Diptera Ceratopogonidae, Biting Midges

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Introduction

Life cycles and phenology

In North Europe ceratopogonid midges of the subfamilies Ceratopogoninae, Dasyheleinae and Forcipomyiinae are present in most semiaquatic and aquatic habitats. The eggs are usually deposited on a moist substrate (soil, stones, emergent vegetation), singly, in scattered loose groups, or in strings and masses with a gelatinous coating. The females of *Mallochohelea* and *Probezzia* of the tribe Sphaeromiini deposit eggs enclosed in long gelatinous ribbons directly on the water surface. At room temperature the eggs of *Culicoides nubeculosus* hatch 48-65 hours after they are laid (Lawson 1951) and larvae exit the egg chorion rapidly, usually within 2-5 minutes of effort. At temperature 22-24°C embryogenesis lasts 3 days in *C. nubeculosus*, *C. riethi*, and *C. algecirensis*; 4-7 days in *C. punctatus*, *C. obsoletus*, *C. fascipennis*; and 9-10 days in *C. pallidicornis*. Embryonic diapause is characteristic for some univoltine species, such as *Culicoides grisescens* and *C. vexans*, or some species living in temporary habitats like rock pools, algae, mosses, or tree holes (*Dasyhelea, Forcipomyia*).

Larvae pass through four instars. The duration of each instar of *Culicoides nubeculosus* when reared in laboratory at 28-30°C was as follows: I - 4-5, II - 3-4, III - 7-11, and IV - 8-11 days, i.e. 22-32 days for the total development (Glukhova 1989).

The pupal stage lasts about 3-5 days and adults may live as long as 1-2 months after emergence. The pupae are not able to swim, but move slowly by twisting their abdomen. The pupae of *Mallochohelea* and *Probezzia* can move quickly by rapidly moving their abdomen vertically and horizontally and using their ventral glandular discs to fasten themselves to submerged solid substrates. In water, pupae of aquatic and semiaquatic forms hang from the surface film by their nonwettable respiratory horns.

Gutsevich (1973) determined that in temperate climates, at an optimal temperature of 20-25°C, an average of about one month is required for the development of most *Culicoides* from egg to adult with 4-6 days for the egg stage, 20-25 days for larvae, and 3-5 days for the pupal stage. If *Culicoides* females suck blood within 4-5 days after their emergence and start to oviposit eggs within 5-7 days after the blood sucking, then 1.5 months are necessary to complete their life cycle from egg to egg (Gutsevich 1973). Low temperatures and general lack of available food may markedly reduce the speed of the development.

Most biting midges overwinter as instar III or IV larvae. For example, *Culicoides impunctatus* overwinters exclusively in instar IV, while *C. nubeculosus*, *C. stigma* and *C. circumscriptus* overwinter in instars II-IV. Adults fly from early spring to late autumn and usually emerge during the first half of May in the more southern regions of North Europe, or in June or early July in boreal or subarctic regions. The first adult biting midges appear together with mosquitoes of the genus *Aedes*. In North and Central Europe *Culicoides obsoletus* and *C. nubeculosus* are the earliest species to appear in spring. Adults disappear in October or early November depending on the weather conditions. The latest species active in the field are *C. obsoletus*, *C. grisescens*, *C. fascipennis*, and *C. punctatus*.

Among the Ceratopogonidae there are both univoltine and multivoltine species. The distinction between these phenological groups is not well-defined because the number of generations produced by some species may depend on climatic conditions. In Karelia, all *Culicoides* species produce one generation per year (except for *C. pulicaris* and *C. stigma*) whereas in more southern regions of Europe most species produce 2 or rarely 3 generations a year.

The seasonal dynamics of flight activity of biting midges as a whole exhibits 2 distinct maxima. The first or spring maximum (May-June) produces adults emerging from overwintering larvae, while the second maximum (August) results from their second generation. The adults of univoltine species emerge after the spring maximum and usually have an influence on the summer maximum. Univoltine species fly from June to August and include *Culicoides albicans* in spring, *C. pallidicornis* in early summer, and *C. fascipennis* in late summer. Univoltine biting midges usually overwinter as eggs (*Culicoides grisescens*, *C. vexans*, *Dasyhelea versicolor*), or larvae (*Culicoides albicans*, *C. pallidicornis*, *C. fascipennis*), whereas multivoltine species overwinter exclusively as instar III-IV larvae.

Habitats

The larvae of biting midges are common inhabitants of different types of aquatic and semiaquatic habitats. Their habitats range from fresh to salt water, and from damp to wet soil. A clear ecological classification of species into aquatic, semiaquatic or terrestrial groups is difficult, since many of them inhabit a wide range of habitats from true aquatic to true terrestrial.

A few minor taxa exclusively inhabit typically

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terrestrial habitats like: (1) animal dung and rotting fungi [*Culicoides chiopterus* (Meigen), *C. dewulfi* Goetghebuer, *C. scoticus* Downes & Kettle, *Forcipomyia brevipennis* (Macquart)]; (2) ant nests [*F. braueri* (Wasman), *F.myrmecophila* (Egger)]; (3) rotting wood, bark, touchwoods, plant debris, mosses in dry places (probably all *Forcipomyia* larvae of the subgenera *Forcipomyia*, *Lasiohelea* Kieffer, *Caloforcipomyia* Saunders, *Microhelea* Kieffer; and of the subgenus *Meloehelea* Wirth of *Atrichopogon*). Larvae of *Dasyhelea versicolor* and of some *Culicoides* species have been recorded from sap flows. They are included in the check list since they may occupy also aquatic or semiaquatic habitats.

Other species are aquatic, semiaquatic or included here because their immature stages are unknown. Their larvae live in a great variety of habitats like lakes, ponds, rivers, streams, springs, tree holes, rock pools and similar temporal water bodies, wet edges of all kinds of water reservoirs, swamps, peat bogs, damp meadows, mosses and blanket algae at water body margins and on wet soil, etc.

All truly aquatic forms with swimming larvae belong to the subfamily Ceratopogoninae. Despite the fact that most species inhabit shallow waters, they were recorded by Ekman in a German lake at a depth of 34-43 m (Mayer 1934). Glukhova (1979) found larvae of *Sphaeromias fasciatus* and *Mallochohelea inermis* (Kieffer) in the profundal zone of eutrophic lakes to a depth of 14 m. Only members of the tribe Sphaeromiini have been recorded from these great depths. At sublittoral and littoral depths of freshwater lakes are most common Palpomyiini (*Bezzia*, *Palpomyia*) and Sphaeromiini. The mean annual density of the Palpomyiini and Sphaeromiini in Lake Norman (USA, North Carolina) was 179 and 501 larvae per m^2 at depths of 8 and 4 m, respectively (Bowen 1983). The shallow littoral areas of lakes and ponds are typical breeding places of *Culicoides*, Palpomyiini, Ceratopogonini, and semiaquatic Forcipomyiinae and *Dasyhelea*. It appears that rivers have no characteristically unique ceratopogonid fauna but contain larvae of the same groups as in lakes and ponds. In streams and springs swimming larvae of *Culicoides*, *Bezzia*, *Palpomyia* and *Clinohelea*, and creeping larvae of *Dasyhelea* and *Atrichopogon* have been found. Apparently, *Atrichopogon muelleri* is the only rheophilic species, that is restricted to cold streams.

Rock pools and similar temporary water bodies are breeding places for *Dasyhelea saxicola* and other species of the subgenus *Dasyhelea (s. str.)* while tree holes are inhabited by larvae of *Culicoides fagineus* Edwards.

Wet meadows are mostly inhabited by *Dasyhelea* and *Culicoides* larvae. Peat bogs are breeding places for mostly *Culicoides impunctatus*, *C. heliophilus*, *C. albicans*, and *C. clintoni*. The larvae of *Culicoides nubeculosus* and *C. riethi* prefer small water bodies with high contents of organic matter.

Biting midges of the genera *Culicoides*, *Dasyhelea*, *Forcipomyia*, *Atrichopogon*, and *Bezzia* are common in inland and coastal saline, aquatic and semiaquatic habitats (Szadziewski 1983). In Central Europe *Culicoides longicollis* Glukhova is an aquatic halobiont whose larvae live on the bottom and in the filamentous algae of the higly mineralized inland reservoirs and were recorded up to over 80,000 larvae per m^2. Other halobionts in the genera *Dasyhelea* and *Forcipomyia* are semiaquatic and live in or on wet soils covered by a thick layer of green algae. In samples taken from March to November in wet, highly saline soils under *Salicornia patula* Duv. in Poland, *Dasyhelea* represented 13.3% of all Diptera larvae. Truly marine species are unknown among the European Ceratopogonidae.

Pupation usually takes place on or in more or less solid substrates, which enable pupae to remain in contact with air, such as on floating vegetation, and at edges of reservoirs. Sometimes, pupation occurs under water on the bottom of reservoirs.

Trophic relationships

Larvae of the subfamily Ceratopogoninae are primarily predators. They feed on any small animals found in the larval habitat like eggs and larvae of chironomids, mosquitoes, Trichoptera, nematods, rotifers, annelids, protozoa, other biting midges, and they may be cannibalistic. They also consume mobile algae, dead ceratopogonid and mosquito larvae.

Nearly all Ceratopogoninae larvae are good swimmers and also can easily move through wet particulate and fibrous matter. Movement in both water and wet particulate media is by sinuous or eel-like side to side flexions of the body. In water, these movements are characteristically rapid and are a means by which larvae of that subfamily may be recognized and collected. When larvae move through particulate or semisolid media they do so by slow undulations of the body (Linley 1986). Larvae of the Forcipomyiinae and Dasyheleinae are not able to swim, they creep on the solid substrate. A few hours or up to a day before the pupation, fully developed instar IV larvae usually stop swimming and become nearly motionless. Only larvae of some *Bezzia* and *Palpomyia* remain active until 10-20 minutes before pupation (Glukhova 1979).

Boorman (1974) observed that the larvae of *Culicoides nubeculosus* and *C. riethi* in laboratory colonies feed on a wide range of bacteria and protozoa and on particles of decaying organic matter. However he was unable to find which of these provided the major food source. The instar I larvae ingested also algae, but could not be reared to maturity on this diet. Glukhova (1979, 1989) observed some *Culicoides* species feeding on yeast, detritus and green algae, and concluded that they are primarily saprophagous and take only prey that is small enough to be ingested entirely. Larvae of aquatic and semiaquatic *Dasyhelea* and Forcipomyiinae feed on filamentous and other algae including diatoms, and rotting plant debris.

Adult habits are diverse. The biting habit, and fully functional biting mouthparts, are restricted to the females. The males take only meal of sugar and water from the nectar of flowers or honeydew. In all *Dasyhelea* and some

Forcipomyia both sexes feed exclusively on nectar from flowers. Females of other biting midges usually supplement their normal protein-rich diet with nectar. The umbelliferous flowers (Apiaceae) are preferred by biting midges (personal observations).

A protein-rich meal is necessary for ovarian development in most species. Some haematophagous species lay the first clutch of eggs without taking a blood meal (autogeny) but require a blood meal to initiate the second and additional ovarian cycles. The females of *Culicoides* and *Forcipomyia (Lasiohelea) sibirica* Bujanova suck blood from mammals and birds and are often notorious pests especially in mountains and cold northern regions. *Forcipomyia (Lasiohelea) velox* females feed on frogs. Some species of *Forcipomyia* and *Atrichopogon* are ectoparasitic on larger insects such as caterpillars and adults of Lepidoptera, Odonata, Coleoptera or Neuroptera from which they suck their haemolymph. For example, females of the Holarctic *Forcipomyia (Trichohelea) eques* are known to feed upon haemolymph taken from wing veins of Chrysopidae (Neuroptera). At least one species is pollinivorous, as females of *Atrichopogon pollinivorus* Downes obtain the protein and fat rich food from pollen grains of honeysuckle (Downes 1955).

The females of all Ceratopogoninae, except *Culicoides*, are predators on small insects. In most cases the prey consists of males of Chironomidae, Ceratopogonidae, or small Ephemeroptera. In most higher lineages, the females kill and eat the male during copulation and may carry his genitalia still attached in the copulatory position on her abdomen for several days. Females inject into their prey a saliva rich in proteolytic enzymes which dissolves tissues and the resulting digested fluid is then sucked out (Downes 1978).

Natural enemies of biting midges include predators, pathogens and parasites. Larvae of biting midges are eaten by fish, and in the sea by *Nereis diversicolor* (Polychaeta). Adults are preyed upon by many predatory insects including *Lispe loewi* Ringdahl (Diptera, Muscidae). Among the pathogens and parasites are viruses, rickettsiae, bacteria, fungi, protozoa, nematodes (Filarioidea, Mermithoidea), mites (Trombidiiformes, Parasitiformes, Hydracarina) and insects of the families Diapriidae and Encyrtidae (Hymenoptera) (Wirth 1977, Miahle et al. 1982a, b, Rieb et al. 1982).

The blood sucking adults are important vectors of various pathogenic organisms (arboviruses, filarial parasites, protozoan blood parasites) in frogs, birds and mammals (Linley 1985a).

State of knowledge

The classification of Ceratopogonidae includes almost 5,000 species in over 90 genera currently placed into five subfamilies (Ceratopogoninae, Forcipomyiinae, Dasyheleinae, Leptoconopinae and Austroconopinae) (Borkent et al. 1987). The subfamily Ceratopogoninae is usually divided into six tribes (Culicoidini, Ceratopogonini, Heteromyiini, Sphaeromiini, Palpomyiini and Stenoxenini) and these are well-founded and generally accepted (Downes & Wirth 1981, Wirth & Grogan 1988, De Meillon & Wirth 1991). In the recent Russian literature there are tendencies to treat the Leptoconopinae as a separate family, and to split the Ceratopogoninae into two subfamilies, Palpomyiinae and Ceratopogoninae (Glukhova 1979, 1989, Remm 1988). The subfamilies Leptoconopinae and Austroconopinae and the tribe Stenoxenini of Ceratopogoninae are absent in North Europe.

