

# The zoogeographical distribution of Chironomidae (Insecta : Diptera)

P. Ashe<sup>1</sup>  
D. A. Murray<sup>2</sup>  
F. Reiss<sup>3</sup>

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A review of present information on the zoogeography of Chironomidae at subfamily and generic levels is given. The known distribution, including some previously unpublished records, of all recognisable genera (307) and subgenera (56) is tabulated according to zoogeographical region. The greatest number of genera is known from the Nearctic (202) followed by the Palaearctic (187), Neotropical (109), Australasian (107), Afrotropical (104) and Oriental (100). 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. An account of the distribution and ecology of each of the ten subfamilies is included. To date, some 3 700 species are described representing only 30 % of the estimated world chironomid fauna. The fossil record of the group is briefly discussed and the Chironomidae are estimated to be at least 200 million years old dating back to the Triassic period.

**Répartition biogéographique des Chironomidés (Insecta : Diptera).**

**Mots clés :** Chironomidés, répartition, biogéographie, écologie, Diptera.

Une révision des connaissances actuelles de la biogéographie mondiale des sous-familles, genres et sous-genres de Chironomidae est présentée. La répartition de 307 genres et 56 sous-genres dans les différentes régions biogéographiques est établie à partir des données de la littérature et de données originales.

La région néarctique compte le plus grand nombre de genres (202), suivie par les régions paléarctique (187), néotropicale (109), australasienne (107), afrotropicale (104) et orientale (100). Le nombre d'espèces connues dans chaque région, leur proportion relative dans les 10 sous-familles, sont comparées ; leur répartition et leur écologie sont examinées.

A ce jour, quelque 3 700 espèces sont décrites ; elles représenteraient seulement 30 % de la faune totale présumée des Chironomidae du monde. Les découvertes fossiles permettent d'estimer la présence des Chironomidés dès la période triasique, il y a au moins 200 millions d'années.

## 1. Introduction

The family Chironomidae is a cosmopolitan group of dipteran insects representatives of which occur in all zoogeographical regions of the world, including Antarctica. There are few areas where the Chironomidae can be regarded as being absent. The

immature stages of most species occur in freshwater but many terrestrial, marine and brackish water species are known.

Most of the early entomologists lived and worked in western Europe and consequently the fauna of the Palaearctic, in particular the western Palaearctic, was most intensively studied. It is not surprising therefore that the chironomid fauna of this region has been most thoroughly studied, followed by the Nearctic, Afrotropical and Australasian regions. The fauna of the Neotropical and Oriental regions is particularly poorly known.

1. Department of Zoology, Trinity College, Dublin 2, Ireland.  
2. Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland.  
3. Zoologische Staatssammlung, Münchenstrasse 21, D-8000 München 60, Federal Republic of Germany.

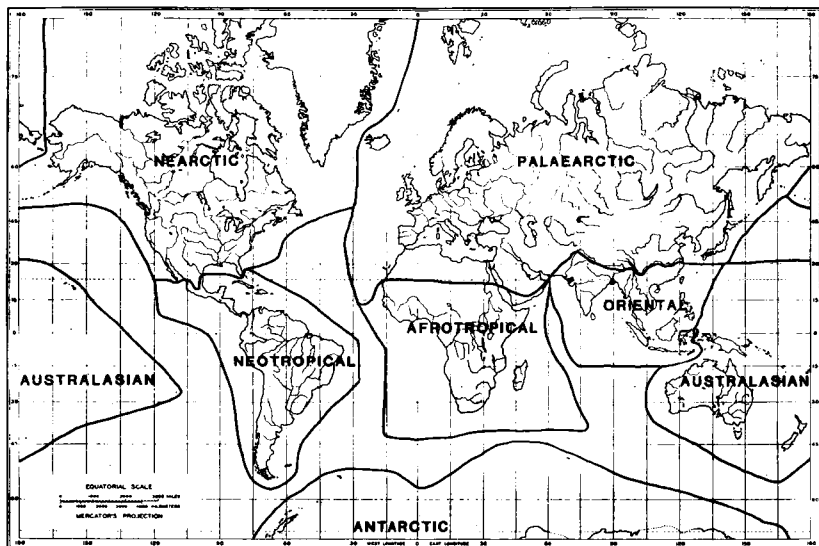


Figure 1: The zoogeographical regions of the world.

Ashe (1983) recognised 355 valid genera within the ten chironomid subfamilies. Some of those genera, though technically valid, are of uncertain status. A few of the valid genera have since been synonymized with other genera and some new genera have been recently described. The 307 genera treated in this work are recognisable genera (i.e. identifiable using recent taxonomic works) excluding those genera which are of doubtful status or those which colleagues have indicated are unpublished synonyms. A total of 56 subgenera are currently recognised. Representatives of six subfamilies, Telmatogetoninae, Tanypodinae, Podonominae, Diamesinae, Orthoclaudiinae and Chironominae, have been recorded from all zoogeographical regions. The remaining four subfamilies appear to have a more restricted distribution. The Chilenomyiinae are known from the

Neotropical region, the Buchonomyiinae from the Palearctic and Oriental, the Aphroteniinae from the Neotropical, Afrotropical and Australasian regions and the Prodiamesinae from the Palearctic, Nearctic, Neotropical and Oriental regions.

There has been no previous attempt to give an account of the global distribution of chironomid genera. In this work the definition of zoogeographical regions in general follows the classical divisions with the main difference being that all continental and oceanic islands are assigned to zoogeographical regions (Fig. 1). The proposed boundary of the Antarctic region has been extended to include some of the subantarctic islands. Further comments on the boundaries between some zoogeographical regions are given later in the text.

## 2. Chironomid fauna of the zoogeographical regions

The known zoogeographical distribution of all currently recognised genera and subgenera is listed (p. 10-18) and a summary of the subfamily generic representation in the zoogeographical zones is given in Table 1.

### 2.1. Palaearctic and Nearctic regions

These two regions, which together constitute the Holarctic, are best considered together because of faunal similarity. There are many monographs and revisions of various genera available, especially on the Palaearctic fauna. Eight of the ten chironomid subfamilies are found in the Holarctic. The two subfamilies which do not occur are the Chilenomyiinae and Aphroteniinae although fossil representatives of the latter have been described from northern U.S.S.R. The most important taxonomic work on identifying the genera of the region is the collaborative work « Chironomidae of the Holarctic Region » edited by Wiederholm (1983 *et seq.*). Volumes dealing with the larvae and pupae are published and one further volume dealing with adult males is in preparation.

In the Palaearctic and Nearctic respectively the subfamily Tanypodinae is represented by 29 and 36 genera with 26 genera common to both regions (Table 1). Genera which occur in the Nearctic not yet recorded from the Palaearctic are: *Alotanypus*, *Brundiniella*, *Cantopelopia*, *Coelotanypus*, *Fittkauimyia*, *Helopelopia*, *Hudsonimyia*, *Meropelopia*, *Pentaneura* and *Radotanyus*. Genera currently unique to the Palaearctic are *Anatopynia*, *Pentaneurella* and *Telmatopelopia*. The majority of these genera may ultimately be found in both regions with the possible exception of *Alotanypus*, *Anatopynia*, *Pentaneura* and *Telmatopelopia*.

Among the smaller subfamilies the representation of genera in the Palaearctic and Nearctic is very similar or identical. The Buchonomyiinae (sole genus: *Buchonomyia*) within the Holarctic is only known from the Palaearctic (Ireland through Middle Europe to Iran). The same five genera of Podonomiinae occur in both regions. Only one additional genus of Diamesinae, *Lappodiamesa*, occurs in the Palaearctic. Representatives of this genus have been found in high northern latitudes and it could be

Table 1: The number of genera of each subfamily recorded from the six zoogeographical regions.

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical
Telmatogtoninae	2	2	2	2	2	2
Chilenomyiinae	0	0	1	0	0	0
Tanypodinae	29	36	15	16	17	19
Buchonomyiinae	1	0	0	0	1	0
Podonomiinae	5	5	5	7	2	2
Aphroteniinae	0	0	2	3	0	1
Diamesinae	11	10	5	3	6	2
Prodiamesinae	3	4	2	0	2	0
Orthoclaadiinae	74	79	34	36	33	31
Chironominae	62	66	43	40	37	47
TOTAL	187	202	109	107	100	104

expected to occur in the arctic-subarctic regions of the Nearctic. Three of the four genera of Prodiamesinae are recorded from the Holarctic but the fourth genus, *Compteromesa*, is only known from the S.E. Nearctic.

The subfamily Orthoclaadiinae is represented in the Holarctic by 91 genera of which 74 are found in the Palaearctic, 79 occur in the Nearctic and 62 genera are common to both. Twelve genera are currently unique to the Palaearctic region: *Boreosmittia*, *Dratnalia*, *Eurycnemus*, *Lappokiefferiella*, *Lindebergia*, *Propsilocerus*, *Semioclaadius*, *Stackelbergina*, *Tavastia*, *Tokunagayusurika*, *Trissocladius* and *Tsudayusurika*. Ten genera are only found in the Nearctic: *Baeocarterus*, *Doithrix*, *Oreadomyia*, *Platysmittia*, *Pluhudsonia*, *Saetheriella*, *Sublettiella*, *Tethymyia*, *Trichochilus* and *Unniella*.

In the Holarctic the Chironominae are represented by 74 genera. The Palaearctic and Nearctic contain 62 and 66 genera respectively of which 54 are common to both regions. Twelve Nearctic genera (*Asheum*, *Beardius*, *Caladomyia*, *Gillotia*, *Goeldichironomus*, *Hyporhygma*, *Nimbocera*, *Oschia*, *Skutzia*, *Stelechomyia*, *Sublettea* and *Xestochironomus*) do

not occur in the Palaearctic and of these *Oschia* and *Stelechomyia* are unique to the Nearctic. Eight Palaearctic genera (*Baetendipes*, *Fleuria*, *Kloosia*, *Lithotanytarsus*, *Neostempellina*, *Nilodorum*, *Thienemanniola* and *Virgatanytarsus*) are not recorded from the Nearctic and five of these, *Fleuria*, *Kloosia*, *Lithotanytarsus*, *Neostempellina* and *Thienemanniola*, are unique to the Palaearctic.

In summary, the close zoogeographical relationships between the Palaearctic and Nearctic regions is reflected in the fact that of the 307 world genera 227 (74%) occur in the Holarctic and 162 of these are common to both regions. There are 40 genera in the Nearctic which are not known from the Palaearctic while the latter region has 25 genera which are not known from the Nearctic - a combined difference of 65 genera (Table 2). This discrepancy seems to give support to the idea of major differences between the two regions. However, a more detailed examination reveals the fact that slightly over half of these genera (33) are currently monotypic and the immature stages of 42 are recently described or unknown while most of the remaining genera contain only 2-6 species (Table 2). Genera with few species are often restricted to very specific habitats and thus less likely to be collected in random sampling. More intensive collecting in the future may redress this situation. Genera currently endemic to the Palaearctic or the Nearctic only and which occur in high northern latitudes can be expected to occur in the other region (e.g. *Pentaneurella*, *Lappodiamesa*); however, those genera confined to southern latitudes within the Palaearctic or Nearctic regions are unlikely to occur in the other region unless those genera also show a much wider distribution beyond adjoining zoogeographical regions. Most of the genera which are found in the southern Nearctic (but not in the Palaearctic) are essentially Neotropical elements which have spread northwards (e.g. *Pentaneura*, *Lopescladius*, *Beardius*, *Caladomyia*, *Goeldichironomus*, *Nimbocera* and *Xestochironomus*) and if they do not occur at least in the Australasian and Oriental regions then they cannot be expected from the Palaearctic. It is probable that some essentially Oriental elements will be discovered in the southern Palaearctic (especially the lowlands of central China) similar to the situation in the southern Nearctic which receives some Neotropical elements. Insufficient data on the distribution of individual genera and species makes it difficult to make statements

regarding some of the genera listed in Table 2 and some are so recently described that it is impossible to predict the distribution of a particular genus. Very few truly endemic genera in either the Palaearctic or the Nearctic are to be expected.

