

rounded (but shrivelled in some); aedeagus (as in Fig. 10A) with lateral prongs, directed anterolaterally, distal portion a simple, gradually tapering projection, about twice as long to markedly longer than lateral prongs, very apex directed ventrally.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Fig. 5D; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on fore, mid femora, ventrally on hind femur; claws of hind leg equal, small.

Wing: macrotrichia restricted to apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially to somewhat truncate but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Pupa. Described under generic description.

Distribution and bionomics. *S. atra* is known from England to Latvia, south to Belgium and Hungary (Fig. 18B). Adults have been collected from 13 May to 6 July.

Little can be said about the bionomics of this species. Goetghebuer (1936b) noted that adult *S. atra* were associated with rivers in northern Belgium but we were unable to confirm his identifications. Two specimens from Britain had labels which noted that the specimens came from fens (Chippenham, Wood Walton (Hunts)). Strenzke (1950) collected a pupa from the shore of Schöhsee, F.R.G.

Taxonomic discussion. The association of the males and females was based on specimens collected at the same place and time in Latvia (by Remm), Belgium (by Goetghebuer: types of *S. nitens*) and Amsterdam (by Meijere, 1946: reported as *S. atra*).

Neotypes have been designated for *Ceratopogon ater*, *Serromyia micronyx* and *Serromyia albitarsis* because type specimens could not be located and have probably been destroyed.

The description of *Ceratopogon ater* by Meigen (1818) and the accompanying plate drawn by Meigen (in Morge, 1975) showing the extent of leg pigmentation, corresponds to the concept of *S. atra* as proposed where. Meigen (1818) noted that his description of *Ceratopogon*

ater was based on material from Megerle. Megerle's material was destroyed in the fire of 1848 at the Vienna Museum (Pont, 1986). We examined three specimens from the Winthem collection (in NHMW) which were labelled as 'ater', but unfortunately not in Meigen's handwriting. These could therefore not be considered as type material and the type material of *S. atra* is considered to be lost.

The description of both *S. micronyx* and *S. albitarsis* by Kieffer (1919) as having females with a brilliantly shiny thorax and short, equal hind claws can only refer to *S. atra* as described here. The neotypes are proposed to ensure stability of the names applied to Palaearctic species.

It is clear from Kieffer's (1919) list of nine localities for *S. spinosipes* that he based his description on a number of specimens. The only available material of Kieffer's type series was the lectotype and a paralectotype housed in the BMNH. The single paralectotype of *S. spinosipes*, however, is a female adult of *S. morio*.

Kieffer's (1919) description of *S. spinosipes* does not quite fit the description of *S. atra* here in that the femora and tibiae of *S. atra* are nearly completely darkly pigmented. Kieffer (1919) reported *S. spinosipes* with the fore and mid femora and tibiae as mostly yellow. However, the lectotype here designated fits the description of *S. atra* in this study.

One female pupa (ZSMC, material from Strenzke, 1950) we examined contained a pharate adult and was somewhat dirty. What few differences between this specimen and other available material of *Serromyia* pupae we could detect (size and number of spiracular openings) are noted in the generic description. The label on the slide noted 'femorata (?) morio?' and '246' (therefore collected at Schöhsees according to Strenzke's (1950) records).

The male genitalia of *S. atra* are indistinguishable from those of *S. morio*. However, the characters given in the keys and significant differences in the ratio of antennal flagellomeres 10/11 indicates that these are separate species.

Material examined. 59 males, 11 females and 1 female pupa.

Derivation of specific epithet. The name *ater* (black) presumably refers to the overall dark appearance of adults of this species noted by Meigen.

***Serromyia bicolor* Borkent sp.n.**

Diagnosis. Male and female: only Palaearctic species with palpal segments 1–3 pale, segment 4 light brown and segment 5 dark brown.

Description. Male adult. Descriptive statistics: see Tables 2–7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus with segments 1–3 pale, segment 4 light brown, segment 5 dark brown.

Thorax: dark brown; scutum pruinose.

Legs: coloration pattern as indicated in Fig. 3E; strong bristles of femora, tibiae distributed as follows: ventrally on mid femur, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta₁ straight; Ta₄ setae with slight curve or some slightly sinuate near their apex.

Wing: slightly infuscated with veins of cells r₁, r₂₊₃ darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 9C): gonostylus sinuous at midlength, tapering gradually for basal half, with swollen apex; paramere (Fig. 9B) blade-like, with pointed apex, directed posteriorly; aedeagus (Fig. 9A) lacking lateral prongs, distal portion truncate, with jagged margin, with posterolateral lobes, extreme apex directed posteriorly.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Fig. 5B; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on mid femur, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: macrotrichia restricted to anteroapical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially, with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. *S. bicolor* is known from Bonn, West Germany, and from Dilizan in the Caucasus Mountains of the Armanakaja S.S.R. (Fig. 18B). Adults have been collected from 10 May to 7 June.

Taxonomic discussion. We have associated the single female with the males on the basis of

the uniquely (amongst Holarctic *Serromyia*) bicoloured palpus.

The male of *S. bicolor* is unusual in a number of characters and is the most distinctive of all the Holarctic species (other than *mangrovi*). Colour pattern of both male and female palpus, the peculiar apex of the aedeagus, the sword-like parameres and a markedly slender (for a species of *Serromyia* in the Holarctic) hind femur of the male are all unique to this species.

Havelka & Caspers (1981) partially described this species under the name *S. subinermis* Kieffer (males are those of *S. bicolor* as recognized here, females are actually those of *S. bicolor* and *S. subinermis*). However, the name *subinermis* cannot apply to the present species as Kieffer (1919) noted that *S. subinermis* had spines (strong bristles) on the fore and mid femora in the female and none in the male. Male *S. bicolor* have strong bristles on the mid femur only and in the female these were either present or absent. As far as we can discern, there are no Palaearctic names which could apply to this species and have accordingly described it as new.

In their drawing of the male genitalia of *S. bicolor* (as *S. subinermis*), Havelka & Caspers (1981) misinterpreted the apex of the aedeagus as elongate and slender.

Types. Holotype, ♂ adult on microscope slide, labelled 'Holotype *Serromyia bicolor* Borkent, Bonn, Federal Republic of Germany, June 7, 1976, P. Havelka, A551' (PEHC); allotype, ♀ adult on microscope slide, labelled as for holotype but collected 24 May 1976 (PEHC); paratypes: 2♂ from holotype locality, dated 10.v.1976 (CNCI), 11.v.1976, (PEHC); 1♀ U.S.S.R., Caucasus, Dilizan, 5.vi.1969 (CNCI).

Derivation of specific epithet. The name *bicolor* (two-coloured) refers to the distinctive bicoloured palpus of males and females of this species.

***Serromyia femorata* (Meigen)**

Ceratopogon femoratus Meigen 1804: 28. Lectotype, here designated, ♂ adult on microscope slide, labelled 'Lectotype *Ceratopogon femoratus* ♂ Meigen, ex coll. Meigen 291/40 (158a), prép. J. Clastrier, 1985 baume phénolé, Museum Paris, *Serromyia femorata*

- Det. A. Borkent' (MNHN); paralectotypes: 2♀ labelled as for holotype (MNHN). Staeger 1839: 598 (in part). Zetterstedt 1838: 822 (in part), 1850: 3665 (in part), Schiner 1864: 584 (in part).
- Chironomus femoratus*: Fabricius 1805: 45.
- Prionomyia femorata*: Stephens 1829: 237.
- Ceratolophus femoratus*: Kieffer 1899: 69.
- Johannseniella femoratus*: Williston 1907: 1.
- Serromyia femorata*: Kieffer 1901: 157. Kieffer 1906: 65. Goetghebuer 1934: 61 (in part). Edwards 1926: 410 (in part).
- Ceratopogon armatus* Meigen 1818: 83. Lectotype, here designated, ♂ adult on microscope slide, labelled 'Lectotype *Ceratopogon armatus* ♂ Meigen, ex coll. Meigen 291/40 (161), prép. J. Clastrier, 1985 baume phénolé, *Serromyia femorata* Det. A. Borkent, Museum Paris' (MNHN).
- Prionomyia armata*: Stephens 1829: 238.
- Ceratolophus armatus*: Kertész 1902: 157.
- Serromyia armata*: Kieffer 1906: 65.
- Ceratopogon foersteri* Meigen 1838: 21. Neotype, here designated, ♂ adult on microscope slide, labelled 'Neotype *Serromyia foersteri* Meigen, ♂, Newcastle-u-Lyme, Staff., England 3-VI-1960, J. R. Vockeroth CNC No. 20249, *Serromyia femorata* Det. A. Borkent' (CNCI).
- Ceratolophus foersteri*: Kertész 1902: 157.
- Serromyia foersteri*: Kieffer 1906: 65.
- Ceratopogon flavipes* Gimmerthal 1847: 144, not *Ceratopogon flavipes* Meigen 1804: 28. Neotype, here designated, ♂ adult on microscope slide, labelled 'Neotype *Ceratopogon flavipes* Gimmerthal, ♂, Oxford, England, 6-V-1953, J. R. Vockeroth, Neotype CNC No. 20272, *Serromyia femorata*, Det. A. Borkent' (CNCI). **New synonym.**
- Palpomyia flavicrus* Kieffer 1906: 63. New name for *Ceratopogon flavipes* Gimmerthal. **New Synonym.**
- Serromyia flavicrus*: Remm 1988: 35.
- Serromyia inermipes* Kieffer 1919: 73. Neotype, here designated, adult on microscope slide, labelled 'Neotype *Serromyia inermipes* Kieffer, Brockenhurst, Hants [= Hampshire], England 3-V-1951, J. R. Vockeroth, CNC No. 20273, *Serromyia femorata* Det. A. Borkent' (CNCI).
- Ceratopogon rufitarsis*: authors, not Meigen. Meigen 1818: 83 (in part).
- Serromyia europaea*: authors, not Clastrier. Clastrier 1963: 61 (in part).
- Ceratopogon morio*: authors, not Fabricius. Staeger 1839: 598 (in part). Zetterstedt 1850: 3666 (in part).
- Diagnosis.** Male: only Palaearctic species with three rows of strong bristles on the fore femur, scutum pruinose and a pale wing. Female: only Palaearctic species with palpus darkly pigmented, the scutum pruinose, nearly the entire fore and mid tibiae yellow with only very apicies pigmented in some, strong lateral bristles absent from hind coxa and a pale wing.
- Description.** *Male adult.* Descriptive statistics: see Tables 2–7.
- Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.
- Thorax: dark brown; scutum pruinose.
- Legs: coloration pattern as indicated in Figs 3F, 4A; strong bristles of femora, tibiae distributed as follows: anteriorly, ventrally, posteriorly on fore femur, dorsally, posteriorly on fore tibia, present or absent anteriorly on fore tibia, anteriorly, ventrally, posteriorly on mid femur, posteriorly on mid tibia, present or absent anteriorly or dorsally on mid tibia, anteriorly, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta₁ straight or with slight basal curvature; Ta₄ setae straight or with slight curve.
- Wing: pale or slightly infuscated with veins of cells r₁, r₂₊₃ very lightly pigmented.
- Abdomen: dark brown.
- Genitalia (Fig. 9F): gonostylus with outer margin evenly curved, tapering gradually for basal half to tapering gradually to rounded or somewhat swollen apex; paramere (Fig. 9E) with apical half markedly swollen, apex rounded; aedeagus (Fig. 9D) with lateral prongs, directed posterolaterally, to dorso-laterally, distal portion a simple, slender projection, about twice to markedly longer than lateral prongs, extreme apex directed ventrally.
- Female adult.* Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:
- Head: mandible serrate.
- Legs: coloration pattern as indicated in Figs 5B, C; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on fore femur, present or absent ventrally on mid

femur, present or absent at extreme apex of mid tibia, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: macrotrichia absent or a few restricted to very apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially to somewhat truncate but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex (one specimen with three fully developed spermathecae present).

Distribution and bionomics. *S.femorata* is known from northern Fennoscandia south to northern Spain, northern Yugoslavia and Moscow (Fig. 19A). The locality in the Kola Peninsula shown on the map is based on a specimen with no further specific distributional data. Adults have been collected from 6 May to 14 August.

Havelka (1978, 1979) and Gil Collado (1957, 1985) noted records of *S.femorata* (Meigen) from Spain. We have examined one female from Santander housed in the MZLU but have been unable to confirm these previous records. Remm (1967) reported two specimens of *S.femorata* from the Caucasus and these identifications, too, could not be confirmed.

Strenzke (1950) noted the presence of larvae of *S.femorata* in lake-side mosses in Germany but we have been unable to confirm these identifications (material was examined, see under generic description).

We examined five pairs of *S.femorata* collected *in copula* from Norway, Sweden and Britain which allowed for confident association of the sexes.