The Ceratopogonidae of North Europe are poorly known. Of the 24 genera which probably should be present, records are still wanting of *Ceratoculicoides*, *Kolenohelea*, *Monohelea*, *Neurohelea*, *Macropeza*, and *Phaenobezzia*. A total number of 112 species which are recognized as aquatic or semiaquatic have been recorded to date and these probably include about 2/3 or less of the actual number of species which live there. Only *Culicoides* has been studied recently in Karelia (Glukhova 1957, 1958, 1979, 1989) and in Denmark (Nielsen 1963, 1964, 1971, Nielsen & Christensen 1975, Nielsen et al. 1986, 1988). All stages of some Danish aquatic and semiaquatic *Atrichopogon* were carefully studied by A. Nielsen (1951). The Finnish biting midges were listed by Hackman (1980), and Greve (1968, 1969) reported *Forcipomyia eques* from Norway. Clastrier (1961, 1962a,b), Dow & Wirth (1972), Szadziewski (1986), and Borkent & Bissett (1990) published modern descriptions of some Scandinavian biting midges. At present almost all species described by Staeger, Zetterstedt, Lundström, Kieffer, Mayer and Storå from North Europe are revised and interpreted. Many old faunistic records are still not revised including that by Goetghebuer & Lindroth (1931) from Iceland.

The immature stages of the Ceratopogonidae are poorly known by comparison with those of other economically important families of aquatic Diptera. They are often collected by limnologists and ecologists but seldom identified below the family level. Larvae are difficult to identify to species because of their small size, and the fact that larvae of relatively few species have been associated with their adult stage. The immature stages are completely unknown for *Ceratoculicoides*, *Kolenohelea*, *Schizohelea*, and *Neurohelea*, or insufficiently described outside of the Palaearctic Region for *Macropeza*, *Allohelea*, and *Nilobezzia*. No comprehensive comparative studies on European immature stages exist which would enable confident determination of all species to the generic level. Keys for larvae and pupae are constructed on the basis of descriptions of some species of some genera which almost certainly cannot represent the entire range of characters for species in these genera. The best guide for beginning students is a compilation provided by De Meillon & Wirth (1991) for Afrotropical biting midges.

The keys for the identification of larvae and pupae presented here should be treated with a great caution and each reliable determination should be supported by associated reared adults.

Morphology

Eggs

Eggs elongate cigar- to banana-shaped or more or less oval in the Forcipomyiinae and Ceratopogoninae (Figs 2-3), or horse-shoe shaped (Fig. 1) in the Dasyheleinae. They are smooth or with a sculptured surface showing significant differences between species. Length from 278 to 460 µm. Newly deposited eggs are usually pale, and they become dark brown or grayish within some hours. At hatching, a small cap splits off from the anterior end and the opening is further enlarged by a short longitudinal slit. The number of eggs produced by *Culicoides* averages 80-120, but can be as high as 212 in the first clutch. Most haematophagous species usually produce 2-4 clutches.

Larvae

The larval stage consists of 4 instars. They are apneustic, with the unique heavily sclerotized pharyngeal apparatus usually visible through the head capsule. The body is composed of the head, 3 thoracic and 9 abdominal segments. The prothoracic segment has a short to long neck (Figs 6-8). In life, the body is white, creamy or grayish, often with a characteristic pattern of pigmentation. Total length up to 17 mm (in *Sphaeromias*).

The instar I larva may be distinguished by having an egg burster on the dorsal surface of the head capsule. In many *Culicoides* there are small prolegs which are absent in subsequent instars. Larvae of instars II and III are difficult to separate since they have similar chaetotaxy, which is like that of the other instars. Instar IV larvae are distinguishable when signs of pupation are visible through the larval skin (respiratory horn in the prothoracic segment, and caudal processes in the caudal segment). Younger instar IV larvae have distinctly stouter thoracic segments and most abdominal segments with readily visible imaginal discs.

Head. Prognathous and usually elongate in the Ceratopogoninae (Fig. 11), slightly hypognathous and broader in *Dasyhelea* (Fig. 10), and fully hypognathous, short and high, in Forcipomyiinae (Fig. 9). Colour of head capsule varies from pale yellow to dark brown. Head capsule well sclerotized and composed of dorsal sclerite (frontoclypeus), and ventrolateral U-shaped sclerite forming ventral and lateral walls. Frontoclypeus delineated by epicranial suture (Figs 12-13). At posterior head lumen with ring-like sclerite called a collar which is usually readily visible in Ceratopogoninae and *Dasyhelea*. Eye spots usually located under cuticle of upper lateral walls of head capsule just below epicranial suture. Eyes usually not recognizable in specimens treated with NaOH or KOH.

The anterior end of head capsule with a well sclerotized oral ring (subgenal ring) to which non-opposable mandibles, maxillae and hypostoma are attached. Antenna 4-segmented; attached just anterior of oral ring in Ceratopogoninae (Fig. 11) and *Dasyhelea* (Fig. 10) or on distal half of head in Forcipomyiinae (Fig. 9).

Labrum forms roof of preoral cavity, while hypostoma is an anterior projection of ventral subgenal ring forming ventral border of preoral cavity. Below labrum is a pair of usually fork-like structures located at bases of mandibles called premandibles or messors. At posterior margin of palatum is a group of weakly sclerotized labral hooks or scopae. Membranous maxillae form lateral borders of preoral cavity. All parts of maxillae more or less fused into a subrectangular plate bearing a small 2-segmented maxillary palpus.

Pharyngeal apparatus is the most heavily sclerotized structure within the head capsule. It consists of a ventral hypopharynx and a dorsal epipharynx (Fig. 14). Ventral surface of hypopharynx usually membranous, while lateral margins usually well sclerotized, especially on distal end. Hypopharynx usually bears a fringe of small setae at posterior median end. Often of important diagnostic value is epipharynx which is suspended above distal end of hypopharynx by two heavily sclerotized lateral arms. Its median portion in lower position forms a curtain in trough of hypopharynx. Median portion consists of 1-4 combs armed with teeth on its posterior margin. Combs best visible when viewed ventrally. Dorsal comb divided medially into two lateral parts; other combs, when present, entire. In some species each lateral arm bears toothed comb as well.

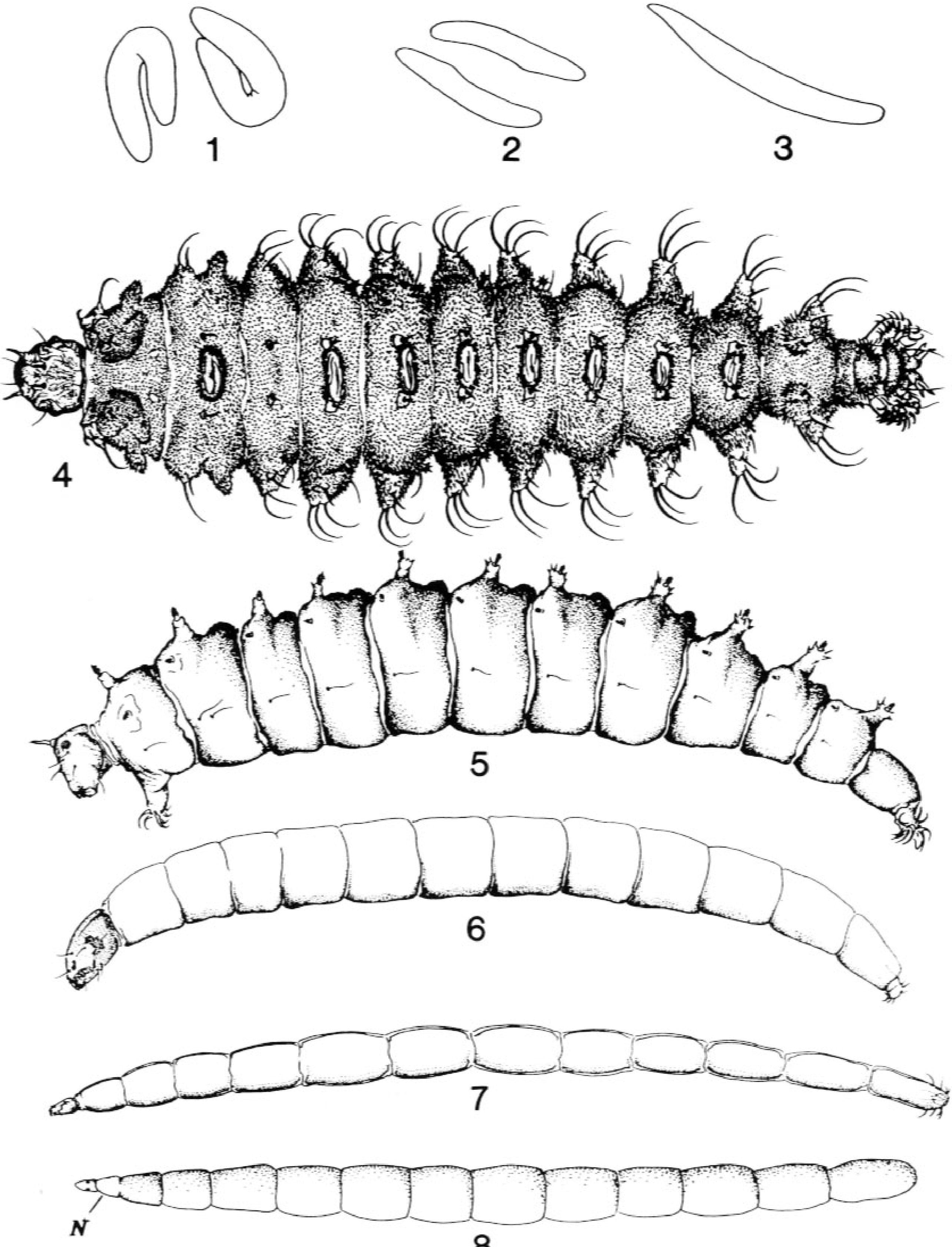
Head capsule bears 13 pairs of setae and 7 pairs of sensory pits (Figs 12-13). In most Ceratopogoninae setae s, u, o and x are multiple, in *Forcipomyia (s. str.)* setae p and q are lanceolate.

Length to width ratio of head (HR) characteristic for some taxa. Head length measured from anterior margin of labrum to posterior edge of collar, while width is measured at widest point of head.

Body. With 11 well-defined segments; 3 thoracic and 8 abdominal segments. Body smooth and almost bare in Ceratopogoninae and Dasyheleinae or with conspicuous tubercles, processes and setae in Forcipomyiinae, and often with a characteristic pattern of pigmentation. Cuticle smooth, in some *Bezzia* with longitudinal regular ridges, or with distinct tubercles and nodules as in *Atrichopogon* or *Forcipomyia*. Characteristic body pigmentation caused by colour of fat body under transparent cuticle in some Ceratopogoninae; well visible in live or recently preserved larvae. In Forcipomyiinae body colouration caused by more or less heavily sclerotized cuticle. In some *Atrichopogon* including *A. muelleri* some body segments have dorsal ovoid fields of modified thin, smooth cuticle which probably have a respiratory function. Similarly, in *Atrichopogon alveolatus*, there are peculiar very densely tracheated alveolate structures on lateral processes of body segments that are covered with thin walled nodules which serve as special gills (A. Nielsen 1951).

All body segments bear setae which in Ceratopogoninae and Dasyheleinae are very fine and difficult to observe, in which case only chaetotaxy of anal segment has diagnostic value. In Forcipomyiinae body setae-well developed and with important diagnostic value. Some dorsal setae of *Forcipomyia (s. str.)* are secretory in function and may play a certain role in cuticular respiration (Szadziewski 1990).

Prothorax usually with well-defined more or less long proximal neck or cervix. Chaetotaxy of this segment



Figs 1-8. Ceratopogonidae, immature stages. -1-3. Eggs. -1. *Dasyhelea obscura* (Winnertz). -2. *Culicoides dewulfi* Goetghebuer. -3. *Mallochohelea munda* (Loew). -4-8. Larva in dorsal (4, 8) and lateral aspect (5-7). -4. *Atrichopogon muelleri* (Kieffer). -5. *Forcipomyia (Synthyridomyia) knockensis* Goetghebuer. -6. *Dasyhelea versicolor* (Winnertz). -7. *Sphaeromias fasciatus* (Meigen). -8. *Serromyia* sp., (N) neck. Fig. 8 redrawn from Glukhova (1979).

different from other thoracic and abdominal segments. Anal segment possesses better developed setae of diagnostic value in most biting midges. Extrusible (2 bilobed pairs) anal papillae of osmoregulatory function are readily visible only in specimens killed in hot water or alcohol.

Pupae

The stout pupae, like those of other nematocerous Diptera possess characteristic respiratory horns with spiracular openings which contact the atmosphere. Total length 2-8 mm. Colour pale brown to dark brown or almost blackish.

