

Identification and ecology of the genus *Smittia* Holmgren in the Netherlands (Diptera: Chironomidae)

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Keys for the identification of males, females, pupae and larvae of the genus *Smittia* are presented. A subdivision of the genus in three groups is proposed and the systematic position and ecological characteristics of each species are described. Seven species are common in the Netherlands. They differ only slightly with respect to most ecological factors, and various species can often coexist in the same place. In describing the general ecology of the genus the influence of humidity of the soil is emphasized. A part of or a whole larval population may go into dormancy or die as a result of weather conditions. Changes in species composition are thought to be a consequence of lowered densities and recolonisation by egg-laying females of species living in the surrounding landscape.

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Introduction

Terrestrial species of Chironomidae have received much less attention than aquatic species, although Karl Strenzke investigated the species of terrestrial habitats in the 1950s. More recently, Sæther revised various genera, e.g. *Limnophyes* Eaton, 1875 (Sæther 1985) and *Paraphaenocladus* Thienemann, 1924 (Sæther & Wang 1995), and Delettre (e.g. Delettre 1984, 1988a, 1988b, 1994) and Frouz (e.g. Frouz 1994a, 1994b) in particular have contributed to a deeper understanding of their ecology.

The present paper is part of a study on terrestrial chironomids and concentrates on the ecology and distribution of the species. The ecology of each genus will be described, drawing on the literature, my own data and unpublished results of other Dutch workers, primarily H. van den Hammen, H. Siepel and H. Vallenduik. The use of 'we' and 'our' in the text refers to the work and results of one or more of these workers and myself. As stated earlier (Moller Pillot 1994), no single sampling method provides a complete quantitative description of the fauna. However, my aim was not to investigate the exact influence of one factor, but to obtain a picture of the most

important differences in the ecology of all the species. Therefore, it seemed to be more useful to give an impression on the ground of different methods. This paper on the genus *Smittia* Holmgren, 1869 is the first of a series on terrestrial chironomids. As there is no recent revision of this genus, I present provisional keys for adult males and females, and for larvae.

Material and methods

Study area. Most terrestrial chironomids for this study were sampled in the Netherlands. Adults and larvae were sampled from locations across the whole country, although the majority of the data relates to the area around Tilburg (province of Noord-Brabant). A few samples were taken in Belarus.

Material. All material in the Moller Pillot collection (HMP), including the archives with comments on identification, aberrations, etc., will be deposited in the National Museum of Natural History Naturalis, Leiden, the Netherlands (RMNH).



Fig. 1. Mini-emergence trap.

Identification. Pinder (1978) was used for identifications and I use his author's names without having checked type material. Any differences from the descriptions or figures given by Pinder are mentioned.

Terminology. Generally Sæther (1980) is followed. Some additions are:

- *Apical part of the costa*: see costal extension, but measured from the point where costa and R_{4+5} meet for the first time (fig. 2). This apical part of the costa is on an average 20 μm higher than the costal extension.
- *Costal extension*: distance from the very end of R_{4+5} to the end of the costa (fig. 2).
- *The setae on sternite VIII* are measured in a straight line.
- *Female cerci* are measured in the exact dorsoventral position, without the narrow stalk.

Sampling methods. This publication is not the result of one systematical investigation. Much unpublished material obtained by others has been used. More than one thousand terrestrial samples, using different methods, were taken at more than 300 localities throughout the Netherlands. Nearly all landscape types were investigated, but woodland and fields are

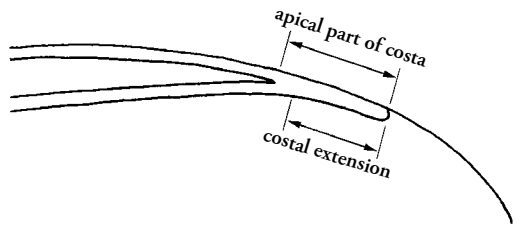


Fig. 2. *Smittia*, male wing: end of the costa.

rather under-represented, and we have hardly any data for pine forests and reed-beds. As a rule, all adult chironomids (at least the males) were identified to species level. In total we identified more than 3,000 adults of *Smittia* from approximately 70 localities.

Different sampling methods were used for different purposes. The most commonly used methods were emergence traps, mini-emergence traps, sweepnet and the Tullgren method, where the larvae are extracted by desiccation of a soil sample. Our soil samples were spread out on a sieve below a lamp and the larvae were collected in a tray partly filled with water. Depending on the nature of the soil material, we sometimes interrupted the irradiation. Some larvae were put into Petri dishes for rearing. The emergence traps we used were developed at the Institute for Forestry and Nature Research (now Alterra) for investigations by H. Siepel. These traps are shaped like a four-sided pyramid, 80 cm high, with a basal area of 25 dm^2 . The mini-emergence trap was developed by H. Vallenduuk for use in the laboratory (fig. 1). It consists of a bucket with an area of 2.5 dm^2 , covered with a cone of black material and a plastic jar near the top with a layer of 5% chloral hydrate. Soil samples, usually consisting of three to six subsamples, were collected in nature and taken to the laboratory. This procedure was sometimes employed with the emergence traps, which usually contained a 8 dm^2 sample. Samples in emergence traps and mini-traps stored in the laboratory were kept moist by sprinkling for at least two months. H. Siepel placed his emergence traps in the field and moved them weekly. Other methods included catching adults with a sweep net, and catching larvae in inundated grasslands with a hand net (see Moller Pillot 2005) and in pitfalls. Larvae in Petri dishes were observed during rearing.

The Tullgren samples and samples in mini-traps consisted of three or more subsamples because the density of larvae can vary substantially (Eijsackers et al. 1988). Often two or more samples were taken at different spots. The different methods gave clearly different numbers for the genus *Smittia*. The Tullgren

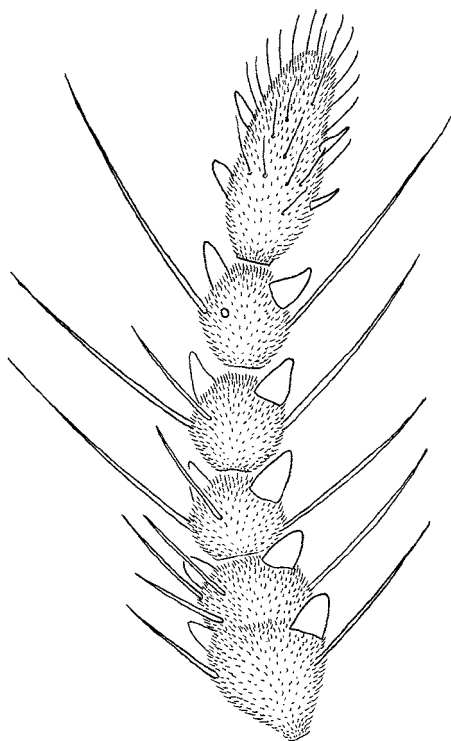


Fig. 3. *Camptocladius stercorarius*, female antenna.

method, in particular, is not very suitable for estimating the numbers of larvae because the proportion of larvae going into dormancy depends on the specific environmental conditions (see below). Rearing yields only the numbers of specimens, which grow into adults after larval and pupal mortality by predation, etc. In our experience, *Smittia* females never deposited eggs in our emergence traps. The fact that so many different methods were used often made it impossible to combine the basic data into a single, well-ordered table.

Systematics

Introduction. This paper does not intend to be a revision of the genus *Smittia*. As to the nomenclature I follow exclusively Langton & Pinder (2007), the manuscript of which was kindly sent to me by Dr. P. Langton. This was to ensure as few differences as possible between this article and usual identification practice in Europe. The inclusion of the parthenogenetic *S. terrestris* within this genus is provisional (see below). For diagnoses and descriptions of the genus in larval, pupal and adult stage (males only),

the reader is referred to Cranston et al. (1983, 1989) and Coffman et al. (1986). My findings differ in only one respect: contrary to Cranston et al. (1989), males and females have small acrostichals. The 2–4 acrostichals of *S. terrestris* are 7–10 μm in length. The other species have 2–7 acrostichals, which are 8–14 μm long. Rossaro (1988), Caspers (1988) and Rossaro & Delettre (1992) also found acrostichals on the thorax of *Smittia*.

Contrary to Ashe & Cranston (1990) and Sæther & Ferrington (2003), who assign *S. terrestris* to *Pseudosmittia* or *Bryophaenocladus* Thienemann, 1934, I consider *S. terrestris* a genuine *Smittia*, since this genus is well-defined in the larval stage and quite different from the other two genera. However, the antennal sensilla of *S. terrestris* are unique, and the absence of anteprenotal setae in the pupa of *S. terrestris* is an important difference from both *Bryophaenocladus* and *Smittia*. It is possible, therefore, that a new genus will have to be erected for *S. terrestris*.

The genus *Smittia* is in need of revision. Many species have been described (see Goetghebuer 1943, Rossaro 1988) and some of these will turn out to be synonyms. I have found a rather large variability in many characters of adult males and hybridisation is probably not rare either.

Species groups. Three species groups are distinguished within the genus: the *terrestris* group, *aterrima* group and *pratorum* group. The *terrestris* group probably merits the status of subgenus or genus. Adults can be recognised easily by their small size, the sensilla on the antenna and the coarse wing punctuation. Anteprenotal setae are absent in the pupa. The setae submenti of the larva are divided. The *aterrima* group is characterised by the leaf-shaped sensilla on the antenna of the female and the 2nd and 3rd segment of the male. The anal lobe of the male wing is nearly right-angled. Sternite VIII of the female has 8–16 pairs of setae, the longest being 50–87 μm . In the *pratorum* group, the antennal sensilla of the female and the basal segments of the male are narrow (in the male of *S. nudipennis* some sensilla are a little broader). The anal lobe of the male wing is more or less reduced. The sternite VIII of the female has 4–7 pairs of setae, the longest being 33–57 μm .

Identification of adults. For ecologists it is important to identify large numbers of specimens within a short time. Therefore some easily observable characters are given here.

A first indication of the genus is given by the relatively fine punctuation of the wing, the bare squama and the usually pubescent eyes. These characters apply to both males and females. In females, the

pubescent eyes and sensilla chaetica on the antenna are especially useful for identification. In *Pseudosmittia* the sensilla have a rather broad base and gradually narrow towards the top; in *Camptocladius* Van der Wulp, 1874 they are (as a rule) leaf-shaped without a long point (fig. 3). In *Smittia* these sensilla are long and nearly parallel-sided or very broad at the base and narrowing to a point (figs. 4-5). Spherical antennal segments 2-4 and the absence of an apical seta are characteristic for *Camptocladius* (fig. 3). At 40 × magnification it is easy to see that the vulva (in sternite IX) is parallel-side in *Smittia* and has the sides converging anteriorly in *Camptocladius* (figs. 6-7).

Identification of larvae. The larvae are easily separable from other genera (except for *Parasmittia*) by the absence of procerci and the circle of claws around the reduced posterior parapods. *Smittia* larvae can be distinguished from *Parasmittia* by the well developed first antennal segment.

Intra- and interspecific variability. Nearly all adult Dutch specimens can be easily identified; they belong to eight species (*S. aterrima*, *contingens*, *foliacea*, *leucopogon*, *pratorum*, *edwardsi*, *nudipennis* and *terrestris*). However, some specimens are aberrant and show combinations of characters of different species: for instance, a male with the crista dorsalis of the gonostylus as in *S. aterrima*, but inferior volsella as in *S. leucopogon* and AR 1.3 (sample nr 44151, collection HMP separate tube under *S. leucopogon* × *aterrima*). Moreover, most characters are highly variable. For example: AR in *S. aterrima* 1.5-2.2; in *S. edwardsi* in the Netherlands 1.15-1.8, in Sweden up to 2.16 (Brundin 1947: 43). There seems to be no doubt that *S. edwardsi* described by Brundin is the same species as *Euphaenocladus edwardsi* described by Strenzke (1950) and the Dutch material (see also the note in Strenzke (1950: 255). The anal point of *S. aterrima* can be 25-53 µm long and either narrow or very broad at the base; small microtrichia can be present or absent in the apical part. The length of the apical part of the costa of *S. edwardsi* in the Netherlands is 55-90 µm, but in the Belarus up to 130 µm. Also the shape of the crista dorsalis is variable in some species.

