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# Distribution of Chironomidae (Diptera) in the river continuum

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## Introduction

Vannote *et al.* (1980) described a framework - the river continuum system - for integrating predictable and observable biological features in lotic systems. They grouped running waters into headwaters (orders 1-3), medium-sized streams (4-6), and large rivers (>6). Many headwaters are characterized by low temperatures and high water velocity resulting in a stony substrate. Further they are often strongly influenced by the riparian vegetation which reduces autotrophic production by shading and provides large amounts of allochthonous material. Accordingly the invertebrate fauna in headwaters is dominated by cold-stenothermous shredders or collectors. As stream size increases, temperature increases, slope and water velocity decrease resulting in a varied substrate of stone, gravel and sand. The reduced importance of terrestrial organic input is replaced by an increased autochthonous production and transport of fine organic matter from upstream increasing the importance of grazers and detrital collectors at the expense of shredders. In large rivers maximum temperatures occur and the substrate often tends to be gravel, sand and silt. The rivers receive quantities of fine particulate organic matter from upstream. A phytoplankton production can occur, but may be limited by depth and turbidity. The invertebrates are dominated by eurythermic detrital collectors.

Thienemann (1954) described a number of chironomid communities in primarily high altitude streams, but had at that time only few data from lowland streams and very little from large rivers. The aim of this paper is to review the faunistic studies on running water chironomids in order to see if the observed chironomid communities fit into the proposed conceptual river continuum framework.

## Material and methods

Data were extracted from the studies listed in Table 1, which cover 104 sites in 80 different watercourses. Further data from 11 sites in New Zealand and Australia are listed in Table 2. A criterium for including these studies was that they all had identified chironomids to the same taxonomic level (prevailing to species level), and this had to be consistent for all subfamilies and tribes. In fact, many studies had to be excluded due to inadequate identification especially for Chironomini and Tanytarsini. Also studies published in national reports were in most cases neglected. Because sampling was done in many different ways quantitative aspects were omitted and species lists were based only on presence or absence of a species. In a number of studies altitude was mentioned, otherwise it was determined from topographic maps. Altitude and latitude are important factors determining the temperature. Informations on temperature and substrate types when available were also listed in Table 1. Species composition were extracted from 70 European studies (marked with an (*) in Table 1) and stored in an unpublished database.

Because environmental data and chemical/physical descriptions of sampling sites often are scarce or missing, two indirect ordination techniques were used to summarize and arrange sites and species in an ordination diagram, in the hope that ecological relationships would emerge. A principal components analysis (PCA), based on the percentage composition of the six most common subfamilies/tribes in 104 studies, and a detrended correspondence analysis (DCA) based on presence/absence data (1/0) of 251 species in 67 studies, were carried out through the computer program CANOCO (ter Braak, 1992a). PCA and DCA assume a linear and a unimodal (bell shaped) model for the relationships between the response of each subfamily/species to the ordination (environmental) axes, respectively.

## Results

### *Percentage distribution of chironomid subfamilies/tribes*

From each site the percentage of species in each chironomid subfamily and the tribes Chironomini/Tanytarsini was calculated (Table 1). From the original descriptions of the localities, it was decided to delimit eight northern temperate river types: (1) glacial brooks, (2) alpine streams, (3) subalpine streams, (4) mountain streams, (5) lower mountain streams, (6) lowland cold streams, (7) lowland warm streams and (8) lowland warm rivers. Further a few localities in subtropical and tropical streams were established as a separate group. This delimitation was based on a combination of latitude, altitude and temperature. In fact it did not include stream order, because most European studies unfortunately did not state stream order and without very detailed topographic maps this was impossible to determine. However, if we applied the river continuum to this typing, (1), (2) and (3) all would be headwaters, (7) medium-sized streams and (8) large rivers, whereas (4), (5) and (6) included both headwaters and medium-sized streams.

The zoocenoses of chironomids in the eight categories of northern hemisphere temperate running waters (Table 1, nos 1-95) can be described in the following way. In a typical glacial brook, where temperature is low, rarely exceeding 4°C in summer, and substrate is composed mainly of boulders and large stones, there are few species (average 7) characterized by the cold-stenothermous Diamesinae making up 45 to 67% of the taxa. The remaining species are Orthocladiinae. In lower altitudes the temperature increases as does species richness which in the alpine brook on average is 23. The Orthocladiinae takes over the dominance with 60-80% and the Tanytarsini comes in with about 5%.

In subalpine streams, the temperatures in summer may reach 10°C and the substrate becomes more varied with an increase in smaller stones and gravel. Species richness increases to an average of 49 species and most subfamilies/tribes are represented. Orthocladiinae dominates with about 60%, although Diamesinae is still important making up 20%.

The mountain or montane streams are physically very similar to low alpine streams, but always have finer particles in their substrate. Further, water temperature in summer during the day-time may be quite high. This results in a further increase in species richness, with an average of 71 species. This increase occurs in all subfamilies/tribes except the Diamesinae, resulting in lower relative abundances (average 11%).

The lower mountain or lower montane streams are a mixture between the montane and lowland streams with substrate types ranging from boulders to sand and silt; often macrophytes occur. In the preceding water types, primary producers mainly are mosses and periphytes. Average monthly temperatures may still be quite low, but short-termed maximum temperatures may exceed 20°C. Maximum species richness (on average 95 species) is recorded here. The Diamesinae and Orthocladiinae decrease to 6% and 59%, respectively, while Chironomini increases to 10%.

The summer-cold lowland streams are fed mainly by ground water causing similar temperature regimes to lower montane streams. However, the prevailing substrate is more soft and macrophytes are nearly always present. The species richness averages only 60, indicating fewer habitats than in the lower montane streams. The percentage of Diamesinae is unchanged, but the Orthocladiinae averages only 53%, while contribution of the Chironomini increases to 15%.

In the summer-warm lowland streams, the average monthly temperature in summer exceeds 20°C, otherwise they physically resemble summer-cold streams. The species richness is on average somewhat higher, but the average percentage of Orthocladiinae decreases to 46% while Chironomini increases to 19%. The summer-warm lowland rivers correspond the large rivers of the river continuum concept. The temperature in summer is always high, the substrate is mainly sand and silt though areas with stone and gravel occur. Macrophytes, if present, occur only in minor extension along the banks. Species richness is on average 67. Diamesinae and Orthocladiinae decrease to 1% and 36%, respectively, while Chironomini makes up 39%.

The described changes in Diamesinae, Orthocladiinae and Chironomini along the river continuum are - in spite of large fluctuations within the single running water type - distinct and significant (Fig. 1). The changes in the remaining subfamilies/tribes are less distinct. Tanypodinae increases in average from 4-5% in the subalpine and montane streams to 10-15% further downstream the river continuum. In alpine streams Tanytarsini constitutes about 5% and remains stable with 10-15% further downstream. Prodiamesinae is found when water temperature reach 10°C and makes up 1-3% further downstream. They apparently have their maximum in the summer-cold lowland streams and may eventually disappear in the very large rivers. The species poor Podonominae is found scattered in the range from subalpine to lower montane streams, while the single species of Buchonomyiinae is found only from a few lower montane streams to warm lowland rivers.

The chironomid communities in subtropical/tropical streams and rivers are very poorly known (Table 1, nos 96-104, Table 2), but apparently the higher average temperatures benefit Chironomini, which makes up a higher percentage compared to otherwise similar temperate running waters.

