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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of non-biting midges (Chironomidae; Insecta-Diptera) in freshwater

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Abstract Chironomidae are common inhabitants of most aquatic habitats, and often dominate aquatic insect communities in both abundance and species richness. Species occur in all continents, including Antarctica, and most major oceanic islands that have been investigated. The family is divided into 11 subfamilies and 22 nominal tribes. Although individual species occur in a wide range of habitats from terrestrial to fully aquatic, a total of 339 genera and 4,147 species are unambiguously aquatic in their immature stages. Greatest species and generic richnesses occur in the Palaearctic Region and Nearctic Region, respectively, but this pattern may largely reflect historical patterns of past taxonomic research efforts.

Keywords Chironomidae · Diversity · Zoogeography · Endemicity · Historical processes

Introduction

Chironomidae is a family of aquatic flies (Diptera) with world-wide distribution. It is the most widespread of all aquatic insect families, with individual species occurring from Antarctica at 68° S latitude (*Belgica antarctica* Jacobs) and sub-antarctic islands (*Parochlus steinenii* (Gerke)) (Edwards & Usher, 1985, Sugg et al., 1983) to Lake Hazen at 81° N on Ellesmere Island (Oliver & Corbet, 1966). They also exhibit extreme elevational ranges, occurring in a glacial-melt stream at 5,600 m in the Himalaya Mountains (Koshima, 1984) to more than 60 m depths in Lake Hovsgol (Hayford & Ferrington, 2006) and >1,000 m depths in Lake Baikal (Linevich, 1971). They are among the most tolerant of aquatic insects to water and air temperatures, with larvae of *Paratendipes thermophilus* Townes occurring in hot springs at temperatures of 38.8°C (Hayford et al., 1995) and adults of *Diamesa mendotae* Muttkowski able to depress their freezing point and survive air temperatures less than –20°C (Carrillo et al., 2004, Bouchard et al., 2006). Although most species appear to be univoltine to trivoltine in seasonal environments (Tokeshi, 1995), life cycle strategies of individual species can also be extreme, with *Apedilum elachistus* Townes maturing from egg to adult in less than 7 days (Nolte, 1996) in rock pool habitats in the Brazilian Pantanal. By contrast, Butler (1982) proposed a 7-year life cycle for two species of *Chironomus* in Alaskan tundra ponds.

Chironomidae are divided into 11 subfamilies and nominally into 22 tribes (not including five additional provisional tribes resulting from dividing Orthocladiini as proposed by Sæther 1979). Overviews of 10

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Freshwater Animal Diversity Assessment

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subfamilies are provided in Cranston (1995a), the phylogeny of subfamilies was cladistically analyzed by Sæther (2000b), and zoogeographical patterns were summarized by Ashe et al. (1987) and Sæther (2000a). A list of generic and subgeneric names and synonyms for Chironomidae was published by Ashe (1983). Table 1 lists the subfamilies in approximate phylogenetic order and tribes alphabetically, based primarily on publications by Brundin (1966, 1983), Brundin and Sæther (1978), Sæther (1977, 1979, 1989, 2000b) and Spies (2005). No world catalogs or checklists have been published recently, however regional catalogs that are somewhat dated but have been valuable sources of distributional data for this article are: Ashe & Cranston (1990) for the Palaearctic Region; Sæther & Spies (2004) for Europe; Oliver et al. (1990) for the Nearctic Region; Spies & Reiss (1996) for the Neotropical Region (and Mexico); Freeman & Cranston (1980) for the Afrotropical Region; Cranston & Martin (1989) for the Australian and Oceanic regions and the Antarctic; and Sublette & Sublette (1973) for the Oriental Region. All new taxonomic papers post-dating the respective regional catalogs (and published as of 2006) have been reviewed and incorporated into the totals provided in Table 2 (see Figs. 1, 2).

When developing estimates of richness for aquatic species of Chironomidae, several problematic issues arise. Notwithstanding difficulties associated with differing species interpretations and incorporating new publication data into this overview, which have required continuous refinement of the richness estimates, a more difficult issue deals with a workable definition of "aquatic". Our working group has discussed this issue and have labored to develop a standardized definition (Lévêque et al., 2005). Among Chironomidae it is the larval and pupal stages that typically are constrained to aquatic habitats while adults are aerial and often collected at substantial distances from potential natal habitats. Species descriptions have, by tradition, been based primarily on adults, and knowledge of immature stages of species is disparate among tribes or even among species within a genus. Some genera are known to have terrestrial immature stages and by our workable definition are excluded from the totals. However, in other genera some species may be clearly aquatic as immatures, others recorded only from terrestrial habitats, and still others unknown as immatures. Cases like this make application of our criterion subjective. In these cases, I have opted not to count species unless (1) the collection records specifically say they are recorded from in or near aquatic habitats or (2) unless I have firsthand knowledge of them occurring in one or more of the types of "aquatic conditions" defined by Lévêque

