SPIXIANA	Supplement 11	109–137	München, 30. Dezember 1985	ISSN 0177-7424

A review of Diamesa davisi Edwards and the davisi group

(Diptera, Chironomidae)*

By **Endre Willassen**

Zoological Museum, Bergen, Norway

WILLASSEN, E. (1985): A review of *Diamesa davisi* Edwards and the *davisi* group (Diptera, Chironomidae). – Spixiana, Suppl. 11: 109–137.

The *Diamesa davisi* group comprizes an aggregate of morphologically very similar populations. Imagines of the group have been examined and sources of nomenclatorial confusion in previous literature are pointed at. It is submitted that application of the biological species concept in this case, could have masked data which seem potentially informative in biogeographical studies, and that regarding the *D. davisi* group as composed of 7 different species has greatest heuristic potentials with the presently available data. *Diamesa davisi* Edwards apparently occurs primarily in the E. Nearctic. *Diamesa alpina* Tokunaga is distributed from Japan via Kamchatka down the west coast of Alaska. Its sister species, *Diamesa sonorae* spec. nov. is found in the mountains of California. *Diamesa saetheri* spec. nov. is known from glacier brooks in Scandinavia and from arctic and alpine Siberia. *Diamesa serratosioi* spec. nov. occurs in Scandinavia, *Diamesa lupus* spec. nov. in the W. Nearctic, and *Diamesa amplexivirilia* Hansen in the Nearctic and E. Palaearctic. The sister species of the *D. davisi* group is the W. Nearctic *Diamesa nivicavernicola* Hansen. Body size in *Diamesa serratosioi* gradually is declining throughout the emergence period, and seasonal variation is seen in the leg ratio. Both phenomena are regarded as effects of temperature. Wing reduction in female *Diamesa saetheri* and *Diamesa steinboecki* Goetghebuer is accompanied by a reduced number of tarsal sensilla chaetica.

Dr. Endre Willassen, Zoological Museum, Muséplass 3, N-5000 Bergen.

Introduction

The present paper attempts to clarify and deal with taxonomic problems concerning *Diamesa davisi* Edwards and the *davisi*-group (KOWNACKI 1980).

EDWARDS (1933) described *Diamesa davisi* from material collected by the Oxford Expedition to Hudson Strait in 1931. Recordings of *D. davisi* from Norway, Sweden, and Greenland were later published by THIENEMANN (1942), and a description of the species given by PAGAST (1947) was based on Thienemann's material from Sweden. Since then, the European *D. davisi* has been considered in a number of papers (SAETHER 1968; SERRA-TOSIO 1969, 1973; STEFFAN 1971; AAGAARD 1978; KOWNACKI 1980) and recently, recordings of *D. davisi* from Siberia have been published (MAKARCHENKO 1980).

* This paper was submitted as one of three manuscripts to the University of Bergen, Norway, August 1982, in partial fulfillment of requirements for the degree of Dr. scient.

In a revision of Nearctic *Diamesa* Meigen, HANSEN and COOK (1976) examined one of the syntypes and redescribed the male imago from material collected in Alaska, California, Canada, Montana, New Hampshire, Washington, Wyoming, and Utah. Referring to figures of the hypopygium of the Scandinavian *D. davisi* presented by PAGAST (1947) and SERRA-TOSIO (1971), they suggested that this might be a different species, more similar to *D. amplexivirilia* Hansen.

I have compared the type material of *D. davisi* to specimens collected at different sites in Western Norway and recognize two new species, both previously described as *D. davisi.* Additional material from the Nearctic which I have had the opportunity to examine, contains three more species, one is identical to *D. alpina* Tokunaga sensu MAKARCHENKO (1980). Another was included in *D. davisi* by HANSEN and COOK (1976) but is distinctly different from the types of *D. davisi.* The third species would key out to *D. amplexivirilia* in the key to Nearctic males of the genus given by HANSEN and COOK (1976), but differs in details of the male hypopygium.

Four new species are thus added to the *davisi* group in the sense of KOWNACKI (1980). These are *D. sonorae* spec. nov., *D. lupus* spec. nov., *D. serratosioi* spec. nov., and *D. saetheri* spec. nov. The following descriptions include the imagines of these species, as well as *D. davisi* and *D. alpina.* Detailed descriptions of *D. amplexivirilia* have been published by HANSEN and COOK (1976) and MAKARCHENKO (1980, 1981), and reference to some diagnostic features is regarded as sufficient for the purpose of this paper.

Taxonomical problems pertaining to body size and variation are briefly elucidated. A tentative reconstruction of the phylogenetic relationships within the *davisi* group is presented and some biogeographic interpretations are based on this.

Methods and morphology

Specimens were mounted on slides following the procedure described by SAETHER (1969). Measurements follow SCHLEE (1966, 1968). In the descriptions measurements are given as ranges.

Terminology generally follows SAETHER (1980) with a few exceptions. I regard the ocelli (SAETHER 1980) as probably being campaniform sensilla and have here called them frontal sensilla (WILLASSEN 1983). Their position relative to the frontal protrusion (Fig. 4.2) are useful taxonomic characters in some cases. A flap (Fig. 5.3) characterizes the female genitalia of some *Diamesa* Meigen and other genera of Diamesinae.

Diagnosis to imagines of the davisi group

Male imago with eight flagellomeres, female with seven. Ultimate flagellomere somewhat swollen, basal flagellomere more slender. Head of both male and female with separate, weak frontal protrusions. Frontal sensilla far apart. Eyes hairy. Frontal setae few or absent. Tentorium tubelike. Wings, when not reduced, with small anal lobe. Alula without setae. Tibial spurs fairly short with dense prickles basally. Male hypopygium with conspicuous laterosternites usually extending beyond posterior margin of tergite IX. Sternapodeme shaped like an arrowpoint. Anal point directed more or less ventrad and often strongly reduced. Male gonocoxite with a knoblike superior volsella. Gonostylus with apical teeth and subterminal peg and erect short setae. Female genitalia with large sternum VIII covering gonocoxites in ventral view, sternal setae 1–2 or wanting. Flap well developed. Tergite VIII nearly devoid of setae. Gonocoxite IX roughly triangular, poorly delineated from tergite IX and without prominent lateral projection, with short setae distributed essentially along dorsal margin. Tergite IX strongly divided with small, setaebearing protrusions appearing as part of gonocoxite in lateral view. Cerci small, rounded to trapezoid, sometimes with ventrolateral knee-like protrusion, occasionally with dorsal protrusion near base.

Key to males of the davisi group

1 Laterosternites not extending beyond posterior margin of tergite IX (Fig. 2.2) . . . . *Diamesa sonorae* spec. nov.

– Laterosternites projecting beyond margin of tergite IX 2

2 Sternapodeme blunt anteriorly, anal point usually pigmented and blunt-tipped, gonostylus with strong bend (Fig. 1.3) . . . . *Diamesa amplexivirilia* Hansen

– Sternapodeme pointed, anal point hyaline and pointed or completely reduced, gonostylus less bent 3

3 Posterior part of laterosternite membraneous, delineated from normally sclerotised anterior part with sickle-shaped apodeme (Figs. 2.3–4) . . . . *Diamesa lupus* spec. nov.

– Sclerotisation of laterosternite uniform 4

4 Tergal bands U-shaped . . . . *Diamesa alpina* Tokunaga

– Tergal bands Y- to V-shaped 5

5 Laterosternites obliquely cut mesally (Figs. 1.1–2, 1.7, 1.9) (Fig. 1.8 illustrates the difficulty of evaluating this character in squeezed mounts) and with minute setae 6

– Laterosternites with relatively long setae and dorsomesal margin almost straight (Figs. 1.3–5) . . . . *Diamesa serratosioi* spec. nov.

6 Posterior margin of tergite IX rounded (Figs. 1.7–9) . . . . *Diamesa saetheri* spec. nov.

– Posterior margin straight (Figs. 1.1–2) . . . . *Diamesa davisi* Edwards

Diamesa amplexivirilia Hansen
(Fig. 1.3)

Diamesa amplexivirilia Hansen, HANSEN and COOK 1976: 53–57, fig. 119 (description of males from Canada and USA).

Diamesa amplexivirilia Hansen, MAKARCHENKO 1980: 86–88, fig. 4 (description of males from the Kolyma area and Wrangel I.). MAKARCHENKO 1981: 108–110, fig. 11 (description of larva and pupa).

Diagnosis: The male is characterized by a gently rounded posterior margin of tergite IX; tergal bands weak, widely U-shaped (semi-circular); anal point relatively well developed and blunt-tipped; laterosternites very extended, evenly sclerotized and with relatively dense and long setae; gonocoxite with weak medial field; gonostylus very strongly curved.

Remarks

The very strong bend of the gonostylus is the most striking autapomorphy of *D. amplexivirilia*. Although the anal point is variable, it seems generally more conspicuous than in other members of the *davisi* group. The specimen figured by MAKARCHENKO (1980) shows a less truncate sternapodeme than the Nearctic specimens available to me, but otherwise the hypopygia appear almost identical.

The female of *D. amplexivirilia* is unknown.

Material studied

USA, Washington, 3 mi. E, 6 mi. S of Glacier, Mt. Baker, Sept. 7, 1967, D. Hansen leg., 3 male paratypes; Montana, Glacier National Park, elev. 5800 ft. July 24, 1968, R. A. Hellenthal, 1 male paratype. Deposited in Department of Entomology, University of Minnesota, St. Paul.

Diamesa davisi Edwards

(Figs. 1.1–2, 3)

Diamesa davisi Edwards 1933: 614–615, fig 2a (descriptions of male and female).
Diamesa davisi Edwards *pro parte*, HANSEN and COOK 1976: 81–85, figs. 62, 120 (description based on Nearctic males, question previous records of *D. davisi* from Scandinavia).

Diagnosis: The male is characterized by Y-(types) to V-shaped tergal bands, a partly straight posterior margin of tergite IX, reduced anal point; moderately extended laterosternites with very weak setae. Confer remarks for the female.

Description

Male imago (type material, n = 2, and additional material, n = 1, in parentheses)

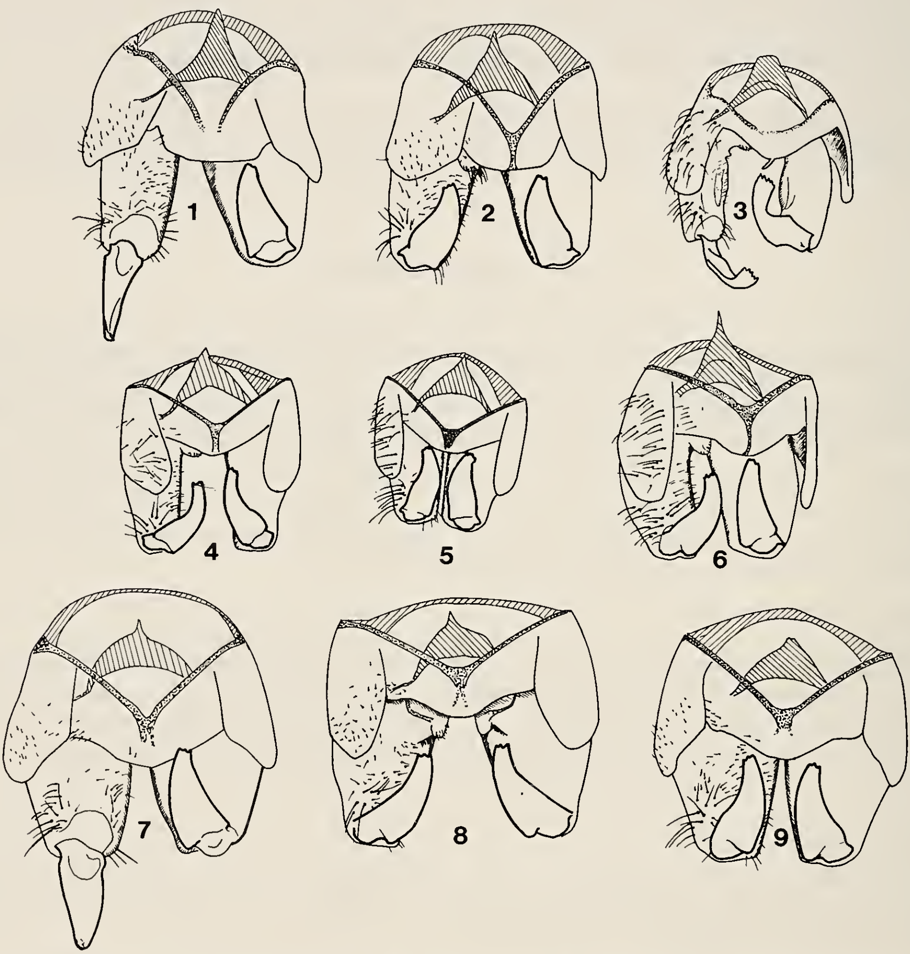

Fig. 1. *Diamesa* spp., male hypopygia. 1.1 *D. davisi* Edwards, Wyoming; 1.2 *D. davisi,* Akpatok Island (paralectotype); 1.3 *D. amplexivirilia* Hansen, Washington; 1.4–6 *D. serratosioi* spec. nov., W. Norway; 1.7–9 *D. saetheri* spec. nov., W. Norway.

Total length 3.07–3.08 (3.17) mm. Wing length/width 2.47–2.59 (2.59)/0.78 (n = 1) (0.95) mm. Total length/wing length 1.19–1.24 (1.24). Wing length/length of profemur 1.58–1.64 (1.54).

Antenna (n = 2): Length/width of pedicel 33 (52)/77 (73) µm. Length/width of flagellomeres (µm): 109 (105)/36 (40), 47 (47)/33 (33), 44 (40)/31 (32), 31 (32)/28 (31), 33 (36)/27 (30), 29 (28)/27 (31), 33 (40)/35 (39), 109 (106)/37 (40). AR 0.29 (0.33). Scape and pedicel without setae. Flagellomeres 1–7 respectively with setae: 6 (4), 2 (3), 1 (2), 0 (1), 1 (1), 0 (0), 6 (6). Ultimate flagellomere with 4 (4) strong setae and 1 (2) weak apical setae.

