

Taylor, P.D., Turnbull, D.A. and Smith, S.M. 1992.
Mating and oviposition behavior of *Tabanus gibensis* (Diptera: Tabanidae).
Journal of African Zoology, **106**: 303–311.

Philip D. Taylor, Dept. of Biology, Carleton University, Ottawa, ON Canada K1S 5B6. David A. Turnbull and Stephen M. Smith (to whom correspondence should be addressed), Dept. of Biology, University of Waterloo, Waterloo, ON Canada N2L 3G1.

Abstract Adult males and females of *Tabanus gibensis* were collected on a bridge over the Gibe River in Ethiopia during November 1986. Males perched on top of the bridge, and pursued females in attempts to copulate with them; 3 copulations were observed. Females perched on the side and the underside of the bridge and oviposited communally in large aggregations on the underside of the bridge. Half the females collected on the bridge were gravid, and were probably there to oviposit; 2 were uninseminated and were probably there to be mated. Both sexes had only small amounts of carbohydrate in their esophageal diverticula.

Introduction

Several recent studies of the biology of Tabanidae have focused on aspects of the life history other than host-seeking and blood-feeding by females, especially the biology and behavior of males (e.g. Magnarelli 1985; Taylor and Smith 1989, 1990). In Africa, little work has been conducted on these other aspects of the biology of any members of the family since Haddow and others published on their work at the Mpanga and Zika forests in Uganda (Haddow *et al.* 1961). Here we present the results of some investigations of the mating and oviposition behavior of a recently described species of Tabanidae, *Tabanus gibensis*, discovered in Ethiopia in 1986 (Turnbull *et al.* 1992).

The mating behaviors of only a few African Tabanidae have been studied (Corbet and Haddow 1962), and we know little about how species in the family respond to the seasonal, tropical environment of East Africa. On a visit to a field station of the International Livestock Centre for Africa (ILCA) on the Gibe River in Ethiopia during October and November 1986, we discovered male and female *Tabanus gibensis* aggregating on a bridge over the river. We examined aspects of the mating behavior and the physiological states of individuals at the mating arena, and the unusual oviposition behavior of the species. Although our investigations and results were constrained by time, they contribute to a broader understanding of the mating and oviposition behavior of Tabanidae and offer significant new observations of the biology of the Tabanidae of a biologically poorly known part of Africa.

Materials and Methods

Description of the study site

The study site was a bridge crossing the Gibe River (Universal Transverse Mercator: 37P CV 20 31; 8°24' N; 37°24' E; elevation approx. 1400 m), on the border of Shewa and Kefa Provinces, Ethiopia. The bridge was concrete, *ca.* 100 m long and *ca.* 6 m above water. The banks of the river were forested for distances of *ca.* 10–100 m inland and at least 1–2 km up and downstream from the bridge; the dominant vegetation in the surrounding valley was relatively undisturbed savanna. Becker (1988) gives a general account of riverine vegetation and topography in this part of Ethiopia.

Few humans or domestic livestock inhabited the immediate area. Black-and-white Abyssinian colobus (*Colobus abyssinicus* (Primates: Colobidae)), baboons (*Papio* sp. (Primates: Cercopithecidae)) and hippopotamus (*Hippopotamus amphibius* (Artiodactyla: Hippotamidae)) were locally abundant, and fresh tracks of more than one species of antelope were observed on the roads most mornings. Any of these mammals may have been hosts for female *Ta. gibensis*.

We worked at the site between 10 October and 16 November 1986. Seasonal rains ended in mid-September, and, consequently, the Gibe River was fast-flowing, turbid, and deep. The level of the river dropped rapidly after the rains ended; by mid-November, the level was *ca.* 1.5 m lower than in early October and there were large areas of exposed vegetation and rocks. After first discovering males on the bridge, we conducted general observations, noting behaviors of males and females; censuses and dissections were made later, on 6 days in mid-November.

Behavior

On 14 and 15 November 1986, we censused flies to determine patterns of activity. We traversed the length of the bridge every 15 or 30 min and counted the number of individuals of each sex alighted on the top edge and on one side and abutments. (Flies were present on the south side of the bridge only, the side that was insolated for most of the day.) At the end of each census period, the ambient temperature and relative humidity above the bridge were measured with a sling psychrometer and the percent cloud cover and wind direction were estimated. During the afternoon of 14 November, we discovered that females were ovipositing on the underside of the bridge, so on 15 November we periodically (at *ca.* 1-h intervals) counted the number of fresh egg masses along the bridge using a mirror on the end of a pole (fresh egg masses were white; they turned gray 1–2 h after being laid).

