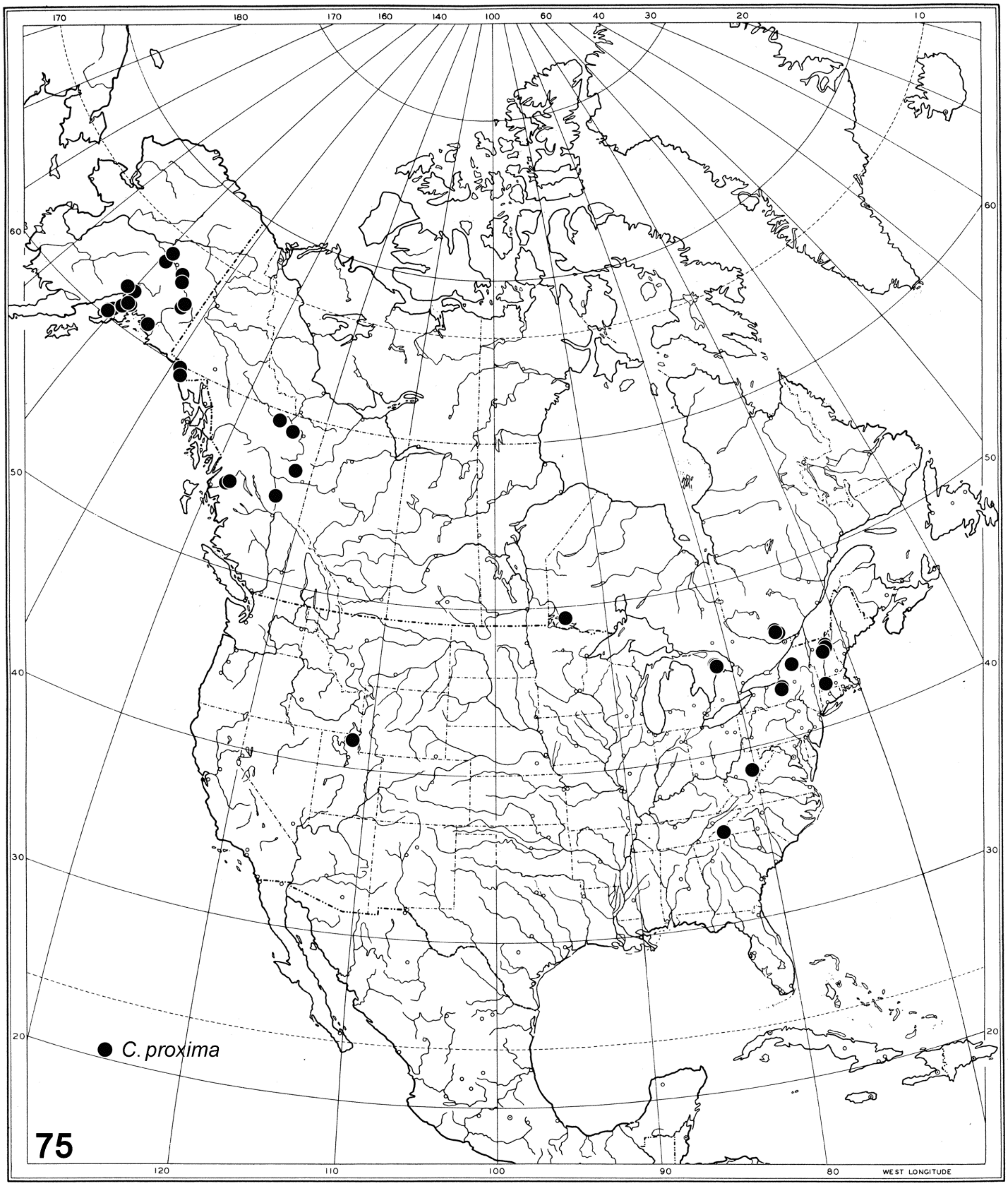


Figure 75. Known distribution of *C. proxima*.