One of the mated pairs (from Sweden) had the male abdomen broken between the sixth and seventh abdominal segments with the male's genitalia firmly attached to that of the female. This indicates a mating behaviour similar to that recorded for various species of Heteromyiini, Sphaeromyiini and Palpomyiini (Downes, 1978). Edwards (1920) noted that he collected mating pairs of *S.femorata* in which the females were feeding on males. We were unable to locate the specimens upon which these observations were based and therefore cannot confirm the identification. The presence of the broken male abdomen and attached male genitalia noted above would correspond to the presence of such a feeding behaviour.

The specimens which Edwards (1920) noted as preying on *Cricotopus pulchripes* Verr. and *Bezzia ornata* (Meigen) were examined and are indeed members of *S.femorata*.

The following are literature records of prey or feeding for which we were unable to examine the original material and confirm the identifications. Edwards (1923) noted *Trichocladius* sp. (Chironomidae) as prey. Gad (1951) reported *S.femorata* attacking *Isohelea sociabilis* (Goetghebuer) and *Culicoides impunctatus* Goetghebuer. Goetghebuer (1949) reported that *S.femorata* males fed on flowers and females preyed on *Metriocnemus* (Chironomidae).

Edwards (1926) noted that male *S.femorata* swarm at mid-day and Downes (1955) reported female swarms composed of 3–20 individuals of *S.femorata* under the tips of alder branches at Loch Lomond, Scotland. Although these records are consistent with the distribution of this species, we were unable to examine any of this material and thereby confirm the identifications.

Taxonomic discussion. The type of *Ceratopogon foersteri* Meigen is not present in Paris (Clastrier, pers. comm.) or in Halle (Dorn, pers. comm.) and we have accordingly designated a neotype for the species. Meigen's (1838) description is so general that this species might actually be one of any number of European species. His drawing of the female (in Morge, 1975) shows a unique leg coloration with apically darkened fore and mid femora and completely pigmented fore and mid tibiae. However, some pinned specimens of *S.femorata* may have somewhat darkened tibiae (as in Fig. 5C). Previous workers (Goetghebuer, 1920, 1934; Remm, 1988) have considered this species to be a synonym of *S.femorata* and the designation of the neotype here will establish this.

The type of *Serromyia inermipes* Kieffer could not be located. Remm (1988) considered the name a synonym of *S.femorata* although the general description given by Kieffer (1919) could apply to several European species. We have designated a neotype to confirm Remm's synonymy.

Remm (1988) recently placed *Ceratopogon flavipes* Gimmerthal as a species of *Serromyia*. Based on the brief description given by Gimmerthal (1847), in which he noted that the underside of the hind femora of the two female syntypes were spinose, this is probably correct.

The rest of the description, however, is so general that it does not allow for a confident placement of the name. The mention that the fore and mid 'Schenkel' [probably = femur] and 'Gelenke' [probably = base of tibia] were brown is approximately a condition occurring in some female *S.femorata*. The designation of the neotype here places *Ceratopogon flavipes* Gimmerthal as a synonym of *S.femorata*.

Goetghebuer (1922a) noted that the syntype series of *Ceratopogon femoratus* was composed of one male and four females. We examined only the male and two females.

The male paratype of *S.europaea* from Norway and the male paralectotype of *S.rufitarsis* were actually specimens of *S.femorata*.

Edwards (1926) suggested that female *S.femorata* lack macrotrichiae on the wing membrane but this is true for only some specimens.

Material examined. 199 males and 246 females.

Derivation of specific epithet. The name *femoratus* (pertaining to the femora) presumably refers to the swollen hind femur of members of this and several other genera of Ceratopogonidae.

***Serromyia mangrovi* Delecolle & Braverman**

Serromyia mangrovi Delecolle & Braverman 1987: 57. Holotype, ♀ adult, not seen, from EGYPT: Sinai, Ras Muhammad (MZSF); allotype, ♂ adult, not seen, labelled as for holotype (MZSF); paratypes (not seen): EGYPT: 9♂, 9♀, Sinai (MZSF, MNHN).

Diagnosis. Male and female: only Palaearctic species with body coloration uniformly pale yellow.

Description. As given by Delecolle & Braverman (1987). Additional character states as follows:

Male adult. Descriptive statistics: see Tables 2–7.

Head: antennal flagellomere 10 with plume arranged in a single whorl.

Thorax: scutum pruinose.

Legs: strong bristles of femora, tibiae distributed as follows: 1 anteriorly, 1 posteriorly on apex of fore femur, posteriorly on fore tibia, 1 anteriorly, 1 posteriorly on apex of mid femur, 2 ventrally on mid tibia, 1 anteriorly, ventrally on hind femur, dorsally on hind tibia; ventral

bristles on hind femur arising directly from flat cuticle or from very slightly developed tubercles; hind Ta₁ with marked basal bend; Ta₄ setae straight or with slight curve.

Wing: pale.

Female adult. Descriptive statistics: see Tables 8–13.

Legs: strong bristles of femora, tibiae distributed as follows: apically on mid tibia, mventrally on hind femur.

Genitalia: sternite 9 truncate medially.

Distribution and bionomics. *S.mangrovi* is known only from the Sinai Peninsula, Egypt. The specimens we examined were collected from 4/5 June to 18/19 November at a light trap.

Taxonomic discussion. Although Delecolle & Braverman (1987) designated only nine males and nine females as paratypes, they also examined an additional thirteen males and 122 females from the Sinai.

Material examined. Two males and two females collected at E-Shira el Gharkana and Ras Muhammad, Sinai Peninsula, Egypt (deposited in CNCI).

Derivation of specific epithet. The name *mangrovi* refers to the mangrove swamp where the specimens were collected.

***Serromyia morio* (Fabricius)**

Culex morio Fabricius 1775: 800. Neotype, here designated, ♂ adult on microscope slide, labelled 'Neotype *Serromyia morio* Fabricius, Oxford, England 13-V-1953, J. R. Vockeroth CNC No. 20131' (CNCI).

Ceratopogon morio: Meigen 1818: 84. Staeger 1839: 598 (in part). Zetterstedt 1850: 3666 (in part).

Prionomyia morio: Stephens 1829: 238.

Ceratolophus morio: Kertész 1902: 158.

Serromyia morio: Kieffer 1906: 65. Edwards 1926: 410. Goetghebuer 1934: 62.

Serromyia nudipennis Kieffer 1913: 10. Neotype, here designated, ♂ adult on microscope slide, labelled 'Neotype *Serromyia nudipennis* Kieffer, Oxford, England 13-V-1953, J. R. Vockeroth CNC No. 20248, *Serromyia morio* Det. A. Borkent' (CNCI). **New synonym.**

Ceratopogon femoratus: authors, not Meigen. Schiner 1864: 584 (in part).

Serromyia femorata: authors, not Meigen. Edwards 1926: 410 (in part). Goetghebuer 1934: 61 (in part).

Serromyia atra: authors, not Meigen. Goetghebuer 1934: 61.

Serromyia spinosipes: authors, not Kieffer. Kieffer 1919: 72.

Serromyia ledicola: authors, not Kieffer. Remm 1969: 214 (in part).

Ceratopogon flavicornis: authors, not Staeger. Zetterstedt 1850: 3667.

Diagnosis. Male: only Palaearctic species with fore femur with three longitudinal rows of strong bristles and with the prongs on the aedeagus directed anterolaterally. Female: only Palaearctic species with the scutum lacking pruinosity, the mid femur distinctly paler basally, and with an elongate, single hind claw.

Description. *Male adult*. Descriptive statistics: see Tables 2–7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.

Thorax: dark brown; scutum bare of pruinosity.

Legs: coloration pattern as indicated in Fig. 4A; strong bristles of femora, tibiae distributed as follows: anteriorly, ventrally, posteriorly on fore femur, dorsally, posteriorly on fore tibia, present or absent anteriorly on fore tibia, anteriorly, ventrally, posteriorly on mid femur, posteriorly on mid tibia, present or absent anteriorly, dorsally on mid tibia, anteriorly, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta_1 straight or with slight basal curvature; Ta_4 setae straight or with slight curve.

Wing: slightly infuscated with veins of cells r_1 , r_{2+3} darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 10C): gonostylus with outer margin evenly curved, tapering gradually for basal half, with swollen, rounded apex; paramere (Fig. 10B) with apical half markedly swollen, apex rounded (but shrivelled in some); aedeagus (Fig. 10A) with lateral prongs, directed anterolaterally, distal portion a simple, gradually tapering projection, about twice as long to markedly longer than lateral prongs, extreme apex directed ventrally.

Female adult. Descriptive statistics: see

Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Figs 4E, 5E; strong bristles of femora, tibiae distributed as follows: absent or present ventrally on fore femur, absent or present on mid femur, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: macrotrichia with very few to many, restricted to apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially to somewhat truncate but with anteromedial margin developed, pointed; 2 spermathecae, additional spermathecal duct terminating in pigmented apex (one specimen with 3 fully developed spermathecae).

Distribution and bionomics. *S. morio* is known from England to Estonia south to France, Austria and Greece (Fig. 19B). Adults have been collected from 7 May to 16 August. The extension into August was due to two specimens, one female from Hiiumaa Is., Estonia, 8 August and a male from Hamburg, Federal Republic of Germany, 16 August. Otherwise the latest date of collection is 18 July. It is possible that the two August specimens were mislabelled.

The most southerly locality of *S. morio* is Lake Ochrid, Macedonia, Yugoslavia. Edwards (1928) recorded this species from Calvi, Corsica, but the single female was actually a specimen of *S. subinermis*.

Remm (1967) reported *S. morio* from the Caucasus, but we have been unable to confirm this identification.

In Zetterstedt's collection at Lund there were three instances of a male and female placed on the same pin. On the label of one of these, Zetterstedt specifically noted that they were caught *in copula*. We were therefore able to confidently associate the sexes.

Little can be said about the bionomics of this species. Zetterstedt (1850) stated that males swarm near marshes in Lund, but unfortunately his identifications of *S. morio* included both this species and *S. femorata*.

Goetghebuer (1936b) suggested that *S. morio* was restricted to eutrophic lentic habitats in southern Belgium but we were unable to confirm this identification from his material.

Labels on some specimens we examined noted the following: 'from saline meadow', 'coastal

flat' (from Bar, Yugoslavia), 'at stream', 'at light'. Two female specimens deserve special mention; they have the intriguing statement 'reared from nest of mole' (from near Beaconsfield, Bucks., U.K.).

Strenzke (1950) and Thienemann (1950) recorded larvae of *S. morio* from lake-side mosses in Germany but we have been unable to confirm these identifications. One pupa from Strenzke's collection labelled 'Strenzke No. 246 *Serromyia femorata* (?) morio?' is actually a specimen of *S. atra* (see under that species and under generic discussion). Strenzke (1950: 349) also recorded a specimen as *S. morio* (?) from Plöner Sees, but we have not been able to examine this specimen and confirm the identification.

Taxonomic discussion. The type of *S. morio* has been destroyed and only the label is left (Zimsen, 1964). The type locality was given by Fabricius (1775) as 'Anglia' [= England] and was collected on 13 May. We have accordingly designated a specimen from Oxford, U.K., collected at the same time of year, as neotype.

The type of *S. nudipennis* could not be located and is probably also destroyed. Kieffer's (1913) rather general description of the female of this species does not allow for a definite application of the name to any known European species. However, most of the characters he does record correspond to the concept of *S. morio* as recognized here (i.e. pale wings, elongate hind claw). Kieffer (1913) recorded this species from Bitche (France). We examined two females from France but these were somewhat damaged. We therefore are designating a neotype (male) from the same place and date as the neotype of *S. morio* (from England).

We examined a male of *morio* identified by Zetterstedt as *Ceratopogon flavicornis* which was a misinterpretation of Staeger's description. *Ceratopogon flavicornis* is actually a member of the genus *Bezzia* (syntypes examined). Similarly, some specimens identified by Meijere, Schiner, Edwards and Goetghebuer as *S. femorata* were in fact *S. morio*. Goetghebuer also misidentified a specimen of *S. morio* as *S. atra*. Remm had misidentified a female as *S. ledicola*.

The single paralectotype of *S. spinosipes* from Budapest (BMNH) is a female adult of *S. morio*.

Material examined. 111 males and 129 females.

Derivation of specific epithet. The name *morio*

(fool) may refer to the unusual appearance of this species as compared to the other species Fabricius placed in *Culex*.

***Serromyia pacifica* Remm sp.n.**

Diagnosis. Male: only Palaearctic species with an AR = 1.17, the scutum pruinose, the fore femur entirely dark brown, with one row of ventral strong bristles and 1–2 posteriorly, and the parameres rounded apically. Female: only Palaearctic species with palpus dark brown, nearly entire fore tibia darkly pigmented, scutum pruinose, mid coxa with strong, lateral bristles, and with a single elongate hind claw, longer than Ta₅.

Description. Male adult. Descriptive statistics: see Tables 2–7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.

Thorax: dark brown; scutum pruinose.

