

Global diversity of dipteran families (Insecta Diptera) in freshwater (excluding Simuliidae, Culicidae, Chironomidae, Tipulidae and Tabanidae)

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Abstract Today's knowledge of worldwide species diversity of 19 families of aquatic Diptera in Continental Waters is presented. Nevertheless, we have to face for certain in most groups a restricted knowledge about distribution, ecology and systematic, particularly in the tropical environments. At the same time we

realize a dramatically decline or even lack of specialists being able, having the time or the opportunity to extend or even secure the present information. The respective families with approximate numbers of aquatic species are: Blephariceridae (308), Deuterophlebiidae (14), Nyphomyiidae (7), Psychodidae (~2.000), Scatopsidae (~5), Tanyderidae (41), Ptychopteridae (69), Dixidae (173), Corethrellidae (97), Chaoboridae (~50), Thaumaleidae (~170),

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Ceratopogonidae (~6.000), Stratiomyidae (~43), Empididae (~660), Lonchopteridae (2), Syrphidae (~1.080), Sciomyzidae (~190), Ephydriidae (~1.500), Muscidae (~870). Numbers of aquatic species will surely increase with increased ecological and taxonomical efforts.

Keywords Aquatic Diptera · Continental waters · Diversity · Distribution · State of knowledge

Foreword

With few exceptions it is difficult to extract from the numerous Diptera families those with aquatic or ‘water dependent’ species. A key problem for most groups is the lack of knowledge on larval ecology and morphology of many taxa on the one hand, and the great ecological plasticity on the other hand. In general, the majority of ‘water dependent’ larvae and pupae live in moist to wet grounds (providing substratum, shelter and food) in the surrounding of springs, streams, rivers, ponds lakes or in wetlands where they may occupy a multitude of spatially and temporally variable habitats.

A restricted amount of families show unquestionable aquatic life cycles, i.e. Chaoboridae and Corethrellidae, that are almost exclusively found in the pelagic zone of standing water bodies, or in the families of Blephariceromorpha whose larvae live almost only in torrential mountain streams. Recently, a few Diptera families have been reported from aquatic habitats, e.g. Lonchopteridae (Vaillant, 2002), Scatopsidae (Haenni, Vaillant pers. comm.), and Bibionidae (own observation). Another example is the family Dolichopodidae; several thousand species have been described until now. Some species exhibit aquatic development of larvae; however, larval ecology of most species remains totally unknown. A compilation of ‘water dependent other Diptera’ (to our best knowledge) is given in Table 1.

Some families were left out of this assessment because we could not find available specialists to deal with the worldwide diversity of these groups (e.g. Athericidae, Rhagionidae, Tabanidae). This is a strikingly clear indication of a dramatic loss or even lack of taxonomic specialists—not only in aquatic Diptera—all over the world.

Authors have tried to provide most complete up to date information, however, in many cases knowledge and existing databases are still far from being complete.

Introduction

Family Blephariceridae (P. Zwick)

For a long time, the slender, long-legged net-winged midges (wing lengths between 4 and 12 mm) were first known by the name Blepharoceridae in the 1840s. Blepharicerid larvae and pupae were only discovered in 1881. They inhabit fast flowing, often torrential waters, from sea-level to high mountains.

Larvae attach to smooth rock substrata with their suckers, head upstream, some resisting speeds of flow over 1 m s^{-1} . Locomotion is by successive detachment of suckers and is slow, except during sideways (!) escape gate.

Distribution on inhabited lands is not uniform, for ecological reasons, plains and terrain without rock substrata cannot be colonized. Blephariceridae are also absent from sandstone and other coarse grained rocks to which suckers cannot attach. Most species occur in permanent streams, but some taxa with long egg diapause survive or even specialize (*Dioptopsis*) in intermittent water courses.

Family Deuterophlebiidae
(G. Courtney & R. Wagner)

Deuterophlebiidae (mountain midges) is one of the most specialized dipterous insects. The larvae and pupae of these small flies (<4 mm) are aquatic, found mostly in cold torrential streams, but ranging from small high-gradient creeks to large low-gradient rivers (Turner et al., 1986; Courtney, 1991a). Larvae and pupae are restricted to riffle habitats where they adhere to larger stones. Among the structural and ecological adaptations are eversible larval prolegs and flattened streamlined pupae. Adults have comparatively large wings and males extremely long antennae. Adults that have vestigial mouthparts, live for only a few hours (Courtney, 1991a, 1994a). Univoltine, synchronous life cycles are typical of most Nearctic species but bivoltine, asynchronous

Table 1 Compilation of 'water dependent' Diptera families

Suborder: Nematocera	Suborder: Brachycera
Infraorder: Blephariceromorpha	Infraorder: Tabanomorpha
Superfamily: Blepharicerioidea	Superfamily: Tabanoidea
Family: Blephariceridae	Family: Tabanidae
Family: Deuterophlebiidae	Family: Rhagionidae
Superfamily: Nymphomyioidea	Superfamily: Stratiomyoidea
Family: Nymphomyiidae	Family: Stratiomyidae
Superfamily: Bibionoidea	Infraorder: Asilomorpha
Family: Bibionidae	Superfamily: Empidoidea
Infraorder: Psychodomorpha	Family: Empididae
Superfamily: Psychodoidea	Family: Dolichopodidae
Family: Psychodidae	Infraorder: Muscomorpha
Family: Scatopsidae	Section: Aschiza
Infraorder: Ptychopteromorpha	Superfamily: Platypezoidea
Family: Tanyderidae	Family: Lonchopteridae
Family: Ptychopteridae	Superfamily: Syrphoidea
Infraorder: Culicomorpha	Family: Syrphidae
Superfamily: Culicoidea	Section: Schizophora
Family: Dixidae	Subsection: Acalyptratae
Family: Corethrellidae	Superfamily: Lauxanioidea
Family: Chaoboridae	Family: Sciomyzidae
Family: Culicidae	Superfamily: Sphaeroceroidea
Superfamily: Chironomoidea	Fam: Heleomyzidae
Family: Thaumaleidae	Fam: Sphaeroceridae
Family: Simuliidae	Superfamily: Ephydroidea
Family: Ceratopogonidae	Family: Ephydriidae
Family: Chironomidae	Subsection: Calyptratae
	Superfamily: Muscoidea
	Family: Muscidae

life cycles were also reported by Courtney (1991a); seasonal, habitat and reproductive isolation of sympatric species occurs North American and Himalayan species (Courtney, 1991a, 1994a).

Family Nymphomyiidae (G. Courtney & R. Wagner)

This peculiar Diptera family was discovered by Tokunaga as recently as 1930, when six specimens were collected along a torrential mountain stream near Kyoto, Japan. Nymphomyiidae were established as a new family based on a single species, *Nymphomyia alba* (Tokunaga 1932, 1935a, b). Phylogenetic relationships have been discussed controversial, but recent studies (Wood & Borkent, 1989; Oosterbroek

& Courtney, 1995) suggest the Nymphomyiidae are sister group to the superfamily Blepharicerioidea (Blephariceridae + Deuterophlebiidae). Only few observations of larval and adult biology exist (Cutten & Kevan, 1970; Harper & Lauzon, 1989; Courtney 1994b). Larvae and pupae are cold stenothermous, found mostly in small perennial streams and cold headwaters (Courtney & Jedlicka, 1997). Details of their life cycle and habits were summarized by Courtney (1994b). Adults apparently do not feed and their life span is very short. One or two generations per year were observed in some species. Although some authors have suggested that eggs or pupae pass the winter (Cutten & Kevan, 1970; Back & Wood, 1979), most data on Nearctic nymphomyiids indicate that the larva is the overwintering stage (Harper & Lauzon, 1989; Courtney 1994b).

Psychodidae (R. Wagner)

Adult Psychodidae are small to medium sized Nematocera, the hump-backed body is covered by a dense vestiture of hairs and setae.

Larvae of Phlebotominae and Bruchomyiinae are terrestrial. Probably all Trichomyiinae larvae are xylophageous. Aquatic in the strict sense are Horaiellinae, Sycoracinae and most Psychodinae. The general appearance differs strongly between subfamilies. Larvae of the Old World Sycoracinae are small and asselliform. *Horaiella* larvae have only one curious ventral sucker. The head of Psychodinae larvae is strongly sclerotized, non-retractile. Thoracic and abdominal segments divided into 26 or 27 ring-shaped pseudosegments (annuli). They are more or less heavily sclerotized, with dorsal plates. Arrangement of hairs and setae on these plates are specific in most cases.

Scatopsidae (J.-P. Haenni)

Scatopsidae are minute to small, rather stoutly built, generally blackish midges. Both sexes are holoptic (except in few genera), with typical eye-bridge above antennae, ocelli present and palpi one-segmented. Larvae peripneustic, with the last abdominal segment bearing a pair of large spiracles generally placed at the apex of more or less elongate posterior processes. Larvae of only a few genera are known, with species-specific or at least genus-specific chaetotaxy. Larvae of most genera are terrestrial, saprophageous, living in a wide variety of organic matter in all degrees of decomposition, consequently often in liquid or semi-liquid media. Few larvae are aquatic living under the surface of a thin water film among water-logged dead tree-leaves, while few others are dendrolimnobiontic (Haenni & Vaillant 1990, 1994). Pupae are typically enclosed in last larval skin.

Family Tanyderidae (R. Wagner)

Tanyderidae (primitive crane-flies) are mid-sized to large nematocerans, resembling Tipulidae, wing with five radial veins and only one anal vein reaching the margin of the variously patterned wings. Larvae of five genera are known, they occur in two types of

habitats, the hyporheic zone of cobble and sand bottom streams or in the outer layers of submerged rotting wood (Exner & Craig, 1976; Krzeminski & Judd, 1997). They prefer unpolluted mountainous streams. Males sometimes swarm in the evening, at day they hide in the bank vegetation.

Family Ptychopteridae (P. Zwick)

The family Ptychopteridae comprises the genus *Ptychoptera* in the Ptychopterinae, and *Bittacomorpha* and *Bittacomorphella* in the subfamily Bittacomorphinae. Numerous differences in structural detail among the subfamilies exist in all life stages. The best general account of the family remains Peus (1958).

Ptychopteridae have petiolate slender wings 5–12 mm long. The family name refers to sharp longitudinal folds in the membrane that may at first glance be taken for veins. *Ptychoptera* has two of these, the more slender Bittacomorphinae with narrower wings only one. Eggs are laid at the edge of soft aquatic sediments in which larvae and pupae live. However, they breathe atmospheric oxygen with long respiratory tubes. From personal observations of European fauna, habitat specificity seems to be high, and habitats may be small. Preferred habitats range from pristine spring seeps in some species to anoxic sediments with H₂S in others. Studied European *Ptychoptera* (Hodkinson, 1973; Hansen, 1979; Wolf & Zwick, 2001; PZ personal data on all seven German species) are seasonal and univoltine, the last larval instar overwinters. *Bittacomorpha* can be aseasonal and plurivoltine (Bowles, 1998). Adult life seems to last only for some days. Adult habits are poorly known.

