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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of caddisflies (Trichoptera: Insecta) in freshwater

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Abstract The not yet uploaded Trichoptera World Checklist (TWC) [http://entweb.clemson.edu/database/trichopt/search.htm], as at July 2006, recorded 12,627 species, 610 genera and 46 families of extant and in addition 488 species, 78 genera and 7 families of fossil Trichoptera. An analysis of the 2001 TWC list of present-day Trichoptera diversity at species, generic/subgeneric and family level along the selected Afrotropical, Neotropical, Australian, Oriental, Nearctic and Palaearctic (as a unit or assessed as Eastern and Western) regions reveals uneven distribution patterns. The Oriental and Neotropical are the two most species diverse with 47–77% of the species in widespread genera being recorded in these two regions. Five Trichoptera families comprise 55% of the world's species and 19 families contain fewer than 30 species per family. Ten out of 620 genera contain 29% of the world's known species. Considerable underestimates of Trichoptera diversity for certain regions are recognised. Historical processes in Trichoptera evolution dating back to the middle and late Triassic reveal that the major phylogenetic differentiation in Trichoptera had occurred during the Jurrasic and early Cretaceous. The breakup of Gondwana in the Cretaceous led to further isolation and diversification of Trichoptera. High species endemism is noted to be in tropical or mountainous regions correlated with humid or high rainfall conditions. Repetitive patterns of shared taxa between biogeographical regions suggest possible centres of origin, vicariant events or distribution routes. Related taxa associations between different regions suggest that an alternative biogeographical map reflecting Trichoptera distribution patterns different from the Wallace (The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface, Vol. 1, 503 pp., Vol. 2, 607 pp., Macmillan, London, 1876) proposed biogeography patterns should be considered. Anthropogenic development threatens biodiversity and the value of Trichoptera as important functional components of aquatic ecosystems, indicator species of deteriorating conditions and custodians of environmental protection are realised.

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Freshwater Animal Diversity Assessment

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Introduction

The order Trichoptera (caddisflies) comprises a group of holometabolous insects closely related to the Lepidoptera. Together the two orders form the superorder Amphiesmenoptera. Adult Trichoptera range in size over two orders of magnitude, from minute with a wing span of less than 3 mm, to large with a wing span approaching 100 mm. Some species have striking colours and wing patterns but they generally range in colour from dull yellow through grey, or brown to black. They are moth-like insects with wings covered by hairs, not scales as in Lepidoptera. Adults have prominent, and in some species exceptionally long, antennae (more than double the length of the forewing). With some exceptions they have well-developed maxillary and labial palps, but never the coiled proboscis that characterises most adult Lepidoptera.

Trichoptera larvae are probably best known for the transportable cases and fixed shelters that many, though not all, species construct. Silk has enabled Trichoptera larvae to develop an enormous array of morphological adaptations for coping with life in almost any kind of freshwater ecosystem (Wiggins, 1996, 2004). Larvae can be distinguished from all other insects with segmented thoracic legs by the presence of a pair of anal prolegs, each with a single curved terminal claw and very short, sometimes almost invisible, antennae consisting of a single segment. The trichopteran pupa is exarate and covered by a semitransparent pupal integument and if fully developed reveals the pharate adult inside. The pupa usually possesses a pair of strong functional mandibles, non functional in the adult, and the abdomen has a number of segments adorned with characteristic sclerotised, dorsal hook-bearing plates. The larval and pupal stages of Trichoptera are, with a few exceptions, entirely dependent on an aquatic environment and are usually abundant in all freshwater ecosystems, from spring sources, mountain streams, large rivers, the splash zones of waterfalls and marshy wetlands, along shorelines and in the depths of lakes, to temporary waters. Certain species are tolerant of high salinities and species in one family, the Chathamiidae, have managed to colonise tidal pools along the sea shore in New Zealand and eastern Australia; some species inhabit the brackish inshore waters of the Baltic and White seas.

The phylogeny of Trichoptera has been studied intensively with explicit methods for 50 years (Ross, 1956, 1964, 1967; Weaver, 1984, 1992a, 1992b; Weaver & Morse, 1986; Wiggins & Wichard, 1989; Wiggins, 1992, 2004; Frania & Wiggins, 1997; Ivanov, 1997, 2002; Morse 1997; Kjer et al., 2001, 2002) (Fig. 1). Morphological, molecular and behavioural features of the adults, larvae and pupae have been used to assess specific and higher taxonomic relationships and form the basis of the hierarchical classification system developed. Subdivision into two suborders—Annulipalpia and Integripalpia—is accepted here, because of their strong support from recent phylogenetic studies. Four families—Hydrobiosidae, Hydroptilidae, Glossosomatidae and Rhyacophilidae—sometimes included in a controversial third group ("Spicipalpia"), remain uncertain in their placement. A detailed comprehensive review of ordinal, familial and infrafamilial phylogenies was provided by Morse (1997, 2003).

Species diversity

Fischer (1960–1973) produced a world catalogue that recorded 5,546 species. The recently updated TWC currently records 12,627 species (Morse, personal communication, July 2006, see also Morse, 1999, 2003). These species are arranged in 610 genera and 46 extant families. In addition, 488 species and 78 genera in seven families are known only from fossil records. New species continue to be described at a considerable rate and it seems—particularly from ongoing studies in the Neotropics, Madagascar, humid regions of Africa, south-east Asia, China and the Phillipines—that the prediction of Schmid (1984), Flint et al. (1999) and Morse (personal communication, 2005), although considered an overestimate by Malicky (1993), that there are in excess of 50,000 species may be closer to the actual figure. If these estimates are correct, this leads to the assumption that only around 20–25% of the world species of Trichoptera have been described.