Cephalothorax with convex dorsum. Dorsal head surface covered with operculum (vertex). Operculum often with tubercles, wrinkles, and setae, all of which may be of diagnostic value. Prothorax with short or long variously shaped respiratory horns bearing 1-2 rows of spiracular openings. Mesothorax forms a dorsal convex shield covered with setae, processes, and tubercles of taxonomic value. Triangular caudomedian projection of mesothorax short in most biting midges. In European *Forcipomyia*, caudomedian projection elongate and covers at least half of first abdominal segment (Fig. 28). Metathorax indistinct, often separated dorsally into two lateral halves by mesothorax (Fig. 42).

Abdomen 9-segmented and bearing various setae, tubercles, spines or processes, often of taxonomic value. Last abdominal segment, or anal segment, with single or paired (*Dasyhelea*) apicolateral processes (Figs 31, 33). In Forcipomyiinae, terminal 3-4 caudal segments covered with retained larval skin. Pupae of most Sphaeromiini bear membranous glandular discs on ventral surface of some distal abdominal segments (Fig. 30). Discs secrete an adhesive to attach pupa to emergent vegetation or other solid substrates.

Adults

Biting midges are small nematocerous flies (Fig. 44) with wing length 0.6-4.8 mm, very similar to Chironomidae. The latter family can usually be distinguished from biting midges by the absence of wing vein M_2. Male antennae with a recumbent plume, whereas in male non-biting midges long hairs of plume perpendicular to long axis of flagellum. Females always have long flagella composed of 13 flagellomeres; usually larger than males. Body often completely dark or brown with or without yellowish or pale pattern of spots, stripes or bands.

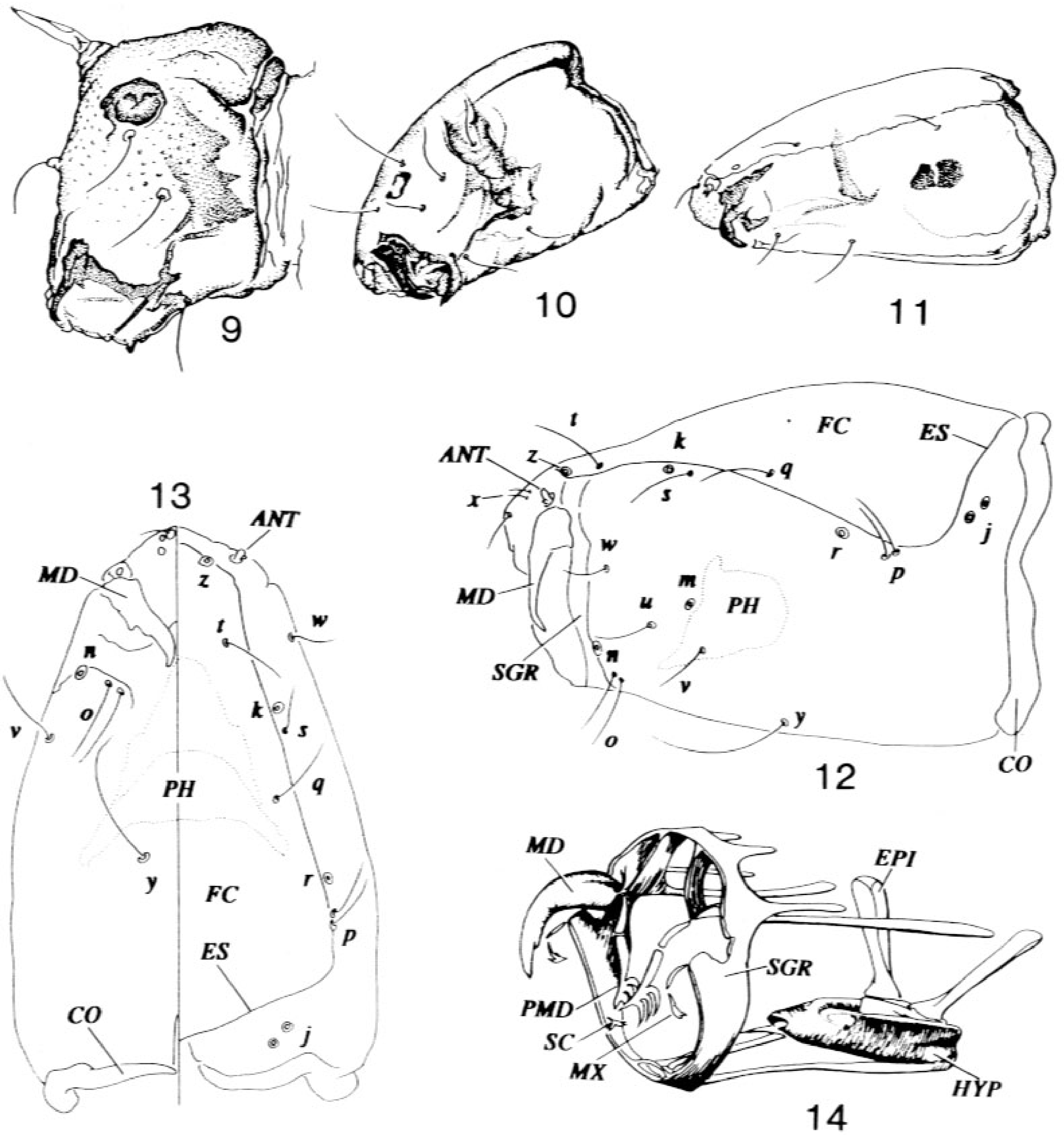
Head. Eyes contiguous or more or less narrowly separated by vertex or by frons and vertex; bare or with minute pubescence between facets; ocelli absent. Frons fused with clypeus into frontoclypeus. Antennal scape reduced to ring-shaped structure covered by enlarged pedicel, which is considerably larger in males. Flagellum composed of 13 segments or flagellomeres in both sexes; rarely reduced in number in males. Proximal 8 flagellomeres of female shorter than elongated distal 5. Proximal female flagellomeres usually bear basal ring of long setae or verticils (sensilla chaetica) and a subapical pair of hyaline setae (sensilla trichodea); distal 5 flagellomeres with shorter basal verticils and scattered short setae and short cone-shaped sensilla basiconica. All *Culicoides* and some other genera of Ceratopogonini have sensilla coeloconica on at least flagellomere 1, usually visible as pits surrounded by ring of short setae (Fig. 57).

Proboscis well-developed, usually adapted for piercing and stronger in female than in male. It consists of three unpaired elements, i.e. labrum forms dorsal wall, labium forms ventral wall and hypopharynx projects between labrum and labium; and two paired lateral elements arising between labium and labrum. These are mandibles, which are usually armed with strong teeth on their median margins and laciniae (portions of maxillae), which are usually armed with fine teeth. Maxilla bears 5-segmented maxillary palpus; in some genera some segments may be fused. Segment 3 of palpus bears on its mesal surface a characteristic sensory area with hyaline capitate sensilla, often invaginated into sensory pit.

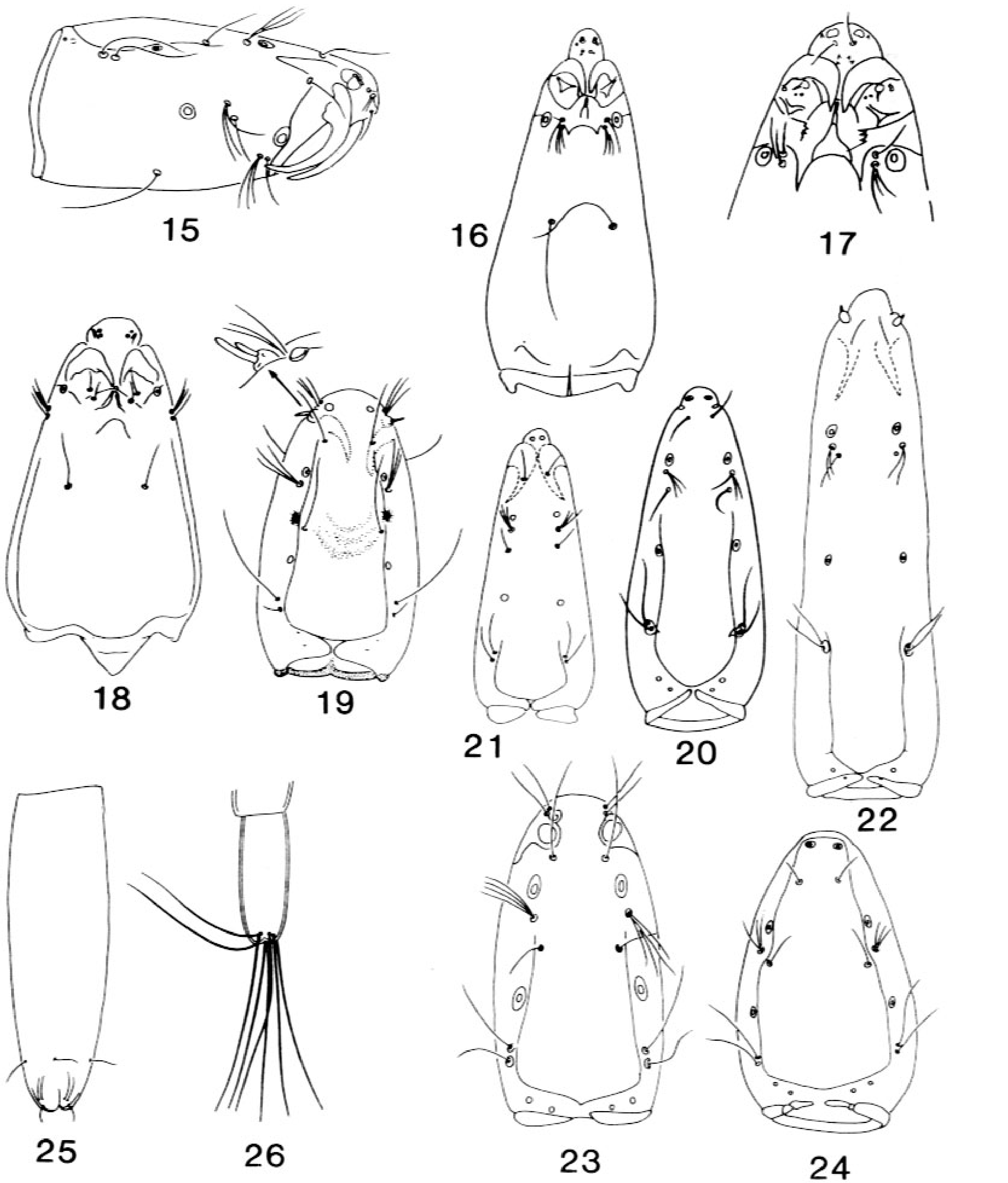
Thorax. Dorsally convex and extends anteriorly over head (Fig. 44). Antepronotum divided by anterior portion of scutum into lateral halves hidden below postpronotum (humerus). In predaceous genera antepronotum often well-developed, collar-like. Mesothorax greatly developed and mesonotum includes entire dorsum, i.e. prescutum, scutum, scutellum and postscutellum (postnotum). Prescutum is greatly reduced and its position coincides with prescutal or humeral pits visible in some genera. In keys, dorsal part of prescutum treated as part of scutum. Anterolateral margin of scutal area with well separated lateral sclerite (paratergite), which is bare in all biting midges other than *Atrichopogon* (Fig. 48). In some species, scutum bears a small tubercle at mid portion of anterior margin. Postnotum bare and without longitudinal suture. Pleural sclerites usually bare. Anepisternum divided into 3 more or less distinct sclerites: anterior, median and posterior (Fig. 47).

Legs. Rather short and stout, often with characteristic modifications, especially in female. One or more pairs of femora may be swollen and armed with distinct ventral and/or lateral spines. Apex of protibia bears articulated spur and transverse row of modified fine hairs, mesotibia without spur, while metatibia usually possesses indistinct spur and tibial comb composed of strong spines. Tarsomeres with or without spines. Tarsomere 1 (basitarsus) longer, equal or shorter than tarsomere 2. Hind basitarsus often bent near base, somewhat swollen and bearing ventral spine near base and usually with ventral palisade of spine-like setae. Tarsomere 4 cylindrical, subcylindrical or cordiform. Female claws usually with simple apices, may be short and equal, long and equal, long and more or less unequal, with or without basal inner and outer teeth, which may be similar on all legs or not. Empodium rudimentary, well-developed only in most Forcipomyiinae. Male claws simple and equal and similar on all legs, apices usually bifid.

