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Revision of the Holarctic genus *Gloma* Meigen (Diptera: Empidoidea: Brachystomatidae: Trichopezinae)

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Abstract

The Holarctic genus *Gloma* Meigen is revised and includes five species (*G. fuscipennis* Meigen, *G. fuscipes* Melander, *G. luctuosa* Melander, *G. pectinipes* Melander, *G. pyricornis* Saigusa & Sinclair **sp. nov.**) and two undescribed species from China, presently known only from females. The monotypic Baltic amber genus *Palaeoparamesia* Meunier is discussed as possibly congeneric with *Gloma*. The Baltic amber species *Gloma hirta* Loew is considered a *nomen dubium*. A lectotype is designated for *Gloma luctuosa*. All species are described or diagnosed, and their geographic distributions mapped. A World key to the species of *Gloma* is provided. Phylogenetic placement of the genus, including a possible new relationship with *Oreogeton* Schiner is considered, and the relationships and zoogeographic history of the species are discussed based on a morphological cladistic analysis.

Key words: Nearctic, Palaearctic, distribution, male terminalia, new species, Baltic amber, *Palaeoparamesia*, *Oreogeton*, World key, phylogeny, zoogeography

Introduction

The Holarctic genus *Gloma* Meigen (Figs 1–4) is a poorly-known group of empidoid flies that are sporadically taken and seldom found in collections. The genus, which was originally characterized primarily on the basis of a reniform antennal postpedicel (Figs 2, 5), is assigned to the empidoid family Brachystomatidae, subfamily Trichopezinae (Sinclair & Cumming 2006), although a different classification has recently been proposed (Wahlberg & Johanson 2018). *Gloma* currently includes four described species, plus a new species that lacks the characteristic antenna (Fig. 6). Two possible undescribed species are also known from single female specimens from China. The purpose of this article is to redefine and revise *Gloma*, in order to incorporate the new species and update collection data for all previously described species. A key to the World species of *Gloma* is also provided for the first time. In addition, the phylogenetic placement of the genus is discussed based on newly recognized features of the male terminalia. The relationships and zoogeographic history of the species of *Gloma* are discussed based on a cladistic analysis of morphological characters.

Material & methods

This study is based on specimens borrowed or deposited in the following collections: California Academy of Sciences, San Francisco, USA (CAS); Canadian National Collection of Insects, Ottawa, Canada (CNC); California State Collection of Arthropods, Sacramento, USA (CSCA); University of Guelph Insect Collection, Guelph, Canada (DEBU); Geowissenschaftliches Zentrum der Georg-August-Universität, Göttingen, Germany (GZG); Biosystematics Laboratory, Kyushu University, Fukuoka, Japan (KUMF); Royal British Columbia Museum, Victoria, Canada

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(RBCM); United States National Museum of Natural History, Washington D.C., USA (USNM); William J. Turner collection, Pullman, USA (WJTC); M.T. James Museum, Washington State University, Pullman, USA (WSU); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

Terms used for adult structures follow those of Cumming & Wood (2017). Male and female terminalia were macerated in 85% lactic acid heated in a microwave oven. Each microwave heating interval comprised 15–30 seconds and was followed by a 1–2 minute cooling period during which macerated muscle tissue was removed with a fine probe. Terminalia were subsequently examined in glycerin on a depression slide. Photographs were taken with a Leica camera model DFC5400 using Leica Application Suite X. Photo montages were created using Zerene Stacker 1.04.

Label data for primary types are cited from the top downward, with the data from each label in quotation marks. Labels are cited in full, with original spelling, punctuation, and date, and label lines are delimited by a slash (/). Additional information is included in square [ ] brackets. The repository of each type is given in parentheses. Secondary type data are abridged and listed alphabetically.

Legs from specimens of *Gloma luctuosa* were sent to the Biodiversity Institute of Ontario in Guelph, ON, Canada for sequencing and alignment of the "Barcoding" region (Hebert *et al*. 2003) of the Cytochrome *c* Oxidase I (COI) mitochondrial gene, a 658 base-pair region of this gene. These specimens are listed in the "Additional material examined" section under that species. GenBank accession numbers are also included in this list. No other species of *Gloma* were submitted because of a lack of available fresh material when barcode analyses were being conducted for a broad spectrum of empidoids in the CNC.

Sixteen morphological characters were used in the phylogenetic analysis, including 15 binary characters and 1 multistate character (see "Appendix 1"). All characters were equally weighted and the multistate character was treated as unordered. Characters were scored for the five ingroup species of *Gloma* and two outgroup taxa. The outgroup taxa selected for the analysis were single exemplar species in the genera *Oreogeton* Schiner (Oreogetoninae) and *Heterophlebus* Philippi (Trichopezinae). Parsimony analysis of the character state matrix (Appendix 2) was performed using PAUP* version 4.0b10 (Swofford 2002). A heuristic search using stepwise addition, random addition sequence of taxa and tree-bisection-reconnection (TBR) branch swapping with a 1000 random replications, was conducted to find the most parsimonious tree. Tree statistics, specifically the consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated to assess the fit of data to the cladograms.

Gloma Meigen

Gloma Meigen, 1822: 14. Type species, *Gloma fuscipennis* Meigen, 1822: 14 (by monotypy).

Diagnosis. The genus is readily distinguished by the following combination of characters: Eyes bare, male holoptic, radial fork V-shaped, veins without setae, postpedicel pyriform or reniform with sub-dorsal or dorsal arista-like extension, female frons without setae; male cercus with apical prolongation of posterior face (= hypoproct), bearing setulae, surstylus divided into dorsal and ventral lobes with a ventral surstylar process, phallus fused apically with paired hypandrial bridge processes, female tergite 8 with internal medial apodeme and female tergite 10 with numerous short thickened setae.

Redescription. Male. Head: holoptic, eyes bare, with upper facets enlarged (Fig. 2); face concave, mostly membranous; ocellar triangle prominent with pair of ocellar setae inserted anteromedial to lateral ocelli and 1–2 pairs of shorter setae; postocular row of setae arched over margin of eye. Vertical bristles not differentiated from surrounding setae. Antenna (Figs 5, 6) dark, scape subequal in length to pedicel; scape with stout dorsal setae and pedicel with circlet of stout setae; postpedicel pyriform or somewhat reniform and drooping, bearing long subdorsal or dorsal terminal arista-like elongation; arista-like stylus comprising short basal article, longer than wide; second article half-length of eye height, bearing seta-like apical sensillum. Proboscis folded up into face; shorter than eye height. Palpus slightly shorter than labrum, narrowed at apex with subapical sensory pit; cylindrical, only slightly expanded apically; bearing long ventrolateral setae. Lacinia shorter than palpus, blade-like; stipes short and stout. Labrum stout, straight, apex pointed with V-shaped notch; epipharyngeal blades weakly differentiated, not articulated, bearing several pairs of knob-like proximal sensillae; epipharyngeal carina absent. Hypopharynx stout, straight, subequal in length to labrum. Labellum well developed, fleshy, with numerous short setae; prementum

with several setae; more than 10 pseudotracheae. Clypeal ridge long and slender, longer than cibarium, articulated together with labrum at labrofulcral articulation point.

Thorax: mesoscutum somewhat arched. Setae long and conspicuous. Acrostichals biserial, slightly shorter than dorsocentral setae, ending at prescutellar depression; dorsocentral setae uniserial, 7 or more setae, anterior pair divergent from row and increasing in length posteriorly; 1 long postpronotal seta and several shorter setae; 1–2 post-humeral setae; 3 long notopleural setae; 2–3 presutural and postsutural supra-alar setae; 1 postalar seta; 2 or more pairs of scutellar setae. Laterotergite bare; prosternum separate from proepisternum; upper and lower proepisternum bearing setae; dorsal mesepimeron pocket present. **Wing** (Fig. 4): length 3.2–4.5 mm; broad, infuscate; anal lobe well developed; alula weakly developed, alular incision obtuse; basal costal bristle present; stigma elongate-oval overlapping apex of R_1. Costa gradually weakened beyond R_1; circumambient; Sc weakened at costa; all veins bare; R_{4+5} branched, acute at base; R_4 straight, closer to R_{2+3} than to R_{4+5}; R_{4+5} and M_{1+2} strongly arched toward posterior wing margin subapically; cell dm truncate apically, emitting 3 veins; cell cua (anal cell) rounded with CuA recurved; CuA+CuP (A_1) reduced to inconspicuous fold, not reaching wing margin. Halter brownish. **Legs:** long and clothed in dark setae, pale to entirely dark. Fore tibia with anteroventral apical comb; hind tibia with posteroventral apical comb. Hind femur and tibia with long dorsal setae, longer than width of segment; hind tibia dilated towards tip. Tarsomere 1 of hindleg broader than other legs. Tarsomere 5 flattened with long claws; pulvillus pale, long and broad, nearly as long as claw; empodium slender, short with sparse ventral pubescence.

Abdomen: segments gradually tapered, conspicuously setose, especially posteromarginally. Tergite 8 slender, one-sixth length of tergite 7. Terminalia: symmetrical, arched dorsally, unrotated (Fig. 3). Proctiger narrow laterally, with thinly sclerotized anterior face (= cercus) and well sclerotized posterior face (= hypoproct) continuous with subepandrial sclerite and extending beyond apex of cercus. Epandrium rounded, with narrow dorsal bridge. Subepandrial plate narrow, extended along base of dorsal surstylus and arched to base of ventral surstylar process. Surstylus divided into broad dorsal and ventral components and slender, often strongly arched ventral surstylar process. Hypandrium prolonged posteriorly, tapered to pair of lateral lobes; narrow gonocoxal apodemes extending little beyond anterior margin; inner distal margin with complex series of strap-like sclerites or processes. Dorsal bridge articulated with pair of digitiform postgonites; dorsal bridge extended posteriorly as narrow plate-like sclerite to apex of phallus, encircling phallus and divided into pair of sickle-shaped hypandrial bridge processes. Phallus narrow, arched at apex; apex fused with paired hypandrial bridge processes; ejaculatory apodeme broad, flattened, articulated at base of phallus.

Female. Similar to male except as follows: dichoptic; frons bare; dorsal setae on hind leg shorter; hind tibia not distinctly dilated towards tip; claws and pulvilli much shorter. Abdomen truncate, caudal segments withdrawn into segment 7; posterior margin of tergite 7 without row of fine setae, with outstanding marginal setae only. Terminalia: sclerites of segment 8 articulated anterolaterally; anterodorsal margin of tergite 8 with elongate, narrow apodeme, extending into segment 7; posterior margin of tergite 8 with deep, median membranous cleft, medially with transverse row of short setae. Sternite 8 with elongate posterior marginal setae, overlapping apical segments. Tergite 9+10 (acanthophorites) divided dorsomedially, subtriangular, with row(s) of pale, stout, erect setae. Cercus heavily sclerotized, slightly arched posterodorsally. Spermathecal receptacle spherical to oblong, darkly pigmented on long, unpigmented duct; genital fork small, subrectangular.

Remarks. Loew (1850) mentioned a species of *Gloma* from Baltic amber, that he stated resembled the type species, *G. fuscipennis*, in the form of the antenna. He referred to this fossil species as *Gloma hirta* Loew, 1850: 41, but did not describe it further. The whereabouts of the type specimens remain uncertain and we hereby consider this name to be a *nomen dubium*.

Gloma fuscipennis Meigen

(Figs 11–13, 28, 32, 39)

Gloma fuscipennis Meigen, 1822: 14. Type locality: not given.

Gloma ossicula Becker, 1887: 132. Type locality: not given [Switzerland, St. Moritz].

G. fuscipennis: Melander, 1928: 102 [checklist, figure of male terminalia and habitus]; Engel, 1941: 194 [redescription, figures of male terminalia, head]; Bährmann, 1960: 515 [male terminalia]; Krystoph, 1961: 852 [mouthparts]; Collin, 1961: 313 [redescription, figures of habitus, head, male genitalia]; Gorodkov & Kovalev, 1969: 613 [key]; Chvála, 1983: 43 [figures of male terminalia, antenna]; Chvála & Wagner, 1989: 229 [catalogue]; Ceianu, 1992: 22 [new records]; Ulrich, 1994: 11

[mesepimeron]; Bährmann *et al*., 1999: 100 [checklist]; Chvála & Barták 2000: 177 [new records]; Papp & Földvári, 2000: 241 [new records]; Yang *et al*., 2007: 450 [catalogue]; Kahanpää, 2014: 195 [checklist]; Meyer & Stark, 2015: 54 [checklist, bibliography]; Shamshev, 2016: 17 [checklist].