Species recognition is based primarily on morphological features of the adults, strongly influenced

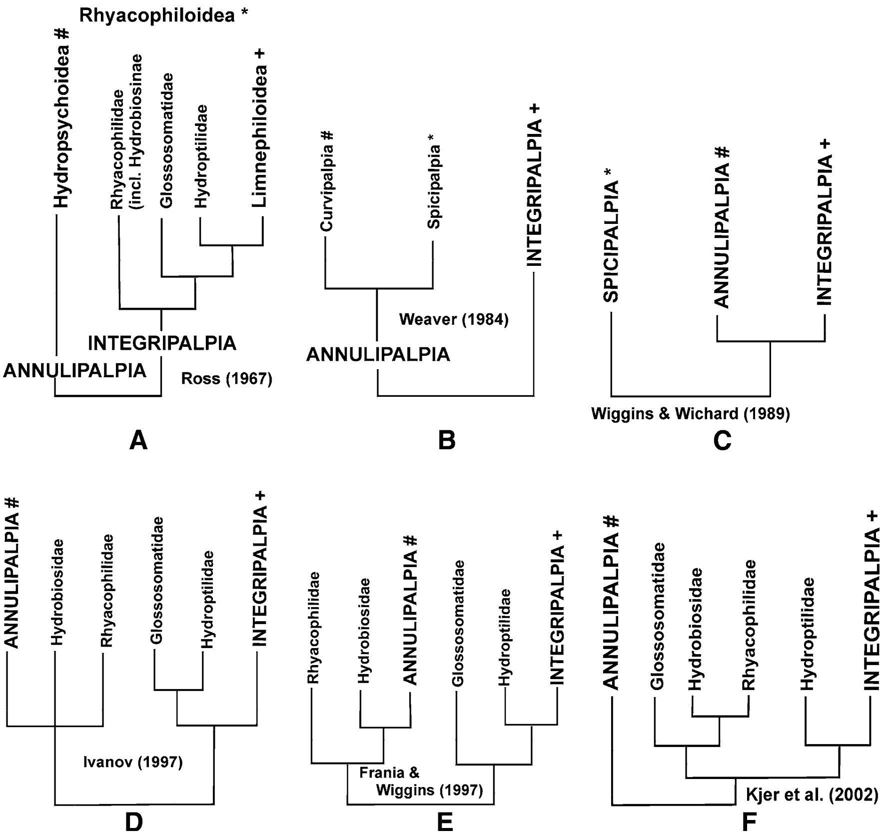

Fig. 1 Six contemporary hypotheses of subordinal relationships of the Trichoptera. Equivalent taxonomic units are indicated by like symbols (e.g. Ross' Hydropsychoidea = Weaver's Curvipalpia = Wiggins & Wichard's Annulipalpia). **A**. From Ross (1967). **B**. From Weaver (1984). **C**. From Wiggins & Wichard (1989), based on pupation only (Wiggins, 1992). **D**. From Ivanov (1997). **E**. Strict consensus of five trees from Frania & Wiggins (1997; Figs. 24, 25). **F**. Simplified phylogram from differentially weighted parsimony analysis of combined data from Kjer et al. 2002. Spicipalpia as used here includes the families Rhyacophilidae, Hydrobiosidae, Glossosomatidae and Hydroptilidae

by detailed studies of the external genitalia of adult male Trichoptera. More recently, molecular sequences in selected RNA and mitochondrial DNA segments have been used to assess species diversity and phylogenetic relationships (Kjer et al., 2001, 2002). The identification of cuticular hydrocarbons in adult Trichoptera presents a further technique that can be used to discern species (Nishimoto et al., 2002). These techniques offer new insights into species diversity and also diversity within species, making it possible to recognise two different species that are morphologically indistinguishable but show considerable genetic diversity, thus making the identification of "sibling" or "aphanic" species possible (Steyskal, 1972).

Generally the world distribution of Trichoptera is considered in a common framework of regions proposed for vertebrates and terrestrial arthropods (Wallace, 1876). The zoogeography of amphibiotic orders, including Trichoptera, differs sufficiently from this to suggest that a different regional classification should be used. In order to present conformity of data to enable comparison with all freshwater fauna reviewed in the other articles in this volume but with one modification, separating the east and west Palaearctic Regions for synthesis, the selection of biogeographical regions for assessing Trichoptera distribution patterns in this article has followed the six major biogeographical regions according to Wallace (1876) (Table 1). A synthesis of the number of genera and species based on the earlier edition of the TWC (last updated 8 January 2001) reveals a total of 11,532 extant species in 620 genera and 94 sub-genera. More than half of these

Table 1 The number of extant genera and species (in parentheses) recorded in Trichoptera families in the major biogeographical regions of the world