Physiological States

On 11–13 and 16 November we collected individuals of both sexes for dissection. Individuals were collected by quickly placing an insect net over them while they perched. Flies were then dissected. Dissections were done using watchmaker's forceps under stereoscopic microscopy at $\times 60$. Individuals were immersed in a physiological saline (Hagedorn *et al.* 1977) containing a drop of liquid detergent. The ventral surface of the abdomen was torn open near the thorax and then down the side. The ventral esophageal diverticulum (crop) was grasped at the point where it joins the esophagus, and pulled out intact. Its surface was dried by blotting lightly with bibulous paper. Crop-volume was estimated for both sexes and assigned to an open-ended series of ordinal categories as follows: 0 (nothing visible); 0–0.5 μl (some liquid); and further categories that increased from 0.5 μl by 1- μl increments. These visual rankings were tested periodically by measuring actual crop-volumes using microcapillary tubes. We then measured the refractive index of crop contents (a relative index of the amount of sugar present in the crop) using a hand-held temperature-compensated refractometer (Reichert model 10235). The amount of fat present was assessed qualitatively in 3 categories: none or little (at most, small quantities of translucent fat on the body wall); some (small quantities of fat on the body wall as well as covering the viscera); and much (substantial quantities of fat on the body wall and covering the viscera). For females, the ovarian state was ranked according to Detinova (1962), and the presence or absence of sperm in the spermathecae was noted. The number of ovarioles in one ovary of each of 20 females was counted.

The STATS and DATA procedures in SYSTAT (Wilkinson 1986) were used to compute means and variances. All means are reported ± 1 SE.

Results

Species identification

When we first examined material at the British Museum (Natural History), we suspected that male *Ta. gibensis* was the undescribed male of *Tabanus kingi* (Austen). Closer examination of the females we collected revealed that 2 similar species occurred at the study site during our investigations, viz. *Ta. kingi* and *Ta. gibensis*. Voucher specimens (40) of males aggregating on the bridge are all *Ta. gibensis*, but unfortunately we have no vouchers of ovipositing females. Vouchers of the 4 females we collected on the bridge (1 *in copula*) are all *Ta. gibensis*, and photographs of females ovipositing on the underside of the bridge show that they are *Ta. gibensis*. Thus we are confident that all observations and dissections reported here refer to *Ta. gibensis* in spite of the fact that we were unaware of the 2 species at the time. Turnbull *et al.* (1992) discuss the taxonomy of the new species and its relationship to *Ta. kingi*.

Environmental profile of the bridge

All observations in mid-November were conducted under similar environmental conditions. Air temperatures during the period of fly activity ranged from 17–33°C; relative humidity ranged from 19–54%. Until *ca.* 1100, a cool breeze flowed up from the river and (or) under the bridge and depressed air temperatures by as much as 2°C. Cloud cover increased from nil in the morning to *ca.* 40% by mid-afternoon (1400). A light breeze blew from SE to SW until *ca.* 1700.

Behavior

Males

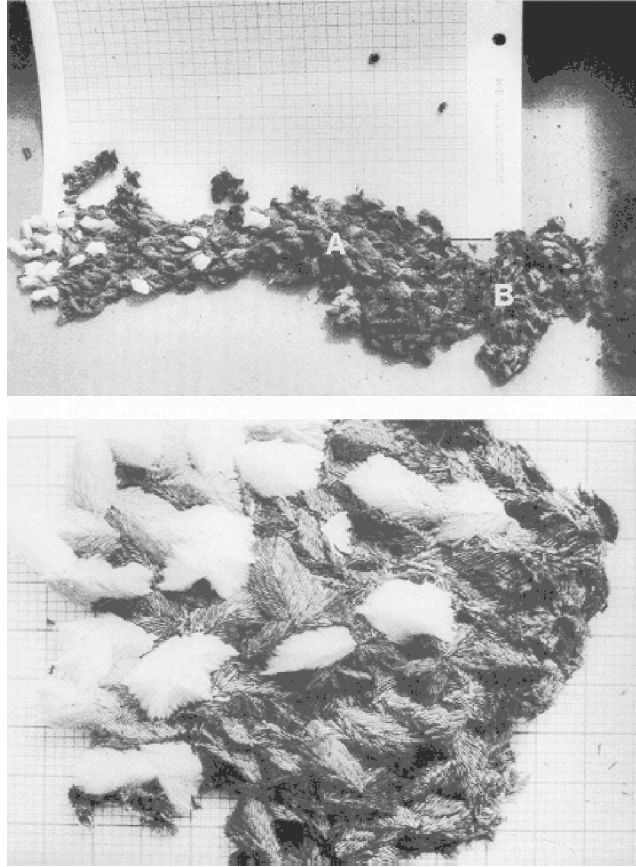
On 18 October, males were first observed perched on railings on top of the bridge. We collected several of these individuals but could not determine the species. Until 21 October, up to 10 males were seen for short periods, only in the mornings. The few males observed suggests that we were observing individuals near the beginning of the flight season. We conducted no further observations until 11 November, when we returned to the site. By that time, large numbers of males were present on the top of the bridge.

