Zootaxa 3682 (1): 143–150
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3682.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:A652476E-EBB7-42EB-B5B6-5E391CA4318F

Rediscovered at last: a new enigmatic genus of Axymyiidae (Diptera) from western North America

BRADLEY J. SINCLAIR
Canadian National Collection of Insects and Ottawa Plant Laboratory - Entomology, CFIA, K.W. Neatby Bldg., C.E.F., 960 Carling Ave., Ottawa, ON, CANADA K1A 0C6. E-mail: bradley.sinclair@inspection.gc.ca

Abstract

An unusual and undescribed genus and species of Axymyiidae known from a single specimen collected more than 50 years ago in Alaska is rediscovered in Mt. Rainier National Park (USA: WA). Based on two female specimens, *Plesioaxymyia vespertina* **gen. nov.**, **sp. nov.** is described. A preliminary phylogenetic tree of the Axymyiidae is presented, showing *Plesioaxymyia* as sister group to all remaining axymyiid genera.

Key words: Diptera, Axymyiidae, Alaska, Washington, Mt. Rainier, new genus, new species

Introduction

The Axymyiidae are a small family of nematocerous Diptera, currently comprising three extant genera (*Axymyia* McAtee, *Mesaxymyia* Mamaev, *Protaxymyia* Mamaev & Krivosheina) and seven described species, known from the Holarctic Region, Taiwan and southern China (Krivosheina 2000; Wihlm & Courtney 2011; Wihlm *et al*. 2012). In addition, three fossil species in three genera are known from the Jurassic (Zhang 2010). The family is considered semi-aquatic with larvae and pupae of all three genera inhabiting galleries in wet, saturated decomposing wood lying partially submerged in seeps and small streams (Wood 1981; Wihlm & Courtney 2011). Adults usually emerge in early spring (April and May) and live only a few days, with swarms having been observed for Palearctic species (Krivosheina 2000; Wihlm & Courtney 2011). In North America, *Axymyia furcata* McAtee is widespread from southern Ontario and Quebec to Georgia and South Carolina and an undescribed autumn species of *Axymyia* is recorded from Oregon (Wihlm & Courtney 2011).

A second very interesting undescribed North American species from Alaska has been known for several decades (Wood 1981). This species was represented by a single female specimen collected in 1962 by Peter Skitsko who accompanied Robin Leech on an expedition for the Northern Insect Survey (Riegert 1999) to Alaska and the Yukon Territory. This specimen was collected at Isabel Pass on the Richardson Highway (likely extracted from a dry malaise trap set in mixed forest), and according to field notebooks, the season was unusually late, very rainy and cold, with occasional snow at higher elevations. The female specimen was later studied by the curators of the Diptera Unit at the Canadian National Collection of Insects (CNC) in Ottawa, who considered it an undescribed genus and species of the family Axymyiidae. The specimen was shown to Willi Hennig during his visit to the Diptera Unit at the CNC in the autumn of 1967 (Cumming *et al*. 2011). Hennig (1973) assigned this undescribed genus to the Perissommatidae on the basis of the reduction of the anal vein, whereas Wood (1981) considered the thoracic structure and the rest of the wing venation more consistent with that of Axymyiidae.

Following its discovery, Monty Wood travelled three times to the Alaskan locality, spending hours sweeping vegetation and ripping open water-saturated logs and branches. Toyokei Saigusa made similar efforts to collect this species at Isabel Pass on three separate occasions and Art Borkent searched the region 10 years ago, but they were also unsuccessful in rediscovering this enigmatic taxon. Over the years the original specimen was damaged, with the loss of the antennae, most leg segments and one wing, and more recently the abdomen was dissected and cleared.

Accepted by V. Blagoderov: 13 May 2013; published: 26 Jun. 2013

In mid July 2012, the author was collecting at Mt. Rainier National Park, primarily in search of seepage midges (Thaumaleidae). The region around Narada Falls and Paradise Park appeared to be in early spring conditions, with small to extensive patches of snow cover. Streams were at high flow rates, and spring flowers were very common and widespread. While sweeping along a wooded trail, the author collected a single axymyiid female. Unfortunately, it was not recognized until the sweep sample was sorted, dried and mounted back at the CNC. The specimen was immediately determined as something unusual, identified as belonging to the family Axymyiidae and comparison to the Alaskan specimen quickly proved they were conspecific.

After discussions with colleagues, it was decided that the best course was to publicize the rediscovery of this enigmatic axymyiid, rather than wait until additional specimens were found. Consequently, in this study a new genus and species is described based on these two female specimens. It is hoped that the more accessible Washington state locality will result in collection of male specimens and immature stages. Hopefully it will not take another 50 years for further discoveries of this genus.

