The karyotype, morphology and ecology of *Glyptotendipes aequalis* Kieffer (Diptera, Chironomidae)

Mauri Hirvenoja & Paraskeva Michailova

Hirvenoja, M. & Michailova, P. 1991: The karyotype, morphology and ecology of *Glyptotendipes aequalis* Kieffer (Diptera, Chironomidae). — Entomol. Fennica 2:87–96.

The karyotype, morphology of adult, pupae and larvae, and the ecology of *Glyptotendipes aequalis* Kieffer (1922) are described from material from Finland, and a neotype from the (probably) original German material is designated. 2n = 8. Ist, IInd and IIIrd chromosomes are metacentric, IVth acrocentric. The IVth chromosome has a nucleolus and a Balbiani ring. *G. aequalis* is karyologically closely related to *G. caulicola*, differing by a simple inversion step.

Mauri Hirvenoja, Sotilaskorventie 13, 01730 Vantaa, Finland Paraskeva Michailova, Bulgarian Academy of Sciences, Boul. Rouski 1, 1000 Sofia, Bulgaria

1. Introduction

The male of *Glyptotendipes aequalis* Kieffer (1922:79) was originally described from material collected in Westfalen, Germany by A. Thienemann. Up to now, however, no original adult specimens have been found in any collection.

Lenz (1954–1962: 176) gives a short description of the pupa of *G. aequalis* as a species of the *caulicola* group in the subgenus *Phytochironomus* Kieffer:

"Analkamm mit nur 2–3 Zähnen, die bei der einzigen vorhandenen Exuvie sogar auf der einen Seite fehlen. Auf der Analflosse oral-median ein Paar helle, starre, mittelgroße Borsten."

According to the same paper, *G. aequalis* was at that time known only from Westfalen (Münster), Germany. Thus the cast pupal skin which Lenz has seen may be a part of the original material. Dr. F. Reiss (Zoologische Staatssammlung, Munich, Germany) in 1988 found and prepared one pupal skin from Thienemann's collection. Although information about the sampling

locality is missing (there being no data label), this is very probably the specimen mentioned by Lenz, because only one side is provided with an anal comb.

The origin of the specimen is, however, not completely certain and thus we cannot know if it is the cast skin of the lost holotype. Thus, (ICZN, Opinion 1147, 1980) it cannot be considered as a lectotype, but the probability that this specimen belongs to the original material is very great. Because it may thus provide the best existing evidence of the characters of the original *G. aequalis*, this pupal skin (cf. below p. 93) has here been designated as the neotype of the species.

According to "Limnofauna Europaea" (Fittkau & Reiss 1978) *G. aequalis* is still known from southern Germany only. By contrast, *Glyptotendipes foliicola* Kieffer according to the same paper is widely distributed and has perhaps in some cases been confused with *G. aequalis*. The correct identification of *G. foliicola* seems so far to be impossible and this has been considered as a nomen dubium (Hirvenoja 1990). A species determined as *G. aequalis* by the aid of the neotype and the literature is found in two different parts of Finland. An attempt to give more definitive descriptions of adults and immature stages follows in the present paper.

In addition the present work deals with the first description of the karyotype under the name G. *aequalis*. We demonstrate the photomap of the polytene chromosomes, as well as present information about the chromosome polymorphism in one Finnish population. The karyotype relationships with other species of the genus *Glyptotendipes* Kieffer are also investigated.

2. Morphology of adults and immature stages

2.1. Material and methods

A great number of adults were reared from larvae from a garden pond in Vantaa near Helsinki (May 1988). Measurements were made on nonmacerated material mounted in Euparal. Morphologically identical specimens had been reared earlier from a forest clay pond on the Hirvenoja farm, Riihimäki (May to August 1970), also in southern Finland. Some of the latter were also included in the measurements in addition to the neotype (Fig. 1G) mentioned above.

