

Global diversity of dragonflies (Odonata) in freshwater

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Abstract Larvae of almost all of the 5,680 species of the insect order Odonata (dragonflies and damselflies) are dependent on freshwater habitats. Both larvae and adults are predators. The order is relatively well studied, and the actual number of species may be close to 7,000. Many species have small distributional ranges, and are habitat specialists, including

inhabitants of alpine mountain bogs, seepage areas in tropical rain forests, and waterfalls. They are often successfully used as indicators for environmental health and conservation management. The highest diversity is found in flowing waters in rain forests of the tropics, the Oriental and Neotropical regions being the most speciose. This paper discusses diversity, summarises the biogeography of dragonflies in the different biogeographical regions and gives the total number of species and genera per family per biogeographical region. Examples are given of areas of particular diversity, in terms of areas of endemism, presence of ancient lineages or remarkable recent radiations but no well-based review of areas with high endemism of dragonflies is available so far. The conservation status of dragonflies is briefly discussed. Species confined to small remnants of forest in the tropics are most under threat of extinction by human activities.

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Introduction

With 5,680 extant species, dragonflies are a relatively small order of insects. Their size and colour and their diurnal and often conspicuous behaviour make them a popular group for both professional and amateur entomologists.

Dragonflies are among the most ancient of winged insects, dating back well into the Permian (Grimaldi & Engel, 2005). They include the largest insect that ever lived, the griffenfly *Meganeuropsis permiana* Carpenter, with a wingspan of c. 70 cm. Dragonflies are recognised by their long, slender abdomen; large globular eyes, often making up a large portion of the head; short antennae; and long wings, which have a conspicuous nodus and usually a pterostigma. They possess a unique mechanism of indirect sperm transfer: sperm are produced in the testes situated at the abdomen tip, but the secondary copulatory organs that transfer them to the female lie on the ventral side of the abdomen base. Sperm must be transferred externally to this organ before copulation. This copulatory organ is used not only to inseminate, but also to remove the sperm of the female's previous mates. Sperm competition in Odonata was first reported by Waage (1979) and stimulated numerous studies, making dragonflies one of the most studied animal groups in terms of reproductive behaviour. Another unique feature of odonates is the strongly modified labium of the larva, which can be extended at great speed to seize prey.

The extant dragonflies are divided into two suborders, the Zygoptera or damselflies and the Anisoptera or true dragonflies (Fig. 1). Until recently a third suborder, Anisozygoptera, was recognised,



Fig. 1 The damselfly *Pseudagrion kersteni* and the dragonfly *Orthetrum julia* sitting on the same perch. (photo: Viola Clausnitzer)

with two extant species from Japan and the eastern Himalayas. The Anisozygoptera, which have some features recalling Zygoptera, are now often included in Anisoptera (as done here), or combined with them under the new name Epirocta. Zygopterans have a broad head with widely separated eyes and similar fore and hind wings. Most species rest with wings closed. The larvae are slender and rely mainly on two or three caudal gills for respiration. Anisoptera are on average larger and more robust than Zygoptera. Their hind wings are distinctly broader at their base than the fore wings and in most families the eyes touch on top of the head. At rest most species spread their wings. The larvae are typically much sturdier than those of Zygoptera and lack caudal gills: oxygen is absorbed through gills in the rectum. A general outline of odonate diversity is given by Silsby (2001). A checklist of all dragonflies including synonyms and references is found on <http://www.odonata.info> (van Tol, 2005)

Dragonfly larvae live in freshwater environments and only a few species tolerate brackish conditions, two of which even live in salt marshes and mangroves. Both running and standing waters are used, while a few species are semi-terrestrial or inhabit water held in tree holes, leaf axils and other phytotelmata. Many species have small distributional ranges, and are habitat specialists, including inhabitants of alpine mountain bogs, seepage areas in tropical rain forests, and waterfalls. Larvae prey on all kinds of small animals up to the size of tadpoles and small fish. Larvae take from a few weeks to 7 years to develop. Emergence takes place above water on plants or on the shore, after which most species leave the water edge to mature. Males return to the water to search for females or to establish territories. Females often only return to mate and to oviposit. Information on the life history and behaviour of odonates is thoroughly summarised in Corbet's (1999) review of odonate behaviour and ecology.

Species diversity

Information on the number of species of odonates is derived from the Global Species Database Odonata prepared for the Catalogue of Life (van Tol, 2005). Taxa were assigned to one or more of the biogeographical regions based on the authors information

and several key references (e.g., Lieftinck, 1949; Watson et al., 1991; Westfall & May, 1996; Okudaira et al., 1999; Needham et al., 2000; Tsuda, 2000; Wang, 2000). Subspecies were not considered. Table 1 enumerates the number of genera and species per family for each biogeographical region. Family-level classification of odonates is poorly resolved, although most families are broadly accepted. The most recent contribution to the higher classification of dragonflies was published by Rehn (2003). With the advent of molecular techniques, revision of family-level classification may be expected.

