

WOLFGANG FRIEDRICH WÜLKER, ON THE OCCASION OF HIS 85TH BIRTHDAY

Wolfgang Wülker was born on 25 September 1925 at Frankfurt, Germany.

In 1952 he began working as a scientific assistant at the Hydrobiological Station Falkau

(later the Limnological Institute of the University of Freiburg, Walter Schlienz-Institut). His initial publications were on fish, but papers on chironomids began appearing from 1956. He was at Falkau for about 10 years and added to the collection of the station both specimens from the Black Forest area, and specimens collected on his research trips to Spain (1954), Fennoscandinavia (1956), Sudan (1963), USA and Canada (1964).

He did his Habilitation in Zoology and Limnology on intersexuality in *Chironomus* and the biology of *Sergentia* at the University of Freiburg, in 1960. Then in 1962 he joined the University of Freiburg.

After his official retirement Wolfgang continued to work at the University, later transferring his laboratory to his home.

Wolfgang was involved in collaborations with colleagues in many countries during his long career, some of which lasted for many years and produced many publications. A photograph of Wolfgang with Jim Sublette in Portales, N.M. in 1964 was reproduced on page 6 of volume 21 of this newsletter. His collaboration with Jim Sublette, Jon Martin and later Mac Butler, has produced 16 papers from 1967 to the present; that with the Russian workers, notably Iya Kiknadze and her group, 15 since about 1993; seven with the Swiss group of Adolf Scholl; four with György Dévai and colleagues from Hungary; and numerous others with students or colleagues from Germany. Wolfgang's full bibliography of chironomid publications is attached.

Jon Martin
Melbourne

My wife, Mary, and I first met Wolfgang and his wife, Dorothea, in Vienna at the 1959 SIL meeting. It was a most auspicious meeting for us which laid the groundwork for a collaborative 40+ years research team of Wuelker, Sublette and Sublette, which shortly thereafter was joined by Jon Martin who was then doing a postdoctoral in Ottawa at Canada Agriculture. The Sublettes were able

to get grants to visit Wuelker in Freiburg. In their brief stay there Jim and Wolfgang held endless discussions on midge taxonomy and Mary focused on getting a camera lucida drawing of some of the Keyl arms. Wolfgang became more entranced with the possibility of using polytene chromosomes in Chironomid taxonomy and phylogeny and spent some time in other labs in Germany becoming acquainted with methodology and cytotaxonomy in general.



Wolfgang Wülker. Photo NN

In 1965 Wolfgang was still working in the field of mermithid parasitism in Chironomidae and he was funded to come to the U.S. to attempt cross-inoculation of mermithid infective larvae into Nearctic samples. Wolfgang had worked with *Sergentia* and wanted to locate nearctic populations. He knew that John Stahl at the University of Indiana had worked on *Sergentia* in Crooked Lake. The Sublette family and Wuelker family met up in Indiana and spent a week together at Shafer Lake, where Jim's brother had lakeside acreage and a home. The Wuelkers pitched their camping trailer on the lawn and Jim and Wolfgang set out in search of *Sergentia*. We located a Crooked Lake on a topographic map, near Ft. Wayne. However, sampling that lake showed it was a shallow lake with only plumosus type larvae. The Wuelkers were anxious

to start a grand tour of the west and bought an old VW microbus in Monon from a dealer recommended by Jim's brother. Seven miles from where the dealership was, the motor fell out of the old VW. Jim's brother did a bit of arm twisting and they replaced the motor gratis. THEN the Wuelkers set off on the grand trip. After touring all of the national parks in the western United States, the Wuelkers ended up in Portales, NM where Jim was teaching. The University provided a guest apartment for the Wuelkers and they stayed there about 4 months. Wolfgang's infective larvae had moulted once as I recall but were still infective. We attempted to infect them into a plumosus type larva and a decorus type larva and a *Glyptotendipes* larva. No *Sergentia* were available. Infections occurred at a low rate but in all cases the mermithid died before moulting again.

Mary acquired the technique of making polytene chromosome squashes and produced several thousand over the next several years. Over the years Wolfgang returned again to Portales to sort through the growing collection of squashes accumulated there. We were most fortunate to make the association and receive the help from Patrick L. Hudson, U.S. Fish and Wildlife Service, who sent innumerable mature, fixed larvae with associated adults and larval/pupal skins. Much of this material was examined by Wolfgang and later by Jon Martin. Jon and Wolfgang were responsible for cytology and Jim and Mary, the larva, pupa and adults. Jim, in ENMU administration, was instrumental in establishing an in-house journal, *Studies in Natural Science* (Portales) which served as the publication vehicle for several of these joint studies.

Jim Sublette
Tucson

Chironomidae publications of W. Wülker

- 1 Wülker, W. 1956. Zur Kenntnis der Gattung *Psectrocladius* Kieff. (Dipt., Chironomidae). - *Arch. Hydrobiol., Suppl.* 24: 1-66
- 2 Wülker, W. 1957. Eine spanische *Halliella* (Dipt. Chironomidae). - *Arch. Hydrobiol., Suppl.* 24: 281-296
- 3 Wülker, W. 1957. Ober die Chironomiden der *Parakiefferiella*-Gruppe. (Diptera, Tendipedidae, Orthoclaadiinae). - *Beitr. Entomol.* 7: 411-429.
- 4 Wülker, W. 1958. Die Bedeutung der Chironomiden für die limnologisch-tiergeographische Charakterisierung des Hochschwarzwaldes. - *Verh. int. Ver. Limnol.* 13: 805-813.
- 5 Wülker, W. 1958. Parasitäre Intersexualität bei Chironomiden des Schluchsees. - *Gewässer und Abwässer (Krefeld) Jhg.* 20: 61-67.
- 6 Wülker, W. 1959. Diamesarien-Studien (Dipt., Chironomidae) im Hochschwarzwald. - *Arch. Hydrobiol., Suppl.* 24: 338-360.
- 7 Wülker, W. 1959. Drei neue Chironomiden-Arten (Dipt.) und ihre Bedeutung für das Konvergenzproblem der Imagines und Puppen. - *Arch. Hydrobiol., Suppl.* 25: 44-64.
- 8 Wülker, W. 1960. Neue Ergebnisse zur parasitären Intersexualität der Chironomiden. - *Naturwiss.* 47: 21-22.
- 9 Wülker, W. 1960. Studien zur Morphologie, Biologie und Verbreitung der Gattung *Sergentia* Kieff. (Dipt., Chironomidae). - *Arch. Hydrobiol., Suppl.* 25: 307-331.
- 10 Wülker, W. 1961. Lebenszyklus und Vertikalverteilung der Chironomide (Dipt.) *Sergentia coracina* Zett. im Titisee. - *Verh. int. Ver. Limnol.* 14: 962-967.
- 11 Wülker, W. 1961. Untersuchungen über die Intersexualität der Chironomiden (Dipt.) nach Paramermis-Infektion. - *Arch. Hydrobiol., Suppl.* 25: 127-181.
- 12 Wülker, W. 1961. Parasitäre und nicht parasitäre Zwischengeschlechtlichkeit bei Chironomiden (Dipt.). - *Zool. Anz., Suppl.* 25: 132-139.
- 13 Wülker, W. 1962. Bedeutung des Wirtes im Leben tierischer Endoparasiten. - *Naturw. Rundschau* 15: 469-474.
- 14 Wülker, W. 1963. Parasitologische und biochemische Verwandtschaft in der Gattung *Chironomus* (Dipt.). - *Naturwiss.* 50: 49-50.
- 15 Wülker, W. 1963. Prospects for biological control of pest Chironomidae in the Sudan. - *Rep. World Organization (WHO/EBL)* 11: 1-23.
- 16 Wülker, W. 1963. Investigations on the chironomid fauna of the Nile (Khartoum, Wadi Medani, Sennar, Wadi A Halfa). - *Ann. Rep. Hydrobiol. Res. Unit. Khartoum* 9-10: 20-21.
- 17 Wülker, W. 1964. Parasite-induced changes of external and internal sex characters in insects. - *Exper. Parasitol.* 15: 561-597.
- 18 Wülker, W. 1965. Der Mechanismus des Eindringens parasitärer Mermithiden (Nematoda) in *Chironomus*-Larven (Dipt., Chironomidae). - *Z. Parasitenkd.* 26: 29-49.