Legs: coloration pattern as indicated in Fig. 3D; strong bristles of femora, tibiae distributed as follows: ventrally, posteriorly on fore femur, posteriorly on fore tibia, anteriorly, ventrally, posteriorly on mid femur, posteriorly on mid tibia, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta₁ with slight basal curvature; Ta₄ setae straight or with slight curve.

Wing: slightly infuscated with veins of cells r₁, r₂₊₃ darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 10F); gonostylus with outer margin every curved, tapering gradually for basal half, with swollen, rounded apex; paramere (Fig. 10E) with apical half somewhat swollen, apex rounded (somewhat shrivelled); aedeagus (Fig. 10D) with lateral prongs, directed dorsolaterally, distal portion a tapering, simple projection, markedly longer than lateral prongs, extreme apex directed ventrally.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Fig. 4E; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on mid femur, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: a few macrotrichia restricted to apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially, with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. *S. pacifica* is known from eastern Siberia (Fig. 18C). Adults examined were collected from 25 May to 27 June.

The specimens from the type locality were collected in mire. The material from Yakut A.S.S.R. was taken from a taiga bog.

Taxonomic discussion. The description provided here is based on the single male and two females housed in the CNCI and a manuscript description provided by Mrs E. Remm. *S. pacifica* will also be described in a separate paper, currently in press (Academy of Sciences, Tartu) and written by H. Remm before his untimely death in 1986. Mrs E. Remm (pers. comm.) indicated that the species description could be included in the present revision, to ensure that this work is inclusive, and consequently whichever paper appears first will provide the date and citation for *S. pacifica*.

Types. Holotype, ♂ adult, from Sakhalin Island, vicinity of Juzhno-Sakhalinsk, 16.vi.1970, mire (IZBE); paratypes: 6♂, 7♀ labelled as for holotype (IZBE, CNCI); U.S.S.R.: 3♀, Kunashir island, Juzhno-Kurilsk vicinity, 27.vi.1970 (IZBE); 1♀, Primorye Territory, NP 'Kedrovaya Pad', 1.vi.1970 (IZBE); 1♀, from Amur Territory, Klimoutzy, 25.v.1957 (ZMAS); 1♂, 4♀, Yakut A.S.S.R., Yakutsk vicinity, 14.vi.1968 (IZBE).

Derivation of specific epithet. The name *pacifica* refers to the proximity to the Pacific Ocean, where this species was collected.

***Serromyia rufitarsis* (Meigen) new status**

Ceratopogon rufitarsis Meigen 1818: 83. Lectotype, here designated, ♂ adult on microscope slide, labelled 'Lectotype *Ceratopogon rufitarsis* ♂ Meigen, ex coll. Meigen 293/40 (160b), prép. J. Clastrier, 1985 baume phénolé, Museum Paris' (MNHN); paralectotype ♂ adult labelled as for holotype but with '160a' instead of '160b' and identified as *Serromyia femorata* (MNHN).

Prionomyia rufitarsis: Stephens 1829: 238.

Ceratophus rufitarsis: Kertész 1902: 158.

Serromyia rufitarsis: Kieffer 1906: 65.

Serromyia gelida Kieffer 1925b: 429. Neotype, here designated, ♂ adult on microscope slide, labelled 'Serromyia gelida Kieffer, Neotype, Latvia, Sivera Lake, E. Remm, 17-6-67 CNC No. 20250, *Serromyia dipetala* R. det. H. Remm, *Serromyia rufitarsis* Det. A. Borkent' (CNCI). **New synonym.**

Serromyia bispinosa Goetghebuer 1936a: 321. Lectotype, here designated, ♂ adult on microscope slide, labelled 'La Panne [=De Panne, Belgium], ♂, 16-6-36, M. Goetghebuer', '*Serromyia bispinosa*', 'R.I.Sc N.B. 18.073 Coll. et det., M. Goetghebuer', '♂ Type Lectotype Goetghebuer, *Serromyia rufitarsis* Det. A. Borkent' (ISNB); paralectotype labelled as for lectotype except with '♀' (ISNB). **New synonym.**

Serromyia dipetala Remm 1965: 182. Holotype, ♂ adult, not seen, from Estonian S.S.R., Valga District, shores of Lake Yakhivavr, 11 July 1952 (IZBE); paratypes: ESTONIA S.S.R.: 111♂, 69♀ (not seen) from Valga, Vyru, Pyarnu, Tartu and Khařy districts, 13 June to 28 July, 1951-61; LATVIA S.S.R.: 13♂, 6♀, Daugavpils and Kraslava districts, 21-24 June 1961 (IZBE). **New synonym.**

Ceratopogon morio: authors, not Fabricius. Staeger 1839: 598 (in part).

Diagnosis. Male: only Palaearctic species in which the parameres bifurcate apically. Female: only Palaearctic species with a shiny scutum, a completely darkly pigmented mid femur and a single elongate hind claw.

Description. *Male adult.* Descriptive statistics: see Tables 2-7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.

Thorax: dark brown; scutum bare of pruinosity.

Legs: coloration pattern as indicated in Fig. 4B; strong bristles of femora, tibiae distributed as follows: present or absent posteriorly on fore femura (one bristle), present or absent posteriorly on mid femur, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta₁ straight or with slight basal curvature; Ta₄ setae straight or with slight curve.

Wing: slightly infuscated with veins of cells r₁, r₂₊₃ darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 11C): gonostylus with outer margin evenly curved, tapering gradually for basal half, with rounded to somewhat pointed apex; paramere (Fig. 11B) with apical portion bifurcate, the ventral arm slender, the dorsal, posteriorly directed arm tapering sharply to point; aedeagus (Fig. 11A) with lateral prongs, directed laterally, dorsolaterally or slightly anterolaterally, distal portion a tapering projection about twice as long to markedly longer than lateral prongs, extreme apex directed ventrally.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Fig. 5F; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on mid femur, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: very few macrotrichia restricted to apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially to somewhat truncate but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. *S. rufitarsis* is known from England to Estonia south to Belgium and Hungary (Fig. 19C). Adults have been collected from 26 May to 23 July.

Remm (1965) recorded specimens from a few additional localities from Estonia and Latvia (as *S. dipetala*), which are also probably members of this species.

The only available bionomic information is from Remm (1965) who noted that this species (as *S. dipetala*) was most plentiful from 1 to 10 July and could be found not only in shrubs and thickets near water but also in damp meadows some distance from any larger body of water.

Taxonomic discussion. Although we were unable to examine any type material of *S. dipetala*, Dr H. Remm kindly sent other material of this species. Both the specimens and the detailed description by Remm (1965) leave little doubt that this name is a junior synonym of *S. rufitarsis*. The material sent by Remm also allowed correct association of males with females.

The type of *Serromyia gelida* Kieffer could not be located and is presumed to be lost. The

description by Kieffer (1925b) of a male with brilliantly shiny thorax and a single spine on the fore femur could apply to either *S. atra* or *S. rufitarsis*. On the basis of the general description of leg pigmentation, we have placed the species here. However, the type locality of *S. gelida* was given as northern Norway (just north of Tromsø [=Tromsø]) which is markedly farther north than any locality of *S. rufitarsis* (Fig. 19C) or *S. atra* (Fig. 18B). The only species with far northern distributions are *S. femorata* (Fig. 19A) and possibly *S. morio* (Fig. 19B) and *S. ledicola* (Fig. 18A). These species, however, have either a pruinose scutum or have many spines on the legs. It may be that *S. rufitarsis* does occur in northern Norway but only future collecting will confirm this. However, the name *S. gelida* now must be considered a synonym of *S. rufitarsis*.

Remm (1965) noted that his *S. dipetala* differed from *S. bispinosa* in lacking strong bristles (his spines) on the fore and mid femora but we found this character to be variable, with a few strong bristles present in some individuals (including some of those identified by Remm as *S. dipetala*).

Goetghebuer (1922a) noted that the syntype series of *Ceratopogon rufitarsis* consisted of two males. The male paralectotype of *S. rufitarsis* is actually a specimen of *S. femorata*.

Although Goetghebuer (1936a) based his description on only one male and one female of *S. bispinosa*, it was uncertain which represented the holotype. Accordingly we have designated the male as lectotype.

Material examined. Thirteen males and ten females.

Derivation of specific epithet. The name *rufitarsis* (red tarsi) refers to the red-yellow tarsi reported for this species by Meigen (1818) (see generic taxonomic discussion for comments on reports of red coloration by previous authors).

***Serromyia subinermis* Kieffer**

Serromyia subinermis Kieffer 1919: 73 (as variety of *S. spinosipes*). Neotype, here designated, ♂ adult, labelled 'Serromyia subinermis Kieffer, ♂, Neotype, Ocsa, Hungary, láprét, 1965.V.19, leg. Mihályi' (HNHM).

Serromyia femorata: authors, not Meigen. Zetterstedt 1838: 822 (in part), 1850: 3665

(in part). Edwards 1926: 410 (in part).

Goetghebuer 1934: 61 (in part).

Serromyia morio: Edwards 1928: 173, not Fabricius.

Diagnosis. Male: only Palaearctic species with the parameres curved subapically and with the pointed apex directed laterally. Female: only Palaearctic species with the palpus dark brown, scutum pruinose, wing slightly infuscated with veins of cells r_1 , r_{2+3} darkly pigmented, lacking strong lateral bristles on the hind coxa, and with a single elongate hind claw.

Description. *Male adult*. Descriptive statistics: see Tables 2–7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.

Thorax: dark brown; scutum pruinose.

Legs: coloration pattern as indicated in Figs 4C, D; strong bristles of femora, tibiae distributed as follows: anteriorly, posteriorly on fore femur, present or absent ventrally on fore femur, posteriorly on fore tibia, present or absent dorsally, anteriorly, posteriorly on mid femur, present or absent dorsally, ventrally on mid femur, posteriorly on mid tibia, present or absent anteriorly, dorsally, posteriorly on mid tibiae, anteriorly, dorsally, ventrally on hind femur, dorsally on hind tibia, ventral bristles on hind femur arising from slightly developed tubercles; hind Ta_1 straight or with slight basal curvature; Ta_4 setae straight or with slight curve.

Wing: slightly infuscated with veins of cells r_1 , r_{2+3} darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 11F): gonostylus with outer margin evenly curved, tapering gradually to pointed apex; paramere (Fig. 11E) with subapical portion somewhat expanded dorso-ventrally (expansion best seen in lateral or posterior view), with pointed apex directed laterally or anterolaterally; aedeagus (Fig. 11D) with lateral prongs, directed posterolaterally to laterally, distal portion a simple, somewhat broadened projection, about twice as long to markedly longer than lateral prongs, extreme apex directed ventrally.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Figs

4F, 5E; strong bristles of femora, tibiae distributed as follows: 0–4 ventrally on fore femur, 0–2 ventrally on mid femur, 0–2 apically on mid tibia, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: a few to many macrotrichia restricted to apical margin.

Genitalia (as in Fig. 12D): sternite 9 truncate medially to somewhat truncate but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. *S. subinermis* is known from England to Estonia south to Corsica, Yugoslavia and Hungary (Fig. 19D). Adults have been collected from 10 April to 5 July.

Taxonomic discussion. We have applied the name *S. subinermis* to this species by designating a neotype. The type material of this species is almost certainly lost.

Kieffer's (1919) brief description of this species noted that the fore and mid femora of the female had one or two spines while the male lacked spines altogether. Our description of the female fits Kieffer's concept but that of the male does not. It may well be that Kieffer incorrectly associated the sexes as he did for *S. spinosipes* (see under *S. morio* and *S. atra*). We prefer to retain a given European name where possible, rather than propose a new one.

We have examined specimens identified by Edwards and Goetghebuer as *S. femorata*, which in fact are members of *S. subinermis*. Edwards (1928) recorded *S. morio* from Corsica but it is actually a specimen of *S. subinermis*.

The association of the sexes of *S. subinermis* is somewhat tentative. None of the males and females we examined were collected at the same place and time. Males and females collected in Hejőbába (8 km W Leninváros), Hungary, in May and males and females identified by H. Remm as *S. spinosipes* from Estonia were considered correctly associated members of this species.

In addition, we are not certain that all the females placed here are conspecific. Although some appear to be correctly associated with the males, some may belong to another, unnamed species. Further collecting and study are required to clarify this problem.

Material examined. Twenty-five males and forty-one females.

Derivation of specific epithet. The name *subinermis* (somewhat unarmed) probably refers to the lack of spines on the fore and mid femora which Kieffer (1919) attributed to males of this species.

***Serromyia tecta* Borkent sp.n.**

Diagnosis. Male: only Palaearctic species lacking spines on fore and mid femora and tibiae, each of which is entirely dark brown, AR = 1.00–1.03, pruinose thorax and with parameres rounded apically and swollen in apical half. Female: only Palaearctic species with small, equal hind claws and a pruinose thorax.

Description. Male adult. Descriptive statistics: see Tables 2–7.

Head: dark brown; antennal flagellomere 10 with plume arranged in more than one whorl; palpus dark brown.