Material examined. GERMANY: Bonn, Kottenforst, 2.vi.2002, B.J. Sinclair (1 ♂, CNC); Bonn, Kottenforst, Katzenlochbachtal, 50°40′N 7°05′E, 16.v.2004, B.J. Sinclair (1 ♀, CNC); Bonn, Venusberg, 24.v.1990, J. Emoto (4 ♂, 3 ♀, KUMF). **NORWAY:** Sandnes, 10.vi.1994, Sorbus wood, J.R. Vockeroth (1 ♀, CNC). **SCOTLAND:** Bonhill, Dumbartonshire, vii.1912, J.R. Malloch (2 ♂, 1 ♀, USNM); Dunoon, vii.1912, J.R. Malloch (1 ♂, USNM); Loch Assynt, Sutherland, 5.vi.1911. Lt.-Col. Yerbury (1 ♂, KUMF). **SWITZERLAND:** Canton de Vaud, Cudrefin, 435 m, 22.vi.1976, P.H. Arnaud (1 ♂, USNM).

Diagnosis. This species is distinguished from other species of *Gloma* by the combination of reniform postpedicel, elongate hypoproct extension, short ventral surstylar process, boot-shaped dorsal lobe of the surstylus and two long, strong setae arising from apex of the ventral lobe of the surstylus.

Redescription. Male. Antenna with postpedicel reniform; circlet of setae on pedicel longer ventrally. Pair of greyish vittae between acrostichals and dorsocentral setae. Scutellum with 2–5 pairs of setae. Legs brownish, with coxae and sometimes apex of femora and base of tibiae yellowish brown. Terminalia (Figs 11–13): hypoproct with very narrow extension, 5X apical width; margin of apex with short, stout setae. Epandrium rounded, with row of strong setae. Dorsal lobe of surstylus boot-shaped with short setae on apical outer face; inner apex with several strong setae directed medially. Ventral surstylar process short, with asymmetrical forked apex; lower fork slender and longer than upper; ventral lobe of surstylus with subtriangular apex, bearing 2 long, strong, curved setae. Hypandrium prolonged posteriorly, tapered into pair of narrow lateral lobes; inner distal margin infolded beneath phallus, narrowed anteriorly and arched dorsally as outer sickle-shaped hypandrial process; inner infolded margin forming thinly sclerotized convoluted complex, extended dorsally becoming associated with apex of postgonite. Postgonite lying parallel to hypandrium, with apex strongly arched dorsally and tapered; without lateral basal process. Hypandrial bridge process with broad base, strongly tapered to near apex of phallus; paired sickle-shaped processes on either side of phallus slightly longer than exposed phallic apex.

Female. Similar to male except as follows: Terminalia (Fig. 28): tergite 8 with sparse row of very short setae. Sternite 8 subtriangular in ventral view, desclerotized medially; tapered apically to narrow margin, about as wide as sternite 10; marginal setae shorter than length of sternite. Tergite 9+10 with single row of pale, stout, erect setae. Spermathecal receptacle oblong (Fig. 32).

Distribution. This species occurs across Europe (Austria, Belgium, Czech Republic, Finland, Germany, Great Britain, Hungary, Ireland, Norway, Romania, Slovakia, Sweden, Switzerland) and European Russia (Chvála 1987; Chvála & Barták 2000; Collin 1961; Ceianu 1992; Papp & Földvári 2000; Kahanpää 2014; Shamshev 2016) (Fig. 39).

Remarks. Collin (1961) redescribed this species, including habitus, head and male genitalia illustrations. In addition, Collin (1961) stated that he examined the male type of *G. fuscipennis*, as well as a male from the type series of *G. ossicula* Becker and considered them conspecific. *Gloma fuscipennis* appears to be active primarily during the spring and early summer seasons (i.e., May to July), and males are stated to form swarms towards evening (Collin 1961).

Gloma fuscipes Melander

(Figs 1–4, 14–16, 17, 26, 27, 31, 36)

Gloma fuscipes Melander, 1945: 84. Type locality: Puget, Washington, USA.
G. fuscipes: Melander, 1965: 454 [catalogue]; Poole, 1996: 156, 468 [checklist]; Yang *et al*., 2007: 451 [catalogue].

Type material examined. HOLOTYPE, ♂ labelled: "Puget WASH/ 4July 1925/ ALMelander"; "HOLOTYPE/ Gloma/fuscipes/ Mel. [red label]"; "ALMelander/ Collection/ 1961" (USNM). **PARATYPES: USA. Idaho:** Lookout Mtn., Priest Lake, 20.viii.1919, A.L. Melander (1 ♀, USNM); Moscow Mtn, 10.viii.1924 (3 ♂, USNM); **Oregon:** Mt. Hood, 3000 ft, 29.vii.1921, A.L. Melander (1 ♂, 1 ♀, USNM). **Washington:** Canyon Creek, 26.vii.1925, A.L. Melander (1 ♀, USNM); Mt. Constitution, 31.vii.1908 (1 ♀, USNM); Potlach, Hoods Canal, 28.vii.1917, A.L. Melander [allotype] (1 ♀, USNM).

Note on type specimens. Seven paratypes (4 ♂, 3 ♀) and the female allotype are listed in Melander (1945), but an additional female paratype was found labelled as such. Since all localities match those listed by Melander (1945), it is assumed the original number of female paratypes listed was incorrect.

Additional material examined. CANADA. Alberta: Peter Lougheed Prov. Pk, Boulton/ Fox Ck Tr, 14.vii.2015, 1730 m, 50°37.03N′, 115°06.67′W, B.J. Sinclair (1 ♀, CNC). **British Columbia:** Bear Lake, Crooked River Prov. Pk, 16.viii.1978, P.H. Arnaud (1 ♂, USNM); Mt. Thornhill nr. Terrace, 30.vii.1960, W.R. Richards (5 ♂, 1 ♀, CNC; 1 ♂, KUMF); Squamish, Diamond Head Tr., 4000 ft, 19.viiii.1953, G.J. Spencer (1 ♂, CNC); Vancouver Is., 2.3 km from Lk Cowichan, cold spring run beside S Shore Rd, MT, 19–28.vii.1985, I.M. Smith (73 ♂, 1 ♀, CNC). **USA. California:** El Dorado Co., Echo Lake, 26.vii.1966, P.H. Arnaud (11 ♂, 11 ♀, USNM); Humboldt Co., Humboldt Bay NWR, Lanphere Dunes, 40°53′29.28″N, 124°8′34.80″W, 10.iv.–18.viii.2008, MT #1, P.H. Kerr & P. Haggard (1 ♂, CSCA); Fresno Co., Huntington Lk, 13.viii.1984, D.J. Burdick (1 ♂, CNC); Fresno Co., Huntington Lk, Kaiser Ck, 2700 m, 17.viii.1984, 13.viii.1989, J. MacDonald (3 ♂, 1 ♀, CNC); Fresno Co., Huntington Lk, Rancheria Ck, 2600 m, 30.vii., 10.viii.1984, J. MacDonald (2 ♂, 1 ♀, CNC); Fresno Co., Sierra NF, Badger Flat Cpgd, Rancheria Ck, 2500 m, 30.vii.1979, D.D. Wilder (1 ♂, CAS); Inyo Co., Mosquito Pk, E side Mono Pass, 10,000 ft, 17.viii.1988, P.H. Arnaud (1 ♂, USNM); Nevada Co., Sagehen Ck Field Station, MT, N39°25′54.6″ W120°14′26.0″, 19.vii.–10.viii.2012, C.J. Borkent, J.M. Cumming, S.E. Brooks (2 ♂, CNC); Nevada Co., Sagehen Ck Field Station, MT, N39°25′54.6″ W120°14′26.0″, 10.ix.–15.x.2012, C.J. Borkent, J.M. Cumming, S.E. Brooks (2 ♂, CNC); Nevada Co., Big Culvert along Sagehen Ck, N39°26′04.4″ W120°16′52.2″, 17.vii.–10.viii.2012, 6 m MT, C.J. Borkent, J.M. Cumming, S.E. Brooks (8 ♂, 7 ♀, CNC); Nevada Co., Big Culvert along Sagehen Ck, N39°26′04.4″ W120°16′52.2″, 10.viii.–10.ix.2012, 6 m MT, C.J. Borkent, J.M. Cumming, S.E. Brooks (10 ♂, 9 ♀, CNC). **Idaho:** Latah Co., Little Sand Creek nr Laird Park, 2900 ft, 16 mi E Potlatch, 5.viii.1979, N.E. Woodley (1 ♀, USNM); Latah Co., L. Sand Ck, nr Bonami Ck, 16 mi E Potlach, 2900 ft, 9.viii.1979, W.J. Turner (7 ♀, WJTC). **Oregon:** Linn Co., Hackleman Ck, 0.6 mi E Tombstone Pass, 44°23′51″N, 122°7′53″N, MT, 1.viii.–22.ix.2016, S. Fitzgerald (4 ♂, 22 ♀, CNC). **Washington:** Grays Harbor Co., Humptulips Rest Area on Hwy 101, 20.vii.1978, D.D. Wilder (1 ♀, CAS); Grays Harbor Co., Olympic NF, Willaby Cpgd Rec. Loop Tr., 21.vii.1978, D.D. Wilder (13 ♂, 6 ♀, CAS); Jefferson Co., Olympic NP, T26NR13W Sec. 28, sweeping coastal forest, 22.vii.1978, D.D. Wilder (3 ♂, 1 ♀, CAS); Mt. Rainier NP, 10.viii.1941, Lipovsky (1 ♀, WSU); Mt. Rainier, NP, West End Rd., 3 mi N Jct Hwy 706 on Tahoma R., 2500 ft, 12.viii.1977, W.J. Turner (22 ♂, 18 ♀, WJTC; 1 ♂, 1 ♀, USNM); Pacific Co., Fort Canby SP nr Ilwaco, 19.vii.1978, D.D. Wilder (1 ♀, CAS); Pierce Co., Tacoma. 17.viii.1911 (1 ♀, USNM); Pierce Co., Mt. Rainier NP, White River Cpgd, 4400 ft, 9–10.viii.1977, R.S. Zack & W.J. Turner (1 ♀, WSU); Mt. Rainier NP, West End Rd, nr Puyallup R., Pierce Co., 3500 ft, 12.viii.1977, W.J. Turner (68 ♂, 42 ♀, WJTC); Mt. Rainier NP, White River Cpgd on White R., 4400 ft, 9–10.viii.1977, sweeping, W.J. Turner (8 ♂, 5 ♀, WJTC); Mt. Rainier NP, Comet Falls Tr. above van Trump Ck, 4500 ft, 13.viii.1977, sweeping, W.J. Turner (13 ♂, 1 ♀, WJTC); Mt. Rainier NP, van Trump Ck, above Christine Falls, 3900 ft, 11.viii.1977, W.J. Turner (5 ♂, 6 ♀, WJTC).

Diagnosis. This species is distinguished from other species of *Gloma* by the combination of reniform postpedicel, pale legs especially coxae, short hypoproct extension, long, sickle-shaped ventral surstylar process, broad, rounded dorsal lobe of the surstylus and numerous strong setae on the ventral lobe of the surstylus.

Redescription. Male. Antenna with postpedicel reniform; circlet of setae on pedicel longer ventrally. Pair of faint vittae between acrostichals and dorsocentral setae. Scutellum with 2 pairs of setae. Legs brownish, with coxae, trochanters, femora and fore tibia yellowish brown. Terminalia (Figs 14–16): hypoproct with short, triangular extension, extending 2–3X apical width; margin of apex with short, stout setae. Epandrium rounded, with row of strong setae. Dorsal lobe of surstylus broadly sickle-shaped with short setae on apical outer face; inner apex with several short setae directed medially. Ventral surstylar process very long, slender and strongly curved, filament-like; outer margin of apical third jagged; ventral lobe of surstylus broad, rounded apically, bearing numerous long, strong marginal setae, shorter setae on outer face. Hypandrium prolonged posteriorly, tapered into pair of triangular lateral lobes; inner distal margin infolded beneath phallus, narrowed anteriorly and arched dorsally as outer sickle-shaped hypandrial process, with weakly pigmented lateral expansion bearing broad sensillum; inner infolded margin forming thinly sclerotized complex, extended dorsally as ear-like lobes. Postgonite lying parallel to hypandrium, with apex strongly arched dorsally, with rounded and laterally flattened apex. Hypandrial bridge process with narrow base, strongly tapered to near apex of phallus; paired long to very long sickle-shaped processes on either side of phallus, more than twice length of exposed phallic apex (Fig. 17).