Specimens showing intermediate characters or combinations of the characters of two species illustrate the need for taking a cautious approach to describing new species. The ecology of the different species shows much overlap. I often found different species swarming together, for instance *S. foliacea* among *S. leucopogon* (HMP 37127) and *S. aterrima* among *S. foliacea* (HMP 37158). In any case, it seems likely that different species of *Smittia* interbreed. Parasitism

can also influence the morphology of adult chironomids (see below).

Problems with identification of females. The pubescence of the eyes is very short in some females of *S. edwardsi* and *S. foliacea*. The punctuation of the wing has to be studied in alcohol and interpretation may depend on the quality of the microscope and the visual acuity of the investigator. Some characters not mentioned in the key appeared to be unreliable when studying a larger number of specimens: (a) the intermediate vein in cell r_{4+5} , (b) the ending of vein M compared with R_{4+5} and Cu_1 , (c) the number of setae on R and R_1 , (d) the form and length of the notum.

Identification of females to species level is sometimes not possible. The females of *S. aterrima*, *S. foliacea*, *S. leucopogon* and *S. contingens* may prove to be identifiable after close examination of the genitalia as Sæther (1977: figs. 58 and 59) has shown.

Key to males of *Smittia* in the Netherlands

1. Crista of gonostylus (in exactly dorsoventral position) absent or low (fig. 8). If not in exactly dorsoventral position the crista looks higher, but ending not very far into distal part of gonostylus. Inferior volsella with characteristic shape or nearly absent 2
 - Crista present, at least as clear as in figs. 9-14. Inferior volsella as in figs. 9-14 3
2. Inferior volsella as in fig. 8 ... *Smittia contingens*
 - Gonocoxite without protruding lobe, the more basal superior volsella strongly rounded (Rossaro & Delettre 1992). Only known from Brittany *Smittia celtica*
3. Crista distally strongly swollen (figs in Caspers 1988 and Rossaro 1988: E, FZ); megaseta nearly in a direct line with the gonostylus. Not known from the Netherlands 4
 - Crista no more swollen than in figures 9-14. Megaseta more or less perpendicular to the longitudinal axis of the gonostylus 5
4. Inferior volsella more or less finger-shaped, anal point extremely long .. *Smittia scutellosetosa*
 - Inferior volsella weakly developed, anal point moderately long *Smittia amoena*
5. AR 2.2-2.8. Crista slightly flattened (fig. 9). Resembling *S. aterrima* (7b; for differences see description) *Smittia foliacea*
 - AR 1.0-2.1 (in *S. aterrima* up to 2.2?) 6
6. At least half of anal point with microtrichia, sometimes extending to apex, at most 20 µm bare at the top. Anal lobe of the wing nearly right-angled (fig. 15). Sensilla on 2nd and

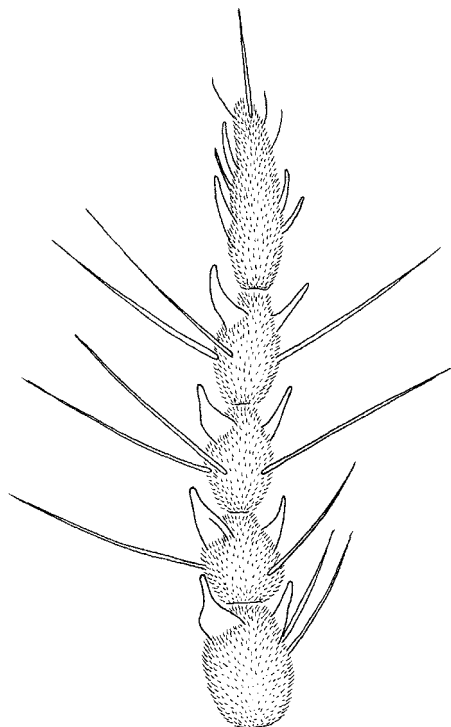


Fig. 4. *Smittia contingens*, female antenna.

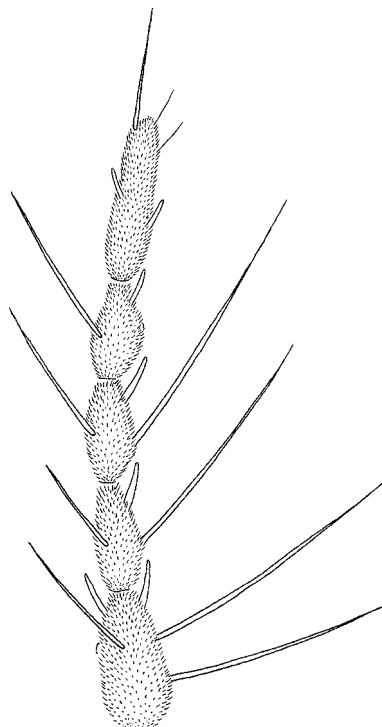


Fig. 5. *Smittia nudipennis*, female antenna.

- 3rd antennal segment with strongly broadened base 7
- At least distal half of anal point, or more than 22 μm at the top of the point, bare. Anal lobe obtuse or absent (figs. 16-17). Sensilla on 2nd and 3rd antennal segment long and narrow, only in *S. nudipennis* partially a little broadened towards the base 8
7. Crista confined to the most distal part of the gonostylus (fig. 10). Inferior volsella more or less finger-shaped. AR 1.0–1.8. Antennal plume whitish (setae in the distal part more or less pale) *Smittia leucopogon*
- Crista of the gonostylus more extensive, occupying nearly half of the total length of the gonostylus (fig. 11). AR 1.5–2.1(?–2.2) *Smittia aterrima*
8. Anal point long, broadened and flattened towards the end (fig. 12). Crista beginning in the proximal half of the gonostylus. Eyes bare. Anal lobe of the wing obtuse, well developed *Smittia pratorum*
- Anal point tapering to a point distally (figs. 13-14). Crista confined to the distal half of the gonostylus. Eyes pubescent 9

9. Anal lobe of the wing nearly absent (fig. 16). Apical part of the costa more than 100 μm . AR 1.1–1.3 *Smittia nudipennis*
- Anal lobe of the wing obtuse (fig. 17). Apical part of the costa in Dutch material 55–90 μm . AR 1.15–1.8 *Smittia edwardsi*

Key to the females of *Smittia* in the Netherlands

1. Total length less than 1.4 mm; wing length less than 1 mm. Five or six sensillae at the top of last antennal segment. Anal vein not reaching further than fCu. Wing punctuation clearly visible at 70 \times magnification. Abdomen yellow to yellowish brown *S. terrestris*
- Total length at least 1.5 mm; wing length more than 1.1 mm. Top of antennal segment without long sensilla, but usually a long bristle. Anal vein reaching further than fCu. Wing punctuation not or barely visible at 70 \times magnification. Abdominal tergites brownish ... 2
2. Antennal sensilla long and narrow, not broadened at base (fig. 5). Sternite VIII with 4–7 pairs of setae, the longest seta 33–57 μm .

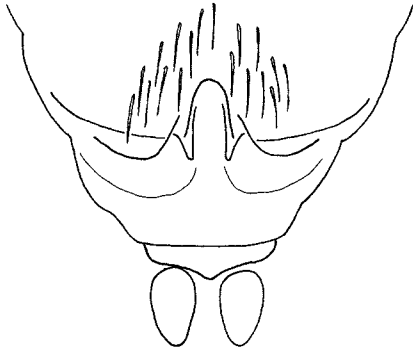


Fig. 6. *Smittia contingens*, female genitalia (ventral view).

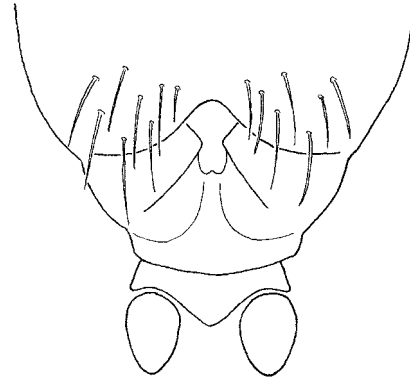


Fig. 7. *Camptocladius stercorarius*, female genitalia (ventral view).

- Cerci (seen from ventral) 45–55 μm long (*S. gr. pratorum*) 3
- Antennal sensilla broadened at base: leaf-shaped to ovoid (fig. 4). Sternite VIII with (?7)8–16 pairs of setae, the longest seta 50–87 μm long (fig. 6). Cerci 45–80 μm long (*S. gr. aterrima*) 5
3. Wing membrane with relatively coarse punctation, in alcohol visible at 120 \times magnification. Anal lobe of the wing nearly absent. Last antennal segment with a very long apical seta: 0.6–0.87 of the length of the segment *S. nudipennis**
- Wing punctation not or barely visible at 120 \times magnification. Wing with obtuse anal lobe. Apical seta of the antenna 0.38–0.6 of the length of last segment 4
4. Eyes bare *S. pratorum***
- Eyes pubescent to hairy *S. edwardsi****
5. Wing punctation very fine: in alcohol not or hardly discernable at 120 \times magnification *S. leucopogon* / *S. contingens*****
- Wing punctation coarser: in alcohol clearly visible at 120 \times magnification *S. aterrima* / *S. foliacea*

Notes

* The female of *S. nudipennis* sensu Brundin could be have a finer punctation, only visible at 140 \times magnification. In the male, and probably also the female, the anal lobe of the wing is a little more developed.

** *S. pratorum* is the only *Smittia* species with bare eyes.

*** Difference between *S. pratorum* and *S. edwardsi* is rather difficult to discern: the hairs on the eyes of *edwardsi* can be short. Other characters are not

very reliable. As a rule, the last antennal segment of *edwardsi* is shorter (not more than 1.5 times the length of the 4th segment; in *S. pratorum* often longer). The width of the last segment is not reliable (often flattened).

**** *S. leucopogon* is usually smaller than the other species of gr. *aterrima* (including *S. contingens*). The cerci of *S. leucopogon* are usually 45–55 μm long, in dung up to 67 μm or more; in the other three species 60–80 μm .

Key to the pupae and exuviae

According to Langton (1991), pupae of the species of *Smittia* are extremely similar, but it is highly probably that he did not investigate pupae of *S. terrestris*. According to Strenzke (1950: 312), the pupae of *S. terrestris* can be identified as follows:

- 1 Median anteprenotal setae absent; total length 1.0–1.5 mm. Three very small pre-corneal setae, approx. 6 μm long ... *S. terrestris*
- Median anteprenotal setae present; total length more than 1.5 mm. Three precorneal setae, the longest 30–120 μm other *Smittia* species

Key to the fourth instar larvae

Partly according to Thienemann & Strenzke (1941) and Strenzke (1950).

1. First antennal segment longer than second segment. Central mental tooth protruding before first lateral teeth. Setae submenti not quite at the external edge of the submentum, with two or three branches. Eye relatively

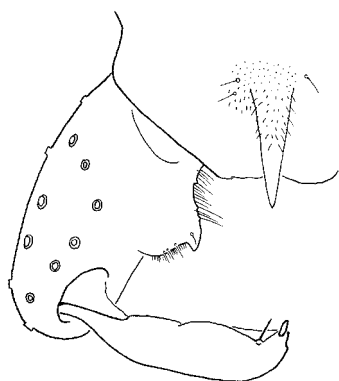


Fig. 8. *Smittia contingens*, hypopygium (dorsal view).

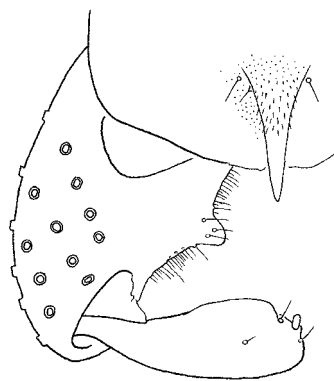


Fig. 9. *Smittia foliacea*, hypopygium (dorsal view).

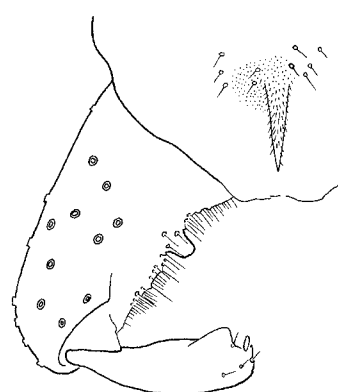


Fig. 10. *Smittia leucopogon*, hypopygium (dorsal view).