Family Dixidae (R. Wagner)

The Greek word Dixos means bifurcate and refers to the two forked veins of the wing. Adults are small, frail, and they do not feed. They remain near their biotops (streams, ponds), and rest in the vegetation. Males of some species form swarms. Eggs are deposited in masses at the water's edge. The life cycle includes four larval instars and pupa. Larvae are pale greyish filter-feeders that lie on the water surface

(meniscus-midges). They were attributed to the 'Fauna Hygropetrica', i.e. the microhabitat where a thin water film flows permanently (or intermittently) over emergent structures. Pupae are much less active than the larvae; they prefer drier microhabitats. *Dixa* larvae prefer stream banks, *Dixella* larvae are found at the edge of standing waters. Some species are restricted to bog or mesotrophic lakes and are appropriate bioindicators.

Life history studies are from Wood (1934; afro-tropical *Dixa bicolor*, pupal stage 3–4 days). Peach & Fowler (1986) describe all instars of the palaeartic *D. autumnalis* (life cycle about 60 days). Peters & Adamski (1982) give an outline of larval morphology (Nearctic *Dixella nova*). Early cytogenetic studies are from Frizzi et al. (1966). Disney (1999) provided an outstandingly nice compendium of west-palaeartic Dixidae that can be used worldwide as a base of knowledge.

Family Corethrellidae (A. Borkent & R. Wagner)

Corethrellidae are close relatives of Culicidae and Chaoboridae, and at one time were placed in the latter family. The predaceous larvae are restricted to bodies of small standing water, in various phytothelmata such as treeholes, epiphytes and leaf axils or in small isolated ground pools, with these sometimes at the margins of springs or lakes. The larvae feed on a variety of small invertebrates (e.g. crustaceans, nematodes, mosquitoes). The female adults feed on the blood of male frogs and are attracted by their calls.

Family Chaoboridae (R. Wagner & Goddeeris)

Chaoboridae or phantom midges are medium-sized, non-biting Nematocera. The larvae live in standing waters; they possess hydrostatic air bladders (except *Eucorethra*) and they are predators of small arthropods, oligochaetes, rotifers, but also unicellular algae (except the filter feeder *Australomochlonyx*). In *Chaoborus*, larvae are mostly planctonic, transparent and they display circadian vertical migration. Pupae are free living in the pelagial. Some species (*Mochlonyx* and *Cryophila*) live in small, often temporary water bodies. Eggs of species from intermittent

biotops overwinter and are resistant to desiccation (Montshadsky, 1960).

Family Thaumaleidae

(B. J. Sinclair & R. Wagner)

Thaumaleidae are small, stout, brownish nematoceros Diptera, very uniform in appearance, sometimes confused with Psychodidae or Simuliidae. Both sexes are holoptic and no ocelli are present. They are considered members of the 'Fauna Hygropetrica', i.e. larvae are restricted to vertical, thin water films flowing over rocks alongside waterfalls and torrents, and hold on to the substrate with anterior and posterior prolegs (Boussy et al., 1994). Larvae are categorized as scrapers, grazing on diatoms. Rapid larval movement is unique and diagnostic, traversing with quick zigzag strokes. Pupae are free-living in the hygropetric zone, bearing leaf-shaped appendages in some Southern Hemisphere species. Parasitism by *Entomacis* sp. (Hymenoptera: Proctotrupiodea: Diapriidae) upon immature *Austrothaumalea denticulata* Theischinger is the only known example (Sinclair, 2000b).

Family Ceratopogonidae (A. Borkent)

The Ceratopogonidae are an extremely diverse and abundant group of flies, commonly known as biting midges or no-see-ums. Biting midge adults are relatively easy to recognize to family. Adult females of four genera suck blood from vertebrates but most of the remaining 99 genera suck blood from other insects. The immatures occur in a wide array of environments where there is at least some moisture, such as rotting vegetation or manure, semiaquatic to fully aquatic habitats, including rivers and lakes. They are most common, both in terms of individuals and in numbers of species, in smaller aquatic habitats such as epiphytic plants, treeholes, pools, rice fields and the margins of marshes, pools and running water. The Ceratopogonidae, in nearly every regard, are one of the most poorly understood of all aquatic groups. Numerous surveys indicate that the group is abundant in many habitats, but because the larvae and pupae cannot be identified even to the generic level with any confidence, they remain largely unstudied.

Family Stratiomyidae

(R. Rozkošný & N. E. Woodley)

Adults of Stratiomyidae range from 2.0 to 26.0 mm in length. They belong to the suborder Brachycera. Larval habitats are very diverse, with both terrestrial and aquatic taxa. The typical aquatic larvae, with the exception of *Ptecticus* (Sarginae) and semi-aquatic larvae of *Beris* (Beridinae) and *Nemotelus* (Nemotelinae), are characterized by a more or less lengthened anal segment (breathing tube) (Rozkošný, 1982–1983).

Hymenopteran parasitoids of aquatic stratiomyid larvae have been known for a long time; reviews are given by McFadden (1967) and Rozkošný (1982).

Family Empididae (B. J. Sinclair)

The Empidoidea (excluding the Dolichopodidae) or dance flies, is a morphologically diverse group, with wing length ranging in size from less than two to over 12 mm. The aquatic larvae are apneustic (except *Oreogeton*) and characterized by paired prolegs or raised pads, partially sclerotized head capsule, with paired metacephalic rods. The aquatic empidoids are predaceous as adults and larvae (Steyskal & Knutson, 1981; Sinclair, 1995; Sinclair & Harkrider, 2004).

In the Northern Hemisphere, surveys of aquatic habitats (mostly running water) that include detailed species lists of empidoids, have been conducted in Canada (Harper, 1980; Landry & Harper, 1985), Germany (Wagner & Gathmann, 1996) and a recent short-term study in the Himalayas (Wagner et al., 2004).

Family Lonchopteridae (M. Bartak)

Lonchopteridae are small, strongly setose yellow to brownish black Brachycera. Both sexes are dichoptical, with conspicuously pointed wing with sexually dimorphic venation. Antennae small, with a rather elongate subapical arista (detailed description and illustrations in e.g. de Meijere, 1906; Smith, 1969; Baud, 1973; Peterson, 1987; Drake, 1996). Larvae live in wet microenvironment of decaying organic matter, among dead leaves, in plant debris, under stones on shores of water courses or they are

semiaquatic. They are saprophagous, microphagous or presumably, mycetophagous. Puparium resembles larva. For more details about biology consult Baud (1973), Bährmann & Bellstedt (1988) and Drake (1996).

Family Syrphidae (G. E. Rotheray)

Syrphidae are small to large (4–25 mm long), slender to robust Lower Cyclorrhaphan flies. Many species resemble noxious Hymenoptera in a general way having white, yellow, orange or red markings but some are highly specific mimics of bees or wasps. Adults are often abundant and occur at low and high altitudes and they are found in a wide range of habitats, from deserts to rain forests. They are frequent flower visitors and important pollinators (Thompson & Rotheray, 1998). Larvae are unusually diverse in form and habit with saprophagous, predatory, parasitic and phytophagous species. Information on larva three stages, morphology and life cycle is available from Rotheray & Gilbert (1999), Rotheray et al. (2000), and Rotheray (2003). Larval morphology is modified in various ways for an aquatic way of life (Varley, 1937; Hartley, 1958, 1961; Rotheray & Gilbert, 1999; Rotheray et al., 2000).

Away from ponds and lakes, aquatic breeding sites used by syrphids include a wide range of phytotelmata i.e. water-based container habitats (Frank, 1983; Kitching, 2000) such as tree holes, water tanks of Neotropical bromeliads (Bromeliaceae) and pitchers of oriental pitcher-plants (Nepenthaceae). Some species are coastal in distribution such as the common European syrphid, *Eristalinus aeneus* (Hartley, 1961).

Family Sciomyzidae (R. Rozkošný & L. Knutson)

The Sciomyzidae represent a family of acalyptate flies which belong, with several related families, to the superfamily Sciomyzoidea. According to recent authors the family includes three subfamilies Huttonininae, Salticellinae and Sciomyzinae, the latter with tribes Sciomyzini and Tetanocerini, but there may be reasons to reinstate a further subfamily (Sepedoninae) for distinctly apotypic genera around *Sepedon* (cf.

Knutson & Ghorpadé, 2004). Sciomyzid larvae feed as aquatic predators or terrestrial parasitoids (and/or predators) of snails and pea mussels, a few attack slugs, aquatic oligochaetes or consume snail eggs. Only two species are known to live as scavengers and feed on various dead invertebrates in addition to living terrestrial snails. The Sciomyzidae thus have colonized a great variety of ecosystems from different types of chiefly stagnant waters, moist habitats of semi-aquatic forms, mesophytic woods and even some xerothermic sites. Information on the development, food preference, ecology, behaviour and biology of Sciomyzidae is unusually rich. In the last 50 years several hundreds of specialized papers and comprehensive reviews have been published, including cladistic analyses of the family (Marinoni & Mathis, 2000; Barker et al., 2004) and evolutionary scenario based on a revised classification of behavioural groups (Knutson & Vala, 2002). Special papers dealing with morphology and biology of immature stages were summarized by e.g. Berg & Knutson (1978), Knutson & Vala (2002) and Barker et al. (2004) and comprehensive information devoted particularly to regional aquatic forms was given by Knutson (1981—Neotropical Region, 1982—Mexico, Central America and West Indies), Rivošecchi (1984—Italy), Rozkošný (1997b, 2002—Europe), Knutson & Ghorpadé (2004—Oriental Region) and Sueyoshi (2005—Japan).

Family Ephydriidae (T. Zatzwornicki)

Adults are small to moderate-sized flies, typical length 1.0–8.0 mm, sometimes up to 12.0 mm. Adults of shore flies usually occur in close association with moist substrates and may often be observed on seashores, and along lake shores, rivers, streams, ponds, marshy habitats and also on the water surface of pools. Many adults are known to be polyphagous, feeding on yeast, various algae, and other microscopic organisms. There are few non-specialized predators, capturing and feeding on small insects. Most larvae are aquatic or semi-aquatic and occur in many different microhabitats. Some are uniquely adapted to such inhospitable habitats as inland alkaline or saline lakes, hot springs, crude oil pools and maritime habitats. The most wide-spread larvae develop in semi-liquid media, faeces, or moist shore

mud. The majority of shore-flies feeds on various micro-organisms, e.g. algae, protozoa, and bacteria, and/or utilize detritus. Others are leaf-miners of limnic emergent macrophytes, active predators or parasitoids of spiders and frog eggs. A large group of scavengers develops in decomposing organic matter, e.g. carcasses of small animals, carrion and faeces.

Family Muscidae (A. Pont)

Muscidae are small to medium-sized flies (wing-length 1.5–20.0 mm) belonging to the superfamily Muscoidea of the series Calyptrata. Adult flies may be recognised by the absence of strong meral setae, an incomplete anal vein (A_1), the absence of a true dorsal seta on hind tibia, and, in the female sex, the absence of postabdominal spiracles. Larvae are typical maggots, though there are some variations from this ground-plan among aquatic forms. Adults are found in all zoogeographic regions, and in all biotopes except for the most arid. Many species are dark and drab in general appearance, but some tropical genera contain more colourful and patterned species. Larvae are mainly terrestrial, but genera in two subfamilies contain species with aquatic larvae. These may be found around lakes and ponds, rivers and streams, living in mud, wet sand and in the water among mosses, vascular plants and algae. They live as predators of other small aquatic invertebrates, and the adults are also predaceous, mainly on other small insects.

