**Zeitschrift:** Mitteilungen der Schweizerischen Entomologischen Gesellschaft =

Bulletin de la Société Entomologique Suisse = Journal of the Swiss

**Entomological Society** 

Herausgeber: Schweizerische Entomologische Gesellschaft

**Band:** 82 (2009)

**Heft:** 3-4

**Artikel:** Redescription of the Alaskan species Drosophila populi (Diptera,

Drosophilidae)

Autor: Vilela, Carlos R. / Bächli, Gerhard

**DOI:** https://doi.org/10.5169/seals-402994

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### MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE

80: 259-269, 2007

# Redescription of the Alaskan species *Drosophila populi* (Diptera, Drosophilidae)

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Abstract. The Nearctic species *Drosophila populi* Wheeler & Throckmorton, 1961 (Diptera, Drosophilidae) is redescribed based on the male holotype. It differs from *Drosophila ingrica* Hackman, 1957, its Palaearctic counterpart, by subtle but reliable details of the component sclerites of the male terminalia. The diagnosis of the *Drosophila populi* species group is updated. Line drawings and photomicrographs of the terminalia are provided.

Keywords. *Drosophila populi* group, male terminalia, Cottonwood, *Populus* sp., Salicaceae, Sophophora.

#### INTRODUCTION

In 2003, while dissecting and preparing line drawings of the male terminalia of a specimen of *Drosophila ingrica* Hackman, 1957, collected at Suistamo (Karelia, Russia, deposited in the Eläinmuseo, Helsingin Yliopisto, Helsinki, Finland), the first author realized they were remarkably similar to those depicted by Takada (1961: 145) for *Drosophila populi* Wheeler & Throckmorton, 1961, from southern Alaska. The dissected specimen was used in the redescription of *Drosophila ingrica* included in the monograph on the Drosophilidae of Fennoscandia and Denmark (Bächli *et al.* 2004: 233), and a photomicrograph of its internal male terminalia in left lateral view was published later (Bächli & Vilela, 2007: 242, fig. 55). This similarity has been overlooked since the description of the Nearctic *Drosophila populi*, which was later (Throckmorton, 1975: 426) considered a unique species in a «group» of its own.

Not having analyzed any Nearctic specimen of the latter species, Bächli *et al.* (2004: 235) just opted to include *Drosophila ingrica* in the *populi* group, considering the subtle differences observed between the male terminalia of the Russian specimen of *Drosophila ingrica* and those pictured for an Alaskan specimen of *Drosophila populi* as most probably an indication of individual variability. However, they did not take any further decision regarding the status of those two taxa, which remained unsolved.

We recently had the opportunity to analyze the male holotype of *Drosophila populi* which allowed a detailed morphological comparison of these two Subarctic species and prompted the present paper.

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#### MATERIAL AND METHODS

Two male specimens were analyzed in the present redescription, i.e. the holotype of *Drosophila populi* and a male specimen of *Drosophila ingrica* from Tyresta NP, Sweden. They were borrowed from the National Museum of Natural History, Washington, D.C. (NMNH) and the Zoologisches Museum der Universität Zürich, respectively.

Label data attached to the quoted type specimen are cited in full with a backslash indicating a label change, and a double space between words a line change.

Preparations of microscope slides were made following Wheeler & Kambysellis (1966) and Kaneshiro (1969). The abdominal sclerites, including the disarticulated terminalia, are preserved in microvials filled with glycerin and attached by the stopper to the pin of the respective specimen. Refer to Vilela & Bächli (2000) and Bächli *et al.* (2004) for further details.

Male terminalia were drawn using a camera lucida (1.4x; except Fig. 1B = 1,23x) attachment on a compound microscope under a 40x objective. They were photographed with a photomicroscope under a 6.3x objective.

Photomicrographs were taken of non-disarticulated internal male terminalia in left lateral and dorsal views.

All figures of one plate were drawn to the same scale and all photomicrographs were taken and enlarged to the same magnification, unless otherwise indicated. For measurements and indices see Vilela & Bächli (1990), for morphological terminology see Vilela & Bächli (2000) and Bächli *et al.* (2004).

#### **TAXONOMY**

## Drosophila populi species group Throckmorton, 1975

*Drosophila populi* species group Throckmorton, 1975: 426 [first reference to a group name]; Lemeunier & Ashburner 1976: 276 [group name]; Bächli *et al.* 2004: 233 [diagnosis]; Ashburner *et al.* 2005: 1214 [affiliation].

