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A revision of the Holarctic species of *Serromyia* Meigen (Diptera: Ceratopogonidae)

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Abstract. This revision recognizes sixteen extant species of *Serromyia* in the Holarctic Region including seven described as new: *S.bicolor* Borkent, *S.borealis* Borkent, *S.nudicolis* Borkent, *S.pacifica* Remm, *S.sierrensis* Borkent, *S.tecta* Borkent and *S.vockerothi* Borkent. In addition, eleven new synonyms are indicated. Keys and descriptions of the male and female adults, and their known distributions, are given for all species. The egg and first instar larva of *Serromyia nudicolis* Borkent n.sp., the pupa of *S.atra* (Meigen) and the fourth instar larvae of an unidentified *Serromyia* are also described.

All available fossil specimens were examined, some redescribed, and two named as new: *S.ryszardi* Borkent and *S.sinuosa* Borkent.

New combinations are *S.alpheus* (Heyden), *Atrichopogon trichopus* (Thomson) and *Monohelea scirpi* (Kieffer).

Limited phylogenetic interpretation indicates that all extent Holarctic species, with the exception of *S.mangrovi* Delecolle and Braverman, form a monophyletic group. Six Baltic amber species are not members of this clade. *Metacanthohelea* is recognized as the sister group of the genus *Serromyia*.

Introduction

The genus *Serromyia* Meigen is a rather distinctive taxon within the Ceratopogonidae. Within the Holarctic Region its members can be easily recognized with the naked eye, or perhaps with a hand lens, by their swollen hind femora which bears strong ventral spines.

We began a revision of this genus with two purposes in mind. The first was to provide the basis for accurate identification of the known species in the Holarctic Region. Although the species outside the Holarctic Region have been recently revised (Meillon & Wirth, 1983; Meillon & Downes, 1986; Giles & Wirth, 1982), the Holarctic species remain very poorly understood. A number of new species from the Nearctic Region were known to us and the identification of Palaearctic species was a jumble of confused synonymy and conflicting, generally uninterpretable, descriptions.

The second motive for initiating a revision was to examine the phylogenetic relationships between the species of *Serromyia*. Because we were initially confident that the genus was monophyletic and exhibited a reasonable degree of interspecific structural variation, we considered the genus a good candidate for phylogenetic analysis. On the whole, our expectations were only partially met. One major difficulty was the current status of our understanding

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of the phylogenetic relationships between the genera of Ceratopogonidae. Enough uncertainties exist that virtually all other Ceratopogonidae must be used in outgroup comparisons.

The genus is relatively well represented by Eocene and Oligocene fossils and we have incorporated these into our revision to better understand the diversification of the extant species in the Holarctic Region.

Materials and Methods

Specimens examined. This study was based on the examination of 657 males, 1154 females, five pupae and nine larvae of *Serromyia*. These included representatives of all named species in Table 1 noted with an asterisk. We were unfortunately unable to examine some African species housed in the South African Institute for Medical Research, Johannesburg.

Generally, the genus was poorly represented in most of the collections from which we requested loans. We were able to study the immatures of only two *Serromyia* identified to species. The eggs and first instar larvae of *S.nudicolis* sp.n. were secured from field-collected female adults which were decapitated to induce egg laying. A pupa of *S.atra* (Meigen) and three larvae and four pupae of unidentified *Serromyia* were also available from the collections of Thienemann and Strenzke (ZSMC).

Finally, to obtain better outgroup comparisons for phylogenetic analysis and to estimate potential for parallelism of character states, we examined adult material of virtually every described genus of Ceratopogonidae.

We were able to examine type material of all *Serromyia* species described in this analysis unless otherwise noted. Details about the location of type material as well as sex and details of labelling are recorded under each species.

We were able to examine most of the material housed in the HMHN and interpreted by Remm (1973b).

The abbreviations used to represent various museums from which material was received and where specimens are deposited are those provided by Arnett & Samuelson (1986). Private collections are abbreviated according to the procedure used in that work. Those used in this study are as follows:

AMNH: Department of Entomology Collection, American Museum of Natural History, Central Park West at 79th St., New York, New York, 10024, U.S.A.

BMNH: Department of Entomology, British Museum (Natural History), London SW7 5BD, U.K.

BPBM: Department of Entomology Collection, Bernice P. Bishop Museum, P.O. Box 19000A, Honolulu, Hawaii 96819, U.S.A.

CASC: Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

CNCI: Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario K1A 0C6, Canada.

CUIC: Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14850, U.S.A.

HNHM: Zoological Department, Hungarian Natural History Museum, Baross utca 13, H-1088, Budapest, Hungary.

INHS: Illinois Natural History Survey Insect Collection, 607 E. Peabody Drive, Champaign, Illinois 61820, U.S.A.

ISNB: Institute Royal des Sciences Naturelles de Belgique, Rue Vautier 29, B-1040, Bruxelles, Belgium.

IZBE: Institute of Zoology and Botany, Vanemuise str. 21, Tartu 202400, U.S.S.R.

KUPC: Katedra Systematické Zoologie, Prirodovedecké Fakulty, University Karlovy, Vinicná 7, 128 44 Praha 2, Czechoslovakia.

LACM: Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A.

MCZC: Entomology Department, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, Massachusetts 02138, U.S.A.

MNHN: National Collection of Insects, Museum National d'Histoire Naturelle, 45 rue Buffon, Paris 75005, France.

MZW: Museum of the Earth, Al. Na Skarpie 20/26, 00–488 Warsaw, Poland.

MZLU: Department of Zoology, Zoological Museum, Helgonavägen 3, S-223 62 Lund, Sweden.

MZSF: Museum Zoologique, Université de Strasbourg, 29, Blvd. de la Victoire, F-67 Strasbourg, France.

NHMW: Naturhistorisches Museum Wien, Postfach 417, Burgring 7, 1040 Wien, Austria.

Table 1. Checklist of *Serromyia* species of the world. For each species the sex examined in this study is noted with an asterisk. The type locality is given for each species.

M	F	
	*	*aethiopiae* Clastrier & Wirth 1961: 219. Gambia.
*	*	*agathae* Meillon & Wirth 1983: 388. Republic of South Africa.
		alpheus Heyden 1870: 251 (*Ceratopogon*). Rott, Federal Republic of Germany. Miocene. **New combination.**
*	*	*anomalicornis* (Loew) 1850: 30 (*Ceratopogon*). Baltic amber. Eocene.
*	*	*atra* (Meigen) 1818: 84 (*Ceratopogon*). Latvia.
		albitarsis Kieffer 1919: 71. Hungary.
		micronyx Kieffer 1919: 70. Hungary. **New synonym.**
		nitens Goetghebuer 1920: 73. Belgium. **New synonym.**
		spinosipes Kieffer 1919: 72. Hungary. **New synonym.**
*	*	*barberi* Wirth 1952: 205. California.
*	*	*bicolor* Borkent n.sp. Federal Republic of Germany.
*	*	*borealis* Borkent n.sp. Alberta.
	*	*colorata* Statz 1944: 150. Rott, Federal Republic of Germany. Miocene.
		austera Statz 1944: 150. Rott, Federal Republic of Germany. Miocene. **New synonym.**
		spinofemorata Statz 1944: 150. Rott, Federal Republic of Germany. Miocene. **New synonym.**
*	*	*crassifemorata* Malloch 1914: 218. Illinois.
*	*	*esakii* Tokunaga 1940: 218. Caroline Islands.
*	*	*femorata* (Meigen) 1804: 28 (*Ceratopogon*). Europe.
		armata (Meigen) 1818: 83 (*Ceratopogon*). Germany.
		flavicrus (Kieffer) 1906: 63 (*Palpomyia*). New name for *flavipes* Gimmerthal. **New synonym.**
		flavipes Gimmerthal 1847: 144 (*Ceratopogon*), not Meigen 1804: 28. England. **New synonym.**
		foersteri (Meigen) 1838: 21 (*Ceratopogon*). England.
		inermipes Kieffer 1919: 73. England.
*		*festiva* Kieffer 1911: 346. Seychelles.
	*	*heveli* Giles and Wirth 1982: 442. Sri Lanka.
*	*	*ledicola* Kieffer 1925a: 156. Estonia.
		europaea Clastrier 1963: 61. Austria.
		macronyx Goetghebuer 1933: 355. Belgium.
	*	*maculipennis* Giles & Wirth 1982: 444. Sri Lanka.
*	*	*mangrovi* Delecolle & Braverman 1987: 57. Egypt.
		meiswinkeli Meillon & Wirth 1983: 390. Republic of South Africa.
*	*	*morio* (Fabricius) 1775: 800 (*Culex*). England.
		nudipennis Kieffer 1913: 10. England. **New synonym.**
		neethlingi Meillon & Wirth 1983: 392. Republic of South Africa.
*	*	*nocticolor* Kieffer 1914: 268. Republic of South Africa.
*	*	*nudicolis* Borkent n.sp. Maine.
*	*	*pacifica* Remm n.sp. Sakhalin Island, East Siberia, U.S.S.R.
	*	*pendleburyi* Macfie 1934: 280. Malaya.
	*	*polonica* Szadziewski 1988: 135. Baltic amber. Eocene.
	*	*punctata* Giles & Wirth 1982: 446. Sri Lanka.
*	*	*reyei* Debenham 1970: 161. North Territory, Australia.
		rossi Meillon & Wirth 1983: 396. Republic of South Africa.
*	*	*rufitarsis* (Meigen) 1818: 83 (*Ceratopogon*). Europe.
		gelida Kieffer 1925: 429. Latvia. **New synonym.**
		bispinosa Goetghebuer 1936a:321. Belgium. **New synonym.**
		dipetala Remm 1965: 182. Estonia. **New synonym.**
*		*ryszardi* Borkent n.sp. Baltic amber. Eocene.
*	*	*sierrensis* Borkent n.sp. California.
	*	*silvatica* Meillon & Downes 1986: 175. Republic of South Africa.
*	*	*sinuosa* Borkent n.sp. Baltic amber. Eocene.
	*	*spinigera* (Loew) 1850: 30 (*Ceratopogon*). Baltic amber. Eocene.
		elongatus Meunier 1904: 231 (*Ceratopogon*). Baltic amber. Eocene.

Table 1 (*continued*)

M	F	
	*	*stuckenbergi* Meillon & Wirth 1983: 398. Republic of South Africa.
*	*	*subinermis* Kieffer 1919: 73 (as var. of *spinosipes*). Hungary.
*	*	*succinea* Szadziewski 1988: 135. Baltic amber. Eocene.
*	*	*tecta* Borkent n.sp. Federal Republic of Germany.
*	*	*vockerothi* Borkent n.sp. Manitoba.
*	*	*zuluensis* Meillon and Wirth 1981: 589. Republic of South Africa.

NHRS: Naturhistoriska Riksmuseet, Sektionen för Entomologi, 104 05 Stockholm, Sweden.

OXAM: Hope Entomological Collections, University Museum, Parks Road, Oxford OX1 3PW, U.K.

PEHC: P. Havelka, Landesanstalt für Umweltschutz Baden-Württemberg, Postfach 21 13 10, 7500 Karlsruhe 21, F.R.G.

RYSC: R. Szadziewski, Department of Invertebrate Zoology, University of Gdansk, Czolgistow 46, 81–378 Gdynia, Poland.

UCDC: Department of Entomology, University of California, Davis, California 95616, U.S.A.

USNM: United States National Entomological Collection, Department of Entomology, U.S. National Museum of Natural History, Washington, DC 20560, U.S.A.

UZMH: Division of Entomology, Zoological Museum, SF-00100, Helsinki 10, Finland.

ZMAN: Instituut voor Taxonomische Zoologie, Universiteit van Amsterdam, Plantage Middenlaan 64, Amsterdam, The Netherlands.

ZMAS: Zoological Museum, Academy of Science, Universitetskaya, Naberzhnayal, B-164, Leningrad, U.S.S.R.

ZMUC: Zoologisk Museum, Universitetsparken 15, DK 2100, Kobenhavn, Denmark.

ZMUH: Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Papendamm 3, 2 Hamburg 13, F.R.G.

ZSMC: Zoologische Sammlung des Bayerischen Staates, Munchhausenstrasse 21, D-8000 Munchen 60, Bayern, F.R.G.

Collecting, preservation and examination techniques

We had the greatest success in obtaining both individuals and species by sweeping vegetation. In general, *Serromyia* adults were collected in habitats where either pools, seeps or small creeks were found. Although we found adults at any time of the day, during full daylight adults of some species occurred very close to the ground. In these instances the net edge was held on the ground while sweeping vegetation. At dusk, individuals were more common in vegetation well above ground level.

The invariable reaction of *Serromyia* adults when swept up was to feign death and fall to the bottom of the net, remaining there sometimes for several minutes. They would then slowly crawl from amongst other insects and debris. It was therefore important to observe the net catch for several minutes to determine whether adults were present. Individuals found resting on vegetation had a similar reaction of collapsing and falling to the ground when disturbed (see bionomic section under *S.nudicolis*). This may explain why adults were often collected near ground level during daylight hours.

Further specific bionomic information which influenced collecting success is given with the account of the pertinent species.

We found that light trapping with a UV light failed to attract *Serromyia*. In one location at Mary's Peak, 21 km W Corvallis, Oregon, such a trap was placed within 5 m of resting females of *S.barberi* Wirth and still did not attract individuals. However, several European species have been collected using light trapping methods.

We attempted to collect immatures of *Serromyia*, but efforts to extract larvae or pupae from moss and bottom samples by various flotation techniques failed.

Adults were preserved in 70% ethanol. They were then examined in one of several ways. Most specimens were mounted on microscope slides using a method developed by Leo Forster

of our centre. Adults had their wings removed and placed in 15% acetic acid. The head and abdomen were dissected from the thorax and all were placed in 10% KOH which was then heated in a hot water bath. When fully cleared these were placed with the wings in the acetic acid. All parts were then taken through successive baths of 100% 2-propanol, 2-propanol layered over clove oil, pure clove oil (where the antennae and left legs were further separated from the head and thorax respectively) and finally into Canada Balsam on the slide. The antennae and legs were sometimes removed while the specimen was in the Canada Balsam.

Many adults were critical point dried and glued to pins. Such dried material allowed examination of pruinosity and some other character states. We left no material preserved in alcohol because such material becomes bleached, distorted, and unfit for study in only a few years.

We also examined specimens of most species cleared, dissected and placed in glycerine. This allowed for careful side by side comparison of many structures of two or more species. These specimens were subsequently slide mounted in Canada Balsam at the end of the study.

At the beginning of this study we searched for character states which could be used to recognize species of *Serromyia* using pinned, glycerine immersed and slide mounted material. Although conscious of characters previously used by ceratopogonid workers, our approach was to search for any character that might be useful for recognizing taxa. Several characters not previously used are therefore incorporated into this analysis. Some characters which have been traditionally viewed as 'good taxonomic' characters were found to be of no value and are either relegated to the generic description or are ignored.

This examination of specimens for significant characters provided the rational basis for the measurements and ratios given in Tables 2–13.

Antennal and wing measurements were taken as described by Grogan & Wirth (1979). Aedeagus length/width was the maximum median, longitudinal distance (median base to tip of aedeagus) divided by the distance between the tips of lateral apodemes of the aedeagus. Length of female hind claws was the minimum distance between the base of the claw and its tip, regardless of the degree of curvature of the claw.

On many of the labels of material housed in the CNCI, there are numbers referring to further collecting data or bionomic information. These are numbers beginning with either 'JAD' or 'CD', referring to specimens collected or dealt with by either Mr J. Antony Downes or the senior author, respectively. Such further information is recorded on data sheets housed in the Diptera Unit of our Centre.

Most photomicrographs were taken with

Table 2. Descriptive statistics for the antennal ratio (flagellomeres 10–13/1–9) of male *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	21	1.04	0.91	1.12	0.054
borealis	3	0.89	0.82	0.93	–
crassifemorata	9	0.95	0.90	1.00	0.029
nudicolis	14	1.08	0.98	1.20	0.061
sierrensis	1	1.16	1.16	1.16	–
vockerothi	2	0.90	0.89	0.91	–
ledicola	25	1.03	0.86	1.15	0.071
atra	14	1.03	0.93	1.11	0.066
bicolor	2	1.14	1.03	1.25	–
femorata	15	1.22	1.04	1.56	0.121
mangrovi	2	1.02	1.00	1.05	–
morio	13	1.11	1.04	1.21	0.043
pacifica	1	1.17	1.17	1.17	–
rufitarsis	8	1.01	0.92	1.10	0.056
subinermis	8	1.15	1.06	1.21	0.047
tecta	2	1.02	1.00	1.03	–

Table 3. Descriptive statistics for ratio of antennal flagellomeres 10/11 of male *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	21	0.76	0.68	0.83	0.038
borealis	3	0.92	0.83	0.98	—
crassifemorata	9	0.97	0.81	1.16	0.090
nudicolis	15	0.84	0.77	0.90	0.045
sierrensis	1	0.80	0.80	0.80	—
vockerothi	2	0.93	0.90	0.95	—
ledicola	26	0.71	0.58	0.84	0.060
atra	15	0.74	0.63	0.81	0.046
bicolor	3	0.85	0.82	0.88	—
femorata	16	0.94	0.83	1.04	0.055
mangrovi	2	0.54	0.53	0.55	—
morio	13	0.89	0.78	0.99	0.064
pacifica	1	1.03	—	—	
rufitarsis	8	0.78	0.72	0.87	0.054
subinermis	13	1.22	1.12	1.37	0.086
tecta	2	0.91	0.87	0.96	—

Table 4. Descriptive statistics for the wing length of male *Serromyia* (in mm).

Species	*n*	Mean	Min.	Max.	SD
barberi	18	2.15	1.50	2.32	0.193
borealis	3	1.62	1.50	1.80	—
crassifemorata	9	1.65	1.38	1.84	0.145
nudicolis	14	1.95	1.80	2.36	0.147
sierrensis	1	1.86	1.86	1.86	—
vockerothi	2	1.64	1.62	1.66	—
ledicola	25	2.35	1.70	2.88	0.265
atra	17	1.66	1.36	1.84	0.115
bicolor	3	2.21	2.02	2.38	—
femorata	22	2.49	2.12	2.84	0.182
mangrovi	2	1.21	1.20	1.22	—
morio	13	2.31	2.02	2.46	0.127
pacifica	1	2.24	2.24	2.24	—
rufitarsis	8	1.56	1.48	1.72	0.078
subinermis	11	2.25	1.82	2.52	0.190
tecta	2	1.69	1.62	1.76	—

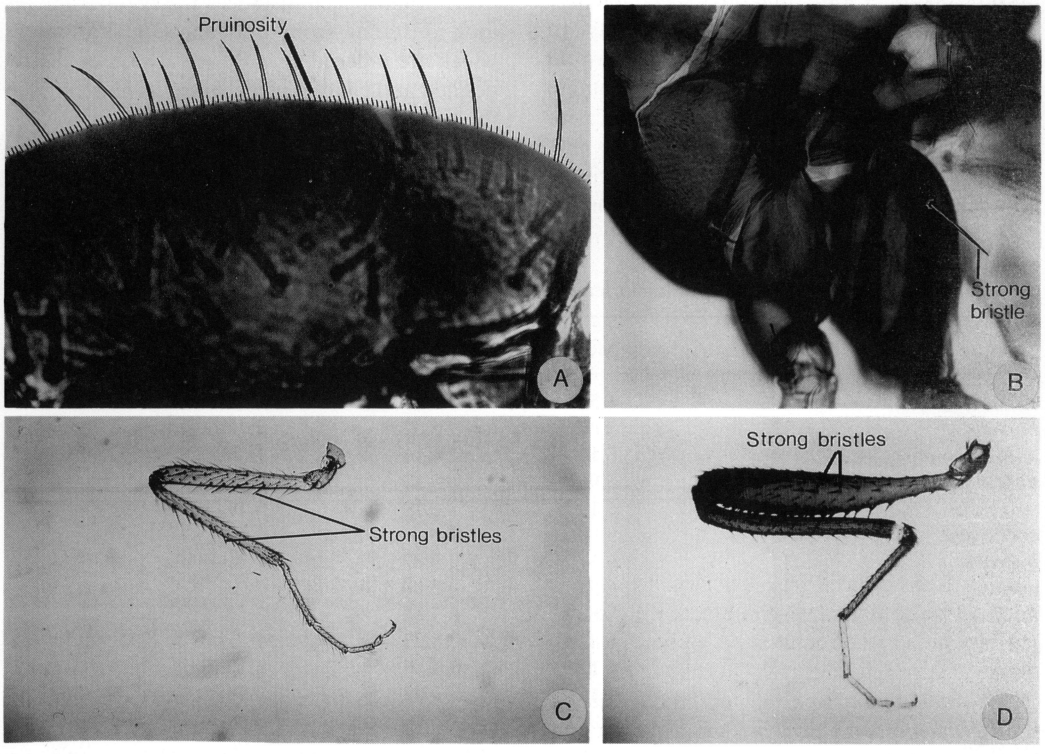
either a Reichert Zetopan or a Nikon Optiphot microscope equipped with interference contrast optics. The larval structures were photographed using a scanning electron microscope. Most structures were measured using a micrometer in a Nikon compound microscope. Wing characters were measured using a micrometer in a Wild M8 steroscope. Subsequent analysis of data was through computer programs.