The morphological terminology as used here is in regard to some details more classical than, for instance, in "Chironomids of the Holarctic region" (Wiederholm ed. 1983, 1986, 1989). The nomenclature of the male genitalia used here is illustrated, for instance, in Reiss & Fittkau (1971: fig. 1) and in Pinder (1978:13). The classical nomenclature of the genitalia has been used because (according to the opinion of the author MH, cf. Hirvenoja 1973) most appendages of the gonocoxite are of phallic origin, arising during the evolution of the chironomid midges and having no true homological connections with Hymenoptera. In the nomenclature of the larval head Gouin's (1959, 1968) school of thought is accepted; defining the ventral wall of the head capsule of the larva as a submentum in recent papers represents an oversimplified morphological concept.

2.2. Male (N=6, Fig. 1A)

A quite dark species with more or less pale scutellum and more or less pale parts on legs as follows: bases of femora, middle of mid and hind tibia; the tarsi darken towards the last joints in the mid and hind legs.

Antennal ratio 3.0–4.2. Frontal tubercles about 10–15 μ m. Palp segments (2–5): 90–115, 205–275, 205–230 and 240–275 μ m. Clypeus with < 35 and postocular region with < 24 setae. Number of acrostichals < 18; dorsocentrals (16–34) in 2–3 rows, sometimes also mostly irregular standing scutellars (25–29) in two rows. Tracheal scar of pupal respiratory organ about 3/5 length of postpronotum. Wings 3.0–3.2 μ m. Costa not extended over R₄₊₅; setae on R₁ and on the distal part of R₄₊₅; squama with 16–18 setae.

About 15-mm-long sensilla chaetica near distal end of basitarsus of mid leg 6–11 in number. Fore leg: leg ratio 1.23–1.35; beard ratio 2.5–3.2. Mid leg: leg ratio 0.48–0.50; beard ratio 2.8–3.0. Hind leg: leg ratio 0.57–0.62; beard ratio 3.8–4.5. Legs in μ m:

	Fore leg	Mid leg	Hind leg
Femur	1200-1400	1315-1570	1430-1630
Tibia	1115-1285	1230-1455	1515-1715
Tarsus ₁	1430–1640	585-745	855-1055
Tarsus ₂	785-855	415-455	540-630
Tarsus ₃	630-700	300-370	385-485
Tarsus ₄	1500-515	1215-255	255-285
Tarsus ₅	230-240	155-185	145-185

Hypopygium (Fig. 1A) resembles that of the common type in the genus *Glyptotendipes*. Processus analis dark, apically rounded and broadest near the apex. Appendage 1 dark, quite straight, proximally haired, apically with a strong hook. Appendage 2 relatively broad compared to its length. About 10 setae on the pale spot of tergite IX, not differing from the nearest setae in surroundings of the pale area.

2.3. Female (*N*=6, Fig. 1B–C)

Colouration as well as type of chaetotaxy as in the male, but the number of setae a little higher. Antennae with 5 flagellomeres or occasionally with 6 if first is more or less clearly divided.



Fig. 1. *Glyptotendipes aequalis* Kieffer. — Adults. A: Male hypopygium; B: Genitalia of female; C: Genitalia and shape of cercus seen more laterally. — Pupa. D: Variation of anal combs; E: Basal ring of the respiratory organ; F: Variation of cephalic tubercles in the slides; G: Variation of the racket-shaped plates of tergite (II) III—VI (first row left drawn from the neotype). — Original.