Diagnosis. Blackish flies; legs completely pale yellow; pleura pale yellow in lowest fourth; males without sex combs; surstylus dorsally bearing a thumb-like process, aedeagus shorter than paraphyses, most of its surface microtrichose; two pairs of paraphyses; outer paraphysis boomerang-shaped in lateral view; inner paraphysis well developed, triangular in lateral view and fused to laterodistal inner surface of hypandrium by a long, dorsal, ribbon-shaped, sclerotized process; hypandrium fused to gonopods; oviscapt with long trichoidlike, instead of the usual peglike, outer ovisensilla (updated from Bächli et al. 2004).

Taxa included (2). Drosophila ingrica Hackman, 1957; Drosophila populi Wheeler & Throckmorton, 1961.

Comments. While proposing the first diagnosis ever published for the *Drosophila populi* species group, we (Bächli *et al.* 2004: 233) mistakenly attributed the authorship of the informal taxon named *Drosophila populi* group to Lemeunier & Ashburner (1976: 276), which in fact was cited as a group one year before, in a table, by Throckmorton (1975: 426), although without giving it a formal diagnosis.

This Holarctic group of species is apparently restricted to the northernmost subarctic forest zone (sensu Toda 1984). All known records for the two species cur-

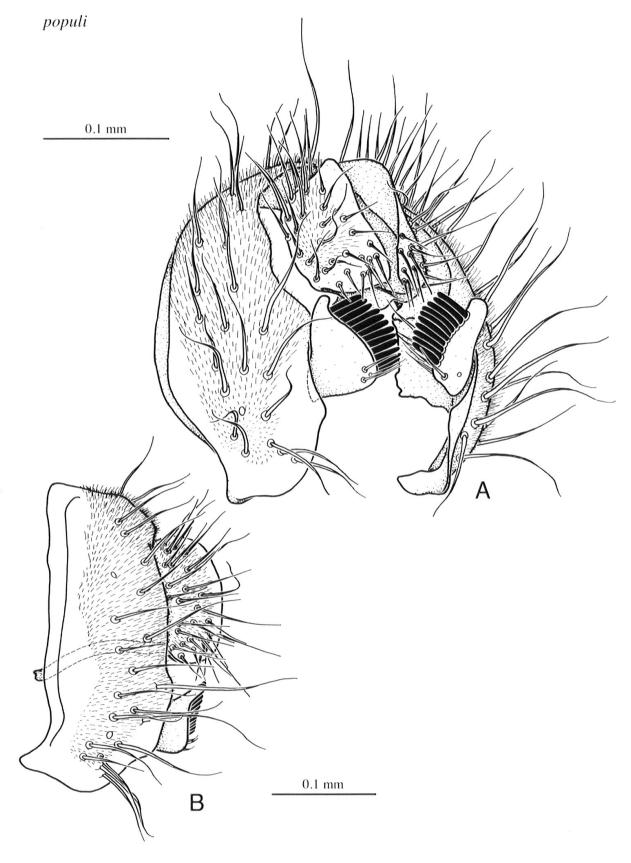


Fig. 1. *Drosophila populi* Wheeler & Throckmorton, male holotype. A, epandrium, cerci, surstyli, and decasternum, oblique posterior view. B, epandrium, cercus and surstylus, left lateral view.

rently included in the group lie in latitudes of  $\sim 60^\circ$  N and therefore not far from the Arctic Circle (66° 32' N). Both species are apparently associated with cotton-wood (*Populus* spp.; Salicaceae). However, it is not known if they utilize this substrate (tree sap fluxes) as feeding and/or breeding sites, or if their larvae live in rotting phloem under decaying bark, as known for some species of *Drosophila* belonging to the *virilis* group and most species of the genus *Chymomyza* (e.g. Spieth 1951, Blight & Romano 1953). It should be stressed that according to Carson *et al.* (1956) adult flies do not regularly feed on their breeding sites.