In total 5,680 species of Odonata are known, 2,739 belonging to the suborder Zygoptera (19 families) and 2,941 to the suborder Anisoptera (12 families). Table 1 and Fig. 2 show that the tropics support by far the most species of dragonflies. Besides higher diversity at the species level, the number of families is also much greater in the tropics (Fig. 3). Twelve of the 31 families are restricted mostly to running waters within tropical forest habitats. The two largest families (Coenagrionidae and Libellulidae) are believed to be relatively recent (Rehn, 2003). Almost all ubiquitous species belong to these two families and they dominate in unshaded habitats with stagnant water (both artificial and natural, e.g., savannas). Both families include species with the greatest migratory capacity, including those with distributions spanning more than one continent and almost all species found on isolated islands.

It is estimated that between 1,000 and 1,500 species of dragonflies await description (Table 1). If this is true, the actual number of extant species may be close to 7,000. The Oriental, Australasian and especially the Neotropical regions hold the highest number of undescribed species. In the latter, new species are still discovered more rapidly than descriptions are published (Paulson, 2004). The fauna of Africa is relatively well known and relatively depauperate. Overall the families Platystictidae, Protonneuridae, Gomphidae and Corduliidae are believed to hold relatively many undescribed species. They are typically inconspicuous odonates with small ranges, often confined to seepages or small runnels in tropical forest. Gomphidae, Corduliidae and also Chlorogomphidae in Southeast Asia are difficult to collect as they spend little time at the waterside. The two largest families, Coenagrionidae and Libellulidae, are relatively well known, because most species are

conspicuous and many favour open habitats, although in absolute numbers they still represent a large proportion of species to be described. This is especially so for the Coenagrionidae in South America. Since 1970 an average of 38 species have been described annually (Fig. 4). With an undiminished rate of description an estimated 95% of all species will be described in 2030.

Processes influencing diversity of dragonflies

Factors influencing the distribution of dragonfly diversity can be divided into historical (geological) and ecological factors. Both determine current species diversity, while composition at family and genus level is predominantly determined by the first. Dragonflies are an ancient group, and present-day distribution reflects the distribution of the families before the break-up of Pangaea and subsequent supercontinental schisms. However, more well-founded phylogenetic reconstructions are needed before a satisfactory synthesis of this subject can be written.

Today's patterns of dragonfly diversity correspond largely with the present climatological zones. Temperature accounts for a sharp increase of diversity from the poles to the equator, while precipitation obscures this pattern by reducing diversity in areas of low precipitation, resulting in 'gaps' in diversity. Diversity of tropical odonates is at least partly explained by the high diversity of aquatic habitats in tropical forests (Orr, 2006), especially in montane areas (Oppel, 2005). Mountains not only provide a greater contemporary diversity of habitats, but also a greater potential for survival in regional refugia. The relative long-term stability of forest habitats (also in the short term, the limited seasonality), which provides opportunities for animals with a specialist lifestyle, might also explain the high diversity of tropical odonates.

Speciation events in dragonflies can be directly linked to isolation events in the geological past such as Andean orogeny (De Marmels, 2001) and isolation in refugia in southern Europe during the ice ages (Sternberg, 1998). Polhemus (1997) showed how a single coenagrionid founder evolved into 22 species of *Megalagrion* on the Hawaiian Islands. Speciation was not only promoted by isolation after the colonisation of newly formed volcanic islands, but also by

Table 1 (a) Number of species per family per biogeographical region. (b) Number of genera per family per biogeographical region