Table 1 Subfamilies and tribes of Chironomidae

Subfamily	Tribe
Telmatogetoninae	
Usambaromyiinae	
Aphroteniinae	
Chilenomyiinae	
Podonominae	
	Boreochlini
	Podonomini
Tanypodinae	
	Anatopynyiini
	Coelopyiini
	Coelotanypodini[a]
	Macropelopiini
	Natarsiini
	Pentaneurini
	Procladiini
	Tanypodini
Buchonomyiinae	
Diamesinae	
	Boreoheptagyiini[b]
	Diamesini
	Harrisonini
	Heptagyiini[b]
	Lobodiamesini
	Protanypodini[b]
Prodiamesinae	
Orthocladiinae	
	Corynoneurini[c]
	Metriocnemini[c]
	Orthocladiini[c]
Chironominae	
	Chironomini
	Pseudochironomini
	Tanytarsini

[a] Please refer to Spies (2005) for information about validity of this tribe name

[b] Please refer to comments by Spies (2005) for further information about this spelling

[c] Please refer to opinion by Spies (2005) for comments on usage and/or recommendations related to these tribes

Table 2 Genera and species of aquatic Chironomidae by biogeographic region (Fig. 1)

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Total Genera	181	211	154	104	105	116	29	6	339
Total Species	1,321	1,092	618	406	359	471	155	9	4,147

Continental distribution of freshwater lizards. PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

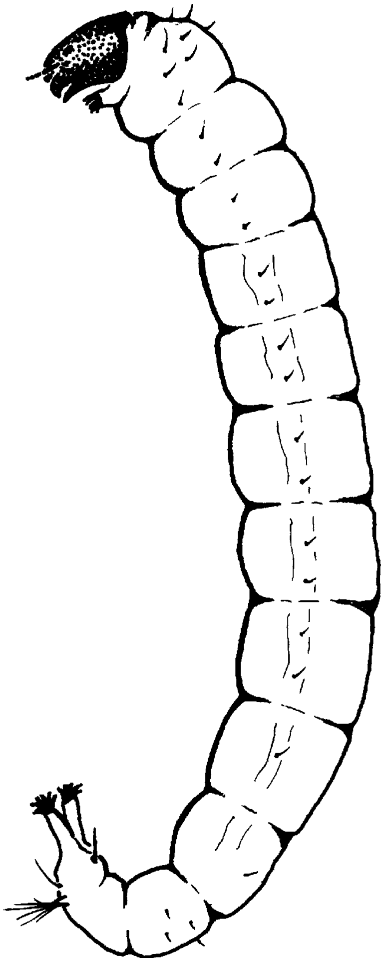

Fig. 1 A chironomid larvae

et al. (2005). However, I have summarily included other species in the genus that are not described as immatures in the totals when all taxa that are known as immatures have been collected from an aquatic habitat. Consequently, the figures provided in this article may be disputed as overly inflated. Without full knowledge, however, of the biology of larvae it is therefore debatable if a general consensus can be obtained for the number of described aquatic species of Chironomidae. However, review of collection records and species accounts confirms a total of 339 genera and 4,147 species can be considered unambiguously aquatic in their immature stages.

Species/generic diversity

When sampled comprehensively, species richness of Chironomidae is usually among the highest of aquatic insect families detected in most aquatic settings, often approaching 80 or more species and occasionally exceeding 100 species per site. Coffman (1989) summarized 152 species richness estimates as a function of stream order and concluded that average richness increased with increasing stream order up to third order, then leveled off or decreased in higher order rivers. Mean species richness (and range of estimates) varied from: 26 (10–64) for first order streams; 44 (13–144) for second order; 63 (25–157) for third order; 51 (25–83) for fourth order; 47 (11–86) for fifth order; 47 (10–99) for sixth order; 45 (12–148) for seventh order and higher.

Although predicted to have lower species richness, some studies of springs, spring runs and intermittent streams show remarkably high values, especially in heterogeneous spring settings or when studied over periods with differing precipitation and hydrologic conditions (e. g., Chou et al., 1999). Ferrington et al. (1995) reported 66 species for an isolated spring in the high plains of western Kansas, but concluded that 48 species were restricted to only one of the five habitats occurring in the spring source. Springs occurring over broad geographic areas show considerable individual variation in richness, however cumulative richness can exceed 100 or more species (e.g., Blackwood et al., 1995; Ferrington, 1998; Lindegaard, 1995).

