Biogeography of afrotropical Chironomidae (Diptera), with special reference to Gondwanaland

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This paper reviews current knowledge of the biogeography of the dipterous family Chironomidae, on a worldwide basis with special reference to Gondwanaland. Afrotropical, transantarctic and Inabrezian distribution patterns are discussed together with palaearctic connections. Species and area cladograms are presented and these data are interpreted to indicate associations. The chironomid fauna of the Afrotropical Region includes about 500 species and 28 endemic genera. Three genera basal in the subfamilies Podonominae and Aphroteniinae show cold-stenothermic transantarctic relationships. Nine genera or subgenera are found on other continents but not in the west Palaearctic Region. Most of these distributions clearly represent warm-eurythermic northern Gondwanan vicariance patterns, while others appear to be due to extensive dispersal. On the generic level the connection between Africa and other continents appear dominated by the warm-eurythermic Gondwanan or Inabrezian distribution. The northern Gondwanan pattern is apparent within all recently revised chironomine genera. The transantarctic Gondwanan distribution in recent revisions is exclusively between Australia and Africa. Faunal exchange between the Afro-Arabian continent and Laurasia probably took place during the Miocene. The only genera occurring exclusively in the west *Palaearctic* (including West Asia) and the Afrotropical Regions are *Lobosmittia* Sæther & Andersen and *Virgatanytarsus* Pinder. However, several species and species-groups show such a distribution. More than half of the about 25 species recorded from the Seychelles are limited to the Malagasy Region, while less than one fifth of the about 45 species recorded from Madagascar are known only from that region. Overall, the Eastern Arc, connected with minor core areas of endemism from Tanzania to Kwazulu-Natal in South Africa, appears to be the most important area of endemism for chironomids. The Western Cape Province of South Africa is the core area for chironomids with a transantarctic Gondwanan pattern. In western Africa three more or less interconnected main centres of endemism representing forest refuges can be identified. Other apparently less important areas of endemism includes the Congo basin refuge and the East African highlands of Ethiopia and Kenya. The widespread Nilotic fauna is relatively well known, while the fauna of the rainforests is likely to contain numerous undescribed species.

INTRODUCTION

The Chironomidae is a cosmopolitan family of dipteran insects occurring in all zoogeographical regions of the world including Antarctica. The immature stages of most species occur in freshwater, but many terrestrial or marine species are known. Ashe *et al.* (1987) provide a review of the zoogeographical information on chironomids at subfamily and generic levels. The chironomid fauna of each zoogeographical region is discussed and a comparison of the number of known species and percentage representation of each subfamily for each region is given. Sæther (2000) provides an overview of different generalised zoogeographical patterns in chironomids based to a large extent on phylogenetic analyses of several recently revised genera.

According to Banarescu (1990, 1991, 1995), the generally accepted zoogeographical regions do not fit well for the freshwater fauna. For instance, the

Yangtse River in China, dividing the Palaearctic and Oriental Regions, obviously is not a good barrier for aquatic organisms. The writers here follow the divisions of Banarescu in, for example, regarding East Asia as part of a Sino-Indian Region rather than of a Palaearctic Region, and dividing the Sino-Indian Region in the subregions East Asia, High Asia and South Asia with West Asia as an intermediary area between the Euro-Mediterranean, Sino-Indian and Afrotropical Regions.

Prior to 1995 geographic coevolutionary analyses and studies in vicariance biogeography were rare in chironomids. Although the distribution of the species in many genera is quite well known, specific phylogenies are limited, and when they do exist, they have not been subjected to zoogeographical analyses. The best evidence, perhaps because it is the clearest and most easily obtained, are the increasingly well understood austral vicariant patterns shown by the chironomids of the southern continents. This pattern has been recognised primarily from systematic studies concerning the smaller subfamilies Podonominae, Aphroteniinae and the tribe Heptagyini of the Diamesinae (Brundin 1966; Cranston & Edward 1992, 1998; Cranston *et al.* 1987). Recently however, Cranston & Edward (1999) analysed a new genus of the large subfamily Orthocladiinae, *Botryocladius*, from Australia and Patagonia and showed that there is a multiple sister species relationship between the species occurring on the different continents. Other chironomid genera unique to the Andean/Patagonian region and Australia and/or New Zealand include *Austrocladius* Freeman, 1961, *Stictocladius* Edwards, 1931, *Megacentron* Freeman, 1961, and *Riethia* Kieffer, 1917, but species-groups within several more widely distributed basal genera will most certainly exhibit the austral pattern.

Sæther (2000) provides an overview of the different general distribution patterns or tracks (concurrent patterns) obtained by geographic coevolutionary analyses using Brooks' Parsimony Analysis (BPA) (Brooks 1990) on different chironomid genera or subgenera (Figure 1). The tracks may in some cases extend further and be interconnected and there are certainly additional patterns not included, such as the vicariance pattern for *Propsilocerus* Kieffer, 1923, which apparently split into two species pairs during the last Ice Age, one in southeastern Europe and northeastern Asia, and one in extreme northeastern Europe and southern China (Sæther & Wang 1996).