- 19 Wülker, W., Sublette, J.E., Martin, J. 1967. Zur Cytotaxonomie nordamerikanischer *Chironomus*-Arten. - *Ann. Zool. Fenn.* 5: 155-158.
- 20 Wülker, W., Götz, P. 1968. Die Verwendung der Imaginalscheiben zur Bestimmung des Entwicklungszustandes von *Chironomus*-Larven (Dipt.). - *Z. Morphol. Tiere* 62: 363-388.
- 21 Wülker, W., Maier, W., Bertau, P. 1969. Untersuchungen über die Hämolympheproteine der Chironomiden (Dipt.). - *Z. Naturforsch.* 24:110-116.
- 22 Wülker, W. 1969. Parasitismus des Nematoden *Gastromermis rosea* in *Chironomus anthracinus* (Diptera). Unterrichtsfilm C 1024, Institut Wiss.Film Göttingen. - *Publ. Wiss. Film* (Göttingen) 7: 299-312 1974.
- 23 Wülker, W., Winter, G. 1970. Untersuchungen über die Ultrastruktur der Gonaden von *Chironomus* (Dipt.). 1. Normalentwicklung der Ovarien im 4. Larvenstadium. - *Z. Zellforsch.* 106: 348-370.
- 24 Wülker, W. 1971. Untersuchungen über die Ultrastruktur der Gonaden von *Chironomus* (Dipt.). 2. Ovarstruktur nach Schädigung durch parasitäre Mermithiden. - *Z. Parasitenkd.* 36: 73-93.
- 25 Krieger-Wolf, E., Wülker, W. 1971. Chironomiden (Diptera) aus der Umgebung von Freiburg Bg. (mit besonderer Berücksichtigung der Gattung *Chironomus*). - *Beitr. naturk. Forsch. SüdwDtI.* 30: 133-145.
- 26 Wülker, W., Sublette, J.E., Sublette, M.F., Martin, J. 1971. A review of the genus *Chironomus* (Chironomidae, Diptera) 1. The *staegeri*-group. - *Stud. Nat. Sci.* (Portales) 1: 1-89.
- 27 Martin, J., Wülker, W. 1971. Inversion polymorphism in *Chironomus staegeri* Lundbeck. - *Can. J. Gen. Cytol.* 13: 306-321.
- 28 Wülker, W. 1973. Revision der Gattung *Chironomus* Meig. III. Europäische Arten des thummi-Komplexes. - *Arch. Hydrobiol.* 72: 356-374.
- 29 Wülker, W., Klötzli, A. 1973. Revision der Gattung *Chironomus* Meig. IV. Arten des lacunarius (commutatus)-Komplexes. - *Arch. Hydrobiol.* 72: 474-489.
- 30 Wülker, W., Martin, J. 1974. A review of the genus *Chironomus* (Diptera, Chironomidae). VI. Cytology in the *Chironomus matorus*-complex. - *Stud. Nat. Sci.* (Portales) 1(9):1-17
- 31 Martin, J., Wülker, W. 1974. A review of the genus *Chironomus* (Diptera, Chironomidae). VIII. *Chironomus stigmaterus* Say, Cytology. - *Stud. Nat. Sci.* (Portales) 111.: 1-17.
- 32 Martin, J., Wülker, W., Sublette, J.E. 1974. Evolutionary cytology in the genus *Chironomus* (Diptera, Chironomidae). - *Stud. Nat. Sci.* (Portales) 112.: 1-12.
- 33 Wülker, W. 1974. Parasitismus und Symbiose, Studieneinheit 19, Funkkolleg Biologie, Systeme des Lebendigen, In: Todt, D. (ed.) *Begleittexte*. Beltz-Verlag, Weinheim, Basel.
- 34 Wülker, W. 1974. Die großen Kreisläufe der Natur. Studieneinheit 23, Funkkolleg Biologie, Systeme des Lebendigen, In: Todt, D. (ed.) *Begleittexte*. Beltz-Verlag Weinheim Basel.
- 35 Wülker, W. 1975. Parasite-induced castration and intersexuality in insects. In: Reinboth, R. (ed.) *Intersexuality in the animal kingdom*. Springer-Verlag Heidelberg. p. 121-134.
- 36 Wülker, W. 1976. Influence of mermithids (Nematoda) on insect imaginal discs. - *Proc. 1st. Intern Coll. Invertebr. Pathol.* Queens Univ., Kingston Ontario, p. 255-258.
- 37 Wülker, W. 1978. Parasitäre Einflüsse auf undifferenzierte Gewebe. - *Z. Parasitenkd.* 57: 255-257.
- 38 Wülker, W. 1978. Morphology and ultrastructure of the ejaculatory duct in normal, parasitized and experimentally (UV)-treated *Chironomus*. - *Acta Univ. Carol. Biol. Praha*, 1-2: 285-290.
- 39 Wülker, W., Rössler, R., v. Essen, S. 1979. Studies on the development of imaginal discs of *Chironomus* (Dipt.). The female genital disc in abdominal segment VIII. - *Zool. Jb. Anat.* 101: 136-153.
- 40 Wülker, W. 1980. Basic pattern in the chromosome evolution of the genus *Chironomus* (Dipt.). - *Z. zool. Syst. Evolutionsforsch.* 18: 112-123.
- 41 Ryser, H.M., Geiger, H.J., Scholl, A., Wülker, W. 1980. Untersuchungen über die Verbreitung der Zuckrücken-gattung *Chironomus* in der Schweiz, mit besonderer Berücksichtigung von drei cytologisch nicht beschriebenen Arten. In: Murray, D.A. (ed.) *Ecology, Systematics, Cytology and Physiology*. Pergamon-Press Oxford New York. pp. 17-24.
- 42 Schmidt, K., Wülker, W. 1980. Parasitäre Intersexualität des Johnstonschen Organes in den

- Antennen von *Chironomus* (Dipt.). - *Z. Parasitenkd.* 64: 1-15.
- 43 Wülker, W., Ryser, H.M., Scholl, A. 1981. Revision der Gattung *Chironomus* Meigen (Dipt.). VI. *C. holomelas* Keyl, *C. saxatilis* n.sp., *C. melanescens* Keyl. - *Rev. Suisse Zool.* 88: 903-924.
- 44 Wülker, W., Eisele, H. Rössler, R. 1982. Tarsal sensilla of *Chironomus* (Diptera: Chironomidae): number, parasitogenic changes, ultrastructure and function. - *Int. J. Insect Morphol. Embryol.* 11(2.): 137-146.
- 45 Ryser, H.M., Scholl, A., Wülker, W. 1983. Revision der Gattung *Chironomus* Meigen (Diptera) VII: *C. muratensis* n.sp. und *C. nudiventris* n.sp., Geschwisterarten aus der plumosus-Gruppe. - *Rev. Suisse Zool.* 90: 299-316.
- 46 Wülker, W., Butler, M.G. 1983. Karyosystematics and morphology of Northern *Chironomus* (Diptera: Chironomidae): Freshwater species with larvae of the salinarius-type. - *Ent. scand.* 14: 121-136.
- 47 Wülker, W., Ryser, H.M., Scholl, A. 1983. Revision der Gattung *Chironomus* Meigen (Diptera), VIII. Arten mit Larven des fluviatilis-Typs (obtusidens-Gruppe): *C. acutiventris* n.sp. und *C. obtusidens* Goetgh. - *Rev. Suisse Zool.* 90: 725-745.
- 48 Dévai, G., Wülker, W., Scholl, A. 1983. Revision der Gattung *Chironomus* Meigen (Diptera). IX. *C. balatonicus* sp.n. aus dem Flachsee Balaton (Ungarn). - *Acta Zool. Acad. Sci. Hung.* 29: 357-373.
- 49 Wülker, W. 1983. Mermithiden (Nematoda) - *Chironomus* spec. (Insecta, Diptera) Kopulation und Eiablage der Parasiten, Wirtsfindung und Eindringvorgang, parasitäre Intersexualität, humorale Einkapselung des Parasiten- In: Boeckeler, W., Wülker, W. (eds.) *Parasitologisches Praktikum*, Verlag Chemie, Weinheim -Deerfield Beach, Florida -Basel.
- 50 Wülker, W., Lörincz, G., Dévai, G. 1984. A new computerized method for deducing phylogenetic trees from chromosome inversion data. - *Z. zool. Syst. Evolutionsforsch.* 22: 86-91.
- 51 Wülker, W. 1985. Karyosystematics and morphology of two North European species of the *Chironomus matorus*-complex (Diptera: Chironomidae). - *Entomol. Gener.* 10: 125-132.
- 52 Wülker, W. 1985. Changes in behaviour, flight tone and wing shape in nematode-infested *Chironomus* (Insecta, Diptera). - *Z. Parasitenkd.* 71: 409-418.
- 53 Ryser, H.M., Wülker, W., Scholl, A. 1985. Revision der Gattung *Chironomus* Meigen (Diptera). X. *Lobochironomus* n.subg. (*C. montuosus* n.sp., *C. storai* Goetgh., *C. mendax* Stora). - *Rev. Suisse Zool.* 92: 385-404.
- 54 Morisch, U., Wülker, W. 1987. Formation of the cerci, abdominal Segment X and postgenital plate in the genital imaginal discs of female larvae and pupae in *Chironomus* (Diptera). - *Ent. scand., Suppl.* 29: 91-96.
- 55 Kaiser, H., Wülker, W., Skofitsch, G. 1987. *Limnomermis anthracini* n.sp. and *L. bathophilii* n.sp., sympatric species of Mermithidae (Nematoda) in different Chironomid (Diptera) hosts. - *Zool Jb. Syst.* 114: 141-156.
- 56 Wülker, W. 1987. Der Karyotyp von *Chironomus (Chaetolabis) macani* Freeman 1948. - *Entomol. Gener.* 12: 281-286.
- 57 Webb, C.J., Martin, J., Wülker, W. 1987. Ultrastructure of larval ventromental plates of European and North American representatives of *Chironomus* Meigen (subgenus *Chaetolabis* Townes) (Diptera: Chironomidae). - *Ent. scand.* 18, 205-211.
- 58 Wülker, W., Herrmann, I. 1987. Die weiblichen Gonodukte in normalen und parasitierten *Chironomus* (Dipt.) Imagines. - *Spixiana Suppl.* 14: 17-24.
- 59 Wülker, W., Sublette, J.E., Morath, E., Martin, J. 1989. *Chironomus columbiensis* n.sp. in South America and *Chironomus anonymus* Williston in North America- closely related species. - *Stud. neotrop. Fauna Environ.* 34: 121-136.
- 60 Dévai, G., Miskolczi, M., Wülker, W. 1989. Standardization of chromosome arms B, C and D in *Chironomus* (Diptera: Chironomidae). - *Acta Biol. Debrecina., Suppl. Oecol. Hungar.* 2: 79-92.
- 61 Wülker, W., Dévai, G., Dévai, I. 1989. Computer assisted studies of chromosome evolution in the genus *Chironomus* (Dipt.). Comparative and integrated analysis of chromosome arms A, E and F. - *Acta Biol. Debrecina Suppl. Oecol. Hungar.* 2: 373-387.
- 62 Wülker, W., Morath, E. 1989. South American *Chironomus* (Dipt.) - karyotypes and their relations to North America. - *Acta Biol. Debrecina, Suppl. Oecol. Hungar.* 2: 389-397.