Material and methods

All specimens examined and studied are housed in the Canadian National Collection of Insects, Ottawa, Canada (CNC). Morphological terms follow Cumming and Wood (2009), except wing venation where the terms of Saigusa (2006) were used. Saigusa (2006) homologized the dipteran vein A_1 (as used in Cumming & Wood 2009) with *CuP* of Mecoptera. Consequently, the following wing venation terms are used here: CuA_1 (of Cumming & Wood) = M_4, CuA_2 = *CuA*, and anal vein (A_1) = *CuP*.

Photographs were taken using a Canon EOS 50D camera with a Canon MP-E 65mm f/2.8 1-5x Macro Lens and a Canon Speedlite 430EX II flash. The camera was attached to a StackShot (Cognisys Inc.) computerized rail, which was used to take a series of images of the specimen. These images were montaged with ZereneStacker version 1.04 (Zerene Systems LLC) to produced one image. The montaged image was edited with Adobe Photoshop.

Plesioaxymyia gen. nov.

(Figs 1–5)

Type-species: *P. vespertina* **sp. nov.**

Etymology. The genus is named in reference to its plesiomorphic position in comparison to *Axymyia*. Its gender is feminine.

Diagnosis. This is the only extant axymyiid genus with well developed mouthparts; R_{2+3} fork V-shaped; R_2 distant from apex of R_1; distal stem of M_{1+2} elongate; CuP very short, two-thirds length of cell bm.

Description. Head: Compound eyes broadly separated in female, each eye divided longitudinally into upper and lower hemispheres by fine groove starting at deep, broad, triangular incision at antennal bases, extending for more than 10 facets (Fig. 2); upper hemisphere smaller than lower hemisphere with facets uniform in size in both sections; facets with numerous ommatrichia; ocellar triangle elevated above eye with three prominent ocelli. Antenna with 14 moniliform flagellomeres, scape and pedicel with circlet of setulae. Mouthparts well-developed; clypeus prominent, strongly convex; palpus apparently 4-segmented (segment 1 possibly obscured), second segment broader than other segments; labellum developed, distinct. **Thorax**: Postpronotum depressed, triangular, separated by prominent prescutum; prescutal suture not prominent, very short, terminating at shallow, shiny rectangular depression. Scutum not distinctly swollen; transverse suture arising at base of wing, distinctly invaginated, terminating before midline of scutum; postsutural area of scutum shallowly concave medially. Scutellum rounded, strongly domed. Mediotergite twice length of scutellum, not as strongly prominent as scutellum. Prosternum large, separated by broad membrane. Anepisternum large, divided by anepisternal cleft into large anterior portion and narrow posterior portion; katepisternum prominent, overhanging mid coxa. Meron large, more than half as long as katepisternum. **Legs**: Fairly short, lacking spurs and long setae. Fore coxa shorter than katepisternum; mid and hind coxae half as long as fore coxa, entirely sclerotized medially; hind coxa broader than mid coxa. Hind tibia with posteroventral apical comb.

Mediolobus spatulate and elongate, more than half length of tarsomere 5, apex truncate; pulvillus shorter than claw. **Wing**: Costa greatly reduced slightly beyond apex of R_{4+5} (Fig. 3). Sc very short, extended to basal quarter of wing, strongly curved to costa proximal to vein Rs; sc-r reduced to faint streak. Rs with kink at mid-length; R_{2+3} branched slightly beyond apex of R_1; R_2 reaching costa well-separated from R_1; R_{2+3} fork V-shaped. Crossvein r-m perpendicular to R_{4+5}. Medial veins weaker than radial veins, distinctly pale in comparison; M_{1+2} with long distal stem, branching proximal to R_{2+3} fork; M_4 straight. Stem of M vein with apex distinct, basal portion reduced to faint crease, indistinctly separating basal cells. CuP very short, extended to half length of cell bm. Alula greatly reduced; anal lobe well-developed. Halter with very long stem, lacking cluster of setae. **Abdomen**: Sparsely setose. Segments 1–7 each with spiracles in membranous pleural region. Tergites considerably broader than sternites; tergite 8 one-third length of sternite, undivided; sternite 8 greatly lengthened, slender, tapered apically, clothed in short setae. Genital fork (sternite 9) with V-shaped ventral portion, dorsal portion prolonged posteriorly as pair of slender rod-like extensions to apex of sternite 8 (Fig. 4). Spermathecae spherical, paired, well-sclerotized; spermathecal ducts paired, separated throughout, slightly inflated distally to genital fork; duct broad exiting spermatheca. Cercus two-segmented; basal segment very small reduced, slender, flap-like, surrounding anus; apical segment longer than wide, bearing several rod-like sensilla (Figs 4,5). **Male and immatures**: Unknown.

