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CHIRONOMIDAE (INSECTA: DIPTERA) COLLECTED FROM *HYDRILLA VERTICILLATA* (HYDROCHARITACEAE) AND OTHER SUBMERSED AQUATIC MACROPHYTES IN LAKE BISINA AND OTHER UGANDAN LAKES

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ABSTRACT

A survey of the aquatic weed *Hydrilla verticillata* was conducted in selected Kenyan and Ugandan lakes, and emerging chironomid adults were collected from samples of *Hydrilla* and seven other aquatic macrophytes. *Hydrilla* was absent from Lake Victoria, in sites where it previously occurred. *Hydrilla* was found in four of nine lakes examined in Uganda, *i.e.* Bisina, Kyoga, Bunyonyi and Mutanda. From 7424 collected chironomid adults, 43 species were identified, 21 (49%) representing new Ugandan records. Thirty-nine (91%) of the species were found on *Hydrilla.* Three species represent probable undescribed taxa. At our primary site, Lake Bisina, the genera *Tanytarsus* and *Dicrotendipes* dominated the chironomid community, comprising 76% of emerged adults. A species accumulation curve for chironomid species associated with Lake Bisina macrophytes suggested that further plant sampling would uncover additional species. *Polypedilum wittei*, formerly considered for possible biological control of *Hydrilla,* was not specific to that plant, emerging from six of the seven other species of submersed macrophytes we sampled. A second candidate *Polypedilum* species, *P. dewulfi*, was not found in Uganda. No insect-related damage to *Hydrilla* was observed. Chironomid data were compared between Uganda collections and those from a concurrent, similar study in lake Tanganyika. Alpha- and ß-diversity values indicated that the chironomid communities on aquatic plants from Lake Bisina and Lake Tanganyika (Burundi) were markedly different. Studies of chironomids and other invertebrates associated with macrophytes in other African lakes will add significantly to knowledge of the natural history of these important aquatic environments.

Keywords: Lake Victoria, weed, biodiversity, biological control, Lake Tanganyika

INTRODUCTION

Hydrilla verticillata (L.f.) Royle is an important weed of fresh water habitats in many parts of the world but only in places where it grows to, or near, the water surface forming dense mats of long, stringy stems that foul boat propellers and impede water movement. In areas where it is a weed, control costs can be great. In Florida, for example, estimates of *Hydrilla* control exceed $12 million annually (Schardt & Ludlow, 2000). Additionally, resistance to the primary herbicide used in its control has recently appeared in *Hydrilla* populations (Michel *et al.*, 2004), making the search for alternate control strategies of immediate importance.

Hydrilla in Africa has a spotty distribution (Cook & Lüönd, 1982). Although it can be found in dense clumps, in Africa *Hydrilla* usually does not grow to the water's surface and is only considered a weed in South Africa into which it was recently introduced from Malaysia (Madeira *et al.*, 2007). The first record of *Hydrilla* from Africa was Grant's collection of it from the Nile in 1862 (Speke, 1863; appendix, p. 585, as *Hydrilla dentata* Casp.). This early collection, in what is now Uganda, suggested that *Hydrilla* might be native to the continent. Plants long resident in a location are more likely to have a suite of herbivores associated with them than are recent invaders, and one possible explanation for *Hydrilla* not being a weed in eastern Africa is herbivory by insects and other animals. Earlier short surveys in eastern Africa for herbivores of *Hydrilla* found evidence of insect (and fish) damage to plants growing in Lake Tanganyika (Tanzania, Pemberton, 1980; Burundi, Markham, 1985). In particular, Chironomidae larvae of the genus *Polypedilum* were suspected to bore into the growing tips and stems of *Hydrilla* (Pemberton, 1980). The larvae were identified as *P.* (*Polypedilum*) *dewulfi* (Goetghebuer) and *P.* (*Pentapedilum*) *wittei* Freeman (Buckingham, 1994). These reports suggested that a more intensive exploration for natural enemies was warranted.

Apart from these Lake Tanganyika collections and Grant's early Uganda record, confirmed collections of *Hydrilla* from non-artificial wetlands in East Africa are known for Kenya (Lake Victoria; Lukala, Port Victoria, J.P. Glasgow, 3 Dec 1950 Makerere University Herbarium [MUH]); Tanzania (Lake Victoria [Pemberton, 1980; Simpson, 1989; Eggermont *et al.*, 2008]); and Uganda (Lakes Bisina [Katende, 2004], Bunyonyi [Denny, 1973], Mutanda [E.M. Lind, 1953, MUH], Kyoga (as Kioga, [Markham, 1985]) and Victoria [G.H.S. Wood, no. 466, 3 Oct 1952, 0.5 miles SW of Buluba Leper Colony, 10 miles E of Jinja, MUH; Entebbe, Lind, no. 2069, 1956, MUH; same data except no. 2695, 1959; Bugonga ferry opposite Jinja, E.M. Lind, no. M.C. 136, 1953, MUH). In November 2006 we began a survey for *Hydrilla* and potential chironomid herbivores in selected areas of eastern Africa. Although we did not find insects suitable for biological control of *Hydrilla*

(Copeland *et al.*, 2011), our survey generated substantial data on chironomids associated with *Hydrilla* and other aquatic macrophytes. In a recent paper (Copeland *et al.*, 2012) we discussed the chironomid species associated with *Hydrilla* and related plants collected from Lake Tanganyika in Burundi. Here, we report on exploration for *Hydrilla* in Kenya and Uganda, and on the diversity of chironomid species reared from *Hydrilla* and associated aquatic plants in some Ugandan lakes.

MATERIALS AND METHODS

Study sites

In Kenya, surveys for *Hydrilla* focused on Lake Victoria where the species was previously collected near Port Victoria. Other *Hydrilla* collections previously reported from Kenya were from artificial sites (Waas, coastal Kenya, Markham, 1985; Karen, central highland Kenya, Simpson, 1989), and no attempt was made to find these sites.

In Uganda, Lake Bisina (1°38'56"N, 33°58'12"E, 1044 m) was our most important site. Bisina is part of the Kyoga lakes system in central and eastern Uganda. The Victoria Nile provides most of the water that flows through Lake Kyoga, but a series of smaller lakes to the east, fed largely by streams originating on Mount Elgon, also drain into the system through a network of Papyrus swamps (Green, 2009). Bisina is one of these lakes and, lying upstream of Kyoga (1035 m), is slightly higher in elevation and not directly influenced by it or the Nile. In addition to the fluvial input of streams from Mount Elgon to the east, Bisina is also fed by the Apendura River to the north. Lake Bisina is a shallow lake that grows and shrinks depending on rainfall, but in a typical year covers about 150 km^2 with a mean depth of 3 m (Vanden Bossche & Bernacsek, 1990) and a maximum, at the time we sampled it, of 5 m (Gidudu *et al.* 2011). It is a designated wetland of international importance (RAMSAR site) because of its unique biodiversity and support of rare and endangered species (Byaruhanga & Kigoolo, 2005).

Lake Victoria was also investigated in Uganda, at two sites (Buluba and Jinja) from which *Hydrilla* was previously collected (see above). Seven additional freshwater lakes were surveyed across Uganda, (figure 1). With the exception of Lake Nabugabo, all were tectonically formed. Two of the lakes, Bunyonyi and Mutanda, were influenced later by volcanic activity, with lava flows plugging outlets (Denny, 1971; Temple, 1971). Nabugabo was formed recently by shoreline buildup on the windward side of Lake Victoria, essentially budding off the latter (Temple, 1971). Like Bisina, Lakes Kachira, Kyoga and Nabugabo are shallow (4-7 m maximum depth; Temple 1971). Bunyonyi and Mutanda are 40 and 50 m deep, respectively (Temple, 1971; Denny, 1973) and the depths of Chahafi (sometimes spelled Cyahafi) and Kiugi are unknown. At 1790, 1891, and 1945 m respectively, Lakes Mutanda, Chahafi and Bunyonyi were the highest lakes we sampled, while Lake Kyoga at 1035 m was the lowest. Data on Chironomidae that emerged from aquatic plants were collected from all lakes in which we found *Hydrilla*.

Plant collection

For the survey, we rented small wooden boats from local fisherman, or used an inflatable boat with a small outboard motor. *Hydrilla* and other plants were located by casting an 8-pronged grapple and dragging it back manually by rope. Areas within approximately 20 m of the shoreline were examined. Plant specimens were pressed, and identified using the literature, by direct comparison with herbaria holdings (East African Herbarium, Nairobi, Kenya; Makerere University Herbarium, Kampala, Uganda), and by examination of photographic vouchers (Chris Cook, pers. comm.).

In lakes where it was found, *Hydrilla* was collected on all field trips and held in the laboratory for emergence of chironomids. From each collection, a sub-sample of approximately 200 stems and growing tips of *Hydrilla* were viewed with a stereomicroscope and examined for evidence of damage attributable to insect herbivory; particularly tip-boring damage of the type described by Pemberton (1980) and Markham (1985). Most of our sampling was concentrated in Lake Bisina, where collections were made on 22 visits between 25 Feb 2007 and 17 Jan 2010, and included all months except October. To compare chironomid species sampled from other aquatic plants with those from *Hydrilla*, other species of submersed macrophytes were collected from a Lake Bisina site (Alelesi) where they grew together with *Hydrilla*. Alelesi was sampled 13 times between 17 November 2007 and 17 January 2010, and on eight of those sampling dates (4 June 2008 to 17 January 2010) in addition to *Hydrilla, Najas horrida* Magn. (six samples), *Potamogeton schweinfurthii* A.Benn (5), *Ceratophyllum demersum* L. (6), and *Ottelia ulvifolia* (Planch.) Walp. (5) were also collected. *Utricularia reflexa* Oliv. was sampled once in Lake Bisina, but not at Alelesi where it did not occur.

Insect rearing and identification

Plants were initially separated by species in the field and placed in water in 50 l plastic buckets. When plants were uprooted, clots of mud around roots were often large enough to substantially limit the amount of plant material that would fit in our collection buckets. On those occasions, plants were first gently swirled in lake water to reduce the mud load. In the laboratory, a second more thorough sorting produced "pure" cultures of individual plant species that were then placed in separate 50 l buckets, to half the volume of the bucket, whereupon they were submerged in filtered water from the collection site.

Laboratory rearing was done under ambient conditions. Air was bubbled into each bucket. The opening of the bucket was covered with mesh netting that had a ~20-cm hole cut out of the center. The bucket then was sealed with a plastic lid that had an opening of the same diameter cut out of its center. The mesh netting allowed newly emerged insects to rest on a partially dry surface, rather than on the condensation-covered inner surface of the plastic lid. Emerging adult insects escaped through the hole cut in the lid and were captured as they emerged through the neck (~3 cm diameter) of an inverted funnel that covered the hole and was fitted into the opening of a Perspex cage (15 x 15 x 20 cm). Adults were killed in 75% ethanol. Chironomids were identified primarily by reference to the work of Freeman (1955a, 1956, 1957a, 1958) and Harrison (1991, 1992, 1994, 1996) with male and, for several species, female imagos. Initial identifications of chironomid species or confirmations of identifications were made by one of us (JHE). After 3-4 weeks, plants were discarded.