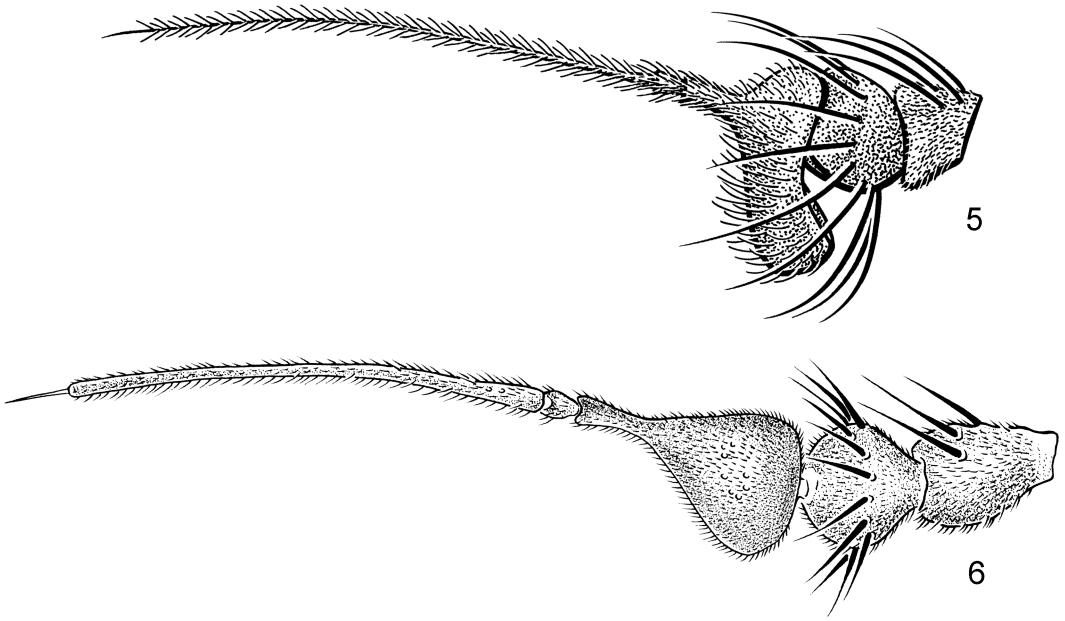
Female. Similar to male except as follows: Terminalia (Figs 26, 27): tergite 8 with sparse row of short setae.

Sternite 8 slightly tapered in ventral view, not desclerotized medially with broad rounded posteriorly margin, broader than width of sternite 10; marginal setae nearly as long as length of sternite. Tergite 9+10 with 2 or more rows of pale, stout, erect setae. Spermathecal receptacle spherical (Fig. 31).

FIGURES 1–4. *Gloma* morphology. **1.** *Gloma fuscipes* Melander, pinned male; **2.** Same, male head in lateral view; **3.** Same, male terminalia in lateral view; **4.** Same, male wing. Abbreviations: an lb—anal lobe; CuA—anterior branch of cubital vein; cua—anterior cubital cell; CuP—posterior branch of cubital vein; dm—discal medial cell; dm-m—discal medial crossvein; M_1, M_2, M_4—medial veins; pped—postpedicel; R_1, R_{2+3}, R_4, R_5—radial veins; Sc—subcostal vein.

Distribution. This species occurs in western North America from British Columbia south to California, including records from Alberta, Idaho, Washington and Oregon (Fig. 36).

Remarks. There is variation in the length and density of setae on the sclerites of the female terminalia of *G. fuscipes*. Some specimens have longer and denser setae on tergite and sternite 8, as well as denser setae on tergite 9+10, than the setae depicted in Figures 26 and 27. *Gloma fuscipes* appears to be active primarily in late summer and early fall.



FIGURES 5–6. *Gloma* antennae. **5.** *Gloma luctuosa* Melander, male antenna; modified from Steyskal & Knutson (1981, fig. 36); **6.** *Gloma pyricornis* **sp. nov.**, male antenna.

Gloma luctuosa Melander
(Figs 5, 19–21, 33, 37)

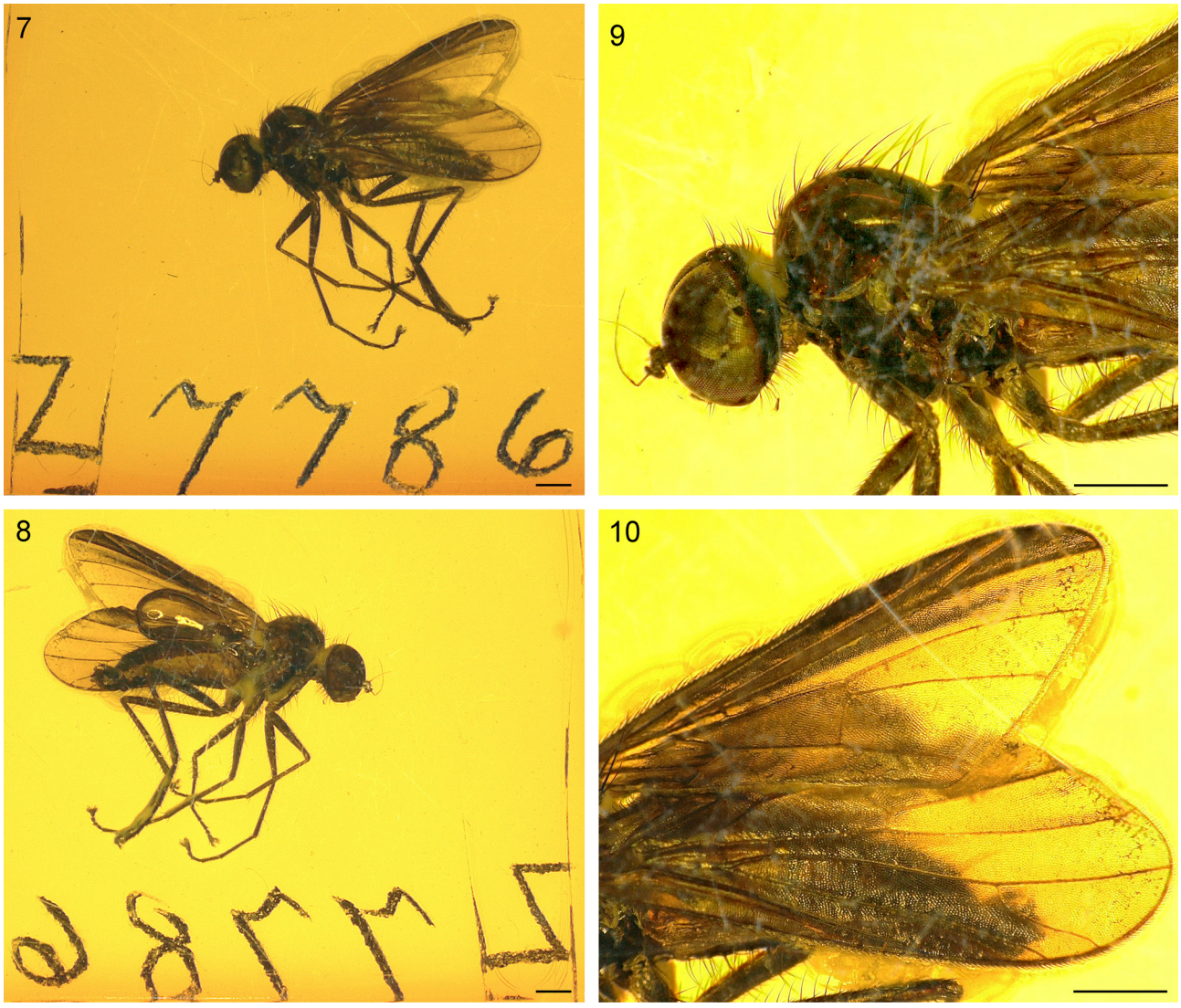
Gloma luctuosa Melander, 1928: 102. Type locality: Mt. Rainier, Washington, USA.
G. luctuosa: Melander, 1965: 454 [catalogue]; McAlpine, 1967: 233, 234 [male terminalia]; McAlpine, 1981: 48 [male terminalia]; Cumming *et al*., 1995: 149 [male terminalia]; Poole, 1996: 156, 499 [checklist]; Yang *et al*., 2007: 451 [catalogue].

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labeled: "Mt. Rainier/ Fairfx Trl/ 9 Aug 1922/ ALMelander"; "TYPE/ Gloma/ luctuosa/ Mel. [red label]; "ALMelander/ Collection/ 1961"; "LECTOTYPE/ of *Gloma*/ *luctuosa* Melander/ des. B.J. Sinclair *et al*. 2019 [red label] (USNM). **PARALECTOTYPES:** Same data as lectotype (3 ♂, 3 ♀, USNM).

Note on type specimens. The original type series includes four male and four female specimens. One female syntype was missing from the USNM collection and its location is unknown.

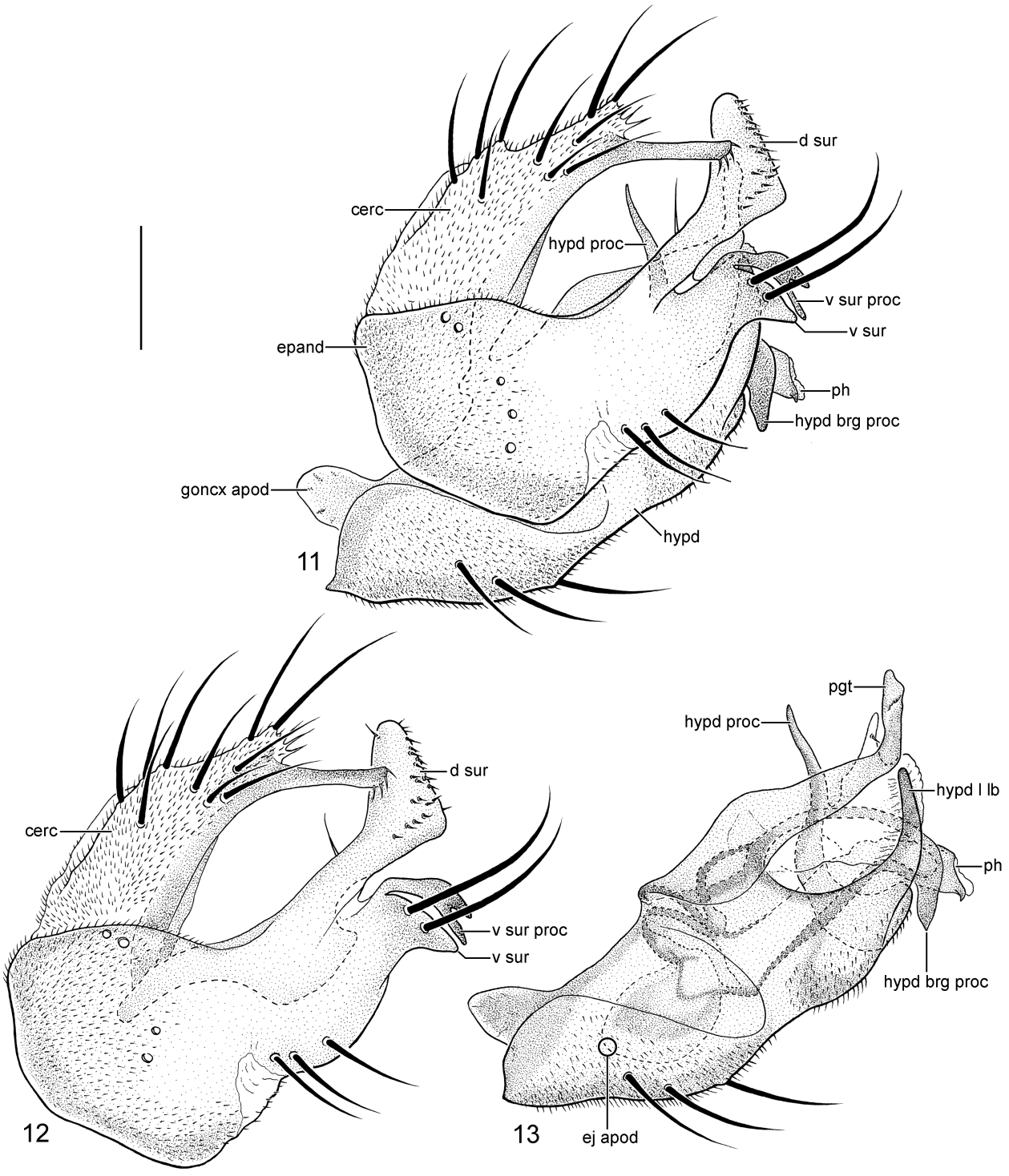
Additional material examined. CANADA. British Columbia: Exchamsiks River, 58 km SW Terrace, 54°20′00″N 129°17′81″W, 18.viii.2008, J.M. Cumming, S.E. Brooks (1 ♂, 1 ♀, CNC); same data except, CNC161459 (GenBank# MN134670), CNC161460 (GenBank# MN134669), CNC161462 (GenBank# MN134666) (1 ♂, 2 ♀, barcoded, CNC); same locality, MT, 15–17.viii.2008, S.E. Brooks, J.M. Cumming (2 ♀, CNC); same data except, 17–18.viii.2008, CNC161461 (GenBank# MN134668), CNC161463 (GenBank# MN134667) (1 ♂, 1 ♀, barcoded, CNC); Graham Is, Bonanza Ck, 4.viii.1983, R.A. Cannings (4 ♀, RBCM); Mt. Thornhill nr. Terrace, 29 & 30.vii.1960, W.R. Richards (3 ♂, 1 ♀, CNC; 1 ♂, KUMF); same locality, 30.vii.1960, B. Heming (1 ♂, CNC); Mt. Thornhill, Terrace, 8.viii.1960, C.H. Mann (1 ♂, 4 ♀, CNC); Prince Rupert, Ridley Is., shoreline of rocks, logs, 54°14.13′N 130°19.80′W, 17.viii.2008, J.M. Cumming (1 ♀, CNC); Prince Rupert, Park Avenue Cpgd, FIT, 8.viii.1996, P.H. & M.M. Arnaud (1 ♂, 1 ♀, USNM); Queen Charlotte Islands, Graham Is, road from QCC to Rennel Sound, first river before Port Clements, 53°22′45″N 132°16′33″W, 8.viii.2001, S. Allombert (2

