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The Diversity of Chironomidae (Diptera) Associated With *Hydrilla verticillata* (Alismatales: Hydrocharitaceae) and Other Aquatic Macrophytes in Lake Tanganyika, Burundi

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ABSTRACT To search for potential biological control agents of the aquatic weed, *Hydrilla verticillata* (L.f.) Royle, emerging chironomid adults were collected from aquatic macrophytes sampled between 2007 and 2009 from near shore sites in Lake Tanganyika, Burundi. Initial surveys identified *H. verticillata* populations at all sampled locations between Bujumbura and Nyanza Lac. Twenty-six (26) species of Chironomidae emerged from collections of four plant species; *Hydrilla*, *Ceratophyllum demersum* variety *apiculatum* (Cham.) Asch., *Potamogeton schweinfurthii* A.Benn., and *Vallisneria spiralis* f. *aethiopica* (Fenzl) T.Durand and Schinz. Twenty-four of the chironomid species were new country records, but none of them represented undescribed species. *Dicrotendipes fusconotatus* (Kieffer) dominated the chironomid community, comprising 82% of 32,090 reared adults. The six most common species contributed over 96% of the total midge fauna. Most species were uncommon or rare; nine species were represented by 10 or fewer specimens. A species accumulation curve for the 25 chironomid species reared from *Hydrilla* suggested that our sampling completely describes the community associated with this plant in northern Lake Tanganyika. Quantitative β -diversity values indicated that chironomid communities of the two Hydrocharitaceae species, *Hydrilla* and *Vallisneria*, were most similar to each other, even though they have very different growth forms. Chironomids also emerged in greater numbers from the two Hydrocharitaceae than from the other plants. No chironomid species, including *Polypedilum wittei* Freeman and *Polypedilum dewulfi* Goetghebuer, two species formerly considered for possible biological control of *Hydrilla*, were specific to that plant. *Polypedilum* species emerged from all sampled aquatic macrophytes. No chironomid-caused damage was seen on *Hydrilla*. African Chironomidae do not appear to be suitable candidates for biological control of *Hydrilla*.

KEY WORDS Africa, biodiversity, submersed plant, biological control, aquatic weed

Hydrilla verticillata (L.f.) Royle (Hydrocharitaceae) is a globally widespread aquatic plant, and an adventitious weed in many freshwater habitats. In areas where it is a weed, *Hydrilla* grows to the water surface, forming dense clumps of stringy vegetation that foul boat propellers, and impede the flow of water. Control costs can be great, particularly because some populations have recently evolved resistance to fluridone, the most economical herbicide used for its control (Mi-

chel et al. 2004). Thus, the search for alternate control strategies is of immediate importance. Classical biological control focuses its search for natural enemies in areas of pest endemicity. The native range of *Hydrilla* is reported to include much of Asia, northern Australia, parts of Europe and a few lakes in east and central Africa (Cook and Lüönd 1982). Evidence of nativity in east and central Africa includes the following: 1) although it can be found in scattered patches in African lakes, its growth pattern differs from that of weedy populations in that it rarely reaches the water's surface. As a consequence, in Africa *Hydrilla* is only considered to be a noxious weed in South Africa where it was recently introduced from Malaysia (Madeira et al. 2007, Coetzee et al. 2009). 2) *Hydrilla* is known to have been in African waters since at least 1862 when it was collected in present-day Uganda by the Victorian explorer James Grant (Speke, 1863; appendix, p. 585, as *Hydrilla dentata*), implying that it might be indigenous to Africa. These facts suggested that it might be useful to search for potential biological con-

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trol agents there. Earlier, short surveys (Pemberton 1980) for herbivores found evidence of insect (and fish) damage to *Hydrilla* growing in Lake Tanganyika. In particular, Chironomidae of the genus *Polypedium* were suspected of boring into the growing tips and stems of *Hydrilla* (Pemberton 1980). These reports argued for a more intensive exploration for natural enemies and, thus, we began a survey of *Hydrilla* in eastern Africa in 2007, including intensive sampling in that part of Lake Tanganyika that falls within the borders of Burundi.

Lake Tanganyika is Africa's deepest lake, reaching $\approx 1,470$ m in depth and, at $\approx 19,690$ km³, its largest by volume (McGlue et al. 2008). Although it shrank to $\approx 56\%$ of present day volume during the African megadrought interval in the late Pleistocene, it has probably never been divided into separate lakes or pools (McGlue et al. 2008). Lying in the Albertine rift, it extends north to south for over 650 km, spanning $>5^\circ$ of latitude and bordering four nations; Democratic Republic of the Congo, Burundi, Tanzania, and Zambia. The lake has a deep, oxygenated water column to ≈ 100 m (Eggermont et al. 2008). It is slightly alkaline (pH range ≈ 8.5 – 9.5), with conductivity (≈ 600 μScm^{-1}) well within the range of freshwater (Bootsma and Hecky 2003, Eggermont et al. 2008). Being relatively low in altitude at ≈ 773 m above sea level, it is warm year-round with temperatures varying only between 25.5 and 27.5°C , measured at a depth of 10 m (Hecky et al. 1991). From April to August, strong, dry-season southerly winds cause upwelling and vertical mixing of the top column of water, resulting in nutrient cycling, with some nutrients eventually reaching the northern part of the lake (Coulter and Spigel 1991). In addition, nutrients are carried into the lake by numerous tributary streams and rivers, particularly the Rusizi in the north, bordering Burundi and D. R. Congo, and the Malagarazi separating Burundi and Tanzania in the east.

The best estimate of the lake's age places the beginning of formation of its oldest basin at between 9 and 12 Ma (Cohen et al. 1993). Because of its long isolation and variety of habitats, the conditions for speciation have been optimal, whereas lake stability probably has been responsible for species accumulation. Lake Tanganyika is renowned for its endemic fish and aquatic invertebrate species, particularly molluscs and noninsect arthropods, and Coulter (1991) judges that it possesses "... a richer fauna and probably also flora than any other African lake, and perhaps than any lake in the world." However, in an exhaustive list of the animals, including insects, and plants known from Lake Tanganyika, not a single chironomid species was included (Coulter 1991), despite the importance of chironomids as fish prey in east African lakes (Macdonald 1956) and the widespread recognition of their utility in assessing water quality (e.g., Saether 1979, Janssens de Bisthoven et al. 1998).

Dejoux (1981) produced a map of Africa with the number of chironomid species known at that time indicated within the border of each country; a map in which the outline of Burundi and Rwanda encloses a

conspicuous "0". Technically, this was incorrect, but not by much. Earlier, Freeman (1955b) had listed five species from Rwanda-Urundi (the name, before independence, of present-day Rwanda and Burundi, when it was a UN trust territory). Of the two specimens collected in what is now Burundi, both were from high altitude collections, and could only be identified to genus (*Trichocladius* and ?*Smittia*; Freeman 1955b). Since then, Janssens de Bisthoven et al. (1993) reported sampling 32 "larval types" from lacustrine and riverine sites in and near Bujumbura, and these data were restated in Theunissen (1993). Soon after, Verschuren et al. (1996) reported 25 fossil chironomid larval-types from cores taken from an upland bog in Burundi. Among these, only one species, *Chironomus formosipennis* Kieffer, was identified unambiguously. In greater Lake Tanganyika, recent studies of subfossil larval remains have revealed the richness of the lake's chironomid fauna (Eggermont and Verschuren 2003a,b). However, it was impossible to assign complete names to most of the specimens collected in those studies so that, at the species level, comparisons with other published research on African Chironomidae could not be made.

As part of a project to explore for natural enemies of *Hydrilla*, we collected insects emerging from *Hydrilla* and associated submersed macrophytes, looking particularly for *Polypedium* species, previously suggested as possible herbivores of *Hydrilla* in Lake Tanganyika (Pemberton 1980, Bennett and Buckingham 2000). Specimens of the suspect *Polypedium* from these earlier studies had been identified by one of us (JHE) as *Polypedium* (*Polypedium*) *dewulfi* Goetghebuer and *Polypedium* (*Pentapedium*) *wittei* Freeman (Buckingham 1994). Elsewhere, we report on the source of tunneling damage to *Hydrilla* in Lake Tanganyika (Copeland et al. 2011). In the present paper, we consider chironomid distribution and diversity among four aquatic macrophytes in Lake Tanganyika, and evaluate the specificity of *Polypedium* species among those plants. We also add significantly to records of Chironomidae from Burundi.

Materials and Methods

Sampling Sites. Rapid surveys for *Hydrilla* were conducted in November 2006 in four areas encompassing most of the length of Lake Tanganyika's shoreline in Burundi. *Hydrilla* was found at all four sites; Nyanza Lac (-4.34892° , 29.59693°); Rumonge (-3.98255° , 29.43285°); Magara (-3.72143° , 29.31110°); and Bujumbura (Cercle Nautique; -3.38996° , 29.35023°) (Fig. 1). For the survey, we rented small wooden boats from local fisherman, and *Hydrilla* was located by casting a large 8-pronged grapple and dragging it back manually by rope. When it was apparent that both *P. dewulfi* and *P. wittei* were reared from *Hydrilla* found at locations in or near Bujumbura, we concentrated our sampling in these areas, in part because of security concerns. Thereafter, collections were made at Cercle Nautique, a partially protected, small bay. Later, supplementary collections were

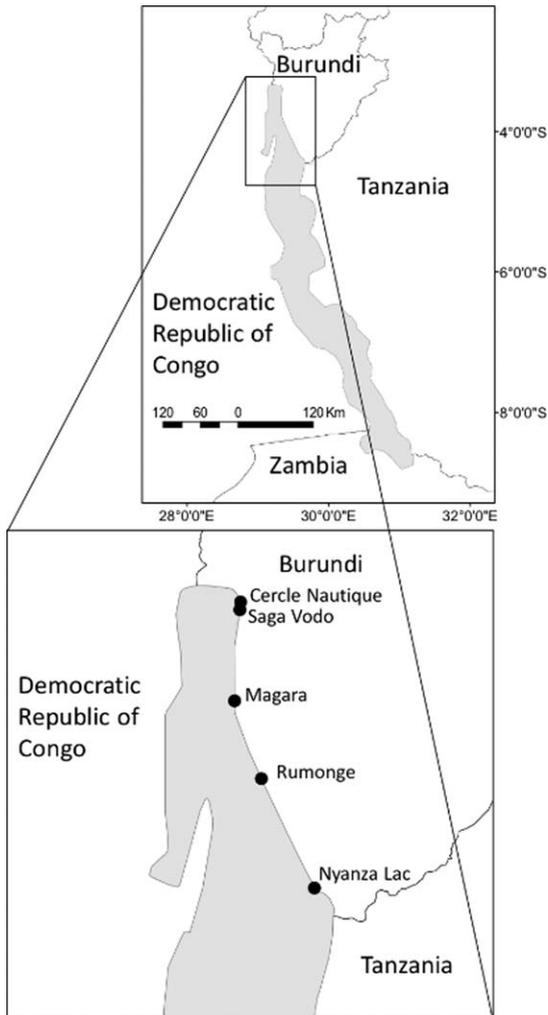


Fig. 1. Map of Lake Tanganyika. Inset shows the sampling sites for the study.

made at Saga Vodo (-3.41414° , 29.34137°), slightly south of Bujumbura (Fig. 1, inset).