- 63 Wülker, W., Sublette, J.E., Martin, J. 1990. *Chironomus utahensis* Malloch and *Chironomus harpi* new species and their karyosystematic relationships to other species in the decorus-group of *Chironomus*. - *Spixiana* 14: 71-94.
- 64 Wülker, W. 1991. Chromosomal and morphological differences between *Chironomus tenuistylus* Brundin 1949 and *C. longistylus* Goetghebuer 1921 in Fennoscandia and the USA. - *Ent. scand.* 22: 231-24.
- 65 Wülker, W. 1991. *Chironomus fraternus* n.sp. and *C. beljaninae* n.sp., sympatric sister species in Fennoscandian reservoirs. - *Ent. Fenn.* 2: 97-109.
- 66 Wülker, W., Weiser, J. 1991. *Helmichia glandulicola* n. sp. (Microspora, Thelohanidae): Morphology, development and influence on salivary glands of *Chironomus anthracinus* (Diptera, Chironomidae). - *Parasitol. Res.* 77:335-340.
- 67 Wülker, W. 1992. Problems of karyosystematics in the Genus *Chironomus* Meigen (In Russian). In: *Biologie der Süßgewässer. Inform. Bull. Russ. Acad.Sci.* St. Petersburg 93:57-62.
- 68 Kiknadze, I.I., Siirin, M.I., Wülker, W. 1993. Siberian species of the *riihimakiensis*-group in the genus *Chironomus* (Diptera, Chironomidae) 1. Karyotypes and morphology. - *Netherl. J. Aquat. Ecol.* 26: 163-171.
- 69 Kiknadze, I.I., Siirin, M.I., Wülker, W. 1994. Siberian species of the *riihimakiensis*-group of the genus *Chironomus* (Diptera, Chironomidae) 2. Inversion polymorphism and cytophylogeny. - *Spixiana Suppl.* 20:115-125.
- 70 Wülker, W. 1996. *Chironomus pilicornis* Fabricius 1787 and *C. heteropilicornis* n.sp (Diptera, Chironomidae) in Fennoscandian reservoirs: karyosystematic and morphological results. - *Aquat. Insects* 18:209-221.
- 71 Wülker, W. 1996. Zoogeographische Verbreitung sibirischer *Chironomus*-Arten (In Russian). In: Shobanov, N.A., Zinchenko, T.D. (eds.) *Ecology, evolution and systematics of chironomids*. Togliatti and Borok Russ. Acad. Sci., pp. 24-27.
- 72 Wülker, W. 1997. *Chironomus esai* n.sp (Diptera:Chironomidae) in lakes and reservoirs of central Fennoscandia. - *Ent. Fenn.* 8: 171-176.
- 73 Wülker, W., Kerkis, I.E., Kiknadze, I.I., Nevers, P. 1998. Chromosomes, morphology, ecology and distribution of *Sergentia baueri* n.sp., *S. prima* Proviz and Proviz 1996 and *S. coracina* Zett. 1824. - *Spixiana* 22: 69-81.
- 74 Wülker, W., 1998. A *Lobochironomus*-species with 3 chromosomes (2n=6. - the true *Chironomus* (*Lobochironomus*) *mendax* Stora (Diptera, Chironomidae). - *J. Kansas Entomol. Soc.* 71: 304-314.
- 75 Wülker, W. 1999. Fennoscandian *Chironomus* species (Dipt., Chironomidae) - identified by karyotypes and compared with the Russian and Central European fauna. - *Stud. dipt.* 6: 425-436.
- 76 Butler, M.G., Kiknadze, I.I., Golygina, V.V., Martin, J., Istomina, A.G., Wülker, W., Sublette, J.E, Sublette, M.F. 1999. Cytogenetic differentiation between Palearctic and Nearctic populations of *Chironomus plumosus* L. (Diptera, Chironomidae). - *Genome* 42: 797-815.
- 77 Wülker, W., Martin, J. 2000. Northernmost *Chironomus* karyotypes (Insecta, Diptera, Chironomidae). In: Baehr, M., Spies, M. (eds). *Contributions to chironomid research in memory of Dr. Friedrich Reiss (Insecta, Diptera)*. - *Spixiana* 23: 151-156.
- 78 Butler, M.G., Kiknadze, I.I., Golygina, V.V., Istomina, A.G., Wülker, W., Martin, J., Sublette, J.E, Sublette, M.F. 2000. Macrogeographic patterns of banding sequences in Holarctic *Chironomus plumosus* L. In: Hoffrichter, O. (ed.) *Late 20th Century Research on Chironomidae: An Anthology from the 13th International Symposium on Chironomidae*, Freiburg, 5-9 September, 1997, Shaker Verlag GmbH, Aachen: 51-57.
- 79 Kiknadze, I.I., Butler, M.G., Golygina, V.V., Martin, J., Wülker, W., Sublette J.E., Sublette, M.F. 2000. Intercontinental karyotypic differentiation of *Chironomus entis* Shobanov, a Holarctic member of the *C. plumosus* - group (Diptera, Chironomidae). - *Genome* 43: 857-873.
- 80 Kiknadze, I.I., Butler, M.G., Golygina, V.V., Wülker, W., Martin, J., Sublette J.E., Sublette, M.F. 2000. Macrogeographic patterns of banding sequences in Holarctic *Chironomus entis* Shobanov. In: Hoffrichter, O. (ed.) *Late 20th Century Research on Chironomidae: An Anthology from the 13th International Symposium on Chironomidae*, Freiburg, 5-9 September, 1997, Shaker Verlag GmbH, Aachen: 135-141.
- 81 Istomina, A.G., Siirin, M.T., Makarevich, I.F., Scherbik, S.V., Wülker, W., Polukonova,