Frontal tubercles 6–10 μ m. Palp segments 2–5: 70–80, 170–210, 185–220 and 220–345 μ m. Wings 3.1–3.8 μ m. Sensilla chaetica on middle and/or more on the apical part of the basitarsus of mid leg (39–55) and on middle of basitarsus of hind leg (39–54 in number). Fore leg: leg ratio 1.37–1.41; beard ratio 2.0–2.3. Mid leg: leg ratio 0.47–0.48; beard ratio 2.5–3.1. Hind leg: leg ratio 0.56–0.57; beard ratio 3.8–4.0. Legs in μ m:

	Fore leg	Mid leg	Hind leg
Femur	1170-1285	1300-1430	1315-1430
Tibia	1085-1170	1270-1355	1485-1570
Tarsus ₁	1530-1600	600-655	840-885
Tarsus ₂	770-830	385-415	515-555
Tarsus ₃	630-655	315-315	415-415
Tarsus ₄	500-515	200-230	240-255
Tarsus ₅	240-245	155-155	145-170

Genitalia as in Fig. 1; spermathecae round or somewhat oval, 140–185 μ m long. Gonocoxite IX with 3 setae; segment X with 7–11 setae on each side.

2.4. Pupa (N=12, Fig. 1E–G)

Length of the cast skins 8-10 µm. Frontal apotome with about 85-115 long cephalic tubercles, the preapical seta present. Thorax dorsomedially granulated, more orally smooth but darkened with reticulate pale lines. Small, furrowed, sometimes not very clearly visible anterolateral tubercles on the first abdominal segment present; small PB and 76-88 hooklets present on segment II; ordinary pedes spurii A on segment IV, the whole conjunctiva on segment V with chagrin, segment VI with few small spines on the hind corner. Structures of the abdominal segments much as in fig. 10.26 by Pinder & Reiss (1986). Racket-shaped plates on tergites III–VI, in every fourth skin at the same place a pigmented spot found on tergite II. A plate (up to $350 \,\mu\text{m}$) covers about 1/4 - 1/3 of the total length of the tergites; there is great individual variability in the size of the plates, but the first (on segment III) is a little smaller than the others, which are all quite similar (Fig. 1D). Anal comb consists of some more or less loose curved spines. The anal segment is bordered with (one side) 64-90 often uniserial filaments but sometimes these

are situated in 2–3 rows, especially on the anal part of the lobes; dorsal pair of setae on the anal segment often present but found in variable places.

2.5. Larva (N=9, Fig. 2)

Length < 9 mm. Anterior parapods with simple, nearly invisible plumose or distictly serrate claws. Behind the parapods, near the claws an unpaired, triangular group of very small clawlike chaetae, about 40-50 in number (in some species of Glyptotendipes this group has been divided into two groups!). One pair about 150-200 µm long and 50-70 µm thick ventral tubules present on segment IX; the anal tubules about 200-250 (the upper pair) up to 300 µm long. Head brownish, about 600-630 µm long, 460-470 µm broad. Antennal sockets and boundaries of frontal apotome a little darkened, forming a V-shaped figure, seen in the unprepared specimens but may partly disappear in slides. Borders of foramen occipitale dark, a quite large triangulum brown beginning at the tentorial pits; ventral part of the postgenal bridge a little darkened between the foramen occipitale and hind margin of the postmentum; also a narrow unsclerotized, pale sulcus of this length ventromedially in the area of fusion of both sides. Dorsal sclerites of the head (Fig. 2K) agree with fig. 10.30.E in Pinder & Reiss (1983:381).

The setae SI about 40 μ m long, proximally with one side feathered but apically with strong, somewhat variable serration on both sides; setae SII simple. Great lateral chaetae feathered, few simple spinulae also present; between these groups a group of very small, hardly visible chaetae (in some other species of *Glyptotendipes* clearly to be found). Pecten epipharyngis with 19–23 teeth, chaetulae lateralis strongly serrated, chaetulae basales (2) rudimentary.