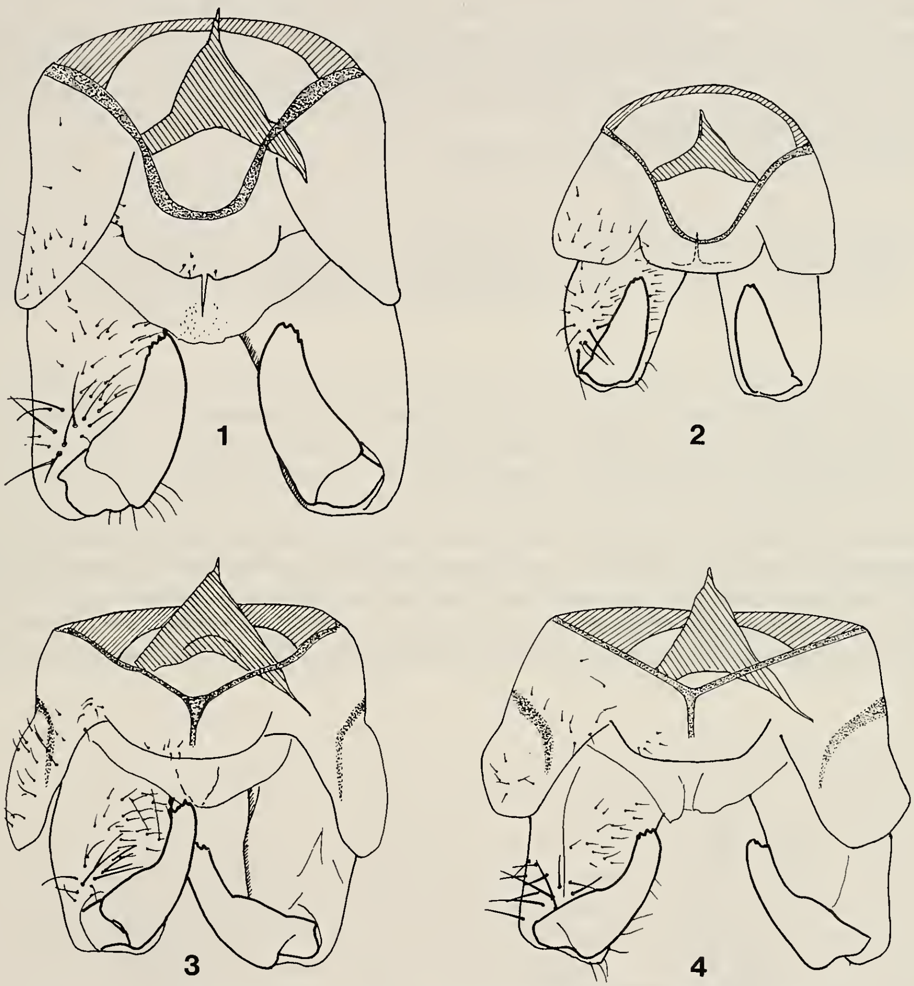

Fig. 2. *Diamesa* spp., male hypopygia. 2.1 *D. alpina* Tokunaga sensu Makarchenko, Alaska; 2.2 *D. sonorae* spec. nov., California; 2.3–4 *D. lupus* spec. nov., Alaska.

Head: Coronal suture complete, 170–176 (162) µm long. Frontal sensilla 165 (160) µm apart. Temporal setae (n = 2) 25 (19), including 8 (3) postorbitals, 13 (15) verticals, 2 (0) orbitals, and 2 (1–2) frontal setae. Clypeus length/width 84–89 (94)/144–165 (144) µm, with 1–3 (1) setae. Length/width of palpal segments (n = 2) µm: 40 (39)/39 (40), 61 (61)/40 (45), 106 (101)/48 (59), 89 (85)/44 (45), 122 (113)/36 (40). Palpal stoutness 2.25 (1.90).

Thorax: Antepronotum nearly reaching scutal projection, with 7–10 (11) lateral setae. Dorsocentrals 6 (7–9), acrostichals absent, prealars 5–6 (7); epimeron II with 0–1 (0) setae, preepisternum II without setae. Scutellars 15–22 (13).

Wing (n = 2): VR 1.03 (1.00). Brachiolum with 4 (3) setae distally; R with 5 (6) setae, R_1 with 5 (12), R_{4+5} with 6 (13) setae. Subcosta with 2 (1) sensilla campaniformia, R_1 with 2 (2), R_{2+3} with 1 (1), R_{4+5} with 2 (2) sensilla campaniformia.

Legs: Spur of front tibia 35–36 (35) µm long, spurs of middle tibia 39–43 (47) and 31–35 (37) µm, spurs of hind tibia 60–65 (69) and 32–40 (41) µm long. Width at apex of front tibia 70–75 (67) µm, of middle tibia 69–75 (72) µm, of hind tibia 86 (86) µm. Comb on hind tibia with 16–19 (18) setae; longest seta 56–69 (63) µm, shortest seta 33–41 (43) µm long. Each leg with 2 apical pseudospurs (may be weak) on ta $_{1-3}$ respectively. Preapical pseudospurs on ta_{1-3} respectively: 0–10, 0, 0 on p_1; 7–9 (3), 2 (2), 0 on p_2; 11–17 (12), 4–6 (3), 0–1 (0) on p_3. Sensilla chaetica ? (3) distributed from (0.72) to (0.77) of posterior ta_1. Claws of posttarsus pointed.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4
p_1	1560–1573 (1651)	1443–1456 (1430)	845–858 (884)	370 (391)	204–231 (233)	84–92 (94)
p_2	1612–1716 (1560)	1326 (1274)	533–549 (528)	215–253 (306)	114–160 (170)	71–79 (85)
p_3	1716–1833 (1651)	1547–1625 (1521)	897–910 (897)	449–459 (468)	220–229 (248)	76–92 (97)

	ta_5	LR	BV	SV	BR
p_1	118 (126)	0.59 (0.62)	4.74–5.01 (4.70)	3.53–3.55 (3.49)	1.0–1.2 (1.1)
p_2	97–100 (113)	0.40–0.41 (0.41)	6.10–6.55 (4.99)	5.51–5.54 (5.37)	1.1 (1.2)
p_3	107–110 (118)	0.56–0.58 (0.59)	4.80–5.03 (4.37)	3.64–3.80 (3.54)	1.1–1.4 (1.4)

Hypopygium (Figs. 1.1–2): Tergite with posterior margin partly straight, tergal bands Y-shaped (type material) to V-shaped, anal point not visible in dorsal view. Laterosternite moderately extended, posterior margin inclined with very weak setae; length ratio of laterosternite to gonocoxite 0.61–0.64 (0.62). Volsella with microtrichia and setae (at least in type material). Gonostylus weakly curved and evenly tapering distad, with 3–4 apical teeth and subterminal peg. HR 1.96–2.15 (1.86). HV 1.39–1.58 (1.36).

Female imago (allolectotype)

Total length 3.35 mm. Wing length/width 2.96/1.08 mm. Total length /wing length 1.13. Wing length/length of profemur 2.59.

Antenna: Length/width of pedicel 44/73 µm. Length/width of flagellomeres (µm): 106/35, 52/32, 39/28, 35/27, 35/27, 47/31, 93/35. AR 0.28. Scape and pedicel without setae. Flagellomeres 1–6 respectively with setae: 4, 3, 1, 0, 2, 5. Ultimate flagellomere with 3 strong setae and 2 weak apical setae.

Head: Coronal suture 131 µm long. Frontal sensilla 167 µm apart. Temporal setae 20, including 8 postorbitals, 11 verticals, 0 orbitals, and 1 frontal seta. Clypeus length/width 89/157 µm, with 2 setae. Length/width of palpal segments (µm): 27/36, 44/44, 80/36, 69/36, 109/35. Palpal stoutness 2.00.

Thorax: Antepronotum with 9 lateral setae. Dorsocentrals 7, acrostichals absent, prealars 5; epimeron II with 1 (?) seta, preepisternum II without setae. Scutellars 21.

Wing: VR 1.01. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 2 setae distally; R with 5 setae, R_1 with 10, R_{4+5} with 6 setae. Alula without setae. Squama with 11 setae. Subcosta with 2 sensilla campaniformia R_1 with 3, R_{2+3} with 1, R_{4+5} with 3 sensilla campaniformia.

Legs: Spur of front tibia not measurable, spurs of middle tibia 43 and 33 µm long, spurs of hind tibia 64 and 33 µm long. Width at apex of front tibia 40 µm, of middle tibia 68 µm, of hind tibia 82 µm.

Comb on hind tibia with 17 setae 53 μm to 36 μm long. Each leg with 2 apical pseudospurs on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 9, 2, 0 on p_2; 14, 2, 0 on p_3. Sensilla chaetica 41 distributed from 0.18 to 0.74 of posterior ta_1.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	1144	1105	702	285	170	–	–	0.64	–	3.20	1.6
p_2	1235	1066	443	197	131	81	97	0.41	5.42	5.19	1.3
p_3	1339	1287	767	433	169	72	–	0.60	–	3.42	1.5

Genitalia (Fig. 3.): Sternum VIII without setae. Gonocoxapodeme weak, nearly parallel to flap margin. Ventrolateral lobe almost entirely covered by flap. Apodeme lobe with weak scattered microtrichia. Seminal capsules slightly oblong with very short neck, punctuation of surface distinct at 500X magnification, length/with 77/39 μm. Spermathecal ducts with loop, apparently with separate openings. Labial microtrichia indistinct at 750X magnification. Gonocoxite IX almost flat, evenly tapering distad and slightly bent mediad behind protrusion of tergite IX, with 8–11 setae about 25–50 μm long. Tergite IX with small knob-like protrusions, 6 setae about 65 μm long on each protrusion. Segment X slightly protruding posteriad (ventral aspect). Cerci more or less rounded with group shagreenation on lateral side, ventral knee-like protrusion apparently missing.

Remarks

A male lectotype has been selected in accordance with recommendation 74B of the International Code of Zoological Nomenclature. One male of the syntype series apparently is lost. *D. davisi* is very similar to *D. alpina* sensu Makarchenko (1980) in the male hypopygium. Distinguishing characters are the U-shaped tergal band and a slightly more developed anal point in *D. alpina* (see below). These characters are also shared by *D. sonorae* spec. nov. which has shorter laterosternites than both *D. davisi* and *D. alpina*. *D. davisi* sensu Makarchenko (1980) is identical to *D. davisi* sensu Saether (1968). This species is clearly different from *D. davisi* Edwards and has been named *D. saetheri* spec. nov. (see below). The female of *D. davisi* was not recognizable from the original description. Hansen and Cook (1976: 81) suggested that the cercus drawn by Edwards (1922, fig. 11) (as *D. ursus* Kieffer) might belong to *D. davisi*. This they did by stating that Saether (1968: 441) questioned the determina-

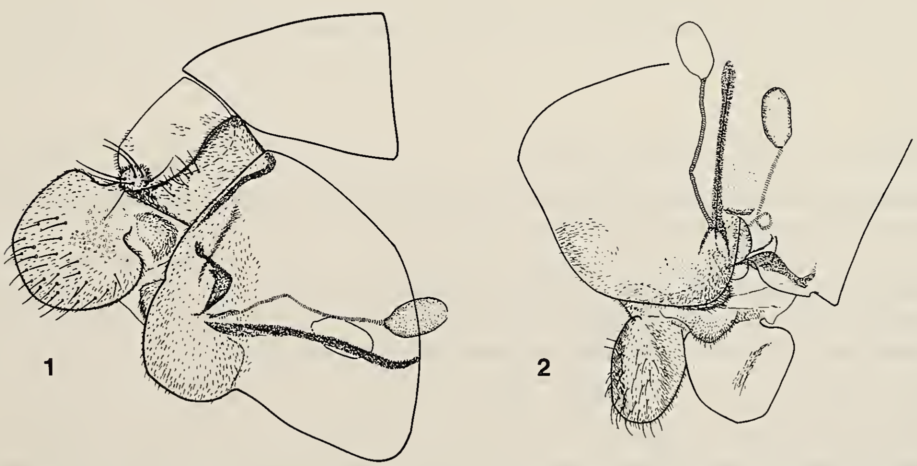

Fig. 3. *D. davisi* Edwards, female genitalia (allolectotype). 3.1 lateral aspect, 3.2 ventral aspect (slightly tilted).

tion by Edwards. However, they refer to the wrong figure. The reference should be to EDWARDS: 1922, fig. 12, concerning *D. hyperborea* Holmgren, which according to PAGAST (1947: 573), and referred to by SAETHER (1968), was regarded as a possible synonym of *D. davisi.* As will be pointed out elsewhere, the cercus in EDWARDS (1922, fig. 11) belongs to *D. bohemani* Goetghebuer (WILLASSEN, MS). A knee-like ventrolateral protrusion of the cercus apparently is missing in *D. davisi.* This seems to be the case also for *D. alpina* (TOKUNAGA 1936) and *D. sonora* spec. nov.

Material studied

Lectotype male, allolectotype female, paralectotype male (by designation); Boulders in watercourse, 21. Aug. 1931, O. U. Exp. 1931, S. E. Akpatok I., Ungava Bay, N. Canada, D. H. S. Davis d. d. 1931, BM 1933 588. USA, Wyoming, 4457′42″ N 10929′00″ W, alt. 10300′, 31mi. N 21mi. W of Cody, Under rocks in small rocky stream feeding Frozen Lake, Aug. 13. 1969, leg. Dean Hansen, DH 69-303, BM 1970 585; 1 male. Above material deposited in the British Museum (NH), London. White Mt. Nat. Forest, Ammonoosuc R., N. H., 26. May 1981, D. R. Oliver and M. E. Roussel leg., 1 male, 1 female, 3 pupae, and 2 larvae. Deposited in the Canadian National Collections, Ottawa.

Diamesa serratosioi spec. nov.
(Figs. 1.4–6, 4.1–3, 5)

? *Diamesa* spec. VI Pagast 1947: 526 (description of *davisi* like male exuvium).
Diamesa davisi Serra-Tosio 1971: 195–198, figs. 82.1–3 (Description of male adult from Sweden; records from Aurland, W. Norway; *pro parte,* distribution and ecology) Serra-Tosio 1973: 59 *pro parte* (distribution and ecology)
Diamesa serratosioi Willassen. Serra-Tosio 1983: 13 (reference to manuscript by Willassen). Nomen nudum.

