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JUNGLESKIMMERS, GRENADIERS, AND ASSOCIATES



While the subfamily Libellulinae’s dominance at open and disturbed habitats may have been facilitated by a reduced dependence on plant matter (p. 36), its diversity appears to have originated in lush tropical climes. Between these extremes, a staggering (but confusing!) variety of sizes, shapes, and colors evolved.

Retaining water in the smallest spaces, rainforests abound in potential habitat: even the squelching forest floor may provide

ABOVE | A male of the Common Grenadier (*Agrionoptera insignis*) on Sulawesi in Indonesia.

RIGHT | Madagascar Jungleskimmer (*Thermothermis madagascariensis*) female laying eggs by propelling them in drops onto the bank.

DIVERSITY

147 species at almost any water in the tropics where odonates occur

TAXONOMY

Genera *Aethiothemis* (13 species), *Agrionoptera* (8), *Amphithemis* (3), *Cannaphila* (3), *Cratilla* (2), *Dasythemis* (4), *Diplacina* (28), *Epithemis* (2), *Hadrothemis* (7), *Hylaeothemis* (4), *Hypothemis* (1), *Lathrecista* (1), *Lyriothemis* (19, including *Boninthemis*),

Micromacromia (4), *Misagria* (4), *Neodythemis* (14), *Nesciothemis* (5), *Nesoxenia* (2), *Notolibellula* (1), *Orchithemis* (3), *Oxythemis* (1), *Pacificothemis* (1), *Palaeothemis* (1), *Phyllothemis* (2), *Pornothemis* (2), *Potamarcha* (2), *Protorthemis* (4), *Pseudagrionoptera* (1), *Tapeinothemis* (1), and *Thermothermis* (2). All (probably) belong to Libellulinae, but position of *Akrothemis* (2) unconfirmed



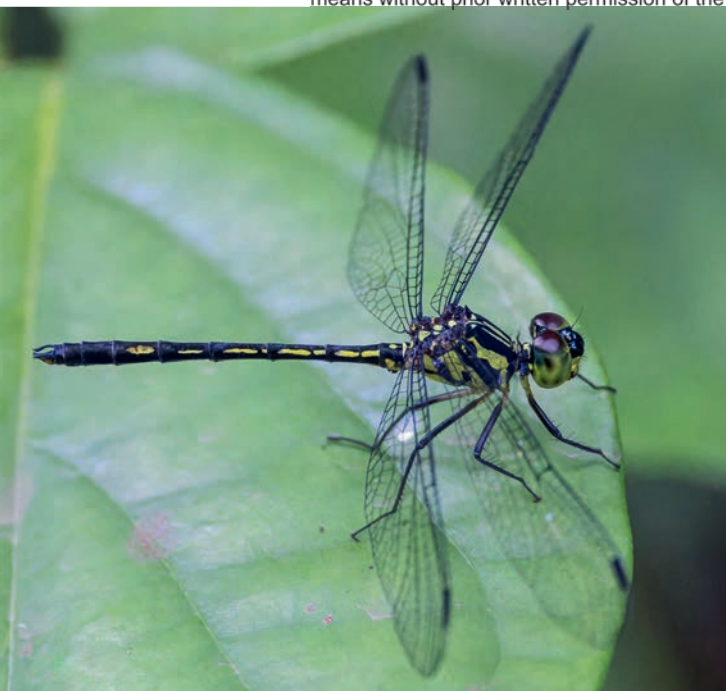
a place to breed. To profit from the limited resources in such constricted habitats, some species are tiny, while others may be very large in order to compete (compare p. 156).

Throughout the tropics, for example, the puddles mushing up the forest roads are guarded by big fat libellulines, such as the Malagasy jungleskimmers (*Thermothemis*), *Protorthemis* in New Guinea and Sulawesi, and the Americas' burliest *Libellula* and *Orthemis* (pp. 37–8). Most bombardiers (*Lyriothemis*) in Asia and the African jungleskimmers (*Hadrothemis*) also breed in muddy pools, but some favor water-filled cavities in trees.

