Taxonomy and diversity of Afroalpine Chironomidae (Insecta: Diptera) on Mount Kenya and the Rwenzori Mountains, East Africa

Hilde Eggermont* and Dirk Verschuren

Limnology Unit, Department of Biology, Ghent University, B-9000 Ghent, Belgium

ABSTRACT

Aim Anthropogenic climate change is expected to result in the complete loss of glaciers from the high mountains of tropical Africa, with profound impacts on the hydrology and ecology of unique tropical cold-water lakes located downstream from them. This study examines the biodiversity of Chironomidae (Insecta: Diptera) communities in these scarce Afroalpine lake systems, in order to determine their uniqueness in relation to lowland African lakes and alpine lakes in temperate regions, and to evaluate the potential of Afroalpine Chironomidae as biological indicators to monitor future changes in the ecological integrity of their habitat.

Location Mount Kenya (Kenya) and Rwenzori Mountains (Uganda).

Methods The species composition of Afroalpine chironomid communities was assessed using recent larval death assemblages extracted from the surface sediments of 11 high-mountain lakes between 2900 and 4575 m. Results were compared with similar faunal data from 68 East African lakes at low and middle elevation (750–2760 m), and with literature records of Chironomidae species distribution in sub-Saharan Africa, the Palaearctic region and elsewhere. All recovered taxa were fully described and illustrated.

Results The 11-lake analysis yielded 1744 subfossil chironomid larvae belonging to 16 distinct taxa of full-grown larvae, and three taxa of less differentiated juveniles. Eleven of these 16 are not known to occur in African lakes at lower elevation, and eight taxa (or 50% of total species richness) appear restricted to the specific habitat of cold lakes above 3900 m, where night-time freezing is frequent year-round. The faunal transition zone coincides broadly with the Ericaceous zone of terrestrial vegetation (c. 3000–4000 m). Snowline depression during the Quaternary ice ages must have facilitated dispersion of cold-stenothermous species among the high mountains of equatorial East Africa, but less so from or to the Palaearctic region via the Ethiopian highlands.

Main conclusions Chironomid communities in glacier-fed lakes on Africa's highest mountains are highly distinct from those of lowland African lakes, and potentially unique on a continental scale. By virtue of excellent preservation and their spatial and temporal integration of local community dynamics, chironomid larval death assemblages extracted from surface sediments are powerful biological indicators for monitoring the hydrological and ecological changes associated with the current retreat and loss of Africa's glaciers.

Keywords

Aquatic biodiversity, biogeography, Chironomidae, lake temperature, lake zoobenthos, mountain lakes, Mount Kenya, Rwenzori, taxonomy.

*Correspondence: Hilde Eggermont, Limnology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat 35, B-9000 Ghent, Belgium.
E-mail: hilde.eggermont@ugent.be

INTRODUCTION

Concerns about the environmental effects of anthropogenic climate change are motivating considerable effort to model and predict the impact of global warming on regional ecosystems. This is particularly true for the high-mountain regions of tropical Africa, where climate change is expected to result in complete loss of ice caps and glaciers. On Mount Kilimanjaro (Tanzania), the ice cap covering its western (Kibo) top has shrunk by 80% in the last century; at this rate, all 'eternal' snow will disappear within two decades (Thompson *et al.*, 2002). Glaciers on Mount Kenya (Kenya) have shrunk by 40% since 1963 (Hastenrath, 1995). Likewise, in the Rwenzori Mountains (Uganda, Democratic Republic of the Congo) the ice field of Elena Glacier is thinning, and its front has retreated several hundreds of metres in the last 50 years (Kaser & Osmaston, 2002; Mölg *et al.*, 2003). This rapid retreat is consistent with warming of the tropical middle troposphere in recent decades (Hastenrath & Kruss, 1992; Gaffen *et al.*, 2000), though a longer-time decrease of precipitation and air humidity may be the principal cause of the near-continuous retreat of the African glaciers since 1850 (Hastenrath, 2001; Kaser *et al.*, 2004). Clearly, loss of permanent ice from the tops of Africa's highest mountains will have profound effects on the hydrology and temperature regime of alpine lakes located downstream from those glaciers. This by itself may have a severe impact on the integrity and function of these scarce Afroalpine aquatic ecosystems, and add to the direct effects of a regional rise in air temperature. Consequently, there is an urgent need to characterize the aquatic fauna and flora of these (still relatively) undamaged Afroalpine lakes, to determine their uniqueness in relation to both African lowland lakes and alpine lakes in temperate regions, and to find adequate means to monitor future changes in their biological diversity.

Chironomid larvae (Insecta: Diptera, non-biting midges) are a dominant component of bottom-dwelling invertebrate communities in lakes and streams around the world (Armitage *et al.*, 1995). Previous surveys of the chironomid fauna of African highland regions have mainly focused on flowing waters in the montane forest zone, e.g. mountain streams and rivers in Ethiopia (Harrison & Hynes, 1988; Harrison, 1991, 1992, 1996), Democratic Republic of the Congo (Lehmann, 1979, 1981), South Africa (Scott, 1958; Harrison & Agnew, 1962; Harrison, 2000a,b) and north-eastern Tanzania (Sæther & Wang, 1992; Andersen & Sæther, 1993, 1994a,b; Sæther & Andersen, 1993, 1995, 1996; Sæther, 1996; Stur & Ekrem, 2000). With the exception of a few streams at 2850–3500 m a.s.l. (above sea level) in Ethiopia (Harrison, 1991, 1992, 1996), most chironomid habitats studied so far are actually cool forest streams at modest elevations of c. 1400–2400 m. Standing waters within this altitude range in tropical Africa are still quite warm (surface temperatures of 18–26°C), and their chironomid fauna is similar to that of low-elevation lakes (Eggermont & Verschuren, 2004a,b). Little information is available on the chironomid fauna in Africa's true high-mountain lakes, which occur above the tree line within the Afroalpine zone of the few

sizeable mountain massifs higher than 3000 m. Their unique, perennially cold tropical standing-water habitat (Löffler, 1964) may well be reflected in a distinct and vulnerable aquatic fauna.

In this context we conducted a study of larval Chironomidae in 11 lakes situated between 2900 and 4575 m a.s.l. on Mount Kenya and the Uganda side of the Rwenzori Mountains. This paper presents diagnoses, illustrations and biogeographical notes for all encountered taxa, followed by an evaluation of species diversity compared to other groups of aquatic biota in these lakes, and of the uniqueness of this Afroalpine chironomid fauna compared with that of African lakes at low and middle elevations. Instead of studying collections of the living larval communities, we examined their remains preserved in recently deposited lake sediments. In the small lakes considered here, recent death assemblages yield a spatially and seasonally integrated picture of present-day species diversity (Frey, 1988), which would otherwise require intensive live collecting that in these remote locations is challenging to realize.

MATERIAL AND METHODS

Study area

Mount Kenya, at 5199 m the second highest peak in Africa, is an extinct volcano c. 3 Myr old, located on the equator in the central Kenya highlands (Fig. 1). The original mountain cone was possibly over 6000 m high, but glacial erosion during the Quaternary has worn away the top part and left in its place a jagged topography with U-shaped glacial valleys and cirque basins. Between 3500 and 4700 m a.s.l. these contain about 20 small glacier-fed lakes and isolated tarns. Lower down on the mountain several volcanic crater lakes occur; the highest of these is Rutundu at 3080 m a.s.l. Above the present-day snowline at 4500 m there are 12 remnant glaciers on Mount Kenya, which are all receding and thinning rapidly. The mountain climate is characterized by large diurnal temperature oscillations and small seasonal variation, heavy long rains in March–June, and short rains in October–November.

Mount Kenya, like other tropical mountains, exhibits discrete vegetation belts distributed over the altitudinal gradient (Fries & Fries, 1948; Hedberg, 1951, 1955; Coe, 1967). The studied surface-sediment samples (August 2000, authors' own collection; and 1995–96, courtesy of Alayne Street-Perrott, University of Wales, and Philip Barker, University of Lancaster, UK) are from one lake at the upper limit of the Bamboo zone (c. 2600–3000 m, with bamboo forest: Bandasa), two lakes in the Ericaceous zone (c. 3000–4000 m, characterized by low-lying heath-like shrubs and grasses: Rutundu and Ellis), two lakes in the Alpine zone [c. 4000–4500 m, dominated by giant groundsel (*Dendrosenecio*) woodland, giant lobelias and grassland: Large Hall Tarn and Hausburg Tarn], and one on the boundary between the Alpine and Nival zone (generally above 4500 m, with glaciers, snowfields and grass only in sheltered areas: Simba Tarn). These six lakes vary in surface-water conductivity from 8.8 to

Figure 1 Map of East Africa showing the position of mountain (>2000 m a.s.l.) and high-mountain (>3000 m a.s.l.) areas.

61 $\mu\text{S cm}^{-1}$, pH from 6.1 to 8.9 and water depth from 0.6 to 10.1 m (Table 1). For comparison we also analysed sediment samples from two lakes on the lower slopes of Mount Kenya,

i.e. in the Cultivation and Basal plateau belt (c. 1600–2000 m, dominated by grasses and agricultural crops: Rurie Swamp and Lake Nkunga). Their surface-water conductivities are 82.9 and 316 $\mu\text{S cm}^{-1}$, respectively, their pH is 7.3 and 6.7, and they are 1.0 and 1.6 m deep.