Type area: W. Norway, Hordaland, Eksingedalen, Ekse.

Type material: Holotype male, Z. M. Bergen Type no. 81; Ekse, HOi, Vaksdal, 60°50′N 6°15′E, 10–16/8 1976, leg. T. Andersen. Paratypes (and allotype): 24–30/6–76 9 males; 17–24/6–76 12 males; 15–20/7–76 7males, 2 females; 20–27/7–76 7 males; 3–10/8–76 1 male; 10–16/8–76 5 males, 2 females; 16–26/8–76 2 males, 2 females; 26/8–1/9–76 10 males; 24–30/9–76 2 females; same loc. as holotype. Lundeelv, Jölster, Sogn og Fjordane, Sep. 1980, leg. G. A. Halvorsen; 7 males, 1 reared from larva, 1 female. Nedre ende Vassbygdvatnet, SFi, Aurland, 16/8 1968, leg. G. Hansteen, 5 males.

Diagnosis: The male is characterized by having Y-shaped tergal bands, a rounded posterior margin of tergite IX, weak anal point usually not visible in dorsal view, very extended laterosternites with weak and long setae. Confer remarks for the female.

Etymology: The species is named as a tribute to dr. Bernard Serra-Tosio, Grenoble, for his contributions to the knowledge of the Diamesini.

Description

Male imago (n = 11 unless otherwise stated)

Total length 2.47–3.73 mm. Wing length/width 2.21–2.81/0.74–0.96 mm. Total length/wing length 0.79–1.41. Wing length/length of profemur 1.54–1.98.

Antenna (n = 8): Length/width of pedicel 27–53/67–97 µm. Length/width of flagellomeres (µm): 84–125/26–39, 42–60/24–39, 29–50/23–34, 26–39/24–34, 25–39/24–32, 16–34/24–31, 25–39/26–39, 81–128/29–47. AR 0.26–0.37. Flagellomeres 1–2 and 7–8 occasionally partly fused. Scape without setae. Pedicel with 1–3 setae. Flagellomeres 1–7 respectively with setae: 2–7, 2–5, 2–3, 1–2, 1–3, 0–2, 4–6. Ultimate flagellomere with 2–5 strong setae and 2–3 weak apical setae. Longest antennal seta 47–93 µm long.

Head: Coronal suture complete, 131–197 µm long. Frontal sensilla 133–170 µm apart, situated 49–60 µm from apex of frontal protrusion. Temporal setae 16–24, including 5–8 postorbitals, 7–13 verticals, 0–4 orbitals, and 0–2 frontal setae. Clypeus length/width 68–89/101–157 µm, with 2–6 setae.

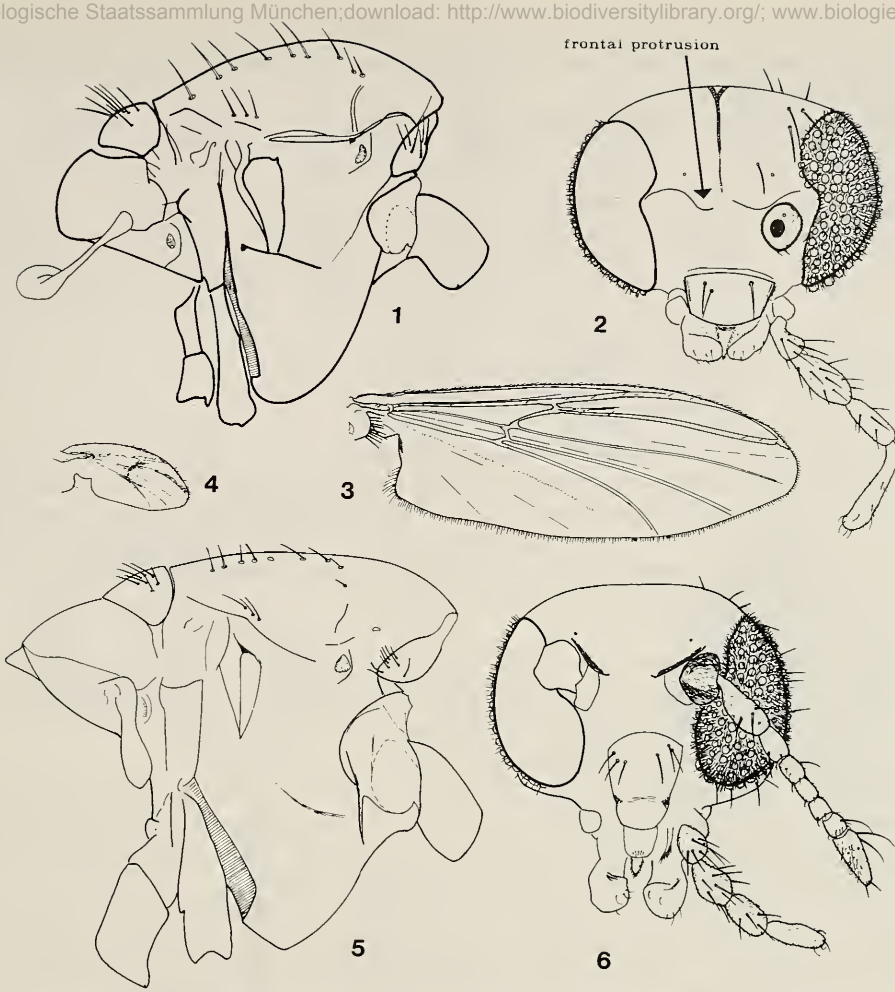

Fig. 4. *Diamesa* spp., head, wing, thorax. 4.1–3 *D. serratosioi* spec. nov., female; 4.4–6 *D. saetheri* spec. nov., brachypterous female (4.4 drawn to same scale as 4.3).

Length/width of palpal segments (μm): 21–43/27–40, 43–66/28–52, 83–118/35–55, 72–100/24–49, 122–168/26–42. Palpal stoutness 2.29–3.10.

Thorax: Antepronotum not reaching scutal projection, with 6–12 lateral setae. Dorsocentrals 6–12, acrostichals absent, prealars 2–5; epimeron II with 0–2 weak setae, preepisternum II without setae. Scutellars 10–18.

Wing: VR 0.92–0.96. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 2–3 weak setae distally and 1 strong seta basally; R with 6–12 setae, R_1 with 5–13, R_{4+5} with 3–9 setae. Alula without setae. Squama with 17–32 setae. Subcosta with 2–4 sensilla campaniformia, R_1 with 2–4, R_{2+3} with 1–2, R_{4+5} with 1–5 sensilla campaniformia.

Legs: Spur of front tibia 20–41 μm long, spurs of middle tibia 37–43 μm and 29–41 μm, spurs of hind tibia 51–79 μm and 31–45 μm long. Width at apex of front tibia 72–105 μm, of middle tibia 54–85 μm, of hind tibia 72–105 μm. Comb on hind tibia with 15–21 setae, longest seta 51–67 μm, shortest seta 26–39 μm long. Each leg with 2 apical pseudospurs (often very weak) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 4–11, 0–2, 0 on p_2; 9–24, 2–8, 0–2 on p_3. Sensilla chaetica 4–11 distributed from 0.36–0.63 to 0.69–0.78 of posterior ta_1. Claws of posttarsus pointed with 1–3 serrations. Pulvilli small.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	1066–1820	1144–1794	689–1131	333–533	167–275	69– 94	93–119
p_2	1079–1807	980–1547	448– 676	225–338	152–308	66– 92	97–118
p_3	1196–1872	1248–1870	754–1131	417–559	222–289	79–105	109–137

	LR	BV	SV	BR
p_1	0.60–0.67	4.13–4.74	2.72–3.73	1.0–1.8
p_2	0.41–0.48	4.52–5.66	4.33–4.96	1.1–1.7
p_3	0.59–0.66	3.84–4.62	3.00–3.36	1.1–2.3

Hypopygium (Figs. 1.4–6): Tergite IX with a few weak setae laterally, posterior margin rounded, tergal band Y-shaped; anal point minute, occasionally visible in dorsal view. Laterosternite strongly produced beyond posterior margin of tergite IX, with several weak but fairly long setae; length ratio of laterosternite to gonocoxite (n = 44) 0.71–0.82, mean value 0.77. Gonocoxite fairly slender; volsella with microtrichia, without setae. Gonostylus broad at base, more or less strongly curved, with 3–5 apical teeth and subterminal peg. HR 1.72–2.14. HV 1.58–2.19.

Female imago (n = 5 unless otherwise stated)

Total length 2.59–3.81 mm. Wing length/width 2.20–2.82/0.82–1.14 mm. Total length/wing length 1.11–1.46. Wing length/length of profemur 2.22–2.68.

Antenna (n = 3): Length/width of pedicel 36–49/63–76 µm.

Length/width of flagellomeres (µm): 66–107/24–27, 37–50/21–26, 29–43/24, 24–31/21–26, 24–31/26–31, 21–36/26–33, 76–92/26–29. AR 0.24–0.44. Scape without setae. Pedicel with 1–3 setae. Flagellomeres 1–6 respectively with setae: 2–5, 2–5, 2–3, 0–2, 2–3, 2–3. Ultimate flagellomere with 2–3 strong setae and 1–2 weak apical setae. Longest antennal seta 52–56 µm.

Head (Fig. 4.2): Coronal suture complete, 73–164 µm long. Frontal sensilla 143–154 apart, situated 56–69 µm from apex of frontal protrusion. Temporal setae 20–24, including 6–8 postorbitals, 13–15 verticals, 0–3 orbitals, and 1–2 frontal setae. Clypeus length/width 52–76/93–147 µm, with 3–4 setae. Length/width of palpal segments (µm): 16–41/26–38, 34–62/33–48, 63–100/36–43, 71–93/29–41, 105–150/26–42. Palpal stoutness 1.82–3.04.

Thorax (Fig. 4.1): Antepronotum not reaching scutal projection, with 7–15 lateral setae. Dorsocentrals 7–12, acrostichals absent, prealars 2–5; epimeron II with 0–2 very weak setae, preepisternum II without setae. Scutellars 10–18.

Wing (Fig. 4.3): VR 0.94–0.99. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 2–5 weak setae distally, R with 8–11 setae, R_1 with 8–12, R_{4+5} with 5–9 setae. Alula without setae. Squama with 19–26 setae. Subcosta with 1–3 sensilla campaniformia, R_1 with 3–4, R_{2+3} with 1–3, R_{4+5} with 1–3 sensilla campaniformia.

Legs: Spur of front tibia 29–38 µm long, spurs of middle tibia 36–40 µm and 31–38 µm, spurs of hind tibia 60–101 µm and 31–64 µm long. Width at apex of front tibia 47–64 µm, of middle tibia 50–68 µm, of hind tibia 66–131 µm. Comb on hind tibia with 14–20 setae, longest seta 47–79 µm, shortest seta 26–53 µm long. Each leg with 2 apical speudospurs (particularly weak on ta_3) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 2–9, 0–2, 0 on p_2; 5–15, 2–6, 0–1 on p_3. Sensilla chaetica 36–67 distributed from 0.14–0.18 to 0.63–0.72 of posterior ta_1. Pulvilli small.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	949–1187	975–1283	663–840	322–404	170–233	63–83	89–120
p_2	918–1289	988–1264	396–490	228–269	142–173	68–77	89–115
p_3	1040–1410	1066–1354	708–879	401–475	194–250	73–96	92–134

	LR	BV	SV	BR
p_1	0.59–0.65	3.42–4.10	2.90–3.72	1.2–1.6
p_2	0.40–0.43	4.50–4.71	4.48–5.15	1.4–1.6
p_3	0.61–0.67	3.68–4.54	2.95–3.33	1.3–1.8

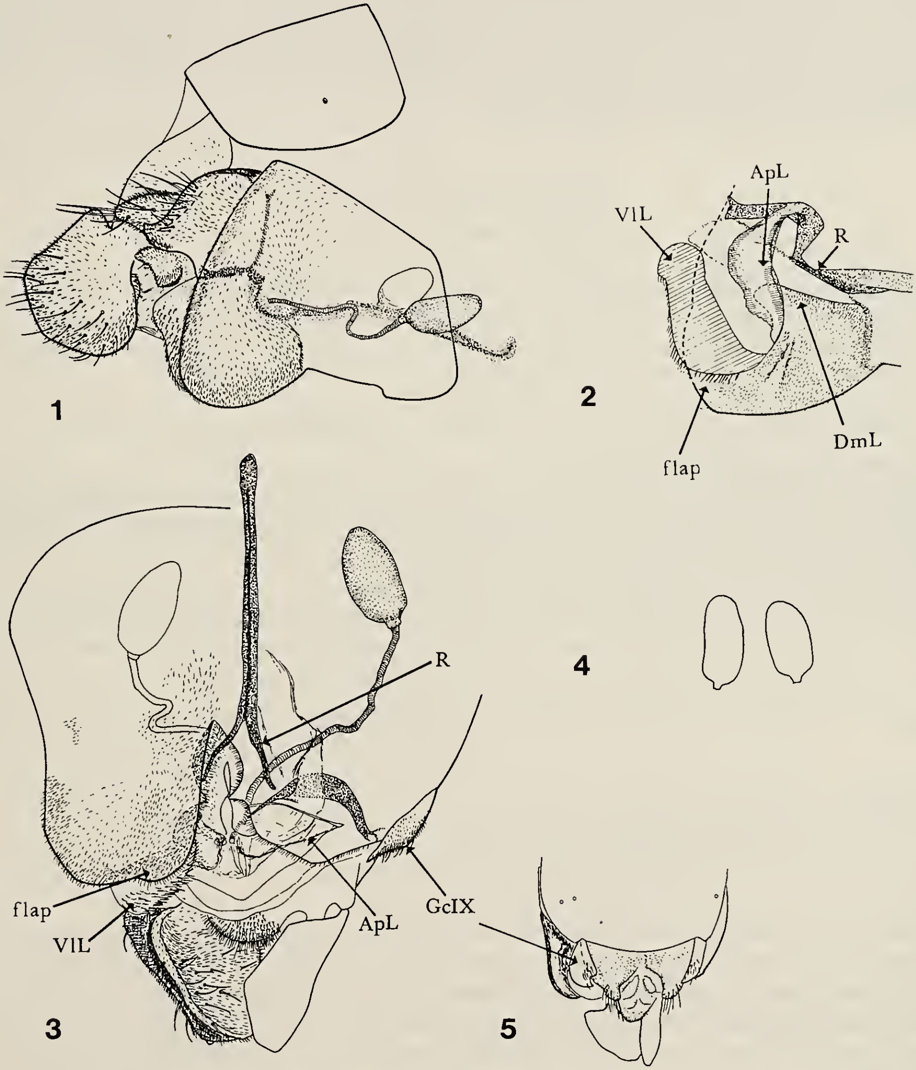

Fig. 5. *D. serratosioi* spec. nov., female genitalia. 5.1 lateral aspect, 5.2 sagittal section of genital atrium, 5.3 ventral aspect, 5.4 variation of seminal capsules, 5.5 dorsal aspect (ApL = apodeme lobe, DmL = dorsomesal lobe, Gc IX = gonocoxite IX, VlL = venrolateral lobe).