- large. Abdomen yellow to pale brownish. Head less than 0.2 mm long *S. terrestris*
- First antennal segment shorter than second segment. Central mental tooth not protruding before first lateral teeth. Setae submenti at the external edge of the submentum, simple. Eye relatively smaller. Abdomen usually with a violet (in alcohol greyish) pattern. Head length in third instars 0.2 mm or more, in fourth instar about 0.3 mm 2
 - 2. Longest claws of anterior parapods not more than 15 μm long. (Length of longest claw of posterior parapods about 30 μm) *S. contingens* *
 - Longest claws of anterior parapods 20–35 μm long. (Length of longest claw of posterior parapods about 40 μm) other *Smittia* species **

Notes

* See the description and comments below

** According to Strenzke (1950), *S. edwardsi* can be distinguished by the form of the S I on the labrum. In *S. edwardsi* the S I has a long median tooth; in all or most other species the S I has teeth all the same length.

Species treatments

The description of each species contains additional diagnostic information. In some cases, aberrant specimens are described, but aberrant forms or hybrids can be found in all species. In the Section 'Synonymy', nomenclatural problems or errors in the literature are discussed.

Our data concerning the ecology of the different

species is based on the results of very different types of investigations (see above). Sufficient information on the sites where living larvae were found could be obtained only for *S. edwardsi* and *S. pratorum*, for which the majority of the data were obtained by rearing. The ecology of most of the species can therefore only be described in general terms.

Smittia amoena Caspers

Smittia amoena: Caspers, 1988: 179

At least one male of *S. amoena* is known, collected near a dry gravel soil in southern Germany. A male from Italy described by Rossaro (1988) as *Smittia* sp. FZ resembles this species, but has a much higher antennal ratio (2.2) and a longer anal point compared with the specimen described by Caspers (antennal ratio 1.15).

This species has been included in the new key for Britain and Ireland (Langton & Pinder, 2007: 140, fig. 73K, 191C).

Smittia aterrima (Meigen)

Chironomus aterrimus Meigen, 1818: 47
? *Camptocladius foliata*: Kieffer, 1906: 344

Material examined. Netherlands: 26 localities.

Diagnosis

Smittia aterrima is a relatively large species within the genus: wing length of female rarely less than 1.5 mm; cerci 60–80 μm . Despite the name, colour often brownish and wing membrane usually also

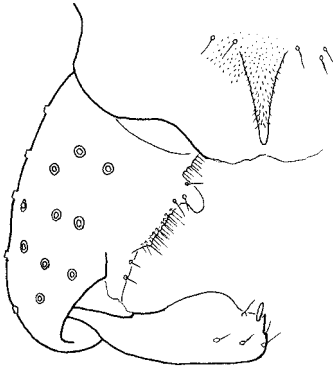


Fig. 11. *Smittia aterrima*, hypopygium (dorsal view).

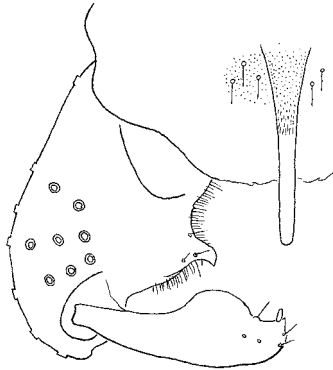


Fig. 12. *Smittia pratorum*, hypopygium (dorsal view).

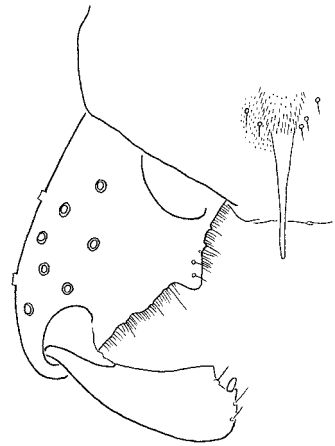


Fig. 13. *Smittia nudipennis*, hypopygium (dorsal view).

somewhat brownish. The male can be identified by the following combination of characters: anal point is rather short (25–53 μm), with microtrichia extending almost to apex, or present on more than half the length of the anal point (up to 20 μm can be bare), with some longer setae near the base (sometimes absent?). AR 1.5–2.1 (–2.2?). There is some overlap with the AR of *S. foliacea*, in which the anal point is more robust, with 20–30 μm bare (or nearly bare) distally. Small differences were found in the shape of the crista and the inferior volsella (see the description of *S. foliacea*). The crista dorsalis is always clearly visible, and usually a little longer than illustrated by Pinder (1978: Fig. 138 D). Viewed in exact dorsoventral position, the highest part of the crista is distal from the middle. Sometimes, however, it seems to resemble the crista of *S. pratorum*, but difference from the crista of *S. leucopogon* is always clearly visible. Shape of inferior volsella exhibits some variation and can resemble that of the latter species. At least one male seemed to be a hybrid between *S. aterrima* and *S. leucopogon*.

Female with relatively coarse punctation on wing, clearly visible at 120 \times magnification (sometimes at 70 \times magnification). Within the *aterrima* group, this character is the same in *S. foliacea*. In the whole group the antennae bear leaf-shaped sensilla that clearly narrow towards the tip (rarely with split tips). Colour of halteres seems to be variable.

Ecology

According to Delettre & Lagerlöf (1992), Frouz (1994a, under *S. nudipennis*), Weber & Büchs (1995) and Frouz & Kindlmann (2001), *S. aterrima*

is a common and often numerous species on different types of agricultural fields, including fallows and grass leys. In accordance with this we found the species in the Netherlands very numerous in fields and we collected the adults flying above different types grassland, but also sometimes in woods. In one instance the species was reared from a dense vegetation of reed, nettles and grasses. *Smittia aterrima* is a rather common species in gardens and on lawns in the centre of Tilburg. In grassland (also in lawns) the species is much less common than *S. pratorum*. It can sometimes be found in nutrient-poor conditions, no less frequently than other species of the genus (except *S. nudipennis*). On bare black soil, for example in gardens, fields and fallow land, it is nearly always more common than *S. pratorum* and it can be found together with nearly all species of the genus. We also reared the species from cow pats and horse dung, but only in low numbers. *Smittia aterrima* seems to be the least specialised member of the genus, but usually we found it not to be the dominant species.

Our data do not give sufficient information about reaction to drought or inundation. In this respect *S. aterrima* is most probably no different from other species of the genus. Regarding the influence of vegetation development, Frouz (1994a) has shown that larvae of *S. aterrima* are scarce in plots with dense vegetation.

Based on our investigations and those of Frouz (1994a), the species can be placed most probably between *S. edwardsi* and *S. pratorum* (see under *S. edwardsi*, table 1). The most striking difference from *S. edwardsi* is that we never found *S. aterrima* in pioneer situations other than fields. On the whole,

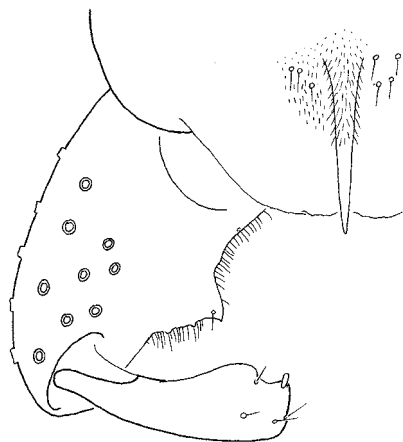


Fig. 14. *Smittia edwardsi*, hypopygium (dorsal view).

S. aterrima can be characterised as a species of soils rich in nutrients.

On five occasions we found males of *S. aterrima* swarming. All these swarms were seen along grassland near or above a shrub, a trench or another object. Since the species does not seem to have exacting requirements regarding swarming locations, this tells us no more about the species habitat.

Smittia celtica Rossaro & Delettre

Smittia celtica Rossaro & Delettre, 1992: 365

Smittia sp. 1: Delettre, 1984: 157 vv

Smittia sp.: Delettre et al., 1992

This species has been found only in Brittany (France). Larvae were present only in dry heathland and adults were not found flying above adjacent habitats (Delettre et al. 1992). Delettre's description does not give enough information to justify allotting the species to one of the systematic groups. For descriptions and ecology see Rossaro & Delettre (1992) and Delettre (1984).

Smittia contingens (Walker)

Chironomus contingens Walker, 1856: 191

? *Euphaenocladius* sp. C: Strenzke, 1950: 264–266, Figs 45 and 46

Material examined. Netherlands: Tilburg, 10.ix.2004 (HMP 44151; arch. nr XXXII-113). Tilburg, 7.i.2005: larvae (HMP 45101; arch. nr XXXIII-25). Tilburg, 12.i.2005 (HMP 45104; arch. nr XXX-

III-79). Tilburg, 4.ii.2005 (HMP 45106; arch. nr XXXIII-26). Esbeek, 6.ii.2005 (HMP 45107; arch. nr XXXIII-76, 78). Lelystad, 20.ii.2005 (HMP 45108 and 45109; arch. nr XXXIII-77, 78).

Synonymy

Thienemann & Strenzke (1941) and Ashe & Cranston (1990) report that *S. aquatilis* Goetghebuer could be a synonym of *S. contingens* (Walker). In any case this is not true for *S. aquatilis* sensu Thienemann & Strenzke (1941) and sensu Goetghebuer (1943: 86, Fig. 150), and therefore not sensu Strenzke (1950). The gonostylus of *S. aquatilis* in their figures is totally different from the gonostylus of *S. contingens*. For *Euphaenocladius* sp. C of Strenzke (1950), see under the section below (Diagnosis of the larva).

Diagnosis

Male. The male can easily be identified by the shape of the gonostylus and the inferior volsella. However, the gonostylus can have a low crista, higher than in Fig. 138A of Pinder (1978), sometimes flattened as in *S. foliacea*. The gap between crista and megaseta is not a reliable character for distinguishing between *S. contingens* and *S. aterrima*, but the megaseta of *S. aterrima* stands nearly perpendicular to the gonostylus (Fig. 138C of Pinder). The anal point of *S. contingens* is more robust than in *S. aterrima*, with a longer bare apex (total length 43–63 µm, the distal half usually without setae and at most with a few microtrichia; in *S. aterrima* 25–53 µm, usually much less than half of it bare). AR 1.4–2.1 (n = 15).

Female. The female resembles *S. aterrima* and *S. foliacea*. The punctuation of the wing, however, is much finer than in these species and barely visible at 120 × magnification. We found no reliable difference between *S. contingens* and *S. leucopogon*. The latter species is usually smaller, but sometimes (especially when living in dung?) about as large as *S. contingens*.

Larva. The larva of *Euphaenocladius* sp. C described by Strenzke (1950) was sampled from dung by H. Franz in Austria. The larva is rather different from all other species of the genus because of the smaller claws of the anterior parapods and the shape of the labral setae. The S I has three wide teeth (other species have more and narrower teeth) and the S II is branched (in other species simple).

Larvae of *S. contingens* reared from horse dung in the Netherlands had an S I with 3–7 wide to narrow teeth. The claws of the anterior parapods were much smaller than the claws of normal *Smittia* larvae (about 13 µm as opposed to 30 µm in other species). However, in cow pats, from which I reared

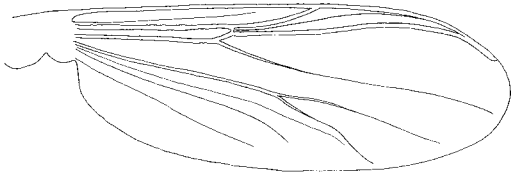


Fig. 15. *Smittia aterrima*, male wing.

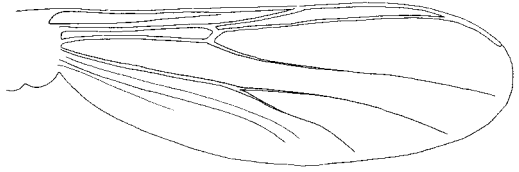


Fig. 16. *Smittia nudipennis*, male wing.