Thorax: dark brown; scutum pruinose.

Legs: coloration pattern as indicated in Fig. 3D; strong bristles absent on femora, tibiae except ventrally on hind femur, present or absent dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta₁ straight or with slight basal curvature; Ta₄ setae straight or with slight curve.

Wing: slightly infuscated with veins of cells r₁, r₂₊₃ darkly pigmented.

Abdomen: dark brown.

Genitalia (Fig. 12C): gonostylus with outer margin evenly curved, tapering gradually for basal half, with rounded, somewhat swollen apex; paramere (Fig. 12B) with apical half somewhat swollen, with rounded apex (shrivelled in some); aedeagus (Fig. 12A) with lateral prongs, directed laterally to posterolaterally, distal portion a simple, slender projection, markedly longer than lateral prongs, extreme apex directed ventrally.

Female adult. Descriptive statistics: see Tables 8–13. Similar to male except for usual sex differences and as follows:

Head: mandible serrate.

Legs: coloration pattern as indicated in Fig. 5D; claws of hind leg equal, small.

Wing: a few macrotrichia restricted to very apical margin.

Genitalia (as in Fig. 12D): sternite 9 somewhat truncate medially but with anteromedial margin developed, pointed; two spermathecae,

additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. *S. tecta* is known from only from the type locality in the Federal Republic of Germany (Fig. 19D). The date of collection on the labels is given as 6.5.1935 and Dr R. Contreras-Lichtenberg (NHMW) (pers. comm.) has informed us that this means 6 May 1935. This clarification was added to the labels on the slide material.

Taxonomic discussion. Males and females of *S. tecta* are very similar to those of Nearctic *S. borealis* and they may be conspecific. However, males have different antennal ratios. Larger series of specimens from a variety of localities are needed to determine whether this is due to geographical variation or is indeed indicative of genetic discontinuity.

Types. Holotype, ♂ adult on microscope slide, labelled 'Holotype *Serromyia tecta* Borkent, ♂, Traun [Austria], Czerny, 6.5.1935, May 6, 1935' (NHMW); allotype on microscope slide labelled as for holotype (NHMW); paratypes: 3♂, 2♀ labelled as for holotype (NHMW, CNCI).

Derivation of specific epithet. The name *tecta* (disguised) refers to the long hidden identity of this European species.

Fossil species

Several species of fossil *Serromyia* have been described, all from Holarctic localities, and these shed some light on the history of the genus. We were fortunate in being able to examine all of these, except one male of *S. spinigera* (Loew). Szadziewski (1988) has recently described the Baltic amber fauna of Ceratopogonidae and included six taxa of *Serromyia*. These are: *S. anomalicornis* (Loew), *S. spinigera* (Loew), *S. succinea* Szadziewski, *S. polonica* Szadziewski and two unnamed species (sp. A and B). His excellent and comprehensive study provides descriptions of these species and we add here only a few further details. Because of the good preservation and presence of some important character states, we have given names to Szadziewski's (1988) species A and B.

***Serromyia anomalicornis* (Loew)**

Ceratopogon anomalicornis Loew 1850: 30.

Types as indicated by Szadziewski (1988).
Serromyia anomalicornis: Szadziewski 1988: 142.

Diagnosis and description. As indicated by Szadziewski (1988). Additional character states as follows: male antennal flagellomere 10 setae in a single whorl; male, female with Ta₄ with straight setae.

Distribution. From Baltic amber.

Material examined. One male and one female.

Derivation of specific epithet. We were uncertain why the name *anomalicornis* (unusual horn) proposed by Loew (1850) was applied to this species.

***Serromyia colorata* Statz**

Serromyia colorata Statz 1944: 150. Holotype ♀, both halves of split rock present, mounted on wooden block, labelled 'Serromyia colorata Stz. Original!', '3527', 'Serromyia colorata Sz. nov. sp.' (LACM).

Serromyia austera Statz 1944: 150. Holotype ♀, both halves of split rock present, mounted on wooden block, labelled 'Serromyia austera Stz. Original!', '3526', 'Serromyia austera Sz.', 'Serromyia colorata Det. A. Borkent' (LACM). **New synonym.**

Serromyia spinofemorata Statz 1944: 151. Holotype ♀, only one half of split rock present, mounted on wooden block, labelled 'Serromyia spinofemorata Statz Original!', '3528', 'Serromyia spinofemorata Sz.', 'Serromyia colorata Det. A. Borkent' (LACM). **New synonym.**

Diagnosis. Female: apical portion of fore femur and tibia pigmented, hind claw elongate with HC/Ta₅ = 1.09–1.38.

Description. *Male adult.* Not known.

Female adult. Legs: coloration pattern with apical portion of fore and mid femora, basal portion of fore and mid tibiae darkly pigmented (Fig. 13D); strong bristles absent on femora, tibiae except present ventrally on hind femur (Figs 13A, C); hind femur length = 0.86–1.07 mm; claw of hind leg single, elongate (Figs 13B, F), with basal tooth, HC/Ta₅ = 1.09–1.38.

Wing: wing venation not discernible.

Genitalia (as in Fig. 13D): sternite 9 truncate medially, two spermathecae present (additional spermathecal duct not discernible).

Distribution and bionomics. *S. colorata* is known from compression fossils from the type locality at Rott, Siebengebirge, Rheinland, Federal Republic of Germany. Although earlier thought to be Oligocene in age the Aquitanian epoch is now dated as Miocene (Szadziewski, pers. comm.).

Taxonomic discussion. The above description is based on the examination of the holotypes of the species listed above and the single female described by Statz (1944: 149) as *Serromyia* sp. We were unable to find any significant differences between these specimens, based on the character states used in recognizing extant species of *Serromyia*. We accordingly consider all to be conspecific.

Statz (1941) provided the names *Serromyia spinofemorata* and *Serromyia austera* under photographs of these, but failed to give any diagnostic features. The names are therefore *nomina nuda*. However, the descriptions by Statz (1944) do validate these names. Sphon (1973) incorrectly considered the earlier naming by Statz (1941) to invalidate his later use of the names (see ICZN Art. 23:m).

Statz (1944) stated that the antennae of *S. colorata*, *S. austera* and *S. spinofemorata* each had 14 segments but each actually has 13 flagellomeres. The macrotrichia visible at the wing apex reported for *S. colorata* were actually those at the very margin.

We consider some of the slight colour differences noted by Statz (1944) to be artefacts of preservation.

Material examined. Four females.

Derivation of specific epithet. The name *colorata* (colour) presumably refers to the differences in color Statz (1944) attributed to this species.

***Serromyia polonica* Szadziewski**

Serromyia polonica Szadziewski 1988: 135.

Types as indicated by Szadziewski (1988).

Diagnosis and description. As indicated by Szadziewski (1988); additional character state as follows: Ta₄ with straight setae.

Distribution. From Baltic amber (Eocene).

Taxonomic discussion. We could not confirm the presence of the prescutal pits as reported by Szadziewski (1988). If well developed, they would be unique in the genus.

Material examined. Two females (all the type material).

Derivation of specific epithet. The name *polonica* presumably refers to the type locality in Poland.

***Serromyia ryszardi* Borkent sp.n.**

Serromyia sp. B Szadziewski 1988: 139.

Diagnosis and description. Described by Szadziewski (1988: 139) as *Serromyia* sp. B. Additional character states as follows: antennal flagellomere 10 with plume arranged in a single whorl; strong bristles of femora, tibiae distributed as follows: anteriorly, ventrally, posteriorly on fore femur, anteriorly, dorsally, posteriorly on fore tibia, anteriorly, ventrally, posteriorly on mid femur, dorsally, posteriorly on mid tibia, anteriorly, dorsally, ventrally on hind femur, 2–3 rows dorsally on hind tibia; aedeagus with trifold apex; Ta₄ with straight setae.

Distribution. From Baltic amber (Eocene).

Taxonomic discussion. The trifold aedeagus of *S.rysardi* is somewhat similar to that of several extant species in the Holarctic (see Figs 8A, D, 9D), with the lateral prongs and the apex directed in a posterior direction.

Type. Holotype, ♂ adult in amber, in paper envelope labelled 'Diptera Nematocera Ceratopogonidae *Serromyia* sp. B, Szadziewski ♂. MZ 16110, *Serromyia ryszardi* Borkent' (MZW).

Derivation of specific epithet. The name *rysardi* is named in honour of the many contributions that Ryszard Szadziewski had made to our understanding of ceratopogonid systematics and, in particular, his comprehensive work on Baltic amber material.

***Serromyia sinuosa* Borkent sp.n.**

Serromyia sp. A Szadziewski 1988: 138.

Diagnosis and description. Described by Szadziewski (1988: 138) as *Serromyia* sp. A. Additional character states as follows: antennal flagellomere 10 with plume arranged in a single whorl; Ta₄ with sinuate setae.

Distribution. From Baltic amber (Eocene).

Taxonomic discussion. The sinuate setae on the fourth tarsomere are unique amongst the Baltic amber and extant Holarctic species of *Serromyia*.

Type. Holotype, ♂ adult in amber, in paper envelope labelled 'Diptera Nematocera Ceratopogonidae *Serromyia* sp. A, Szadziewski 1988 ♂. MZ 14972, *Serromyia sinuosa* Borkent' (MZW).

Derivation of specific epithet. The name *sinuosa* (windings) refers to the sinuate setae found on the fourth tarsomeres of this species.

***Serromyia spinigera* (Loew)**

Ceratopogon spiniger Loew 1850: 30. Types as indicated by Szadziewski (1988).

Serromyia spinigera: Kieffer 1906: 2. Szadziewski 1988: 140.

Ceratopogon elongatus Meunier 1904: 242.

Types as indicated by Szadziewski (1988).

Serromyia elongatus: Szadziewski 1988: 140.

Diagnosis and description. As indicated by Szadziewski (1988). Additional character state as follows: Ta₄ with straight setae.

Distribution. From Baltic amber (Eocene).

Material examined. Two females.

Derivation of specific epithet. The name *spinigera* (spine bearer) presumably refers to the noted spines on the hind femur of this species.

***Serromyia succinea* Szadziewski**

Serromyia succinea Szadziewski 1988: 136.

Types as indicated by Szadziewski (1988).

Diagnosis and description. As indicated by Szadziewski (1988).

Distribution. From Baltic amber (Eocene).

Taxonomic discussion. Flagellomere 10 of the male could not be seen clearly. Both male and females had only straight setae on ta₄.

The male was correctly reported to have a few macrotrichia at the wing tip (discussed below under 'Phylogeny').

Material examined. One male and two females (all type material).

Derivation of specific epithet. The name *succinea* (amber) clearly refers to the state of preservation of this species.

Discussion of fossil material

Our examination of many specimens of extant species as well as of available fossils of extinct

species allows for some improvements in the key given by Szadziewski (1988). In particular, our studies show that the ratio of the second radial cell to the first is highly variable and a poor tool for recognizing extant species. This suggests that the same would be true for the fossil species. The suggested changes replace the use of that character in the key and are as follows:

Couplet 6

- Fourth tarsomere with both straight and one pair of sinuate setae *S.sinuosa*
 Fourth tarsomere with only straight setae 7

Couplet 8

- Fore and mid femur with strong bristles anteriorly, ventrally and posteriorly *S.ryszardi*
 Fore and mid femur with only a few strong bristles ventrally *S.succinea*

Because *S.colorata* is known as a compression fossil, it was not included in the key by Szadziewski (1988). If keyed out, it would run to *S.succinea*. Although *S.colorata* has darker leg pigmentation restricted to the apex of the fore femur and tibia and *S.succinea* females have completely dark fore legs, it is unlikely that this can be used to distinguish them. Virtually all Baltic amber ceratopogonids lack contrasting pigmentation and this may be an artefact of preservation (Szadziewski, 1988). We can suggest no other distinguishing feature.

Another fossil, described by Heyden (1870) as *Ceratopogon alpheus*, is probably a member of *Serromyia*. The male specimen was collected from the brown coal deposits at Rott, Siebengebirge, Federal Republic of Germany. The figure clearly shows plumose antennae and markedly swollen hind femora and we know of no other Nematocera with such a combination of characters. Some *Monohoelea* and *Schizohelea* also have swollen hind femora but not to such a degree. We therefore recognize this species as a new combination: *Serromyia alpheus* (Heyden). Unfortunately, the type was reported as lost (Szadziewski, 1988), and we too have tried without success to locate it at the BMNH and OXUM. It is possible that this male was conspecific with the females described as *S.colorata*. However, we prefer to leave the

name available until such time as further specimens become available for study and a neotype can be designated.

Phylogeny

A fundamental question to the interpretation of phylogenetic relationships within *Serromyia*, concerns the monophyly of the genus itself. Throughout the course of this study the presence of a swollen hind femur bearing a ventral patch of strong bristles arranged as a single row of 1–3 bristles basally, forming 2 rows at mid length and scattering distally into an indistinct pattern up to 4 bristles wide, was interpreted as a derived character state. This character state appears to be unique within the Ceratopogonidae and Culicomorpha.