Remarks. *Plesioaxymyia* will key with some difficulty to *Protaxymyia* in the key to genera in Zhang (2010). The new genus clearly differs from the latter genus in the shape of R_2, shortened Sc and CuP, and the very long distal stem of M_{1+2}.

A preliminary phylogenetic assessment of the infrafamilial relationships of Axymyiidae is summarized in Figure 6 and characters listed and described in Table 1. The Bibionidae was used to polarize the characters. The assignment of *Plesioaxymyia* to the family Axymyiidae is supported on the basis of the four family-level synapomorphies: female cercus with rod-like sensilla (1); vein Rs with kink at mid-length (2); compound eye divided longitudinally (3); and prescutal suture ending at an elongate depression (shiny spot in *Axymyia*) (4). All axymyiid genera, exclusive of *Plesioaxymyia* form a clade, supported by the reduction of the mouthparts (5), presence of a cluster of setae on the stem of the halter (6) (although both characters scored as unknown in the fossil genera) and R_2 directed towards R_1 (7). The monophyly of *Plesioaxymyia* is supported on the basis of four synapomorphies: shortened Sc (8), elongate distal stem of M_{1+2} (longer than M_2) (9), greatly weakened M vein (10), and shortened CuP (anal vein), two-thirds length of cell bm (11). Four genera are apparently most closely related (Fig. 6) on the basis of the closely positioned apex of veins R_1 and R_2 (12). The three fossil genera (*Juraxymyia* Zhang, *Psocites* Hong and *Sinaxymyia* Zhang) clearly belong to the sister group of *Plesioaxymyia* and provides strong evidence that this genus has its roots in the Jurassic or earlier.

The shape and size of the female ovipositor (e.g., length and shape of sternite 8 and cercus) requires further evaluation. The apical segment of the cercus is longer than wide in *Plesioaxymyia* and sternite 8 is greatly lengthened in *Plesioaxymyia* and *Protaxymyia japonica* (Ishida).

TABLE 1. Characters for the analysis of Axymyiidae.

1. *Female cercus*: lacking rod-like sensilla (0); rod-like sensilla present (1).
2. *Vein Rs*: straight (0); with kink (1).
3. *Compound eye*: undivided longitudinally (0); divided longitudinally (1).
4. *Prescutal suture*: unmodified (0); ending at elongate depression (1).
5. *Mouthparts*: unmodified (0); shortened and reduced (1).
6. *Stem of halter*: bare (0); with cluster of setae (1).
7. *R_2 orientation*: directly apically (0); directed towards apex of R_1 (1).
8. *Sc vein*: elongate, extending to beyond Rs (0); short, not reaching Rs (1).
9. *Stem of M_{1+2}*: short, less than half length of M_2 (0); elongate nearly subequal in length to M_2 (1).
10. *M vein*: well defined (0); greatly weakened (1).
11. *CuP length*: elongate, at least three-quarters length of cell bm (0); short, two-thirds length of cell bm (1).
12. *R_1 and R_2*: separated by length of R_2 (0); nearly touching (1).

***Plesioaxymyia vespertina* sp. nov.**
(Figs 1–3)

Material examined. HOLOTYPE ♀, labelled: "USA: WA: Mt Rainier NP/ Narada Falls to Reflection Lk/ trail; N46°46' W121°44'/ 1400 m, 17.vii.2012/ B.J. Sinclair"; "HOLOTYPE/ *Plesioaxymyia*/ *vespertina*/ Sinclair [red label]" (CNC). **PARATYPE**: **USA. Alaska**: Isabel Pass, mi 206 Richardson Hwy., 2900', 13.vii.1962, P.J. Skitsko (1 ♀, CNC).

Etymology. The species name is from the Latin *vespertinus* (western), in reference to its distribution in North America.

Description. Female. Body length: 3.7 mm (not including antenna). **Head**: Antenna longer than width of head; scape and pedicel somewhat paler than dark brown flagellum; pedicel slightly longer than scape. Frons with setulae along inner eye margin and above antennal bases. **Thorax**: Scutum dark brown, concolorous, clothed in fine pruinescence and short setulae; lacking prominent setae. Pleura somewhat paler than scutum, subshiny. Coxae concolorous with pleura; femora pale brown, darker towards apices; tibiae pale brown with proximal and distal portions darker; tarsomeres dark brown; mediolobus and pulvilli bright white. **Wing**: Length: 3.8 mm, subequal to body length, excluding antenna; pterostigma distinct, brown, otherwise wing unmarked; M_{1+2} with long stem, longer than M_2. Halter stem with 2–3 scattered setulae, lacking dense cluster of setae. **Abdomen**: Basal segment dark; segments 2–6 pale brown; segment 7 with anterior half pale brown and posterior half dark brown; pleural region dark brown. **Male and immatures**. Unknown.