Recently, faunal linkages between more tropical areas north of the Equator involving eurythermic and warm-stenothermic chironomids have begun to appear. Most of the chironomid area cladograms analysed show evidence of a linkage between tropical Africa and the South and East Asia subregions of the Sino-Indian Region (Adam & Sæther 1999; Oyewo & Sæther 1998; Sæther & Sundal 1999; Sæther & Wang 1995; Vårdal *et al.* 2002), and several phylogenetically based biogeographic analyses of other taxa show a clear relationship between Africa and the Indo-Pacific and/or Australia (e.g. Coscarôn & Morrone 1995; Schuh 1991; Schuh & Stonedahl 1986 for Heteroptera; Lansbury 1981 for Hemiptera; and Grehan 1991 for Lepidoptera). This pattern is apparently part of a northern Gondwanian or Inabrezian (tropical fragment of Gondwana) distribution which can be divided in an afrotropical - South American pattern often extending into the Caribbean and/or Central America and further to North America, and an afrotropical - South Asia pattern which often extends to East Asia and/or Australia and may be connected with the Beringian track (Sæther 2000). The afrotropical - South-east Asian - Australian pattern is in accordance with Burton (1970) and Ridd (1971) who, based on stratiographic and plant fossil evidence, claimed that eastern South Asia initially belonged to Gondwanaland, where it was placed in between the Indian and Australian plates. Thus, although the eastern Inabrezian distribution pattern in some cases is probably due to later dispersal over the Middle East, it is also likely to be caused by vicariance. Several examples from other aquatic groups (Bǎnǎrescu 1990, 1991, 1995; Croizat 1958) indicate that the vicariance pattern between tropical South America and Africa precedes that between Africa and South Asia. According to the current theory, the opposite should have been the case since India, and supposedly eastern South Asia, separated from Africa earlier than the
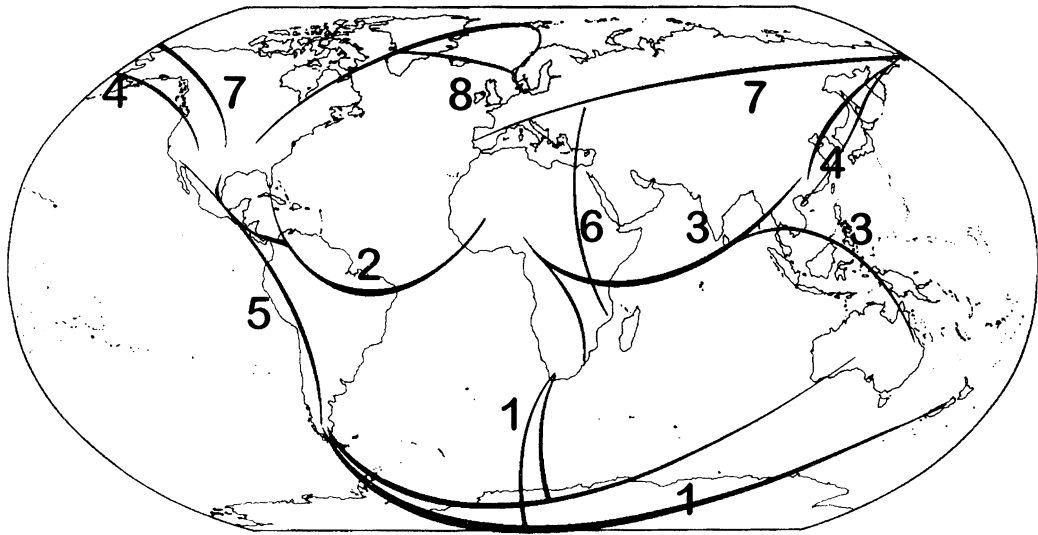
Figure **1**. Generalised tracks of chironomid distribution worldwide (after Sæther 2000).

final separation between South America and Africa. However, India and associated landmasses apparently have been close to the African continent when drifting northward, allowing for dispersal from Africa to the drifting continents.

Several primarily holarctic groups have apparently dispersed along the mountain chains in eastern Africa (Sæther 2000).

BIOGEOGRAPHY

AFROTROPICAL DISTRIBUTION PATTERNS

Here the writers focus on the distribution, phylogeny and geographic coevolution of afrotropical genera and species. There are 28 endemic afrotropical genera or subgenera (Table 1). Most of these genera are, however, monotypic or contain very few species and some are in need of redescription. *Harrisonina* Freeman, 1956, known from South Africa with the single included species *Harrisonina petricola* Freeman, 1956, according to Brundin (1966) forms a tribe of its own: Harrisonini. This tribe forms the plesiomorphic sister group of the holarctic tribes Diamesini and Protanypodini combined, suggesting a vicariance pattern between

Laurasia and Gondwanaland. There are few character states, however, that suggest that the genus truly belongs in the Diamesinae. The writers regard a placement among the more plesiomorphic Orthocladiinae, perhaps close to *Chasmatonotus* Loew, 1864, known from Japan and North America, to be the more likely.

TRANSANTARCTIC DISTRIBUTIONS

Only three genera, the aphrotenine *Aphrotenia* Brundin, 1966, and the podonomines *Archaeochlus* Brundin, 1966, and *Afrochlus* Freeman, 1964, are part of typical transantarctic Gondwanan patterns (Figure 1, track 1), but involving only Australia and South Africa (Cranston & Edward 1992, 1998; Cranston *et al.* 1987). These intergeneric South African/Australian disjunctions date from at least the Jurassic Period. The distribution and historical biogeography of *Aphrotenia* and the Aphroteniinae is discussed by Cranston & Edward (1992). Kalugina (1980) described an amber fossil, *Electrotaenia brundini*, from the Upper Cretaceous in Siberia, which clearly belongs to the Aphroteniinae.

Brundin (1966) together with Cranston & Edward (1998) regarded the monotypic *Afrochlus* Freeman, 1964, as sister to the South African-Australian ge-

Table 1. Known distribution of non-cosmopolitan afrotropical chironomid genera. Abbreviations: **AF** = afrotropical, **WP** = west palaearctic (Euro-Mediterranean region); **WA** = West Asia; **SA** = South Asia; **EA** = East Asia; **IP** = Indo-Pacific; **NZ** = New Zealand; **AU** = Australia; **NEO** = neotropical; **NEA** = nearctic.

	AF	WP	WA	SA	EA	IP	NZ	AU	NEO	NEA
Aphroteniinae										
Aphrotenia Brundin	x							x		
Podonominae										
Afrochlus Freeman	x									
Archaeochlus Brundin	x							x		
Tanypodinae										
Cantopelopia Roback	x									x
Chrysopelopia Harrison	x									
Djalmabatista Fittkau	x				x			x	x	x
Kamelopelopia Harrison	x									
Lepidopelopia Harrison	x									
Usambaromyiinae										
Usambaromyia Andersen & Sæther	x									
Diamesinae										
Harrisonina Freeman	x									
Orthocladiinae										
Allocladius Kieffer	x									
Colosmittia Andersen & Sæther	x									
Doithrix Sæther & Sublette	x				x					x
Freemaniella Sæther	x									
Ionthosmittia Sæther & Andersen	x				x					
Knepperia Kieffer	x									
Lerheimia Andersen & Sæther	x									
Lobosmittia Sæther & Andersen	x		x							
Notocladius Harrison	x									
Paradoxocladius Harrison	x									
Semiocladius Sublette & Wirth (New to Africa = Seychelles)	x				x	x	x	x		
Tokyobrillia Kobayashi & Sasa	x				x					
Chironominae										
Acinoretracus Epler, Harrison & Hare	x									
Collartomyia Goetghebuer	x									
Conochironomus Freeman	x							x		
Friederia Sæther & Andersen	x									
Henrardia Goetghebuer	x									
Kribiocosmus Kieffer	x									
Kribiodosis Kieffer	x									
Kribiomyia Kieffer	x									
Kribiothauma Kieffer	x									
Lepidopodus Freeman	x									
Lunditendipes Harrison	x									
Manoa Fittkau	x								x	x
Nilodorum Kieffer	x		x	x	x			x		
Nilodosis Kieffer	x									
Polypedilum (*Cerobregma* Sæther & Sundal)	x	x		x	x				x	
Seppia Ekrem & Sæther	x									
Skusella Freeman	x									
Virgatanytarsus Pinder	x	x	x							
Xestotendipes Harrison (prob. African larval form of *Stenochironomus*)	x									
Zuluchironomus Harrison	x									

nus *Archaeochlus* Brundin, 1966. Molecular evidence (*vide* Cranston *et al.* 2000) indicates, however, that the Australian clade of three species of *Archaeochlus* is monophyletic, forming the sister clade to the *Archaeochlus* from southern Africa, which includes the monotypic genus *Afrochlus*. Re-examination of the morphology in the light of this hypothesis demonstrates that Cranston & Edward (1998) overlooked a structure of the male genitalia, evidently synapomorphic, involving an attenuation of segment IX, and an associated shortening of the transverse sternapodeme in the African taxa, including *Afrochlus*. This feature overturns the previous morphological support for *Archaeochlus* monophyly, and confirms the molecular-based relationship (Cranston *et al.* 2000).