- N.V. 2000. The fixation of polytene chromosome species-specific band sequences is the main differentiating factor in the obtusidens group of the genus *Chironomus* (Diptera, Chironomidae). In: *Biodiversity and dynamics of ecosystems in North Eurasia. V. 1. Part 3. Molecular-genetic bases of biodiversity (animals and plants)*, Inst. Tsitol. Genet., Sib. Otd. Russ. Akad. Nauk, Novosibirsk: 57-59.
- 82 Spies, M., Sublette, J.E., Sublette, M.F., Wülker, W., Martin, J., Hille, A., Mitchell, M. A., Witt, K. 2002. Pan-American *Chironomus calligraphus* Goeldi, 1905 (Diptera, Chironomidae): species or complex? Evidence from external morphology, karyology and DNA sequencing. - *Aquat. Insects* 24: 91-113.
- 83 Shobvanov, N., Wülker, W., Kiknadze, I.I. 2002. *Chironomus albimaculatus* sp.n. and *C. trabicola* sp.n. (Diptera, Chironomidae) from polar Russia. - *Aquat. Insects* 24: 169-188.
- 84 Kiknadze, I.I., Wülker, W., Istomina, A.G., Andreeva, E.N. 2005. Banding sequences pool of *Chironomus anthracinus* Zett. (Diptera, Chironomidae) in Palearctic and Nearctic. - *Euroasian Ent. J.* 4: 13-27.
- 85 Martin, J., Andreeva, E.N., Kiknadze, I.I., Wülker, W. 2006. Polytene chromosomes and phylogenetic relationships of *Chironomus atrella* (Diptera: Chironomidae) in North America. - *Genome* 49: 1384-1392.
- 86 Wülker, W., 2007. Two new *Chironomus* species with fluviatilis-type larvae from the near-shore sandy sediments of Lake Michigan (Diptera: Chironomidae). In: Andersen, T. (ed.) *Contributions to the Systematics and Ecology of Aquatic Diptera - A Tribute to Ole A. Sæther*, The Caddis Press, Columbus, Ohio: 321-333.
- 87 Kiknadze, I.I., Gunderina, L., Butler, M.G., Wülker, W., Martin, J. 2008. Chromosomes and continents. In: Dobretsov, N., Kolchanov, N., Rozanov, A., Zavarzin, G. (eds.) *Biosphere origins and evolution*, Springer, New York, N.Y.: 349-369.
- 88 Wülker, W., Martin, J., Kiknadze, I.I., Sublette, J.E., Michiels, S. 2009. *Chironomus blaylocki* n.sp. and *C. bifurcatus* n.sp., North American species near the base of the decorus-group. - *Zootaxa* 2023: 28-46.
- 89 Wülker, W. 2010. The role of chromosomes in chironomid systematics, ecology and phylogeny. In: Ferrington, L.C., Jr. (ed.) *Proceedings of the XV International Symposium on Chironomidae*. Chironomidae Research Group, University of Minnesota, Saint Paul, Minnesota: 1-13.
- 90 Kiknadze, I.I., Istomina, A.G., Wülker, W., Vallenduuk, H.J. 2010. The karyotype of *Chironomus uliginosus* Keyl (Diptera, Chironomidae). - *VOGiS Herald* 14: 22-30

Jon Martin
Melbourne

Odwin Hoffrichter
Freiburg

PROFESSOR IYA I. KIKNADZE: 80TH BIRTHDAY AND 55 YEARS IN SCIENCE AND TEACHING

Professor Iya Ivanovna Kiknadze is a leading expert in cell biology, cytogenetics, karyosystematics, and comparative and evolutionary genomics of Chironomidae.

On February 9, 2010, this honoured worker of science of the Russian Federation celebrated her 80th anniversary. She is among the oldest researchers at the Institute of Cytology and Genetics (ICG), Novosibirsk, and Professors of the Novosibirsk State University (NSU). In addition, in 2010 it will be 55 years since the beginning of her research work, of them, three years at the Laboratory of Cytology, Zoological Institute, Leningrad, later transformed into the Institute of Cytology. She has been working at ICG, Novosibirsk, for 52 years, since January, 1958. For 32 years, from 1962 till 1994, she headed a laboratory at the institute and from 1963 to 1986, at NSU.

Iya Kiknadze is the founder in Russia of the new research field: functional organization of chromosomes and differential gene activity in Diptera. She developed the notion of puffing as the basis for differential gene transcription and described the pattern and dynamics of puffs at major stages of chironomid development. With her supervision, the role of tissue-specific puffs was analyzed and an insight into the genetic control of tissue-specific secretory proteins was obtained. She pioneered in microdissection of the disk containing genes of the tissue-specific Balbiani ring, investigation of the molecular study of these genes, description of transposable elements in Chironomidae, and study of the cytogenetic control of the fine structure of chironomid salivary glands in the course of induced gene repression and expression. This study provided grounds for the original hypothesis of periodic genome reprogramming. Construction of high-resolution cytophotographic maps of chironomid polytene chromosomes allowed these species to be enrolled on the list of models for studies of evolutionary transformations in genomes and genetic impact of industrial factors on organisms. In particular, these results were extensively used in the assessment of radioactive pollution in the integrated projects: *Remote Consequences of the Radioactive Impact of Nuclear Tests at the Semipalatinsk Test Site on the Population of the Altai Territory* and *Study of the Genetic Consequences of Nuclear Tests at the Semipalatinsk Test Site on Plant and Animal Populations*. Iya Kiknadze supervised the development of inversion genomics of chironomids, based on global analysis of the disk

(gene) sequence polymorphism on various continents: Eurasia, North and South America, Africa, and Australia. Putative ancestral disk sequences were recognized in each of the chromosome arms of the genome (primitive karyotype). Phylogenetic trees were constructed for the first time for the genus *Chironomus* on the basis of inversion polymorphism in cooperation with researchers of the Institute of Mathematics, Novosibirsk, and the cytogenetic history of the genus was reconstructed.



Iya I. Kiknadze at the Symposium of Cytogenetics of Invertebrates, August 2010. Photo W. Wülker.

Iya Kiknadze was the first to obtain experimental evidence against the involvement of endomitosis in somatic polyploidization. It allowed revision of the endomitosis concept. Functional organization of chromosomes and differential gene activity are also among the subjects of Kiknadze's seminal studies. Her monograph "Functional organization of polytene chromosomes" summarizes studies in this field. Iya Kiknadze applied the polytene chromosome model to the development of the essentials of the functional organization of interphase chromosomes and introduced the notion of chromomeres as functional units of these chromosomes.

When working at ICG, Iya Kiknadze commenced studies of interphase chromosomes, chromomeres, and nucleoli. In collaboration with Dr. E. S. Belyaeva, she proved that the nucleolus was a transcriptionally active region of an interphase chromosome.

One more field of research conducted under Kiknadze's supervision since 1980s is the molecular and cytological organization of specific regions in eukaryotic chromosomes, including the organization of multigenic loci and their transformation in the course of evolution.

Long-term monitoring of chromosome pools of natural chironomid populations is conducted in permafrost regions of Yakutia in cooperation with the Institute of Ecology, Yakutian Academy of Sciences.

Iya Ivanovna Kiknadze was born in the old merchant city of Tyumen on February 9, 1930. Her mother Antonina Reshetnikova and father Ivan Balakin were clerks.

Iya spent all her childhood and school years in Tyumen, never going further than ten miles from it. She entered first School No. 1 and graduated from girl's school No. 25. In wartime, Tyumen gave home not to only evacuated industrial enterprises but also many higher educational institutions from Moscow and other Russian cities. They included the staff of the Moscow Medical Institute. As it later turned out, the embalmed body of Vladimir Lenin was kept there during the Second World War. The cultural standard of the provincial town was notably improved by performances of companies of the Moscow Academic Art Theatre and other theatres. The metropolitan culture influenced the artistic taste of Tyumen inhabitants, in particular, teenagers. In 1947, Iya graduated school with a School Gold Medal and went to the "northern capital" to enter the Leningrad State University.

In 1952, Iya Kiknadze graduated from the Faculty of Biology and Soil Science cum laude and became specialist in a field rare at that time: Darwinist-Geneticist. She started her research activity when learning at the University. From 1952 to 1955, she took a postgraduate course at the Leningrad State University and defended a candidate's dissertation entitled *Dynamics of DNA and RNA in oogenesis and early cleavage in invertebrates*. Then she obtained her first position of Junior Researcher at the Laboratory of Cytology, Zoological Institute (In 1956, the laboratory was transformed into the Institute of Cytology). Her research advisor at the University and Zoological Institute was Ivan I. Sokolov, a prominent cytologist. For years, he remained her tutor and standard of dedication and ethics. In 1957 Iya was advised by A. A. Prokof'eva-Bel'govskaya to move to the just established Akademgorodok in Novosibirsk and obtain a job at ICG. She was promised she would have an apartment and interesting work. Iya was a daughter of Siberia, and she

did not resist it. In 1957 Iya Kiknadze, her husband the botanist Georgii Sergeevich Kiknadze, and their small daughter Irene left for Novosibirsk.

At ICG, Iya Kiknadze became Junior Researcher at the Department of Physical, Chemical, and Cytological Basics of Heredity. It was headed by Prof. Ivan Dmitrievich Romanov till 1961. It was a remarkable time with a remarkable scientist. Even now, his portrait is on the wall in Iya Kiknadze's study. During her first decade in Novosibirsk, Kiknadze made friends with older colleagues, Vera V. Khvostova and Raisa P. Martynova, and colleagues of her age, Ninel B. Khristolyubova and Klavdia K. Sidorova.

In 1961–1962, Kiknadze worked as a Senior Researcher. Since October, 1962, she has headed the Laboratory of General Cytology. She defended her doctoral dissertation *Functional Organization of Chromosomes* in 1967, at a session of the Joint Dissertation Council in Biological Sciences, Siberian Branch of the USSR Academy of Sciences. She was awarded Professor's rank at the Chair of Cytology and Genetics on December 10, 1970.