Plant Collection. Although the primary focus of our study was to search for insect herbivores of *Hydrilla*, on four sampling dates in 2009 we collected three additional plant species to compare the chironomid communities associated with each plant and, especially, to determine if the two *Polypedilum* species being evaluated for possible biological control of *Hydrilla* were restricted to that plant. These collections were made at Cercle Nautique and spanned the period between the final months of the dry season (July and August) and the beginning months of the rainy season (October and November). On these four dates, in addition to *Hydrilla*, we sampled *Ceratophyllum demersum* variety *apiculatum* (Cham.) Asch. (Ceratophyllaceae), *Potamogeton schweinfurthii* A.Benn. (Potamogetonaceae), and *Vallisneria spiralis* f. *aethiopica* (Fenzl) T.Durand and Schinz (Hydrocharitaceae).

At Cercle Nautique, water level was always low enough to collect *Hydrilla* and other plants by hand. Plants were uprooted and, because agglomerations of mud around roots were often large enough to substantially limit the amount of plant material that would fit in our collection buckets, they were gently swirled to reduce the mud load. At Saga Vodo, plants also were collected by hand. However, depending on the season, deeper water sometimes necessitated collection by diving and this often resulted in plant breakage above the root system. Consequently, Saga Vodo samples sometimes had little mud associated with them. A standard collection was ≈ 25 liters of plant material (by volume) in a 50-liter plastic bucket. Plants were submersed in lake water and transported immediately to the laboratory in Bujumbura, located ≈ 20 min away.

Separate collections were made for each plant species, but no species grew in pure stands. However, the very different morphologies of these four plant species facilitated their separation during sampling. Nonetheless, although efforts were made to completely segregate plant species during collection and transport, some mixing was unavoidable. Complete separation of plant species was done immediately on returned to the laboratory. Finally, because removal of mud from roots was substantial but never complete, our sampling method did not rule out the possibility that some of the chironomids we reared developed in the bottom substrate.

Insect Rearing. At the laboratory, after a complete sorting of plants, separate species were placed in clean 50-liter plastic buckets and submersed in water from the collection site. Air was bubbled into the water through a tube connected to a small aquarium pump. The bucket opening 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. A large plastic funnel was inverted and placed over the opening in the lid of the bucket. To capture emerging insects, the top was removed from a white, translucent plastic bottle (10 cm diameter by 17.5 cm high with a 5.8 cm opening at the top) that was then placed upside-down over the funnel's 3-cm-wide tube. The bottom of the bottle (now facing up) had been cut away and replaced with fine, white-mesh netting. This limited the formation of condensation within the collecting bottle, and also provided purchase for newly emerged midges. Collection bottles were inspected daily and any insects that had emerged were knocked down by chilling and placed in vials in 75% ethanol. After 3–4 wk, plants were removed and discarded. Initial identifications of Chironomidae and confirmations of identifications were made by J.H.E.

To compare chironomid emergences among species of aquatic macrophytes, we calculated plant dry weight as follows. After separating plant species, water was decanted from the buckets containing each spe-

cies. A subsample was then removed and weighed (v). It was then air-dried until its weight stabilized (w). The bucket, with remaining plant material, was weighed (x). Later, the bucket was weighed dry (y). Thus;

$$\text{sample dry weight} = (w/v) * (x-y).$$

To eliminate adverse effects on chironomid development, and because the volume of collected plants was standardized across samples, this estimate was made once for each species.

Chironomid Diversity. At our primary site, Cercle Nautique, α - and β -diversity were computed for Chironomidae that emerged from the four aquatic macrophytes. For each plant species, the numbers of emerged adults of each chironomid species were pooled over the four sampling dates. Alpha-diversity was measured with the Shannon index (H'), incorporating species richness and evenness, and compared statistically between pairs of plant species by using a t -test (Magurran 1988). Beta-diversity, comparing similarity of chironomid communities among habitats (plant species), was determined qualitatively using Jaccard's measure and Sorenson's qualitative measure, and quantitatively with Sorenson's quantitative measure (Magurran 1988).

To examine the possible effect of site differences on chironomid communities, midges that emerged from *Hydrilla* were compared between two locations, Cercle Nautique and Saga Vodo, sampled during the same 3 mo; August and November 2007, and September 2008.

Sources for Information on the Geographic Distribution of Chironomidae. Information on the geographic distribution of the Chironomidae species we reared was taken from several sources; the groundbreaking work of Freeman (1955a, 1956, 1957a, 1958); general country surveys (usually focusing on one major lake); revisions of particular groups; paleoecological studies; and single species descriptions. The most important resources that we used are listed in Appendix 1. In the interest of space we do not list here the other, less inclusive papers that, nonetheless, added information on the distribution of at least one species not covered in the papers listed in Appendix 1. Those papers are indicated in the references: Kugler 1978, Ghonaim et al. 2005, and Eggermont et al. 2007.

Voucher Specimens. Voucher specimens of reared Chironomidae have been deposited in the Biosystematics Unit, the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, and at the Institut National pour l'Environnement et la Conservation de la Nature (INECN), Bujumbura, Burundi.

Results

Summary of Chironomidae Reared From Submerged Aquatic Plants. We reared 26 species of Chironomidae from aquatic plants, 24 of which were first records for Burundi (Table 1). None of them represented undescribed species. In total, 32,090 chironomids emerged, of which *Dicrotendipes fusconotatus*

was, by far, the most common species, contributing over 80% of all chironomid specimens (Table 1). Most species were uncommon or rare. Fourteen species produced <100 specimens each, with the rarest nine species contributing <10 each. The six most frequently reared species made up 96.4% of the total.

For *Hydrilla*, recruitment of novel species was nil over the last six sampling dates, suggesting that our sampling completely described species richness ($n = 25$) for this plant at this site (Fig. 2). The final five species were reared from collections made in February and May of 2008. Collections of *Hydrilla* made over the same months during 2007 did not yield these species, indicating that rare or uncommon species can be overlooked without adequately comprehensive sampling.

Between-site Differences in Chironomids Reared From *Hydrilla*. From the three *Hydrilla* collections made during the same months, six of the species from Saga Vodo were not reared at Cercle Nautique, and some taxa common at one site, e.g., *Parachironomus* species at Cercle Nautique and *Cladotanytarsus pseudomancus* at Saga Vodo, were uncommon or absent from the other (Table 2). In addition, Saga Vodo *Hydrilla* yielded more chironomid species than Cercle Nautique *Hydrilla* on all three sampling dates (8, 11, and 8 versus 7, 5, and 4), although the difference was not significant ($\chi^2 = 0.89$, $df = 2$, $P = 0.64$).

Composition of Chironomid Emergences From Four Submerged Aquatic Plant Species at Cercle Nautique. During our four-sample comparison of plant species, with the exception of *T. balteatus*, all commonly reared chironomids (i.e., species emerging from >25% of all *Hydrilla* collections; $n = 22$) were recovered from more than one plant species (Table 3). Although *T. balteatus* was often (nine of 22 samples) reared from *Hydrilla* over the entire course of our study, it was not reared from any plants, including *Hydrilla*, during the four-sample comparison.

An examination of chironomid emergence from the four plants across our four sampling dates revealed both plant-specific and seasonal differences (Fig. 3). Chironomid emergence was highest from the two Hydrocharitaceae species, *Hydrilla* and *Vallisneria*. For all plant species except *Ceratophyllum*, from which chironomid numbers were always very low, abundance plummeted by two or more orders of magnitude between July and October.

Rank abundance curves of chironomids that emerged from the four plant species showed distinct differences among plants in the importance of individual midge species to overall chironomid emergence (Fig. 4). Particularly striking was the importance of *K. brevipalpis* in the complex of chironomid species from both *Potamogeton* and *Ceratophyllum* and its relative unimportance in populations reared from the two species of Hydrocharitaceae; ranking fifth from *Hydrilla* and near absent from *Vallisneria* (Fig. 4). A similar, but opposite effect was observed for *Cricotopus cf. harrisoni*, whereas *K. chloronotus* was the third most common species on *Potamogeton* and absent, or nearly so, from the other three species.