Species Diversity

Family Blephariceridae (P. Zwick)

A forthcoming world catalogue (Hogue & Zwick, in prep.) recognizes 308 species in 27 genera (as of 2004) which are assigned to four tribes in two subfamilies. All taxa are strictly aquatic.

Family Deuterophlebiidae (G. Courtney & R. Wagner)

The family contains a single genus, *Deuterophlebia*, with fourteen described species, six in western North

America and eight from east and central Asia. Although the immature stages of several Himalayan species have been described, some remain unnamed until properly associated with adults of named species (Courtney, 1994a). The Himalayas and other parts of Asia may harbour additional new species, but it seems likely that the number of undiscovered species will be few.

Family Nymphomyiidae (G. Courtney & R. Wagner)

Seven species in one genus are known to date. Since the first discovery during the past 40 years additional species have been found, in eastern Canada (Ide, 1965), eastern Himalayas (Cutten & Kevan, 1970), Far East Russia (Rohdendorf & Kalugina, 1974), Sakhalin Island (Makarchenko, 1979), Hong Kong, and the south-eastern US (Courtney, 1994b). Larvae discovered recently in Nepal (Courtney, 1998) remain unassociated with adults and, therefore, unnamed.

Psychodidae (R. Wagner)

Six subfamilies are recognized to date, but larval development of Phlebotominae and Bruchomyiinae is obviously terrestrial; larvae of Trichomyiinae as far as we know live in dead wood. Three subfamilies include aquatic or semi-aquatic species.

The monogeneric subfamily Horaiellinae includes four known species. *Horaiella* is not well known but it seems to be restricted to the Himalayas and the mountainous areas of SE Asia and China, where larvae are found in unpolluted mountain streams.

More than 20 Sycoracinae (monogeneric) species are known from the Palaearctic, Afrotropic and Australian regions. The occurrence of Sycoracinae in the Nearctic and in the Neotropical regions is unlikely. All *Sycorax* species are aquatic.

A total of 2,000 species of Psychodinae in approximately 100 genera are currently described but species number is still increasing. Particularly the Neotropical, Afrotropical and Oriental regions are hardly discovered. The description of new species genera or even higher taxa is very probable. Most Psychodinae are aquatic and almost all are water dependent (Table 2).

The current numbers likely underestimate real diversity that is expected to be ten times higher, main issues concern nomenclatural problems and lack of phylogenetic analyses. However, there are several fine revisions of some groups and some phylogenetical attempts (among others Hogue, 1973; Vaillant, 1971–1983; Duckhouse, 1990, 1991).

Scatopsidae (J.-P. Haenni)

About 350 species in 32 genera have been described worldwide, but an aquatic development is known from only few species. But this figure is only provisional since faunas of large regions remains practically unstudied. Aquatic or semi-aquatic larvae are known till now only from five Palaearctic species of the following genera: *Ectactia*, with *E. platyscelis* (Loew), *Holoplagia*, with *H. richardsi* (Edwards), both in water-filled tree-holes in France (Haenni & Vaillant, 1994); *Reichertella*, with *R. geniculata* (Zetterstedt) among water-logged dead tree leaves (Europe, Haenni, unpublished); finally in an unidentified genus of Scatopsinae, with two different species in little permanent springs and subsequent brooklets in forested areas of France (Haenni & Vaillant, 1994). There is little doubt that aquatic representatives will also be discovered in other zoogeographic regions.

Family Tanyderidae (R. Wagner)

Tanyderidae include more than 40 species in ten extant genera (Krzeminski & Judd, 1997—Table 2). Several are known only from larva and remain unnamed (Judd, homepage).

Family Ptychopteridae (P. Zwick)

Less than a 100 species were named from the Palaearctic, Oriental and Afrotropical Regions, and from Madagascar. Species numbers in Table 2 follow the taxonomic interpretation of regional catalogues and lists (e.g. Zwick, 2004). Many more species may await discovery, even in well-studied Europe new species were recently found.

Table 2 Number of aquatic and water dependent (FW) species per zoogeographic region

	PA	NA	NT	AT	OL	AU	PAC	ANT	World FW Species
Blephariceridae	124	34	76	28	22	19	0	0	322
Edwardsiinae	0	0	10	8	0	19	0	0	37
Blepharicerinae	124	34	66	20	22	0	0	0	285
Deuterophlebiidae ¹	8	6	0	0	[1]	0	0	0	14
Nymphomyiidae	3	2	0	0	2	0	0	0	7
Psychodidae	692	114	362	159	279	370	62	0	1,988
Horiaellinae	0	0	0	0	4	0	0	0	4
Sycoracinae	11	0	(1)	4	(1)	5	0	0	22
Psychodinae	681	114	361	155	274	365	62	0	1,917
Scatopsidae	5	?	?	?	?	?	?	?	5
Tanyderidae ²	9	6	3	1	[3]	22	0	0	41
Ptychopteridae	27	18	?	9	?	15	?	0	69
Dixidae	67	51	17	8	21	16	1	0	180
Corethrellidae ³	2	7	69	6	4	12		0	97
Chaoboridae ³	10	15	11	8	6	7		0	50
Thaumaleidae	87	28	6	2	16	33	1	0	174
Ceratopogonidae ^{3,4}	1,028 ^b	600	1,066	622 ^a	521 ^c	761 ^d			5,600
Stratiomyidae	240	181	252	131	56	76		0	889
Empidoidea (exclusive Dolichopodidae)	296	125	52	51	87	58	2	0	671
“Oreogetoninae”	5	8	0	0	0	10	0	0	23
Ceratomerinae	0	0	1	0	0	34	0	0	35
Clinocerinae	200	58	8	30	37	9	2	0	344
Hemerodromiinae	77	58	43	21	45	5	0	0	299
Trichopezinae	14	1	0	0	5	0	0	0	19
Lonchopteridae	2	?	?	?	?	?	?	0	2
Syrphidae ³	354	402	257	165	202	68		0	1,341
Sciomyzidae	52	82	30	7	10	8		0	154
Ephydriidae	352	329	317	218	113	104	49	2	1,251
Discomyzinae	43	22	25	40	13	6	4	0	120
Hydrelliinae	63	73	54	93	40	22	4	0	312
Gymnomyzinae	75	52	58	36	34	28	6	0	232
Ilytheinae	35	38	50	18	8	8	4	0	127

Table 2 continued

	PA	NA	NT	AT	OL	AU	PAC	ANT	World FW Species
Ephydrinae	136	144	130	31	18	40	31	2	460
Muscidae	128	45	105	140	91	137	28	0	599
Mydinae	1	1	0	0	1	0	0	0	1
Coenosinae Limmophorini	115	39	104	139	89	137	26	0	580
Coenosinae Coenosini	12	5	1	1	1	0	2	0	18

PA = Palaearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

¹ Species mentioned in Oriental Catalog, but attributed to PA

² *Protoplasma fitchii* and *Protoplasma fitchii* ssp. *Carolinensis*, [] Palaearctic species in Oriental region

³ Data in AU include PAC

⁴ Ceratopogonidae in the biogeographical regions of the world, catalogues and recent additions. Numbers for the Nearctic and Neotropical Regions, and the total are current. Others are dated and need revision: ^afrom Wirth et al. (1980); ^bfrom Remm (1988), cataloged to 1982; ^cfrom Wirth (1973), notably out of date; ^dfrom Debenham (1989). Most species are water dependent

Family Dixidae (R. Wagner)

More than 170 species in seven genera have been described. Species diversity is highest in sources and in headwater streams, river banks are hardly populated. Low species numbers in regions depend on inadequate exploration. Most species are known from the Palaearctic and Nearctic regions. *Dixa* and *Dixella* are mainly distributed in the northern hemisphere with relations to Afrotropical and Oriental regions. Most Oriental species have been described from the Himalayas. Only few species are known from the Neotropic and Australian regions. It is unlikely that the present generic concept will remain the same in future.

Family Corethrellidae (A. Borkent & R. Wagner)

The family Corethrellidae is monogeneric with a nearly pantropical distribution. A total of 97 extant species are recognized but many more remain undescribed. The genus is generally restricted to subtropical and tropical climates but some species are known from as far north as southern Canada and eastern Siberia and as far south as New Zealand. A world catalogue of fossil and extant Corethrellidae (and Chaoboridae) was provided by Borkent (1993). A world revision is near completion (Borkent, in prep.).

Family Chaoboridae (R. Wagner & Goddeeris)

Chaoboridae include about 50 extant species in six genera and two subfamilies (Borkent, 1993). *Eucoethra* is monobasic in the Nearctic, the also monobasic *Promochlonyx* and *Australomochlonyx* are endemic to Australia (Colless, 1986). *Mochlonyx* has Holarctic distribution, *Cryophila* is Palaearctic, *Chaoborus* is cosmopolitan (Saether, 2002).

Family Thaumaleidae (B. J. Sinclair & R. Wagner)

Some 170 species of Thaumaleidae in eight genera are known and typically restricted to small distributional areas.

Family Ceratopogonidae (A. Borkent)

The Ceratopogonidae are an extremely diverse, worldwide group, with 5,598 validly named species, placed in 103 genera, in four subfamilies (Borkent & Wirth, 1997). However, large areas of the planet have been poorly sampled and some, like the otherwise species rich South American Andes, have been barely collected at all. It is reasonable to estimate that there are currently at least 15,000 morphologically distinct species on our planet. Most species are assumed to be aquatic or water dependant, but the ecology of many species remains unknown.

Identification guides to genera and species are listed by Borkent & Spinelli (2000; area south of the US); Borkent & Grogan (in press; Nearctic); Boorman (1997; Palaearctic); de Meillon & Wirth (1991); and the other relevant catalogs.

Family Stratiomyidae

(R. Rozkošný & N. E. Woodley)

More than 2,650 species are known from all the main biogeographical regions (Woodley, 2001). Aquatic or at least semi-aquatic larvae are known in 75 spp. (though specific diagnostic characters are sometimes unknown) and presumed in 889 species. The majority of descriptions are based on larvae originating from the Nearctic and the western part of the Palaearctic Regions. The number of aquatic larvae known from other regions is only very limited.

Family Empididae (B. J. Sinclair)

The majority of empidoids breed in damp soil and rotting wood, with larval development in aquatic habitats mostly restricted to two subfamilies, Clinocerinae and Hemerodromiinae. Although larvae are only known for about 1% of the species, the taxa included in Table 2 are classified as aquatic based on where adults are most often collected (e.g. emergent rocks, riparian vegetation), congeneric larvae have been collected elsewhere from aquatic habitats, or adults have been found in emergence traps set over aquatic habitats. Some 660 species in 26 genera are known, with several species found in more than one biogeographical region, e.g. Holarctic species (*Clinocera stagnalis*, *C. nivalis*).

Many species remain undescribed from most regions of the world, especially the Southern Hemisphere, (e.g. *Proagomyia* and *Asymphyloptera*). In North America, the genera *Proclinopyga* and *Dolichocephala* require taxonomic revision. Large numbers of undescribed species of *Hemerodromia* remain unexamined worldwide.

Family Lonchopteridae (M. Bartak)

About 49 species (and two subspecies) are known worldwide all of them cited mostly in a single genus, *Lonchoptera*, but sometimes in combination with other nominal genera (e.g. *Neolonchoptera*, *Dipsa*, *Spilolonchoptera*), but their taxonomic status remains unclear. An aquatic development is known from only two or three palaearctic species.