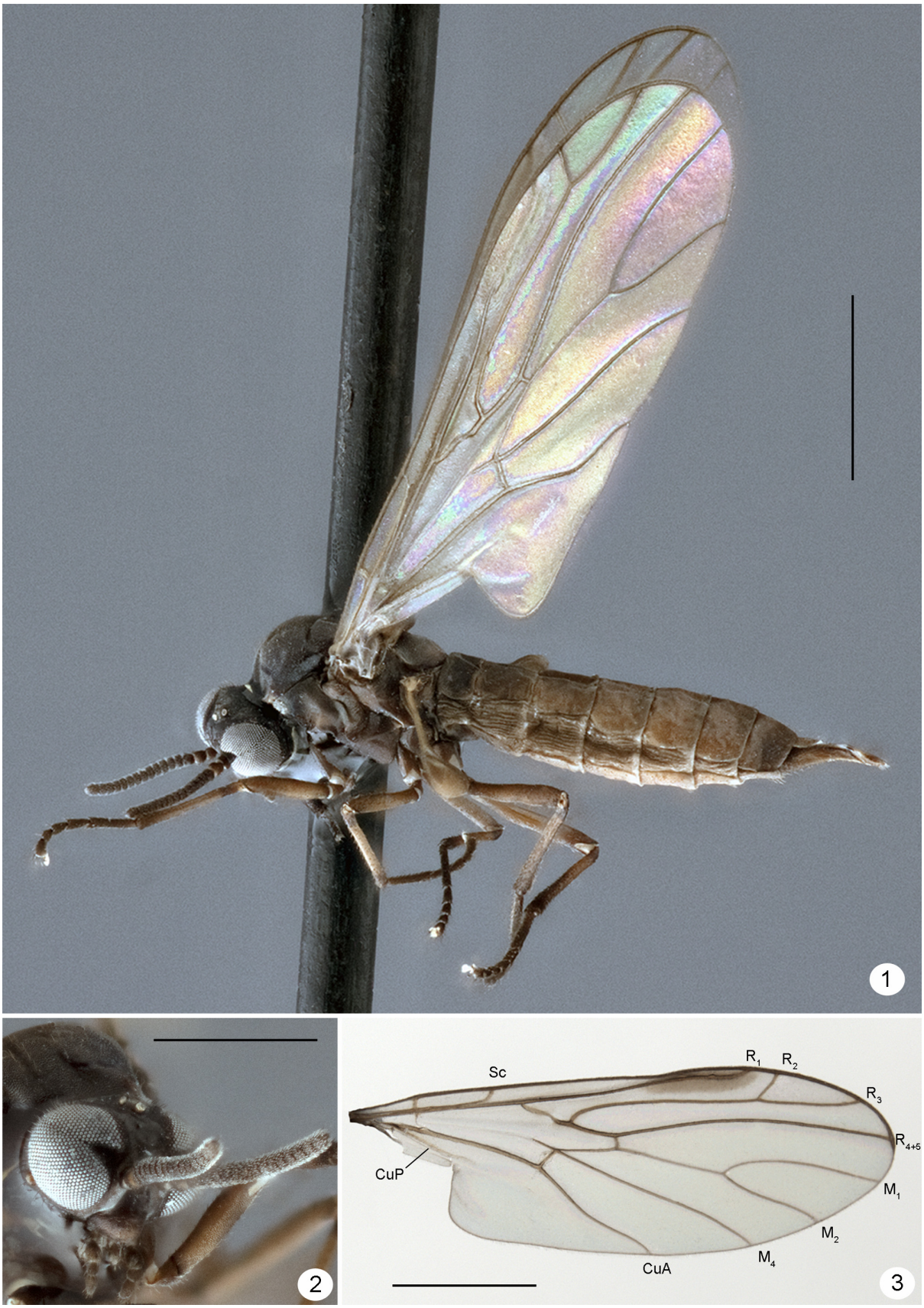
Remarks. This species was collected by sweep net while walking along the Woodland hiking trail from the base of Narada Falls to Reflection Lake in Mt. Rainier National Park. This trail runs below Hwy 706, through mid-elevation conifer forests at approximately 1400 m. The season appeared to be early spring, with many small snowmelt streamlets and broad, major streams often retaining thick snow caps. However the daytime air temperatures reached 27–29°C and spring flowers were in full bloom.

The immature stages of *P. vespertina* are assumed to occur in saturated logs and branches as recorded for the other three extant axymyiid genera. But given the unsuccessful attempts to collect the immature stages at the Alaskan locality, perhaps the immature stages reside in wet leaf litter or decomposing fungi. Larvae of the family Perissommatidae, which has been suggested as closely related to Axymyiidae (see following section), have been found in decomposing fungi (Colless 1962).