Family taxa	W. PA	E. PA	PA	NA	AT	NT	OL	AU	World total
Annulipalpia									
Philopotamidae	5 (51)	5 (41)	7 (91)	5 (56)	4 (87)	4 (257)	10 (346)	5 (60)	17 (886)
Stenopsychidae	–	1 (14)	1 (14)	–	1 (1)	1 (3)	1 (64)	1 (10)	3 (89)
Hydropsychidae	6 (120)	11 (69)	11 (179)	17 (165)	13 (148)	16 (355)	24 (489)	17 (87)	49 (1,409)
Dipseudopsidae	1 (1)	3 (3)	3 (4)	1 (5)	4 (48)	–	4 (47)	2 (3)	6 (104)
Polycentropodidae	8 (88)	9 (38)	11 (118)	8 (77)	7 (20)	7 (173)	10 (230)	8 (42)	23 (656)
Ecnomidae	2 (10)	1 (5)	2 (14)	1 (3)	3 (80)	1 (35)	1 (120)	2 (78)	6 (327)
Xiphocentronidae	–	1 (3)	1 (3)	2 (8)	1 (2)	3 (47)	5 (76)	–	7 (133)
Psychomyiidae	5 (103)	6 (28)	6 (130)	4 (18)	3 (16)	–	7 (234)	2 (5)	8 (400)
"*Spicipalpia*"									
Rhyacophilidae	2 (120)	2 (110)	3 (221)	2 (127)	–	–	3 (350)	1 (1)	4 (696)
Hydrobiosidae	–	1 (2)	1 (2)	1 (5)	–	23 (168)	1 (31)	27 (183)	50 (384)
Glossosomatidae	3 (78)	5 (63)	6 (135)	5 (85)	1 (4)	14 (160)	6 (125)	1 (22)	22 (530)
Hydroptilidae	11 (181)	10 (61)	15 (236)	19 (295)	13 (142)	33 (498)	17 (318)	21 (224)	68 (1,679)
Integripalpia									
Oeconesidae	–	–	–	–	–	–	–	6 (19)	6 (19)
Brachycentridae	2 (30)	5 (28)	6 (56)	5 (37)	–	–	2 (22)	–	7 (112)
Phryganopsychidae	–	1 (2)	1 (2)	–	–	–	1 (2)	–	1 (3)
Lepidostomatidae	6 (25)	9 (55)	12 (79)	3 (75)	3 (37)	1 (18)	23 (187)	–	30 (389)
Pisuliidae	–	–	–	–	2 (15)	–	–	–	2 (15)
Rossianidae	–	–	–	2 (2)	–	–	–	–	2 (2)
Kokiriidae	–	–	–	–	–	1 (1)	–	4 (7)	6 (8)
Plectrotarsidae	–	–	–	–	–	–	–	3 (5)	3 (5)
Phryganeidae	9 (26)	7 (27)	10 (44)	7 (21)	–	–	5 (19)	–	14 (77)
Goeridae	7 (24)	3 (20)	8 (44)	2 (6)	1 (1)	–	5 (110)	1 (2)	12 (160)
Uenoidae	1 (6)	2 (6)	3 (12)	5 (51)	–	–	2 (15)	–	7 (78)
Apataniidae	2 (31)	15 (69)	15 (97)	5 (34)	–	–	5 (60)	–	18 (185)
Limnephilidae	50 (388)	29 (167)	64 (514)	39 (222)	–	10 (45)	17 (102)	1 (3)	95 (861)
Tasimiidae	–	–	–	–	–	2 (2)	–	2 (6)	4 (9)
Odontoceridae	1 (3)	2 (9)	3 (12)	6 (12)	–	2 (25)	4 (41)	2 (4)	12 (103)
Atriplectididae	–	–	–	–	1 (1)	1 (1)	–	1 (1)	4 (5)
Limnocentropodidae	–	1 (1)	1 (1)	–	–	–	1 (14)	–	1 (15)
Philorheithridae	–	–	–	–	–	2 (5)	–	6 (15)	8 (23)
Molannidae	2 (6)	2 (7)	2 (10)	2 (7)	–	–	2 (19)	–	3 (34)
Calamoceratidae	1 (2)	5 (11)	6 (13)	3 (5)	1 (5)	2 (39)	3 (46)	1 (25)	9 (125)
Leptoceridae	14 (127)	13 (102)	18 (212)	8 (116)	18 (302)	12 (143)	16 (597)	18 (207)	48 (1,549)
Sericostomatidae	5 (50)	1 (2)	6 (52)	3 (15)	5 (12)	5 (16)	2 (4)	–	19 (97)
Beraeidae	5 (45)	2 (2)	6 (47)	1 (4)	1 (1)	–	–	–	7 (52)
Anomalopsychidae	–	–	–	–	–	2 (22)	–	–	2 (22)
Helicopsychidae	1 (5)	1 (2)	1 (7)	1 (10)	1 (13)	1 (62)	1 (55)	2 (52)	2 (194)
Chathamiidae	–	–	–	–	–	–	–	2 (5)	2 (5)
Helicophidae	–	–	–	–	–	5 (13)	–	3 (8)	8 (21)
Calocidae	–	–	–	–	–	–	–	7 (20)	7 (20)

Table 1 continued

Family taxa	W. PA	E. PA	PA	NA	AT	NT	OL	AU	World total
Conoesucidae	–	–	–	–	–	–	–	12 (42)	12 (42)
Barbarochthonidae	–	–	–	–	1 (1)	–	–	–	1 (1)
Antipodoeciidae	–	–	–	–	–	–	–	1 (1)	1 (1)
Hydrosalpingidae	–	–	–	–	1 (1)	–	–	–	1 (1)
Petrothrincidae	–	–	–	–	2 (6)	–	–	–	2 (6)
Total genera	149	145	229	157	87	148	169	143	619
Total species	1,520	947	2,349	1,461	944	2,100	3,723	1,140	11,532

The Palaearctic region has been divided into eastern and western regions but is also recorded as a single region for comparative purposes. Zoogeographic regions: PA, Palaearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian

known species were recorded from only two regions, the Oriental and Neotropical Regions (Fig. 2). This indicates a high capacity for supporting large numbers of different species in tropical ecosystems, lower rates of species extinctions during the most recent glaciations, and probably a significantly higher rate of speciation in these two regions than in the other regions. This is borne out by the large proportion of the recorded world species in widely distributed genera such as *Chimarra* (35% and 40%), *Orthotrichia* (47% and 27%), *Oecetis* (40% and 7%) and *Setodes* (71% and 0%) found, respectively, in these two regions.

The highest species diversity is recorded in the Oriental Region. With more than 3,700 species, it contains more than double the recorded species for each of the other regions, except the Neotropics. Without exception, all eight families of the suborder Annulipalpia attain their greatest species richness in the Oriental Region. The family Rhyacophilidae and

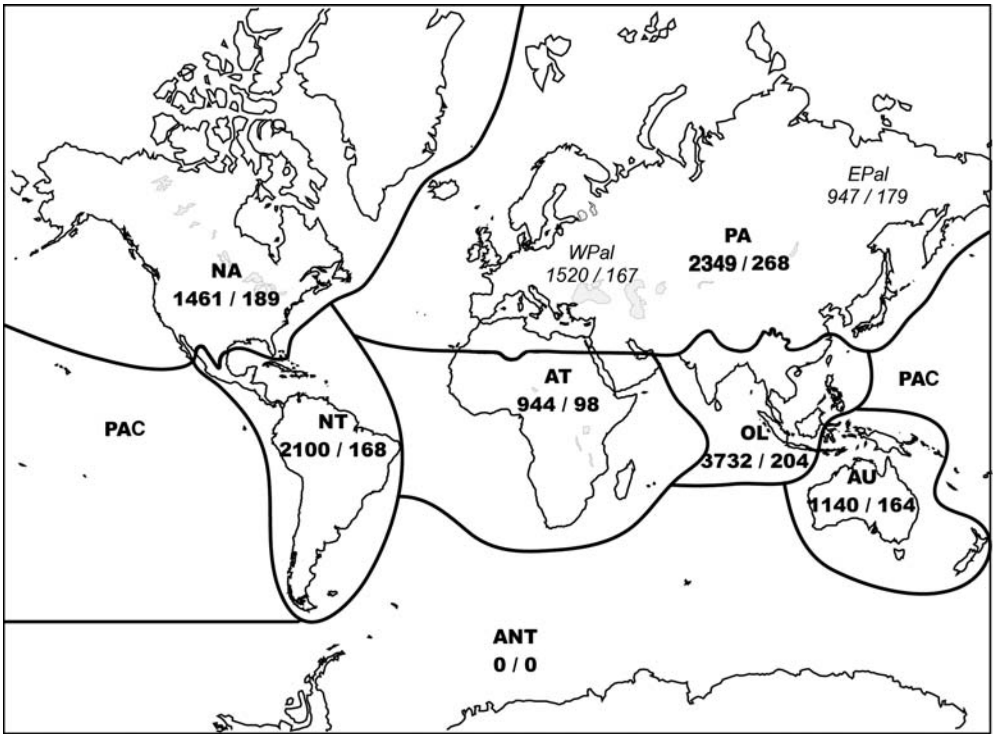

Fig. 2 The current number of species/genera plus subgenera for each of the seven major biogeographical regions. AT, afrotropical; numbers for AU, Australasian include Pacific Oceanic Islands (PAC); PA (WPal), West Palaearctic; PA (EPal), East Palaearctic; NA, Nearctic; NT, neotropical; OL, Oriental