The Rwenzori Mountains are a group of six glaciated massifs stretching from Lake Edward to Lake Albert on the border between Uganda and the Democratic Republic of the Congo (Fig. 1). The high massifs (reaching between 4626 and 5109 m a.s.l.) are all topped with glaciers, and dissected by deep glacier-eroded valleys. Vegetation distribution is largely similar to that on Mount Kenya with some difference in altitudinal extent of the vegetation belts, and in the plant species present (Hedberg, 1951). The Rwenzori mountains are wetter than Mount Kenya because of heavier and more regular rainfall, with main rainy periods from mid-March to May, and from September to mid-December. An estimated 30 glacier-fed lakes and tarns occur on the Ugandan side, and another 10 or so on the Democratic Republic of the Congo side of the range. We studied samples (authors' own collection, July 2002) from five highly dilute lakes (surface-water conductivity between 6 and 26 $\mu\text{S cm}^{-1}$) situated in the Alpine zone (Bujuku, Lower Kitandara, Upper Kitandara and Josephat's Pool; with mosses, giant heather, lobelias and groundsels around the lakes) and the Nival zone (Green Pool; an isolated permanent pool surrounded by rocks with lichens, no real vegetation), spanning elevations between 3909 and 4341 m. Due to logistic constraints at the time of sampling, data on lake depth and temperature are currently not available for these Rwenzori lakes; their pH ranges between 6.1 and 7.8 (Table 1). In contrast to the study sites on Mount Kenya, where bottom-sediment samples were collected from a boat, larval chironomid communities in the Rwenzori lakes were studied using

Table 1 Overview of the study sites listed per region (Mount Kenya, Kenya; Rwenzori Mountains, Uganda) with environmental data, total number of chironomid fossils recovered, raw taxon richness, number of taxa expected in a sample of 50 fossils (ES_{50}) and Hill's N2 diversity measure. Surface-water temperatures are spot measurements at the time of sampling; pH values for the Rwenzori lakes are based on measurement 2–5 days after sampling

No.	Lake	Altitude (m a.s.l.)	Depth (m)	<i>T</i> (°C)	Conductivity ($\mu\text{S cm}^{-1}$)	pH	Sample code	No. of specimens	No. of taxa	ES_{50}	N2
Mount Kenya											
1	Rurie Swamp	1320	1.0	19.4–26	82.9	7.3	1995	138.5	18	10.7	3.4
2	Nkunga	1840	1.6	16.2–16.7	316	6.7	1995	140.5	21	13.2	3.7
3	Bandasa	2900	0.6	18	20.2	6.1	1995	133	7	6.4	3.2
4	Rutundu	3080	–	15.1–15.9	33.5	8.9	1995	240	6	5.2	3.1
5	Ellis	3500	7.0	12.3	33	8.2	1996	294	7	6.2	3.0
6	Large Hall Tarn	4300	1.0	9.8	8.8	7.2	1996	187	6	5.4	3.2
7	Hausburg Tarn	4352	10.1	4.8	23.4	6.9	HT 00-1G	139	9	8.3	3.4
8	Simba Tarn	4575	5.0	8.1	18.9	6.4	1996	75.5	5	4.0	2.4
Rwenzori											
9	Bujuku	3909	14.0	–	61	7.8	02-1S	115.5	5	4.0	2.6
10	Lower Kitandara	3990	11.0	–	25	6.7	02-1S	69	5	4.9	2.8
11	Upper Kitandara	4060	15.0	–	26	6.3	02-1S	112	8	5.9	2.9
12	Josephat's Pool	4109	–	–	23	6.4	02-1S	181	4	4.4	2.6
13	Green Pool	4341	–	–	6	6.1	02-1S	197.5	3	12.4	6.4

bottom sediments collected nearshore. We cannot assume that these present a fully integrated picture of faunal diversity in these lakes (Frey, 1988). However, cold polymixis (frequent mixing) and lack of submerged littoral vegetation (Löffler, 1964) creates similar well-oxygenated bottom habitat in both deepwater and nearshore environments. Consequently, recently deposited chironomid death assemblages are probably fairly homogeneous lake-wide.

Sample processing and analysis

Surface-sediment samples (0–5 cm) were prepared by dispersing the sediment in warm 10% KOH (Walker & Paterson, 1985), and rinsing through 150- and 100- μ m mesh sieves. Retained residues were scanned at 30 $\times$ magnification under transmitted light. All chironomid head capsules were picked and mounted in glycerine on microscope slides; cover slips were sealed with a synthetic epoxy. Identification was done at 100–400 $\times$, by comparison with reference collections from Lake Tanganyika (Eggermont & Verschuren, 2003a,b) and about 70 other low- and mid-elevation lakes in East Africa (Verschuren, 1997; Eggermont & Verschuren, 2004a,b), alpha-taxonomic literature (see Eggermont & Verschuren, 2003a), and general works on Holarctic and Nearctic Chironomidae (Wiederholm, 1983; Møller-Pillot, 1984a,b; Epler, 1995, 2001). Representative specimens were photographed with a Nikon Coolpix 990 digital camera. The illustrations presented here are Adobe Photoshop® collages of stacked partial images, each with certain skeletal elements in focus.

To ensure consistency of identification throughout the collection, all fossils were looked at several times until all specimens possessing a minimum set of diagnostic characters could be assigned to a distinct morphotype. Differences in diagnostic characters between these taxa resemble differences at the species level in live material from the Holarctic region, so we regard most of our fossil morphotypes to be equivalent to morphospecies. Morphological terminology follows Sæther (1980), supplemented by Kowalyk (1985), Rieradevall & Brooks (2001) and Webb & Scholl (1985) for the relevant taxa. Species attribution of the subfossil morphotypes follows criteria set out by Eggermont & Verschuren (2003a), using both morphological and biogeographical considerations. Specimens were attributed to a known morphotype when the minimum set of required diagnostic characters were recorded at least once per site. Morphotypes bearing no explicit resemblance with known African or Holarctic species and larval types are designated by their genus or tribe name followed by the name of the lake in which the most complete specimen was found, e.g. '*Larsia* type Kitandara'. If no single diagnostically complete specimen was found, we used the name of a lake in which the taxon was sufficiently abundant to construct a composite diagnosis.

Species richness was evaluated using the raw number of taxa present, and the number of taxa expected with constant sample size (ES_{50}) using Hurlbert's rarefaction method (Magurran, 1988); species diversity was evaluated using Hill's (1973)

diversity measure N_2 ; the two latter values were calculated using Primer® version 5.2.4 (Primer-E Ltd, 2001). The significance of differences in sample size between lakes and in taxonomic diversity between regions was assessed with the Student's *t*-test and Mann–Whitney *U*-test using STATISTICA 5.0 (StatSoft Inc., 1998).

RESULTS

Taxonomic overview

Analysis of the 11 surface-sediment samples from high-elevation lakes (>2900 m a.s.l.) yielded subfossil remains of 1744 chironomid larvae, of which 1731 (99.3%) could be assigned to 16 different taxa of full-grown larvae, and three morphotypes of less differentiated juveniles. The faunal inventory of full-grown larvae includes one species of Diamesinae, two Tanypodinae, six Orthoclaadiinae and seven Chironominae (four Chironomini and three Tanytarsini) (Table 2). All 19 taxa are diagnosed and illustrated below. A further 15 taxa were encountered only in the two mid-elevation lakes on Mount Kenya (Nkunga and Rurie Swamp) studied here for comparison. For completeness these are listed in Table 3, but not treated in the taxonomic section of this paper; we refer to Verschuren (1997) and Eggermont & Verschuren (2003a,b, 2004a,b) for a taxonomic diagnosis.

Subfamily Diamesinae

Diamesa rwenzoriensis Freeman (Figs 2 & 3)

Head capsule heavily sclerotized. Mentum with simple median tooth flanked by four pairs of well-developed lateral teeth, and another three to four pairs of smaller lateral teeth steeply sloping back on the curved lateral portions of the mentum. Ventromental plates inconspicuous, vestigial.

There are three known species of *Diamesa* in Africa, of which *Diamesa kenya* Freeman and *Diamesa freemani* Willassen and Cranston have been described as larvae (both from Mount Kenya; Willassen & Cranston, 1986). The present morphotype differs from *D. freemani* in having a mentum with only about eight pairs of lateral teeth (not 12), and from *D. kenya* in the more steeply sloping arrangement of the outer teeth. Our species designation is based on the reported occurrence of *Diamesa rwenzoriensis* at Lake Bujuku in the Rwenzori (Freeman, 1955). We did not find this species in Lake Bujuku but recovered it from two other Rwenzori lakes in the Alpine and Nival zone, above 4000 m.

Subfamily Tanypodinae

Tribe Macropelopiini

Procladius brevipetiolatus Goetghebuer (Figs 4 & 5). Ligula with concave row of five black, straight-pointed teeth, median tooth distinctly shorter and narrower than the lateral teeth.