Our collection and rearing methods did not eliminate several possible sources of contamination or errors and these may have influenced the results, particularly if their effects on chironomid species were not uniform. These factors included (1) washing away of larvae during sampling of plants, (2) mixing of larvae with benthic species in the buckets in the field, (3) predation by other insects (*e.g.* dragonfly larvae) during incubation time in the laboratory, (4) larval mortality, (5) adult mortality in rearing buckets.

Chironomid biodiversity

At Alelesi, our primary sampling site in Lake Bisina, α- and β-diversity were computed for Chironomidae that emerged from four aquatic macrophytes, *Hydrilla, Ceratophyllum* *demersum, Najas horrida* and *Potamogeton schweinfurthii.* For the analyses, data were used only from those collections (three) during which all four of the plant species were sampled. Alpha–diversity was expressed with the Shannon index (H'), incorporating species richness and evenness, and compared statistically between pairs of plant species using a t-test (Magurran, 1988). Beta-diversity, comparing similarity of habitats (plant species), was determined qualitatively using Jaccard's measure and Sorenson's qualitative measure, and quantitatively with Sorenson's quantitative measure (Magurran, 1988).

Additionally, for *Hydrilla* samples only, we compared α- and β-diversity of Chironomidae among sites at three widely separated lakes of varying size and altitude; Lakes Bisina and Bunyoni in Uganda and Lake Tanganyika in Burundi (see Copeland *et al.* 2012). Sampling at the three sites was carried out using the same methods and over the same period (2007-2010). For those comparisons, data from our primary sampling site in each of the three lakes were used: Cercle Nautique (3°23'24"S, 29°21'0"E, 773 m) in Lake Tanganyika, Bujumbura, Burundi, Alelesi (1°39'11"N, 33°58'41"E, 1044 m) in Lake Bisina, and a site in Lake Bunyonyi (*ca.* 1°16'16"S, 29°55'52"E, 1945 m). In this case β-diversity compared similarity among locations.

Sources for information on the geographic distribution of Chironomidae

Information on the geographic distribution of African Chironomidae was taken from published sources (see Copeland *et al.*, 2012; Appendix 1) and an unpublished checklist with distributional data for all African Chironomidae (available from Hilde Eggermont; hr.eggermont@gmail.com).

Voucher specimens

Voucher specimens were retained at the National Fisheries Resources Research Institute, Jinja (Uganda) with duplicates at the herbarium of Makerere University (MHU) for the plants, and at the International Centre of Insect Physiology and Ecology, Nairobi (Kenya), for the insects.

RESULTS

Hydrilla survey

Hydrilla was found in four Ugandan lakes, Bunyonyi and Mutanda (1°12'36"S, 29°40' 44"E, 1783 m) in the far southwest, Kyoga (1°33'32"N, 32°53'6"E, 1035 m) in the north-central area, and Bisina in the northeast (figure 1). There was no evidence of seasonality in the presence of *Hydrilla*, and sites in these four lakes that were resampled always produced *Hydrilla.* We found no evidence of its presence in Lakes Kyugi (0°19'19"S, 31°50'49"E, 1164 m), Nabugabo (0°21'58"S, 31°54'0"E, 1140 m), and Kachira (0°37'52"S, 31°5'38"E, 1231 m) in the south-central part of the country and Chahafi (1°20'42"S, 29°46'12"E, 1891 m) in the southwest.

In spite of considerable sampling effort, *Hydrilla* was not found in Lake Victoria (figure 1; figure 2, maps 2 and 3). In Kenya, the species was absent from 70 sites between 1°1'44"S and 0°3'40"N (figure 2, map 3). Samples were taken along the lakeshore of much of the Winam (=Kavirondo) Gulf and areas to the south and the north of it, including Port Victoria, where *Hydrilla* was previously found. Some areas, especially in the Winam Gulf, were inaccessible because of the presence of large stands of *Eichhornia crassipes* (Mart.) Solms. In Uganda, *Hydrilla* was absent from both the Jinja and Buluba areas of Lake

Victoria (figure 2, map 2) from where it had been recorded previously. Neither was there evidence of broken stems or dead plants. However, *Egeria densa* Planch. (Brazilian Egeria), an exotic Hydrocharitaceae that closely resembles *Hydrilla*, was common in both areas, including very dense patches in Buluba (figure 3).

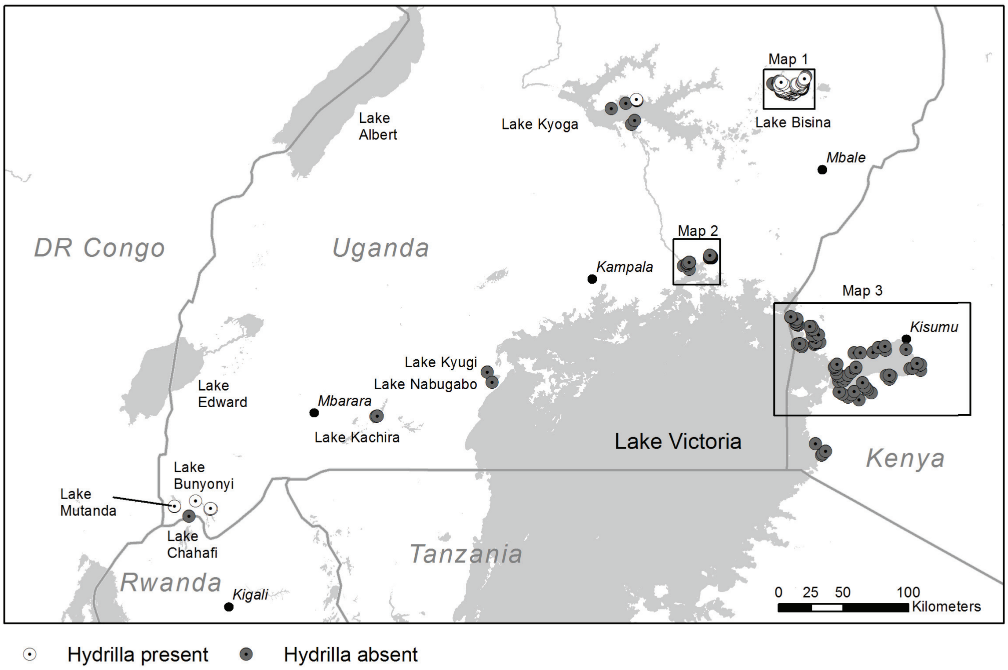

Figure 1. Hydrilla *survey sites in Kenya and Uganda. Maps 1, 2 and 3 enlarged in figure 2.*

In Lake Bisina we conducted an extensive survey mapping the distribution of the major aquatic macrophytes (Gidudu *et al.* 2011). Figure 2, map 1 presents the mapping data for presence/absence of *Hydrilla* at 199 sampling points. *Hydrilla* was uncommon in the western portions of the lake where the substrate was usually sandy. It was commonly found in the central and eastern portions growing in the muddy (but not flocculent) lake bottom, and was particularly abundant in the Alelesi area where it grew together with *Najas horrida, Potamogeton schweinfurthii*, *Ceratophyllum demersum*, and *Ottelia ulvifoli*a.

Chironomidae reared from *Hydrilla* and associated aquatic plants

We collected 7424 adults representing 43 species of Chironomidae from submersed macrophytes in Ugandan lakes (table 1). Nearly half of the species (21, 49%), including three putative new species, *Paramerina* sp. and *Cladotanytarsus* sp. U1 and U2, represent new records for Uganda. Thirty-nine (39) of the species (91%), emerged from *Hydrilla*. Only *Paramerina* sp. n., *Chironomus calipterus*, *Cryptochironomus lindneri*, and *Cladotanytarsus* sp. U1 were not associated with *Hydrilla* samples.

Fourteen of the 43 species (33%) emerged only from *Hydrilla* samples. However, *Polypedilum wittei*, a possible herbivore of *Hydrilla* (Buckingham, 1994) was not specific to it, emerging from collections of six other aquatic plant species (table 2). *Polypedilum dewulfi*, the other potential chironomid herbivore of *Hydrilla* (Buckingham, 1994) was not found in Uganda.

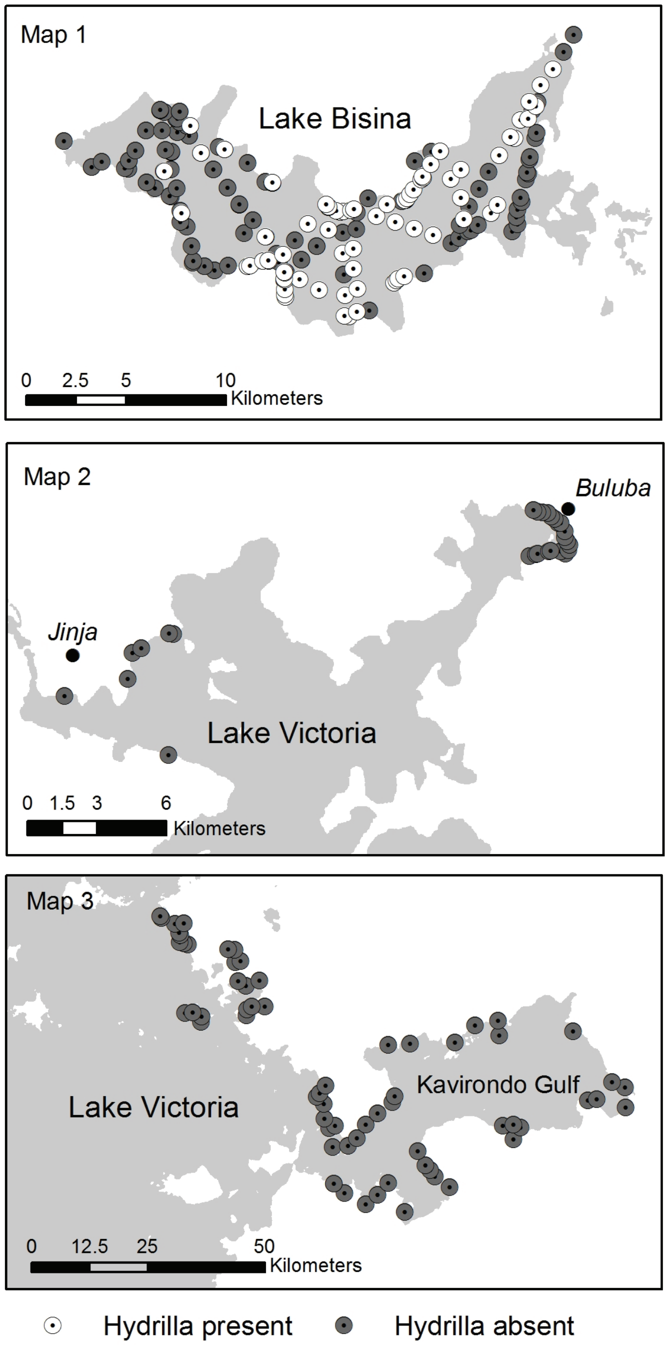

Figure 2. Higher resolution of three Hydrilla *survey areas. Sites in Lake Bisina, Uganda (map 1, top); Lake Victoria, Uganda, Jinja and Buluba areas (map 2, middle); Lake Victoria, western Kenya (map 3, bottom).*

Figure 3. Dense surface mat of Egeria densa *in small bay near Buluba, Uganda. Photograph taken 31 August 2009 by Robert Copeland.*

At Lake Bisina, our main sampling site, 37 species emerged from aquatic macrophytes and 33 (89.2%) of these emerged form *Hydrilla* (table 2). Although nearly 2/3 of species found in Lake Bisina had been collected by the third sampling date, new species were still being recovered from plants up to the penultimate sampling date (figure 4). Four of the six species that emerged from sampling dates 19-21 were from plants other than *Hydrilla*.