INABREZIAN DISTRIBUTIONS

Several genera, subgenera and species-groups exhibit a warm-eurythermic Gondwanan distribution or what Bànàrescu terms 'Inabrezian' distribution (Figure 1, tracks 2+3). Some of the genera have extended their distribution to Australia and/or Japan and some occur in North America. Sæther & Wang (1992) described *Tokyobrillia anderseni* from Tanzania, which is clearly the sister species of *Tokyobrillia tamamegaseta* Kobayashi & Sasa, 1991, from Japan and China. The monotypic genera *Pseudobrillia* Niitsuma, 1991, known from Japan and China, and *Irisobrillia* Oliver, 1985, known from St. Vincent in the Caribbean and from Venezuela are most likely the closest related genera of *Tokyobrillia* Kobayashi & Sasa, 1991.

Sæther & Andersen (1996) described two new species of the genus *Doithrix* Sæther & Sublette, from Ghana, a genus otherwise known only from North America, Japan and China. They also described two new species of *Georthocladius* Strenzke, 1941, from Ghana, both with their apparent sister species in Japan.

The Pseudochironomini genus *Manoa* Fittkau, 1963, previously known only from Brazil, also exhibits an extended Inabrezian distribution following the discovery of one species from Tanzania

(Andersen & Sæther 1997) and one from the Everglades in Florida (Jacobsen & Perry 2002).

The genus *Djalmabatista* Fittkau, 1968, has its main distribution in South America. There is one afrotropical species, several nearctic species, and the genus is also present in East Asia and Australia, apparently exhibiting a complete Inabrezian distribution (Figure 1, tracks 2+3). However, the presence in East Asia and Australia could be a result of a Beringian connection (Figure 1, track 4) rather than a northern Gondwanan connection (Figure 1, track 3).

Ionthosmittia Sæther & Andersen (1995) known from Africa and Japan, *Cantopelopia* Roback, 1971, known from Africa and North America and *Doithrix* Sæther & Sublette, 1983, known from North America, Africa and China all exhibit a probable Inabrezian distribution which would be confirmed by finding representatives of these genera in South America.

Cranston & Hare (1995) revised the genus *Conochironomus* Freeman, 1961, which includes three afrotropical and four Australian species with the afrotropical genus *Skusella* Freeman, 1961, as its sister group. It is obvious that there is a close relationship between the Australian and afrotropical (including Madagascan) clades, and if dispersal gave rise to the current generic distribution, *Conochironomus* ought to be found in Saudi Arabia, on the Indian Sub-continent and in Southeast Asia. The genus so far appears to be absent from these intervening landmasses.

The afrotropical genus *Nilodosis* Kieffer, 1921, forms the sister group of *Fissimentum* Cranston & Nolte, 1996, from South America and Australia (Cranston & Nolte 1996; Cranston & Spies 1999). *Fissimentum* is also recently recorded from Japan and North America. The Australian genus *Imparipecten* Freeman, 1961, forms the sister group of the pair, and all genera are closely related to the above-mentioned *Conochironomus* and *Skusella*. This group of genera obviously again demonstrate an Inabrezian distribution, and contributes to the formation of tracks 2+3 in Figure 1.
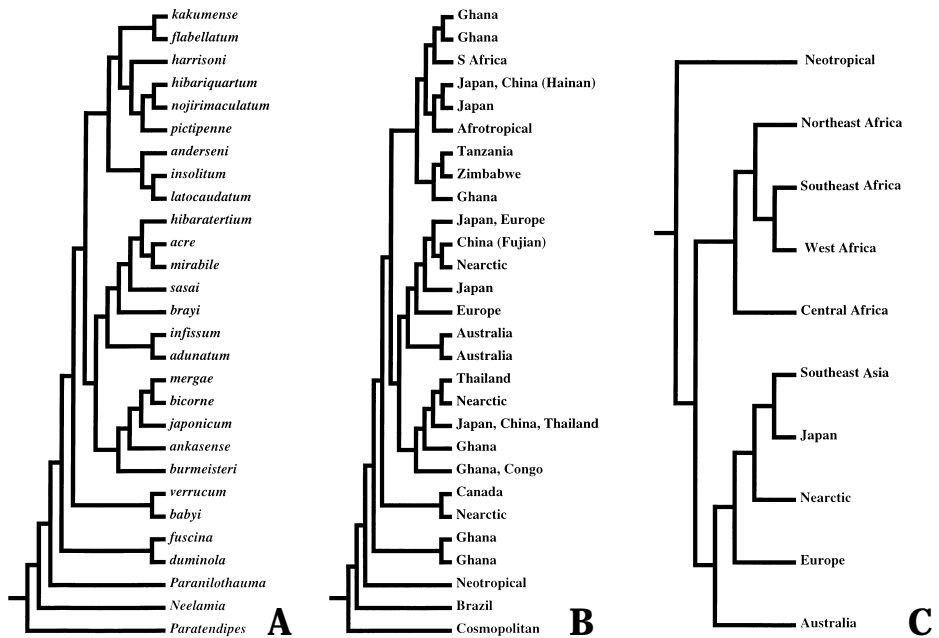
Figure **2**. Cladograms of the chironomid genus *Nilothauma* Kieffer. **A** = preferred manual tree, **B** = area cladogram, **C** = results from Brooks' parsimony analysis.
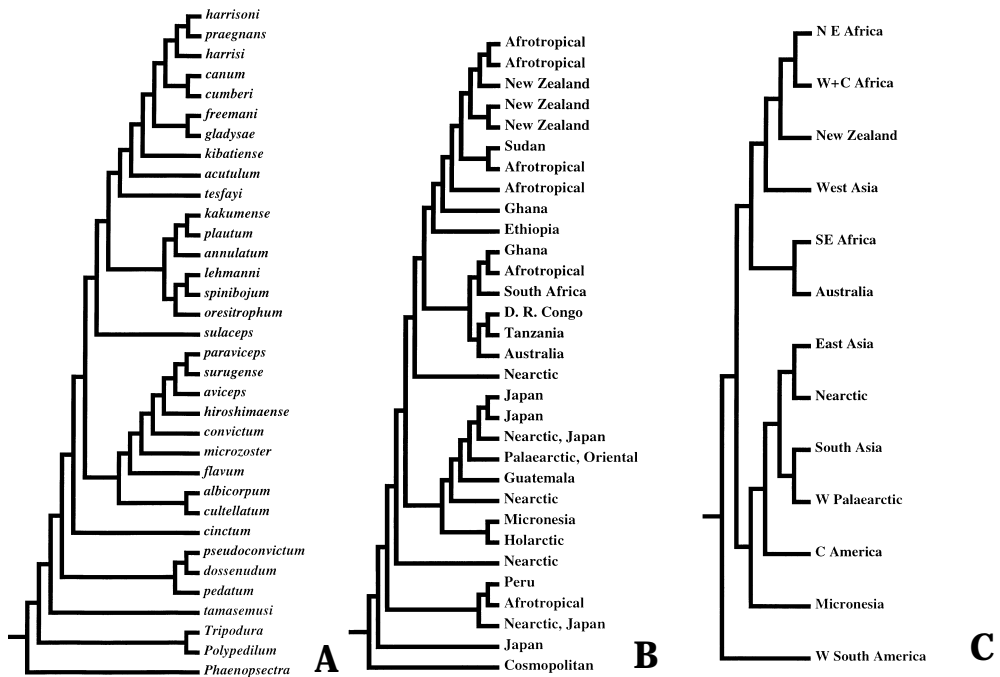