Terms and abbreviations for structures

In general we use the terms provided by Downes & Wirth (1981) for adults. Although not in keeping with some of the terms traditionally used by ceratopogonid workers, their work provides names for structures which are consistent with those utilized in the rest of the Diptera. General terms for larval structures follow

Table 5. Descriptive statistics for the number of elongate strong bristles on the hind coxa of male *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	22	0	0	0	0
borealis	3	0	0	0	—
crassifemorata	9	0	0	0	0
nudicolis	16	0	0	0	0
sierrensis	1	0	0	0	—
vockerothi	3	0	0	0	—
ledicola	27	1.41	0	4	1.01
atra	15	1.13	0	3	0.99
bicolor	3	0	0	0	—
femorata	22	0	0	0	0
mangrovi	2	0	0	0	—
morio	14	0.29	0	2	0.61
pacifica	1	1	1	1	—
rufitarsis	10	0	0	0	0
subinermis	11	0	0	0	0
tecta	2	0	0	0	—



Figs 1A–D. A, scutum of male *Serromyia femorata* in lateral view; B, thorax of female *S.ledicola* in lateral view; C, foreleg of male *S.barberi*; D, hindleg of male *S.morio*.

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

W: width
AR: antennal ratio; length of flagellomeres 10–13 divided by length of flagellomeres 1–9 for males and flagellomeres 9–13 divided by length of flagellomeres 1–8 for females
CR: costal ratio; costa length/wing length as measured from MA
HC/Ta_5: length of hind leg claw divided by length of hind leg tarsomere 5
MA: arculus
Ta: tarsomere

Rearing

We were able to obtain eggs and first instar larvae of *Serromyia nudicolis* by decapitating females collected in the field. We found that females kept in the laboratory for 2–3 days before decapitation would be more likely to lay eggs. Resultant first instars did not survive on a nematode culture offered to them. The technique followed that successfully implemented for other species of Ceratopogonidae by Linley (1985) using *Panagrellus redivivus*.

Criteria for species recognition and phylogenetic analysis

Reproductive isolation is the criterion for objective species recognition (Mayr, 1969: 26), but lack of bionomic and field observations in this study limited species determination to the interpretation of morphological discontinuities.

Although this study has little phylogenetic interpretation, readers should know that our approach is cladistic, as more fully described by Borkent (1984). We emphasize the importance of outgroup comparisons for the determination of character state polarity and recognize that cladistic analyses are often only as good as are those comparisons. The general lack of cladistic information in this study is due to a paucity of interpretable character states.

Traditionally, the genus *Serromyia* has generally been considered a member of the tribe Stilobezziini, but most recently Wirth & Grogan (1988) have dealt with the historic difficulty of distinguishing the Stilobezziini from the Ceratopogonini by combining the two tribes. *Serromyia*, therefore, is now considered to be a member of the Ceratopogonini. Nevertheless, the relationships between the genera in these two tribes remains problematic and the combining of the two groups can only be regarded as a interim measure until phylogenetic relationships become better understood.

A consequence of this lack of understanding of phylogenetic relationships between the genera is that outgroup comparisons must include virtually all other genera of Ceratopogonidae. As such, virtually every character state that we examined within *Serromyia* was also present

Table 7. Descriptive statistics for ratio of aedeagus length/width of male *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	21	0.63	0.54	0.75	0.057
borealis	3	0.68	0.65	0.71	—
crassifemorata	9	0.70	0.65	0.81	0.054
nudicolis	13	0.65	0.56	0.73	0.047
sierrensis	—	—	—	—	—
vockerothi	1	0.61	0.61	0.61	—
ledicola	22	0.46	0.39	0.54	0.041
atra	17	0.57	0.49	0.62	0.038
bicolor	3	0.52	0.48	0.59	—
femorata	20	0.54	0.41	0.62	0.053
mangrovi	2	0.61	0.56	0.65	—
morio	14	0.62	0.56	0.68	0.039
pacifica	1	0.70	0.70	0.70	—
rufitarsis	11	0.61	0.50	0.64	0.040
subinermis	11	0.59	0.49	0.72	0.063
tecta	2	0.55	0.55	0.56	—

Table 8. Descriptive statistics for antennal ratio of female *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	50	1.23	1.04	1.38	0.076
borealis	2	0.96	0.93	0.99	–
crassifemorata	12	0.96	0.88	1.04	0.051
nudicolis	42	1.12	1.00	1.21	0.044
sierrensis	1	1.24	1.24	1.24	–
vockerothi	1	1.20	1.20	1.20	–
ledicola	33	1.27	1.06	1.40	0.074
atra	5	1.17	1.08	1.21	–
bicolor	2	1.10	1.04	1.16	–
femorata	15	1.21	1.10	1.28	0.051
mangrovi	2	1.14	1.10	1.19	–
morio	17	1.23	1.14	1.38	0.078
pacifica	1	1.13	1.13	1.13	–
rufitarsis	3	1.22	1.20	1.23	–
subinermis	10	1.25	1.17	1.39	0.072
tecta	2	1.06	0.96	1.15	–

Table 9. Descriptive statistics for the ratio of antennal flagellomeres 8/9 of female *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	53	0.62	0.55	0.68	0.031
borealis	3	0.78	0.77	0.80	–
crassifemorata	13	0.77	0.69	0.95	0.074
nudicolis	43	0.68	0.62	0.82	0.041
sierrensis	1	0.61	0.61	0.61	–
vockerothi	2	0.60	0.59	0.60	–
ledicola	34	0.60	0.54	0.68	0.042
atra	5	0.69	0.65	0.76	–
bicolor	2	0.74	0.74	0.74	–
femorata	15	0.63	0.58	0.70	0.038
mangrovi	2	0.66	0.65	0.67	–
morio	17	0.63	0.59	0.68	0.026
pacifica	1	0.66	0.66	0.66	–
rufitarsis	4	0.68	0.62	0.72	–
subinermis	12	0.61	0.50	0.67	0.049
tecta	2	0.71	0.68	0.74	–

at least somewhere in the outgroup and the polarity (plesiomorphic/apomorphic) was therefore uninterpretable.

Fresh clues to interpret the phylogenetic relationships between the genera in the Stilobezziini and Ceratopogonini indicate that current concepts need to be modified (Borkent, in prep.) and we have therefore not used the phylogenetic interpretations proposed by Remm (1975) or Szadziewski (1988).

Classification and descriptive format

Because the *Serromyia* species we examined had so few interpretable apomorphies, we have arranged species as follows: the Nearctic species in alphabetical order, the Holarctic species *S. ledicola* Kieffer, followed by the Palaearctic species in alphabetical order.

All new species are to be attributed to the senior author.

The characters described are those that are either useful for species discrimination or for phylogenetic interpretation. Because we examined as many species of *Serromyia* as possible on a world basis, the descriptions reflect variation of character states throughout the genus.

Extent of leg pigmentation is shown diagrammatically in the illustrations. Significant variation is represented by two drawings for a particular leg.

The diagnosis of the genus allows recognition once the specimen is determined to belong to the family and the species diagnoses allow separation from other *Serromyia* species.

When given localities on specimen labels or in past literature are now named differently, the current locality is given in square brackets.

We have listed the previous descriptions of species of *Serromyia* under the appropriate name but only have done so when certain of that author's concept. For European workers,

Table 10. Descriptive statistics for the wing length of female *Serromyia* (in mm).

Species	*n*	Mean	Min.	Max.	SD
barberi	50	2.11	1.68	2.54	0.181
borealis	3	1.65	1.60	1.72	—
crassifemorata	13	1.63	1.42	1.98	0.156
nudicolis	44	1.84	1.62	2.48	0.151
sierrensis	2	2.11	1.94	2.28	—
vockerothi	2	1.75	1.72	1.78	—
ledicola	36	2.25	1.66	2.74	0.234
atra	6	1.66	1.58	1.82	—
bicolor	2	2.08	2.06	2.10	—
femorata	19	2.35	1.96	2.68	0.209
mangrovi	2	1.42	1.39	1.45	—
morio	19	2.07	1.56	2.28	0.171
pacifica	1	2.16	2.16	2.16	—
rufitarsis	4	1.62	1.56	1.68	—
subinermis	10	1.97	1.72	2.16	0.134
tecta	2	1.56	1.55	1.57	—

Table 11. Descriptive statistics for the number of elongate strong bristles on the hind coxa of female *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	54	0	0	0	0.00
borealis	3	0	0	0	—
crassifemorata	13	0	0	0	0.00
nudicolis	43	0.05	0	1	0.21
sierrensis	2	0	0	0	—
vockerothi	3	0	0	0	—
ledicola	32	2.53	0	4	1.11
atra	7	1.57	1	2	—
bicolor	2	0	0	0	—
femorata	20	0.05	0	1	0.22
mangrovi	2	0	0	0	—
morio	17	0.53	0	2	0.72
pacifica	1	4	4	4	—
rufitarsis	4	0	0	0	—
subinermis	12	0	0	0	0.00
tecta	2	0	0	0	—

Table 12. Descriptive statistics for the ratio of hind Ta_1/Ta_2 of female *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	54	2.14	1.91	2.79	0.150
borealis	3	1.92	1.83	1.97	—
crassifemorata	13	1.91	1.66	2.03	0.092
nudicolis	45	2.25	2.00	2.42	0.124
sierrensis	2	2.18	2.10	2.25	—
vockerothi	2	2.42	2.23	2.63	—
ledicola	39	2.40	2.11	3.12	0.191
atra	7	1.84	1.71	1.98	—
bicolor	2	2.50	2.43	2.56	—
femorata	19	2.34	2.19	2.78	0.121
mangrovi	2	1.84	1.84	1.84	—
morio	18	2.27	1.93	2.48	0.186
pacifica	1	2.32	2.32	2.32	—
rufitarsis	3	2.01	1.91	2.10	—
subinermis	12	2.45	2.27	2.69	0.109
tecta	2	2.07	2.03	2.11	—

Table 13. Descriptive statistics for the ratio of length of hind claw/length of hind tarsomere 5 (HC/Ta_5) of female *Serromyia*.

Species	*n*	Mean	Min.	Max.	SD
barberi	47	1.34	1.19	1.65	0.090
borealis	3	0.38	0.36	0.42	—
crassifemorata	13	0.35	0.30	0.44	0.040
nudicolis	40	0.84	0.62	1.06	0.103
sierrensis	2	1.33	1.27	1.39	—
vockerothi	2	1.03	0.98	1.08	—
ledicola	35	1.28	1.07	1.49	0.109
atra	4	0.33	0.31	0.38	—
bicolor	2	1.20	1.16	1.24	—
femorata	18	1.16	1.04	1.29	0.068
mangrovi	2	1.30	1.25	1.35	—
morio	19	1.14	0.97	1.35	0.107
pacifica	1	1.17	1.17	1.17	—
rufitarsis	3	0.76	0.67	0.89	—
subinermis	11	1.13	0.88	1.39	0.177
tecta	2	0.40	0.38	0.43	—

most descriptions could only be reinterpreted when a given author's original material was available for examination.

Type specimens in the Canadian National Collection are given numbers in a reference text and these numbers are reported here with the description of the type locality of each named species as 'CNC No.'.

Distribution maps are based entirely on material actually examined during the course of this study. Further possible records from the literature which may extend the range of a given species are discussed under 'distribution and bionomics' or 'taxonomic discussion' of that species.

Serromyia Meigen

Serromyia Meigen 1818: 83. Type-species *Ceratopogon femoratus* Meigen (by monotypy). Generic name cited in specific synonymy.

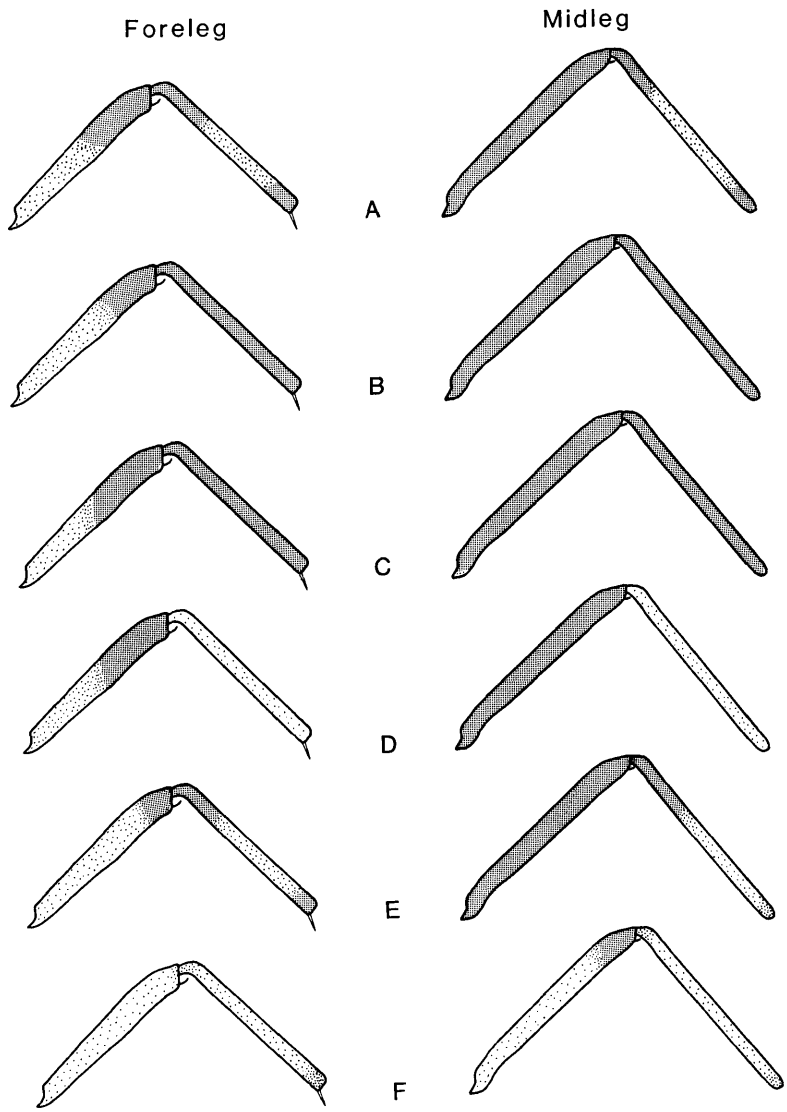
Prionomyia Stephens 1829: 237. Type-species *Ceratopogon femoratus* Meigen (subsequent designation by Westwood 1840: 126).

Ceratolophus Kieffer 1899: 69, not Barboza de Bocage 1873. Type-species *Ceratopogon femoratus* Meigen (by monotypy).

Johannseniella Williston 1907: 1 (new name for *Ceratolophus* Kieffer). Type-species *Ceratopogon femoratus* Meigen (automatic).

Ceratolophana Strand 1928: 48 (new name for *Ceratolophus* Kieffer). Type-species *Ceratopogon femoratus* Meigen (automatic).

Diagnosis. Male adults: with hind femur markedly swollen, bearing at least two rows of strong, stout bristles ventrally, on more than apical 0.58 of hind femur. Female adults: with hind femur markedly swollen, bearing at least two rows of strong, stout bristles ventrally, with base of claws straight or rounded and distal portion curved. Pupae: with only very short,

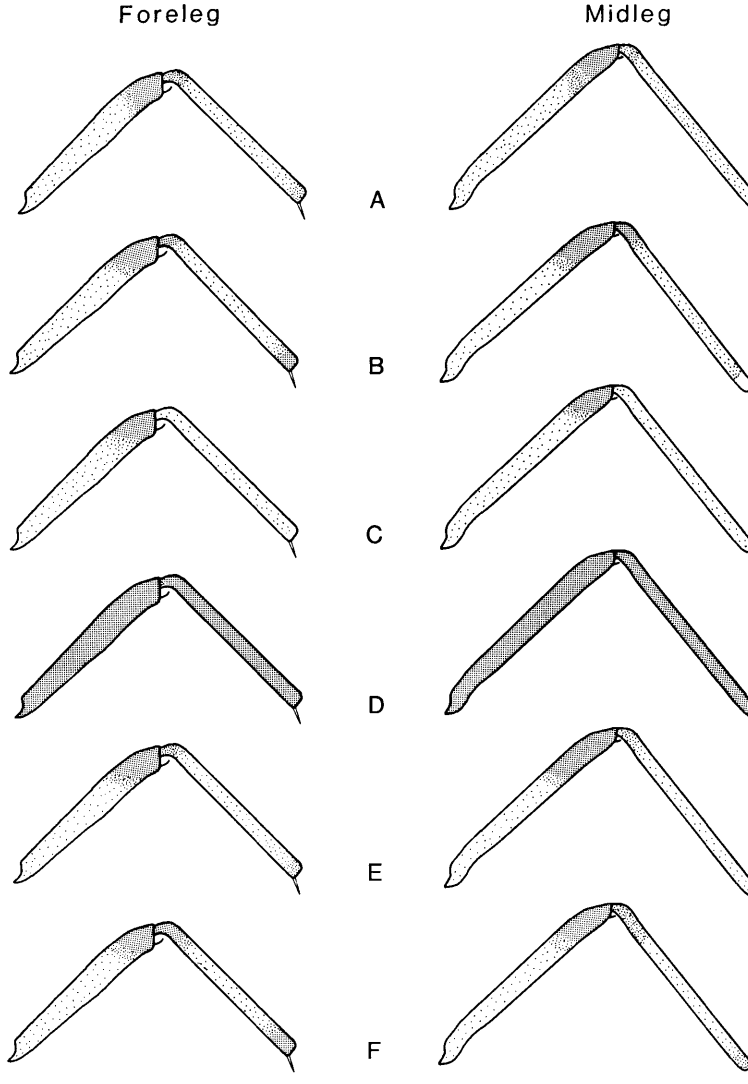


Figs 2A–F. Pigmentation of male fore and mid legs; A–B, *Serromyia barberi*; C, *S.borealis*; D, *S.crassifemorata*; E, *S.nudicolis*; F, *S.sierrensis*.

rounded abdominal tubercles and with body setae very small. Fourth instar larvae: head very small in relation to body and all head capsule setae simple (not bifurcating) including setae s, o.