Table 1. Chironomid species reared from aquatic macrophytes in Lake Tanganyika, Burundi

Subfamily	Tribe	Species	No. (%)	Synonyms ^a	General distribution	African distribution ^{b,c}
Tanyptodinae	Pentaneurini	<i>Ababesomyia cf. dusoleili</i> Goetghebuer	3 (0.01)		Widespread Afrotropical (incl. Madagascar)	ben, bur, cam, cha, <u>CON</u> , egypt, eth, gha, ken, mad, mali, niger, rco, sen, sou, sud, uga, zim
		<i>A. cf. melaleuca</i> Goetghebuer	2 (0.01)		Widespread West and Central Africa	cha, <u>CON</u> , gha, gui, ivo, nige, sen, sie, uga
Orthocladiinae		<i>A. rimae</i> Harrison	23 (0.07)		Widespread Afrotropical (incl. Madagascar)	Buru ^{d,e} , <u>ETH</u> , nam ^f , tan ^{d,e}
		<i>Nilotanyptus comatus</i> (Kieffer)	1 (0.00)	<i>Pentaneura nitra</i> Freeman	Widespread Afrotropical (incl. Madagascar)	Buru ^{d,e} , cha, con, eth, gui, mad, mali, nige, sen, <u>SOU</u> , tan ^{d,e} , uga, zim
		<i>Cricotopus albitibia</i> Walker	1 (0.00)	<i>Chironomus bicinctus</i> var. <i>plumbeus</i> Goetghebuer; ? <i>Tricholadus</i> <i>kribiensis</i> Kieffer	Widespread Afrotropical (incl. Madagascar)	cha, con, eth, mad, nam ^f , nige, niger, <u>SIE</u> , sou, uga, zim ^f
		<i>C. cf. harrisoni</i> Freeman	1263 (3.94)		East and South Africa	con, eth, <u>KEN</u> , sou
Chironominae	Chironomini	<i>Nanocladius saellleri</i> Harrison	4 (0.01)		Eastern Africa	<u>ETH</u> , ken ^f , uga ^f , sou
		<i>Chironomus imicola</i> Kieffer	116 (0.36)	<i>C. palpatis</i> Goetghebuer; <i>C. reginae</i> Goetghebuer; ? <i>Cryptochironomus</i> <i>fasciatus</i> Kieffer	widespread Afrotropical, incl. Madagascar	ben, bur, cha, con, eth, gha, gui, <u>KEN</u> , mala, mali, niger, nige, sou, sen, sud, uga, zim
		<i>Cryptochironomus cf. dicerus</i> Kieffer ^g	27 (0.08)	<i>Cladopelma fimbriatum</i> Kieffer	Widespread West and southern Africa,	bur, cam, cha, con, eth, gha, ivo, mad, mala, niger, nige, sen, <u>SUD</u> , sou, zim
		<i>C. lindneri</i> (Freeman)	15 (0.05)	<i>C. pseudolabis</i> Kieffer	Madagascar	cam, cha, con, eth, gha, niger, nige, sen, sou, <u>SUD</u> , uga, zam, zim
		<i>Dicrotendipes fusconotatus</i> (Kieffer)	26398 (82.25)	<i>D. ? trilabis</i> Kieffer; <i>Calochironomus</i> <i>griseonotatus</i> Kieffer; <i>C.</i> <i>griseosparvus</i> Kieffer; <i>D. forficula</i> Kieffer; <i>D. nilicola</i> Kieffer;	Widespread Afrotropical, eastern Mediterranean	bur, buru ^{d,e} , cha, con, egypt, eth, gha, ^h mala, niger, nige, niger, <u>SUD</u> , tan ^{d,e} , uga, sou, zim
		<i>D. kribicola</i> (Kieffer)	1 (0.00)	<i>Polypedium quatuor punctatum</i> Goetghebuer	West and central Africa	bur, buru ^{d,e} , <u>CAM</u> , cha, con, gha, mala, tan ^{d,e} , uga
		<i>D. sudanicus</i> Freeman	129 (0.40)		Widespread equatorial Africa	bur, buru ^{d,e} , cam, cha, gha, gui, mali, nam, nige, sen, sou, <u>SUD</u> , tan ^{d,e} , zim
		<i>Harnischia curtillamellata</i> Malloch	1 (0.00)	<i>Cryptochironomus nudiforceps</i> Kieffer; <i>Chironomus monilis</i> Freeman; <i>C.</i> <i>atrofasciatus</i> Freeman	Widespread Africa, USA, Europe, West Asia	bur, cam, cha, con, gha, ivo, mali, niger, nige, rco, sen, sou, sud, zim
		<i>Kiefferulus brevipalpis</i> (Kieffer)	1711 (5.33)	<i>Nilodorium devulfi</i> Goetghebuer; <i>Chironomus sordellus</i> Goetghebuer;	Widespread Afrotropical	cam, cha, con, <u>ETH</u> , gha, ken, mala, moz, nam, niger, nige, sou, sud, uga, zim
		<i>K. chloronotus</i> (Kieffer)	129 (0.40)	<i>C. vitsumbiensis</i> Goetghebuer <i>Chironomus niloticus</i> Kieffer; <i>C.</i> <i>latilobus</i> Kieffer; <i>C. hewardi</i> Goetghebuer	Widespread Afrotropical (incl. Madagascar), western Asia	ben, bur, cam, cha, con, eth, gha, gui, ken, mad, mala, mali, nam, niger, nige, rco, sen, <u>SEY</u> , sou, sud, tan, uga, zim
<i>Parachironomus acutus</i> (Goetghebuer)	497 (1.55)		Widespread Afrotropical (incl. Madagascar), N. Africa, western Asia	bur, cam, cha, <u>CON</u> , egypt, eth, gha, mad, mala, mali, niger, nige, sou, zim		
<i>P. devulfi</i> (Goetghebuer)	262 (0.82)		Widespread Afrotropical, N Africa, western Asia	alg, bur, cam, cha, <u>CON</u> , egypt, eth, gha, niger, nige, sud, uga, zim		
<i>Polypedium (Pentapedilum)</i> <i>micra</i> Freeman	1 (0.00)		Widespread Central, West, and southern Africa	bur, car, gha, nam, nige, <u>SUD</u> , tog, zim		
<i>P. (Pentapedilum) wittei</i> Freeman	294 (0.92)		Widespread Afrotropical, western Asia, S Europe	bur, buru ^{d,e} , <u>CON</u> , egypt, eth, gha, gui, ken ^{d,e} , nige, sen, sou, sud, tan ^{d,e} , uga, zim		

Table 1. Continued

Subfamily	Tribe	Species	No. (%)	Synonyms ^d	General distribution	African distribution ^{b,c}
		<i>Polypedium</i> (<i>Polypedium</i>) <i>deвуlfi</i> Goetghebuer ^e	660 (2.06)	<i>P. scotti</i> Freeman	widespread West and southern Africa	bur, <u>CON</u> , eth, gha, gui, nam, nige, sen, sou, sud, zim
		<i>P. (Polypedium) tenuitarse</i> (Kieffer)	3 (0.01)	<i>Polypedium fenestratum</i> Goetghebuer; <i>Kribiomimus leucolabis</i> Kieffer; <i>K. leucolabis</i> var. <i>tibialis</i> Kieffer; ? <i>Kribiocharis flitarsis</i> Kieffer	Widespread Afrotropical	<u>CAM</u> , cha, con, gui, nige, sen, sou, sud
Tanytarsini		<i>Cladotanytarsus pseudomancus</i> (Goetghebuer)	411 (1.28)		Widespread Afrotropical (incl. Madagascar), eastern Mediterranean	bur, cam, car, cha, <u>CON</u> , egypt, eth, gha, gui, ken, mad, mala, mali, nam, niger, nige, sen, sou, sud, uga, zim
		<i>Rhectanytarsus guineensis</i> Kieffer	4 (0.01)		Widespread Afrotropical	con, eth, <u>GUI</u> , ken, sen, sou, uga, tan, zim
		<i>Tanytarsus balteatus</i> Freeman	122 (0.38)		Widespread West, central and southern Africa, India, Nepal	car, cam, cha, con, nam, niger, nige, sou, <u>SUD</u> , uga, zim
		<i>T. formosanus</i> Kieffer	12 (0.04)	<i>T. formosae</i> Kieffer; <i>T. horni</i> Goetghebuer; <i>T. aculeus</i> Chaudhuri et al.; <i>T. fuscimarginalis</i> Chaudhuri et al.; <i>T. nigrocinctus</i> Freeman	Widespread Afrotropical, North Africa, Palearctic, S and E Asia	ben, bur, car, cam, cha, <u>CON</u> , egypt, eth, gha, ken, niger, nige, sen, sou, sud, tog, <u>UGA</u>

^a Only synonyms with different species epithets are included; e.g. for *Polypedium tenuitarse*, *P. fenestratum* is included, whereas *P. tenuitarsis* is not.
^b ben, Benin; bur, Burkina Faso; buru, Burundi; car, Central African Republic; cam, Cameroon; cha, Chad; con, Democratic Republic of Congo; egypt, Egypt; eth, Ethiopia; gab, Gabon; gha, Ghana; gui, Guinea; ivo, Ivory Coast; ken, Kenya; mad, Madagascar; mala, Malawi; mali, Mali; moz, Mozambique; nam, Namibia; niger, Niger; nige, Nigeria; reu, Reunion; rco, Republic of Congo; sen, Senegal; sey, Seychelles; sierra, Sierra Leone; sou, South Africa; sud, Sudan; tan, Tanzania; tog, Togo; zam, Zambia; zim, Zimbabwe.
^c Countries from which holotypes were described are indicated in bold, underlined capital letters; countries from which synonymized species were described are underlined.
^d Larvae not unequivocally identified; rather listed as "cf." (conferatur = compare) or "near".
^e Lake Tanganyika collections, national boundaries not specified (Eggermont and Verschuren 2003a,b); probably includes both Burundi and Tanzania.
^f 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.
^g Species recorded by Freeman (1957b) from Albertville and Kabinba, Lake Tanganyika, DR Congo.
^h as *Dicrotendipes* sp. 2 (Petr 1972), and identified as *D. fuscitatus* by Verschuren (1997).