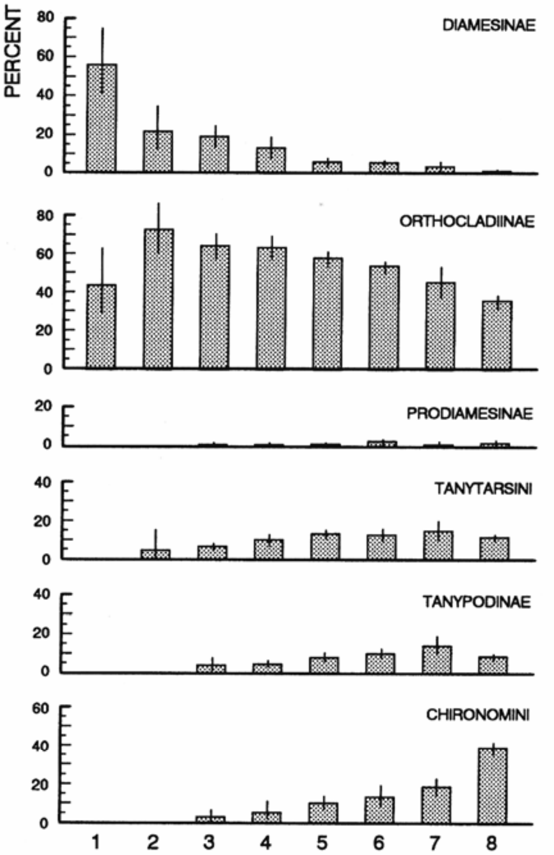


**Figure 1.** Average percentage composition (± 95% confidence limits) of six subfamilies/tribes in eight running water categories: (1) glacial brooks, (2) alpine streams, (3) subalpine streams, (4) montane streams, (5) lower montane streams, (6) lowland summer-cold streams, (7) lowland summer-warm streams and (8) lowland large rivers.

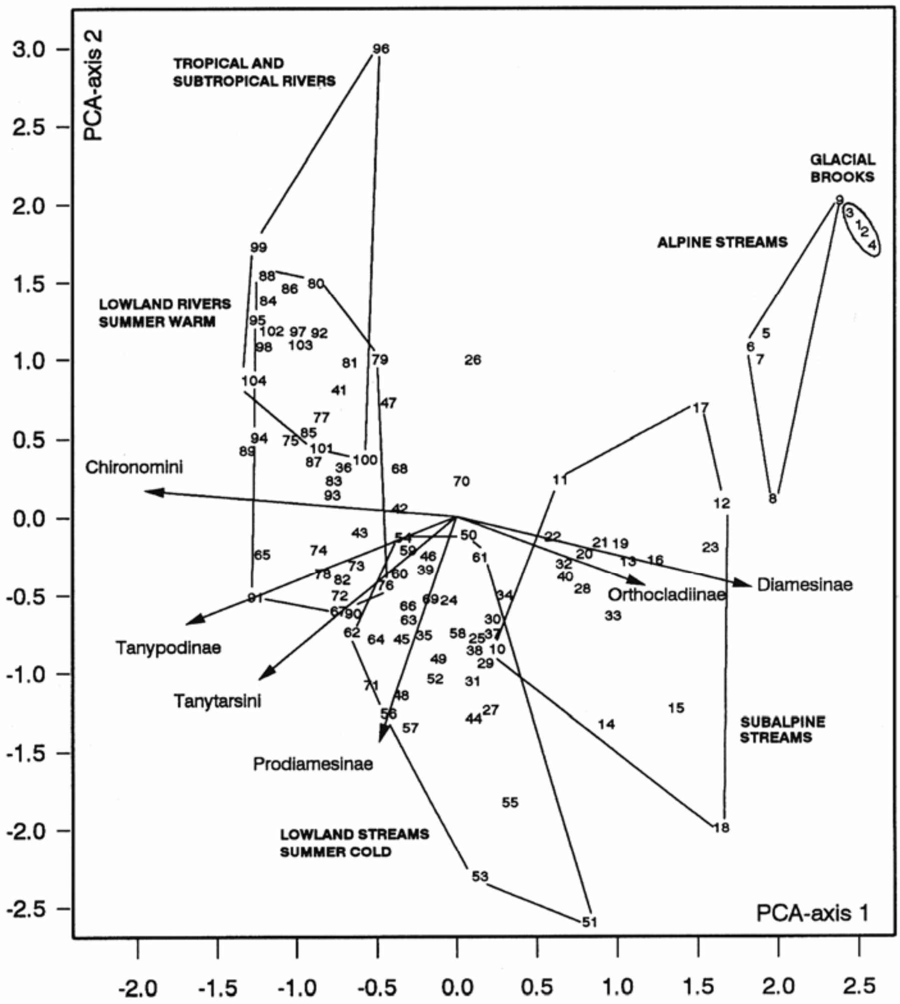


**Figure 2.** PCA-biplot showing the separation of six running water categories based on the percentage distribution of chironomid subfamilies/tribes in 104 running water sites. Arrows are pointing in the directions of maximum variation in percentage contribution of subfamilies.

Chironomid studies from Australia and New Zealand demonstrate a somewhat similar zonation as in the northern hemisphere, except that other subfamilies/tribes complicate the patterns (Table 2). Aphroteniinae occur in low order streams (Cranston and Edward, 1992); in headwaters and cooler streams Podonominae are abundant; Diamesinae are species-poor although sometimes abundant; Prodiamesinae are absent and Pseudochironomini (*Riethia* spp.) may be numerous (especially in individuals) in middle order streams. These patterns are evident in temperate south-eastern Australia (Metzeling *et al.*, 1984) and Mediterranean south-west Australia even though the headwaters here are of low elevation (Bunn *et al.*, 1986, Storey and Edward, 1989). In tropical, monsoonal northern Australia, where catchment areas are also of modest elevation, subfamily representation is restricted. Diamesinae is absent, Aphroteniinae rare only in the upper reaches and Orthocladiinae frequent only in low order streams. In the middle sections and lowland flood-plains Chironomini dominate; Tanypodinae and Tanytarsini are distributed throughout the continuum (Cranston, 1991).

Wilson (1980) characterized chironomid groups as "rhithral" (Pentaneurini, Diamesinae, Orthocladiinae, Chironomini connectentes) or "potamal" (Tanypodini, Macropelopiini, Prodiamesinae, Chironomini genuini, Tanytarsini) arguing that the first group occurs primarily in rhithron and the latter in potamon according to the zonation suggested by Illies and Botosaneanu (1963). The calculated percentage of rhithral groups declines gradually from 100% in glacial brooks to an average of 58% in lowland warm rivers (Table 1, nos 1-95). Thus, this approach shows a great similarity to the succession described on the basis of the Diamesinae/Orthocladiinae/Chironomini relationships.

In a PCA ordination biplot (Fig. 2) a high separation (69% of variance) was found along axis 1, and six of the named running water categories could be outlined without major overlap. The arrows point in the direction of maximum variation in percentage contribution of subfamilies (ter Braak and Prentice, 1988), and a water temperature and/or altitude gradient could be interpreted along axis 1, mainly due to the distribution of Diamesinae and Chironomini. This was shown by plotting the maximum water temperature and the altitude for each site to the corresponding axis 1 site score from the ordination analyses (Fig. 3). Temperature appears to better explain the separation along axis 1 than does the altitude. However, these two factors are related.

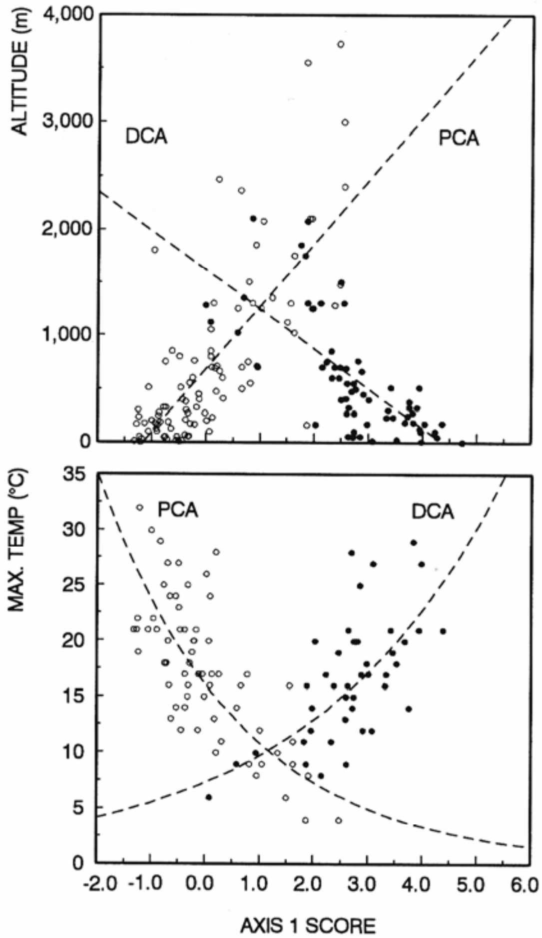


**Figure 3.** Correlation between ordination-axis 1 site score and the corresponding altitude (m a.s.l.) and maximum temperature (°C) for the site.