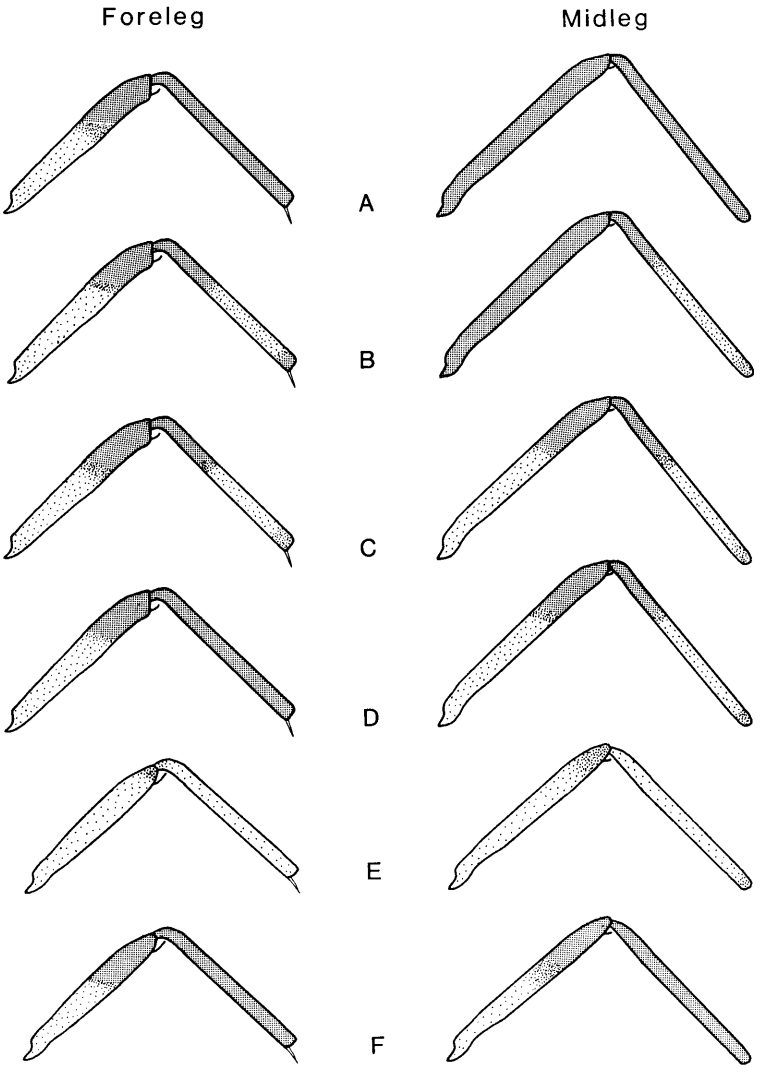
Description

Adults. Moderately sized (wing length of males = 1.0–2.9 mm, of females = 1.2–2.7 mm); general body coloration patterned or dark brown, either bare or with light pruinosity; eyes broadly separated (*S.mangrovi* Delecolle & Braverman, *S.reyei* Debenham) or narrowly separated to contiguous, bare; male antenna with flagellomeres separate or with all or some of flagellomeres 1–10 fused, with well-developed plume, with flagellomeres 10–13 or 11–13 elongate; female antenna with each of flagellomeres 9–13 more elongate than each of flagellomeres 1–8, though in some species 9 is only slightly longer than 8, sensilla coeloconica absent; 5 palpal segments; third palpal segment with shallow pit or lacking sensory pit but



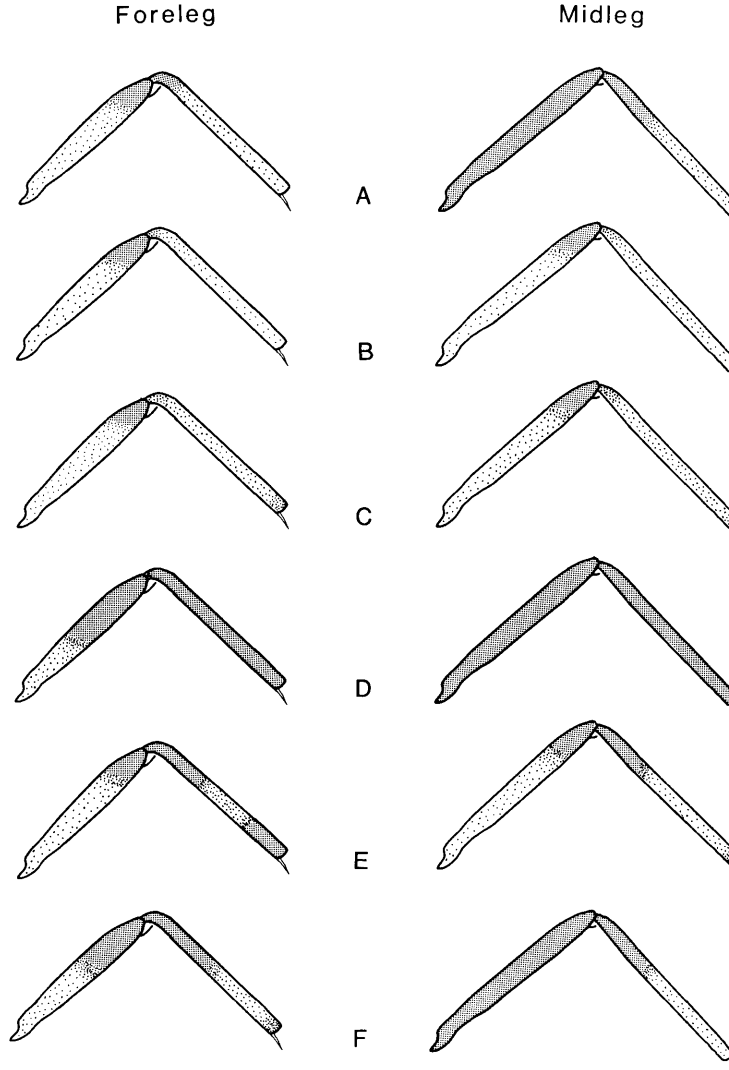
Figs 3A–F. Pigmentation of male fore and mid legs; A, *Serromyia vockerothi*; B–C, *S.ledicola*; D, *S.atra*; E, *S.bicolor*; F, *S.femorata*.

bearing on surface a patch of sensilla which are bulbous apically (as in Rowley & Cornford, 1972: Fig. 2); female mandible lacking or with 7–14 teeth; thorax dull or shiny (with or without light pruinosity), scutum lacking anteromedial tubercle; humeral pits shallow, evident in pruinose species as shiny bare patches; legs either without strong bristles or variously armed; female with claws of fore and mid legs equal and short, with base of claws straight or rounded and distal portion curved (Figs 16D–G); hind leg claws either equal, short, lacking short inner tooth, or with only a single elongate claw present, with spur near base present or absent (lacking in *S.zuluensis*, *S.aethiopiae*); hind femur markedly swollen, with ventral patch of strong bristles arranged as a single row of 1–3 bristles basally, forming two rows at mid length, scattering distally into an indistinct pattern up to 4 bristles wide; hind tibia basally arcuate to fold against swollen hind femur, with dorsal row or rows of bristles; hind first tarsomere with single ventral row of palisade setae, with additional stout subbasal



Figs 4A–F. Pigmentation of fore and mid legs; A, male *Serromyia femorata*; B, male *S.rufitarsis*; C–D, male *S.subinermis*; E, female *S.barberi*; F, female *S.borealis*.

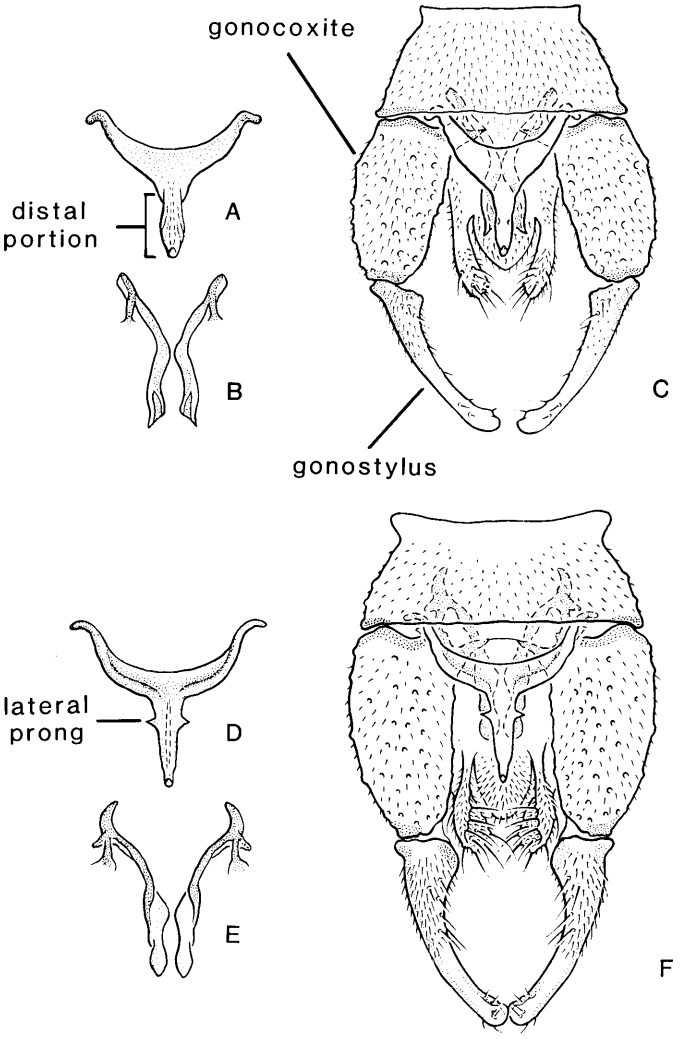
setae present or absent; some species with fourth tarsomeres bearing pair of sinuate setae (*S.reyei*, *S.agathae* Meillon & Wirth, *S.stuckenbergi* Meillon & Wirth, *S.festiva* Kieffer); wing with well-developed microtrichia, female wing lacking or with scattered macrotrichia at apex; CR=0.41–0.73 for males, 0.52–0.85 for females; cells r_1 and r_{2+3} distinct, cell r_1/cell r_{2+3} = 0.39–1.42 for males, 0.33–1.14 for females; stem of media very short to distinct, M2 indistinct to well developed at base; abdominal tergite 2 with anteromedial triangular apodeme; male genitalia rotated in some individuals of all species, lacking apicolateral processes on tergite 9; with well-developed gonocoxite, gonostylus; most species with anteromedial apodeme ventral to gonocoxal apodeme; parameres separate or fused, fused or articulated basally with gonocoxal apodeme; aedeagus articulated laterally with base of gonocoxite, some species with apex of aedeagus directed ventrally; male cercus large, situated



Figs 5A–F. Pigmentation of female fore and mid legs; A, *Serromyia nudicolis*; B, *S.vockerothi*; C, *S.ledicola*; D, *S.atra*; E, *S.morio*; F, *S.rufitarsis*.

on lateral margin of segment 10, directed posteriorly; female genitalia with posterior margin of sternite 8 somewhat bilobed to completely cleft (*S.aethiopae* Clastrier & Wirth), with each lobe bearing a sometimes indistinct patch of setae; sternite 9 divided medially, either truncate or with anteromedial margin projecting medially; segment 10 bearing 2–7 strong bristles ventrally, cercus well developed; 1–2 spermathecae, most species also with an additional blind spermathecal duct, pigmented apically; spermathecae ovoid to ellipsoidal, with or without surface pores; a few members of some species with three fully developed spermathecae.

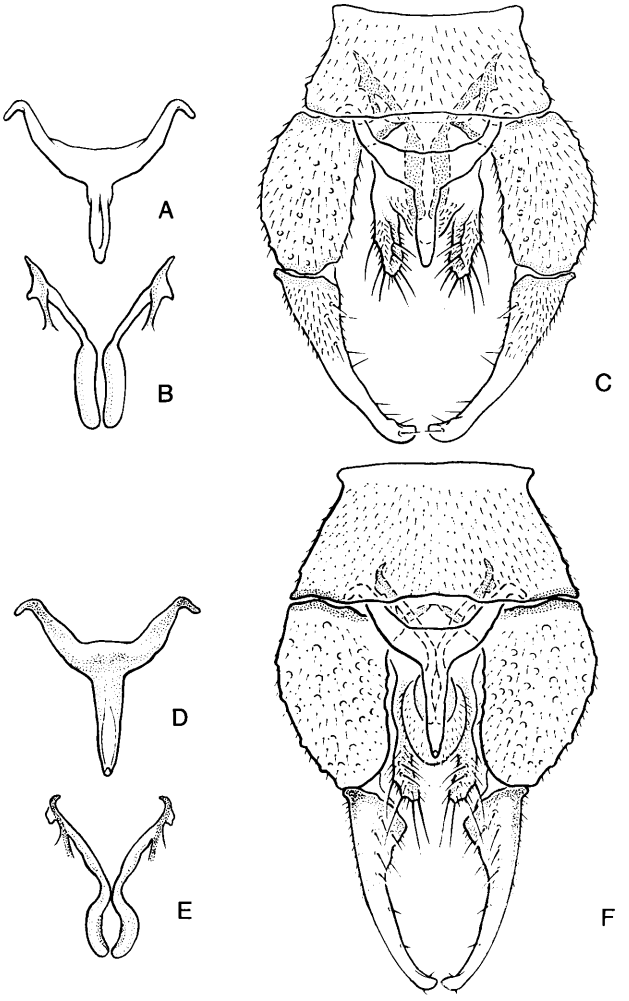
Pupa. Length 3.1 (for *S.atra*) or 3.6–4.2 mm; general coloration light brown; dorsum of thorax, dorsum and ventrum of abdomen covered with short spicules; all body setae very short, simple, tapering; operculum with apical medial knob (similar to that described by Kettle & Lawson, 1952: Fig. 90); anteromedial seta present, with sensory pit located just ventrally, anterodorsal seta single with associated sensory pit, 2 dorsolaterals present, ventrolateral and ventromedian setae absent, thoracic dorsals with i, ii on abutting low tubercles, iv posterolateral to v; respiratory organ (as shown in Kettle & Lawson, 1952: Fig. 75, but somewhat



Figs 6A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia barberi*; D–F, *S.borealis*.

wider at apex) dark brown except light brown at very base, length 0.85–1.26 mm, L/W = 2.2–2.9, with 6 (for *S.atra*) or 8–11 spiracular openings, each on a slight protuberance; metathorax indentate medially but not completely divided (Kettle & Lawson, 1952: Fig. 102); setae on abdomen situated on low, rounded tubercles, those on segment four distributed as follows (Fig. 16B): 2 d.a.s.m., 3 d.p.m., 4 l.p.m. (3 on one tubercle), 3 vent.; caudal spine with dark apex, directed laterally at about 60° from longitudinal axis.

Larva (partially after Glukhova, 1979). Head short-oval, medium brown, collar weakly developed, very narrow, barely darker than the rest of head, ventral side with small medial expansion and ventral suture, posterior margin of frontal sclerite slightly acuminate in middle, frontal suture terminating at pronotal sensory pit; sensory pits medium-sized, sensory pit j around collar large, anterior one somewhat smaller, all setae simple, of average length and thickness, setae p short with small base, setae o with approximated bases abutting subgenal ring, setae y of medium length, u and v with abutting bases, seta w situated more anteriorly and a short distance from subgenal ring, setae q, s, t, x present; antenna prominent with short, wide segments, segment 2 bearing 2-segmented short rod and 4 small sensilla; eyes of medium size,



Figs 7A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia crassifemorata*; D–F, *S.nudicolis*.

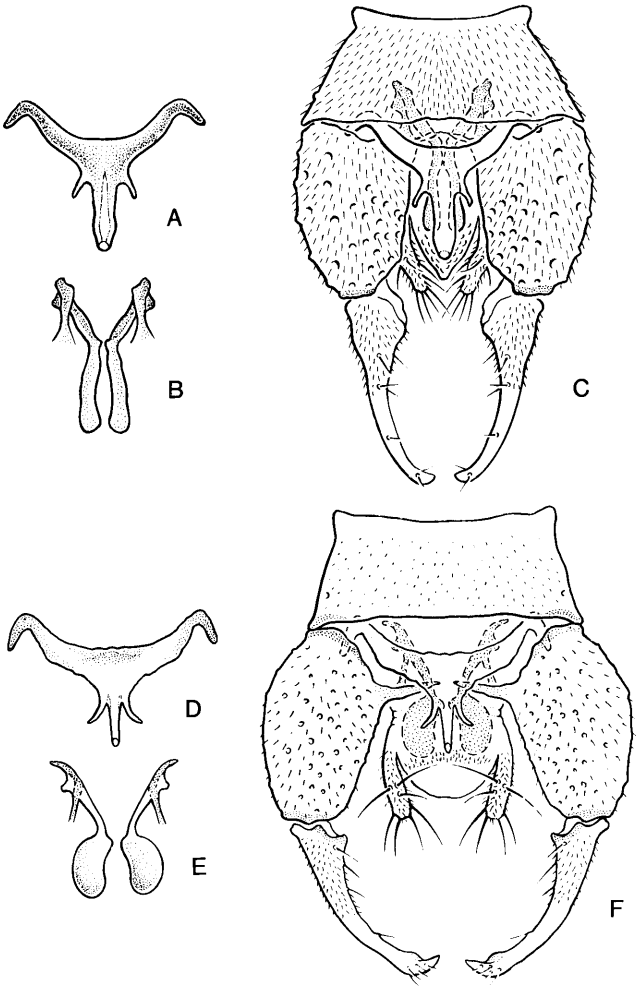
somewhat spherical; labrum short, wide, sensillae as reported for *S.nudicolis* below, mandible short, brown, external surface concave, one denticle basally, maxillary palpus short, hypostoma spherical, moderately convex, lacking denticles; labium narrow, anteriorly acuminate plate; epipharynx with 2 sets of plates; body very thick in relation to head, lacking pigmentation, anal segment (segment 10) with very short setae, 4 dorsal setae not paired.

Eggs. Markedly elongate, rounded anteriorly, somewhat tapered posteriorly (Fig. 16A); in *S.nudicolis* with longitudinal rows of spicules (see under that species); egg shell known only for *S.nudicolis* (see under that species).

Distribution and bionomics

The genus *Serromyia* is virtually cosmopolitan but has not been recorded from the Neotropical Region or from New Zealand. Several records in the literature extend distributions of described species in Europe but we have unfortunately have been unable to confirm these. Without reidentification, such records cannot be used: Havelka (1978) reported *S.femorata* from North Africa, and Remm (1973a) noted *S.ledicola* from Mongolia. Remm (1967) reported *S.femorata* and *S.morio* (Fabricius) from the Caucasus.