Genitalia (Fig. 5): Sternum VIII with 0–1 setae on each side. Gonocoxapodeme inconspicuous. Apodeme lobe with scattered microtrichia. Seminal capsules ovoid to oblong with short neck, punctuation of surface visible at 375X magnification. Gonocoxite with sigmoid dorsal margin, with 12–20 setae about 30–45 µm long. Protrusion of tergite IX knob-like to weakly digitiform, with 9–12 setae about 50 µm long. Segment X weak, slightly protruding posteriad (ventral view). Cerci trapezoid with ventrolateral knee-like protrusion (may be difficult to detect in small individuals).

Remarks

Males of *D. serratosioi, D. amplexivirilia,* and *D. lupus* can be separated by the diagnostic characters given for each of them. Female *D. lupus* has a well-developed dorsal projection on the cercus and so is distinct from *D. serratosioi.* Female *D. amplexivirilia* is unknown. The pupal exuvium described by Pagast (1947) probably belonged to *D. serratosioi* (as *Diamesa spec.* VI). As noted by Pagast, the thorns on the tergites are reduced and have a much lighter coloration when compared to *D. saetheri* (which he described as *D. davisi).* Males of *D. serratosioi* from Norway and Sweden were previously described as *D. davisi* by Serra-Tosio (1971).

Diamesa saetheri spec nov.

(Figs. 1.7–9, 4.4–6, 6, 7)

Diamesa davisi auct., nec Edwards 1933. Pagast 1947: 477–478, 525–526, figs. 37, 79 (description of male adult and pupa from Sweden). Saether 1968: 430, 440, 441–445, 448 (description of male adult, pupa, and larva from Finse, Norway). Makarchenko 1980: 80–83, tabs. 1–2, figs. 1–2 (description of male adults from Siberia). Doughman 1983: 25, fig 17B–C, 34 (description of larva).

nec *Diamesa davisi* sensu Saether 1968: fig. 17B (female, figured seminal capsule).

nec *Diamesa hyperborea* Holmgren 1869. Pagast 1947: 573 (as possible synonym of *D. davisi).*

Type area: W. Norway, Hordaland, Finse.

Type material: Holotype male, Z. M. Bergen Type no. 82; Finse, Blåisen, 13–8 1980, leg E. Willassen. Paratypes (and allotype): 15 males, 4 females, 2 pupae reared from larvae; same loc. and date as holotype. Finse near Blåisen, 9–10 1979, leg. P. Ottesen, 1 brachypterous female. Mjölkedöla, Jotunheimen, 12–8 1981, leg. G. A. Halvorsen, 1 intersex reared from pupa, 1 male with damaged hypopygium.

Diagnosis: The male is characterized by having Y-shaped tergal bands, a gently rounded posterior margin of tergite IX, reduced anal point, moderately extended laterosternites with minute setae, massive gonocoxites, and weakly curved gonostyli. See remarks for the female.

Etymology: The species is named after professor Ole A. Saether, Bergen, who previously studied the population at Finse.

Description

Male imago (n = 10 unless otherwise stated)

Total length 4.03–5.03 mm. Wing length/width 2.64–3.06/0.87–1.18 (n = 8) mm. Total length/wing length 1.32–1.91. Wing length/length of profemur 1.59–2.02.

Antenna: Length/width of pedicel 42–54/78–90 µm. Length/width of flagellomeres (µm): 105–131/31–42, 39–57/29–37, 31–45/29–36, 26–38/29–35, 24–39/30–36, 22–33/31–37, 31–43/37–45, 85–123/39–45. AR 0.24–0.34. Adjacent flagellomeres often partially fused. Scape and pedicel usually without setae. Flagellomeres 1–7 respectively with setae: 3–8, 1–3, 1–4, 0–2, 1–2, 1–2, 3–6. Ultimate flagellomere with 1–5 strong setae and 1–2 weak apical setae. Longest antennal seta 60–79 µm long.

Head: Coronal suture weak, reaching frontal sensilla or completely reduced. Frontal sensilla 147–174 µm apart, situated 50–62 µm from apex of frontal protrusion. Temporal setae 13–21, including 2–6 postorbitals, 9–15 verticals, and 0–1 orbitals; frontal setae absent. Clypeus length/width

73–97/123–174 µm, with 2–4 setae. Length/width of palpal segments (µm): 29–45/32–54, 39–58/47–58, 89–116/39–54, 67–90/37–57, 94–126/31–39. Palpal stoutness 1.74–2.00.

Thorax: Antepronotum reaching or almost reaching scutal projection, with 9–18 lateral setae. Dorsocentrals 7–14, acrostichals absent, prealars 3–6; epimeron II with 0–4 weak setae, preepisternum II without setae.

Wing: VR 0.89–0.99. Microtrichia of wing membrane visible at 40–100X magnification. Brachiolum with 2–4 weak setae distally and 1 strong seta basally; R with 4–9 setae, R_1 with 4–9, R_{4+5} with 6–12 setae. Alula without setae. Squama with 14–24 setae. Subcosta with 1–4 sensilla campaniformia, R_1 with 1–4, R_{2+3} with 1–2, R_{4+5} with 1–7 sensilla campaniformia.

Legs: Spur of front tibia 31–42 µm long, spurs of middle tibia 39–47 µm and 35–45 µm, spurs of hind tibia 52–72 µm and 28–42 µm long; spur of front tibia occasionally bifid. Width at apex of front tibia 76–99 µm, of middle tibia 79–110 µm, of hind tibia 94–126 µm. Comb on hind tibia with 16–25 setae, longest seta 52–66 µm, shortest seta 29–49 µm long (n = 8). Each leg with 2 apical pseudospurs (often weak) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 5–16, 0–6, 0–2 on p_2; 11–33, 2–10, 0–2 on p_3. Sensilla chaetica 1–41 distributed from 0.14–0.74 to 0.72–0.75 of posterior ta_1. ta_5 slightly enlarged distally. Claws of posttarsus pointed with 1–2 serrations. Pulvilli small.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	1456–1690	1508–1768	910–1207	396–520	186–285	68–100	110–131
p_2	1625–1859	1352–1625	598– 741	264–343	148–201	79– 92	100–136
p_3	1625–1976	1521–1859	884–1066	433–611	211–275	84–102	115–136

	LR	BV	SV	BR
p_1	0.57–0.67	4.24–5.20	2.86–3.55	1.2–1.6
p_2	0.42–0.47	5.47–6.36	4.44–5.36	1.1–1.5
p_3	0.54–0.63	4.37–5.12	3.27–3.97	1.2–2.3

Hypopygium (Figs. 1.7–9): Tergite IX with weak setae along posterior margin, margin gently rounded, tergal bands roughly Y-shaped; anal point not visible in dorsal view. Laterosternite well produced beyond posterior margin of tergite IX, obliquely truncate on medial margin, and bearing very short setae; length ratio of laterosternite to gonocoxite (n = 15) 0.65–0.73, mean value 0.69. Gonocoxite massive, inner side densely covered with microtrichia and short setae, volsella with setae and microtrichia. Gonostylus weakly curved with 3–5 apical teeth and subterminal peg. HR 1.40–2.11. HV 1.46–2.00.

Female imago (n = 5 unless otherwise stated)

Total length 4.23–4.42 mm. Wing length/width 0.53–3.35/0.3–1.26 mm. Total length/wing length 1.38–7.93. Wing length/length of profemur 0.59–2.87.

Antenna (Fig. 4.6): Length/width of pedicel 40–71/73–88 µm. Length/width of flagellomeres (µm): 96–188/31–36, 37–83/28–31, 34–72/28–31, 29–56/28–33, 30–53/29–38, 32–59/36–38, 85–196/37–43. AR 0.22–0.30. Scape and pedicel without setae. Flagellomeres 1–6 respectively with setae: 2–7, 1–3, 1–3, 1–2, 2–3, 3–4. Ultimate flagellomere with 3–5 strong setae and 2 weak apical setae. Longest antennal seta 52–117 µm.

Head (Fig. 4.6): Coronal suture and triangle faint or completely reduced. Frontal sensilla 137–173 µm apart, situated 49–57 µm from apex of poorly developed frontal protrusions. Temporal setae 19–24, including 5–7 postorbitals, 10–15 verticals, 0–4 orbitals; frontal setae absent. Clypeus length/width 75–133/97–177 µm, with 4–6 setae; labrum well sclerotized. Length/width of palpal segments (µm): 27–38/33–48, 34–52/40–45, 69–100/47–53, 53–79/36–45, 82–114/29–39. Palpal stoutness 1.47–2.16. Palpal segment 1 occasionally with 1 seta.

Thorax (Fig. 4.5): In brachypterous individuals modified and very weakly sclerotized. In macropterous individuals more like in Fig. 4.1. Antepronotals 8–14. Dorsocentrals 11–13, acrostichals absent,

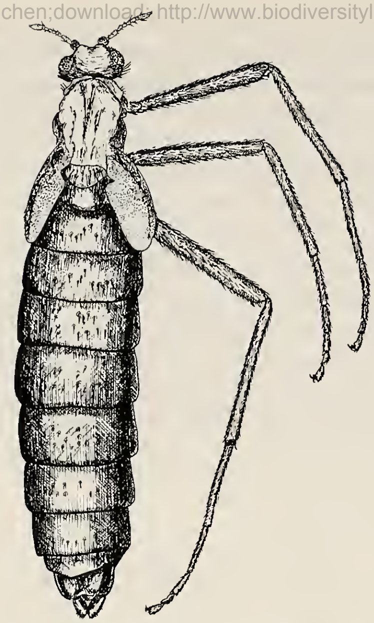

Fig. 6. *D. saetheri* spec. nov., brachypterous female.

prealars 3–8; epimeron II with 0–2 weak setae, preepisternum II without setae. Scutellars 22–36.

Wing (Fig. 4.4): General outline as in Fig. 4.3 or strongly reduced. VR (n = 2) 0.94. Reduced wing with ill defined vein pattern. Microtrichia of normal wing membrane visible at about 100X magnification, reduced wing very densely covered over entire surface. Brachiolum with 2–3 setae distally, R with 5–7 setae, R_1 with 6–11, R_{4+5} with 6–15 setae. Alula without setae. Squama with 22–26 setae, in brachypterous individual only 1 seta. Subcosta with 2 sensilla campaniformia, R_1 with 2–3, R_{2+3} with 2, R_{4+5} with 2–4 sensilla campaniformia. Reduced wing nearly devoid of marginal setae.

Legs: Spur of front tibia 29–33 μm long, spurs of middle tibia 34–45 μm and 32–39 μm, spurs of hind tibia 67–83 μm and 31–45 μm long. Comb on hind tibia with 20–23 setae, longest seta 47–68 μm, shortest seta 30–32 μm long. Width at apex of front tibia 56–93 μm, of middle tibia 58–79 μm, of hind tibia 86–106 μm. Each leg with 2 apical pseudospurs (may be very weak) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 8–13, 1–3, 0–2 (n = 3) on p_2; 19–26, 6–9, 0–4 (n = 4) on p_3. Sensilla chaetica 54–61 distributed from 0.16–0.17 to 0.73–0.77 of posterior ta_1 in macropterous individuals (n = 4), in brachypterous individual (n = 1) 11 sensilla chaetica distributed from 0.27 to 0.69. ta_5 slightly enlarged distally. Pulvilli small.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	897–1313	897–1365	544–871	269–422	162–238	85–100	104–127
p_2	923–1259	806–1300	333–547	190–284	131–192	77– 96	100–125
p_3	1131–1560	1114–1473	591–903	343–578	170–365	84–106	104–144

	LR	BV	SV	BR
p_1	0.61–0.65	3.75–4.12	2.91–3.30	1.2–2.2
p_2	0.40–0.46	4.54–5.16	4.58–5.19	1.2–2.2
p_3	0.57–0.61	3.36–4.17	3.21–3.63	1.0–1.8

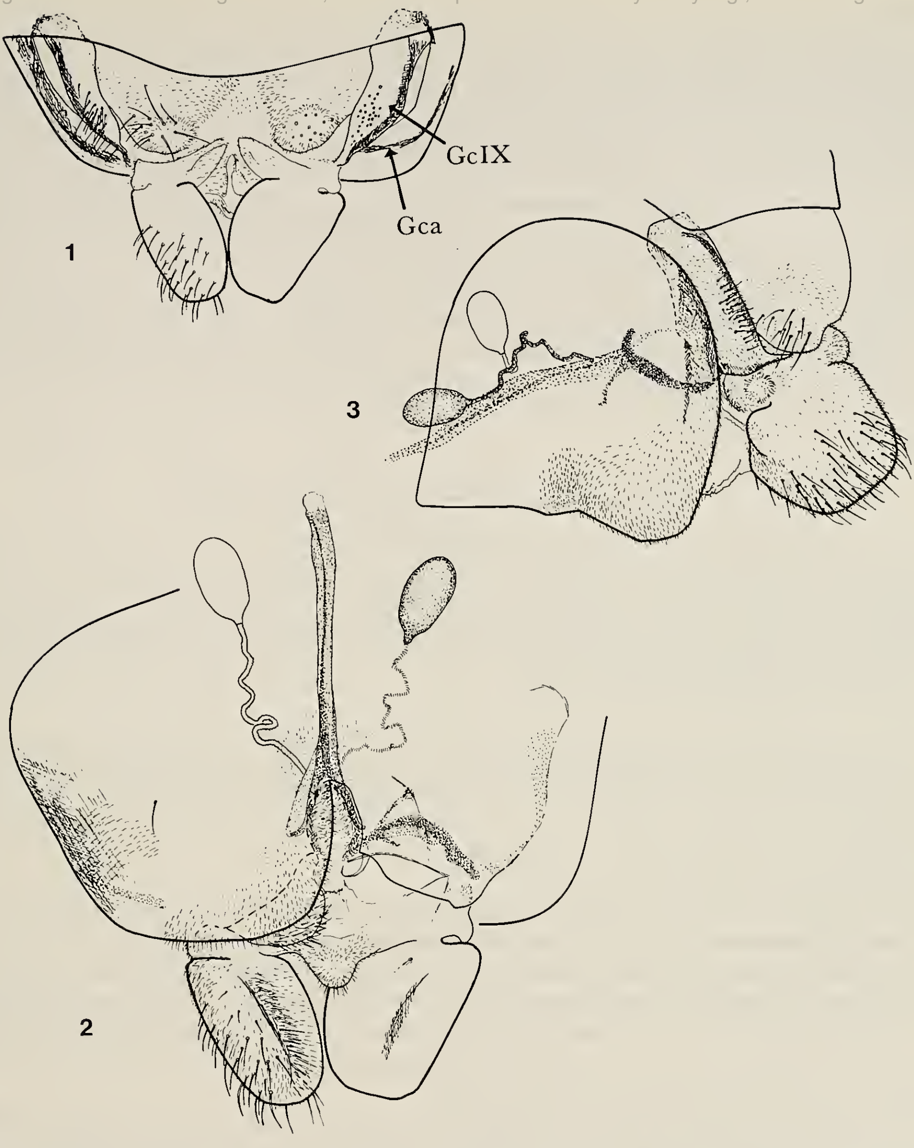

Fig. 7. *D. saetheri* spec. nov., female genitalia. 7.1 dorsal aspect, 7.2 ventral aspect, 7.3 lateral aspect (Gca = gonocoxapodeme).