Chironomid biodiversity

Comparison of diversity of chironomids associated with Hydrilla among sites on three lakes

Alpha-diversity of chironomids from *Hydrilla* was virtually identical at the sites on Lakes Bisina (Alelesi) and Bunyonyi, while it was significantly lower at the Lake Tanganyika site (Cercle Nautique) than at either of the other sites (table 3), even though Cercle Nautique produced as many or more chironomid species than did the two Ugandan sites. This is because the Shannon index (H') is sensitive to both species richness (numbers of species) and the evenness of their distribution, so that H_{max} occurs when all species are equally abundant (Magurran, 1988). This is shown graphically (figure 5) in the relatively flattened rank abundance curves of chironomids from the sites in Lakes Bisina and Bunyonyi compared to that of samples from our site in Lake Tanganyika, where one species comprised over 80% of all individuals (Copeland *et al.*, 2012).

Table 1. Chironomidae associated with submersed aquatic macrophytes in Uganda.

Subfamily	Tribe	Species[1]	Synonyms[2]	African distribution[3,4,5]
Tanypodinae	Coelotanypodini	*Clinotanypus claripennis* Kieffer	*C. niligena* Kieffer; *C. nigripalpis;* Goetghebuer; *C. nigrovittatus* Goetghebuer r	buru[6,7], cam, cha, **con**, **EGY**, eth, gha, ken, mala, mali, nam, niger, nige, sen, sou, **sud**, tan[6,7], uga, zam, zim
	Pentaneurini	*Ablabesmyia dusoleili* Goetghebuer		ben, bur, buru[8], cam, cha, **CON**, egy, eth, gha, ken, mad, mali, nige, rco, sen, sou, sud, uga, zim
		A. melaleuca Goetghebuer		buru[8], cha, **CON**, gha, gui, ivo, nige, sen, sie, uga
		A. nilotica **(Kieffer)**	*?Tanypus congoensis* Kieffer; *?T. kribiensis* Kieffer; *A. tricolor* Goetghebuer	bur, cam, **cha**, **con**, eth, gha, mala, mali, nam, nige, rco, sou, **SUD**, tan, zim
		A. rimae **Harrison**		buru[8], **ETH**, nam[9], tan[6,7]
		Paramerina **sp. nov.**		
Orthocladiinae		***Cricotopus scottae*** **Freeman**		buru[7], cha, con, eth, gha[10], niger, nige, **SOU**, tan[7], zim
		Nanocladius saetheri **Harrison**		buru[8], **ETH**, ken[6], uga[6], sou
Chironominae	Chironomini	*Chironomus calipterus* Kieffer	*Chironomus tavetae* Kieffer; *Calochironomus niliacus* Kieffer; *Calochironomus hexastictus* Kieffer	ben, bur, con, **egy,** **ken,** mad, **NAM,** sen, sou, **sud,** uga
		Chironomus callichirus Kieffer	*?C. apicalis* Kieffer; *C. seychelleanus* Kieffer; *C. albomarginatus* Kieffer; *C. nivalis* Freeman	bur, con, eth, ken, mad, mala, **nam**, reu, **SEY**, **sou**, sud, tan, uga, zam, zim
		C. formosipennis Kieffer	*C. palustris* Kieffer; *C. tricolor* Kieffer; *C. oxylabis* Kieffer; *C. nilicola Kieffer;* *C. pictiventris* Kieffer; *C. oxylabis* var. *linea* Kieffer	bur, buru[7], cam, cha, con, **egy**, eth, gha, **ken**, mad, mala, mali, **NAM**, niger, nige, sen, **sou**, **sud**, tan[7], uga, zam

Subfamily	Tribe	Species[1]	Synonyms[2]	African distribution[3,4,5]
		Cryptochironomus lindneri(Freeman)	*?Cladopelma pseudolabis* Kieffer	buru[8], cam, cha, con, eth, gha, niger, nige, sen, sou, **SUD**, uga, zam, zim
		Dicrotendipes chambiensis (Goetghebuer)		cha, **CON**, sen, sou, sey, uga
		D. fusconotatus (Kieffer)	*?D. trilabis* Kieffer; *Chalochironomus griseonotatus* Kieffer; *C. griseosparsus* Kieffer; *D. forficula* Kieffer; *D. nilicola* Kieffer; *Polypedilum quatuorpunctatum* Goetghebuer	bur, buru[8], cha, con, egy, eth, gha[11], mala, niger, nige, **SUD**, tan[6,7], uga, sou, zim
		D. kribiicola (Kieffer)		bur, buru[8], **CAM**, cha, con, gha, mali, tan[6,7], uga
		***D. peringueyanus* (Kieffer)**	*Polypedilum griseovittatum* Goetghebuer	bot, bur, cam, cha, **con**, ken, moz[9], sen, **SOU**, zam, zim
		D. septemmaculatus (Becker)	*Chironomus (Prochironomus) punctatipennis* Kieffer; *Dicrotendipes pictipennis* Kieffer; *Tendipes punctatipennis* Kieffer; *D. formosanus* Kieffer; *D. formosanus var. frontalis* Kieffer; *D. speciosus* Kieffer; *Stictochironomus sexnotatus* Goetghebuer; *C. hirtitarsis* Johannsen; *Polypedilum quatuordecimpunctatum* Goetghebuer; *Dicranotendipes speciosus* Kieffer; *D. frontalis* Kieffer; *D. punctatipennis* (Kieffer); *D. rajasthani* Singh and Kulshrestha; *D. hiritarsis* (Johannsen)	alg, cha[12], con, egy, eth, ken, mad, nam, nige, sou, sud, uga, zim
		***D. sudanicus* (Freeman)**		bur, buru[8], cam, cha, gha, gui, mali, nam, nige, sen, sou, **SUD**, tan[6,7], zim
		***Harnischia cf. lacteiforceps* (Kieffer)**		bur, buru[6,7], cam, cha, gha, gui, mali, nam, nige, sen, sou, **SUD**, tan[6,7], zim

Subfamily	Tribe	Species[1]	Synonyms[2]	African distribution[3,4,5]
		Kiefferulus brevibucca (Kieffer)	*Nilodorum stilatum* Kieffer (as var.); *N. caffarium* Kieffer (as var.); *N. nigritarse* Goetghebuer; *N. burgeoni* Goetghebuer	bur, buru[6], cam, cha, **con**, egy, eth, gab, gha, ken, niger, nige, sen, sou, **SUD**, tan[6], uga, zam, **zim**
		K. brevipalpis (Kieffer)	*Nilodorum dewulfi* Goetghebuer; *Chironomus surdellus* Goetghebuer; *C. vitshumbiensis* Goetghebuer	buru[8], cam, cha, **con**, **ETH**, gha, ken, mala, moz, nam, niger, nige, sou, sud, uga, zim
		K. chloronotus (Kieffer)	*Chironomus niloticus* Kieffer; *C. latilobus* Kieffer; *C. henrardi* Goetghebuer	ben, bur, buru[8], cam, cha, **con**, eth, gha, gui, ken, mad, mala, mali, nam, niger, nige, sen, **SEY**, sou, sud, tan[6], uga, **zim**
		K. fractilobus (Kieffer)	*Chironomus caligans* Goetghebuer; *Nilodorum elongatum* Freeman	bur, cha, **con**, eth, gha, ken, nige, sou, **SUD**, uga, zim
		***Nilothauma cf. latocaudatum* Adam & Saether**		**ZIM**
		***Parachironomus acutus* (Goetghebuer)**		bur, buru[8], cam, cha, **CON**, egy, eth, gha, mad, mala, mali, niger, nige, sou, zim
		P. dewulfianus (Goetghebuer)		alg, bur, buru[8], cam, cha, **CON**, egy, eth, gha, niger, nige, sud, uga, zim
		***Polypedilum* (*Pentapedilum*) *micra* Freeman**		bur, buru[8], car, gha, nam, nige, **SUD**, tog, zim
		P. (*Pentapedilum*) *vittatum* Freeman		eth, ken, mala, nige, sou, uga, **ZIM**
		***P.* (*Pentapedilum*) *wittei* Freeman**		bur, buru[8], **CON**, egy, eth, gha, gui, ken[6], nige, sen, sou, sud, tan[6,7], uga[6], zim

Subfamily	Tribe	Species[1]	Synonyms[2]	African distribution[3,4,5]
		***P.* (*Polypedilum*) *tenuitarse* (Kieffer)**	*Polypedilum fenestratum* Goetghebuer; *Kribiomimus leucolabis* Kieffer; *K. leucolabis var. tibialis* Kieffer; ? *Kribiocharis filitarsis* Kieffer	buru[8], **CAM**, cha, con, gui, nige, sen, sou, sud
		***Xenochironomus trisetosus* (Kieffer)**		bur, cam, cha, con, gha, gui, ivo, nam[9], rco, sen, **SUD**
		X. ugandae (Goetghebuer)		cam, cha, con, nam, nige, sou, sud, **UGA**, zim
		***Zavreliella marmorata* (Wulp)**	*Lauterborniella fuscoguttata* Kieffer; *Polypedilum fuscoguttatum* Kieffer	bur, cam, cha, gha, gui, nige, sen, sou, **SUD**, zim
	Tanytarsini	*Cladotanytarsus pseudomancus* (Goetghebuer)		bur, buru[8], cam, car, cha, **CON**, egy, eth, gha, gui, ken, mad, mala, mali, nam, niger, nige, sen, sou, sud, uga, zim
		***Cladotanytarsus* sp. U-1**		
		Cladotanytarsus* sp. *U-2		
		***Rheotanytarsus ceratophylli* (Dejoux)**		**CHA**, gha, ken[6], nige, sen, sud, uga[6]
		Tanytarsus balteatus Freeman		buru[8], car, cam, cha, con, nam, niger, nige, sou, **SUD**, uga, zim
		***T. bifurcus* Freeman**		**BUR**, cam, cha, eth, gha, mali, nige
		***T. flexistilis* Freeman**		bur, cam, cha, gha, **NIGE**
		T. formosanus Kieffer	*T. formosae* Kieffer; *T. horni* Goetghebuer; *T. aculeus* Chaudhuri *et al.*; *T. fuscimarginalis* Chauduri *et al.*; *T. nigrocinctus* Freeman	ben, bur, buru[8], car, cam, cha, con, egy, eth, gha, ken, niger, nige, sen, sou, sud, tog, uga

Subfamily	Tribe	Species[1]	Synonyms[2]	African distribution[3,4,5]
		***T. harei* Ekrem**		ivo, **<u>NIGE</u>**, sen
		Virgatanytarsus nigricornis (Goetghebuer)		bur, **<u>CON</u>**, eth, gui, sou, uga, zim

[1]Species in bold represent new, unequivocal collection records for Uganda; larvae of some species may have been collected earlier (see footnote 6).