Patterns of lotic chironomid richness across biotopes were discussed by Coffman (1989). Factors identified as contributing to regional species richness

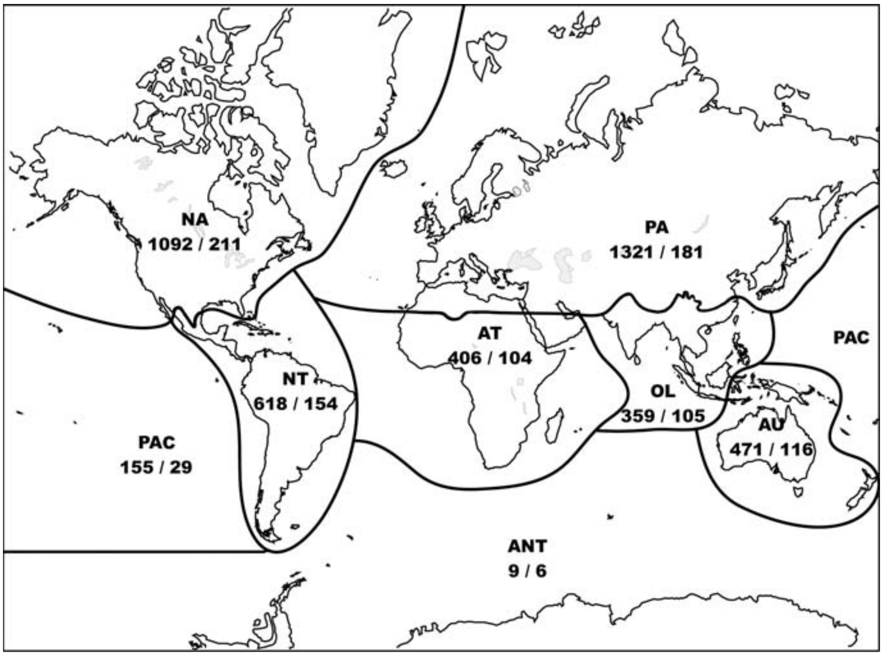

Fig. 2 Global distribution of species and genus diversity of Chironomidae by zoogeographic region (Species number/genus number). PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical ; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands; ANT—Antarctic

included (1) ecological heterogeneity, (2) size of stream, (3) altitude, (4) latitude, and (5) "biogeographical potential". Consideration of these factors led him to predict highest species richness would occur in 3rd order, temperate, lowland streams in the Holarctic Region. However, in subsequent papers Coffman and de la Rosa (1998) reported 250 species from three streams in Costa Rica, and Coffman et al. (1992) documented 299 species in 31 West African streams, including 175 species in a large river. Consequently, it is likely that regional species richness in some tropical streams approaches or exceeds richness in temperate lowland streams.

Species richness of lakes is generally lower than average stream estimates. However, some estimates for large, heterogeneous systems reach or exceed richness for streams (e.g., Reiss (1968) detected 184 species in Bodensees). When a large array of lake types are considered, the cumulative number of species detected can also be high. For example Ruse (2002) detected 275 species in 30 lakes in England and Wales.

Phylogeny and historical processes

A phylogeny of subfamilies was developed by Sæther (1977). Based strongly on considerations of the structure of female genitalia, the Telmatogetoninae were placed as the primitive sister group to all remaining subfamilies of Chironomidae, a position differing from Brundin's (1966) view of Telmatogetoninae as the apomorph sister group of Diamesinae. In a subsequent paper, Sæther (1979) provided an historical review of earlier classifications and proposed relationships, and additional arguments for the basal placement of Telmatogetoninae. This placement has been criticized by Ashe et al. (1987), based on re-interpretation of homologies of female genitalia and the predominantly marine habits of larvae. However, no compelling arguments have been proposed for an alternative placement of Telmatogetoninae, although preliminary molecular evidence presented by Cranston et al. (2000) appears to support a basal placement of the subfamily.

Chilenomyiinae with one described species, *Chilenomyia paradoxa* Brundin, was considered by Ashe et al. (1987) as a logical replacement for Telmatogetoninae as the primitive sister to all other chironomid subfamilies. Brundin (1983) proposed a placement of Chilenomyiinae as sister group to all subfamilies less the Telmatogetoninae.

The subfamily Usambaromyiinae, with one species known from Tanzania, is considered to be the sister group of Tanypodinae + Aphroteniinae + Podonominae (=semifamily Tanypodoinae of Sæther, 1983) (Andersen and Sæther, 1994).

The monophyly of Tanypodinae + Aphroteniinae + Podonominae is well supported morphologically and generally accepted. Within this clade Tanypodinae form the sister subfamily to Aphroteniinae.

Sæther (1983) proposed the semifamily Chironomoinae to include the remaining subfamilies Buchonomyiinae, Diamesinae, Prodiamesinae, Orthocladiinae and Chironominae. The placement of Buchonomyiinae within the semifamily was disputed by Murray and Ashe (1985), based on re-interpretation of morphology of male genitalia and new characters from the female genitalia, who proposed placement within the semifamily Tanypodoinae. The latter placement appears to be favored by Cranston (1995a), who considered the apparent lack of premandibles in early instar larvae combined with a labral rod and SII setae on pedestals as characters supporting placement in Tanypodoinae.

Sæther (2000b) performed a cladistic analysis of the subfamilies and (using parsimony) concluded the results supported previous findings, placing Buchonomyiinae and Chilenomyiinae basally within the Chironomoinae, and Usambaromyiinae as the sister group of the Tanypodoinae.