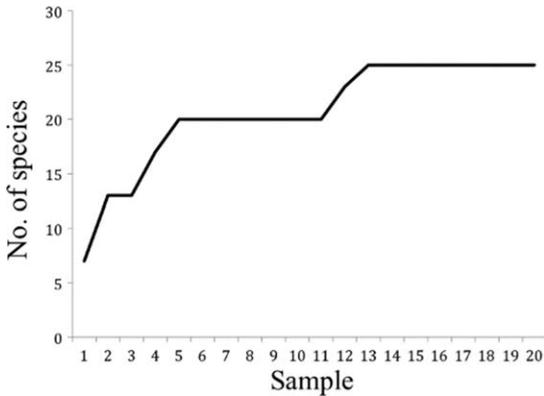


Fig. 2. Species accumulation curve for Chironomidae reared from *Hydrilla* at Cercle Nautique.

Chironomidae: α - and β -diversity. Differences in α -diversity (H') of chironomids sampled from four aquatic macrophytes were significant for all pair-wise combinations of plants (Table 4). Using either Jaccard's or Sorenson's qualitative measures to measure β -diversity, presence-absence data showed very similar chironomid species distributions across the six possible plant species-pairs comparisons (Fig. 5). However, Sorenson's quantitative measure, which incorporates abundance along with presence or absence data, demonstrated substantial differences between pairs of plant species (Fig. 5). For example, the chironomid communities of *Hydrilla* and *Vallisneria*, both Hydrocharitaceae, were much more similar than were other pairs, reflecting considerable overlap in both species composition and abundance of dominant species, in this case *D. fusconotatus* and *Cricotopus cf. harrisoni* (Fig. 4).

Other Insects Reared From Aquatic Plants. We reared few other insect species from plants. Small Trichoptera, particularly *Orthotrichia* (Hydroptilidae), were reared from a majority of collections. *Orthotrichia sanya* Mosely was reared from 13 of 22 of samples of *Hydrilla* from Cercle Nautique as well as

from *Hydrilla* collections from Rumonge, Magara, and Saga Vodo. It also was reared from two collections of *Vallisneria*, and a second *Orthotrichia* species was reared once from that plant. *Ecnomus tomasseti* Mosely (Trichoptera: Ecnomidae) was reared once from *Hydrilla* at both Cercle Nautique and Rumonge. Numbers of Trichoptera usually were modest, with a mean of 9.2 *O. sanya* (median = 2; maximum = 68; $n = 20$) reared from *Hydrilla* collected at Cercle Nautique. In addition, a single *Paraponyx* larva (Lepidoptera: Crambidae) was found eating a *Hydrilla* leaf collected at Cercle Nautique, a single specimen of Curculionidae (Coleoptera), probably a *Bagous* sp., was found associated with *Hydrilla* from the same site, and three scelionid parasitoids were reared from *Hydrilla* collected at Cercle Nautique and Saga Vodo. Damselflies and mayflies also occasionally emerged, but the relatively short time that we held plants and our rearing apparatus might not have created conditions favorable for the development and emergence of nonchironomid taxa.

Discussion

Chironomidae of Burundi and Lake Tanganyika.

Except, perhaps, for its butterflies, the insects of Burundi are poorly known, and 24 of the chironomid species we collected represent new country records. *Polypedilum dewulfi* and *P. wittei* were previously identified by one of us (J.H.E.) from larvae associated with damaged *Hydrilla* collected in Lake Tanganyika, Burundi (Buckingham 1994). *Kiefferulus chloronotus* (Kieffer) has been identified previously from Lake Tanganyika (Eggermont and Verschuren 2003b), but from a Tanzanian site (H. Eggermont, personal communication). Adults of *Cryptochironomus cf. diceras* were previously identified from material collected at Albertville on the shore of Lake Tanganyika, but in DR Congo (Freeman 1957b). The number of chironomid species recorded from Burundi doubtless will increase with collections made in other habitats, particularly lotic ones. Hints of the unknown diversity of Burundi's

Table 2. The number of chironomids reared from two sites in Lake Tanganyika

Chironomid species	Cercle Nautique			Saga Vodo		
	7 Aug.	7 Nov.	8 Sept.	7 Aug.	7 Nov.	8 Sept.
<i>Cricotopus cf. harrisoni</i>	52	1		2	103	44
<i>Nanocladius saetheri</i>					1	2
<i>Chironomus imicola</i>					26	
<i>Cryptochironomus cf. diceras</i>					13	
<i>Dicrentodipus fusconotatus</i>	868	8	40	17	15	7
<i>D. sudanicus</i>	3				1	
<i>Kiefferulus brevivalpis</i>		292		90		2
<i>K. chloronotus</i>					8	
<i>Parachironomus acutus</i>	146			1		2
<i>P. dewulfianus</i>	52		29			
<i>Polypedilum wittei</i>	2				3	3
<i>P. dewulfi</i>	39	1	52	1	123	102
<i>P. tenuitarsis</i>				1		
<i>Cladotanytarsus pseudomancus</i>		8	1	2	102	97
<i>Tanytarsus balteatus</i>				4	1	
Totals	1,162	310	122	118	396	259

Table 3. Percentage of samples from which chironomid species emerged from four aquatic macrophytes in Lake Tanganyika, Burundi

Subfamily	Tribe	Species	All samples (n = 22) of <i>Hydrilla verticillata</i> (L.f.) Royle	Samples collected Jul, Aug, Oct, and Nov 2009			
				<i>H. verticillata</i>	<i>Ceratophyllum demersum</i> var. <i>apiculatum</i> (Cham.) Asch.	<i>Potamogeton schweinfurthii</i> A.Benn.	<i>Vallisneria spiralis</i> f. <i>aethiopica</i> (Fenzl) T.Durand & Schinz
Tanypodinae	Pentaneurini	<i>Ablabesmyia cf. dusoleili</i>	5	0	0 ^a	0 ^a	0 ^a
		<i>A. cf. melaleuca</i>	5	0	0	0	0
		<i>A. rimae</i>	32	50	25	0	0
Orthocladiinae		<i>Nilotanytus comatus</i>	0	0	25	0	0
		<i>Cricotopus albitibia</i>	5	0	0	0	0
		<i>C. cf. harrisoni</i>	82	50	50	50	75
Chironominae	Chironomini	<i>Nanocladus saetheri</i>	14	0	0	0	0
		<i>Chironomus imicola</i>	27	25	0	25	0
		<i>Cryptochironomus cf. dicerus</i>	9	0	0	0	25
		<i>C. lindneri</i>	5	0	0	0	0
		<i>Dicrolentipes fusconotatus</i>	100	100	100 ^a	100 ^a	100 ^a
		<i>D. kribicola</i>	5	0	0	0	0
		<i>D. sudanicus</i>	55	50	25 ^a	25	50 ^a
		<i>Harnischia curtilamellata</i>	5	0	0 ^a	0 ^a	0
		<i>Kiefferulus brevipalpis</i>	64	25	25	75	25
		<i>K. chloronotus</i>	27	25	0	25 ^a	0
		<i>Parachironomus acutus</i>	55	50	75	25	50
		<i>P. devulfianus</i>	45	50	25	50	50
		<i>Polypedilum (Pentapedilum) micra</i>	5	0	0	0	0
		<i>P. (Pentapedilum) wittei</i>	55	50	50	25	75
		<i>Polypedilum (Polypedilum) devulfi</i>	86	100	50	25	100
Tanytarsini		<i>P. (Polypedilum) tenuitarse</i>	14	0	0	0	0
		<i>Cladotanytarsus pseudomaneus</i>	59	50	0	25	50
		<i>Rheotanytarsus guineensis</i>	9	25	0	0	0
		<i>Tanytarsus balteatus</i>	41	0	0	0	0
		<i>T. formosanus</i>	18	0	0 ^a	0 ^a	0 ^a

^a Collected from this plant species in Lake Chad (Dejoux 1972).

chironomid fauna were provided by Janssens de Bisthoven et al. (1993) who reported that four of the larval types they collected from the Ntahangwa River, a small tributary of Lake Tanganyika, were representatives of genera previously unknown from Africa. Sampling of moist forest and forest wetlands also may yield new species. Sampling in or near such sites has yielded many endemic chironomids elsewhere in Africa (Hare and Carter 1987).

One chironomid species, *D. fusconotatus*, made up a disproportionate number (>80%) of individuals

that emerged from our plant samples. It is possible that environmental conditions at Cercle Nautique were particularly favorable for development of *D. fusconotatus*. Alternatively, our results may reflect the general case, or at least that seen in some African lakes, where one species dominates the fauna associated with submersed macrophytes. In Volta Lake, Ghana, over 90% of chironomid larvae sampled from *Ceratophyllum demersum* and *Pistia stratiotes* L. were of one species, *Kiefferulus fractilobus* (Petr 1968).

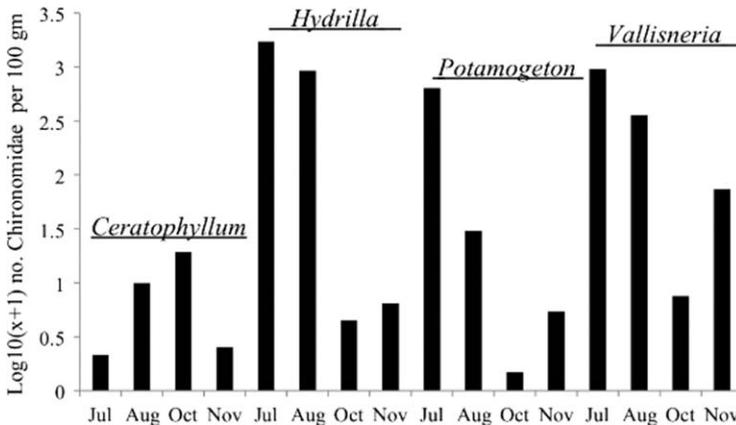


Fig. 3. Abundance (chironomids per 100 gm plant dry weight) of midges that emerged from four aquatic plants at Cercle Nautique, July–November 2009.