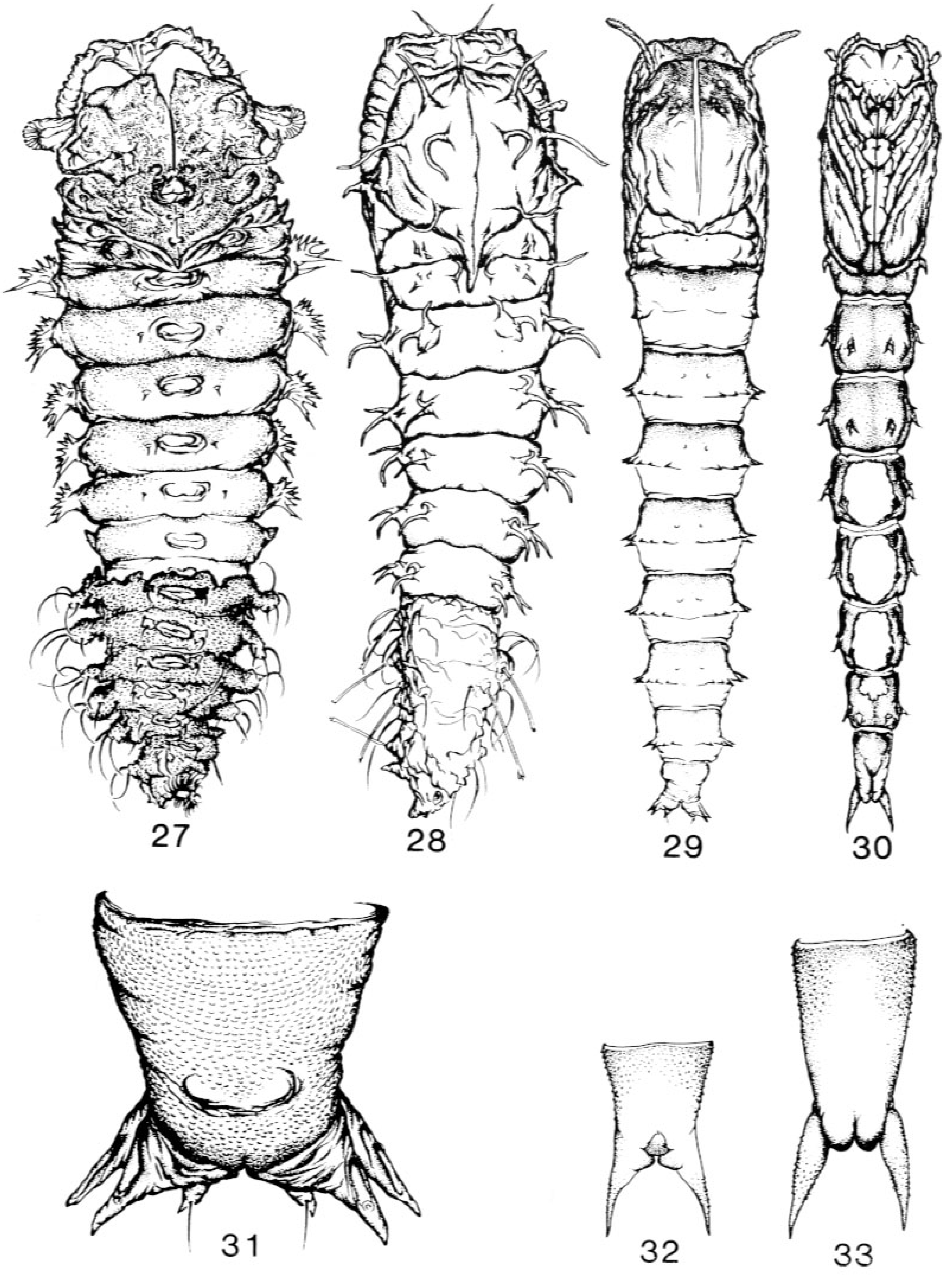
Wings. Moderately broad, in male narrower, alula indistinct. Wing membrane usually covered with short microtrichia of uniform density, and long macrotrichia varying in density, distribution and size. Development or reduction of macrotrichia and microtrichia are important diagnostic characters. Wing often infuscated and/or with pattern of dark patches on light backgroud or with light



Figs 9-14. Ceratopogonidae, head of larva. -9-11. Lateral aspect. -9. *Forcipomyia knockensis* Goetghebuer. -10. *Dasyhelea versicolor* (Winnertz). -11. *Sphaeromias fasciatus* (Meigen). -12-13. *Culicoides longicollis* Glukhova, lateral (12), dorsal (13 right) and ventral aspects (13 left). -14. *C. nubeculosus* (Meigen), subgenal ring and pharyngeal apparatus. Fig. 14 redrawn from Lawson (1951). Abbreviations: (CO) collar, (EPI) epipharynx, (ES) epicranial suture, (FC) frontoclypeus, (HYP) hypopharynx, (MD) mandible, (MX) maxilla, (PH) pharyngeal apparatus, (PMD) premandible, (SC) scopae, (SGR) subgenal ring, (j, k, m, n, r, z) pits, (o, p, q, s, t, u, v, w, x) setae.



Figs 15-26. Ceratopogonidae, head (15-24) and anal segment (25-26) of larva. -15. *Clinohelea unimaculata* (Macquart), lateral aspect. -16-18. Ventral aspect. -16. *Probezzia seminigra* (Panzer). -17. *Mallochohelea inermis* (Kieffer), proximal portion. -18. *Sphaeromias fasciatus* (Meigen). -19-24. Dorsal aspect. -19. *Brachypogon (Isohelea)* sp., head and antenna. -20. *Palpomyia flavipes* (Meigen). -21. *Bezzia nobilis* (Winnertz). -22. *Phaenobezzia rubiginosa* (Winnertz). -23. *Monohelea estonica* Remm. -24-25. *Stilobezzia flavirostris* (Winnertz). -26. *Alluaudomyia quadripunctata* (Goetghebuer). Figs 15-17, 20-26 redrawn from Glukhova (1979); 19 from Kettle & Lawson (1952).



Figs 27-33. Ceratopogonidae, pupa: dorsal (27-29), ventral (30) aspect, and anal segment (31-33). -27. *Atrichopogon muelleri* (Kieffer). -28. *Forcipomyia nigra* (Winnertz). -29, 31. *Dasyhelea versicolor* (Winnertz). -30, 33. *Mallochohelea munda* (Loew). -32. *Probezzia seminigra* (Panzer).

spots on dark background that are usually present in *Culicoides*, *Alluaudomyia*, and some other genera. Costal vein usually short, rarely elongated to wing tip. First radial vein R_1 usually reaches wing margin at middle of wing length. R_s typically branching into veins R_{2+3} and R_{4+5} to form cell r_1 and r_{2+3} which usually are called 1st and 2nd radial cells respectively (Fig. 64). Cell r_{4+5} with simple or forked intercalary or false vein. Veins M_1 and M_2 usually well-developed, sessile or petiolate, sometimes base of M_2 atrophied or vein totally reduced. Wing length measured from basal arculus (transverse short vein at wing base) to wing tip.

Abdomen. 10-segmented; tergites of segments 1-2 sometimes fused. Female abdomen short to moderately elongated and bears on its caudal end short one-segmented cerci; in Palpomyiini with one or more pairs of long tubular structures that extend forward just beneath abdominal tergites from openings in dorsal intersegmental regions (Fig. 75). They lie beside long paired apodemes (gland-rods) that originate from front margins of corresponding tergites. Although it was suggested by earlier authors that these structures are glandular, a recent study indicates that they are not glandular nor do they produce substances. Instead, the long filaments that everted from these eversible structures during the flight of the female may have a mimicry function of those species that prey on Ephemeroptera. Conversely, they may serve as a sort of parachute to slow their fall to the ground after the female has captured her prey (Borkent & Craig 1994). Male abdomen more slender than in female; genitalia (Fig. 79) formed by modified elements of segments IX-XI. They may be inverted, rotated or remain in normal position.

Methods

Collecting

Techniques for collecting and isolating the immature stages are described in detail by Kettle & Lawson (1952), Gutsevich & Glukhova (1970), Glukhova (1979), and Wirth & Hubert (1989). The larvae and pupae may be concentrated by sieving and flotation with sugar, salt or magnesium sulphate, which quickly float the immature stages to the surface where they may be sorted and counted. Flotation is recommended for samples with small amount of debris, since all living and dead organic material floats. Immature stages may be collected when a sample of their semiaquatic substrate is placed in a white dish and broken up in water. Within some minutes pupae will float on the water surface and swimming larvae become visible as the water clears. The larvae and pupae may be easily collected directly from their breeding sites in rock pools, tree holes or floating filamentous algae. In larger bodies of water, floating pupae or those fastened to submerged vegetation may be picked up directly with forceps or droppers. Berlese funnels are useful for exctracting larvae and pupae from semiaquatic substrates. Generally all methods used in limnological and pedobiological studies may be used for the extraction of immature stages.

Adults in the field may be collected by a fine-mesh entomological net from swarms, or trees, bushes and other vegetation in moist habitats. The best results are when sweeping from spruce trees and umbelliferous flowers (Apiaceae). A Malaise trap provides an effective method for collecting all biting midges while a light trap is the most satisfactory method to determine incidence and relative abundace of *Culicoides* species. A variety of emergence traps set over aquatic and semiaquatic larval habitats may be used in order to locate specific breeding sites. Haematophagous females may be collected while feeding on man or animals by an aspirator or with an entomological net.

Rearing

Samples of all possible larval habitats may be collected and placed in suitable rearing vials where they can continue their development, pupate and emerge as adults. For rearing individual specimens of Ceratopogoninae, full developed instar IV larvae should be placed separately in watch glasses in small amounts of clean water. Glukhova (1979) recommends putting a small piece of cotton there for larvae of Sphaeromiini and other predaceous genera. Then the watch glasses may be placed in Petri dishes with moist blotting paper on the bottom. Upon pupation, each pupa is then transferred to moist cotton in the bottom of a small tube stoppered with a cotton plug and the larval skin placed in alcohol. After the adult has emerged and allowed to harden for about 24 hours, it and the pupal exuvium are preserved with the larval skin.

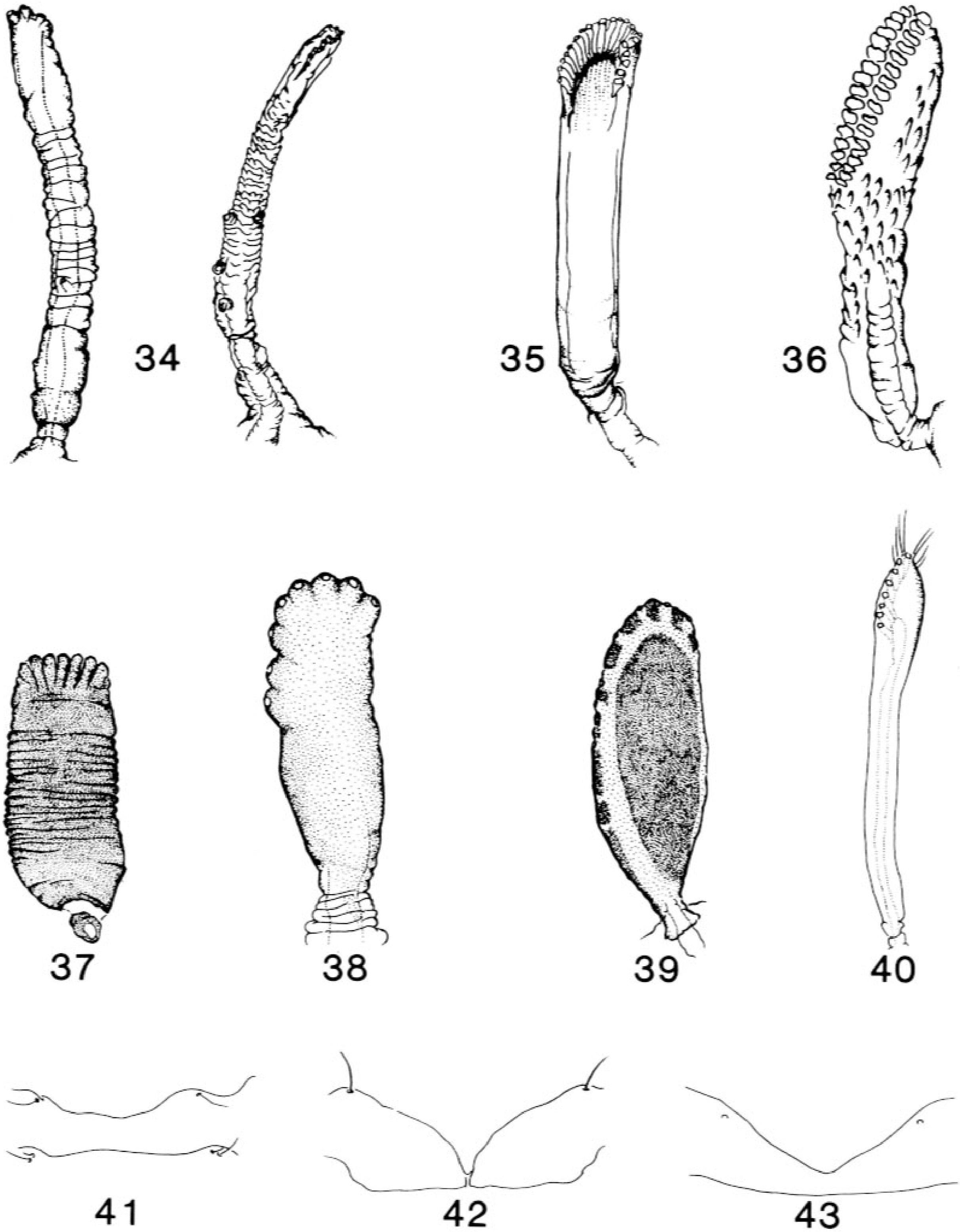
Modern procedures for the successful laboratory colonization of medically important species of the genus *Culicoides* using microorganisms and nematodes as larval food were developed mainly by Linley (1968, 1969, 1979, 1985b) and Boorman (1974).

Preparation and conservation

Living larvae should be killed by submersing them in hot water for a few seconds in order to force out prolegs and anal papillae, then preserved in 70-75% alcohol or 2-3% formalin. Pupae and adults are preserved for taxonomic study by killing and preserving them directly in 70-75% alcohol. It is usually necessary to mount all stages on microscope slides for accurate identification with a compound microscope. We prefer the quick method of making permanent preparations on slides as described by Wirth & Marston (1968). In this method, liquified phenol (or KOH for heavily sclerotized adults and larvae) is used for clearing specimens, which are then directly dissected and mounted in a mixture of phenol-Canada balsam on glass slides.