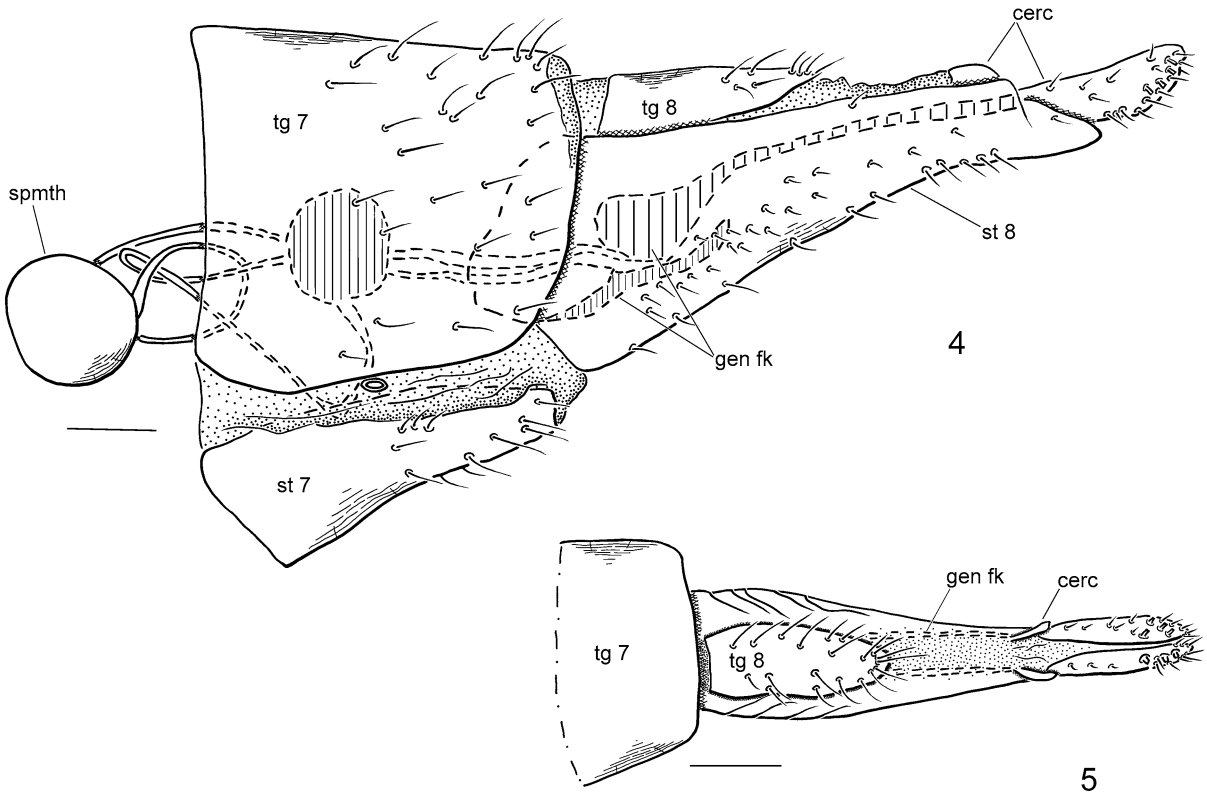
Recent phylogenetic history of the Axymyiidae

The phylogenetic relationships and systematic assignment of the Axymyiidae remains disputed and largely tentative. As stated by Wood & Borkent (1989), the debate started almost immediately with the description of the type-genus *Axymyia* by McAtee (1921) and the immediate assignment of the genus to its own subfamily in the Anisopodidae by Shannon (1921). More recently, Hennig (1973) assigned axymyiids to the Bibionomorpha on the basis of reduction of the costa on the posterior margin of the wing and considered them closely related to *Pachyneura* Zetterstedt and *Perissomma* Colless on the basis of a forked R_{2+3} and unbranched R_{4+5}. Wood & Borkent (1989) considered the forked condition of R_{2+3} as plesiomorphic and assigned the single family Axymyiidae to the infraorder Axymyiomorpha, with no apparent synapomorphies showing conclusive relationships to other nematocerous Diptera. Krzemińska *et al*. (1993) accepted the wing venation characters of Hennig (1973), assigning the fossil family Elliidae, Axymyiidae, Pachyneuridae, Perissommatidae, and Thaumaleidae to the Axymyiomorpha; the latter family was later removed by Krzemiński and Krzemińska (2003).