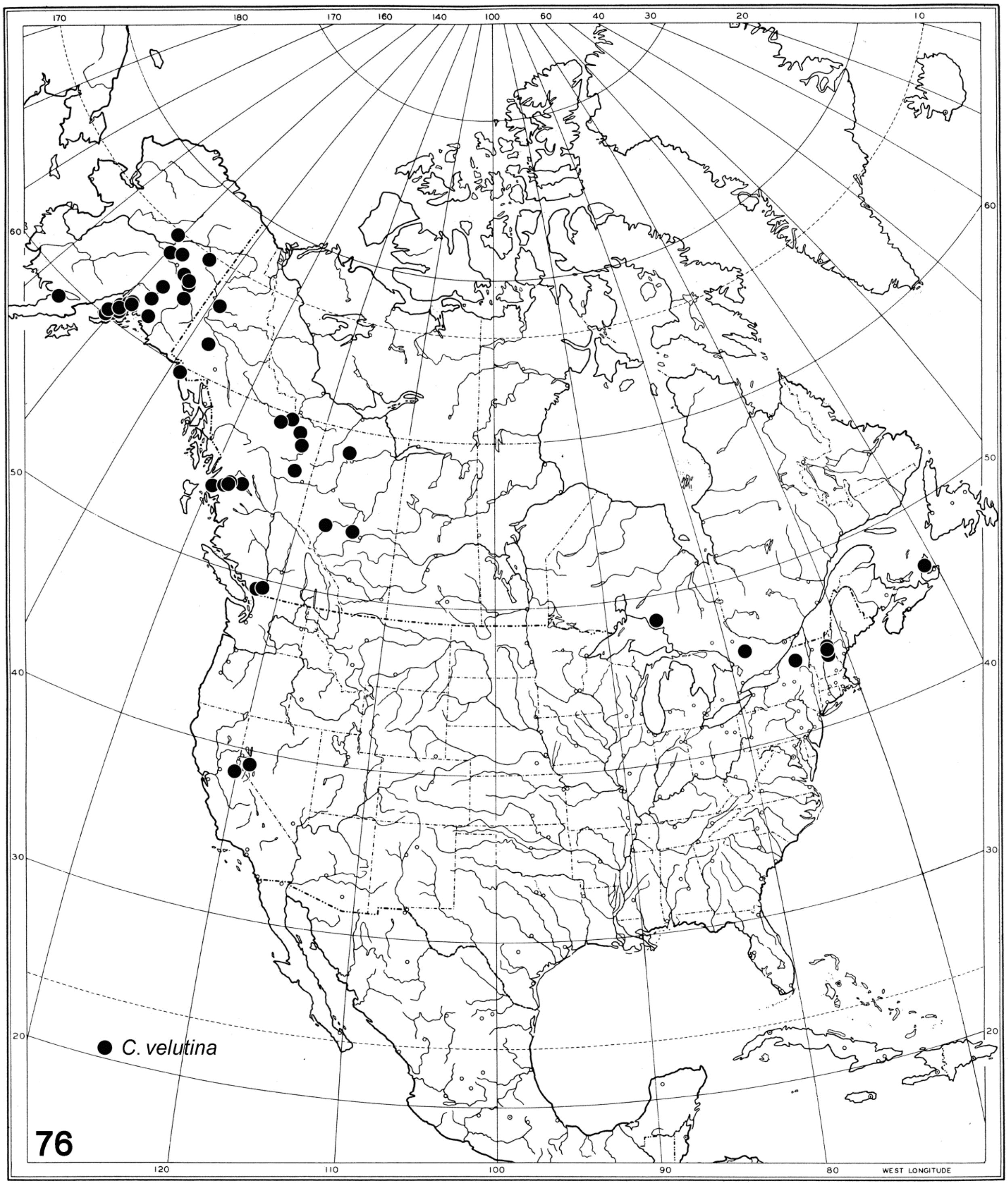


Figure 76. Known distribution of *C. velutina*.