Other subfamilies assigned to Chironomoinae are generally considered monophyletic and appropriately placed, with the relationships following Sæther (1977). Cranston (1995a), however, speculated on possible paraphyly of both Diamesinae and Prodiamesinae.

Zoogeography and Endemicity

Estimates of aquatic species richness by region are presented in Table 2. Based on published data the Chironomidae appear to be more species rich in the northern hemisphere than the southern hemisphere, and with greatest richnesses in northern mid-latitudes. The latter pattern does not conform to the more generalized trend of greatest richness in the tropics for many groups of organisms, and Coffman (1989) has argued that a variety of factors contribute to the higher richness of lotic chironomids in mid-latitudes (see earlier text). However, it can also be expected that the apparent patterns of species richness of Chironomidae are largely the result of differing efforts to describe local faunas rather than actual biological patterns, and more recent studies of Costa Rican and West African streams support this conclusion (Coffman and de la Rosa, 1998; Coffman et al., 1992).

Several taxonomic levels of chironomids show strong, but alternative, patterns of endemism and/or zoogeographical distributions. At the subfamily level, the southern hemisphere patterns of endemism for Podonominae and Aphroteniinae conform to patterns of transantarctic diversification and vicariance (Brundin, 1966). The Heptagyiae group (Diamesinae), defined by Brundin (1966) as consisting of five genera, also conforms to this pattern. Other conspicuous examples of endemism at the genus or sub–genus level, but on more restrictive geographic scales, are discussed in Sæther (2000a) and Sæther & Ekrem (2003). Based on phylogenetic hypotheses derived from morphological and limited distributional data, several Gondwanian (early Cretaceous), Laurasian (Quaternary Ice Age) and Inabrezian distributions were postulated. These conclusions provide the basis for developing hypotheses that can be tested when better information about immature stages can be generated. Another example of endemism, but with very strong support from morphological and molecular data, was presented by Papoucheva et al. (2003) for species flocks of *Sergentia* species in Lake Baikal, which they conclude date to tectonic activities 25–27 MY ago. On a more restrictive scale, the distributional pattern of the two described species of *Oliveridia*, with *O. tricornis* widespread in lakes at high latitudes in North America, Greenland, Iceland, northern Norway and *O. hugginsi*, by contrast, limited to one watershed in extreme southern Kansas (Ferrington & Sæther, 1987), strongly suggest post-glacial events since the Kansan Glaciation as contributing to the disjunct distributions of these two species. Vicariance events with intervening dispersal during climatic optima were argued by Willassen and Cranston (1986) as contributing to range extension of the cold-water adapted genus *Diamesa* into Africa and the present day distribution of species within montane habitats.

Hot spots

Areas where large numbers of undescribed species are known to occur include north western Costa Rica, the

Brazilian lowlands, West Africa and high elevation streams in the steppes on the eastern edge of the Andes in Patagonia. In a more general sense, habitats that are widespread geographically but are likely to have high concentrations of undescribed species include: (1) intermittent and ephemeral aquatic habitats; (2) streams and lakes of most extreme low latitudes of major north/south orientated mountain chains (example, southern Rockies in Arizona, New Mexico and southern Appalachians in North America); (3) high-elevation springs and seeps; and (4) oceanic archipelagos. Timing of field work to correspond to early spring collecting soon after ice melt in mid-latitude streams and lakes, will also likely result in undescribed species even in areas where the summer emerging fauna is relatively well known. Similarly, collecting during winter in streams that are strongly dominated by groundwater inputs and remain free of ice and relatively warm in winter may also provide substantial numbers of undescribed species.

Human-related issues

Chironomidae have both positive and negative interactions with humans. Negative interactions include species that are considered as nuisance species (Ali, 1995), species that act as known or suspected sources of environmental allergens (Cranston, 1995b), and species that host and transport pathogenic bacteria (Broza and Halpern, 2001).

Species with dense populations and synchronized emergences from water bodies in highly urbanized landscapes are often considered to be nuisance species when attracted as adults by light to shops, restaurants, homes, or other places where people congregate such as sports stadiums and outdoor banquet or concert halls. Adults can stain buildings as meconium is produced and deposited, and can clog screened air intakes to furnaces (personal observation), air conditioner cooling systems and compressors, or indoor building environment systems. Estimates of maintenance costs and business losses in Florida amounted to millions of dollars annually (Anonymous, 1977) and control efforts were estimated at approximately one million dollars in Venice in the late 1980s/early 1990s (Ali et al., 1992). Possible consequences to the aviation industry have been proposed by Barbato et al. (1990). Larval stages have often been considered as nuisances by infesting drinking-water supply systems (Berg, 1996; Langton et al., 1988), by damaging rice seedlings (Darby, 1962; Ferrarese 1993), or by grazing on apical meristem or leaf-mining in other ornamental aquatic hydrophytes (Tokunaga and Koroda, 1936).