Fig. 17. *Smittia edwardsi*, male wing.

no *S. contingens*, but three other species, I found larvae which had an S I with 3–7 teeth and the longest claw of the anterior parapods varying from 13 μm (one specimen) to 30 μm . I cannot exclude the possibility that *S. contingens* larvae were present here, but the labral setae in particular were nearly the same in all the larvae found in dung. In view of this, I suspect that at least the labral setae are not a reliable character, and that one or more other species also have shorter claws.

Ecology

I reared the species from horse dung found in different parts of the Netherlands, sometimes together with other *Smittia* species. I have only been able to rear the species from horse dung and never from any other substrate. In Austria H. Franz also found *Euphaenocladus* sp. C only in dung. For more information about *Smittia* in dung (see Discussion on ecology – Dung).

Smittia edwardsi Goetghebuer

Smittia edwardsi Goetghebuer, 1932: 123
Euphaenocladus edwardsi: Strenzke, 1950: 255–257,
 Figs 37–39

Material examined. Netherlands: 33 localities. **Belarus:** Hlupin (52°03' N, 28°08' E), 4.vi.1999, 2 males from swarm; iv.2004, 2 males, 8 females reared (HMP 44106; arch. nr XXXII-92). Hvoensk (52°03' N, 27°56' E), 24.iv.2004, 9 females (HMP 44539; arch. nr XXXII-121).

Diagnosis

Male. The male can be identified only by a combination of characters: fairly long anal point, crista in distal part of gonostylus, pubescent eyes (sometimes difficult to see and overlooked by Goetghebuer), wing with obtuse anal lobe, R_1 with 1–3 setae, An fairly long and curved. In the Netherlands length of apical part of costa of *S. edwardsi* 55–90 μm , in Belarus up to 130 μm . The location of the tip of R_{4+5} and the antennal ratio are not very reliable. We found an AR of 1.15–1.6; Brundin (1947) mentions an AR of 1.80–2.16. In some specimens the anal point is rather short (40 μm), but always at least 20 μm of the point is bare. The base of the anal point has a number of setae, which is a distinguishing character between *S. edwardsi* and both forms of *S. nudipennis*.

Female. The female differs from *S. pratorum* primarily by the pubescent eyes, and from *S. nudipennis* by the more developed anal lobe of the wing and the finer wing punctation (see however the comments under *S. nudipennis*). Apical seta of antenna 0.4–0.6 of the length of last segment ($n = 5$). According to Goetghebuer (1943: 83, 89) and Edwards (1950: 165) the sensilla are short and fairly broad. This must be a mistake: I have checked five different populations and always found long and narrow sensilla. The last antennal segment is fairly short, between 1.3 and 1.5 times longer than the penultimate segment. The hairy eyes and the obtuse anal lobe makes it possible to distinguish *S. edwardsi* from the related species.

Larva. Quite similar to other *Smittia* species. A possible diagnostic character is that S I and chaeta media on the labrum have a long central tooth (Strenzke, 1950: p. 257, Fig. 39).

Distribution and ecology

Very few exact ecological data are mentioned in the literature. The species seems to be less common than *S. aterrima* and *S. pratorum*. According to Ashe & Cranston (1990) and Strenzke (1950), the species has been found in Austria, Germany, Great Britain, Ireland, Rumania and Sweden. In the Netherlands

Table 1. Number of samples from which *S. edwardsi* and *S. pratorum* were reared in relation to percentage of open soil, vegetation type and height of the vegetation.

Not included:

more samples from the same locality;

samples from outside the Netherlands;

samples for which the relevant data were not available;

samples from sites where the relevant factors at the time of egg depositing were not the same as at the time of sampling;

samples which could not be classified for other reasons.

	% open soil				vegetation type					height of vegetation			total number	
	no open space	< 10%	10 – 50%	> 50%	field	grassland	wood	herbs (and reed)	pioneer-vegetation	no vegetation	< or = 5 cm	5 – 20 cm		> 20 cm
<i>S. edwardsi</i>	0	7	7	12	3	5	0	4	15	1	7	13	6	26 (28)
<i>S. pratorum</i>	10	10	12	10	2	18	8	6	7	1	22	10	10	42

we collected or reared *S. edwardsi* at 33 localities, in 15 10 × 10 km squares, spread throughout the country. In Belarus I found the species in several places. The densities are usually very low, at most about 10 adults emerging from 1 dm².

Table 1 shows that *S. edwardsi* is a species of pioneer situations, although it can also live in grassland. In comparison with *S. pratorum* we found *S. edwardsi* more often in places with open soil. Five localities were in poor grassland or heathland, about fifteen on shores and banks or in soils that were dug off. In such pioneer situations we often found no other *Smittia* species and it appears to be a specialisation of *S. edwardsi*. The height of the vegetation does not seem to be critical: some of the plants may reach a height of 20 cm or more as long as there is enough open space. *S. pratorum* is present more often in meadows grazed by cattle and with a dense vegetation of low grasses. However, the larvae of *S. edwardsi* are able to live in grassland and the adults emerge there, usually together with other species such as *S. pratorum* and *S. leucopogon*. Elsewhere these species rarely live together.

Also soil fertility seems to play a role. We rarely found *S. edwardsi* in lawns within the town or in manured or fertilised grassland, but the species was reared three times from a corn field (in two cases the eggs had probably been laid when the maize was very young; the third case was in winter). We reared two males from cow pats, but in this case too the soil was poor and supported a pioneer vegetation.

The role of moisture in the habitat choice of these two species cannot be deduced clearly from our data. Soils overgrown by dense vegetations are less vulnerable to desiccation, which is why Frouz & Kindlmann (2001) did not find *S. aterrima* in open areas during summer. *Smittia edwardsi* may be more resistant to desiccation than *S. pratorum*. The former species has often been found in shores and banks and consequently also often in wet soils. Elsewhere however, there seems to be no difference between *S. pratorum* and *S. edwardsi* with respect to soil moisture. Both species inhabit moist to wet soils. They are rarely found on very wet or inundated sites and are not found in dry soils.

In very acid soils *S. edwardsi* is almost the only *Smittia* species in the Netherlands and this does not seem to be an effect of low pH only (see the section on pH under Discussion on ecology below).

Seddon (1986) found some females in emergence traps in an English woodland; however identification of females with Edwards (1950) is not reliable as Seddon stated. Nevertheless, the species sometimes flies in woodland, as I found in Belarus.

Swarming and mating. A copulating pair was caught in Tilburg near the top of a block of flats at a height of 45 m. No other *Smittia* species were found there, although *S. pratorum*, *S. leucopogon* and *S. aterrima* are common in the city. On 19 October 1997 a small group was swarming (between aphids) above blackberry (*Rubus spec.*) bushes near a road at Hilvarenbeek, only two metres above the soil.

***Smittia foliacea* (Kieffer)**

Smittia foliacea (Kieffer, 1921) sensu Pinder, 1978: 96, figs 47C and 138B

Psectrocladius foliaceus Kieffer, 1921: 797–798, figs 17 and 18

Trichocladius foliatus: Kieffer 1921: 799–800, figs 20 and 21

Smittia foliata Goetghebuer 1943: 91–92, fig. 160
nec *Camptocladius foliata*: Kieffer, 1906: 344 (= ? *S. aterrima*)

nec *Camptocladius foliaceus*: Kieffer 1921: 789

Material examined. Netherlands: 25 localities, two of which in Tilburg.

Synonymy

Identification of this species has been problematic in the past. In any future revision of the genus it would be useful to check the identity of *Psectrocladius foliaceus* Kieffer, 1921. The female antenna (his fig. 17) seems to belong to another species and Kieffer wrote that *P. foliaceus* has bare eyes. Both may be mistakes due to inaccurate association and the low magnification used by Kieffer. Provisionally I follow Pinder (1978) and Langton & Pinder (2007) in maintaining the name *S. foliacea*.

According to Ashe & Cranston (1990) *S. foliata* (Kieffer, 1921, not 1906) must be *S. foliacea*. My males and the females associated with these males at different localities correspond with *Trichocladius foliatus* Kieffer, 1921. This is also true for the description and illustration of this species by Goetghebuer (1943), although he mentions an AR of only 2.0. Rossaro (1988) gives an AR of 2.0–2.5.

Diagnosis

Male. In most cases males can be identified without any problem because of the high antennal ratio (?2.1–2.8). In some cases there may be some doubt about whether the specimen belongs to *S. foliacea* or *S. aterrima*. In such cases special attention should be given to the anal point (see below).

In comparison with other *Smittia* species, *S. foliacea* is usually a little more robust and often blacker. The anal lobe of the wing is right-angled, as in other species of gr. *aterrima*. The hypopygium resembles that of the related *S. aterrima*. The crista is large, more or less flattened, as in fig. 9. However, when examined from behind it seems to be more rounded, as in *S. pratorum*. The hairy inferior volsella is as illustrated by Pinder (1978: fig. 138B), but when not positioned exactly dorsoventrally a small bare point is visible and the distal side of the lobe is more concave. The anal point is more robust (approx. 60 µm) than in *S. aterrima* and a longer apical part (usually 20–30 µm) is bare (or only has a few scattered

microtrichia). The lower half of the anal point (between the microtrichia) has some longer setae (up to 17 µm). In all or most specimens one or two of the sensilla on the basal segments of the male antenna are wider than in *S. aterrima*.

Female. For the female I found no reliable differences with *S. aterrima*. In alcohol, the punctation on the wing membrane is visible at 120 × magnification, sometimes as low as 70 ×.

Ecology

In the Netherlands the species is widespread, but rarely numerous. We found *S. foliacea* at 25 localities on sand and clay, in fields and meadows, on lawns in the city and sometimes along water margins. The species has been found together with *S. aterrima* and *S. pratorum*, but hardly ever with *S. edwardsi*. No specific ecological characteristic can be given, but most probably the species has a slight preference for fertilised conditions, and in one instance males have been reared from cow pats. Adults were caught twice on grassland that was not fertilised at all, but in these cases the soil was rich in organic matter. Swarms have been seen at heights between 5 and 60 cm, two times in small groups above a meadow, once above a plastic bag.

***Smittia leucopogon* (Meigen)**

Chironomus leucopogon Meigen, 1804: 17

Smittia leucopogon: Goetghebuer, 1943: 94; Brundin, 1947: 43, fig. 73 (?*leucopogon*); Edwards, 1950: 167; Pinder, 1978: 96, figs 47A and 138C

Smittia spec. D': Rossaro, 1988: 306, fig. 2

Material examined. Netherlands: 27 localities.

Synonymy

There is some confusion about this species in the literature. I agree with Pinder (1978) that the most distinguishing mark is the distal expansion of the gonostylus. However, the inferior volsella in the Dutch and Belarussian material is not shaped as in Pinder's fig. 138C. It is commonly swollen and more or less rounded, as illustrated by Brundin (1947: fig. 73). My material corresponds with the figures of spec. D' in Rossaro (1988), see fig. 10.

Diagnosis

Smittia leucopogon is a rather small species within gr. *aterrima*. Wing length of female 1.2–1.65 mm (in the other species of the group 1.4–1.75 mm). Cerci of *S. leucopogon* 45–55 µm long (rarely up to 67 µm) and in the other species 60–80 µm. In distal part of male antenna setae are usually more or less white. Various authors give different ARs: Pinder 1.0–1.3, Edwards approx. 1.3, Rossaro 1.6, and Brundin

1.53, while in my material it is 1.4–1.9 ($n = 30$). The species is a typical representative of gr. *aterrima*: male wing with large anal lobe and antenna of female with leaf-shaped sensilla. Anal point rather short (37–56 μm long) and only the last 1–14 μm (sometimes about 20 μm) may be without microtrichia. Some longer setae are present on the base of the anal point (not drawn in Pinder's figure). Punctuation on the wing of female strikingly finer than that of *S. aterrima* and at a magnification of 120 \times punctuation cannot be seen or is just discernable. According to Goetghebuer (1943: 83) the sensilla of the female are not broadened but this must be an error. I did not find differences between the female of *S. leucopogon* and (the usually larger) *S. contingens*, of which the larvae only live in dung. When *S. leucopogon* is reared from dung it seems to be larger.