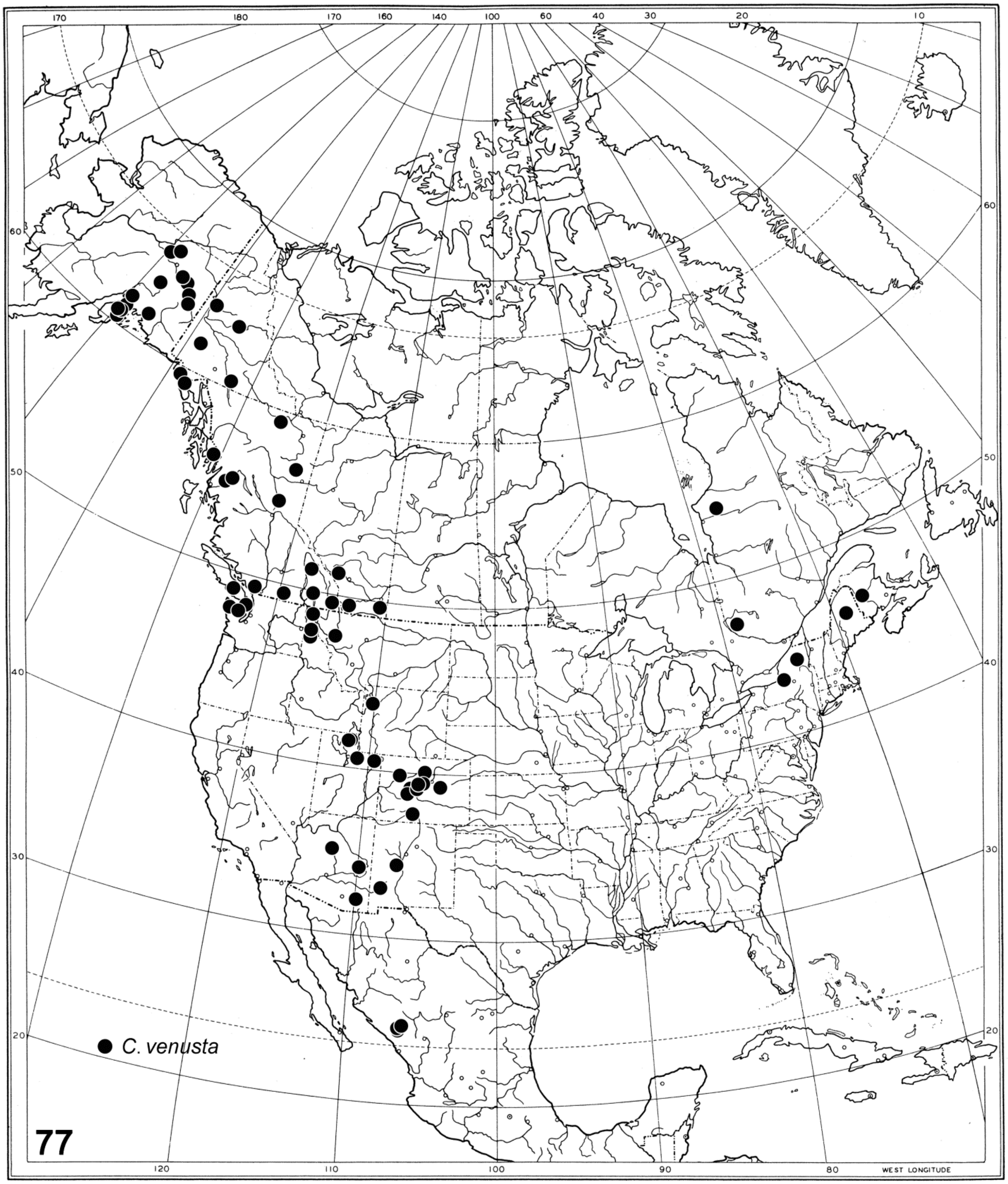


Figure 77. Known distribution of *C. venusta*.