Premandibles with 2 apical teeth, inner tooth more or less sharply pointed, a little smaller than outer. In mandibles with pale dorsal tooth, other 4 teeth darkened. Apex of maxillary sclerite clearly dentate with 5–7 rounded denticles; outer side of the galeolacinia (region of palpifer; Imms 1957:24) with lengthened chaetae. Prementum conical; lateral chaetulae quite narrow, not



Fig. 2. *Glyptotendipes aequalis* Kieffer. — Larva. A: Head in ventral view; B: Front border of the maxillary sclerite; C: Eye spots; D: Seta SI; E: Pecten epipharyngis; F: Apex of premandible; G: Front border of paralabial plate; H: Claws of parapods; I: Maxille antiaxially; J: Prementum; K: Head in dorsal view; L: Last abdominal segments. — Original.

markedly differentiated, abundantly present and those standing most laterally seem to bend inwards in direct ventral view. Middle tooth of the chin or hypochilum (Gouin 1959) with small lateral denticles; from the six other teeth the outermost 3rd clearly smallest. Paralabials totally striated, front border smooth but figured (depends somewhat on preparation technique) as in Fig. 2G. Antennae about 180 µm long. RO in first third of basal segment. Proportions of lengths of the antennal segments in fourth instar (6 larvae):

100:30:24:20:6	100:35:28:23:7
100:32:29:24:6	100:37:27:23:7
100:32:21:18:6	100:38:27:19:5

(One smaller, obviously third instar larva: 100:45:24:24:10.)

3. Karyological studies

3.1. Material and methods

Nine larvae from the garden pond in Vantaa were fixed in 3 : 1 ethanol : acetic acid. The analysis was performed on squashed preparations of salivary gland polytene chromosomes made by the standard aceto-orcein technique. The chromosome arms of *G. aequalis* have been called A to G on the basis of their homology with some sections of *G. glaucus* (Meigen) chromosomes. The latter species has been suggested as a standard (Michailova 1989). *G. aequalis* polytene chromosomes have distinctive banding patterns, making them advantageous for karyological analysis. Every chromosome is divided conditionally into sections.



Fig. 3. Ist, IInd, IIIrd and IVth chromosomes of Glyptotendipes aequalis Kieffer. Original.

3.2. Karyotype.

2 n = 8. Ist (AB), IInd (CD), and IIIrd (EF) chromosomes are metacentric, IVth (G) acrocentric. The centromere region is the darkest band in every chromosome. *C. aequalis* has no cytologically obvious sex-differential segment or chromosomes.

Ist (AB) chromosome (Fig. 3). This chromosome is divided into 15 sections. The centromere region is in section 5/6. Arm A: all investigated individuals exhibit heterozygous inversion in this arm. Arm B: in section 5/6 - 6/7 is a constriction. Such a constriction has been observed in the Ist chromosome of *G. caulicola* Kieffer, *G. glaucus* Kieffer, *G. paripes* Edwards, *G. man*- *cunianus* Edwards and *G. gripekoveni* Kieffer (Michailova 1979). The double bands in section 12/13 - 13/14 are typical to this chromosome. Section 9/10 - 12 is similar to region 7/8 - 9/10 in *G. caulicola* (Michailova 1979:29). Near the telomere 13/4 - 14/15) there is a pale section which looks like a constriction. Such a section exists in *G. caulicola*, *G. glaucus*, *G. gripekoveni* and *G. paripes*, but has a different localization in this chromosome.

IInd (CD) chromosome (Fig. 3). This chromosome contains 18 sections. The centromere region is localized in section 9/10. Arm C: at the telomere there is a group of dark bands. This region is very often active. This arm is very similar in gross morphology to the arm C in G.

1

92



Fig. 4. *Glyptotendipes aequalis* Kieffer. — a: Heterozygous inversions in IInd chromosome. b: IVth chromosome, different functional activity. c: Telomere heterochromatin "Dark knob" in IVth chromosome. Original.