In such wet environments, suitable habitat is typically closeby, so many species adapted with narrow wings, suitable for taking off quickly into the canopy but not for going far. Consequently, their veins were often rearranged and reduced, inspiring

the description of numerous genera (p. 26). The name *Agrionoptera*, for example, means damselfly-wing. Genetics show this genus should not only include the grenadiers found at leafy pools and forest swamps from tropical Asia to the Pacific, however, but also the bulky *Protorthemis* and the smaller Bicolored Skimmer (*Notolibellula bicolor*) from north Australia's rock pools. In Asia, the *Nesoxenia* grenadiers and Bloodtail (*Lathrecista asiatica*) are also related, as may be the pursuers (*Potamarcha*) and forestskimmers (*Cratilla*). Even the structurally and ecologically similar *Cannaphila*, *Misagria*, and especially *Dasythemis* might well have been placed in *Agrionoptera* if they were not from Central and South America! Forest libellulines everywhere have the piebald thorax stripes for which those genera have been named "convict skimmers."





To absorb the reduced sunlight in their shady environs, or to blend in, adults can also be largely black, marked only with dabs of yellow or green. Larger spots frequently lie near the abdomen tip, perhaps serving as signals. Such unshowy males may need other ways to woo females, perhaps with elaborate claspers or genitalia (compare p. 99).

From the study of genitalia, nymphs, and genetics, it has become clear that some libellulids have changed so much that they are barely still recognizable as such. Earlier odonatists considered the smallest and darkest species with the narrowest wings to be more primitive, like an ancestral group from which larger and more colorful ones evolved (p. 72). The opposite, however, appears to be true. The claspers of some junglewatchers (*Hylaeothemis*, *Neodythemis*) and micmacs (*Micromacromia*), small dragonflies inhabiting forest streams and seeps in tropical Asia, Africa, and Madagascar, for example, put the similarly black-and-yellow Gomphidae to shame (p. 92). The stream-living *Diplacina* from the

Philippines, Sulawesi, the Moluccas, and New Guinea, as well as the streamwatchers (*Phyllothemis*) in Southeast Asia, are similarly disparate.

Sometimes only the female's sideflaps (p. 37), or details of nymphs or genitalia, reveal that species are part of Libellulinae. Uncovering their exact affinities to infer their history and ecology, and classify them correctly, is even harder. In tropical Africa, the flashers (*Aethiothemis*) have a distinctively exposed penis in common, but were initially described in five different genera. Longfield's confusing blacktails and peppertails (*Nesciothemis*) proved close to the Pepperpants (*Oxythemis phoenicosceles*) (p. 39).

Much work remains to be done. Restricted to Sundaland's swamp forests and mangroves, the sentinels (*Orchithemis*; photos p. 28) and marshals (*Pornothemis*) recall miniature and thin-bodied *Lyriothemis*. The similarly small hawklets from India's Western Ghats (*Epithemis*) and Indochina (*Amphithemis*) appear close too.



Some of the most modified genera are so poorly known that identifying their true affinities is still quite impossible. Fiji's *Hypothemis*, Pohnpei's *Pacificothemis*, Myanmar's *Palaeothemis*, Borneo's *Pseudagrionoptera*, and the Solomon Islands' *Tapeinothemis*, all with a single species, do appear to be near Libellulinae.

Two species of *Akrothemis* from New Guinea, however, might in fact belong to one of the groups treated next.

ABOVE LEFT | This male Spring Micmac (*Micromacromia zygoptera*) from Ghana is one of many inconspicuous libellulids confined to rainforest streams.

ABOVE MIDDLE | The male Pepperpants (*Oxythemis phoenicosceles*) from tropical Africa shows off his brightly colored legs.

ABOVE RIGHT | This male *Diplacina phoebe* from Halmahera, Indonesia, and its relatives from New Guinea are likely to form a separate genus from the true *Diplacina* species found on Sulawesi and the Philippines.

RIGHT | Red-rumped Hawklet (*Epithemis wayanadensis*) male. Only the second of its genus, this southern Indian species was first described in 2023.



SCARLETS, DRAGONLETS, AND KIN

Humans have moved many insect species around the globe, often with dire consequences. The only truly invasive odonate, however, is the Oriental Scarlet (*Crocothemis servilia*); besides Hawaii (where five species introduced from North America have become established), this Asian species gained a foothold in Florida in the 1970s and on Cuba in the 1990s, and now occurs on all islands of the Greater Antilles. There is no trade and thus no deliberate transport of odonates. As odonates

often disperse well, there may be fewer unoccupied niches available for invasion than is the case for other insects. So how did this species succeed?