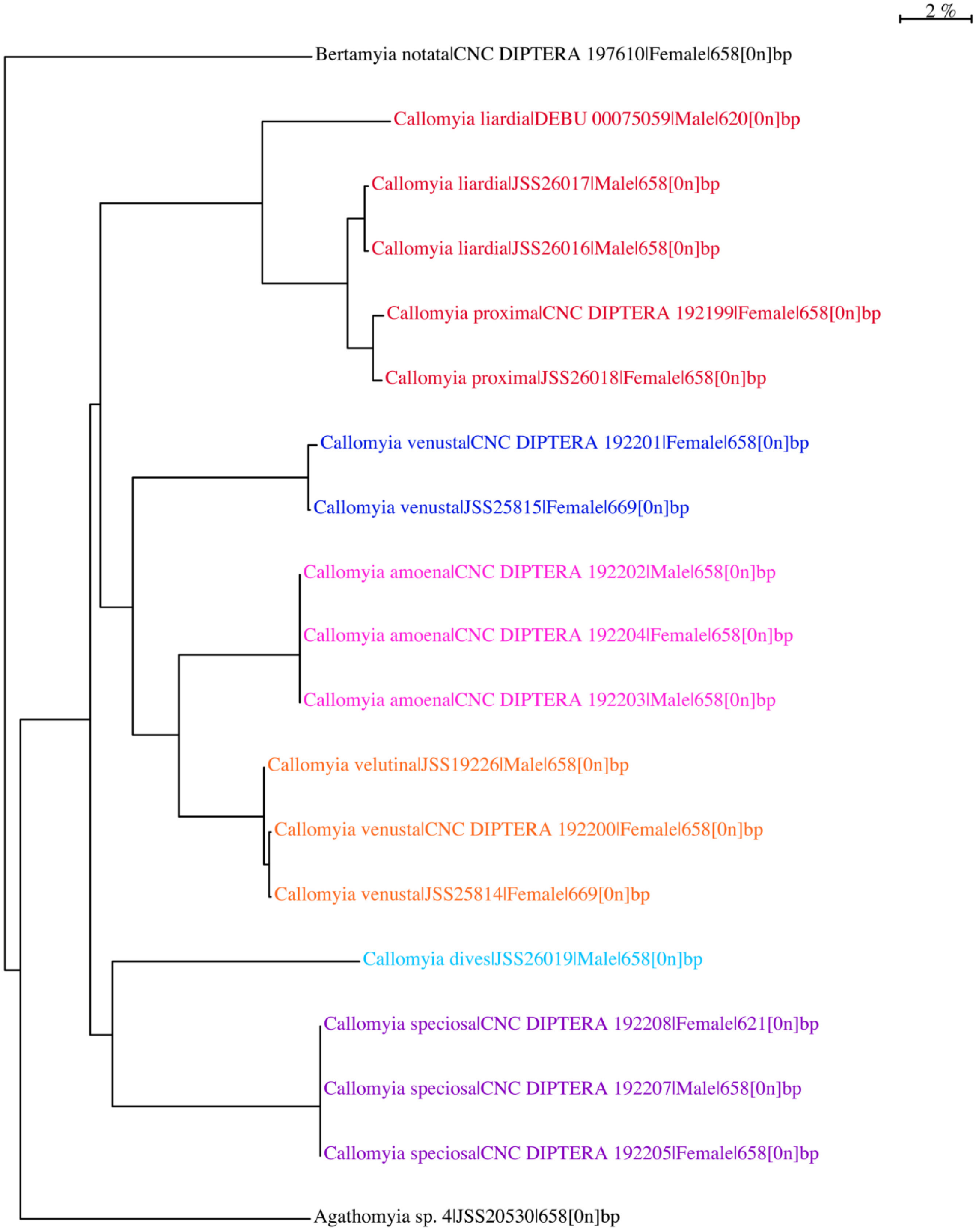


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Figure 78. Neighbour-joining tree of 17 *Callomyia* specimens and two outgroup specimens. Nearctic species names as used by Kessel & Buegler (1972). Current species concepts shown by different colours (red = *C. proxima*, blue = *C. venusta*, pink = *C. amoena*, orange = *C. velutina*, aqua blue = *C. dives*, purple = *C. speciosa*) with outgroup specimens shown in black.