On January 21, 1988, the Department of Cell Biology was founded on the base of the Laboratory of General Cytology. It included the Laboratory of Evolutionary Cytogenetics and several sectors: Genetics of Tissue-Specific Traits, Molecular Neurogenetics, and Genomics.

Since 1994, Prof. Kiknadze has held the position of Chief Researcher at the Laboratory of Evolutionary Biology, ICG.

Professor Iya Kiknadze convened several All-Union and international conferences: the 2nd All-Union Symposium *Chromosome Structure and Function* (Novosibirsk, 1970) and the All-Union Symposium *Chironomidae Evolution, Speciation, and Systematics* (Novosibirsk, 1985). In 1982, the international symposium *Organization and Expression of Tissue-Specific Genes* was held in Akademgorodok in 1982. It marked the beginning of regular workshops on chironomid Balbiani rings. At present, I. Kiknadze is participating in the preparation of the conference *Invertebrate Karyosystematics* (Novosibirsk) as Chairlady of the Organizing Committee.

Professor Iya Kiknadze is the founder of the Novosibirsk school of dipterologists, experts in Chironomidae and Drosophilidae. Twenty-nine candidate's dissertations were defended with her scientific supervision. She generously presents her ideas to her students. She has dozens of followers and disciples who have chosen their own research

ways in many countries. Many of Kiknadze's students have raised their own students.

Professor Iya Kiknadze applied much effort to teaching of cytology at the Chair of Cytology and Genetics, Biological Department, Faculty of Sciences, NSU. From the foundation of the Chair of Cytology and Genetics in 1962 to 1986, she performed the offices of Vice-Chairholder. She was the first not only at NSU but in the USSR to develop and deliver the course *Cytology/Cell Biology* after decades of the stranglehold of Michurin's biology. She also held and supervised seminars and laboratory courses on branches of cytology and genetics.

Iya Kiknadze introduced her experience acquired from the Leningrad biological research school to ICG and NSU. She started with the system of biologist tutorship. Major and minor laboratory courses on cytology and genetics and summer practicals in the field were conducted in the image and likeness of corresponding activities at the Chair of Biology of the Leningrad University. This was how the famous Leningrad school of cytology and genetics, created by the famous scientists Yu. A. Filipchenko, M. E. Lobashov, D. N. Nasonov, and M. S. Navashin, sprouted in Siberia.

Since 1965, Iya Kiknadze has been a member of the Joint Academic Board in Biology, Siberian Branch of the USSR Academy of Sciences. She was a permanent member of the Academic Board of ICG since its establishment, a member of the Academic Board of the Faculty of Sciences, NSU, and a member of the Dissertation Council at the Novosibirsk State Medical University. Now Prof. Kiknadze is also a member of the Dissertation Council at the Institute of Systematics and Ecology of Animals.

For 28 years, from 1974 to 2001, Iya Kiknadze was a member of the Editorial Board of the journal *Tsitologiya (Cytology)*, and for 5 years, from 1984 to 1989, of the Editorial Board of *Ontogenez (Development)*. Since 2003, she has been a member of the Editorial Board of *Evroaziatskii Entomologicheskii Zhurnal (Eurasian Entomological Journal)*, and since 2008, of the Editorial Board of *Comparative Cytogenetics*.

The Honoured Worker of Science of the Russian Federation (since 1998), Professor Kiknadze was awarded the Order of the Badge of Honour in 1967 for participation in the development of the Novosibirsk Research Centre and scientific contribution; in 1970, the Medal for Valorous Labour. She has the titles of Honoured Veteran of the Siberian Branch of the USSR Academy of Sciences and Honoured

Veteran of Labour. Certificates of Merit: from SB RAS on the occasion of the 275th Anniversary of the Academy of Sciences in 1999, from the Ministry of Education and Science on the occasion of the 50th Anniversary of the Siberian Branch of the RAS in 2007, and from the Novosibirsk Governor V. A. Tolokonsky in 2010.

Iya Kiknadze is an earnest and fruitful worker. It is apparent from her numerous publications in the recent decade and enormous work on reviewing and editing of research papers. Her desk is always covered by fans of photographs of her favourite polytene chromosomes. Their banding patterns serve as barcodes. They allow the features and evolutionary history of each species to be understood. With the help of her students, A. G. Istomina, L. I. Gunderina, V. V. Golygina, and A. D. Broshkov, as well as with numerous Russian and foreign colleagues, Iya Kiknadze works in the enormous field of chromosome pools, chromosome polymorphism, and speciation in Holarctic Chironomidae species. These studies contribute to cytogenetics of natural chironomid populations in the context of the role of chromosome rearrangements in population adaptation and chromosome set divergence during speciation. They have revealed profound cytogenetic divergence between Palearctic and Nearctic populations of Holarctic species.

Iya Kiknadze is among authors of over 350 publications, including 10 monographs.

During all scientific activity Prof. I. Kiknadze had fruitful contacts with many specialists from different countries. She took part in many international symposia and other scientific meetings. While studying the structure and function of chironomid polytene chromosomes she had associated with Prof. B. Daneholt, Prof. E.R. Schmidt, Prof. M. Lezzi, Prof. J.E. Edström, Prof. U. Grossbach, Prof. R. Panitz, Prof. S. Case, H. Bäumlein, U. Wobus. Joint work with Prof. W. Wülker, Prof. J. Martin, Prof. M. Butler, Prof. X. Wang, Prof. R. Contreras-Lichtenberg, H. Vallenduuk, H. Moller-Pilot result in the description of new species, their karyotypes and chromosomal polymorphism. Iya Kiknadze collected chironomid larvae with M. Butler in North America. The fruitful interactions with Prof. W. Wülker and Prof. J. Martin resulted in revision and making cytomaps of polytene chromosomes of many *Chironomus* species more precise. In joint work with Prof. W. Wülker, Prof. J. Martin, Prof. M. Butler and Dr. L. Gunderina it has been shown that the banding sequence pools of populations of the same species on different continents differed much in the sets and frequencies of

gene inversion orders. Banding sequence pools of populations on each continent were found to contain continent-specific banding sequences in addition to sequences occurring on several continents.

We wish Iya Kiknadze many more interesting years full with new ideas and successes.

I.K. Zakharov, A.G. Istomina, W. Wülker

Iya Kiknadze's selected publications

- Kiknadze I.I. 1972. The functional organization of the chromosomes. - L. Nauka, 212p. (In Russian).
- Kiknadze I.I., Shilova A.I., Kerkis I.E. *et al.* 1991. *Karyotypes and larval morphology in tribe Chironomini*. An Atlas. Novosibirsk: Nauka. 113 p. (In Russian with English Summary).
- Kiknadze, I.I., Istomina, A.G., Gunderina, L.I., Salova, T.A., Aimanova, K.G. & Savvinov D.D. 1996. *The banding sequences pool of chironomids from permafrost zone of Yakutia: tribe Chironomini*. Nauka Publishing, Novosibirsk, 166 pp. (In Russian).
- Kiknadze I.I., Kokoza V.A., Kolesnikov N.N., Karakin E.I., Scherbakov D.Yu., Aimanova K.G., Agapova O.A., Zainiev G.A., Kopantsev E.P., Sebeleva T.E. 1985. *Organization and expression of tissue specific genes in Diptera*. Novosibirsk: Nauka Publ. 237 p. (In Russian).
- Kiknadze I.I., Blinov A.G., Kolesnikov N.N. 1989. The molecular-cytological organization of chironomid genome; (pp. 4-59) in Shumny V.K. (Ed.) *Structural and functional organization of genome*. Novosibirsk, 189 p. (In Russian with English summary).
- Kiknadze I.I. 1967. The chromosomes of Diptera. The evolutionary and practical significance of karyotype study. - *Genetika* 3: 145-165. (In Russian with English Summary).
- Kiknadze I.I. 1970. The transcriptional activity of chromosomes during differentiation. - *Soviet Journal of Developmental Biology*, 1: 7-27. (In Russian with English Summary).
- Kiknadze .I.I. 1971. Polytene chromosomes as a model of interphase chromosome. - *Tsitologia* 13: 716-732. (In Russian with English Summary).
- Kiknadze I.I., Perov N.A., Chentsov Yu.S. 1976. Ultrastructural organization of salivary gland polytene chromosomes of *Chironomus thummi*. - *Chromosoma* 55: 91-102.
- Kiknadze I.I. 1976. Comparative characteristics of puffing pattern in salivary gland *Chironomus* during larval development and metamorphosis. I. Puffing pattern in chromosome IV. - *Tsitologia* 18: 1322-1329. (In Russian with English Summary).
- Kiknadze I.I. 1978. Comparative characteristics of puffing pattern in salivary gland *Chironomus* during larval development and metamorphosis. II. Puffing pattern in chromosomes I, II, III. - *Tsitologia* 20: 514-521. (In Russian with English Summary).
- Kiknadze I.I., Valeeva F.S., Vlasova I.E., Panova T.M., Sebeleva T.E., Kolesnikov N.N. 1979. Puffing and specific function of salivary gland in *Chironomus thummi*. I. Quantitative changes of proteins and glycoproteins in the salivary gland at different larval stages. - *Soviet Journal of Developmental Biology* 10: 161-172. (In Russian with English Summary).
- Kiknadze I.I. Chromosomal polymorphism in natural populations of the *plumosus* species-group of West Siberia (Diptera: Chironomidae). - *Entomol. Scand.* 1987, Suppl. 29: 113-121.
- Kiknadze I.I., Kolesnikov N.N., Panova T.M., Gydamakova E.K., Blinov A.G., Filippova M.A. 1987. Transposable elements in Chironomidae I. Location of pCth C1.2HR sequence in the polytene chromosomes of closely related subspecies *Chironomus thummi thummi* Kieffer, *C. th. piger* Strenzke and their hybrids. - *Genetika* 23: 1366-1376. (In Russian with English Summary).
- Kiknadze I.I., Butler M.G., Aimanova K.G. *et al.* 1998. Divergent cytogenetic evolution in Nearctic and Palearctic populations of sibling species in subgenus *Camptochironomus* Kieffer. - *Can. J. Zool.* 76; 361-376.
- Butler M.G., Kiknadze I.I., Golygina V.V. *et al.* 1999. Cytogenetic differentiation between Palearctic and Nearctic populations of *Chironomus plumosus* L. (Diptera, Chironomidae) - *Genome* 42: 797-815.
- Kiknadze I.I., Butler M.G., Golygina V.V. *et al.* 2000. Inter-continental cytogenetic differentiation in *Chironomus entis* Shobanov, a Holarctic species in the *plumosus*-group (Diptera, Chironomidae) - *Genome* 43: 857-873.
- Kiknadze I.I., Gunderina L.I., Istomina A.G. *et al.* 2003. Similarity analysis of inversion banding sequences of *Chironomus* species (breakpoint phylogeny) In: Kolchanov N., Hofstaedt R..