Crocothemis belongs to Palpopleurinae, the second-largest subfamily in Libellulidae, with almost 170 species currently classified. Like Libellulinae (p. 36), they are abundant and conspicuous at most standing, open, warm waters, which are often recent or seasonal, forming after the ground has been disturbed or rain has fallen.



LEFT | Africa's most widespread dragonfly, the Broad Scarlet (*Crocothemis erythraea*), is superficially identical to its Asian counterpart, the Oriental Scarlet (*C. servilia*).

RIGHT | This female Indian Rockdweller (*Bradinopyga geminata*) has excellent camouflage.

DIVERSITY

118 species in a wide range of warmer waters (mostly open and standing, often temporary) around the world

TAXONOMY

Genera *Bradinopyga* (4 species), *Crocothemis* (9), *Diplacodes* (10), *Erythrodiplax* (61), *Hemistigma* (2), *Indothemis* (2), *Nannodiplax* (1), *Neurothemis* (17), *Palpopleura* (7), and *Thermochoria* (2) appear close, but *Anatya* (2) and *Pseudoleon* (1) treated here somewhat tentatively





Unlike libellulines, most palpopleurine nymphs are smooth with large eyes and slender legs, indicating they roam freely rather than burrow, and appear to lack dorsal abdominal spines.

While these can be absent in other subfamilies too, most libellulid genera and their presumed ancestors have them. As spines protect against fish, their consistent absence in such a dominant group suggests that their nymphs manage best in small, isolated, ephemeral waters without fish, or in microhabitats fish cannot penetrate.

Rockdweller (*Bradinopyga*) nymphs, for example, amble about fearlessly in rock pools (and cement basins and water tanks!) in Africa and Asia. The speckled adults sit flat on rockfaces and walls nearby, blending in completely. Nymphs of most palpopleurines clamber among submerged plants, however. The females place their eggs onto these plants, organic matter or mud, using the genital opening's extended (and often downcurved) lip (compare Libellulinae; p. 37).

Scarlets and rockdwellers are among almost 60 such species from the Old World's warmer reaches. Found at any rice paddy or roadside pool, their often colorful wings mean they may be the most photographed odonates: in Africa, perhaps the black-winged Lucia Widow (*Palpopleura lucia*) wins; from Asia across to Australia, one of the parasols (*Neurothemis*) with their black-and-white or largely

RIGHT | This male Lesser Red Parasol (*Neurothemis fluctuans*) from Thailand must be agitated, as most parasols hold their colorful wings down, shading the body like an umbrella.



red wings. The perchers (*Diplacodes*) too are very numerous on these continents.

Also in the warmer parts of the New World, about 60 species are among the most-seen dragonflies. The majority are classified as dragonlets (*Erythrodiplax*), which have diversified into an even wider array of habitats: Costa Rica's Canopy Dragonlet (*E. laselva*) breeds in bromeliads holding water high in rainforest trees; the Seaside Dragonlet (*E. berenice*) favors brackish water in mangroves, saltmarsh, and deserts.

The tropical distribution and success of the subfamily Palpopleurinae suggests that only cold winters limit its conquests. The shallow and well-vegetated waters they favor might warm up

in summer, but leave the nymphs exposed when temperatures drop. Nonetheless, all Africa's most widespread odonate, the Broad Scarlet (*C. erythraea*), needed to expand across Europe was some eutrophic ponds and a bit of global heating.

Perhaps all its near-identical Asian counterpart needed in America, therefore, was a head start. The Oriental Scarlet is one of the commonest species in tropical Asia, where many aquarium and pond plants are cultivated for export. Unsurprisingly, therefore, it is the dragonfly imported accidentally most often, of 40 odonate species reported so far (see also p. 136).

The ecologically varied but closely related species of this subfamily have often converged





in appearance: separating some *Diplacodes* and *Erythrodiplax* is hard without knowing the continent they are from. Others look more distinct than they are. Despite its grizzled body, tiger-striped eyes, and blotched wings, the Filigree Skimmer (*Pseudoleon superbus*), adapted to rocky streams in Middle America, is near *Erythrodiplax*, for example. Two blue-eyes (*Anatya*) from rainforest pools seem near that genus too.