We studied a series of eight females from Japan, labelled 'Japan, Hokkaido, Daisetzusan,



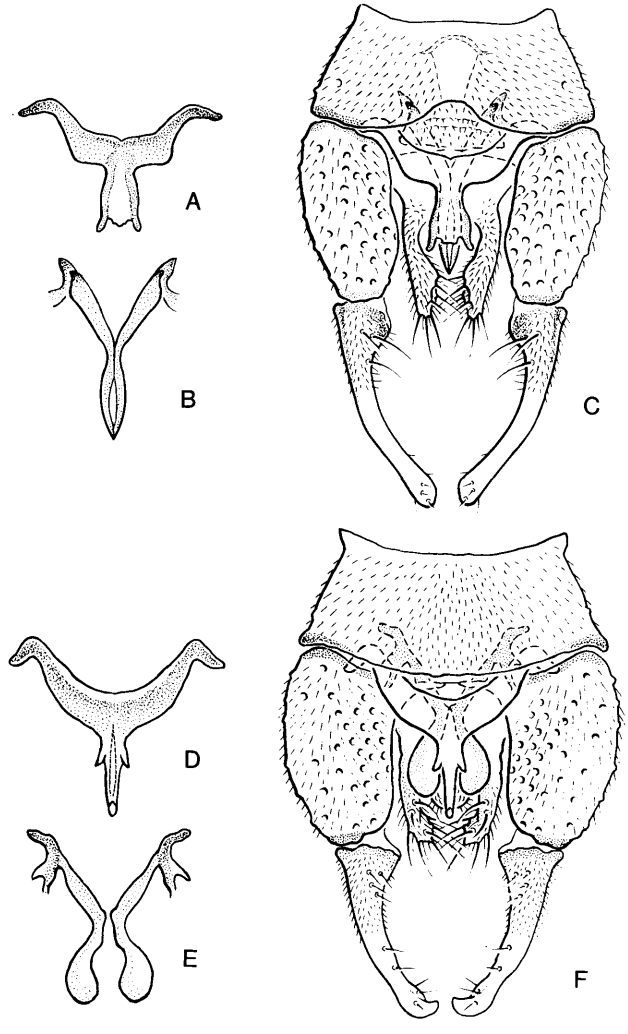
Figs 8A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia vockerothi*; D–F, *S.ledicola*.

Aizankei, 17-VII-1986, D.M. Wood CD812' (CNCI). These were very similar to the female of *S.subinermis* Kieffer, but, considering the similarity between females of most *Serromyia* species, could well represent another, unnamed species. Further collecting will hopefully obtain an associated male which will allow interpretation of this species.

Yu (1978) included the genus *Serromyia* in his key to Chinese genera, though no species has yet been identified from that country. We have examined an undescribed species from Taiwan (one female) and considering the material of uncertain status from Japan noted above, members of the genus are certainly expected to be present in China.

Although Fox (1946) considered *Johannseniella fluviatilis* Lutz from the Neotropical Region to be a species of *Serromyia*, Ortiz (1958) correctly assigned the species to the genus *Culicoides* Latrielle.

Because so little bionomic information is available, it is uncertain what general statements can be made about the genus. All the Holarctic species seem to be associated with bogs, fens, wet meadows, streams or small rivers. Furthermore, south of treeline, all species are restricted to wooded regions (i.e. absent from prairie).

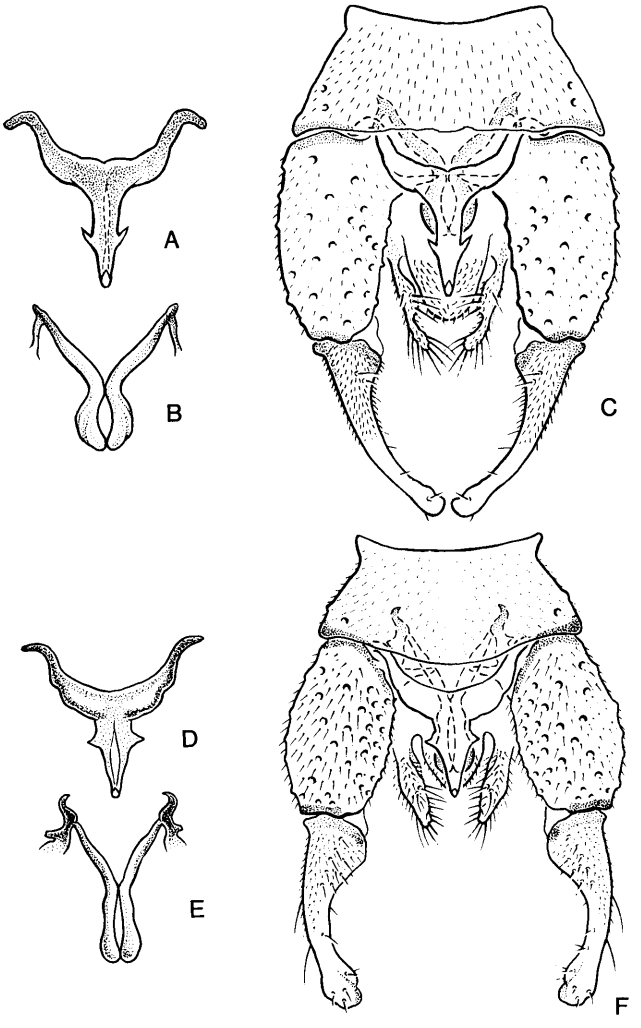


Figs 9A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia bicolor*; D–F, *S.femorata*.

We have discussed further, more detailed habitat observations under each of the pertinent species.

Female adults of nearly all species of *Serromyia* (*S.crassifemorata* Malloch excepted) have serrate mandibles, and limited observations indicate that they capture and feed on other insects (Edwards, 1920, 1923, 1926; Gad, 1951; Downes, 1955, 1978; see below under *barberi*, *femorata*). Edwards (1920) also noted that the females of *S.femorata* prey on the males during mating (see below under that species). Females probably also take nectar from flowers (see below under *S.barberi*). Szadziewski & Krzywinski (1988) reported unidentified *Serromyia* from flowers of *Anthriscus silvestris* in Poland.

Information on immatures is very limited. We were able to observe the eggs and first instar larvae of *S.nudicolis* as discussed below under that species. Strenzke (1950) and Thienemann (1950) found larvae of *S.femorata* and *S.morio* in mosses at lake margins. Kettle & Lawson (1952) found *Serromyia femorata* larvae in mud associated with marshlands. Because of uncertainty of identification, it should be noted that the larvae collected by these authors may actually belong to another species



Figs 10A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia morio*; D–F, *S.pacifica*.

of *Serromyia*. One pupa in the Strenzke (1950) collection was a member of *S.atra* (see below under that species).

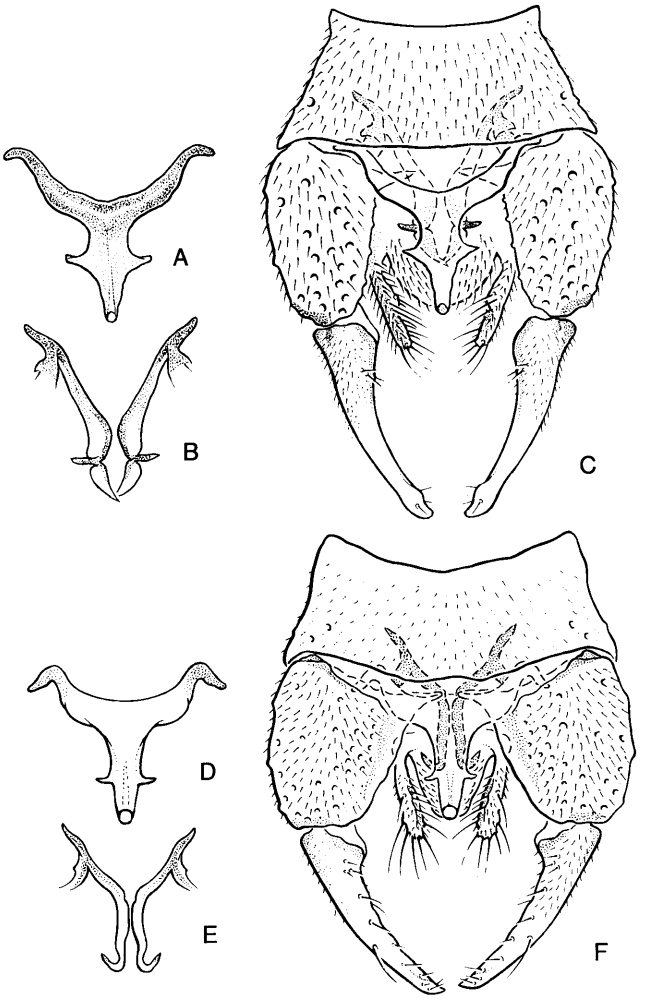
Taxonomic discussion

This study indicates that the genus *Serromyia* contains thirty-two extant and eight fossil species, reflecting some changes in taxonomic status and the description of several new species. A list of included species is given in Table 1.

Wirth & Grogan (1988) included *Ceratopogon trichopus* Thomson 1869 from China, in *Serromyia* while Wirth (1973) considered the species as an unplaced species of Sphaeromiini. However, we have examined the female type, housed in the NHRS, and found it belongs in *Atrichopogon* Kieffer. This change results in a new combination for the species.

Kieffer (1901) provided a brief description (as part of a key) of a new species *Serromyia scirpi* based on a female from Germany and subsequently (1913, 1919) gave more complete descriptions (also as part of keys). Remm (1988) most recently also included the name in his Palaearctic catalogue as a species of *Serromyia*.

Several characters, however, suggest that *S.scirpi* is not actually a member of *Serromyia*.

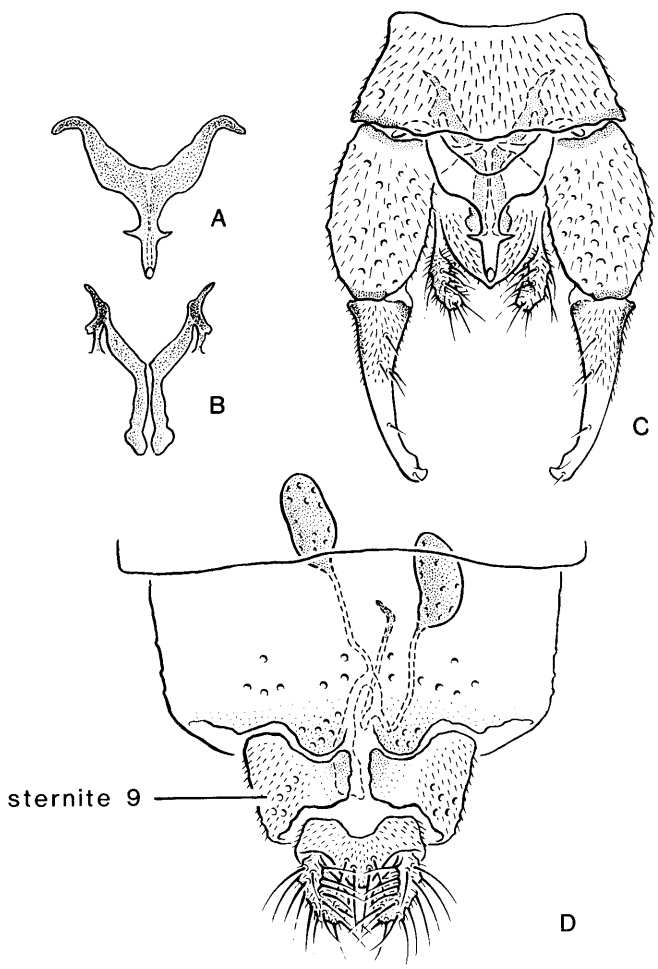


Figs 11A–F. Male genitalia C, F; aedeagus A, D; paramere B, E; A–C, *Serromyia rufitarsis*; D–F, *S.subinermis*.

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



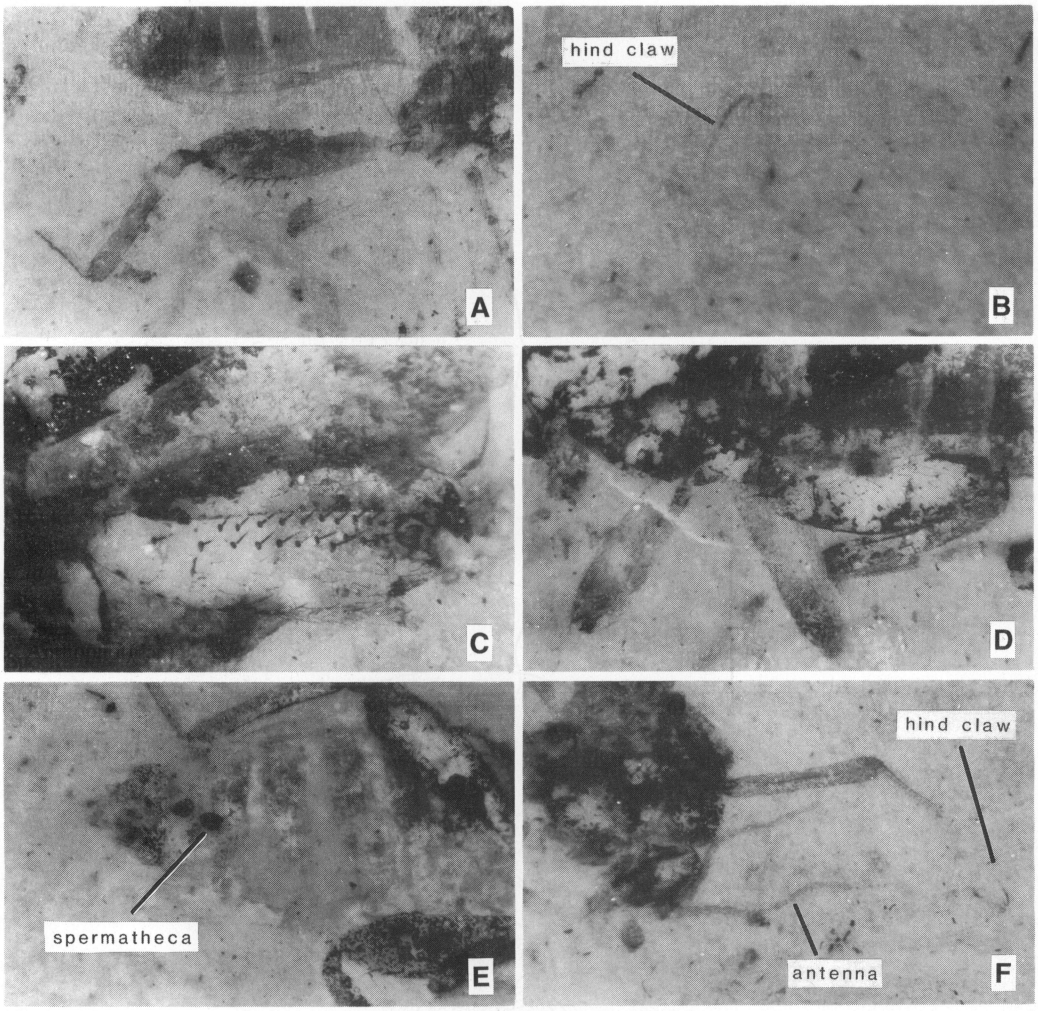
Figs 12A–D. A aedeagus, B paramere, C male genitalia of *Serromyia tecta*; D, female genitalia of *S.borealis*.

this species as a synonym of *Ceratopogon niveipennis* Meigen.

Stephens (1829) named *Prionomyia pusilla* as a new species among other members of *Serromyia* (all of which he placed in *Prionomyia*) but, without any description, the name is clearly a *nomen nudum*.

Some confusion has surrounded the authorship and validity of the generic name *Serromyia*. Although first published in synonymy with *Ceratopogon*, it is available under I.C.Z.N. Code Article 11(e).

The species outside the Holarctic Region are well described and keyed. Debenham (1970) described those in the Australian Region, Giles & Wirth (1982) dealt with those in the Oriental and Australasian Regions and Meillon & Wirth (1983) described and keyed those from the Afrotropical Region. The recently described *S.silvatica* Meillon & Downes from South Africa (Meillon & Downes, 1986) has not been incorporated into a key but is the only *Serromyia* in the Afrotropical Region in which the female has equal hind claws.

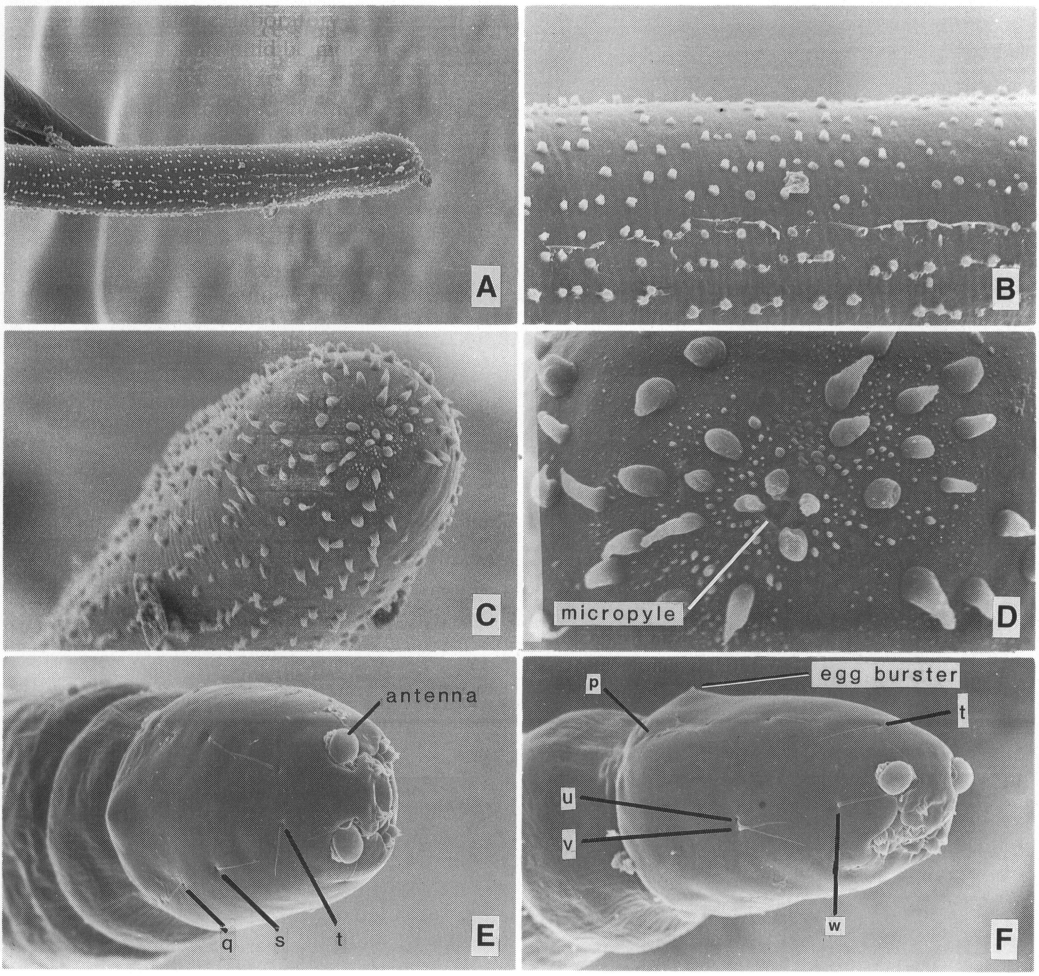


Figs 13A–F. Photomicrographs of *Serromyia colorata*; A, hind leg (from holotype of *S.spinofemorata*); B, hind claw (from holotype of *S.spinofemorata*); C, hind femur (from holotype of *S.austera*); D, fore, mid, and hind legs (from holotype of *S.austera*); E, abdomen (from holotype of *S.colorata*); F, antenna and hind claw (from holotype of *S.spinofemorata*).