[2]Only synonyms with different species epithets are included; e.g. for *Polypedilum tenuitarse*, *P. fenestratum* is included, while *P. tenuitarsis* is not.

[3]Based on the principal literature sources for the distribution of African Chironomidae (see Appendix 1, Copeland *et al*., 2012) plus records from an unpublished distributional list of all African Chironomidae (available from Hilde Eggermont, hr.eggermont@gmail.com).

[4]alg=Algeria; ben=Benin; bot=Botswana; bur=Burkina Faso; buru=Burundi; cam=Cameroon; car=Central African Republic; cha=Chad; con= Democratic Republic of Congo; egy=Egypt; eth=Ethiopia; gab= Gabon; gha=Ghana; gui=Guinee; ivo=Ivory Coast; ken=Kenya; mad=Madagascar; mala=Malawi; mali=Mali; moz=Mozambique; nam=Namibia; niger=Niger; nige=Nigeria; rco=Republic of Congo (Brazzaville); reu=Reunion; sen= Senegal; sey=Seychelles; sie=Sierra Leone; sou=South Africa; sud=Sudan; tan=Tanzania, tog=Togo; zam=Zambia; zim=Zimbabwe.

[5]Countries from which holotypes were described are indicated in bold, underlined capital letters; countries from which synonymized species were described are underlined.

[6]Larvae not unequivocally identified; rather listed as "cf." (conferatur=compare) or "near".

[7]Lake Tanganyika collections, national boundaries not specified (Eggermont & Verschuren, 2003a,b); probably includes both Burundi and Tanzania.

[8]Copeland *et al.* (2012).

[9]Personal communication (H. Eggermont); formerly included in online list of southern Africa fauna (Harrison, 2000; see Eggermont *et al*., 2008), but no longer posted on internet.

[10]as ? *Cricotopus* sp. (Petr, 1972), and identified as *C. scottae* in Verschuren (1997).

[11]as *Dicrotendipes* sp. 2 (Petr, 1972), and identified as *D. fuscontatus* in Verschuren (1997).

[12]as *Dicrotendipes pilosimanus* (Dejoux, 1968).

Table 2. Distribution of Chironomidae among Ugandan lakes and aquatic plants[1] .

	Lake and plant species										
	Bisina						Bunyonyi		Kyoga	Mutanda	Victoria
Chironomid species	*Hydrilla verticillata*	*Ceratophyllum demersum*	*Najas horrida*	*Ottelia ulvifolia*	*Utricularia reflexa*	*Potamogeton schweinfurthii*	*H. verticillata*	*Lagarosiphon* sp.	*H. verticillata*	*H. verticillata*	*Egeria densa*
Clinotanypus claripennis	x										
Ablabesmyia dusoleili	x		x				x				
A. melaleuca	x										x
A. nilotica	x	x					x	x			x
A. rimae	x	x	x			x			x		x
Paramerina sp. nov.					x						
Cricotopus scottae	x						x				
Nanocladius saetheri	x	x	x	x		x			x		
Chironomus calipterus					x						
C. callichirus					x					x	x
C. formosipennis	x				x		x				x

Chironomid species	Lake and plant species										
	Bisina						Bunyonyi		Kyoga	Mutanda	Victoria
	Hydrilla verticillata	*Ceratophyllum demersum*	*Najas horrida*	*Ottelia ulvifolia*	*Utricularia reflexa*	*Potamogeton schweinfurthii*	*H. verticillata*	*Lagarosiphon* sp.	*H. verticillata*	*H. verticillata*	*Egeria densa*
Cryptochironomus lindneri		x									
Dicrotendipes chambiensis							x				
D. fusconotatus	x		x				x		x	x	x
D. kribiicola	x	x	x			x	x		x		x
D. peringueyanus							x	x		x	
D. septemmaculatus	x	x	x			x	x	x		x	x
D. sudanicus	x										
Harnischia cf. lacteiforceps	x				x						
Kiefferulus brevibucca									x		
K. brevipalpis	x	x	x	x	x	x	x	x	x	x	x
K. chloronotus	x						x				x
K. fractilobus	x						x			x	x

Chironomid species	Lake and plant species										
	Bisina						Bunyonyi		Kyoga	Mutanda	Victoria
	Hydrilla verticillata	*Ceratophyllum demersum*	*Najas horrida*	*Ottelia ulvifolia*	*Utricularia reflexa*	*Potamogeton schweinfurthii*	*H. verticillata*	*Lagarosiphon* sp.	*H. verticillata*	*H. verticillata*	*Egeria densa*
Nilothauma cf. *latocaudatum*	×										
Parachironomus acutus	×						×		×		×
P. dewulfianus	×		×			×	×		×		×
Polypedilum (Pentapedilum) micra	×						×		×		
P. (Pentapedilum) vittatum							×				
P. (Pentapedilum) wittei	×	×	×	×	×	×	×	×		×	
P. (Polypedilum) tenuitarse	×										
Cladotanytarsus pseudomancus	×	×	×			×	×			×	
C. sp. U-1								×			
C. sp. U-2	×										
Rheotanytarsus ceratophylli	×						×				×
Tanytarsus balteatus	×	×	×	×	×	×	×		×		×

Chironomid species	Bisina: *Hydrilla verticillata*	Bisina: *Ceratophyllum demersum*	Bisina: *Najas horrida*	Bisina: *Ottelia ulvifolia*	Bisina: *Utricularia reflexa*	Bisina: *Potamogeton schweinfurthii*	Bunyonyi: *H. verticillata*	Bunyonyi: *Lagarosiphon* sp.	Kyoga: *H. verticillata*	Mutanda: *H. verticillata*	Victoria: *Egeria densa*
T. bifurcus	x	x	x		x	x					
T. flexistilus	x	x	x		x	x			x		
T. formosanus	x	x	x	x	x	x	x	x	x		x
T. harei	x	x	x			x	x				
Virgatanytarsus nigricornis							x				
Xenochironomus trisetosus	x								x		
X. ugandae	x	x							x		
Zavreliella marmorata	x										x

[1]Occurrence of chironomid species indicated with an "x".

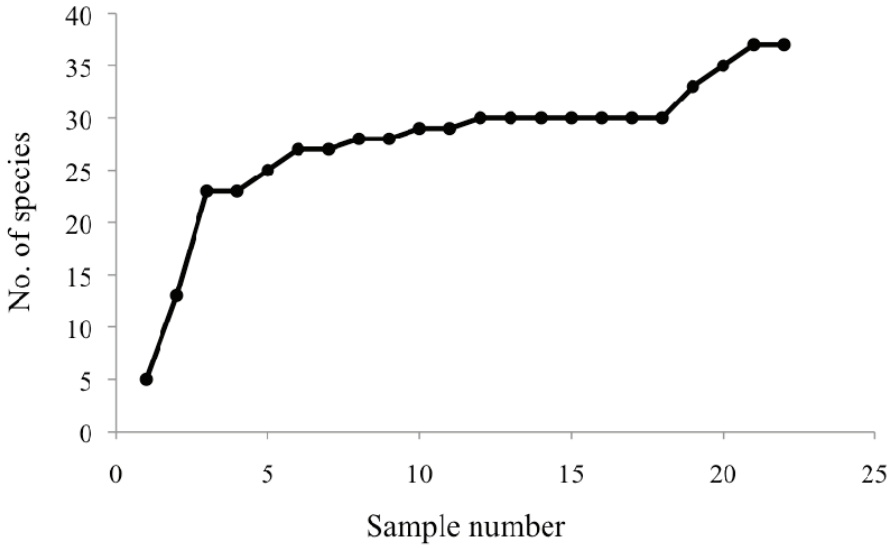

Figure 4. Species accumulation curve for Chironomidae from aquatic macrophytes in Lake Bisina, Uganda.

Table 3. Shannon α-diversity measures for Chironomidae emerging from Hydrilla *sampled at three discrete sites in widely separated areas; Lakes Bunyonyi and Bisina (Alelesi site) in Uganda, and Lake Tanganyika (Cercle Nautique site) in Burundi[1].*

Site	Latitude	Longitude	Altitude (m)	Shannon index
Lake Bunyonyi, Uganda	1°16’15”S	29°55’51”E	1951	2.161
Lake Bisina, Uganda	1°39’15”N	33°57’44”E	1042	2.174
Lake Tanganyika, Burundi	3°23’24”S	29°21’1”E	786	0.606

Paired site comparison	t-statistic	df	p
Bisina/Bunyonyi	0.316	1337	>0.500
Bisina/Tanganyika	75.79	2787	<0.001
Bunyonyi/Tanganyika	40.88	951	<0.001

[1]Data for Lake Tanganyika from 22 sampling dates at a site near Bujumbura (see Copeland *et al.* 2012).