### *Distribution of chironomid species*

A total of 514 chironomid species are recorded from 70 European running water sites representing 52 different watercourses. This is about 50% of the total number of Chironomidae known from Europe (Table 3). The species-rich subfamilies are equally represented (44-54%), while the occurrence of Tanypodinae and Diamesinae in running water make up 64% and 71% of total numbers, respectively. About half of the recorded running water chironomids occurred in less than four localities and we eliminated these from the DCA analysis. This did not alter the proportion between the subfamilies/tribes (Table 3). The distribution of the remaining 67 running water sites in a DCA analysis with 251 species is shown in Fig. 4. The alpine, subalpine and montane streams are found to the left, the large rivers are placed to the right, and the lower montane and lowland streams overlap in the centre of the diagram. In fact, the groups which can be distinctly delineated are placed in the same geographically region. Thus, for example, the alpine, subalpine and montane streams in Norway, France and Poland are well separated, and the Mittel and Nieder Rhein are found to be different from other lowland rivers in Germany.

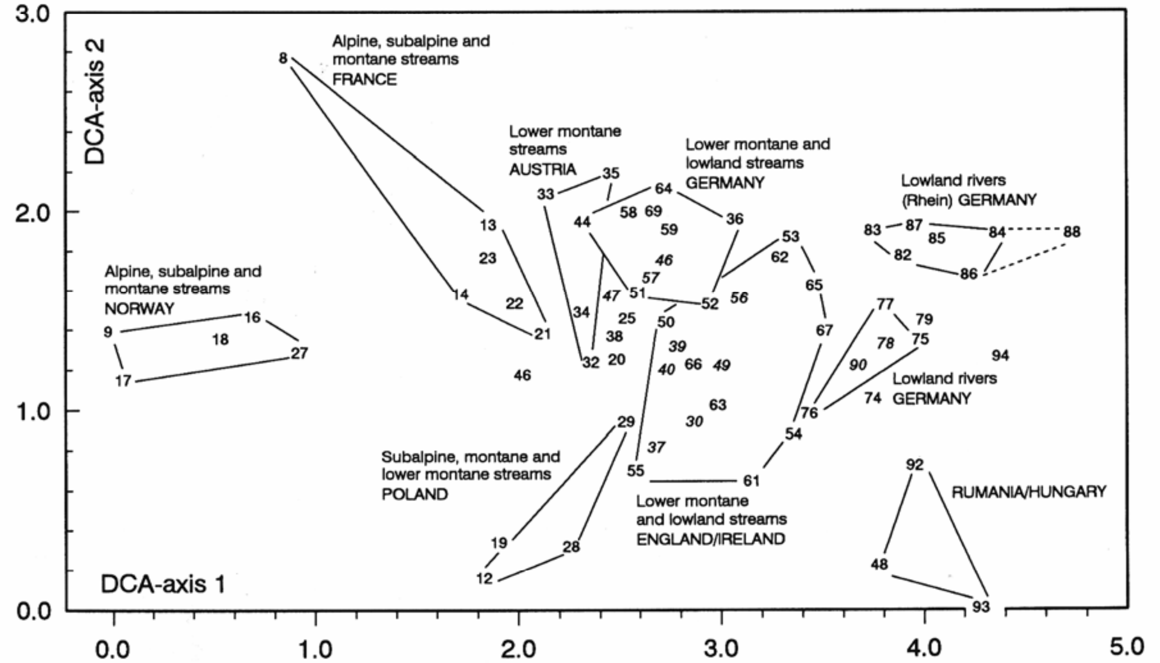


**Figure 4.** Ordination by DCA showing the scores of 67 European running water sites based on presence/absence data of 251 chironomid species. Sites in *cursive* do not belong to the outlined categories.

The distribution of the 251 species in the same DCA-diagram is shown in Fig. 5. The Diamesinae and Podonominae species are mainly placed to the left with few species in the centre, while the Chironominae concentrates to the right in the diagram. The Orthocladiinae is distinctly placed in the middle section of the diagram with some species to the left. The Tanypodinae is also centred though with a tendency to the right. The Tanytarsini is evenly distributed from left to right although they avoid the extreme margins. The Prodiamesinae is centred but with *Prodiamesa rufovittata* to the right.

The gradient from left to right along axis 1 in Figs 4-5 can be clearly correlated to increasing maximum temperature and less distinctly to decreasing altitude (Fig. 3). The gradient along axis 2 is less obvious, but may to a large degree reflect geographic distribution. The distribution along the temperature gradient reflects again the cold-stenothermic nature of most Diamesinae and of some Orthocladiinae and Tanytarsini, while many Chironomini can be considered warm-stenothermic. Many Orthocladiinae centred in the diagram (Fig. 5) have a wide distribution along the river continuum indicating an eurythermic nature.

## Discussion

Although great overlaps occur, especially in the lower mountain and summer-cold lowland stream categories, it was possible to demonstrate distinct shifts in the chironomid community along the river continuum. Also it was possible to correlate these shifts to temperature, which was the only environmental factor stated in nearly all papers. Rossaro (1992) lists optimum mean water temperature (range 4-25°C) for 127 chironomid species from Italian streams and rivers based on their abundance in 991 sites. The cold-stenothermic species were represented by mainly Diamesinae and Orthocladiinae,