There have been several characters which have been discussed and used extensively by previous authors to recognize species of *Serromyia* in the Palaearctic. Goetghebuer (1922b, 1934) noted the difference in number of acrostichal and dorsocentral setae between *S.femorata* and *S.morio*. Although the differences are probably statistically significant, there is overlap in the number of setae. We did not include this character in our study because we could not count it consistently.

Several authors have noted differences in leg coloration (red, yellow, brown) which we have been unable to confirm (e.g. Meigen, 1818; Kieffer, 1919; Goetghebuer, 1934; Zihali-Sebess, 1940). However, it may be that freshly collected material from Europe exhibits differences in colour that were not detected in this study. The legs of specimens in the material we examined were various shades of yellow, brown and black.

Extent of leg coloration has also been used by a number of authors to recognize species of *Serromyia*. Winnertz (1852) considered such pigmentation to be intraspecific variation. The results of this study indicate that extent of pigmentation can be used to recognize some species.



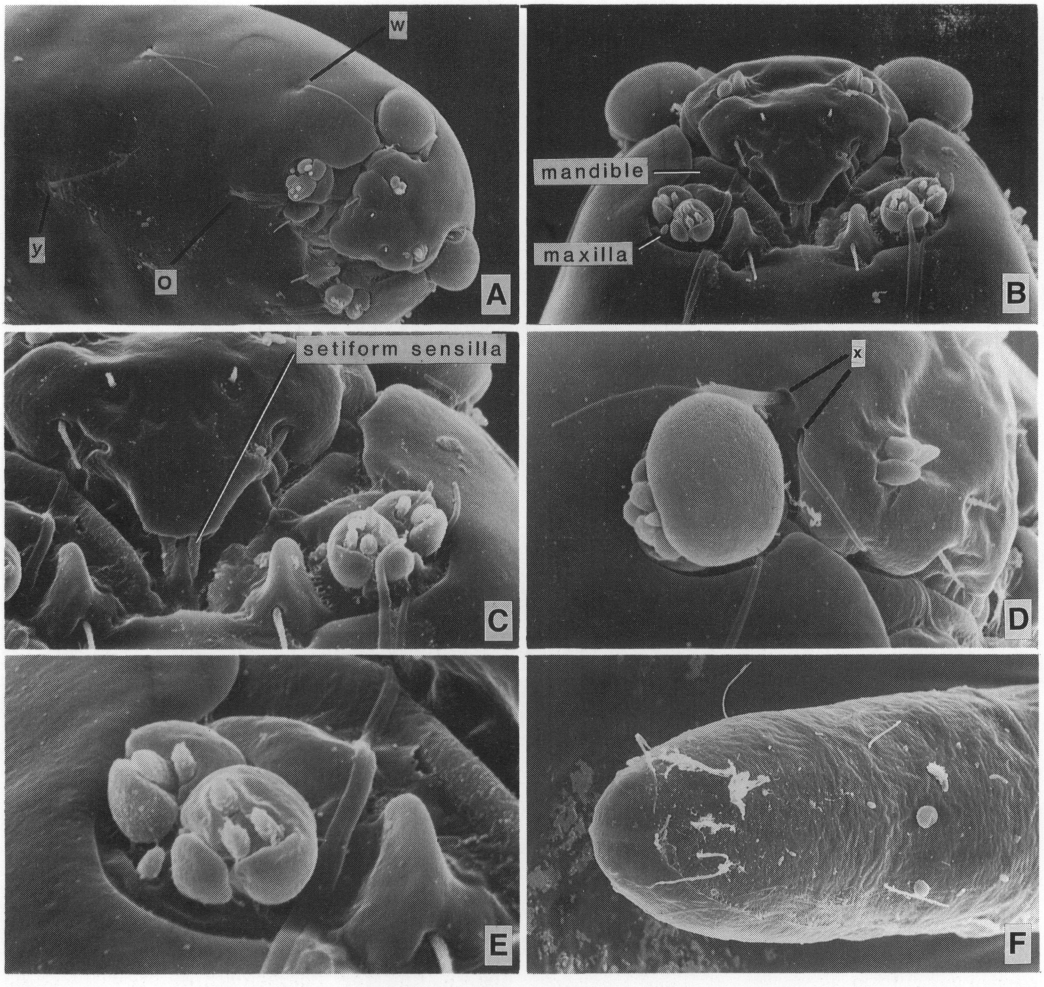
Figs 14A–F. SEM photomicrographs of *Serromyia nudicolis*; A–D, egg; E, first instar head capsule in anterodorsal view; F, first instar head capsule in anterolateral view.

Zihali-Sebess (1940) used the ratio of wing vein m/r-m to distinguish some *Serromyia* species but we found no statistically significant differences between the species.

Szadziewski (1988), in his study of Baltic amber ceratopogonids, used the ratio of hind femur length/width to distinguish some fossil *Serromyia* species. Because of marked variation within extant species, we found the character to be of very limited value for males (Table 6) and of no value for characterizing females, where total range values for all Holarctic species was 3.97–7.73. Intraspecific variation for females of some species was also large; for example *S. ledicola* had a range from 4.09 to 7.73 (n= 37). Szadziewski (1988) recorded some values for the fossil material, however, that exceeded these values.

Meillon & Wirth (1983) and Wirth & Grogan (1988) noted in their generic diagnoses that male genitalia are 'concealed beneath the tip of the pregenital terga' [= tergite 8]. Although true for some specimens of some species, we have been unable to confirm this for living or freshly killed specimens. It is possible that such a position is an artefact of preservation.

Meillon & Wirth (1983) mistakenly drew the female genitalia of *Serromyia aethiopiae* as



Figs 15A–F. SEM photomicrographs of first instar larva of *Serromyia nudicolis*; A, anterior portion of head capsule in anteroventral view; B, mouthparts in ventral view; C, mouthparts in ventral view; D, antenna and labrum in anterolateral view; E, right maxillary palp; F, terminal abdominal segments in dorsal view.

having a very broad sternite 8. The lateral margin of sternite 9 was included as part of sternite 8, which is, in fact, more narrow posteriorly.

It is likely that spermathecal shape differs between at least some species of *Serromyia* but we were unable to examine these in a consistent enough manner to categorize those differences. Apparent shape changes dramatically with different orientations of the spermatheca within the body cavity.

The only previous description of the pupal stage has been by Kettle & Lawson (1952), who characterized the pupa of *S.femorata* (perhaps misidentified to species; not seen), and by Mayer (1957), who tabulated some setal distributions. Our description of the pupa above is based on a few specimens (n=5) from the Strenzke and Thienemann collections (ZSMC). One of these contained a pharate adult of *S.atra* but the others could not be confidently identified.

Kettle & Lawson (1952) drew the respiratory organ of the pupa of *S.femorata* with the apex more narrow than that of any of the specimens we studied. This may indicate real variation but may also be due to drawing the specimen at an angle.

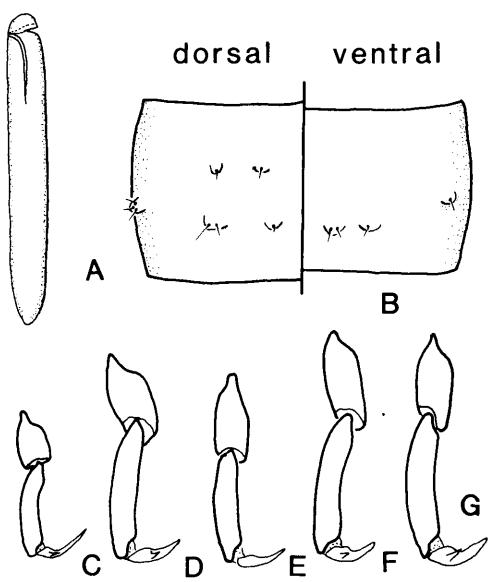


Fig. 16. A, egg shell of *Serromyia nudicolis*; B, setal distribution on fourth abdominal segment of pupa of unidentified *Serromyia*; C–G, medial view of posterior claw of female right fore leg: C, *Metacanthohelea cogani*; D, *S.nudicolis*; E, *S.silvatica*; F, *S. maculipennis*; G, *S.agathae*.

Mayer (1957) noted that members of the Heteromyiini, Sphaeromiini and Palpomyiini all have 3 anterior and 4 posterior dorsal setae on abdominal segment four. Each of these two groups of setae actually included a sensory pit. In the somewhat dirty pupal material of *Serromyia* examined we could not be certain whether sensory pits were present or not. The different sensilla counts, therefore, may not be significant.

Descriptions of larvae have been previously provided by Kettle & Lawson (1952) and Glukhova (1977, 1979). In addition, the first instar larva of *S.nudicolis* is described below. Our diagnosis above should allow recognition of the genus. The simple anal segment with very short setae is unusual but not unique, being characteristic in some *Paradasyhelea* Macfie, *Stilobezzia* Kieffer and *Sphaeromias* Curtis.

We examined three fourth instar larvae of an unidentified *Serromyia* from the Strenzke and Thienemann collections (ZSMC). These matched in nearly every detail the excellent description by Glukhova (1979: 160). Glukhova, however, in drawing seta w in her ventral view of the head capsule, failed to draw it in her lateral view. The seta is just dorsal of the subgenal ring. We failed to confirm the observation that the posterior margin of the eye was slightly triangularly elongated. The specimens we examined had eyes which were generally spherical with a somewhat ragged edge. In addition, we could not locate sensory pits r and k.

We were unable to locate the specimens used by Kettle & Lawson (1952) in their description of *S.femorata* larvae. Considering the uncertainty in species identification at that time, these may have been the larvae of one or more other *Serromyia* species.

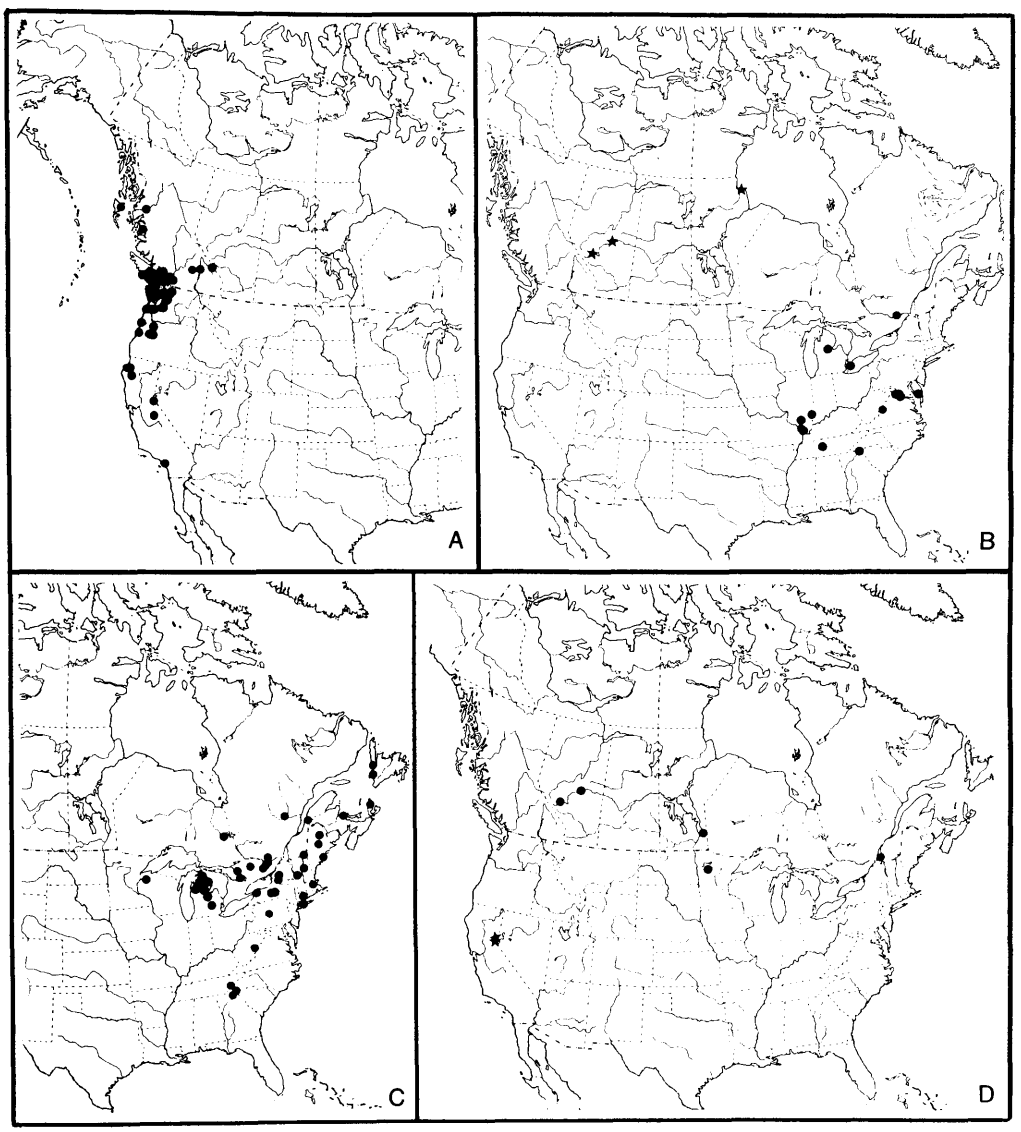
The description of the egg above is based mostly on the undeveloped ova within preserved female abdomens. Otherwise, only the egg of *S.nudicolis* is known (described below). A recent investigation of the surface sculpturing of eggs of *Culicoides* (Kariya *et al.*, 1989) show significant differences between species, indicating that this character may provide useful information in distinguishing the eggs of different *Serromyia* species.

The way the egg shell chorion is split is similar

to that reported for *Culicoides circumscriptus* Kieffer by Becker (1961) and *Bezzia varicolor* (Coquillett) by Thomsen (1937), suggesting that this is a widespread characteristic at least within the Ceratopogoninae. Otherwise, so few egg shells have been described that no further comparisons are possible.

Meillon & Wirth (1983) noted the variation among species of southern hemisphere Old World *Serromyia* as compared to the relative homogeneity of species in the Holarctic. They intimated the possibility of splitting the group into two or more genera but could find no evidence to support clear distinctions. We too could find no evidence to support the recognition of more than one genus.

Wirth & Grogan (1988) recently described the new monotypic genus *Metacanthohelea* from Africa. Further examination of two males and two females of *M.cogani* indicates that most character states which were indicated as distinguishing this genus also occur in at least some



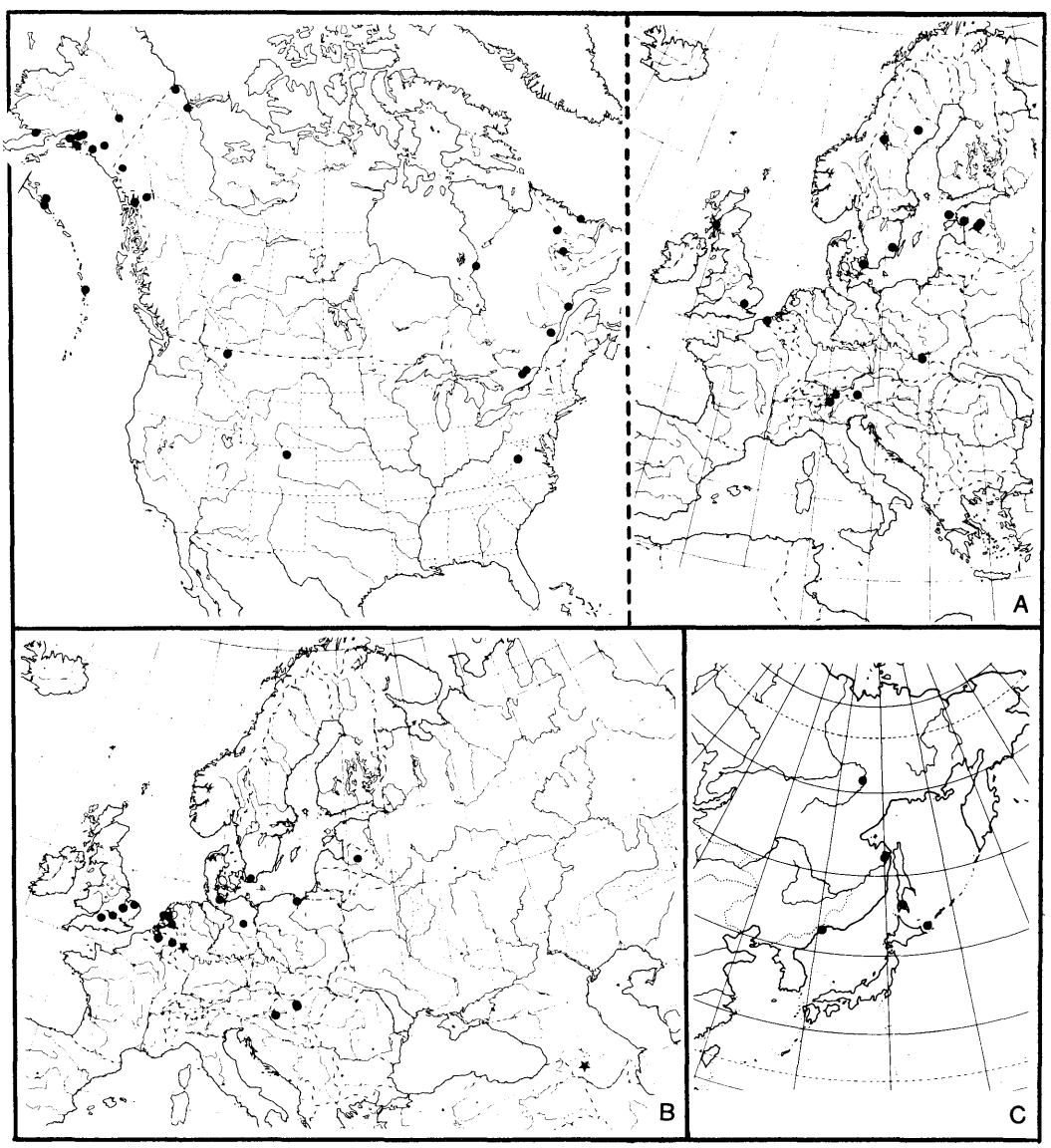
Figs 17A–D. Distributions of: A, *Serromyia barberi*; B, *S.borealis* (*), *S.crassifemorata* (•); C, *S.nudicolis*; D, *S.sierrenis* (*), *S.vockerothi* (•).

species of *Serromyia* (see discussion below under 'Phylogeny'). The key provided by Wirth & Grogan (1988) is therefore revised as follows:

22. Female claws with rounded or straight base, distal portion curved (Fig. 16D–G); female hind claws either single and elongate or, if short and equal, lacking inner tooth; male with more than 0.58 of apex of hind femur bearing strong bristles ..... *Serromyia* Meigen

22. Female claws with marked bend at base, distal portion straight (Fig. 16C); female hind claws short and equal, with well-developed inner tooth; male with less than 0.43 of apex of hind femur bearing strong bristles ..... *Metacanthohelea* Wirth & Grogan

Boorman & Rowland (1988) recently provided a generic key to the ceratopogonid adults of Great Britain. However, many female specimens of *Serromyia* found there will not key out properly because of the presence of



Figs 18A–C. Distributions of: A, *Serromyia ledicola*; B, *S.atra* (•), *S.bicolor* (*): C, *S.pacifica*.