Hemoglobin produced by larvae for respiration, but carried over to the adult, has been shown to have allergenic properties among atopic individuals (Cranston, 1995b; Miyamoto, 1988) that may be of worldwide significance (Sublette and Sublette, 1988). Symptoms can range from mild urticaria, pruritis and conjunctivitis to more severe reactions varying from allergenic rhinitis to asthmatic symptoms or even leading to anaphylaxis.

Occupational allergic reactions are known among aquarists, owners of pet fish stores and employees of fish-food production facilities (Baur, 1982, 1992; Fuchs and Kleinhaus, 1982). In most cases the allergen is known or suspected to be associated with freeze-dried larvae incorporated into the commercial fish food (Cabrerizo Ballesteros et al., 2006). Contact dermatitis is also reported in a person handling bloodworms (Brasch et al., 1992).

Vibrio cholerae, the causative agent of Cholera, has been isolated from chironomid egg masses by Broza and Halpern (2001). They concluded the gelatinous matrix was the sole source of carbon for the bacteria and considered masses to act as natural reservoirs of the bacteria. More recently, Broza et al. (2003) have isolated two non-pathogenic serotypes of *V. cholerae* from adults and have proposed chironomids as a potential air born dispersal mechanism.

Positive interactions with humans have not been extensively quantified, however both adults and immatures provide essential roles in ecosystem processes such as nutrient cycling and energy flow. Consequently chironomids, and other aquatic invertebrates, contribute to ecosystem goods and services upon which human society depends. Other more readily conceptualized interactions benefiting humans are summarized by Armitage (1995) and include serving as food for freshwater commercial and sport fisheries (e.g., Mackay, 1979, Rasmussen, 1990), food for other species of invertebrates and amphibians (e.g., Avery, 1968; Johnson, 1985), and as ingredients in production of insect flour (Bergeron et al., 1988). Mating swarms of adults attract swifts and swallows (Lack and Owen, 1955; St Louis et al., 1990), at least some species of bats intermittently consume large quantities of adults (Griffith and Gates, 1985), and larvae can be important in diets of migratory waterfowl during breeding seasons (e.g., Austin et al., 1990). Chironomids are also a major component of some live and freeze-dried commercial tropical fish foods (Armitage, 1995).

Larvae, pupae, and even eclosing adults have served as models and mimics for fly fishing. Publications explaining the concept of "match the hatch" provide directions on how to determine if chironomids are emerging and how to tie or select flies that match particular life stages or colors of chironomids. A few random web searches yielded an impressive array of fly-types such as "*Brassie, Griffith's gnat, midge, olive midge, blood midge, disco midge, black palomino midge, AK's midge larva, paramidge, midge pupa, ascending midge pupa, blood midge pupa, hatching midge pupa, parachute Adams, serendipity*", attesting to the interest and enthusiasm of some fly-fishers to mimic the habitus of chironomids.

References

Ali, A., 1995. Nuisance, economic impact and possibilities for control, In: Armitage P. D., P. S. Cranston & L. V. C. Pinder (eds), The Chironomidae: Biology and Ecology of Non-biting Midges. Chapman & Hall, London, UK, 339–364, Chapter 13.

Ali, A., L. Barbato, G. Ceretti, S. Della Sala, R. Riso, G. Marchese & F. D'Andrea, 1992. Efficacy of two temephos formulations against *Chironomus salinarius* (Diptera: Chironomidae) in the saltwater lagoon of Venice, Italy. Journal of the American Mosquito Control Association 8: 353–356.

Andersen, T. & O. A. Sæther, 1994. *Usambaromyia nigrala* gen. n., sp. n., and Usambaromyiinae, a new subfamily among the Chironomidae (Diptera). Aquatic Insects 16: 21–29.

Anonymous, 1977. Economic Impact Statement, Blind Mosquito (Midge) Task Force. Report by Sanford Chamber of Commerce, Seminole County, Florida.

Armitage, 1995. Chironomidae as food. In: Armitage P. D., P. S. Cranston & L. V. C. Pinder (eds), The Chironomidae: Biology and Ecology of Non-biting Midges. Chapman & Hall, London, UK, 423–435, Chapter 17.

Ashe, P., 1983. A catalogue of chironomid genera and subgenera of the world including synonyms (Diptera: Chironomidae). Entomologica Scandinavica Supplement 17: 1–68.

Ashe, P. & P. S. Cranston, 1990. Chironomidae. In: Soos A. & L. Papp (eds), Catalogue of Palaearctic Diptera. Elsevier Science Publishers, Amsterdam, The Netherlands, 113–355.

Ashe, P., D. A. Murray & F. Reiss, 1987. The zoogeographical distribution of Chironomidae. Annales de Limnologie 23: 27–60.

Austin, J. E., J. R. Serie & J. H. Noyes, 1990. Diet of canvasbacks during breeding. Prairie Naturalist 22(3): 171–176.