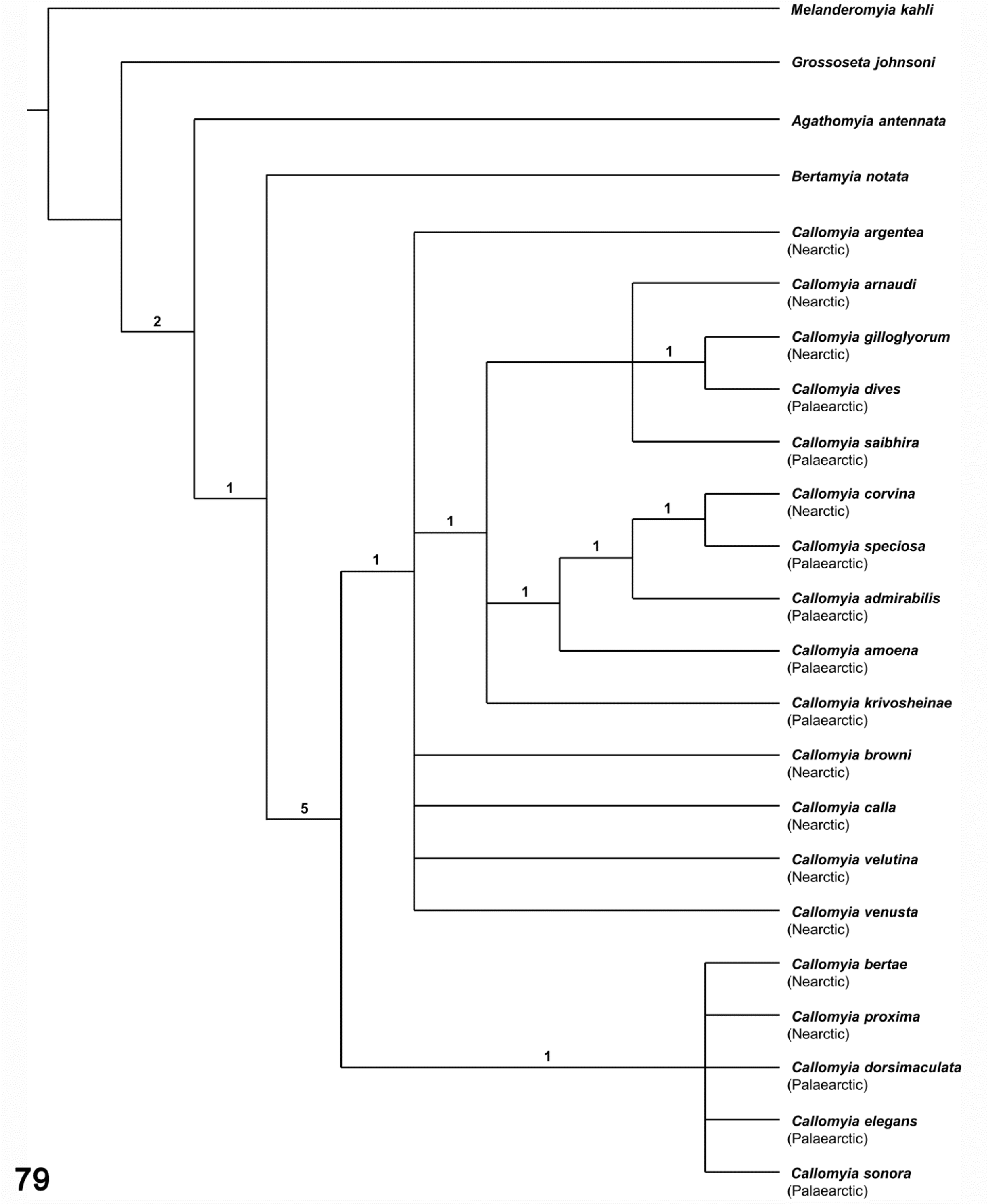

Figure 79. Strict consensus tree of the 136 most parsimonious cladograms of the world species of *Callomyia* and outgroups, produced by analysis of the data matrix in Table 2. Bremer support values are listed above each internode. The Oriental species, *Callomyia coei* Kessel and *C. triangulata* Tkoč, were excluded from the analysis because they are only known from females.