(eds) *Bioinformatics of genome regulation and structure* Boston/Dordrecht/London: Kluwer Acad. Publ.. pp. 245–253.

Kiknadze I.I. 2008. The role of chromosome polymorphism in divergence of populations and species of the genus *Chironomus*. - *Entomol. Rev.* 88: 509–524.

Kiknadze I.I., Golygina V.V., Broshkov F.D. *et al.* 2008. Mystery of *Chironomus dorsalis* karyo-

type (Diptera, Chironomidae) - *Comp. Cytogenet.* 2: 21–35.

Kiknadze I.I., Gunderina L.I., Butler M.G. *et al.* 2008. Chromosomes and continents. In: Dobretsov N., Rozanov A., Kolchanov N., Zavarzin G., (eds.) *Biosphere Origin and Evolution*. Springer-Verlag pp. 349-369.

ARTHUR DESMOND HARRISON (24.12.1921 - 30.12.2007) – AN APPRECIATION

Arthur D. Harrison, the doyen of African limnology and studies of the Afrotropical Chironomidae, died in Canada over 3 years ago with little or no posthumous scientific recognition. This piece is an attempt to rectify the situation, and to recognise the significance of Arthur as a clear-thinking and often pioneering biogeographer, entomologist, educator and above all as a limnologist in the broadest sense. His life and career spanned Africa and Canada, although his influence remains very much associated with Africa, from Ethiopia to the Cape.



Arthur D. Harrison. Photo Helen James

Arthur was born in the Western Cape of South Africa, at Kalk Bay, on 24th December 1921, and he lived for a period at Fish Hoek (where he returned in retirement – see photograph). He attended school in Rondebosch and then studied at the University of Cape Town where he gained B.Sc and M.Sc. He then obtained teaching qualifications (B.Ed) and took up a teaching appointment before deciding that research was to be his career. He gained a po-

sition at CSIR (South Africa’s Council for Scientific and Industrial Research) undertaking limnological surveys in rivers and estuaries. This led to the award of a Ph.D. for his pioneering studies of the Great Berg River (of the Western Cape), published in two parts in the Transactions of the Royal Society of South Africa (Harrison 1958; Harrison & Elsworth 1958) and revisited subsequently (e.g. Harrison 1964). These papers (‘beacons’ in the literature according Allanson 2003) remain well-cited and show Arthur’s early recognition of the downstream effects (zonation) in river structure and function from headwaters to estuaries. From the outset Arthur balanced his limnological studies with the applied – one of his earliest papers concerned the effects of acidic mine pollution on the streams of the Transvaal. Throughout his career, by himself or others with his assistance, revealed a range of human impacts on aquatic ecosystems.



Fish Hoek. Photo P. Cranston

After relocations with CSIR (Witwatersrand University, then Pretoria) Arthur took up a Rockefeller-funded position studying *Bilharzia* at the University of Salisbury, in what was then (early-1960s) Rhodesia. Arthur clearly had some time on his hands aside from studying the effects of molluscicides. He observed the recovery of a Rhodesian stream, post-drought, including documenting

the chironomids, and finding the adults of the first known podonomine midge from Africa, described as *Afrochlus harrisoni* by Freeman (1964). Following the Unilateral Declaration of Independence (from the UK) in November 1965, Rockefeller funding was withdrawn under sanctions, and Arthur returned to South Africa to become Professor of Zoology at the University of Natal, in Pietermaritzburg.

This was a short-lived appointment as Arthur accepted an invitation to join the faculty of the University of Waterloo in Ontario, Canada, where under Noel Hynes he joined a dynamic group of tropical limnologists. At this time Arthur's deepening personal interest in the chironomids became more evident. Although he had collected the midges throughout his career, including finding in 1954 *Harrisonina petricola* Freeman in an ephemeral stream in Oliphants Valley and recognising it as curious, he passed many of his specimens onto others, first to Marjorie Scott, and then to Paul Freeman at the Natural History Museum, London (BMNH). However his own first publications on the group started to appear in the early 1970s, with his interest in the Tanypodinae evident when he took Sepp Fittkau's (1962) revision of the Tanypodinae and placed the somewhat neglected African species into the modern generic concepts (Harrison 1971). In the course of this study, he described his first midge genus (*Lepidopelopia*) for the 'one that didn't fit' the Fittkau scheme (Harrison 1970). It was at this time that I first met Arthur as he came through London to view the types of the African Tanypodinae held in the BMNH – he asked me to make microscope slide preparations in advance of his visit so that he could see features such as the spurs on the adult legs that characterised Fittkau's new taxa. Arthur was a stickler for correct preparations, and it gave me some pleasure to 'pass the test'. He was very alert to the 'modern' means of doing chironomid taxonomy, and made slides of most of his specimens as he collected them. Further, he reared much and tried to incorporate the immature stages.

For many subsequent years our paths did not cross, as Arthur spent his time either in Waterloo, or seconded to the University of Addis Ababa in Ethiopia. From 1981 to 1989 he was a major contributor to the Canadian International Development Agency (CIDA)-funded Institutional Enhancement project, spending 4 years living there. Another of the Waterloo faculty engaged in this project, Herbert Fernando, recalled 'At the best of times Ethiopia is not an easy country to work in. But these were not good times. We needed permission from

the highest government authorities to leave Addis Ababa even for field work.' Despite this situation, experienced Africa-hand Arthur succeeded in doing much publishable research, and he produced a series of papers on the Chironomidae of Ethiopian lakes, extending distributions of known taxa, and describing new species and new life histories. He managed to get himself to the high elevation streams as well as the Rift Valley lakes, and published general invertebrate reviews with Noel Hynes and some particular chironomid papers. Arthur published this work especially in *Archiv für Hydrobiologie* and *Spixiana*, and always he tried to get his research out to the appropriate audience. When *Aquatic Insects* started, he was a contributor and supporter from the outset (e.g. Harrison 2000). Further, he seemed never to decline an invitation to summarise his compendious and very broad understanding of the ecology and distribution of African invertebrates (e.g. Harrison 1978, 1995). He wrote fluently and with a highly readable style – and was a frequent correspondent and an early adopter of e-mail.