Males perched on the tops and sides of the railings, on the road surface and on the side of the bridge, always in full sun. They were attentive (*sensu* Taylor and Smith 1990) and pursued other insects that flew by. On 3 occasions we observed pursuit flights that resulted in copulations with females.

Females

In October, we observed few females on either the top or side of the bridge. By mid-November, however, many females could be seen, mainly on the side of the bridge. During observations on 14 November, we saw females walking and flying from the side to the underside of the bridge. Observations with a ×20 telescope from below the bridge at the edge of the river revealed large groups of females ovipositing communally at 4 sites along the underside of the bridge.

The acervuli¹ of egg masses were concentrated at the center of the bridge, over open water; each comprised up to several hundred individual egg masses (Figs. 1, 2). Egg-mass acervuli were situated only where the concrete had eroded slightly, leaving a rough surface. Several sites with corroded concrete had no egg masses and 6 or 7 sites had only acervuli from previous seasons. Females oviposited toward one side of the agglomeration so that it grew linearly and in one direction (Fig. 1). As many as 20 females could be seen together on a single acervulus, close together and frequently touching one another. Females frequently laid their eggs on top of other egg masses (Fig. 2).



Figs. 1–2. Egg masses of *Tabanus gibensis*. **1.** A portion of an acervulus of *Tabanus gibensis*, scraped from the underside of the bridge. Note the freshly laid (white), tanned (gray in color) (A) and previous-season's (B) egg masses. The smallest squares in the background graph paper are 1×1 mm. **2.** A portion of the egg-mass accumulation shown in Fig. 1, showing fresh, tanning, and tanned egg masses. The smallest squares in the background graph paper are 1×1 mm.

Activity profile

The results of the 15-November census are presented in Fig. 3. (Results from 14 November were similar.) Males were active during a short period in the morning (0900–1130) that coincided with the times that copulations were observed (1016, 1030, 1130). Females on the side of the bridge were active for a more prolonged period, 1030–1700, that began toward the end of the major period of male activity. The number of fresh egg masses (a cumulative index of daily oviposition activity) shows a slight phase shift from the numbers of females on the side of the bridge, evidence that females on the side of the bridge were preparing to oviposit. We also observed small numbers of females on the top of the bridge, primarily in the morning; these females were likely recently emerged and(or) mated, and not at the site to oviposit.