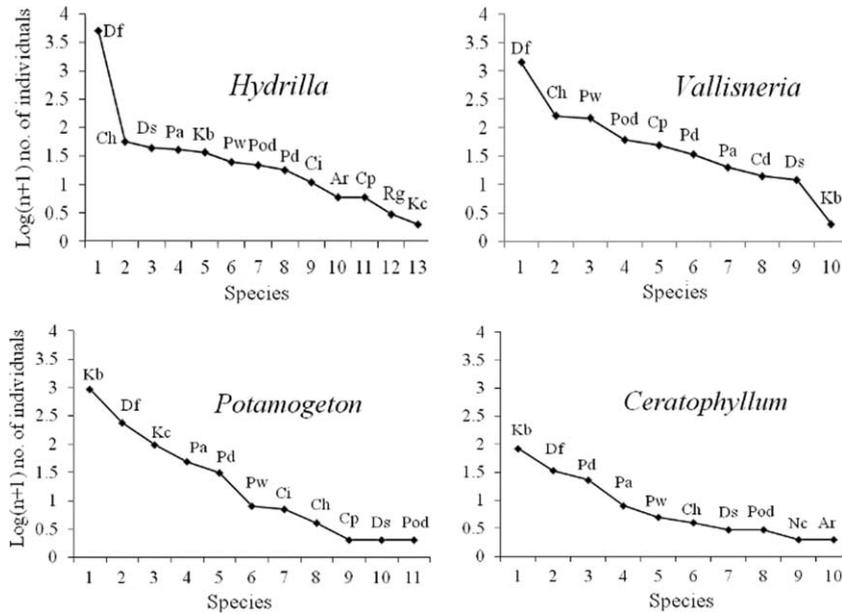


Fig. 4. Rank Abundance plots of Chironomidae species reared from four species of aquatic plants. Ar, *Ablabesmyia rimae*; Cd, *Cryptochironomus cf. dicerus*; Ch, *Crictopus cf. harrisoni*; Ci, *Chironomus imicola*; Cp, *Cladotanytarsus pseudomancus*; Df, *Dicrondipis fusconotatus*; Ds, *Dicrondipis sudanicus*; Kb, *Kiefferulus brevipalpis*; Kc, *Kiefferulus chloronotus*; Nc, *Nilotanytarsus comatus*; Pa, *Parachironomus acutus*; Pd, *Parachironomus dewulfianus*; Pod, *Polypedilum dewulfi*; Pw, *Polypedilum wittei*; Rg, *Rheotanytarsus guineensis*.

Recently, knowledge of Lake Tanganyika’s chironomid diversity has increased indirectly, incidental to research in northern Lake Tanganyika on the use of 1) living chironomid larvae for studying contemporary habitat preferences (Eggermont et al. 2008); and 2) sub-fossil larval remains (Eggermont and Verschuren 2003a, b) and recent death assemblages of larvae (Eggermont and Verschuren 2003c) for assessing natural and human-related causes of environmental change. However, studies of the African chironomid fauna by rearing individually isolated larvae, thereby unambiguously associating the adult with cast larval and pupal exuviae, are still in the early stages. As a result, although the publications of Eggermont and Verschuren (2003a,b,c) and Eggermont et al. (2008) have greatly increased knowledge of Lake Tanganyika’s

chironomid diversity, only six of the 78 larval types they recorded could be assigned, unequivocally, complete species names. A further 16 (20%) were accompanied by the qualifiers “cf.” (conferatur, “compare”) or “near”, while the remaining 56 (72%) were morphotypes. Nonetheless, combined with the larval types unique to Theunissen’s (1993) lake samples, the number of species previously known from Lake Tanganyika was 83 (Eggermont et al. 2008). Currently, we can unequivocally add only two of the species we collected to that number, because some or most of the adults reared during our study may already be represented among the larval types identified by Eggermont and Verschuren (2003a, b). *Chironomus imicola* and *Kiefferulus brevipalpis*, for which larval identifications were available (Verschuren 1997) were not listed among the species collected by Eggermont and colleagues. Future studies associating larval and adult forms of the same species may reveal that other species we sampled are also new to the lake fauna. Even so, among African lakes, the present conservative figure of 85 is second only to that of Lake Chad’s 105 species; 93 listed in Dejoux (1968) plus 12 more species attributed to the lake in a later report (Dejoux 1973).

The importance of the deep-water African rift lakes in conserving the lacustrine chironomid fauna over geologic time is not known. However, in times of extended drought, and particularly during the African mega-drought interval over 106 Ka (McGlue et al. 2008), Lake Tanganyika, which never dried up, prob-

Table 4. Shannon α -diversity measures for Chironomidae on four aquatic macrophytes

Plant species	Shannon index		
<i>Ceratophyllum</i>	1.43		
<i>Hydrilla</i>	0.30		
<i>Potamogeton</i>	1.03		
<i>Vallisneria</i>	1.01		
Paired comparison	t-statistic	df	p
<i>Ceratophyllum</i> / <i>Hydrilla</i>	13.25	168	<0.001
<i>Ceratophyllum</i> / <i>Potamogeton</i>	4.43	200	<0.001
<i>Ceratophyllum</i> / <i>Vallisneria</i>	6.04	204	<0.001
<i>Hydrilla</i> / <i>Potamogeton</i>	21.68	2119	<0.001
<i>Hydrilla</i> / <i>Vallisneria</i>	16.88	2864	<0.001
<i>Potamogeton</i> / <i>Vallisneria</i>	3.33	3220	<0.001

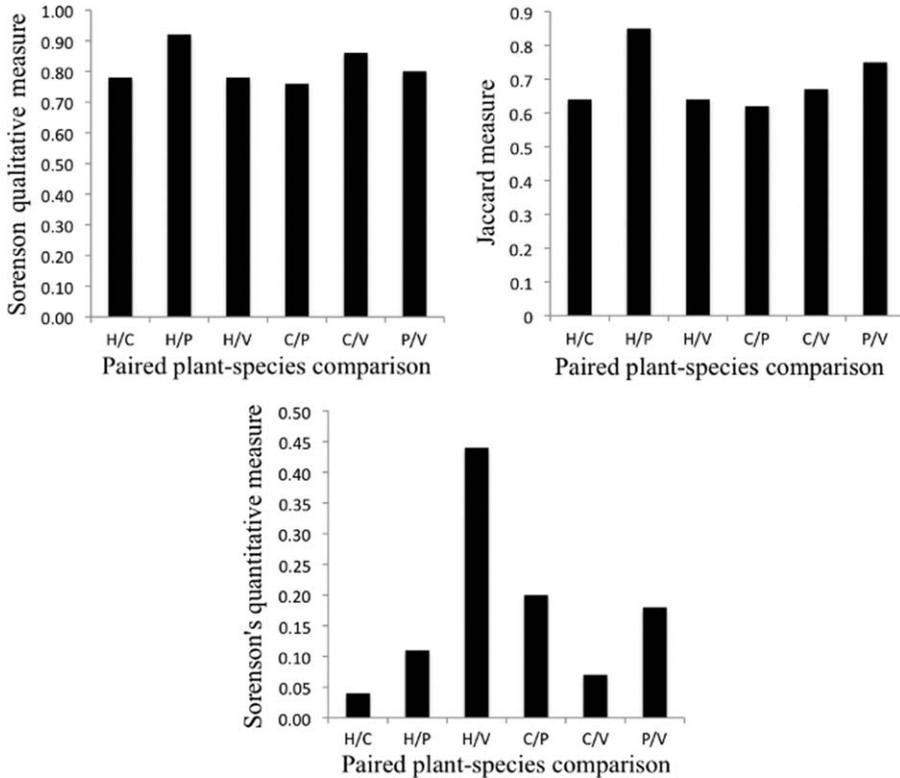


Fig. 5. β -diversity measures comparing chironomid diversity between pairs of aquatic plants from Cerle Nautique. C, *Ceratophyllum demersum* variety *apiculatum*; H, *Hydrilla verticillata*; P, *Potamogeton schweinfurthii*; V, *Vallisneria spiralis* f. *aethiopica*.

ably acted as a refugium for many species of flying insects whose immature stages are lake dependent.

Lack of Evidence of Herbivory Among Lake Tanganyika Chironomidae. Although substantial work has been conducted on chironomid feeding behavior, little has focused on the African fauna. In a recent review (Berg 1995), only one out of 149 citations referred to African chironomids. Some chironomid communities on aquatic plants demonstrate great complexity in exploiting plant resources. For example, in a community of chironomids reared from *Potamogeton* species in midwestern USA, Berg (1950) described true leaf mining (consumption of mesophyll tissue while tunneling between epidermal layers), channel feeding (ingesting one layer of epidermis in addition to the mesophyll) and tube makers/net spinners that live in short burrows in stems or unopened leaves.

To our knowledge, there are no unequivocal reports of herbivory by Chironomidae on aquatic plants in Africa, and we found no evidence in our study of plant damage attributable to chironomid activity. Like us, Petr (1968), working in Volta Lake, found no evidence of feeding by any insect on aquatic macrophytes, except for a single instance where a pyralid moth larva was observed feeding on a plant. Mining in growing buds and stems of *Hydrilla* by suspected *Polypedilum* species as described by Pemberton (1980) was not observed by us either at Cerle Nautique or Saga

Vodo. Late in the current study, tunneling damage to growing buds similar to that figured by Pemberton (1980) was seen in *Hydrilla* collected from Rumonge and Magara, but no insects were seen boring in plants. Recent experimental evidence suggests that nymphs of the mayfly *Povilla adusta* Navás (Polymitarcidae) are responsible for these tunnels (Copeland et al. 2011). In terms of niche utilization, the plant-associated chironomid community in Lake Tanganyika appears to be an exceptionally simple one, exploiting leaf and stem surfaces solely for anchorage and, for browsers and predators, active foraging for food. Nonetheless, plant damage caused by *Polypedilum* cannot be ruled out unequivocally. Petr (1970b) reported tunneling behavior by *P. adusta* in flooded trees in Volta Lake, Ghana, and commented that *Polypedilum* larvae also might be burrowers, as they were often found inside the wood.