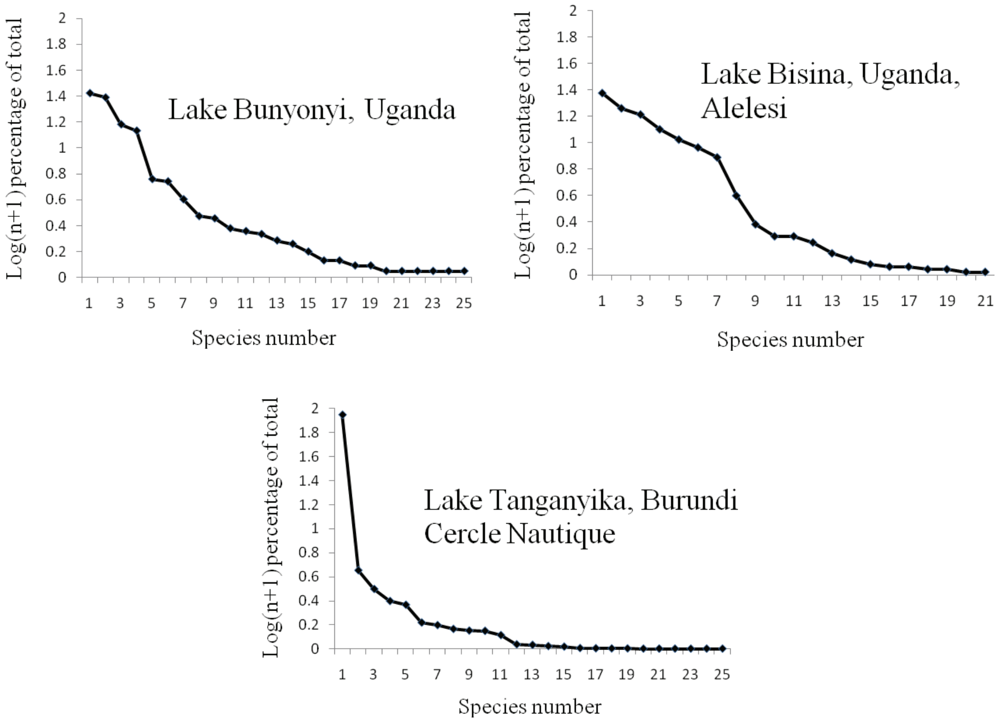

Figure 5. Species abundance curves for Chironomidae emerging from Hydrilla *sampled at three discrete sites in widely separated areas: Lakes Bunyonyi and Bisina (Alelesi site) in Uganda, and Lake Tanganyika (Cercle Nautique site) in Burundi (Lake Tanganyika data collected concurrently; see Copeland* et al.*, 2012).*

β-diversity of chironomids reared from *Hydrilla* was also compared among the same three sites. The chironomid faunas from the sites on the two Ugandan lakes were more similar to each other than they were to the fauna of the Lake Tanganyika site (figure 6). When quantitative data was included (Sorenson's quantitative measure) these differences were more pronounced.

Species composition and quantitative differences between the chironomid faunas of aquatic macrophytes of Lake Bisina and Lake Tanganyika

The species composition of chironomids emerging from all sampled plant species in Lakes Bisina and Tanganyika was strikingly different (table 4). *Dicrotendipes* contributed the most common species in each lake (*D. septemmaculatus* in Bisina and *D. fusconotatus* in Tanganyika), but each of the two species was absent or rare in the other lake. Except for populations of a single species, *Kiefferulus brevipalpis,* this pattern repeated itself among paired species comparisons between the two lakes. Among the Orthocladiinae, Chironomini and Tanytarsini, different species dominated the Bisina and Tanganyika faunas (table 4). Additionally, the relative proportions of the overall chironomid population contributed by the four higher taxa of Chironomidae (Tanypodinae, Orthocladiinae, Chironominae: Chironomini and Chironominae: Tanytarsini) differed greatly between lakes. Most pronounced was the marked difference between the two lakes in the importance of the

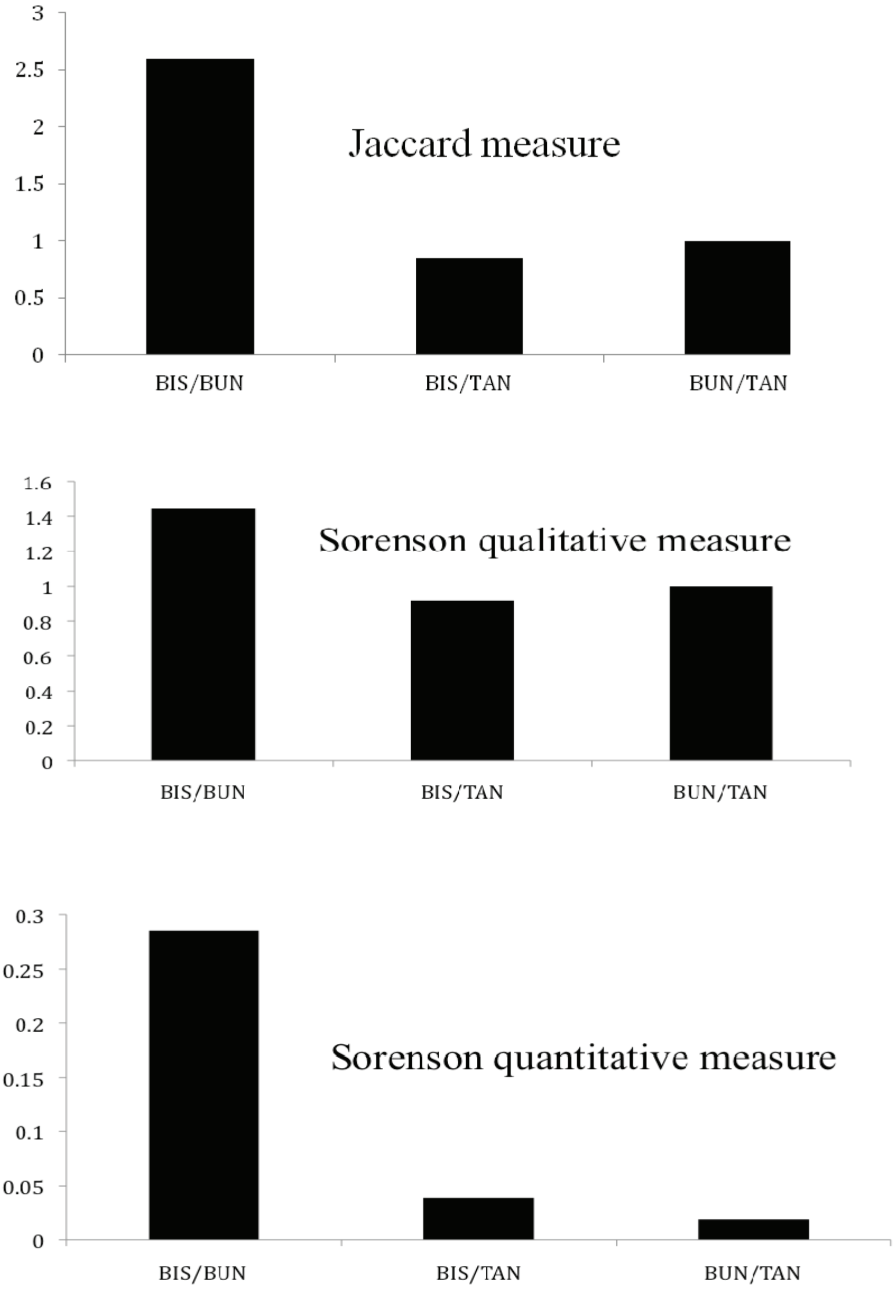

Figure 6. Beta-diversity measures of Chironomidae emerging from Hydrilla *sampled at three discrete sites in widely separated areas: Lakes Bunyonyi and Bisina (Alelesi site) in Uganda, and Lake Tanganyika (Cercle Nautique site) in Burundi. BIS=Lake Bisina; BUN=Lake Bunyonyi; TAN=Lake Tanganyika (Lake Tanganyika data collected concurrently; see Copeland* et al.*, 2012).*

Tanytarsini populations; this being substantial in Bisina (8 species, 39.5% of all individuals) and negligible in Tanganyika (4 species, 2.2% of individuals; table 4).

Comparison of diversity of chironomids associated with different aquatic macrophytes at a site on Lake Bisina

At Alelesi on Lake Bisina, α-diversity of chironomids was compared among four aquatic plants. Shannon indices (range 1.87-2.09) were remarkably similar for all of them (table 5). Pairwise comparisons of Shannon indices showed slight, but significant, differences between *Ceratophyllum*/*Hydrilla*, *Hydrilla/Najas* and *Najas*/*Potamogeton.* Indices of the remaining three combinations of plants were not significantly different. β-diversity measures of chironomids from the four plants also showed limited differences among the six pairwise comparisons (table 6). Even when quantitative data were included, the range of values (0.338-0.641) was not great. Among the six possible pairwise combinations, chironomid populations from *Hydrilla*/*Ceratophyllum* and *Hydrilla*/*Potamogeton* were most different while the populations that emerged from *Hydrilla*/*Najas* were most alike.

DISCUSSION

Apparent local eradication of *Hydrilla* from Lake Victoria

Despite intensive searches in Lake Victoria, *Hydrilla* was not found at any of the 97 sites sampled in Kenya and Uganda. In contrast, *Egeria densa*, an invasive Hydrocharitaceae closely resembling *Hydrilla* in habit, was sampled at several sites near Buluba and Jinja, Uganda where *Hydrilla* was formerly found. Although the reasons for the disappearance of *Hydrilla* from areas where it was previously found may never be known, various factors could account for it. Earlier records of *Hydrilla* from Lake Victoria may have been misidentifications of the very similar looking *Egeria densa.* However, confirmation of the identity of two Lake Victoria *Hydrilla* specimens was made by one of us (RSC) (*G.H.S. Wood 466*, 3 Oct 1952, 0.5 miles SW of Buluba Leper Colony, 10 miles E of Jinja, Makerere University Herbarium, Kampala, Uganda; *E.M. Lind M.C. 136*, Bugonga ferry opposite Jinja, 1953, Makerere University Herbarium, Kampala, Uganda). Alternatively, *Egeria* may tolerate higher levels of organic pollution than *Hydrilla*, and compete better in a lake under stress from an expanding human population (Verschuren *et al.,* 2002). In experiments, however, *Hydrilla* generally outcompeted *Egeria* under varying levels of nutrient (fertilizer) availability, except when pure sand was used as a substrate (Mony *et al.*, 2007). The characteristics of the bottom substrate may influence establishment of the two plant species. Presently, the bottom substrate of Lake Victoria in the area of Buluba and Jinja is soft, flocculent mud with large amounts of decaying vegetation. In lakes where we collected *Hydrilla*, it grew in non-flocculent mud and in the absence of rotting plants. Finally, *Hydrilla* may have been driven to extinction by one of the periodic blooms of the invasive weed, *Eichhornia crassipes* (water hyacinth), first reported from Lake Victoria, Uganda, in 1989 (Twongo, 1991). These blooms cause transient blanketing of large areas of the lake, particularly in protected bays and inlets, and *Eichhornia* may remain stationary long enough to kill the submersed plants beneath it (Gichuki *et al.*, 2001). Such an event may have eliminated the *Hydrilla* populations in and around the Winam Gulf in Kenya, which was severely impacted by *Eichhornia,* and near Jinja and Buluba in eastern Uganda, which experienced similar hyacinth blooms. However, for the Jinja area, at least, there is evidence that the disappearance of *Hydrilla* from the lake predated the reported appearance of water

Table 4. Comparison of Chironomidae species associated with plants in Lake Bisina, Uganda and Lake Tanganyika, Burundi[1].