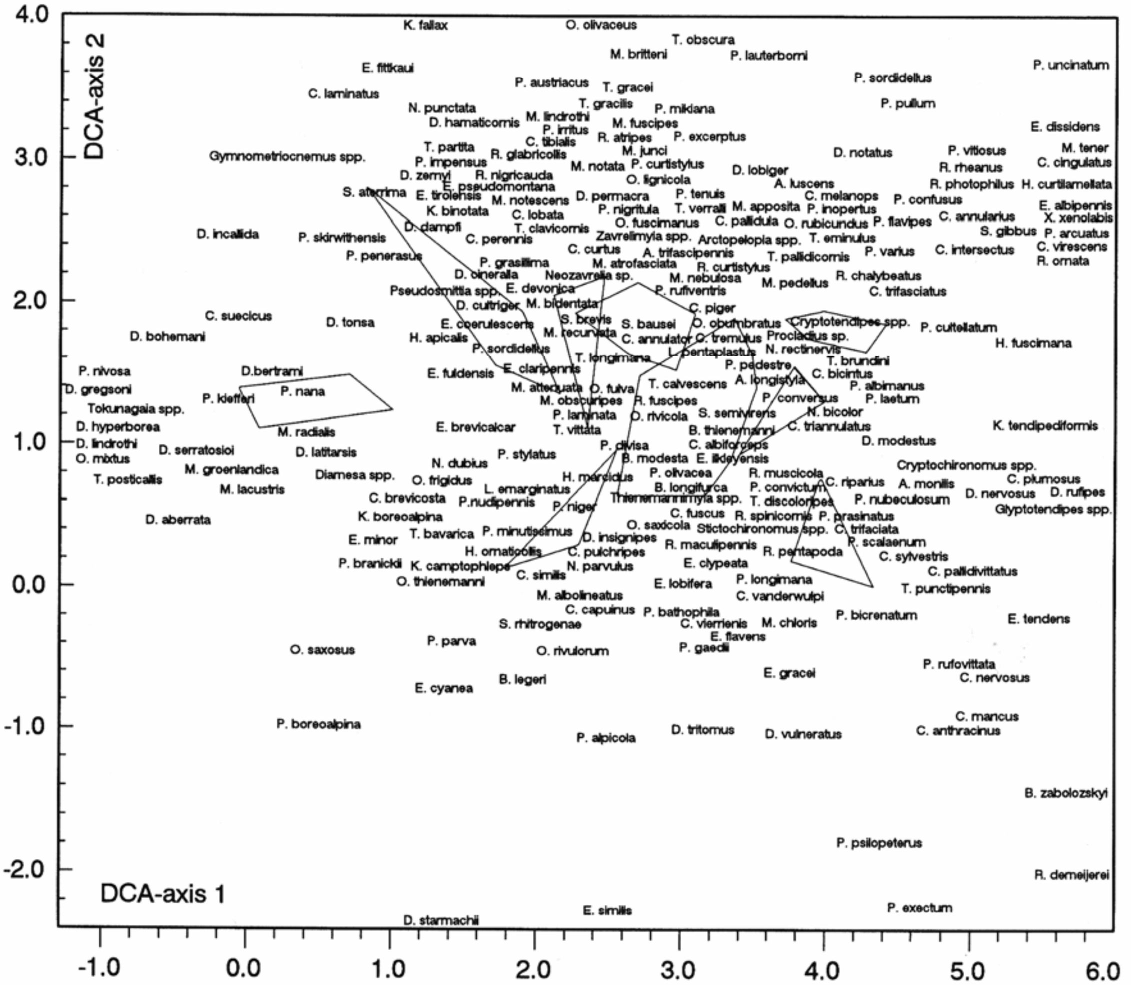


**Figure 5.** DCA-ordination diagram showing the 251 chironomid species scores of Fig. 4.

while the Chironomini dominated in the range from 17-25°C. A comparison between these optimum mean temperatures of 88 species and the corresponding DCA-axis 1 coordinates (Fig. 5) shows a fairly high correlation (Fig. 6). This correlation makes possible a rough estimate of the remaining species optimum temperature. Rossaro (1992) stated furthermore that most species were cold-stenothermous with an optimum temperature near their minimum tolerance value, whereas the warm water species were more or less eurythermous. This means that temperature may be the key factor for distribution of Diamesinae and cold-stenothermic Orthocladiinae, while other factors may be more important for Chironomini.

Substrate type and available food are supposed to influence chironomid distribution fully as much as temperature. However, these two factors are to some degree linked to temperature as they - according to the river continuum concept - change downstream within the continuum. Functional feeding groups have been linked to the river continuum concept. However, because there is an absence of shredders among Chironomidae, this notion has to be modified if chironomids are considered in isolation. Further, high latitude or altitude headwaters may deviate from the general pattern with regard to autotrophy/heterotrophy by lacking the shading riparian vegetation (Statzner and Higler, 1985). Accordingly algal grazers such as Diamesinae and some Orthocladiinae can dominate glacial brooks, alpine and subalpine streams. At lower altitudes, the shading effect of riparian vegetation may diminish algal grazers in headwaters and increase the importance of scrapers and collectors feeding on a more detritus rich food (many Orthocladiinae and Tanytarsini, some Chironomini). In lowland streams and rivers low water velocity and high amounts of particulate organic matter will benefit some filterers (e.g. *Rheotanytarsus* spp.) and deposit feeders as many Chironomini. Ward and Williams (1986) found a similar zonation of chironomids along the Rouge River in Ontario, Canada, and demonstrated a difference in available food and food uptake along this gradient.

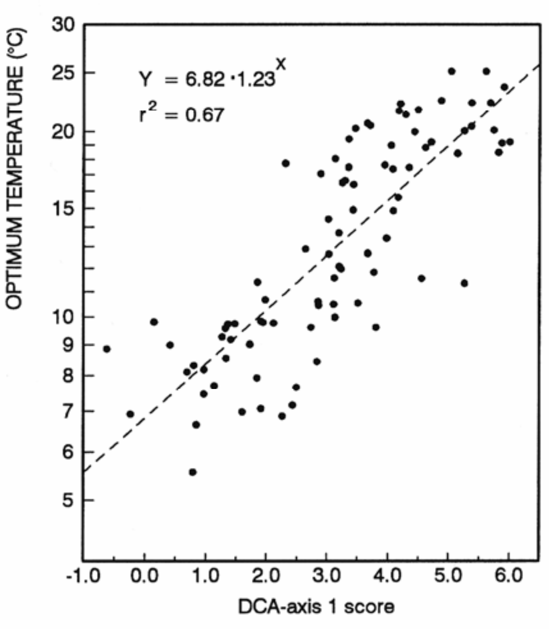


**Figure 6.** Correlation between DCA-axis 1 species score and weighted average optimum temperature (Rossaro, 1992) for 88 species.

They interpreted this zonation to be influenced by both temperature and substrate. The importance of substrate in determining species composition is demonstrated in Little Boulder Creek, where Tilley (1989) found three species of Chironomini in a canyon site with boulders and stones. Upstream he recorded six species of Chironomini at the same low temperature, but in a meadow site with a gravel and sand dominated substrate. Furthermore, Rae (1985) demonstrated strong differences in habitat preference for deposit-feeding chironomid species when offered a choice of different sediment grain size, sediment heterogeneity and content of organic matter.

The discussed subfamilies/tribes of chironomids all are very rich in species (cf. Table 3) and large differences in temperature optimum, substrate and food preference occur between species within these groups. Therefore, any generalization based on these large systematic groups will be broad. A better delimitation should be achieved by selected groups of species. However, the large number of species (> 500) in European running waters makes a clustering difficult and confused even when the number of species is reduced to about 250 species. Further, a large number of species occur in many of the outlined running water categories, leaving the remaining Diamesinae and Chironomini species to characterize the uppermost and lower parts of the river continuum (cf. Fig. 5). The DCA analysis also grouped running water sites more to geographic position than to running water categories (Fig. 4). A similar separation of running water sites in geographic groups was found by Aagaard (1993) by analyzing 42 sites in 16 different watercourses. This was unexpected, because most European chironomid species seem to be widely distributed throughout Europe (cf. Ashe and Cranston, 1990) and Lindegaard (1995) found 75% of the known European species reported from the Nordic Countries (Denmark, Sweden, Norway, Finland and Iceland). A high separation to geographic areas might therefore be due to either a real difference in geographic distribution or to the fact that identification is not good enough. Some high altitude chironomid species seem to be restricted to single mountain massifs (cf. Laville and Vinçon, 1991; Casas and Vilches-Quero, 1993) or to Scandinavian mountains *versus* the Alps (e.g. Sæther, 1968). Lower mountain and lowland chironomids, however, seem to be very widely distributed.

The steady increase in species richness from glacial brooks to a maximum in lower mountain streams followed by a decrease further downstream agrees with Coffman (1989), who stated a maximum richness of lotic chironomids in 3rd order streams due to primarily a high ecological heterogeneity. These findings are consistent with the river continuum concept.

The observed changes in Chironomidae along the river continuum are - with the implicated modifications - applicable to the river continuum concept. The river continuum concept was proposed by Vannote *et al.* (1980) to be of world-wide applicability. This statement has subsequently been discussed by a number of authors (e.g. Winterbourn *et al.*, 1981, Statzner and Higler, 1985). The described changes in chironomid communities are based almost exclusively on data from northern hemisphere temperate streams. If these changes can be considered valid world-wide, then we must await further progress in southern hemisphere taxonomic and basic faunistic studies on chironomids.