A total of 1285 valid species is known from the Palaearctic (Cranston & Ashe, in press) which possesses the richest described chironomid fauna of any region. The Nearctic has 978 valid species (Table 3). Figures for the Nearctic region have been provided by Cranston (pers. comm.). When the subfamily representation in each region is compared with regard to numbers of species and percentage of the total fauna some major differences in the main subfamilies are apparent (Table 3). These figures represent the stage of taxonomic knowledge of the particular subfamily within the region rather than any real major differences in subfamily representation. The Tanytopodinae possess 139 species in the Nearctic and 116 species in the Palaearctic reflecting the more intensive work done on this subfamily throughout North America in recent years compared with more localised studies in the Palaearctic. In the Orthocladiinae the differences between the two regions are not very significant but the Chironominae with 348 species in the Nearctic is 192 species poorer than the Palaearctic with 540 species. This anomaly can be partly explained by the fact that the Tanytarsini are very under-represented in the Nearctic (Table 4). Very few new species of Tanytarsini have been described in North America over the last two decades pending a revision of the group by Prof. J.E. Sublette and when complete the imbalance between the two regions should be less marked. The lower number of Chironomini in the Nearctic is due to the less active study of the group there. The higher number of Pseudochironomini in the Nearctic reflects the proximity to the Neotropical region where this group is abundant with at least 43 species reported (Fittkau & Reiss 1979).

As the present paper was being written we became aware that a paper on the problems of Holarctic biogeography was at the same time being prepared (Cranston & Oliver, in press). Although different aspects of the Holarctic generic fauna are discussed in varying detail in this paper and in Cranston & Oliver (in press) it is interesting to note that similar or identical conclusions are reached on topics such as monotypic and endemic genera, origin of certain genera, etc. However, the « Antillean

Table 2: Genera within the Holarctic which are currently only known from either the Palaearctic or the Nearctic (numbers in parentheses refers to the number of described species; \* = Palaearctic endemic; + = Nearctic endemic; § = immatures unknown or only recently described, since 1980).

PALAEARCTIC	TANYPODINAE	NEARCTIC
* <i>Anatopynia</i> (1)		<i>Alotanypus</i> (3)
*§ <i>Pentaneurella</i> (1)		+ <i>Brundiniella</i> (1)
* <i>Telmatopelopia</i> (1)		§ <i>Camtopelopia</i> (3)
		<i>Coslotanypus</i> (13)
		<i>Fittkauimyia</i> (2)
		+§ <i>Helopelopia</i> (2)
		+ <i>Hudsonimyia</i> (2)
		+§ <i>Meropelopia</i> (2)
		<i>Pentaneura</i> (4)
		+§ <i>Radotanypus</i> (1)
	BUCHONOMYIINAE	
§ <i>Buchonomyia</i> (2)		
	DIAMESINAE	
*§ <i>Lappodiamesa</i> (1)		
	PRODIAMESINAE	
		+§ <i>Compteromesa</i> (1)
	ORTHOCLADIINAE	
*§ <i>Boreosmittia</i> (2)		§ <i>Antillocladius</i> (3)
*§ <i>Dratnalia</i> (1)		+ <i>Baeoetenus</i> (1)
*§ <i>Eurycnemus</i> (1)		§ <i>Compterossmittia</i> (2)
*§ <i>Lappokiefferiella</i> (1)		§ <i>Diplosmittia</i> (2)
*§ <i>Lindebergia</i> (1)		+§ <i>Doithrix</i> (5)
* <i>Propsilocerus</i> (4)		§ <i>Eretmoptera</i> (2)
§ <i>Semiocladius</i> (2)		§ <i>Lipurometriocnemus</i> (2)
* <i>Stackelbergina</i> (1)		§ <i>Lopescladius</i> (5)
*§ <i>Tavastia</i> (1)		+§ <i>Oreadomyia</i> (1)
* <i>Tokunagayusurika</i> (1)		+§ <i>Platysmittia</i> (2)
*§ <i>Trissoccladius</i> (2)		+§ <i>Pluhdsonia</i> (1)
*§ <i>Tsudayusurika</i> (1)		+§ <i>Saetheriella</i> (1)
		+§ <i>Sublettiella</i> (1)
		+ <i>Tethymyia</i> (1)
		+§ <i>Trichochilus</i> (1)
		+§ <i>Unniella</i> (1)
		§ <i>Xylotopus</i> (2)
	CHIRONOMINAE	
* <i>Baeotendipes</i> (1)		<i>Ashewi</i> (1)
* <i>Fleuriia</i> (1)		§ <i>Beardiis</i> (3)
*§ <i>Kloosia</i> (1)		§ <i>Caladomyia</i> (8)
* <i>Lithotanytarsus</i> (1)		<i>Gillotia</i> (2)
*§ <i>Neostempellina</i> (1)		<i>Goeldichironomus</i> (9)
<i>Nilodorum</i> (6)		§ <i>Hyporhygma</i> (1)
* <i>Thienemanniola</i> (1)		<i>Nimbocera</i> (2)
§ <i>Virgatanytarsus</i> (7)		+§ <i>Oschia</i> (1)
		§ <i>Sletsia</i> (2)
		+§ <i>Stelechomyia</i> (1)
		<i>Sublettea</i> (1)
		§ <i>Xestochironomus</i> (12)

Table 3 : The number of described species and the percentage representation of each subfamily in the six zoogeographical regions (figures given for the Palaearctic, Nearctic and Australasian regions, are based on unpublished manuscripts, and may differ slightly from those which appear in forthcoming published catalogues).

	PALAEARCTIC		NEARCTIC		NEOTROPICAL		AUSTRALASIAN		ORIENTAL		AFROTROPICAL	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<b>Telmatogetoninae</b>	5	0.4	7	0.7	10	2.7	16	4.0	3	0.9	3	0.7
<b>Chilenomyiinae</b>	-	-	-	-	1	0.3	-	-	-	-	-	-
<b>Tanypodinae</b>	116	9.0	139	14.2	51	13.8	43	10.7	67	19.2	65	15.3
<b>Buchonomyiinae</b>	1	0.1	-	-	-	-	-	-	1	0.3	-	-
<b>Podonominae</b>	13	1.0	13	1.3	83	22.5	33	8.2	3	0.9	3	0.7
<b>Aphroteniinae</b>	-	-	-	-	2	0.5	4	1.0	-	-	2	0.4
<b>Diamessinae</b>	99	7.7	55	5.6	12	3.3	8	2.0	15	4.3	4	0.9
<b>Prodiamessinae</b>	11	0.9	10	1.0	1	0.3	-	-	-	-	-	-
<b>Orthocladiinae</b>	500	38.9	406	41.5	86	23.3	109	27.0	78	22.4	111	26.1
<b>Chironominae</b>	540	42.0	348	35.6	123	33.3	190	47.1	181	52.0	238	55.9
<b>TOTAL</b>	1285		978		369		403		348		426	

Table 4 : Comparison of Chironominae species numbers within tribes in the Palaearctic and Nearctic regions.

	Palaearctic	Nearctic
	<b>Chironomini</b>	333
<b>Pseudochironomini</b>	1	13
<b>Tanytarsini</b>	206	74
<b>TOTAL</b>	540	348

element » as discussed by Cranston & Oliver (in press) appears to be a Neotropical component which has migrated northwards (supported by the recent discovery of *Diplosmittia* from mainland South America - see chapter 5) rather than an endemic Nearctic or Antillean component.

The total area of the Palaearctic region (approx. 48 million sq. km.) is over twice that of the Nearctic region (approx. 22 million sq. km.) and on the basis of land area alone the Palaearctic requires twice the effort and resources to obtain the same level of knowledge as in the Nearctic.

## 2.2. Neotropical region

The available monographs on Chironomidae of this region only cover a small part of the total fauna. Edwards (1931) deals with the fauna of Patagonia and South Chile and the species described only represent a small part of the chironomid fauna of this region of South America. However, the generic taxonomy of Edwards (*op. cit.*) is outdated. In his excellent monograph on transantarctic relationships Brundin (1966) deals extensively with the subfamilies Podonominae, Aphroteniinae and Diamessinae (except Diamessini) of this region. Fittkau and Reiss in several publications have dealt with the subfamilies Tanypodinae and Chironominae in the Amazon basin but as yet only a small fraction of the known species have been described. Reiss (1972) has reported on the Tanytarsini fauna of Patagonia and South Chile. The subfamily Orthocladiinae is the most poorly known although it probably has a rich and varied fauna in the high mountain and cold temperate regions.

A recent catalogue of Chironomidae in the Neotropics is not available. The number of recognisable species presented here was compiled from a wide range of published literature and cross-checked against « Zoological Record ». In this region

109 genera have been reported of which 15 are endemic and currently there are 369 recognisable species. All subfamilies except Buchonomyiinae have been recorded from the region. The subfamily Chironominae is dominant with 123 species (33.3 %) followed by the Orthocladiinae and Podonominae with 86 (23.3 %) and 83 (22.5 %) species respectively and the Tanypodinae with 51 (13.8 %) species (Table 3). The balance of 24 (7.1 %) species represent the five remaining subfamilies.

Some additional information is available for the Neotropical region which shows the contrast in the chironomid fauna, at the subfamily level, between the tropical-subtropical lowlands (below 500 m) and the temperate mountain fauna of flowing waters in the Andean-Patagonian region (Table 5). Figures for the tropical-subtropical lowlands are from Fittkau & Reiss (1979). However, the single Diamesinae species mentioned (op. cit. : 276) in their table belongs to *Prodiamesa* which is now included in the Prodiamesinae and was collected as a larva in the foothills of the Peruvian Andes between 100-200 metres (Roback 1966) - this subfamily cannot be regarded as typical of the tropical lowlands. It is evident that the Chironominae are by far the most important group with nearly 80 % of the species, followed by the Tanypodinae with 13.1 % and the Orthocladiinae with only 8.2 %. Neotropical Telmatogetoninae, which are only found on the coast can be expected on rocky shores throughout the region. The Prodiamesinae, which in the Neotropical region may occur in peripheral areas bordering on the tropical lowlands, can be regarded as more typical of temperate latitudes and cool high mountain regions. Significantly, the Podonominae, Diamesinae, Aphroteniinae and Chilenomyiinae have not been reported from the tropical-subtropical lowlands. The figures for the Andean-Patagonian flowing waters are estimated from Brundin (1966 : 440-441) : « podonomine fauna... makes up no less than 38 % of the chironomid species of the running waters... Diamesinae + Orthocladiinae (42 %) ». Brundin's (loc. cit.) 38 % Podonominae figure is equivalent to 87 species and by taking account of the described Diamesinae (11 species) the percentage and number of Orthocladiinae can be estimated. The figures given here (Table 5) are estimates but are probably reasonably accurate. No figures are given for the Tanypodinae, Prodiamesinae or Chironominae but all three together only make up 18.5 % of the fauna. The

Table 5 : The number of known species and the percentage representation of each subfamily in the tropical lowlands of South America (modified from Fittkau & Reiss 1979) compared to the fauna of Andean-Patagonian flowing waters (estimated from Brundin 1966).

	Tropical lowlands of South America		Andean-Patagonian flowing waters	
	No.	%	No.	%
Telmatogetoninae	4	0.8	0	-
Chilenomyiinae	0	-	1	0.2
Tanypodinae	66	13.1	?	?
Podonominae	0	-	87	38.0
Aphroteniinae	0	-	3	1.3
Diamesinae	0	-	11	4.8
Prodiamesinae	1	0.2	?	?
Orthocladiinae	41	8.2	85	37.2
Chironominae	391	77.7	?	?
TOTAL	503	100.0	187	81.5

Chironominae would probably constitute about 10-12 %, the Tanypodinae about 6-8 % and the Prodiamesinae about 1 % or less. The subfamily Chilenomyiinae is only recently described (Brundin 1983a), probably occurs in flowing water, and is included in the table for the sake of completeness. Significant, from these figures for the Andean-Patagonian flowing waters, compared with those of the tropical-subtropical lowlands, is the presence of the Podonominae, Diamesinae, Aphroteniinae and Chilenomyiinae. In addition the Podonominae and Orthocladiinae, each with about 38 % of the fauna, together constitute 75 % of the total fauna and are the dominant groups.

### 2.3. Australasian region

The principal taxonomic works on this region include those of Freeman (1959, 1961) dealing with New Zealand and Australia respectively ; Brundin (1966) on the representatives of the subfamilies Aphroteniinae, Podonominae and Diamesinae in Australia and New Zealand ; Glover (1973) on with the Tanytarsini of Australia. The fauna of New Zealand's subantarctic islands is treated by Sublette & Wirth (1980). The only recent monograph on the Micronesian fauna is by Tokunaga (1964) although the taxonomy at the generic level is outdated. The generic placement of the Australian Tanypodinae

dealt with by Freeman (1961) has been updated by Roback (1982b, c). A catalogue of the fauna of the region is in preparation (Cranston, pers. comm.) and the previously uncertain generic placement of many species has been resolved - figures given in Table 3 reflect this information.