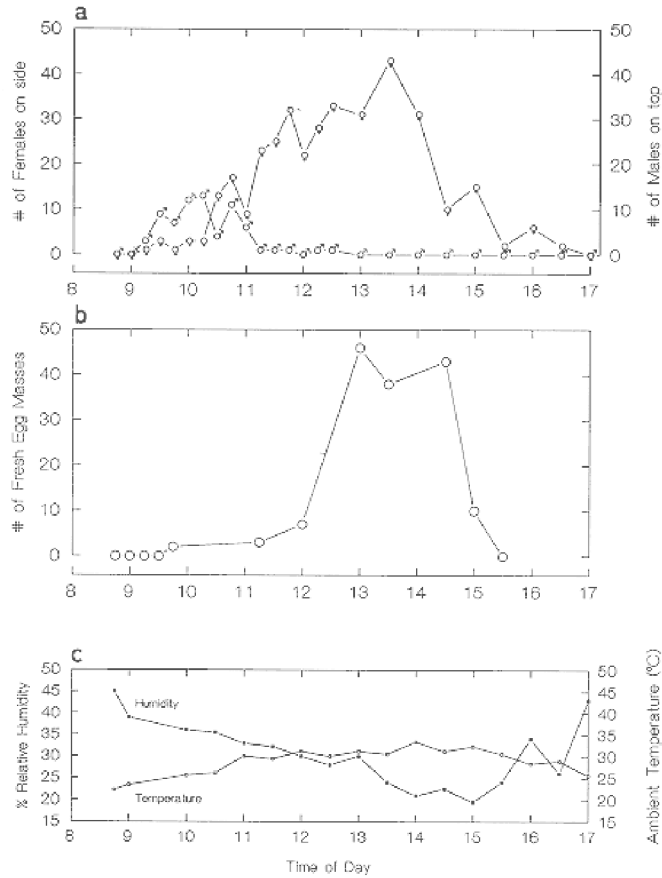


Fig. 3. Temporal-activity profiles of male and female *Tabanus gibensis*, oviposition rate and weather conditions on the bridge on 15 November 1986. **a.** Number of male *Tabanus gibensis* on the top of the bridge, and the number of female *Ta. gibensis* on one side of the bridge. **b.** Number of fresh (white) egg masses at 4 mass-oviposition sites on the underside of the bridge, as a function of the time of day. **c.** Weather conditions (temperature and relative humidity) on the bridge.

Physiological states

Crop contents and fat body

In both males and females, crop volumes were small. Only $4/59$ (7%) of females collected from the bridge had $>0.5 \mu\text{l}$ of liquid in the crop; $17/65$ (26%) of males collected from the bridge had $>0.5 \mu\text{l}$ of liquid in the crop. There were insufficient data to explore possible relationships between crop volumes and temporal variables. Refractive indices of the crop contents of 14 males ranged from 41–75% ($\bar{x} = 56 \pm 2.8\%$). Most individuals of both sexes had little or no fat body (females, $45/59=76\%$; males, $50/74=68\%$).

Female gonotrophic states

Of 58 females collected from the bridge, 33 (57%) were gravid, 8 (14%) had follicles in early ovarian stages (stage 1a, 1b) and 17 (29%) had follicles in stages 2a and 2b, the ovarian resting stages in other Tabanidae (Thomas 1972; Troubridge and Davies 1975). 2 females were uninseminated; 1 of these had ovarian follicles in stage 1, meconium in the gut and a large amount of fat; the other had stage-2a follicles, no meconium and a medium amount of fat. Both females were nulliparous and had empty crops. 13 of the 25 females with early-stage ovarian follicles were nulliparous; these females are likely to have emerged and(or) been inseminated recently.

The mean number of ovarioles in one ovary of each of 20 females was 373 ± 7.0 .

Discussion

Mating behavior

The co-occurrence of aggregating males, uninseminated females and pairs *in copula* at the aggregation site links the aggregation behavior with mating. These observations do not preclude the possibility that mating also occurred elsewhere. 2 fundamentally different strategies are used by aggregating male tabanids — hovering in place and perching; hovering is the better-known activity but perching strategies are known in *Chrysops* and some species of *Hybomitra* and *Tabanus* (Wilkerson *et al.* 1985). Male *Ta. gibensis* use the “perch-and-pursue” mating strategy, similar to that used by the temperate-zone tabanid, *Hybomitra illota* (Osten Sacken) (Taylor and Smith 1990); males perch on substrates within a “mating arena” and pursue passing females. Although there are similarities in behavior, the daily patterns of activity in the 2 species differ markedly. Male *Ta. gibensis* ceased aggregation at *ca.* 1130, whereas male *Hy. illota* remained active at the mating arena as late as 1700. Some male *Hy. illota* moved into shady parts of their mating arena at high ambient temperatures, possibly as a means of behavioral thermoregulation (Taylor and Smith 1990). There were no parts of the *Ta. gibensis* arena that contained shade, with the possible exception of the underside of the bridge. The lack of areas of shade, in an exposed, hot, mating arena, may make it difficult for the species to behaviorally thermoregulate, resulting in a truncated aggregation period. Females were active throughout the day, but primarily on the side and underside of the bridge, where the temperature was probably cooler.

We spent some time along the banks of the Gibe River up- and downstream from the bridge, searching for natural analogues of the *Ta. gibensis* mating arena. We propose 2 possibilities: rock outcrops and vegetation overhanging the river. We searched overhanging branches and leaves near the bridge site but no aggregations of males were found. Stream-side rock outcrops were absent from the immediate area and it was not possible to examine mid-stream exposed rocks. Nevertheless, we believe that the rock outcrops are the most likely natural analogue because of the similarity of that substrate to the bridge and because of our lack of success seeing males on overhanging vegetation.