the integripalpian families Lepidostomatidae, Goeridae, Calamoceratidae and Leptoceridae also record their highest number of species in this region. With the large number of species previously described from India by Schmid & Mosely (see expanded reference list on web site), this region also records the highest density of species per unit area at 1.6 species per kilohectare (Morse, 2003). The Neotropical Region records the greatest number of species in the families Hydroptilidae and Glossosomatidae (Table 1). There are no Rhyacophilidae in this region but Hydrobiosidae, confined mostly to southern Patagonia and Chile, are second in species richness after the Australian Region. The West Palaearctic Region records the greatest number of integripalpian species in the families Limnephilidae, Sericostomatidae and Beraeidae.

The distribution of species in the 45 families of Trichoptera is also very uneven with the five most species-rich families comprising 55% of the recorded species. Nineteen families, all in the suborder Integripalpia, comprise fewer than 30 species per family. Ten genera out of the 620 world genera account for 3,299 species, representing 29% of the world total. The numbers of genera within families is also very unevenly distributed. The family Rhyacophilidae, with 696 species, comprises only four extant genera, with 93% of the family's species in the genus *Rhyacophila*. The closest sister family—the Hydrobiosidae—includes 384 species classified in 50 genera, with the most species-rich genus, *Atopsyche*, split into four subgenera containing 30% of the known species in the family. In the family Hydroptilidae there are 20 monobasic genera and a single genus *Hydroptila* records 375 species, contributing 22% of the species in that family. Within the suborder Annulipalpia, the family Philopotamidae (with 17 world genera) has 61% of its species recorded in three subgenera of the genus *Chimarra*. The family Hydropsychidae (with 49 world genera) contains 36% of 1,409 recorded species in two genera (*Cheumatopsyche* and *Hydropsyche*).

Molecular techniques, and more detailed morphological and cladistic techniques have revealed that many of the presently classified large genera are paraphyletic or even polyphyletic. Consequently, some genera need refining to represent monophyletic lineages. Thus the estimations on abundances in generic and higher-level classifications are rather tentative. Larger families like Hydropsychidae, Limnephilidae and Rhyacophilidae await revisions to provide a more reliable basis for determining zoogeographic distribution patterns and phylogenies.

The regional biogeographic diversity of the species and genera recorded in each of the 45 extant families (Table 1) represents considerable underestimates for regions like the Afrotropical and Oriental realms where large numbers of species have been described recently or are awaiting description. Studies in Madagascar (Gibon et al., 2001) reveal that there are at least a further 416 undescribed Madagascan species. Based on the current database and considering only described and recorded species there was a 13% increase in the number of known world species between 2001 and 2006.

A number of regional species lists, catalogues and atlases of Trichoptera, including web sites such as the Trichoptera World Checklist (TWC) (Morse, 1999 http://entweb.clemson.edu/database/trichopt/index.htm), Fauna Europaea (http://www.faunaeur.org) and Checklist of the New Zealand Trichoptera (Ward, 2003 http://www.niwa.co.nz/ncabb) can be consulted for an understanding of Trichoptera diversity.

Historical processes and phylogeny

If representatives from fossil families in the Permian suborder Protomeropina (=Permotrichoptera), which are part of the ancestral Amphiesmenoptera lineage, are considered not to belong in the direct lineage to Trichoptera, then the earliest records of recognisable Trichoptera—in the extinct families Prorhyacophilidae and Necrotauliidae and species recognisable as belonging to the extant family Philopotamidae—are from the Middle and Late Triassic times around 230 mybp (Morse, 1997; Ivanov & Sukatsheva, 2002). It is assumed that all the continents were united in a supercontinent Pangea with a remarkably homogeneous biota, emphasised by the indistinctness of floristic boundaries, recorded throughout (Eskov & Sukatsheva, 1997). This suggests that relatively uniform climatic conditions existed and allowed rapid dispersion of insect groups all over Pangea. The extinct family Necrotauliidae were considered to be the dominant Triassic and Jurassic Trichoptera until the recent revision of old collections by Ansorge (2002) revealed large numbers of Lepidoptera among them. The overall number of Trichoptera recorded from the Triassic is low, both in species and specimen numbers. The earliest aquatic stages of Trichoptera are dated to Late Jurassic times. Trichoptera diversity increased in the Jurassic, with the Lower and Middle Jurassic deposits revealing a number of extinct families (Ivanov & Sukatsheva, 2002). Major phylogenetic differentiation in Trichoptera appeared in the Late Jurassic and Cretaceous (Ivanov & Sukatsheva, 2002) and the biogeographical patterns of those times can therefore help us to understand the present-day peculiarities of Trichoptera distribution.

The earliest Philopotamidae were discovered from late Triassic deposits in the then tropical belt of what would constitute the present day North America and Western Europe (Eskov & Sukatsheva, 1997). Middle Jurassic fossil sediments in Angaraland (which included present-day Siberia) record the earliest species that can be placed in the Integripalpia. The origins of the earliest Rhyacophilidae (Middle Jurassic) and Polycentropodidae (Upper Jurassic) are also recorded from this region. The Rhyacophilidae penetrated the tropical realm in the Early Cretaceous but Polycentropodidae are not recorded there until the Caenozoic from Oligocene-Miocene Dominican Amber. The oldest supposed Hydroptilidae fossils (larval or pupal cases) were found in the Upper Jurassic of Siberia (Ivanov & Sukatsheva, 2002). Presumably the place of origin for this family was somewhere within the non-tropical Old World areas. Originally the species in this family were phytophagous and found in lotic ecosystems. The Hydroptilidae were preadapted to survive in warm waters because of their small size and larval hypermetamorphosis (with very tiny caseless younger instars). Since low oxygen in overheated, organic-rich waters is the most important limiting factor for apneustic immature stages of aquatic insects in the tropics, members of this family are well adapted to tropical situations. Their small size also makes it easy to survive in hygropetric ecosysytems (in a thin film of water over stones, in waterfalls and rapids). The Hydroptilidae show remarkable speciation in the tropics and the diverse S. American fauna clearly demonstrates this (Flint et al., 1999). It is assumed that there were several independent invasions of Hydroptilidae from north to south (from N. America to S. America, from Europe to Africa, and from Asia to Australia). Some species of Hydroptilidae are readily dispersed by wind, and this manner of dispersal is possibly responsible for the peculiar patchy distribution pattern shown by some species. So although the origin of the above family was not considered as tropical, it was adapted to readily invade the tropics and subsequently, with isolation and speciation, developed a diverse fauna (Eskov et al., 2004).