Figure **3**. Cladograms of the chironomid genus *Polypedilum* subgenus *Uresipedilum* Oyewo & Sæther. **A** = preferred manual tree, **B** = area cladogram, **C** = results from Brooks' Parsimony Analysis.

RECENT ZOOGEOGRAPHICAL ANALYSES

The above records concern relatively few species, while studies showing multiple sister group relationships between tropical South America, Africa and South Asia have been found in larger revisions of *Nilothauma* Kieffer, 1921, *Rheotanytarsus* Thienemann & Bause, 1913, *Polypedilum* Kieffer, 1912, and *Tanytarsus* v. d. Wulp, 1874. These studies, also demonstrate the difficulties inherent in performing geographic coevolutionary studies on genera with a global distribution. Several patterns are present simultaneously, leading to reciprocal obscurity. Both synapomorphic diagrams or cladograms and BPA area cladograms are hierarchical, while several geographical relationships can be better demonstrated with a reticulate diagram.

In the *Nilothauma* revision (Adam & Sæther 1999) the preferred manual tree (Figure 2A) differed only slightly from the various most parsimonious cladograms obtained. Note that *Neelamia* Soponis, 1986, and *Paranilothauma* Soponis, 1986, are both neotropical genera, while *N. duminola* Adam & Sæther, 1999, and *N. fuscina* Adam & Sæther, 1999, are both from West Africa and *N. babiyi* (Rempel, 1937) and *N. verrucum* Adam & Sæther, 1999, are nearctic (Figure 2B). The most parsimonious reduced area cladogram from the BPA analysis (Figure 2C) does not have the Nearctic Region near the base, but shows the Beringian connection (Figure 1, track 4). This is caused by several nearctic species placed higher in the synapomorphy diagram. *Nilothauma babiyi* and *N. verrucum* are probably Gondwanan elements exhibiting the Inabrezian track, while the remaining nearctic species show the Beringian connection. Although no neotropical *Nilothauma* were included in the revision, Adam & Sæther (1999) postulated that they should be present in the region, but only from more plesiomorphic groups with one, not two projections on the anal tergite. The genus has been found in South America, but the species are presently undescribed.

The basal subgenus *Uresipedilum* Oyewo & Sæther (1998) of *Polypedilum* appear to exhibit a trans-antarctic Gondwanan vicariance between South Africa and Australia, and possibly between New Zealand and Africa (Figure 3). This may be an artefact, as the relationship is between New Zealand and northeast plus west and central Africa, and West Asia is in the same group. It appears more likely that this is a pattern of dispersal from South Asia and Micronesia. The two known neotropical species, from Guatemala and Peru, appear to be part of a Beringian track continuing into a Cordilleran track (Figure 1, tracks 4+5) although nearctic records are lacking.

In the paper on *Polypedilum* subgenus *Cerobregma,* Sæther & Sundal (1999) combine parsimony analyses with a zoogeographical analysis (Figure 4A). The area cladogram resulting from the BPA is shown in Figure 4C. The subgenus displays a northern Gondwanan or Inabrezian distribution with a secondary East Asian- nearctic vicariance.

Vårdal *et al.* (2002) include a phylogeny and a geographic coevolutionary analysis of the 135 species within the *Polypedilum* subgenus *Tripodura* Townes, 1945, in their revision of the 30 afrotropical species. BPA of the subgenus as a whole and of the major groups were performed and the areas most likely to be part of the original areas were estimated. Eastern South America and Africa were most likely part of the ancestral area. There are multiple sister group relationships and generalised tracks between South and East Asia and Africa, between Africa and the Palaearctic Region, between South and East Asia, between tropical Brazil and Africa, between East Asia and North America across a former Beringian land bridge, and between the Indo-west Pacific Region and New Zealand, but no evidence for transantarctic relationships (Figure 5). For the full genus (Figure 5A) as well as for the *acifer*- (Figure 5B), *halterale-* (Figure 5D) and *pullum*-groups, the relationships with the west palaearctic and West Asia are the predominant. In the *aferum*-group (Figure 5C) the connection between West Africa and Brazil is clear.