♂, RBCM); Squamish, Diamond Head Tr., 3500 ft, 17.viii.1953, G.J. Spencer (1 ♂, CNC); same locality, 3200 ft, 12.viii.1953, G.J. Spencer (1 ♀, CNC). **USA. Alaska:** Douglas Island, Fish Ck, 6.viii.1958, W.C.F. coll. (1 ♀, WSU); Ketchikan, 28.vii.1958, F. Baker (1 ♀, WSU); Ketchikan, Deer Mtn, 100–200 m, 5.viii.1970, N.L.H. Krauss (2 ♂, 1 ♀, USNM); Kukak Bay, 5.viii.1953, W.C.F. coll. (1 ♂, WSU); Thane, 13.viii.1952, W.C.F. coll. (4 ♂, 2 ♀, WSU); Valdez, Glacier Cpgd, 1–2.viii.1978, P.H. Arnaud (20 ♂, 1 ♀, USNM; 1 ♂, CAS); Valdez, 3 mi W, 24.viii.1948, R.I. Sailer, Alaska Ins Project (1 ♀, UNSM). **Washington:** Jefferson Co., Olympic NP, T26NR13W Sec. 28, sweeping coastal forest, 22.vii.1978, D.D. Wilder (1 ♂, CAS); Mt. Rainier NP, Paradise River near Paradise, moist meadow seep, 20.viii.1977, N.E. Woodley (3 ♂, 2 ♀, USNM); Mt. Rainier NP, Sunbeam Ck, above Louise Lk, 1520 m, 4.viii.1977, D.D. Wilder (1 ♂, CAS); Mt. Rainier NP, West End Rd, 3 mi W jct Hwy 706 on Tahoma R., 2500 ft, 12.viii.1977, sweeping, W.J. Turner (4 ♂, 5 ♀, WJTC); Mt. Rainier NP, White River Cpgd on White R., 4400 ft, 9–10.viii.1977, Malaise, sweeping, W.J. Turner (4 ♂, WJTC); Mt. Rainier NP, Comet Falls Tr. above van Trump Ck, 4500 ft, 13.viii.1977, W.J. Turner (1 ♂, WJTC); Mt. Rainier NP, Paradise River nr Paradise, 20.viii.1977, N.E. Woodley (1 ♂, 1 ♀, KUMF).

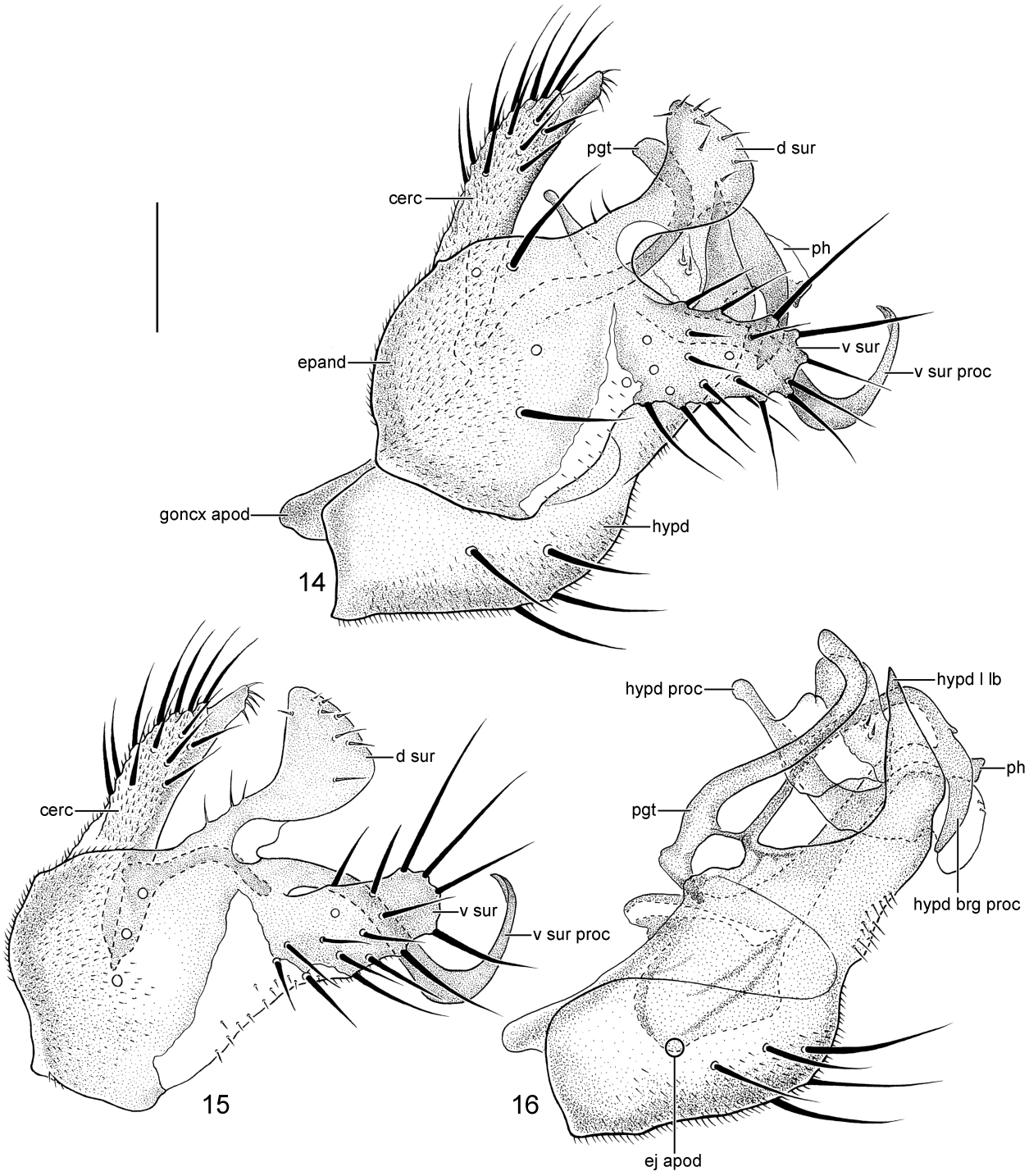


FIGURES 7–10. *Palaeoparamesia proosti* Meunier, specimen No. 7786 (GZG.BST.00056) in Baltic amber. **7.** Left side of fossil showing Meunier's specimen number below inclusion; **8.** Right side of fossil; **9.** Close-up of head and thorax viewed from left side of fossil; **10.** Close-up of wings viewed from left side of fossil. Scale bars = 0.5 mm (photographs @ GZG Museum, B. Ilsemann).

Diagnosis. This species is distinguished from other species of *Gloma* by the combination of reniform postpedicel, dark legs, elongate hypoproct extension, corkscrew-shaped ventral surstylar process, broadly subtriangular dorsal lobe of the surstylus and numerous strong setae on the margin of the ventral lobe of the surstylus.



FIGURES 11–13. *Gloma fuscipennis* Meigen, male terminalia, left lateral view. **11.** Hypopygium; **12.** Epandrium and proctiger; **13.** Hypandrium and phallus. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; ej apod—ejaculatory apodeme; epand—epandrium; goncx apod—gonocoxal apodeme; hypd—hypandrium; hypd brg proc–hypandrial bridge process; hypd l lb–hypandrial lateral lobe; hypd proc–hypandrial process; pgt—postgonite; ph—phallus; v sur—ventral lobe of surstylus; v sur proc—ventral surstylar process. Scale bar = 0.1 mm.



FIGURES 14–16. *Gloma fuscipes* Melander, male terminalia, left lateral view. **14.** Hypopygium; **15.** Epandrium and proctiger; **16.** Hypandrium and phallus. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; ej apod—ejaculatory apodeme; epand—epandrium; goncx apod—gonocoxal apodeme; hypd—hypandrium; hypd brg proc–hypandrial bridge process; hypd l lb–hypandrial lateral lobe; hypd proc–hypandrial process; pgt—postgonite; ph—phallus; v sur—ventral lobe of surstylus; v sur proc—ventral surstylar process. Scale bar = 0.1 mm.

Redescription. Male. Antenna with postpedicel reniform; circlet of setae on pedicel longer ventrally (Fig. 5). Pair of greyish vittae between acrostichals and dorsocentral setae. Scutellum with 2 pairs of setae. Legs brownish. Terminalia (Figs 19–21): hypoproct with long, narrow extension, extending nearly 4X apical width; margin of apex with short, stout setae. Epandrium rounded, with row of strong setae. Dorsal lobe surstylus broadly subtriangular

with short setae on apical outer face; inner apex with numerous short setae directed medially. Ventral surstylar process very long, slender, apex curled into tight swirl or corkscrew; ventral lobe of surstylus narrow, digitiform, rounded apically, bearing double row of long, strong marginal setae. Hypandrium prolonged posteriorly into pair of laterally flattened lateral lobes with pointed apex; inner distal margin infolded beneath phallus, narrowed anteriorly and arched dorsally as outer sickle-shaped hypandrial process, with curved apex; lateral margin of hypandrial process with weakly pigmented lateral lobe bearing small sensillum on inner apical face and enlarged sensillum on lower inner face; inner infolded margin forming thinly sclerotized complex. Postgonite projected obliquely from hypandrium, with apex strongly bent dorsally, with rounded and laterally flattened apex; slender process arising proximal to apical bend. Hypandrial bridge process with narrow base, strongly tapered to near apex of phallus; pair of pointed, sickle-shaped processes on either side of phallus, slightly longer than length of exposed phallic apex.

Female. Similar to male except as follows: Terminalia: generally indistinguishable from *G. fuscipes*. Spermathecal receptacle oblong (Fig. 33).

Distribution. This species occurs in western North America from Alaska south to Washington, including records from British Columbia (Fig. 37) (see Brooks & Cumming 2012, fig. 7 for example of habitat).

Remarks. Melander (1928, pl. 8, fig. 73) illustrated the male terminalia of *G. luctuosa* as did McAlpine (1967, figs 21–24; 1981, figs 124–126). Cumming *et al*. (1995, figs 13a, b) reinterpreted the homologies of the hypopygium of this species in light of their revised epandrial hypothesis. Here (Figs 19, 20) we modify the colour coding of some of the parts presented in Cumming *et al*. (1995), to reflect Sinclair & Cumming's (2006) discovery of postgonites throughout most of the Empidoidea and our new interpretation of phallic and hypandrial structures in *Gloma* (see "Discussion" below).

Barcode sequences that were obtained from two male and three female specimens (listed in "Additional material examined" above) clustered together with <2% genetic divergence, supporting the species identity of those female specimens. Adults of *G. luctuosa* are found primarily in late summer and early fall.

Gloma pectinipes Melander

(Figs 22, 29, 34, 38)

Gloma pectinipes Melander, 1945: 84. Type locality: Seward, Alaska, USA.
G. pectinipes: Melander, 1965: 454 [catalogue]; Poole, 1996: 156, 537 [checklist]; Yang *et al*., 2007: 450 [catalogue].

Type material examined. HOLOTYPE, ♂ labelled: "Seward Alsk/ VII.26.21"; "JM Aldrich/ coll"; "ALMelander/ Collection/ 1961"; "Gloma/ pectinipes [hand written]"; "Gloma/ pectinipes/ Mel./ TYPE [hand written]" (USNM). **PARATYPES** [not examined]: **USA. Alaska:** same data as holotype (1 ♀, allotype, USNM); Anchorage, 20.vii. J.M. Aldrich (USNM). Only the holotype is currently present in USNM collection.

Additional specimens examined. CANADA. Alberta: Banff, Bow River, 45 ft, 12.vii.1928, O. Bryant (1 ♂, CAS). **British Columbia:** Chilkat Pass, 3200 ft, mi 94, 17.vii.1948, Mason & Hughes (1 ♀, CNC). **Yukon:** Whitehorse, Wolf Ck Cpgd, FIT, 17.vi.–14.vii.1987, Spruce, Equisetum, S.A. Marshall (1 ♂, DEBU). **USA. Alaska:** Bison Gulch, mi 224 George Park Hwy, 21.vii.1993, T. Saigusa (1 ♂, KUMF); One Mile Ck nr Paxson, 16.vii.1993, T. Saigusa (18 ♂, 7 ♀, KUMF); Phelan Ck, mi 204 Richardson Hwy, 8 and 15.vii.1993, T. Saigusa (1 ♂, 1 ♀, KUMF); Savonoski, Naknek Lk, 1919, A.J. Basinger (1 ♀, CAS). **Colorado:** Doolittle Ranch, 9800 ft, Mt. Evans, 3.viii.1961, J.G. Chillcott (1 ♀, CNC); ditto, 6.viii.1961 (1 ♂, CNC); ditto, 23.vii.1961 (1 ♂, CNC); Mt. Evans, 11300 ft, marshy clearing, 10.viii.1961, J.G. Chillcott (1 ♂, 2 ♀, CNC).