It appears likely that the climate during the Jurassic and Cretaceous was sub-tropical to warm temperate throughout most of the landmasses, without the climatic extremes of the present-day tropical deserts and rainforests. There are notably no Jurassic fossil records from any region of Gondwana (Eskov & Sukatsheva, 1997). Hydrobiosidae appear to have originated in the tropical Jurassic belt (in present day-western Mongolia) and from there spread into more temperate regions. During the Late Jurassic, Leptoceridae were found in the extratropical, warm temperate latitudes of Laurasia (England and Siberia); they dispersed in the Early Cretaceous across other landmasses including Gondwana (Brazil). In contrast, the families Calamoceratidae and Phryganeidae originated in the Early Cretaceous in higher latitudes in the Northern Hemisphere and dispersed to lower latitudes later. The early Cretaceous reveals rapid progress and diversification in Trichoptera case constructions (Ivanov & Sukatsheva, 2002 and the references therein) reflecting extensive speciation. In the Late Cretaceous the Sericostomatidae and Hydroptilidae appear for the first time in deposits in high latitudes in the Northern Hemisphere. Between the early and late Cretaceous the extinction of many of the earlier taxa and dispersal of the taxa described above led to a complete change in pattern of overall Trichoptera diversity. This was caused largely by general transformation of the freshwater ecosystems through the proliferation of angiosperms which resulted in additions of large quantities of foliage debris in surface waters, leading to eutrophication and oxygen depletion (Eskov & Sukatsheva, 1997; Ivanov & Sukatsheva, 2002). During the Cretaceous the breakup of Gondwana further facilitated the isolation of populations of Trichoptera on the newly formed southern continents.

Caenozoic fossil resins and a few poorly studied sedimentary depositional sites reveal a domination of recent Trichoptera at the level of families, a few extinct genera and many extinct species generally related to the extant ones (Ulmer, 1912; Ivanov & Sukatsheva, 2002). The most recent fossil Trichoptera (Middle Miocene Dominican amber) show no significant difference from the Holocene fauna for the same area, indicating that most major evolutionary and dispersal events, at least for these tropical areas, happened before the Miocene (Ivanov & Sukatsheva, 2002). The main feature of the Eocene Baltic amber Trichoptera is the total absence of the large modern family Limnephilidae and the relative paucity of the generally-abundant Hydropsychidae while the family Polycentropodidae is extremely diverse. Based on a number of Caenozoic amber fossils, Limnephilidae are believed to have originated in North America and subsequently spread out across Angaraland/Angarida via the Beringian land bridge into Siberia and Europe (Ivanov & Sukasheva, 2002). Fossil *Wormaldia* species are closely related to extant North American species. In contrast to its present-day paucity in Europe, Caenozoic amber-fossil records of Ecnomidae suggest the previous diversity of this family in the Palaearctic. Similarly, fossil evidence shows the presence of Stenopsychidae and tentatively-identified Dipseudopsidae, now absent from Europe.

Although there were earlier general classifications of subordinal taxa within the Trichoptera, the first hypotheses—linking phylogeny to the dispersal of Trichoptera—to assess phylogenetic relationships were put forward by Ross (1967). He proposed a number of distribution patterns for the explanation and support of his phylogenies but most of his dispersal schemes had no palaeontological evidence. Historical biogeography has been used to identify tracks of phylogenetic relationships across recognised biogeographic regions. This more rigorous testable method produces reduced area cladograms and has been used to identify repeated patterns of biogeographic vicariance events to explain present day distribution patterns in Leptoceridae (Yang & Morse, 2000; Morse & Yang, 2002).

Present distribution and main areas of endemism

The present-day distribution of Trichoptera is nearly cosmopolitan, with only the Polar Regions and small islands remote from continents being excluded. The larvae are almost always aquatic and the adults seldom move far from the water-source on which they are dependent for production of future generations.

The origin and early diversification of Trichoptera are currently considered to have occurred in the early Mesozoic prior to the breakup of Gondwana (see discussion above, Morse, 1997; Ivanov, 2002). Wiggins (1984) noted the uneven distribution pattern of Trichoptera families in the world, with distinct northern and southern hemisphere differences being particularly discernible in the Integripalpia. This pattern reflects the Mesozoic split of the land masses separated by the Tethys Ocean in the North and a series of epicontinental seas in the South. Long isolation between the northern and southern continents could have led to the parallel evolution of separated ancestors of each of the major phylogenetic lineages, so there are southern counterparts of many northern families, forming pairs or triads: Phryganeidae (northern)–Plectrotarsidae (southern); Lepidostomatidae (northern, Laurasian-Oriental)–Oeconesidae (southern, Gondwana-Australian)–Pisuliidae (southern, Gondwana-African); Rhyacophilidae (northern)–Hydrobiosidae (southern). The Hydrobiosidae are especially notable: the family originated in the northern landmasses, then penetrated the southern continents where it evolved into several species-rich lineages, while it became extinct on the northern continents except for a few secondarily migrated species of the genera *Apsilochorema* in the East Palearctic and *Atopsyche* in the West Palearctic regions (Schmid, 1989).

Note should be taken that the present-day distribution of Trichoptera presents a snap-shot in a geological time scale of a continuously changing pattern driven by two major processes; a slow process of evolution, and a more rapid process of vicariance and dispersal moving and mixing of the different faunal elements. The Pleistocene has seen several periods of glaciation when cooling and increased aridity caused rainforests to be reduced to small isolated patches and the great lakes in Africa nearly dried out. This increased aridity would have reduced the suitability of large areas for colonisation by Trichoptera and would have created many small refuge areas for both warm and cold adapted species. The glacial periods were followed by interglacials when temperatures were often considerably warmer than present-day ones. Ocean levels rose by more than 10 m higher than present-day levels and large areas became suitable for colonisation by Trichoptera.