The preferred tree for the genus *Rheotanytarsus* (Sæther & Kyerematen, 2001) was also analysed using constraints based on pupal types and species pairs. The results of the BPA of the genus as a whole (Figure 6A) show both the Brazil – Africa pattern and that the presence in Central America as well as in western South America are extensions
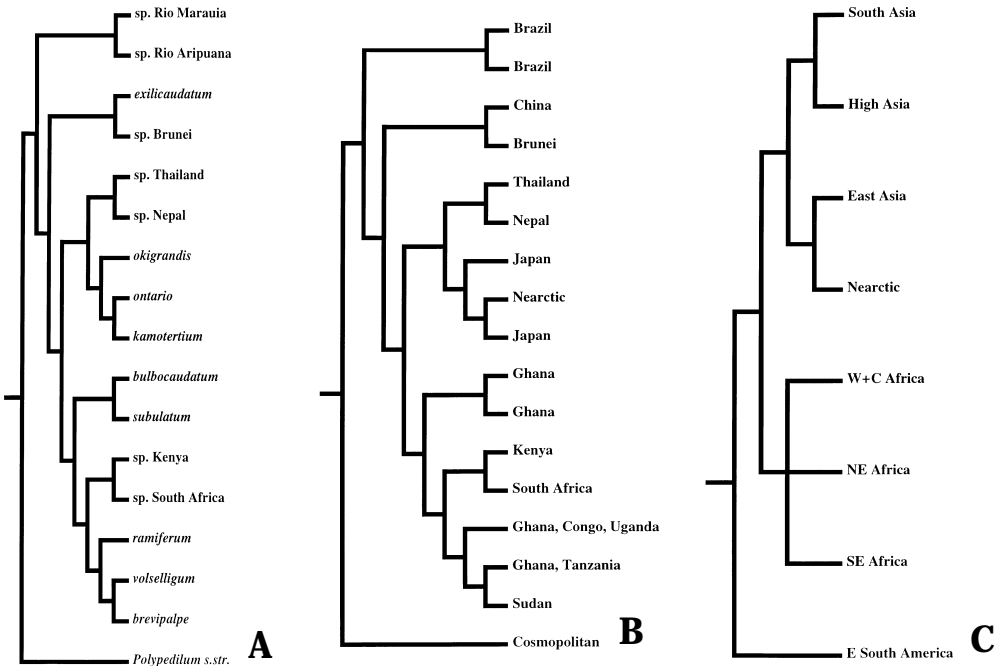
Figure **4**. Cladograms of the chironomid genus *Polypedilum* subgenus *Cerobregma* Sæther & Sundal. **A** = preferred manual tree, **B** = area cladogram, **C** = results from Brooks' Parsimony Analysis.
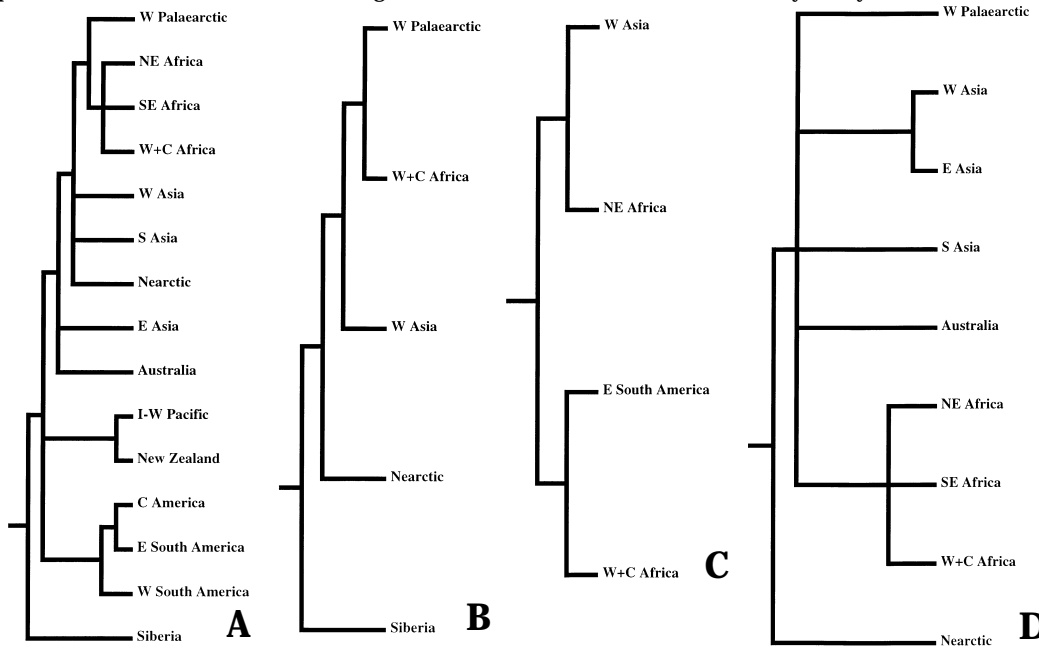

Figure **5**. Results from Brooks' Parsimony Analysis of the chironomid genus *Polypedilum* subgenus *Tripodura* Townes. **A** = Adams consensus tree of the 16 trees obtained for the full subgenus, **B** = the single tree obtained for the *acifer*-group, **C** = the single tree obtained for the *aferum*-group, **D** = consensus tree of the four trees obtained for the *halterale*-group

of the Beringian pattern. Examination of the area cladogram indicate that the position of the west palaearctic in the BPA cladogram is due to secondary dispersal as most of the 14 species also occur outside Europe, including three species in the Afrotropical Region and five in North Africa and/ or West Asia. The position of Australia in this cladogram would have been expected to be closer to South Asia. Apparently, however, South Asian *Rheotanytarsus* species have more connections with East Asian than with Australian species, and the East Asian *Rheotanytarsus* fauna shows greater affinities with the American than with the Australian taxa. The Inabrezian pattern in the *acerbus*-group (Figure 6B) appear relatively clear. In the large *guineensis*-group (Figure 6C) the patterns both with west palaearctic and with Brazil is clear. In the *trivittatus*-group (Figure 6D) there is a tropical vicariance pattern between Africa and South Asia/ Australia. It is not clear whether the connection with the other species, all from Central America, are from South America to Africa or possibly a direct trans-Pacific track between Central America and South Asia/Australia. The *trivittatus*-group is apparently the only group of the genus containing members living in stagnant water, often with high salinity, and it is not unlikely that they may occur in the inter-tidal zone. A further indication of the direct trans-Pacific relationship is the presence of species on Okinawa and the Nansei Islands.

A collection of Chironomidae from the Seychelles substantiates the direct trans-Indian Ocean pattern. The dominant species includes *Semiocladius brevicornis* (Tokunaga, 1964), previously known only from Micronesia (Caroline Is.); *Clunio* sp. nov. near *C. tuthilli* Tokunaga, 1964, known from Marshall Is., Micronesia; *Pseudosmittia triangula* (Tokunaga, 1964) known from Caroline and Marshall Islands; and *Tanytarsus esakii* Tokunaga, 1940, of the '*maritimus*'-group, previously known from the Caroline and Marshall Islands. In addition, the genus *Pseudosmittia* Goetghebuer, 1932, contains a large monophyletic group of inter-tidal species, extending from the coast of East Africa across the Indian Ocean and the Pacific to the Caribbean (L.C. Ferrington & O.A. Sæther unpub.).

T. Ekrem (2003) undertook a phylogenetic analysis of the species of *Tanytarsus* v. d. Wulp, 1874, previously placed in the *eminulus, gregarius, lugens* and *mendax* species-groups. This analyses resulted in the suggested erection of an additional group, the *mcmillani*-group, forming the basal sister group of the other groups combined. The species of this group occur in Africa, South Asia, New Zealand and Australia and most likely indicate an eastern Gondwanan pattern, or perhaps a northern Gondwanan pattern with dispersal to New Zealand and Australia.