Differences Between Sites in the Chironomid Fauna Associated with *Hydrilla*. Dejoux and Saint-Jean (1972) reported that chironomid species richness on submersed aquatic plants was greater in a more exposed area of Lake Chad than in a protected area with little wind disturbance. Some of this difference was attributed to the presence of more Orthoclaadiinae species at the former site. Orthoclaadiinae generally require higher levels of dissolved oxygen than do other chironomid taxa (Eggermont and Verschuren 2007;

Petr 1970a). The bulk of our collections were made at Cercle Nautique, a small and relatively well-protected bay. Aquatic plant communities in areas of Lake Tanganyika that have greater, but not damaging, exposure to wind action may possess a richer chironomid fauna. Compared with Cercle Nautique, Saga Vodo has higher exposure to wind and wave action. During the three-month comparison of chironomids reared from *Hydrilla* at these distinct, but closely situated, sites in Lake Tanganyika, differences were seen in chironomid composition and species richness (Table 2). Although no species was reared from Saga Vodo *Hydrilla* that was not also reared from that plant at Cercle Nautique over the course of the entire study (Table 1), our limited comparative data suggest that real differences in chironomid species composition probably exist between the two sites. A larger study, with multiple sites, that focuses on a comprehensive characterization of habitat differences and their relation to chironomid populations could help to elucidate the hydrologic features that affect the distribution of midge species in Lake Tanganyika.

The chironomid Fauna of Aquatic Macrophytes. Aquatic plants are important microhabitats for lacustrine invertebrates (Krecker 1939, Schramm and Jirka 1989, Taniguchi et al. 2003, Tarkowska-Kukuryk and Kornijów 2008). Besides providing autecological information for individual midge species, documentation of the contemporary species of Chironomidae associated with aquatic plants is a necessary first step in generating paleoenvironmental reconstructions using fossil larvae, and some advances have already been made in this direction (Eggermont and Verschuren 2006, Verschuren and Eggermont 2006, Eggermont et al. 2006, Eggermont et al. 2008, Eggermont et al. 2010). Species that are presently restricted to plants and whose fossils are found in dated core samples of lake sediment can, by inference, reveal environmental conditions that prevailed at that time.

Although most studies of African chironomids have relied on benthic sampling or light trapping, published data on plant-associated species does exist for some African lakes (Appendix 2). Petr (1968) examined densities of individual larvae of several taxa, but only at the family level, in Volta Lake, Ghana, and did not address diversity of chironomid species. In most of the other studies, chironomid species richness was relatively low. In highland Ethiopia, Kibret and Harrison (1989) recorded only 13 chironomid species from aquatic plants in Lake Awasa, but these represented nearly half of the 27 total species collected at light or by sweep net. Two other studies focused on unstable lake systems; Kariba in Zimbabwe, a manmade, recently-dammed lake (MacLachlan 1969a), and the shallow, intermittently saline Lake Chilwa in Malawi (MacLachlan 1975). Both lakes were prone to radical shifts in water volume and they each lacked permanent populations of aquatic macrophytes. Nonetheless, these studies demonstrated the importance of aquatic plants in (1) the establishment of insect faunas during lake recovery after a complete drying out of Lake Chilwa (MacLachlan 1975), and (2) increasing

the species richness and biomass of invertebrates as Lake Kariba matured (MacLachlan 1969a). Aquatic macrophytes supported >5x the faunal biomass as mud, and nearly 18x that of submerged trees in Lake Kariba (MacLachlan 1970). Additionally, the establishment of aquatic plants had effects beyond the simple addition of epiphytic chironomid species to the species lists of lentic habitats. Aquatic macrophytes were also associated with increased species richness of the purely benthic fauna (MacLachlan 1969a, Petr 1972). Plants probably improve the local conditions for establishment of bottom-dwelling chironomid populations. Their roots stabilize lake-bottom sediments, and detritus from dying plant parts adds nutrients and material for tube construction. For species of Chironomidae that do not live within tubes, plants also may provide intermittent protection against predators, particularly fish, and food resources in the form of periphyton and, for the predaceous chironomids, other smaller invertebrates.

In contrast with studies reporting low chironomid species richness on aquatic macrophytes, 60 chironomid larval-types were sampled from plants in chironomid-rich Lake Chad (Dejoux and Saint-Jean 1972), implying that the majority of species ($n = 105$) recorded from that lake use aquatic macrophytes during at least some stage of their life cycle. Most of the chironomid species we reared have been collected previously from aquatic vegetation. Appendix 3 lists these species and the studies in which they were reported. It also lists other substrates from which the species were sampled in those studies.

Lack of Specificity of Chironomid Species Among Aquatic Macrophytes. Except for rare species, there was no evidence of a specific relationship between chironomid species and individual plant species. More importantly, neither *Polypedilum dewulfi* nor *P. wittei*, the two species being investigated for possible herbivory of *Hydrilla*, was specific to that plant. Both species were generalists, and emerged from samples of all four aquatic macrophytes in three plant families (Table 3). A similar lack of specificity was seen during a concurrent study in Uganda, where *P. wittei* (but not *P. dewulfi*) was found. There, in addition to *Ceratophyllum demersum*, *Potamogeton schweinfuthii* and *Hydrilla*, *P. wittei* emerged from species of *Lagarosiphon*, *Najas*, and *Ottelia* (all Hydrocharitaceae) as well as *Utricularia* (Lentibulareaceae) (RSC, unpubl. data). Even if we had found evidence of herbivory of *Hydrilla* by *P. wittei* or *P. dewulfi*, as suggested in an earlier study (Pemberton 1980), it appears that neither midge has the degree of host specificity required of a classical biological control agent.

Effect of Season and Plant Species on Chironomid Emergences. Like Janssens de Bisthoven et al. (1993) we also observed a marked decrease in chironomid abundance during the rainy season in Burundi. In Burundi, August–September normally marks the transition from dry to wet season. The major differences between the two periods are a switch from a strong southerly wind to a mild northerly one and the appearance in the wet season of intermittent violent

showers with attendant rapid changes in water chemistry and sediment input from rivers and seasonal streams (Coulter and Spigel 1991). Presumably, these changes in conditions disrupt the habitat sufficiently to depress chironomid population growth.

In our comparison of four aquatic macrophytes, *Ceratophyllum* yielded far fewer chironomids than did the other species. The only other African study that included quantitative data for chironomids among different aquatic plant species was conducted on Lake Chad, in which *Hydrilla* did not occur. In that study, Dejoux (1983) compared larval densities of nine chironomid species on three plants, *Potamogeton schweinfurthii*, *Ceratophyllum demersum*, and *Najas* sp. Over five sampling dates, chironomid larval densities were highest on *Najas*, another Hydrocharitaceae, averaging just over 10^4 larvae per 100-g dry weight. However, in Lake Chad larval density was higher on *Ceratophyllum* than on *Potamogeton*.

Biodiversity of Chironomids

Alpha-diversity. *Ceratophyllum* had the highest Shannon index value (Table 4) although, along with *Vallisneria*, it had the lowest species richness (10), and also yielded far fewer chironomids than did the other plant species. The higher Shannon index value reflects the index's sensitivity to both species richness and the evenness of distribution of chironomid individuals among species, so that H_{\max} occurs when all species have the same abundance (Magurran 1988). This is shown graphically in the relatively flattened rank abundance curve of chironomids from *Ceratophyllum* compared with those of the other sampled plants (Fig. 4). It is also the reason that the value for *Hydrilla* was so low, being influenced negatively by the great disparity in number between *D. fusconotatus* and the other chironomid species reared from it.

Plant Architecture and β -diversity of Chironomidae. In a survey of seven aquatic macrophytes growing in protected areas of Lake Erie Krecker (1939) found that chironomid larvae, *Nais* spp. (Annelida) and *Melicerta* spp. (Rotifera) dominated across all plant species. Species of *Potamogeton* and *Myriophyllum* were most favored, whereas *Vallisneria* had many fewer genera, and individuals, of invertebrates. Krecker (1939) proposed that these distributions were related to the architecture of preferred and avoided plants, with the former having conformations that make it easy for organisms to attach, whereas the latter (*Vallisneria*), a genus whose species have simple, elongate, smooth leaves, offered poor attachment sites.

In contrast, in Lake Chad, Chironomidae species were distributed remarkably evenly across *Vallisneria* (36 species), *Ceratophyllum* (38), and *Potamogeton* (37) (Dejoux and Saint-Jean 1972). Similarly, in our limited comparison of plants in Lake Tanganyika, we saw no evidence that *Vallisneria*, with its simple architecture was less attractive to colonization by chironomids than were the more complex *Ceratophyllum*, with its brush-like aggregations of leaves, and *Hydrilla*, with its multiple, small leaves arranged in whorls along

the stem. Over four sampling dates, species richness of Chironomidae on *Vallisneria* ($n = 10$) was similar to that on *Ceratophyllum* ($n = 10$), *Potamogeton* ($n = 11$), and *Hydrilla* ($n = 13$), and *Vallisneria* yielded the second highest number of chironomids. Moreover, chironomid β -diversity, a measure of habitat similarity, was much higher between *Hydrilla* and *Vallisneria* than for any other plant-plant comparison. Although the architecture of *Hydrilla* and *Vallisneria* are very different, they are both Hydrocharitaceae, suggesting that plant-relatedness may play a more important role in chironomid distribution than does plant architecture. Although it is true that over our entire study *Hydrilla* had the highest species richness, it was sampled many more times than the other plants, greatly increasing the chances of recovering uncommon or rare species.