Table 2 Chironomidae recovered from the 11 African high-elevation lakes (>2900m a.s.l.) studied, with number of lakes where each taxon was recorded, number of specimens analysed and the slide-collection codes of illustrated specimens

Morphotype	No. of lakes	No. of specimens	Collection code
Subfamily Diamesinae			
<i>Diamesa rwenzoriensis</i> Freeman	2	2	Green-3-1
Subfamily Tanypodinae			
Tribe Macropelopiini			
<i>Procladius brevipetiolatus</i> (Goetghebuer)	2	106	Ellis-4-21; 7-8
Tribe Pentaneurini			
<i>Larsia</i> type Kitandara	3	29.5	Lower Kitandara-2-5; 3-17;1-6
Pentaneurini larvula	1	1	Bujuku-3-7
Subfamily Orthoclaadiinae			
<i>Chaetocladius melaleucus</i> (Meigen)	7	280.5	Josephat's Pool-2-8; 2-43; 3-33; 2-35; Hausburg Tarn-5-3; Simba Tarn-1-9
<i>Limnophyes minimus</i> (Epler) group	9	374	Green-3-9; 2-34; 2-9
Near <i>Paraphaenocladus</i> type Ol Bolossat	1	1.5	Nkunga-3-3
<i>Paratrachocladus</i> type Hausburg Tarn	3	77	Hausburg Tarn-3-6; 5-4; Simba Tarn-2-10
<i>Paratrachocladus</i> type Simba Tarn	6	108.5	Simba-1-22; Hausburg Tarn-3-4
<i>Pseudosmittia</i> type Tanganyika	3	13.5	Hausburg Tarn-5-17
Subfamily Chironominae			
Tribe Chironomini			
<i>Chironomus</i> type Kibos	3	7	Hausburg Tarn-1-2
<i>Chironomus</i> near <i>imicola</i> (Kieffer)	5	182.5	Rutundu-4-20; 2-5
<i>Dicrotendipes</i> near <i>pilosimanus</i> (Kieffer)	5	90.5	Nkunga-3-12; Bandasa-2-17
<i>Polypedilum</i> type Bandasa	2	43.5	Bandasa-1-23
Chironomini larvula type 1	5	173	Hausburg Tarn-10-3
Chironomini larvula type 2	2	15	Ellis-7-28
Subfamily Tanytarsini			
<i>Rheotanytarsus</i> type Kitandara	1	1.5	Upper Kitandara-2-16
Tanytarsini indet. type Ellis	3	164	Ellis-6-41
Tanytarsini indet. type Large Hall Tarn	2	60	Large Hall Tarn 2-1; 4-2

Paraligula with a tall apical point, barbed on both sides (about four to six teeth on the outer side and two or three points on the inner side). Dorsomentum with two rows of seven or eight teeth on either side of the median, but always fewer in early instars (usually about five). Mandible with a uniformly curved apical tooth about a third of the length of the mandible, a large pale basal tooth with blunt apex pointing distally, and a small pale accessory basal tooth lodged between them on the inner mandibular margin. Pecten hypopharyngis well-developed with a strong medial tooth and about 11 more teeth of equal length. Basal segment of the antenna stout about four to five times its basal width, ring organ about a third from the distal end. Cephalic setation as for the genus, with DP present, S8 and S7 in an angulated line, and S5 anteromesial to S8 (not illustrated). First-instar larvae of this type (Fig. 5) have a ligula with constricted base, and four teeth, of which the outer dark-coloured pair are distinctly swollen and point outward, while the median teeth are very small and pale; dorsomentum with at least three teeth on either side of the median; mandible with indication of a developing basal tooth; basal segment of antenna short, about three times its basal width.

There are seven known *Procladius* species in sub-Saharan Africa, of which at least two species (*Procladius brevipetiolatus*

Goetghebuer and *Procladius shibrui* Harrison) have been collected at high-elevation sites (Freeman, 1955; Harrison, 1991, 2000a). This particular fossil type is identical to larval *P. brevipetiolatus* described from various East African lakes and reservoirs (Chrispeels, 1959; McLachlan, 1969; Harrison, 1991), and widely distributed in lakes at low and middle elevations (Verschuren, 1997; Eggermont & Verschuren, 2004a). Here we found it to be common at two lakes in the Ericaceous zone of Mount Kenya (Fig. 2); it also occurs lower down on the mountain (Table 3).

Tribe Pentaneurini

Larsia type Kitandara (Figs 6–9). Head capsule yellowish brown, with two longitudinal grooves positioned symmetrically above the ventrobasal margin (Fig. 6). Ligula with weakly concave row of five teeth, three central teeth roughly equal in size with apices pointing forward, middle section moderately narrowed, and shallow stripe-like muscle-attachment area. Paraligula bifid, about half the length of the ligula, outer point about two and a half times the length of the inner point, inner point arising from immediately above a weakly thickened base. Mandible narrow and strongly curved,

Morphotype	Rurie Swamp	Nkunga	Reference
Subfamily Tanypodinae			
Tribe Tanypodini			
<i>Tanytus</i> near <i>guttatipennis</i> Goetghebuer	5	1	1, 4
Tribe Macropelopiini			
<i>Procladius</i> <i>brevipetiolatus</i> (Goetghebuer)*	2	1	1, 4
Tribe Pentaneurini			
<i>Paramerina</i> cf. <i>ababae</i> Harrison	13	6	4
Pentaneurini indet. type Naivasha	3	3	4
Pentaneurini larvula*	0	1	4
Subfamily Orthocladiinae			
<i>Corynoneura</i> cf. <i>coronata</i> Edwards	1	0	2, 4
<i>Limnophyes minimus</i> (Epler) group*	15.5	7	6
near <i>Paraphaenocladus</i> type Ol Bolossat*	0	4.5	4
<i>Psectrocladius viridescens</i> Freeman	0	10.5	1, 2, 4
<i>Pseudosmittia</i> type Tanganyika*	10.5	3	2, 4
Orthocladiinae indet. type Amboseli NP Pool 3	1	0	4
Subfamily Chironominae			
Tribe Chironomini			
<i>Acinoretractus</i> near <i>multispinosus</i> (Freeman)	0	2	5
<i>Chironomus</i> near <i>alluaudi</i> Kieffer	5	0	1, 3, 5
<i>Chironomus</i> type Kibos *	4	12	5
<i>Chironomus</i> near <i>imicola</i> (Kieffer)*	3	0	5
<i>Dicrotendipes</i> near <i>pilosimanus</i> (Kieffer)*	1	24	6
<i>Kiefferulus chloronotus</i> (Kieffer)	8.5	5	1, 3, 5
<i>Parachironomus</i> type Naivasha	1	4	5
<i>Polypedilum</i> cf. <i>trigonus</i> Townes	13	3	5
<i>Polypedilum</i> type Bandasa*	1	3	6
<i>Polypedilum</i> type Narasha	0	19	5
Chironomini larvula type 1*	0	3	5
Chironomini larvula type 2*	0	1	5
Subfamily Tanytarsini			
<i>Cladotanytarsus pseudomancus</i> (Goetghebuer)	1	0	1, 5
<i>Tanytarsus</i> near <i>formosanus</i> Kieffer	49	8	1, 5
Tanytarsini indet. type Kifuruka	0	13	5

Table 3 Chironomidae recovered from Rurie Swamp (1320 m a.s.l.) and Lake Nkunga (1840 m a.s.l.) on Mt. Kenya, with primary reference(s) for the taxonomic diagnosis (1, Verschuren, 1997; 2, 3, Eggermont & Verschuren, 2003a,b; 4, 5, Eggermont & Verschuren, 2004a,b; 6, this study). Taxa also recovered from the high-elevation sites are marked by an asterisk

with a large basal tooth, a smaller accessory tooth, and a pronounced projection at its base. Pecten hypopharyngis with about 15 pointed teeth, the innermost corner tooth larger than the remaining teeth. Dorsomentum a sclerotized complex without teeth, extending by ridges to the ventral region of the premento-hypopharyngeal complex, and apically ending in a blunt process, with a large, apically directed dorsal tooth. Basal segment of the maxillary palp undivided, with ring organ at about a quarter of the distance from the distal end. Basal segment of the antenna relatively long, about nine to ten times its basal width, with ring organ at about a third of the distance from the distal end. Cephalic setation as typical for the genus, with seta 10 (S10) posterolateral to seta 9 (S9), ventral pore (VP) posterolateral to S9, closer to S9 than S10, and greater than the setal sockets; dorsally, seta 5 (S5) anterior to the dorsal pore (DP), close grouping of seta 8 (S8) and seta 7 (S7) (Fig. 8).

Some six species of *Larsia* are known to occur in sub-Saharan Africa (Freeman & Cranston, 1980), but none have

been described as larva. This morphotype was found in three Alpine lakes in the Rwenzori (Fig. 2), comprising up to 15.9% of the recovered local fauna.

Pentaneurini spp. larvula (Fig. 10). Ligula slightly concave, with four teeth, of which the outer lateral teeth are wide and the median teeth narrower and smaller. Paraligula bifid, but very small and usually unclear in fossil specimens. Mandible with a pointed apical tooth, otherwise no other details visible. Pecten hypopharyngis with about four or five teeth. Basal segment of the antenna up to six times its basal width.

This morphotype groups first instar larvae of various *Pentaneurini* taxa. In East African low-elevation lakes it most likely represents larvae of *Ablabesmyia* and *Paramerina* species (Eggermont & Verschuren, 2004a). In this collection, a specimen found at Lake Bujuku (Rwenzori) is possibly *Larsia*; and a specimen from Lake Nkunga (Mount Kenya) is possibly *Paramerina* near *ababae* or *Pentaneurini* indet. type Naivasha.

Figure 2–10 Subfossil remains of larval Diamesinae and Tanypodinae from East African mountain lakes: (2, 3) *Diamesa rwenzoriensis* Freeman; (4) *Procladius brevipetiolatus* Goetghebuer; (5) *Procladius brevipetiolatus* Goetghebuer, early instar; (6–9) *Larsia* type Kitandara; (10) *Pentaneurini* sp. larvula. Scale bar = 25 μ m.