Many genera are ill-defined, therefore. The piedspots (*Hemistigma*) and piedfaces (*Thermochoria*) from Africa and Madagascar differ only in their veins' density. One of six widows (*Palpopleura*) there (the seventh is Asian) looks so deceptively like the

former that it was once named *Hemistigmoides deceptor*! The Pygmy Percher (*Nannodiplax rubra*) from Australasia is just a tiny *Diplacodes*, while tropical Asia's two demons (*Indothemis*) look like rather robust, black examples of that genus.

LEFT | This female Asian Widow (*Palpopleura sexmaculata*) strongly recalls the Americas' distantly related amberwings (p. 66).

TOP RIGHT | The male of Middle America's unique Filigree Skimmer (*Pseudoleon superbus*).

LOWER RIGHT | Band-winged Dragonlet (*Erythrodiplax umbrata*) male from the Cayman Islands.



PONDHAWKS, PINTAILS, PYGMYFLIES, AND KIN

The bright colors of the male Bluebolt (*Cyanothemis simpsoni*) in Africa, Greenbolt (*Viridithemis viridula*) on Madagascar, and redbolts (*Rhodothemis*) from south Asia to Australia inspired both their common and scientific names (p. 38). Their American counterparts are just as colorful: the redskimmers (*Rhodopygia*) are a particularly

vivid red, while some pondhawks (*Erythemis*) are red or black and others largely green. Like many libellulids, pruinosity can affect their look too, with age turning two green *Erythemis* species wholly blue and a red *Rhodopygia* purple; Brazil's *Carajathemis simone* is pruinose with a red tip.



RIGHT | A female Great Pondhawk (*Erythemis vesiculosa*) in Suriname feeding on a close relative, a male Black Pondhawk (*E. attala*).

LEFT | The weirdly shaped pintails (*Acisoma*), such as this male Stout Pintail (*A. inflatum*) from Ghana, are found within grassy verges from tropical Africa to Madagascar and Asia.



DIVERSITY

43 species of richly vegetated (standing and sometimes running) waters; almost global, but absent from much of Eurasia

TAXONOMY

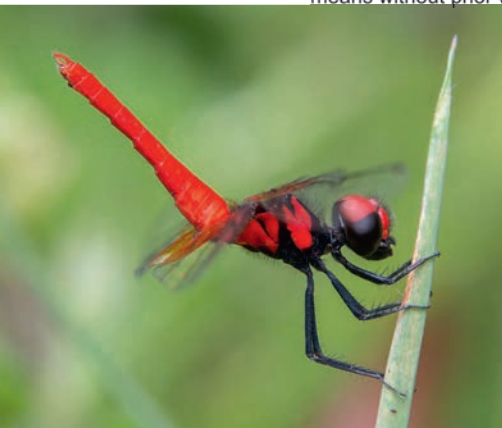
Genera *Nannophya* (8 species) and *Nannothemis* (1), **both blue on map**, appear closer to each other than to *Acisoma* (6), *Carajathemis* (1), *Cyanothemis* (1), *Erythemis* (10), *Porpax* (6), *Rhodopygia* (5), *Rhodothemis* (4), and *Viridithemis* (1) **in pink**



Representing only 43 species of the dragonflies' largest and gaudiest family (p. 35), this group is indeed unrivaled in color range. The Bluebolt and some pintails (*Acisoma*) and pricklylegs (*Porpax*) in Africa are the only libellulids whose deep blue markings are not caused by pruinosity but, as damselflies (p. 148) and aeshnid dragonflies (p. 112), by pigments. And while many dragons have touches of green, notably those in dark habitats, that color rarely covers the entire body of those sitting out in the sun; its red tail-end makes the Greenbolt male look like a popsicle!

Remarkably, the group's size range is unequalled too. The $2\frac{1}{3}$ in (6 cm) Great Pondhawk (*E. vesiculosa*) habitually takes butterflies and other dragonflies as prey. While the Bluebolt is almost as big, its cousins in the genus *Porpax* include Africa's smallest dragonfly, less than $\frac{3}{4}$ in (2 cm) long. Down to $\frac{3}{5}$ in (15 mm), the pygmyflies (*Nannophya*) from Japan to Tasmania are even the shortest odonates. Their North American sister, the Elfin Skimmer (*Nannothemis bella*), is almost as tiny.