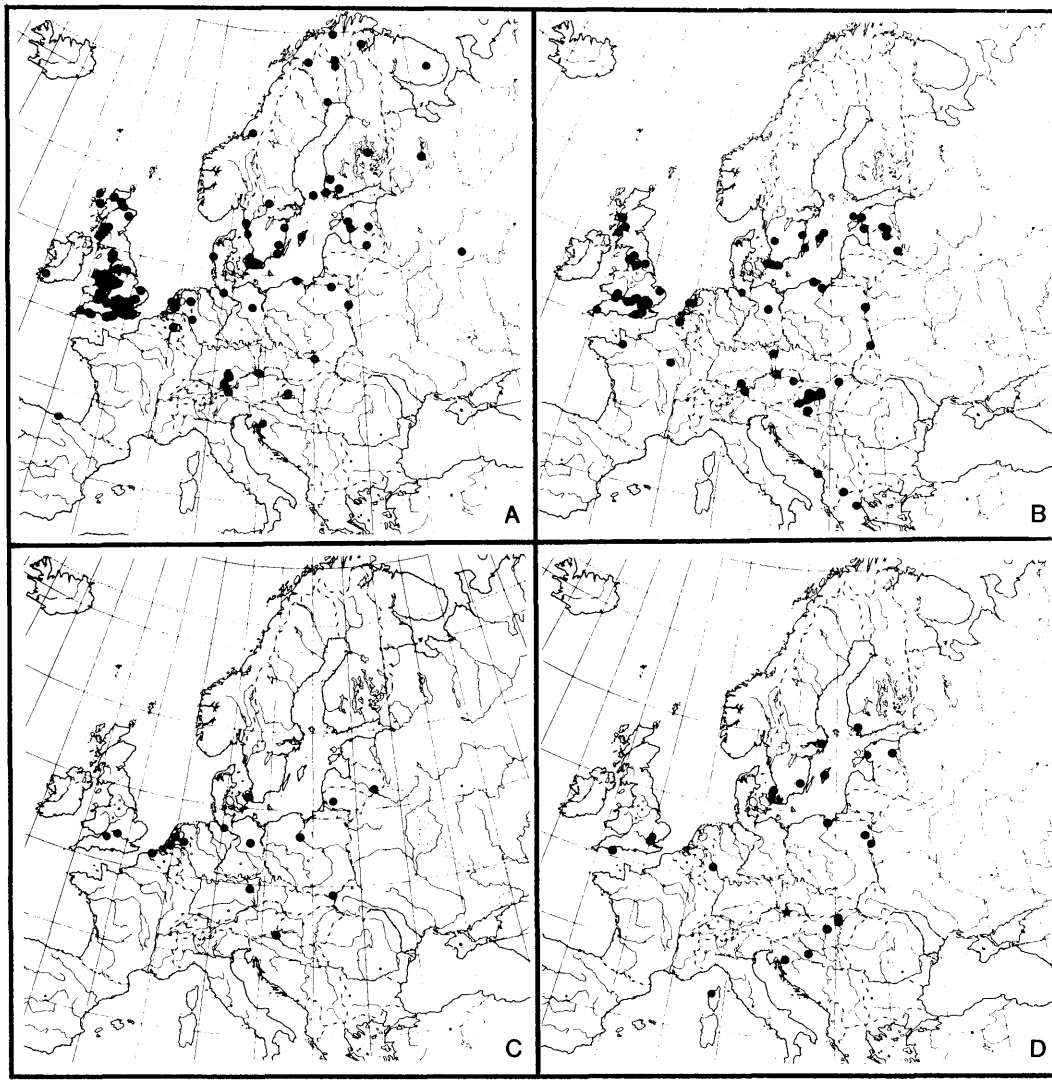
macrotrichia on the wing tip. The key will work if all specimens, regardless of sex, are treated as if they were male.

Keys

Members of the genus *Serromyia* may be recognized as such in the Holarctic Region using Downes & Wirth (1981) or on a worldwide basis using Wirth & Grogan (1988) with the modifications suggested above allowing for better separation of *Metacanthohelea* and *Serromyia*.

Some terms in the keys presented below require special attention or interpretation and the reader is directed to the above section 'Terms and abbreviations for structures'.

Males are generally easier to identify than females, especially those of species from the Palaearctic.



Figs 19A–D. Distributions of: A, *Serromyia femorata*; B, *S.morio*: C, *S.rufitarsis*; D, *S.subinermis* (•), *S.tecta* (*).

Key to adult males of Nearctic *Serromyia* species

1. Mid femur yellow with apical portion more darkly pigmented 2

   Mid femur uniformly dark brown 4

2. Hind coxa with 0–4 elongate lateral setae (Fig. 1B); fore femur with or without strong ventral bristles; scutum pruinose (as in Fig. 1A); adults present 13 July to 6 November (broadly Holarctic) ..... *ledicola*

   Hind coxa lacking elongate lateral seta; fore femur with or without strong bristles, if present situated at least anteriorly; scutum pruinose or lacking pruinosity; adults present 2 June to 3 July 3

3. Fore femur with strong bristles anteriorly and posteriorly; scutum pruinose (Canada, northern United States) ..... *vockerothi*

   Fore femur with one strong bristle anteroapically; scutum lacking pruinosity (Sierra Nevada) ..... *sierrensis*

4. Paramere with a distinctly pointed apex (Fig. 6B); west of continental divide (western Nearctic) ..... *barberi*

   Paramere with a rounded (sometimes difficult to see) apex (Figs 6E, 7B, 7E); east of continental divide 5

5. Fore femur with stout bristles at least anteriorly and posteriorly (eastern Nearctic) ..... *nudicolis*

   Fore femur lacking strong bristles 6

6. Scutum pruinose; aedeagus with lateral prongs (Fig. 6D) (Alberta, Manitoba) ..... *borealis*

   Scutum lacking pruinosity; aedeagus lacking lateral prongs (Fig. 7A) (eastern Nearctic) ..... *crassifemorata*

Key to adult females of Nearctic *Serromyia* species

1. Claws of hind leg equal, markedly shorter than tarsomere 5 2

   Hind leg claw single and elongate, with one small side tooth; claw equal to or longer than tarsomere 5 3

2. Mandible serrate; fore and mid tibiae darkly pigmented (Fig. 4F); scutum pruinose (Alberta, Manitoba) ..... *borealis*

   Mandible reduced, lacking teeth; fore and mid tibiae pale or yellow; scutum lacking pruinosity (eastern Nearctic) ..... *crassifemorata*

3. Cells r_1 and r_{2+3} pale to dark brown; hind claw longer than tarsomere 5 (HC/Ta_5 = 1.07–1.65) 4

   Cells r_1 and r_{2+3} dark brown; hind claw equal to or shorter than tarsomere 5 (HC/Ta_5 = 0.62–1.08) 6

4. Cells r_1 and r_{2+3} dark brown; fore and mid tibiae brown (Sierra Nevada) ..... *sierrensis*

   Cells r_1 and r_{2+3} pale to light brown; fore and mid tibiae pale or with just apex of mid tibia darkly pigmented 5

5. Coxa of hind leg with one or more strong lateral setae (as in Fig. 1B); scutum pruinose (broadly Holarctic) ..... *ledicola*

   Coxa of hind leg lacking strong lateral setae; scutum lacking pruinosity (western Nearctic) ..... *barberi*

6. Ratio of antennal flagellomeres 8/9 = 0.62–0.82 (eastern Nearctic) ..... *nudicolis*

   Ratio of antennal flagellomeres 8/9 = 0.59–0.60 (Canada, northern States) ..... *vockerothi*

Key to adult males of Palaearctic *Serromyia* species

1. Body pale yellow (Egypt) ..... *mangrovi*

   Body dark brown to black 2

2. Parameres tapered apically to a definite point (Figs 9B, 11B, E) 3

   Parameres rounded apically, shrivelled in some, but apex not pointed (Figs 8E, 9E, 10B, E, 12B) .5

3. Scutum lacking pruinosity; each paramere bifurcate (Fig. 11B) apically (Europe) ... *rufitarsis*

   Scutum pruinose; each paramere ending in a single point (Figs 9B, 11E) 4

4. Apex of paramere bent laterally at about a 45–90° angle (Fig. 11E) (Europe) ..... *subinermis*

   Apex of paramere straight, sword-like (Fig. 9B) (Federal Republic of Germany, Caucasus) *bicolor*

5. Thorax shiny; cells r_1 and r_{2+3} dark brown; aedeagus with side prongs directed anterolaterally (Fig. 10A) 6

   Thorax pruinose; cells r_1 and r_{2+3} light to pale brown; aedeagus with side prongs directed dorsolaterally, laterally or posterolaterally (Figs 8D, 9D, 10D, 12A) 7

6. Fore femur with three rows of strong bristles; wing length = 2.0–2.5 mm (Europe) ..... *morio*

Fore femur with one ventral row of strong bristles and 0–2 anterior or posterior strong bristles; wing length = 1.3–1.9 mm (Europe) ..... *atra*

7. Fore femur with three rows of strong bristles; hind femur with anterior strong bristles (as in Fig. 1D) (Europe) ..... *femorata*

   Fore femur lacking strong bristles or with one row of strong bristles in some composed of only a few spines, some with 1–2 additional strong posterior bristles; hind femur lacking anterior strong bristles 8

8. Each of fore and mid femora and tibiae at most only partly pigmented (Fig. 3B, C); parameres markedly swollen in apical half (Fig. 8E); gonostylus narrow and pointed apically (Fig. 8F) (broadly Holarctic) ..... *ledicola*

   Fore and mid femora and tibiae entirely brown (as in Fig. 3D); parameres sausage shaped, apical half about equal in diameter for entire length (Figs 10E, 12B); gonostylus with rounded apex (Figs 10F, 12C) 9

9. AR = 1.17; wing length 2.2 mm; apex of gonostylus markedly swollen (Fig. 10F) (eastern Palearctic) ..... *pacifica*

   AR = 1.00–1.03; wing length 1.6–1.8 mm; apex of gonostylus at most only slightly swollen (Fig. 12C) (Federal Republic of Germany) ..... *tecta*

Key to adult females of Palaearctic *Serromyia* species

1. Body pale yellow (Egypt) ..... *mangrovi*

   Body dark brown to black 2

2. Hind claws equal, similar to fore and mid leg claws 3

   Hind claws unequal (a single claw present), longer than fore and mid leg claws 4

3. Scutum pruinose; hind coxa lacking strong lateral bristles (Federal Republic of Germany) ..... *tecta*

   Scutum lacking pruinosity; hind coxa with 1–2 strong lateral bristles (as in Fig. 1B) (Europe) ..... *atra*

4. Palpus mostly pale, with only segments 4 and 5 darkly pigmented (Federal Republic of Germany, Caucasus) ..... *bicolor*

   Palpus uniformly dark brown 5

5. Scutum pruinose 6

   Scutum lacking pruinosity 10

6. Fore tibia nearly entirely darkly pigmented (as in Fig. 4F) 7

   Fore tibia only partially pigmented (Figs 4E, 5B, C, E, F) 8

7. Hind coxa lacking strong lateral bristles (Europe) ..... *subinermis* (in part)

   Hind coxa with about 4 strong lateral bristles (eastern Palearctic) ..... *pacifica*

8. Coxa of hindleg with 0–4 strong lateral bristles; collected 20 July to 6 November (broadly Holarctic) ..... *ledicola*

   Coxa of hindleg lacking strong lateral bristles; collected before 14 August 9

9. Wing slightly infuscated, with cells r_1 and r_{2+3} dark brown (Europe) ..... *subinermis* (in part)

   Wing pale, with cells r_1 and r_{2+3} pale or slightly pigmented (Europe) ..... *femorata*

10. Mid femur entirely dark brown; HC/Ta_5 = 0.67–0.89 (Europe) ..... *rufitarsis*

    Mid femur pale basally; HC/Ta_5 = 0.97–1.32 (Europe) ..... *morio*

Serromyia barberi Wirth

Serromyia barberi Wirth 1952: 205. Holotype, ♂ adult, pinned, labelled 'Eureka, Cal. 22.5', 'HS Barber Collector', 'Holotype Serromyia barberi W.W. Wirth' (USNM); allotype ♀ labelled as for holotype but collected 6.vi (USNM); paratypes: 17♂, 2♀ from type locality collected either 22.v or 6.vi (USNM); U.S.A.: 1 ♀, Cal., Humboldt Co., Hely Creek, 11.viii.1948 (USNM); 1♀, Cal., San Luis Obispo Co., Black Lake Canyon (not found).

Diagnosis. Male: only Nearctic species with a paramere with a distinctly pointed apex. Female: only Nearctic species with the fore and mid tibae pale or with only apex of mid tibia pigmented, with the scutum lacking pruinosity, 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 bare of pruinosity.

Legs: coloration pattern as indicated in Fig. 2A, B; strong bristles on femora, tibiae distributed as follows: 1 present anteriorly, to 21 present anteriorly, ventrally, posteriorly on fore femur, present or absent posteriorly on fore

tibia, present or absent anteriorly, ventrally, posteriorly on mid femur, present or absent posteriorly on mid tibia, present ventrally on hind femur, present or absent anteriorly on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind ta_1 straight; ta_4 setae straight or slightly curved.

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

Abdomen: dark brown.

Genitalia (Fig. 6C): gonostylus with outer margin evenly curved, tapering gradually to slightly swollen, rounded or somewhat pointed apex; paramere (Fig. 6B) slender, with pointed apex; aedeagus (Fig. 6A) lacking lateral prongs, distal portion a simple, slender projection, 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 absent on femora, tibiae except ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: pale or pale with veins of cells r_1, r_{2+3} darkly pigmented; 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.barberi* is known from the southern half of British Columbia south to California (Fig. 17A). The only other species west of the continental divide are *S.sierrensis* from the Sierra Nevada of California and *S.ledicola* which has been collected just west of the continental divide in Montana and Colorado. Adults of *S.barberi* have been collected from 17 May to 11 August.

The most southerly locality of *S.barberi* was a specimen labelled 'S. Fork Santa Ana R., Calif., 18 June, 1945'. This disjunct indicates further profitable collecting in southern California.

We found *S.barberi* most common in areas of seeps and along the margins of small streams, nearly always associated with flowing water. A few specimens were found along the margins of larger rivers. However, we found one female at the margin of a fen, 3 km E Salmon Arm, British Columbia, with no flowing water nearby.

Although rarely abundant, a large collection of six males and 100 females was made at Mary's Peak (Parker's Creek), 21 km W Corvallis, Oregon on 19.vii.1985. In most other areas, however, it often took 1–2 h to locate one specimen.

During broad daylight *S.barberi* adults were most commonly collected low in the vegetation and the edge of the net was held on the ground, while sweeping, to obtain these individuals. However, some specimens were collected by sweeping at arm level, especially along the margins of streams. Adults were restricted to a limited area within a habitat so that, for example, the margin of a stream could be swept for several hundred metres without finding a specimen and then suddenly two or three would be collected in the space of 5 m. We are unable to report any generalization which would predict where these specimens might be located.

In general, females were collected more frequently than males and this is reflected in their relative numbers in the collections made and in the museum collections examined.

Observations of female feeding were made at two localities. At 6.5 km SE of Hebo, Oregon, female *S.barberi* flew out of stream margin vegetation throughout the afternoon to dart into small chironomid swarms which formed in dark enclaves in the stream bank. At least some of these were of males of *Nilotanypus* Kieffer. Female *S.barberi* assumed a ragged up and down flight, somewhat mimicking the chironomid flight pattern, and then left the swarm to return to the vegetation. We succeeded in collecting one female with a chironomid male but could make no detailed observations as to how the prey was captured or held. At Parker's Creek on Mary's Peak, 21 km W Corvallis, Oregon, females were quiescent until after dusk when they could be collected along the narrow gravel road which bisected the stream where many had been resting earlier. They were especially common between 09.00 and 09.30 p.m. Females flew in directed flight at the height of about 2–2.5 m until they met with chironomid swarms which formed along this road. They then joined the swarm and assumed a similar ragged up and down flight. We were unable to make further observations on prey capture or feeding. We placed white sheets under such swarms but no *S.barberi* females landed on

these, as may happen with prey capture in other groups (Downes, 1978).

W. W. Wirth collected a male at Revelstoke, British Columbia, on an Umbelliferae, where the specimen was presumably feeding on flower nectar.

We examined a gynandromorph female from Cowichan Lake, B.C. (CNCI) in which flagellomeres 1–8 of the right antenna are male-like and plumose.

Taxonomic discussion. One character, generally of good diagnostic value within the genus, exhibited a puzzling degree of variation in male *S. barberi*. The number of strong bristles on the fore femur varied from 1 to 21, representing individuals with a near total lack of strong bristles on all the legs to very bristly specimens. In some areas, such as southern Vancouver Island, variation ranged virtually continuously from 2 to 21 bristles, while on Mary's Peak, 21 km W Corvallis, Oregon the senior author collected 6 males on 19.vii.1985 with 1, 1, 1, 10, 13 and 17 bristles on the fore femur. We were unable to find any correlation with size, geographical or temporal distribution, although it should be noted that only sixty-six males were available for study.

The sex of one of the paratypes from Eureka was incorrectly given as male by Wirth (1952). We were unable to locate the paratype from Black Lake Canyon.

Material examined. Seventy-two males and 268 females.

Derivation of specific epithet. The name *barberi* refers to the collector of the type series, H. S. Barber.

Serromyia borealis Borkent sp.n.

Diagnosis. Male: only Nearctic species with mid femur completely pigmented brown and aedeagus with lateral prongs. Female: only Nearctic species with claws of hind leg equal, short (male-like) and mandible well developed, with teeth.

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. 2C; strong bristles absent on femora, tibiae except ventrally on hind femur, arising from slightly developed tubercles; hind Ta_1 straight to with slight basal curvature; Ta_4 setae straight or with slight curve.

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

Abdomen: dark brown.

Genitalia (Fig. 6F): gonostylus with outer margin evenly curved, tapering gradually for basal half, with rounded, slightly to moderately swollen apex; paramere (Fig. 6E) with apical half somewhat swollen, somewhat rounded, but with apex difficult to discern; aedeagus (Fig. 6D) with lateral prongs, directed laterally, 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. 4F; claws of hind leg equal, small.

Wing: pale with veins of cells r_1, r_{2+3} darkly pigmented; macrotrichia absent.

Genitalia (Fig. 12D): sternite 9 truncate medially; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. S. borealis is known from Alberta to Manitoba (Fig. 17B). Adults have been collected from 15 June to 4 July.

We collected this species at two localities. At 10 km E Spruce Grove, Alberta, two males were swept from the upper branches of short (3–4 m) spruce trees in a well-developed sphagnum bog. At the type locality, both males and females were swept from grassy tussocks, very near to the ground, in a black spruce bog. Adults were restricted to a small patch of ground about 15 m in diameter, which was a little drier than the surrounding area.

Taxonomic discussion. The association of males and females was based on the number of each collected at the type locality. It should be noted, however, that one female of *S. vockerothi* was also collected at this site.

Types. Holotype, ♂ adult on microscope slide, labelled 'Holotype Serromyia borealis Borkent, CNC No. 20128, ♂, 3.2 km. N. Nordegg, Alta., 28-VI-1985, A. Borkent CD379', allotype on microscope slide labelled as for holotype (CNCI); paratypes: 9♂, 9♀

labelled as for holotype (CNCI, USNM); CANADA: 1♂, Alberta, Nordegg, 15.vi.1921 (CNCI); 2♂, Alberta, 10 km E Spruce Grove (Wagner Bog), 24–26.vi.1985 (CNCI); 1♀, Manitoba, Churchill, 4.vii.1947 (CNCI).

Derivation of specific epithet. The name *borealis* (northern) refers to the perceived boreal habitat of this species.