The Chilenomyiinae, Buchonomyiinae and Prodiamesinae are the only subfamilies not reported from the Australasian region. The fauna of this region consists of 107 genera, of which 25 are currently endemic, and 403 valid species. The number of species and the percentage representation of each subfamily is given in Table 3. The Chironominae (47.1%), Orthocladiinae (27.0%), Tanypodinae (10.7%) and the Podonominae (8.2%) are the dominant subfamilies with the Telmatogetoninae, Diamesinae and Aphroteniinae making up the remainder. The immature stages of most of the endemic genera are unknown as are the immatures of most of the described species. The strong relationship between the fauna of S.E. Australia + New Zealand and the Chile/Patagonian fauna of the Neotropics is seen in the fact that 12 genera and one subgenus are unique to the two areas (Table 6). The discovery of the subfamily Chilenomyiidae, which so far is only known from Southern Chile, would not be unexpected in S.E. Australia and New Zealand. As our knowledge of the fauna of these areas increases it is likely that this trend will be more conclusively demonstrated. The chironomid fauna of New Zealand is generally regarded as being impoverished and at present consists of 86 species or 21% of the total fauna of the Australasian region of which only four species are reported to occur in both New Zealand and Australia. According to Brundin (1966: 449) the fauna of New Zealand shows closer relationship to that of Chile/Patagonia than to the continent of Australia.

## 2.4. Oriental region

The chironomid fauna of the Oriental region is the least well known of all the zoogeographical regions. The adults of many described species are poorly and incompletely illustrated and described so that recognition of many described or even new species is very difficult. The immature stages have been largely ignored and are mostly unknown or undescribed. A catalogue of the Chironomidae of the Oriental region has been published (Sublette & Sublette 1973). It is evident from this catalogue that many

Table 6: Genera and one Subgenus unique to the Andean/Patagonian region and S.E. Australia/New Zealand.

<i>Podoohlus</i>	<i>Austrocladius</i>
<i>Podonomopsis</i>	<i>Rhinocladius</i>
<i>Podonomus</i>	<i>Stictocladius</i>
<i>Rheochlus</i>	<i>Symbiocladius (Aoletius)</i>
<i>Aphroteniella</i>	<i>Megacentron</i>
<i>Paraphrotenia</i>	<i>Riethia</i>
<i>Paraheptagya</i>	

of the species described from this region by Kieffer, now regarded as *nomina dubia*, require re-examination and re-description in line with currently accepted diagnostic and illustrative methods. In recent years Chaudhuri and co-workers have begun working on the taxonomy of the fauna of the Indian subcontinent. The dividing line between the Oriental and Australasian Region's, as given in the « Catalogue of the Diptera of the Oriental Region », is Weber's Line but a detailed study on the island faunas in the area is required to determine if this represents the true boundary. At the boundary between the Oriental and Palaearctic regions Reiss (1971) regards those taxa in the Himalayan range within the Oriental region occurring above 2,000 metres to be essentially of Palaearctic origin whereas he (Reiss *op. cit.*) considered those occurring below this altitude to be Oriental elements.

Only two of the ten chironomid subfamilies (Chilenomyiinae and Aphroteniinae) have not been recorded from the Oriental region. A total of 100 genera are now known from the region and there are, at present, only four genera - *Neopodonomus*, *Asclerina*, *Eusmittia* and *Trichotendipes* which are unique to this region. The larvae and pupae of all four endemic genera are unknown. *Neopodonomus* and *Asclerina* are known from high altitude (over 2,000 m) in Bhutan and Nepal respectively and are probably really Palaearctic elements. The genus *Eusmittia* is only known from the Batu Caves in Malaysia (Freeman 1962) and the recently described *Trichotendipes* occurs on the Andaman Islands, Bay of Bengal (Guha & al. 1985). The region possesses a fauna of 348 valid species (compiled from the catalogue of Sublette & Sublette 1973, Zoological Record and various



individual taxonomic publications). The figures available for the number of species and percentage representation of each subfamily (Table 3) shows that the Chironominae, Orthocladiinae and Tanyptodinae are the dominant groups with 181 (52.0%), 78 (22.4%) and 67 (19.2%) species respectively. The balance of 22 (6.4%) species represent the remaining five subfamilies. The Diamesinae is well represented, mainly concentrated in the Himalayas, and it is likely that the species inventory of this subfamily and other cold adapted groups will increase with more intensive work on the high mountain fauna.

### 2.5. Afrotropical Region

After the Palaearctic and Nearctic the chironomid fauna of the Afrotropical region is the next best known of all the regions. Our present understanding of the fauna of this region is mainly due to the work of Freeman (1955, 1956, 1957, 1958) who resolved most of the problems with Kieffer's inadequate descriptions, redescribed all the known species as well as describing a number of new species. However, the generic taxonomy of Freeman's early papers is outdated and when identifying species the works mentioned above should be used in conjunction with the recently published Afrotropical catalogue (Freeman & Cranston 1980) in which the species are placed into their modern generic concept. Recently, Lehmann (1979, 1981) studied the fauna of two streams in Zaïre adding more new species to the faunal inventory.

Seven subfamilies are known from the region and those which have not been recorded are the Chironomyiinae, Buchonomyiinae and Prodiamesinae. To date, 104 genera are known and 18 genera are currently endemic (List, Table 1). The region has a described fauna of 426 valid species (compiled from Freeman & Cranston 1980; Lehmann 1979, 1981; Willassen & Cranston 1986). The species and percentage representation of each subfamily is given in Table 3. Interestingly the Chironominae, with 238 species, represents 55.9% of the total chironomid fauna whereas the Orthocladiinae with 111 species and 26.1% of the fauna is poorly represented when compared with the Palaearctic or Nearctic faunas. The Tanyptodinae with 65 species (15.3%) has a relatively rich fauna. The Chironominae, Orthocladiinae and Tanyptodinae combined make up 97.3% of the fauna or 414 species. The balance of 2.7% and 12 species represents the remaining four subfamilies i.e. Podonominae, Aphroteniinae, Telmatogetoninae and

Diamesinae. The Diamesinae are poorly represented in the Afrotropical fauna with only four known species of which three belong to *Diamesa* and one species in the endemic genus *Harrisonina*. The possible origin of Afrotropical *Diamesa* is discussed by Willassen & Cranston (1986) who suggest that they are derived from species that existed in northern latitudes and that the sister-group relationship of the three Afrotropical species is with species or species-groups from the high mountain ranges in the Himalayas and the southern Palaearctic. *Diamesa* is not known to occur further south than Mount Kenya and according to Cranston (pers. comm. to P. Ashe) the genus has not been discovered in any of the extensive samples examined from rivers in the Drakensberg Range in Southern Africa where ideal conditions for *Diamesa* exist. The Prodiamesinae and Buchonomyiinae are unknown from the region, although their presence cannot be ruled out, and if they occur the most likely area would be the East African Highlands.

### 2.6. Antarctic region

The Antarctic region as defined here includes the land-mass of Antarctica as well as the islands or island groups of: South Shetlands, South Orkneys, South Georgia, South Sandwich, Bouvet, Prince Edward, Crozet, Kerguelen, Heard and Balleny (Ile Saint Paul and Ile d'Amsterdam are regarded as belonging to the Afrotropical region). Due to the fact that so few chironomid species (or other insects) are known or can be expected from the region it seems best not to assign the region a status similar to that of the major zoogeographical regions and for this reason a separate column for the Antarctic region is not included in the various tables. The known chironomid fauna of the Antarctic region, as defined here, consists of nine species (Table 7) and the total chironomid fauna will probably consist of not more than 20-30 species. Two genera, *Microzetia* and *Belgica*, are endemic to the region. *Belgica* contains two described species, *B. antarctica* which is the only chironomid known from mainland Antarctica as well as being the most southerly known free-living holometabolous insect (Usher & Edwards 1984). The second species, *B. albipes*, is only known from the Crozet Islands as is the monotypic genus *Microzetia*.

The fauna of Antarctica, particularly in the Graham Land area, may in reality be merely an

List of chironomid genera and subgenera (indented) and their zoogeographical distribution (\* = worldwide distribution; + = published record; U = previously unpublished record (see Chapter 5); § = refers to a taxonomic note in Chapter 5; numbers in the right hand column are the sources for published records, see references).

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
TELMATOGETONINAE (2)							
* <i>Telmatogeton</i>	+	+	+	+	+	+	23
* <i>Thalassomya</i>	+	+	+	+	+	+	23, 31
CHILENOMYIINAE (1)							
<i>Chilenomyia</i>			+				6
TANYPODINAE (44)							
* <i>Ablabesmyia</i>	+	+	+	+	+	+	23
* <i>Ablabesmyia</i>	+	+	+	+	+	+	23
<i>Asayia</i>			+				60
<i>Karelia</i>	+	+	+		+	+	13, 38, 55, 59
<i>Sartaia</i>			+				59
<i>Alotanypus</i>		+		+			24
<i>Anatopynia</i>	+						24
§ <i>Apspectrotanypus</i>	+	+		+		+	24, 28, 56
<i>Arctopelopia</i>	+	+					24
<i>Brundiniella</i>		+					24
<i>Cantopelopia</i>		+				+	24, 28
<i>Chrysopelopia</i>						+	28
* <i>Clinotanypus</i>	+	+	+	+	+	+	24
<i>Aponteus</i>		+					55
* <i>Clinotanypus</i>	+	+	+	+	+	+	24
<i>Coslopynia</i>				+			26
<i>Coelotanypus</i>		+	+	+		+	24
* <i>Conchapelopia</i>	+	+	+	U	+	+	24
<i>Derotanypus</i>	+	+					24
§ <i>Djalmbatiata</i>	+	+	+		+		24
<i>Fittkauimyia</i>		+	+	+	+	+	24, 56
<i>Gressittius</i>				+			85
<i>Outtipelopia</i>	+	+					24
<i>Hayesomyia</i>	+	+					43
<i>Helopelopia</i>		+					24
<i>Hudsonimyia</i>		+					24
<i>Krenopelopia</i>	+	+			+		24
§ <i>Labrundinia</i>	+	+	+		+		23

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
* <i>Larsia</i>	+	+	+	+	+	+	24, 28, 56
<i>Lepidopelopia</i>						+	28
* <i>Macropelopia</i>	+	+	+	+	+	+	24
<i>Meropelopia</i>		+					24
<i>Monopelopia</i>	+	+			+	+	24, 28
<i>Naerotanypus</i>			+				58
<i>Natarisia</i>	+	+					24
* <i>Nilotanypus</i>	+	+	U	U	U	+	24
<i>Paramerina</i>	+	+		+	+	+	24, 28
<i>Pentaneura</i>		+	+				24
<i>Pentaneurella</i>	+						24
§* <i>Procladius</i>	+	+	+	+	+	+	24
<i>Holotanypus</i>	+	+			U	U	56
<i>Procladius</i>			+	+	U		24
<i>Pelotanypus</i>	+	+	+		U	+	22, 28, 55, 57
<i>Pseotrotanypus</i>	+	+	+			+	23
<i>Radotanypus</i>		+					21
<i>Rheopelopia</i>	+	+			U		24
* <i>Tanypus</i>	+	+	+	+	+	+	24
<i>Apelopia</i>		+					55
* <i>Tanypus</i>	+	+	+	+	+	+	24
<i>TeImatopelopia</i>	+						24
<i>TeLopeLopia</i>	+	+					24
<i>Thienemannimyia</i>	+	+		+	+	+	24, 28, 48
<i>Trissopelopia</i>	+	+				+	24, 28
<i>Xenopelopia</i>	+	+					24
<i>Zavrelimyia</i>	+	+			+		24
<b>BUCHONOMYIINAE (1)</b>							
<i>Buchomyia</i>	+				+		40
<b>PODONOMINAE (14)</b>							
<i>Afrochilus</i>						+	4
§ <i>Archaeochilus</i>				+		+	4, 20
<i>Boreochilus</i>	+	+			+		7
<i>Lasiodicmesa</i>	+	+					7
<i>Microsetia</i>			Crozet Islands				77
<i>Neopodonomus</i>					+		9
<i>Paraboreochilus</i>	+	+					7
<i>Parochilus</i>	+	+	+	+			7
<i>Podochilus</i>			+	+			4
§ <i>Podonomopsis</i>			+	+			4
<i>Podonomus</i>			+	+			4
<i>Rheochilus</i>			+	+			4