PALAEARCTIC CONNECTIONS

Brundin (1966) regarded the East African mountains as an important dispersal route for chironomids from southern centres of origin to the Northern Hemisphere. According to Serra-Tosio (1972) this route was probably the principal manner in which ancestral Diamesini reached Europe and North America, with the relict East African *Diamesa* Meigen, 1835, providing evidence for the southern origin of the tribe Diamesini. Kalugina (1976) showed, however, the presence of Diamesinae in the upper Cretaceous of the Taymir area of northern Russia, thus refuting this timing of the colonisation of Europe. Willassen & Cranston (1986) indicate that the three species found in the East African mountains belong to a relatively plesiomorphic lineage with sister species occurring in the Himalayas, the Caucasian mountains and the Alps. As argued by Willassen & Cranston, the ancestors of the African *Diamesa* were probably cold-stenotherms like modern species. The spread of ancestral *Diamesa* into Africa depended on contact between Laurasia and the Afro-Arabian continent and the presence of a cold, montane route between the ancestral area and the present locations of East African *Diamesa*. According to plate tectonic models, the Tethys Ocean provided a broad barrier to faunal exchange between the Afro-Arabian continent and Laurasia. The disruption of the Tethys by collision of the Arabian plate with Asia probably occurred more than once during the last 65 million years but, in contrast with earlier land connections through global falls in sea levels, the final Miocene closure (about 16-18 million years ago) was caused by a

Table 2. European chironomid species occurring in the Afrotropical Region. Distribution in other regions is provided in parenthesis.

Bryophaenocladius brincki (Freeman) (West Asia)
Chaetocladius melaleucus (Meigen) (West Asia)
Cricotopus (*C.*) *bicinctus* (Meigen) (cosmopolitan)
Limnophyes minimus (Meigen) (cosmopolitan except Australia)
Limnophyes natalensis (Kieffer) (holarctic, South Asia)
Paratrichocladius micans (Kieffer) (North Africa, West Asia)
Pseudosmittia danconai (Marcuzzi) (West Asia)
Pseudosmittia subtrilobata (Freeman) (Italy only)
Chironomus calipterus Kieffer (palaearctic, West Asia, South Asia)
Dicrotendipes fusconotatus (Kieffer) (Spain, North Africa, West Asia)
Dicrotendipes pilosimanus (Kieffer) (Greece, North Africa, West Asia, South Asia, Australia)
Dicrotendipes septemmaculatus (Becker) (palaearctic, East Asia, South Asia, Australian)
Harnischia curtilamellata (Malloch) (cosmopolitan except neotropics)
Microchironomus deribae (Freeman) (palaearctic including North Africa, West Asia)
Microchironomus tener (Kieffer) (palaearctic, West Asia, South Asia, East Asia, Australian)
Paralauterborniella nigrohalteralis (Malloch) (cosmopolitan except Australia)
Polypedilum (*Polypedilum*) *albosignatum* Kieffer (doubtful record from Germany)
Polypedilum (*Tripodura*) *aegyptium* Kieffer (Europe, North Africa, West Asia, South Asia)
Rheotanytarsus montanus Lehmann (Italy only)
Tanytarsus formosanus Kieffer (palaearctic, East Asia, South Asia, Australian)
Zavreliella marmorata (v. d. Wulp) (cosmopolitan except neotropics)

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general elevation of the region (Adams *et al.* 1983; Willassen & Cranston 1986). Most recent Holocene climatic conditions might not have been suitable for the range extension of cold stenotherms, but past conditions were certainly more favourable. The Semian Mountains of Ethiopia, Mount Elgon and the Aberdares all had glaciers in the Pleistocene, and the glaciers of Mount Kenya, Kilimanjaro and the Ruwenzori were more extensive (Hamilton 1982). Thus, at latest during the Pleistocene, cold stenothermic insects could extend their range.

Although most of the chironomid genera occurring in the Afrotropical Region are shared with Europe only 21 species are currently known to be in common (Table 2). This is nearly as low a number as the number of species shared between Europe and the Neotropical Region (20 species) or between Europe and Australia (12 species). In contrast North America has 344 species in common with Europe, North Africa 275 species and West Asia 319 species.

The larvae of the genus *Paraphaenocladius* Thienemann, 1924, occur in semi-terrestrial or semi-aquatic habitats, but are also truly aquatic in springs, streams, ponds and lakes (Sæther & Wang 1995). Three species are known from Africa: *P. auneipennis* (Freeman, 1961) from Madagascar, *P. crassicaudatus* Sæther & Wang, 1995 from Tanzania, and *P. dewulfi* (Goetghebuer, 1936) widespread in Africa and also present in Saudi Arabia. The distributions of other species are nearly exclusively holarctic (including East Asia), but one species is known only from India and two species have subspecies with apparent recent dispersals to Central America and to India respectively. The South Asian and the Central American regions in the BPA cladogram (Figure 7) can thus be regarded as expansions of a holarctic distribution pattern (Figure 1, tracks 7+8) and the distribution may follow the pattern of *Diamesa* (Figure 1, track 6). An early dispersal could, however, equally well have been from the Afrotropical Region to Laurasia. The afrotropical species does not form a monophyletic group, but this could be an artefact, which may dissipate when immatures become known.
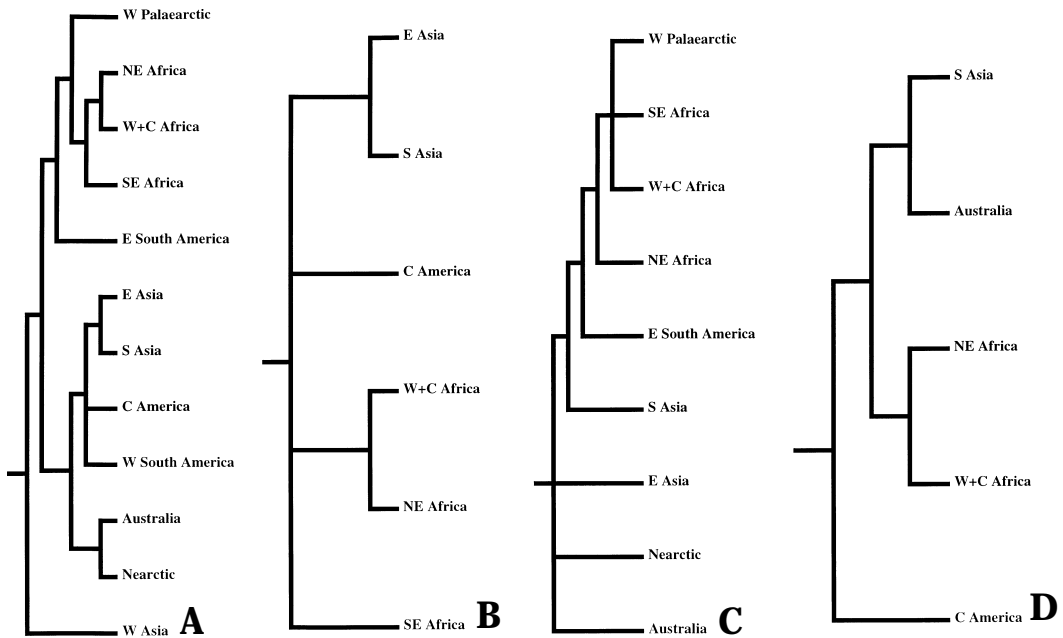
Figure **6**. Results from Brooks' Parsimony Analysis of the chironomid genus *Rheotanytarsus* Thienemann & Bause. **A** = strict consensus tree of the four trees obtained for the genus as a whole, **B** = strict consensus tree of the two trees obtained for the *acerbus*-group, **C** = strict consensus tree of the eight trees obtained for the *guineensis*-group, **D** = the single tree obtained for the *trivittatus*-group.
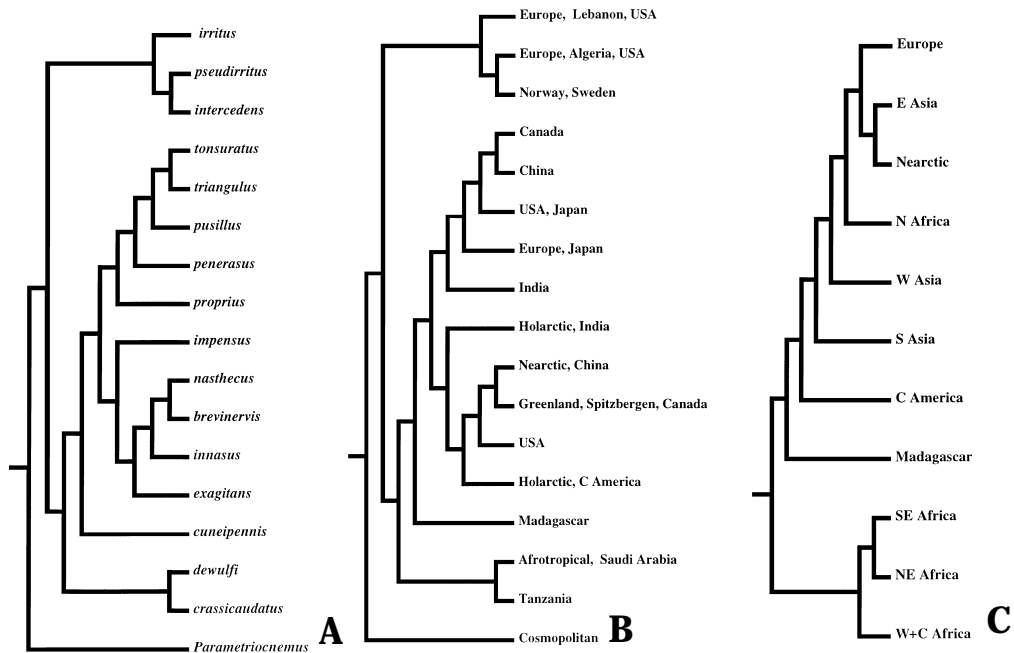