Mobility and dispersal capacity differ from species to species. A number of species in the genus *Drusus* are endemic to specific mountain valleys in the Balkans, whereas others are widespread over Europe and Asia (Malicky, 1979, 1983). The radiation of certain genera resulting in the formation of large concentrations of endemic species in small regions—as seen in the genus *Drusus* in mountain valleys in the Balkans, Apataniidae in Lake Baikal, and *Athripsodes* in the Cape Fold mountains of South Africa—can be considered to have been a result of recent speciation events with ensuing limited dispersal. This was described by Mayr (1942) as "explosive speciation" that resulted in the formation of flocks of closely related species and was inferred for the genus *Drusus* by Malicky (1979). Malicky (1983) proposes a Dinodal biome for explaining the restricted distribution of specialised mountain-stream Trichoptera that could have survived several glacial and interglacial epochs because mountain stream conditions during these periods were relatively stable when compared to lowland areas that show much larger fluctuations of temperature regimes.

The present day distribution of Hydroptilidae shows that generic and species proliferation in this family has occurred mostly in the tropical regions. All fossil records of hydroptilids from amber resins date back to the late Cretaceous from regions that were in the warm to hot belts of the corresponding epochs (Eskov et al., 2004). They are not found in any of the fossil amber from the cool Sibero-Canadian palaeofloristic region (Meyen, 1987). Hydroptilidae do also not track a temperate Gondwana distribution which is revealed by the paucity of genera in the temperate areas of the Australian and Neotropical Regions and the lack of any transoceanic relationships in this family. Hydroptilidae are conservative as regards their dispersal capacity this is borne out by the present-day restriction of the genera *Agraylea* and *Palaeagapetus* to the Holarctic region since the late Cretaceous, as evidenced from fossil resins (Eskov et al., 2004).

Knowledge on the world distribution of Trichoptera is unevenly skewed, with some regions very well known and others hardly explored, a measure of the present state of knowledge is nevertheless presented. The database prepared from the TWC (Morse, 1999) is summarised in Table 1. The strength of association of the 714 genera and subgenera of Trichoptera between each of the seven selected biogeographical regions was assessed through a two-way regional comparison using Sorensen's coefficient of biotic similarity [$SC = 2a/(2a + b + c)$, where a is the number of genera/subgenera common between two regions, b the number of genera/subgenera unique to first region, c the number of genera subgenera unique to second region] (Table 2).

The highest value for Sorensen's coefficient, and thus the greatest regional generic/subgeneric similarity, is between the Oriental and East Palaearctic Regions which shared 111 taxa. This is followed by the East Palaearctic and West Palaearctic Regions sharing 85 taxa. Only one other association (East Palaearctic and Nearctic) is above 0.4 with 63 taxa shared between these two regions.

The seven selected regions for the TWC, essentially represent an artificially imposed biogeography for the Trichoptera. There is clearly a temperate (Chile and Patagonia) and tropical (Brazil and Argentina) Gondwana region for the Neotropical realm, as indicated by many of the Trichoptera families. The Nearctic also shows a strong link on the western side with the Eastern Palaearctic. The similarity of NW American and NE Asian faunas supports the concept of " Angarida/Angaraland" or "Beringia" as a special faunistic region that existed in the past. This was evidently an area of rapid faunistic exchanges in times immediately preceding

Table 2 Sorensen's coefficient produced from a two-way analysis of the relative affinities of 714 Trichoptera genera/subgenera for the seven major biogeographical regions covered

	AT	WP	EP	NA	NT	OL
WP	0.23					
EP	0.28	0.49				
NA	0.17	0.35	0.46			
NT	0.12	0.09	0.10	0.32		
OL	0.33	0.34	0.58	0.31	0.12	
AU	0.20	0.14	0.19	0.15	0.11	0.22

AT, Afrotropical; WP, West Palaearctic; EP, East Palaearctic; NA, Nearctic; NT, Neotropical; OL, Oriental; AU, Australasian glaciation or shortly after glacial meltdown, when the ocean level was sufficiently low to expose the Beringian landbridge along the Bering Strait (Ross, 1967; Levanidova, 1982; Wiggins & Parker, 2002). The corresponding link between the East Nearctic and West Palearctic is less evident because the continental break has led to an increasing distance and longer period of isolation across the Atlantic Ocean. The recent glaciation events also greatly altered the European and American faunas. The most evident present-day faunal relations are in the Arctic regions revealing a Circumboreal type of distribution. There is significant asymmetry in Trichoptera distribution in northern Europe showing distinct penetration of the cold-adapted species from Asia to the boreal regions spreading from the Urals to Fennoscandia (Spuris, 1986, 1989).

The present-day distribution of families in the seven selected biogeographical regions gives a somewhat less refined analysis but adequately reveals major patterns. There are six endemic families in the Australian Region making it the region with the highest rate of endemism (Fig. 3). The Afrotropical Region comes second with four endemic families, three of which are restricted to the south-western region of South Africa or Madagascar and are considered to be relict populations from temperate Gondwana (Scott & de Moor, 1993). Species in the remaining family, Pisuliidae, are specialised ecological shredders that have populations confined to patches of coastal or montane rainforest in the central and southern half of the African continent and in rain forests in Madagascar. The Neotropical and Nearctic Regions each have one endemic family. All 12 families endemic to any region have low numbers of species; the highest number recorded is 22 species for the Anomalopsychidae. Six additional families share their distribution over two biogeographical regions. Four families are shared between the Neotropical and Australian Regions and two families have species in the East Palaeartic and Oriental Regions. The family Atriplectididae has representative species in the Australian, Afrotropical and Neotropical Regions (Fig. 3, Table 1).

An assessment of the number of endemic genera/subgenera in each region also shows the highest endemism to be in the Australian Region with a figure of 73%, followed by the Neotropical Region with 69% (Fig. 3). The Afrotropical Region (43%) and West Palaearctic Region (41%) also have quite high endemism at generic/subgeneric levels. The Oriental Region with the highest number of genera/subgenera (204) has a similar number of endemics to the West Palaearctic Region, but this only represents 33% of its generic/subgeneric component.