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
<i>Trichotanytus</i>	+	+					7
<i>Zelandochilus</i>				+			4
<b>APHROTEINIINAE (4)</b>							
<i>Anaphrotenia</i>				+			8
<i>Aphrotenia</i>						+	4
<i>Aphroteniella</i>			+	+			4
<i>Paraphrotenia</i>			+	+			4
<b>DIAMESINAE (18)</b>							
‡ <i>Arctodiamesa</i>	+	U					39
<i>Boreoheptagyia</i>	+	+			+		45, 79
<i>Diamesa</i>	+	+	+		+	+	4, 45
<i>Harrisonia</i>						+	4
<i>Heptagyia</i>			+				4
<i>Lappodiamesa</i>	+						45
<i>Lumaya</i>			+				4
<i>Lobodiamesa</i>				+			4
<i>Maoridiamesa</i>				+			4
<i>Pagastia</i>	+	+					45
<i>Parahepagyia</i>			+	+			4
<i>Potthastia</i>	+	+			+		4, 45
<i>Protanytus</i>	+	+			+		4, 45
<i>Pseudodiamesa</i>	+	+			+		45
<i>Paohydiamesa</i>		+					44
<i>Pseudodiamesa</i>	+	+			+		45
<i>Pseudokiefferiella</i>	+	+					45
<i>Reissia</i>			+				5
<i>Symptothastia</i>	+	+			+		45
<i>Syndiamesa</i>	+	+					45
<b>PRODIAMESINAE (4)</b>							
<i>Compteromesa</i>		+					64
<i>Monodiamesa</i>	+	+	+		U		64
<i>Odontomesa</i>	+	+			+		4, 64
<i>Prodiamesa</i>	+	+	+				23
<b>ORTHOCLADIINAE (118)</b>							
<i>Abiakomyia</i>	+	+					18
<i>Acampocladius</i>	+	+					18
<i>Aericoptopus</i>	+	+			+		18
<i>Alliocladius</i>						+	28
<i>Allometriocnemus</i>				+			26
<i>Allotriasocladius</i>				+	+		12, 27

	Palaearctic	Nearctic	Neotropical	Austroalasian	Oriental	Afrotropical	References
<i>Ancylocladius</i>			+				84
<i>Antillocladius</i>		+	+				18
<i>Apometriocnemus</i>	U	+		.			68
<i>Asclerina</i>					+		49
<i>Austrobrillia</i>				+			26
<i>Austrocladius</i>			+	+			26
<i>Baeocetus</i>		+					18
<i>Belgica</i>	Antarctica; Crozet Islands						78
<i>Boreosmittia</i>	+						92
<i>Brillia</i>	+	+			+		18
<i>Bryophaenocladus</i>	+	+	+		+	+	18
<i>Campocladius</i>	+	+		+			18
* <i>Cardiocladius</i>	+	+	+	+	+	+	23
<i>Chaetocladius</i>	+	+			+	+	10, 18
<i>Chasmatonotus</i>	+	+					18
* <i>Clunio</i>	+	+	+	+	+	+	23
<i>Comptosmittia</i>		+	+				18
* <i>Corynoneura</i>	+	+	+	+	+	+	23, 86
* <i>Cricotopus</i>	+	+	+	+	+	+	18
* <i>Cricotopus</i>	+	+	+	+	+	+	18
<i>Isocladius</i>	+	+			+	+	33, 37, 80, 86
<i>Maurius</i>						+	38
<i>Nostococladus</i>	+	+					1, 80
<i>Diplocladius</i>	+	+					18
§ <i>Diplosmittia</i>		+	+				72
<i>Dothrix</i>		+					18
<i>Doloplastus</i>				.			26
<i>Donaricotopus</i>	+	+					18
<i>Dratnalia</i>	+						18
<i>Epoicocladus</i>	+	+			U		18
<i>Eretmoptera</i>			+	Antarctica			18
* <i>Eukiefferiella</i>	+	+	+	+	+	+	18
§ <i>Euryanemus</i>	+						41
<i>Euryhapsis</i>	+	+					18
<i>Eusmittia</i>					+		83
<i>Freemantella</i>						+	28
<i>Geothaocladus</i>	+	+					18
<i>Ateuropodella</i>		+					18
<i>Geothaocladus</i>	+	+					18
<i>Gymmetriocnemus</i>	+	+		+		+	18
<i>Gymmetriocnemus</i>	+	+		+		+	18
<i>Raphidocladus</i>	+	+					65
<i>Gymnidocladus</i>				+			85
<i>Halocladus</i>	+	+					18

	Palearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
<i>Halocladus</i>	+	+					18
<i>Pannocladus</i>	+						18
<i>Heleniella</i>	+	+			+		18
<i>Heterotanytarsus</i>	+	+					18
<i>Heterotrissocladius</i>	+	+			+		18, 83
<i>Hevelius</i>				+			85
<i>Hydrobaenus</i>	+	+					18
<i>Ichthyocladus</i>			+				23
<i>Irisobrillia</i>			+				46
<i>Kiefferophyes</i>				+			26
<i>Knepperia</i>						+	28
<i>Krenomittia</i>	+	+			U	+	18, 28
<i>Kuschlius</i>				+			85
<i>Lappokiefferiella</i>	+						92
<i>Lappomittia</i>	+	+					15, 22
* <i>Limnophyes</i>	+	+	+	+	+	+	18
<i>Lindebergia</i>	+						89
<i>Lipumetricoenus</i>		+	+				18
<i>Lopesoladius</i>		+	+				18
<i>Cordiella</i>		+	+				16
<i>Lopencladus</i>		+	+				67
<i>Maryella</i>				+			85
<i>Mecaenus</i>				+			85
<i>Mesocricotopus</i>	+	+					18
<i>Mesosmittia</i>	+	+	+			+	18, 37, 71
* <i>Metricoenus</i>	+	+	+	+	+	+	18
<i>Nakataia</i>				+			85
* <i>Nanocladus</i>	+	+	+	+	+	+	18, 86, 88
* <i>Nanocladus</i>	+	+	+	+	+	+	18, 86, 88
<i>Plecopteraoluthus</i>		+					18
<i>Nasutioladius</i>				+	+		26, 81
<i>Nesiocladius</i>				+			85
<i>Oliveridia</i>	+	+					18
<i>Oreadomyia</i>		+					18
* <i>Orthocladus</i>	+	+	+	+	+	+	18
<i>Eudactylocladius</i>	+	+			+	U	19, 22, 83
<i>Euorthocladus</i>	+	+					22, 63
* <i>Orthocladus</i>	+	+	+	+	+	+	18
<i>Pogonocladus</i>	+	+					19, 22
<i>Parahaetocladus</i>	+	+					18
<i>Paracadius</i>	+	+					18
<i>Paracricotopus</i>	+	+			U		18
<i>Parakiefferiella</i>	+	+	+		+	+	3, 18
<i>Paralimnophyes</i>	+	U					18

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
* <i>Parametricnemus</i>	+	+	+	+	+	+	18
<i>Paraphaenocladius</i>	+	+	+			+	18, 61
<i>Parasmittia</i>	+	U					18
* <i>Paratrioocladius</i>	+	+	+	+	+	+	18, 34
<i>Paratrioocladius</i>	+	+	U			+	18
<i>Parorthocladius</i>	+	+				+	18
<i>Fetalocladius</i>			+				84
<i>Platymittia</i>		+					18
<i>Plundeonia</i>		+					18
<i>Propilocerus</i>	+						18
<i>Psectrocladius</i>	+	+	+		+	+	18
<i>Allopectrocladius</i>	+	+					18
<i>Mesopsectrocladius</i>	+	+					18
<i>Monopsectrocladius</i>	+	+					18
<i>Psectrocladius</i>	+	+	+		+	+	18
<i>Pseudorthocladius</i>	+	+				+	18
<i>Lordella</i>		+					74
<i>Pseudorthocladius</i>	+	+				+	18
<i>Pseudomittia</i>	+	+	+	+		+	18, 26, 28, 61
<i>Psilometricnemus</i>		+					18, 91
<i>Pterosia</i>				+			85
§* <i>Rheocricotopus</i>	+	+	+	+	+	+	18, 61, 87
<i>Psilocricotopus</i>	+	+				+	73
<i>Rheocricotopus</i>	+	+			+		73
<i>Rheomittia</i>	+	+			+		17
<i>Rhinocladius</i>			+	+			26
<i>Saethaviella</i>		+					18
<i>Semiocladius</i>	+			+	U		85
* <i>Smittia</i>	+	+	+	+	+	+	18
<i>Stackelbergina</i>	+						18
§ <i>Stictocladius</i>			+	+			26
<i>Stilocladius</i>	+	+					18
<i>Sublettiella</i>		+					65
<i>Symbiocladius</i>	+	+	+	+			15, 22, 35, 54
<i>Aclletius</i>			+	+			35, 54
<i>Symbiocladius</i>	+	+					15, 22
<i>Symposiocladius</i>	+	+					18
<i>Synorthocladius</i>	+	+				+	18
<i>Tavastia</i>	+						90
<i>Tethymia</i>		+					18
<i>Thalassomittia</i>	+	+					18
<i>Thienemannia</i>	+	+					69
* <i>Thienemannella</i>	+	+	+	+	+	+	23, 86
<i>Tokunagaia</i>	+	+					18

	Palaearctic	Holarctic	Neotropical	Australasian	Oriental	Afrotropical	References
<i>Tokunagayusurika</i>	+						18
<i>Trichochilus</i>		+					70
<i>Trissocladius</i>	+						18
<i>Tsudayusurika</i>	+						76
<i>Tvetenia</i>	+	+			+	+	18
<i>Umrella</i>		+					18
<i>Xylotopus</i>		+			+		18
<i>Zalutschia</i>	+	+					18
CHIRONOMINAE (101)							
<i>Acaloarella</i>	+	+					47
<i>Aedokritus</i>			+				23
<i>Ashmun</i>		+	+				47, 53
<i>Azarus</i>	+	+	+				47
<i>Baetendipes</i>	+				+	+	47
<i>Beardius</i>		+	+				53
<i>Beckidia</i>	+	+				+	47
<i>Caladomyia</i>		+	+				75
<i>Camposomyia</i>			+				75
<i>Chernovskiiia</i>	+	+			U		47
* <i>Chironomus</i>	+	+	+	+	+	+	47
<i>Camptochironomus</i>	+	+			+		22, 36
<i>Chaetolabis</i>	+	+					93
* <i>Chironomus</i>	+	+	+	+	+	+	47
<i>Lobochironomus</i>	+						62
* <i>Cladopelma</i>	+	+	+	+	+	+	23, 87
* <i>Cladotanytarsus</i>	+	+	+	+	+	+	75
<i>Collartomyia</i>						+	28
<i>Conochironomus</i>				+		+	26
<i>Constempellina</i>	+	+					47
<i>Corynooera</i>	+	+		+			47
* <i>Cryptochironomus</i>	+	+	+	+	+	+	47
§ <i>Cryptotendipes</i>	+	+			U	U	47
<i>Cyphomella</i>	+	+		+		+	47
<i>Demetjerea</i>	+	+					47
<i>Demicryptochironomus</i>	+	+				+	37, 47
* <i>Dicrotendipes</i>	+	+	+	+	+	+	47
<i>Einfeldia</i>	+	+			+		32, 47
<i>Endochironomus</i>	+	+		+	+	+	47, 88
<i>Fleuvia</i>	+						47
<i>Gillotia</i>		+	+			+	47, 50
<i>Glyptotendipes</i>	+	+	+		+	+	3, 47
§ <i>Goeldichironomus</i>	+	+	+	+			47, 53
<i>Gracvus</i>	+	+					47