caulicola. Section 3/4 - 6/7 of *G. aequalis* differs from section 1/1 - 3/4 of *G. caulicola* by an homozygous inversion. Arm D has a constriction in section 11/12, and distinct bands in section 12/ 13 and 13/14. The band sequence in section 14/ 15 - 16 is inverted in comparison with the band pattern in section 6/7 - 8 of *G. caulicola*. Section 14/15 - 15/16 is similar to section 5/6 - 6/7 of *G. gripekoveni* and section 8-9 of *G. glaucus* (Michailova 1979). Heterozygous inversions were observed in both arms in telomere regions in 3.22 % (Fig. 4a). IIIrd (EF) chromosome (Fig. 3). This is divided into 8 sections. The centromere region is localized in section 3/4. Arm E: section 1/1 - 1/2 is similar to section 1 - 2/3 of *G. gripekoveni*. Section 1/1 - 2/3 is similar to section 1 - 2/3 of *G. caulicola*. The banding pattern in section 3/4 is characteristic in this arm of the chromosome. Arm F: Sequences of bands in sections 5 - 6/7 of *G. aequalis* differs by homozygous inversion from sequence of bands 4/5 - 5/6 of *G. gripekoveni*.

IVth (G) chromosome (Fig. 3). This is the shortest of the complement, and is divided into 6 sections. There is a Balbiani ring and a nucleolus. The last one is in the telomere region. Very often in connection with the nucleolus there is a "Dark knob" (Fig. 4c). The band pattern in section 6/7 is similar to section 4/5 of *G. caulicola*. Section 1/2 - 2/3 is a functionally active heterozygous puff or different thickness of a dark band (Fig. 4b).

4. Discussion.

4.2. Morphology

The adults were originally determined as *G. aequalis* with the aid of the key in "Lindner" (Goetghebuer 1937–1954). The comparison between the neotype (pupal skin) and the cast skins from Finland shows that some specimens of the latter material are quite similar. Most of the skins of Finnish origin, however, have stronger racket-shaped dorsal plates on tergites III–VI, but for the present there do not exist sufficient taxonomical differences to make it possible to reject the determination of the populations from Finland as *G. aequalis*.

Kieffer (1922:79) describes the male foreleg of *G. aequalis* as follows: "..., extremite du metatarse et 2e article briévement barbus, poils trois fois aussi longs que la grosseur des articles,..."

The latter agrees well with the specimens described above as *G. aequalis*. The genitalia of many species of *Glyptotendipes* are very similar. The structure of the male foreleg, the colouration of the adult, and the characters of the pupa considered together make the correct identification of the species possible.

Pinder & Reiss (1983, 1986) divide the known pupae and larvae of the genus *Glyptotendipes* into three groups: A, B and C, a division which in some details differs from the older grouping of Lenz (1954–1962). The new key characters bring, however, new problems:

The pupa of *G. aequalis* has an anterolateral tubercle present on the sides of the first abdominal segment as in species of the species group A, but it is very small and moreover the features otherwise match group B better. The dark "mark" on the tergite II in some individuals from Finland gives, however, an intermediate impression between the groups A and B.

Key characters of group A also include lateral denticles in the median tooth of the hypochilum of the larva of *G. aequalis*, although in many respects the larva agrees with those of group B. Furthermore in smaller details, for instance the front border of the paralabials and the apex of the maxillary sclerite, it agrees more with *G. barbipes* sensu Pankratova (1983) than with *G. caulicola* figured in the same paper. The presence of the ventral tubuli should likewise not be included in the characteristics of *Phytochironomus* sensu Lenz (1954–1962), to which for instance *G. aequalis* and *G. caulicola* were referred by this author.

The karyological comparison (see above) shows *G. aequalis* and *G. caulicola* to be closely related species. Morphologically the relations between these species are not so clear, but there is no true disagreement: if the features discussed above, distinguishing *G. aequalis* from *C. caulicola*, are not interpreted as synapomorphies, they can be discarded in the definition of species group B. It seems therefore better to change the key characters for groups A and B in Pinder & Reiss (1983, 1986), rather than to create a new group for *G. aequalis*.