Avery, R. A., 1968. Food and feeding relations of three species of *Triturus* (Amphibia: Urodela) during the aquatic phases. Oikos 19: 408–412.

Barbato, L. C., L. A. Filia, B. Maraga, O. Pancino & E. Tsuroplis, 1990. Problematiche relative al controllo dei Chironomidi nella Laguna di Venecia. In: D'Andrea F. & G. Marchese (eds), *Chironomidi*, Culicidi, Simulidi—Aspetti Sanitari ed Ecologici. Regione Veneto, ULSS 16, S. I. P., Venezia, Italy, 113–127.

Baur, X., 1982. Chironomid hemoglobin. A major allergen for humans. Chironomus 2: 24–25.

Baur, X., 1992. Chironomid midge allergy. Japanese Journal of Immunology 41: 81–85.

Berg, M. B., 1996. Infestation of enclosed water supplies by chironomids: Two case studies. In: P. Cranston (ed.). Chironomids: From *Genes to Ecosystems*. CSIRO Publications, East Melbourne, Australia, 241–246.

Bergeron, D., R. J. Bushway, F. L. Roberts, I. Kornfield, J. Okedi & A. A. Bushway, 1988. The nutrient composition of an insect flour sample from Lake Victoria, Uganda. Journal of Food Composition and Analysis 1: 371–377.

Blackwood, M. A., S. M. Hall & L. C. Ferrington Jr, 1995. Emergence of Chironomidae (Diptera) from springs in the central high plains of the United States. Journal of the Kansas Entomological Society 68: 132–151.

Bouchard, R. W., Jr, M. A. Carrillo & L. C. Ferrington Jr, 2006. Lower lethal temperature for adult male *Diamesa mendotae* Muttkowski (Diptera: Chironomidae), a winter-emerging aquatic insect. Aquatic Insects 28: 57–66.

Brasch, J., H. Brüning & E. Paulke, 1992. Allergic contact dermatitis from chironomids. Contact Dermatitis 26: 317–320.

Broza, M. & M. Halpern, 2001 Chironomid egg masses and *Vibrio cholerae* . Nature 412: 40.

Broza, M., M. Halpern, H. Gancz & Y. Kashi, 2003. Do chironomids play a key role in onset of Cholera epidemics. Abstract on-line at: http://www.entomology.umn.edu/midge/XVSymposium.htm.

Brundin, L., 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kunglica Svenska Vetenskapsakademiens Handlungar 11: 1–472 + plates.

Brundin, L., 1983. *Chilenomyia paradoxa* gen. n., sp. n. and Chilenomyiinae, a new subfamily among Chironomidae (Diptera). Entomologica scandinavica 14: 33–45.

Brundin, L & O. A. Sæther, 1978. *Buchonomyia burmanica* sp. n. and Buchonomyiinae, a new subfamily among the Chironomidae (Diptera). Zoologica Scripta 7: 269–275.

Butler, M. G., 1982. A 7-year life cycle for two *Chironomus* species in arctic Alaskan tundra ponds (Diptera: Chironomidae). Canadian Journal of Zoology 60: 58–70.

Cabrerizo Ballesteros S., M. de Barrio, M. L. Baeza, M. Rubio Sotés, 2006. Allergy to chironomid larvae (red midge larvae) in non professional handlers of fish food. Journal of Investigational Allergology and Clinical Immunology 16: 63–68.

Carrillo, M. A., C. A. Cannon & L. C. Ferrington Jr, 2004. Effect of sex and age on supercooling point of winter-active *Diamesa mendotae* Muttkowski (Diptera: Chironomidae). Aquatic Insects 26: 243–251.

Chou, R. Y. M., L. C. Ferrington Jr, B. L. Hayford & H. M. Smith, 1999. Composition and phenology of Chironomidae (Diptera) from an intermittent stream in Kansas. Archives für Hydrobiology 147: 35–64.

Coffman, W. P., 1989. Factors that determine the species richness of lotic communities of Chironomidae. Acta Biologica Debrecina Oecologica Hungarica 3: 95–100.

Coffman, W. P. & C. de la Rosa, 1998. Taxonomic composition and temporal organization of tropical and temperate species assemblages of lotic Chironomidae. Journal of the Kansas Entomological Society 71: 388–406.

Coffman, W. P., C. de la Rosa, K. W. Cummins & M. A. Wilzbach, 1992. Species richness in some Neotropical (Costa Rica) and Afrotropical (West African) lotic communities of Chironomidae. Netherlands Journal of Aquatic Ecology 26: 229–237.

Cranston, P. S., 1995a. Systematics. In: Armitage P. D., P. S. Cranston & L. V. C. Pinder (eds), The Chironomidae: Biology and Ecology of Non-biting Midges. Chapman & Hall, London, UK, 31–61, Chapter 3.