A possible reason for the difference between our results and those of Krecker (1939), that concluded that plant architecture was an important factor influencing colonization by aquatic invertebrates, was the presence of a rich periphyton, a layer of biotic (e.g., algae and bacteria) and abiotic (e.g., sand and silt) material, on our plants. Periphyton provides not only a nutritional source for both grazing and tube-dwelling species but also a texture on which larvae can establish purchase. Many of the species we reared live inside tubes constructed of sediment and mucilaginous larval secretions, and these probably also aid in attachment. The species of chironomids from plants in the study of Krecker (1939) are not indicated and may have been depauperate in the number of tube dwellers. Other studies have tested the hypothesis that aquatic plant architecture influences the diversity and abundance of epiphytic fauna, and these have produced conflicting results. For example, Boerger et al. (1982) found that plants with the highest ratio of surface area to weight supported higher densities of chironomid larvae, whereas Cyr and Downing (1988) found that macrophytes with finely dissected leaves did not, in general, have higher densities of chironomids than did broad-leaved plants. Interestingly, when all invertebrate taxa were included in the analysis, of the two species in their study that had highly dissected leaves, *Myriophyllum* sp. and *Ceratophyllum demersum*, the former supported a significantly higher abundance of individuals than did broad-leaved species, whereas *C. demersum* did not (Cyr and Downing 1988).

In our study, because plant species occurred in mixed stands, it is not impossible that individual chironomid larvae could have been transferred from one plant to another during sampling. However, many of the chironomid species we sampled are tube dwellers and it seems more likely that a disturbance would cause them to retreat into the safety of their tube, reducing the chances of transfer between plants. In addition, normal wave action and occasional heavy storms on the lake also create the conditions for possible transfer of midge larvae between plants, so that the local turbulence created during our sampling probably mimicked the natural condition at some level. Nonetheless, we have no way of knowing what

role, if any, the possible movement of insects between sampled plants affected our results and they should, therefore, be treated with some caution.

Notes on the Chironomid Taxa From Aquatic Plants

Orthocladiinae and Tanypodinae. The presence of a high proportion (25%, $n = 77$) of orthocladiine larval types among sub-fossil chironomids collected by Eggermont and Verschuren (2003a) in Lake Tanganyika is curious. Previous surveys have generally demonstrated a paucity of orthocladiine species from African lowland lakes whether collected at light (1%, $n = 93$, Dejoux 1968, Lake Volta, Chad, Chad; 0%, $n = \approx 50$, Petr 1970a, Lake Volta, Ghana), by bottom sampling (4%, $n = 25$, McLachlan 1969a, 0%, $n = 17$, McLachlan and McLachlan 1971, Lake Kariba, Zimbabwe; 5%, $n = 19$, Petr 1972, Lake Volta, Ghana), by bottom sampling plus emergence traps (2%, $n = 46$, Hare and Carter 1987, Opi Lake, Nigeria), or by undisclosed methods (4%, $n = \approx 57$, Bidwell and Clarke 1977, Lake Kainji, Nigeria). Most Orthocladiinae are dependent on highly oxygenated water (Petr 1970a), and in tropical regions comprised a large proportion of chironomids from cool, lotic habitats (63%, $n = 16$, Harrison and Hynes 1988, rivers in highland Ethiopia; 53%, $n = 45$, Lehmann 1979, rivers in eastern, highland DR Congo), perhaps because oxygen is less soluble in warmer water, and higher temperatures speed up decomposition of organic material which also depletes oxygen (Eggermont and Verschuren 2003b). Consistent with this interpretation, the proportion of orthocladiines was lower in lower altitude rivers and streams (29%, $n = 38$, Lehmann 1981, rivers in central DR Congo) and in highland lakes (21% $n = 32$, Verschuren 1997, Lake Naivasha, Kenya); 15%, $n = 27$, Kibret and Harrison 1989, Lake Awasa, Ethiopia). Although they acknowledge that some of their sub-fossil types may have washed in with sediment from feeder streams and rivers, Eggermont and Verschuren (2003b) argue that the consistently strong wave action characteristic of the large Rift Valley lakes may create the conditions for oxygenation usually encountered in fast moving streams and rivers and, by extension, an environment favorable to at least some orthocladiine species. This phenomenon may explain the higher number of orthocladiine species collected from plants at an exposed site, compared with a protected one, as was found in Lake Chad (Dejoux and Saint-Jean 1972). During our survey, Orthocladiinae made up 12% (3/26) of reared species (Table 1), a figure that lies between the proportion (25%) found by Eggermont and Verschuren (2003b) and those cited above (mean <3%) for six other low to midaltitude lakes in Africa. In discussing potential contamination of their core samples by upland, lotic species having been washed into Lake Tanganyika, Eggermont and Verschuren (2003b) considered *Nilotanypus* near *comatus* (a Tanypodinae) among the species most likely to have appeared in this way, as this species was previously recorded from stoney torrents (Harrison 1991). How-

ever, our rearing records show that this species, at least, definitely occurs in Lake Tanganyika. Therefore, it appears reasonable to believe that some of the orthocladiine subfossil types reported in Eggermont and Verschuren (2003a) did develop in Lake Tanganyika, although association of larvae with reared adults is required to confirm this.

Of the orthocladiine species we reared, both *Cricotopus albitibia* and *Nanocladius saetheri* previously have been associated with lacustrine vegetation (Harrison 1992, Harrison 1994) (Appendix 3). Similarly, the predaceous larvae of the tanypodine species *Ablabesmyia dusoleili* and *A. rimae* have been collected from near-shore aquatic macrophytes (Dejoux and Saint-Jean 1972, Harrison 1991). Aquatic plants probably provide *Ablabesmyia* with abundant prey in the form of chironomid larvae and other small invertebrates.

It is possible that our *Cricotopus cf. harrisoni* may not be true *C. harrisoni*. The latter is known from cold, high elevation streams, including torrential ones (Lehmann 1979, Harrison and Hynes 1988, Harrison 1992). However, chironomid species often are tolerant of different environmental conditions, and four other species we reared, *Nilotanypus comatus*, *Cryptochironomus cf. dicerus*, *Polypedilum dewulfi* and *C. albitibia* also have been recorded from fast and slow moving mountain streams and rivers (Lehmann 1979, 1981; Harrison and Hynes 1988; Harrison 1996). Lehmann (1981) describes *C. dicerus* as a "eurytop" (=euryoecious), capable of developing in a wide range of aquatic habitats, and the other species may be similarly tolerant. The possibility that these "tolerant" taxa may actually represent cryptic-species groups should be investigated.

Chironominae. *Chironomus imicola* was thought by McLachlan (1988) to be primarily a species of small, ephemeral bodies of freshwater (puddles, pools, and ponds) that used rock pools in seasonal rivers as dry season refugia. Over 10 yr of sampling, he was unable to find *C. imicola* in two large lakes, Chilwa in Malawi and Karibe in Zimbabwe. Similarly, Harrison (1996) was unable to find *C. imicola* larvae in Lake Awasa, Ethiopia, and felt that the species must develop in peripheral swampy areas. McLachlan (1988), however, did not exclude the possibility that *C. imicola* might occur, undetected, in low densities in large lakes. The collection of *C. imicola* in the current study from Lake Tanganyika and by others from Opi Lake (Hare and Carter 1987) and Kainji Lake (Bidwell and Clarke 1977) in Nigeria, Volta Lake, Ghana (Petr 1972), Lake Chad (Dejoux 1968), and Lake George, Uganda (Darlington 1977) shows this species to be capable of using a wide range of habitats including, rarely, streams (McLachlan 1988). A larval morphotype that is probably *C. imicola* was commonly recovered from surface sediment samples from lakes in Kenya, Ethiopia, Tanzania, and Uganda (Eggermont and Verschuren 2004b).

In a table showing the salinity distributions of various chironomids, Verschuren (1997) indicated that *Kiefferulus chloronotus* was recorded only from water

with low conductivity (c. 100 μScm^{-1} or less) suggesting that this species had a very low tolerance for salinity. Although we did not measure conductivity at our sites, reported values for Lake Tanganyika are $\approx 600 \mu\text{Scm}^{-1}$ (Bootsma and Hecky 2003; Eggermont et al. 2008). Thus, the distribution of *K. chloronotus* probably is not markedly limited by conductivity, and a recent survey showed that this species was commonly found in tropical African lakes with conductivity to 700 $\mu\text{S/cm}$ (Eggermont et al. 2006). Of the species we reared, *Cladotanytarsus pseudomancus* is the only one known to have a wide tolerance to salinity, having been found in Lake Chala, Ethiopia, with a conductivity of 21,000 μScm^{-1} (Tudorancea and Harrison 1988), although its conductivity optimum among African lakes was 510 $\mu\text{S/cm}$ (Eggermont et al. 2006). The report of a salt tolerant population of *Tanytarsus formosanus* (as *Tanytarsus horni*) from the same lake (Tudorancea and Harrison 1988) was based on a mistaken larval identification (Verschuren 1997).

We collected only four *Polypedilum* species, although two, *P. (Polypedilum) dewulfi* and *P. (Pentapedilum) wittei*, were relatively common (Tables 1 and 2). West African lakes are rich in *Polypedilum* species (Dejoux 1974), particularly subgenus *Polypedilum*, as is Lake Chad (Dejoux 1968), but members of this subgenus seem to be less diverse in east African lakes. Two (7.7%) of our reared species were members of this subgenus. Of 77 larval types from sediments in Lake Tanganyika, Eggermont and Verschuren (2003b) recorded at most five (6.5%) in the subgenus *Polypedilum (Polypedilum)*. Similarly, in a list of chironomids reared from plants in Ugandan lakes, only two of 44 (4.5%) species were representatives of this subgenus (R.S.C., unpublished data). In contrast, of 15 chironomid species-lists from 12 central and west African countries, a mean of 20.0% (range, 6.5–40%) of the chironomid fauna was contributed by *Polypedilum (Polypedilum)* species (Freeman 1955c, 1957b; Dejoux 1968, 1973, 1974, 1976; Petr 1970a; Bidwell and Clarke 1977; Hare and Carter 1987). Eggermont et al. (2005) pointed out that the chironomid fauna of West African lakes is richer than that of East Africa's and suggested that environmental stability was probably a major reason for the difference. Among African Chironomidae, *Polypedilum (Polypedilum)* species may be particularly sensitive to environmental perturbation and less likely to successfully colonize areas that have a greater probability of exposure to extended dry periods.