Geographic ranges are mostly restricted to relatively small areas except broadly distributed Palaearctic species (*L. fallax*), cosmopolitan *L. bifurcata*, Palaearctic + Oriental *L. lutea* and Holarctic *L. unisetata*). Recently two Palaearctic species were mentioned to have water dependent larvae; these were found in rheo- and limnocratic environments and in madicolous habitats along streams (Vaillant, 2002).

Family Syrphidae (G. E. Rotheray)

About 6,000 species of Syrphidae are known occurring on all continents except the Antarctic. Three subfamilies and about 177 genera are recognised: Microdontinae, Syrphinae and Eristalinae (Thompson & Rotheray 1998). So far as is known microdontines are myrmecophilous (ant associated) and do not include aquatic species and only a few Syrphinae are aquatic. Most aquatic syrphids belong to the Eristalinae. However not all members of this subfamily are aquatic (Rotheray & Gilbert, 1999; Stahls et al., 2003). More than 1,000 species in more than 90 genera are aquatic or water-dependant.

Family Sciomyzidae (R. Rozkosny & L. Knutson)

The known world fauna of Sciomyzidae embraces 533 described species (Rozkošný 1995; Vala et al. in prep.). However, there is a large number of

distinguished but still undescribed species and the tropical faunas appear insufficiently investigated. A number of species with aquatic and at least semi-aquatic larvae may be estimated to about 280 spp., though the number of species with known biology of larvae belonging to these ecological groups reach, for the time being, 156 species.

The known aquatic forms are dominant in the subfamily Sciomyzinae (521 spp.) where differences in the larval morphology of the two tribes have been found. Semi-aquatic larvae of Sciomyzini chiefly are parasitoids and predators of exposed aquatic snails whereas aquatic larvae of Tetanocerini mainly include (at least in the last, third instar) overt predators of aquatic molluscs and aquatic oligochaetes.

Family Ephydriidae (T. Zatwarnicki)

About 1,800 valid species in 127 genera (five treated also as subgenera) are distributed in all zoogeographic regions and on most oceanic islands, except continental Antarctica (Mathis & Zatwarnicki, 1998). Although inadequately known, larvae of following genera and tribes are not strictly aquatic: parasitoids [*Rhynchopsilopa* and *Trimerina* (Psilopini)], scavengers [Discomyzini (Discomyzinae)], macrophyte leaf-miners [Hydrelliini (Hydrelliinae)], parasitoids or carcasses feeders [Gastropini, Hecamedini, Gymnomyzini (Gymnomyzinae)], and soil algae feeders [*Garifuna*, *Nostima* and *Philygria* (Hyadinini, Ilytheinae)]. Members of five subfamilies (89 genera; 1,251 species) are aquatic: Discomyzinae (120 species), Hydrelliinae (312), Gymnomyzinae (232), Ilytheinae (127) and Ephydrinae (460).

Family Muscidae (A. Pont)

There are probably some 4,500 described species of Muscidae, but the biology and immature stages of only a relatively small number (less than 10%) are known (Skidmore, 1985). The larvae of the more basal subfamilies are terrestrial (Achanthipterinae, Atherigoninae, Azeliinae, Muscinae, Phaoniinae, Cyrtoneurinae), but include a few that live in water accumulations in tree holes, bamboos, etc. The truly aquatic and subaquatic larvae belong to the more apical subfamilies: Mydaeinae (*Graphomya* Robineau-

Desvoidy), Coenosiinae tribe Limnophorini (*Spillogona* Schnabl, *Lispoides* Malloch, *Xenomyia* Malloch, *Limnophora* Robineau-Desvoidy, *Lispe* Latreille), and Coenosiinae tribe Coenosiini (*Lispocephala* Pokorny, *Schoenomyza* Haliday). Several hundred species of eight genera are aquatic or water dependant. The Limnophorini are the most abundant and diverse of the aquatic groups, although some of the known larvae are terrestrial not aquatic. What is known about the predatory activity of the adults has been summarised by Werner & Pont (2005): species of *Lispe* are predaceous mainly on the adults and immature stages of mosquitoes (Culicidae) and swarming midges (Chironomidae), whilst species of *Limnophora* and *Xenomyia* are predaceous mainly on adults and immature stages of black flies (Simuliidae). When more is known about the biology of Muscidae in tropical regions, especially in the Neotropical and Afrotropical regions, it is certain that other genera will also be found to have aquatic larvae.

Phylogeny and historical processes

Family Blephariceridae (P. Zwick)

Families Blephariceridae, Deuterophlebiidae and Nymphomyiidae together form the monophyletic Blephariceromorpha (Courtney, 1991b) all of which develop exclusively in streams.

The monophyly of the blepharicerid subfamilies and of the tribes Paltostomatini and Apistomiini is well established (Zwick, 1977; Stuckenberg, 2004); monophyly of Blepharicerini is weakly supported. The Edwardsininae are apparently Gondwanan relicts, with *Paulianina* in Madagascar and *Edwardsina* in Andean South America and south-eastern Australia.

The area of origin of the Blepharicerinae is not clear, extant representatives occur world-wide. The only fossil reliably assigned to the family comes from Far Eastern Siberia and is a close relative and possible ancestor of extant local genera (Lukashevich & Shcherbakov, 1997).

Tribal assignment of *Hapalothrix* (Europe) and *Neohapalothrix* (Central to East Asia) is doubtful. They share some derived characters with Paltostomatini, but also some with Blepharicerini. Additional investigation and re-evaluation of character expressions are needed, also because genera *Blepharicera*

and *Tianschanella* (Tien-Shan) lack structures distinctive of other Blepharicerini.

The case of *Hapalothrix* and *Neohapalothrix* is decisive for interpretations of evolution and distributional history of the Blepharicerinae. If these two genera should eventually prove to be Blepharicerini, Paltostomatini would be endemic, and disjunct, in the Afrotropical (only *Elporia*) and Neotropical regions (several endemic genera).

Sister-group to the Paltostomatini is the Apistomyiini (Stuckenberg, 2004) which have their most ancient representatives on New Zealand and New Caledonia. More advanced genera occur in the Oriental region and in East Australia (not Tasmania) (Zwick, 1977, 1998). Genus *Apistomyia* attains its greatest diversity in the Oriental region. It extends into eastern Australia and apparently profits from aerial distribution, with outlying species on Bougainville, Taiwan, and islands in the European Mediterranean region.

Family Deuterophlebiidae (G. Courtney & R. Wagner)

Deuterophlebiidae + Blephariceridae form a monophyletic group (Blephariceroidae) supported by several synapomorphies (Wood & Borkent, 1989; Courtney, 1991b; Oosterbroek & Courtney, 1995). No fossil records of the group are available. The Nearctic fauna is not monophyletic at least two successive invasions into North America are assumed (Courtney, 1994a). Dispersal along Beringia was assumed because during the Pleistocene this area provided ideal conditions to cool adapted taxa; however, a mid Tertiary transgression was more probable than a Pleistocene invasion (Courtney, 1994a). Transatlantic dispersal (until 20–35 million years ago (mya)) is highly improbable.

Family Nymphomyiidae (G. Courtney & R. Wagner)

Some early workers considered the Nymphomyiidae the most primitive Diptera family (e.g. Ide, 1965; Cutten & Kevan, 1970). Courtney (1994b) suggested a relation to the Culicomorpha. Recent analyses (e.g. Oosterbroek & Courtney, 1995) recognised it as sister-group of the Blephariceroidae.

Hoffeins & Hoffeins (1995) found fossil European Nymphomyiidae in the Eocene Baltic and Bitterfeld amber that were described by Wagner et al. (2000). With the discovery of this species, a gap in the distribution pattern of extant Nymphomyiidae was closed. It is probable that the Nymphomyiidae colonised the eastern Nearctic Region via the Thule landbridge approximately 25–30 mya. In Europe, Nymphomyiidae probably became extinct with the Pleistocene climatic alteration. They survived only at some distance from the borders of glaciation with sufficient environmental conditions in areas with torrential streams.

Psychodidae (R. Wagner)

The entire system of Psychodidae sensu lato needs urgent revision. Existing phylogenetical analyses are contradictory even at the subfamily level. Comparison of the extant and Baltic amber Psychodinae faunas shows great differences even on the subfamily and generic level, probably as a consequence of glaciation. On the other hand, psychodids in Caribbean amber are quite similar to the extant fauna, at least on generic level.

Scatopsidae (J.-P. Haenni)

The older still undescribed fossil Scatopsidae date back to the Cretaceous (Siberian and Canadian ambers), and even to the early Cretaceous from Mongolia (Kovalev, 1986), although their relation to the extinct family Protoscatopsidae still must be investigated. Four species from Paleocene/Eocene Baltic amber are the older described taxa (Meunier, 1907) but several additional undescribed species are known (Haenni, unpubl.). Scanty information on fossil history of the family is summarized in Haenni (1997).

Family Tanyderidae (R. Wagner)

Since 1919 Tanyderidae have been given family rank, before they had been included into Tipulidae or Ptychopteridae. There is still some debate about the sister-group of Tanyderidae in the phylogenetical system.

Family Ptychopteridae (P. Zwick)

Generic relationships and distributions suggest a Holarctic origin of the family and its subsequent spread into Africa. Palaeontological evidence is not in conflict with this interpretation. Assignment of several European Liassic fossils to the family is doubtful (Peus, 1958). Ptychopterid pupae were recorded from the Mesozoic of Siberia (Lukashevich, 1995). A Tertiary *Bittacomorphella* from Colorado (Alexander, 1927, 1981) and European Tertiary *Ptychoptera* resemble extant forms (Peus, 1958).

Bittacomorpha appears more derived than *Bittacomorphella*. For further inferences, relations between individual species would have to be known but are not. Many individual species have been compared with some other for selected diagnostic characters, but a comparative morphological study permitting phylogenetic analyses was never made. Distributional pathways of the Ptychopteridae remain therefore unknown. *Paraptychoptera* Tonnoir is a monophyletic endemic European clade and was assigned subgeneric rank within *Ptychoptera*, in order not to turn *Ptychoptera* s. str. paraphyletic (Zwick & Starý, 2003).

Family Dixidae (R. Wagner)

Dixidae are placed in the superfamily Culicoidea, but were also considered a subfamily of the Culicidae. Hennig (1966) mentioned Dixidae from Baltic amber described by Loew and Meunier; he described three additional species in the genus *Paradixa* Tonnoir, 1924 (a synonymy of *Dixella* Dyar & Shannon, 1924). But there are earlier remnants of Dixidae or related taxa (Hennig, l.c.). The Baltic amber species are not very different from extant Palaearctic species, concerning the figured male genitalia.

Dixa and *Dixella* seem to be of northern hemisphere origin with radiation into the adjacent Afrotropical and Oriental regions. *Dixina*, *Neodixa* and *Nothodixa* are exclusively distributed in the southern hemisphere. *Nothodixa* occurs in the Neotropical and Australian regions and probably is a Gondwanan element. Climatic changes from Tertiary to the present may have affected at least the northern hemisphere Dixidae. Probably the warmer postglacial climate and an increasing number of permanently

running waters may have led to an increased number of *Dixa* species.