Ecology

About 25% of my data on *S. leucopogon* are from rearing, the remainder is based on sweep net catches. The species has been found in the Netherlands at 27 localities, many of which meadows, but in the city of Tilburg the adults were rarely caught on lawns and more frequently in gardens with bare soil, along the edges of ponds, etc. One male emerged from the soil of a wet birch wood and some males were collected in a carrot field. Near Tilburg the species was much more common in a manured meadow than in a nutrient-poor meadow, but the species has been reared from very poor grassland as well. However, in comparison with *S. pratorum*, *S. leucopogon* seems to prefer places with more decaying organic matter. This would also explain the scarcity of *S. leucopogon* on lawns, where *S. pratorum* is often numerous. The species was reared quite frequently from horse dung and once from cow pats (more than other species of *Smittia*, except for *S. contingens*) (see Discussion on ecology - Dung).

Smittia nudipennis Goetghebuer

Smittia nudipennis Goetghebuer, 1943: 97, fig. 166; Brundin, 1947: 44, figs 19 and 74; Edwards, 1950: 168; Pinder, 1978: fig. 139C

Smittia paranudipennis: Brundin, 1947: 44, figs 18 and 75
 ? *Smittia vesparum*: Goetghebuer, 1921: 169
 nec *Smittia nudipennis* Frouz, 1994a, 1994b (= *S. aterrima*)

Material examined. Netherlands: Ederveen, v.1992, 1 δ ; Westbroek, v.1992, 4 δ ; Belt-Schutsloot, v.1992, 8 δ ; Vogelenzang, 1993–1994, δ δ and δ δ ; Oirschot, 1994–1995, δ δ and δ δ ; Tilburg, 1994–2004, δ δ and δ δ ; Bakkum, leg. H. v.d.Hammen 27.ii.1999, reared to 1 δ , 1 δ ;

Veenendaal, 22.iv.2005, 2 δ ; De Wijk, 23.viii.2005, 1 δ , 1 δ . (All data HMP arch. XXI–XXVII; XXXIII.)

Synonymy

According to Brundin (1947) there are at least two or three species resembling *Smittia nudipennis* Goetghebuer, 1913. He described one of them as *S. paranudipennis*. Pinder (1978) and also Langton (personal communication) do not consider this to be a separate species, although the differences seem to be rather constant. These differences are described below, but it would be better to wait for a total revision of the genus before separating related species. Brundin (1947) gives the following characters for distinguishing *S. nudipennis* (from *S. paranudipennis*): (a) Anal lobe of the wing slightly developed while lacking in *S. paranudipennis*; (b) Anal point short while long and bare in *S. paranudipennis*; (c) Only one seta near the base of the anal point while with three setae in *S. paranudipennis*; (d) Interior volsella not protruding while protruding and more or less pointed in *S. paranudipennis*.

Brundin found only one male in Sweden. In the Netherlands I found it at two sites: Oirschot (samples HMP 35206 and HV 3237; arch. XXIV-7, 84) and Veenendaal (HMP 45135, arch. XXXIII-39). These specimens exhibited not only the above mentioned characters, but also had a clearly finer punctuation on the wing: in *S. nudipennis* hardly or not discernable at 120 \times magnification while clearly visible in *S. paranudipennis* at this magnification. Further, the sensilla on the second antennal segment seem to be narrower than in *S. paranudipennis*.

In some specimens of the Dutch material of both species, vein R_{4+5} ends above the tip of vein M_{3+4} , which is a character of *S. vesparum* according to Goetghebuer and Brundin. In this respect I found differences within a population. In two typical *paranudipennis*, vein R_{4+5} even ended beyond the tip of M_{3+4} . Also, the antennal ratio seems to be an unreliable character: all my specimens of *S. nudipennis* sensu Brundin and some of the specimens of *S. paranudipennis* have an AR of about 1.3.

Females belonging to *S. nudipennis* sensu Brundin are not available. The investigations of Frouz (1994a, 1994b) refer to *S. aterrima*.

Diagnosis

Most males can be identified by the nearly total absence of the anal lobe of the wing. In females the anal lobe is also almost absent. A main difference from other species of gr. *pratorum* is the coarse punctuation of the wing (see also the key and the section on Synonymy). The sensilla on the second segment

of the male antenna are a little wider at the base (except in *S. nudipennis* sensu Brundin) and sometimes only the longest sensilla on the third segment is long and narrow, as in the female. This distinguishes *S. nudipennis* from the other species of gr. *pratorum*. The length of the apical seta on the female antenna is 0.6–0.87 of the length of the last segment ($n = 7$). The female of *S. nudipennis* sensu Brundin, 1947 is unknown and may resemble *S. edwardsi*, probably with a more slightly developed anal lobe of the wing. One male of *S. nudipennis* sensu Brundin had more microtrichia on the rather short (34 μm) anal point, leaving only about 17 μm bare, as in some specimens of *S. aterrima*. One other male seemed to be a hybrid between these two species. Specimens from Italy comparable with this male are described by Rossaro (1988) as *Smittia* sp. D.

Ecology

The species has been found at twelve localities in the Netherlands. In contrast with other species of the genus, all the localities where *S. nudipennis* were found were more or less nutrient-poor and partly very wet grasslands. In only one instance the species was numerous (more than 10 specimens/dm²). Other species of *Smittia* were usually absent in these samples, but the larvae can live together with *S. pratorum*. In a heavily investigated meadow near my house, where *S. pratorum* was the dominant species, *S. nudipennis* was found almost only in spring and in a wet part of the meadow.

An interesting sample was taken in this meadow on 5 May 1995. After a very wet winter the soil was already rather dry at the sampling site. Within 4 weeks (after sprinkling), 28 adults of *S. pratorum* emerged in the mini-trap, followed in weeks 6–9 by 30 adults of *S. nudipennis*. In mini-emergence traps the normal emergence time for all species of *Smittia* at this time of the year is within five weeks. The reason for this difference is probably not (or not only) that the eggs had been laid on a later date, or that *S. nudipennis* needs longer time for development, but more likely that *S. nudipennis* goes into dormancy earlier than *S. pratorum* under conditions of desiccation.

Our data give little information about nutrient levels. The species may not have been found in heavy fertilised grassland because such grasslands in the Netherlands are also more or less dry. In any case, some of the localities where *S. nudipennis* was found had very poor soils; others were not fertilised, but were nevertheless rich in nitrogen.

Smittia pratorum (Goetghebuer)

Camptocladus pratorum Goetghebuer, 1927: 101

Material examined. Netherlands: 66 localities. Belarus: Hlupin (52°03' N, 28°08' E), 21/22.iv.2004, 5 females (HMP 44529, 44534; arch. nr XXXII-120).

Diagnosis

Male. Can easily be identified by the length and shape of the anal point, the rather characteristic crista and the bare eyes. The anal point is about 70–95 μm long and about half of it is bare. Some long setae are present near the base of the point. Goetghebuer (1943: fig. 167) illustrated a completely aberrant hypopygium without the characteristic broadened tip of the anal point and the long crista on the gonostylus.

Female. Differs from all other species by its bare eyes. The very fine wing punctuation (not or barely visible at 120 × magnification) and narrow sensilla on the antenna are also characteristic. The differences between *S. pratorum* and *S. edwardsi* are small (see Key). The length of the apical seta of the antenna in the female is 0.38–0.54 of the length of the last segment ($n = 7$). In some cases only females were found and it seemed to be a special form or separate species (see section on sex ratio under Discussion on ecology).

Ecology

Delettre (1984) found larvae of *S. pratorum* mostly in the soil, but could also find larvae in *Cladonia* vegetation on heathland in Brittany, especially in winter. The species was sometimes present in dry heathland, but usually in small numbers (Delettre et al. 1992). Delettre (1984: 247) supposes that the larvae normally use natural holes in the soil and become immobile in dry periods, during which they lie in a U-form. My own observations in the laboratory indicate that the larvae are free living, but often make a kind of chamber or tube of gathered material, in which they can remain for a long time.

In the Netherlands the species has been found to be very common and often numerous in fertilised grassland and on lawns. Moreover, *S. pratorum* has been reared regularly from woodland soils and from pond banks with pioneer vegetation (table 1). The numbers reared from woodland soils were always low, although flying adults were more numerous. The species seems to be less common in agricultural fields and between high herbs or reed.

We rarely found *S. pratorum* in very nutrient-poor habitats (including nutrient-poor grassland), consistent with Delettre (1994) who found the species to

be scarce and only incidentally more numerous in heathland. The species appears to be scarce in dung (see the section Dung under Discussion on ecology below) and it is possible that the eggs are never laid on dung itself. *S. pratorum* is the dominant and often the only species on lawns in Tilburg. The larvae are equally numerous in grasslands with open or dense vegetation (see table 1), at least when this vegetation is short. They live in grassland on sand or peaty soil, but also often on clay.

Delettre (1988a) stated that *S. pratorum* flies less often than other terrestrial chironomids, avoiding downwind transport, despite its relatively large wing area. However, the species has been found flying in all types of habitat, also where no larvae were living (Delettre et al. 1992). In habitats where the soil becomes very dry in summer, like corn fields, the species can be present in spring. This must be the result of recolonisation, as Frouz & Kindlmann (2001) reported for *S. aterrima* on a field in the Czech Republic. Similar behaviour has been observed in *Limnophyes minimus* (Meigen, 1818), which dies off during a short dry period and quickly recolonises after a wet period. The absence of *S. pratorum* on some temporarily suitable sites may be due to the lack of egg-depositing females at such times. According to Delettre (1988a) *S. pratorum* is more or less a resident species in predictable habitats, with some larval resistance to drought and persistence of the populations on the site.

Nevertheless, in Tilburg *S. pratorum* is a common species in silt and dead leaves in street gutters. This is without doubt the result of the large numbers of flying adults of this species, which disperse from the lawns, where the species is numerous.

Smittia pratorum has been reared from the same site, along with all other *Smittia* species (except *S. terrestris*), most often with *S. leucopogon*, *S. aterrima* and *S. foliaceae* and rarely with *S. contingens*.

Smittia scutellosetosa Caspers

Smittia scutellosetosa Caspers, 1988: 175

? *Smittia* sp. E: Rossaro, 1988: 307, fig. 2E

The type material was collected near gravel banks in southern Germany, and probably by Rossaro in Italy. The larva is unknown. For descriptions and ecology see Caspers (1988).

Smittia terrestris Goetghebuer

Smittia (*Pseudosmittia*) *terrestris* Goetghebuer, 1941: 289.

Euphaenocladius (*Smittia*) *terrestris* (Goetghebuer): Thienemann & Strenzke, 1941: 251

Pseudosmittia terrestris (Goetghebuer): Ashe & Cranston, 1990: 224

Bryophaenocladus terrestris (Goetghebuer): Sæther & Ferrington, 2003: 3

? *Pseudosmittia strenzkei*: Goetghebuer, 1943: 108, fig. 56

Material examined. Netherlands: Helmond: Stipdonk, 13.iv.1982, 1 larva (HMP 22018; arch. nr XXXIII-5); Tilburg, 4.x.2004, 1 ♀ (HMP 44156, arch. nr XXXII-115); Veenendaal, 22.iv.2005, 1 ♀, 3 larvae, 1 larva reared to pupa, 8 larvae reared to ♀ (HMP 45138–41, arch. nr XXXIII-37, 70–73).

Diagnosis

Smittia terrestris is easily distinguished from other species of the genus by its small size, the yellowish abdomen, the antenna without strong apical seta, the short anal vein and the coarse wing punctuation. The pupa and larva also can be easily identified. Some authors (for example Ashe & Cranston 1990) assign the species to *Pseudosmittia* or to *Bryophaenocladus* (Sæther & Ferrington 2003). The larva, however, is a typical *Smittia* larva. It seems more correct to treat *S. terrestris* as a separate subgenus of *Smittia* or as a separate genus (see under Systematics in the introduction of this article).

Most Dutch specimens show a combination of the characters used to distinguish between *S. terrestris* and *S. strenzkei*, which leads me to think the latter is not a separate species, as has already been suggested by Strenzke (1950: 261, note 5).

Larva. Described in detail by Thienemann & Strenzke (1941) and Strenzke (1950), the latter also giving possible differences between *S. terrestris* and *S. strenzkei*. The total length is about 3 mm; the Dutch larvae are somewhat smaller. Strenzke's larvae were pale brownish; the Dutch ones yellow. The differentiating characters that distinguish this species from other *Smittia* species are mentioned in the key.