Africa-wide Distribution. Of the 26 species we collected, *P. acutus*, *P. wittei*, *D. fusconotatus*, *H. curtilamellata*, and *T. formosanus* also are recorded from Europe, with *H. curtilamellata* known from North America as well. This is a relatively high percentage given that only 25 total species are known to occur in both Europe and the Afrotropical region (Saether and Ekrem 2003). We were not surprised that there were no Burundi endemics among our sampled chironomid species. Those groups comprising the bulk of Lake Tanganyika's endemic fauna are restricted primarily to flightless taxa, particularly fish, noninsect Arthro-

poda, and Mollusca with 219, 157, and 46 endemics each, respectively (Coulter 1991). In stark contrast, of the 155 identified insects recorded from the lake, none are endemic (Coulter 1991). As flying insects, chironomid distributions would be expected to be wide in contemporary aquatic habitats if suitable bodies of water, now extinct but present during wetter geological periods, were available as "stepping stones" for dispersing adults. Such was the case at the beginning of the Holocene when bridging ponds and lakes were spread across the Soudanienne region from Mauritania to Sudan, and present in Mali, Niger and even the now-desolate Hoggar of southern Algeria (Dejoux 1981). Twenty-four of our 26 species are distributed across Africa and into southern Africa, at least to Zimbabwe and most to South Africa. Only two, *Abblabesmyia cf. melaleuca* and *Dicrotendipes kribiicola* have not been recorded from southern subtropical Africa. Several workers have noted the similarity of chironomid faunas across the present-day Sahelian and Sudanian zones stretching from west to central Africa, across the Nile Basin and into Kenya and Tanzania (Dejoux 1974, Saether and Ekrem 2003, Eggermont et al. 2005). Current distributions also suggest a migratory connection between east and South Africa (Dejoux 1974). The Albertine and Southern Rift Valleys, with their deep-water Great Lakes, Tanganyika and Malawi, provide both a flyway to facilitate migration and permanent water sources for conserving species during mega-droughts. The lakes probably also contribute colonizing individuals for dispersal during favorable periods.

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Appendix 1. Principle literature sources for distribution and identification of African Chironomidae

Country records		Pan-African distribution, taxonomy and identification	
Country	Citation	Higher taxon	Citation
Burkina Faso	Dejoux (1974, 1976, 1977)	Chironomidae, Afrotropical catalogue	Freeman and Cranston (1980)
Cameroon	Dejoux (1973, 1976)	Tanypodinae	Freeman (1955a), Harrison (1978)
Central African Republic	Dejoux (1976)	Orthocladiinae	Freeman (1956)
Chad	Dejoux (1968, 1971, 1973)	Orthocladiinae, <i>Nanocladius</i> , Afrotropical species	Harrison (1994)
Congo Republic	Dejoux (1976)	Chironominae, Chironomini	Freeman (1957a)
D.R. Congo	Chrispeels (1959); Freeman (1955c,d; 1957b); Lehmann (1979, 1981)	Chironominae, Chironomini, Tanytarsini	Freeman (1958)
Ethiopia	Harrison (1991, 1992, 1996)	Chironominae, Chironomini, <i>Dicrotendipes</i> , revision	Epler (1988)
Ghana	Petr (1970a)	Chironominae, Chironomini, <i>Polypedilum</i> (<i>Pentapedilum</i>) revision	Oyewo and Saether (2008)
Guinea	Dejoux (1984)	Chironominae, Tanytarsini, <i>Tanytarsus</i> , review of Afrotropical species	Ekrem (2001)
Ivory Coast	Dejoux (1974)	Chironominae, Tanytarsini, <i>Rheotanytarsus</i> species, worldwide distribution	Saether and Kyerematen (2001)
Kenya	Eggermont and Verschuren (2004a,b)		
Malawi	McLachlan (1975)		
Mali	Dejoux (1974, 1976)		
Niger	Dejoux (1973)		
Nigeria	Dejoux (1973), Bidwell and Clark (1977), Hare and Carter 1987		
Senegal	Dejoux (1974, 1976)		
South Africa	Freeman 1955e, Allanson (1961)		
Tanzania	Eggermont and Verschuren (2003a,b)		
Uganda	Eggermont and Verschuren (2004a,b)		
Zimbabwe	Munro (1966); McLachlan (1969a,b); McLachlan (1970); McLachlan and McLachlan (1971)		

Appendix 2. Studies of Chironomidae associated with aquatic plants in Africa

Country	Lake	Plant family	Plant species	Chironomid profile	Reference
Zimbabwe	Kariba	Salviniaceae	<i>Salvinia auriculata</i> Aubl.	14 species; <i>Stolonifera</i> was species-poor	McLachlan 1969a
		Onagraceae	<i>Ludwigia adscendens</i> subsp. <i>diffusa</i> (Forsk.) P.H. Raven		
Ethiopia	Awasa	Potamogetonaceae	<i>Potamogeton pusillus</i> L.	13 species; <i>Potamogeton</i> was species-poor but undersampled	Kibret and Harrison 1989
		Potamogetonaceae	<i>Potamogeton schweinfurthii</i> A.Benn.		
		Nymphaeaceae	<i>Nymphaea nouchali</i> var. <i>caerulea</i> (Savigny) Verdc.		
		Cyperaceae	<i>Cyperus exaltatus</i> (sic) ^a		
		Poaceae	<i>Paspalidium geminatum</i> (Forsk.) Stapf		
Chad	Chad	Potamogetonaceae	<i>P. schweinfurthii</i> ^b	60 species; <i>Potamogeton</i> (37), <i>Ceratophyllum</i> (38), <i>Vallisneria</i> (36), <i>Cyperus</i> (18)	Dejoux and Saint-Jean 1972, Dejoux 1983
		Ceratophyllaceae	<i>Ceratophyllum demersum</i> L.		
		Hydrocharitaceae	<i>Vallisneria</i> sp.		
		Cyperaceae	<i>Cyperus papyrus</i> L.		
Ghana	Volta	Ceratophyllaceae	<i>C. demersum</i>	No list, larval biomass 10 × higher on <i>Ceratophyllum</i>	Petr 1968
		Araceae	<i>Pistia stratiotes</i> L.		
Malawi	Chilwa	Fabaceae	<i>Aeschynomene pfundii</i> Taub.	18 species; <i>Aeschynomene</i> was species-poor	McLachlan 1975
		Poaceae	<i>Leptochloa fusca</i> (L.) Kunth ^c		
		Typhaceae	<i>Typha domingensis</i> Pers.		

^a Probably *Cyperus exaltatus* Retz., or possibly *Cyperus cristatus* var. *exaltatus* Merxm, now a synonym of *Kyllinga alba* Nees subsp. *alba*.
^b All species, except *Cyperus*, actually represent facies, mixed stands of submersed aquatic plants dominated (>90% of individual plants) by one species.

^c as *Diplacne* (sic) *fusca* (L.) Beaur.

Appendix 3. Reared Burundi Chironomidae reported previously from aquatic macrophytes and other substrates in Africa

Subfamily	Tribe	Species	Vegetation	Submerged tree	Mud	Lake(s), and country
Tanypodinae	Pentaneurini	<i>Ablabesmyia dusoleili</i>	X ^a			Chad, Chad
		<i>Ablabesmyia rimae</i>	X ^b		X ^b	Various, Ethiopia
Orthoclaadiinae		<i>Cricotopus albitibia</i>	X ^{a,c}			Chad, Chad Awasa, Ethiopia
		<i>Nanocladius saetheri</i>	X ^d			Awasa and Ziwai, Ethiopia
Chironominae	Chironomini	<i>Chironomus imicola</i> ^f	X ^{e,f}	X ^{f,j}	X ^e	Kariba, Zimbabwe
		<i>Cryptochironomus dicerus</i>	X ^{e,g}		X ^b	Kariba, Zimbabwe Chilwa, Malawi
		<i>Dicortendipes fusconotatus</i>	X ^{a,g,i}			Chad, Chad Chilwa, Malawi Tanganyika, Tanzania
		<i>Dicortendipes sudanicus</i>	X ^{a,e,i}	X ^{f,j}		Chad, Chad Kariba, Zimbabwe Tanganyika, Tanzania
		<i>Harnischia curtilamellata</i>	X ^a			Chad, Chad
		<i>Kiefferulus brevipalpis</i>	X ^{e,g}			Awasa, Ethiopia Chilwa, Malawi
		<i>Kiefferulus chloronotus</i>	X ^a	X ^{f,j}		Chad, Chad Kariba, Zimbabwe Volta, Ghana
		<i>Parachironomus acutus</i>	X ^g			Chilwa, Malawi
		<i>Parachironomus dewulfianus</i>	X ^a			Chad, Chad
		<i>Polypedilum cf. wittei</i>	X ^{e,f}	X ^{f,i}	X ^e	Kariba, Zimbabwe
Chironominae	Tanytarsini	<i>Cladotanytarsus pseudomancus</i>	X ^{e,g}	X ^j	X ^{e,j}	Kariba, Zimbabwe Chilwa, Malawi
		<i>Tanytarsus formosanus</i>	X ^a			Chad, Chad

^a Dejoux and Saint-Jean 1972.

^b Harrison 1991.

^c Kibret and Harrison 1989.

^d Harrison 1994.

^e McLachlan 1969a.

^f McLachlan 1969b.

^g McLachlan 1975.

^h McLachlan and McLachlan 1971.

ⁱ Eggermont et al. 2008.

^j McLachlan 1970.

^k Petr 1970b.

^l Misidentified as *Nilodorum fractilobus* by McLachlan (1969b), identification corrected in Darlington (1977).