Diagnosis. This species is distinguished from other species of *Gloma* by the combination of reniform postpedicel, dark legs, short hypoproct extension, long ventral surstylar process, apically expanded dorsal lobe of the surstylus and digitiform lobe bearing pair of setae extending from the ventral lobe of the surstylus.

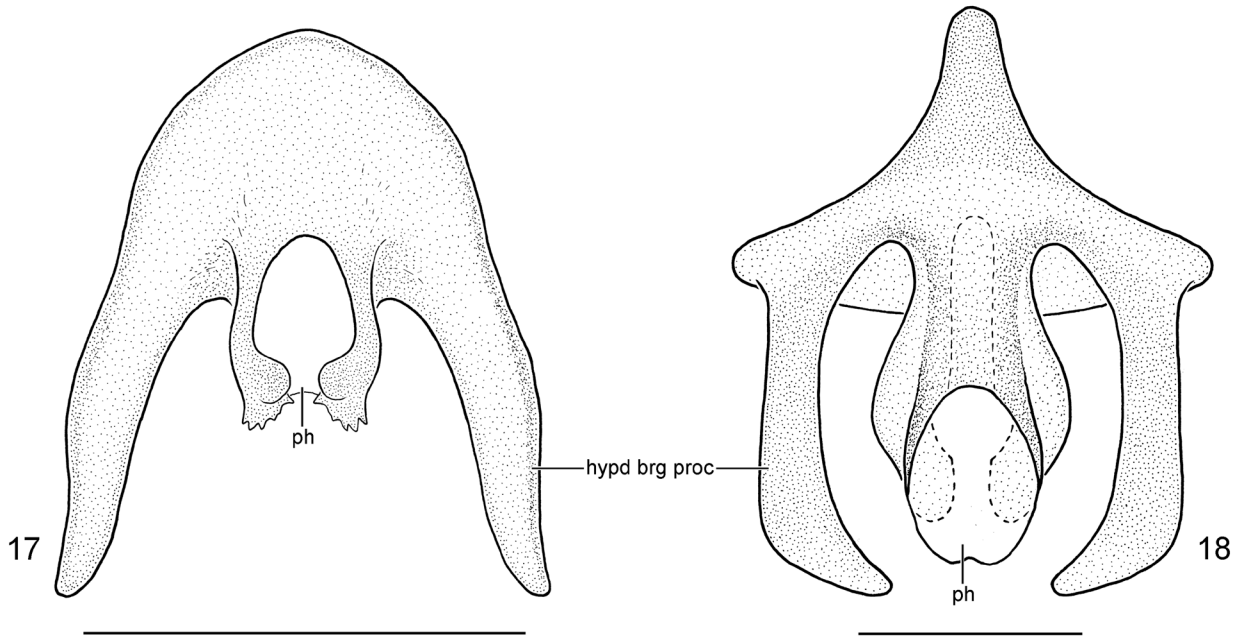
Redescription. Male. Antenna with postpedicel reniform; circlet of setae on pedicel longer ventrally. Pair of subshiny vittae between acrostichals and dorsocentral setae. Scutellum with 3–5 pairs of setae. Legs brownish, with apex of femora and base of tibia paler, especially foreleg. Terminalia (Fig. 22): hypoproct with short, slightly tapered extension, extending nearly 2–3X apical width; margin of apex with short, stout setae. Epandrium rounded, with scattered strong setae. Dorsal lobe of surstylus broadly expanded, boot-shaped with numerous setae on apical outer face; inner apex with several longer setae directed medially. Ventral surstylar process long, gradually arched ventrally; ventral lobe of surstylus produced into narrow upper digitiform process, rounded apically, bear-

ing 2 strong apical setae, lower portion expanded with strong setae. Hypandrium prolonged posteriorly into pair of laterally flattened lateral tapered lobes with pointed apex; inner distal margin infolded beneath phallus, narrowed anteriorly and arched dorsally as outer slender hypandrial process; lateral margin of hypandrial process with weakly pigmented lateral expansion bearing enlarged sensillum on inner face; inner infolded margin forming thinly sclerotized complex. Postgonite projected obliquely from hypandrium, with apex strongly bent dorsally, with rounded and laterally flattened apex; slender process arising proximal to apical bend. Hypandrial bridge process with narrow base, strongly tapered to near apex of phallus; paired very long sickle-shaped processes on either side of phallus, more than twice length of exposed phallic apex.

Female. Similar to male except as follows: Terminalia (Fig. 29): tergite 8 with sparse row of short setae. Sternite 8 slightly tapered in ventral view, not desclerotized medially with broad rounded posteriorly margin, broader than width of sternite 10; marginal setae nearly as long as length of sternite. Tergite 9+10 with 2 rows of pale, stout, erect setae. Spermathecal receptacle oblong (Fig. 34).

Distribution. This species is known from the Rocky and Coastal Mountains of western North America from Alaska south to Colorado, including records from Yukon, British Columbia and Alberta (Fig. 38).

Remarks. Adults of *G. pectinipes* occur from mid- to late summer.



FIGURES 17–18. Male terminalia of *Gloma* and *Oreogeton*, hypandrial bridge process and phallus in posterior view. **17.** *Gloma fuscipes* Melander; **18.** *Oreogeton scopifera* (Coquillett). Abbreviations: hypd brg proc—hypandrial bridge process; ph—phallus. Scale bars = 0.1 mm.

Gloma pyricornis Saigusa & Sinclair sp. nov.

(Figs 6, 23–25, 30, 35, 40)

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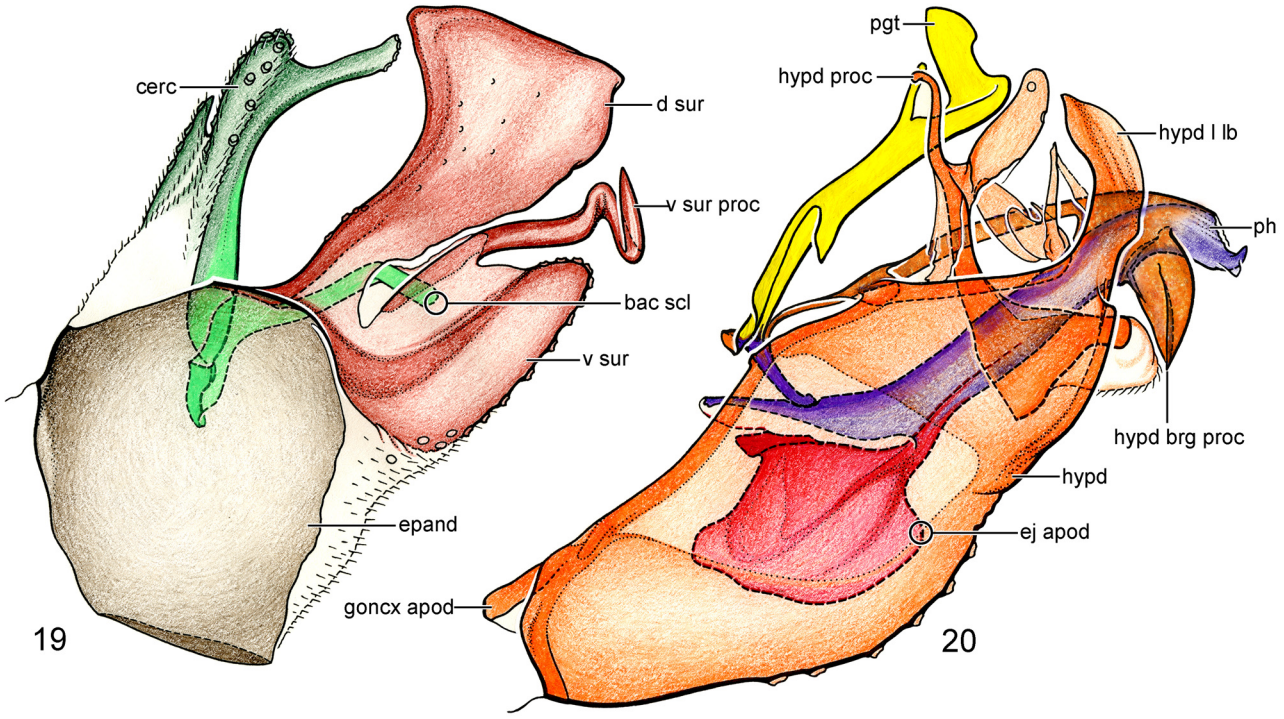
Type material. HOLOTYPE, ♂ labelled: "[HONSHU]/ Kanayama/ Sudama/ YAMANASHI/ 1962.VI.7/ T. SAIGUSA"; "HOLOTYPE/ *Gloma*/ *pyricornis*/ Saigusa & Sinclair [red label]" (KUMF). **PARATYPES: JAPAN. Nagano Pref.:** Kamikochi, Tokugo-toge, 29.vi.1964, A. Kato (2 ♀, KUMF); Shimashimadani, 26.v.1975, A. Nakanishi (2 ♂, 2 ♀, KUMF); Shimashimadani, 28.v.1976, A. Nakanishi (6 ♂, 3 ♀, KUMF; 6 ♂, 3 ♀, CNC); Shimashimadani, Azumi-mura, 23.v.1975, A. Nakanishi (1 ♂, KUMF); Yarisawa, Uarigatake, 6.vii.1964, T. Naito (1 ♀, KUMF). **Tokushima Pref.:** Minokoshi, Tsurugisan, 18.v.1988, T. Saigusa (2 ♂, 1 ♀, KUMF); Minokoshi, Nishijima, Tsurugisan, 22.vi.1988, T. Saigusa (1 ♀, KUMF); Mt. Tsurugisan, 7.v.1987, T. Saigusa (1 ♂, KUMF); Mt. Tsurugisan, 3.vi.1981, K. Ohara (1 ♀, KUMF). **Yamanashi Pref.:** Hirogawara, 13.vi.1966, A. Katô (11 ♂, 2 ♀, KUMF); ditto, 7.vi.1960 (2 ♂, KUMF).



FIGURES 19–20. *Gloma luctuosa* Melander, male terminalia, left lateral view; modified from Cumming *et al*. (1995, figs 13a, b). **19.** Epandrium and proctiger; **20.** Hypandrium and phallus. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; ej apod—ejaculatory apodeme; epand—epandrium; goncx apod—gonocoxal apodeme; hypd—hypandrium; hypd brg proc–hypandrial bridge process; hypd l lb–hypandrial lateral lobe; hypd proc–hypandrial process; pgt—postgonite; ph—phallus; v sur—ventral lobe of surstylus; v sur proc—ventral surstylar process. Colour code: grey-brown—epandrium; orange—hypandrium + gonocoxites; yellow—postgonite; dark green—cercus + proctiger; reddish-brown—surstylus; pale green—subepandrial sclerite + bacilliform sclerite; red—ejaculatory apodeme + aedeagal structures; purple—phallus.

Diagnosis. This species is distinguished from other species of *Gloma* by the combination of pyriform postpedicel, dark legs, short hypoproct extension, long, outwardly curved ventral surstylar process, digitiform dorsal lobe of the surstylus and numerous strong setae on the ventral lobe of the surstylus.