Distribution and life history

Strenzke (1950) records *S. terrestris* from northern Germany and Iceland and *S. strenzkei* from Austria. In the Netherlands the species has been found in three different areas. It is probably not rare, but under-recorded.

Some adults were caught in the Netherlands at the end of April and in early October. Thienemann & Strenzke (1941) reared adults from June until September. The number of generations is unknown. All collected and reared adults were females and the species is probably parthenogenetic.

Table 2. Numbers of males/females of *Smittia pratorum* caught with a sweep net (100 ×) on a lawn in Tilburg
- = no sample

Month	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
2004	-	-	-	-	14/4	-	/2	8/2	1/	
2005	3/2	1/2	10/12	3/0	9/17	3/2	9/8	7/11	-	-

Ecology

Thienemann & Strenzke (1941) found the larvae on wet soils, mostly in mossy vegetation and often near the margin of a lake. Strenzke (1950) characterises the larvae as typical inhabitants of moist or wet moss. In the Netherlands, all samples in which the larvae were found were also moist to wet and rich in moss. None of the three localities where the larvae were found was influenced by manuring and two of them are in nature reserves with groundwater seepage.

During rearing the larvae lived more at the surface than other *Smittia* larvae. They fed on algae and fine particulate detritus.

Discussion on ecology

Life cycle

Own results. In the Netherlands adults of *S. pratorum* were found all year round, but the numbers are low in winter (see table 2). Adults were caught in several places in December and February and they were sometimes numerous in March and April. The numbers in different months seem to be determined more by local circumstances and weather conditions than by life cycle. If reared indoors, the adults emerge during the whole winter, in contrast to some terrestrial chironomids of other genera, which have a winter diapause. When reared indoors, the development time from egg to adult lasted about five weeks in summer and up to several months in winter or in soil, which was not regularly moistened.

I caught adults of most other *Smittia* species also the whole year round, depending only on temperature and moisture. Swarming of *S. aterrima* and *S. pratorum* was seen even in January (for instance, on 11 January 1998 swarming males of *S. pratorum* at 12° C). For *S. terrestris* I do not have sufficient data.

The development time of the larvae proved to be rather short. In mini-traps and emergence traps in the laboratory the soil was moistened and in summer nearly all adults emerged within five weeks after sampling. Reared Chironomidae always have a much shorter development time than in nature (Lindegaard & Mortensen, 1988). In winter the time required for development in the mini-traps was some weeks longer if kept at a temperature of about 10° C.

From a sample taken at the end of October and temporarily dried out in early spring the last females of *S. pratorum* emerged at the end of April.

Discussion. Delettre (1984) reports that *Smittia celtica* (as sp. 1) and *S. pratorum* on heathland in Brittany have only one generation a year. Delettre & Lagerlöf (1992) found (in *S. aterrima*) two generations in Swedish fields: in spring and in autumn. The authors suggest that the autumn generation was established by midges originating from adjacent habitats with more favourable moisture regimes. Seddon (1986) in England and Frouz (1994a) and Frouz & Kindlmann (2001) in the Czech Republic also found two generations of *S. aterrima* a year: in spring and in late summer or autumn. Weber (1993) found no clear annual periodicity and supposed that on fields in Central Germany *Smittia* has a short life cycle, with several generations during spring and summer. Our investigations in the Netherlands give no indication of clear spring and autumn generations (see for instance *S. pratorum* above). In soils that dry out in summer I could demonstrate that the larvae go into dormancy (see below under Experiment). In wet periods in summer I never found a gap in the emergence of *Smittia*. In general, adults of all species (including *S. aterrima*) emerged throughout the year, even in mid-summer and winter. The absence of young larvae in Swedish fields in July may be the result of a dry period in June and July 1982.

In England Edwards (1950) also mentions a flying period from January to December.

Conclusion. My conclusion is that in favourable conditions in the Netherlands development can be continuous and there can be at least four (overlapping) generations a year. The data in the literature mentioned above refer to environments that dry out or are densely overgrown in summer, and partly to regions with colder winters than in the Netherlands. Under less favourable conditions a part of the population may go through a restricted number of generations (Delettre 1984). I disagree with the statement by Frouz et al. (2003) that *Smittia* species in unpredictable habitats are characterised by resistance in situ and have few generations per year. In most cases when there are only one or two generations this must be the result of a temporary absence of the species.

Sex ratio

Sometimes the numbers of males and females are almost equal, but in many cases either males or females are strikingly more abundant. In nature the sex ratio varies from place to place and can depend on many factors. The data given below refer to reared samples unless stated otherwise. No causes of aberrant sex ratios in *Smittia* were ever established. This needs further investigation with carefully designed experiments. The data indicate five possible causes.

Different genetic forms or species. Some data in the literature and a number of cases in my own investigations seem to be attributable to genetic differences. The most striking examples are mentioned here.

Dettinger-Klemm (2003: 311–312) found a possibly parthenogenetic form or species resembling *S. pratorum*. He caught more than 300 females but no males in his emergence traps. Strenzke (1950: 259) mentions a population of only females in asparagus beds (*Euphaenocladus puripennis* Kieffer, 1924). A further example is a population of about 300 females I caught in a mini-emergence trap from detritus in street gutters in the summer of 2005 (HMP 45158; arch. nr XXXIII-61,64). In late summer a further 43 females were reared from the same site (HMP 45180; arch. nr XXXIII-55). In both cases no difference from *S. pratorum* could be found and in both cases the explanations c, d and e below can be excluded. Moreover, the contents of the trap were checked. From another street I reared two males and 61 females (HMP 45162; arch. nr XXXIII-59,62). On 18 May 2005 I caught 12 males and 108 females on a lawn, where the numbers were usually found to be more or less equal (HMP 45155; arch. nr XXXIII-42).

Most samples of *S. edwardsi* gave a normal sex ratio. From two samples near Riethoven I reared one male and eleven females (sampling date 9 September 1995) and one male and six females (sampling date 11 May 1996). From one sample taken near Heiloo we reared 15 females and no males. A sample from a *Scorzonera* field near Hornerheide, taken on 21 December 1994 (mostly *S. aterrima*, but a few *S. foliacea* and *S. pratorum*) contained 43 males and 135 females; the last 23 adults emerged in March and were all females (HMP 34215; arch. nr XXIII-59,61). In some of these cases either the presence of two different forms or facultative parthenogenesis could be the explanation (see b).

S. terrestris is most probably a parthenogenetic species because males have never been found.

Facultative parthenogenesis (thelytoky). It may be possible that females that do not find a partner produce only female offspring by asexual reproduction.

In most cases this explanation seems improbable, but is not impossible in some of the cases mentioned under a. *Smittia* females never laid fertile eggs in the emergence traps and I found no second generations.

Influence of rearing method. More males than females of *S. pratorum* always emerged in the big emergence trap (70 cm high) used for rearing samples from a meadow in Tilburg. In the mini-trap (30 cm high) I sometimes collected many more females than males. Females may possibly be less disposed to fly and tend to stay at the bottom of the trap, depending on temperature and other conditions. It seems unlikely, though, that this explanation plays a significant role because under more or less consistent conditions the results from the mini-traps are too irregular. One of the mini-traps used to sample *S. pratorum* in the study mentioned under a (above) was checked and contained no males.

Differences in mortality or behaviour. Many samples taken in winter or mid summer contained more females than males. One explanation is that the female larvae are probably slightly larger and better able to survive drought, frost, etc. However, my investigations of the influence of drought (see below) do not provide any strong evidence to support this explanation, which surely would not explain all cases where females were more abundant. It is possible that the larger female larvae crawl deeper into the soil in less favourable conditions. If this were true, males would be found nearer to the place of oviposition than females, or (in samples with more males) the samples were not taken at sufficient depth to catch all females. No investigations have been carried out to test this and there is also no evidence to back up this supposition.

Faster development of males. Strenzke (1966) has stated that males often emerge before females. In some of our samples the males were also observed to emerge on average earlier than females; in other samples there was no difference. However, this difference can rarely explain the differences between the numbers of males and females in a sample. In some cases it is possible that the total population came from one egg mass or from egg masses deposited on the same day. In such cases the possibility that most males had already emerged before sampling cannot be excluded. According to Nolte (1993) simultaneous appearance of many egg masses at one site is not unusual in Chironomidae.

Conclusion. For the moment it is impossible to provide a reliable answer to the question of the differences in sex ratio. My own impression is that genetic

differences (a) and differences in mortality or behaviour (d) are the most likely explanations. Further investigations are needed to resolve this issue.

Flying and swarming

Dispersion. Passive as well as active movements play an important role in the dispersion of *Smittia* species. As in other chironomids, *Smittia* adults are seen flying or swarming in periods with light wind or in sheltered places. In periods with strong wind most specimens are found between vegetation; I sometimes saw that many specimens were blown away from the open field into more enclosed vegetation. Delettre (1984, 1988a) found that swarming of *Smittia celtica* was interrupted when wind speed exceeded 0.8 m/sec. In addition, he found that *S. celtica* flew only over heathland where the larvae lived, whereas *S. pratorum* flew everywhere, although the larvae were absent or rarely found in woodland and pond banks. I observed swarming only during daytime, in most places probably only when the air and the vegetation were dry. In winter only few days seem to be suitable for swarming.

Differences between species. In swarms of *Smittia* I often found only one species, sometimes accompanied by one or more males of another species (sample nrs HMP 36108, 37127, 37158). The number of swarms I investigated were too small to draw any firm conclusions, but there seem to be slight differences in the location of swarming places between species. For instance, swarms of *S. aterrima* were observed only in the vicinity of a change in ground level or vegetation cover, for example near a shrub or above the lip of a trench. Swarms of *S. pratorum*, *S. foliaceae* and *S. leucopogon* were seen above open grassland without any other visible physical feature or patches of different vegetation, although they can also be found above a striking irregularity in the landscape. In general, *Smittia* swarm at a height of about 50 cm or more (*S. aterrima* often a little higher?), but a copula of *S. edwardsi* was found at a height of 45 m on a block of flats, probably after swarming there. I also found a number of males of this species swarming between aphids at a height of 10–50 cm above blackberry bushes.

Larval density

From the literature it appears that low densities (less than 10 larvae dm^{-2}) are normal; more than 50 larvae dm^{-2} is rarely stated. Our own investigations supplied corresponding results.

In an investigation with high gradient extractors in a field, a fallow and a meadow, Frouz (1994a) reported rarely more than 10 larvae from one dm^2 . In an experimental field with a sieving and flotation

method, Weber (1993) found maxima of almost 50 *Smittia* larvae dm^{-2} , normally 5–20 dm^{-2} , and with an emergence trap a maximum of 8 adults from one dm^2 in two weeks. In a Lucerne field Delettre & Lagerlöf (1992) found, as an exception, a maximum of about 95 *Smittia* larvae dm^{-2} (extraction in a Tullgren funnel).

Most authors mention that their methods were not very efficient for younger instars. With the Tullgren method we rarely found more than 10 larvae dm^{-2} . Once, however, in December in a sample from grassland on clay, we found 110 mainly third and fourth instar larvae on 2 dm^2 . From samples reared in a mini-trap, the highest numbers were about 60 adults dm^{-2} (in grassland and street gutter detritus). Normally, in grassland, the numbers emerging were no larger than 5–10 dm^{-2} , often much lower. The very high densities mentioned above were found in *S. pratorum*, *S. aterrima* and *S. contingens* and once in *S. leucopogon*; the numbers of other species rarely exceeded 10 emerging adults dm^{-2} . In samples containing high densities of one species, one or more other species can also be present in lower numbers. In horse dung the densities of *Smittia* larvae can be high, but never equal to those of *Camptocladius stercorarius* (De Geer, 1776) (up to more than 1000 larvae dm^{-3}). More exact data are given in table 5. Only dung with a favourable moisture content has been investigated.

Most authors also state that the numbers of larvae and/or emerging adults often change considerably between years, and also within a single year (Frouz 1994a, Delettre 1994). This is also my experience. In many cases the reason cannot be only because younger instars were not efficiently sampled. It is clear that sites are often not permanently suitable for the development of *Smittia* larvae. This matter will be addressed below. It is important to note here that very low densities are normal, also at sites where higher densities are found during longer periods with optimal moisture content. Competition for food, therefore, seems to be less important, but other competitive interactions, such as insufficient adequate pores in the soil, cannot be excluded.