On his retirement from Waterloo, he lived on Vancouver Island for some years, but he felt the health of his wife, Jessie, might benefit from returning to South Africa where more help was available. Although she died in 1994, Arthur remained in Fish Hoek, making periodic visits to his family in Canada and to Perth, Australia. It was in the Western Cape, post-apartheid, that I resumed 'in person' acquaintance with Arthur as I started to visit the 'rainbow nation' and adjacent countries. Arthur guided me by hand-drawn maps and photographs and detailed verbal instructions to localities including for *Afrochlus* in Zimbabwe (see photograph of Ngoma Kurira) and *Aphrotenia* in the Western Cape. He had immense knowledge (and profound memory) of aquatic locations and their inhabitants throughout southern Africa. In the 1990s and early years of this century, this knowledge continued to be extended as he identified chironomids, seemingly for all aquatic research groups in South Africa. Fortunately he continued to publish from his immense collections and those provided by his collaborators, although his field work was curtailed. When Don Edward (University of Western Australia) and I visited the Cape in 1998, Arthur accompanied us to the upper Eerste River in Jonkershoek. We collaborated subsequently, including over an orthoclad, *Elpiscladius*, a member of the *Brillia* group for which Arthur had a pharate male (Harrison & Cranston 2007). Little did we know but the then-unknown larva was in the Eerste – mining in immersed wood as its phylogeny predicted (Cranston 2008).



Ngome Kurira. Photo: P. Cranston.

My last meeting with Arthur in person was in Fish Hoek in early 2004 when he announced that he was to return to be nearer to the trusted medical facilities of Vancouver. Arthur continued to write wonderful e-mails, full of biogeographic and taxonomic insights from the vast range of organisms with which he was familiar. If a communication silence went on too long he would write simply to enquire 'where in the world was I?'. The last silence though was on his part: the precursor to his death at the end of 2007, although sadly this news was slow to spread.

Arthur Harrison was an immensely knowledgeable, insightful and very productive scientist to the end. Justifiably, his major works continue to be well cited – he was a limnological pioneer in Africa at the time the field was in its infancy. His breadth of knowledge of invertebrates and their distributions was unrivalled, and his biogeographic insights (e.g. Harrison 1978) have stood the test of time. Further, although he had a tremendous empathy with local peoples, he showed that quality biological research can be produced under most arduous circumstances. We will not see his like again.

I am grateful to Ferdy de Moor for provoking this article – I hope that my heartfelt appreciation is better late than not at all.

Peter S. Cranston
University of California, Davis

References

- Allanson, B.R. 2003. Beacons in the limnological landscape. - *African Journal of Aquatic Science* 28: 89-101
- Cranston, P.S. 2008. Phylogeny predicts larval biology in a wood-mining chironomid (Diptera: Chironomidae). - *African Entomology* 16: 1-6.
- Fittkau, E.J. 1962 Die Tanypodinae (Diptera: Chironomidae). (Die Tribus Anatopyniini, Macropelopiini und Pentaneurini). - *Abhandlungen zur Larvalsystematik der Insekten* 6: 1-453.
- Freeman, P. 1964. Notes on Chironomidae (Diptera, Chironomidae). - *Proceedings of the Royal Entomological Society of London (B)* 33: 147-150.
- Harrison, A.D. 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part 2. Quantitative studies on sandy bottoms, notes on the tributaries and further information on the fauna, arranged systematically. - *Transactions of the Royal Society of South Africa* 35: 227-276.
- Harrison, A.D. 1964. An ecological study of the Berg River, pp.143-158, in *Ecological Studies in Southern Africa*, ed. D.H.S. Davis, The Hague: W. Junk, 415pp. (Monographiae Biologicae 14).
- Harrison, A.D. 1970. Lepidopelopia, a new chironomid genus with scale-like setae on the legs (Dipt., Chironomidae). - *Journal of the Entomological Society of South Africa* 33: 295-301.
- Harrison, A.D. 1971. A conspectus of the Macropelopiini and Pentaneurini (Tanypodinae: Chironomidae) of Africa south of the Sahara. - *Canadian Entomologist* 103: 386-390.
- Harrison, A.D. 1978. Freshwater invertebrates (except Molluscs), pp. 1139-1152, in *Biogeography and Ecology of Southern Africa*, ed. M.J.A. Werger, with the assistance of A. C. Van Bruggen. 2 parts. The Hague: Dr W. Junk. 1-660 p. (pt. 1); 661-1439 p. (pt. 2). (Monographiae Biologicae, 31).
- Harrison, A.D. 1995. Northeast Africa Rivers and Streams, pp. 507-517, in *Ecosystems of the world: 22. River and stream ecosystems*, eds. C. E. Cushing, K. W. Cummins, and G. W. Minshall, Amsterdam, The Netherlands, Elsevier, 817 pp.
- Harrison, A.D. 2000. Four new genera and species of Chironomidae (Diptera) from southern Africa. - *Aquatic Insects* 22: 219-236.
- Harrison, A.D. & Cranston, P.S. 2007. Elpiscladius Harrison and Cranston, a new orthoclad (Diptera: Chironomidae) in the Brillia group from South Africa. - *Annals of the Eastern Cape Museum* 6: 1-11.
- Harrison, A.D. & Elsworth, J.F. 1958. Hydrobiological studies on the Great Berg River, Western Cape Province. Part I General Description, Chemical Studies and Main Features of the Flora and Fauna. - *Transactions of the Royal Society of South Africa* 35: 125-226.

PAUL FREEMAN – AN APPRECIATION OF HIS STUDIES ON CHIRONOMIDAE



Paul Freeman, August 1960. Photo G.W. Byers

Dr. Paul Freeman died at the age of 94 at the end of July this year. To many contemporary chironomologists he will be known principally for his contribution to untangling the taxonomy of the sub-Saharan African Chironomidae. The results were published in 4 parts in the *Bulletin of the British Museum (Natural History)*, Entomology series, between 1955 and 1958 (Freeman 1955, 1956, 1957, 1958), followed by the Chironomidae of New Zealand (Freeman 1959) and of Australia (Freeman, 1961). One third of Freeman's scientific publications (of 86 in total) concerned the Chironomidae: the others ranged across several other families of nematoceros Diptera. After his first publication on chironomid midges (adding two new species to the United Kingdom list in 1948), the remainder concerned non-European species, especially, but not exclusively, from Africa, Australia and New Zealand. Freeman apparently never visited these countries but relied on an extensive network of colleagues who sent him adult midges. Amongst these scientists based in Africa were Arthur Harrison (whose commemoration can be found elsewhere in this issue) and Margaret (K.M.F.) Scott from the University of Cape Town, who are expressly thanked at the outset of the sub-Saharan studies for their big collection of adult midges 'in excellent condition'. From the Sudan, David (D.J.) Lewis is acknowledged for much material including the asthma-inducing Nile midge that Freeman named for its collector (*Cladotanytarsus lewisi* (Freeman, 1950)). From throughout colonial Africa people sent material to London, providing the impetus for a series of short papers on particular National Parks, especially those in central Africa. This material led Freeman to understand the problematic influence of the Abbe J.J. Kieffer – whose work

he described as 'very erratic', noting the 'very uncertain' concepts of genera, paucity of illustrations and redescription of the same species 'over and over again not only in different papers but even in the same one' (Freeman 1955: pp. 5–6). Although Freeman examined as many of Kieffer's types as could be found (many are lost amongst the 300 Kieffer described from the region), and he disentangled the taxonomic confusion as best he could, he concluded that more collecting was needed in type localities, picking out Kribi (tropical Cameroon) as especially important. Sadly this situation remains essentially as true today as it was during the 1950s.

Freeman's African studies were important in placing the midges of a large continent into more modern generic (including subgeneric) concepts, yet he published at a time of turn-over in our ideas and methods. Freeman used pinned adults, but prepared hypopygial mounts and drew quite detailed and accurate figures of these structures. The days of routine slide mounting of the complete adult were yet to come, but the warning that Freeman gave of the tendency of coverslips to 'distort' genitalia remains as pertinent today as then. The post-WWII years was the time when European entomologists were building on an increased understanding of the significance of the immature stages in classification – led by what has been termed the 'Thienemann school' of ecologists-turned-taxonomists. These disciples often reared their larvae to adulthood, retained the immature stages (the larvae and the quite critical pupal exuviae) and had sent the adults to Kieffer for description. The outcome became a more synthetic (and coherent) generic concept, often parallel to that derived from adults alone, but generally narrower. What is more, the Hennigian revolution was starting 'on the continent' with early adherents amongst some of the chironomid workers. One could cite Strenzke's (1960) explicit application to the chironomids (for *Clunio* and relatives), and phylogenetic thinking was evident earlier amongst the Thienemann group. Actually such thinking pre-dated Willi Hennig, as F.W. Edwards, one of Freeman's predecessors in studying Nematocera in the British Museum (*Natural History*), was remarkably prescient about these issues (Edwards, 1926). However Freeman's African studies were at the cusp of this transformation, and his higher level taxonomic work remained closer to the traditional adult-based scheme of Goetghebuer. This is not to criticise these studies for not being 'ahead of their time' from an ecological or phylogenetic perspective – history certainly has

been kind to Freeman's species concepts: his keys work, there is little or no synonymy, and the 'tidying-up' of so much of Kieffer's African concepts was of immense value to later taxonomists. For a more modern allocation of the taxa to genera, Freeman (with some help from an acolyte) did this in the *Catalogue of the Diptera of the Afrotropical Region* (Freeman & Cranston 1980) – his last publication on the family.