Table 1. Number of chironomid taxa and percentage distribution of chironomid subfamilies/tribes in a wide range of temperate and a few subtropical and tropical running waters representing major sections of the river continuum. Subfamilies/tribes are: Podonominae (1), Tanypodinae (2), Buchonomyiinae (3), Diamesinae (4), Prodiamesinae (5), Orthocladiinae (6), Chironomini (7) and Tanytarsini (8). Rhithral groups are Pentaneurini, Diamesinae, Orthocladiinae, Chironomini connectentes (Wilson 1980). Substrate "types" are delimited as boulder (bo), stone (st), gravel (gr), sand (sa), silt (si), periphyton (pe), macrophytes (ma), mosses (mo), detritus (de), riffles (ri), leave packs (lp), and snag (sn). An (*) indicate localities used in a DCA analyses of species distribution in European running waters.

| No | River | Country | Lati-tude | Altitude m a.s.l. | Tempera. °C | | % of subfamilies/tribes | | | | | | | | Total no. taxa | % rhit. gr. | Substrate | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ra | mean | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | | | |
| **Glacial brooks** | | | | | | | | | | | | | | | | | | |
| * 1 | Finse Brook | Norway | 60°N | 1550-1400 | 1- 4 | | 0 | 0 | 0 | 50 | 0 | 50 | 0 | 0 | 4 | 100 | bo, st | Sæther 1968 |
| 2 | "The Alps" | Europe | 47°N | c. 3000 | | 1 | 0 | 0 | 0 | 63 | 0 | 37 | 0 | 0 | 8 | 100 | bo | Thienemann 1954 |
| 3 | North Boulder Cr. | CO, USA | 40°N | 3800-3650 | | 1 | 0 | 0 | 0 | 5 | 0 | 55 | 0 | 0 | 11 | 100 | bo | Elgmork and Sæther 1970 |
| * 4 | Rio Plima | Italy | 46°N | 2800-2000 | | | 0 | 0 | 0 | 67 | 0 | 33 | 0 | 0 | 6 | 100 | st | Kownacki 1991 |
| Average | | | | | | | 0 | 0 | 0 | 56 | 0 | 44 | 0 | 0 | 7 | 100 | | |
| **High mountain brooks, "alpine"** | | | | | | | | | | | | | | | | | | |
| 5 | "The Alps" | Europe | 47°N | > 2100 | 1- 8 | | 0 | 0 | 0 | 16 | 0 | 80 | 0 | 4 | 25 | 96 | bo | Thienemann 1954 |
| 6 | North Boulder Cr | CO, USA | 40°N | 3650-3450 | | 4 | 0 | 0 | 0 | 14 | 0 | 81 | 0 | 5 | 21 | 95 | bo, mo | Elgmork and Sæther 1970 |
| 7 | Bathurst Island | NWT, Canada | 75°N | 163- 0 | 1- 4 | | 0 | 0 | 0 | 15 | 0 | 80 | 0 | 5 | 20 | 95 | st, gr | Hayes and Murray 1987 |
| * 8 | Ossau Valley | France | 43°N | > 2100 | | | 0 | 0 | 0 | 29 | 0 | 59 | 0 | 12 | 17 | 88 | bo | Laville and Vinçon 1991 |
| * 9 | Atna, Vidjedalsb | Norway | 62°N | 1280 | | | 0 | 0 | 0 | 35 | 0 | 65 | 0 | 0 | 31 | 100 | | Aagaard *et al.* 1989 |
| Average | | | | | | | 0 | 0 | 0 | 22 | 0 | 73 | 0 | 5 | 23 | 95 | | |
| **High mountain brooks, "subalpine"** | | | | | | | | | | | | | | | | | | |
| 10 | Ll. Boulder Cr. me | Idaho, USA | 44°N | 2466 | | | 1 | 8 | 0 | 10 | 4 | 62 | 12 | 4 | 52 | 85 | gr, sa | Tilley 1989 |
| 11 | Ll. Boulder Cr. ca | Idaho, USA | 44°N | 2362 | | | 1 | 5 | 0 | 15 | 0 | 63 | 7 | 7 | 41 | 90 | bo, st, gr | Tilley 1989 |
| * 12 | High Tatra streams | Poland | 49°N | 2000-1500 | 1-11 | | 0 | 4 | 0 | 20 | 0 | 73 | 0 | 4 | 56 | 96 | bo, st, gr, mo | Kownacki 1971 |
| * 13 | Estaragne | France | 43°N | 2300-1850 | 1- 9 | | 0 | 5 | 0 | 19 | 0 | 65 | 2 | 9 | 58 | 91 | bo | Laville and Lavandier 1977 |
| * 14 | Ossau Valley | France | 43°N | 2100-1600 | | | 0 | 6 | 0 | 16 | 2 | 70 | 2 | 9 | 56 | 89 | bo, mo | Laville and Vinçon 1991 |
| 15 | "The Alps", übergb. | Europe | 47°N | | 2-10 | | 0 | 6 | 0 | 14 | 2 | 73 | 0 | 6 | 51 | 88 | st, mo | Thienemann 1954 |
| * 16 | Blesbekken | Norway | 62°N | 1350 | < 10 | | 0 | 3 | 0 | 26 | 0 | 59 | 2 | 10 | 54 | 87 | bo, st | Aagaard *et al.*1987 |
| * 17 | Atna, Skrangleh. | Norway | 62°N | 1120 | 0- 6 | | 5 | 0 | 0 | 32 | 0 | 51 | 3 | 8 | 37 | 89 | bo, st | Aagaard *et al.* 1989 |
| * 18 | Atna, Dørålsæter | Norway | 62°N | 1020 | 0- 9 | | 0 | 3 | 0 | 32 | 3 | 53 | 0 | 11 | 38 | 87 | | Aagaard *et al.* 1989 |
| Average | | | | | | | 1 | 4 | 0 | 20 | 1 | 63 | 3 | 8 | 49 | 89 | | |
| **Mountain streams, "montane"** | | | | | | | | | | | | | | | | | | |
| * 19 | High Tatra streams | Poland | 49°N | 1500-1000 | 1-12 | | 0 | 4 | 0 | 17 | 1 | 70 | 3 | 4 | 69 | 93 | bo, st, gr, mo | Kownacki 1971 |
| * 20 | V.- & H. Rhein | Switzerland | 47°N | 2000-1000 | | | 0 | 4 | 0 | 9 | 0 | 69 | 2 | 16 | 45 | 84 | | Wilson and Wilson 1985 |
| * 21 | Ossau Valley | France | 43°N | 1600-1000 | | | 0 | 2 | 0 | 13 | 1 | 64 | 4 | 9 | 75 | 88 | | Laville and Vinçon 1991 |
| * 22 | Neste d'Aure | France | 43°N | 1500-1000 | 1-14 | | 0 | 6 | 0 | 12 | 0 | 66 | 5 | 11 | 65 | 88 | st, gr, pe | Gazagnes and Laville 1985 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| * 23 | L'Eau d'Olle | France | 45°N | 1900- 713 | 3-16 | | 0 | 3 | 0 | 18 | 0 | 73 | 0 | 8 | 40 | 93 | bo, st, gr | Gay 1982 |
| 24 | "Mittelgebirge" | Germany | | | 2-17 | | 0 | 10 | 0 | 5 | 1 | 62 | 10 | 12 | 126 | 82 | st, gr, mo | Thienemann 1954 |
| * 25 | Sierre Nevada | Spain | 37°N | 1700- 900 | | | 0 | 8 | 0 | 9 | 1 | 57 | 10 | 14 | 144 | - | | Casas and Vilchez-Quero 1989 |