## Drosophila (Sophophora) populi Wheeler and Throckmorton, 1961

(Figs. 1-4)

Drosophila populi Wheeler & Throckmorton 1961: 138 [description, egg, female terminalia, male reproductive system, ecology]; Takada 1961: 145 [male terminalia]; Throckmorton 1962: 217 [paragonia and vasa deferentia], 228 [phylogeny], 234 [ejaculatory bulb and apodeme], 244, 252, 269, 279, 292, 318, [phylogeny], 256 [testes], 258 [spermatheca], 273 [ventral receptacle], 280 [Malpighian tubules, phylogeny]; Wheeler 1965: 768 [Nearctic catalog]; Takada 1966: 45 [external male terminalia]; Throckmorton 1966: 339 [spermatheca], 357 [egg]. 369 [abdominal sternites]; Okada 1968: 145 [egg]; Throckmorton 1968: 360ff. [phylogeny]; 1975: 433 [phylogeny]; Starmer 1981: 49 [ecology]; Val et al. 1981: 156 [phylogeny]; Wheeler 1981a: 62 [World catalog], 1981b: 116 [endemism]; Ferrar 1987: 156 [egg];

*Material examined* (1 ♂). Male holotype (dissected, deposited in the USNM): «Anchorage Alaska July 1960 \ MRWheeler Collector \ HOLOTYPE [red label] \ Dros. populi \ Drosophila populi Wheeler & Throckmorton \ ♂ \ Drosophila populi Wheeler & Throckmorton Bächli & Vilela det. 2007».

Type locality. Rabbit Creek, south of Anchorage, Alaska, USA.

Diagnosis. Aedeagus microtrichose, rice-seed-like in lateral view (Fig. 3C); outer paraphysis boomerang-shaped, not microtrichose on inner surface, with a sinuate row of ca. 8 setulae along the outer surface (Figs 3B, C); inner paraphyses distally sharply pointed in lateral view (Fig. 4A) and distally clearly fused to each other (Fig. 4B), as seen in dorsal or ventral aspect.

Description. ♂.

Head. Frons generally blackish-brown, greyish microtrichose, paler above face, frontal length 0.29 mm; frontal index = 0.77, top to bottom width ratio = 1.41. Frontal triangle about 76 % of frontal length; ocellar triangle slightly prominent, about 41 % of frontal length. Orbital plates parallel to eye margin, about 71 % of frontal length. Orbital setae black, or2 outside and slightly behind or1, distance of or3 to or1 = 71 % of or3 to vtm, or1 / or3 ratio = 0.79, or2 / or1 ratio = 0.55, post-vertical setae = 59 % of frontal length, ocellar setae = 88 % of frontal length; vibris-sal index = 0.33. Face brownish. Carina short, narrow, dorsally flat, not noselike. Cheek pale yellow, ventral margin brown, eye/cheek index about 10. Eye with short pile, L/W index = 1.26. Antennae brownish. Flagellomere 1 with slightly elongated setulae, about one fourth width of flagellomere, length to width ratio = 1.14. Arista with 3 short dorsal, 2 short ventral and about 6 small inner branches, plus short terminal fork. Proboscis and palpus yellowish.

Thorax length 0.71 mm. Scutum blackish-brown, somewhat microtrichose, 6 rows of acrostichal setae. h index = 1.00. Transverse distance of dorsocentral setae about 21 % of longitudinal distance; dc index = 0.73. Scutellum medially brownish, with paler margin, scutellar setae nearly equidistant; scut index = 0.70. Pleura

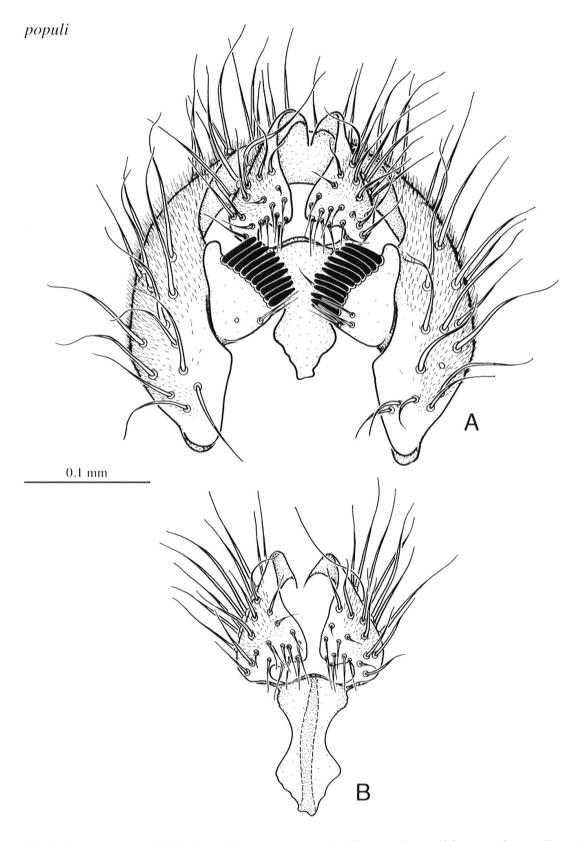


Fig. 2. *Drosophila populi* Wheeler & Throckmorton, male holotype. A, epandrium, cerci, surstyli, and decasternum, posterior view. B, cerci and decasternum, posterior view.