Serromyia crassifemorata Malloch

Serromyia crassifemorata Malloch 1914: 218. Lectotype designated by Frison (1927), ♀ adult, pinned, labelled '1789', 'Serromyia crassifemorata Malloch (Type)', '♀', 'Lectotype ♀ Serromyia crassifemorata Malloch', 'Property of the Illinois Natural History Survey' (INHS); paralectotype ♀ on pin from same locality (as indicated by Malloch, 1914), with additional labels stating: '#1789 IL, Mt. Carmel 28 May 1884 from leaves of *Quercus*' 'Serromyia crassifemorata Det. A. Borkent' (INHS).

Diagnosis. Male: only Nearctic species lacking strong bristles on legs, with mid femur uniformly dark brown, with aedeagus lacking side prongs and paramere with rounded apex. Female: only Nearctic species with short, equal hind claws and reduced, nonserrate mandibles.

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

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

Thorax: medium to dark brown; scutum bare of pruinosity.

Legs: coloration pattern as indicated in Fig. 2D; 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 Ta_1 straight; 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. 7C): gonostylus with outer margin evenly curved, tapering gradually to slightly swollen, rounded to somewhat pointed apex; paramere (Fig. 7B) with apical half sausage shaped, rounded apex; aedeagus (Fig. 7A) lacking lateral prongs, distal portion a simple, slender projection, 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 vestigial, no teeth evident.

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

Wing: macrotrichia absent or 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.crassifemorata is known from southern Ontario and Quebec, south to Tennessee and Georgia (Fig. 17B). Adults have been collected from 2 May to 22 June. Johannsen (1928, 1943) reported this species from Lewiston, New York, and, though the species almost certainly does occur in New York, we failed to examine any material from that state.

The nonfunctional mandibles of the female, unique in the genus, indicates that it does not feed on other insects.

The localities from which this species have been collected suggest that *S.crassifemorata* occurs in both lotic and lentic habitats. W. W. Wirth collected a series of females in Virginia in *Osmunda* bogs (a genus of fern, characteristic of wet woodland and some open swamps) and a few from a stream margin at Alexandria, Virginia. We collected one specimen from Rondeau Provincial Park in southern Ontario in a malaise trap located in a wet swampy area.

Taxonomic discussion. The recognition of the previously unknown male is based on the association of twenty males with two females of *S.crassifemorata* from Cobden, Illinois, collected 7–9.v.1918. One additional male was from Roaring Spring, Jonesboro, Illinois.

Wirth & Grogan (1981) provided a description of the female of *S.crassifemorata*.

Material examined. Twenty-one males and seventy-six females.

Derivation of specific epithet. The name *crassifemorata* means thickened femora and presumably refers to the thick hind femora of this and all other species in the genus.

***Serromyia nudicolis* Borkent sp.n.**

Diagnosis. Male: only Nearctic species with mid femur completely darkly pigmented, with numerous strong bristles on legs (at least fore femur with anterior and posterior strong bristles) and paramere with rounded apex. Female: only Nearctic species with a ratio of antennal flagellomeres 8/9 = 0.62–0.82, and an elongate, single hind claw, with HC/Ta_5 = 0.62–1.06.

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. 2E; strong bristles of femora, tibiae distributed as follows: anteriorly, posteriorly on fore femur, present or absent dorsally, ventrally on fore femur, posteriorly on fore tibia, present or absent anteriorly, dorsally on fore tibia, at least some present but present or absent anteriorly, dorsally, ventrally, posteriorly on mid femur, posteriorly on mid tibia, present or absent anteriorly, dorsally on mid tibia, 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. 7F): gonostylus with outer margin evenly curved, tapering gradually for basal half, with pointed apex or with slightly swollen, somewhat rounded apex; paramere (Fig. 7E) with apical half sausage shaped (sometimes somewhat shrivelled), apex rounded; aedeagus (Fig. 7D) lacking lateral prongs, distal portion a simple, slender projection, 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, 5A; strong bristles of femora, tibiae distributed as follows: 1–2 apically on mid tibia (absent on one specimen), 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 somewhat truncate but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

First instar larva. Total length = 0.74–0.91 mm (n=4).

Head: length = 78.4–84.0 μm (n = 5), length/width = 1.40–1.53 (n = 3); capsule medium brown, with well developed, darkly pigmented egg burster (Fig. 14F); eye spot pigmented black, shaped as simple, elongate oval, oriented dorsoventrally; antenna large, flat disc, with 7 short sensilla at anterolateral margin of base (Figs 14E, 15D), setae x on medial margin of antennal base (Fig. 15D); labrum with anterolateral group of 4 short, thick sensilla with very fine spicules at bases, a more medial, short seta, an elongate ventrolateral seta, an apical setiform sensillum (Figs 15B, C, D); mandible sickle shaped, elongate, extending in adducted state to level of setae o, apex longitudinally corrugated but mandible not seen well enough to describe further; maxilla with 1 elongate seta at base of anteriorly projecting lobe, palpus reduced with 8 sensilla distributed as follows: 1 small aboral, 2 large, stout aboral sensilla, 2 on anterolateral lobe, 3 on anteromedial lobe (Figs 15C, E); labium with single, anteriorly projecting tooth (Fig. 15C); otherwise following setae present (Figs 14E, F, 15A, D): t, s, q, p, w, u, v, o, y (j could not be seen), distribution similar to that given by Glukhova (1979) for fourth instar but seta u directly dorsal to v; sensory pits z, k, r, m, n absent; epipharynx with lateral arm well developed, with barely discernible, posteriorly directed comb.

Thorax, abdomen: lacking pigmentation; thorax with well-developed collar; proleg absent; perianal setae short, poorly developed, restricted to lateral, dorsal surface of segment 9 (Fig. 15F); no evidence of anus, anal papillae.

Egg. Dark brown, elongate, slightly curved (Fig. 14A), length = 592–632 μm, width = 79–87 μm, length/width = 6.8–8.0 (n=10); with short tubercles arranged in somewhat scattered, longitudinal rows (Figs 14A, B) (easily seen at ×100 under compound microscope); tubercles longer around micropyle, arranged in circular pattern, amongst which are

very small, blunt tubercles (Figs 14C, D); egg shell with circular cap at very anterior end and dorsal, longitudinal fissure restricted to anterior 1/3 (Fig. 16A).

Distribution and bionomics. S.nudicolis is known from Ontario to Newfoundland, south to Tennessee and Georgia (Fig. 17C). The southern localities are restricted to the Appalachian Mountains and probably reflect the cool, wet habitat of this species. Adults have been collected from 23 May to 30 July, but seem most common, at least in southern Ontario and Quebec and the northeastern states, from mid June to mid July.

We collected adults of this species in moist deciduous or mixed deciduous–coniferous woods, always in the presence of small running seeps or streams. In some but not all instances these waters led to wet meadows or fens.

We made some observations on male adult behaviour at the type locality, 33.5 km S Ashland, Maine. At this place the vegetation had been recently cut and trees and shrubs were only about 2–3 m high. We were able to collect males from the very tops of small *Abies balsamea*. Sampling at regular intervals led to repeated collections, indicating that the males were actively seeking out these sites. In general, we were able to collect mostly females of *S.nudicolis* and these observations of tree topping may indicate that the males were scarce in collections because they swarm, or at least congregate, at the apices of tree tops where we, and most other collectors, have been unable to collect at most sites.

We were able to observe on two separate occasions female avoidance behaviour. We initially found each of two females hanging on the underside of leaves about 1 m above the ground. Upon being slowly approached to a distance of about 50 cm, each of these females dropped to the ground. Net collected specimens of this and of every other Nearctic species we collected, exhibited a similar behaviour of dropping to the net bottom when disturbed.

The eggs and first instar larvae of *S.nudicolis* were obtained by decapitating field caught females and placing these in petri dishes on a shallow layer of agar. Eggs from such females were laid at the rate of 12–16 per minute with some laid in a group and abutting laterally, while others were scattered on the agar. Fertile eggs were dark brown, while non-fertilized (i.e. those which failed to develop) were pale or pale brown. Larvae hatched about 12–15 days after eggs were laid on agar plates and held at about 20°C. Emerging first instars were very active, moving with a slow snake-like motion characteristic of many other ceratopogonid larvae. We introduced nematodes (as described in Materials and Methods) but, in spite of observing one larva feeding, failed to rear these to even the second instar.

Taxonomic discussion. Wirth (1952: 206, 1965) identified members of *S.nudicolis* as *S.femorata*.

Types. Holotype, ♂ adult on microscope slide, labelled 'Holotype Serromyia nudicolis Borkent, CNC No. 20126, ♂, Maine, 33.5 km S Ashland CD587, 2-VII-1986, A. Borkent' (CNCI); allotype on microscope slide labelled as for holotype (CNCI); paratypes: 11♂, 17♀, 2 first instar larvae, 1 egg, 1 egg shell labelled as for holotype (CNCI, USNM); CANADA: 7♀, Ontario, Iroquois Falls, various dates ranging 18.vi–7.vii.1987 (CNCI); 1♀, Ontario, Black Lake, 15 km SW Lanark, 23.vi.1975 (CNCI); 1♀, Ontario, Algonquin Park, 8.vi.1960 (USNM); 2♀, 2 first instar larvae, 13 egg shells, Ontario, 10 km SW Richmond, 17.vi.1987 (CNCI); 8♀, Ontario, Ottawa, 17.vi.1946, 19.vi.1946, 8.vi.1951, 25.vi.1964, 23.vi.1980 (CNCI); 2♀, Ontario, Waubamik, 14.vi.1915 (USNM); 1♀, Ontario, Finland, 17.vii.1960 (CNCI); 3♀, Ontario, Maynooth, 19.vi.1953 (CNCI); 1♀, Ontario, Midland, 30.vii.1956 (CNCI); 1♀, Quebec, Mistassini, 12.vii.1956 (CNCI); 2♀, Quebec, Beechgrove, 7.vi.1955, 29.vi.1962 (CNCI); 2♀, Quebec, Gatineau Park, Black Lake, 27.vi.1985, 9.vii.1985 (CNCI); 4♀, Quebec, Gatineau Park, Bourgeois Lake, 11.vi.1987 (CNCI); 9♀, 1 first instar larva, 6 egg shells, Quebec, 5 km W Old Chelsea, 10.vi.1987 (CNCI); 5♀, Quebec, Old Chelsea, 21.vi.1959, 16.vi.1961, 8.vi.1964 (CNCI); 1♀, Quebec, Kam. Co., Parke Reserve, [32 km S Riviere du Loup], 4.vii.1957 (CNCI); 2♀, Quebec, Meach Lake, 21.vi.1916, 5.vii.1916 (CUIC); 1♂, 6♀, New Brunswick, Kouchibouguac National Park, vii.1977, 9–11.vii.1977, 11–12.vii.1978 (CNCI); 3♀, Nova Scotia, Cape Breton Highlands National Park, North Mountain, 1–4.ii.1983 (CNCI); 1♀, Newfoundland, mountains east of Codroy, 19–22.vii.1905 (MCZC); 1♀, Terra Nova National Park, Newfoundland, 6.vii.1961

(USNM); U.S.A.: 6♀, Wisconsin, Washburn Co., 20–21.vi.1953 (USNM); 2♀, Michigan, Gladwin Co., 14.vi.1958, 19.vi.1943 (USNM); 1♀, Michigan, Kalkaska Co., 23.vi.1951 (USNM); 1♀, Michigan, Livingston Co., E.S. George Reserve, 4.vi.1950 (USNM); 1♀, Michigan, Saginaw Co., 9.vi.1952 (USNM); 1♀, Michigan, Alpena Co., 4.vii.1941 (USNM); 2♀, Michigan, Wexford Co., 14.vi.1952 (USNM); 10♀, Michigan, Crawford Co., 17.vi.1951, 21.vi.1953 (USNM); 5♀, Michigan, Cheboygan Co., 4.vii.1953 (USNM); 3♀, Michigan, Midland Co., 14.vi.1952, 16.vi.1952 (USNM); 1♀, New York, Caroline-Harford, 15.vi.1904 (CUIC); 12♀, New York, Tompkins Co., Ringwood Reservoir, 16–17.vi.1963 (USNM); 3♀, New York, Orleans Co., Albion, 11.vi.1963 (USNM); 5♀, New York, St Lawrence Co., Cranberry L., 25.vi.1963 (USNM); 4♀, New York, St Lawrence Co., Benson Mines, 25.vi.1963 (USNM); 7♂, 14♀, New York, Lewis Co., Whetstone Gulf, 20–23.vi.1963 (USNM); 1♀, New York, North Beach, L.I., 30.v.1930 (MCZC); 1♀, New York, Slaterville [nr Candor], 13.vi.1904 (INHS); 2♂, 12♀, 1 first instar larva, 14 egg shells, Vermont, 5 km E Danby, 25–26.vi.1986 (CNCI, INHS, USNM, RYSC, NHMW); 1♀, New Hampshire, Third Connecticut Lake [10 km N Idlewilde], 9.vii.1952 (USNM); 1♂, New Hampshire, Franconia (AMNH); 7♀, Maine, 14 km NW Camden, 1.vii.1986 (CNCI, RYSC); 1♀, Maine, Katahdin, 4.v.1959 (USNM); 1♀, Connecticut, Redding, 27.v.1933 (USNM); 1♀, Pennsylvania, Centre Co., Pine Grove Mills, 16.vi.1975 (CASC); 1♀, Pennsylvania, Centre Co., 4.vii.1972 (CASC); 1♀, Massachusetts, Burgess, 15.vi.1876 (USNM); 4♂, 4♀, Massachusetts, Holliston 26.v, 9.vi.1956 (MCZC, USNM); 1♀, West Virginia, Cranberry Glades [= 23 km E Richwood], 4.vi.1955 (USNM); 1♀, Tennessee, Gatlinburg, 29.vi.1947 (USNM); 1♂, 6♀, North Carolina, Highlands, 23.v.1957, 29.v.1957 (CNCI); 1♀ Georgia, Unicoi State Park (nr Helen), 17.v.1979 (CNCI).

Derivation of specific epithet. The name *nudicolis* (nude, penis) refers to the aedeagus which lacks side prongs.

Serromyia sierrensis **Borkent sp.n.**

Diagnosis. Male: only Nearctic species with mid femur yellow with apical portion more darkly pigmented and scutum lacking pruinosity. Female: only Nearctic species with fore and mid tibiae dark brown and with an elongated, single hind claw with the claw longer than Ta_5.

Description. Male adult. Descriptive statistics: see Tables 2–6.

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. 2F; strong bristles of femora, tibiae distributed as follows: one anteroapically on fore femur, one anteriorly, one posteriorly on mid femur, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta_1 straight; 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: broken from specimen, lost.

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. 4F; strong bristles of femora, tibiae distributed as follows: single bristle at apex of mid tibia, ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: slightly infuscated with veins of cells r_1, r_{23} darkly pigmented; a 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.sierrensis is known only from the Sierra Nevada of California (Fig. 17D). Adults have been collected from 2 June to 3 July.

Taxonomic discussion. This is the only species described as new in which the holotype is a female. The single male was missing its genitalia, and although we are confident that it is correctly associated with the two females, we are reluctant to designate such a damaged specimen as the holotype.

The male of *S.sierrensis* has an unusually high

antennal ratio and this feature, once more material becomes available, may prove to be distinctive, at least within the western Nearctic.

CASC provides type numbers for all its holotypes and has assigned *S.sierrensis* no.16472.

Types. Holotype, ♀ adult on microscope slide, labelled 'Holotype Serromyia sierrensis Borkent, ♀, CAL [California] Placer Co., E. end Bear Val., 2-VI-1964, P.H. Arnaud, Jr.', 'Serromyia barberi Det. W. Wirth, '76', (CASC); allotype ♂ on microscope slide. U.S.A: Cal., Nevada Co., Sagehen Creek, 26.vi.1974 (CASC); paratype: 1♀, Cal., Sierra Co., Webber Lake, 3.vii.1964 (CASC).

Derivation of specific epithet. The name *sierrensis* refers to the type locality in the Sierra Nevada of California.

Serromyia vockerothi Borkent sp.n.

Diagnosis. Male: only Nearctic species with mid femur yellow and pigmented only apically, with strong bristles on fore femur (at least present anteriorly and posteriorly) and with scutum pruinose. Female: only Nearctic species with a ratio of antennal flagellomeres 8/9 = 0.59–0.60 and an elongate, single hind claw about the same length as Ta_5.

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. 3A; 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 anteriorly, dorsally on fore tibia, anteriorly, ventrally, posteriorly on mid femur, posteriorly on mid tibia, present or absent on mid tibia, anteriorly, ventrally on hind femur, present or absent posteriorly 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. 8C): gonostylus with outer margin evenly curved, tapering gradually for basal half, with rounded or somewhat pointed apex; paramere (Fig. 8B) with apical half sausage shaped (sometimes somewhat shrivelled), apex rounded; aedeagus (Fig. 8A) with lateral prongs directed posterolaterally, somewhat reduced in some, 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. 5B; strong bristles of femora, tibiae distributed as follows: absent or 1 present on fore femur, 1 present apically on mid tibia, 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 somewhat truncate medially but with anteromedial margin developed, pointed; two spermathecae, additional spermathecal duct terminating in pigmented apex.

Distribution and bionomics. S.vockerothi is known from Alberta to southern Quebec and from one locality in Minnesota (Fig. 17D). Adults have been collected from 4 to 26 June. The holotype and allotype were collected near the margin of a shallow, small (i.e. 7–8 m by 2 m, woodland pool with thick moss and rich vegetation growing around its margin. The single female from 3.2 km N Nordegg was taken in a black spruce bog (habitat described more fully under *S.borealis*).

Taxonomic discussion. Although we are reasonably confident of the conspecificity of the three males and the allotype, we are less sure that the two female specimens from Alberta are accurately interpreted. It may be that they are actually members of *S.nudicolis* or of another undescribed species. Further collecting, especially of males in Alberta, is required.

The allotype is somewhat damaged and is missing all tarsomeres and flagellomeres 6–13. When first collected, this female was believed to be a specimen of *S.nudicolis* and was kept alive in the hopes of obtaining some eggs. Unfortunately, she died and was damaged before being properly preserved.

A male from Abbotsford, Quebec (11.vi.

1937, CNCI) may be a member of this species but lacked the lateral prongs on the aedeagus. One of the paratypes of *S.vockerothi* had somewhat reduced lateral prongs, indicating that lack of lateral prongs may be within the variation of the species. Further material is required to determine whether the Abbotsford specimen is *S.vockerothi* or represents an undescribed species.

Types. Holotype, ♂ adult on microscope slide, labelled 'Holotype Serromyia vockerothi Borkent CNC No. 20127, ♂, 10 km S Victoria Beach, Manitoba, 18.VI.1985, A. Borkent CD368', allotype ♀ on microscope slide labelled as for holotype (CNCI); paratypes: CANADA: 1♂, Quebec, Mt. St. Hilaire, 500–700 ft, 4.vi.1963 (CNCI); 1♀, Alberta, Edmonton, 1932 (CASC); 1♀, Alberta, 3.2 km N Nordegg (Wagner Bog), 28.vi.1985 (CNCI); U.S.A.: 1♂, Minnesota, Itasca Park [30 km N Park Rapids], 17.vi.1938 (USNM).

Derivation of specific epithet. The name *vockerothi* is proposed in appreciation of our friend and colleague Dr J. Richard Vockeroth. His outstanding collecting efforts in all the Diptera are reflected in this study. He collected specimens of nearly every Nearctic *Serromyia* species (including this one) as well as important series of *S.femorata*, *S.ledicola* and *S.morio* from Europe. In addition, his unstinting willingness to share his vast knowledge of Diptera, his knowledge of the literature and location of often difficult to find museum specimens added immeasurably to this study.