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
(a)									
Aeshnidae	57	42	127	44	138	76	13	–	441
Amphipterygidae	–	–	3	2	5	–	–	–	10
Austropetaliidae	–	–	7	–	–	4	–	–	11
Calopterygidae	37	8	61	20	60	4	–	–	171
Chlorocyphidae	3	–	–	41	80	15	–	–	135
Coenagrionidae	95	101	370	197	185	170	88	–	1084
Cordulegastridae	18	9	1	–	27	–	–	–	49
Chlorogomphidae	5	–	–	–	40	–	–	–	41
Corduliidae	20	50	37	17	57	54	12	–	239
Dicteriadidae	–	–	2	–	–	–	–	–	2
Epiophlebiidae	1	–	–	–	1	–	–	–	2
Euphaeidae	11	–	–	–	65	1	–	–	69
Gomphidae	127	100	273	149	358	42	–	–	966
Hemiphlebiidae	–	–	–	–	–	1	–	–	1
Isostictidae	–	–	–	–	–	41	5	–	46
Lestidae	17	19	38	17	39	29	3	–	148
Lestoideidae	2	–	–	–	4	9	–	–	13
Libellulidae	121	107	352	245	190	184	32	–	1012
Macromiidae	6	9	2	37	50	16	–	–	122
Megapodagrionidae	2	–	130	38	28	57	5	–	260
Neopetaliidae	–	–	1	–	–	–	0	–	1
Perilestidae	–	–	18	1	–	–	–	–	20
Petaluridae	1	2	1	–	–	6	–	–	10
Platycnemididae	23	–	–	33	130	37	–	–	210
Platystictidae	–	1	42	–	119	29	1	–	191
Polythoridae	–	–	58	–	–	–	–	–	58
Protoneuridae	1	3	94	37	57	52	–	–	245
Pseudolestidae	7	–	–	–	15	–	–	–	22
Pseudostigmatidae	–	–	18	1	–	–	–	–	19
Synlestidae	6	–	1	10	17	8	–	–	37
Synthemistidae	–	–	–	–	–	35	9	–	43
Total	560	451	1636	889	1665	870	168	0	5680
Undescribed	75–100	5–10	400–500	100–125	300–400	175–250	30–40	0	1085–1425
(b)									
Aeshnidae	14	13	15	6	18	19	7	–	48
Amphipterygidae	–	–	2	1	1	–	–	–	4
Austropetaliidae	–	–	2	–	–	2	–	–	8
Calopterygidae	8	3	3	3	10	1	–	–	16
Chlorocyphidae	3	–	–	3	14	4	–	–	18
Coenagrionidae	15	15	38	15	23	24	12	–	90
Cordulegastridae	3	1	1	–	5	–	–	–	5
Chlorogomphidae	1	–	–	–	1	–	–	–	1
Corduliidae	6	8	2	6	7	16	3	–	41
Dicteriadidae	–	–	2	–	–	–	–	–	2

Table 1 continued

	PA	NA	NT	AT	OL	AU	PAC	ANT	World
Epiophlebiidae	1	–	–	–	1	–	–	–	1
Euphaeidae	5	–	–	–	12	1	–	–	12
Gomphidae	33	14	26	20	43	9	–	–	92
Hemiphlebiidae	–	–	–	–	–	1	–	–	1
Isostictidae	–	–	–	–	–	11	1	–	12
Lestidae	3	2	2	1	5	3	3	–	8
Lestoideidae	1	–	–	–	1	2	–	–	3
Libellulidae	31	27	44	53	56	45	16	0	143
Macromiidae	2	1	2	1	2	2	–	–	4
Megapodagrionidae	2	–	14	6	10	6	3	–	39
Neopetaliidae	–	–	1	–	–	–	–	–	1
Perilestidae	–	–	2	1	–	–	–	–	3
Petaluridae	1	2	1	–	–	2	–	–	5
Platycnemididae	4	–	–	9	8	11	–	–	25
Platystictidae	–	1	1	–	5	2	1	–	6
Polythoridae	–	–	8	–	–	–	–	–	8
Protoneuridae	1	2	14	4	8	1	–	–	25
Pseudolestidae	1	–	–	–	3	–	–	–	3
Pseudostigmatidae	–	–	5	1	–	–	–	–	6
Synlestidae	2	–	1	2	2	3	–	–	8
Synthemistidae	–	–	–	–	–	4	1	–	4
Total	137	89	186	132	235	169	47	0	642

habitat specialisation (stagnant water, seepage, phytotelmata and swift streams) within an island. Speciation has also been promoted by the isolation of patches of tropical forest due to climatological factors (Dijkstra & Clausnitzer, 2006). Large river systems such as the Amazon and Congo basins, forming an ever-changing mosaic of land and water, probably also facilitated speciation, but distribution patterns in these regions are known insufficiently to verify this hypothesis.

A brief outline of odonate biodiversity within the biogeographical regions

Palaeartic

Large parts of the Palaeartic are relatively species poor when compared with areas at the same latitude in North America. Europe for instance has only slightly more than half the number of species of Texas. Exceptions are Japan, Korea and the part of China

included in the Palaeartic. The faunal diversity in these areas is at least as high as in North America and is far richer than in Europe. In China the Palaeartic fauna merges gradually into the Oriental fauna. This transition zone is very rich compared to the other parts of the Palaeartic and harbours many species not occurring elsewhere in the Palaeartic. The large differences in diversity between different parts of the Palaeartic are largely due to the advance of glaciers during the Pleistocene ice ages, which impoverished the fauna in the western two-thirds of the Palaeartic. Here the main mountain ranges and seas run east–west (e.g., the Mediterranean Sea, the Pyrenees, Alps and Himalayas) thus forming a barrier for northern species retreating southwards. Similar factors also apply today as Oriental species can easily penetrate into the Palaeartic, but northward expansion of African and Oriental species into the western Palaeartic is hampered by the same barriers as those limiting southward retreat in the past. The ice ages also promoted speciation by isolating species in various refugia, especially evident in Europe. Most Palaeartic-