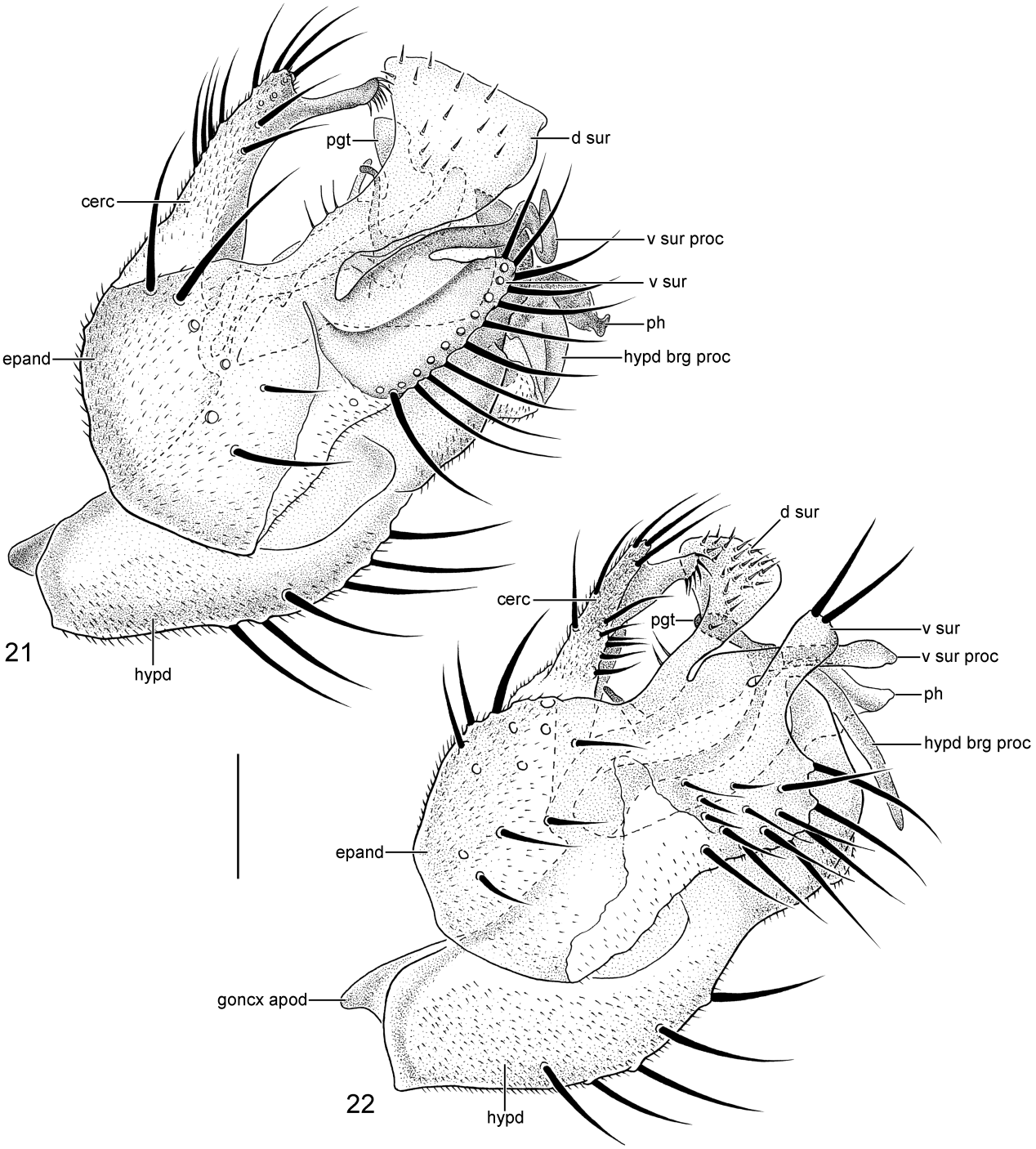
Description. Male. Antenna with postpedicel pyriform; circlet of setae on pedicel subequal dorsally and ventrally (Fig. 6). Pair of greyish vittae between acrostichals and dorsocentral setae. Scutellum with 2 pairs of setae. Legs dark brown. Terminalia (Figs 23–25): hypoproct with short, broad extension, extending nearly 2X apical width; margin of apex with short, stout setae. Epandrium rounded, with strong marginal setae. Dorsal lobe of surstylus digitiform, parallel-sided, not expanded apically with rounded apex; with short setae on outer face; inner apex with several short, slender setae directed medially. Ventral surstylar process very long, slender, strongly curved at mid-length and directed outwards; base of ventral surstylar process with triangular expansion bearing strong setae; ventral lobe of surstylus rounded, not prolonged, bearing several rows of setae, shorter than upper setae. Hypandrium prolonged posteriorly into pair of laterally flattened lateral lobes, prolonged dorsally, slender with flattened, slightly expanded apex; inner distal margin infolded beneath phallus, narrowed anteriorly and arched dorsally as outer sickle-shaped hypandrial process, with curved apex; lateral margin of hypandrial process with weakly pigmented lateral lobe bearing enlarged sensillum on lower inner face; inner infolded margin forming thinly sclerotized complex with several short setae. Postgonite projected parallel to hypandrium, with apex tightly twisted around apex of hypandrial lateral lobe, tapered to narrow apex; long, slender process arising proximal to apical bend. Hypandrial bridge process narrow with narrow base; pair of long, flattened sickle-shaped processes on either side of phallus, nearly 3X length of exposed phallic apex.

Female. Similar to male except as follows: Terminalia (Fig. 30): tergite 8 with sparse row of long setae, longer than dorsal length of tergite. Sternite 8 strongly tapered in ventral view, partially desclerotized medially with narrow rounded posteriorly margin, narrower than width of sternite 10; marginal setae much longer than length of sternite. Tergite 9+10 with 2 rows of pale, stout, erect setae. Spermathecal receptacle short oblong (Fig. 35).

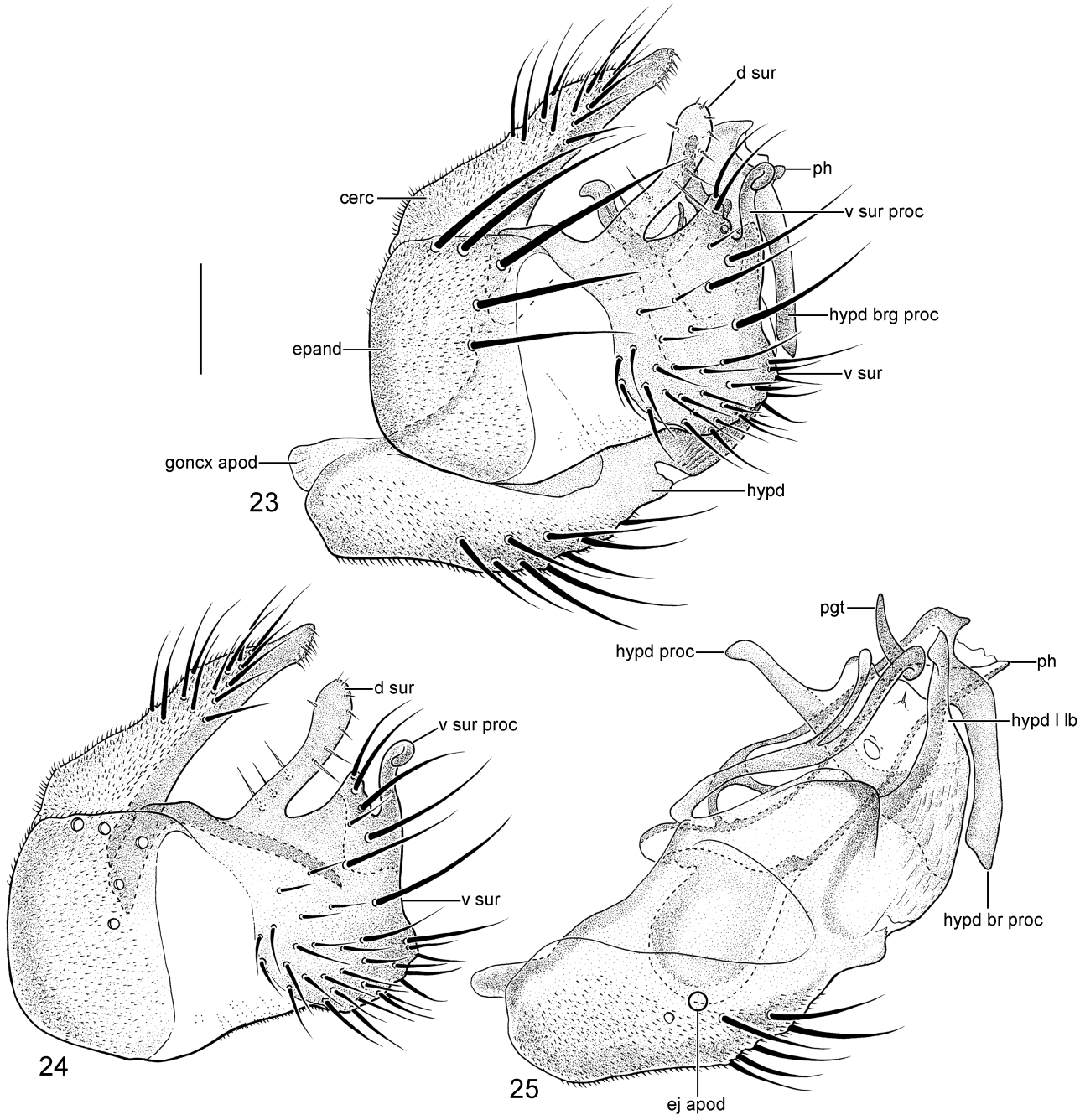
Etymology. The species name is from the Latin *pyrus* (pear) and *cornus* (horn) in reference to the pyriform-shaped postpedicel.

Distribution. This species occurs in Japan on the island of Honshu in the Prefectures of Nagano and Yamanashi, and on the island of Shikoku in the Prefecture of Tokusima (Fig. 40).

Remarks. Adults of this species are found in early summer.



FIGURES 21–22. *Gloma*, male terminalia, left lateral view. **21.** *Gloma luctuosa* Melander, Hypopygium; **22.** *Gloma pectinipes* Melander, hypopygium. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; goncx apod—gonocoxal apodeme; hypd—hypandrium; hypd brg proc–hypandrial bridge process; pgt—postgonite; ph—phallus; v sur—ventral lobe of surstylus; v sur proc—ventral surstylar process. Scale bar = 0.1 mm.



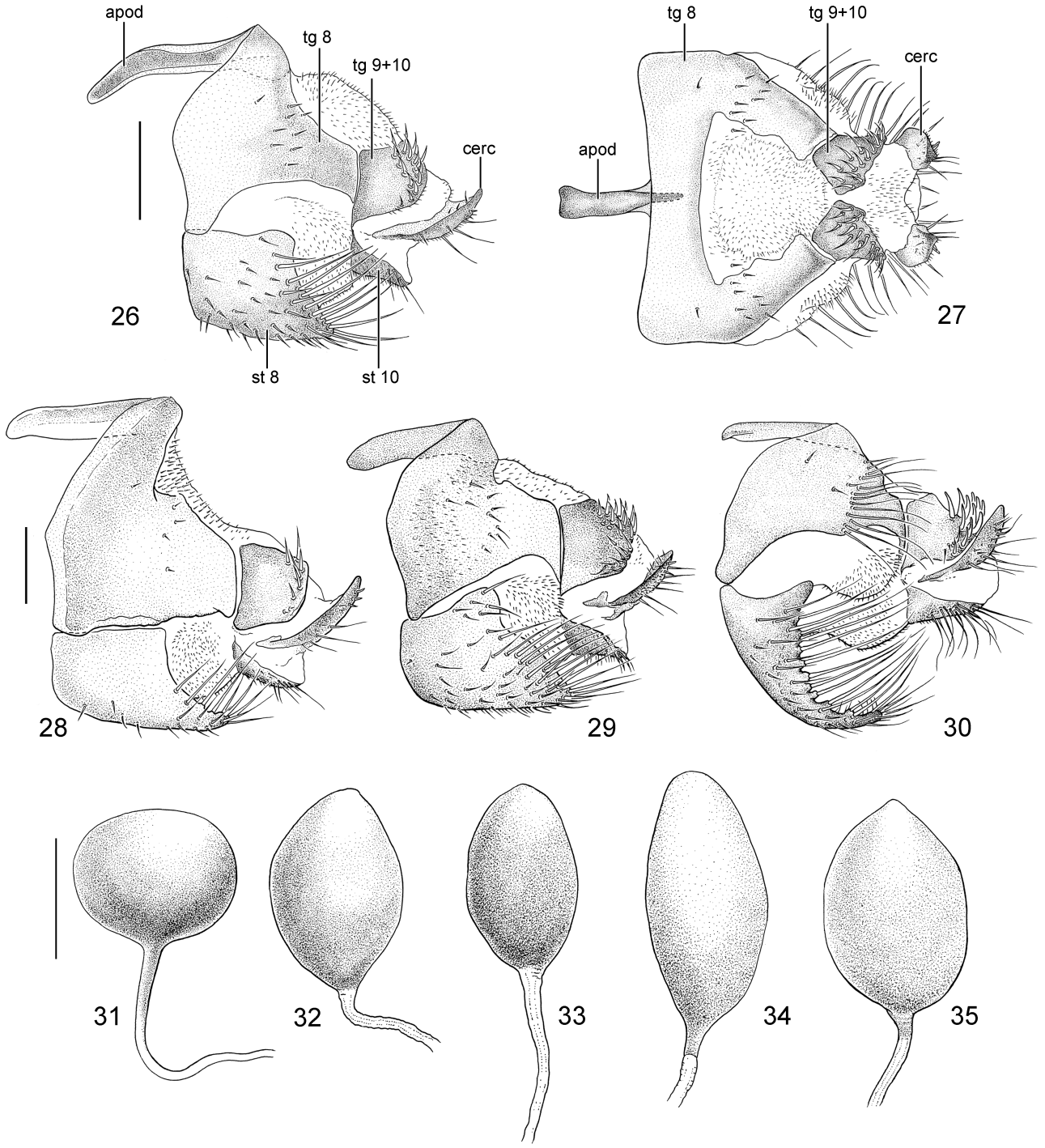
FIGURES 23–25. *Gloma pyricornis* **sp. nov.**, male terminalia, left lateral view. **23.** Hypopygium; **24.** Epandrium and proctiger; **25.** Hypandrium and phallus. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; ej apod—ejaculatory apodeme; epand—epandrium; goncx apod—gonocoxal apodeme; hypd—hypandrium; hypd brg proc–hypandrial bridge process; hypd l lb–hypandrial lateral lobe; hypd proc–hypandrial process; pgt—postgonite; ph—phallus; v sur—ventral lobe of surstylus; v sur proc—ventral surstylar process. Scale bar = 0.1 mm.