	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
<i>Harrischia</i>	+	+		+	+	+	47
<i>Harrisius</i>				+			26
<i>Henrardia</i>						+	28
<i>Hyporhygma</i>		+	+				47, 53
<i>Imparipecten</i>				+			26
<i>Kiefferulus</i>	+	+		+	+	+	11, 47
<i>Kiefferulus</i>	+	+		+	+	+	11, 47
<i>Wirthiella</i>		+					15
<i>Kloosia</i>	+						94
<i>Krenopsectra</i>	+	+					47
<i>Kriblocoemus</i>						+	28
<i>Kribidosia</i>						+	28
<i>Kribiomyia</i>						+	28
<i>Kribiothama</i>						+	28
<i>Kribioxenus</i>						+	28
* <i>Lauterborniella</i>	+	+	+	+	+	+	26, 28, 47, 83
<i>Lepidopodus</i>						+	28
<i>Lipiniella</i>	+	+					47
<i>Lithotanytarsus</i>	+						47
<i>Manoa</i>			+				23
<i>Megaecentron</i>			+	+			26
<i>Microchironomus</i>	+	+		+	+	+	26, 47
<i>Miaropsectra</i>	+	+		+	+		30, 75
* <i>Microtendipes</i>	+	+	+	+	+	+	23, 86
<i>Neostempellina</i>	+						51
<i>Neozavrelia</i>	+	+			+		15, 47
<i>Niduarbia</i>						+	75
§ <i>Nilodorum</i>	+			+	+	+	23
<i>Nilodosia</i>						+	28
<i>Nilothama</i>	+	+	+			+	47
<i>Nimbocera</i>		+	+				47
<i>Omisis</i>	+	+					47
<i>Ophryophorus</i>				+			25
<i>Oschia</i>		+					66
<i>Pagastiella</i>	+	+					67
<i>Parabornielle</i>				+			26
* <i>Parachironomus</i>	+	+	+	+	+	+	47
§ <i>Paracadopelma</i>	+	+			U		47
<i>Paralauterborniella</i>	+	+	+	U			47
<i>Parapsectra</i>	+	+					47
<i>Paratanytarsus</i>	+	+	+	+	+		75
<i>Paratendipes</i>	+	+	U		+	+	47
<i>Parwitergum</i>				+			26
<i>Paucispinigera</i>				+			25

	Palaearctic	Nearctic	Neotropical	Australasian	Oriental	Afrotropical	References
<i>Phaenopæctra</i>	+	+	+	+		+	3, 38, 47, 88
* <i>Polypedilum</i>	+	+	+	+	+	+	47
<i>Pentapedilum</i>	+	+		+	+	+	22, 26, 28, 83
* <i>Polypedilum</i>	+	+	+	+	+	+	47
<i>Tripodura</i>	+	+	+		U		37, 42, 61, 80
<i>Pontomyia</i>	+	U	+	+	+		14, 47
<i>Pseudochironomus</i>	+	+	+				47
<i>Feilochironomus</i>			+				23
* <i>Rheotanytarsus</i>	+	+	+	+	+	+	47
<i>Riethia</i>			+	+			26
<i>Robackia</i>	+	+	+		U	U	47, 50
<i>Saetheria</i>	+	+	U				22, 66
<i>Sergentia</i>	+	+					47
<i>Baicalosergentia</i>	+						47
<i>Sergentia</i>	+	+					47
<i>Skusella</i>				+		+	26, 28
<i>Skutzia</i>		+	+				52
<i>Stelechomyia</i>		+					47
* <i>Stempellina</i>	+	+	+	+	+	+	47
<i>Stempellinella</i>	+	+			+	U	75
* <i>Stenochironomus</i>	+	+	+	+	+	+	47
<i>Petalopholeus</i>	+	+	+	+			2
* <i>Stenochironomus</i>	+	+	+	+	+	+	47
<i>Stictochironomus</i>	+	+		+	+	+	26, 47
<i>Sublettea</i>		+	+		+		47, 50
* <i>Tanytarsus</i>	+	+	+	+	+	+	47
<i>Thienemanniola</i>	+						47
<i>Toumsia</i>			+				23
<i>Tribelos</i>	+	+					47
<i>Trichotendipes</i>					+		29
<i>Virgatanytarsus</i>	+					+	47
* <i>Xenochironomus</i>	+	+	+	+	+	+	23
<i>Xestochironomus</i>		+	+				47
<i>Yama</i>				+			48
<i>Zavrelia</i>	+	+			+	+	47
* <i>Zavreliella</i>	+	+	+	+	+	+	47

Table 7: Known Chironomidae of the Antarctic region and their distribution.

Species	Distribution
<i>Telmatogeton amphibius</i> (Eaton)	Kerguelen Is. Crozet Is.
<i>Microzetia mirabilis</i> Seguy	Crozet Is.
<i>Parochlus steinenii</i> (Gercke)	South Sandwich Is., South Georgia Is.
<i>Parochlus</i> n.sp. Edwards & Usher 1985	South Georgia Is.
<i>Belgica albipes</i> (Seguy)	Crozet Is.
<i>Belgica antarctica</i> Jacobs	offshore islands and mainland Antarctica
<i>Eretmoptera murphyi</i> Schaeffer	South Georgia Is., South Orkney Is.
<i>Limnophyes minimus</i> (Meigen)	Kerguelen Is.
<i>Limnophyes</i> sp. Brundin 1970	South Georgia Is.

extension of the Patagonian fauna. More work is required in south Patagonia (Tierra del Fuego) to investigate the possible occurrence of Antarctic elements which may contradict recognition of a true Antarctic region. *P. steinenii* from South Georgia is not conspecific with the Patagonian « *steinenii* » of Brundin (1966) and the latter represents an undescribed species.

### 3. Subfamily ecology and zoogeography

#### 3.1. Telmatogetoninae

The Telmatogetoninae is the sixth largest subfamily in terms of described species and now contains only two valid genera, *Telmatogeton* and *Thalassomya*, both of which have a worldwide distribution.

The subfamily is almost exclusively marine, the only freshwater representatives known belong to the genus *Telmatogeton* where five species inhabit rapid mountain streams in the Hawaiian Islands. The immature stages of the marine species are found in the intertidal zone on rocky coasts where the larvae feed on algae and algal detritus. Larvae of the marine species construct tubes in various algae including *Enteromorpha*, *Monostroma*, *Porphyra* and *Ulva* (Tokunaga 1935). Recently, Robles (1984) has shown that the heavily chitinized anterior end and the peculiar development of the terminal segments in the pupa protect it from eviction from its tube by aggressive larvae of the same, or allied, species.

#### 3.2. Chilenomyiinae

This is the most recently recognised subfamily as well as one of the most primitive. The Chilenomyiinae is the smallest subfamily with only a single species, i.e. *Chilenomyia paradoxa* Brundin. The subfamily is exclusively Neotropical and has only been found to date in Southern Chile (Brundin 1983a). Several genera in other subfamilies e.g. Podonomiinae and Aphroteniinae, exhibit a circumantarctic distribution with sister species and/or genera occurring in the southern Neotropics, Australia-New Zealand and southern Africa (Brundin 1966). It would not therefore be very surprising if the Chilenomyiinae were discovered in New Zealand or S.E. Australia.

Little is known regarding the ecology of this subfamily since the larvae and pupae have yet to be discovered. The adults were found flying near small brooks in dense *Notofagus* forests (Brundin 1983a). The immature stages, as in the majority of species in the family, will probably prove to be aquatic.

#### 3.3. Tanytopodinae

This subfamily is the third largest in terms of the number of genera and species. Currently there are 44 recognisable genera with subgenera in *Ablabesmyia*, *Clinotanypus*, *Procladius* and *Tanytus*. Only eight genera, *Ablabesmyia*, *Clinotanypus*, *Conchapelopia*, *Larsia*, *Macropelopia*, *Nilotanypus*, *Procladius* and *Tanytus*, are known from all zoogeographical regions

(List). The information currently available indicates that there are several other genera which could be expected to have a worldwide distribution: these include *Apsectrotanypus*, *Coelotanypus*, *Fittkauimyia*, *Labrundinia*, *Paramerina*, *Psectrotanypus* and *Thienemannimyia*. On present evidence the Nearctic region is the richest in genera with 36 recorded, followed by the Palaearctic with 29, the Afrotropical with 19, the Oriental with 17, the Australasian with 16 and the Neotropical with 15 genera. The Neotropical and Oriental regions, which theoretically should have rich generic faunas, are among the poorest which reflects the lack of work done on the chironomid fauna in these areas when compared to the Palaearctic and Nearctic. Although the numbers of described tanypodine genera recorded from the Neotropical and Oriental regions is quite low some undescribed genera have been discovered in these regions. In addition, the discovery of genera already known from other regions is to be expected.

The Tanypodinae are generally adapted to warmer waters (middle to higher range of temperature) and mostly prefer standing water. Representatives of some genera (e.g. *Tanypus*) have been reported from hot springs at temperatures up to 44.5° C (Thienemann 1954 : 567, *sub Protenthes*). When they occur in rivers they are usually more common in the slow flowing lower course or in marginal lentic areas in upland or mountain regions where the current is weaker. Some genera, such as *Rheopelopia* and *Nilotanypus*, are secondarily adapted to running waters and may be found in moderately strong currents. Some genera which possess haemoglobin are able to survive in warm stagnant water bodies with typically low oxygen concentrations. Representatives of the subfamily are commoner in the warmer climatic regions, especially in tropical and subtropical areas. The diversity decreases towards colder regions or with increasing altitude. The larvae are generally regarded as being carnivorous but some species are known to feed on diatoms and detritus (Oliver 1971). The true situation in many species is probably a combination of both types of feeding with reliance on diatoms and detritus when prey items are scarce. The larvae of the majority of species are free-living and none are known to produce larval or pupal cases. However, one species, *Abla besmyia* (A.) janta Roback is known to be symbiotic on Mollusca (Unionidae : *Quadrula*) (Roback 1982).

### 3.4. Buchonomyiinae

This subfamily contains a single genus, *Buchonomyia*, and two described species, *B. thienemanni* Fittkau from the western Palaearctic and *B. burmanica* Brundin & Saether from the Oriental region. *B. thienemanni* occurs in western and central Europe in a band stretching from Ireland through southern Britain, France and Germany apparently as far as Iran (pupal exuvia from Iran probably belong to *B. thienemanni*) (Murray & Ashe 1981). This species, therefore, could be expected to occur in Italy, Yugoslavia, Hungary, Greece, Bulgaria, Turkey and Iraq. *B. burmanica* is only known from Kambaiti in Northern Burma close to the border with China. In Iran (Dowling pers. comm.) and Burma (Brundin + Saether 1978) *Buchonomyia* has been found at altitudes over 2,000 m so that the genus could be expected to occur at similar altitudes in Pakistan, India and China (Yunnan Province). The genus has not yet been discovered in the Eastern Palaearctic or the Nearctic region. The description of the distinctive pupa (Murray & Ashe 1981), 1st instar larva (Ashe 1985) and 4th instar larva (Ashe, in prep.) will ensure recognition of the immature stages. The subfamily Buchonomyiinae in the northern hemisphere seems to have a more southern distribution with all reported occurrences between 25° N-53° N.

The larvae and pupae are only known for *B. thienemanni* and are found in rivers in areas of moderate currents. It is likely that *B. burmanica* also occurs in lotic habitats. The subfamily seems to be adapted to the middle range of water temperature and in Western Europe *B. thienemanni* emerges mainly during the summer months. Recently a single 4th instar larva has been discovered which was obtained from a probable trichopteran case, indicating that there may be an association between *Buchonomyia* and a trichopteran species.

### 3.5. Podonominae

There are 14 genera currently recognised in the Podonominae (List). None of these genera are worldwide in distribution but every zoogeographical region is represented by at least two genera. *Parochlus*, which occurs in four regions, i.e. Palaearctic, Nearctic, Neotropical and Australasian regions, is the most widely distributed genus. The genus contains 47 described species but only one, *P. kiefferi*.

is found in the northern hemisphere where it has a Holarctic distribution. The remaining species occur only in the southern hemisphere. *Boreochlus* is the next most widely occurring genus and it has been found in the Holarctic and the Oriental regions. The Palaearctic and Nearctic share five genera in common i.e. *Boreochlus*, *Lasiodiamesa*, *Paraboreochlus*, *Parochlus* and *Trichotanypus*. Five genera are found in both the Neotropical and Australasian regions: *Parochlus*, *Podochlus*, *Podonomopsis*, *Podonomus* and *Rheochlus*. The Australasian region contains two further genera, *Zelandochlus* which is endemic to New Zealand and *Archaechlus* which has been found in Southern Africa and Western Australia. The Oriental region contains two genera, *Boreochlus* (with two species from Northern Burma) and *Neopodonomus* from Bhutan. The genus *Microzetia* is only known from the isolated Crozet Islands between the African continent and Antarctica.