Physiological states

In the adults of *Ta. gibensis* examined in this study, the crop reserves of carbohydrates were low, particularly in comparison with temperate-zone tabanids (Auroi and Briegel 1985; Taylor and Smith 1990). Not only do many species of temperate-zone tabanids store large quantities of carbohydrate in the crop, but such reserves, at least in males, must also be replenished frequently, probably on a daily basis (Schutz and Gaugler 1989; Taylor and Smith 1990). Given the limited time frame of the present study, it would be imprudent to speculate on a temperate/tropical divergence in energy strategies. However, if the carbohydrate reserves in *Ta. gibensis* are low, then the daily activity may be constrained.

Mass oviposition

Most species of Tabanidae lay their eggs, usually on vegetation, in discrete masses, each egg mass the output from a single female (Oldroyd 1964). Communal oviposition has been reported in only 2 other species of Tabanidae, viz. *Tabanus kingi* Austen (King 1910) and *Tabanus fairchildi* (Schwardt 1936). We have doubts about the association of King's observations with the species *Ta. kingi*. King found 3 rocks that had traces of egg-masses on them; on only one rock were there many eggs together in a group:

"Such rocks [for oviposition] occur only every here and there; in the mile or so of stream searched by the writer, only three rocks bearing traces of having been used by this Tabanid [*Ta. kingi*] for purposes of ovipositing were found. On one of them were the remains of several hundred egg-masses lining a small crack in the face of the rock from 2 ft. to 3½ ft. above the water level. As none of the fresh egg-masses found were situated more than 15 inches above the water level, these old masses had probably been deposited when that level was higher."

In total, King saw about 7 females ovipositing; we infer that these were individual females because he indicates their locations with X's in his Fig 5 (King 1910, p. 270). King states that the acervulus of several hundred egg masses that he observed was older, and had probably been laid at a different time of year when the water-level was higher. We suspect that these egg-masses were from a different species, possibly *Ta. gibensis*.

Schwardt (1936) described mass oviposition by *Ta. fairchildi* (as *Ta. vivax*) and included a picture of an egg-mass acervulus similar to that of *Ta. gibensis*. Both species are riverine, and it may be that communal oviposition in such species reflects a paucity of suitable egg-laying sites. Similar egg-laying behavior is known in the riverine species of the dipteran *Atherix* of the family Athericidae, known to be closely related to the Tabanidae (Wesenberg-Lund 1943; Nagatomi 1962).

Communal oviposition could be advantageous to *Ta. gibensis* in several ways. It might reduce desiccation of eggs or offer some protection from egg parasites or predators; both King (1910) and Schwardt (1936) reported large numbers of hymenopteran parasites around tabanid egg masses. Due to impairment of oxygen delivery to lower-level eggs, multi-layered egg masses could be expected to show high variance in embryonation rates, as has been observed in communally ovipositing blackflies (Imhof and Smith 1979); communal oviposition might therefore serve to ensure a staggered age structure of the larval stages. Alternatively, lower-level eggs might suffer high mortalities due to failure to embryonate or inability of first-instar larvae to escape (Imhof and Smith 1979); if this should occur in *Ta. gibensis*, mass oviposition may be an important density-dependent regulatory factor.

Acknowledgements

We are indebted to ILCA for the provision of accommodation in Addis Ababa and in the field; we especially appreciate the support of Ato Getechew Tikubet and the use of his field laboratory at Tolley. The friendship and willing help of the ILCA field staff at Tolley, particularly the field manager, Ato Chemellis, and our driver, Ato Mekonnen T/Selassie, were significant contributors to our work. Special thanks to Ato Meta for indispensable and continuous support during our sojourn in Ethiopia. We are grateful for the help of Gloria Smith in the field. John Chainey of the British Museum (Natural History) generously assisted us in identifying pinned material. This project was carried out while SMS was on secondment to the Department of Biology at Addis Ababa University, under the aegis of a joint University of Waterloo/University of Addis Ababa project, funded by the Canadian International Development Agency. Most of the equipment and other support for this project came from a grant to SMS from the Natural Sciences and Engineering Research Council of Canada. We are grateful to Drs Wayne Hawthorn, Kit Kovacs and Bill Taylor, for their critical comments on a draft of the manuscript.