Subfamily Orthocladiinae

Chaetocladius melaleucus (Meigen) (Figs 11–16). Head capsule strongly sclerotized. Mentum with a double median tooth and five pairs of pointed lateral teeth with apices in slightly convex alignment; median tooth about two and a half to three times as wide as the first laterals, and two small nipples in unworn specimens; in early (first and second) instars, the incision between the first and second laterals is sometimes deeper than adjacent incisions; setae submenti located near the posterior margin of the ventromental plates, below the second laterals. Ventromental plates well developed, with a strongly sclerotized triangular plate extending scarcely beyond the basal margin of the mentum. Apical tooth of mandible shorter than the combined width of the three inner teeth; mola nearly as dark as the inner teeth; seta subdentalis stubby, placed well below the mola; seta interna with at least six strong branches, all toothed at one side of distal quarter (Fig. 16); dorsal surface of the mandible with flanged inside margin, coloured light brown (Fig. 15). Pre-mandible with two apical, and one blunt

subapical tooth (Fig. 15). Pecten epipharyngis with three teeth; about six pairs of chaetulae laterales present; S I toothed at both sides. Antenna with five segments; first antennal segment about twice its basal width; third and fourth segment subequal; blade shorter than flagellum (Fig. 13).

At least two *Chaetocladius* species occur in East Africa (Freeman & Cranston, 1980; Harrison, 1992), but their larvae are unknown. Our species designation is based on adult *Chaetocladius melaleucus* having been netted in the vicinity of Lake Bujuku (Freeman, 1956), where this morphotype occurs. It appears restricted to the Alpine and Nival zones, but is fairly common both in the Rwenzori (five lakes) and on Mount Kenya (two lakes). The other East African species, *Chaetocladius awasae* Harrison, has been recorded only from the Ethiopian Rift Valley and South Africa (Harrison, 1992, 2000a).

Limnophyes minimus group (Epler) (Figs 17–19). Mentum uniformly pale brown with double median tooth and five pairs of lateral teeth; median tooth about two and a half times as wide as the first laterals; lateral portions of the mentum concave, with second to fourth laterals gradually diminishing

Figure 11–23 Subfossil remains of larval Orthocladiinae from East African mountain lakes: (11–16) *Chaetocladius melaleucus* (Meigen); (17–19) *Limnophyes minimus* (Epler) group; (20) near *Paraphaenocladus* type Ol Bolossat; (21–23) *Paratrachocladus* type Hausburg Tarn. Scale bar = 25 µm.

in size; fifth laterals small. Ventromental plates narrow anteriorly, widened and sclerotized posterolaterally into a rounded plate extending beyond the basal margin of the mentum. Mandible with apical tooth much shorter than the combined width of the three inner teeth; seta subdentalis stout, not extending beyond the third inner tooth (Fig. 18). Pre-mandible with two rounded apical, and two subapical teeth. Antenna with five segments; fourth segment longer than third segment; blade about as long as the flagellum (Fig. 19).

Sæther (1990) recognized four African species of *Limnophyes*, of which *Limnophyes bubo* Sæther, *Limnophyes lobiscus* Sæther and *Limnophyes minimus* (Meigen) appear to be restricted to high-elevation sites in East Africa (including the Rwenzori and Mount Kenya; Sæther, 1990), whereas *Limnophyes natalensis* (Kieffer) is also widely distributed in lowland lakes and streams throughout eastern and southern Africa. All four African *Limnophyes* species belong to the *L. minimus* group as defined by Epler (2001), but their larvae cannot reliably be separated without associated adults (Sæther, 1990; Epler, 2001). This morphotype matches larval *L. minimus* described from the Kerguelen Islands (Sæther, 1990), but also *L. natalensis* (Sæther, 1990; Eggermont & Verschuren, 2004a).

Given the possible occurrence of all four African *Limnophyes* species in the study area, we attribute this morphotype to the species group. It occurs at all altitudes (Fig. 2) both in the Rwenzori and on Mount Kenya, most abundantly in the Alpine and Nival zones (making up 97.0% of the fauna in Green Pool).

Near *Paraphaenocladus* type Ol Bolossat (Fig. 20). Mentum with a broad single median tooth, and five pairs of lateral teeth pointing inward; median tooth about two and a half to three times as wide as first laterals, nipped in unworn specimens but the small point is often broken off; first and second laterals large and pointed; fourth and fifth laterals small and pointing inwards; lateral margin of the mentum with indentation below the fifth laterals; setae submenti positioned below the incision between the median tooth and first laterals. Ventromental plate conspicuous, laterally extending beyond the mentum. Mandible with apical tooth shorter than the combined width of the four inner teeth, and wide mola extending to behind the second inner tooth; seta subdentalis short and pointed.

Mentum, ventromental plates and mandible of this taxon resemble *Paraphaenocladus*, which has two African represent-

atives (Freeman & Cranston, 1980), but skeletal elements that would permit definitive generic assignment (labro-epipharyngeal region, antenna) were missing in our material. This morphotype also occurs in both fresh and saline waters in the lowlands of Kenya and Uganda, suggesting it may group a number of sibling species (Eggermont & Verschuren, 2004a). Here we recovered it from the alpine Upper Kitandara Lake (Rwenzori), and from the mid-elevation Lake Nkunga (Mount Kenya).

Paratrachocladus type Hausburg Tarn (Figs 21–23). Head capsule strongly sclerotized. Mentum with a simple median tooth and first two pairs of lateral teeth pale brown, separated from the rest of the mentum by a deep incision; median tooth broadly domed, about two to two and a half times as wide as the first laterals; first laterals with rounded apex; second laterals pointed and smaller than both first and third laterals, leaning against the first laterals, but still clearly separated from them; third to sixth laterals about equal in size, dark brown with pointed apices; setae submenti located below the lateral margin of the mentum. Ventromental plates conspicuous and

sclerotized, starting from below the second laterals. Mandible with a narrow apical tooth shorter than the combined width of the three inner teeth, inner teeth gradually decreasing in size; outer margin always smooth; seta subdentalis short and pointed, placed below a well-developed mola (Fig. 23). Pre-mandible with one apical tooth (Fig. 23). Antenna with five segments gradually becoming smaller; ring organ at basal third of first antennal segment.

The genus *Paratrachocladus* includes three known African species, of which *Paratrachocladus micans* (Freeman) and *Paratrachocladus pretorians* (Freeman) are known to occur in the highlands (Lehmann, 1979; Freeman & Cranston, 1980). This morphotype was fairly common in Hausburg Tarn, Large Hall Tarn (both Mount Kenya), and Lower Kitandara (Rwenzori), all situated in the Alpine zone.

Paratrachocladus type Simba Tarn (Figs 24 & 25). This morphotype closely resembles *Paratrachocladus* type Hausburg Tarn as described above, but the median tooth is only about as wide as a first lateral tooth, and scarcely protruding them; second laterals pointing forwards, separate

Figure 24–34 Subfossil remains of larval Orthocladiinae and Chironomini East African mountain lakes: (24, 25) *Paratrachocladus* type Simba Tarn; (26) *Pseudosmittia* type Tanganyika; (27, 28) *Chironomus* type Kibos; (29, 30) *Chironomus* near *imicola* (Kieffer); (31–33) *Dicrotendipes pilosimanus* (Kieffer); (34) *Polypedilum* type Bandasa. Scale bar = 25 µm.

from the first laterals in unworn specimens but frequently worn down to nothing more than a rounded shoulder on the side of the first laterals.

This species was fairly common throughout the study region (four lakes in the Rwenzori and two on Mount Kenya), but it appears to be restricted to the Alpine and Nival zone (up to 78% of the fauna in Simba Tarn, Mount Kenya). In Hausburg Tarn (Mount Kenya) and Lower Kitandara (Rwenzori), it occurs together with *Paratrichocladius* type Hausburg Tarn.

Pseudosmittia type Tanganyika (Fig. 26). Mentum with a single domed median tooth which sometimes has a central nipple, and four pairs of lateral teeth; first laterals protruding, pointing outwards in unworn specimens, second to fourth laterals about equal in size; lateral margin of mentum constricted below the fourth laterals. Ventromental plates distinct, also a second plate is present and extends beyond the mentum laterally but the latter is often worn down. Mandible with apical tooth shorter than the combined width of the three inner teeth.

Pseudosmittia occurs with at least four species in equatorial Africa (Harrison, 1992, 2000a), but their larvae are unknown. One species, *Pseudosmittia rectilobus* (Freeman) is known from highland regions (Freeman, 1955; Harrison, 1992). Specimens in the present material are indistinguishable from *Pseudosmittia* sp. diagnosed from Lake Tanganyika (Eggermont & Verschuren, 2003a) and reported from various other African lakes (Eggermont & Verschuren, 2004a). We found it in alpine lakes both on Mount Kenya and the Rwenzori, and in the mid-elevation lakes Nkunga and Rurie Swamp (Mount Kenya).

Subfamily Chironominae

Tribe Chironomini

Chironomus type Kibos (Figs 27 & 28). Mentum with trifid median tooth and six pairs of lateral teeth; the central median tooth accounts for distinctly less than half the total width of the median, and the lateral median teeth reaching at least half the height of the central median tooth; their apices point forward; lateral median teeth separate from the central tooth and well-developed, but always less than half the height of the central tooth (unlike *Chironomus* near *imicola*, see below); the first and second pair of the lateral teeth stand close together but are not fused; the configuration of the fourth to sixth laterals is usually according to mentum type I of Webb & Scholl (1985), i.e. with apices of the third to fifth laterals placed in line (Fig. 27). Ventromental plates fan-shaped, 1.0–1.1 times the width of the mentum, anterior margin smooth. Mandible with row of radially arranged grooves on the ventral surface as characteristic for *Chironomus*, and with an apical, one dorsal, and three inner teeth; third inner tooth small and slightly paler than the remaining teeth, i.e. *Chironomus* mandible type II of Webb & Scholl (1985); seta interna with four plumose branches; inner mandibular margin with about

three spines in the basal quarter; seta subdentalis with broad base, stout and pointed. Pre-mandible bifid with outer tooth stiliform, narrower than the inner tooth. Pecten epipharyngis with around 13–17 subequal teeth.