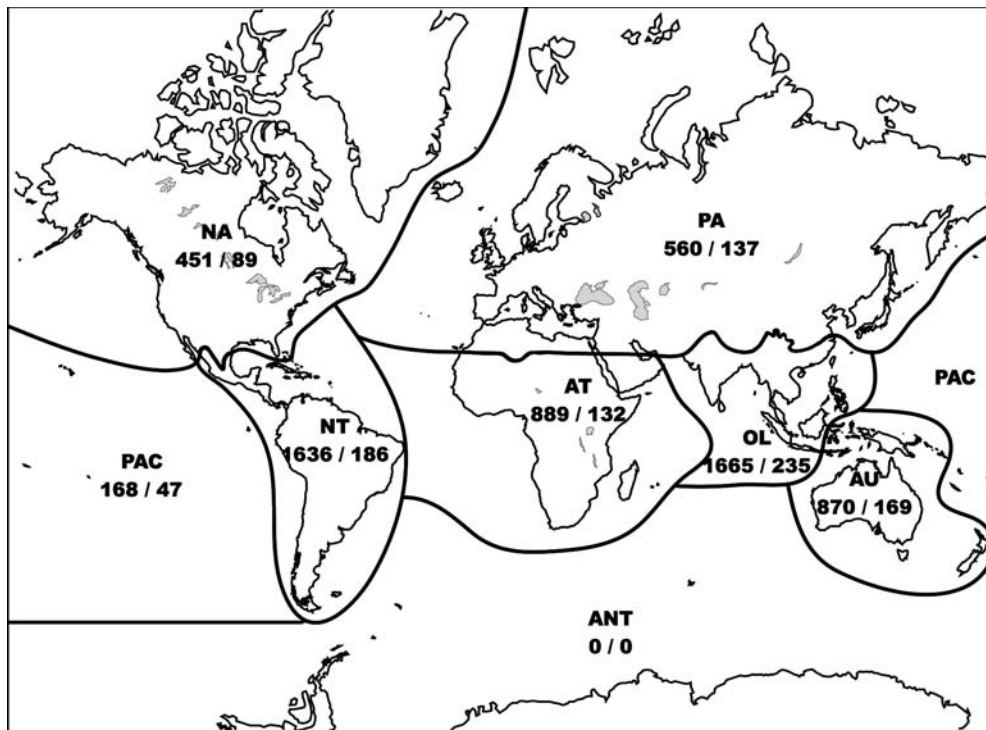


Fig. 2 Diversity of dragonflies per biogeographical region (species number/genus number). PA—Palearctic, NA—Nearctic, NT—Neotropical, AT—Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, ANT—Antarctic

tic species with a more northern distribution are widespread, several ranging from Europe to eastern Russia or even into the Nearctic. Whether after the ice ages these wide-ranging species colonised the eastern Palearctic from the western Palearctic or vice versa is still a point of debate (Kosterin, 2005).

Nearctic

The dragonfly fauna of the Nearctic is richer than that of most of the Palearctic. As in the Palearctic, the eastern part of the Nearctic is richer than the western part, and most eastern states in the USA have larger species lists than all of Europe. This is presumably because the humid East has had a continuous connection with the wet tropics to the south, and numerous tropical species have moved into south-eastern USA, while the West has gone through arid periods when odonate dispersal was interrupted and aquatic faunas were presumably extirpated by glaciation. The species of the wet forests on the west coast of Mexico are restricted from advancing northward

by thorn forest and then desert, but species of the moister uplands of the Mexican Plateau have also moved north into the southwestern states. Thus the latter region is a centre of diversity and endemism in North America, as are the north-eastern and south-eastern coastal plains, Allegheny-Appalachian

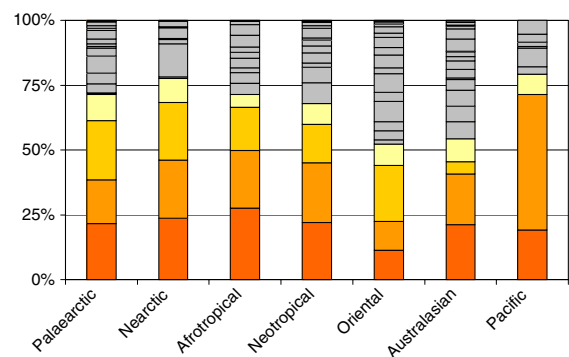


Fig. 3 Percentages of species belonging to a family for the seven different biogeographical regions. The four largest families are at the bottom with from bottom to top: Coenagrionidae, Libellulidae, Gomphidae and Aeshnidae