Figure **7**. Cladograms of the chironomid genus *Paraphaenocladius* Thienemann. **A** = preferred manual tree, **B** = area cladogram, **C** = results from Brooks' Parsimony Analysis.

DISTRIBUTION WITHIN THE AFRO-TROPICAL REGION

Many zoogeographers recognise a Malagasy Region encompassing Madagascar and some neighbouring archipelagos: the Comoros, the Mascarenes (Réunion, Mauritius and Rodriguez) and even the much smaller and more eastern Seychelles. Only one species, *Cricotopus rodriguensis* Edwards, 1923, is known from Rodriguez. This species is limited to Rodriguez and Réunion. Réunion has records of five additional species, two of which are restricted to the Malagasy Region. More than half of the approximate 25 species recorded from the Seychelles are limited to the Malagasy Region, while less than one fifth of the approximate 45 species recorded from Madagascar are known only from the region (Freeman & Cranston 1980). The monotypic genus *Lepidopodus* Freeman, 1958, is limited to the Seychelles. It is likely, however, that some of the apparent endemic species may have a wider distribution. Particularly the species from the Seychelles could be part of the trans-Indian Ocean distribution mentioned above.

The chironomids of islands of the South Atlantic Ocean are poorly known. One exception is Gough Island, where the so-called 'Gough Island Terrestrial Invertebrate Survey' (GITIS) project led by A. G. Jones, University of Sheffield, United Kingdom, has extensively deployed Malaise traps. The total chironomid fauna consists of five species. Two of these are fully marine, a new species of *Telmatogeton* close to *T. sanctipauli* Schiner, 1866, and *Clunio africanus* Hesse, 1937. The three remaining species consist of a parthenogenetic population of *Limnophyes minimus* (Meigen, 1818) (a species with facultative parthenogenetic populations where all populations on the sub-Antarctic islands of Kerguelen, Marion Island and Prince Edward Island are parthenogenetic); and two new parthenogenetic species of *Bryophaenocladius* Thienemann, 1934 and *Thalassosmittia* Strenzke & Remmert, 1957.

The freshwater fauna of tropical and southern Africa is more homogeneous than that of similarly wide areas such as North America, South America and southern Asia. This fact is due to past and present geographical and climatic conditions. The climate is tropical to subtropical throughout the continent, there are no continuous mountain ranges acting as barriers, and the rich riverine network favours contact between river basins. Africa south of the Sahara has almost always been a single landmass, either as a part of Gondwanaland, fully isolated or attached to Eurasia.

Dejoux (1974) gave an overview of the contemporarily known distribution of the afrotropical chironomid fauna. His conclusions, that the fauna of the Sahelian and sub-Equatorial Regions show great affinity with the fauna of the Sudanese Region, appear confirmed by later findings. That very widespread chironomids are also part of the Nilotic fauna appears correct. Dejoux mentions two distinct high-forest faunas; one in Guinea and the other in the Congo basin, but there appear to be several additional centres of endemism.

The Eastern Arc, a chain of mountains stretching along the coast of Tanzania, is much older than the mountains of Kenya and Ethiopia and these are among the most interesting centres of endemism in Africa (Hamilton 1982; Kingdon 1971). These mountains are more or less connected with minor core areas of endemism in Eastern Transvaal and the Natal Province in South Africa (Hamilton 1989). The mountains are covered with montane evergreen forest, which due to a stable and most favourable coastal climate are considered to be very old. In the above BPA-cladograms these areas combined are named Southeast Africa. These areas are mainly mentioned as hot spots for birds (perhaps partly due to collection efforts). Several interesting chironomids are, however, recorded only from this region. The subfamily Usambaromyiinae with the single included species *Usambaromyia nigrala* Andersen & Sæther (1994a) is named after the Usambara Mountains, the most northerly of the Eastern Arc Mountains, and is not known from other localities. The record of the genus *Manoa* Fittkau, 1963, otherwise known only from Brazil and Florida, constitute the only find of the tribe Pseudochironomini in Africa.