Family Corethrellidae (A. Borkent & R. Wagner)

Corethrellidae have traditionally been placed as subfamily in the related Chaoboridae, but are now recognized as the sister group of Culicidae + Chaoboridae (Wood & Borkent, 1989). In the world catalogue of fossil and extant Corethrellidae and Chaoboridae Borkent (1993) provides substantial information and references on both groups. Fossils are known from various ambers, including one from Lebanese amber, 121 million years old.

Family Chaoboridae (R. Wagner & B. Goddeeris)

Chaoboridae and Culicidae are the sister-group of the Corethrellidae (Wood & Borkent, 1989; Saether, 1997). Together with Dixidae they form the superfamily Culicoidea of the infraorder Culicomorpha. Two synapomorphies, (1) precocious development of adult eyes in the larva, (2) articulate, membranous anal paddles in pupae indicate the monophyly of Chaoboridae and Culicidae (Wood & Borkent, 1989). Within Chaoboridae Eucorethrinae are the plesiomorphic sister group of Chaoborinae (features in Saether, 1970, 1992). Intrafamilial classification remains unsolved. Only the position of the monobasic *Eucorethra* in its own subfamily is generally accepted. A number of fossil Chaoboridae has been described. The group probably diverged in the Upper Jurassic (Refs. in Saether, 2002). Borkent (1993) presented a world catalogue of fossil and extant Corethrellidae and Chaoboridae with substantial references on both groups.

Since then several new species have been described. Several fossil taxa were grouped in the subfamily Chironomapterinae that is probably paraphyletic (Borkent, 1993). Higher classification needs new studies with classical and molecular methods.

Family Thaumaleidae (B. J. Sinclair & R. Wagner)

Hennig (1973) assigned the Thaumaleidae to the Culicomorpha, and an assumed phylogenetic

relationship with Chironomoidea, although they appear to be a somewhat isolated group. This classification has been followed ever since (e.g. Wood & Borkent, 1989; Oosterbroek & Courtney, 1995). Relations among most genera have yet to be clearly analysed, although it appears the Southern Hemisphere species form a monophyletic clade (Sinclair, unpubl. data). Kovalev (1990) described *Mesothaumalea fossilis* from the late Jurassic or early Cretaceous (~ 110 to 130 mya), which represents the only known fossil thaumaleid.

Family Ceratopogonidae (A. Borkent)

The basics of Ceratopogonidae phylogeny are reasonably well understood and the family has one of the best fossil records of any group of insect. The relationships between the four subfamilies are well established and the early lineages within these groups at least partially understood. The Leptoconopinae are the sister group of all remaining Ceratopogonidae and the Forcipomyiinae + Dasyheleinae are the sister group of the Ceratopogoninae. There remains a great need to interpret the relationships between the genera in the tribes Ceratopogonini, Heteromyiini, Sphaeromiini, Palpomyiini and Stenoxenini. A molecular study supported the relationships previously indicated by morphological and fossil studies.

Ceratopogonidae are an ancient family, likely arising in the Jurassic. Remarkably, two extant genera, *Leptoconops* and *Austroconops*, the only members of the Leptoconopinae, are present in Lebanese amber, 121 million years old (Borkent & Craig, 2004). Other extinct genera have been described and abundant fossils from a variety of ambers of different ages show a strong congruence with the cladistic relationships based on morphological analysis (Borkent, 2000). Successively younger ambers include successively younger lineages.

The habit of adult females sucking blood from vertebrates is a plesiotypic feature within the family and is homologous with vertebrate feeding in the related families Simuliidae, Corethrellidae and Culicidae. Similarly, the occurrence of Ceratopogonidae in small aquatic habitats is a plesiotypic feature, shared with at least the early lineages of all other Culicomorpha (Borkent & Craig, 2004). Those Ceratopogonidae which are in large rivers and lakes represent derived lineages.

Family Stratiomyidae (R. Rozkošný & N. E. Woodley)

The first comprehensive phylogenetic information concerning the Stratiomyidae on a world level, a definition of the Xylomyidae as a sister-group of Stratiomyidae and a cladistic analysis of all 12 subfamilies were presented by Woodley (1995, 2001). Subfamilies with aquatic larvae are all in clade six which includes the Raphiocerinae, Stratiomyinae and Nematelinae. The recently discovered larva of *Raphiocera* in a semi-aquatic situation seems to point to an aquatic or semi-aquatic existence for the subfamily. In the Nematelinae only semi-aquatic larvae of *Nematelus* are widely distributed, (though aquatic larvae are not excluded in *Brachycara* spp. occurring in littoral marine habitats). Thus, current information indicates that the aquatic lifestyle has evolved once at clade six in the Stratiomyidae (Woodley, 2001), with a few convergent species in other clades such as two *Beris* spp. and *Ptecticus flavifemoratus* discussed above.

The primitive Brachycera probably arose during the Triassic because flies with well-developed brachycerous characters are known from the lower Jurassic. However, no fossils that can be assigned to any extant families are known from these early periods (Woodley, 1989). Only a small number of fossils belonging undoubtedly to the Stratiomyidae are included in a catalogue by Evenhuis (1994). Out of seven species with presumed aquatic larvae, five lived apparently in the Oligocene and were found in Europe or USA, one is from the Eocene or Oligocene (England) and one from the Oligocene or Miocene (Dominican Republic). No reliable information about the time when stratiomyid larvae colonized water environment is available.

Family Empididae (B. J. Sinclair)

Fossils with empidoid-like venation are known from the upper Jurassic, with empidoid subfamilies present by the early Cretaceous (Grimaldi, 1999; Grimaldi & Cumming, 1999). In fact, the Empidoidea are among the best known lineages from the Cretaceous (Grimaldi, 1999). Divergence time estimates for the Empidoidea range between 144 and 163 mya

(Wiegmann et al., 2003). During the past few years, there have been attempts to establish a stable phylogeny using molecular characters (Collins & Wiegmann, 2002a; Moulton & Wiegmann, 2004). A quantitative phylogeny of the empidoidea by Sinclair & Cumming (2006), based on morphological characters has also helped to stabilize classification.

Family Lonchopteridae (M. Bartak)

The origin and relationships of the family Lonchopteridae are not known certainly, hence, taxonomic position remains unclear. The family Lonchopteridae is usually placed in the paraphyletic basal cyclorhaphan taxon “Aschiza” (e.g. Peterson, 1987) of the infraorder Muscomorpha. Within Aschiza, it is either placed to the superfamily Platypezoidea (as sister group to Opetiidae—Collins & Wiegmann, 2002b) or it forms a single taxon on superfamily (Lonchopteridae) or higher taxonomic levels (e.g. Griffiths, 1972). No reliable fossils are described in details except recent treatments of *Lonchopterites ptisca* and *Lonchopteromorpha asetocella* by Grimaldi & Cumming (1999).

Family Syrphidae (G. E. Rotheray)

Phylogenetic relationships between Syrphidae are under assessment and although some clades are well supported, a consensus has yet to be reached (Rotheray & Gilbert, 1999; Stahls et al., 2003). The earliest fossil syrphids are aged at about 120–130 million years, the time when the supercontinent was breaking apart (Grimaldi & Cumming, 1999). During the break up, basal syrphid lineages probably became separated in South America, South Africa and possibly Australia. When syrphids reached the Palearctic probably from South Africa, diversity rose and lineages spread east into the Oriental and perhaps across the Bering Strait into the Nearctic. Others spread into the Australasian region. In the other direction, lineages also spread west from the Palearctic into first the Nearctic and from the Nearctic, a subset of lineages crossed into South and Central America and diversified in the Neotropics (Vockeroth, 1969; Thompson, 1972).

Family Sciomyzidae (R. Rozkosny & L. Knutson)

The potential evolution of malacophagy in Diptera, probable origin of Sciomyzidae, their ecological specialisation and generalisation as well as subsequent radiation and some further aspects of sciomyzid evolution are discussed in detail by Knutson & Vala (2002) and Barker et al. (2004). The Sciomyzidae probably evolved from a dryomyzid-like ancestor during the Lower Cretaceous. This generally adapted, saprophagous, acalyptrate ancestor had probably developed a requirement for a diet rich in proteins as a base for a subsequent great variety of malacophagous behaviour. A probable biology of sciomyzid ancestors may be demonstrated by the extant *Atrichomelina pubera* (NA). Its larvae are capable to live as saprophages, predators and parasitoids and their feeding habits are dependant on circumstances.

Very probably the specialised forms developed in different microhabitats, from the original damp situations to the almost strictly aquatic forms on one side and to the terrestrial, hygrophilous and even xerothermic forms, on the other side. This specialisation was, however, markedly influenced by the availability of molluscs (or other invertebrates) as a suitable source of food.

According to the cladistic morphoanalysis of the Sciomyzidae presented by Marinoni & Mathis (2000) and Barker et al. (2004), *Salticella* is at the base of the cladogram and it is more closely related to the Sciomyzini than to the Tetanocerini. Also the monophyly of both tribes of Sciomyzinae was confirmed but *Eutrichomelina* (NT) was transferred from the Sciomyzini to the Tetanocerini. *Renocera* and *Anticheta*, which share some intermediate larval characters, are placed at the base of the Tetanocerini and the genera around *Sepedon* (forming a potential subfamily Sepedoninae) form the most specialised group of the family.

Fossil records of Sciomyzidae (13 described species in five genera, see Vala et al. in prep.) are relatively rich in the framework of acalyptrate flies. All are restricted to the Tertiary. Four genera are extinct and two extant, all species are known from the Eocene/Oligocene and Miocene, and many from the Baltic amber. Species of *Sciomyza* and *Tetanocera* were apparently numerous already in that time. It is not excluded that some fossils from the Upper Jurassic/Lower Cretaceous of Spain belong also to

this family (Evenhuis, 1994). Unfortunately, no information on feeding habits or ecological requirements of immature stages of fossil forms is available.

Family Ephydriidae (T. Zatwarnicki)

Ephydriidae is a family of the Ephydroidea (=Drosophiloidea) within the cyclorrhaphous Schizophora. They are related to Risidae (also treated as a sublineage within shore flies) and Diastatidae due to the possession of a female ventral receptacle (Hennig, 1973). The family is divided into five subfamilies; Discomyzinae and Hydrellinae are one evolutionary line, and Gymnomyzinae, Ilytheinae and Ephydriidae are a second morphologically more advanced line (Zatwarnicki, 1992). Probably ancestors fed on decomposing organic material, parasitoids, leaf miners and larvae living in carcasses of small animals developed later. Predators and the use of microorganisms and/or detritus in water and mud evolved independently. Few fossils (4 genera) are known from the Oligocene and related ages.

Family Muscidae (A. Pont)

For at least a century there has been little dispute over the definition and scope of the family Muscidae, and the only fundamental change has been the removal of the subfamily Fanniinae to a separate family Fanniidae. The phylogenetic classification of the family was dealt with comprehensively by Hennig (1965) and, whilst some details have changed since 1965, there has been no new overall review. Some cladistic lineages were outlined by de Carvalho (1989), and a cladistic analysis of the tribe Coenosiini was made by Couri & Pont (2000). A few species, but none belonging to the aquatic groups, have been described from Dominican amber, 15–20 mya (Pont & Carvalho, 1997). A cladistic analysis of the Limnophorini is urgently needed.

Present Distribution and Main Areas of Endemicity

Family Blephariceridae (P. Zwick)

Blephariceridae occur on all continents except Antarctica (Table 2), and on many continental islands,

but also on the Oceanic islands of St. Vincent and Bougainville.