All species favor waters rich in vegetable matter, such as swamps and pools with lush vegetation or



ABOVE | This male Scarlet Pygmyfly (*Nannophya pygmaea*) from east Asia may be the world's tiniest dragonfly.

BELOW | While many libellulids appear blue, the male of Africa's Bluebolt (*Cyanothemis simpsoni*) is among very few species where this color is not produced by pruinosity.

thick deposits of leaf-litter, rivers with floating organic debris, or seeps with wet cushions of peatmoss. Males perch persistently near preferred microhabitats, often defending them vigorously. Deep within grassy borders, pygmyfly territories are under a square meter in size. Strong evolutionary selection on size and color either led them to fit into such specific niches, therefore, or rather stand out from them. Catching big prey might even have evolved from aggressive territoriality, literally eating the competition!

Many species press their body, wings, and legs against leaves or the ground when perched. Perhaps that is why their bright colors are often concentrated dorsally and the occiput (the triangle separating the top of the eyes) is diagnostically large: to make them more visible. Large spines and dense setae on the hind femora, especially in some males, may be linked to this posture too. These can aid the capture of large prey but, judging from their diversity in pricklylegs, also have a sexual function.

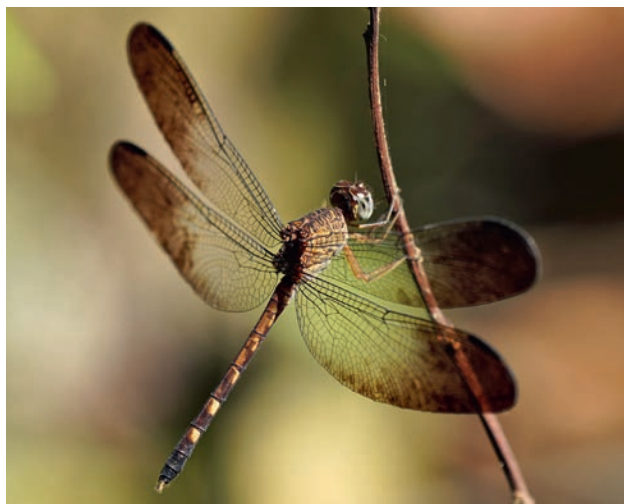


WOODSKIMMERS

Many palpopleurines breed in seasonal waters, the adults sheltering in woodland for months and only attaining their mature colors as the first rains flood the landscape. In lowland forest in Central or South America, great numbers of dull dragonflies with dark-marked wings perch among the undergrowth just above the ground. Brown with a unique wood-grain pattern of fine transverse lines on the thorax, they eventually become dark and dusted with gray pruinosity.

Males of *Uracis* species, and the much smaller Little Woodskimmer (*Ypirangathemis calverti*), differ mostly in their wings, which are black-tipped in some, broadly banded in others. Alongside the black bands, the White-banded Woodskimmer (*U. siemensi*) develops pruinose flashes in the wing bases, a piebald pattern that stands out as it hovers over small shaded waterholes.

Female woodskimmers jab their eggs in flight into muddy pools, damp earth, and even dry soil in shallow depressions before those inundate. While drawn out in most Palpopleurinae (p. 45), the plate below the female's genital opening is developed most dramatically here, even projecting far beyond the abdomen like a stinger (thus recalling Cordulegastridae; p. 86) in the Spike-tailed Woodskimmer (*U. oviposित्रix*).



DIVERSITY

8 species of seasonal puddles on the forest floor in Central and South America

TAXONOMY

Genera *Uracis* (7 species) and *Ypirangathemis* (1)

TOP | A male of the Large Woodskimmer (*Uracis fastigiata*) in Panama.

ABOVE | Female of the Common Woodskimmer (*Uracis imbuta*) demonstrating the group's characteristic wood-grain pattern.