Amorim (1993) assigned Axymyiidae as sister to the Perissommatidae, primarily on the basis of the divided compound eye and incomplete CuP, and along with Pachyneuridae (comprising *Pachyneura*) the three families were assigned to the Axymyiomorpha. Grimaldi & Engel (2005) also recognized Axymyiidae, Pachyneuridae (incl. *Cramptonomyia* Alexander) and Perissommatidae as a clade, and assigned it as sister to the remaining Bibionomorpha. Oosterbroek & Courtney (1995) assigned the Axymyiidae as sister to the Bibionomorpha, whereas Blagoderov *et al*. (2007) assigned *Axymyia* to a mostly unresolved and paraphyletic Bibionomorpha. In the search for new morphological characters, the internal male genital tract of Axymyiidae was recently examined (Borkent & Sinclair 2012). The configuration of the male genital tract appeared highly autapomorphic and no shared features were



FIGURES 1–3. *Plesioaxymyia vespertina*. **1**, female holotype, habitus (scale bar: 1.0 mm); **2**, female holotype, head, oblique view (scale bar: 0.5 mm); **3**, wing, paratype (scale bar: 1.0 mm). Abbreviations: CuA—anterior branch of cubital vein; CuP—posterior branch of cubital vein; $M_{1,2,4}$ —medial vein; $R_{2,3,4,5}$— radial vein; Sc—subcostal vein.



FIGURES 4–5. Female terminalia of *Plesioaxymyia vespertina*. **4**, lateral view; **5**, dorsal view (scale bar: 0.1 mm). Abbreviations: cerc—cercus; gen fk—genital fork; spmth—spermatheca; st—sternite; tg—tegite.

found with other nematocerous families. Specifically the family lacked the multi-chambered accessory gland present in Bibionomorpha s.str. (Borkent & Sinclair 2012; Sinclair *et al*. 2013). In an analysis of the male postabdomen, Spangenberg *et al*. (2012) placed Bibionidae, Anispodidae and Axymyiidae together in a clade, assigned as sister group to the Brachycera. Among synapomorphies supporting the entire clade was fusion of the hypandrium with the gonocoxites and parameres fused into a dorsal sclerite.

The establishment and recognition of the Neodiptera [Bibionomorpha *sensu* Hennig (1973) + Brachycera] by Michelsen (1996) on the basis of characters of the pronoto-cervical region was a significant advancement in Diptera phylogenetics. Michelsen (1996) included the Axymyiidae in the Neodiptera, which represents the first phylogenetic assignment of this family that is not based in part on wing venation (although Wood & Borkent (1989) assigned Axymyiidae to 'Diptera, exclusive of Tipulidae', based on the larval mandible).

The advancement of molecular based analyses has so far produced mixed results in regards to the placement of the Axymyiidae. Bertone *et al*. (2008) could not confidently resolve the phylogenetic relationship of the family. Wiegmann *et al*. (2011) recognized the Neodiptera and within this clade assigned Axymyiidae as sister group to the Bibionomorpha s.str. Additional molecular analyses are required to test the proposed relationships.

Discovery of the male of *P. vespertina* could potentially be significant in the classification and placement of the Axymyiidae. In the clade Bibionomorpha + Brachycera (i.e., Neodiptera), the parameres are fused dorsally forming a sheath that encircles the desclerotized aedeagus (Sinclair *et al*. 2013). In contrast, the aedeagus of Axymyiidae is well-sclerotized, tubular and distinctly separate from the dorsally fused parameres (Wood 1991, fig. 9e). Given the strong morphological and molecular support for the Neodiptera (Michelsen 1996; Wiegmann *et al*. 2011), lack of a parameral sheath in Axymyiidae suggests a possible sister-group relationship with the rest of the Neodiptera. Is the aedeagus and paramere of *Plesioaxymyia* similar to other Axymyiidae, or are these structures modified as in Perssommatidae and the Bibionomorpha? The discovery of the male of this unusual genus is certainly anxiously awaited.

In summary, *Plesioaxymyia* certainly appears to be the sister group of all remaining genera of Axymyiidae, and consequently there is a logical possibility that the male adult and/or immatures will be sufficiently different (and

hopefully plesiomorphic) from known axymyiids. Knowledge of these missing life stages is expected to clarify for the first time the relationship of Axymyiidae to other nematocerous Diptera.