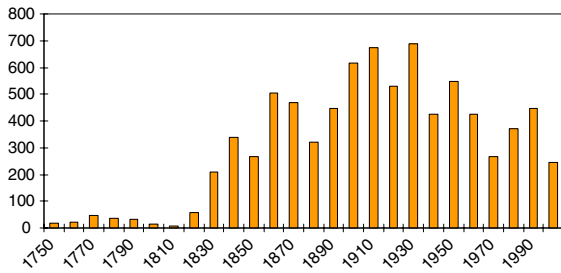


Fig. 4 Rate of description of new taxa in Odonata

uplands, Ozarks, Great Plains, and Pacific coast. Stream-dwelling gomphids are especially likely to show restricted distributions and diversification, and they comprise the largest odonate family in the eastern Nearctic. However, many odonate species, both northern and southern, are wide-ranging over the entire moist eastern half or all across the continent. Others are restricted to the West, often both arid and humid parts of it, as ultimately it is the presence of water bodies that determines their distributions. Some of even the largest odonate families appear to show different origins in the Nearctic, for example coenagrionids and libellulids mostly from the tropics and gomphids and corduliids mostly from northern latitudes. There is a substantial boreal fauna; Canada holds 208 species, but many of them are restricted to the southeastern border region, including tropical genera such as *Hetaerina*, *Argia*, and *Pantala* (Cattling et al., 2005). Special features of the Nearctic include the presence of two petalurids, a Pacific Northwest montane species (*Tanypteryx hageni*) with nearest relative in Japan and a southeastern lowland species (*Tachopteryx thoreyi*); certain genera (*Tanypteryx*, *Lanthus*, *Stylogomphus* and *Hagenius*) that show a distinct relationship between eastern Asia and eastern Nearctic; and a very recent radiation of *Enallagma* (Brown et al., 2000).

Afrotropical

It is notable that, among tropical faunas, the Afrotropical fauna is relatively poor and its composition is nearest that of the Holarctic, with few families and a large proportion of Coenagrionidae and Libellulidae (Dijkstra & Clausnitzer, 2006). This may be explained by the relatively unstable climatological history of the continent, which favoured species capable of colonis-

ing recent or temporary habitats. The extent of tropical forest in Africa is believed to have contracted substantially during periods with a cooler and drier climate. As a consequence the 'old' African fauna seems to be largely gone, although relicts remain in isolated areas that were apparently more stable. Examples are the genera *Pentaplebia* (Amphipterygidae) and *Nubiolestes* (Perilestidae) in the Cameroon highlands and *Coryphagrion* (Pseudostigmatidae) in the East Coast forests, which all have their only relatives in tropical America. The families Synlestidae and Megapodagrionidae, which have a global but rather fragmented distribution, are largely restricted to South Africa and Madagascar, respectively. On the other hand, the present-day extent of forest and other tropical habitats, such as the continent's famous savannahs, has allowed remarkable speciation in a few genera (e.g., *Chlorocypha*, *Pseudagrion*, *Paragomphus*, *Phyllo-macromia*, *Orthetrum* and *Trithemis*). These groups often have strong Asian affinities, suggesting palaeotropical faunal exchange followed by rapid radiation in periods with a more favourable climate. A small but interesting element in the fauna of the eastern coast and Indian Ocean islands are genera of probably Papuan-Australian origin (*Hemicordulia*, *Teinobasis*), that probably reached Africa by wind-aided trans-oceanic dispersal. The highest odonate diversity, as well as the greatest number of range-restricted species, is found in the Guineo-Congolian forest, which stretches from Senegal to western Kenya. The richest area is the Cameroon highlands and the surrounding Lower Guinea lowland forest. The Upper Guinean forest, Congo Basin and Albertine Rift are other core areas within this forest belt. Outside it, coastal East Africa (including the Eastern Arc Mountains), the Ethiopian highlands and South Africa are notable for their endemism. Although the approximately 175 odonate species of Madagascar include distinctly Afrotropical elements, 60% of Anisoptera and almost 95% of Zygoptera species are endemic. Endemism and diversity is greatest on the island's wet eastern coast.