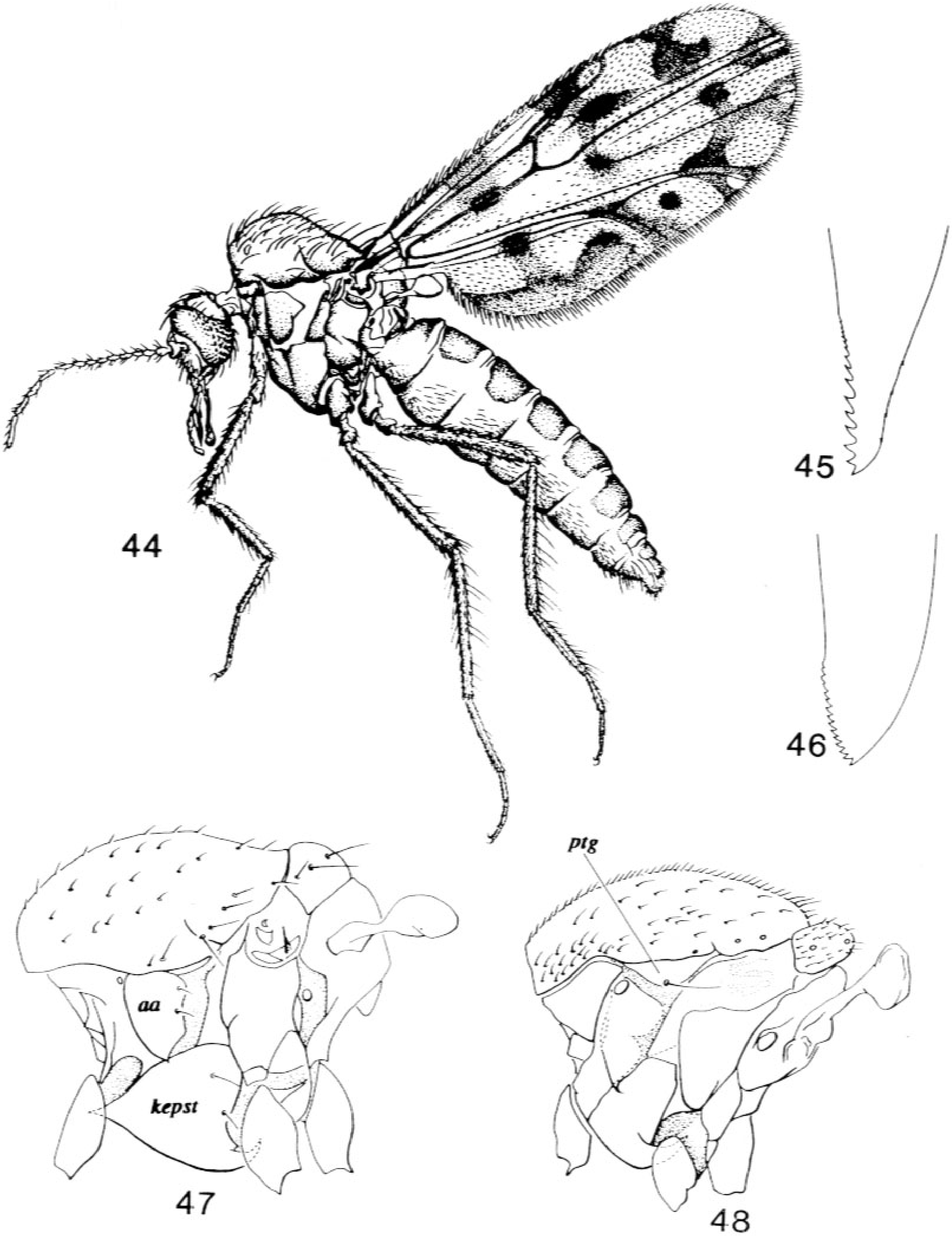
Key to genera for adults

1. Terminal flagellomere of antenna with apical prolongation nipple-shaped (Fig. 53), apex slightly bilobed. Legs with empodium usually large, and claws strongly curved (Fig. 66) (Forcipomyiinae) 2
- Terminal flagellomere of antenna with blunt rounded apex (Figs 52, 54); when apical prolongation present then cylindrical or conical with simple tip, and

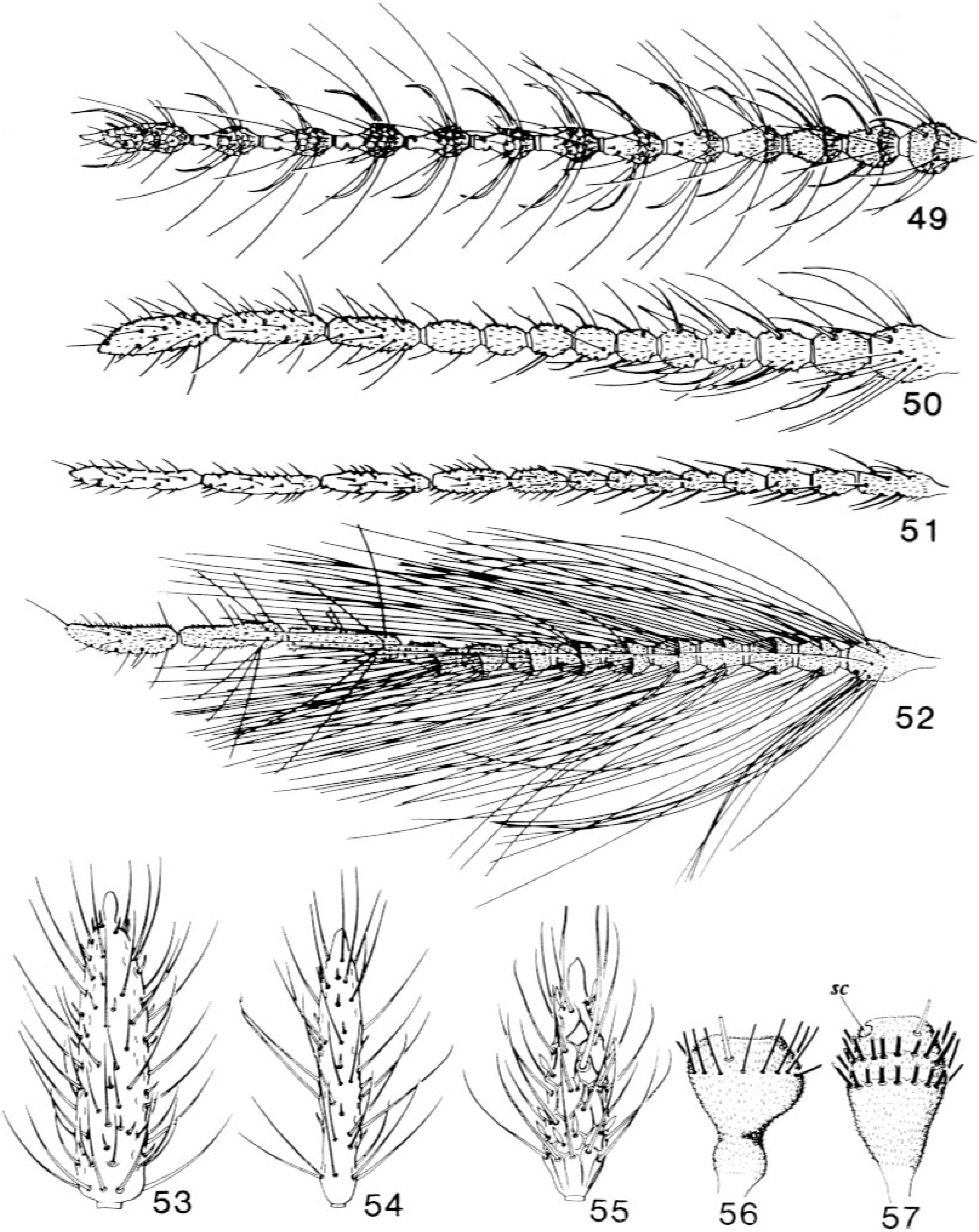


Figs 34-43. Ceratopogonidae, pupa: respiratory horn (34-40) and metathorax in dorsal aspect (41-43). -34. *Culicoides* sp. -35. *Palpomyia* sp. -36. *Alluaudomyia pentaspila* Remm & Glukhova. -37. *Brachypogon incompletus* (Kieffer). -38. *Serromyia femorata* (Meigen). -39. *Ceratopogon* sp. -40. *Stilobezzia ochracea* (Winnertz). -41. *Ceratopogon* sp. -42. *Culicoides* sp. -43. *Serromyia femorata* (Meigen). Fig. 36 redrawn from Remm & Glukhova (1971); 38-41, 43 from Kettle & Lawson (1952).

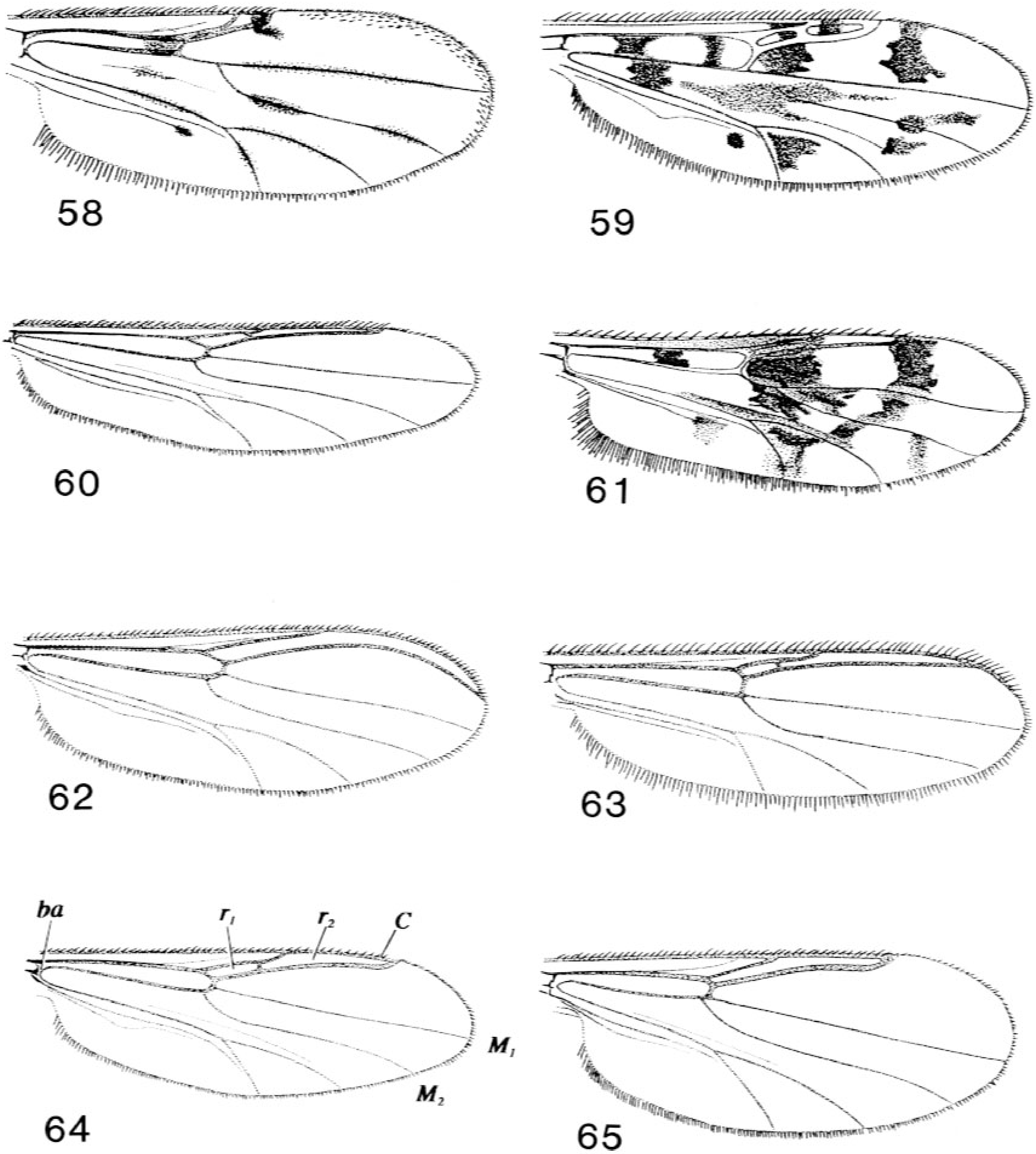
flagellomeres sculptured (Figs 49, 55). Empodium indistinct, claws gently curved (Figs 67-72) 3
2. Paratergite of scutum with 1 or more setae (Fig. 48) .. .. *Atrichopogon* Kieffer
- Paratergite bare .... *Forcipomyia* Meigen
3. Antenna with at least distal flagellomeres sculptured (Figs 49, 55); male flagellomere 1 with single whorl of setae (Fig. 56) (Dasyheleinae) .... *Dasyhelea* Kieffer
- Antenna with all flagellomeres without sculpture; male flagellomere 1 usually with 2 whorls of long setae (Fig. 57), or plume totally reduced (Figs 50-51) (Ceratopogoninae) 4
4. Wing veins M_2 and M_1 forking distal of crossvein r-m (Figs 44, 58, 61) or vein M_2 totally or partially reduced (Ceratopogonini, Culicoidini) 5
- Vein M_2 and M_1 forking at or proximal of crossvein r-m (Figs 60, 62-65); M_2 well-developed from base to apex 15
5. First flagellomere of antenna with sensilla coeloconica (Culicoidini, Ceratopogonini part) (Fig. 57) 6
- First flagellomere without sensilla coeloconica 9
6. Katepisternum of thorax with 1 or more setae (Fig. 47) 7
- Katepisternum lacking setae 8
7. Anterior anepisternum of thorax with 2-3 setae on posterior margin (Fig. 47). Female claws smaller on hind leg. Male antenna with flagellomeres (6)7-11 fused .... *Ceratoculicoides* Wirth & Ratanaworabhan
- Anterior anepisternum bare. Female claws of similar size on all legs. Male flagellomeres 2-11 fused .... *Brachypogon* Kieffer
8. Legs with tarsomere 4 cylindrical. Wing membrane with abundant macrotrichia, usually with pattern of dark and light spots (Fig. 44). Metatibial spur well-developed (Fig. 73). Female mandible armed with small teeth (Fig. 46). Female claws small, equal and simple (Fig. 67) (Culicoidini) .... *Culicoides* Latreille
- Tarsomere 4 cordiform or subcylindrical. Wing milky, membrane with very few macrotrichia at wing apex in female, bare in male. Metatibial spur greatly reduced or absent. Female mandible with coarse teeth (Fig. 45). Female claws large with inner tooth .... *Ceratopogon* Meigen
9. Wing with prominent colour pattern 10
- Wing without colour pattern 12
10. Wing with 1st and 2nd radial cells confluent (Fig. 58) .... *Alluaudomyia* Kieffer
- Wing with 1st and 2nd radial cells separate 11
11. Wing with 4 dark areas on anterior margin (Fig. 59). Female metatarsal claws single .... *Monohelea* Kieffer
- Wing with 3 dark areas on anterior margin (Fig. 61). Female metatarsal claws with short basal barb .... *Allohelea* Kieffer
12. Metafemur armed with ventral spines (Fig. 74) .... *Serromyia* Meigen
- Metafemur without ventral spines 13
13. Metafemur slender .... *Stilobezzia* Kieffer
- Metafemur swollen 14
14. Female claws unequal on all legs (Fig. 68). Male genitalia with very long club-shaped apicolateral processes of tergite IX (Fig. 76) .... *Kolenohelea* De Meillon & Wirth
- Female tarsal claws equal on fore and mid legs, greatly unequal on hind leg. Male genitalia with short apicolateral processes of tergite IX *Schizohelea* Kieffer
15. Antenna without plume. Abdomen apically with short cerci (females) 16
- Antenna in most species with adpressed plume. Abdomen apically with male genitalia (Fig. 79) (males) 25
16. Legs with tarsomere 5 armed ventrally with stout black blunt spines (Figs 69, 72) (Sphaeromiini) 17
- Tarsomere 5 without black blunt spines 21
17. Tarsal claws with slender internal basal barb (Fig. 69) .... *Sphaeromias* Curtis
- Tarsal claws with blunt external basal tooth (Fig. 72) 18
18. Wing with costa short, extending to about 0.8 of wing length (Fig. 60) 19
- Costa long, extending nearly to wing tip (Fig. 62) .. 20
19. Body slender. Scutum shining .... *Mallochohelea* Wirth
- Body stout. Scutum dull .... *Nilobezzia* Kieffer
20. Metatarsomere 1 very long. Antenna with proximal flagellomeres with lanceolate setae. Scutum with simple setae .... *Macropeza* Meigen
- Metatarsomere 1 short. Antenna with proximal flagellomeres with simple setae. Scutum with strong erect spines .... *Probezzia* Kieffer
21. Abdomen without internal sclerotized gland rods. Protarsomere 5 inflated or swollen (Fig. 70) (Heteromyiini) 22
- Abdomen with internal sclerotized rods (Fig.75). Protarsomere 5 not inflated or swollen (Palpomyiini) 23
22. Wing with costa extending beyond tip of R4+5 (Fig. 63). Tarsal claws equal on all legs. Protarsomere 5 inflated .... *Neurohelea* Kieffer
- Wing with costa ending at tip of R4+5. Tarsal claws unequal on mid and hind legs. Protarsomere 5 greatly swollen (Fig. 70) .... *Clinohelea* Kieffer
23. Wing with 1st and 2nd radial cells separate (Fig. 64) .... *Palpomyia* Meigen
- Wing with 1st and 2nd radial cells confluent (Fig. 65) 24
24. Protarsomere 5 with stout ventral spines having sharp bent tips (Fig. 71) .... *Phaenobezzia* Haeselbarth
- Protarsomere 5 without stout ventral spines .... *Bezzia* Kieffer
25. Wing with 1st and 2nd radial cells confluent 26
- Wing with 1st and 2nd radial cells separate 29
26. Genitalia with gonostylus greatly reduced (Fig. 77) . ... *Phaenobezzia* Haeselbarth
- Gonostylus normal 27
27. Antenna with plume of flagellum totally reduced (Fig. 51) .... *Macropeza* Meigen
- Plume of flagellum more or less well-developed 28