Blephariceridae are often disjunctly distributed. Distinctness of the separate subfaunas in the Andes and the Brazilian Shield, respectively, or the Rocky Mountains and the Appalachians (only *Blepharicera*), respectively, suggests long lasting separations maintained by present ecological conditions. The four western Nearctic genera are shared with East Asia and provide evidence of past Trans-Beringian connections. The presence of net-winged midges in the East of Australia and their absence from the rest of the continent has parallels among other stream fauna and is probably due to past and present ecological conditions. The relictual Edwardsininae are well represented in Tasmania, Victoria and New South Wales but lack further north. Conversely, Apistomiini which seem to be immigrants from the tropical north during relatively recent land connections with Papua New Guinea occur all along the Australian East coast, but are absent from Tasmania.

The holarctic fauna is sharply divided into a western part including the Caucasus and adjacent highlands in Iran (endemic genera *Dioptopsis*, *Liponeura*, *Hapalothrix*) and an eastern part extending west to Kazakhstan and Afghanistan (endemic genera *Asioreas*, *Horaia*, *Neohapalothrix*, *Tianschanella*).

The distribution of West Palaeartic species reflects Pleistocene impact. Net-winged midges are absent from suitable habitats in the British Isles and Scandinavia, and there are only five species in the Alps and the same species plus two more in mountains north of the Alps. The largest number of West Palaeartic species occurs on mountains in the Mediterranean area, each of the Mediterranean peninsulas and Anatolia harbour a high endemic diversity.

East Palaeartic species may range from Kazakhstan to Kamchatka and Japan, respectively, but most Japanese species are endemic. The genera *Agathon*, *Bibiocephala*, *Philorus* are shared between the East Palaeartic and the West Nearctic regions, *Philorus* extends also into the Oriental region.

The most widespread northern hemisphere genus is *Blepharicera* whose three species groups are very distinct. One occurs in eastern North America, another in the Oriental region where it overlaps with the third which is also widespread in the Palaeartic region and western North America where the most ancient representatives of this third group occur.

Family Deuterophlebiidae (G. Courtney & R. Wagner)

The extant species are restricted to the northern temperate regions of the earth, although Kennedy (1973) mentioned “one undescribed collection from South America”. The distribution is amphi-pacific and appears relictual, but there are no species with a Holarctic distribution (Courtney, 1994a). Six species are known from the western Nearctic region, and eight described and perhaps some undescribed species in the Palaearctic region (including the Himalayas). Within the Palaearctic and Nearctic fauna there are two widespread species and several species known from only a few localities. Courtney (1990, 1994a) provided an extensive account of mountain midges with distribution data. The Cascade- and Coast Ranges (North America), Himalayas, Japan and the Korean peninsula appear as main areas of deuterophlebiid endemicity.

Family Nymphomyiidae (G. Courtney & R. Wagner)

The distribution of extant Nymphomyiidae seems to be restricted to the Holarctic and Oriental Regions (Table 2). Two geographical and phylogenetic ‘lines’ can be distinguished (Courtney, 1994b): the ‘*N. alba*-group’, consisting of *N. alba* + (*N. rohdendorfi* + *N. levanidovae*) in the eastern Palaearctic Region, and the ‘*N. walkeri*-group’ (*N. walkeri* + *N. dolichopeza*) in the eastern Nearctic Region, including also (*N. brundini* + *N. holoptica*) from the Oriental Region.

Psychodidae (R. Wagner)

Psychodidae occur on all continents except Antarctica (Table 2). Several species (mainly Psychodini and *Clogmia albipunctata*) have been transported by man with organic material (e.g. vegetables) from continent to continent and this is still the case for some other species. Recently, species with larvae developing in Brazilian Bromeliaceae have been detected in Sweden passively transported within these ornamental plants. Our attempt to describe distribution patterns indicates that the tribe Psychodini is distributed worldwide partly due to passive

transport by man. Pericomini and Paramormiini are particularly distributed in the northern hemisphere (Holarctic elements), Paramormiini with few more genera in the neighbouring Afrotropical and Oriental regions. Maruinini and Mormiini are probably of southern origin but with large expansion into the northern hemisphere. Setomimini are most abundant in the Neotropical region. Endemicity is often related to specific habitat requirements for water dependant taxa therefore several genera are endemic to individual realms. In general, Psychodid larvae occur in almost all types of wetlands, in springs, streams and along rivers. Even Bromeliads and other small water bodies may be inhabited by specialized taxa. Endemicity is higher in mountainous areas under moderate and tropical climate but endemics are also present in wetlands in the tropics.

Scatopsidae (J.-P. Haenni)

This family of tiny midges is represented in all zoogeographic regions with about 350 described species, but water dependant scatopsids have been recorded only from the Palaearctic region, with five species in three genera (plus one unidentified genus). Their larvae live under the surface of a thin water film among water-logged tree-leaves or are dendrolimnobiotic (Haenni & Vaillant, 1990, 1994), while larvae of most genera are terrestrial, saprophagous, living in a wide variety of organic matter in all degrees of decomposition, consequently often in liquid or semi-liquid media. Due to fragmentary present knowledge, no inference may be made upon the real distribution and areas of endemicity of genera with aquatic representatives.

Family Tanyderidae (R. Wagner)

Most genera are endemic to the southwestern Nearctic region, southern Neotropic, South Africa, Australia or New Zealand (Table 2). Only *Protanyderus* has a wider distribution in the Holarctic and the adjacent parts of the Oriental region, and *Radinoderus* in the Australian and Oceanian regions. Genus *Mischoderus* is endemic in New Zealand, *Nothoderus* in Australia, *Radinoderus* in Australia and south-east Asian Islands. *Protanyderus* occurs in the Palaearctis and W-Nearctis, *Protoplasa* in

the eastern Nearctic. (D. Judd presents substantial information at: http://mgd.nacse.org/cgi-bin/sqml2.0/judd/Pictdb.qml?qml_screen=Picturelist&none=)

Family Ptychopteridae (P. Zwick)

Many species are known only from types, their actual distribution remains unknown. There are no examples of confirmed narrow regional endemism. Instead, ranges of individual species may be very large. For example, *Ptychoptera contaminata* (L.) ranges from Great Britain to Kazakhstan (leg. Devyatkov, P.Z. collection), and *P. hugoi* Tjeder from Mongolia to North Sweden (Krzeminski & Zwick, 1993). Several North American and African species also seem to be widespread.

Family Dixidae (R. Wagner)

Faunas of the western and eastern borders of the Palearctic and Nearctic regions are quite well known. More than 40 species occur in the West-Palaeartic, and about a dozen in Japan. Spreading of these taxa into Central Asia remains unknown, but so far four endemic species have been mentioned from that area. Two species are of Holarctic distribution (*Dixella naevia* Peus, N-Europe, N-Russia and Alaska, *Dixella dyari* (Garrett), Sweden, Alaska, Canada). Information on the other biogeographic regions is fragmentary, in particular concerning tropical South America, Africa, Southeast Asia, and partly Australia. At least two species are endemics on oceanic islands (Canary, Madeira). Many species still remain undiscovered in the tropics and in the mountain ranges all over the world in general. Certainly species numbers mentioned represent at most 15–20% of the world biodiversity of Dixidae.

Family Corethrellidae (A. Borkent & R. Wagner)

Out of the 97 extant species known, more than 2/3 is from the Neotropical realm (Table 2). However, the Neotropical Region has been far more extensively sampled and it is likely that the genus will be diverse in other areas, especially in south-east Asia and New Guinea. Two species occur in both the Nearctic and Neotropical Regions and one Japanese species occurs

in the Ryukyu Islands in the Oriental Region. Otherwise there are no species occurring in more than one region.

Family Chaoboridae (R. Wagner & Goddeeris)

Most Chaoboridae (even species) have large distribution areas that cover continents, or even one or two biogeographical regions. Two genera are restricted to Australia, one to the Nearctic region. Five species (*C. crystallinus*, *C. flavicans*, *M. fuliginosus*, *M. velutinus*, *C. nyblaei*) are distributed in the Nearctic and Palaeartic regions (Holarctic). *C. festivus* occurs in the Nearctic and Neotropical regions, and *C. queenslandensis* the Australian and Oriental regions.

Family Thaumaleidae

(B. J. Sinclair & R. Wagner)

The degree of endemism in Thaumaleidae is particularly high, because adults are weak fliers and larvae are restricted to their small, local habitats. Consequently, Thaumaleidae are particularly suitable for biogeographical studies. For example, only six of over 80 species of west-Palaeartic Thaumaleidae are distributed over wide areas within Europe. Most are restricted to islands, mountainous areas or even individual massifs. Most mountainous areas of the earth remain undiscovered. Adult Thaumaleidae are inconspicuous, larvae and pupae are not striking, and many species are on the wing for only a short period. The total amount of species is assumed to be several times higher than the number of species known today.

The most substantial knowledge exists for the west-Palaeartic (European) (Vaillant, 1977; Wagner, 2002) and west- and east-Nearctic Thaumaleidae (Arnaud & Boussy, 1994; Sinclair, 1996). *Thaumalea* is widely distributed in the W Palaeartic, *Andropopsopa* is Holarctic, *Protothaumalea* is endemic in the SW-Palaeartic, and *Trichothaumalea* is widely disjunct with species in the eastern and western Nearctic and in Japan (Sinclair & Saigusa, 2002). Only about five European species are distributed over greater areas, the others are restricted to mountainous regions (e.g. Alps, Pyrenees, Balkans). Only *Th. verralli* is distributed in two biogeographical regions

(amphi-Atlantic). Sinclair (1996) suggested that its presence in North America was human assisted; larvae may have been transported over centuries step-by-step in water barrels from NE Europe via Iceland and Greenland to Newfoundland. Neotropical and Australian genera *Niphtha*, *Oterere* and *Austrothaumalea* have close affinities to *Afrothaumalea* and all four are unequivocal Gondwanan elements (Sinclair & Stuckenberg, 1995). Up to date publications on Thaumaleidae of the Neotropics (Edwards 1932), Australia and New Zealand (McLellan, 1983, 1988; Theischinger, 1986, 1988) and South Africa (Sinclair & Stuckenberg, 1995) form a good basis for future research.

Family Ceratopogonidae (A. Borkent)

Members of the family occur on all continents other than Antarctica, from sea level to as high as 4,200 m (in Tibet). They occur within 150 km of permanent polar ice in the north and have been recorded from most subantarctic islands. A few genera are particularly good dispersers and there are representatives of the family on every island of even moderate size (Borkent, 1991). Although as a family, Ceratopogonidae are very broadly distributed, many species are known from restricted areas. Lowland, continental species tend to have broader distributions within various regions but at higher elevations, especially above 1,500 m in the tropics, species are increasingly endemic and it is common to have species restricted to a given mountain range. Likewise, many species on continental islands and distant volcanic islands are endemic. In the Palaearctic 1028 species have been recorded, different numbers occur in the Nearctic (600), Afrotropical (622), Neotropical (1,066), Oriental (521) and Australasian (761) regions.

Family Stratiomyidae (R. Rozkošný & N. E. Woodley)

Stratiomyids are found throughout the world but they are particularly diverse in tropical areas. Almost 1,000 species are known from the Neotropical Region but many fewer species have been recorded in the Palaearctic (426), Nearctic (267), Afrotropical (387), Australasian (407) and Oriental (321) regions. It is

evident that especially in the last region many new species await description as indicated by a set of recent studies.