Genitalia (Fig. 7): Sternum VIII with 0–1 setae on each side. Gonocoxapodeme weak. Apodeme lobe with scattered microtrichia. Seminal capsules ovoid, slightly narrowed posteriad, with short but distinct neck; punctuation of surface visible at 500X magnification; length/width 81–89/39–45 µm. Spermathecal ducts winded with indistinct openings. Gonocoxite IX strongly sclerotized except at caudal apex, dorsal margin slightly protruding laterad, with 23–34 short setae (about 30–75 µm long). Tergite IX with 9–16 setae on each protrusion. Segment X slightly protruding posteriad (ventral view). Cerci trapezoid to rounded with conspicuous kneelike ventrolateral protrusion.

Remarks

PAGAST's (1947) description of *D. davisi* from Swedish Lapland presumably refers to *D. saetheri* but he figured the hypopygium in a lateral position. Pagast also examined pupae collected at Finse and identified these to *D. davisi*. SAETHER (1968: fig. 17) figured the male hypopygium in a distorted mount. *D. saetheri* obviously is the same species as described by MAKARCHENKO (1980) as *D. davisi*. MAKARCHENKO (1980: fig. 1b) also reported wing reduction in males of *D. saetheri*. Wing reduction in an even more drastic form is here demonstrated in a female specimen. Morphological modifications accompanying wing reduction, such as the altered shape and weaker sclerotization of the thorax, have recently been discussed by SERRA-TOSIO (1974) and HANSEN and COOK (1976) in studies of *D. steinboecki* Goetghebuer and *D. leona* Roback. One new observation is that the number of tarsal sensilla chaetica is drastically reduced in brachypterous females. I have observed this in specimens of *D. steinboecki* as well. The phenomenon might be a pleiotropic effect. An unusually high number of sensilla chaetica was found in two males of the material. This was probably caused by mermithid (Nematoda) parasitism (SAETHER and GALLOWAY 1980), as infected larvae were found at the site.

Diamesa alpina Tokunaga sensu Makarchenko

(Fig. 2.1)

?*Diamesa alpina* Tokunaga 1936: 539–542, figs. 5, 6, 11, 20–23, 32 (description of male, female and pupa from Japan).

Diamesa alpina Tokunaga. MAKARCHENKO 1980: 82–86, tab. 3, fig 3 (description of male imagines from Koryakskiy Range and Kamchatka Peninsula, USSR).

nec. *Diamesa alpina* (Goetghebuer). Sec. junior homonym.

Diagnosis: The male is characterized by having U-shaped tergal bands, anal point visible in dorsal view, and laterosternites extending beyond posterior margin of tergite IX. See remarks for the female.

Description

Male imago (n = 6 unless otherwise stated)

Total length (n = 5) 2.82–4.04 mm. Wing length/width 2.14–3.23/0.81–1.15 mm. Total length/wing length (n = 5) 1.20–1.31. Wing length/length of profemur 1.67–1.96.

Antenna (n = 4): Length/width of pedicel 39–48/69–84 µm. Length/width of flagellomeres (µm): 96–114/30–42, 39–48/25–33, 27–39/26–36, 27–39/27–36, 27–36/30–38, 24–36/30–38, 36–51/36–42, 111–135/39–45. AR 0.35–0.38. Scape without setae. Pedicel with 0–2 setae. Flagellomeres 1–7 respectively with setae: 5, 3, 2–3, 0–1, 1–2, 1–2, 5–6. Ultimate flagellomere with 3–4 strong setae and 2 weak apical setae. Longest antennal seta 72–90 µm long.

Head: Coronal suture complete or incomplete, 133–249 µm long. Frontal sensilla 132–190 µm apart, situated 48–86 µm from apex of frontal protrusion. Temporal setae 21–26, including 7–8 postorbitals, 13–18 verticals, 1–2 orbitals, and 0–1 frontal setae. Clypeus length/width 76–95/99–167 µm, with 2–3 setae. Length/width of palpal segments (µm) (n = 2): 24–38/30–38, 51–62/39–48, 90–110/45–52, 75–95/36–43, 105–133/35–39. Palpal stoutness 2.02–2.25.

Thorax: Antepronotum not reaching or just reaching scutal projection, with 7–14 lateral setae. Dorsocentrals 6–8, acrostichals absent, prealars 3–5; epimeron II with 0–2 weak setae, preepisternum II without setae. Scutellars 20–26.

Wing: VR 0.90–0.99. R_{2+3} occasionally fused with R_{4+5}. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 1–3 setae distally, occasionally 1 seta medially, and 1 strong seta basally; R with 4–10 setae, R_1 with 4–7, R_{4+5} with 4–13 setae. Alula without setae. Squama with 11–23 setae. Subcosta with 2 sensilla campaniformia, R_1 with 2–4, R_{2+3} with 1–2, R_{4+5} with 2–4 sensilla campaniformia.

Legs: Spur of front tibia 23–57 μm long, spurs of midle tibia 38–45 μm and 30–43 μm, spurs of hind tibia 56–76 μm and 30–43 μm long. Width at apex of front tibia 56–81 μm, of middle tibia 53–94 μm, of hind tibia 71–110 μm. Comb on hind tibia with 17–21 setae, longest seta 41–67 μm, shortest seta 26–48 μm long. Each leg with 2 apical pseudospurs (may be weak) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 7–9, 1–3, 0–2 on p_2; 12–23, 1–8, 0–2 on p_3. Sensilla chaetica 2–7 distributed from 0.26–0.76 to 0.71–0.82 of posterior ta_1. Claws of posttarsus pointed with 0–3 serrations. Pulvilli small.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	1093–1932	1164–1872	750–1117	354–523	203–314	83–120	102–135
p_2	1164–2053	1045–1750	510– 755	245–363	150–238	83–120	102–132
p_3	1259–2174	1235–2083	760–1208	413–634	215–315	87–131	113–145

	LR	BV	SV	BR
p_1	0.60–0.64	3.96–4.60	3.01–3.41	1.1–1.4
p_2	0.43–0.49	4.69–5.73	4.33–5.03	1.1–1.5
p_3	0.60–0.64	3.93–4.50	3.28–3.52	1.2–1.5

Hypopygium (Fig. 2.1): Tergite IX with weak setae along margin, posterior margin partly straight to slightly rounded; tergal bands broad and distinctly U-shaped; anal point usually visible in dorsal view. Laterosternite extending beyond posterior margin of tergite IX, with weak setae; length ratio of laterosternite to gonocoxite 0.57–0.62. Volsella with microtrichia, with or without setae. Gonostylus weakly curved with 3–4 apical teeth and subterminal peg. (According to MAKARCHENKO [1980], a peg may be missing.) HR 1.79–2.04. HV 1.53–1.78.

Remarks

This species obviously is very similar to *D. davisi.* My material originates from Glacier Bay, Alaska, and the male hypopygia of these specimens show the same characteristics as those described by MAKARCHENKO (1980). The typical U-shape of the tergal bands apparently separates this species from *D. davisi.*

Provided that *D. alpina* in the sense of Makarchenko corresponds to *D. alpina* Tokunaga, this is the first record of this species from N. America. The female of *D. alpina* described by TOKUNAGA (1936) shows no indication of projections on the cercus. *Syndiamesa alpina* Goetghebuer (1941), a species described from the Alps, is listed by THIENEMANN (1954) and FITTKAU and REISS (1978) as *D. alpina.* The transfer of this taxon to *Diamesa* probably can be traced back to JANETSCHEK (1949). (Reference not seen by author.)

Material studied

Alaska, Glacier Bay, Nunatak Creek, 12. 8. 1979, 2 males; Wolf Creek 13. 8. 1979, 4 males, A. Milner leg. In coll. British Museum (Nat. Hist.).

Diamesa sonorae spec. nov.
(Fig. 2.2)

Diamesa davisi Hansen and Cook 1976: 81–85, *pro parte, nec* EDWARDS 1933.

Type area: California, Sonora Pass.

Type material: Holotype male, Mono Co., Calif., nr. Sonora Pass, Elev. 8500', 18-VII-68, R. A. Hellenthal. Paratypes, 2 females, same labelling as holotype. Types in coll. Dr. J. E. Sublette, Univ. S. Colorado, Pueblo, Colorado.

Diagnosis: The male is characterized by having U-shaped tergal bands and laterosternites not surpassing tergite IX caudally. Confer remarks for the female.

Etymology: The name refers to the collection site, Sonora Pass.

Description

Male imago (n = 1)

Total length not measurable. Wing length/width 2.00/0.71 mm. Wing length/length of profemur 1.71.

Antenna: Length/width of pedicel 36/63 µm. Length/width of flagellomeres (µm): 96/21, 42/23, 30/24, 24/24, 24/24, 21/24, 30/30, 93/45. AR 0.34. Scape and pedicel without setae. Flagellomeres 1–7 respectively with setae: 4, 2, 2, 0, 1, 0, 3. Ultimate flagellomere with 2 strong setae and 2 weak apical setae. Longest antennal seta 66 µm.

Head: Coronal suture complete, 148 µm long. Frontal sensilla 124 µm apart, situated 38 µm from apex of frontal protrusion. Temporal setae 17, including 8 postorbitals, 8 verticals, 0 orbitals, and 1 frontal seta. Clypeus without setae, length/width of clypeus 60/150 µm. Length/width of palpal segments (µm): 21/30, 42/27, 78/39, 69/33, 150/30. Palpal stoutness 2.30.

Thorax: Antepronotum just reaching scutal projection, with 5–6 lateral setae. Dorsocentrals 4–5, acrostichals absent, prealars 2, epimeron II with 2 setae, preepisternum II with 1 seta. Scutellars not countable.

Wing: VR 0.97. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 1 seta distally, R with 4 setae, R_1 with 6, R_{4+5} with 5 setae. Alula without setae. Squama with 12 setae. Subcosta with 2 sensilla campaniformia, R_1 with 1, R_{2+3} with 1, R_{4+5} with 2 sensilla campaniformia.

Legs: Spur of front tibia 38 µm long, spurs of middle tibia 38 µm and 30 µm, spurs of hind tibia 59 µm and 31 µm long. Width at apex of front tibia 45 µm, of middle tibia 60 µm, of hind tibia 62 µm. Comb on hind tibia with 12 setae 48 µm to 31 µm long. Each leg with 2 apical pseudospurs on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 7, 1, 0, on p_2; 8, 3, 0 on p_3. Sensilla chaetica 5 distributed from 0.62 to 0.71 of posterior ta_1. Claws on posttarsus not serrated. Pulvilli visible at 300X magnification.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	1164	1140	760	374	207	75	102	0.67	4.04	3.03	1.5
p_2	1116	1021	452	218	135	72	102	0.44	4.91	4.74	1.4
p_3	1235	1188	760	390	207	79	109	0.64	4.05	3.19	1.8

Hypopygium (Fig. 2.2): Tergite IX with a few very weak setae. Tergal band U-shaped. Anal point well developed, directed anteriad under tergite. Laterosternite not surpassing tergite IX in length, posterior margin parallel to margin of tergite, with very weak setae; length ratio of laterosternite to gonocoxite 0.50. Volsella with setae and microtrichia. Gonostylus only slightly curved, lateral margin almost straight; with 2 small apical teeth and subterminal peg. HR 2.19. HV not measurable.

Female imago (n = 2 unless otherwise stated)

Total length 3.26–3.62 mm. Wing length/width 2.54–3.23/0.94–1.09 mm. Total length/wing length 1.12–1.29. Wing length/length of profemur 2.37–2.41.

Antenna: Length/width (n = 1) of pedicel 45/78 µm. Length/width of flagellomeres (µm) (n = 1): 117/30, 48/27, 39/30, 30/29, 33/30, 39/36, 93/42. AR 0.31–0.38. Scape and pedicel without setae. Flagellomeres 1–6 respectively with setae: 4–5, 3–5, 1–2, 0–2, 1–2, 2–4. Ultimate flagellomere with 3–4 strong setae and 2 weak apical setae. Longest antennal seta 54–57 µm long.

Head: Coronal suture complete or incomplete, 114–129 μm long. Temporal setae 15–20, including 6 postorbitals, 5–10 verticals, 1–3 orbitals, and 1 frontal seta. Clypeus with 2–3 setae, length/width of clypeus 63–81/120–156 μm. Length/width of palpal segments (μm): 14–29/30–38, 57–67/33–38, 90–105/42–48, 76–81/30–33, 114–138/30–43. Palpal stoutness 2.41–2.50.