Subfamily	Tribe	genus	species	No. (%) from Lake Bisina (n=5649)	No. (%) from Lake Tanganyika n=32090)
Tanypodinae	Coelotanypodini	*Clinotanypus*	*cf. claripennis*	4 (<1)	0
	Pentaneurini	*Ablabesmyia*	*cf. melaluca*	3 (<1)	2 (<1)
			dusoleili	21 (<1)	3 (<1)
			nilotica	10 (<1)	0
			rimae	143 (2.5)	23 (<1)
		Nilotanypus	*comatus*	0	1 (<1)
		Paramerina	sp. nov.	1 (<1)	0
Ortthocladiinae		*Cricotopus*	*albitibia*	0	1 (<1)
			cf. harrisoni	0	1263 (3.9)
			scottae	1 (<1)	0
		Nanocladius	*cf. saetheri*	138 (2.4)	4 (<1)
Chironominae	Chironomini	*Chironomus*	*calipterus*	1 (<1)	0
			callichirus	1 (<1)	0
			formosipennis	13 (<1)	0
			imicola	0	116 (<1)
		Cryptochironomus	*cf. diceras*	0	27 (<1)
			lindneri	1 (<1)	15 (<1)
		Dicrotendipes	*fusconotatus*	3 (<1)	26398 (82.3)
			kribiicola	370 (6.6)	1 (<1)
			septemmaculatus	1554 (27.5)	0
			sudanicus	5 (<1)	129 (<1)
		Harnischia	*curtilamellata*	0	1 (<1)
			cf. lacteiforceps	22 (<1)	0

Subfamily	Tribe	genus	species	No. (%) from Lake Bisina (n=5649)	No. (%) from Lake Tanganyika n=32090)
		Kiefferulus	*brevipalpis*	517 (9.2)	1711 (5.3)
			chloronotus	1 (<1)	129 (<1)
			fractilobus	8 (<1)	0
		Nilothauma	*cf. latocaudatum*	1 (<1)	0
		Parachironomus	*acutus*	1 (<1)	497 (1.6)
			dewulfianus	174 (3.1)	262 (<1)
		Polypedilum	*dewulfi*	0	660 (2.1)
			micra	11 (<1)	1 (<1)
			tenuitarse	1 (<1)	3 (<1)
			wittei	186 (3.3)	294 (<1)
		Xenochironomus	*trisetosus*	16 (<1)	0
			ugandae	5 (<1)	0
		Zavreliella	*marmorata*	1 (<1)	0
	Tanytarsini	*Cladotanytarsus*	*pseudomancus*	28 (<1)	411 (1.3)
			sp. U-2	2 (<1)	0
		Rheotanytarsus	*ceratophylli*	10 (<1)	0
			guineensis	0	4 (<1)
		Tanytarsus	*balteatus*	811 (14.4)	122 (<1)
			bifurcus	699 (12.4)	0
			flexistilis	100 (1.8)	0
			formosanus	363 (6.4)	12 (<1)
			harei	415 (7.4)	0

[1]Grey areas highlight major differences between lake faunas. Data represent chironomids emerging from all plant samples collected in Lake Bisina (22 sampling dates) and Lake Tanganyika (25 sampling dates, collections made concurrently with those of Lake Bisina; see Copeland et al., 2012).

Table 5. Shannon α-diversity measures for Chironomidae from four submersed macrophytes at Alelesi, Lake Bisina.

Plant species	Shannon index		
Ceratophyllum demersum	1.91		
Hydrilla verticillata	2.09		
Najas horrida	1.87		
Potamogeton schweinfurthii	2.06		
Paired comparison	t-statistic	df	p
Ceratophyllum/Hydrilla	2.58	390	<0.01
Ceratyophyllum/Najas	0.41	598	>0.05
Ceratophyllum/Potamogeton	1.87	463	>0.05
Hydrilla/Najas	3.63	684	<0.001
Hydrilla/Potamogeton	0.53	322	>0.05
Najas/Potamogeton	2.59	547	<0.01

Table 6. Beta-diversity measures for chironomids from four submersed macrophytes at Alelesi, Lake Bisina.

	Pairwise comparison of plant species[1]					
Beta-diversity measure	CER HYD	CER NAJ	CER POT	HYD NAJ	HYD POT	NAJ POT
Jaccard (qualitative)	0.556	0.611	0.667	0.706	0.563	0.733
Sorenson (qualitative)	0.714	0.759	0.8	0.828	0.72	0.846
Sorenson (quantitative)	0.45	0.624	0.641	0.649	0.338	0.493

[1]CER, *Ceratophyllum demersum*; HYD, *Hydrilla verticillata*; NAJ, *Najas horrida*; POT, *Potamogeton schweinfurthii*

hyacinth in 1989 (Twongo, 1991). Surveys conducted in 1983-84 that specifically targeted *Hydrilla* failed to find any submersed aquatic macrophytes in the Jinja area of Lake Victoria (Markham, 1985). Regardless of how *Hydrilla* was extirpated, its reestablishment would depend on reintroduction of the plant by natural or artificial means, and *Egeria* may be a more effective colonizer.

Chironomids sampled from aquatic macrophytes in Uganda

Including the 21 new country records for the species collected during the present study, 97 Chironomidae are now known from Uganda. An updated list of Ugandan Chironomidae is provided in the appendix. Because much of the data presented in the appendix is from an unpublished report (see footnote in the appendix), these distributional data should be viewed with some caution.

Because our study was designed to maximise the chances of finding natural enemies of *Hydrilla*, only lacustrine habitats were sampled. Streams, swamps, temporary pools, small dambos, rock pools and natural and artificial container habitats were not examined. Furthermore, only submersed macrophytes were sampled. Other lacustrine habitats such as lake bottom substrates (rocks, mud or sand) and rotting wood were likewise ignored. We also did not explore forest wetlands, which in other studies have yielded many interesting species (*e.g.* Hare & Carter 1987). It is likely that a thorough search of these habitats would greatly increase the number of species known from Uganda.

Three rare species, *Paramerina* sp., *Cladotanytarsus* sp. U-1, *Cladotanytarsus* sp. U-2, were each represented in our collections by a single specimen. These individuals apparently represent undescribed species but we are hesitant to describe new species based on single specimens.

There were differences in the composition of chironomid species among the lakes sampled in Uganda. Adults of four species, *Polypedilum vittatum, Dicrotendipes chambiensis, D. peringueyanus* and *Virganatanytarus nigricornis* emerged from plants collected in Lake Bunyonyi which was only sampled six times, but were not recovered elsewhere, including Bisina which was sampled intensively. Similarly, *Kiefferulus brevibucca* was found in Lake Kyoga, but not in Bisina, just upstream from it. Comparatively few collections were made in lakes other than Bisina, and additional sampling is needed before conclusions can be drawn regarding the distribution of Ugandan midge species found, to date, only in Lake Bisina.

Chironomidae from Lake Bisina

Chironomid species richness on plants in Lake Bisina was substantial. Microscopic inspection of plants did not reveal any evidence of endophytic larvae in our plant samples. Although we do not rule out the possibility that some primarily benthic species might have been sampled in mud attached to the roots of sampled plants, our swirling of plants in lake water eliminated clotted mud, limiting the chances of sampling benthic species. The 37 species we sampled may come close to the actual number of epiphytic chironomid species that occur in the lake. However, more species will probably be found on plants, and this is suggested by the species accumulation curve (figure 4) that showed a departure from flatness near the end of our sampling programme. Non-*Hydrilla* plants were sampled on only eight occasions and mostly late in the project, and four of the last six chironomid species recovered from plants were from species other than *Hydrilla*. One of these, *Utricularia reflexa*, was sampled only once but contributed three unique species, one probably undescribed, to the total from the lake. Furthermore, at least 10 other species of aquatic macrophytes occur in Lake Bisina in addition to those we sampled (Gidudu *et al.*, 2011). Intensive sampling in Lake Bisina of species other than *Hydrilla* would likely produce additional chironomid species.

Interestingly, *Hydrilla* and *Najas horrida* were most alike in the composition of their chironomid populations, while *Hydrilla*/*Ceratophyllum* and *Hydrilla*/*Potamogeton* were most different. *Hydrilla* and *Najas* each have relatively complex plant architecture and both are

Hydrocharitaceae; more closely related to each other than to either of the other two plant species.

Lake Chad is the only African lake for which estimates have been made of both the total number of chironomid species and the number associated with aquatic plants. At Lake Chad, 105 species of chironomid adults were collected at light (Dejoux, 1968, 1973), while larvae of 60 chironomid morphospecies were sampled from aquatic macrophytes (Dejoux & Saint-Jean, 1972). These data suggest that about 57% of species collected at light were associated, as larvae, with aquatic plants in Lake Chad (the actual percentage may be higher because some of the adults collected at light may have developed in other, nearby aquatic habitats). If a similar relationship between epiphytic and total chironomid species richness holds for Lake Bisina, then the total number of chironomid species breeding in the lake is undoubtedly much higher than the 37 species we sampled. Even when based solely on the sampling data from aquatic macrophytes, Bisina is currently the 7th most species-rich lake in Africa (table 7).

Eggermont & Verschuren (2004a,b) identified sub-fossil larvae from surface-sediment samples from 73 lakes in Uganda (40), Kenya (20), Tanzania (1) and Ethiopia (12). They considered that their samples from small- and medium-size lakes gave an "... adequate representation of the full range of local benthic microhabitat in mid-lake fossil assemblages" (Eggermont & Verschuren, 2004b; p. 452). In their study, Ugandan lakes had the highest taxon richness, led by Lakes Kayihara (30 taxa), Kyaninga (29), and Wanjkenzi (29) (Eggermont & Verschuren, 2004b). Without any targeted sampling of the benthic fauna, Lake Bisina had 37 species associated with it and probably has many more. These data suggest either that surface-sediment collections of recent chironomid death assemblages in small- and medium-size lakes undersample the epiphytic fauna or that Lake Bisina is particularly species rich. The latter is probably the case. Most of the Ugandan lakes sampled by Eggermont & Verschuren (2004a,b) are crater lakes while all of the Kyoga system lakes, including Bisina, were tectonically formed. Crater lakes are often characterized by their steep walls and normally have a smaller littoral zone than do tectonically formed lakes. A larger littoral area may offer more niches to aquatic plant and animal species.