brownish, paler along ventral one fourth, sterno index = 0.76, median katepisternal seta about 38 % of the anterior one. Halter pale brownish. Legs brownish-yellow.

Wing hyaline, veins R4+5 and M almost parallel, length 2.48 mm, length to width ratio = 2.22. Indices: C = 2.39, ac = 2.25, hb = 0.39, 4C = 0.95, 4v = 1.68, 5x = 1.29, M = 0.47, prox. x = 0.53.

Abdomen. Unicolorous dark brown.

Terminalia (Fig. 1–3, 4A, B). Epandrium for greatest part microtrichose, with ca. 12 lower setae, ca. 11 long upper setae and a convex ventral margin; ventral lobe almost indistinct, distally slightly sinuate, mostly bare. Cercus anteriorly connected to epandrium by membranous tissue, mostly microtrichose and without ventral lobe. Surstylus not microtrichose, dorsally bearing a prominent thumb-like process (Figs 1A, 2A), distally with a slightly convex row of ca. 12 peg-like roundish-tipped prensisetae, ventrally with ca. 3 outer and ca. 4 inner setae. Decasternum (Figs 2A, B) 8-shaped, medially bearing a distinct longitudinal sclerotized stripe, laterally linked to surstyli by membranous tissue, posteriorly connecting ventral margins of cerci. Hypandrium (Fig. 3) rectangle-shaped, as long as epandrium, anterior margin convex, posterior margin deeply sinuate; posterior hypandrial process and dorsal arch absent; gonopods completely fused to hypandrium but recognizable because of their protruded, medioapical connection to outer paraphyses, and presence of their setae on submedian distal area of hypandrium. Aedeagus almost completely microtrichose, oblong, slightly narrowing towards tip, roundish at tip in ventral and dorsal views (Figs. 3A and 4B, respectively), anteriorly connected to posterior end of aedeagal apodeme by membranous tissue, flanked by two pairs of paraphyses. Outer paraphysis boomerang-shaped in lateral view (Fig. 3C), not microtrichose, roundish at tip, laterally with a sinuate row of ca. 8 setulae on outer surface, anteriorly connected both to posterolateral end of aedeagal apodeme, and to the submedially protruding distal margin of hypandrium (gonopods), by membranous tissue. Inner paraphyses unusually large, distally fused to each other, thereby embracing aedeagus like a dorsal arch, pointed at tip and somewhat triangular in lateral view (Fig. 3C), microtrichose at very tip, and fused to laterodistal inner surface of hypandrium by means of a long, dorsal, ribbon-shaped, sclerotized process (Figs 3B, C). Aedeagal apodeme rod-shaped, longer than aedeagus, anteriorly expanded; ventral rod narrow, ca. 1/5 of length of aedeagal apodeme, anteriorly fused to sub-posterior ventral area of aedeagal apodeme, distal tip connected to median region of posterior margin of hypandrium by membranous tissue [a similar ventral rod is indeed also present in *Drosophila ingrica*, although we have overlooked it in its redescription (Bächli et al. 2004: 234, 235; see fig. 551)].

Distribution. USA (apparently endemic to Alaska). However, its geographical distribution may be much larger, including southern Canada and northern areas of the United States. It is rarely attracted to fruits baits, the most usual method for collecting species of *Drosophila*. According to Wheeler & Throckmorton (1961: 138, 139) an estimated 98 % of the sampled *Drosophila populi* in Alaska were collected by sweeping among fallen cottonwood branches and only about 2 % were attracted to banana baits placed nearby.

*Biology*. Apparently associated with cottonwood tree (*Populus* sp.; Salicaceae).