Some 15 *Chironomus* species are reported to occur in equatorial Africa (Freeman & Cranston, 1980), six of which have been described as larvae (Dejoux, 1968, 1970; McLachlan, 1969; Petr, 1972; Harrison, 1996) but none of these is similar to the present morphotype, which was first described from Kibos Swamp in Lake Victoria (Eggermont & Verschuren, 2004b) and found to be widespread throughout Uganda and Kenya. The specimens here were recovered from five lakes distributed across the altitudinal gradient on Mount Kenya.

Chironomus near *imicola* (Kieffer) (Figs 29 & 30). Head capsule of full-grown larvae mostly dark brown, with pigmentation often extending forward beyond halfway to the gula; early instars scarcely pigmented. Mentum with trifid median tooth of which the central median tooth is prominent, almost half the total width of the median tooth; lateral median teeth separate from the central tooth and well-developed, but always less than half the height of the central tooth (unlike *Chironomus* type Kibos, see above), and pointing slightly inward; first and second laterals strongly protruding and fused over much of their length, incision between second and third laterals distinctly deeper and wider than adjacent incisions; fourth laterals always smaller and less wide than fifth laterals, and placed as in *Chironomus* mentum type II (i.e. with apex of fourth laterals clearly below the line connecting the apices of the third and fifth laterals, and the line connecting the apices of the fourth and fifth laterals nearly horizontal relative to the axis of symmetry), *Chironomus* mentum type III (having the fifth laterals slightly higher than the fourth laterals), or an intermediate configuration. Ventromental plates, mandible and pre-mandible as in *Chironomus* type Kibos. Pecten epipharyngis with at least 13–15 teeth of irregular length.

This taxon was previously described from low-elevation lakes in East Africa (Eggermont & Verschuren, 2004b). Here it was found only on Mount Kenya, but fairly commonly at all altitudes (seven lakes, spanning elevations between 1320 and 4575 m a.s.l.). In the alpine lakes it was more common than *Chironomus* type Kibos, discussed above.

Dicortendipes pilosimanus (Kieffer) (Figs 31–33). Mentum very dark brown to black, with single median tooth and six pairs of lateral teeth; median tooth not protruding beyond the first laterals, and with barely noticeable lateral incisions; second laterals small, fully fused with the first laterals so as to form no more than a notch on the side of the first laterals just below the apex of the third laterals; third to sixth laterals normally developed, gradually diminishing in size. Ventromental plates compact fan-shaped, about 0.7 times the width of the mentum, with about 40–46 striae, and a mostly smooth or very finely crenulated anterior margin. Mandible with pointed apical tooth, a pale dorsal tooth at the base of which a small accessory dorsal tooth is sometimes

visible, three inner teeth of equal size, and a weakly developed mola; seta subdentalis spatulate but pointed, extending just beyond the apex of the third inner tooth (Fig. 32). Pre-mandible with two teeth of which the inner tooth is the largest, and some two rounded subapical teeth. Pecten epipharyngis with about five robust, blunt teeth. Anterior margin of the frontal apotome without irregular crenulation (Figs 31 & 33); labral sclerite 1 smooth. Antenna with five segments of which the fourth segment is slightly shorter than the second, but distinctly longer than both third and fifth segments; antennal blade slightly longer than the flagellum; ring organ in proximal third of the basal segment.

The present morphotype matches the larva of *Dicrotendipes pilosimanus* described from Kebena River (Ethiopia) and Lake Noordhoek (South Africa; Harrison, 1993). It differs from larvae of the related *Dicrotendipes septemmaculatus* (Becker) mainly in having ventromental plates with more striae (c. 40–46 rather than c. 26–32), and a frontal apotome with smooth anterior margin, not displaying the irregular tubercles present in *D. septemmaculatus* (Contreras-Lichtenberg, 1988; Epler, 1988; Harrison, 1993). Records of *D. pilosimanus* are restricted to South Africa and cool montane streams and ponds in East Africa (Harrison, 1993, 2000a), whereas *D. septemmaculatus* seems to occur in warm low- and mid-elevation lakes throughout East and North Africa (Freeman, 1957; Epler, 1988). Also *Dicrotendipes collarti* (Goetghebuer) has been reported from the East African mountains (Nyandarua Range in Kenya; Freeman, 1957), but its larva is unknown. We found *D. pilosimanus* only on Mount Kenya, at all elevations (seven lakes between 1320 and 4575 m a.s.l.) but most abundantly in lakes below tree line. As its frontal apotome is not always preserved and the ventromental striae often difficult to count, we are aware that our material may include some *D. septemmaculatus*, especially in the mid-elevation lakes Nkunga and Rurie Swamp. Lake Nkunga *Dicrotendipes* include at least three true *D. pilosimanus* specimens, but some others are more likely to belong to *D. septemmaculatus*. Also some incomplete *Dicrotendipes* from mid-elevation Kenya lakes such as Ol Bolossat (c. 2358 m a.s.l.) and Narasha (c. 2764 m a.s.l.) which Eggermont & Verschuren (2004b) assigned to *D. septemmaculatus* may actually be *D. pilosimanus*, yet none of the several 100 *Dicrotendipes* specimens recovered from these and other lakes could be unambiguously assigned to it.

Polypedilum type Bandasa (Fig. 34). Mentum uniformly brown or black with four median teeth of which the outer pair are small, and six pairs of lateral teeth; two central median teeth wide with slightly outward pointing apices; first laterals as tall as central median teeth; third laterals often set slightly forward, and taller than the fourth laterals; fourth to sixth laterals small, with apices somewhat turned outward; lateral sides of mentum slanted. Ventromental plates fan-shaped, in some cases nearly trapezoidal, about 1.1–1.3 times as wide as the mentum, with smooth anterior margin, medial margin with a distinct corner halfway, pointed posterolateral ends, and pointed anteromedian ends directed towards each other or

slightly upturned, with well-expressed but fine striation running over their entire surface. Mandible with apical tooth, a strong dorsal tooth, and two inner teeth.

At least 40 *Polypedilum* species have been reported from equatorial Africa, and nine of these were (partly) described as larvae (McLachlan, 1969; Dejoux, 1971; Lehmann, 1979; Oyewo & Sæther, 1998), but no one particularly resembles the present morphotype. Our material closely resembles subfossil *Polypedilum* type Narasha from mid-elevation Lake Narasha (2764 m a.s.l.) on the western shoulder of the Kenya Rift Valley (Eggermont & Verschuren, 2004b), but small differences in the shape of the ventromental plates (*P.* type Narasha never has the anteromedian ends upturned, and striation is less well expressed) and the mentum (in *Polypedilum* type Narasha the fourth laterals are not taller than the third laterals) warrants separating the two morphotypes. Nine other *Polypedilum* species have been found as fossils in lowland African lakes (Eggermont & Verschuren, 2004b), but these are all unambiguously distinguishable from the present morphotype. It was recovered from four lakes on Mount Kenya, all located below 3100 m a.s.l.; in Lake Bandasa, it represented 29.6% of the recovered fauna.

Chironomini larvula type 1 (Fig. 35). Mentum not greater than c. 40 µm, pale brown with clearly trifid median tooth, and six pairs of lateral teeth gradually diminishing in size; all laterals clearly separated from each other, or first and second laterals pressed against each other. Ventromental plates fan-shaped, less wide than the mentum, their anteromedian ends pointing up towards central part of the mentum, and their posteromedian corners tapering backward; anterior margin very finely crenulated. Mandible with apical, one dorsal, and three inner teeth. Pre-mandible with at least two teeth. Pecten epipharyngis with at least seven teeth. Antenna with five segments.

This previously described morphotype (Eggermont & Verschuren, 2004b) here most probably groups first-instar larvae of *Chironomus* type Kibos and *Chironomus* near *imicola*. It was only encountered on Mount Kenya (seven lakes, spanning elevations between 1840 and 4352 m a.s.l.), most abundantly in lakes above 3000 m a.s.l.

Chironomini larvula type 2 (Fig. 36). Mentum not greater than about 40 µm, laterally compressed, with laterally notched median tooth and six pairs of lateral teeth; median tooth protruding beyond first laterals, first to sixth laterals gradually decreasing in size. Ventromental plates, mandible and pre-mandible as in *Chironomini* larvula type 1; pecten epipharyngis not clearly recorded. S I toothed; S II simple. Antenna with five segments, fourth segment longer than both third and fifth segment, but smaller than the second segment.

In low-elevation African lakes this morphotype includes first-instar larvae of *Nilodorum*, *Dicrotendipes* and other closely related *Chironomini* (Eggermont & Verschuren, 2004b). Here we found it almost exclusively in two Mount Kenya lakes

Figure 35–41 Subfossil remains of larval Chironomini and Tanytarsini from East African mountain lakes: (35) Chironomini larvula type 1; (36) Chironomini larvula type 2; (37) *Rheotanytarsus* type Kitandara; (38, 39) Tanytarsini indet. type Ellis; (40, 41) Tanytarsini indet. type Large Hall Tarn. Scale bar = 25 µm.

(Bandasa and Ellis) where *Dicrotendipes pilosimanus* is common.