Wirth & Grogan (1988), however, recently described the new monotypic genus *Metacanthohelea* which exhibits this same character state. On the basis of this modification, we suggest that these two together form a monophyletic group (Fig. 20).

Wirth & Grogan (1988) suggested several characters which may serve to distinguish *Metacanthohelea* from *Serromyia*. Our study indicates that many of these also occur in at least some species of *Serromyia*. The proposed distinguishing character of *Metacanthohelea*, followed by the character states within *Serromyia* are given below:

—slightly arcuate hind tibia: indistinguishable from that of *S.reyei*, *S.maculipennis*, *S.mangrovi*, *S.silvatica*, *S.stuckenbergi*, *S.nocticolor*. The degree of bend of the base of the hind tibia seems strongly correlated with the thickness of the hind femur. Thicker hind femora are associated with a stronger bend at the base of the tibia.

—reduced number of hind femur spines: within *Serromyia*, the number of spines (here called strong bristles) is generally correlated with the size of the hind femur. However, the extent to which the hind femur bears strong bristles does vary. Female *S.reyei*, *S.silvatica* and *S.mangrovi* have the same or a smaller percentage of the hind femur covered with strong bristles when compared with *M.cogani*.

The male of *M.cogani* has the distal 0.39–0.43 of the hind femur bearing spines. Within *Serromyia* the least amount of the hind femur bearing strong bristles is exhibited by *S.reyei* with a minimum of 0.58. Otherwise, all *Serromyia* have an even more extensively spinose femur.

—female with equal hind claws: also present in *S.silvatica*, *S.atra*, *S.crassifemorata*, *S.borealis*, *S.tecta*. However, in each of these *Serromyia* species, each claw does not bear an inner tooth, which is present in *Metacanthohelea cogani*.

—female with relatively short hind fourth tarsomere: we failed to find any significant differences between the hind fourth tarsomeres of *Metacanthohelea* and species of *Serromyia*.

—eyes broadly separated: also present in *S.reyei*, *S.mangrovi*, *S.stuckenbergi* and *S.noticolor*.

—male antenna with flagellomeres 1–8 fused: flagellomeres fused in *S.mangrovi* and *S.noticolor* or at least partially fused basal flagellomeres in all Holarctic species other than *S.nudicolis*.

—parameres fused: also fused in *S.reyei*, *S.festiva* and *S.esaki*.

—sensory pit on palpal segment 3: also present in male and female *S.agathae* and *S.noticolor* and in at least the male of *S.festiva*.

—radically different genitalia: although the male genitalia of *Metacanthohelea* are somewhat different from those of most *Serromyia* species, they are similar to those of *S.reyei*. In addition, some *Serromyia* also have rather different genitalia when compared to those in the rest of the genus (e.g. *S.esakii*, *S.mangrovi*).

From the above comparisons, it appears that the only possible distinguishing character of *Metacanthohelea* is the reduced extent to which the male hind femur bears strong bristles. In addition, re-examination of the original material (Wirth, pers. comm., and ourselves) indicates that the female claws are distinctive. They are bent sharply at their base and with the distal portion straight (Fig. 16C), in comparison to species of *Serromyia*, where the base of the claws are either straight or evenly curved and the distal portion of the claw is always curved (Figs 16D–G). In addition, the claws of the hind leg of *M.cogani*, although equal and shorter than the fifth tarsomere, bear a well-developed inner tooth. In those *Serromyia* species which have equal hind claws, the inner tooth is lacking.

Of the above character states we can interpret only the degree to which the male hind femur bear strong bristles for phylogenetic analysis. Outgroup comparisons indicate that most genera of Ceratopogonidae lack thick strong bristles on the hind femur but that some bear a single row of thick spines. Two alternate hypotheses are therefore possible.

The first suggests that the plesiomorphic state is the total lack of strong bristles (as in most Ceratopogonidae), developing to a state where strong bristles are restricted to the distal portion of the hind femur (as in *Metacanthohelea*), and ultimately to the extensive strong bristles of *Serromyia*. This hypothesis would suggest that *Metacanthohelea* is the sister group of *Serromyia*.

The second hypothesis suggests that the plesiomorphic condition is a single, but extensive row of strong bristles (as in *Echinohelea* Macfie, some *Austrohelea* Wirth & Grogan, some *Fanthamia* de Meillon and some *Stilobezzia*), which develop into the more complex pattern typical of most species of *Serromyia*. This suggests that *Metacanthohelea cogani* is merely an autapomorphic member of *Serromyia*, with a somewhat reduced distribution of strong bristles on the hind femur.

In our opinion, the first hypothesis seems most likely and we therefore recognize *Metacanthohelea* as a valid genus (Fig. 20). We are unable to suggest an apomorphy for *Metacanthohelea*, but, considering the genus is monotypic, it must be monophyletic.

In spite of a diligent search for character states which might be useful in interpreting the phylogenetic relationships between species of *Serromyia*, only a few clues were discovered.

In all extant Holarctic species of *Serromyia*, other than *S.mangrovi*, the tenth flagellomere exhibits a series of whorls of elongate bristles. In all other Ceratopogonidae, including all *Serromyia* examined from the Oriental, Australian and Afrotropical Regions, the tenth flagellomere has a single whorl of elongate bristles, similar to that of the preceding flagellomeres. The multi-whorled condition is therefore logically interpreted as a synapomorphy (Fig. 20). This character state is also reflected in the ratio of antennal flagellomere 10/11 (Table 3), where *S.mangrovi* has a single whorl and a low ratio and all other species have a higher ratio and have more than one whorl.

Considering the monophyly of the Holarctic species (except *S.mangrovi*), another character state may give further resolution. All Palaearctic species (except *S.mangrovi*) and several Nearctic species exhibit lateral prongs on the aedeagus. This tripartite condition is also present in various configurations, in some African species: *S.agathae*, *S.neethlingi*,

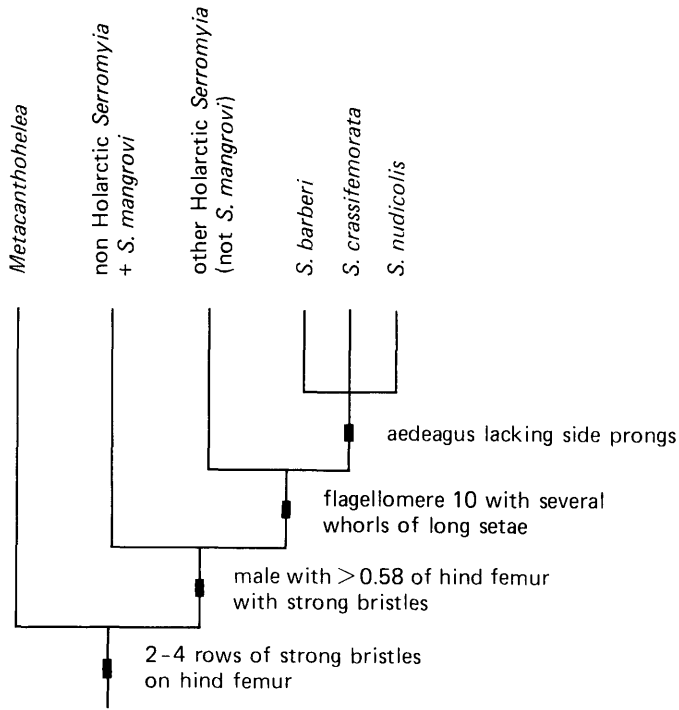


Fig. 20. Cladogram showing relationships within *Serromyia* and its sister lineage. Black rectangles and accompanying descriptions represent synapomorphic character states.

S. meiswickeli, *S. nocticolor* and *S. stuckenbergi*. This includes all those *Serromyia* south of the Holarctic in which the body coloration is entirely dark brown and for which the male is known. This may allow for interpretation of the two character states found within the Holarctic lineage where the aedeagus either has lateral prongs or is lacking these. Using the African species as the outgroup, those species lacking lateral prongs in the Nearctic would form a monophyletic group: *S. barberi*, *S. crassifemorata* and *S. nudicolis* (Fig. 20).

Although based on phenetic similarity, it seems likely to us that *S. morio* and *S. atra* are sister species. The male genitalia of these two species were inseparable.

Szadziewski (1988: 142) has suggested that those species where the females have short, equal hind claws may form a monophyletic group, which he called the *crassifemorata* group. This hypothesis seems unlikely to us. It does seem clear that the character state of having short claws is derived from a plesiomorphic longer, single claw, based on the widespread

presence of long claws in the genus and similar genera such as *Monohelea* and *Stilobezzia*. Although the presence of short claws is probably apomorphic within *Serromyia*, incompatibility with other character states suggests that this character state is susceptible to homoplasy and argues against such a grouping. *S. silvatica*, an African species known only from the female, has short hind claws. It is unlikely that the male will have the synapomorphy of possessing more than one whorl of setae on flagellomere 10, a synapomorphy grouping all Holarctic species (except *S. mangrovi*), including four species which have short hind claws: *S. atra*, *S. borealis*, *S. tecta* and *S. crassifemorata*. Considering the overall morphological similarity between *S. borealis* and *S. tecta*, these two are probably sister species. However, as argued above, *S. crassifemorata* is more closely related to two long-clawed species than to other short-clawed species. In addition, also as suggested above, the short-clawed *S. atra* is probably most closely related to *S. morio*, a species with an elongate hind claw. Finally, two of the fossil species

S. spinigera and *S. anomalicornis* have short hind claws and assuming these are correctly associated with the males, definitely do not belong to the clade including the extant Holarctic species (three species of which have short claws). We conclude, therefore, that short hind claws have evolved independently at least three times amongst the extant Holarctic lineage and that it is a poor indicator of relationship. The question may be further tested by discovery of the male of *S. silvatica* and further resolution of phylogenetic relationships amongst the Holarctic lineage.

As noted above, *S. mangrovi* is not part of clade formed by all other Holarctic species. This, its distinctive morphology (as compared to Holarctic species), and its presence in the Sinai, may indicate an Afrotropical or Oriental phylogenetic connection for this species.

Our examination of fossil material provided some clues about the history of the genus. All males of the fossil species had a single whorl of setae on flagellomere 10, indicating that they were not members of that clade which includes all extant Holarctic species (except *S. mangrovi*). Either the Holarctic species diversified since the Eocene (Baltic amber age) or they evolved elsewhere.

S. ryszardi was unique in the fossil material in exhibiting 2–3 rows of strong dorsal bristles on the hind tibia. The only extant *Serromyia* species which has a similar condition is *S. nocticolor* from South Africa. This character state is probably a valid synapomorphy. Only some members of *Echinohelea* have a similar condition.

Two other clues indicate that the Baltic amber *Serromyia* may not be immediately related to the assemblage of extant Holarctic species. The sinuate setae on the fourth tarsomere of *S. sinuosa* (Baltic amber) is shared only with some more southerly members of the genus: *S. reyei* (Australasian), *S. stuckenbergi* (Afrotropical) and *S. agathae* (Afrotropical). It is uncertain, however, which character state is derived. Both conditions of sinuate and straight setae on the fourth tarsomere are widespread throughout the Ceratopogonini.

A second character state is shared by *S. succinea* (Baltic amber) and *S. agathae* (Afrotropical). Males of both have a few macrotrichia at the wing apex. Although the presence of wing macrotrichia are widespread on the wings of females, they are not present on any other

Serromyia males. However, this character state cannot be interpreted as synapomorphic, as male wing macrotrichia also occur in a number of other ceratopogonid genera.

Previous workers have used some characters states to recognize new taxa (particularly genera) which show homoplasy within *Serromyia*. If *Serromyia* is indeed monophyletic, this may indicate that those character states are susceptible to homoplasy in other groups of ceratopogonids as well and that they should be interpreted with caution. The character states are as follows: separate or fused male flagellomeres; terminal three or four male flagellomeres elongate; presence or absence of sensory pit on third palpal segment; female mandible vestigial or well developed; distance between eyes; presence or absence of pruinosity on scutum; base of M_2 indistinct or well developed; presence or absence of macrotrichiae on male or female wings; presence or absence of strong bristles on legs; presence or absence of sinuate setae on fourth tarsomeres; short and equal or elongate and single hind female claws; straight or basally curved hind first tarsomere; presence or absence of stout spine near base of hind first tarsomere; female with sternite eight bilobed or completely cleft; separate or fused parameres; 1–3 functional spermathecae.

Debenham (1987) recently described the new, monotypic genus *Chimaerohelea* and suggested that it was closely related to *Serromyia*. This conclusion was based on shared similarities between *Chimaerohelea* and some species of *Serromyia*. These stated similarities require comment, based on our study of *Serromyia*. The following gives the character state which Debenham (1987) suggested was shared by *Chimaerohelea* and various *Serromyia*, followed by our observations:

—fusion of the veins between cells r_1 and r_{2+3} present in *S. barberi*, male *S. reyei*, *S. femorata* and possibly *S. nocticolor*: our examination showed that no *Serromyia* species showed such fusion except as intraspecific variation in a few species (*S. nudiculis*, *S. femorata*, *S. atra*).