Thorax: Antepronotum nearly reaching scutal projection, with 7–9 lateral setae. Dorsocentrals 5–7, acrostichals absent, prealars 3–6, epimeron II with 1 seta, preepisternum II with 1 setae. Scutellars 21–32.

Wing: VR 0.94–0.96. Microtrichia of wing membrane visible at about 100X magnification. Brachiolum with 3–4 setae, R with 4–9 setae, R_1 with 4?–13, R_{4+5} with 8–12 setae. Alula without setae. Squama with 20–23 setae.

Subcosta with 2 sensilla campaniformia, R_1 with 2 (n = 1), R_{2+3} with 1, R_{4+5} with 2–3 sensilla campaniformia.

Legs: Spur of front tibia 29–33 μm long, spurs of middle tibia 43 μm and 33 μm, spurs of hind tibia 57–71 μm and 39–43 μm long. Width at apex of front tibia 57–62 μm, of middle tibia 57–71 μm, of hind tibia 78–100 μm. Comb on hind tibia with 16–19 setae 33–24 (n = 1) μm long. Each leg with 2 weak apical pseudospurs on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 6–8, 0–1, 0 on p_2; 11–22, 4–8, 0–1 on p_3. Sensilla chaetica 73–83 distributed from 0.14–0.17 to 0.75 of posterior ta_1. Pulvilli visible at about 250X magnification.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4
p_1	1154–1358	1090–1449	763– 957	351–460	200–252	76–95
p_2	1087–1389	1026–1268	467– 574	229–279	148–194	67–85
p_3	1208–1509	1177–1540	815–1042	452–581	219–279	76–85

	ta_5	LR	BV	SV	BR
p_1	105–129	0.66–0.70	3.97–4.02	2.81–2.93	1.7–2.0
p_2	95–109	0.45–0.46	4.79–4.85	4.52–4.63	1.6–1.8
p_3	110–133	0.68–0.69	3.73–3.79	2.93	1.2

Genitalia: Sternum VIII with 0–1 setae on each side. Gonocoxapodeme weak. Seminal capsules slightly narrowed anteriad with weak neck; punctuation of surface visible at 500X magnification; length/width 67–84/38–39 μm. Spermathecal ducts winded. Gonocoxite IX apparently fused with protrusion of tergite IX, with 8–18 setae. Tergite IX with 5 setae on each protrusion. Segment X and cerci as in *D. davisi.*

Remarks

D. sonorae shares an apomorphy with *D. alpina* in the U-shaped tergal bands of the male hypopygium. Another common feature is the relatively well developed anal point (this may be reduced occasionally). The female is not distinct from *D. davisi.*

Diamesa lupus spec. nov.
(Figs. 2.3–4.8)

Type area: Alaska, Glacier Bay, Wolf Creek.

Type material: Holotype male, Z. M. Bergen Type no. 83; Alaska: Glacier Bay, Wolf Creek, 12-VII-1979, S. Milner. Paratypes, 11 males, same labelling as holotype; Wolf Creek, Glacier Bay, National Monument, August 1980: 2 females, 1 female reared from pupa, 3 females reared from larva. Canada: Jasper-Banff area, 13. 9. 1957 L. Brundin, 10 males.

Holotype and 13 paratypes in Mus. Zool. Bergen, remaining paratypes in Brit. Mus. (Nat. Hist.), London.

Diagnosis: The male is characterized by Y-shaped tergal bands, a partly straight posterior margin of the tergite IX, reduced anal point; very extended laterosternites, divided into two parts by curved apodeme. Confer remarks for the female.

Etymology: The epithet is standing in apposition to the generic name and thus takes the meaning of: the wolf (associated with Wolf Creek) (from Latin lupus, wolf).

Description

Male imago (n = 10 unless otherwise stated)

Total length (n = 8) 2.20–3.84 mm. Wing length/width (n = 9) 1.16–3.14/0.62–1.21 mm. Total length/wing length 1.08–1.37. Wing length/length of profemur 1.83–2.05.

Antenna (n = 8): Length/width of pedicel 33–45/51–81 µm. Length/width of flagellomeres (µm): 69–111/24–42, 33–54/21–39, 27–39/21–33, 24–30/21–36, 21–30/21–36, 18–33/24–36, 27–42/27–42, 90–129/33–51. AR 0.35–0.43. Scape without setae. Pedicel usually without setae, occasionally with 2 (n = 1) setae. Flagellomeres 1–7 respectively with setae: 4–5, 2–5, 1–2, 0–2, 1–2, 0–2, 4–6. Ultimate flagellomere with 3–4 strong setae and 2 weak apical setae. Longest antennal seta 51–96 µm long.

Head: Coronal suture complete or incomplete, 78–190 µm long. Frontal sensilla 128–162 µm apart, situated 36–67 µm from apex of frontal protrusion. Temporal setae 15–28, including 4–10 postorbitals, 8–15 verticals, 0–2 orbitals, and 0–5 frontal setae. Clypeus length/width 57–114/110–180 µm, with 2–4 setae. Length/width of palpal segments (µm) (n = 6): 21–36/24–42, 45–57/27–42, 63–114/30–51, 75–96/27–48, 90–150/30–42. Palpal stoutness 2.28–2.53. Palpal segment 1 occasionally with 1 seta.

Thorax: Antepronotum not reaching or just reaching scutal projection, with 5–12 lateral and occasionally 1 dorsal setae. Dorsocentrals 5–8, acrostichals absent, prealars 1–4; epimeron II with 1–3 setae, preepisternum II without setae. Scutellars 11–21.

Wing: VR 0.93–0.99. R_{2+3} occasionally fused with R_{4+5}. Microtrichia of wing membrane visible at 50–100× magnification. Brachiolum with 1–3 setae distally, 0–1 medially, and 1 strong seta basally; R

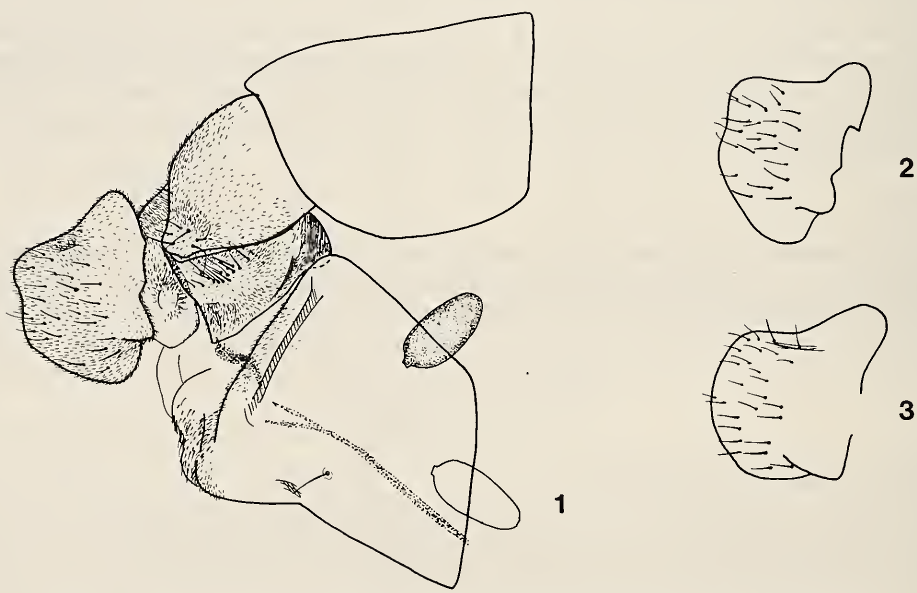

Fig. 8. *D. lupus* spec. nov., female genitalia. 8.1 lateral aspect, 8.2–3 variation of cerci.

(n = 9) with 0–7 setae, R_1 with 6–12, R_{4+5} with 3–7 setae. Alula without setae. Squama with 12–29 setae. Subcosta with 2–3 sensilla campaniformia, R_1 with 2–4, R_{2+3} with 1, R_{4+5} with 1–4 sensilla campaniformia.

Legs: Spur of front tibia 24–49 μm long, spurs of middle tibia 21–48 μm and 16–43 μm, spurs of hind tibia 33–76 μm and 24–43 μm long. Width at apex of front tibia 45–72 μm, of middle tibia 38–72 μm, of hind tibia 52–95 μm. Comb on hind tibia with 12–19 setae, longest seta 28–64 μm, shortest seta 24–41 μm long. Each leg with 2 apical pseudospurs (often very weak) on ta_{1-3} respectively. Preapical pseudospurs on ta_{1-3} respectively: 0, 0, 0 on p_1; 4–10, 0–4, 0–3 on p_2; 9–22, 4–6, 0–2 on p_3. Sensilla chaetica (n = 5) 3–6 distributed from 0.60–0.75 to 0.68–0.80 of posterior ta_1. Claws of posttarsus pointed with 1–3 very weak serrations. Pulvilli visible at about 300× magnification.

Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
p_1	751–1720	787–1690	545–1026	244–521	147–303	57–119	90–135
p_2	760–1811	694–1636	324– 760	162–373	113–230	53– 98	71–129
p_3	854–1932	826–1781	518–1116	278–594	139–310	53–110	71–139

	LR	BV	SV	BR
p_1	0.60–0.69	3.71–4.23	2.82–3.33	1.1–1.7
p_2	0.46–0.50	4.30–5.04	4.22–4.64	1.1–1.4
p_3	0.61–0.66	3.57–4.28	3.07–3.39	1.2–1.7

Hypopygium (Figs. 2.3–4): Tergite with posterior margin gently rounded to partly straight, tergal bands Y-shaped, anal point apparently completely reduced. Laterosternite very extended, divided into two parts by curved apodeme, ventrocaudal part more weakly sclerotized than rest of hypopygium, with weak setae and microtrichia arranged in groups; length ratio of laterosternite to gonocoxite 0.74–0.90. Volsella with dense microtrichia, apparently without setae. Gonostylus curved, narrowed about 0.5 from base, with 2–5 apical teeth and subterminal peg. HR 1.52–1.89. HV 1.49–1.88.

Female imago

Genitalia (Fig. 8): Gonocoxapodeme weak. Seminal capsules ovoid to conspicuously oblong. Gonocoxite poorly delineated from tergite IX, with 12–19 setae near dorsal margin. Tergite IX with 4–8 setae on each protrusion. Cerci with weakly sclerotized dorsal projection near base and small ventrolateral, kneelike protrusion. Other characters about as in *D. serratosioi.*

Remarks

D. lupus would key out to *D. amplexivirilia* in the key to Nearctic males of *Diamesa* given by HANSEN and COOK (1976). The hypopygium, however, is quite distinct from both *D. davisi* and *D. amplexivirilia.* The female genitalia are most similar to those of *D. serratosioi,* differing in the more developed dorsal projection of the cerci.

D. lupus is presently known only from Glacier Bay, Alaska, and the Jasper-Banff area, Alberta, Canada.

Phenology and temporal variation

In a study of *Diamesa* larvae *(D. valkanovi* Saeth. and *D. saetheri* [as *D. davisi*]) in a glacier brook at Finse, Norway, SAETHER (1968) found that larvae in the upper reaches needed two years to reach full maturity, whereas larvae further downstream completed their life cycle in only one year. The length of the life cycle was regarded as a function of temperature and the duration of the ice free period.

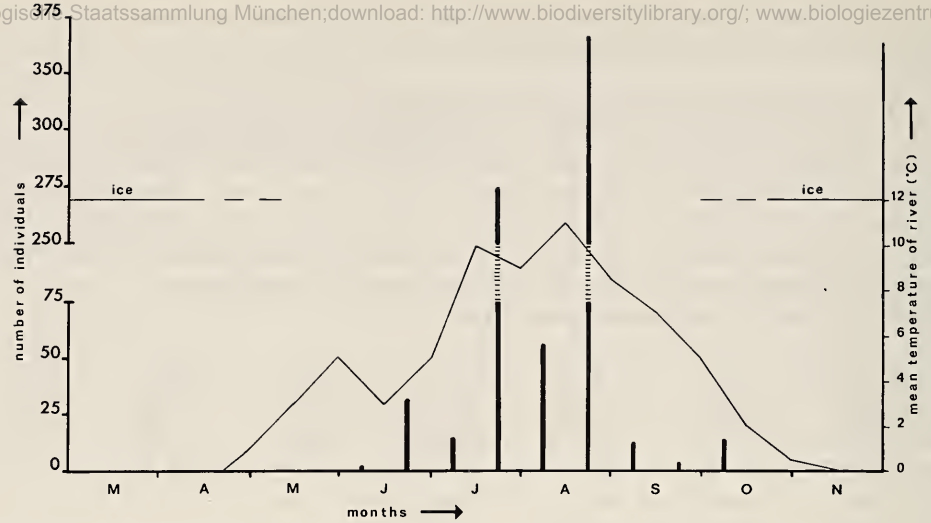

Fig. 9. Light trap catches per week of male *D. serratosioi* spec. nov. (bars) and mean temperature (curve) in the river Ekso at Ekse, W. Norway, 1976.

At Ekse in W. Norway *D. serratosioi* emerges throughout most of the ice free period (perhaps even in winter) and thus exhibits a rather asynchronous eclosion pattern. Figure 9 shows the number of males of this species caught in a light trap at Ekse in 1976. Remembering the limitations of the light trap as a quantitative sampling device, we can still accept the histogram in the figure as a crude reflection of the true emergence pattern of the species at this particular site. When superimposed, the curve for the mean temperature of the river (data from ANDERSEN et al. 1978) shows a fairly good congruence with the emergence pattern. Thus, emergence seems to follow fluctuations of the mean temperature. Moreover, the phase delay between temperature peaks and maxima of catch is longer early in the season than later in the summer. This may reflect a slower development at lower temperatures. Individuals emerging in June most likely represent overwintering larvae with a life cycle of approximately one year. These individuals give rise to a succeeding generation of which the larger part probably emerges the same season.

The duration of life cycles has important implications for taxonomic work. EDMONDSON (1971: 155, with reference to manuscript by COOPER) states: "At colder temperatures animals will remain in the fourth instar and grow larger before pupation." As can be seen from Fig. 10, the body size (measured as the length of the gonocoxite) in males of *D. serratosioi* gradually declines throughout the summer season. This probably is a cumulative effect of temperature. Increased temperature will speed up the metabolic rate in the larvae and thus shorten the time of development. It is perfectly clear, therefore, that caution must be observed when size and size-related characters are used as taxonomical units.