Tribe Tanytarsini

Rheotanytarsus type Kitandara (Fig. 37). Mentum with weakly notched median tooth (probably because of wear) and five pairs of lateral teeth gradually decreasing in size; median tooth about twice as wide as the first laterals. Ventromental plates compact, only c. 0.8 times as wide as the mentum, and about two and a half times as long as wide; anterior margin strongly curved, with behind it a narrow zone without striae, a band of square surface sculpturing, and then a band of striae taking up the middle third; the plates touch each other medially with their upper anteromedian ends only. Antennal pedestal tubular and curved, about as wide as long.

Three *Rheotanytarsus* species have been reported from African mountain streams (*Rheotanytarsus bufemoratus* Kyrmaten and Sæther, *Rheotanytarsus guineensis* (Kieffer), *Rheotanytarsus montanus* Lehmann), but the associated larvae are unknown. This morphotype mainly differs from larvae of the African lake species *Rheotanytarsus ceratophylli* (Dejoux, 1973) in having more compact ventromental plates, and a mentum with wider, scarcely notched median tooth. In this respect, it resembles the Nearctic *Rheotanytarsus* sp. A (Epler, 2001). Only a few partial specimens of this type were recovered, from the alpine Upper Kitandara Lake (Rwenzori).

Tanytarsini indet. type Ellis (Figs 38 & 39). Head capsule of older instars with circular gula pigmentation, ventrobasal margin well-sclerotized, sclerotization extending forward in two Y-shaped thickened ridges (Fig. 39). Mentum dark brown, with single median tooth and five pairs of lateral teeth; median tooth and first laterals separated from the rest of the mentum by a deep incision, and set backward; lateral teeth gradually decreasing in size, fifth laterals small and pressed against the fourth laterals; mentum somewhat constricted towards its base; setae submenti inserted below the fifth laterals. Ventromental plates rectangular, with a curved anterior margin, c. 1.2–1.3 times as wide as the mentum, clearly striated, anteromedian part of the posterior margin often more sclerotized. Mandible with one dorsal, an apical, and three inner teeth, all dark brown; seta subdentalis long and curved; pecten mandibularis well-developed, with one or more setae quite stiff and extending beyond the dorsal tooth. Pre-mandible with at least four teeth, the outermost being stiliform, other teeth more or less spatulate and decreasing in size; brush present. Labral lamella well-developed, with about 20 teeth. Pecten epipharyngis consisting of three serrated platelets. Antennal pedestal tubular, broadening towards the base, about as high as wide, with irregular surface and short distal spur. Antenna consisting of five segments; first antennal segment about six times its basal width, with ring organ two-fifths from its base; second antennal segment cylindrical, about a quarter of the length of the first antennal segment.

Attribution of this morphotype to the genus *Tanytarsus* s.s. is uncertain because of the lack of a complete antenna. This taxon differs from *Tanytarsini* indet. type Large Hall Tarn (below) in having a mentum which is not constricted at its base, and with first laterals gradually decreasing in size (not smaller than both the median and second laterals). All 11 *Tanytarsini* morphotypes previously described from Lake Tanganyika (Eggermont & Verschuren, 2003b) and African lakes at lower elevation (Eggermont & Verschuren, 2004b) can be distinguished from *Tanytarsini* indet. type Ellis by details in mental teeth configuration, shape of the antennal pedestal, and/or the mandible. This morphotype was found in three alpine lakes on Mount Kenya. In Lake Ellis, it made up 54.8% of the recovered fauna.

Tanytarsini indet. type Large Hall Tarn (Figs 40 & 41). Mentum with broad median tooth and five pairs of robust lateral teeth; median tooth about twice as wide as the first laterals, and slightly notched in unworn specimens; first laterals pointing outward, smaller than both the median tooth and second laterals, and separated from them by a deep incision; second to fifth laterals gradually diminishing in size and slightly turned outward; mentum constricted towards its base. Ventromental plates relatively high rectangular, about as wide as the mentum, with a curved anterior margin. Mandible with one dorsal, an apical, and three well-developed inner teeth. Antennal pedestal tubular, c. 1.3–1.7 times as high as wide, and with a short distal spur.

Generic attribution to *Tanytarsus* s.s. remains uncertain since the examined material lacks essential skeletal components, such as pre-mandible, pecten epipharyngis, and antenna. It mainly differs from *Tanytarsini* indet. type Ellis (above) by having a mentum with constricted base (lateral margins not straight) and first laterals smaller than both the median and second laterals (laterals not gradually decreasing in size). This morphotype was found in two alpine tarns (Hausburg Tarn and Large Hall Tarn) on Mount Kenya, being most abundant in Large Hall Tarn (31.6% of the recovered fauna).

Species diversity and altitudinal distribution

The altitudinal distribution of the 16 chironomid taxa inhabiting high-elevation lakes (>2900 m a.s.l.) on Mount Kenya and the Rwenzori displays the following trends:

1. eight taxa appear restricted to the Alpine and Nival zones (>3900 m a.s.l.): the Diamesinae species *Diamesa* type Kitandara, one Tanypodinae (*Larsia* type Kitandara), three Orthocladiinae (*Chaetocladius melaleucus*, *Paratrichocladius* type Hausburg Tarn and *Paratrichocladius* type Simba Tarn) and three *Tanytarsini* (*Rheotanytarsus* type Kitandara, *Tanytarsini* indet. type Ellis, and *Tanytarsini* indet. type Large Hall Tarn);
2. two taxa occur at low and middle elevations up to the Ericaceous zone, but are excluded from the Alpine and Nival zones: *Procladius brevipetiolatus* and *Polypedilum* type Bandasa;

3. four taxa occur at all elevations from the Basal Plateau belt to the Alpine zone: *Limnophyes minimus* group, *Chironomus* type Kibos, *Chironomus* near *imicola* and *Dicerotendipes pilosimanus*;

4. two taxa appear to occur both in low- and mid-elevation lakes and in the Alpine zone but not at intermediate altitudes: *Pseudosmittia* type Tanganyika and near *Paraphaenocladus* type Ol Bolossat.

Combination of this East African mountain data set with similar chironomid death-assemblage data from 68 East African lakes (Uganda–Kenya–Ethiopia) at low to intermediate elevations (750–2760 m a.s.l.; Eggermont & Verschuren, 2004a,b) reveals the highly distinct character of African high-mountain chironomid communities. This is illustrated in Fig. 42, where the altitudinal distributions of the 16 taxa recorded in this study are shown together with those of eight chironomid taxa widely distributed in East African freshwater lakes, along a combined altitudinal gradient ranging from 935 to 4575 m a.s.l. These eight common taxa each occur in at least 35% of the 55 freshwater lakes (conductivity < 1000 $\mu\text{S cm}^{-1}$) at low and middle elevations sampled to date (Eggermont *et al.*, 2006; Lake Nkunga and Rurie Swamp in this study), but are lacking in the 11 high-mountain lakes studied here. Among the 90 chironomid taxa recorded to date in low- and mid-elevation East African lakes, only six (*Procladius brevipetiolatus*, *Polypedilum* type Bandasa, *Pseudosmittia* type Tanganyika, near *Paraphaenocladus* type Ol Bolossat, *Chironomus* type Kibos and *Chironomus* near *imicola*) are here recorded from lakes above 2900 m, and only the latter four appear to penetrate into the Afroalpine zone (but see Discussion below). Consequently a marked faunal transition occurs in lakes between c. 2900 and 4000 m a.s.l., i.e. broadly corresponding with the Ericaceous zone of terrestrial vegetation.

Chironomid species diversity in the sampled high-mountain lakes (Table 4: 6.0 taxa on average; $ES_{50} = 6.1$; $N_2 = 3.2$) is significantly lower than that in the two mid-elevation lakes on Mount Kenya (mean 19.5 taxa; $ES_{50} = 12.0$; $N_2 = 3.6$) or in the 68 East African low- and mid-elevation lakes (mean 15.0 taxa; $ES_{50} = 10.6$; $N_2 = 5.5$).

DISCUSSION

The biodiversity and biogeography of Afroalpine ecosystems have long attracted interest from both botanists and zoologists. Today these ecosystems occur on seven mountain ranges in equatorial Africa (Mount Kenya, the Nyandarua (Aberdare) Range, Mount Kilimanjaro, Mount Meru, Mount Elgon, the Rwenzori Mountains and the Virunga Mountains) and three mountain massifs in Ethiopia (Simien, Arsi and Bale), which are typically treated as a separate biogeographical region. The origins of Afroalpine biota are predominantly local (tropical African) or Palaearctic depending on the group, with typically smaller contributions from temperate South Africa and other distant sources (Harmsen *et al.*, 1991). In poorly dispersing terrestrial biota such as vascular plants (Hedberg, 1957; Harmsen *et al.*, 1991), mosses (Spence & Pocs, 1987), flightless

Figure 42 Distribution of selected chironomid taxa in surface-sediment death assemblages from 25 freshwater lakes situated along an altitudinal and temperature gradient between 935 and 4575 m a.s.l. in Uganda and Kenya. Lakes on Mount Kenya and Rwenzori are indicated with an asterisk. Grey circle surface areas show the relative abundance of each taxon per sample; grey crosses indicate uncertain records.