—a single spermatheca present in *S. aethiopiae*: this is the only species of *Serromyia* with a single spermatheca. However, the character state appears to be homoplastic in numbers of other genera of Ceratopogonini (*Alluaudomyia* Kieffer (1–2), *Brachypogon* Kieffer (1–2), *Ceratoculicoides* Wirth & Ratanaworabhan (1–2), *Kolenohelea* de Meillon

& Wirth (1–2), *Macrurohelea* Ingram & Macfie (1–2), *Stilobezzia* Kieffer (1–3)) and is probably a poor indicator of relationship.

– wing fold extending basally from point where M_2 curves toward M_1 : we confirm that *S.aethiopiae* is the only *Serromyia* with a barely discernable, slightly pigmented line extending basally.

– male flagellomeres 4–11 fused in *S.dipetala* (named *S.rufitarsis* here), possibly *S.nocticolor*, and some other genera of Ceratopogonini: we found fused flagellomeres present in *S.mangrovi*, *S.nocticolor* and at least partial fusion in all Holarctic species other than *S.nudicolis*.

– aedeagus similar to *S.femorata*, *S.pendleburyi*, *S.dipetala* (named *S.rufitarsis* here): we failed to see distinctive similarities between *Chimaerohelea* and any species of *Serromyia*.

Of the characters discussed by Debenham (1987), the only character state which may possibly be interpreted as a synapomorphy is the dark line extending basally from M_2 . We could find no other Ceratopogonini with such a character state. However, this would indicate that the monopoly of *Serromyia* plus *Metacanthohelea* would be in doubt. We consider this to be unlikely and that the above similarities are all due to homoplasy.

We are unable, however, to present an alternative hypothesis of the phylogenetic position of *Chimaerohelea*. Further research is require to interpret the position of this and many other genera of Ceratopogonini.

Zoogeography

The above phylogenetic interpretation is so sketchy that it is presently impossible to interpret the historical zoogeography of the extant Holarctic species. However, some distributions allow for some general zoogeographic statements to be made.

The distributions of all species of *Serromyia* in the Nearctic are restricted to temperate habitats. The southern extensions are otherwise present only in the mountainous regions. No *Serromyia* are known from the Neotropical Region.

Within the Nearctic, *S.nudicolis* and *S.crassifemorata* are restricted to eastern North America. *S.barberi* is present only west of the continental divide while the remaining species are too poorly represented for their

distributions to be confidently interpreted. The only Holarctic species, *S.ledicola*, is widespread in the Nearctic but appears to be absent from most of the area west of the continental divide in more southerly latitudes.

Within the Palaearctic, all the European species which were well represented in collections, seem to be broadly distributed in central Europe. In southern Europe, however, species appear to be restricted to mountainous regions.

Although *S.femorata* is the only species definitely known from northern Fennoscandia, it seems likely that at least *S.morio* (based on its presence in Scotland) and *S.ledicola* (based on its northern distribution in North America) will also be found there.

Szadziewski (1988) has suggested a European origin for the genus *Serromyia*. We can see no logical basis for such a conclusion. We recognize that zoogeographic interpretation must be based on an understanding of the phylogenetic relationships within the group under consideration. Until further interpretation of the relationships between the known species is available, it will be impossible to identify the early lineages of *Serromyia* and thereby suggest where the genus may have originated.

Szadziewski (1988) also interpreted his 'crassifemorata group' as exhibiting a recent Euro-North American distribution. As indicated above, however, evidence suggests that this group is polyphyletic (grouped on the basis of parallelism). As such, no zoogeographic interpretation could be validated.

The fossil data indicate that the extant Holarctic lineage was probably not present in Europe during the Eocene. We are inclined to think that the extant Holarctic species, as a monophyletic group, are most closely related to those species from Africa which are darkly coloured. However, there is no logical evidence to support this at present, other than some of the unpolarized shared similarities between Holarctic species (other than *S.mangrovi*) and some of the African species noted above.

Acknowledgments

This study was the result of 4 years of investigation. A few years ago, when the senior author was new to the study of Ceratopogonidae, Dr Willis W. Wirth gave generously of his time and expertise to help in initiating my studies. He

already had a draft key of the Nearctic species of *Serromyia* (including *S. nudicolis*) as well as some notes on the species. He unstintingly gave these to us. We express our thanks to him for his magnanimous approach and support.

Leo Forster mounted on microscope slides nearly all the specimens used in this study. His remarkably clear and carefully prepared mounts added immeasurably to the information gathered during this work. He also helped with some field collecting. Without his assistance this study would not have compiled the information it has. His retirement at the end of 1988 was sorely felt!

We also appreciate the assistance of the staff of the Electron Microscope Unit of the Cell Biology Research Centre, Agriculture Canada.

Barry Flahey drew and inked all the genitalia drawings. His skills in illustrating these small creatures are much appreciated.

Ms Mary Dillon kindly identified some chironomids which were recorded as prey.

We also extend our thanks to Mrs Evi Remm, who kindly provided advice on how to deal with *S. pacifica* Remm.

Our thanks also extends to all those curators who lent specimens of *Serromyia*: Dr R. Abraham (ZMUH), Dr P. H. Arnaud (CASC), Mr B. Brugge (ZMAN), Dr M. Chvala (KUPC), Dr J. Clastrier (MNHN), Dr R. Contreras-Lichtenberg (NHMW), Dr P. S. Cranston and Mr B. Townsend (BMNH), Mr R. Danielson (MZLU), Dr J. C. Delecolle (MZSF), Dr A. Dely-Draskovits (HNHM), Dr N. L. Evenhuis (BPBM), Dr W. L. Grogan (Maryland), Dr P. Grootaert (ISNB), Dr P. Havelka (PEHC), Dr J. K. Liebherr (CUIC), Dr B. Lindeberg (UZMH), Dr L. Lyneborg (ZMUG), Dr G. C. McGavin (OXAM), Ms K. C. McGiffen (INHS), Ms P. I. Persson (NHRS), Dr W. W. Wirth and Dr B. V. Peterson (USNM), Dr F. Reiss (ZSMC), Dr H. Remm (IZBE), Mr L. Saul (LACM), Dr R. T. Schuh (AMNH), Dr R. O. Schuster (UCDC), Dr R. Szadziwski (Gdansk). In addition Dr G. C. McGavin gave us substantial help with interpreting otherwise impossible British place names, Ms Evi Remm provided much appreciated help with Latvian, Estonian and Lithuanian localities, Dr L. Papp interpreted Hungarian place names and Dr P. Grootaert kindly did the same with difficult Belgian localities.

We thank the following who provided

thorough reviews of this manuscript: Dr William L. Grogan, Dr Evert E. Lindquist and Dr Michael Sharkey, Dr Ryzard Szadziwski, Dr Richard J. Vockeroth and Dr Willis W. Wirth. Their suggestions and criticisms greatly improved the text.

Finally, the senior author thanks his wife Annette and his three children for sharing several field trips and assisting in many of the tasks demanded by these excursions. His son Chris also helped with an attempt to interpret strong bristle variation in *S. barberi* males.

References

- Arnett, R.H. & Samuelson, G.A. (1986) *The Insect and Spider Collections of the World*, 220pp. E. J. Brill/Flora and Fauna Pub., Gainesville, Florida.
- Becker, P. (1961) Observations on the life cycle and immature stages of *Culicoides circumscriptus* Kieff. (Diptera, Ceratopogonidae). *Proceedings of the Royal Society of Edinburgh* (B), **67**, 363–386, Plates 1, 2.
- Boorman, J. & Rowland, C. (1988) A key to the genera of British Ceratopogonidae (Diptera). *Entomologist's Gazette*, **39**, 65–73.
- Borkent, A. (1984) The systematics and phylogeny of the *Stenochironomus* complex (*Xestochironomus*, *Harrisius*, and *Stenochironomus*) (Diptera: Chironomidae). *Memoirs of the Entomological Society of Canada*, **128**, 269pp.
- Clastrier, J. (1960) Notes sur les Cératopogonidés. X. Cératopogonidés de la République du Congo (2). *Archives de l'Institut Pasteur d'Algérie*, **38**, 258–298.
- Clastrier, J. (1963) Notes sur les Cératopogonidés. XVIII. Espèces du genre *Stilobezzia* Kieffer ou Apparentées de la Région Paléarctique. *Archives de l'Institut Pasteur d'Algérie*, **41**, 41–68.
- Clastrier, J. & Wirth, W.W. (1961) Notes sur les Cératopogonidés. XIII. Cératopogonidés de la région éthiopienne. *Archives de l'Institut Pasteur d'Algérie*, **39**, 190–240.
- Coquillett, D.W. (1900) Papers from the Harriman Alaska Expedition. IX. Entomological results (3): Diptera. *Proceedings of the Washington Academy of Sciences*, **2**, 389–464.
- Debenham, M.L. (1970) Australasian Ceratopogonidae (Diptera, Nematocera). Part XIV: The genus *Serromyia* Meigen. *Proceedings of the Linnean Society of New South Wales*, **94**, 160–165.
- Debenham, M.L. (1987) *Chimaerohelea*, a new genus of Ceratopogonidae (Diptera) from North Queensland. *Invertebrate Taxonomy*, **1**, 801–806.
- Delecolle, J.-C. & Braverman, Y. (1987) Description de *Serromyia mangrovi* n.sp. du Sinai (Dipt.

- Ceratopogonidae). *Bulletin de la Société Entomologique de France*, **92**, 57–65.
- Downes, J.A. (1955) Observations on the swarming flight and mating of *Culicoides* (Diptera: Ceratopogonidae). *Transactions of the Royal Entomological Society of London*, **106**, 213–236, pls. 1–2.
- Downes, J.A. (1978) Feeding and mating in the insectivorous Ceratopogoninae (Diptera). *Memoirs of the Entomological Society of Canada*, **104**, 62pp.
- Downes, J.A. & Wirth, W.W. (1981) 28. Ceratopogonidae. Pp. 393–421 in *Manual of Nearctic Diptera*. Vol. 1. *Agriculture Canada Research Branch Monograph* No. 27. 674pp.
- Edwards, F.W. (1920) Some records of predaceous Ceratopogoninae (Diptera). *Entomologist's Monthly Magazine*, **6**, 203–205.
- Edwards, F.W. (1923) New and old observations on Ceratopogonine midges attacking other insects. *Annals of Tropical Medicine and Parasitology*, **17**, 19–29.
- Edwards, F.W. (1926) On the British biting midges (Diptera, Ceratopogonidae). *Transactions of the Entomological Society of London*, **74**, 389–426, 2 pls.
- Edwards, F.W. (1928) The Nematocerous Diptera of Corsica. *Encyclopédie Entomologique, Série B*, **4**, 157–189.
- Fabricius, J.C. (1775) *Systema entomologiae, sistens insectorum classes, ordines, genera, species adiectis synonymis, locis, descriptionibus, observationibus*, 832pp. Flensburgi et Lipsiae (=Flensburg and Leipzig).
- Fabricius, J.C. (1805) *Systema Anliatorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. 372pp. + 30pp. Brunsvigae [=Brunswick].
- Fox, I. (1946) A review of the species of the biting midges of *Culicoides* from the Caribbean Region. *Annals of the Entomological Society of America*, **39**, 248–258.
- Frison, T.H. (1927) A list of the insect types in the collections of the Illinois State Natural History Survey and the University of Illinois. *Bulletin of the Illinois Natural History Survey*, **16**, 137–309.
- Gad, A.M. (1951) The head-capsule and mouth-parts in the Ceratopogonidae (Diptera – Nematocera). *Bulletin de la Société Fouad Ier d'Entomologie*, **35**, 17–75.
- Gil Collado, J. (1957) Estudios sobre Dipteros hematofagos. La familia Helicidos (=Ceratopogonidos). *Medicina Tropica*, **30**, 245–262.
- Gil Collado, J. (1985) Claves de identificación de Ceratopogonidae de España peninsular. II. Subfamilia Ceratopogoninae (Dip., Nematocera). *Graellsia*, **41**, 43–63.
- Giles, F.E. & Wirth, W.W. (1982) Three new species of *Serromyia* (Diptera: Ceratopogonidae) from Sri Lanka, with new records and a key to the Oriental and Australasian species. *Proceedings of the Entomological Society of Washington*, **84**, 440–447.
- Gimmerthal, B.A. (1847) Vierter Beitrag zur Dipterologie Russlands. *Bulletin de la Société des Naturalistes de Moscou*, **20**, 142–151.
- Glukhova, V.M. (1977) Midges of the family Ceratopogonidae (synonym Helicidae) [in Russian]. Pp. 431–457 in *Determination of the freshwater invertebrates of the European regions of the USSR (Plankton and Benthos)* (ed. by L. A. Kutikova and Y. I. Starobogato), 510pp. Zoological Institute of the Academy of Sciences, Hydrometeo, Leningrad.
- Glukhova, V.M. (1979) *Larvae of the Biting Midges of the subfamilies Palpomyiinae and Ceratopogoninae of the Fauna of the USSR (Diptera, Ceratopogonidae = Heleidae)* [in Russian], 230pp. AN SSSR, Opredeliteli po faune SSSR, 121, Nauk, SSSR, Leningrad.
- Goetghebuer, M. (1920) Ceratopogoninae de Belgique. *Mémoires Musée Royal d'Histoire Naturelle de Belgique*, **8**, (3), 1–116.
- Goetghebuer, M. (1922a) étude critique des *Ceratopogon* de la collection Meigen. *Bulletin de la Société Entomologique de Belgique*, **4**, 50–59.
- Goetghebuer, M. (1922b) Nouveaux matériaux pour l'étude de la faune des Chironomides de Belgique. *Annales de Biologie Lacustre*, **11**, 38–62.
- Goetghebuer, M. (1933) Ceratopogonidae et Chironomidae nouveaux ou peu connus d'Europe (Quatrième note). *Bulletin et Annales de la Société Entomologique de Belgique*, **73**, 353–361.
- Goetghebuer, M. (1934) 13a. Helicidae (Ceratopogonidae). Pp. 1–94, Figs. 43–177, Pls. 7–12. In Lindner, E., ed., *Die Fliegen der palaearktischen Region*, Vol. 3. Lfg. 77. Stuttgart.
- Goetghebuer, M. (1936a) Nouvelle contribution a la Connaissance des Cératopogonides et des Chironomides de Belgique. *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **76**, 319–326.
- Goetghebuer, M. (1936b) Les Cératopogonides et les Chironomides de Belgique au point de vue hydrobiologique. *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **76**, 69–76.
- Goetghebuer, M. (1949) Biologie des Cératopogonides (Diptères Némocères). *Biologisch Jaarboek*, **16**, 113–117.
- Grogan, W.L. & Wirth, W.W. (1979) The North American predaceous midges of the genus *Palpomyia* Meigen (Diptera: Ceratopogonidae). *Memoirs of the Entomological Society of Washington*, **8**, vi + 125pp.
- Havelka, P. (1976) Limnologische und systematische Studien an Ceratopogoniden (Diptera: Nematocera). *Beiträge zur Entomologie*, **26**, 211–305.
- Havelka, P. (1978) Ceratopogonidae. Pp. 441–458. In Illies, J., ed., *Limnofauna Europaea*, 2nd edn.