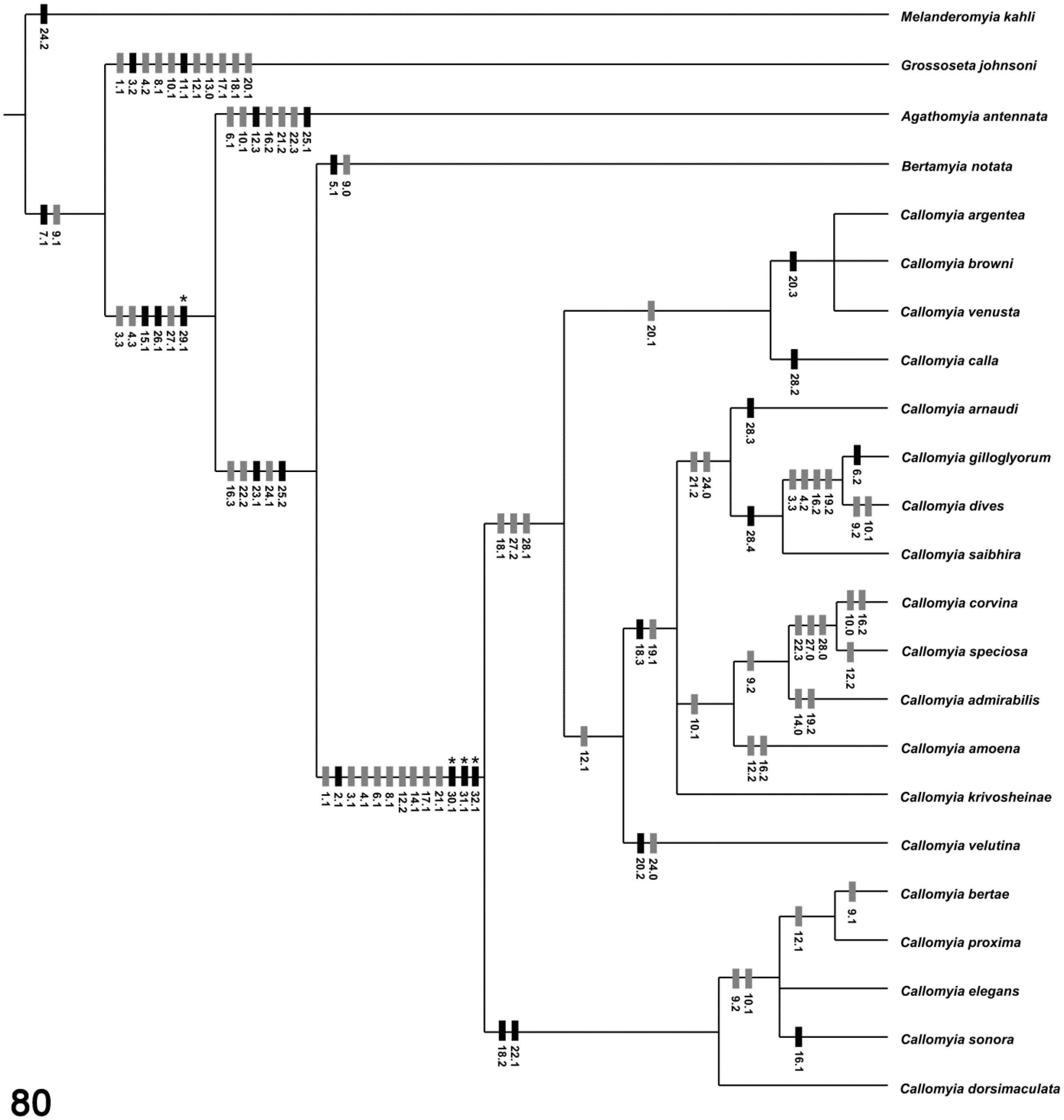

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Figure 80. One of 136 most parsimonious cladograms produced by the analysis of the data matrix in Table 2, and one of 32 trees obtained by successive approximations weighting. Character distribution shown by black hash marks for uniquely derived states and grey hash marks for homoplasious states (including subsequent transformations). * indicates that exact placement of character state is equivocal due to missing data.

CHAPTER 3. GENERAL CONCLUSION

The study presented in this thesis has greatly contributed to our knowledge of the Nearctic diversity and relationships of the world species within the genus *Callomyia*. It provides the first comprehensive Nearctic revision of *Callomyia* that includes detailed species descriptions, diagnoses, accurate illustrations of male terminalia, and thorough figures of distributions, habitus and other important diagnostic characters. A key to the species for both sexes is also included, which uses not only colour but additional morphological characters to identify species. Furthermore, this study presents the first hypothesis of the phylogenetic relationships between the world species of *Callomyia*.