Table 4 Mean taxon richness, ES₅₀ and Hill's N2 diversity (mean and standard deviation) for high-elevation African lakes (this study), East African low- and mid-elevation lakes (Eggermont & Verschuren, 2004a,b) and lakes Nkunga and Rurie Swamp on the lower slopes of Mount Kenya (this study)

	High elevation	Low and mid-elevation	Nkunga and Rurie Swamp
No. of taxa	6.0 (1.7)	15.0 (7.9)	19.5 (2)
ES ₅₀	6.1 (2.4)	10.6 (4.7)	12.0 (1.8)
N2	3.2 (1.1)	5.5 (3.0)	3.6 (0.2)
No. of lakes	11	68	2

insects (Brühl, 1997) and spiders (Scharff, 1992), each mountain has a significant component of locally endemic species. In plants and mosses, this component ranges from c. 2% on the Aberdares and Mount Meru to c. 14% in the Rwenzori, with a positive relationship to the area occupied, age and isolation from other mountains (Harmsen *et al.*, 1991). In flightless insects, genera can be distributed widely over the different mountains but at the species level local endemism is the rule rather than the exception (Brühl, 1997). In contrast, highly mobile terrestrial biota such as mammals, birds and butterflies are mostly represented by eurytopic lowland species, and species diversity above the tree line is typically unimpressive.

The occurrence of standing-water aquatic ecosystems in the Afroalpine zone depends on present or past glacial activity carving out lake depressions or forming barriers to drainage, and on a positive water balance to fill those basins. Consequently they are not evenly distributed across Africa's highest mountains. The large majority occur on Mount Kenya and in the Rwenzori. Mount Kilimanjaro (Tanzania, Fig. 1), Africa's highest mountain, is a relatively young intact volcano with only one known lake at high elevation (Mawenzi Tarn; 4150 m). On Mount Elgon (eastern Uganda) and the Nyandarua Range (central Kenya) only bogs and shallow swamps occur, and on the dry Mount Meru (northern Tanzania) nothing more than a few seasonal ponds. In the Ethiopian highlands, high-altitude depressions are mostly occupied by bogs, with the exception of Lake Garba Guratch in the Bale Mountains (Umer *et al.*, 2004).

Individual Afroalpine lakes are ephemeral on geological time scales, as during Quaternary ice ages most of their basins have repeatedly been occupied by glaciers. Consequently, aquatic biota were not necessarily favoured by the larger and more contiguous Afroalpine zone which occurred when the snowline was depressed (between 570 and 1000 m on individual mountains; Osmaston & Harrison, 2005) and vegetation belts shifted downslope: their local persistence would have depended on the presence of alternative suitable lake habitat at intermediate elevations. This long-term instability of tropical cold-water habitat together with harsh abiotic

conditions has resulted in low species diversity and endemism in most groups of aquatic biota. For example, Afroalpine phytoplankton communities are mainly composed of easily dispersing (aerophilic) cosmopolitan species, complemented by eurytopic tropical species (Löffler, 1964). Zooplankton communities (Cladocera, Rotifera) appear to have modest species diversity and a mix of biogeographical affinities (Löffler, 1964, 1968; Lens, 1978); however, the often exceedingly low population abundances have so far complicated comprehensive sampling and a proper biodiversity assessment. The same being true for aquatic insects (Löffler, 1964), quantitative faunistic and ecological monitoring of Afroalpine aquatic ecosystems is logistically challenging.

Altitudinal distribution

Our present dataset of chironomid communities in African high-mountain lakes (>2900 m a.s.l.) permits distinction between: (1) taxa restricted to the Alpine and Nival zones (>3900 m a.s.l.), (2) taxa occurring at low and middle elevations up to the Ericaceous zone (c. 3000–4000 m), (3) taxa occurring at all elevations up to c. 4500 m in the Alpine zone, and (4) taxa which appear to occur both in low- and mid-elevation lakes and in the Alpine zone but not at intermediate altitudes. The eight group (1) taxa were absent both in lakes below 3900 m (1320–3500 m) surveyed here and from any of 68 East African lakes at low and intermediate altitude (750–2760 m) surveyed earlier (Eggermont & Verschuren, 2004a,b); consequently they must be cold-stenothermal species which are adapted to, and require, the harsh climatic conditions prevailing at the top of Africa's highest mountains. Night-time freezing can occur from c. 3000 m a.s.l. (i.e. the present-day tree line between Bamboo forest and the Ericaceous zone), but at 4000 m (transition between Ericaceous zone and Alpine zone) nocturnal frosts occur on 80–90% of the nights and almost throughout the year (Rundel, 1994). The equatorial position of these mountain ranges creates daily oscillations in air temperature between –5 and 20°C in the Alpine and Nival zones, an order of magnitude greater than the seasonal change in maximum daytime temperature. In the deeper lakes, night-time water-surface cooling and convection creates bottom temperatures approaching 4°C, as in seasonally stratified lakes in cold-temperate regions. Shallow lakes often freeze over at night, and with the exception of the shallowest tarns, daytime warming heats up surface waters to, at most, 8–10°C (Table 1). As almost all life processes in holometabolous insects (egg survival and hatching rate, larval growth and feeding, pupation, emergence, flight and fecundity) are under temperature control (Pinder, 1995), African Chironomidae whose larvae are restricted to these alpine lakes and tarns must evidently be cold-stenothermal.

All but one of the eight recorded cold-adapted taxa are relatively small forms belonging to the subfamilies Diamesinae, Orthocladiinae and Tanytarsini, which also dominate the chironomid fauna of alpine lakes and tarns in north-temperate

regions (Walker & Mathewes, 1989; Lotter *et al.*, 1997). The Diamesinae in particular are a characteristic component of alpine chironomid faunas in the Holarctic region (North America and Eurasia). The three known East African Diamesinae species are restricted to the ultra-oligotrophic waters of glacial tarns and streams on Mount Kenya, Mount Kilimanjaro and the Rwenzori (Freeman & Cranston, 1980; Willassen & Cranston, 1986). A handful of African Orthocladiinae (*Cricotopus scottae*, *Cricotopus albitibia*, *Limnophyes natalensis*, *Nanocladius saetheri*, *Psectrocladius viridescens*) are widely distributed in warm and productive lowland lakes (Tudorancea *et al.*, 1989; Eggermont & Verschuren, 2004a), but as a group the Orthocladiinae contribute significantly to chironomid faunal diversity only in well-oxygenated waters of fast-flowing streams (Harrison & Hynes, 1988), cool forest rivers (Lehmann, 1979) and the rare unproductive African lakes at low elevation (e.g. Lake Tanganyika; Eggermont & Verschuren, 2003a). Here in cold, unproductive mountain lakes we find Orthocladiinae to be common both in number of taxa (6 of 16, or 31.5%) and absolute abundance (49.0% of total yield).

Of the eight taxa constituting groups (2) to (4), i.e. those not restricted to the Afroalpine ecosystem, six have previously been found in lowland African lakes. The group (2) species *Procladius brevipes* and *Polypedilum* type Bandasa can be considered warm-adapted tropical elements, as also are the majority of Tanytarsini and Chironomini which we only encountered in Rurie Swamp and/or Lake Nkunga (Table 2; Fig. 42). Group (3) includes at least two distinct, well-defined species that can be considered as positively eurythermic: *Chironomus* type Kibos and *Chironomus* near *imicola*. Their known distribution in equatorial East Africa now encompasses both alpine tarns of 4°C and lowland tropical lakes with (bottom-water) temperatures of up to 27°C (Fig. 42). The other two morphotaxa of group (3) may include more than one biological species, therefore their apparent altitudinal distribution may be an artefact of inadequate discrimination of subfossil remains. The disjunct distribution of group (4) taxa similarly indicate that their high-mountain populations actually represent a different species, which at present cannot be separated consistently on the basis of morphological features on the larval head and mouthparts.

Faunal diversity and possible endemism

We found that the chironomid communities in African high-mountain lakes are comparatively poor in species: their mean local species richness is significantly lower than that in the two mid-elevation lakes on Mount Kenya studied here or East African low- and mid-elevation lakes in general (Table 4). This is also typical of cold, ultra-oligotrophic alpine lakes elsewhere (Bretschko, 1974). However, the combined chironomid species diversity of 16 taxa now recorded is high compared with that of other groups of resident aquatic insects and crustacean zooplankton (Löffler, 1964, 1968), especially taking into account that this study covers only c. 15% of present-day Afroalpine lake ecosystems. In the present data set, 50% of this

diversity are cold-stenothermal taxa restricted to these systems. These Chironomidae, and their diagnostic remains preserved in lake-sediment records, thus constitute valuable biological indicators to monitor past and future environmental change affecting the hydrology and temperature regime of scarce glacier-fed aquatic ecosystems in tropical Africa.

Our exploratory data set currently lacks the coverage to address conclusively the question of endemism among Afroalpine Chironomidae, either local (individual mountain ranges), regional (e.g. equatorial East African mountains vs. the Ethiopian highlands) or continental (e.g. Afrotropical vs. Palaearctic). Given efficient long-distance dispersal of adult midges (Armitage *et al.*, 1995), there is no reason to expect a high proportion of local endemics (i.e. restricted to just one mountain range) among the Chironomidae inhabiting Africa's high-mountain lakes, unlike the situation in less mobile Afroalpine biota such as vascular plants, mosses and flightless insects. Among the eight cold-stenothermous taxa encountered only *Chaetocladius melaleucus*, *Paratrichocladius* type Hausburg Tarn and *Paratrichocladius* type Simba Tarn were found both on Mount Kenya and in the Rwenzori, but with only c. 15% of potential habitat on the two mountains sampled, this small proportion of shared species is not likely to be a true reflection of the shared fauna. Afrotropical *Diamesa* do show species differentiation between mountains (*D. kenya* and *D. freemani* on Mount Kenya, *D. rwenzoriensis* in the Rwenzori; *Diamesa* has not yet been recorded on Mount Kilimanjaro: Freeman, 1955; Willassen & Cranston, 1986), but with the caveat that distribution records for the adult midges are as fragmentary as they are for larvae.