- Stuttgart.
- Havelka, P. (1979) Situation der Ceratopogonidenforschung auf der Iberischen Halbinsel (Dipt. Ceratopogonidae). *Eos*, **53**, 55–74, pl. II.
- Havelka, P. & Caspers, N. (1981) Die Gnitzen (Diptera, Nematocera, Ceratopogonidae) eines kleinen Waldbaches bei Bonn. *Decheniana*, **25**, 1–100.
- Heyden, L. von (1870) Fossile Dipteren aus der Braunkohle von Rott im Siebengebirge. *Palaeontographica*, **17**, 237–266, Pls. 44–45.
- Johannsen, O.A. (1928) Order Diptera. Pp. 687–868 in M. D. Leonard, ed., List of the insects of New York with a list of the spiders and certain other allied groups. *Memoirs of the Cornell University Agricultural Experiment Station*, **101**, 1–1121.
- Johannsen, O.A. (1943) A generic synopsis of the Ceratopogonidae (Heleidae) of the Americas, a bibliography, and a list of the North American species. *Annals of the Entomological Society of America*, **36**, 763–791.
- Kariya, Y., Imai, S., Ishii, T. & Morii, T. (1989) Ultrastructural comparison of egg surface structure of seven *Culicoides* species (Diptera: Ceratopogonidae) from Japan. *Japan Journal of Sanitary Zoology*, **40**, 55–59.
- Kertész, K. (1902) *Catalogus dipterorum hucusque descriptorum*, Vol. 1, 339pp. Lipsiae, Budapestini [=Leipzig, Budapest].
- Kettle, D.S. & Lawson, J.W.H. (1952) The early stages of British biting midges *Culicoides* Latreille (Diptera: Ceratopogonidae) and allied genera. *Bulletin of Entomological Research*, **43**, 421–467, pls. 14–19.
- Kieffer, J.J. (1899) Description d'un nouveau genre et tableau des genres européens de la famille des Chironomides (Dipt.). *Bulletin de la Société Entomologique de France*, **1899**, 66–70.
- Kieffer, J.J. (1901) Synops des représentants européens du groupe *Ceratopogon* avec description de quelques espèces nouvelles. *Bulletin de la Société d'Histoire Naturelle de Metz*, **9**, 143–165.
- Kieffer, J.J. (1906) Diptera. Fam. Chironomidae. Fasc. 42, 78pp., 4 pls. In Wytzman, P., ed., *Genera Insectorum*. Bruxelles.
- Kieffer, J.J. (1911) The Percy Sladen Trust Expedition to the Indian Ocean in 1905. Under the leadership of Mr. J. Stanley Gardiner. Vol. 3. No. XV. Diptera, Chironomidae der Seychellen-inseln, aus der Sammlung von Mr. H. Scott. *Transactions of the Linnean Society of London* (2nd Series), **14**, 331–366.
- Kieffer, J.J. (1913) Nouveaux Chironomides (Tendipédides) d'Allemagne. *Bulletin de la Société d'Histoire Naturelle de Metz*, **28**, 7–35.
- Kieffer, J.J. (1914) South African Chironomidae (Diptera). *Annals of the South African Museum*, **10**, 259–270.
- Kieffer, J.J. (1919) Chironomides d'Europe conservés au Musée National Hongrois de Budapest. *Annales Musei Nationalis Hungarici*, **17**, 1–160.
- Kieffer, J.J. (1925a) 16. Chironomiden der Hochmoore Nordeuropas und des östlichen Mitteleuropas. *Beiträge zur Kunde Estlands*, **10**, 145–163.
- Kieffer, J.J. (1925b) Nouveaux genres et nouvelles espèces de chironomides piqueurs. *Archives de l'Institut Pasteur d'Algérie*, **3**, 405–430.
- Lawson, J.W.H. (1951) The anatomy and morphology of the early stages of *Culicoides nubeculosus* Meigen (Diptera: Ceratopogonidae = Heleidae). *Transactions of the Royal Entomological Society of London*, **102**, 511–570, Pl. 1.
- Linley, J.R. (1985) Growth and survival of *Culicoides melleus* larvae (Diptera: Ceratopogonidae) on four prey organisms. *Journal of Medical Entomology*, **22**, 178–189.
- Loew, H. (1850) Ueber den Bernstein und die Bernsteinfauna. Program könig. *Realschule Meseritz*, **1850**, 1–48.
- Macfie, J.W.W. (1934) Report on a collection of Ceratopogonidae from Malaya. *Annals of Tropical Medicine and Parasitology*, **28**, 279–293.
- Malloch, J.R. (1914) Notes on North American Diptera, with descriptions of new species in the collection of the Illinois State Laboratory of Natural History. *Bulletin of the Illinois State Laboratory of Natural History* (1915), **10**, 213–243.
- Mayer, K. (1957) Die Beschreibung der Puppen von *Dicrohelea albidorsata* de M. und *Xenohelea galatea* de M. mit einem überblick über das System der Heleinae (Dipt. Heleidae). *Deutsche Entomologische Zeitschrift*, **4**, 30–34.
- Mayr, E. (1969) *Principles of Systematic Zoology*, xi + 428pp. McGraw-Hill, New York.
- Meigen, J.W. (1804) *Klassifikation und Beschreibung der europäischen zweiflügeligen Insekten* (Diptera Linn.). Erster Band. Abt. I. pp. i–xxviii + 1–152, pls. 1–8; Abt. II, pp. i–vi + 153–314, pls. 9–15. Braunschweig.
- Meigen, J.W. (1818) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*, Vol. 1, xxxvi + 333pp., Pls. 1–11. Aachen.
- Meigen, J.W. (1838) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*, Vol. 7: 'oder Supplementband', xii + 434pp., Pls. 67–74.
- Meijere, J.C.H. de (1946) Zevende Supplement op de Nieuwe Naamlijst van Nederlandsche Diptera van 1898. (Eerste Supplement op mijne Naamlijst van 1939). *Tijdschrift voor Entomologie*, **87**, 1–25.
- Meillon, B. de & Downes, J.A. (1986) Sub-Saharan Ceratopogonidae (Diptera). X. Report on species collected in the Drakensberg, South Africa. *Canadian Entomologist*, **118**, 141–180.
- Meillon, B. de & Wirth, W.W. (1981) Sub-Saharan

- Ceratopogonidac (Diptera). VII. The biting midges of the Kruger National Park, South Africa, exclusive of the genus *Culicoides*. *Annals of the Natal Museum*, **24**, 563–601.
- Meillon, B. de & Wirth, W.W. (1983) Subsaharan Ceratopogonidac (Diptera). XI. The genus *Serromyia* Meigen. *Annals of the Natal Museum*, **25**, 383–402.
- Meunier, F. (1904) Monographie des Cecidomyiidae, des Sclariidae, des Mycetophilidae et des Chironomidae. *Annales de la Société Scientifique de Bruxelles*, **28**, 12–275.
- Morge, G. (1975) Dipteren-Farbtafeln nach den bisher nicht veröffentlichten Original-Handzeichnungen Meigens: 'Johann Wilhelm Meigen: Abbildung der europaischen zaeiflügeligen Insecten, nach der Natur'. Pars I. Vorwort des Herausgebers — Faksimiles von Original-Legenden und — index: 'Erklärung der Fig.' und 'Alphabetisches Verzeichniss der Gattungen und Arten' — Farbtafeln I — LXXX. *Beiträge zur Entomologie*, **25**, 383–500, Pls. 1–80.
- Ortiz, I. (1958) Sobre *Johannseniella fluviatilis* Lutz, 1914, y *Culicoides pachymerus* Lutz, 1914 (Diptera: Ceratopogonidac). *Bolletín Venezolano de Laboratorio Clínico*, **3**, 37–42.
- Pont, A.C. (1986) A revision of the Fanniidae and Muscidae described by J. W. Meigen (Insecta: Diptera). *Annales des Naturhistorischen Museums Wien*, **87**, 197–253.
- Remm, H. (1965) New species of biting-midges (Diptera, Helicidae) from the European part of the USSR [in Russian, with English summary]. *Entomologicheskoe Obozrenie*, **44**, 182–188 (Translation in *Entomological Review*, **44**, 101–103).
- Remm, H. (1967) On the fauna of Ceratopogonidac (Diptera) in the Caucasus [in Russian]. *Tartu Riikliku Ulukooli Toimetised*, **194**, 3–37.
- Remm, H. (1969) 13. Fam. Ceratopogonidac (Helicidae) (in Russian). *Key to the Insects of the European Part of the USSR*, **5**, 201–218.
- Remm, H. (1973a) 246. Ceratopogonidac Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei (Diptera). *Reichenbachia*, **14**, 171–186.
- Remm, H. (1973b) Beiträge zur Ceratopogoniden-Fauna Ungarns (Diptera). *Folia Entomologia Hungarica*, **26**, 349–357.
- Remm, H. (1975) On the classification of the biting midges (Diptera, Ceratopogonidac) [in Russian]. *Parasitologiya*, **9**, 393–397.
- Remm, H. (1981) New synonyms and new names of the Palaearctic Ceratopogonidac (Diptera). *Eesti NSV Teaduste Akadeemia Toimetised*, **30**, 27–32.
- Remm, H. (1988) Ceratopogonidac. Pp. 11–110 in *Catalogue of Palaearctic Diptera*, Volume 3. Ceratopogonidac – Mycetophilidae. A. Soós Ed., 448pp. Akadémiai Kiadó, Budapest.
- Rowley, W.A. & Cornford, M. (1972) Scanning electron microscopy of the pit of the maxillary palp of selected species of *Culicoides*. *Canadian Journal of Zoology*, **50**, 1207–1210.
- Saunders, L.G. (1924) On the life history and the anatomy of the early stages of *Forcipomyia* (Diptera, Nemat., Ceratopogoninac). *Parasitology*, **16**, 164–213.
- Schiner, J.R. (1864) *Fauna Austriaca. Die Fliegen*, Vol. 2, xxxii + 658pp. Wien [=Vienna].
- Sphon, G.G. (1973) Additional type specimens of fossil Invertebrata in the collections of the Natural History Museum of Los Angeles County. *Contributions in Science, Natural History Museum of Los Angeles County*, No. 250, 75pp.
- Staeger, R.C. (1839) Systematisk fortegnelse over de i Danmark hidtil fundne Diptera. *Naturhistorisk Tidsskrift*, **2**, 549–600.
- Statz, G. (1941) Plagegeister aus dem rheinischen Braunkohlenwalde. *Rheinischer Naturfreund*, **5**, (1), 1–16.
- Statz, G. (1944) Neue Dipteren (Nematocera) aus dem Oberoligozän von Rott. VI. Familie: Tendipedidae (Zuck-oder Schwarmücken). VII. Familie: Helcidae (Ceratopogonidac), (Gnitzen). VIII. Familie: Lycoriidae (Trauermücken). *Palaeontographica* Abt. A, **95**, 123–188, 17 pls.
- Stephens, J.F. (1829) *A systematic catalogue of British insects: being an attempt to arrange all the hitherto discovered indigenous insects in accordance with their natural affinities*, Volume 2, 388 pp. London.
- Strand, E. (1928) Miscellanea nomenclatorica zoologica et palaeontologica. I-II. *Archiv für Naturgeschichte* (1926) Abt. A, **91**, (8), 62–66.
- Strenzke, K. (1950) Systematik, Morphologie und ökologie der terrestrischen Chironomiden. *Archiv für Hydrobiologie*, Supplement-Band, **18**, 207–414.
- Szadziewski, R. (1986) Redescriptions and notes on some Ceratopogonidac (Diptera). *Polskie Pismo Entomologiczne*, **56**, 3–103.
- Szadziewski, R. (1988) Biting midges (Diptera, Ceratopogonidac) from Baltic amber. *Polskie Pismo Entomologiczne*, **58**, 3–283.
- Szadziewski, R. & Krzywinski, J. (1988) Biting midges of the genus *Culicoides*/Ceratopogonidac/visiting umbelliferous flowers in Poland. pp. 155–158 in *Medical and Veterinary Dipterology, Proceedings of the International Conference, Nov. 30 – Dec. 4, 1987*. J. Olejniczek Ed., viii + 305pp. House of Technics CSVTS, Ceske Budejovice.
- Teskey, H.J. (1981) 3. Morphology and terminology – larvae. Pp. 65–88 in *Manual of Nearctic Diptera*, Vol. 1. *Agriculture Canada Research Branch Monograph* No. 27. 674pp.
- Thienemann, A. (1950) Lunzer Chironomiden. Ergebnisse von Untersuchungen der stehenden Gewässer des Lunzer Seengebietes (Niederösterreich). *Archiv für Hydrobiologie, Supplement-*