Unfortunately, none of the lakes of the Kyoga system, of which Bisina is the third largest, was included in their (Eggermont & Verschuren, 2004a,b) study. The Kyoga system in eastern Uganda includes 23 lakes, varying greatly in size (0.3-1800 km^2), though fairly uniform in depth (*ca.* 2-4 m) (LAKIMO, 2004). As such, the Kyoga system lakes provide an opportunity to examine the effect of lake size and environmental factors on invertebrate species richness.

Table 7. Number of chironomid species reported from selected African lakes.

Lake	Country	Sampling method	No. of species	Reference
Chad	Cameroon, Chad, Niger, Nigeria	Light traps and plant sampling	105	Dejoux (1968, 1973)
Tanganyika	Burundi, D.R. Congo, Tanzania, Zambia	Surface-sediment samples and plant sampling	85	Eggermont & Verschuren (2003a,b); Copeland *et al.* (2012)

Kainji	Nigeria	Not stated	57	Bidwell & Clarke (1977)
Volta	Ghana	Light traps	47	Petr (1970)
Opi	Nigeria	Emergence trapping and sediment grabs	46[1]	Hare & Carter (1987)
Victoria	Kenya, Tanzania, Uganda	Surface-sediment samples	39	Eggermont & Verschuren (2004a,b)
Bisina	Uganda	Plant sampling	37	This study
Kayihara	Uganda	Surface-sediment samples	30	Eggermont & Verschuren (2004a,b)
Kyaninga	Uganda	Surface-sediment samples	29	Eggermont & Verschuren (2004a,b)
Wankezi	Uganda	Surface-sediment samples	29	Eggermont & Verschuren (2004a,b)
Awasi	Ethiopia	Sediment grabs and plant sampling	27	Kibret & Harrison (1989)
Kariba	Zambia, Zimbabwe	Sediment grabs	27	McLachlan (1969)

[1]34 other species collected at light were thought by the authors not to have developed in Lake Opi.

Comparison of the epiphytic chironomid communities of Lakes Bisina and Tanganyika

Eggermont & Verschuren (2004a,b) found substantial differences between the species composition of sub-fossil larval Chironomidae extracted from surface-sediment samples from freshwater East African lakes and those from similar samples from Lake Tanganyika in Central Africa (Eggermont & Verschuren, 2003a,b). Of the *ca.* 77 larval taxa they collected in Lake Tanganyika, only 26 (ca. 34%) occurred in at least one of the 66 East African lakes they sampled (Eggermont & Verschuren, 2004b) and the total from Tanganyika nearly equaled the total from all the East African lakes (79 taxa). They suggested two factors that could at least partly explain this low level of correspondence; (1) greater representation in Lake Tanganyika of Congo Basin fauna and (2) generally better environmental conditions in the Lake Tanganyika littoral zone created by wind-driven wave action and the resulting consistent oxygenation of the water column (Eggermont & Verschuren, 2004b). The chironomid faunas of the aquatic macrophytes we sampled in Lakes Bisina and Tanganyika were also markedly different (table 4) but the patterns seen differed from those of the benthic samples of Eggermont & Verschuren (2003a,b; 2004a,b). First, the much smaller (and shallower) Bisina had 42% more chironomid species associated with plants than did Tanganyika (26 species). Second, the differences between faunas were expressed not only by the absolute presence or absence of species, but at least as much by the relative importance of species that were sampled in both lakes. In contrast to the low species correspondence (34%) of benthic samples from Lake Tanganyika and East African lakes (Eggermont & Verschuren, 2003a,b; 2004a,b), 69% of the 26 species we sampled from plants in Lake Tanganyika also occurred in Lake Bisina. But among most of the species shared by the two lakes, the contributions made to the total chironomid population could hardly have been more different, best illustrated by the examples of *Dicrotendipes fusconotatus, D. kribiicola, Parachironomus acutus, Tanytarsus balteatus* and *T. formosanus* (see table 4). Although the factors mentioned by Eggermont & Verschuren (2004b) may contribute to the great differences we saw between Lakes Tanganyika and Bisina, other environmental conditions influencing the distribution of epiphytic chironomid species must also play a significant role. Seasonal differences in chironomid emergence (*e.g.* Macdonald, 1956) were probably not a factor since both lakes were sampled over the same time period (2007-2010) and at approximately the same frequency (Lake Bisina, 22 samples; Lake Tanganyika, 25 samples). Table 8 presents some water chemistry values from Lake Bisina (Gidudu *et al.*, 2011) and Lake Tanganyika at Bujumbura (Plisnier *et al.*, 1999). While water temperature and pH were very similar, conductivity and concentrations of nitrates and phosphates showed some differences, although whether and to what degree they could be responsible for differences in the community structure of epiphytic chironomids in the two lakes is unknown.

Lack of observed damage to *Hydrilla* by *Polypedilum* species and their non-specific occurrence among aquatic macrophytes

The two most important characteristics of an effective weed biological control agent are host specificity and ability to damage a targeted plant. Of the two species of *Polypedilum* suspected of causing boring damage to *Hydrilla* from Lake Tanganyika (Pemberton, 1980; Markham, 1985), *P. wittei* commonly emerged from *Hydrilla* samples collected in Ugandan lakes, whereas *P. dewulfi* was never collected (Table 1). However, insect damage to *Hydrilla* was not observed in any of the four Ugandan lakes from which we collected the plant. Neither was damage seen to *Hydrilla* sampled at our primary site (Cercle Nautique) in Lake Tanganyika, Burundi, from which both *P. wittei* and *P. dewulfi* were reared (Copeland *et al.*, 2012). Furthermore, data reported elsewhere (Copeland *et al.*, 2011) showed that a mayfly, *Povilla adusta* Navas, tunnels in *Hydrilla* and causes boring damage indistinguishable from that illustrated by Pemberton (1980) and that observed by us in wild plants collected in Lake Tanganyika, Burundi at sites south of Cercle Nautique (Copeland *et al.*, 2011). In East and Central Africa, *Povilla* may be responsible for most, if not all, of the tunneling damage to *Hydrilla.*

Even if *P. wittei* were herbivorous on *Hydrilla*, the fact that it was sampled from a wide range of plant species shows that it lacks the host specificity necessary to avoid risk to non-target plants. *Polypedilum witttei* emerged from all of the aquatic plants we collected in Ugandan lakes except *Egeria densa* from Lake Victoria (table 2). A similar lack of specificity was observed in Lake Tanganyika, Burundi where, in addition to emerging from buckets containing *Hydrilla,* both *P. wittei* and *P. dewulfi* were recovered from several other species of submersed macrophytes (Copeland *et al.* 2012). Given the nonspecific relationship of *Polypedilum* species to *Hydrilla* in the present study and the evidence that much of the insect damage to *Hydrilla* in Africa may be due to the mayfly *Povilla adusta* (Copeland *et al.*, 2011), we suggest that available data does not support the idea of using African *Polypedilum* species for biological control of *Hydrilla.*

Geographic distribution and notes on Chironomidae

Excluding the three putative new species we sampled, most of the other chironomid species are distributed widely throughout West, Central, East and Southern Africa, and several (*Dicrotendipes fusconotatus*, *D. septemmaculatus*, *Parachironomus acutus*, *Polypedilum wittei*, *Zavraliella marmorata*, *Tanytarsus balteatus* and *T. formosanus*) also occur in other regions of the world. Previous studies have noted the similarity of chironomid faunas across the Sahelian and Sudanian zones from West to Central Africa, and crossing the Nile Basin into Kenya and Tanzania (Dejoux, 1974; Saether & Ekrem, 2003; Eggermont *et al.,* 2005). Additionally, strong affinities between East and South Africa species point to a migratory connection between these two regions also (Dejoux, 1974).

Table 8. Selected physical and chemical measurements from Lakes Bisina and Tanganyika.

Lake	sampling dates	Temperature	pH	Conductivity uS/cm	PO_4-P ug/L	NO_3-N g/L
Bisina[1]	Jan 2009	26.5±0.14	7.9 ±0.13	276.9 ±1.5	16.1±2.2	21.2±3.1
Bisina	Apr 2009	27.7±0.14	8.1±0.07	254.4±6.1	12.0±1.5	26.3±1.4
Tanganyika[2]	1983-1984	~26.25	~9	~659	~10	~38

[1]Values for Lake Bisina from Gidudu *et al*. (2011).

[2]Estimated values for near surface water at a Bujumbura, Burundi site (Plisnier *et al*., 1999; figures 2A and 2B).

However, there were exceptions to the pattern of widespread species' distributions throughout the major regions of sub-Saharan Africa. Five species we sampled, *Zavraliella marmorata*, *Polypedilum vittatum*, *Rheotanytarsus ceratophylli*, *Tanytarsus bifurcus* and *T. flexistilis* have not been recorded from equatorial Central Africa. Two others, *Ablabesmyia melaleuca* and *Dicrotendipes kribiicola* have not been found in Southern Africa. Three Tanytarsini species, *Rheotanytarsus ceratophylli*, *Tanytarsus bifurcus* and *T. flexistilis* are absent, to date, from both Southern Africa and equatorial Central Africa. Finally, until the present study, *Tanytarus harei* was known only from West Africa and *Nilothauma latocaudatum* only from Zimbabwe.

In West and Central African lakes species richness of *Polypedilum*, particularly subgenus *Polypedilum*, is typically high, the latter taxon comprising 6.5-40% (mean 20%) of chironomid species in lists from 12 lakes (Freeman, 1955b, 1957b; Dejoux, 1968, 1973, 1974, 1976; Petr, 1970; Bidwell & Clarke, 1977; Hare & Carter, 1987). Although these data usually refer to collections of adults at light, Dejoux (1983) identified 10 morphospecies of larval *Polypedilum* representing 16.7% of chironomid species he collected on aquatic plants in Lake Chad. In contrast, *Polypedilum* species were not commonly associated with aquatic macrophytes in Lake Bisina (table 2). In Bisina, the three *Polypedilum* species represented 8.1% of chironomid species and the single specimen of *P. tenuitarse* was the only representative of *Polypedilum* (*Polypedilum*) from that lake. Eggermont *et al.* (2005) noted that the chironomid fauna of West African lakes was richer than those of East Africa and suggested that habitat stability over geological time could account for the difference.

Polypedilum (*Polypedilum*) *dewulfi* was not sampled from Ugandan plants and has not been reported from East Africa. It was the most common *Polypedilum* species sampled in Lake Tanganyika, Burundi where it co-occurs with its congener *P.* (*Pentapedilum*) *wittei* (Copeland *et al.*, 2012). Records of *P. dewulfi* from Sudan and Ethiopia suggest an earlier migration to, or from, the northeast.

Species of *Dicrotendipes* are associated mainly with the surface of submersed vegetation, and also with aufwuchs on rocks and logs, and with algal mats (Epler, 1988). Not surprisingly, members of this genus were an important component of chironomids emerging from plants in both Ugandan lakes and in Lake Tanganyika. In Lake Bisina, four *Dicrotendipes* species comprised 34.2% of the total individuals and in Lake Tanganyika the proportion made up by *Dicrotendipes* was 82.3%, nearly all of them *D. fusconotatus*.