4.2. Karyotype

Comparison of the karyotypic features of *G. glaucus* with those of the other *Glyptotendipes* studied demonstrates similarities with respect to the diploid chromosome set (7 species of this genus have been cytotaxonomically analysed; see Martin & Porter 1973, Michailova 1979, 1987,

1989, Miseiko et al. 1971, Miseiko & Minsarinova 1974; Belyanina 1982). In all species 2n = 8; Ist, IInd and IIIrd chromosomes are metacentric, IVth acrocentric. Comparing the banding pattern of the salivary gland chromosomes of G. aequalis with other species of the genus Glyptotendipes indicates that G. aequalis is closely related to G. caulicola, G. glaucus, G. paripes and G. gripekoveni. The band patterns of all chromosomes of G. aequalis differ from those of G. salinus and G. barbipes. This supports the idea (Michailova 1979) that G. glaucus, G. gripekoveni, G. paripes, G. caulicola and G. aequalis have evolved from one ancestor in one direction while G. barbipes Staeger and G. salinus Michailova have evolved in another direction.

G. gripekoveni, *G. caulicola*, *G. glaucus* and *G. aequalis* showed remarkable stability in some chromosome sections, viz. Ist chromosome, section 13/14 - 14 - 15 and 5/6 - 6/7; IInd chromosome, section 14/15 - 15/16; IIIrd chromosome, section 1 - 1/2. These patterns could be considered as "basic patterns" in the sense of Wülker (1980). Perhaps these common patterns existed in a hypothetical stem species.

G. caulicola and *G. aequalis* are very similar and closely related, certain sequences of their chromosomes being identical. They differ only by a simple inversion step (IInd chromosome, sections 3/4 - 6/7, 14/15 - 16), thus indicating derivation from a common ancestor. They are not far removed from the ancestral species and have a slow rate of divergency.

5. Ecological observations

Kieffer (1922:79), as well as Lenz (1954–1962: 176), mentions that the original specimens were (probably semi-) mining *Alisma plantago* L. According to Thienemann (1954:95, sub *Phytochironomus*) this species was reared in June 1914 from the stem of *Alisma* in Westfalen.

The specimens described here from Vantaa, Finland, were found in an artificial (about 15 m^2) water reservoir in the garden while emptying the former on 15 May 1988. The larvae had overwintered among the leaves of *Populus tremula* L. and *Betula* spp. and in mud in a small amount of completely frozen water on the concrete bottom. The water was somewhat polluted by the decomposing leaves of the trees and especially by the excrement of the ducks that had been living on it during the previous summer. The water was strongly coloured by algae, and the populations of the Cladocera species were dense. The electrical conductivity of the water (on 15 May 1988) was 13.7 mS/m (γ 25), alkalinity 0.50 and the colour about 80 mg Pt/l.

Using the saprobity tables of Sládecek (1973) and the information of Thienemann & Zavrel (1916) it is possible to estimate the (limno)-saprobity index for this biotope. This is at least 2.5 on the basis of the few known indices for single species. This means (spring 1988) at least conditions of beta-mesosaprobity. In autumn 1989, under the ice, however, a BOD₅ value of 9.3 mg O₂/l and an oxygen concentration of 0.3 mg O₂/l were measured in the same pond; this reflects (cf. Sládecek 1973:67) alfa-mesosaprobic conditions, at least at that time (1989). *G. aequalis* was the dominating overwintered species. The others coexisting with it on 15.5.1988 were the following:

Lumbriculus variegatus (Müller) Daphnia pulex de Geer Simocephalus vetulus O.F.Müller Diacyclops bicuspidatus Claus Chaoborus crystallinus (de Geer) Psectrotanypus varius (Fabricius) Psectrocladius octomaculatus Wülker Chironomus riparius Meigen C. ?piger Strenzke Paratanytarsus austriacus Kieffer

G. aequalis was reared in 1970 also from the type locality of *Chironomus riihimakiensis* Wülker. This biotope (at present dried up) was an old, permanent clay pond (2×3 m, depth <0.5 m) at the border of a forest on the Hirvenoja farm in Riihimäki, Finland; conductivity about 8 mS/ m, pH about 6, and colour >80 mg Pt/l. Algal blooms were never observed but *Callitriche* sp. was present in abundance. The bottom consisted of clay ooze and leaves of *Alnus incana* (L.) Willd. The electrical conductivity of the lastmentioned pond represents values about the same as the 7.9 mS/m (γ 25) [= 69 mS/cm (κ_{18})] mean, according to Laaksonen (1970), of natural waters in Finland. *G. aequalis* was the most abundant

overwintered chironomid species in this pond.