Dispersal of larvae

Moller Pillot (2005) notes that different species of terrestrial chironomids exhibit remarkable differences in crawling behaviour. *Smittia* larvae probably crawl less often than some other genera. It is completely unknown whether young *Smittia* larvae disperse quickly from the place of hatching, but first and second instar larvae most probably tend to be concentrated around the oviposition sites. Older larvae in the laboratory may remain for a long time

in their shelter (usually not a self-made tube, except for pupation), from where they move out to feed in the neighbourhood. When disturbed, the larvae can creep for some centimetres over the surface within few minutes and they tend to crawl around more often at night than in daylight. If this is also true in nature, they could move considerable distances in response to worsening conditions. Blanchart et al. (1987) has stated that terrestrial chironomids could creep further than one metre to find a place with a suitable soil structure for pupation. This may also apply to *Smittia* larvae.

In nature, after inundation only a few larvae will be found creeping in the water layer. When tap water is applied, many larvae remain in their shelter. Larvae lying in tap water usually swell up, do not move and they can die within few days.

Pitfalls usually only contain one or two *Smittia* larvae. This method is much less efficient for catching larvae of this genus than other methods. It may be that the larvae rarely crawl on the surface. However, 46 larvae were caught at one locality, on a clayish, moist, fertile soil. It is clear that larvae can cover a distance of at least several decimetres within their life, and distances of several metres cannot be excluded.

Microhabitat of the larva

Smittia larvae are mainly found in the top centimeters of the soil.

Delettre (1984) has investigated the microhabitat of *Smittia celtica* in Brittany in detail. Often more than 20% of the larvae of this species lived in the vegetation during the winter (in this case *Cladonia*) but the majority were found in the litter. In June and July nearly all larvae were found in the litter and the soil, and by September all the larvae had migrated from the litter to deeper layers in the soil. Weber (1993) found the larvae as a rule in the top 7 cm. In June and August 1989 most larvae were found at a depth of 7–14 cm, with a significant proportion even deeper. Such behaviour was also found in *Smittia pratorum* by Blanchet (unpublished), and has also been reported by Delettre (1984) in desiccating compost. These migrations to deeper layers were probably also caused by others factors. In winter Frouz (unpublished) sometimes found larvae of *Smittia aterrima* (as *S. nudipennis*) in deeper layers of the soil than in summer (in the Czech Republic). This may be influenced by frost in winter and/or saturation of the upper layers with water.

In my rearing experiments, I almost always found the larvae of *Smittia pratorum* within the soil material. The larvae crawled around for a short time on the surface only after they were disturbed. They moved out of their shelter at night, and rarely in daylight.

Following inundation they do not like to leave the soil (especially not in daylight?). In winter, after rainfall some larvae were found in the rain pools on grassland, within the vegetation, but the numbers of *Smittia* larvae were always low in comparison with other terrestrial chironomids. In summer the majority of the larvae seemed to live in the top centimetres of the soil.

It may be concluded from the above that the larvae seem to prefer the uppermost layers if the conditions are good, when they live in the vegetation or in the upper two centimetres of the soil. In worsening conditions, larvae can be found in the soil to a depth of 10 cm or more.

Feeding of the larvae

According to Strenzke (1950: 403) the food of terrestrial chironomids depends strongly on local conditions. Mineral particles, organic detritus, fungi, mosses and algae can be found in the gut in varying amounts. Frouz & Lukešová (1995) found the same contents in the gut of *Smittia* larvae. Weber & Büchs (1995) assume that *Smittia* larvae contribute to the decomposition of organic material in fields. When rearing larvae I saw them eating small particles of organic detritus and algae, but never gnawing on larger organic material. Living green algae remained green after passing through the whole gut. According to Strenzke (1950: 255, 258, 259) *Smittia* larvae often live in decaying plant material, but can also cause damage to plant roots.

Soil structure

Own results. We found *Smittia* larvae to be scarce in very compact soil, in clay as well in humic sand, but our data are insufficient to allow us to draw a definite conclusion. Sometimes the larvae were numerous in clay too, especially in winter, when there is no problem of desiccation.

Discussion. According to Wallwork (1976) soil texture can influence egg deposition and the horizontal and vertical distribution of burrowing species. Frouz (1994b) and Delettre & Lagerlöf (1992) suppose that porosity is important in relation to the water content of the soil. Frouz (1994b) supposed that many *Smittia* larvae died when the non-capillary pores were saturated with water. In any case, larvae migrate, when possible, to more aerated parts of the soil. Conditions in which 50% of the capillary pores are filled with water were found to be most favourable for larval development. Blanchart et al. (1987) have stated that the pupae make still higher demands on the porosity of the soil than the larvae, so that the prepupae often move to drier parts of the soil. Freezing in winter and indirect relations between food and soil structure may also play a role.

Ploughing

Delettre & Lagerlöf (1992) have suggested that larval chironomids, which inhabit the upper soil layers, are adversely affected by ploughing. Frouz (1994a: Fig. 6) found few *Smittia* larvae after the soil had been ploughed. In the Netherlands we found many *Smittia* larvae in winter in Scorzonera and corn fields that were not ploughed after summer. Although the soil will be less compact after ploughing and therefore more favourable for the larvae, it will dry more quickly. Such differences may also influence egg deposition (cf. Wallwork 1976).

Hydrology and soil moisture; inundation

In comparison with other terrestrial chironomids, *Smittia* larvae do not live in very wet soil. Frouz (1994b) found a high mortality in very wet conditions. On the other hand, Delettre (1984, 1988b) has shown that the larvae of *S. celtica* and *S. pratorum* do not have ecophysiological adaptations to prevent desiccation. During drought they move to deeper layers in the soil. In summer Delettre found *S. celtica* in U-shaped tubes, where they remained inactive. *S. pratorum* larvae were also found in a U-shape and survive in the same manner. The intestines of the larvae in this condition were empty. The larvae became active again 24 hours after moistening. Frouz (1994b) has suggested that conditions of 50% capillary pores filled with water are most favourable for larval development.

Our own investigations also suggest that the larvae avoid very dry and very wet soils. We found hardly any adults of *Smittia* during long dry periods in summer. Of 40 soils samples from which we reared *S. pratorum*, none were dry, 20 were moist, 6 were moist to wet, 11 were wet, 1 was very wet and 2 were inundated at the moment of sampling. The results from 24 samples of *S. edwardsi* were comparable: 0 dry, 8 moist, 6 moist to wet, 8 wet, 1 very wet and 1 inundated.

We took samples on the 28 February 1994 from a grassland in De Mortelen (near Oirschot) that had been partly inundated during two weeks in early January (see table 3). In early January site A was inundated, site B was almost inundated, and site C remained 'dry'. Of 52 identified specimens, 46 belonged to *S. pratorum* and 6 to *S. leucopogon*. In summer the soil in this meadow dried out and *Smittia* was very scarce.

We obtained comparable results in a grassland at Haarlemmerliede in March 1994, where we reared 65 *S. pratorum* from 4 samples, 58 of which were from the only sample of relatively dry soil and only one specimen from inundated soil.

Table 3. Numbers of *Smittia* obtained from three sites in a grassland in De Mortelen (see text)
* converted to 2.5 dm²

	A	B	C
mini-trap	0	2	43
Tullgren*	0	1	58

A short period of inundation is not necessarily lethal, but the larvae are less active after inundation than *Limnophyes* Eaton, 1875 or *Metriocnemus* Van der Wulp, 1874 for example, probably due to the uptake of water (Moller Pillot 2005). We found no species living in water for a long time. An aquatic species (*S. 'aquatilis*) mentioned by Cranston et al. (1989) is probably a case of inundation.

Experiment on the influence of soil moisture on *Smittia pratorum* larvae

I conducted an experiment to obtain a better understanding of the influence of drought in nature. In the dry summer of 1995 I took soil samples from a meadow with sandy peaty soil. To compare moist and dry soils, each sample was divided into two parts and put into two mini-traps. Bucket 1 was sprinkled with water straight away, bucket 2 was allowed to dry out further and was sprinkled with water after three weeks. (Drying out was more serious in nature than in the buckets before sprinkling). No *S. pratorum* emerged from dry soil; emergence began more than a week after moistening. The emergence of *S. pratorum* is shown in table 4.

There appeared to be a period of dormancy, which ended as soon as the soil was moistened. Some of the larvae in the samples which became seriously dried out (especially bucket 2 of samples B, C, D and H) must have died. The population in the field also diminished during the dry periods (the first half of July and whole of August were very dry). The species showed no signs of reproduction in the mini-traps. From this experiment I concluded that no adults of *S. pratorum* emerge from dry soil in summer. Development continued after moistening and adults emerged within a few weeks, although larval mortality rate seems to be rather high.

We may conclude from the above that many *Smittia* larvae do not survive very wet or very dry periods. As a result, the population density is often lower than the maximum level and concurrence of species is limited. Our dataset on *S. nudipennis* suggests that this species prefers a wetter soil and also goes into dormancy during dry periods.

Table 4. Numbers of *S. pratorum* emerging each week

start of regular sprinkling of the sample
 week week number after sampling date

description of samples

	location	soil moisture before sampling	sampling date	moisture on this date
A	depression	wet from 1/6–20/6	22/6	moist
B	depression	after 20/6 moist	1/7	moist, upper mm dry
C	depression	14/7–31/7 moist	3/8	hardly moist
D	depression	from 1/8 drying	24/8	upper cm dry
H	elevation	moist, drying out	1/7	upper cm dry

Sample A was taken after a wet period (not divided); samples B to D, taken at the same locality, gradually dried out during dry periods; sample H was taken from an adjacent spot.

[HMP archives XXIV: 87–78.

Sample numbers: A 35198, B 1 35200, B 2 35201, C 1 35214, C 2 35215, D 1 35217, D 2 35218, H 1 35202, H 2 35203]

week	0	1	2	3	4	5	6	7	8	9	10	11
A	#	8	9	10	15	3	-	-	-	-	-	-
B1	#	-	5	6	11	6	1	-	1	-	-	-
B2	-	-	-	-	#	4	1	3	3	-	-	-
C1	#	-	8	2	1	-	-	-	-	-	-	-
C2	-	-	-	-	#	1	3	1	-	-	-	-
D1	#	-	8	1	-	-	-	-	-	-	-	-
D2	-	-	-	-	#	-	3	2	1	-	-	-
H1	#	-	1	5	3	-	-	-	-	-	-	-
H2	-	-	-	-	#	-	1	-	-	-	-	-

Nutrient availability

Weber (1993) has shown that higher numbers of *Smittia* developed in agricultural soil fertilised with sewage sludge than in soils without sludge. The sludge provides food for the larvae. These results probably pertain mainly to *S. aterrima* (see Weber & Büchs 1995). The investigations by Delettre & Lagerlöf (1992) do not show any clear differences resulting from the influence of different fertilisers, possibly because ploughing affected the results or because organic material in the upper layers of the soil was a more significant influential factor. In more fertilised grassland in the Netherlands, investigated by Siepel et al. (1987), the numbers of *S. pratorum* increased with larger applications of fertiliser and higher grass yields (unpublished data). He rarely found *Smittia* in poor grasslands on the sandy soils of the elevated Veluwe region (not fertilised). In the grasslands at Bovenbuurt (fertilised with 20 kg N/ha/year; grass yield 8,000 kg) the numbers were obviously lower than at Droevendaal (390 kg N/ha/year; grass yield 15,000 kg). However, this appeared not to be true for other *Smittia* species: *S. edwardsi* was found only once: a large population in the poorest acid grassland

on the Veluwe. In the acid and poor heathlands in the Netherlands *Smittia* proved to be rare. For the relation between acidity and nutrient availability, see the section on pH below.

Data mentioned earlier indicate that *S. edwardsi* and *S. nudipennis* are more common in nutrient-poor soils and *S. leucopogon* in soils with much decomposing organic material. This is borne out by data on the presence of the different species in dung, which is examined in the next section.