Gloma sp. A
(Fig. 40)

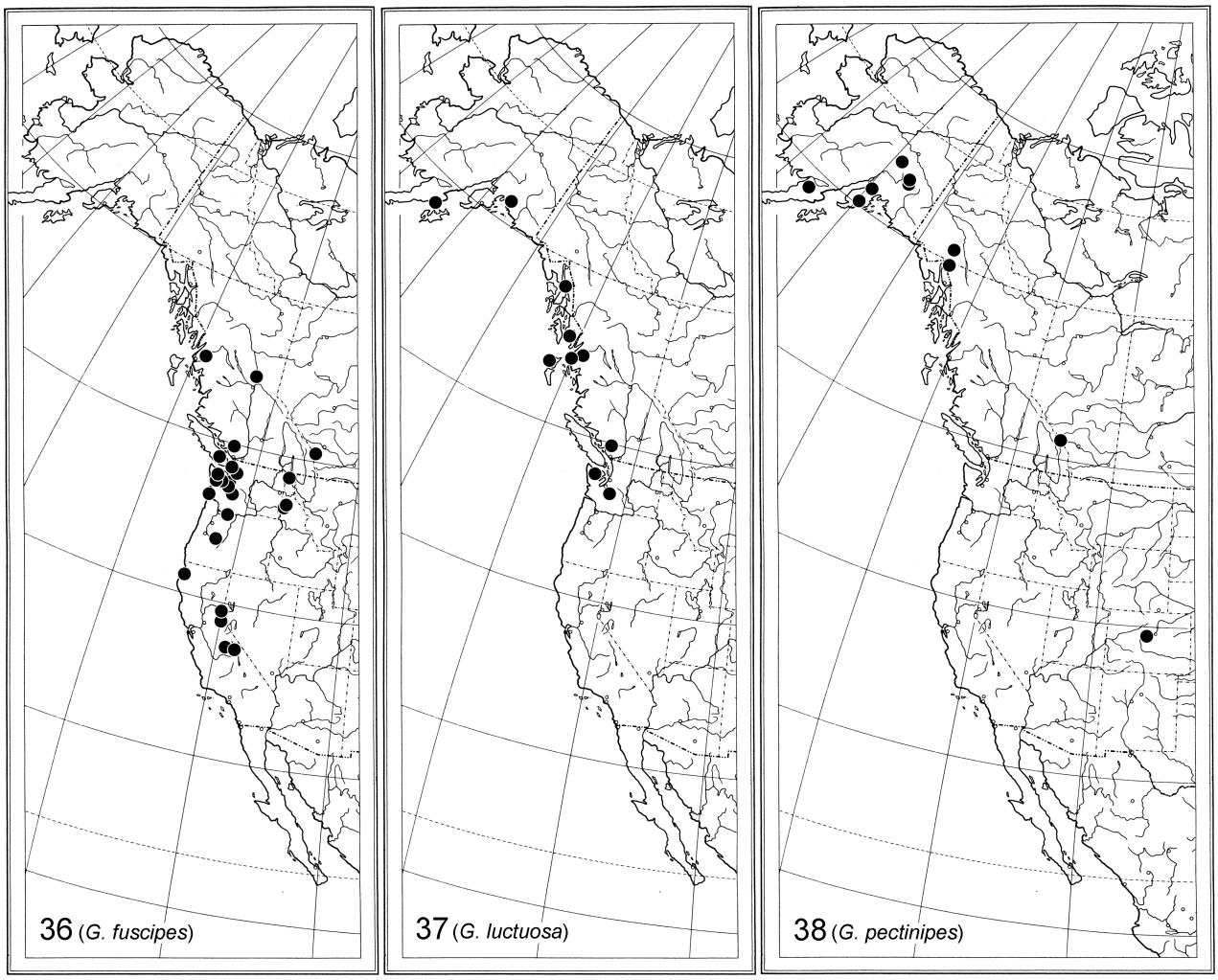
Material examined. CHINA. Yunnan: Yunlong, 3 km NNW of Zhichang, 2500–2600 m, 4.vi.1996, T. Saigusa (1 ♀, KUMF).

Diagnosis. This species is distinguished from other species of *Gloma* in this region by the reniform postpedicel and dark legs.

Remarks. The female terminalia is very similar to *G. fuscipennis* with tergite 9+10 bearing a single row of short, stout setae and the posterior margin of sternite 8 is weakly narrowed and prolonged. Since we have observed some variation in female terminalia (see "Remarks" under *G. fuscipes*), male specimens from this region are required to confirm the identity of this apparent new species.



FIGURES 26–35. *Gloma*, female terminalia. **26.** *Gloma fuscipes* Melander, terminalia, left lateral view; **27.** Same, dorsal view; **28.** *Gloma fuscipennis* Meigen, terminalia, left lateral view; **29.** *Gloma pectinipes* Melander, terminalia, left lateral view; **30.** *Gloma pyricornis* **sp. nov.**, terminalia, left lateral view; **31.** *Gloma fuscipes* Melander, spermatheca; **32.** *Gloma fuscipennis* Meigen, spermatheca; **33.** *Gloma luctuosa* Melander, spermatheca; **34.** *Gloma pectinipes* Melander, spermatheca; **35.** *Gloma pyricornis* **sp. nov.**, spermatheca. Abbreviations: apod—apodeme; cerc—cercus; st—sternite; tg—tergite. Scale bar = 0.1 mm.



FIGURES 36–38. Distribution of *Gloma* in the Nearctic Region. **36.** *Gloma fuscipes* Melander; **37.** *Gloma luctuosa* Melander; **38.** *Gloma pectinipes* Melander.

Gloma sp. B
(Fig. 40)

Material examined. CHINA. Shaanxi: Fuping-x, Liangfengya, 2000–2100 m, 12 km WNW Longcaoping, 24.vi.1997, T. Saigusa (1 ♀, KUMF).

Diagnosis. This species is distinguished from other species of *Gloma* in this region by the pyriform postpedicel and pale legs, especially coxae.

Remarks. This species is similar to *G. pyricornis* on the basis of the pyriform postpedicel, but is distinguished by its pale legs. Given slight changes in leg colouration during preservation, males are required to fully describe, name and confirm the identity of this apparent new species.

Key to world species of *Gloma*
(*Gloma* sp. A not included in the key)

1	Palaearctic	2
-	Nearctic	4
2	Antenna with pyriform postpedicel (Fig. 6)	3
-	Antenna with reniform postpedicel (as in Fig. 5)	*G. fuscipennis*
3	Legs brown, including coxae, similar in colour to thorax; paired hypandrial bridge process long and sickle-shaped; ventral	

surstylar process very long, slender, strongly curved at mid-length and directed outwards (Japan) . . . . . *G. pyricornis* **sp. nov.**

- Legs pale yellowish brown, including coxae, paler than colour of thorax; male unknown (China: Shaanxi). . . . . *Gloma* sp. B

4 Three or more pairs of scutellar setae; paired hypandrial bridge processes long and slender; ventral surstylar process gradually arched ventrally (Fig. 22) . . . . . *G. pectinipes*

- Two or three pairs of scutellar setae; paired hypandrial bridge processes subtriangular in shape, slightly longer than apex of phallus, in lateral view; ventral surstylar process strongly arched or tightly twisted into corkscrew (Figs 14, 21) 5

5 Posterior extension of male cercus (= hypoproct) short, not longer than width of cercus (Figs 14, 15); ventral surstylar process sickle-shaped, arched anteriorly; female legs pale brown, particularly fore and midlegs and all coxae; spermatheca oval, wider than long (Fig. 31) . . . . . *G. fuscipes*

- Posterior extension of male cercus (= hypoproct) elongate, longer than width of cercus (Figs 19, 21); ventral surstylar process twisted into tight twirl or corkscrew (Fig. 19); female legs dark, coxae not distinctly paler; spermatheca oblong, longer than wide (Fig. 33) . . . . . *G. luctuosa*

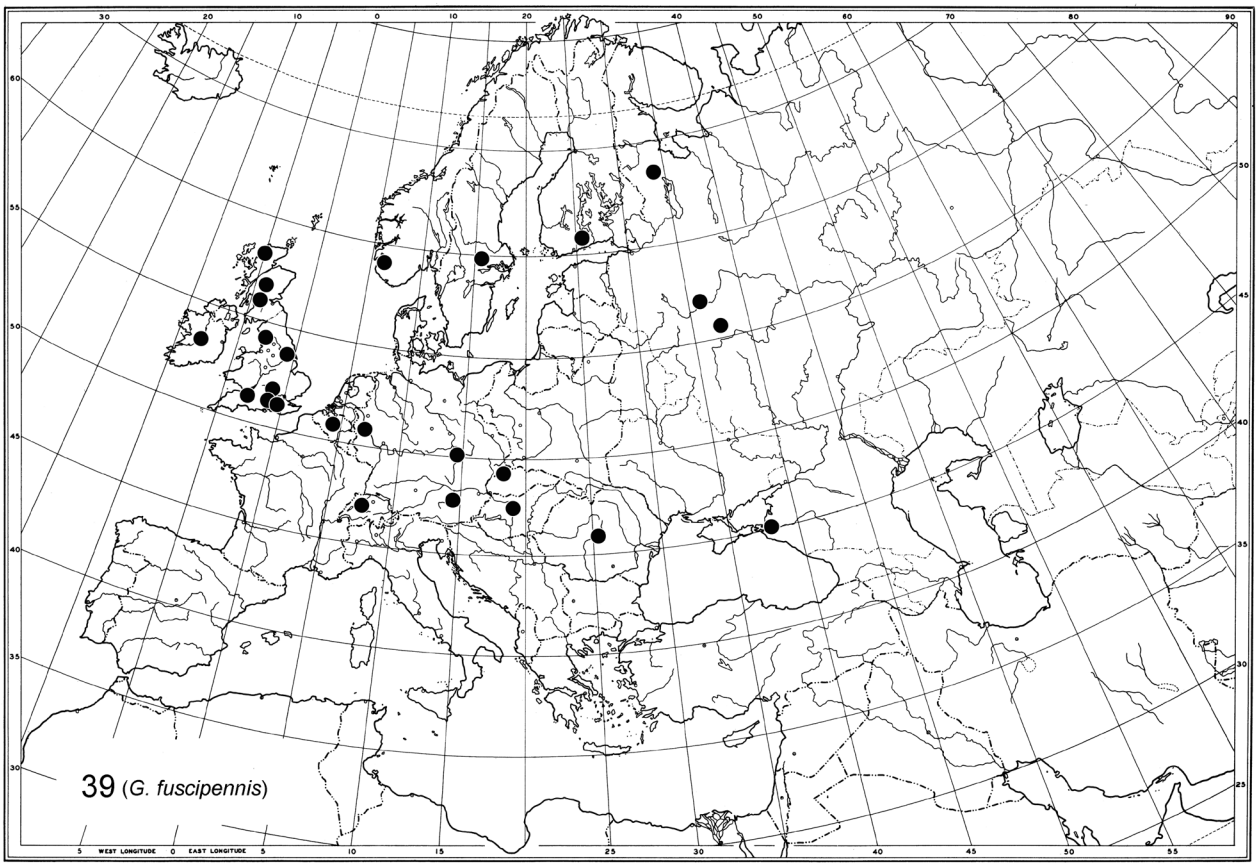


FIGURE 39. Distribution of *Gloma* in the Palaearctic Region based on literature and specimens examined. *Gloma fuscipennis* Meigen.