The Podonominae, in general, can be regarded as an essentially cold-tolerant predominantly rheophilic group requiring high oxygen concentrations. Larvae may be found in waters with a temperature range 0-24° C (Brundin 1966: 96) and are adapted to the lower to middle range of temperature. Most species occur in cool rivers and streams but some are found in warm, more or less, temporary streams (*Archaechlus* and *Afrochilus*), among mosses in cool springs and creeks (*Parochlus kiefferi* (Garrett), *Boreochlus* and *Paraboreochlus*), meltwater tarns at high latitude (*Parochlus steinenii* (Gercke) and *Trichotanypus*) or in standing bog waters (*Lasiodiamesa*) (Brundin 1966). Larvae of some species are found in the most extreme of all freshwater habitats i.e. in glacier fed rivers and streams close to the glacier in very powerful currents, in very low temperatures (0-5° C) and in waters containing large amounts of suspended abraded material (coarse sand and gravel) (Brundin 1966: 97). As far as is known the larvae feed on unicellular algae, mainly diatoms, and algal detritus (Brundin 1966); no carnivorous forms have been reported.

### 3.6. Aphroteniinae

The subfamily Aphroteniinae is confined in its distribution to the southern hemisphere. However, the presence of the fossil amber genus *Electrotenia* in Asiatic Russia (Kalugina 1980) within the Palaearctic indicates that the subfamily historically had a

much wider distribution. It is possible that members of the subfamily still survive in the Palaearctic in an area climatically similar to those areas in the southern hemisphere where the only known living species occur. Four recent genera, *Anaphrotenia*, *Aphrotenia*, *Aphroteniella* and *Paraphrotenia* are recognised. In the Neotropical and Australasian regions both *Aphroteniella* and *Paraphrotenia* occur whereas the recently described *Anaphrotenia* has only been recorded from the latter region. The genus *Aphrotenia* is apparently endemic to Southern Africa.

Aphroteniine larvae are found in mountain streams in the southern temperate zone (Southern Chile, S.E. Australia and Cape Province in South Africa) except for the recently described genus and species, *Anaphrotenia lacustris* Brundin which is found in the littoral zone of a subtropical lake in Queensland, Australia. Larvae and pupae of the rheophilic species occur in the algal layer on stones exposed to the current in water temperatures ranging from 8.8-20.4° C and seem to be adapted to the middle range of temperature. They do not show the tolerance to very low water temperatures exhibited by the Podonominae and are not found in streams coming directly from glaciers. The only known lentic species, *A. lacustris*, occurs in the sandy littoral zone of a warm (25° C), humic, low lying, subtropical lake on Frazer Island, Queensland. The larvae of most species appear to be algal and organic detritus feeders except *Paraphrotenia cf. excellens* Brundin which is carnivorous and feeds on other arthropods such as chironomid larvae and crustaceans (Brundin 1966, 1983c).

### 3.7. Diamesinae

After the Tanypodinae the subfamily Diamesinae is the next largest in both numbers of genera and species. None of the genera are worldwide in distribution but *Diamesa* is the most widely distributed. *Diamesa* is a good example of a cold adapted Holarctic genus which is typical of cool mountain streams and lakes, a habitat which is only found in tropical latitudes on very high mountains. In the Neotropical region *Diamesa* has been found from the Mexican Highlands (Serra-Tosio 1977), the Bolivian Andes and as far south as Patagonia (Brundin 1966: 366) to about latitude 55° S. In the Afrotropical region the most southerly known occurrences

are Mt. Kenya and Mt. Ruwenzori on the equator in the East African Highlands (Willassen & Cranston 1986) and the genus has not been found in Southern Africa where suitable habitats exist. *Diamesa* is not known from the Australasian region but the nearest occurrence is Mount Kinabalu in Borneo (Willassen, pers. comm. to P. Ashe) at about latitude 6° N and it seems unlikely that the genus could occur in the New Guinea Highlands or further south.

The Diamesinae are a cold adapted group which occur in rivers and lakes and, like the Podonominae, are adapted to the low to middle range of temperature (0–22° C) and require high oxygen concentrations. Rheophilic species are more common in upland or mountainous areas being particularly common wherever the current is strongest although some genera such as *Lobodiamesa* and *Potthastia* prefer slower current. The rheophilic forms include *Boreoheptagyia* whose larvae cling to rocks at the splash line in cool mountain or glacier-fed streams (Oliver 1983). *Diamesa* is the most commonly encountered lotic genus but it is also known from springs, shallow still waters (Oliver 1983), meltwater trickles under snow at high altitude (Kohshima 1984) and even exposed wave-washed lake shores (Aagaard 1978). Other genera, e.g. *Potthastia* and *Pseudodiamesa*, also occur in both standing and flowing water. *Protanypus* is the only genus known to be restricted to standing waters and it is usually found in oligotrophic lakes (Oliver 1983) although Brundin (1966 : 366) states that three undescribed species from Northern Burma may be rheophilic.

The larvae of most species are algal feeders (mainly diatoms), *Pseudodiamesa* is regarded as omnivorous and at least two genera, *Lobodiamesa* and *Protanypus*, are carnivorous (Brundin 1966 : 364–366).

### 3.8. Prodiamesinae

This subfamily is the seventh most speciose with four genera currently recognised. No genera of Prodiamesinae are known to have a worldwide distribution but *Monodiamesa*, recorded from four regions, is the most widely distributed. Both *Monodiamesa* and *Prodiamesa* are found in the Palaearctic and Nearctic and south to Patagonia in the Neotropics (Brundin 1966 : 366). In the regions where the subfamily is found it is usually represented by only a few species. If the subfamily exists in the

Afrotropical and Australasian regions it will probably only be discovered by intensive collecting in the preferred habitat. All four genera i.e. *Compteromesa*, *Monodiamesa*, *Odontomesa* and *Prodiamesa*, occur in the Nearctic, three in the Palaearctic (except *Compteromesa*), two (*Monodiamesa* and *Prodiamesa*) from the Neotropical region and two (*Monodiamesa* and *Odontomesa*) from the Oriental region.

Larvae of the « *Prodiamesa* group » (Brundin 1966 : 367) [= Prodiamesinae] are detritivores and live preferably in cool, slow-flowing streams, in the profundal zone of oligotrophic lakes and in the littoral zone of high mountain lakes. Members of the subfamily prefer the low to middle range of water temperature and no species have been reported from warm tropical waters. *Prodiamesa olivacea* (Meigen) is reported to be predatory (Beck 1977).

### 3.9. Orthoclaadiinae

Currently the Orthoclaadiinae is the largest subfamily with 118 recognisable genera and 31 subgenera. Fourteen genera : *Cardiocladius*, *Clunio*, *Corynoneura*, *Cricotopus*, *Eukiefferiella*, *Limnophyes*, *Metricnemus*, *Nanocladius*, *Orthoclaadius*, *Parametricnemus*, *Paratrachoclaadius*, *Rheocricotopus*, *Smittia* and *Thienemanniella* are known from all regions. In addition, there are nine genera (i.e. *Bryophaenoclaadius*, *Gymnometricnemus*, *Krenosmittia*, *Parakiefferiella*, *Paraphaenoclaadius*, *Psectrocladius*, *Pseudosmittia*, *Symbiocladius* and *Tvetenia*) which, based on their present distribution, are likely to have a worldwide distribution. The Nearctic region at present has the richest generic fauna with 79 genera followed by the Palaearctic with 74, the Australasian with 36 and the Neotropical, Oriental and Afrotropical regions with 34, 33 and 31 genera respectively.

The Orthoclaadiinae can be regarded as the most broadly adapted group ecologically. The subfamily includes numerous species in various types of freshwater habitats as well as many terrestrial forms and some marine genera. In general they are cold adapted, become more common towards higher latitudes or with increasing altitude and are poorly represented in tropical standing waters. The majority of species prefer the low to middle temperature range (0–25° C) but some genera (e.g. *Cricotopus*) are common in warm tropical waters and even in hot

springs. Some freshwater genera may be confined to running water (*Eurycnemus*, *Rheosmittia*) or standing water (*Mesocricotopus*, *Tokunagayusurika*) whereas others may occur in rivers, lakes, ponds and puddles (*Heterotrissocladus*, *Hydrobaenus*). Representatives of some genera are found in very restricted habitats such as seeps (*Antillocladius*), plant held water or phytotelmata (*Metricnemus* in pitcher plants, rot holes, etc.) and temporary pools (*Lapposmittia*). Other genera occur not only in freshwater but also in brackish water (*Propilocerus*) or have representatives that occur in aquatic, semi-terrestrial and terrestrial habitats (*Bryophaenocladus*, *Limnophyes*) (Cranston *et al.* 1983). The terrestrial forms include *Belgica* and *Eretmoptera* which are found in peaty soils among mosses and higher plants (Usher *et al.* Edwards 1984, Cranston 1985), *Campyocladus* living in cow dung and *Gymnometricnemus* and *Parasmittia* in the soil of meadows and woodlands (Cranston *et al.* 1983). Marine genera include *Clunio*, which occurs in the littoral to sublittoral zone (to about 20 m), as well as *Halocladus*, *Tethymyia* and *Thalassosmittia* (Neumann 1976). Most aquatic orthoclad genera produce larval/pupal cases constructed from one or more of a variety of materials including detritus, sand grains, salivary secretions, diatoms, plant debris. Such cases may be fixed to solid objects or covered by sediments. Larvae of some genera, *Abiskomyia* and *Heterotanytarsus*, produce transportable cases similar to those constructed by some Chironominae. Within major habitats, e.g. lakes or rivers, some taxa may be severely restricted in where they occur: *Symposiocladus* and *Xyloptopus* mine in saturated dead wood (Cranston *et al.* 1983), *Cricotopus* subg. *Nostococladus* live within colonies of the blue-green alga *Nostoc* (Ashe & Murray 1980), or they may be associated with other animals.

The immature stages of several orthoclad genera and species are associated (i.e. parasitic, symbiotic, phoretic, commensal or inquiline) with other aquatic invertebrates and even aquatic vertebrates. *Epoicocladus* is phoretic on ephemeropteran nymphs (*Ephemerella* and *Hexagenia*) (Steffan 1968) whereas *Symbiocladus* is ectoparasitic on ephemeropteran nymphs (*Atalophlebioides*, *Ecdyonurus*, *Epeorus*, *Habropleptoides*, *Heptagenia*, *Meridialaris*, *Rhithrogena* and *Thraulodes*) (Wiens *et al.* 1975; Hynes 1976; Soldan 1978). *Dratnalia* is phoretic on Trichoptera (Limnephilidae: *Potamophylax*) (Dratnal

1979; Saether & Halvorsen 1981) and *Eurycnemus* was found in trichopteran cases (Hydropsychidae: *Hydropsyche*) although the type of association is unknown (Murray & Ashe 1981). *Cardiocladus* larvae are reported to be ectoparasitic and predatory on trichopteran pupae (Parker & Voshell 1979) and on Diptera (Simuliidae) (Steffan 1968). *Nanocladus* subg. *Plecopteraoluthus* is phoretic on Plecoptera (Perlidae: *Acroneuria* and *Paragnetina*) and both subgenera of *Nanocladus* have been found in phoretic association on Megaloptera (Corydalidae: *Chauliodes*, *Corydalis* and *Nigronia*) (Gotceitas & Mackay 1980) although *Nanocladus* s.str. are more typically free-living. A species, placed originally in *Dactylocladus* (Tonnoir 1922), whose generic affinities are uncertain, is phoretic on Diptera (Blephariceridae: *Neocurupira*). A probable *Eukiefferiella* species is phoretic on aquatic Hemiptera (Naucoridae: *Cryphocricos*) (Roback 1977). In lamellibranchiate molluscs two orthoclad genera, *Baeoetenus* and an undescribed genus, are found among the gills of *Anodonta* species and larvae of *Baeoetenus* are known to feed on the gills of the molluscs (Gordon *et al.* 1978). The only known association between a chironomid and a vertebrate was described by Fittkau (1974) where species of the genus *Ichthyocladus* are found in cases attached to opercular spines in catfish of the families *Austroblepiidae* and *Loricariidae* although the exact type of relationship is unknown.

It is obvious that the Orthoclaadiinae display a wide variety of food preferences which include detritus, diatoms, other algae, living tissues of higher plants, saturated dead wood, dung, etc. and some are predatory on various invertebrates. Some genera feed on only one type of food whereas others are less specific and may feed on a wide range of available food types.