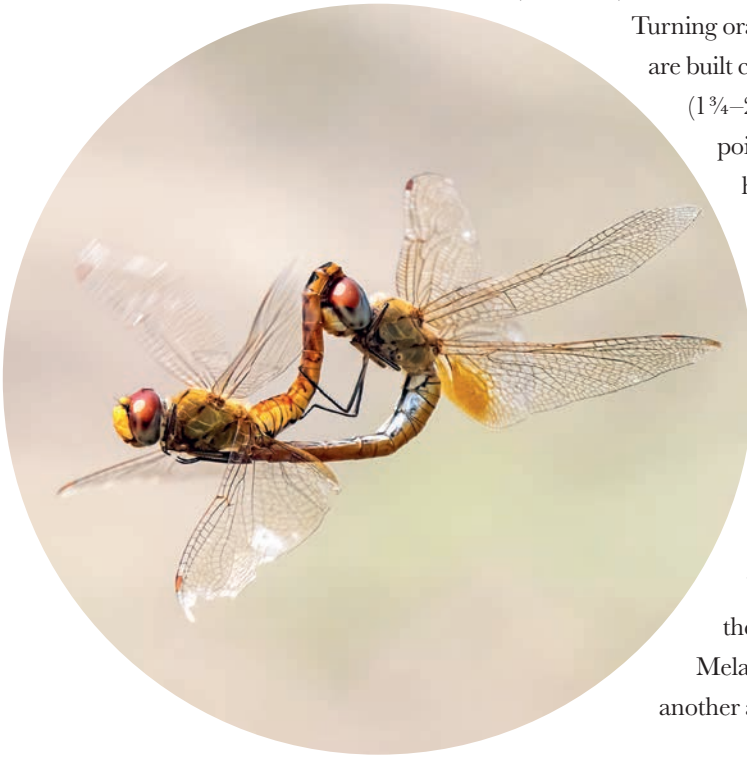
RAINPOOL GLIDERS

BELOW | Wandering Gliders (*Pantala flavescens*) mating in flight in Nepal.

With *Pantala* roughly meaning “throughout-roaming” in Greek, the Wandering Glider (*P. flavescens*) is indeed one of the most widespread insect species and most remarkable odonates. Also called the Globe Skimmer, it is the only one to occur on every continent but Antarctica (rare in Europe), reach the sub-Antarctic island of Amsterdam, and breed on Rapa Nui (Easter Island), over 1,200 miles (2,000 km) from the nearest populations.

Turning orange as they mature, adults are built completely for flight: robust ($1\frac{3}{4}$ –2 in/4.5–5.0 cm long) with long pointed wings, the very broad-based hind pair being distinctly triangular; the abdomen is cylindrical and tapered, almost conical. Built for growth, the big nymphs are just as unmistakable. They are active hunters with prominent eyes and teeth, and long abdominal spines and legs, the latter peculiarly black-tipped, contrasting with the almost translucent body.

Melanin provides sturdiness, perhaps another adaptation to their rapid lifestyle.



DIVERSITY

Two species of open temporary ponds almost everywhere except Antarctica and much of Europe

TAXONOMY

Genus *Pantala* (2 species)



New generations emerge from rain puddles (and other warm and unvegetated waters) within about five weeks, which are among the fastest developments in a relatively slow-developing insect order.

The species is thus optimized entirely for living in the wake of summer rains: as the seasons shift, each generation must move across the equator to find a new bounty of balmy food-filled pools. Wherever a monsoon climate prevails, numbers build up toward the rains, swarming around treetops and patrolling over swimming pools and shiny car roofs. Tending to glide and hover, during rare resting periods they typically hang inside vegetation.

Only in 2009 it was inferred that their annual arrival on the bone-dry Maldives is part of what may be the greatest event of insect dispersal. Masses appear to fly directly from India to Africa each year, benefiting from favorable winds to cross the ocean in as little as four days. To get back, however, their offspring must take the long way around, following the coast.

Although some Trameinae look similar (p. 68), *Pantala* appears to have no direct relatives (but see next pages), the darker and thicker-bodied Spot-winged Glider (*P. hymenaea*) being the only other species. Recognized by a dark blotch in its hind wing expansion, this species has a similar ecology as its global cousin but only extends from Canada to Argentina, and from the Caribbean to the Galapagos.



ABOVE | Distributed globally, the Wandering Glider (*Pantala flavescens*) is the Worldwide Dragonfly Association's mascot. As harbinger of the rains and monsoon mosquito oppressor, it is the perfect focus for global collaboration among odonate enthusiasts (p. 31).