Cranston, P. S., 1995b. Medical significance. In: Armitage P. D., P. S. Cranston & L. V. C. Pinder (eds), The Chironomidae: Biology and Ecology of Non-biting Midges. Chapman & Hall, London, UK, 365–384, Chapter 14.

Cranston, P. S. & J. Martin, 1989. Family Chironomidae. In: Evenhuis N. L. (ed.), Catalogue of the Diptera of the Australasian and Oceanian Regions. Bishop Museum Press, Honolulu, Hawaii, 252–274.

Cranston, P. S., O. A. Sæther & L. Cook, 2000. Molecular evidence supports, fails to refute, or provoke new morphological assessment in Chironomidae (Diptera). Abstract, XXI International Congress of Entomology, 919.

Darby, R. E., 1962. Midges associated with California rice fields, with special reference to their ecology (Diptera: Chironomidae). Hilgardia 32: 1–206.

Edwards, M. & M. B. Usher, 1985. The winged Antarctic midge *Parochlus steinenii* (Gerke) (Diptera: Chironomidae), in the South Shetland Islands. Biological Journal of the Linnaean Society 26: 83–93.

Ferrarese, U., 1993. Chironomids of Italian rice fields. Netherlands Journal of Aquatic Ecology 26: 341–346.

Ferrington, L. C., Jr, 1998. Generic composition of the chironomid fauna in springs of North America. In: L. Botosaneanu (ed.). Studies in Crenobiology: The Biology of Springs & Springbrooks. Backhuys Publishers, Leiden, The Netherlands, 141–155.

Ferrington, L. C., Jr. & O. A. Sæther, 1987. The male, female, pupa and biology of *Oliveridia hugginsi* n. sp. (Diptera: Chironomidae Orthocladiinae) from Kansas. Journal of the Kansas Entomological Society 60: 451–461.

Ferrington, L. C., Jr, R. G. Kavanaugh, F. J. Schmidt & J. L. Kavanaugh, 1995. Habitat separation among Chironomidae (Diptera) in Big Springs. Journal of the Kansas Entomological Society 68: 152–165.

Freeman, P. & P. S. Cranston, 1980. Family Chironomidae. In: Crosskey R. W. (ed.), Catalogue of the Diptera of the Afrotropical Region. British Museum (Natural History), London, England, 175–202.

Fuchs, T. & D. Kleinhaus, 1982. Fischfutter-allergie: Sensibilisierung gegen Chironomiden-Larven (Zuckmückenlarven). Allergologie 5: 81–82.

Griffith, L. A. & J. E. Gates, 1985. Food habits of cave-dwelling bats in the Central Appalachians. Journal of Mammology 66: 451–460.

Hayford, B. & L. C. Ferrington Jr, 2006. Distribution of Chironomidae (Diptera) in Lake Hövsgöl, Mongolia. In Goulden, C. E., T. Sitnikova, J. Gelhaus, B. Boldgiv (eds), The Geology, Biodiversity, Ecology of Lake Hövsgöl (Mongolia). Backhuys Publishers, Leiden, The Netherlands, 433–452, Chapter 26.

Hayford, B. L., J. E. Sublette & S. J. Herrmann, 1995. Distribution of chironomids (Diptera: Chironomidae) and ceratopogonids (Diptera: Ceratopogonidae) along a Colorado thermal spring effluent. Journal of the Kansas Entomological Society (Special Publication 1) 68: 77–92.

Johnson, J. H., 1985. Diel feeding ecology of the nymphs of *Aeshna multicolor* and *Lestes unguiculatus* (Odonata). Freshwater Biology 15: 749–756.

Koshima, S., 1984. A novel cold-tolerant insect found in a Himalayan glacier. Nature 310: 225–227.

Lack, D. & D. F. Owen, 1955. The food of the swift. Journal of Animal Ecology 24: 120–136.

Langton, P. H., P. S. Cranston & P. D. Armitage, 1988. The parthenogenetic midge of water supply systems *Paratanytarsus grimmii* Schneider (Diptera: Chironomidae). Bulletin of Entomological Research 78: 317–328.

Lévêque, C., E. V. Balian & K. Martens, 2005. An assessment of animal species diversity in continental waters. Hydrobiologia 542: 39–67.

Lindegaard, C., 1995. Chironomidae (Diptera) of European cold springs and factors influencing their distribution. Journal of the Kansas Entomological Society 68: 108–131.

Linevich, A. A., 1971. The Chironomidae of Lake Baikal. Limnologica (Berlin) 8: 51–52.

Mackay, A. P., 1979. Trophic dependencies of some larval Chironomidae (Diptera) and fish species in the River Thames. Hydrobiologia 62: 241–247.

Miyamoto, T. (ed.), 1988. International Symposium on Mite and Midge Allergy. Special report of the Ministry of Education, Science and Culture, University of Tokyo, Japan, 372 pp.