Dicrotendipes septemmaculatus, the most common species to emerge from plants in Uganda, was not sampled in Lake Tanganyika (Copeland *et al.*, 2012). Of the 72 known species of *Dicrotendipes*, *D. septemmaculatus* is among the most widely distributed, having been recorded from the Afrotropical (including Madagascar), southern Palearctic, Asian and Australian regions (Epler, 1988). In Asia, *D. septemmaculatus* has been collected from *Hydrilla* in Burma, Indonesia and Malaysia (Epler, 1988). For a species with such a wide distribution, its absence from aquatic plants in Lake Tanganyika is curious (see table 4). Eggermont & Verschuren (2003b) also did not list *D. septemmaculatus* from samples of subfossil remains of chironomid larvae collected in Lake Tanganyika. However, they did recover specimens of a morphotype they designated as *D.* near *sudanicus* and stated that these were not distinguishable by them from *D. septemmaculatus* (Eggermont & Verschuren, 2003b). Eggermont & Verschuren (2003b) explained the assignment of the morphotype name as being based on the fact that a record existed for "… adult *D. sudanicus* from the D. R. Congo side of Lake Tanganyika (Freeman 1957b)". It is possible, then, that *D. septemmaculatus* was represented among the three "*D.* near *sudanicus*" specimens sampled by Eggermont & Verschuren (2003b) in Lake Tanganyika. However, because adults of *D. septemmaculatus* never emerged from *Hydrilla* or three other species of aquatic macrophytes collected from Lake Tanganyika over 25 sampling dates while *D. sudanicus* adults were collected (table 4) it is more parsimonious to assume that the *D.* near *sudanicus* morphotype of Eggermont & Verschuren (2003b) represents true *D. sudanicus* and not *D. septemmaculatus*.

Competitive exclusion by its closely related congener, *D. fusconotatus*, is unlikely to account for the absence of *D. septemmaculatus* from Lake Tanganyika, given the numerical dominance of the latter over *D. fusconotatus* in Lake Bisina (1554 individuals to 3; table 4). However, it is possible that environmental conditions are dissimilar enough between the two lakes to differentially favour one or the other of the two *Dicrotendipes* species in competitive interactions.

In Central and West Africa, *D. septemmaculatus* has been recorded only from less humid areas, north and south of equatorial forest; Jos, Nigeria (9.92°N), Kurra, Sudan (13.28°N), and Lubumbashi (=Elisabethville) Congo (11.66° S) (Epler 1988). Additionally, Dejoux (1968) collected it at Lake Chad (*ca.* 13.33°N). Accordingly, a scenario in which *D. septemmaculatus* dispersed out of East Africa northwestwardly through Sudan into Central and West Africa, and south (and southwestwardly) into southern Africa, and including southern Congo, appears as likely as any other to explain the known distribution of this species in Africa. *Dicrotendipes septemmaculatus* may simply have never reached Lake Tanganyika.

Dicrotendipes peringueyanus, another species closely related to *D. fusconotatus* and *D. septemmaculatus,* was absent from both Lake Bisina and Lake Tanganyika but relatively common in the few collections we made in Lake Bunyonyi, located about halfway between the two former lakes and at a much higher altitude than either of them. All three species occurred in Bunyonyi with *D. peringueyanus* (134 individuals, 14.6 % of total Chironomidae) being the most common followed by *D. septemmaculatus* (110, 12.0%) and *D. fusconotatus* (2, <1%). Possibly the distributions of all three species are at least partly limited by temperature. *Dicrotendipes peringueyanus* has been reported living phoretically on *Potamonautes* spp. river crabs in Cameroon (Disney, 1975), and Epler (1988) verified the identification of the midge. The presence (or absence) of *Potamonautes* spp. may influence the distribution of *D. peringueyanus*, and it would be very interesting to examine the environmental and biological factors influencing the comparative distributions of these three closely related *Dicrotendipes* species.

Species richness of Tanytarsini species on aquatic macrophytes was particularly high in Lake Bisina. The eight species that were associated with plants was twice that sampled from submersed macrophytes in Lake Tanganyika (Copeland *et al.*, 2012) and nearly equal to the much larger Lake Chad's nine species (Dejoux, 1983). The genus *Tanytarsus* was the most common taxon in Lake Bisina, both in number of species and percentage of emerged individuals (5, 42.3%), eclipsing species of the Chironomini genera *Dicrotendipes* (4, 34.2%) and *Kiefferulus* (3, 9.3%), both of which are commonly associated with aquatic macrophytes (Verschuren, 1997; *Nilodorum=Kiefferulus*). These results were in stark contrast to those recorded from Lake Tanganyika plants, where *Tanytarsus* was an insignificant genus (2, <1%).

CONCLUSION

Aquatic macrophytes are an important resource for lacustrine invertebrates (Krecker, 1939; Berg, 1950; Taniguchi *et al.*, 2003). For the Chironomidae, plants provide anchorage for species that build tubes and a substrate on which periphyton can accumulate, to be browsed by larvae. In many cases, complex plant architecture provides protection against predators, particularly fish. However, few studies have been published on the association of chironomid species with aquatic plants in African lakes (see appendix 2, Copeland *et al.*, 2012). The present study focused most closely on the chironomid community associated with submersed macrophytes in Lake Bisina. The richness of this community adds weight to the various factors evaluated to justify the assignment of RAMSAR status to Lake Bisina. Studies of chironomids and other invertebrates associated with macrophytes in other African lakes will add significantly to knowledge of the natural history of these important aquatic environments.

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Appendix. List of Chironomidae currently known from Uganda.

Subfamily	Tribe	Species
Tanypodinae	Coelotanypodini	*Clinotanypus claripennis* Kieffer
		Tanypus fuscus Freeman[1]
		T. guttatipennis Goetghebuer[1]
	Macropelopiini	*Procladius albitalus* Freeman[1]
		Procladius brevipetiolatus (Goetghebuer)[1]
		Psectrotanypus schwetzi (Freeman)[1]
	Pentaneurini	*Ablabesmyia dusoleili* Goetghebuer
		A. melaleuca Goetghebuer
		A. nilotica (Kieffer)
		A. rimae Harrison
		Paramerina sp. nov.
		P. longipes (Freeman)[1]
Diamesinae		*Diamesa ruwenzoriensis* Freeman[1]
Orthocladiinae		*Bryophaenocladius ruwenzoriensis* (Freeman)[1]
		Chaetocladius melaleucus (Meigen)[1]
		Corynoneura dewulfi Goetghebuer[1]
		Cricotopus albitibia (Walker) [1]
		C. flavozonatus Freeman[1]
		C. scottae Freeman
		Limnophyes bubo Saether[1]
		L. lobiscus Saether[1]
		L. natalensis (Kieffer)[1]
		Metriocnemus canus Freeman[1]
		M. conicus Freeman[1]
		M. fletcheri Freeman[1]
		M. wittei Freeman[1]
		Nanocladius saetheri Harrison
		N. vitellinus (Kieffer)[1]
		Parametriocnemus fordi [1]
		P. scotti (Freeman)[1]
		Paratrichocladius micans (Freeman)[1]
		Psectrodadius viridescens Freeman
		Pseudosmittia rectilobus (Freeman)[1]
		Smittia atra Freeman[1]
		S. fletcheri Freeman[1]
		S. nigra (Freeman)[1]
Chironominae	Chironomini	*Acinoretractus multispinosus* (Freeman)[1]
		Chironomus calipterus Kieffer
		C. callichirus Kieffer
		C. formosipennis Kieffer

Subfamily	Tribe	Species
		C. satchelli Freeman[1]
		C. tetraleucus Kieffer[1]
		Collartomyia hirsuta (Goetghebuer)[1]
		Conochironomus acutistilus (Freeman)[1]
		Cryptochironomus lindneri (Freeman)
		C. nigrocorporis (Freeman)[1]
		C. niligenus (Kieffer) [1]
		Dicrotendipes chambiensis (Goetghebuer)
		D. cordatus Kieffer[1]
		D. fusconotatus (Kieffer)
		D. kribiicola (Kieffer)
		D. peringueyanus (Kieffer)
		D. septemmaculatus (Becker)
		D. sudanicus (Freeman)
		Endochironomus woodi (Freeman)[1]
		Harnischia cf. lacteiforceps (Kieffer)
		Kiefferulus brevibucca (Kieffer)
		K. brevipalpis (Kieffer)
		K. chloronotus (Kieffer)
		K. fractilobus (Kieffer)
		K. rugosus (Freeman)[1]
		Microchironomus lendli Kieffer[1]
		Microchironomus tener (Kieffer)[1]
		Nilodosis fusca Kieffer[1]
		Nilothauma cf. latocaudatum Adam & Saether
		Parachironomus acutus (Goetghebuer)
		Parachironomus coronatus (Kieffer)[1]
		P. dewulfianus (Goetghebuer)
		Polypedilum (Cerobregma) ramiferum Kieffer
		Polypedilum (Pentapedilum) anale Freeman
		P. (*Pentapedilum*) *micra* Freeman
		P. (*Pentapedilum*) *vittatum* Freeman
		P. (*Pentapedilum*) *wittei* Freeman
		Polypedilum (Polypedilum) albosignatum Kieffer[1]
		P. (Polypedilum) deletum Goetghebuer[1]
		P. (*Polypedilum*) *tenuitarse* (Kieffer)
		Polypedilum (Tripodura) alboguttatum Kieffer[1]
		P. (Tripodura) longicrus Kieffer[1]
		P. (Tripodura) tridens Freeman[1]
		Polypedilum (Uresipedilum) dossenudum Oyewo & Saether[1]
		P. (Uresipedilum) kibatiense Goetghebuer[1]

Subfamily	Tribe	Species
		Stenochironomus edwardsi Freeman[1]
		Xenochironomus trisetosus (Kieffer)
		X. ugandae (Goetghebuer)
		Zavreliella marmorata (Wulp)
	Tanytarsini	*Cladotanytarsus pseudomancus* (Goetghebuer)
		Cladotanytarsus sp. U-1
		Cladotanytarsus sp. *U-2*
		Rheotanytarsus bufemoratus Kyrematen & Saether[1]
		Rheotanytarsus ceratophylli (Dejoux)
		Rheotanytarusus guineensis (Kieffer)[1]
		Tanytarsus balteatus Freeman
		T. bifurcus Freeman
		T. flexistilus Freeman
		T. formosanus Kieffer
		T. harei Ekrem
		Virgatanytarsus nigricornis (Goetghebuer)

[1]Data from an unpublished distributional checklist list of Afrotropical Chironomidae. Available from Hilde Eggermont; hr.eggermont@gmail.com.