The Nearctic revision of *Callomyia*, presented in Chapter 2, provides a fundamental resource for future taxonomic studies on the genus, as well as an essential foundation for future biodiversity and ecological studies requiring proper identification tools for *Callomyia* species in the Nearctic Region. Although this revision has addressed many of the taxonomic problems that were left unresolved in Kessel & Buelger's (1972) revision, future work is still required on Nearctic *Callomyia*. Three species of Nearctic *Callomyia* (*C. argentea*, *C. bertae*, *C. browni*) are currently known from males only. Because of limited collecting records, in addition to the presence of sexual dimorphism and a lack of rearing events (Chandler 1974), associating the sexes of Nearctic species has been difficult. With further collection of fresh material, particularly series of specimens that include both sexes, discovery of the missing females of the three species mentioned above is attainable, and this revision provides the context necessary to properly associate the sexes or to determine if species are new. Continued collection of fresh material is also needed to help discover the immature stages of species other than *C. gilloglyorum*, which will add to our knowledge of larval morphology and fungal host-associations, and if reared will also assist with the association of sexes. In addition, further collecting of Nearctic *Callomyia* will provide supplementary fresh material for further DNA barcode data and will also expand current information on the geographic range and seasonal occurrence of each species.

The phylogenetic analysis of the world species of *Callomyia*, also presented in Chapter 2, confirmed the monophyly of *Callomyia*. In addition, it revealed that the Nearctic species do not form a monophyletic group, but are instead distributed within at least three separate clades, which show some close relationships with Palaearctic species. Despite these significant findings, future work could supplement the phylogenetic analysis. Because only six of the 21 species of *Callomyia* are known from the immature stages (Kessel 1961b; Krivosheina 2008b; M. Tkoč pers. comm.), there is considerable missing data for the four larval characters scored in the data matrix. Discovery of the immature stages for the remaining 15 species of *Callomyia* will not only add to our knowledge of larval morphology and fungal host-associations, but will also help fill in important missing character data into the matrix. This may provide a higher resolution of relationships between the species of *Callomyia* and give further support for the monophyly of the genus. In addition, the two Oriental species, *C. coei* and *C. triangulata*, were excluded from the phylogenetic analysis because they are only known from females and the characters used in the analysis are largely based on male characters. Discovery of the missing males of these two Oriental species is required to include them in the analysis, in order to produce a complete phylogeny of the world species of *Callomyia.*

Lastly, the phylogenetic analysis of the world species of *Callomyia* could be expanded to analyze the generic relationships within the subfamily Callomyiinae. This would include *Callomyia*, and a more extensive representation of the outgroup genera (i.e., *Grossoseta*, *Bertamyia*, and *Agathomyia*) used in the species level analysis of *Callomyia*, as well as inclusion of the remaining genera *Platypezina* and *Chydaeopeza*. A more extensive analysis, including exemplar species from the other three platypezid subfamilies, would test Chandler's (2001) phylogenetic analysis of Callomyiinae and his hypothesis that the subfamily is monophyletic. This is particularly important because two other studies, i.e., Rotheray et al. (2004) based on larval and pupal characters and Tkoč et al. (2010) based on a preliminary molecular analysis of four mitochondrial markers, suggest the subfamily is paraphyletic.

REFERENCES

Chandler, P.J. (2001) The flat-footed flies (Diptera: Opetiidae and Platypezidae) of Europe. *Fauna Entomologica Scandinavica*, 36, 1–276.

Kessel, E.L. (1961b) The immature stages of *Callomyia*, with the description of a new species of this genus (Diptera: Platypezidae). *Occasional Papers of the California Academy of Sciences*, 30, 1–10.

Kessel, E.L. & Buegler, M.E. (1972) A review of the genus *Callomyia* in North America, with the description of a new species (Diptera: Platypezidae). *The Wasmann Journal of Biology*, 30, 241–278.

Krivosheina, N.P. (2008b) On Biology of xylobiont platypezid larvae of the genus *Callomyia* (Diptera, Platypezidae). *Entomological Review*, 88, 973–982.

Rotheray, G.E., Chandler, P.J. & Gilbert, F. (2004) Final stage larvae and puparia of Platypezidae (Diptera). *Insect Systematics and Evolution*, 35, 79–106.

Tkoč, M., Vaňhara, J. & Tóthová, A. (2010) Phylogeny of flat-footed flies (Diptera, Platypezidae) based on mitochondrial gene analyses. Unpublished poster and handout presented at 7th International Congress of Dipterology, San Jose, Costa Rica, August 2010.