Oriental

The Oriental region is, together with the Neotropical region, by far the most species-rich of the eight regions recognised here. In China the Oriental and Palaearctic faunas merge gradually along a climatic gradient. The Chlorogomphidae and Euphaeidae are

largely confined to the Oriental region although both have outlying species occurring in the Palaearctic, and several families such as the Chlorocyphidae, Platycnemididae, Platystictidae and Pseudolestidae are exceptionally well represented. Within the region, several loosely defined subregions, each with a characteristic dragonfly fauna, may be recognised: i.e., the Indian subcontinent, Sundaland, the Philippines, and the main landmass of southeast and east Asia (including tropical and subtropical China, but excluding the Malaya peninsula). The latter subregion exhibits the highest diversity in both species and genera of the entire Oriental region, presumably owing to its large area, numerous mountain ranges intersected by major rivers, and mosaic of forest types. Particularly speciose is the area including the north of Thailand, Laos and Vietnam together with tropical China, recognised by some as distinct faunistic sub-region (van Tol & Rozendaal, 1995; Wilson & Reels, 2003). Within the Indian sub-region the greatest number of species and endemics occurs in tropical forest refugia. Richest are the tropical and subtropical forests to the south of the Himalayas, including Sikkim, North Bengal and the Khasi Hills, with other centres of diversity in the Western Ghats and Nilgiris and the wet south-western and central part of Sri Lanka (Lahiri, 1989; Bedjanić, 2004). Extensive semi-arid parts of the subcontinent host a depauperate and unexceptional fauna. Present-day Sundaland is divided into several large land masses which were contiguous as recently as 8,000 years ago when sea levels were lower. Highest levels of endemism and species richness occur in north Borneo among forest stream dwellers in montane and mixed dipterocarp forest, but Java, Sumatra and the Malay peninsula all host distinctive faunas. The fauna of the Philippines has a high number of endemics (more than 60% of the named species) sharing elements with both the Oriental and the Australasian fauna. Its numerous islands have facilitated speciation, resulting in a high number of endemic species in genera such as *Drepanosticta*, *Amphicnemis*, *Teinobasis*, *Risioicnemis* and *Oligoaeschna* (Hämäläinen & Müller, 1997).

Australasian region

The Australasian dragonfly fauna is very distinct with a strong representation of small families either largely

confined to the region or showing a relict distribution. For several families a large percentage of the world fauna is restricted to the Australasian region: Austropteraliidae (36%), Isostictidae (89%), Lestoideidae (69%), Petaluridae (60%) and Synthemistidae (81%). Hemiphlebiidae and Cordulephyinae (Corduliidae) are both endemic for continental Australia. The Austropteraliidae are only shared with the southern Andes and are therefore believed to be of Gondwanian origin. The Petaluridae and the Synlestidae are good examples of families showing a relict distribution. The majority of dragonflies of the Australian continent occur in the eastern Great Dividing Range and in the adjacent narrow coastal strip to the east of this, and in the wetter parts of the southwest. Greatest diversity is to be found in the north-eastern wet tropics of Queensland. The dry interior of the continent has a depauperate fauna of widespread eurytopic species. The New Zealand fauna is poor with only 17 species (Rowe, 1992) including two species of Petaluridae. New Guinea is very species-rich with a high percentage of endemics, owing to the perhumid tropical conditions and a highly dissected, mountainous topography that creates numerous isolated stream systems, each including a wide altitudinal range. New Guinea was formed during the mid-late Caenozoic when the northward moving Australian plate collided with island arcs to the north, resulting in massive uplifting and orogenesis. The island arcs were part of a complex archipelago that probably played a part in faunal exchange between the Oriental region and the Australasian region, resulting in unexpected affinities between the Philippines and New Guinea (van Tol & Gassmann, 2005). New Guinea and Australia were connected as recently as 8,000 years ago and generally have strong biogeographical affinities. They share a high diversity of Megapodagrionidae, Isostictidae and Synthemistidae. However considering their shared history the differences in the dragonfly fauna is remarkable. Especially striking is the absence of Platystictidae and Platycnemididae in Australia and conversely the virtual lack of Gomphidae and Brachytroninae (Aeshnidae) in New Guinea (Lieftinck, 1949). The Moluccas and Lesser Sundas (Nusa Tenggara) have probably never been connected to either the Oriental region or the Australasian region. The islands of Lesser Sundas have a drier climate than the rest of the Indonesian archipelago but their faunas are generally commensurate with island area. Most of the species on these islands, including the

many endemics, are of Oriental origin (Lieftinck, 1953). The Moluccan fauna is largely derived from New Guinea, is rather depauperate, and is perhaps most notable for its lack of the genus *Neurobasis* (Calopterygidae), present in New Guinea, Sulawesi and the Philippines. The island of Sulawesi was formed by the collision of several elements of Laurasian origin and Gondwanian origin. The dragonfly fauna is therefore a blend of species of Australasian and Oriental origin, although the latter dominate (van Tol & Gassmann, 2005). No current review of Sulawesi dragonflies is available, but it is known that the fauna is less species-rich than might be expected (van Tol, 1987). The family Chlorocyphidae shows exceptional higher-level diversity, as does Borneo, which perhaps dates back to the most recent connection of the two land masses 42 mya.