| 26 | Llobregat a. dam | Spain | 42°N | 1350- 750 | 1-24 | | 0 | 4 | 0 | 4 | 0 | 73 | 12 | 8 | 26 | 92 | bo, st | Prat *et al.* 1983 |
| * 27 | Atna, Vollen | Norway | 62°N | 710 | 0-10 | | 2 | 8 | 0 | 14 | 2 | 50 | 12 | 12 | 50 | 74 | | Aagaard *et al.* 1989 |
| Average | | | | | | | <1 | 5 | 0 | 11 | 1 | 65 | 6 | 10 | 71 | 87 | | |
| **Lower mountain streams, "lower montane"** | | | | | | | | | | | | | | | | | | |
| * 28 | High Tatra streams | Poland | 49°N | 1000- 500 | 1-17 | | 0 | 4 | 0 | 14 | 1 | 59 | 4 | 8 | 101 | 78 | st, gr, sa, mo | Kownacki 1971 |
| * 29 | Grajcarek Stream | Poland | 50°N | 840- 540 | 0-13 | | 0 | 7 | 0 | 7 | 2 | 61 | 8 | 12 | 74 | 81 | bo, st, gr | Kownacki 1982 |
| * 30 | Rajcianka Stream | Slovakia | 49°N | 940- 384 | 0-17 | | 0 | 3 | 0 | 8 | 3 | 63 | 11 | 11 | 71 | 80 | bo, st, gr, sa | Bitusik and Ertlova 1985 |
| 31 | Windrow Farm St. | Canada | 44°N | 800 | 2-16 | 7 | 0 | 8 | 0 | 3 | 2 | 65 | 4 | 18 | 62 | 79 | bo, st, gr, mo | Singh and Harrison 1984 |
| * 32 | Wagrainer Ache | Austria | 47°N | 700 | -16 | | 1 | 6 | 0 | 15 | 1 | 66 | 6 | 5 | 164 | 91 | bo, st, sa, pe | Moog and Janecek 1991 |
| * 33 | Schreierbach | Austria | 48°N | 700 | 4- 8 | | 0 | 6 | 0 | 12 | 0 | 64 | 1 | 16 | 81 | 84 | st, mo, pe | Caspers 1983a |
| * 34 | Obere Seebach | Austria | 48°N | 600 | 2-11 | | 1 | 7 | 0 | 8 | 1 | 67 | 7 | 10 | 102 | 87 | st, gr, sa, mo | Schmid 1986, Bretschko 1991 |
| * 35 | Teichbach | Austria | 48°N | 600 | 0-19 | | 0 | 17 | 0 | 3 | 1 | 57 | 8 | 14 | 109 | 78 | sa, ma | Caspers 1983a |
| * 36 | Krumbach | Germany | 51°N | | 0-27 | | 0 | 10 | 0 | 1 | 1 | 50 | 21 | 12 | 68 | 85 | gr | Röser 1980 |
| * 37 | Caucasus Mts st. | Grusia? | 41°N | 950-0 | 3-28 | | 0 | 7 | 0 | 13 | 1 | 51 | 13 | 13 | 107 | 79 | bo, st, sa, ma | Kownacki and Zosidze 1980 |
| * 38 | Ossau Valley | France | 43°N | 1000- 400 | | | 0 | 6 | 0 | 6 | 2 | 63 | 9 | 13 | 97 | 81 | | Laville and Vinçon 1991 |
| * 39 | Haute-Lot | France | 44°N | 1295- 223 | 4-20 | | 0 | 6 | 1 | 3 | 1 | 59 | 12 | 19 | 109 | 81 | st, sa, ma | Laville 1981 |
| * 40 | Alpen-Rhein | Switzerland | 47°N | 600- 400 | | | 0 | 2 | 0 | 4 | 2 | 78 | 2 | 12 | 49 | 84 | | Wilson and Wilson 1985 |
| 41 | Adirondack st. | NY, USA | 44°N | 800- 700 | 2-18 | | 0 | 13 | 0 | 0 | 0 | 56 | 11 | 16 | 32 | 75 | | Simpson 1983 |
| 42 | N.Carolina st. | NC, USA | 36°N | | | | 0 | 10 | 0 | 4 | 1 | 54 | 23 | 8 | 168 | 88 | | Lenat and Folley 1983 |
| 43 | Bigoray River | Alb., Canada | 53°N | 850 | 1-13 | | 1 | 18 | 0 | 3 | 0 | 39 | 21 | 19 | 112 | 66 | sa, si, ma | Boerger 1981 |
| * 44 | Fulda, springs | Germany | 51°N | 850 | | | 0 | 13 | 0 | 7 | 1 | 53 | 6 | 20 | 86 | 76 | bo | Lehmann 1971 |
| * 45 | Fulda, city Fulda | Germany | 51°N | 800- 300 | | | 0 | 14 | 0 | 3 | 2 | 59 | 11 | 11 | 100 | 87 | bo, st | Lehmann 1971 |
| * 46 | Atna, Solbakken | Norway | 62°N | 380 | 0-14 | | 0 | 9 | 0 | 4 | 0 | 49 | 11 | 26 | 53 | 60 | st, gr | Aagaard *et al.* 1989 |
| * 47 | Skiftesåa | Norway | 64°N | 170- 160 | 0-20 | 10 | 1 | 8 | 0 | 1 | 0 | 63 | 12 | 15 | 147 | 77 | st | Aagaard *et al.* (in press) |
| Average | | | | | | | <1 | 9 | <1 | 6 | 1 | 59 | 10 | 14 | 95 | 80 | | |
| **Lowland streams, summer cold** | | | | | | | | | | | | | | | | | | |
| * 48 | Bistrita | Rumania | 47°N | 400 | | | 0 | 9 | 0 | 5 | 4 | 49 | 22 | 12 | 78 | 67 | bo, st, sa, mo | Candea-Cure 1971 |
| * 49 | Bityska Stream | Czech Rep. | 49°N | 500- 300 | 1-17 | 7 | 0 | 25 | 0 | 9 | 3 | 44 | 16 | 3 | 32 | 78 | st, gr, sa, si | Zelinka et al. 1977 |
| * 50 | Althahoney | Ireland | 54°N | 160- 40 | 5-20 | | 0 | 14 | 0 | 7 | 0 | 60 | 9 | 10 | 58 | 86 | bo, st, gr, sa | Fahy and Murray 1972 |
| * 51 | Aabach, spring area | Germany | 51°N | 550 | 4- 9 | | 0 | 13 | 0 | 8 | 3 | 53 | 0 | 24 | 38 | 66 | st, sa, mo | Dittmar 1955 |
| * 52 | Aabach, low reach | Germany | 51°N | 550- 350 | 3-12 | | 0 | 7 | 0 | 9 | 2 | 45 | 20 | 16 | 44 | 73 | st, sa, ma | Dittmar 1955 |
| * 53 | River Cynon | England | 52°N | 390-70 | 4-17 | | 0 | 14 | 0 | 11 | 4 | 46 | 7 | 18 | 28 | 79 | st, pe | Learner *et al.* 1971 |
| * 54 | River Wye | England | 52°N | 600- 0 | | | 0 | 80 | | 4 | 1 | 53 | 22 | 12 | 77 | 79 | st, sa, ma | Brooker and Morris 1980 |
| * 55 | River Nent | England | 55°N | 556- 262 | | | 0 | 14 | 0 | 11 | 3 | 57 | 5 | 11 | 37 | 84 | st, gr | Armitage and Blackburn 1985 |
| * 56 | Linding Å | Denmark | 56°N | 20-10 | 2-12 | 7 | 0 | 12 | 0 | 3 | 6 | 55 | 17 | 9 | 67 | 75 | gr, sa, ma | Lindegaard 1972 |
| * 57 | Rabis Bæk | Denmark | 56°N | 55 | 2-16 | 8 | 0 | 12 | 0 | 3 | 6 | 62 | 12 | 9 | 34 | 76 | st, gr, sa, ma | Lindegaard and Mortensen 1988 |
| * 58 | Breitenbach | Germany | 51°N | 270 | 1-15 | | 0 | 7 | 0 | 7 | 2 | 58 | 14 | 11 | 81 | 79 | gr, sa, ma | Ringe 1974 |
| * 59 | Breitenbach | Germany | 51°N | 270 | 1-15 | | 0 | 11 | 0 | 4 | 1 | 54 | 18 | 10 | 134 | 74 | gr, sa, ma | Siebert 1980 |