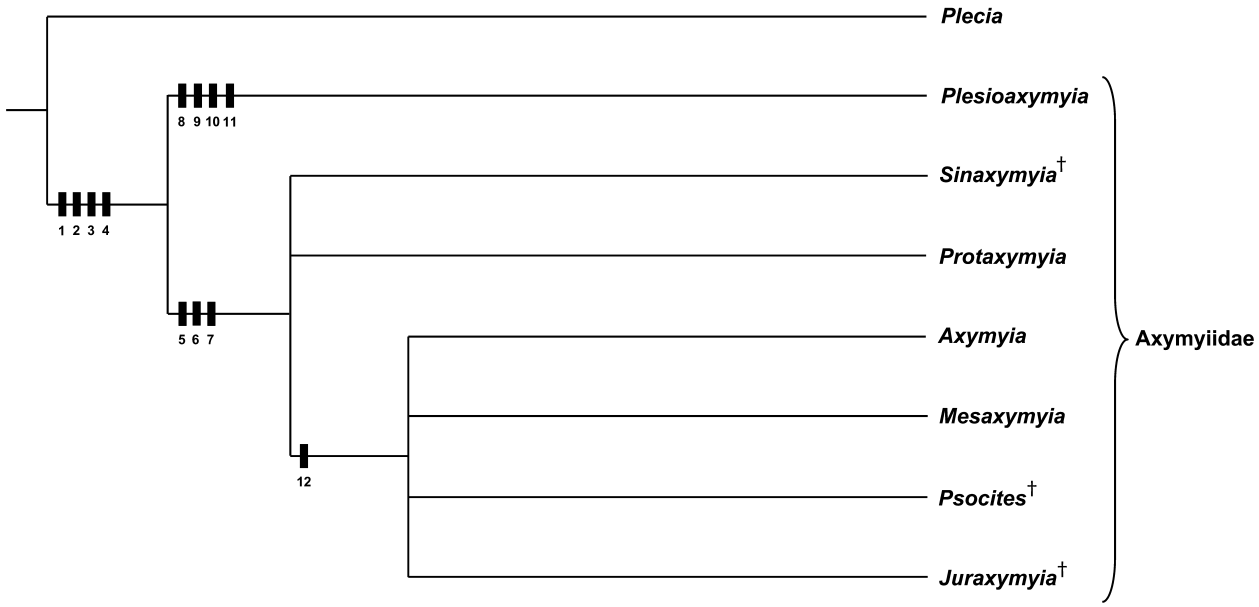


FIGURE 6. Phylogeny of the Axymyiidae. Characters are defined in Table 1 and discussed further in the text. Character distribution for uniquely derived states shown by black hash marks.

Acknowledgements

Art Borkent (British Columbia), Toyohei Saigusa (Fukuoka, Japan) and Monty Wood (CNC) kindly provided encouragement and supporting data on this taxon. Jeff Cumming (CNC), Hume Douglas (Canadian Food Inspection Agency), Art Borkent and an anonymous reviewer critically reviewed earlier drafts of this manuscript. Michelle Locke, Shannon Henderson and Scott Brooks (CNC) are thanked for greatly assisting in producing the photographs. I am grateful to the National Park Service for granting permission to collect in Mt. Rainier National Park (Permit No. MORA-2012-SCI-0017). Research was partially supported by a grant from the United States National Science Foundation (MIDGEPEET, Award No. 0933218).

References

Amorim, D.S. (1993) A phylogenetic analysis of the basal groups of Bibionomorpha, with a critical examination of the wing vein homology. *Revista Brasileira de Biologia*, 52 (3), 379–399. [1992]

Bertone, M.A., Courtney, C.W. & Wiegmann, B.M. (2008) Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology*, 33, 668–687. http://dx.doi.org/10.1111/j.1365-3113.2008.00437.x

Blagoderov, V., Grimaldi, D.A. & Fraser, N.C. (2007) How time flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. *American Museum Novitates*, 3572, 1–39. http://dx.doi.org/10.1206/0003-0082(2007)509[1:HTFFFD]2.0.CO;2

Borkent, A. & Sinclair, B.J. (2012) The male genital tract of Axymyiidae and Tanyderidae (Diptera). *In*: Festschrift commemorating the coordinators of the Manual of Nearctic Diptera and their contributions to building the Canadian National Collection of Insects. Part 3. *The Canadian Entomologist*, 144, 266–272. http://dx.doi.org/10.4039/tce.2012.26

Colless, D.H. (1962) A new Australian genus and family of Diptera (Nematocera: Perissommatidae). *Australian Journal of Zoology*, 10, 519–535. http://dx.doi.org/10.1071/ZO9620519