Pacific

As might be expected, the Pacific is species poor. Species present can be divided into two groups: those with a very small area of distribution, being often confined to a single island or island group, and highly vagile eurytopic species which occur on most Pacific islands, and which generally also occur throughout much of the Oriental or Australasian regions (or both). Even in Hawaii this phenomenon occurs, although the widespread species originate from the Americas. Both the widespread species and the endemics belong mainly to the Coenagrionidae and the Libellulidae. In the Coenagrionidae the colonisation of an island or group of islands was often followed by speciation events leading to a group of closely related species. This has occurred on Hawaii (*Megalagrion*), Pohnpei (*Teinobasis*), Fiji (*Nesobasis* and *Melanesobasis*) and Samoa (*Pacificagrion* and *Amorphostigma*). An exception to this pattern is New Caledonia, which drifted away from continental Australia at the end of the Cretaceous, and is moderately species rich. It has an interesting fauna showing distinct affinities with Australia and New Guinea and has numerous endemic species and several endemic genera (Davies, 2002).

Neotropical

Although North and South America have numerous genera and species in common, this is primarily because the boundary between them is political

rather than biogeographical. Nevertheless, the two faunas are quite distinct, with a strong faunal break at middle elevations around the Mexican Plateau, many Nearctic species in temperate habitats on that plateau, and tropical species surrounding it in the lowlands (Paulson, 1982). Dispersal was apparently much greater from south to north when Panama emerged in the Pliocene to provide a pathway between the continents, and that dispersal continues today. The Polythoridae, Dicteriadidae and Neopetaliidae are endemic to the region, the latter confined to the southern Andes while the former two are distributed in the tropics. Largely confined to this region are the Austropetaliidae, Perilestidae and Pseudostigmatidae. The latter includes 18 species of very elongate spider-eating, phytotelmata-breeding damselflies which are among the most remarkable odonates. Significant regions of odonate diversification include the Mexican Plateau, Chiapas to Honduras highlands, Costa Rica-Panama highlands, northern Andes, eastern Andean foothills, tepuis of the Guyana Shield, Guyana lowlands, Atlantic forests of Brazil, Rio Paraná basin, and southern Andes. In the last, Gondwanian groups, including the Austropetaliidae, Neopetaliidae, Petaluridae, and *Gomphomacromia*, are prominent. This leaves the huge Amazon basin, poorly known but presumably with its own regions of endemism. The Neotropical fauna equals that of the Oriental region in both modern (species) and ancient (family) diversity. The complexity of the mountain ranges extending from Mexico to Chile and the varied climates along their length have produced a great variety of odonate habitats, as well as providing repeated opportunities for speciation, and *Argia*, with 108 named species, is the star of this show. Other characteristic neotropical genera that have diversified widely in the region include *Heteragrion*, *Palaemnema*, *Acanthagrion*, *Telebasis*, *Phyllogomphoides*, *Progomphus*, *Erythrodiplax* and *Micrathyria*. High biodiversity is the rule for all of the countries in this region, but nevertheless, the Neotropical fauna is the least known in the world. The highest known local diversity of odonates is in South America, with 186 species at a single site in southern Peru. Much of the fauna of the West Indies comes from adjacent Mexico and South America, but the large Greater Antillean islands have numerous endemics, including *Hypolestes* of poorly known affinities.

Table 2 Examples of areas with a high number of endemic dragonflies

Biogeographical region	Name of area	Number of species	Number of endemic species	Estimate of endemism (%)
Afrotropical	Ethiopia	96	12	13
	South Africa	160	30	19
	Madagascar	175	135	77
Oriental	Taiwan	142	21	15
	Borneo	272	124	46
	Hainan	127	20	16
	Sri Lanka	116	53	46
Palearctic	Northwest Africa (Morocco, Algeria and Tunisia)	70	4	6
	Japan	215	74	34
Neotropical	Cuba	80	5	6
	Costa Rica	265	32	12
	Venezuela	489	90	18
Australasian	Sulawesi	124	55	44
	New Zealand	17	10	59
Pacific	Hawaii	36	26	72
	New Caledonia	55	22	40

Antarctica

No species are known from this region and it is unlikely that any species of dragonfly will reproduce there although it is not impossible that some species might be found as vagrants.

Areas of endemism

No well-based review of areas with high endemism of dragonflies is available. However, this is intended in the near future as part of a Global Dragonfly Assessment. Regional projects to identify areas of endemism carried out so far include an analysis of endemism in freshwater biotas partly based on Zygoptera for New Guinea and on Zygoptera and Anisoptera in eastern Africa (Polhemus et al., 2004; Darwall et al., 2005) and are presently being prepared for southern and western Africa by the IUCN Freshwater Biodiversity Assessment Programme. Some examples of levels of endemism in different regions are summarised in Table 2, showing large inter-area differences between areas in absolute and relative numbers of endemic species. Species in the temperate region have wide distributions and the percentage of localised species is low, whereas

faunas with both high absolute and relative endemism are mainly found in moist tropical forests. Although at present there is no sound basis for identifying the most important areas of endemism, it goes without question that the faunas of the islands of New Guinea, Sulawesi, Sri Lanka and Madagascar are exceptionally rich in endemics (see Table 2). It is noteworthy that the percentage of endemic Zygoptera is almost always much higher than the percentage of endemic Anisoptera. Examples of this are Madagascar (60% in Anisoptera, 95% in Zygoptera), the Philippines (31%, 86%) and Sri Lanka (30%, 68%).