Tokyobrillia anderseni Sæther & Wang, 1992, from Usambara is the only representative of genera near *Brillia* Kieffer, 1913, or *Irisobrillia* Oliver, 1985, and the African representatives of the genera *Lobosmittia* Sæther & Andersen (1993), *Colosmittia* Andersen & Sæther (1994b) and *Ionthosmittia* Sæther & Andersen (1995) are not found outside this area. Amongst the four species known of *Lerheimia* Andersen & Sæther (1993), three are from the Usambara Mountains, the fourth from Democratic Republic of Congo. *Chrysopelopia* Harrison, 1978, is known only from Zimbabwe, *Lepidopelopia* Harrison, 1970, only from Ghana, Democratic Republic of Congo and Tanzania (Harrison 1997b; Sæther & Andersen 2000). Harrison (2000) recently described four new genera, *viz. Lunditendipes*, *Paradoxocladius*, *Xestotendipes*, and *Zuluchironomus* from Zimbabwe and the Eastern Transvaal and Kwazulu-Natal, South Africa, the southern end of this area of endemism. The second of these genera was also found in the Western Cape Province, South Africa, an additional area of endemism.

The East African highlands of Ethiopia and Kenya consist of much younger mountains (Kingdon 1971). The development of the African Rift system and its associated mountain upheavals in the late Oligocene and Miocene down to the Quaternary, resulted in extensive mountain building, with altitudes over 3 000 to 4 000 m and with a number of glaciated regions. This allowed colonisation by true cold stenotherms, but there is no evidence that the original African fauna contributed to any of this (Harrison & Hynes 1988). The monotypic *Freemaniella* Sæther (1976) was originally described from Kenya, but has also been recorded from Senegal. Several species are recorded from these highlands only and could be endemic. They belong to widespread genera, however, and their apparent limited distribution may be due to lack of sampling effort.

The Western Cape Province of South Africa is the core area for chironomids with a transantarctic Gondwanan pattern. The Aphroteniinae and Podonominae, treated above, are also found in Lesotho, Namibia and Zimbabwe. *Harrisonina* Freeman, 1956, is known from the Eastern Cape

Province, South Africa to Zimbabwe, and probably belongs to this area rather than to the Eastern Arc centres. The monotypic *Notocladius* Harrison (1997a) is so far recorded only from the Table Mountain Sandstone system of the Western Cape Province. The insufficiently known monotypic *Knepperia* Kieffer, 1908, is only known from Namibia and if a valid genus, it may be part of the same area of endemism. The only afrotropical species of *Apsectrotanypus* Fittkau, 1962, and of *Macropelopia* Thienemann, 1916, are recorded from the Western Cape Province (Harrison 1997b). No species of these genera are found in South America, but both are represented with one species each in Australia. This could represent a hitherto overlooked transantarctic connection. A few other species are restricted to the Western Cape Province: *Dicrotendipes penicillatus* Freeman, 1957, *Micropsectra capicola* Freeman, 1955 (the only afrotropical representative of the genus), *Parametriocnemus capensis* (Freeman, 1954), *Polypedilum* (*Polypedilum*) *lobiferum* Freeman, 1954, *Pseudosmittia capicola* (Freeman, 1953), *Smittia capensis* (Kieffer, 1914) and *Synorthocladius conicus* (Freeman, 1953).

The Congo basin refuge contains more than 50 species recorded only from this area, most of them described by Lehmann (1979, 1981), but there are apparently no endemic genera.

In western Africa two main centres of endemism representing forest refuges are usually identified, one in Sierra Leone and one in Cameroon-Gabon (Mayr & O'Hara 1986). Hugueny & Lèvêque (1994) identified a third forest refuge covering the southeast Ivory Coast and southwestern Ghana, recognised as the Eburneo-Ghanean Region. The few species recorded from Sierra Leone all have wide distributions or occur also in other western refuges. The endemic afrotropical genera *Kribiomyia* Kieffer, 1921 and *Kribioxenus* Kieffer, 1921, as well as the doubtful genera *Kribiobius* Kieffer, 1921 and *Kribiopelma* Kieffer, 1921, are up till now only recorded from the Cameroon-Gabon refuge. Nearly 20 additional species, all described by Kieffer and in need of re-examination, are only known from Cameroon. Several additional species are known from Democratic Republic of Congo and Gabon.

Polypedilum (*Tripodura*) *ogoouense* Bjørlo, 2002 and *Polypedilum* (*Tripodura*) *patulum* Bjørlo, 2002 (Vårdal *et al.* 2002) are known only from Gabon. Two tanytarsine genera recorded only from Ghana, *Friederia* Sæther & Andersen (1998) and *Seppia* Ekrem & Sæther (1997), are both from south-western Ghana, and thus part of the Eburneo-Ghanean Region. Seven species of *Rheotanytarsus*, six of *Nilothauma*, five of *Polypedilum* (*Tripodura*), two of *Polypedilum* (*Cerobregma*), two species of *Polypedilum* (*Uresipedilum*) and one of *Tanytarsus* are known only from Ghana (Adam & Sæther 1999; Ekrem 2001; Kyerematen & Sæther 2000; Oyewo & Sæther 1998, Sæther & Kyerematen 2001; Sæther & Sundal 1999; Vårdal *et al.* 2002). Several of these species, however, are likely to have a wider distribution, and amongst the species listed by Amakye (1993) none are restricted to Ghana.

There are apparently clear connections between the different forest refuges in West and central Africa. Some species are recorded from several of these areas; others appear to show a vicariance between areas.

CONCLUSION

Dejoux (1974: figure 8) presented a generalised picture of the known distribution and relationships of afrotropical chironomids. Most of the species belonging to the widespread Nilotic fauna appear, on the one hand, to be relatively well known with comparatively few new species in spite of extensive sampling. This fauna is dominant in large rivers and reservoirs and near heavily populated areas, and the recently described species of this fauna is mostly a result of revisions.

The fauna of the rainforest, on the other hand, is poorly known, and a few days of fieldwork may easily result in more than 70% new species per sample. About 500 species of chironomids are recorded from the Afrotropical Region, much less than the 1 188 species known from Europe. Most of Africa south of the Sahara is, however, in tropical or subtropical regions, with only small areas qualifying as temperate zones. The Afrotropical Region is thus lacking many of the cold-stenothermous genera and species common in Europe. The tropical rainforests, however, have been shown to be very species-rich and are expected to contain numerous undescribed semi-terrestrial and semi-aquatic species.

The relationships between the different chironomid faunal regions in Africa are unclear due to many un-investigated areas. Nevertheless, there appears to be a close relationship between the large forest areas of West Africa and also a connection between these and the Eastern Arc areas of endemism.

Although there are many endemic afrotropical genera, the majority of the species belong to widely distributed, mostly cosmopolitan genera. On the generic level the connection between Africa and other continents appear dominated by the warm-eurythermic Gondwanan or Inabrezian distribution. The transantarctic Gondwanan distribution is exclusively between Australia and Africa. Faunal exchange between the Afro-Arabian continent and Laurasia probably took place during the Miocene (about 16-18 million years ago).

The diversity and distribution of the family Chironomidae makes it well suited for geographic co-evolutionary analyses, and more stable phylogenies in the future will certainly add valuable information to existing hypotheses on zoogeographical patterns.

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