Dung

Literature on the presence of *Smittia* in dung is scarce. I have not been able to find a single article on studies of *Smittia* in dung in which the species involved have been identified. For this reason I took some samples from horse dung and cow pats (without soil material) in different parts of the Netherlands. Every sample contained material from several heaps of dung in a meadow and consisted of about 1 dm³. The number of dung samples from which I reared a *Smittia* species are shown in table 5. By comparison, I found *Camptocladus stercorarius* in six

Table 5. Number of dung samples from which *Smittia* were reared (numbers between brackets are the maximum number of specimens found in a sample of about 1 dm³)

	horse dung	cow pats
number of samples	11	2
<i>S. pratorum</i>	1 (2)	1 (4)
<i>S. edwardsi</i>	0	1 (2)
<i>S. nudipennis</i>	0	0
<i>S. aterrima</i>	1 (1)	1 (2)
<i>S. contingens</i>	4 (39)	0
<i>S. foliacea</i>	0	1 (2)
<i>S. leucopogon</i>	4 (53)	1 (3)

samples of horse dung, up to a maximum of 1,300 specimens. Species of other genera were scarce.

As can be seen from table 5, only *S. contingens* and *S. leucopogon* were more or less regularly present. The former species I only found by rearing from dung or by catching with a sweep net. It is unclear whether the eggs of *S. pratorum* and *S. aterrima* were laid on the horse dung or on the soil around it. The low numbers in one sample of the cow pats, however, are less suspect because ten females (of gr. *aterrima*) were also obtained. The data given by Curry (1994) indicate that the presence of *Smittia* larvae in dung is almost entirely limited to autumn and winter. In our samples we found *S. contingens* only in winter and *S. leucopogon* more in summer, but we had too few samples to draw any conclusions.

pH

As to pH there seem to exist striking differences between literature and the data from the Netherlands.

Delettre (1984, 1994) investigated acid heathland in Brittany (France) with a vegetation of grasses, *Erica cinerea*, etc. and a pH (KCl) of about 3.5. He found *S. celtica* and *S. pratorum* at many sites (often numerous) and locally *S. aterrima*.

In the Pleistocene regions of the Netherlands the heathland vegetation consists mainly of *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea*, and the pH (KCl) is about 3.0. *Smittia* is very rare in these heathlands and nearby acid grasslands, where the pH (KCl) is about 3.5. Almost the only species present here is *S. edwardsi*. The C/N ratio is much lower in the heathlands of Brittany (about 13) and the calcium (and probably also phosphate) content will be higher. These (and possibly other) factors seem to be more important for *Smittia* larvae than pH alone; the availability of food is probably important for *Smittia* (see the section on nutrient availability).

There is usually a strong relation between pH and microbial degradation (Wallwork 1976, Chamier 1987). The key factor for *Smittia* larvae in acid soils remains unclear. Of further interest is the fact that *Smittia* is very scarce in the dune valleys near the sea at Vogelenzang, where the pH is considerably higher. The main species in these dune valleys is *S. nudipennis*.

Brackish environment

According to Strenzke (1950: 364) *Smittia* larvae are only present in soils with a rather low chloride content. In the Netherlands they have been found at different places along the coast, where the chloride content can be more than 2,000 mg/l (unpublished data). One larva was found in the Weevers Inlaag in the province of Zeeland, where the chloride content was usually more than 7,000 mg/l, but this was not measured during the sampling period (Krebs 1990: 82). The soil water content can change rapidly and measurements are almost never comparable; more accurate data are needed.

Grazing and mowing

In the grasslands investigated by Siepel et al. (1987), more *Smittia* appeared to emerge from grazed land than from mown plots, but the results are not very clear. The density of *Smittia* probably depends mainly on the vegetation structure and desiccation of the soil and will vary during the course of the year, especially in plots that are mown.

Vegetation structure

Smittia larvae live in more open ground than other genera. Frouz (1994a) has reported a decreasing abundance of larvae of *S. aterrima* (as *S. nudipennis*) during succession, when annual weeds were replaced by perennial grasses. The lowest abundance was found in the plots with tall vegetation. Delettre (1994), however, found *S. aterrima* in low numbers in tall heathland with a rather homogeneous vegetation of *Ulex europaeus*. In our investigations we found very few *Smittia* in dense and tall vegetation (see under *S. edwardsi* and *S. pratorum*), but there are differences between species: in grassland with more or less enclosed vegetation we found many *S. pratorum*, scarcely *S. aterrima* and hardly any *S. edwardsi*. The height of the vegetation seemed to be less important when there was much open space between the plants. From the investigations mentioned here we can state that *Smittia* is not totally absent in tall and dense vegetation, but vegetation structure is undoubtedly an important factor. Delettre & Lagerlöf (1992) suppose that the vertical structure and density of the vegetation influence the choice of oviposition sites

Table 6. The occurrence of *Smittia* species in one meadow at Tilburg

<i>Smittia aterrima</i>	rarely, usually flying along the edge of a wood
<i>Smittia contingens</i>	only in horse dung
<i>Smittia edwardsi</i>	every year in low numbers, probably often absent
<i>Smittia foliacea</i>	rarely
<i>Smittia leucopogon</i>	first years absent, in later years fairly common
<i>Smittia nudipennis</i>	only in some years, and only locally more abundant
<i>Smittia pratorum</i>	common every year and probably always present

and, thus, the larval stock level. Investigation of this factor must start from the time of oviposition. Also the distance the larvae move during their life can be important: when eggs are laid on more open sites, the larvae may creep to more sheltered places in dry periods.

In woods and forests *Smittia* can be found flying, but the reared numbers are always low. This may be due to the amount of leaf litter present: more litter could prevent the eggs from making direct contact with the soil capillaries (Frouz 1994a). The only species we often reared from forest soil was *S. pratorum*; some species may not be present there at all (see above under Flying and swarming).

Some species seem to swarm only near a structure in the landscape, but we found *S. pratorum* larvae and sometimes other species also in very open grassland, far from any shrubs or tall-herb vegetation. We have insufficient data to draw conclusions about densities. On a day with strong wind we found large numbers of *Smittia* blown into a water body and shrub vegetation.

Parasitism

Aagaard (1974) has described how parasitism by Nematoda can cause intersexuality in chironomids. Such specimens can display abnormal antennae and aberrations in the genitalia. *Smittia* with such antennae or genitalia seem to be relatively rare. We found intersexes in about 1% of all specimens, but we may have overlooked some of them. In most cases a female had one male antenna, which was not always fully developed. The intersexes appeared in at least five species.

In dung, adult chironomids often carry mites, which are sometimes fixed firmly to the midge. Nothing further is known about them. When rearing samples in mini-traps we often caught small Hymenoptera, even when only Chironomidae and Sciaridae were present in the soil sample. Parasitism by small Hymenoptera on *Smittia* larvae seems to be probable.

Predation

Predation of *Smittia* larvae or adults by birds has never been observed. Birds are known to prey on other terrestrial species like *Metriocnemus*, but *Smittia* are slightly smaller. I do not think that predation by birds is significant if it does occur at all.

In the emergence traps we often reared a number of flies with predaceous larvae and the number of emerging chironomids may have been reduced by these predators. The predaceous fly larvae were more abundant in some dung samples and also when the only possible prey consisted of Chironomidae and Sciaridae larvae. In the emergence traps we often saw spiders building their webs above the ground or in front of the outlet. We always removed the latter. In nature it is normal for chironomids to be caught in spider webs and this can incidentally influence the numbers of flying adults.

Irregular presence of species

Eijsackers et al. (1988) state that large fluctuations of soil organisms are normal, especially in soils where moisture and temperature can vary considerably. For micro- and macroarthropods they give a natural fluctuation constant of 10 between minimum and maximum. In many cases, terrestrial chironomids do not live permanently on a site and can be found only temporarily or irregularly after colonisation or recolonisation (Delettre 1984, 1994).

In a meadow near my house I took about 90 soil samples and caught adults with a sweep net nearly 40 times (most within a period of six years). I collected here seven species of *Smittia* (see table 6).

Flying adults of the different species were collected mostly during the same periods in which they were reared from soil samples. From this it appears that the selection of sampling sites is probably not the reason for a species to be absent in the soil samples for a long time. Only *S. edwardsi* was rarely caught as a flying adult and *S. contingens* was only found in or near horse dung. For the other species, temporary absence has not been proven, but is very probable. Because the meadow was sometimes nearly totally inundated, and in summer sometimes too dry for

normal development of *Smittia* larvae, even the dominant species *S. pratorum* was sometimes rare or absent at many sites. In such a dynamic environment, colonisation or recolonisation seems to be an essential aspect of the ecology of *Smittia* species. In this case, the meadow is surrounded by a great diversity of habitats, so that for most species refugia are not far away. For instance, the banks of some pools provide a useful habitat in summer, but are much less appropriate in winter, when the water's edge is covered by dense vegetation.

Coexistence of species with similar autecology

As we have seen, six of the seven common species of the genus *Smittia* are morphologically and ecologically very similar. For example, I found all the species in the meadow near my house (see above). These species seem to coexist easily, although only *S. pratorum* is often more numerous. We very often found two or more species of *Smittia* in the same sample from many other grasslands, and more than one species was present in the majority of grasslands and fields. The proportion of the species could vary over short distances or in a short space of time. These findings contradict those published by Delettre & Lagerlöf (1992), Frouz (1994a) and Frouz & Kindlmann (2001), where the authors claim that only *S. aterrima* was present. My observations are that this species in particular nearly always coexists with other *Smittia* species. This does not alter the valuable conclusions of these authors, but it highlights the necessity of stating what proportion of the specimens has been identified to species level (the authors could not identify most specimens because they were sampling larvae). Anderson (1975) has argued that the existence of ecologically related species of soil animals does not always mean that there is an excess of food available. There may be small differences in food utilisation, for example under the influence of animal/microorganism interaction.

We have seen in *Smittia* that small differences in microhabitat from place to place present advantages for the different species. These differences lie in the amount of organic material, the density of vegetation, soil moisture, etc. Differences in food acquisition are not very probable. In contrast to many genera of the subfamily Chironomini, *Smittia* species have completely similar mouthparts, suggesting a similar acquisition of food.

Still, all these species can develop in the above-mentioned meadow, as well as in other grasslands, and in many cases even on the same patch.

Some of the *Smittia* larvae disappear more than once a year, either going into dormancy or dying off due

to weather conditions. As stated by Delettre (1988a), *Smittia* species are not frequent flyers, but are more resident species and avoid downwind transport. As a result, recolonisation is delayed, often leaving a niche available for immigrants, with food available in sufficient quantities. Competition between the larvae of the same or different species will be more or less insignificant in such cases. In the Netherlands, all species fly all year round and females of different species will nearly always deposit their eggs, so that the proportion of different species is continuously changing. As Frouz & Kindlmann (2001) have shown, many places are only temporarily better or worse than others – and species do not need optimal conditions to survive.

Siepel (1994) has argued that coexistence of microarthropods that hardly differ in their food requirements is possible because of differences in life history traits. He mentions that the competitive exclusion principle appears to fail when mobility of the competing species is limited. In the case of *Smittia*, however, the life cycle and reproduction of most species seem to be very similar or the same. Their level of mobility is fairly high. Here, the frequent changes in the suitability of the sites, combined with moderately quick colonisation, seems to give the same result: coexistence of six related and ecologically very similar species. Almost forty years ago, Westhoff (1969: 11) said that two equivalent species can coexist without exterminating one another when variations in space and time are taken into account. The species can differ a little in their tolerance of an environmental factor, but what is more important is that their opportunities for survival change at different places because of spatial variation and high temporal dynamics. This is why the *Smittia* species can coexist in the same meadow and all survive in the landscape for a long time.

Acknowledgements

Special thanks are due to Dr. H. van der Hammen (deceased), H. Vallenduuk and Dr. H. Siepel for placing many samples at my disposal, which has contributed to my knowledge of the habitats of the different species of terrestrial chironomids. Other colleagues also collected valuable material. Prof. Dr. O.A. Sæther gave a number of improving suggestions. A. van Nieuwenhuijzen drew the many good figures and D. Middleton corrected the English text. I am also indebted to the Uyttenboogaart-Eliassen Stichting for providing financial support for publication.

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Received: 16 February 2007

Accepted: 8 August 2008