After the major African publication, Freeman continued to receive additional chironomids of interest, notably an Afromontane *Diamesa* from Mount Kenya, the southernmost representative of the genus (Freeman 1964a) and the first African species belonging to the 'cool stenothermic' subfamily Podonominae (Freeman 1964b). Paul recounted to me his astonishment when he referred Arthur Harrison's specimens of this first African podonome from Zimbabwe – the genus *Afrochilus* – to Lars Brundin who was revising the subfamily. Lars' postcard thanking Paul for the material was mailed from South Africa where Lars was already seeking more material. I am not sure if Freeman's astonishment concerned the ease with which the Head of Zoology at the Stockholm Museum could head south, or the cost, or both, but Lars was not only Head, but also in charge of the Museum's travel budget.

By this time Freeman had completed his immersion in Australasian Chironomidae – having produced first the study on New Zealand (Freeman 1959) and then his *Chironomidae of Australia* (Freeman 1961). These works differ from the African studies in several ways: the nomenclatural issues were more tractable (less of Kieffer), incompleteness of the survey material available to him was acknowledged (no Arthur Harrison!), more genera were described as new in the works (3 from New Zealand, 12 for Australia), and there was a strong visibility of some modern biogeographic thinking. Although Freeman did not publish on South American Chironomidae, he understood Edwards (1931) studies, and thus was able to recognise Neotropical elements in both New Zealand and Australia (e.g. *Stictocladius*, *Riethia*). Further, he reallocated some African species of Chironomini to groupings that he recognised and described as new from Australia, notably *Conochironomus* and *Skusella*. In the short summary in the introduction to the Australian work ('Distribution and affinities of the Australian Chironomidae'), there is scarcely an incorrect idea. Studies in both countries since Freeman's publications have extended the biogeographic ideas, notably through Brundin (1966) who encountered a much more diverse Podonominae fauna than Freeman had available to him, and

to myself including with Don Edward (e.g. Cranston & Edward 1999), who delved into the 'little black orthoclads' of the austral continents. Nevertheless, Freeman's new Antipodean genera hold up, including against the molecular data becoming available.

That Paul Freeman's research on Chironomidae slowed down, albeit almost ceased in the late 1960s was due to his promotion to lead the Entomology Department of the Natural History Museum (termed 'keeper'). His leadership skills were well demonstrated in 1964 when he organised the International Congress of Entomology, held in London. Further, he had a truly hands-on involvement in the sorely-missed 'new' Insect Gallery of the Museum that lured many a child, and perhaps adults too, with a celebration of insect diversity long before the term became popular. This was all before my time – when I interviewed for a lowly technical position in the Museum in the 'summer of mass unemployment' (1971) Freeman already had occupied the top floor Keeper's Office for 3 years. However he was the Departmental representative on the recruitment panel established for some vacancies, including the one that I had applied for: assistant scientific officer in the Ornithology section. On being told that the vacancy in birds was filled already, the Keeper put the 'soft sell' on me to consider working with insects, leveraging the Museum's generous policy on work release to pursue higher education and extolling the pathways that an enthusiastic junior member of the staff could pursue as a career. My negative experiences with entomology teaching during an incomplete undergraduate degree were no match for this persuasiveness, and so I declined other offers to control yeast quality in a brewery or culture cells in a cancer research hospital. Obituaries for Paul Freeman in the Guardian (<http://www.guardian.co.uk/environment/2010/aug/25/paul-freeman-obituary>) and the Telegraph (<http://www.telegraph.co.uk/news/obituaries/science-obituaries/7960471/Paul-Freeman.html>) both point to his support for his younger staff – he is quoted as stating "It is important to look after the junior staff, as the senior staff can look after themselves". I can affirm that this was especially so in my case – shortly after entry I was given the position of technical support for the nematocerous Diptera families, already a budding career trajectory for two assistants that later became Keepers – Dick Vane-Wright and Richard Lane. After familiarisation with the Diptera families and some work with both Tipulidae and Mycetophilidae I was encouraged, surely with the guiding hand of Paul Freeman, to curate the collections of Tanypodinae (which existed as pinned adults) in the light of Sepp Fittkau's *Die Tanypodinae* (Fittkau,

1962). There was a steep learning curve – it was in German (without Google translator to assist), dealt with features that could only be seen on good slide mounts with high power magnification, and described a plethora of genera compared to what was currently in use in English language guides. The visit to London of Arthur Harrison to review the African Tanypodinae against Fittkau’s work assured me not only that I was on the right track, but that I was not the only one interested in getting the subfamily into a modern framework.

When it came time to undertake a Ph.D., it was natural to stay with the Chironomidae, and I chose to work with the immature Orthocladiinae with guidance from ecologist Alan Hildrew and from Paul Freeman. This was before the days when Museums and like institutions saw a role for themselves in higher education, and certainly I was early into the system of having formal approval for Museum research to be directed towards the goal of a higher degree. As he had promised at outset, Paul Freeman was very supportive throughout the study and although not very conversant with immature stages he knew the broad and specific literature extremely well. Perhaps what has stayed with me most was his questioning of ‘publishability’ of research, long prior to the ‘publish or perish’ days. Simply put, he felt that if the taxpayer has paid for the research then there was an obligation to complete the work by publishing it. With the Keeper coming from a background in Diptera, I often heard it said that the cluster of staff Dipterists were the recipients of some favouritism. Although those were the days when budgets seemed to increase each year, and the Diptera section surely was blessed with a stream of very able technicians and some more senior recruits, Paul argued his strong support for the group was based on their publishing productivity. Amongst these was the multi-collaborative project led by Roger Crosskey’s editing of the *Catalogue of the Diptera of the Afrotropical Region* and for which Paul and I co-authored the Chironomidae contribution.

My career owes its entirety to that recruitment promise made by Paul Freeman, and delivered upon – support his junior staff he surely did, by deeds and example.

Peter S. Cranston
University of California, Davis

References

- Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagytiae. - *Kung. Sv. Vetenskapsakad. Handl.* 11: 1–472.
- Cranston, P.S. & Edward, D.H.D. 1999. *Botryocladius* gen. nov.: a new transantarctic genus of orthocladiine midge (Diptera: Chironomidae). *Syst. Ent.* 24: 305–33.
- Edwards, F.W. 1926. The phylogeny of nematoceros Diptera: a critical review of some recent suggestions. pp. 111–130, Internationaler Entomologen-Kongress, Zurich, July, 1925.
- Edwards, F.W. 1931. Part II. Fascicle 5. Chironomidae. *Diptera of Patagonia and South Chile.* pp. 232–331.
- Fittkau, E.J. 1962. Die Tanypodinae (Diptera: Chironomidae). (Die tribus Anatopyniini, Macropelopiini und Pentaneurini). - *Abhandl. Larvensyst. Ins.* 6: 1–453.
- Freeman, P. 1950. A species of chironomid from the Sudan suspected of causing asthma. *Proc. R. Ent. Soc. Lond. (B)* 19: 58–59.
- Freeman, P. 1955. A study of the Chironomidae (Diptera) of Africa south of the Sahara. Part I. *Bull. Brit. Mus. (Nat. Hist.), Ent.* 4: 1–67.
- Freeman, P. 1956. A study of the Chironomidae (Diptera) of Africa south of the Sahara. Part II. *Bull. Brit. Mus. (Nat. Hist.), Ent.* 4: 285–368.
- Freeman, P. 1957. A study of the Chironomidae (Diptera) of Africa south of the Sahara. Part III. *Bull. Brit. Mus. (Nat. Hist.), Ent.* 5: 321–426.
- Freeman, P. 1958. A study of the Chironomidae (Diptera) of Africa south of the Sahara. Part IV. *Bull. Brit. Mus. (Nat. Hist.), Ent.* 6: 261–363.
- Freeman, P. 1959. A study of the New Zealand Chironomidae (Diptera, Nematocera). *Bull. Brit. Mus. (Nat. Hist.), Ent.* 7: 393–437.
- Freeman, P. 1961. The Chironomidae (Diptera) of Australia. *Austr. J. Zool.* 9: 611–737.
- Freeman, P. 1964a. A new species of *Diamesa* (Diptera, Chironomidae) from Africa south of the Sahara. *Ann. (K.K.) Naturhist. Mus. Wien* 67: 407–408.
- Freeman, P. 1964b. Notes on Chironomidae (Diptera: Nematocera). *Proc. R. Ent. Soc. Lond. (B)* 33: 147–150.
- Freeman, P. & Cranston, P.S. 1980. Family Chironomidae. In Crosskey, R.W. (ed.), *Catalogue of the Diptera of the Afrotropical Region*, pp. 175–202. British Museum (Natural History), London.