Cumming, J.M., Sinclair, B.J., Brooks, S.E., O'Hara, J.E. &. Skevington, J.H. (2011) The history of dipterology at the Canadian National Collection of Insects, with special reference to the Manual of Nearctic Diptera. *In*: Festschrift

commemorating the coordinators of the Manual of Nearctic Diptera and their contributions to building the Canadian National Collection of Insects. Part 1. *The Canadian Entomologist*, 143, 539–577.
Cumming, J.M. & Wood, D.M. (2009) 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.
Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, New York, pp. 755.
Hennig, W. (1973) Diptera (Zweiflügler). *Handbuch der Zoologie*, 4 (2), 1–337.
Krivosheina, M.G. (2000) Family Axymyiidae. *In*: Papp, L. & Darvas, B. (Eds.*), Contributions to a manual of Palaearctic Diptera. Appendix*. Science Herald, Budapest, pp. 31–39.
Krzemińska, E, Blagoderov, V. & Kzwemiński, W. (1993) Elliidae, a new fossil family of the infraorder Axymyiomorpha (Diptera). *Acta Zoologica Cracoviensia*, 35, 581–591.
Kzwemiński, W. & Krzemińska, E. (2003) Triassic Diptera: descriptions, revisions and phylogenetic relations. *Acta Zoologica Cracoviensia*, 46 (Supplement), 153–184.
McAtee, W.L. (1921) Description of a new genus of Nematocera. (Dipt.). *Proceedings of the Entomological Society of Washington*, 23, 49.
Michelsen, V. (1996) Neodiptera: new insights into the adult morphology and higher level phylogeny of Diptera (Insecta). *Zoological Journal of the Linnean Society*, 117, 71–102.
http://dx.doi.org/10.1111/j.1096-3642.1996.tb02149.x
Oosterbroek, P. & Courtney, G. (1995) Phylogeny of the nematocerous families of Diptera (Insecta). *Zoological Journal of the Linnean Society*, 115, 267–311.
http://dx.doi.org/10.1111/j.1096-3642.1995.tb02462.x
Riegert, P.W. (1999) *The survey of insects of northern Canada 1947–1962*. Rampeck Publishers, Regina, 48 pp.
Saigusa, T. (2006) *Homology of wing venation of Diptera*. Unpublished handout distributed at the 6th International Congress of Dipterology, Fukuoka, Japan, 26 pp.
Shannon, R.C. (1921) Another anomalous dipteron added to the Rhyphidae. *Proceedings of the Entomological Society of Washington*, 23, 51–51.
Sinclair, B.J., Cumming, J.M & Brooks, S.E. (2013) Male terminalia of Diptera (Insecta): a review of evolutionary trends, homology and phylogenetic implications. *Insect Systematics & Evolution.* [in press]
Spangenberg, R., Hünefeld, F., Schneeberg, K. & Beutel, R.G. (2012) The male postabdomen and reproductive system of *Bibio marci* Linnaeus, 1758 (Hexapoda: Diptera: Bibionidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 264–288.
http://dx.doi.org/10.1111/j.1439-0469.2012.00669.x
Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.W., Kim, J.-W., Lambkin, C., Bertone, M.A., Cassel, B.K., Peterson, K.J., Bayless, K.M., Heimberg, A.M., Wheeler, B.M., Peterson, K.J., Pape, T., Sinclair, B.J., Skevington, J.H., Blagoderov, V., Caravas, J., Kutty, S., 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*, 108, 5690–5695.
http://dx.doi.org/10.1073/pnas.1012675108
Wihlm, M.W. & Courtney, G.W. (2011) The distribution and life history of *Axymyia furcata* McAtee (Diptera: Axymyiidae), a wood inhabiting, semi-aquatic fly. *Proceedings of the Entomological Society of Washington*, 113, 385–398.
http://dx.doi.org/10.4289/0013-8797.113.3.385
Wihlm, M.W., Sam, R.B. & Courtney, G.W. (2012) Morphology of *Axymyia furcata* (Diptera: Axymyiidae), including scanning electron microscopy of all life stages. *In:* Festschrift commemorating the coordinators of the Manual of Nearctic Diptera and their contributions to building the Canadian National Collection of Insects. Part 3. *The Canadian Entomologist*, 144, 273–290.
http://dx.doi.org/10.4039/tce.2012.27
Wood, D.M. (1981) Axymyiidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Co-ords.), *Manual of Nearctic Diptera, Volume 1*. Agriculture Canada Monograph No. 27, pp. 209–212.
Wood, D.M. (1991) Homology and phylogenetic implications of male genitalia in Diptera; the ground plan. *In*: Weismann, L, Országh, I. & Pont, A.C. (Eds.) *Proceedings of the Second International Congress of Dipterology.* SPB Academic Publishing, The Hague, Netherlands, pp. 255–284.
Wood, D.M. & Borkent, A. (1989) Phylogeny and classification of the Nematocera [Chapter] 114. *In*: McAlpine, J.F. (Ed.) *Manual of Nearctic Diptera. Volume 3.* Agriculture Canada Monograph No. 32, pp. 1333–1370.
Zhang, J. (2010) Two new genera and one new species of Jurassic Axymyiidae (Diptera: Nematocera), with revision and redescription of the extinct taxa. *Annals of the Entomological Society of America*, 103, 455–464.
http://dx.doi.org/10.1603/an09073