Figs 44-48. Ceratopogonidae, female. -44. *Culicoides punctatus* (Meigen), habitus. -45-46. Mandible, apex. -45. *Ceratopogon grandiforceps* Kieffer. -46. *Culicoides nubeculosus* (Meigen). -47-48. Thorax, lateral aspect: (aa) anterior anepisternum, (kepst) katepisternum, (ptg) paratergite. -47. *Ceratoculicoides* sp. -48. *Atrichopogon fusculus* (Coquillett).



Figs 49-57. Ceratopogonidae, flagellum of female (49, 53-55) and male (50-52, 56-57). -49. *Dasyhelea obscura* (Winnertz). -50. *Sphaeromias fasciatus* (Meigen). -51. *Macropeza albitarsis* (Meigen). -52. *Culicoides nubeculosus* (Meigen). -53-55. Terminal flagellomere. -53. *Atrichopogon fusculus* (Coquillett). -54. *Palpomyia distincta* (Haliday). -55. *Dasyhelea obscura* (Winnertz). -56-57. First flagellomere, (sc) sensilla coeloconica. -56. *D. obscura*. -57. *Culicoides nubeculosus* (Meigen).



Figs 58-65. Ceratopogonidae, wing of male (58-59, 61) and female (60, 62-65). -58. *Alluaudomyia quadripunctata* (Goetghebuer). -59. *Monohelea estonica* Remm. -60. *Mallochohelea nitida* (Macquart). -61. *Allohelea tessellata* (Zetterstedt). -62. *Probezzia seminigra* (Panzer). -63. *Neurohelea luteitarsis* (Meigen). -64. *Palpomyia tibialis* (Meigen): (ba) basal arculus, (C) costa, (M_1, M_2) median veins, (r_1, r_2) first and second radial cells. -65. *Bezzia ornata* (Meigen). Fig. 59 redrawn from Remm (1971), 63 from Goetghebuer (1934).

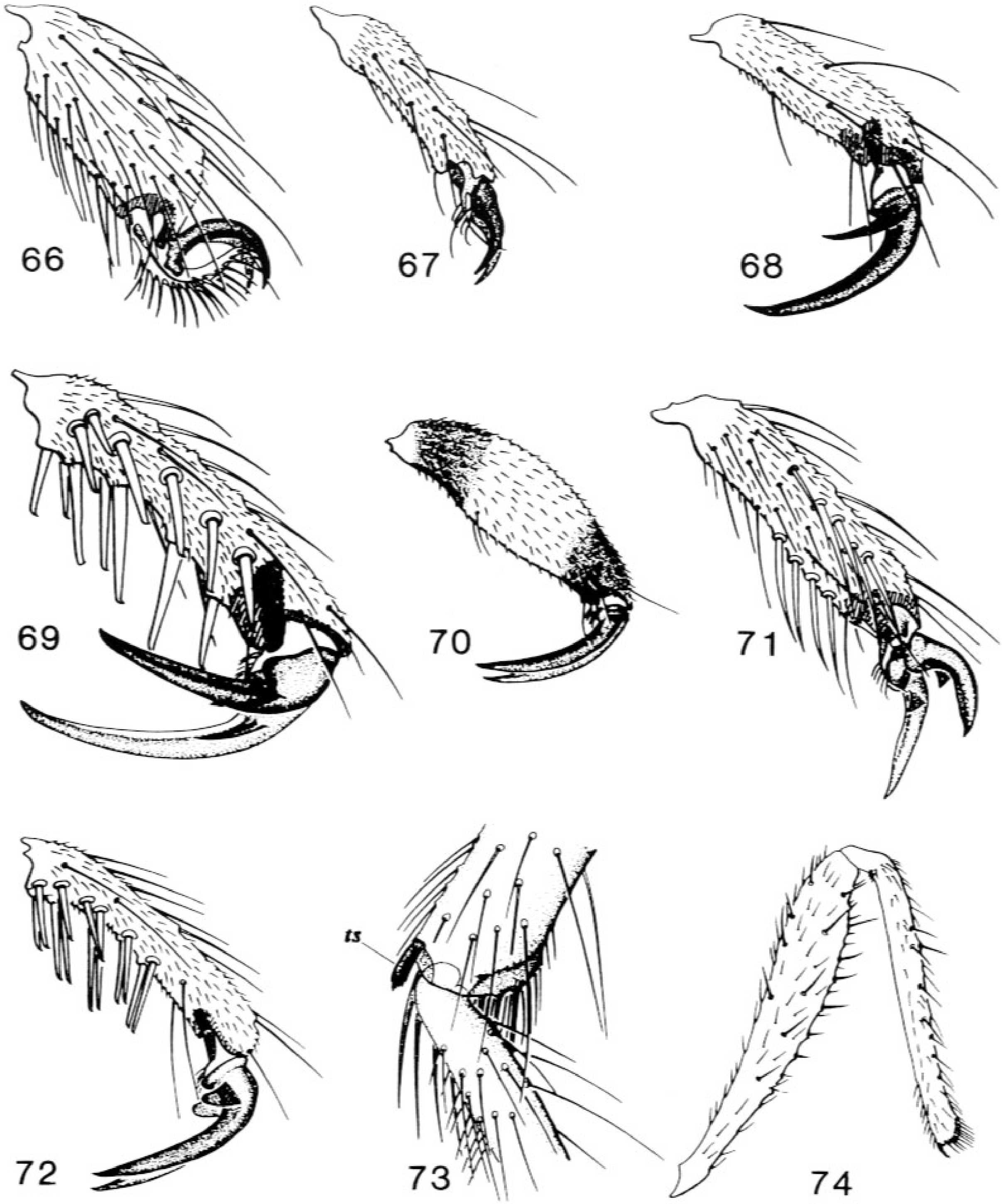
28. Scutum with strong erect spines. Parameres separate distally (Fig. 79) .... *Probezzia* Kieffer
- Scutum without strong erect spines. Parameres totally fused (Fig. 78) .... *Bezzia* Kieffer
29. Genitalia with gonostylus greatly reduced, immovable and bud-like .... *Nilobezzia* Kieffer
- Gonostylus normal, articulated 30
30. Wing with costa extending beyond tip of R_{4+5} (Fig. 63) .... *Neurohelea* Kieffer
- Wing with costa ending at tip of R_{4+5} 31
31. Profemur armed with ventral spines 32
- Profemur without ventral spines 33
32. Legs with tarsomere 5 bearing stout and blunt ventral spines. Antenna with plume almost totally reduced (Fig. 50). Parameres with tonque-like tip setose .... *Sphaeromias* Curtis
- Legs with tarsomere 5 without ventral blunt spines. Antenna with plume more or less well-developed. Tip of parameres bare .... *Palpomyia* Meigen
33. Genitalia small; parameres separate (Fig. 80). Protarsomere 5 swollen. Tarsomere 4 cordiform, on mid and hind legs with lateral lobes armed with apical spines .... *Clinohelea* Kieffer
- Genitalia large; parameres fused at mid portion. Protarsomere 5 slender. Tarsomere 4 on mid and hind legs without lateral lobes armed with apical spines .... *Mallochohelea* Wirth

Key to genera for pupae

1. Last 3-4 abdominal segments covered with larval exuvium (Figs 27-28) (Forcipomyiinae) 2
- Pupa free from larval exuvium (Figs 29-30)............... 3
2. Posteriomedian prolongation long, overlapping abdominal segment 1 (Fig. 28)................ *Forcipomyia*
- Mesothorax with posteriomedian prolongation short, never overlapping abdominal segment 1 (Fig. 27)....... .... *Atrichopogon*
3. Anal segment with pair of setigerous protuberances in addition to apicolateral processes (Fig. 31) (Dasyheleinae) .... *Dasyhelea*
- Anal segment without additional setigerous protuberances (Figs 32-33) (Ceratopogoninae) 4
4. Respiratory horn with double row of spiracles (Fig. 36) .... *Alluaudomyia*
- Respiratory horn with single row of spiracles (Fig. 40) 5
5. Abdominal segments 5-7(8) with glandular discs on ventral side (Fig. 30) 6
- Abdominal segments without glandular discs 7
6. Anal segment not constricted at mid length (Fig. 33). .... *Mallochohelea*
- Anal segment constricted at mid length (Fig. 32)......... .... *Probezzia*
7. Whole respiratory horn dark and broad (Figs 37-39) 8
- Respiratory horn not dark, slender (Figs 34-35, 40) 10
8. Respiratory horn pigmented, but not opaque (Fig. 38). Metathorax widely emarginate (Fig. 43) .... *Serromyia*
- Respiratory horn opaquely dark (Figs 37, 39). Metathorax not emarginate (Fig. 41) 9
9. Respiratory horn with spiracles in cluster at tip (Fig. 37) and with cluster of smaller openings at base .... *Brachypogon*
- Respiratory horn with spiracles more or less regularly distributed around tip and along dorsal edge (Fig. 39) .... *Ceratopogon*
10. Respiratory horn cylindrical (Figs 34, 40). Metathorax completely divided along mid-dorsal line (Fig. 42) 11
- Respiratory horn clavate or spoon-shaped (Fig. 35). Metathorax at most emarginate on anterior border in mid-dorsal line 12
11. Respiratory horn with surface smooth; without scales or transverse convolutions (Fig. 40) .... *Stilobezzia*
- Respiratory horn with surface with distinct scales or transverse convolutions (Fig. 34) .... *Culicoides*
12. Body stout, 7-9 mm long. Integument covered with distinct dark pigmented spots .... *Sphaeromias*
- Body slender, shorter than 6 mm. Integument uniformly coloured, sometimes with indistinct darker spots .... *Phaenobezzia, Bezzia* & *Palpomyia*