As is seen from the values for conductivity, conditions in the forest pond (Riihimäki) were not as eutrophicated as in the garden pond in Vantaa, as is clear also from the species combination. The latter might give a slightly lower saprobity index than that of the pond in Vantaa. The water most probably here too completely freezes in winter. There has been, however, more opportunity for burrowing in the ooze. At least the following species coexisted with *G. aequalis* in Riihimäki (the material preserved in 1970 from the cultures):

Chaoborus crystallinus (de Geer) Psectrotanypus varius (Fabricius) Zavrelimyia hirtimana (Kieffer) Chironomus pseudothummi Strenzke. C. riihimakiensis Wülker Chironomus sp. (Q) Einfeldia cf. pectoralis Kieffer Endochironomus lepidus (Meigen) Pentapedilum tritum (Walker) P. uncinatum Goetghebuer

In both ponds species such as *Cloeon dipterum* (L.) (Ephemeroptera), *Culex pipiens* L. (Culicidae), pond-scaters, water boatmen and water beetles were included in the summer fauna.

G. aequalis has also been found in another very small but permanent forest pond in Riihimäki in 1989–90 together with a fauna similar to that listed above. This indicates a preference for small water habitats, especially as the species has not been found in lakes in Finland.

Acknowledgements: We thank Dr. F. Reiss (Munich) for sending information and material for solving the question of the type specimen.

References

- Belyanina, S. I. (Белянина, С. И.) 1982: The karyotypic variations of Glyptotendipes barbipes Staeg. (Chironomidae, Diptera) examined from various localities. (In Russian with English summary) Tsitologiya 24:78–85.
- Edwards, F. 1929: British non-biting midges (Diptera, Chironomidae). — Trans. R. Entomol. Soc. London 77:279–430.

- Fittkau, E. J. & Reiss, F. 1978: Chironomidae. In: Illies, J. (ed.), Limnofauna Europaea. 2 ed.: 404–420.
- Goetghebuer, M. 1937–1954: Tendipedidae (Chironomidae). b) Subfamilie Tendipedinae (Chironominae).A. Die Imagines. — In: Lindner, E. (ed.): Die Fliegen der palarktischen Region 13c: 1–138.
- Gouin, F. 1959: Morphology of the larval head of some chironomidae (Diptera, Nematocera). — Smithsonian Misc. Coll. 137: 175–201.
- 1968: Morphologie, Histologie und Entwicklungsgeschichte der Insekten und der Myriapoden. — Fortschr. Zool. 19:194–282.
- Hirvenoja, M. 1973: Revision der Gattung Cricotopus van der Wulp und ihrer Verwandten (Diptera, Chironomidae). — Ann. Zool. Fennici 10:1–363.
- 1990: What is Glyptotendipes foliicola Kieffer (Diptera, Chironomidae)? — Nachr.Bl. Bayer. Entomol. 39:29– 30.
- Imms, A. D. 1957: A general textbook of entomology, including the anatomy, physiology, development and classification of insects. 9. ed. — London. 886 pp.
- Kieffer, J. J. 1922: Chironomides nouveaux ou peu connus de la région palearctique. — Ann. Soc. Sci. Bruxelles 42(1):71–128.
- Laaksonen, R. 1970: Water quality in the water systems. A study based on observations carried out by the water pollution control authority 1962–1968. (In Finnish with English abstract) Maa ja vesiteknillisiä tutkimuksia 17:1–132.
- Lenz, F. 1954–1962: Tendipedidae (Chironomidae). b) Subfamilie Tendipedinae (Chironominae). B. Die Metamorphose der Tendipedinae. — In: Lindner, E. (ed.): Die Fliegen der palarktischen Region 13c: 139– 260.
- Martin, J. & Porter, D. 1973: The salivary gland chromosomes of Glyptotendipes barbipes Staeg. (Diptera, Chironomidae) description of inversions and comparison of Nearctic and Palaearctic karyotypes. — Stud. Naatur. Sci. 6:1–25.
- Michailova, P. 1979: Comparative karyological analysis of the species of the genus Glyptotendipes Kieff. (Diptera, Chironomidae). — Caryologia 32:23–44.
- 1987: Comparative karyological studies of three species of the genus Glyptotendipes Kieff. (Diptera, Chironomidae) from Hungary and Bulgaria and Glyptotendipes salinus sp.n. from Bulgaria. — Folia Biol. 35:43–56.
- 1989: The polytene chromosomes and their significance for systematics and phylogeny of fam. Chironomidae, Diptera. — Acta Zool. Fennica 186:1–107.
- Мізеіко, G. N., Мілsarinova, B. Kh. & Kiknadze, I. I. (Мисейко, Г. Н., Минсаринова, Б. X. & Кикналзе,