- Band, 18, 1–202.
- Thomson, C.G. (1869) Diptera species novas descripsit. Pp. 443–614, Pl. 9, in *Kongliga Svenska fregatten Eugenie's resa omkring jorden*. Pt 2: Zoologi. 1. Insekter, 617pp., 9 pls. Stockholm, '1868'.
- Thomson, L.C. (1937) Aquatic Diptera Part V. Ceratopogonidae. *Memoirs of the Cornell University Agricultural Experiment Station*, 210, 57–80, Pls. 10–18.
- Tokunaga, M. (1940) Ceratopogonidae and Chironomidae from the Micronesian Islands. *Philippine Journal of Science*, 71, 205–226.
- Westwood, J.O. (1840) Order XIII. Diptera Aristotle (Antliata Fabricius. Halteriptera Clairv.). Pp. 125–128 (= signature I, part), 129–144 (= signature K), 145–158 (= signature L) in *An Introduction to the modern classification of insects. Synopsis of the genera of British insects*, 158pp. London.
- Williston, S.W. (1907) Dipterological Notes. *Journal of the New York Entomological Society*, 15, 1–2.
- Winnertz, J. (1852) Beitrag zur Kenntniss der Gattung *Ceratopogon* Meigen. *Linnaea Entomologica*, 6, 1–80.
- Wirth, W.W. (1952) The Heleidae of California. *University of California Publications in Entomology*, 9, 95–266.
- Wirth, W.W. (1965) Family Ceratopogonidae. pp. 121–142 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*, 276 pp. United States Department of Agriculture, Agricultural Research Service.
- Wirth, W.W. (1973) Family Ceratopogonidae. Pp. 346–388 in *A Catalog of the Oriental Region*, Volume 1. Suborder Nematocera, 618pp. University Press of Hawaii, Honolulu.
- Wirth, W.W. & Grogan, W.L. (1981) Natural History of Plummers Island, Maryland. XXV. Biting midges (Diptera: Ceratopogonidae). 3. The species of the tribe Stilobezziini. *Bulletin of the Biological Society of Washington*, 5, 1–102.
- Wirth, W.W. & Grogan, W.L. (1988) The predaceous midges of the World (Diptera: Ceratopogonidae: Tribe Ceratopogonini). *Flora and Fauna Handbook* No. 4, xv + 160pp. E.J. Brill, Leiden.
- Yu, Y-X. (1978) Chapter III. The identification of important biting midges of China [in Chinese] pp. 178–224, Pls. 16–22. *Manual of Important Chinese Insect Vectors of Animal Disease*. People's Health Publishing House, China.
- Zetterstedt, J.W. (1838) Diptera Scandinaviae. Sect. 3: Diptera. Pp. 477–868 in *Insecta Lapponica* vi + 1140pp. Lipsiae [=Leipzig].
- Zetterstedt, J.W. (1850) *Diptera Scandinaviae. Disposita et descripta*, Vol. 9, pp. 3367–3710. Lundae [=Lund].
- Zihali-Sebess, G. (1940) Magyarország Heleidái. (Heleiden aus Ungarn). *Folia Entomologia Hungarica*, 5, 10–133.
- Zimsen, E. (1964) *The type material of I. C. Fabricius*. Munksgaard, Copenhagen.

Accepted 27 October 1989

Erratum

Vossbrinck, C.R. & Friedman, S. (1989) A 28s ribosomal RNA phylogeny of certain cyclorrhaphous Diptera based upon a hypervariable region. *Systematic Entomology*, **14**, 417–431.

The tsetse species listed as *Glossina simulans* should be *Glossina morsitans*.

Teskey (1981) and detailed characters (i.e. chaetotaxy) as well as pupal characters follow Saunders (1924) and Lawson (1951).

We use some terms in the keys and descriptions that require further comment. Some adult *Serromyia* lack pruinosity on the scutum and in such specimens the scutum is brilliantly shiny and highly reflective in pinned material (the humeral pits are not distinct from the surrounding shiny cuticle) and utterly lacking fine spicules when viewed laterally in slide-mounted specimens. Specimens which are reported to exhibit pruinosity on the scutum are somewhat dull in reflected light (so that the humeral pits appear as discrete, shiny patches). When slide mounted, such specimens have a short coat of fine spicules visible in lateral view (Fig. 1A). We looked for pruinosity amongst the dorso-central setae on the laterally mounted thorax using interference contrast optics.

When one examines the brilliantly shining scutum of a pinned specimen with a dissecting microscope, one can be confident of the lack of pruinosity; but when the scutum is dull, care must be taken. A somewhat dirty specimen may appear dull when in fact it lacks pruinosity. In most of these instances the humeral pits would also be dull. We generally preferred to examine slide-mounted material to ensure correct interpretation of the state of pruinosity.

We use the term 'strong bristles' in describing armature of the legs. Among ceratopogonids,

some groups have bristles that are more markedly developed than in any species of *Serromyia*. The strong bristles as used here to describe character states refer to those bristles which stand out from the remaining setae as thicker and often appear to be more darkly pigmented. Figs 1C, D indicate examples of typical strong bristles on the fore and hind leg, respectively. The lateral strong bristles on the hind coxa are shown in Fig. 1B. Sometimes strong bristles are broken off at the base and then the enlarged socket needs to be searched for, for accurate interpretation of keys and descriptions.

Leg coloration is illustrated somewhat diagrammatically. Leg pigmentation intensity differed between specimens and varied according to preparation technique. Illustrations therefore are meant to show extent of pigmentation for a given species with the intensity of pigmentation not necessarily comparable between species.

Parameres are described as either rounded or tapered apically. Rounded parameres are sometimes shrivelled and may appear pointed. However, in most such instances the two parameres look different from one another. Parameres which are tapered apically are always of clearly defined and characteristic form, as illustrated in the drawings of the male genitalia.

Ratios and some structures discussed in this study are abbreviated as follows:

L: length

Table 6. Descriptive statistics for hind femur length/width of male *Serromyia*.

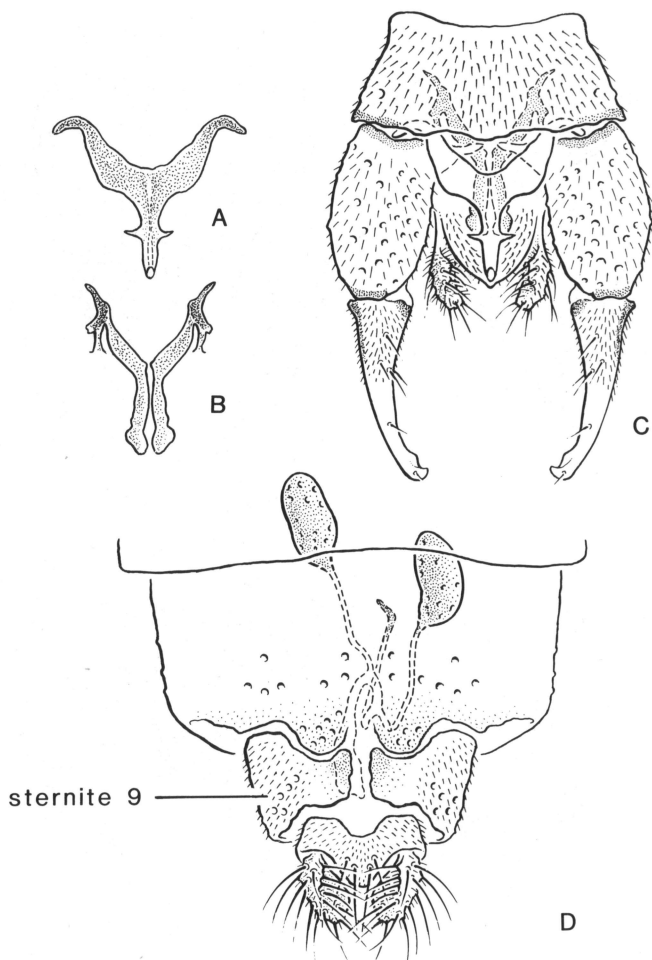
Species	n	Mean	Min.	Max.	SD
<i>barberi</i>	10	6.51	5.62	7.06	0.575
<i>borealis</i>	2	5.67	5.57	5.77	—
<i>crassifemorata</i>	9	6.10	4.16	7.06	0.937
<i>nudicolis</i>	16	5.96	5.38	6.64	0.388
<i>sierrensis</i>	1	6.19	6.19	6.19	—
<i>vockerothi</i>	3	5.90	5.74	6.05	—
<i>ledicola</i>	15	6.51	5.87	7.36	0.445
<i>atra</i>	13	6.55	5.00	7.00	0.539
<i>bicolor</i>	3	7.64	7.52	7.76	—
<i>femorata</i>	19	6.47	5.23	7.52	0.517
<i>mangrovi</i>	2	4.12	4.08	4.15	—
<i>morio</i>	13	7.15	6.32	7.50	0.612
<i>pacifica</i>	1	6.00	6.00	6.00	—
<i>rufitarsis</i>	10	6.68	5.90	7.06	0.367
<i>subinermis</i>	10	6.82	6.46	7.26	0.287
<i>tecta</i>	2	6.28	6.25	6.32	—

Kieffer (1913, 1919) noted that the fork of the cubitus (as posticale) was markedly distal to the position of the crossvein r-m (as transversale) and that the wings were spotted. Combined with the presence of short, equal claws on the fore and mid legs and an elongate hind claw (equal to the length of the fifth tarsomere), this description cannot apply to any known *Serromyia*, but does fit a general description of several species of Palaearctic *Monohelea*. We therefore transfer the name to that genus as a new combination: *Monohelea scirpi* (Kieffer).

Serromyia fuligipennis Clastrier has recently been placed in a new genus *Congohelea* Wirth & Grogan and we agree that it was incorrectly placed in *Serromyia*.

Havelka (1978) considered *Ceratopogon*

communis Fabricius 1805 and *C. palustris* Meigen 1804 as members of *Serromyia* but there is, in our opinion, no evidence for this. Remm (1988) placed *C. communis* in *Ceratopogon* (considering that Fabricius' description of *C. communis* was not a new name but followed Meigen's earlier 1804 description) and *C. palustris* in *Dasyhelea* Kieffer. The date of submission for the catalogue in Remm (1988) was the end of 1982 and Szadziewski (1986), after examining the type specimens, has shown that the *Ceratopogon palustris* is actually a species of *Forcipomyia*. Havelka (1978) also interpreted *Ceratopogon candidatus* Winnertz 1852 as a member of *Serromyia* but considered the name unavailable because of lack of use (50-year rule). Remm (1988) correctly placed



Figs 12A–D. A aedeagus, B paramere, C male genitalia of *Serromyia tecta*; D, female genitalia of *S. borealis*.