*Table 1 (cont. 2)*

| No | River | Country | Latitude | Altitude m a.s.l. | Tempera. °C ra | Tempera. °C mean | % of subfamilies/tribes 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Total no. taxa | % rhit. gr. | Substrate | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 60 | Juday Creek | IN, USA | 42°N | 206 | 2-17 | 10 | 0 | 8 | 0 | 4 | 2 | 52 | 23 | 10 | 48 | 79 | st, gr, sa | Berg and Hellenthal 1991 |
| * 61 | River Frome | England | 51°N | | | | 0 | 2 | 0 | 7 | 2 | 60 | 16 | 13 | 45 | 78 | gr, ma | Pinder 1980 |
| * 62 | Tadnell Brook | England | 51°N | | 6-16 | | 0 | 9 | 0 | 1 | 3 | 52 | 16 | 19 | 75 | 68 | gr, sa, ma | Pinder 1974 |
| * 63 | North Tyne | England | 55°N | 170 | 3-18 | | 0 | 13 | 0 | 6 | 1 | 49 | 18 | 13 | 71 | 79 | st, sa | Brennan *et al.* 1981 |
| * 64 | Fuhlenau | Germany | 54°N | c.50 | 1-14 | | 0 | 7 | 0 | 1 | 3 | 54 | 12 | 22 | 67 | 67 | st, gr, sa | Böttger *et al.* 1987 |
| Average | | | | | | | 0 | 11 | 0 | 6 | 3 | 53 | 15 | 13 | 60 | 76 | | |
| **Lowland streams, summer warm** | | | | | | | | | | | | | | | | | | |
| * 65 | Doulonnes | France | 47°N | 254 - 209 | 3-19 | | 0 | 19 | 0 | 0 | 2 | 35 | 27 | 17 | 48 | 65 | bo, st, gr, sa | Verneaux 1968 |
| * 66 | Caragh River | Eire | 52°N | 90 - 18 | 4-25 | 14 | 0 | 21 | 0 | 3 | 1 | 54 | 10 | 10 | 68 | 84 | bo, gr, sa, si | Dowling *et al.* 1981a, 1981b |
| * 67 | River Chew | England | 51°N | 25 | 4-18 | | 0 | 19 | 0 | 2 | 2 | 40 | 21 | 11 | 86 | 60 | si, ma | Wilson 1977 |
| 68 | Linesville Creek | PA, USA | 40°N | | 1-21 | | 0 | 10 | 0 | 3 | 0 | 55 | 17 | 15 | 143 | 68 | st, gr, ma | Coffmann 1973 |
| * 69 | Rohrweisenbach | Germany | 51°N | 325 | 0-21 | | 0 | 8 | 0 | 7 | 1 | 51 | 19 | 14 | 85 | 76 | gr, sa, dt | Ringe 1974 |
| 70 | Llobregat, b. dam | Spain | 42°N | 400 - 0 | 6-26 | | 0 | 9 | 0 | 9 | 0 | 57 | 17 | 9 | 35 | 83 | st, gr, sa, si | Prat *et al.* 1983 |
| 71 | Kossau | Germany | 54°N | 34 - 0 | 1-24 | | 0 | 15 | 0 | 4 | 1 | 34 | 18 | 28 | 74 | 46 | st, si, ma | Nietzke 1938 |
| 72 | Suså | Denmark | 55°N | 90 - 6 | 1-25 | | 0 | 17 | 0 | 2 | 1 | 38 | 23 | 18 | 87 | 52 | st, sa, si, ma | Berg 1948 |
| Average | | | | | | | 0 | 15 | 0 | 4 | 1 | 46 | 19 | 15 | 78 | 67 | | |
| **Lowland rivers, summer warm** | | | | | | | | | | | | | | | | | | |
| 73 | Warta River | Poland | 52°N | c. 125 | | 11 | 0 | 5 | 0 | 3 | 8 | 30 | 49 | 5 | 37 | 46 | sa | Grzybkowska *et al.* 1990 |
| * 74 | Nida River | Poland | 50°N | c. 490 | | | 0 | 8 | 0 | 1 | 3 | 42 | 33 | 13 | 148 | 57 | gr, sa, si, ma | Srokosz 1980 |
| * 75 | Oberen Alz | Germany | 48°N | 517 - 506 | 2-21 | | 0 | 18 | 1 | 1 | 0 | 28 | 35 | 18 | 79 | 57 | | Caspers 1983b |
| * 76 | Oberen Alz | Germany | 48°N | 517 - 506 | 2-21 | | 0 | 12 | 1 | 5 | 1 | 43 | 26 | 13 | 82 | 66 | | Kownacki and Margreiter-Kownacka 1993 |
| * 77 | Fulda b. city Fulda | Germany | 51°N | 300 - 250 | | | 0 | 11 | 0 | 1 | 1 | 44 | 35 | 8 | 80 | 61 | | Lehmann 1971 |
| * 78 | River Po | Italy | 45°N | 100 - 70 | 2-29 | 18 | 0 | 9 | 0 | 2 | 3 | 37 | 41 | 8 | 148 | 56 | st, sa, si, ma | Rossaro 1984 |
| * 79 | River Po | Italy | 45°N | 7 | 2-27 | | 0 | 3 | 0 | 3 | 0 | 38 | 38 | 18 | 34 | 59 | artificial sub | Battegazzore *et al.* 1992 |
| 80 | Saskatchewan a. ip. | Canada | 54°N | | 1-21 | | 0 | 6 | 0 | 1 | 0 | 32 | 49 | 11 | 79 | - | | Mason and Lemhkuhl 1983 |
| 81 | Saskatchewan b. ip. | Canada | 54°N | | 1-20 | | 0 | 4 | 0 | 2 | 0 | 33 | 40 | 20 | 84 | - | | Mason and Lemhkuhl 1983 |
| * 82 | Hoch Rhein | Germany | 48°N | 400 - 250 | | | 0 | 10 | 0 | 2 | 2 | 39 | 32 | 15 | 59 | 63 | | Wilson and Wilson 1985 |
| * 83 | Hoch Rhein | Germany | 48°N | 400 - 250 | | | 0 | 11 | 0 | 2 | 1 | 43 | 33 | 10 | 107 | 66 | | Caspers 1991 |
| * 84 | Ober Rhein | Germany | 48°N | 250 - 100 | | | 0 | 9 | 0 | 0 | 0 | 40 | 38 | 14 | 58 | 59 | | Wilson and Wilson 1985 |
| * 85 | Ober Rhein | Germany | 48°N | 250 - 100 | | | 0 | 10 | 0 | 1 | 1 | 38 | 39 | 11 | 98 | 59 | | Caspers 1991 |
| * 86 | M. + N. Rhein | Germany | 49-52°N | c. 100 | | | 0 | 13 | 0 | 0 | 0 | 47 | 31 | 9 | 32 | 75 | | Wilson and Wilson 1985 |
| * 87 | M. + N. Rhein | Germany | 50°N | c. 100 | | | 0 | 9 | 0 | 1 | 1 | 39 | 35 | 14 | 74 | 59 | | Caspers 1991 |
| * 88 | Wall | Netherland | 52°N | - 0 | | | 0 | 11 | 0 | 0 | 0 | 33 | 44 | 11 | 18 | 56 | | Wilson and Wilson 1985 |
| 89 | Oder | Germany | 53°N | 21 - 0 | 0-21 | | 0 | 15 | 0 | 0 | 2 | 28 | 45 | 10 | 60 | 60 | sa, si, ma | Harnish 1922 |