The chironomid fauna of Ethiopian mountain streams (34 sites between 700 and 3550 m a.s.l.) is strongly linked with those of East and South African counterparts (Harrison & Hynes, 1988). Likewise, inventory of the forest river Kalengo in the Democratic Republic of Congo (c. 1800 m a.s.l.; Lehmann, 1979) yielded several species with continent-wide African distribution. Part of this pattern of widespread species distribution may be credited to the occurrence of cool forest-river systems over large contiguous areas in East and Central Africa. By contrast, true cold-water lakes with (bottom) temperatures of 4–5°C or less are restricted to the few isolated islands of Africa's highest mountain ranges, which are separated by large expanses of warm lowlands (Fig. 1). Still, regional endemism in Afroalpine Chironomidae between the group of seven equatorial East African mountain ranges and other African highland regions is not likely to be substantial, if only because of the general lack of Afroalpine standing-water ecosystems outside of equatorial East Africa, with the exception of one lake and a handful of bogs in the Ethiopian Arsi and Bale Mountains.

Similarity of cold-stenothermal chironomid faunas among Africa's mountain ranges, and between tropical Africa and the Palaearctic region may, in addition to present-day dispersal, also reflect improved conditions for long-distance dispersal in the past (Kingdom, 1989). Willassen & Cranston (1986) suggested a more or less continuous dispersal route for alpine

aquatic biota between the East African mountains and Eurasia during the mid-Tertiary period. This route would have stretched from the Caucasus through the Near East to the Ethiopian highlands, and allowed colonization of East Africa by strictly cold-stenothermal taxa. Prominent among these are *Diamesa* and African montane Orthoclaadiinae such as *Chaetocladius melaleucus* (Meigen) that are considered to have a Palaearctic or Nearctic origin (Willassen & Cranston, 1986). *Limnophyes minimus* (Meigen) and *L. natalensis* (Kieffer), here combined into Epler's (2001) *Limnophyes minimus* group, are both widely distributed throughout Europe and North America, and even occur on some sub-Antarctic islands (Sæther, 1990). African Chironominae with montane distribution patterns are proposed to have used the same route but in either direction (Harrison & Hynes, 1988). One example is *Dicrotendipes pilosimanus* (Kieffer), which besides Africa's eastern and southern highlands also occurs throughout the Middle East, the Balkans and the Oriental region (Epler, 1988).

Although the reality of intercontinental dispersal of cold-adapted biota between Eurasia and Africa is unquestioned, improved knowledge of Africa's tectonic and palaeoclimatic history argues against a prominent role of mid-Tertiary faunal exchange. First, the Oligocene period of world-wide cooling [34–26 million years ago (Ma)], which is supposed to have created a stepping-stone corridor of cold mountain environments from Eurasia to East Africa, was most probably still as warm or warmer than today (Zachos *et al.*, 2001), and was followed by 12 Myr of late Oligocene and Miocene warming (26–14 Ma), at which time no glaciers can have existed at tropical latitudes. Second, although Eocene volcanic activity in the incipient East African Rift System (c. 45–33 Ma) extruded sequences of flood basalt up to 2.5 km thick in present-day Ethiopia, northern Kenya and southern Arabia (Ebinger *et al.*, 2000; Tiercelin & Lezzar, 2002), there is no evidence for temporal continuity of high-mountain environments in East Africa between this period of early rifting in the north, and the main uplift of the Aberdares in the late Miocene, the Rwenzori in the Pliocene or the formation of Mount Kenya c. 3 Ma (Barker *et al.*, 1988; Pickford *et al.*, 1993; Ebinger *et al.*, 2000).

Abundant palaeoclimatic evidence shows that over the entire period from 65 Ma to the Present global cooling was most extreme during late Quaternary glaciation (Zachos *et al.*, 2001), the major ice ages which occurred at roughly 100,000-year intervals over the past 700,000 years (e.g. Raymo, 1992). During this period, global cooling relative to the Present has been the rule rather than the exception: interglacial climate conditions similar to those of the current Holocene epoch prevailed during c. 20% of the time (EPICA, 2004). Therefore, faunal exchange between Africa's high-mountain environments and Eurasia has almost certainly been most prominent not during the mid Tertiary but during late Quaternary glacial episodes, and as recently as 15,000–20,000 years ago. It is commonly assumed that Afroalpine ecosystems persisted continuously since the late Pliocene (Axelrod & Raven, 1978; Harmsen *et al.*, 1991), but probably not much longer. The

oldest concrete evidence for mountain glaciation in equatorial East Africa is in fact decidedly younger: *c.* 480,000 years on Mount Kilimanjaro (Downie, 1964), *c.* 400,000 years on Mount Kenya (Shanahan & Zreda, 2000) and >300,000 years in the Rwenzori (Osmaston & Kaser, 2001).

Besides the three currently snow-capped mountains, extensive field evidence for late Quaternary glaciation, and by implication the existence of glacier-fed lakes and streams, exists in the Ethiopian highlands (Umer *et al.*, 2004) and on most other East African massifs higher than 3000 m (reviewed in Osmaston & Harrison, 2005). At that time, mean annual temperature in mountainous regions was reduced by 5–6°C (Porter, 2001), and snowlines were depressed by 570–1000 m (Kaser & Osmaston, 2002). Vegetation belts shifted downslope and contracted, extending the Afroalpine zone to *c.* 3200 m a.s.l. (Mahaney, 1989). The seven current Afroalpine enclaves in equatorial East Africa must have increased somewhat in size (Harmsen *et al.*, 1991) but not substantially so, and only very few new enclaves with probable Afroalpine abiotic conditions were formed in the Cherangani Hills of northern Kenya, the Ngorongoro area west of Mount Meru, and the Mitumba Range of eastern Democratic Republic of the Congo. Only when including the entire faunal transition zone (Fig. 42), of which the lower boundary may have extended to *c.* 2200 m, can it be proposed that cold-stenothermal African Chironomidae potentially enjoyed significantly more widespread distributions and increased dispersal between individual mountain systems during Quaternary glaciation periods. Broad swaths of highlands at that elevation lie both among the eastern (Mount Elgon, Mount Kenya, Nyandarua, Mount Kilimanjaro, Mount Meru) and western (Rwenzori, Virunga) equatorial mountains, and among the three Ethiopian massifs, and substantial new stepping stones between these three mountain regions may have occurred in the Uganda–Sudan border region. For the aquatic midge larvae in question, the true limiting factor on glacial-time distribution would have been the occurrence of permanent open water bodies within the altitude range of suitable abiotic conditions, as is the case today.

MAIN CONCLUSIONS

Through study of recent death assemblages of larval remains in surface sediments, we found that the chironomid fauna of high-elevation (>3000 m a.s.l.) lakes and tarns on glaciated mountains of equatorial East Africa is diverse in species and highly distinct from that of low- and mid-elevation African lakes. The faunal transition zone coincides broadly with the Ericaceous zone of terrestrial vegetation, where night freezing becomes increasingly more common with altitude. Eight taxa, or 50% of total species richness, appear restricted to the specific habitat of cold holomictic lakes in the Alpine and Nival zones (>3900 m a.s.l.), and can thus be considered true Afroalpine elements. The question of endemism among Afroalpine Chironomidae at either a local, regional or continental scale remains largely unanswered at this time, but taking into account the restricted occurrence of glacier-fed

lakes and tarns on Africa's highest mountains we surmise that the chironomid fauna of these tropical cold-water ecosystems is potentially unique on a continental scale.

By virtue of their excellent preservation and their spatial and temporal integration of local community dynamics, chironomid larval death assemblages extracted from surface sediments are powerful biological proxy indicators to monitor the potentially dramatic hydrological and ecological changes associated with the retreat of Africa's alpine glaciers. In north-temperate regions, chironomid palaeoecology is already an established instrument to reconstruct past histories of climate-driven temperature and ecological change (Battarbee, 2000). Initial demonstration, from surface-sediment larval death assemblages, of strong altitudinal and latitudinal gradients in chironomid species distribution (Walker & Mathewes, 1989; Walker & MacDonald, 1995) resulted in the development of chironomid-based quantitative inference models for reconstruction of past variations of air and water temperature in both North America and Europe (Lotter *et al.*, 1997; Walker *et al.*, 1997; Larocque *et al.*, 2001). Reconstruction of Africa's climate history from natural climate archives such as lake sediments will be essential to amend the current scarcity of information on natural tropical climate variability and help forecast the fate of Afrotropical ecosystems over the next centuries. Given the difficulty of separating the effects of changes in temperature and moisture balance on geochemical records of African climate change (Gasse, 2002), an independent and reliable proxy indicator for past temperature change in Africa would be most welcome (Verschuren, 2003). Documentation in this study of the distinct character of chironomid communities inhabiting Africa's true cold-water lakes is a first step towards chironomid-based reconstruction of past temperature change in Africa, and improved understanding of past and future tropical climate dynamics.

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BIOSKETCHES

Hilde Eggermont is post-doctoral fellow with the Research Foundation of Flanders (FWO-Vlaanderen), Belgium. She studies subfossil larval Chironomidae preserved in African lake sediments with emphasis on taxonomy, biogeography and their use as quantitative indicators for past environmental changes in lakes. This includes palaeoclimate reconstruction and historical biomonitoring of the various anthropogenic impacts to which African lakes are exposed.

Dirk Verschuren is research professor in Ecology at Ghent University, Belgium. His research interests include African climate history and the long-term dynamics of African lake ecosystems. He exploits multiple proxy indicators preserved in lake-sediment records to reconstruct past climate dynamics at decadal to millennial time scales, and the evolution of human impact on African lakes and their drainage basins.

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