Comments. For comparison purposes we dissected one Swedish male specimen of Drosophila ingrica («SWEDEN: SÖ Tyresta NP: NATUV. verkets dok program:

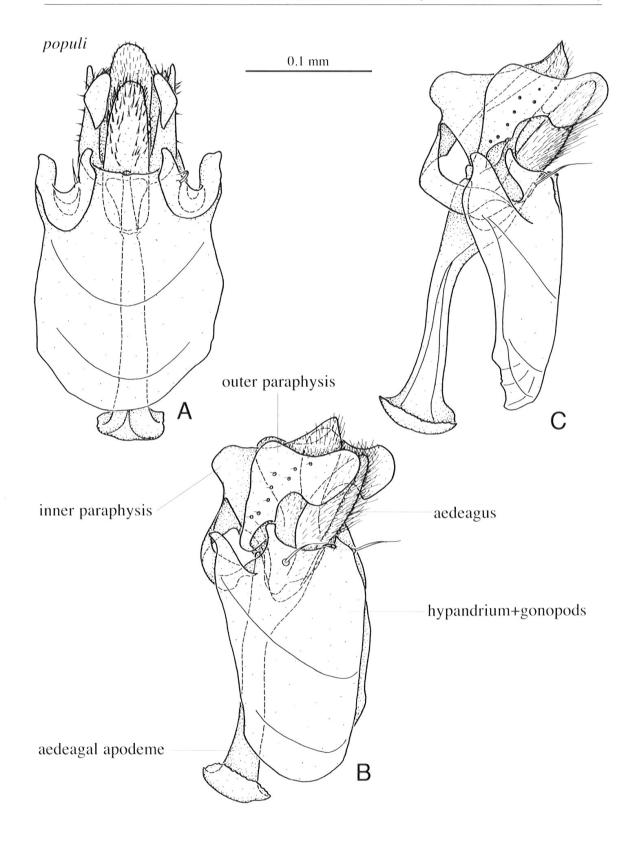


Fig. 3. *Drosophila populi* Wheeler & Throckmorton, male holotype, internal male terminalia. A, ventral view. B, oblique ventral view. C, left lateral view.

Malaise-trap over Populus log: GPS N 59 10 738 E 18 18 630: 28.VII–20.IX.2000: Viklund B, Wikars L-O & Ahnlund H leg. \ Drosophila ingrica Hackman, Bächli et al., 2004 \ ♂ ») from which we took two photomicrographs of the internal male terminalia (Figs 4C, D, respectively in left lateral and dorsal view). This species was redescribed by Bächli *et al.* (2004: 224 (fig. 537), 233–235) based both on males from Karelia and Sweden and females from Sweden and Finland. One photomicrograph of the internal male terminalia of the Karelian specimen in left lateral view was published later (Bächli & Vilela, 2007: 242, fig. 55). Through the comparisons of the male terminalia we have concluded that *Drosophila populi* differs from *D. ingrica* by the following subtle but reliable details of their component sclerites:

- 1) aedeagus rice-seed-like in *D. populi* (Fig. 3C), but with a noticeably broad base in *D. ingrica* (Bächli *et al.*, 2004: 234, fig. 551), as seen in lateral view;
- 2) outer paraphysis with a sinuate row of ca. 8 setulae along the outer surface, and not microtrichose on inner surface in the first species (Figs 3B, C), but with a sinuate row of ca. 4 setulae on the base of outer surface, and partially microtrichose on inner surface in the latter (Bächli *et al.*, 2004: 234, fig. 551, 552);
- 3) inner paraphyses distally clearly fused to each other in the first species (Fig. 4B; blunt at tip, as indicated by an arrow), but distally linked to each other by membranous tissue in the latter (Fig. 4D; sharply pointed at tip, as indicated by an arrow), as seen in dorsal or ventral view;
- 4) inner paraphysis distally sharply pointed in the first species (Fig. 4A), but distally blunt at tip in the latter (Fig. 4C), as seen in lateral view.

Although we have not analyzed any female specimen of *Drosophila populi*, it is possible to compare the published line drawing of its right oviscapt valve (Wheeler & Throckmorton, 1961: 141, fig. 7), with that published for the left oviscapt valve (Bächli *et al.* 2004: 224, fig. 537) of *Drosophila ingrica*. They look very similar in having unusually long, trichoidlike, instead of the usual peglike, outer ovisensilla. We suggest that this state of character might be related to the oviposition substrate, which is unknown for both species. Their trichoidlike outer ovisensilla on the valves are also remarkably similar to these depicted by Bächli *et al* (2004: 224, fig. 535) for *Drosophila subsilvestris* Hardy and Kaneshiro, 1968, an unique character for a species belonging to the closely related *obscura* group of the subgenus *Sophophora*.