Serromyia ledicola Kieffer

Serromyia ledicola Kieffer 1925a: 156. Neotype, here designated, ♂ adult, on microscope slide, labelled 'Estonia Hiiumaa, H. Remm, 8–8–53, Serromyia ledicola K det. H. Remm, Neotype CNC No. 20129'. (CNCI). Remm 1969: 214 (in part).

Serromyia macronyx Goetghebuer 1933: 355. Lectotype, here designated, ♂ adult, pinned but subsequently mounted on microscope slide, labelled 'La Panne 7.9.33 M. Goetghebuer', 'R.I.Sc.N.B. 18.073 Coll et det., M. Goetghebuer', 'macronyx', 'Type Lectotype ♂ M. Goetghebuer. Serromyia ledicola Det. A. Borkent' (ISNB); paralectotype ♀ adult on microscope slide from type locality but dated 1–17.ix.33 (ISNB).

Serromyia europaea Clastrier 1963: 61. Holotype, ♂ adult on microscope slide, labelled 'Autriche [Austria] Heiligenblut 10–VIII–1960 à la lumière Serromyia europaea Holotype ♂ 2356, Serromyia ledicola Det. A. Borkent' (MNHN).

Ceratopogon femoratus: authors, not Meigen. Staeger 1839: 598 (in part).
Zetterstedt 1838: 822 (in part), 1850: 3665 (in part). Coquillett 1900: 396.

Serromyia femorata: of authors not Meigen. Wirth 1965: 136. Havelka 1976: 236 (in part). Havelka & Caspers 1981: 30 (in part).

Diagnosis. Male: only Holarctic species with fore femur, at most, with a few ventral strong bristles, mid femur pigmented only at apex, scutum pruinose, and parameres with apical half markedly swollen and rounded (in Nearctic, only species with short aedeagus, L/W = 0.39–0.54). Female: only Holarctic species with palpus uniformly dark brown, fore and mid tibiae pigmented only apically, hind coxa with 0–4 lateral strong bristles, scutum pruinose, and an elongate, unequal hind claw with HC/Ta_5 = 1.07–1.49.

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 3B, C; strong bristles of femora, tibiae distributed as follows: present or absent ventrally on fore femur, present or absent anteriorly, ventrally, posteriorly on fore tibia, present or absent ventrally on mid femur, present or absent anteriorly, ventrally, posteriorly on mid tibia, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta_1 straight; Ta_4 setae straight or with slight curve.

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

Abdomen: dark brown.

Genitalia (Fig. 8F): gonostylus with outer margin evenly curved, tapering gently for basal half, with pointed apex; paramere (Fig. 8E) with apical half markedly swollen, apex rounded; aedeagus (Fig. 8D) with lateral prongs, directed posterolaterally, distal portion a simple, slender projection, about twice as

long as 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, 5C; strong bristles absent on femora, tibiae except ventrally on hind femur; claw of hind leg single, elongate, with basal tooth.

Wing: pale or pale with veins of cells r_1, r_{2+3} light brown; 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.ledicola is known in Europe from Sweden and Estonia south to England and northern Italy and in North America from Alaska to Newfoundland south to Colorado and Virginia (Fig. 18A). Adults have been collected from 13 July to 6 November.

Remm (1973a) noted the presence of *S.ledicola* in Mongolia, collected at the end of July. We have not examined the specimens but the records are consistent with the conclusion that *S.ledicola* is a Holarctic species.

The two disjunct southern Nearctic records are from Gould, Colorado and Reddish Knob, Augusta Co., Virginia.

The collections from Alaska, particularly along the Aleutian Island chain, support the conclusion that *S.ledicola* is a Holarctic species. Although not yet recorded from the far eastern Palaearctic, it is certainly to be expected there.

The record of *S.femorata* (as *Ceratopogon femoratus*) from Popof Island, Alaska by Coquillett (1900) is actually of a specimen of *S.ledicola*.

The few available records of habitat indicate that this species is associated with boggy areas, sometimes in the vicinity of seeps or small streams but also in areas with only standing waters. Goetghebuer (1936b) suggested that this species (as *S.macronyx*) was restricted to eutrophic lentic habitats in southern Belgium.

S.ledicola is virtually unique in the Holarctic fauna in being a late season emerger. Although the overall emergence period is from 13 July to 6 November, the earlier records are from localities with climatic extremes: Adak and Popof Islands in the Aleutians of Alaska and Lake McDonald, Montana (35 km NE Columbia Falls). If these are excluded, the earliest collection we examined in North America was from 1 August. The only other Nearctic species which overlaps with *S.ledicola* is *S.barberi* of which a few specimens have been collected as late as 11 August. In Europe a similar pattern is apparent. With the exception of a sample from Obergurgl, Tirol, Austria, taken near the foot of a glacier from 20 July to 3 September, the earliest sample was from 1 August. Only the sympatric Palaearctic species *S.femorata* and *S.morio* overlap temporally with late records of 14 and 16 August respectively. *S.mangrovi*, from the Sinai, has been recorded as late as 18–19 November.

Taxonomic discussion. We attempted to locate the Kieffer holotype female of *S.ledicola*, collected by A. Dampf, but failed. Considering that so many of Kieffer's types are known to have been lost or destroyed, it is likely that the type of *S.ledicola* is also gone. We have therefore designated a neotype from the same area from which the holotype was originally collected (Mavli bog on Dago [= Hiiumaa Island], Estonia [U.S.S.R.]).

North American workers have uniformly considered Nearctic material of this species (sometimes also including material of other species) as *S.femorata*. However, it is clear from examination of the type of *S.femorata* that this was a misinterpretation.

Remm (1981) provided the synonymy listed here and we have been able to partially confirm this through examination of the types of *S.macronyx* and *S.europaea*. He correctly states that the late flight period may be taken as evidence of the synonymy, even though as far as *S.europaea* is concerned, some *S.femoratus* and *S.morio* also fly into August. However, we have been unable to confirm that the holotype of *S.ledicola* was collected late in the season and correspondence with Dr Remm questioning him about this reached him after his untimely death. Regardless, the rather general description by Kieffer (1925a) does fit the concept of *S.ledicola* as presented here (female with long hind claw and yellow legs lacking spines) and we accept Remm's suggestion of *ledicola* being the oldest available name.

Goetghebuer (1933) noted that there were

three males and fifteen females in the type series of *S.macronyx* but we were only able to examine the single male and female noted above.

Remm (1969) provided a key to the *Serromyia* species in the European portion of the U.S.S.R. Based on specimens he sent to us, his concept of female *ledicola* included specimens of *S.morio*.

We have examined Zetterstedt's collections and found a male and female of this species in material identified as *S.femorata*. In addition, Zetterstedt (1850) mentioned that he had collected material in September, which can only refer to *S.ledicola*.

One of the specimens identified by Staeger (in ZMUC) as *Ceratopogon femoratus* was in fact *S.ledicola*.

One of the paratypes of *S.europaea* (from Norway) (MNHN) is actually a male of *S.femorata*.

Material examined. 85 males and 109 females.

Derivation of specific epithet. The name *ledicola* (*Ledum* (labrador tea), dweller) probably refers to the boggy habitat of *S.ledicola*, where *Ledum* grows and from which Kieffer (1925a) recorded this species.

Serromyia atra (Meigen)

Ceratopogon ater Meigen 1818: 84. Neotype, here designated, ♂ adult on microscope slide, labelled 'Ceratopogon ater Meigen, ♂, Serromyia atra Mg. H. Remm, Neotype, Latvia, Jumurda Lake [10 km E. Ergli], E. Remm, 21–6–67 CNC No. 20130 Serromyia atra Det. A. Borkent' (CNCI).

Prionomyia atra: Stephens 1829: 238.

Ceratolophus ater: Kertész 1902: 157.

Serromyia ater: Kieffer 1906: 65.

Serromyia atra: Kieffer 1919: 74.

Serromyia micronyx Kieffer 1919: 70. Neotype, here designated, ♂ adult on microscope slide, labelled 'Serromyia micronyx Kieffer, Neotype, ♂, 1967.V.16, leg. Mihályi, Kiskomarom [15 km. W. Marcali], Hungary, erdo, Serromyia atra Det. A. Borkent' (HNHM). **New synonym.**

Serromyia albitarsis Kieffer 1919: 71. Neotype, here designated, ♂ adult, labelled 'Serromyia albitarsis Kieffer, Neotype, 1965.V.19, leg. Mihályi, Ocsa, Hungary, laprét, Serromyia atra Det. A. Borkent' (HNHM).

Serromyia spinosipes Kieffer 1919:72. Lectotype, here designated, ♂ adult on microscope slide, labelled 'spinosipes typus [in red] Kieff. det. Kieffer, ♂, Budapest Kertész, Purchd. from Budapest Mus. B.M. 1922–72. Lectotype, Serromyia atra Det. A. Borkent, Return to Brit. Mus. (N.H.)' (BMNH); paralectotype ♀ adult labelled as for lectotype but identified as Serromyia morio (BMNH). **New synonym.**

Serromyia nitens Goetghebuer 1920: 73. Lectotype, here designated, ♂ adult on microscope slide, labelled 'Wemmel [just north of Brussels, Belgium], 4–6–18 [June 4, 1918], R.I.Sc.N.B. 18.073 Coll. et det., M. Goetghebuer, nitens Goetghe., Lectotype, ♂, Serromyia atra Det. A. Borkent' (ISNB); paralectotype: ♀ labelled as for lectotype but date probably incorrectly given as 4 June 1917 (ISNB). **New synonym.**

Diagnosis. Male: only Palaearctic species with fore femur with only one longitudinal, ventral row of strong bristles plus 0–2 strong bristles anteriorly, and with the prongs on the aedeagus directed anterolaterally. Female: only Palaearctic species with equal hind claws and a scutum bare of pruinosity.

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. 3D; strong bristles of femora, tibiae distributed as follows: ventrally on fore femur, one bristle present or absent anteriorly on fore femur, ventrally on mid femur, present or absent anteriorly, posteriorly on mid femur, 0–3 bristles anteriorly on hind femur, ventrally on hind femur, dorsally on hind tibia; ventral bristles on hind femur arising from slightly developed tubercles; hind Ta_1 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 (as in Fig. 10C): gonostylus with outer margin evenly curved, tapering gradually for basal half, with somewhat pointed to swollen, rounded apex; paramere (as in Fig. 10B) with apical half markedly swollen, apex

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 Ta_1 straight; Ta_4 setae with slight curve or some slightly sinuate near their apex.

Wing: slightly infuscated with veins of cells r_1, r_{2+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 Armanskaja 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 Ta_1 straight or with slight basal curvature; Ta_4 setae straight or with slight curve.

Wing: pale or slightly infuscated with veins of cells r_1, r_{2+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 dorsolaterally, 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 Causcasus 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, Sphaeromiini 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 Ta_1 with marked basal bend; Ta_4 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 Ta_5.

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 Ta_1 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. 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.

Ceratolophus 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 rufitarsus 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 Yakhiyavr, 11 July 1952 (IZBE); paratypes: ESTONIA S.S.R.: 111♂, 69♀ (not seen) from Valga, Vyru, Pyarnu, Tartu and Khaŕyu 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 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. 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 Tromsoe [=Tromso]) 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 dorsoventrally (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 Hejöbába (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 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. 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 Ta_4 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 $HC/Ta_5 = 1.09-1.38$.

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 led single, elongate (Figs 13B, F), with basal tooth, $HC/Ta_5 = 1.09-1.38$.

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: Ta_4 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 trifid apex; Ta_4 with straight setae.

Distribution. From Baltic amber (Eocene).

Taxonomic discussion. The trifid aeadeagus of *S.ryszardi* 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 *ryszardi* 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; Ta_4 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: Ta_4 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 ta_4.

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 *Monohelea* 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 *Metacanthohela* 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 coqani*.

—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.nocticolor*.

—male antenna with flagellomeres 1–8 fused: flagellomeres fused in *S.mangrovi* and *S.nocticolor* 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.nocticolor* 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 aeadeagus. This tripartite condition is also present in various configurations, in some African species: *S.agathae*, *S.neethlingi*,

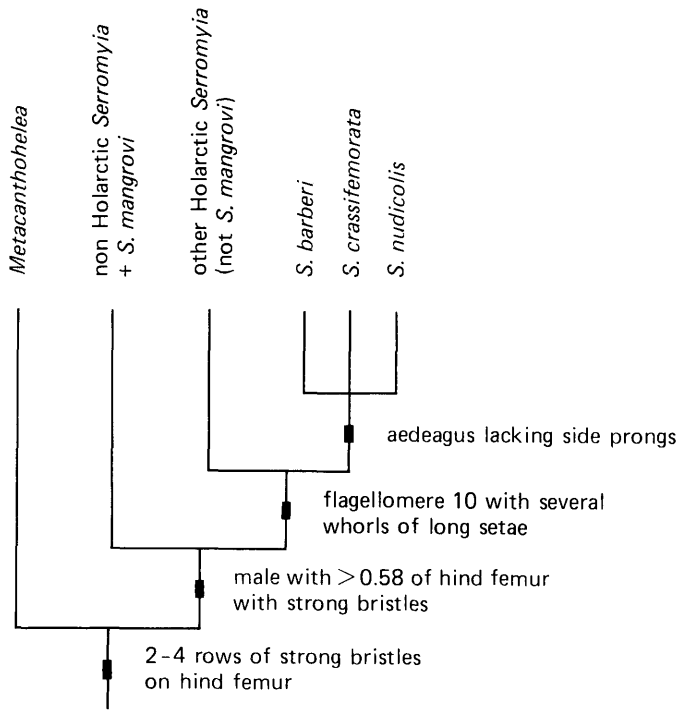


Fig. 20. Cladogram showing relationships within *Serromyia* and its sister lineage. Black rectangles and accompanying descriptions represent synapomorphic character states.

S.meiswinkeli, *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 vestigal 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 *Chimaerohela* 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.nudicolis*, *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 Neotrophical 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.

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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 Antliatorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus*. 372pp. + 30pp. Brunsvigae [=Brunswick].

Fox, I. (1946) A eview 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 1er d'Entomologie*, **35**, 17–75.

Gil Collado, J. (1957) Estudios sobre Dipteros hematofagos. La familia Heleidos (=Ceratopogonidos). *Medicina Tropica*, **30**, 245–262.

Gil Collado, J. (1985) Claves de identificacion 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 Heleidae) [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. Heleidae (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 Ceratopogonides et des Chironomides de Belgique. *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **76**, 319–326.

Goetghebuer, M. (1936b) Les Ceratopogonides 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 Ceratopogonides (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: Ceratogonidae) 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) Synopse des représentants européens du groupe *Ceratopogon* avec description de quelques espéces 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 Wytsman, 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. *Beitrage 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) *Klassifikazion 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) Subsaharan Ceratopogonidae (Diptera). X. Report on species collected in the Drakensberg, South Africa. *Canadian Entomologist*, **118**, 141–180.

Meillon, B. de & Wirth, W.W. (1981) Subsaharan

Ceratopogonidae (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 Ceratopogonidae (Diptera). XI. The genus *Serromyia* Meigen. *Annals of the Natal Museum*, **25**, 383–402.

Meunier, F. (1904) Monographie des Cecidomyidae, des Sciaridae, 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 europaeischen zaeiflügeligen Insecten, nach der Natur'. Pars I. Vorwort des Herausgebers — Faksimiles von Original-Legenden und — index: 'Erklaerung 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: Ceratopogonidae). *Bolletin Venezolano de Laboratorio Clinico*, **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, Heleidae) from the European part of the USSR [in Russian, with English summary]. *Entomologischeskoe Obozrenie*, **44**, 182–188 (Translation in *Entomological Review*, **44**, 101–103.

Remm, H. (1967) On the fauna of Ceratopogonidae (Diptera) in the Caucasus [in Russian]. *Tartu Riikliku Ulikooli Toimetised*, **194**, 3–37.

Remm, H. (1969) 13. Fam. Ceratopogonidae (Heleidae) (in Russian). *Key to the Insects of the European Part of the USSR*, **5**, 201–218.

Remm, H. (1973a) 246. Ceratopogonidae 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, Ceratopogonidae) [in Russian]. *Parasitologiya*, **9**, 393–397.

Remm, H. (1981) New synonyms and new names of the Palaearctic Ceratopogonidae (Diptera). *Eesti NSV Teaduste Akadeemia Toimetised*, **30**, 27–32.

Remm, H. (1988) Ceratopogonidae. Pp. 11–110 in *Catalogue of Palaearctic Diptera*, Volume 3. Ceratopogonidae – 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., Ceratopogoninae). *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: Heleidae (Ceratopogonidae), (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 Ceratopogonidae (Diptera). *Polskie Pismo Entomologiczne*, **56**, 3–103.

Szadziewski, R. (1988) Biting midges (Diptera, Ceratopogonidae) from Baltic amber. *Polskie Pismo Entomologiczne*, **58**, 3–283.

Szadziewski, R. & Krzywinski, J. (1988) Biting midges of the genus *Culicoides*/Ceratopogonidae/visiting umbelliferous flowers in Poland. pp. 155–158 in *Medical and Veterinary Dipterology, Proceedings of the International Conference, Nov. 30 – Dec. 4, 1987*. J. Olejnicek 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 Eugenies resa omkring jorden*. Pt 2: Zoologi. 1. Insekter, 617pp., 9 pls. Stockholm, '1868'.

Thomsen, 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. *Linnea 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.

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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 dorsocentral 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

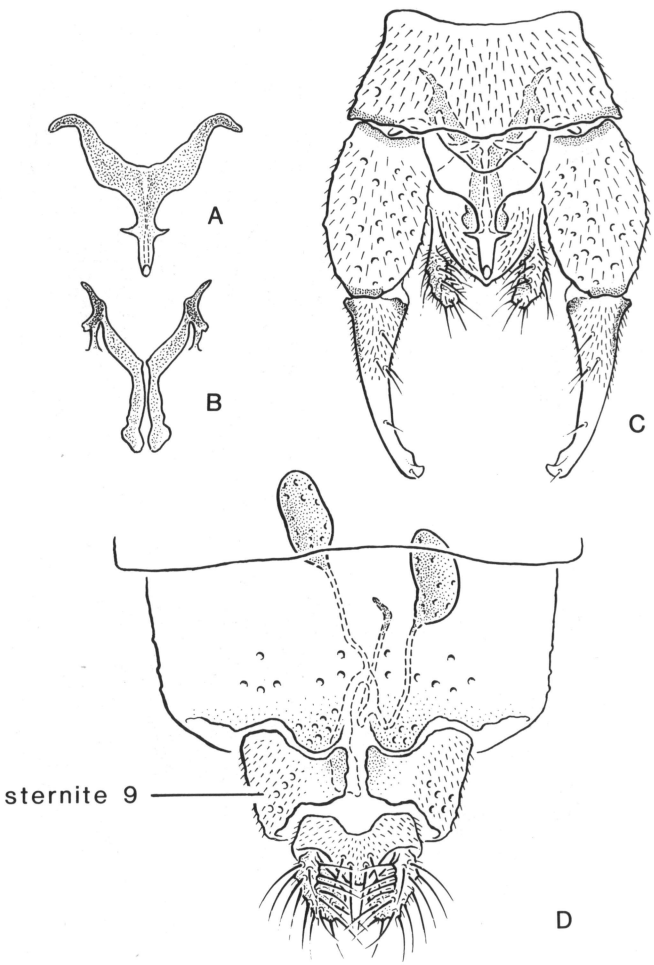
Table 6. Descriptive statistics for hind femur length/width of male *Serromyia*.

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