Key to genera for instar IV larvae

1. Body with anterior and posterior prolegs present (Fig. 5). Antennae attached to posterior half of head (Fig. 9). Head hypognathous. Body segments usually with distinct tubercles or spines and long setae (Figs 4-5) (Forcipomyiinae) 2
- Anterior prolegs absent. Antennae attached to anterior half of head. Head prognathous or slightly hypognathous. Body segments smooth (Figs 6-8) 3
2. Body cylindrical without distinct lateral processes or setae (Fig. 5) .... *Forcipomyia*
- Body usually flattened with distinct lateral processes and setae (Fig. 4) .... *Atrichopogon*
3. Anal segment with retractile prolegs bearing hooks and spines. Head slightly hypognathous (Fig. 6) (Dasyheleinae) .... *Dasyhelea*
- Anal segment without prolegs, smooth, bearing only setae. Head prognathous (Figs 7-8, 11) (Ceratopogoninae) 4
4. Head with simple setae (Fig. 12) 5
- Head with setae s, u, and posterior o multiple (Fig. 15) 6
5. Head small in comparison with thick body. Neck strongly developed (Fig. 8) (Ceratopogonini part) ... *Serromyia*
- Head larger in comparison with body. Neck short (Culicoidini) .... *Culicoides*
6. Mandible very long, about one third of head length (Fig. 15) (Heteromyiini)...................................... *Clinohelea*
- Mandible short, less than one sixth or one seventh of head length 7
7. Head collar with ventral triangular or rounded extention (Fig. 18) 8
- Head collar narrow ventrally (Fig. 19)...................... 12
8. Head collar brownish, not much darker than head capsule (Palpomyiini part) .... *Palpomyia tibialis* (Meigen)
- Head collar dark, much darker than head capsule (Sphaeromiini) 9



Figs 66-74. Ceratopogonidae, female leg. -66-72. Tarsomere 5. -66. *Forcipomyia* sp. -67. *Culicoides nubeculosus* (Meigen). -68. *Kolenohelea calcarata* (Goegthebuer), mid leg. -69-72. Fore leg. -69. *Sphaeromias fasciatus* (Meigen). -70. *Clinohelea unimaculata* (Macquart). -71. *Phaenobezzia rubiginosa* (Winnertz). -72. *Mallochohelea nitida* (Macquart). -73. *Culicoides nubeculosus* (Meigen), metatibial spur (ts). -74. *Serromyia* sp., metafemur and -tibia.

9. Thoracic segments with black spots .... *Nilobezzia*
- Thoracic segments with brownish spots 10
10. Head with ventral extension of collar triangular (Fig. 18). Body length 16-17 mm, length of head exceeding 450 µm .... *Sphaeromias* Curtis
- Ventral extension of collar rounded (Fig. 16). Body smaller 11
11. Labrum elongated (Fig. 16) .... *Probezzia*
- Labrum not elongated (Fig. 17) .... *Mallochohelea*
12. Head long and slender, HR more than 2.2. Labrum narrow (Fig. 22) (Palpomyiini part) 13
- Head short to moderately long, HR less than 2.1. Labrum broad (Fig. 24) (Ceratopogonini) 14
13. Head with epicranial suture long, reaching level of pit r (Fig. 20) .... *Palpomyia* (part)
- Epicranial suture short, not reaching level of pit r (Figs 21-22) ..... *Palpomyia lineata*, *Phaenobezzia* & *Bezzia*
14. Antenna long (Fig. 19) .... *Brachypogon*
- Antenna very short 15
15. Anal setae equal to or longer than anal segment (Fig. 26) .... *Alluaudomyia*
- Anal setae much shorter than anal segment (Fig. 25) 16
16. Head with epicranial suture short, reaching level of seta q (Fig. 23) .... *Monohelea*
- Epicranial suture long, reaching level of pit z or seta t (Fig. 24) 17
17. Anal setae very short (Fig. 25). Bad swimmers .... *Stilobezzia*
- Anal setae moderately long. Good swimmers .... *Ceratopogon*

References

General and identification

Borkent, A. & Bissett, B. 1990. A revision of the Holarctic species of Serromyia Meigen (Diptera: Ceratopogonidae). - Syst. Ent. 15:153-217.

Borkent, A., Wirth, W.W. & Dyce, A.L. 1987. The newly discovered male of Austroconops (Ceratopogonidae: Diptera) with a discussion of the phylogeny of the basal lineages of the Ceratopogonidae. - Proc. ent. Soc. Washington 89:587-606.

Boorman, J. & Rowland, C. 1988. A key to the genera of British Ceratopogonidae (Diptera). - Entomologist's Gaz. 39:65-73.

De Meillon, B. & Wirth, W.W. 1991. The genera and subgenera (excluding Culicoides) of the Afrotropical biting midges (Diptera: Ceratopogonidae). - Ann. Natal Mus. 32:27-147.

Downes, J.A. & Wirth W.W. 1981. Ceratopogonidae. -In: McAlpine J.E. et al., Manual of Nearctic Diptera. Agric. Can. Monogr. 27, 674 pp., Ottawa .

Glukhova, V. M. 1979. Larvae of the biting midges of the subfamilies Palpomyiinae and Ceratopogoninae of the Soviet Union. - Keys to the Soviet Union Fauna, Nauka, Leningrad, 121, 231 pp. [In Russian.]

Glukhova, V. M., 1989. Blood-sucking midges of the genera Culicoides and Forcipomyia (Ceratopogonidae). - Fauna SSSR, Nauka, Leningrad, 3, 5, 408 pp. [In Russian.]

Goetghebuer, M. 1934. Heleidae (Ceratopogonidae). -In: Lindner E. (ed.). Die Fliegen der Paläarktischen Region. Fam. 13. 77, 1-133, 12 plates.

Gutsevich, A.V. 1973. The bloodsucking midges (Ceratopogonidae). - Fauna SSSR, Dipterous Insects, III, 5, Nauka, Leningrad, 270pp. [In Russian.]

Kettle, D.S. & Lawson, J.W.H. 1952. The early stages of British biting midges Culicoides Latreille (Diptera: Ceratopogonidae) and allied genera. - Bull. ent. Res. 43:421-467.

Lawson, J.W.H. 1951. The anatomy and morphology of the early stages of Culicoides nubeculosus Meigen (Diptera: Ceratopogonidae = Heleidae). - Trans. R. ent. Soc. Lond. 102:511-574.

Mayer, K. 1934. Die Metamorphose der Ceratopogonidae (Dipt.). Ein Beitrag zur Morphologie, Systematik, Ökologie und Biologie der Jugendstadien dieser Dipterenfamilie. - Arch. Naturgeschichte, N.F. 3:205-288.

Murphree, C.S. & Mullen, G.R. 1991. Comparative larval morphology of the genus Culicoides Latreille (Diptera: Ceratopogonidae) in North America with a key to species. - Bull. Soc. Vector Ecol. 16:269-399.

Nielsen, A. 1951. Contributions to the metamorphosis and biology of the genus Atrichopogon Kieff. (Diptera, Ceratopogonidae) with remarks on the evolution and taxonomy of the genus. - Kgl. Danske Vidensk. Selskab. Biol. Skr. 6:1-95, 2 pl.

Remm, H. 1988. Family Ceratopogonidae. -In: Soós, À. & Papp, L. (eds). Catalogue of Palaearctic Diptera 3:11-110. Akad. Kiadó, Budapest.

Wirth, W.W. & Grogan W.L. 1988. The predaceous midges of the World (Diptera: Ceratopogonidae; tribe Ceratopogonini). - Flora & Fauna Handbook 4, 160 pp.

Natural history

Borkent, A. & Craig, D.A. 1994. The structure and function of the abdominal eversible sacs of female Bezzia varicolor (Coquilletts) (Ceratopogonidae: Diptera). - Can. Ent. 126:533-541.

Bowen, T.W. 1983. Production of the predaceous midge tribes Sphaeromiini and Palpomyiini (Diptera: Ceratopogonidae) in Lake Norman, North Carolina. - Hydrobiologia 99:81-87.

Downes, J.A. 1955. The food habits and description of Atrichopogon pollinivorus sp. n. (Diptera, Ceratopogonidae). -Trans. R. ent. Soc. Lond. 106:439-453.

Downes, J.A. 1958. The feeding habits of biting flies and their significance in classification. - Ann. Rev. Ent. 3:249-266.

Downes, J.A. 1978. Feeding and mating in the insectivorous Ceratopogoninae (Diptera). - Mem. ent. Soc. Can. 104:1-62.

Glukhova, V.M. 1958a. On the gonotrophical cycle of the midges genus Culicoides (Diptera, Heleidae) of the Karelian ASSR. - Parasitol. sbornik Zool. Inst. AN SSSR 18:239-254. [In Russian.]

Glukhova, V.M. 1958b. Different types of attacking in Culicoides Latr. (Diptera, Heleidae). - Ent. Obozr. 37:330-335. [In Russian.]

Linley, J. R. 1985a. Biting midges (Diptera: Ceratopogonidae) as vectors of nonviral animal pathogens. - J. med. Ent. 22:589-599.

Linley, J. R. 1986. Swimming behaviour of the larva of Culicoides variipennis (Diptera: Ceratopogonidae) and its relationship to temperature and viscosity. - J. med. Ent. 16:473-483.

Miahle, E., Crozier, G., Veyrunes, J. C., Quiot, J. M. & Rieb, J. P. 1982a. Study of a Birnavirus isolated from a natural population of larvae of Culicoides sp. - Mosquito News 42:527-528.

Miahle, E., Louis, C., Quiot, J.-M., Rieb, J.-P. & Vaga, C. 1982b.Evidence and study of a chlamydial infection in Culicoides sp. - Mosquito News 42:528.

Nielsen, B.O. 1963. The biting midges of Lyngby Aamose (Culicoides: Ceratopogonidae). - Natura Jutlandica 10:1-46.

Nielsen, B.O. 1971. Some observations on biting midges (Diptera: Ceratopogonidae) attacking grazing cattle in Denmark. - Ent. scand. 2:94-98.

Nielsen, B.O. & Christensen, O. 1975. A mass attack by the biting midge Culicoides nubeculosus (Mg.) (Diptera, Ceratopogonidae) on grazing cattle in Denmark. A new aspect of sewage discharge. - Nord. Vet.-Med. 27:365-372.

Nielsen, S.A., Nielsen, B.O. & Jespersen, J. 1986. Effekt af vandløbskvalitet på hyppigheden af kvaegmyg- og mittelarver (Simuliidae & Ceratopogonidae: Culicoides). - Flora & Fauna 92:69-74.

Rieb, J.-P., Miahle, E. & Quiot, J.-M. 1982. Ceratopogonidae infected by an Iridovirus. - Mosquito News 42:529.

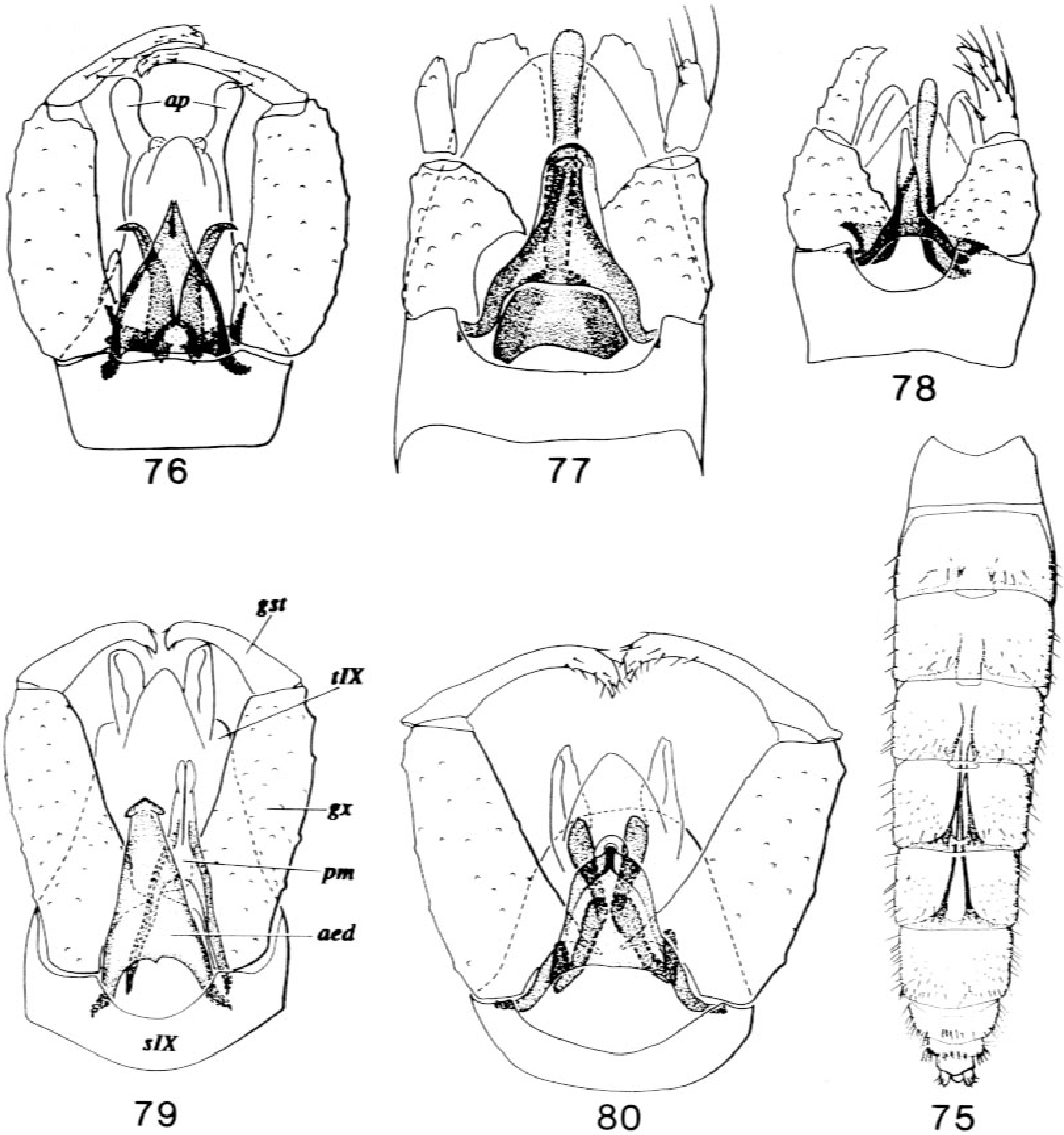
Szadziewski, R. 1983. Flies (Diptera) of the saline habitats of Poland. - Polskie Pismo ent. 53:31-76.