Genus distribution

Forms with confirmed and presumed aquatic larvae occur in all regions (Table 3), though some genera with numerous species predominate in the Palaearctic Region (*Oxycera*, *Nemotelus*, *Stratiomys*) or in the Australasian Region (*Odontomyia*). The species-rich genus *Nemotelus* is evidently absent in the Oriental and Australasian Regions, *Oxycera* in the Neotropical and Australasian Regions, and also *Stratiomys* in the latter region. Some genera occur almost exclusively in the Nearctic Region (*Caloparyphus*), in the Nearctic and Neotropical Regions (*Euparyphus*, *Myxosargus*, *Anoplodontha*, *Hedriodiscus*, *Hoplitimyia*, *Psellidotus*) or only in the Neotropical Region (*Anopisthocrania*, *Chloromelas*, *Metabasis*, *Glariopsis*, *Glaris*, *Pachyptilum*, *Promeranisa*, *Rhingiopsis*, *Stratiomyella*, *Zuerchermyia*).

The described aquatic larvae from the Palaearctic Region (38 spp.) are treated by Vaillant (1951, 1952), Rozkošný (1982–1983, 1997a, 2000) and Rozkošný & Baez (1986). Only three aquatic larvae are described from the Afrotropical Region (Lachaise & Lindner, 1973; Kühbander, 1985). No aquatic larva has been described from the Australasian Region, although species of *Odontomyia* that occur there are almost certainly aquatic. Described aquatic larvae of the Nearctic Region (24 spp.) are summarized by McFadden (1967) and added by Sinclair (1989).

More information on the distribution of genera in individual realms will be presented on the homepage.

Family Empididae (B. J. Sinclair)

Aquatic Empididae are found on all continents except Antarctica (Table 3). The genus *Wiedemannia* predominates in terms of number of species in the Palaearctic Region, especially Europe, in contrast to North America, where *Trichoclinocera* has greater diversity and is more numerous and widespread. These two genera are primarily confined to the Northern Hemisphere, with an endemic species group of *Wiedemannia* known from widely disjunct

Table 3 Number of aquatic and water dependent (FW) genera per zoogeographic region

	PA	NA	NT	AT	OL	AU	PAC	ANT	World FW genera
Blephariceridae	12	4	5	2	4	9	0	0	27
Edwardsiinae	0	0	1	1	0	1	0	0	2
Blepharicerinae	12	4	4	1	4	8	0	0	25
Deuterophlebiidae	1	1	0	0	0	0	0	0	1
Nymphomyiidae	1	1	0	0	1	0	0	0	1
Psychodidae	50	15	37	21	24	22	9	0	102
Horiaellinae	0	0	0	0	1	0	0	0	1
Sycoracinae	1	0	(1)	1	(1)	1	0	0	3
Psychodinae	49	15	36	20	22	21	9	0	98
Scatopsidae	4	?	?	?	?	?	?	0	4
Tanyderidae	1	3	3	1	(1)	4	0	0	10
Ptychopteridae	2	3	?	1	2	?	?	0	3
Dixidae	2	3	4	1	2	5	–	0	8
Corethrellidae ³	1	1	1	1	1	1		0	1
Chaoboridae ³	3	3	1	1	1	3		0	6
Thaumaleidae ⁴	4	3	3	1	2	3	1	0	8
Ceratopogonidae	?	?	?	?	?	?	?	?	?
Stratiomyiidae	16	13	38	16	13	7		0	64
Empidoidea (exclusive Dolichopodidae)	18	13	9	7	11	8	3	0	26
“Oreogetoninae”	1	1	0	0	0	1	0	0	2
Ceratomerinae	0	0	1	0	0	2	0	0	2
Clinocerinae	12	7	4	6	8	3	2	0	16
Hemerodromiinae	3	4	4	1	2	2	1	0	4
Trichopezinae	2	1	0	0	1	0	0	0	2
Lonchopteridae	1	?	?	?	?	?	?	0	1
Syrphidae ³	37	24	33	12	9	10		0	53
Sciomyzidae	16	14	12	3	5	4	1	0	30
Ephydriidae	52	50	46	40	27	33	15	2	93
Discomyzinae	4	5	5	4	3	3	2	0	11
Hydrelliinae	13	7	7	13	8	8	3	0	21
Gymnomyzinae	10	12	11	8	6	8	3	0	17
Ilytheinae	7	6	7	5	3	4	4	0	10
Ephydrinae	18	20	16	10	7	10	3	2	34
Muscidae	6	7	6	7	6	6	0	0	19
Mydaeinae	1	1	1	1	1	1	0	0	1
Coenosiinae Limnophorini	5	4	6	3	2	4	2	0	13
Coenosiinae Coenosiini	4	4	2	1	1	0	1	0	5

PA = Palearctic, NA = Nearctic, NT = Neotropical, AT = Afrotropical, OL = Oriental, AU = Australasian, PAC = Pacific Oceanic islands, ANT = Antarctic

afromontane regions of Africa (Sinclair, 2003) and *Trichoclinocera* distributed as far south as Java (Sinclair & Saigusa, 2005). *Bergenstammia*, *Phaeobalia* and *Clinocerella* do not occur outside of Europe,

whereas a series of species of *Kowarzia* extend from Europe to South Africa (Sinclair, 1999).

In the Southern Hemisphere these northern clinocerine genera are mostly absent and replaced by the

Ceratomerinae, and the clinocerine genera, *Asymphyloptera* and *Proagomyia*. Many aquatic species remain undescribed from New Zealand and this habitat is largely unexplored in Chile.

Clinocera is worldwide in distribution, although only a few species groups occur in the Southern Hemisphere (Sinclair, 1995, 2000a). In the Hemerodromiinae, *Chelifera* and *Hemerodromia* are very widespread and not confined to a specific biogeographic region. In contrast, *Metachela* is a Northern Hemisphere taxon and *Neoplasta* is possibly confined to the New World.

The degree of endemism or “aquatic empidoid hotspots” based on the number of species (incl. undescribed species) can be identified and include for example, New Zealand (*Ceratomerus*—some 40 spp., *Hydropeza*—10 spp.), southeastern Australia (*Ceratomerus*—17 spp., *Clinocera*—7 spp.), western North America (*Clinocera*—+30 spp., other aquatic empidids—+60 spp.), Europe (*Wiedemannia*—+65 spp.) and Himalayas (+45 spp.).

Family Lonchopteridae (M. Bartak)

The main distribution centre of the family is probably the area of south-east Asia. From that area 31 species are known and additional taxa await description. In Europe 13 species occur (four of them restricted to the northern or southern parts), four are known from the Nearctic (one Holarctic and one cosmopolitan), five from the Afrotropis (one cosmopolitan) and 16 species from the Orientalis (one occurring simultaneously in the Palaeartic region), and only a single cosmopolitan, *L. bifurcata* is known from the Neotropical and Australasian regions. Aquatic species are only known from Europe.

Family Syrphidae (G. E. Rotheray)

As stated in the phylogeny section, explanation of distribution and biogeographic patterns remain provisional. At genus-level the greatest region of diversity is the Palaeartic followed by the Oriental. However in terms of species, the richest region is the Neotropical. The Afrotropical and Australasian regions are relatively less biodiverse and include a mix of endemic and more widespread groups.

Family Sciomyzidae (R. Rozkošný & L. Knutson)

Out of 533 described species in 61 genera distributed throughout all the main biogeographical regions aquatic or semi-aquatic larvae are presumed in about 280 species and 31 genera. Most aquatic species are restricted to a single Region (except for holarctically distributed species), but several are slightly to moderately invasive into one or two neighbouring regions and a few are broadly distributed across two regions. The number of aquatic species with the known larvae being found in each region are: Palaeartic (54), Nearctic (79), Afrotropical (6), Australian and Oceanic (8), Neotropical (28), and Oriental (10). The fauna of the northern hemisphere including the Palaeartic and the Nearctic species is apparently more rich (or better known) than that of southern hemisphere.

In the Palaeartic, nine genera are apparently endemic but of them aquatic larvae were proved only in *Ilione*, *Pherbina* and *Psacadina*. Some Palaeartic species reach some parts of the Oriental Region (e.g. *Pherbellia cinerella*, *P. nana*, *Hydromya dorsalis*, *Ilione turcestanica*, *Sepedon sphaegee*).

Of genera with known aquatic larvae only *Hedria* and *Hoplodictya* are apparently of Nearctic origin, though two of the five species of the latter also colonize some parts of Central America. Species of *Dictya* are distributed very asymmetrically, embracing 34 Nearctic, eight Neotropical and one Palaeartic species. The North American populations of *Sepedon spinipes* are considered to represent a separate subspecies (*S. spinipes americana*).

Out of ten Afrotropical genera five are endemic but only *Sepedonella* has aquatic larvae. The Afrotropical complex of *Sepedon* species (all with presumably aquatic larvae) is surprisingly rich (42 spp.) also in comparison with any other region and includes a substantial part of Afrotropical species at all (63 spp.). Only *Hydromya dorsalis* penetrate from the Palaeartic and, on the other hand, only *Sepedon hispanica* and *S. ruficeps* reach the southern areas of the West Palaeartic. There is no species common with the Neotropical or Oriental Regions.

The Australasian Region with its 39 sciomyzid species and eight known aquatic larvae appears to be almost as poor as the Oriental Region. Out of six endemic species of the widely distributed *Dichetophora*, *D. australis* seems to be confined to Tasmania

and some *Sepedon* species are common with the Oriental Region. A totally endemic fauna with 25 species in four endemic genera is known from New Zealand, where the larvae of *Eulimnia* and five of eight reared species of *Neolimnia* has been proved as aquatic. All these forms very probably developed in a long geographical isolation. The Oceanic sciomyzid fauna is scarce (*Pherbellia dives* and *Sepedon lata* on the Fiji Is., *S. plumbella* on some islands). No original species of Sciomyzidae is known from the Hawaiian Is.

A comparatively high number of endemic genera are known in South America. Of 22 genera 13 are confined to the Neotropical region and nine of them include aquatic larvae. Aquatic larvae apparently predominate at least in the endemic genera *Dictyodes*, *Guatemalaia*, *Perilimnia*, *Protodictya*, *Sepedonea*, *Shannonia* and in *Thecomyia*. Some species of distinctly Nearctic origin penetrate from the North (species of *Dictya*, *Ditaeniella*, *Hoplodictya*, *Pherbellia*, *Sepedon*, *Tetanocera*) and Neotropical species have been regularly recorded in southern parts of the Nearctic Region (*Pherbellia guttata* and *Sepedomerus macropus*).

The Oriental fauna of Sciomyzidae is only insufficiently investigated because only ten aquatic larvae from the genera *Ditaeniella*, *Hydromya*, *Ilione* and *Sepedon* are known. Some clearly endemic Oriental species belong to the broadly distributed genera and additional aquatic larvae may be presumed especially in the Oriental species of *Pteromicra*, *Dichetophora*, *Sepedon* and *Tetanocera*. Typical Oriental species that are widely distributed throughout the region belong to *Sepedon* (*S. chalybeifrons*, *S. ferruginosa*, *S. lobifera* and *S. senex*). *Pteromicra leucodactyla* is probably endemic on Taiwan. Some species penetrate from the Palaearctic, other widely distributed species are also known from the Australasian region (e.g. *Sepedon plumbella*).