References

- Auroi, C. and Briegel, H. 1985. Energy reserves and carbohydrate feeding in field-caught female horse flies (*Haematopota pluvialis*) (Diptera: Tabanidae). *Myia*, **3**: 403–414.
- Becker, C.D. 1988. Patterns in bird populations along the Omo River in Ethiopia. *Afr. J. Ecol.*, **26**: 1–10.
- Corbet, P.S. and Haddow, A.J. 1962. Diptera swarming high above the forest canopy in Uganda, with special reference to Tabanidae. *Trans. R. Entomol. Soc. London*, **114**: 267–284.
- Detinova, T.S. 1962. Age-grouping methods in Diptera of medical importance. With special reference to some vectors of malaria. World Health Organization, Geneva.
- Haddow, A.J., Corbet, P.S. and Gillett, J.D. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. *Trans. R. Entomol. Soc. London*, **113**: 249–368.
- Hagedorn, H.H., Turner, S., Hagedorn, E.A., Pontecorvo, D., Greenbaum, P., Pfeiffer, D., Wheelock, G. and Flanagan, T.R. 1977. Post-emergence growth of the ovarian follicles of *Aedes aegypti*. *J. Insect Physiol.*, **23**: 203–206.
- Imhof, J.E. and Smith, S.M. 1979. Oviposition behavior, egg masses and hatching response of the eggs of five Nearctic species of *Simulium* (Diptera: Simuliidae). *Bull. Entomol. Res.*, **69**: 405–425.
- Jaeger, E.C. 1955. *A source-book of biological names and terms*. 3rd ed. Charles C. Thomas, Publishers, Springfield, IL.
- King, H.H. 1910. Some observations on the bionomics of *Tabanus ditaeniatus* Macquart, and *Tabanus kingi* Austen. *Bull. Entomol. Res.*, **1**: 265–274.
- Magnarelli, L.A. 1985. Hovering and swarming behavior of males of *Hybomitra lasiophthalma* and *Hybomitra aurilimba* (Diptera: Tabanidae). *Myia*, **3**: 475–484.
- Nagatomi, A. 1962. Studies in the aquatic snipeflies of Japan. Part V. Biological notes. (Diptera: Rhagionidae). *Mushi*, **36**: 103–149.
- Oldroyd, H. 1964. *The natural history of flies*. W.W. Norton & Company, Inc., New York.
- Schutz, S.J. and Gaugler, R. 1989. Honeydew-feeding behavior of salt-marsh horseflies (Diptera: Tabanidae). *J. Med. Entomol.*, **26**: 471–473.
- Schwardt, H.H. 1936. Horseflies of Arkansas. *Bull. Arkansas Agric. Exp. Station*, no. 332. 66 pp.
- Taylor, P.D. and Smith, S.M. 1989. Activities and physiological states of male and female *Tabanus sackeni*. *Med. Vet. Entomol.*, **3**: 203–212.
- Taylor, P.D. and Smith, S.M. 1990. Behavior, physiological states and thermal characteristics of aggregating male *Hybomitra illota* (Diptera: Tabanidae). *Med. Vet. Entomol.*, **4**: 337–348.
- Thomas, A.W. 1972. Physiological age structure of adult tabanid populations (Diptera: Tabanidae) in Alberta, Canada. *J. Med. Entomol.*, **9**: 295–300.
- Troubridge, D.A. and Davies, D.M. 1975. Seasonal changes in physiological-age composition of tabanid (Diptera) populations in southern Ontario. *J. Med. Entomol.*, **12**: 453–457.
- Turnbull, D.A., Taylor, P.D., Smith, S.M. and Chainey, J.E. 1992. A collection of Tabanidae (Diptera) from west-central Ethiopia, with descriptions of *Tabanus gibensis* sp. n. and the male of *T. pallidifacies* Surcouf. *J. Afr. Zool.*, **106**: 133–140.
- Wesenberg-Lund, C. 1943. *Biologie der Süßwasserinsekten*. J. Springer, Berlin.
- Wilkerson, R.C., Butler, J.F. and Pechuman, L.L. 1985. Swarming, hovering, and mating behavior of male horseflies and deerflies (Diptera: Tabanidae). *Myia*, **3**: 515–546.
- Wilkinson, L. 1986. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.

¹ *Acervulus* (Latin): a heap (Jaeger 1955). In biology, the word has come to mean an accumulation of small heaps.