Discussion

Gloma was first placed in the subfamily Oreogetoninae by Chvála (1976), a mostly paraphyletic grouping of genera. The genus was later transferred to the Trichopezinae by Sinclair (1995) and subsequently assigned to the *Heterophlebus* genus group within that subfamily by Sinclair & Cumming (2006). This group of four genera also includes *Apalocnemis* Philippi and *Hyperperacera* Collin, and all of these genera have similar male genitalia with a dorsal and ventral lobe on each surstylus. Interestingly, *Gloma* has an additional novel structure associated with the intromittent organ, namely a phallus that is fused at the apex with paired hypandrial bridge processes (Figs 17, 20). This structure arises from the hypandrial bridge and projects posteriorly as a single narrow plate that expands over the apex of the phallus and separates into paired processes on either side of the phallic opening (=phallotrema). This feature is found in only one other group within the Empidoidea, namely the genus *Oreogeton* (Fig. 18; Sinclair & Cumming 2006, fig. 269, labelled as pgt). *Oreogeton* is currently placed in the monogeneric subfamily Oreogetoninae and is now classified as *incertae sedis* within the Empidoidea (Sinclair & Cumming 2006). *Oreogeton* also possesses a divided surstylus, although this feature does occur sporadically in other groups of Empidoidea (e.g.,

Hesperempis Melander, *Niphogenia* Melander, most Dolichopodidae *s.lat*.). Given the difficulty in placing *Oreogeton* within the Empidoidea, it is possible that it may actually be the sister group to *Gloma* based on unique possession of the narrow hypandrial bridge plate and paired apical processes that are fused with the phallus. Although *Oreogeton* does not possess a suite of modified female terminalia structures that characterize most Trichopezinae and other brachystomatids (Sinclair & Cumming 2006, characters 69, 78, 80, 82), these features all exhibit some degree of homoplasy within the Trichopezinae. Within Empidoidea, *Oreogeton* is also characterized by differently modified female terminalia that include moderately sclerotized cerci (Sinclair & Cumming 2006, character 85) that are also observed in a more heavily sclerotized condition in Trichopezinae and other brachystomatids. This potential relationship of *Oreogeton* and *Gloma*, needs to be more thoroughly investigated with new phylogenetic analyses that examine additional exemplars of Trichopezinae (see for example, Sinclair 2008) and other little known currently unplaced groups such as *Gondwanamyia* Sinclair, Cumming, Brooks, Plant & Saigusa (Sinclair *et al*. 2016). An undescribed genus from the Pacific Northwest of North America was recently identified by us that also possesses a hypandrial bridge plate and three-lobed surstylus, which is very similar to *Gloma*. This new genus should also be included in any future phylogenetic analyses.

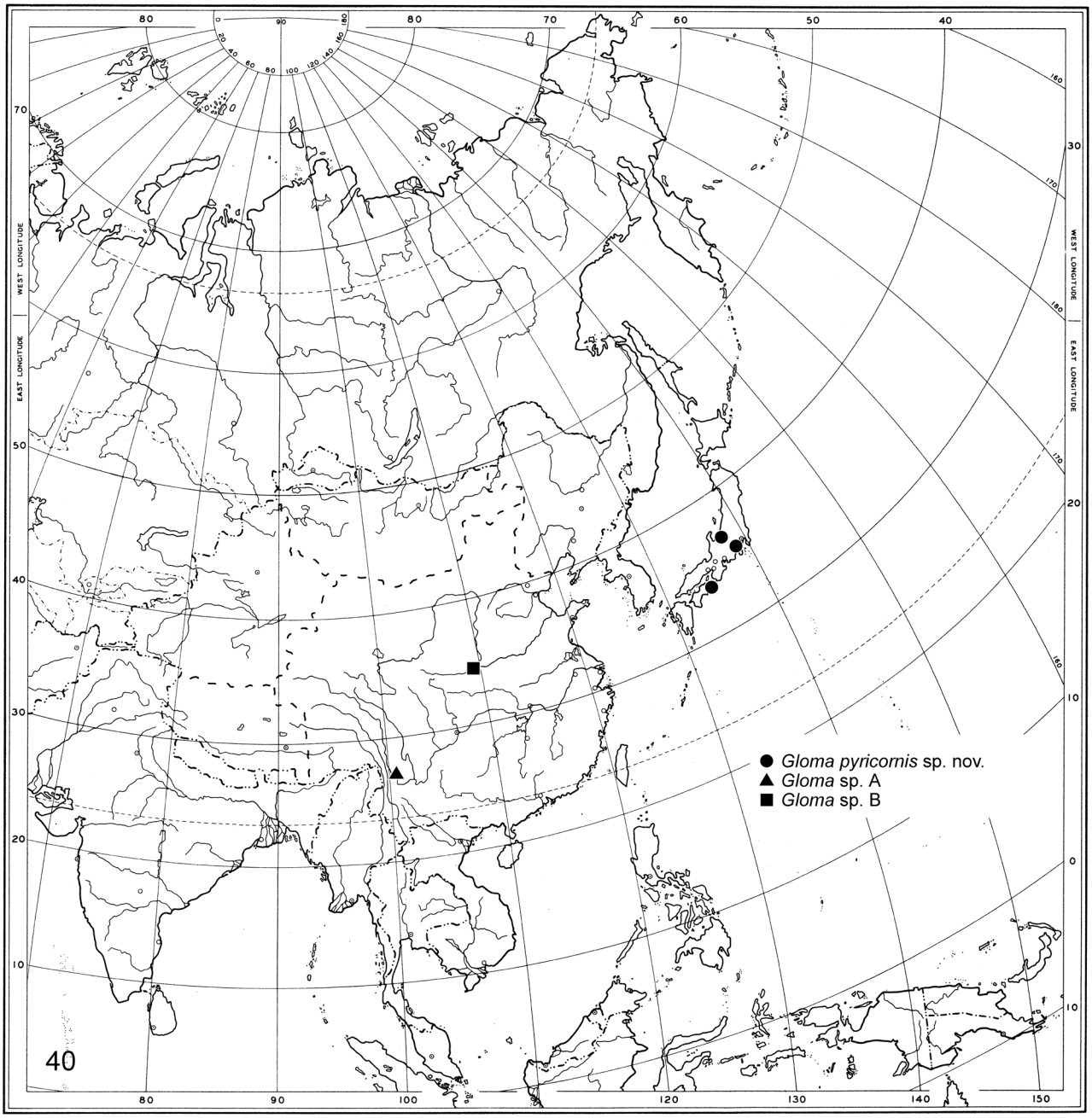


FIGURE 40. Distribution of *Gloma* in the Palaearctic Region. *Gloma pyricornis* **sp. nov.**, *Gloma* sp. A, *Gloma* sp. B.

The cladistic analysis of the species of *Gloma* resulted in a single most parsimonious tree (Fig. 41) with length = 24, CI = 0.75, RI = 0.67 and RC = 0.50. *Gloma* is confirmed as a monophyletic genus primarily on the basis of the presence of a terminal extension on the postpedicel (character 2.1) and a ventral surstylar process (characters 8.1, 8.2). *Gloma pyricornis* is considered the sister group to the other four described extant species because the latter group all share a reniform postpedicel (character 1.1), circlet of setae on the pedicel that are longer ventrally (character 3.1), apically expanded dorsal lobe of the surstylus (character 7.1) and very short setae on female tergite 8 (character 14.1). The relationships within this group of four species are not fully resolved. *Gloma fuscipennis* and *G. luctuosa* are united as sister species on the basis of an elongate male hypoproct (character 6.1) and short thick hypandrial bridge processes (character 12.1). However, the precise sister group to this lineage could be either *G. fuscipes* or *G. pectinipes*.

Neither the Palaearctic nor the Nearctic species form monophyletic groups and appear to be the result of multiple sister lineage connections between the two regions. This pattern plus the northern hemisphere distribution of the genus is suggestive of a Laurasian lineage of probable late Mesozoic age, like many other empidoid groups (e.g., Cumming *et al*. 2014) and is generally considered the result of early to mid-tertiary vicariant events. The presence of the plesiomorphic pyriform postpedicel in temperate eastern Asian *Gloma* suggests the initial diversification of the genus probably occurred in this area. From this region, the reniform postpedicel group appears to have expanded throughout cool temperate Laurasia.

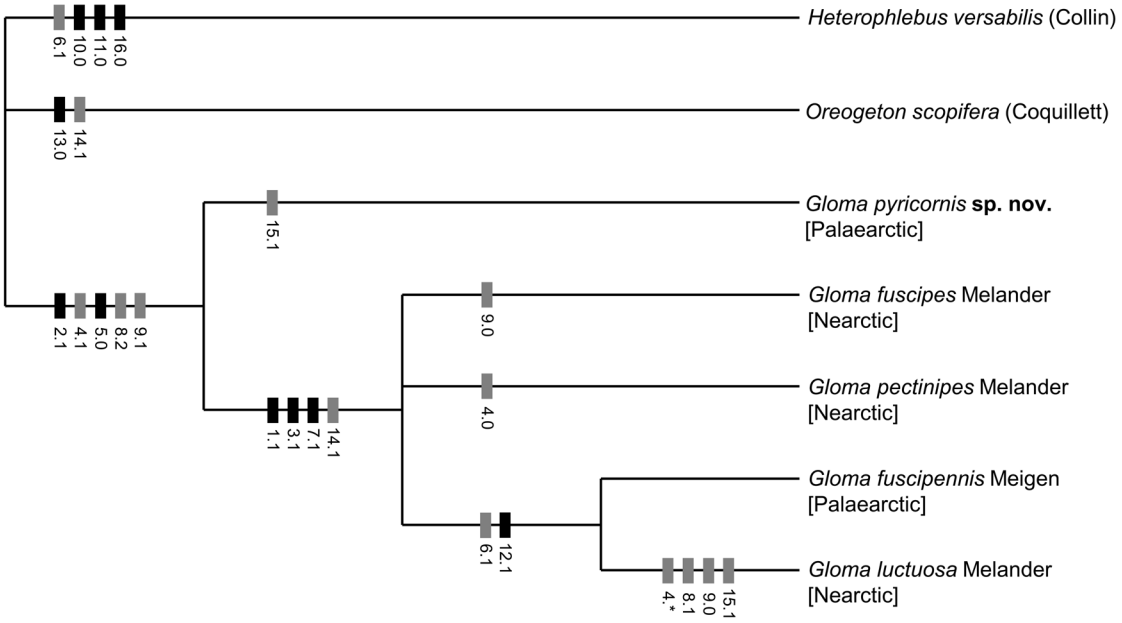


FIGURE 41. Most parsimonious cladogram of the world species of *Gloma* and outgroups, produced by cladistic analysis of morphological data in Appendix 1 and 2. Character distribution for uniquely derived states shown by black hash marks and by grey hash marks for homoplasious states (including subsequent transformations).

The Baltic amber genus *Palaeoparamesia* Meunier was described for the single species *P. proosti* on the basis of a single male specimen (No. 2118) (Meunier 1902). Later Meunier (1908) listed two additional specimens of this species [Nos. 8437 (= GZG.BST.00179) and 7786 (= GZG.BST.00056)] in his monograph on Baltic amber Empididae. Sinclair (2010) reported that only specimen No. 8437 from these original series remained in the Meunier collection in GZG, but recently specimen No. 7786 was also located in that collection. The actual type specimen (No. 2118) is presumed lost. Specimen 8437 and specimen 7786 are not conspecific (or even congeneric) and of the two, the latter specimen most closely resembles Meunier's description (plus two figures) of *Palaeoparamesia*. This specimen is possibly congeneric with *Gloma* on the basis of the apparent extension of the postpedicel and the general shape of the male terminalia. We were only able to examine photographs of this specimen (Figs 7–10) and consequently cannot confirm this possible synonymy.

There is a series of amber inclusions from the personal collection of Hans Ulrich (housed at the ZFMK) that

were provisionally identified by him as *Gloma* or *Palaeoparamesia* (ZFMK DIP 00057721–00057736). However most of these specimens appear to be congeneric with an undescribed genus that includes the Nearctic species of *Apalocnemis* (see Sinclair 2010) and Meunier's specimen No. 8437 discussed above.

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APPENDIX 1. Characters and character state codings as presented in the character matrix (Appendix 2), and used in the cladistic analysis.

1. *Postpedicel shape*. Pyriform or conical (0); reniform (1).
2. *Postpedicel terminal extension*. Absent (0); present (1).
3. *Pedicel circlet of setae*. Subequal dorsally and ventrally (0); longer ventrally (1).
4. *Scutellar setae*. Primarily three to five pairs (0); primarily two pairs (1).
5. *Radial veins*. Without setae (0); with setae (1).
6. *Male hypoproct*. Short (0); elongate (1).
7. *Dorsal lobe of surstylus*. Digitiform (0); apically expanded (1).
8. *Ventral lobe of surstylus*. Without process (0); with short process (1); with long process (2).
9. *Postgonite*. Without basal process (0); with basal process (1).
10. *Phallus apex*. Simple (0); fused to paired hypandrial bridge processes (1).
11. *Hypandrial bridge plate*. Short or absent (0); posteriorly produced (1).
12. *Hypandrial bridge processes* (*lateral view*). Long and slender (0); short and thick (1).
13. *Female tergite 8 median apodeme*. Absent (0); present (1).
14. *Female tergite 8 setae*. Elongate (0); very short (1).
15. *Female sternite 8 apex*. Broad (0); narrowed (1).
16. *Female tergite 10*. Without acanthophorite spines (0); with acanthophorite spines (1).

APPENDIX 2. Character state matrix for cladistic analysis of *Gloma* (characters 1–16). Outgroup taxa are listed at the beginning of the matrix. Inapplicable states are indicated by a "–" and polymorphic states are indicated by a "*".

Taxon	1 111111 1234567890 123456
Oreogeton scopifera	00001000–1 100100
Heterophlebus versabilis	0000110000 0–1001
Gloma fuscipennis	111*011101 111111
Gloma fuscipes	1111001201 101101
Gloma luctuosa	1111011211 111101
Gloma pectinipes	1110001211 101101
Gloma pyricornis	0101000211 101011