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| * 90 | Danube | Austria | 48°N | 187 | 0-20 | 0 | 6 | 0 | 2 | 5 | 42 | 33 | 12 | 66 | 56 | | Schmid 1992 |
| 91 | Danube | Czech Rep. | 48°N | 165 - 150 | | 0 | 7 | 0 | 0 | 7 | 25 | 43 | 18 | 28 | 46 | st, gr, sa, pe | Ertlová 1963 |
| * 92 | Danube | Hungary | 48°N | 150 - 100 | | 0 | 3 | 0 | 0 | 3 | 47 | 40 | 7 | 30 | 63 | st, gr, pe | Berczik 1971 |
| * 93 | Danube | Romania | 45°N | 100 - 0 | | 0 | 10 | 0 | 4 | 1 | 24 | 52 | 10 | 83 | 48 | gr, sa, si | Cure 1964 |
| * 94 | Thames | England | 52°N | | 0-21 | 0 | 8 | 0 | 0 | 4 | 25 | 54 | 8 | 24 | 46 | st, sa, si, ma | Mackey 1976a,b, 1977 |
| 95 | Ohio River | Ohio, USA | 39°N | | | 0 | 16 | 0 | 0 | 0 | 32 | 40 | 12 | 25 | 52 | sa, si | Mason and Sublette 1971 |
| Average | | | | | | 0 | 9 | <1 | 1 | 2 | 36 | 39 | 12 | 67 | 58 | | |
| **Subtropical and tropical rivers** | | | | | | | | | | | | | | | | | |
| 96 | Gt Berg R. spring | South Africa | 35°S | 1300 - 300 | 9-23 | 0 | 15 | 0 | 0 | 0 | 70 | 15 | 0 | 20 | 70 | st, mo | Scott 1959 |
| 97 | Gt Berg R. u. r. | South Africa | 35°S | 300 - 100 | 9-30 | 0 | 11 | 0 | 0 | 0 | 50 | 25 | 14 | 64 | 78 | st, sa, ma | Scott 1959 |
| 98 | Gt Berg R. l. r. | South Africa | 35°S | 100 - 0 | 10-32 | 0 | 14 | 0 | 0 | 0 | 34 | 36 | 16 | 56 | 50 | sa, si, ma | Scott 1959 |
| 99 | Tiga | Nigeria | 12°S | 300 | 20-22 | 0 | 8 | 0 | 0 | 0 | 25 | 55 | 12 | 40 | 50 | st, sa, si, pe | Brown 1983 |
| 100 | Turkey | FA, USA | 30°N | | 12-24 | 0 | 19 | 0 | 5 | 0 | 29 | 38 | 10 | 42 | 67 | sa | Soponis 1980 |
| 101 | Ridge & Valley st. | GA, USA | 33°N | 262 - 154 | | 0 | 23 | 0 | 1 | 0 | 41 | 23 | 13 | 71 | 69 | ri, lp | Caldwell and Parrish 1987 |
| 102 | Costal Plain st. | GA, USA | 32°N | 38 - 20 | | 0 | 25 | 0 | 0 | 0 | 38 | 30 | 8 | 53 | 68 | sa, lp, sn | Caldwell and Parrish 1987 |
| 103 | Kalengo | Zaire | 3°S | 1800 | 16-22 | 0 | 11 | 0 | 0 | 0 | 52 | 22 | 15 | 46 | 80 | st | Lehmann 1979 |
| 104 | Simisi | Zaire | 3°S | | | 0 | 18 | 0 | 0 | 0 | 29 | 34 | 18 | 38 | ? | | Lehmann 1981 |
| Average | | | | | | 0 | 16 | 0 | 1 | 0 | 41 | 31 | 12 | 48 | 67 | | |

Table 2. Number of chironomid taxa and percentage distribution of chironomid subfamilies/tribes in New Zealand and Australian running waters. Subfamilies/tribes are: Podonominae (1), Tanypodinae (2), Aphroteniinae (3), Diamesinae (4), Orthocladiinae (5), Chironomini (6), Pseudochironomini (7) and Tanytarsini (8). Substrate "types" as in Table 1.

| No | River | Country | Latitude | Altitude m a.s.l. | Tempera. °C | | % of subfamilies/tribes | | | | | | | | Total no. taxa | % rhit. gr. | Substrate | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ra | mean | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | | | |
| 105 | Waitakere River | New Zealand | 36°S | 110 - 10 | | 11-23 | 0 | 25 | 0 | 13 | 38 | 13 | 0 | 13 | 16 | | st, sa, si, ma | Towns 1978, 1979 |
| 106 | Devils Creek | New Zealand | 42°S | 360 - 280 | | | 23 | 20 | 3 | 0 | 40 | 11 | 0 | 3 | 35 | | | Cowie 1983 |
| 107 | North Dandalup | WA Australia | 32°S | 300 - 0 | | | 0 | 14 | 0 | 5 | 31 | 36 | 5 | 14 | 42 | | | Storey and Edward 1989 |
| 108 | Canning | WA Australia | 32°S | 300 - 0 | | | 2 | 11 | 0 | 2 | 43 | 34 | 4 | 9 | 56 | | ri | Storey and Edward 1989 |
| 109 | La Trobe River | Vic Australia | 38°S | 930 - 240 | | 2-20 | 5 | 11 | 0 | 3 | 30 | 32 | 3 | 16 | 37 | | st, gr | Metzeling *et al*. 1984 |
| 110 | La Trobe River | Vic Australia | 38°S | 190 - 160 | | 5-20 | 6 | 19 | 0 | 3 | 22 | 34 | 3 | 13 | 32 | | st, gr, sa | Metzeling *et al*. 1984 |
| 111 | La Trobe River | Vic Australia | 38°S | 60 - 50 | | 7-22 | 7 | 21 | 0 | 3 | 17 | 31 | 3 | 17 | 29 | | gr, sa | Metzeling *et al*. 1984 |
| 112 | Cooper Creek | NT Australia | 13°S | | | | 0 | 13 | 0 | 0 | 7 | 60 | 0 | 20 | 30 | | | Cranston 1991 |
| 113 | Radon Spring | NT Australia | 13°S | | | | 0 | 21 | 0 | 0 | 9 | 47 | 0 | 24 | 34 | | | Cranston 1991 |
| 114 | Gulungal Creek | NT Australia | 13°S | | | | 0 | 14 | 0 | 0 | 12 | 51 | 0 | 23 | 43 | | | Cranston 1991 |
| 115 | S. Alligator R. (03) | NT Australia | 13°S | | | | 0 | 17 | 0 | 0 | 10 | 48 | 0 | 26 | 42 | | | Cranston 1991 |

Table 3. Number of chironomid species and percentage distribution of chironomid subfamilies in 70 European running water sites (marked with an (*) in Table 1). Reduced numbers is used in a DCA analyses of species composition (see text). Total number of chironomid species in Europe is enumerated from Ashe and Cranston (1990) and some later descriptions and revisions. (A): Percentage of species found in running water in proportion to species recorded in Europe.

| Subfamily | 70 running water sites | | | | Total | | |
|---|---|---|---|---|---|---|---|
| | total | | reduced | | Europe | | A |
| | no. | % | no. | % | no. | % | % |
| Podonominae | 3 | 1 | 3 | 1 | 8 | 1 | 40 |
| Tanypodinae | 49 | 10 | 22 | 9 | 76 | 8 | 64 |
| Buchonomyiinae | 1 | - | 1 | - | 1 | - | 100 |
| Diamesinae | 42 | 8 | 27 | 11 | 59 | 6 | 71 |
| Telmatogetoninae | - | - | - | - | 3 | - | - |
| Prodiamesinae | 5 | 1 | 3 | 1 | 10 | 1 | 50 |
| Orthocladiinae | 230 | 45 | 107 | 43 | 427 | 44 | 54 |
| Chironominae | | | | | | | |
| Chironomini | 103 | 20 | 52 | 21 | 237 | 24 | 44 |
| Pseudochironomini | 1 | - | 1 | - | 1 | - | 100 |
| Tanytarsini | 80 | 16 | 35 | 14 | 159 | 16 | 50 |
| Total | 514 | 101 | 251 | 100 | 981 | 100 | 52 |

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