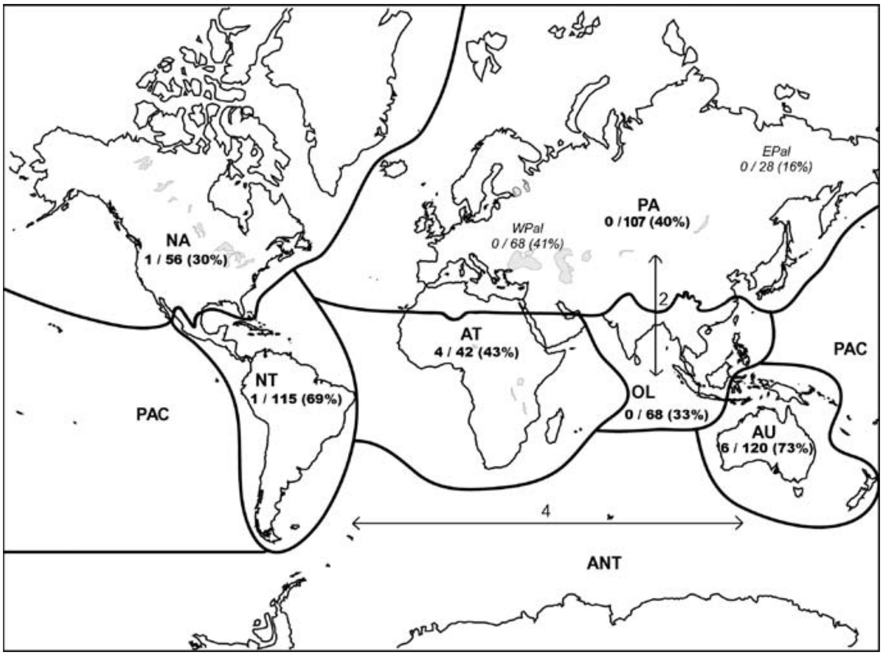

Fig. 3 The number of recorded endemic families and genera plus subgenera (End. Fam./End gen. (% of total genera)) for each major biogeographical region. Arrowed figures indicate the number of families found in two biogeographical regions (two families are common to EPal and OL and four families are common to NT and AU)

One striking aspect is that the areas with the greatest species diversity are not necessarily those with the greatest higher-level taxon diversity. The Neotropical Region, although second highest in species diversity, is only fourth in generic/sub-generic diversity after the Nearctic and East Palaearctic. The subfamily Leptocerinae is most diverse in generic diversity in the Afrotropical Region, but records the highest number of species in the Oriental Region (de Moor 2002a). These discrepancies might indicate rapid speciation in recent times after the formation of rainforest ecosystems in the Late Caenozoic.

Areas with great concentrations of endemic species or with high numbers of species (hotspots of endemism or hotspots of species diversity) can be identified as being in temperate and tropical mountain regions or in areas of high rainfall. The northern Andes, the Amazon basin and mountains of southern and southeastern Brazil are represented in the Neotropics (Flint et al., 1999); the mountain fold belt of the south western and southern Cape in South Africa, the central African highlands and West Africa are represented in the Afrotropics. Numerous endemics are found in the Mediterranean area including Turkey, the southern Caucasus and the Alps (Malicky, 1983, 1986; Malicky & Sipahiler, 1993) as well as the Iberian peninsula in WP. There are smaller centres of endemism in Middle Asia (from Pamir to the Tyan-Shan mountain ranges); in the Altai Mountains, mountain ridges of the Far East and around Lake Baikal. A large amount of endemism occurs in Korea, China and Japan, although the Chinese biogeography is too poorly studied to provide significant detail of smaller regions. Large numbers of local endemic species are found throughout SE Asia, with significant concentrations along the Himalayan slopes and the meridional mountain ridges of Indochina, and also on the islands of Indonesia. The endemism here correlates with the monsoon intensity providing the humid conditions necessary for Trichoptera development.

Repetitive patterns of shared taxa between biogeographical regions suggest possible centres of origin, routes of dispersal or vicariant events. These are apparent from the database of generic/subgeneric distribution and species abundance prepared from the TWC (see internet documents and Morse, 1999). In summarising the foregoing discussions the following biogeographical patterns are proposed:

1. Temperate Gondwana link between Australian and Neotropical Regions with some relict survivors at superfamily level (Sericostomatoidea) also found in the southernmost part of Africa and Madagascar. Several families and closely related genera show this pattern.
2. A shared distribution pattern between the Oriental and Holarctic Regions. This has two alternative routes of dispersal both indicated by species abundances of closely related taxa; the first via the East Palaeartic to the Nearctic Region, and the second to the West Palaearctic Region (the Rhyacophilidae indicate both these patterns).
3. A tropical Gondwana link between Africa, Madagascar and India (genera of Hydropsychidae, Hydroptilidae and Dipseudopsidae). There are also a few instances where Brazilian linkages with West Africa can be discerned with some taxa even extending to the Australian region (family Atriplectididae, genus *Ecnomus* and some Leptocerinae and Hydroptilidae genera).
4. A two-way exchange of Neotropic and Nearctic faunas, indicated by some shared Hydroptilidae and Leptoceridae genera.
5. A more recent link between the Australian and Oriental Region with a number of taxa crossing the Wallace/Weber lines. This is mostly of tropical origin into temperate Australia, but there are some temperate Triplectidinae that have apparently moved into the Oriental realm more recently.

The discovery of Eocene Baltic Amber fossil records of Helicophidae and psyllobetine Hydrobiosidae—groups presently restricted to Australia and New Zealand (Australian Region) and Chile (Neotropical Region)—suggests a very different alternative hypothesis. Possibly these presently-restricted, temperate Gondwana taxa (Southern Hemisphere) had a much wider distribution, previously extending into the Northern Hemisphere, and became extinct in most of their former range (Botosaneanu & Wichard, 1983). The Northern Hemisphere continents in the last 3 million years (Pleistocene) have been exposed to glaciation events which have largely left the southern hemisphere continents unscathed. It is likely that the glaciations led to the local and regional extinction of many widespread taxa that were unable to disperse. Relict populations probably survived in more hospitable climates. Baltic and Dominican Amber fossils also reveal that certain taxa (Leptoceridae: Triplectidinae) were more widespread than indicated by present-day records (Botosaneanu & Wichard, 1981). Some populations of the more plesiomorphic Philopotamidae and Hydrobiosidae—found presently only in temperate Gondwana regions—may therefore also represent a relict fauna of previously widespread taxa that became extinct in other regions in the Northern Hemisphere (Eskov, 1984).