Murray, D. A. & P. Ashe, 1985. A description of the adult female of *Buchonomyia thienemanni* Fittkau and a reassessment of the phylogenetic position of the subfamily Buchonomyiinae. Spixiana Supplement 11: 149–160.

Nolte, U., 1996. From egg to adult in less than seven days: *Apedilum elachistus* Chironomidae. In: P. Cranston (ed.), Chironomids: From Genes to Ecosystems. CSIRO Publications, East Melbourne, Australia, 177–184.

Oliver, D. R. & P. S. Corbet, 1966. Aquatic habitats in a high arctic locality: the Lake Hazen camp study area, Ellesmere Island, N. W. T. Defense Research Board of Canada, Report #26: Operation Hazen.

Oliver, D. R., M. E. Dillon & P. S. Cranston, 1990. A catalog of Nearctic Chironomidae. Research Branch Agriculture Canada, Publication 1857/B.

Papoucheva, E., V. Proviz, C. Lambkin, B. Goddeeris & A. Blinov, 2003. Phylogeny of the endemic Baikalian *Sergentia* (Chironomidae, Diptera). Molecular Phylogenetics and Evolution 29: 120–125.

Rasmussen, K., 1990. Some positive and negative effects of stocking whitefish on the ecosystem redevelopment of Hjarbaek Fjord, Denmark. Hydrobiologia 200: 593–602.

Reiss, F., 1968. Ökologische und systematische Untersuchungen an Chironomiden (Diptera) des Bodensees: Ein Beitrag zur lakustrischen Chironomidenfauna des nördlichen Alpenvorlandes. Archives für Hydrobiologie 64: 176–323.

Ruse, L., 2002. Chironomid pupal exuviae as indicators of lake status. Archives für Hydrobiologie 153: 367–390.

Sæther, O. A., 1977. Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. Bulletin of the Fisheries Research Board of Canada 197: 1–209.

Sæther, O. A., 1979. Hierarchy of the Chironomidae with emphasis on the female genitalia (Diptera). Entomologica scandinavica Supplement 10: 17–26.

Sæther, O. A., 1983. The canalized evolutionary potential: inconsistencies in phylogenetic reasoning. Systematic Zoology 32: 343–359.

Sæther, O. A., 1989. Phylogenetic trends and their evaluation in chironomids with special reference to orthoclads. Acta Biologica Debrecina Oecologica Hungarica 2: 53–75.

Sæther, O. A., 2000a. Zoogeographical patterns in Chironomidae (Diptera). Internationale Vereingung für Theoretische und Angewandte Limnologie 27: 290–302.

Sæther, O. A., 2000b. Phylogeny of the subfamilies of Chironomidae (Diptera) Systematic Entomology 25: 393–403.

Sæther, O. A. & T. Ekrem, 2003. Biogeography of Afrotropical Chironomidae (Diptera), with speciel reference to Gondwanaland. Cimbebasia 19: 175–190.

Sæther, O. A. & M. Spies, 2004. Family Chironomidae (Diptera), on-line @ http://www.faunaeur.org.

St Louis, V. L., L. Breebaart & J. C. Barlow, 1990. Foraging behavior of tree swallows over acidified nonacidic lakes. Canadian Journal of Zoology 68: 2385–2392.

Spies, M., 2005. On selected family group names in Chironomidae (Insecta, Diptera), and related nomenclature. Zootaxa 894: 1–12.

Spies, M. & F. Reiss, 1996. Catalog and bibliography of Neotropical and Mexican Chironomidae (Insecta, Diptera). Spixiana Supplement 22: 61–119.

Sugg, P., J. S. Edwards & J. Baust, 1983. Phenology and life history of *Belgica Antarctica*, an Antarctic midge (Diptera: Chironomidae). Ecological Entomology 8: 105–113.

Sublette, J. E. & M. S. Sublette, 1973. Family Chironomidae. In Delfinado M. & E. D. Hardy (eds), Catalogue of the Diptera of the Oriental Region, Part 1. University Press, Honolulu, Hawaii, 389–422.

Sublette, J. E. & M. Sublette, 1988. An overview of the potential for Chironomidae as a worldwide source for potent allergens. In: Miyamoto T. (ed.), International Symposium on Mite and Midge Allergy. Special report of Ministry of Education, Science and Culture, University of Tokyo, Japan, 190–231.

Tokeshi, M., 1995. Life cycles and population dynamics. In: Armitage P. D., P. S. Cranston & L. V. C. Pinder (eds), The Chironomidae: Biology and Ecology of Non-biting Midges. Chapman & Hall, London, UK, 225–268, Chapter 10.

Tokunaga, M. & M. Kuroda, 1936. *Stenochironomus* midge from Japan (Diptera), with notes on controlling methods of a leaf mining midge. Transactions of the Kansai Entomological Society 7: 1–6.

Willassen, E. & P. S. Cranston, 1986. Afrotropical montane midges (Diptera: Chironomidae, *Diamesa*). Zoological Journal of the Linnaean Society 87: 91–123.