### 3.10. Chironominae

The Chironominae is the second largest subfamily (List) in terms of genera (101) but the largest if the number of described species is taken into account (Table 3). Subgenera are recognised in *Chironomus*, *Kiefferulus*, *Polypedilum*, *Sergentia* and *Stenochironomus*. The Chironominae are the dominant group in the tropical and subtropical lowlands and with more work on the taxonomy in these regions the number of genera and species can be expected to

increase to make this the dominant subfamily. Fourteen genera have a worldwide distribution: *Chironomus*, *Cladopelma*, *Cladotanytarsus*, *Cryptochironomus*, *Dicrotendipes*, *Microtendipes*, *Parachironomus*, *Polypedium*, *Rheotanytarsus*, *Stempellina*, *Stenochironomus*, *Tanytarsus*, *Xenochironomus* and *Zavreliella*. There are over 20 Chironominae genera known from five of the six zoogeographical regions and it is likely that most of these will prove to have a worldwide distribution. The Nearctic is the richest in genera followed by the Palaearctic, Afrotropical, Neotropical, Australasian and Oriental regions.

The Chironominae are adapted to a wide variety of freshwater habitats and also occur in brackish and marine waters. At least one terrestrial species, belonging to the genus *Tanytarsus*, is known to exist (Pinder & Reiss 1983). As a general rule the number of species of Chironominae increases towards the equatorial regions, with decreasing altitude and with reducing current speed in flowing waters. They are the dominant group in lowland standing waters in tropical and subtropical areas of the world. The majority of species prefer the middle to high range of temperature (15-35° C) but some species exist in hot springs or in streams fed by hot springs at temperatures up to 50° C. Many species possess haemoglobin, a factor which may partly account for their dominance in lowland tropical standing waters where oxygen concentrations are likely to be low. Although the ecology of the Chironominae is still poorly known because the tropical forms are little investigated they do not seem to be as broadly adapted ecologically as the Orthoclaudiinae - especially with regard to marine and terrestrial forms. Most genera are represented in standing waters and when they occur in flowing waters it is usually in the lower reaches of large, slow flowing rivers or in marginal lentic areas in fast flowing rivers and streams. Some genera are only known from running waters (*Rheotanytarsus*, *Sublettea*) or standing waters (*Corynocera*, *Goeldichironomus*, *Nilodorum*) whereas other genera occur in a wide range of aquatic habitats including rivers, lakes, thermal springs and brackish water (*Cladotanytarsus*, *Stempellina*). Some genera appear to be restricted to certain types of water bodies: *Omisus* in dystrophic lakes and pools, *Lithotanytarsus* in limestone rich streams and *Baeotendipes* in polyhaline waters (Pinder & Reiss 1983). The only exclusively marine genus, *Pontomyia*, is found near coasts to a depth of 30 m (Bretschko

1982) and the genus *Tanytarsus* has five described marine species from the Pacific area (Hashimoto 1976). Some genera and species are very restricted in their occurrence within major habitats (lake, river, etc.): some mine in and feed on saturated dead wood (*Harrisius*, *Stelechomyia*, *Stenochironomus* s.str.) or in living tissues, leaves and stems, of macrophytes (*Endochironomus* (some species), *Hyporhygma*, *Stenochironomus* sub. gen. *Petalophleus*) (Pinder & Reiss 1983, Borkent 1984) or may be associated with other invertebrates.

Most of the reported cases of Chironominae living in association with other aquatic invertebrates involve molluscs. *Parachironomus* species are known to be parasitic in Gastropoda with *Parachironomus varus* Goetghebuer ectoparasitic in *Physa fontinalis* Linnaeus and *P. varus* var. *limnai* Guibé reported as endoparasitic in *Limnaea limosa* (Guibé 1942). Lamellibranch molluscs are also known to be parasitized by chironomid larvae. *Glyptotendipes* (?) *paripes* Edwards is reported in *Anodonta cygnea* Linnaeus (Beedham 1966) and *Xenochironomus canterburyensis* (Freeman) from New Zealand is found in *Hyridella menziensis* (Gray) (Forsyth & McCallum 1978). *Demeijerea* species mine in and feed on freshwater sponges and Bryozoa (Neff & Benfield 1970) and some species of *Xenochironomus* mine in sponges (Pinder & Reiss 1983). *Polypedium fallax* (Joh.) is reported to be parasitic and predatory on trichopteran pupae of the genus *Potamophylax* (Otto & Svensson 1981) and *Collartomyia* also appears to behave similarly (Borkent 1984: 22 sub *Collartiella*). *Dicrotendipes peringueyanus* Kieffer in tropical Africa is phoretic on freshwater crabs (*Potamonautes*) and was never found free-living (Disney 1975).

The Chironominae, being one of the largest subfamilies, displays a wide range of food preferences and as indicated above includes those that feed on aquatic plants (diatoms, other algae, higher plants, etc.), saturated dead wood, dead leaves, enriched sediments, etc. Predatory forms occur sporadically throughout the Chironominae but members of the *Harnischia*-complex are generally regarded as being carnivorous.

#### 4. Fossil record and the age of Chironomidae

A neglected but very important element for the zoogeography, phylogeny and ageing of chironomid



taxa is the fossil component, primarily fossils in amber. The amber chironomid fossils have not been comprehensively dealt with even though this family of insects is one of the commonest components. A study of the amber fossils would be particularly useful in elucidating past distributions of genera especially in areas where such genera may now be absent. Additionally such a study would help in establishing a minimum geological age for many genera, tribes and subfamilies. Fossil ambers are known from several periods of the Cenozoic and Mesozoic eras. From the collection of Baltic amber in the Zoological Museum, Copenhagen (Larsson 1965) it is evident that the family Chironomidae is by far the largest component represented by 671 specimens which is 27.4 % of the Diptera or 13.2 % of all arthropod inclusions. Around the turn of the century Meunier, in various papers, described numerous chironomids from Baltic and Zanzibar amber but all the descriptions are inadequate and the material needs to be redescribed and compared with extant species. Only three amber chironomid fossils have been adequately described: *Libanochlites neocomicus* Brundin (Podonomiinae: Boreochlini) from the Lower Cretaceous of Lebanon (120-140 million years old) (Brundin 1976); *Electrotenia brundini* Kalugina (Aphroteniinae: Electroteniini) from the Upper Cretaceous of Siberia (Kalugina 1980) and *Cretodiamesa taimyrica* Kalugina (Diamesinae: Cretodiamesini) also from the Upper Cretaceous of Siberia (Kalugina 1976). The subfamilies Tanypodinae, Orthoclaadiinae, Chironominae (Boesel 1937) and Buchonomyiinae (probably *B. thienemanni*) (Brundin 1966: 80) are known from Baltic amber (Upper Eocene, about 40 million years old) but the only subfamily reported from Canadian amber (Upper Cretaceous, about 75 million years old) is the Orthoclaadiinae (Boesel 1937). Only the subfamilies Chilenomyiinae, Telmatogetoninae and Prodiamesinae have not been reported from amber.

« There is strong reason to suppose that the basic adaptations and first steps in the phylogenetic evolution of the family took place in the upper course of small, cool mountain streams and their springs, and that the present widespread occurrence of the chironomid midges in other types of habitats is due to secondary adaptative radiation » (Brundin 1966: 455). The larvae of most rheophilic chironomids feed on diatoms and this diet has permitted chironomids to evolve and radiate independently of higher plants

and have a history which goes back far into the Jurassic (Brundin 1966: 439). Since the adult stage is not dependant on any specialised food source it follows that the evolution of chironomids was not dependant on the presence of vertebrates or higher plants as are some other families of Diptera. The phylogenetic relationships between the chironomid subfamilies have been well documented. Recently the phylogenetic position of the Buchonomyiinae has been resolved with its placement as the sister group of the Podonomiinae + Aphroteniinae (Murray & Ashe 1985). However, the phylogenetic position of the Telmatogetoninae is still uncertain. The Telmatogetoninae were originally considered as the apomorph sister group of the Diamesinae by Brundin (1966: 373) a view which was initially supported by Saether (1976) but later rejected and placed as the plesiomorphic sister group of the other chironomid subfamilies (Saether 1977). The ecology of the Telmatogetoninae (predominantly marine) does not agree with the presumed primitive habitat of the ancestral chironomid in the « upper course of small, cool mountain streams and springs » suggested by Brundin and with its present phylogenetic position as the sister group of all the other chironomid subfamilies. It seems that the Chilenomyiinae should more logically occupy this position with the Telmatogetoninae placed as a sister group of the Diamesinae. There is little evidence to suggest that Gs IX of Telmatogetoninae (Saether 1977: 4) is identical with structures found in Sciaridae and « possibly in some » Nymphomyiidae or that the presence of a gonostylus in the adult female is a plesiomorphic feature throughout the Diptera since such structures are not reported elsewhere in the whole of the Diptera. Two plesiomorphic characters: gonostylus IX (Gs IX) present and gonapophysis VIII (Gp VIII) very large and elongate, are used by Saether (1977: 31, Trends 1, 2) to support the phylogenetic placement of the Telmatogetoninae since most of the apomorphies are autapomorphies. The eggs of Telmatogetoninae, i.e. *Telmatogeton* (and presumably also *Thalassomyia*), are always laid singly, without a gelatinous medium, with the micropyle uppermost (Terry 1913, sub *Charadromyia*). The gonostyli in Telmatogetoninae, with the cerci, probably help in orientation and the correct positioning of the individual eggs during attachment to the substrate. Much more control is required for this kind of oviposition than is found in those chironomids

which lay an egg-mass. It would seem therefore that most of the unique features of the female genitalia of Telmatogetoninae are highly apomorphic and have developed to suit the needs of a very harsh environment. The female genitalia of Telmatogetoninae have developed some remarkable features but practically all these features appear to be apomorphies (loss of the gelatinous egg-mass) or autapomorphies (loss of spermathecae, Gp VIII very large and elongate, Gs IX present with elongated cerci to facilitate ovoposition). It is not within the scope of this work to deal with the phylogeny of the Telmatogetoninae in any greater detail since it requires a much more detailed analysis and because of this no formal change is proposed for the phylogenetic position of the Telmatogetoninae.

According to Brundin (1976 : 153) the S. African/W. Australian vicariance pattern displayed by *Archaeochlus* is a consequence of the Upper Jurassic separation between S. Africa and E. Antarctica and (Brundin, *loc. cit.* : 148) that the existence of the genus in the Upper Jurassic supports the idea that the Podonominae with its two tribes, Boreochlini and Podonomini, are at least 175 million years old. Brundin (1976 : 159) in summary states : « there is good reason to conclude that representatives of all Chironomidae subfamilies and many tribes existed in the Jurassic ». Prior to the breakup of the southern continents India occupied a position between Southern Africa and Western Australia and *Archaeochlus* must have existed in Southern India at that time. Climatic changes that occurred as India drifted northwards were probably not significantly different to that which exists today and it is possible that *Archaeochlus* still survives in Southern India or Sri Lanka.

An estimate of the minimum age of some chironomid genera can be made in a similar way to Brundin's estimate regarding *Archaeochlus*. The shared presence of a particular genus or group of genera on different land masses which are now separated from one another, but which were formerly in close contact, indicates that the minimum age of those genera, can in some cases, be dated to at least that time prior to the break-up of the original land-mass. The shared presence of certain genera and a subgenus in S.E. Australia/New Zealand and the Andean/Patagonian region (Table 6) indicates that all these taxa are at least 45 million years old dating from the separation of Australia from Antarctica

when the continuous land connection from Australia through Antarctica to South America was finally broken. Those genera (and subgenera) which occur in both the Palaeartic and Nearctic regions date back at least to the time just prior to the final separation of Europe and Eastern Russia from North America.

## 5. Taxonomic notes and new faunal records

### *Apsectrotanypus*

According to Fittkau & Roback (1983) species from the Neotropical and Australasian regions identified as *Macropelopia* may belong to *Apsectrotanypus*. Larvae similar to *Apsectrotanypus* are known from the Neotropics.

### *Conchapelopia*

Australasian region : Adult males have been collected from the McLeod River about 18 km west of Mt. Carbine in Queensland (F. Reiss).

### *Djalmabatista*

This genus has been found in a river in the transition zone between the Palaeartic and Oriental regions (Fittkau & Roback 1983) and it is therefore regarded as occurring in both these regions.

### *Labrundinia*

In Fittkau & Roback (1983) *Labrundinia* is erroneously stated to have a worldwide distribution, there are no published records from the Afrotropical or Australasian regions.

### *Nilotanypus*

Neotropical region : Two new species have been discovered in the Amazon basin region (F. Reiss).

Australasian region : Pupal exuviae have been found in recent collections from creeks in New South Wales and Queensland (F. Reiss).

Oriental region : Pupal exuviae have been found in a stream in northern Sulawesi, Indonesia (P. Ashe) and from Yunnan Province, China (F. Reiss).