From the above discussion it is suggested that an alternative map highlighting regions on present day continents reflect a somewhat different biogeographical pattern to the generally accepted seven biogeographical Regions. Detailed distribution patterns of Trichoptera and possibly other amphibiotic insects cannot be expounded here, but what is clear is that Gondwana needs to be divided into several more closely related biogeographical regions reflecting a temperate southern region incorporating Australia, New Zealand, Patagonia and southern Chile and possibly the southern tip of Africa and southernmost part of Madagascar; and a tropical region incorporating parts of the Neotropical, African, Madagascar and the Indian-part of the Oriental regions. The proposed map highlighting distinct biogeographic regions and indicating close relationships illustrates these patterns (Fig. 4).

The Northern Holarctic Region also presents a different pattern with at least five clearly discernible divisions (Fig. 4). Thus, the distribution of Hydrobiosidae in S. America shows great extra-tropical diversity in Patagonia similar to that in New Zealand and Southern Australia, whereas the slopes of the Andes further to the north have increasingly less diversity (Schmid, 1989). The distribution of Trichoptera in Central Asia shows a distinct gap in Eastern Iran and Western Afghanistan between the generally western European fauna of Iran and the Oriental fauna of Afghanistan (Malicky, 1986). The distribution of the "Beringian" species encompasses Eastern Siberia, but generally avoids Western Siberia (Levanidova, 1982).

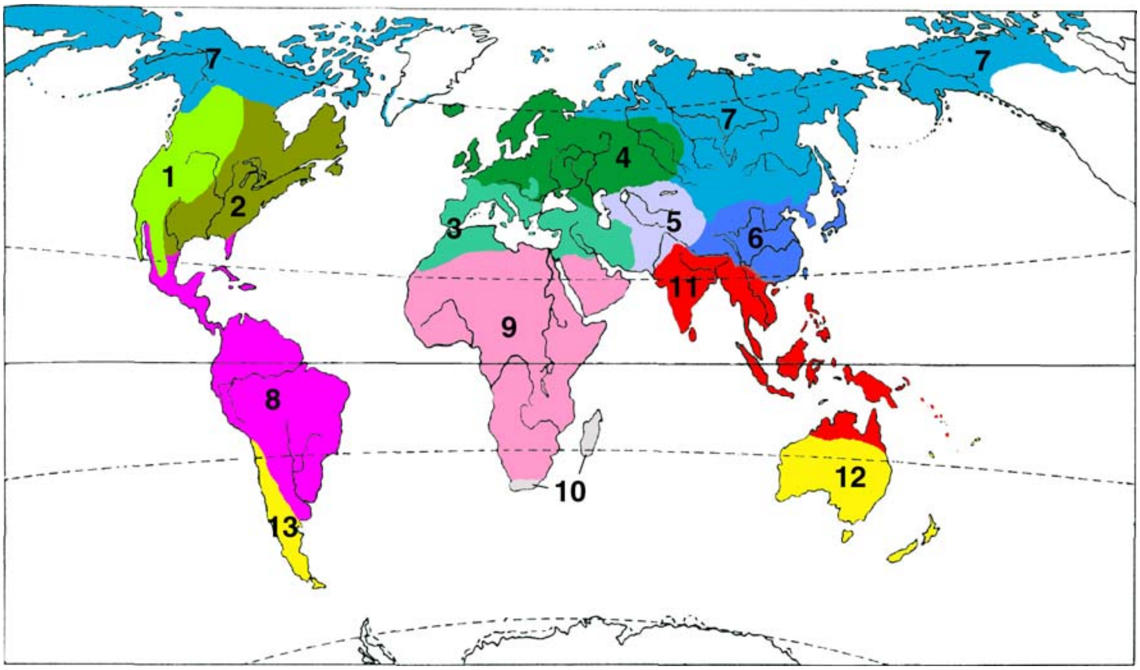

Fig. 4 Preliminary outline for Trichoptera biogeographical regions. 1. West Nearctic, 2. East Nearctic, 3. West Palaearctic, 4. Boreal Palaearctic, 5. South Palaearctic, 6. East Palaearctic, 7. Beringian, 8. Neotropical, 9. Afrotropical, 10. Cape South African, 11. Oriental, 12. Australasian, 13. Patagonian. Similar colours indicate close biogeographical relationships

Human related issues

Trichoptera are abundant in all types of natural aquatic ecosystems. They are apneustic and rely on dissolved oxygen for respiration. With a high diversity of species with both case- and shelter-constructing larvae, they are useful indicators of organic pollution. Trichoptera have been used extensively in biomonitoring assays with indicator species, selected communities or assemblages of species or more broadly based family level identifications of species being used to assess the health status of aquatic ecosystems. Trichoptera, in conjunction with other aquatic insect orders, have also been used to assess aquatic biodiversity EPT (Ephemeroptera, Plecoptera and Trichoptera) or ETS (Ephemeroptera, Trichoptera, Simuliidae: Diptera) and habitat diversity (Hannaford & Resh, 1995; Hewlett, 2000; de Moor, 2002b).

From an ecological perspective, Trichoptera are important processors of organic matter and provide a keystone taxon in the development of the river continuum concept (RCC) (Vannote et al., 1980). As processors of organic matter, collectively known as the functional feeding groups (FFG) of animals, they display the full array of feeding modes (Cummins, 1973). In lotic water filter-feeding, shelter-constructing species are important predators of blackfly larvae and help keep population levels of pest species at acceptable levels (de Moor, 1992). In some instances excessive construction of shelters by collector/filter-feeding larvae have caused the clogging of pipes under bridges and storm-water pipes, creating problems when flooding occurs (McCafferty, 1981). Trichoptera larvae, pupae and adults also form an important link in the food chain and they have also been used extensively by trout fishing enthusiasts as models for "flies" (McCafferty, 1981).

Development and man's activities have considerably reduced Trichoptera species diversity and the need for remedial measures to prevent further damage to ecosystems and loss of Trichoptera species have been discussed by Botosaneanu (1981) and Ivanov (2000). Red data lists for certain countries have been produced and can be used to manage ecosystems to protect vulnerable or rare species of Trichoptera. Anthropogenic development threatens biodiversity and the value of Trichoptera as important functional components of aquatic ecosystems, indicator species of deteriorating conditions and custodians of environmental protection are realised.

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