Szadziewski, R. 1990. Secretory setae of the Forcipomyia brevipennis larvae and their biological significance (Ceratopogonidae). - Second International Congress of Dipterology, Abstract vol., p. 232. Bratislava.

Wirth, W. W. 1977. A review of the pathogens and parasites of the biting midges (Diptera: Ceratopogonidae). - J. Wash. Acad. Sci. 67:60-75.

Faunistics

Dow, M.I. & Wirth, W. W. 1972. Studies on the genus Forcipomyia. 2. The Nearctic species of the subgenera Thyridomyia and Synthyridomyia (Diptera: Ceratopogonidae). - Ann. ent. Soc. Am. 65:177-201.



Figs 75-80. Ceratopogonidae, female abdomen (75) and male genitalia (76-80). -75. *Palpomyia flavipes* (Meigen). -76. *Kolenohelea calcarata* (Goetghebuer). -77. *Phaenobezzia rubiginosa* (Winnertz). -78. *Bezzia nigritula* (Zetterstedt). -79. *Probezzia seminigra* (Panzer). -80. *Clinohelea unimaculata* (Macquart). Abbreviations: (aed) aedeagus, (ap) apicolateral processes of tergite IX, (gst) gonostylus, (gx) gonocoxite, (pm) parameres, (sIX) sternite IX, (tIX) tergite IX.

Clastrier, J. 1961. Notes sur les Cératopogonidés. XV. Ceratopogon et Alluaudomyia de la région palearctique. - Arch. Inst. Pasteur Algér. 39:401-437.
Clastrier, J. 1962a. Notes sur les Cératopogonidés. XVI. Espèces du genre Bezzia Kieffer ou apparentées de la région palearctique. - Arch. Inst. Pasteur Algér. 40:53-125.
Clastrier, J. 1962b. Notes sur les Cératopogonidés. XVII. Nouveaux Palpomyia Meig. et Johannsenomyia Mall. - Arch. Inst. Pasteur Algér. 40:225-288.
Glukhova, V.M. 1957. Genus Culicoides Latr. (Diptera, Heleidae) in Karelia. - Ent. Obozr. 36:248-251. [In Russian.]
Goetghebuer, M. & Lindroth, C.H. 1931. Fam. Ceratopogonidae und Chironomidae. -In: Lindroth, C.H. Die Insektenfauna Islands und ihre Probleme. - Zool. Bidr. Uppsala 13:274-285.
Greve, L. 1968. Forcipomyia eques, (Diptera), ektoparasitt på Gulløye i Norge. - Fauna 21:59-60.
Greve, L. 1969. Fire nye funn av Forcipomyia eques (Diptera) i Norge. - Fauna 22:64.
Hackman, W. 1980. A check list of the Finnish Diptera I. Nematocera and Brachycera (s. str.). - Notulae ent. 60:17-48.
Nielsen, B.O. 1964. Studies on the Danish biting midges, Culicoides Latreille (Dipt., Ceratopogonidae). - Ent. Meddr 32:261-276.
Nielsen, B.O., Nielsen, S.A. & Jespersen, J.B. 1988. The fauna of Diptera visiting tethered heifers in Danish pastures. -Ent. Meddr 56:79-88.
Szadziewski, R. 1986. Redescriptions and notes on some Ceratopogonidae (Diptera). - Polskie Pismo ent. 56:3-103.

Methods

Boorman, J. 1974. The maintenance of laboratory colonies of Culicoides variipennis (Coq.), C. nubeculosus (Mg.) and C. riethi Kieff. (Diptera, Ceratopogonidae). - Bull. ent. Res. 64:371-377.
Gutsevich, A.V. & Glukhova, A.M. 1970. Methods for the study of bloodsucking midges. - Methods in Parasitological Investigations, 3, Nauka, Leningrad, 103 pp. [In Russian.]
Linley, J.R. 1968. Colonization of Culicoides furens. - Ann. ent. Soc. Am. 61:1486-1490.
Linley, J.R. 1969. Studies on larval development in Culicoides furens (Poey) (Diptera: Ceratopogonidae). 1. Establishment of a standard rearing technique. - Ann. ent. Res. Am. 62:702-710.
Linley, J.R. 1979. Nutrient agar mixtures for culture of food organisms for predaceous Culicoides larvae (Diptera: Ceratopogonidae). - J. med. Ent. 16:171-172.
Linley, J.R. 1985b. Growth and survival of Culicoides melleus larvae (Diptera: Ceratopogonidae) on four prey organisms. - J. med. Ent. 22:178-189.
Wirth, W.W. & Hubert, A.A. 1989. The Culicoides of Southeast Asia (Diptera: Ceratopogonidae). - Mem. Am. ent. Inst. 44:1-508.
Wirth, W.W. & Marston, N. 1968. A method for mounting small insects on microscope slides in Canada balsam. - Ann. ent. Soc. Am. 61:783-784.

Check list

[Parts of North Europe coded as: D= Denmark, N= Norway, S= Sweden, F= Finland, K= Fennoscandian parts of Russia, I= Iceland, Fa= Faroes, Sv= Svalbard. A few expected species not yet recorded from NW Europe are listed within parentheses.]

Ceratopogoninae

Culicoidini

Culicoides albicans (Winnertz, 1852) .... DK
C. circumscriptus Kieffer, 1918 .... DNK
C. clintoni Boorman, 1984 .... K
C. duddingstoni Kettle & Lawson, 1955 .... D
C. fascipennis (Staeger, 1839) .... DSK
C. festivipennis Kieffer, 1914 .... DK
C. grisescens Edwards, 1939 .... DK
C. heliophilus Edwards, 1921 .... D
C. helveticus Callot, Kremer & Deduit, 1962 .... K
C. impunctatus Goetghebuer, 1920 .... DK
C. kibunensis Tokunaga, 1937 .... DK
C. manchuriensis Tokunaga, 1941 .... K
C. minutissimus (Zetterstedt, 1855) .... S
C. newsteadi Austen, 1921 .... DN
C. nubeculosus (Meigen, 1830) .... DFK
C. obsoletus (Meigen, 1818) .... DFK
C. pallidicornis Kieffer, 1919 .... DK
C. pictipennis (Staeger, 1839) .... DF
C. pulicaris (Linnaeus, 1758) .... DSFK
C. punctatus (Meigen, 1804) .... DFK
C. riethi Kieffer, 1914 .... DK
C. salinarius Kieffer, 1914 .... D K
C. segnis Campbell & Pelham-Clinton, 1960 .... D
C. sphagnumensis Williams, 1955 .... K
C. stigma (Meigen, 1818) .... DFK
C. subfasciipennis Kieffer, 1919 .... DK
C. truncorum Edwards, 1939 .... D
C. vexans (Staeger, 1839) .... DF

Ceratopogonini

Allohelea tessellata (Zetterstedt, 1850) .... S
Alluaudomyia quadripunctata (Goetghebuer, 1934) .... FK
A. splendida (Winnertz, 1852) .... K
Brachypogon aquilonalis (Clastrier, 1961) .... F
B. borealis (Kieffer, 1919) .... N
B. hyperboreus (Clastrier, 1961) .... NF
B. incompletus (Kieffer, 1925) .... SF
B. nitidulus (Edwards, 1921) .... FK
B. sociabilis (Goetghebuer, 1920) .... NSFI
Ceratopogon crassinervis (Goetghebuer, 1920) .... NK
C. lacteipennis Zetterstedt, 1838 .... NFK
C. longitarsis (Mayer, 1940) .... S
C. niveipennis Meigen, 1818 .... F
(*Ceratoculicoides havelkai* Wirth & Grogan, 1988)
[*Kolenohelea calcarata* (Goetghebuer, 1920)]
(*Monohelea estonica* Remm, 1965)
Schizohelea leucopeza (Meigen, 1804) .... FIFa
Serromyia atra (Meigen, 1818) .... S
S. femorata (Meigen, 1804) .... DNSFK
S. ledicola Kieffer, 1925 .... DS
S. rufitarsis (Meigen, 1818) .... D
S. subinermis Kieffer, 1919 .... DSF
Stilobezzia gracilis (Haliday, 1833) .... S

Heteromyiini

Clinohelea unimaculata (Macquart, 1826) .... F
[*Neurohelea luteitarsis* (Meigen, 1838)]

Sphaeromiini

(*Macropeza albitarsis* Meigen, 1818)
Mallochohelea munda (Loew, 1864) .... DSK
M. nitida (Macquart, 1826) .... DF
M. scandinaviae (Clastrier, 1962) .... N
Nilobezzia posticata (Zetterstedt, 1850) .... N
Probezzia seminigra (Panzer, 1798) .... FK
Sphaeromias candidatus (Loew, 1851) .... F
S. fasciatus (Meigen, 1804) .... SFK
S. pictus (Meigen, 1818) .... F

Palpomyiini

Bezzia affinis (Staeger, 1839) .... DS
B. annulipes (Meigen, 1830) .... FK
B. bicolor (Meigen, 1806) .... FK
B. coracina (Zetterstedt, 1850) .... SF
B. flavicornis (Staeger, 1839) .... D
B. leucogaster (Zetterstedt, 1850) .... DSF
B. nigrita Clastrier, 1962 .... NK
B. nigritula (Zetterstedt, 1850) .... NF
B. nobilis (Winnertz, 1852) .... K
B. ornata (Meigen, 1830) .... S
B. pilipennis Lundström, 1916 .... S
B. signata (Meigen, 1804) .... SK
B. solstitialis (Winnertz, 1852) .... DF
B. transfuga (Staeger, 1839) .... DSF
B. winnertziana Kieffer, 1919 .... F
[*Phaenobezzia rubiginosa* (Winnertz, 1852)]
Palpomyia armipes (Meigen, 1838) .... DF

P. aterrima Goetghebuer, 1921 .... NF
P. bispinosa Kieffer, 1915 .... D
P. concoloripes Clastrier, 1962 .... N
P. distincta (Haliday, 1833) .... SF
P. flavipes (Meigen, 1804) .... F
P. fulva (Macquart, 1962) .... D
P. lineata (Meigen, 1804) .... DFK
P. lundstroemi Remm, 1981 .... DF
P. nigripes (Meigen, 1830) .... S
P. rufipes (Meigen, 1818) .... K
P. serripes (Meigen, 1838) .... DSF
P. spinipes (Meigen, 1818) .... SF
P. tibialis (Meigen, 1818) .... FK

Dasyheleinae

Dasyhelea flavoscutellata (Zetterstedt, 1850) .... NFI
D. holosericea (Meigen, 1804) .... F
D. modesta (Winnertz, 1804) .... F
D. notata Goetghebuer, 1920 I
D. obscura (Winnertz, 1852) .... F
D. saxicola Edwards, 1929 .... F
D. sericata (Winnertz, 1852) I
D. scutellata (Meigen, 1830) .... F
D. versicolor (Winnertz, 1852) .... SF

Forcipomyiinae

Atrichopogon alveolatus Nielsen, 1951 .... D
A. brunnipes (Meigen, 1804) .... F
A. dubius Nielsen, 1951 .... D
A. forcipatus (Winnertz, 1852) .... F
A. fusculus (Coquillett, 1901) .... DS
A. fuscus (Meigen, 1804) .... DF
A. griseolus (Zetterstedt, 1855) .... NS
A. hexastichus Nielsen, 1951 .... D
A. maculatus (Lundström, 1910) .... F
A. minutus (Meigen, 1830) .... F
A. muelleri (Kieffer, 1905) .... DS
A. pavidus (Winnertz, 1852) .... F
A. rostratus (Winnertz, 1852) .... F
A. speculiger Nielsen, 1951 .... D
Forcipomyia eques (Johannsen, 1908) .... NF
F. monilicornis (Coquillett, 1905) .... F
F. murina (Winnertz, 1852) .... S