### *Procladius*

Chaudhuri & Debnath (1983) describe several species of *Procladius* from the Oriental region (India) and assign them to the subgenera *Calotanypus*, *Psilotanypus* and *Procladius* s.str. Roback (1982c)

recently redescribed *Procladius* and its subgenera and it is apparent that the subgenera identified in Chaudhuri & Debnath (*op. cit.*) are incorrect but from their illustrations of the male genitalia it is possible to recognise the correct subgenera. The species included in *Calotanypus* belong in *Djalmabata*, the *Psilotanypus* species appear to belong to *Procladius* s.str. and those included in *Procladius* s.str. belong to *Holotanypus*. One of the Indian species, *Procladius noctivagus* (Kieffer), which also occurs in the Afrotropical region, belongs in the subgenus *Holotanypus* and this subgenus now occurs in both the Oriental and Afrotropical regions.

#### *Rheopelopia*

Oriental region : A male adult has been collected in Guangdong Province, China (F. Reiss).

#### *Archaeochlus*

Downes (1974) reports the presence of an undescribed species of *Archaeochlus* from Western Australia. The species possesses well developed mandibles in the adult.

#### *Podonomopsis*

This genus was incorrectly included as a nomen nudum only in the generic catalogue (Ashe 1983) and the fact that the genus had been validly described by Brundin (1966 : 272) was unfortunately omitted.

#### *Arctodiamesa*

The uncertain presence of *Arctodiamesa* in the Nearctic (Saether et al. 1984) has been confirmed from specimens collected in Alaska (Cranston & Oliver, pers. comm. to P. Ashe).

#### *Monodiamesa*

Oriental region : Two species have been found at Taoyuan, Hunan Province, China (F. Reiss).

#### *Apometriocnemus*

Palaeartic region : This genus has been discovered in material collected in Ireland (Heneghan, pers. comm.).

#### *Diplosmittia*

Neotropical region : This genus which was originally described from the West Indies within the Neotropical region (Saether 1981) has recently been discovered on the mainland of South America as an

adult male collected near Panguana, Peru (F. Reiss).

#### *Epoicocladius*

Oriental region : Pupal exuviae have been collected in surface drift in a tributary of the River Mung Lun, Yunnan Province, China (F. Reiss).

#### *Eurycnemus*

This genus is only known with certainty from the Palaeartic region and reports to date of the genus from the Nearctic, Neotropical and Australasian regions are erroneous.

#### *Krenosmittia*

Oriental region : Pupal exuviae has been collected in drift samples from a stream in northern Sulawesi, Indonesia (P. Ashe).

#### *Orthocladius (Eudactylocladius)*

Afrotropical region : A pupa belonging to this subgenus has been found high on Mount Kenya (Cranston pers. comm. to P. Ashe).

#### *Paracricotopus*

Oriental region : Pupal exuviae have been collected in a stream in northern Sulawesi, Indonesia (P. Ashe).

#### *Paralimnophyes*

Nearctic region : This genus has been recently discovered in the northern Nearctic (Cranston & Oliver, pers. comm. to P. Ashe).

#### *Parasmittia*

Nearctic region : One species of the genus has been found in Canada (Cranston & Oliver, pers. comm. to P. Ashe).

#### *Paratrissocladius*

Neotropical region : Adults of this genus have been discovered in Southern Chile (Halvorsen, pers. comm. to P. Ashe).

#### *Rheocricotopus*

The subgenera to which the Neotropical and Australasian members of the genus belong is at present unknown.

#### *Semiocladius*

Oriental region : This genus has been found recently in the Oriental region (Cranston, pers. comm. to P. Ashe).

*Stictocladius*

*Stictocladius* should not be regarded as a subgenus of *Diptocladius* but warrants full generic status because it has a larva of « Genus nr. *Lopescladius* » type as described by Coffman & Roback (1984) (Cranston & Edward, pers. comm. to P. Ashe).

*Chernovskiiia*

Oriental region : Adults of this genus have been found at Taoyuan, Hunan Province, China (F. Reiss).

*Cladopelma*

Neotropical region : *Cryptocladopelma boydi* (Lichtenberg) from Columbia now belong in *Cladopelma*.

Oriental region : There are unpublished records from Sri Lanka, India and China (Yunnan Province) (F. Reiss).

*Cryptotendipes*

Oriental region : Pupal exuviae collected in a tributary of the River Mung Lun, Yunnan Province, China (F. Reiss).

Afrotropical region : According to Cranston (pers. comm. to P. Ashe) the single African species included in *Paracladopelma* in Freeman & Cranston (1980) is really a *Cryptotendipes* species.

*Goeldichironomus*

*G. holoprasinus* (Goeldi) has been found in Hawaii and is apparently a recent aircraft introduction (Reiss & Sublette 1985).

*Nilodorum*

The concept of *Nilodorum* as used by all recent authors and in this paper is based on *Nilodorum brevibucca* Kieffer which was described from Africa and which was until recently regarded as the type-species of the genus. When compiling a catalogue of chironomid genera (Ashe 1983) it was discovered that the genus was described in an earlier paper and *N. heterochirus* Kieffer automatically became the type-species by monotypy. *N. heterochirus* was described from the Island of Trinidad (Neotropical region) and was regarded by Edwards (1931 : 320) as a synonym of *Chironomus brasiliensis* Wiedemann, 1828. It seems likely that a new name will be required for *Nilodorum* sensu auct. with *N. brevibucca* as the type-species but this cannot be done until a re-examination of the

type-material of *C. brasiliensis* and *N. heterochirus* is completed. Until this problem is resolved the concept of *Nilodorum* should be based on *N. brevibucca* and on the diagnoses of the larva, pupa and adult of the genus as given in the key work on the « Chironomidae of the Holarctic region » (Wiederholm 1983 *et seq.*).

*Paracladopelma*

Oriental region : Adult males, pupae and pupal exuvia have been collected from the Rangeet River, Darjeeling, India ; pupal exuvia which probably belong to this genus have been collected in a tributary of the River Mung Lun, Yunnan Province, China (F. Reiss).

Afrotropical region : See note under *Cryptotendipes*.

*Paralauterborniella*

Australasian region : A single adult male has been discovered near the Mc Leod River, 18 km west of Mount Carbine, Queensland (F. Reiss).

*Paratendipes*

Neotropical region : Adult males belonging to this genus have been found in Venezuela (F. Reiss).

*Polypedilum (Tripodura)*

Oriental region : Several species belonging to the subgenus *Tripodura* have been found in the Oriental part of China (R. Reiss).

*Pontomyia*

Nearctic region : Larvae have been collected in a bottom grab at Sapper Point, near Key Largo, Florida (Caldwell, pers. comm. to P. Ashe).

*Robackia*

Afrotropical region : Adult males have been collected around Samburu Lodge, Kenya (*leg* S. Koch, *det.* Saether).

Oriental region : Pupal exuviae and a mature pupa were collected from the Darjeeling River at 250 m.a.s.l. The genus is also known from pupal exuviae collected from a tributary of the River Mung Lun, Yunnan Province and at Taoyuan, Hainan Province, China (F. Reiss).

*Saetheria*

Neotropical region : Adult males and pupal skins have been found in the Amazonian region (F. Reiss).

*Stempellinella*

Afrotropical region : One species has been found recently at Lake Tana, Ethiopia (F. Reiss).

**6. Overview of chironomid distribution**

Of the 307 described valid genera only 38, representing the subfamilies Telmatogetoninae, Tanypodinae, Orthocladiinae and Chironominae, are known to have a worldwide distribution. The investigation of different habitat types in various areas of each zoogeographical region is important to determine if particular genera are present or likely to be absent. Genera which occur in very specific and difficult to sample habitats are often missed by normal collecting methods and this may account for some of the anomaly in generic representation between the Nearctic and the Palaearctic regions. To date the known world chironomid fauna totals some 3700 valid species (Table 3), representing perhaps only 30% - 35% of the estimated chironomid fauna of 10,000 - 12,000 species. In terms of the numbers of species and our knowledge of the distribution of species within regions the Palaearctic is the best known followed by the Nearctic, Afrotropical, Australasian, Neotropical and Oriental. Most Neotropical and Oriental species are only known from one or two countries with many only known from the original type-locality. Our knowledge of the world fauna outside the Holarctic can be brought into perspective if the figures for the number of genera (Table 1) and species (Table 3) for the other regions are compared with a small, well investigated, region of the Holarctic e.g. Great Britain. Great Britain, with about 128 genera and over 500 species (Langton 1984), occupies a land area of only 229,979 sq.km. and has a fauna which at present is greater than the described fauna of each region except the Palaearctic and Nearctic.

For the major subfamilies the following general rule applies : Progressing from polar regions to the equator (i.e. high latitudes to low latitudes) or from high mountains to lowlands there is an increase in diversity and numbers of specimens of the Chironominae and Tanypodinae with a corresponding decrease in the Orthocladiinae, Podonominae, Diamesinae and Prodiamesinae ; the reverse is true progressing from the equator towards the polar regions or from lowlands to high mountains. This rule is a reflection of the adaptations of the major

subfamilies to prevailing environmental conditions (oxygen concentration, water temperature, climate, altitude, current speed in flowing water, etc.). The Telmatogetoninae are an exception to the above rule in that they are predominantly marine and a different set of factors apply. Our knowledge of the ecology of the three smallest subfamilies, Chilenomyiinae, Buchonomyiinae and Aphroteniinae, is very incomplete but they appear to mostly avoid climatic or environmental extremes.

In chapter 4 we discussed the importance of continental drift in relation to the distribution of some chironomid genera. Such vicariance events have played the primary role in establishing the distribution of chironomid subfamilies, tribes and some genera since the breakup of Pangaea. However, the distribution of all chironomid genera cannot be explained by vicariance events alone and dispersal (e.g. *Diamesa*, Chapter 3.7) has played an important role, in recent times, since the middle to recent Tertiary. A comparison of the chironomid fauna of the Holarctic with that of the Neotropical, Afrotropical and Australasian regions respectively reveals that the Neotropical region has exchanged some cold adapted and many warm adapted groups with the Holarctic ; the Afrotropical region has exchanged mainly warm adapted groups and the Australasian region (as present incomplete knowledge indicates) has exchanged the least (mainly some warm adapted groups). The ability of each of the three regions to exchange faunal elements with the Holarctic is directly related to the physical conditions linking or separating these regions from the Holarctic. An almost continuous mountain chain, which stretches from Alaska through Central America and linking to the Andes mountains (which extend from Colombia to Patagonia), provides a pathway by which cold adapted forms from the Nearctic and Neotropical regions can migrate southwards and northwards respectively. A similar exchange of warm adapted groups between the Neotropics and the Nearctic is possible along the lowland coastal strips of Central America and by island hopping along the Lesser and Greater Antilles to Florida. In the Afrotropical region the lack of a continuous high mountain range between the East African Highlands and the Drakensberg Range has resulted in the fact that most (if not all) cold adapted Palaearctic groups have not reached Southern Africa although a few extend as far south as the East African Highlands. A

considerable number of warm adapted groups have been able to migrate from the Afrotropical region northwards and from the southern Palaearctic southwards mainly via the Middle East and along the Nile Valley (the Sahara, in more recent times at least, has acted as a barrier to migration north or south). The Australasian region is separated from the Palaearctic by the Oriental region and in order for any exchange to take place between the Palaearctic and Australasian regions groups must occur in and have migrated through the Oriental region. Migration between the Palaearctic and Australasian regions is very difficult because there is no continuous land connection and large areas of open sea exist interspersed with numerous islands. Very few cold adapted Palaearctic or Australasian groups are likely to be able to migrate south and north respectively because of the absence of high mountains necessary for temperate conditions to exist and because of the lack of continuity of the mountain ranges of the East Indies with the Himalayas or with the New Guinea Highlands. The main exchange likely is between warm adapted groups but our knowledge of the Australasian fauna and that of the lowlands of the eastern Palaearctic (central China) and S.E. Asia is very incomplete.

An analysis of the zoogeographical distribution of any animal group relies on a vast amount of accurate and reliable data on the distribution of individual taxa. In spite of the detailed information presented here our knowledge of the distribution of individual genera/subgenera throughout the world is still very inadequate and it is not possible to deal with the zoogeography in any greater detail. For the majority of genera it is not yet possible to deal with such topics as « centre of origin », minimum age or even the total distribution within a zoogeographical region. We need to know more about the present distribution of individual taxa, their phylogenetic relationships, ecology and fossil record and relate this data to geological and climatological events in different regions over the time scale of the existence of the group.

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