И.И.) 1971: The karyotype structure in natural populations of Glyptotendipes barbipes (Diptera, Chironomidae). (In Russian with English summary) — Tsitologiya 13: 1501–1505.

- Miseiko, G. N. & Minsarinova, B. Kh. (Мисейко, Γ. Η. & Минсаринова, Б. Х)1974: The karyological structure of natural populations of Glyptotendipes glaucus and G. paripes (Chironomidae). (In Russian with English summary) — Tsitologiya 16:893–897.
- ICZN, Opinion 1147, 1980: Status for the purposes of type fixations of the remains of Chironomid larvae (Insecta, Diptera) provided by Thienemann to Kieffer for the description of new species based on the adults reared from those larvae. — Bull. Zool. Nomencl. 37(1):11– 26.
- Pankratova, V. Ya. (Панкратова, В. Я.) 1983: [Larvae and pupae of midges of the subfamily Chironominae of the USSR fauna (Diptera, Chironomidae = Tendipedidae)]. (In Russian) — Opred. Faune SSSR 134:1–295.
- Pinder, L. C. V. & Reiss, F. 1983: The larvae of Chironominae (Diptera: Chironomidae) of the Holarctic region. — Keys and diagnoses. — Entomol. Scand., Suppl. 19:293–435.
- 1986: The pupae of Chironominae (Diptera: Chironomidae) of the Holarctic region. Keys and diagnoses. Entomol. Scand., Suppl. 28:299–456.
- Reiss, F. & Fittkau, E. J. 1971: Taxonomie und Ökologie europäisch verbreiteter Tanytarsus-Arten (Chironomidae, Diptera). — Arch. Hydrobiol., Suppl. 40:75– 200.
- Sládeček, V. 1973: System of water quality from the biological point of view. — Ergebn. Limnol. 7:1–208.
- Thienemann, A. 1954: Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. — Binnengewässer 20:1–834.
- Thienemann, A. & Zavrel, J. 1916: Die Metamorphose der Tanypinen. — Arch. Hydrobiol., Suppl. 2: 566–654.
- Wiederholm, T. (ed.) 1983: Chironomidae of the holarctic region. Keys and diagnoses. Part 1. — Larvae. — Entomol. Scand., Suppl. 19:1–457.
- 1986: Chironomidae of the holarctic region. Keys and diagnoses. Part 2. — Pupae. — Entomol. Scand., Suppl. 28:1–482.
- 1989: Chironomidae of the holarctic region. Keys and diagnoses. Part 3 — Adult males. — Entomol. Scand., Suppl. 34:1–532.
- Wülker, W. 1980: Basic patterns in chromosome evolution in the genus Chironomus (Diptera). — Zeitschr. Zool. Syst. Evolutionforsch. 18:112–113.

Received 12.I.1990, revised 27.II.1991