The following remark, quoted from Starmer (1981: 49), written in the context of breeding sites containing particular yeasts, favours our suggestion of similarity between the breeding sites (probably slime fluxes of temperate tree, especially cottonwood) of *Drosophila populi* and *Drosophila ingrica*, based on the type of outer ovisensilla of their oviscapt plates: «The Sophophoran radiation also has several members which are known to utilize tree fluxes for feeding and/or breeding (*D. populi, obscura* group and *Chymomyza*), while other groups rely on decaying fruit (willistoni, saltans and melanogaster groups)». According to Starmer (1981: 47), temperate tree flux yeasts have extensive physiological abilities; they produce several fermentation products. We suggest that subtle differences of yeast communities among temperate tree fluxes could be responsible for a putative preference of the species of the *populi* group for cottonwood fluxes, whereas they may be unable to develop in fluxes of other temperate tree species. It is interesting to note that, accord-

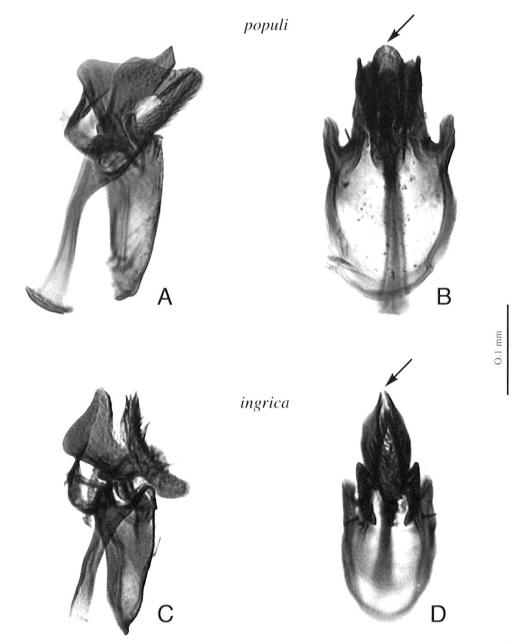


Fig. 4. Photomicrographs of male internal terminalia of the two species of the *Drosophila populi* group in left lateral view (A and C) and dorsal view (B and D). — A and B, *Drosophila populi* Wheeler & Throckmorton, holotype; outer paraphyses not extruded. — C and D, *Drosophila ingrica* Hackman, specimen from Tyresta NP, Sweden, 28.VII – 20.IX.2000; outer paraphyses extruded. The arrows point to the connections between the inner paraphyses: B, fused to each other; D, linked to each other by membranous tissue.

ing to the label, the specimen of *Drosophila ingrica* from Tyresta, just cited above, was collected with a Malaise trap settled over a *Populus* log.

The year of publication of the description of *Drosophila populi* was mistaken by Wheeler (1981a: 97) as 1960 (indeed, on the running title of the description it is stated: December, 1960). However, in the present redescription we follow Brake & Bächli (2008: 113, 358), because according to them the paper by Wheeler & Throckmorton was published only on April 11th, 1961. It is worthwhile to note that the year of publication of the original description of *Drosophila populi* had been previously considered as 1961 by Wheeler himself (1965: 768, 1469).

#### **ACKNOWLEDGMENTS**

We thank B. Viklund for presenting some Swedish specimens of *D. ingrica* to the Zoologisches Museum der Universität Zürich. We are indebted to Pierre Brauchli and Doro Röthlisberger for helping with digital image processing and to Dr. Wayne N. Mathis, of the National Museum of Natural History, Washington, D.C., for kindly loaning the type specimen.