A full analysis of temporal variation is beyond the scope of this study. However, it has been observed that the leg ratio (LR) generally is lower in individuals caught at the beginning of the summer (Tab. I). The leg ratio may to a certain extent be correlated with body size, but according to LINDEBERG (1967) the matter is even more complicated. An instructive study of temporal variation in *Constempellina brevicosta* (Edw.) has been published by GRIMÅS and WIEDERHOLM (1979).

Tab. I: Temporal variation of LR in male *Diamesa serratosioi* spec. nov.

Period	17.–30. 6. (n = 20)		15.–27. 7. (n = 12)		3.–31. 8. (n = 15)	
	$\bar{x}$	range	$\bar{x}$	range	$\bar{x}$	range
p_1	0.60	0.58–0.63	0.64	0.61–0.66	0.64	0.59–0.67
p_3	0.60	0.58–0.63	0.63	0.61–0.66	0.63	0.50–0.67

Temporal variation of the kind described above may be a serious obstacle when evaluating taxonomic differences, especially when small samples of specimens are available. An obvious methodological implication of such variation is that the values of measurements given in descriptions must be critically used. This is certainly the case even if large samples are compared. A biometric comparison of *D. serratosioi* and *D. saetheri* apparently would yield a number of non-overlapping characters if based exclusively on material collected in August (conf. Fig. 10). However, when material from the whole season is considered most meristic characters and measurements intergrade.

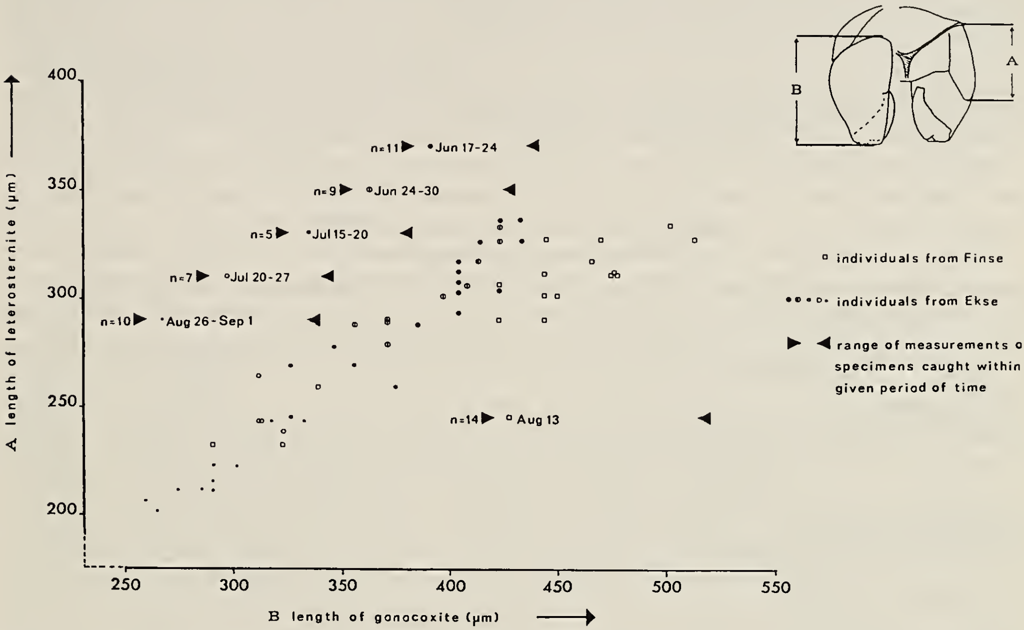

Fig. 10. Temporal variation of "body size" (measurements as figured) in *D. serratosioi* spec. nov. (circles and dots). Squares represent measurements of *D. saetheri* spec. nov., collected at Finse.

From what has already been mentioned about life cycles and size it would seem as a very plausible explanation that *D. saetheri* simply is a large *D. serratosioi.* The different shapes of the male hypopygia could be an allometric phenomenon. Linear regression analysis of the data (Fig. 10) for *D. serratosioi* gives the regression line $y = 0.77x + 2.2$; with a correlation coefficient of 0.97, which indicates isometric growth of the laterosternite. The plot for *D. serratosioi* and *D. saetheri* combined cannot be properly fitted to a logarithmic regression line, which is the usual expression of allometric growth (Hennig 1966). I conclude therefore, that *D. serratosioi* and *D. saetheri* are morphologically distinguishable with the shape of the male genitalia, although measurements show some overlap.

Biogeography and species taxa

Udvardy (1969: 231) states: "Evolutionists want to trace the geographic history of groups within their field of interest, and their use of distribution cues is here fully justified; they are obliged to use the accepted taxa because they have no other nomenclatorial means at their disposal. But since not all zoogeographers are evolutionists or taxonomists, the general recommendation stands that zoogeographical research should be based on the distribution of species or on species areas." UDVARDY writes further: "In summary the higher taxa are abstractions, compromises between the wishful thinking of the evolutionist and the practical need of the systematist and the nomenclator." Although this was written some years ago it expresses the common notion that the species is the only natural taxon. But what is a species? Most biologists consider species as more or less distinct units of nature with an existence independent of man's ability to perceive them. Most biologists would also agree that the general properties of species are that they constitute reproductive communities, ecological units, and genetic units (MAYR 1963: 12). But what, for instance is a reproductive community? Disregarding the risk of being caught in a net of tautologies by this sort of reasoning, the question may be answered in terms of evolutionary process and isolation mechanisms: "Species level is reached when the process of speciation has become irreversible, even if some of the secondary isolation mechanisms have not yet reached perfection" (MAYR 1963: 18). The problem of the taxonomist is to recognize species. Within this narrow perspective the task would be to make judgements about whether or not the process of speciation has become irreversible and to evaluate the efficiency of secondary isolation mechanisms.

Much energy has been used in disputes about whether species are real entities or man-made abstractions. Necessarily they are both parts. Because it is a question of recognizing and defining presumed natural entities, the meaning signified by the word 'species' must have a nominalistic connotation.

HENNIG (1966: 69) writes: "Thus delineation of the living genetic species is a long-continued operation, which has advanced to very different levels in the different groups of animals. In many groups there are still numerous "species" of which no more is known than the morphological characters given in the original description. In other groups the process of approaching a complete delineation of the genetic species and their intraspecific make-up is well advanced, because it was necessary to employ the whole apparatus of the most refined experimental and statistical methods. In either case the ultimate objective is the genetic species concept." Clearly, what we deal with as species are frequently not well defined reproductive communities, but samples of presumed reproductive communities (or evolutionary units), in many cases simply typological kinds. The species taxa, thus, are hypotheses that, due to incompleteness of data at the time the taxon is erected, often run the risk of being rejected. From a purely nomenclatorial aspect the species may be synonymised or subject to splitting. No matter what species concept a biologist claims to use, the different species identified will be products of different and unequal sets of conditions. Included in these conditions are application of method, evaluation of data according to the perspective of the problem, and not least personal opinions about what is sufficiently distinct to be assigned to the species category. In this sense the species taxon is no less apt to be influenced by "wishful thinking and the practical need of the systematist" than higher taxa.

MAYR (1963: 14) defines a taxon as follows: "A taxon is a taxonomic group of any rank that is sufficiently distinct to be worthy of being assigned to a definite category" ... "An essensialist (typological) definition is satisfactory and sufficient at the level of the higher taxa. It is, however, irrelevant and misleading to define species in an essensialistic way because the species is not defined by intrinsic, but by relational properties." Obviously, some relational facet is inevitable in the definition of a taxon, no matter whether we define it "biologically" or typologically. A taxon with feathers cannot be defined without reference to those groups that don't have feathers.

The biological species concept embodies no criteria of morphological differentiation. If we accept that the degree of morphological difference between natural populations is a by-product of the genetic divergence resulting from reproductive isolation, how do we decide when a population is sufficiently distinct to be recognized as a taxonomic group worthy of being assigned to a definite category? Even prominent advocates of the biological species concept may be tempted by typological thinking; e. g. MAYR's (p. 424) definition of a superspecies: "A monophyletic group of entirely or essentially allopatric species that are either morphologically too different to be included in a single species or demonstrate their reproductive isolation in a zone of contact."

Elsewhere Mayr proposes numerical indices to measure degrees of difference as guides for taking sound taxonomic decisions. Such indices are no less typological than similarity indices are for measuring relationships between taxa.

I agree in principle with Rosen (1978) that "a species is a unit of taxonomic convenience and that the population, in the sense of a geographically constricted group of individuals with some unique apomorphous character, is the unit of evolutionary significance". There is certainly a possibility of misjudging the actual or potential gene flow between given populations when taxonomic decisions are made. Moreover, it would be unjustified to conceal the practical difficulties in delineating monophyletic groups in aggregates of closely related species (Brundin 1972). However, if monophyly can be demonstrated and made testable by new data the question whether populations are sufficiently distinct to be recognized as taxa seems irrelevant. Provided that we deal with sister groups, each with some apomorphous feature, the point is that they have differentiated and may provide information with respect to the relationship of their area to other areas.

Thus, biogeographical research should be based not only on the distribution of species, but on monophyletic groups in the sense of Hennig (1966), no matter what rank or category these units are given in classifications.

Relationships within the davisi group

The phylogenetic relationships within the group is attempted assessed by means of the following trends and scheme of argumentation (Fig. 11) (a = apomorphous, p = plesiomorphous).

Trend 1 Laterosternite not extending beyond margin of T IX (a), laterosternite extending beyond T IX (p).

Trend 2 Setae not present on preepisternum II (a), setae usually present on preepisternum (p).

Trend 3 Tergal bands of male U-shaped (a), tergal bands Y-shaped (p).

Trend 4 Anal point inconspicuous (a), anal point usually discernable (p).

Trend 5 Ventrolateral knee-like protrusion on female cercus reduced (a), protrusion present (p).

Trend 6 Male gonocoxite as broad as, or broader than length of gonostylus (a) (refers to undistorted mounts); male gonocoxite narrower than length of gonostylus (p).

Trend 7 Male laterosternite with mesal margin obliquely cut and setae strongly reduced (a); mesal margin more parallel to longitudinal axis, setae usually well developed (p).

Trend 8 Gonostylus constricted at about 0.5–0.7 and more or less strongly bent, volsella without distinct setae (a); gonostylus more evenly tapering distad and less curved, volsella usually with distinct setae (p).

Trend 9 Gonostylus very strongly bent and expanding distad, pupa with 2 setae in front of the thoracic horn (a); gonostylus less strongly bent and narrowing distad, pupa with 3 setae in front of the thoracic horn (p).

Trend 10 Laterosternite very weakly sclerotized distally and with distinct curved apodeme, anal point, if present, very weak and hyaline (a); laterosternite well sclerotized and without such apodeme, anal point relatively well developed (p).

Trend 11 Abrupt constriction and bend at about 0.5 of male gonostylus (a); constriction not abrupt, bend weaker and slightly more distad (p).

Trend 12 Laterosternites held tight to the gonocoxite or slightly directed mesad (a), laterosternites slightly directed laterad (p).

Trends 13 Male hypopygium with extended laterosternites (secondarily reduced in *D. sonorae)*, gonostylus with apical serrations, male antenna reduced to 8 flagellomeres, female genitalia without projection on gonocoxite and practically devoid of setae on tergite and sternite VIII (a); male hypopygium without extended laterosternites, gonostylus without apical serrations, male antenna with more than 8 flagellomeres, female genitalia with projection on gonocoxite and setae on tergite and sternite VIII (p).

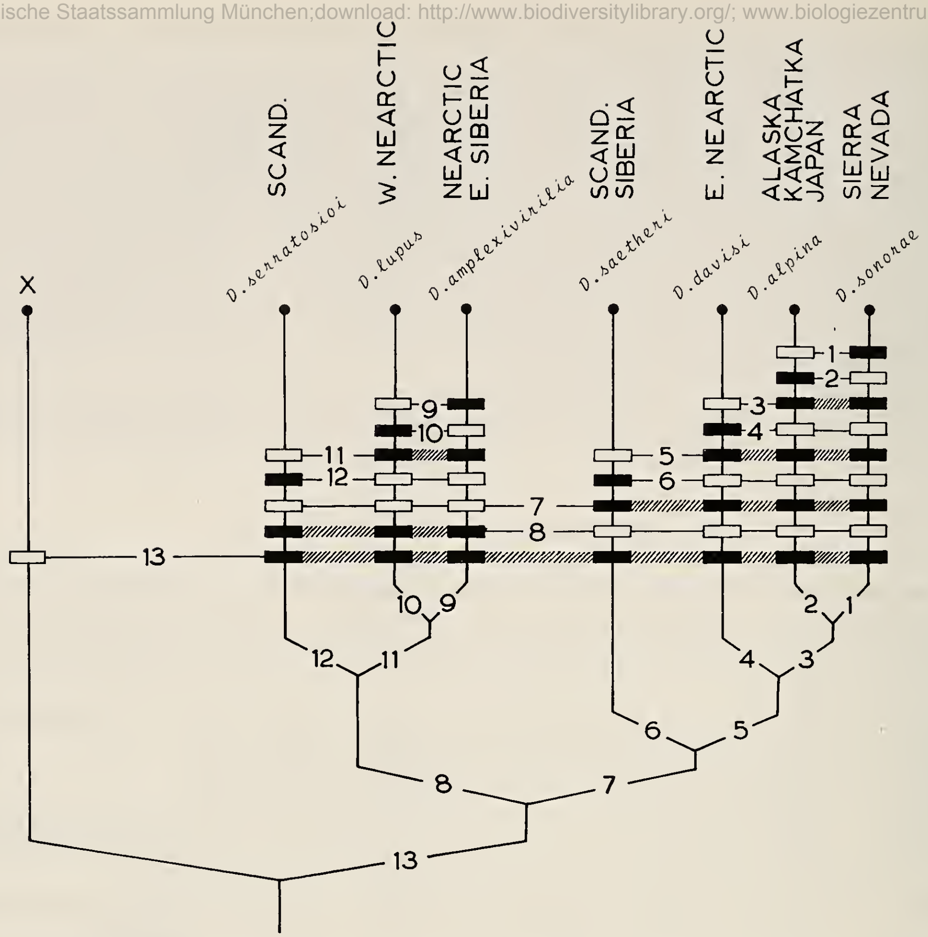

Fig. 11. Scheme of argumentation outlining the apparent phylogenetic relationships within the *D. davisi* group.