Human-related issues

Dragonflies have little economic value, although they are used as food and as magical or medicinal resources at a local scale, and to an unknown extent may influence populations of disease vectors. The group features prominently in nature management in the temperate regions of the world (Westfall & May, 1996; Kosterin et al., 2004; Sahlén et al., 2004) and they are often used as indicators for environmental health and conservation management (Corbet, 1999). Their sensitivity to structural habitat quality (e.g., forest cover, water chemistry) and amphibious habits

make dragonflies well suited for use in evaluating environmental change in the long term (biogeography, climatology) and in the short term (conservation biology), both above and below the water surface (e.g., Clark & Samways, 1996; Sahlén & Ekestubbe, 2001; Clausnitzer, 2003; Foote & Hornung, 2005; Osborn, 2005). Dragonflies are often used in both fundamental and applied research because of the relative ease with which they can be observed and their broad array of behaviours. In many regions reliable identification literature is available, so species can be determined fairly easily by the layman. This enables mapping schemes conducted by volunteers, facilitating the use of distributional data on dragonflies in management. From a global perspective, odonates are among the best known insect groups with respect to taxonomy and distribution, and, apart from butterflies, probably no other group of insects receives so much attention from the general public and has so many organisations devoted to its study. An overview of the conservation and research status of the world's Odonata can be found in Clausnitzer & Jödicke (2004).

Many species in the temperate region have shown a dramatic decline in distribution and abundance since the second half of the 20th century (Westfall & May, 1996; Sahlén et al., 2004; Inoue, 2004). This has been caused by habitat destruction, eutrophication, acidification and pollution of aquatic habitats in general, and the canalisation of streams and rivers. Most of these species are not under immediate threat of extinction as they have wide ranges. A marked exception comes from the Ogasawara Islands, Japan, where five endemic species are on the verge of extinction due to the introduction in the 1980s of an *Anolis* lizard (Karube, 2005). At least in parts of Europe, some of the species considered threatened recovered since the 1990s as result of improved water management. Recently it has become evident that many dragonflies of temperate regions are responding, both in distribution and phenology, to global climate change (Ott, 2001). The ranges of common and widespread southern species are expanding in Europe but there is as yet no strong evidence that northern species are decreasing as a result of the rising temperatures, as might be expected.

Most of the world's dragonflies are restricted to the tropics, especially to forest, where the diversity of the group is greatest. Tropical species of open

landscapes are generally better able to colonise new habitats than species confined to forest, and therefore have wider ranges on average and seem to be less influenced by habitat alteration. A clear exception is a number of South African endemics which declined due to shading of their habitat by invasive alien trees (Kinzig & Samways, 2000), and recovered after removal of the trees (Samways, 2004). Destruction of tropical forest is probably the most important threat to global odonate diversity, potentially resulting in the extinction of numerous species. Unfortunately these species are often poorly known, making it difficult to say whether a species is genuinely rare or merely overlooked. Evaluating the conservation status of most naturally rare species is hardly possible. Examples of data deficiency are known from Africa (e.g., Dijkstra & Clausnitzer, 2006), South America (Paulson, 2006), the Oriental region (Orr, 2004) and New Guinea. More fieldwork is thus essential to establish the true ranges of these species and to determine areas of endemism within larger tropical forest areas. There is, however, no doubt that species confined to small remnants of forest in areas under high human pressure are endangered. Examples of such sites include many of the Philippine islands, Hawaii, the small pockets of forest in the Eastern Arc Mountains of East Africa and the Caribbean islands of Cuba, Hispaniola and Jamaica, but a well-founded overview of threatened areas of high importance for dragonflies is wanting. Especially susceptible are species depending on forest on small islands such as those of the Seychelles (Samways, 2003). Here the disappearance of forest-cover not only results in alteration of the habitat but also may change precipitation patterns.

Dragonflies have shown to be useful for nature management and conservation, and recently an increased effort is being made to make information on dragonflies available for both scientists and policymakers. Important initiatives taken are the update of the IUCN red list, the 'Pan-Africa Freshwater Biodiversity Assessment' started by the IUCN (Darwall et al., 2005), which includes dragonflies among other taxa, and the 'Global Dragonfly Assessment' initiated in 2005. The latter should hopefully result in a more detailed overview of the areas of endemism and conservation priority in the coming years.

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