#### REFERENCES

- Ashburner, M., Golic, K.G. & Hawley, R.S. 2005. Drosophila. A laboratory handbook. Second edition. 1409 pp. Cold Spring Harbor Laboratory Press.
- Bächli, G. & Vilela, C.R. 2007. Photomicrographs of the male terminalia of Scandinavian Drosophilidae (Diptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 80: 231–246.
- Bächli, G., Vilela, C.R., Andersson Escher, S. & Saura, A. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica, vol. 39, 362 pp. Brill, Leiden.
- Blight, W.C. & Romano, A. 1953. Notes on a breeding site of Drosophila americana near St. Louis, Missouri. American Naturalist 87: 111–112.
- Brake, I. & Bächli, G. 2008. Drosophilidae (Diptera). *In*: World Catalogue of Insects 9: 1–412. Apollo, Stenstrup.
- Carson, H.L., Knapp, E.P. & Phaff, H.J. 1956. Studies on the ecology of *Drosophila* in the Yosemite region of California. III. The yeast flora of the natural breeding sites of some species of Drosophila. Ecology 37: 538–544.
- Ferrar, P. 1987. A Guide to the breeding habits and immature stages of Diptera Cyclorrhapha. Entomonograph, 8(1–2): 1–907.
- Kaneshiro, K.Y. 1969. A study of the relationships of Hawaiian *Drosophila* species based on external male genitalia. The University of Texas Publication 6918: 55–70.
- Lemeunier, F. & Ashburner, M. 1976. Relationships within the *melanogaster* species group of the genus *Drosophila* (*Sophophora*). II. Phylogenetic relationships between six species based upon polytene chromosome banding sequences. Proceedings of the Royal Society of London B 193: 275–294.
- Okada, T. 1968. Systematic Study of the Early Stages of Drosophilidae. 188 pp. Bunka Zugeisha, Tokyo.
- Spieth, H.T. 1951. The breeding site of *Drosophila lacicola* Patterson. Science 113: 232.
- Starmer, W.T. 1981. A comparison of *Drosophila* habitats according to the physiological attributes of the associated yeast communities. Evolution 35: 38–52.
- Takada, H. 1961. The male genitalia of *Drosophila populi* Wheeler and Throckmorton (Diptera: Drosophilidae). Bulletin of the Brooklyn Entomological Society [1960] 55(5): 144–147.
- Takada, H. 1966. Differentiation of the external male genitalia in the Drosophilidae. Proceedings of the Kushiro Women's College 1: 39–50, 131–132.
- Throckmorton, L.H. 1962. The problem of phylogeny in the genus *Drosophila*. The University of Texas Publication 6205: 207–343.
- Throckmorton, L.H. 1966. The relationships of the endemic Hawaiian Drosophilidae. The University of Texas Publication 6615: 335–396.
- Throckmorton, L.H. 1968. Concordance and discordance of taxonomic characters in *Drosophila* classification. Systematic Zoology 17:355–387.
- Throckmorton, L.H. 1975. The phylogeny, ecology, and geography of *Drosophila*. *In*: King, R.C. (ed.), Handbook of Genetics, vol. 3, pp. 421–469. Plenum Press, New York.
- Toda, M.J. 1984. The northernmost subarctic Drosophilidae. *Drosophila* Information Service 60: 193–194.
- Val, F.C., Vilela, C.R. & Marques, M.D. 1981. Drosophilidae of the Neotropical region. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 123–168. Academic Press, London.
- Vilela, C.R. & Bächli, G. 1990. Taxonomic studies on Neotropical species of seven genera of Drosophilidae. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 63(Suppl.): 1–332.
- Vilela, C.R. & Bächli, G. 2000. Morphological and ecological notes on the two species of *Drosophila* belonging to the subgenus *Siphlodora* Patterson & Mainland, 1944 (Diptera, Drosophilidae).
   Mitteilungen der Schweizerischen Entomologischen Gesellschaft 73(1–2): 23–47.
- Wheeler, M.R. 1965. Family Drosophilidae. *In*: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H.
  & Coulson, J.R. (eds), A Catalog of the Diptera of America north of Mexico, pp. 760–771. —
  U. S. Department of Agriculture, Washington, D.C.

- Wheeler, M.R. 1981a. The Drosophilidae: A taxonomic overview. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 1–97. Academic Press, London.
- Wheeler, M.R. 1981b. Geographical survey of Drosophilidae: Nearctic species. *In*: Ashburner, M., Carson, H.L. & Thompson, J.N. (eds), The Genetics and Biology of *Drosophila*, vol. 3a, pp. 99–121. Academic Press, London.
- Wheeler, M.R. & Kambysellis, M.P. 1966. Notes on the Drosophilidae (Diptera) of Samoa. The University of Texas Publication 6615: 533–565.
- Wheeler, M.R. & Throckmorton, L.H. 1961. Notes on the Alaskan Drosophilidae (Diptera) with the description of a new species. Bulletin of the Brooklyn Entomological Society [1960] 55(5): 134–143.

(received November 3, 2009; accepted November 17, 2009)