Trends number 2 and 4 are parallel reductions and thus not very strong arguments. Unless trend 5 is interpreted as a reduction, it will be in conflict with trend 7. It could be thought of as going in the opposite direction. Trend 9 is in part based on Makarchenko's description of the pupa of *D. amplexivirilia* (Makarchenko 1981). It is not clear whether the anteriormost precorneal seta is completely reduced or just displaced anteriad. The latter trend is seen in several other species of *Diamesa*. Knowledge of the female of *D. amplexivirilia* will be a test to the hypothesized relationship between this species and *D. lupus*.

Extrinsic relationships

Kownacki (1980) places the *davisi* group as a subgroup of the *D. steinboecki* group. There seem to be no clear synapomorphies holding the *D. steinboecki* group as monophyletic. In the *D. cinerella* group, which is certainly monophyletic, there are two species with male antennae reduced to 8 flagellomeres, showing that antennal reduction must have taken place independently in different monophyletic groups of *Diamesa*. Ongoing studies of females of *Diamesa* have revealed that the most probable sister group of the *davisi* group is *D. nivicavernicola* Hansen (female to be described elsewhere). The female of this species is very close to females of the *davisi* group in overall similarity, but a clear synapomorphy with the *davisi* group is seen in the dorsal position of the setae on the gonocoxite. No other *Diamesa* are known to have this character. The male of *D. nivicavernicola* has antennae with the number of flagellomeres reduced to 10 or 11. This may be thought of as a transitional stage from the normal number which is 13. Saether (1968) discussed antennal reductions in *Diamesa* and regarded this and accompanying morphological features as adaptions to high altitude habitats. The relationship between *D. nivicavernicola* and the *davisi* group is strong support to the conclusions arrived at by Saether.

Further relationships of the *davisi* group cannot be properly inferred until the females of the Nearctic species are better known. It seems probable, though, that the sister group of *D. nivicavernicola* and the *davisi* group is to be found among Nearctic species. A relatively strongly divided tergite IX occurs in species like *D. sommermani* Hansen and *D. heteropus* (Coquillett). Seminal capsules with a relatively short neck are seen both in *D. sommermani* and in a presently unidentified species from the Nearctic.

Distributional patterns of the davisi group

As indicated under the descriptions, distributional data for the members of the *davisi* group are presently scarce and probably will remain so for some time. Nevertheless, there is no reason to refrain from biogeographic inquiry. "What is important is not the degree of completeness per se, but what the data, however scanty they might be, suggest about the distribution of a species or group" (Nelson and Platnick 1981: 382).

The pattern shown by *D. sonorae, D. alpina,* and *D. davisi* is an indication of east-west vicariance which seems to be common in many genera of Nearctic chironomids. The populations in the Sierra Nevada and in White Mts. apparently are left behind by the withdrawal of the Pleistocene glaciers. While this resulted in subsequent differentiation in the west *(D. alpina – D. sonorae),* the population of *D. davisi* in the White Mts. remains undifferentiated from the rest of the population in the northern areas. The records of *D. davisi* from Greenland (Thienemann 1942) has not later been confirmed. It seems likely though, that they actually refer to *D. davisi* in the sense of Edwards.

D. alpina is distributed over the mountain ranges surrounding the northern Pacific Ocean. Provided that *D. alpina* in the sense of Makarchenko (1980) is co-specific with *D. alpina* Tokunaga, it extends as far south as to Japan in the E. Palaearctic. Its sister group, *D. sonorae,* may be an endemic of the Sierra Nevada. If so, it supports the theory (Elgmork and Saether 1970, Serra-Tosio 1973, Kownacki 1980) that isolation of populations in mountain areas during periods of warmer climate is the usual reason for the extensive speciation in *Diamesa. D. alpina* and *D. sonorae* combined show a distribution which coarsely coincides with the range of the East-Palaearctic and West-Nearctic representatives of the genus *Polycelis* (Tricladida) (Ball 1975) and probably reflects the pattern of an ancient biota. The coastal mountain ranges of the W. Nearctic is the only area that *D. nivicavernicola* has been recorded from (Hansen and Cook 1976).

The pattern shown by members of the *davisi* group is of particular interest with respect to Beringia. *D. saetheri,* which occurs in Scandinavia, has been found as far east as to the Chukotskii Peninsula. It seems probable that this distribution is the result of dispersal east after the disappearance of a barrier that once existed further west than the Bering Strait. This assumption is supported by the semicircular distribution shown by *D. alpina,* by the vicariance pattern shown by the European species of the group, and also by the distribution of *D. amplexivirilia* which covers most of the Nearctic but stops in the Kolyma area of the USSR. According to Matthews (1979) geological evidence indicates that some kind of Asian-Alaskan land connection lasted from the late Cretaceous until the Pliocene. The primary barrier to Eurasian-Asiamerican faunal exchange at least up to the early Tertiary probably was the Turgay Strait.

It is evident that the periods of glacial advances, in which Beringia was dry land, must have had an expanding effect on the original distribution of the *davisi* group. Whether the sequences of phylogenetic differentiation can be correlated with certain palaeogeographical events, of Pleistocene or earlier date, depends on the demonstration of similar relationships for other monophyletic groups.

Acknowledgements

I am much indebted to L. Brundin, Stockholm, E. F. Cook, St. Paul, P. S. Cranston, London, D. R. Oliver, Ottawa, P. Ottesen, Oslo, F. Reiss, Munich, and J. E. Sublette, Pueblo for providing me with relevant material. L. Brundin, P. S. Cranston, G. A. Halvorsen and O. A. Saether, both Bergen, B. Serra-Tosio, Grenoble, J. E. Sublette, and T. Wiederholm, Uppsala, read and commented on parts of various draft manuscripts. This study was financially supported by the Norwegian research council NAVF and the University of Bergen.

Literature

AAGAARD, K. 1978: The Chironomidae of the exposed zone of Övre Heimdalsvatn. – Holarctic Ecology **1:** 261–265

ANDERSEN, T., FJELLHEIM, A., LARSEN, R., and OTTO, C. 1978: Relative abundance and flight periods of Ephemeroptera, Plecoptera, and Trichoptera in a regulated West Norwegian river. – Norw. J. Ent. **25:** 139–144

BALL, I. R. 1975: Nature and formulation of biogeographical hypotheses. – Syst. Zool. **24:** 407–430

BRUNDIN, L. 1972: Phylogenetics and biogeography. – Syst. Zool. **21:** 69–79

DOUGHMAN, J. S. 1983: A guide to the larvae of the Nearctic Diamesinae (Diptera: Chironomidae). The genera *Boreoheptagyia, Protanypus, Diamesa,* and *Pseudokiefferiella.* – U.S. Geol. Surv. Wat.-Resources Invest. Rep. 83-4006, Doraville. IV + 58 pp.

EDMONDSON, W. T. 1971: Instar analysis. In: Edmondson, W. T. and Winberg, G. G. (eds.). A manual on methods for the assessment of secondary productivity in fresh waters. IBP handbook no. 17. – Blackwell, Oxford. 358 pp.

EDWARDS, F. W. 1922: Results of the Oxford University Expedition to Spitzbergen, 1921. – Ann. Mag. nat. Hist. Ser. 9, **11:** 235–240

— — 1933: Oxford University Expedition to Hudson's Strait, 1931: Diptera Nematocera. With notes on some other species of the genus *Diamesa.* – Ann. Mag. nat. Hist. Ser. 10, **12:** 611–620

ELGMORK, K. & SAETHER, O. A. 1970: Distribution of invertebrates in a high mountain brook in the Colorado Rocky Mountains. – Univ. Colorado Stud. Ser. Biol. **31:** 1–55

FITTKAU, E. J. & REISS. F. 1978: Chironomidae. In: Illies, J. (ed.). Limnofauna Europaea. – Gustav Fischer Verlag, Stuttgart. 2nd edition. XVII + 532 pp.

GRIMÅS, U. & WIEDERHOLM, T. 1979: Biometry and biology of *Constempellina brevicosta* (Chironomidae) in a subarctic lake. – Holarctic Ecology 2, **2:** 119–124

GOETGHEBUER, M. 1941: Quelques Chironomides du Tyrol. – Bull. Mus. r. Hist. nat. Belg. **17**(37): 1–8

HANSEN, D. C. & COOK, E. F. 1976: The systematics and morphology of the Nearctic species of *Diamesa* Meigen, 1835 (Diptera: Chironomidae). – Mem. Am. Ent. Soc. **30:** 1–203

HENNIG, W. 1966: Phylogenetic systematics. – Univ. Illinois Press, Urbana. 1st edition. 263 pp.

JANETSCHEK, H. 1949: Tierische Successionen auf hochalpinem Neuland. Nach Untersuchungen am Hintereis-, Niederjoch-, und Gepatschferner in den Ötztaler Alpen. – Ber. naturw. med. Ver. Innsbruck 48, **49:** 1–215

KOWNACKI, A. 1980: Ecology and biogeography of the *Diamesa steinboecki* group. – Acta Univ. Carolinae Biol. **1978:** 95–102

LINDEBERG, B. 1967: Sibling species delimitation in the *Tanytarsus lestagei* aggregate (Diptera, Chironomidae). – Ann. zool. fenn. **4:** 45–86

MAKARCHENKO, E. A. 1980: Novye i maloizvestnye vidy khironomid podsemeistva Diamesinae (Diptera, Chironomidae) dal'nego Vostoka SSSR. – Fauna presnyk vod dal'nego Vostoka; Vladivostok: 80–94

— — 1981: Taksonomiya i rasprostranenie nekotorykh vidov khironomid podsemeïstva Diamesinae (Diptera, Chironomidae) dal'nego Vostoka SSSR. – Bespozvonochnye zhivotnye v zkosistemakh lososteyykh rek dal'nego Vostoka, Vladivostok: 89–113

Matthews, J. V. jr. 1979: Tertiary and quarternary environments: historical background for an analysis of the Canadian insect fauna. – Mem. ent. Soc. Can. **108**: 31–86

Mayr, E. 1976: Populations, species, and evolution. – Harvard Univ. Press, Cambridge. 5th edition. 453 pp.

Nelson, G. & Platnick, N. 1981: Systematics and biogeography. – Colombia Univ. Press, New York. 567 pp.

Pagast, F. 1947: Systematik und Verbreitung der um die Gattung *Diamesa* gruppierten Chironomiden. – Arch. Hydrobiol. **41**: 435–596

Rosen, D. E. 1978: Vicariant patterns and historical explanation in biogeography. – Syst. Zool. **27**: 159–188

Rossaro, B. 1980: Descriptions of some larvae of *Diamesa* genus and corrections to previous descriptions (Dipt., Chironomidae). – Arch. Hydrobiol. **90**: 298–308

Saether, O. A. 1968: Chironomids of the Finse area, Norway, with special reference to their distribution in a glacier brook. – Arch. Hydrobiol. **64**: 426–483

— — 1969: Some Nearctic Podonominae, Diamesinae, and Orthocladiinae (Diptera, Chironomidae). – Bull. Fish. Res. Bd Can. **170**: 1–154

— — 1980: Glossary of chironomid morphology terminology (Chironomidae: Diptera). – Ent. scand. Suppl. **14**: 1–51

Saether, O. A. & Galloway, T. D. 1980: Sexual anomalies in Chironomini (Chironomidae: Diptera) from Lake Winnipeg, Manitoba, with observations on mermithid (Nematoda) parasites. – Acta Univ. Carolinae Biol. 1978: 193–211

Schlee, D. 1966: Präparation und Ermittlung von Meßwerten an Chironomiden (Diptera). – Gewäss. Abwäss. **41/42**: 169–193

— — 1968: Vergleichende Merkmalsanalyse zur Morphologie und Phylogenie der *Corynoneura*-Gruppe (Diptera: Chironomidae). Zugleich eine allgemeine Morphologie der Chironomiden-Imago (♂). – Stuttg. Beitr. Naturk. **180**: 1–150

Serra-Tosio, B. 1969: Les chironomides Diamesini de la collection Brundin (Diptera). – Ent. Tidskr. **90**: 203–209

— — 1971: Contribution à l'étude taxonomique, phylogénétique, biogéographique et écologique des Diamesini (Diptera, Chironomidae) d'Europe. – Thèse Univ. scient. med. Grenoble, T. I: 1–303, T. II: 304–462

— — 1973: Ecologie et biogéographie des Diamesini d'Europe (Diptera, Chironomidae). – Trav. Lab. Hydrobiol. Piscic. Univ. Grenoble **63**: 5–175

— — 1974: La mouche des glaciers *Diamesa steinboecki* Goetgh., insecte de montagne à ailes réduites (Diptera, Chironomidae). – Trav. Scient. Natn. Vanoise **7**: 117–138

— — 1983: Nouveaux Diamesinae de la Paléarctide méridionale et orientale (Diptera, Chironomidae). – Spixiana **6**: 1–26

Steffan, A. W. 1971: Chironomid (Diptera) biocoenoses in Scandinavian glacier brooks. – Can. Ent. **103**: 477–486

Thienemann, A. 1942: Lappländische Chironomiden und ihre Wohngewässer. – Arch. Hydrobiol. Suppl. **17**: 1–253

— — 1954: Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. – Binnengewässer **20**: 834 pp.

Tokunaga, M. 1936: Chironomidae from Japan (Diptera). IV Diamesinae. – Philipp. J. Sci. **59**: 525–552

Udvardy, M. D. F. 1969: Dynamic zoogeography. – Van Nostrand Reinholdt Co., New York. 445 pp.

Willassen, E. 1983: Notes on the chironomid (Diptera, Chironomidae) „ocelli". – Zool. Scr. **12**: 221–223

Zeitschrift/Journal: Spixiana, Zeitschrift für Zoologie, Supplement

Jahr/Year: 1984

Band/Volume: 011

Autor(en)/Author(s): Willassen Endre

Artikel/Article: A review of Diamesa davisi Edwards and the davisi group (Diptera, Chironomidae) 109-137