Family Ephydriidae (T. Zatwarnicki)

Some genera, especially those with numerous species are either widespread all over the world or absent in only one or two zoogeographic regions (perhaps because of poor collecting). There are genera restricted to the New World [*Cressonomyia*, *Dimecoenia* (also Tristan da Cunha), *Lipochaeta*, *Hydrochasma*], the Old World [*Dryxo*, *Cerobothrium*, *Donaceus*; Holarctic:

Axysta, *Calocoenia*, *Coenia*, *Dichaeta*, *Eutaenionotum*, *Gymnoclasiopa*, *Lamproscatella*, *Paracoenia*, *Rhinonapaea*, *Schema*, and *Thinoscatella*] or to the Southern Hemisphere [*Oedenopiforma*, *Eleleides* and *Ephydrella*]. A few are distributed in two or three regions: *Diclasiopa*, *Haloscatella* (New Zealand, probably taxonomic artefact), and *Philotelma* in the Holarctic and Afrotropical realms; *Asmeringa*, *Homalometopus* and *Scoliocephalus* in the Afrotropic and Palaearctic regions; *Halmopota* and *Omyxa* in the Palaearctic and Oriental, and *Papuama* in Australasia and the Oriental realms. Twenty seven genera are limited to one zoogeographic region: *Afrolimna*, *Corythophora*, *Isgamera* and *Psilopoidea* (Afrotropical), *Parydroptera*, *Subpelignus* and *Teichomyza* (introduced to Neotropics) (Palaearctic), *Callinapaea*, *Cirrula*, *Thiomyia*, *Tronamyia* and *Trimerinoides* (Nearctic), *Austrocoenia*, *Dagus*, *Diedrops*, *Pelinoidea*, *Physemops*, *Notiocoenia*, *Paraglenanthe*, *Pectinifer* and *Peltopsilopa* (Neotropical), *Psilephydra* and *Sinops* (Oriental), *Galaterina*, *Parahydina* and *Tauromima* (Australian and Oceanian), *Amalopteryx* and *Synhoplos* (remote islands—Falkland and Sub-Antarctic). Most species are distributed in one or two realms and only a few are subcosmopolitan: *Discocerina obscurella* (Fallén), *Hydrellia griseola* (Fallén) and *Scatella stagnalis* (Fallén) (Mathis & Zatwarnicki, 1998).

For historical reasons the Palaearctic region is the best known (325 species: Cogan, 1984), the majority of species are widespread. Large numbers of endemic species are known from well studied countries: Italy (14: Canzoneri & Meneghini, 1983), and Japan (30: Myiagi, 1977; probably artificial). Wirth (1965) mentioned in the catalogue 329 species from Nearctic 38 of which are restricted to the Western USA. In the Afrotropis (218 species) endemic species are predominantly restricted to groups of off-shore islands: Madagascar (16 endemic species of 32), Cape Verde Islands (five of 16) and Seychelles Islands (seven of 39, Mathis & Zatwarnicki, 2003). The fauna of Oriental region for sure contains more than the 113 species recorded; some islands, particularly the Philippines (five of 22) and Taiwan (six of 39) bear endemic species. Characteristic feature of 317 species in the Neotropis is the narrow distribution, both on the continent, e.g. Argentina (25 species: Lizarralde de Grosso, 1989), Chile (29 species) and on the islands: Juan Fernandez Islands (21 of 25 species),

and the West Indies (20 of 41). In Australasia and on Oceanic Islands (146 species) there are several areas with significant rate of endemism, like New Guinea (4 indigenous species of 18), French Polynesia (six of 12), Samoa (four of six), Hawaii (19 of 22: Tenorio, 1980), and New Zealand (11 of 18).

Family Muscidae (A. Pont)

Spilogona species are confined to temperate and montane habitats and are especially abundant at high latitudes of the Holarctic and southern Neotropics. *Lispe* and *Limnophora* are predominantly subtropical to tropical groups, though *Lispe* is poorly represented in the Neotropics. *Xenomyia* is exclusively Afrotropical. *Lispoidea* is entirely New World, and is best developed in the southern Neotropics, and *Schoenomyza*, with a single Old World species, follows the same pattern. *Graphomya* appears to be an ancient genus, found in all zoogeographic regions but with only a small number of species. *Lispocephala* is found in all regions except the Neotropics. Many species are widespread and occur in more than one zoogeographic region, especially Palaearctic/Nearctic (*Spilogona*), Nearctic/Neotropical (*Limnophora*) and Afrotropical/Oriental (*Lispe*, *Limnophora*). Some areas show a high level of endemism, such as the island of New Guinea (*Limnophora*, 87 species (Shinonaga, 2005)), the Hawaiian Islands (*Lispocephala*, 105 species (Hardy, 1981)), and New Zealand (*Spilogona* s. l., circa 200 species, R. A. Harrison, pers.comm).

Human related issues

Psychodidae (R. Wagner)

Phlebotomine sand-flies are of basic medical interest. The main sand-fly born disease (leishmaniasis) occurs in the Old World largely outside the tropics. Females of *Horaiella* have functional mouthparts, but no information on hosts is available. Females of Old World Sycoracinae bite amphibia and reptilia and transmit diseases of frogs and lizards. A few Psychodinae larvae and adults live in sewage treatments. The cosmopolitan ‘trickling filter fly’ (*Tinearia alterana*, Say) may cause several diseases: such as asthmatic attacks in sewage

treatment workers, and the larvae cause myiasis (Europe, Jordan, Japan). *T. alternata* (Say), *Psychoda albipennis* Zetterstedt, *P. cinerea* Banks and other *Psychoda* species have been quoted as members of an eusynanthropic, exophilous Diptera fauna.

Family Dixidae (R. Wagner)

No relation to any human disease is known. Dixid larvae are extremely sensitive indicators of the presence of surfactant or oil-borne pollutants in streams (Thomas, 1979). Larval mortality increased with decreasing surface tension of water (Fowler, Withers & Dewhurst, 1997).

Family Chaoboridae (R. Wagner & B. Goddeeris)

Swarms of *Chaoborus edulis* Edwards, emerging from the large East African lakes may be so dense that they pose a risk of suffocation. People living in the surroundings of the African lakes Victoria and Nyassa/Malawi are known to collect the huge swarms of adult chaoborids for food.

Family Ceratopogonidae (A. Borkent)

The female adults of a few species in a given region are nasty biters that pester humans and domestic animals. Because of their generally small size, some of these can pass through screens and mesh that keeps other biting pests outside and these can make life insufferable. Worldwide, Ceratopogonidae female adults of three genera *Leptoconops*, *Forcipomyia* (*Lasiohelea*) and *Culicoides*, transmit harmful diseases or parasites including 66 viruses, 15 species of protozoa and 26 species of filarial nematodes, to a diversity of vertebrate hosts (Borkent, 2004).

Biting midges also provide important services in ecological systems. Many species, especially in the genera *Forcipomyia*, *Atrichopogon* and *Dasyhelea* are important pollinators of such plants as cacao (without them we would not enjoy chocolate!) and rubber trees, and the larvae of many are significant predators of other organisms in aquatic habitats. The adults of most biting midges actually suck blood from other insects.

Family Syrphidae (G. E. Rotheray)

Most syrphids are beneficial or benign as far as humans are concerned. Direct benefits include pollination of crops (Gilbert, 1986), predation of pests such as greenfly and blackfly (Rotheray, 1989). Some aquatic species are used to indicate water quality and others are being investigated for use in clearing up water polluted by organic waste. A few species are pests in bulbs (*Merodon* and *Eumerus*) and there are occasional reports of aquatic larvae causing health problems (Whittington & Rotheray, 1997). In the UK, a programme of work is underway to conserve two endangered saproxylic syrphids in one of the first attempts at species-level conservation (see Malloch Society website: <http://www.mallochsociety.org.uk>).

Family Sciomyzidae (R. Rozkosny & L. Knutson)

Some freshwater predaceous larvae appear to be suitable potential biocontrol agents of aquatic snails that are intermediate hosts of parasitic flatworms causing schistosomiasis of man and fascioliasis of cattle and sheep. Some species have been thus introduced to Pacific areas as new natural enemies or to support the native populations of sciomyzids.

The most recent review of Sciomyzidae as biological control agents are those of Barker et al. (2004) and Knutson & Vala (2006).

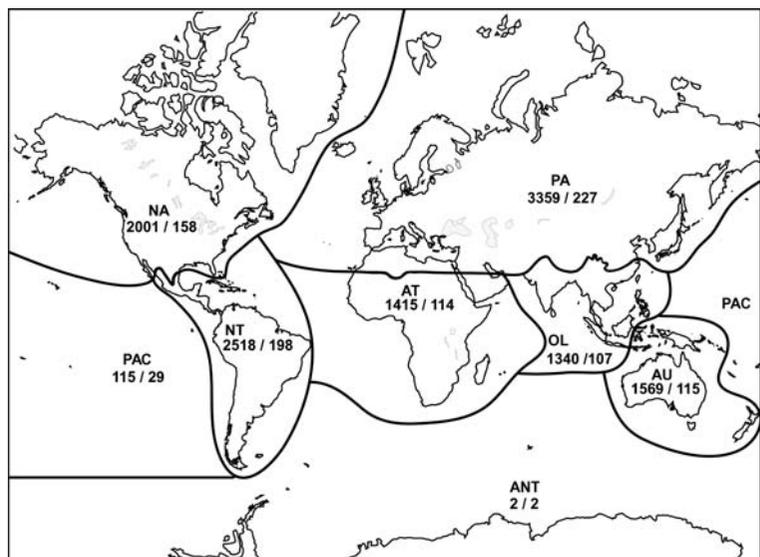
Family Ephydriidae (T. Zlatwornicki)

The leaf or stem mines of *Hydrellia*, particularly *H. griseola* become extensive enough to damage crops of watercress, rice, barley, and other irrigated cereals (Grigarick, 1959). On the other hand the same species had been used as biocontrol agent against noxious weeds that invade wetlands in the USA (Foote, 1995). A *Notiphila* species in Japan (Koizumi, 1949) and *Ephydra macellaria* Egger in Egypt (Andres, 1913) have been reported to damage rice. *Psilopa leucostoma* Meigen is a leaf miner affecting sugar beet production in the USA (Landis et al., 1967). *Teichomyza fusca* Macquart incidentally causes myiasis (Goetghebuer, 1928).

Family Muscidae (A. Pont)

Mosquitoes (Culicidae) and black flies (Simuliidae) are among the most important groups of biting insects from the point-of-view of human and animal health. The species of Limnophorini, both as adults and as larvae, are known to act as significant predators of both these groups. The dipteran predators of black flies have been reviewed by Werner & Pont (2003), and the same authors have recently discussed the adult predaceous behaviour of the entire tribe Limnophorini (Werner & Pont, 2005). Apart from some work on the genus *Xenomyia* in Africa, almost all that

Fig. 1 Distribution of Dipteran species and genera (Species number/Genus number) by zoogeographic regions (excluding Diptera families: Simuliidae, Culicidae, Chironomidae, Tipulidae and Tabanidae). PA—Palaeartic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands; ANT—Antarctic



is known about predation by the Limnophorini is based on work in Europe. This would be a worthwhile field for further investigation anywhere in the world (Fig. 1).

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