OPPOSITE | Wandering Glider (*Pantala flavescens*) nymph.

CASCADERS AND DROPWINGS



As that family dominates ephemeral ponds (p. 34), it makes sense that the Wandering Glider (*Pantala flavescens*)—the farthest-flying and perhaps fastest-breeding odonate—is a libellulid (p. 52). Most pantalines favor permanent streams and rivers, however, forming the family’s largest running-water radiation. Cascaders (*Zygonyx*) guard their domain in sustained flight and rest away from water hanging in vegetation, just like their wandering relative, but their spiny nymphs cling to rocks like limpets in rapid currents, even of waterfalls (see photo p. 9).

Most genera perch frequently, though, such as the dropwings (*Trithemis*) that occupied almost the full complement of freshwater habitats available to them. Genetics suggest that the oldest extant species arose in Africa when forests gave way to savanna 10 mya, but most appeared in the last

TOP LEFT | Many libellulids, such as this male of Africa’s Red-veined Dropwing (*Trithemis arteriosa*), will point their abdomen at the sun and also often lower their wings to minimize exposure, behavior known as obelisking.

LEFT | Africa’s Ringed Cascader (*Zygonyx torridus*) extends to India and southern Europe, patrolling over open streams.



DIVERSITY

75 species mostly in wide range of flowing waters in tropics of Africa and Asia

TAXONOMY

Genera *Trithemis* (43 species including *Thalassothemis*; **both colors on map**) and *Zygonyx* (24; **purple**)

RIGHT | Appearing like a typical dropwing, *T. marchali* from the oceanic island of Mauritius was only separated from *Trithemis* in the genus *Thalassothemis* (“sea-libellulid”) on account of its venation.

BELOW | This photo taken in Angola’s highlands in 2018 was the first evidence of this dropwing’s existence. Still unnamed, this new *Trithemis* species appears to mimic large *Acraea* butterflies.



5 mya. As the climate continued to fluctuate, they became isolated as habitats fragmented, or adapted as new ones appeared. Ultimately over 40 species thus evolved there, dominating dragonfly communities from cool streams to warm temporary pools, rainforests to deserts, and lowlands to highlands today.

Some species left Africa, resulting in another two on Madagascar and five in Asia, of which one got to New Guinea. And the exodus continues. The Violet Dropwing (*T. annulata*) arrived in Spain in the 1970s and is now halfway through France. Even inhabiting swimming pools and fountain basins,

the Orange-winged Dropwing (*T. kirbyi*) crossed over only in 2008 but reached Belgium in 2022!

These species and most others of sunny habitats have red males (see photo p. 13). That color stands out against green plants but also against the open sky. To aid warming, most species in shadier places are largely black, often combined with blue pruinosity to still stand out. The species’ wings, meanwhile, vary from clear and narrow with reduced venation at forest streams (compare p. 41) to broad with dense cells and butterfly-like blotches of color in open swamps (p. 64).

Many species were placed in separate genera to capture this diversity, but most have been sunk back into *Trithemis*. The next may be *Thalassothemis marchali*, restricted to rocky streams on Mauritius. Related to the Dancing Dropwing (*T. pallidinervis*), a south Asian colonist of new ponds, its ancestor must have crossed the Indian Ocean just as the Wandering Glider does annually today.

Indeed, the cascaders’ restless habit and the dropwings’ dramatic diversification show how such a species can evolve and colonize the world. On Rapa Nui, meanwhile, the glider has shorter wings and is said to fly lower, settling as soon as bad weather threatens to carry it offshore. Are these starved castaways or is the evolution of another island specialist like Mauritius’s dropwing already underway?



RIVERDARTERS, STREAMSKIMMERS, AND KIN



Despite the extremes discussed in the previous profiles, most pantalines inhabit streams and rivers, often in forest. Each tropical region, for example, has robust species that fall ecologically between *Zygonyx* and *Trithemis*, with males aggressively defending stretches of rapid water from a conspicuous perch.

In Asia, these are the riverdarters (*Onychothemis*), in America, the streamskimmers (*Elasmothermis*) **(both marked pink on the map)**. The related *Orionothemis* is known only from its extremely spiny nymphs found on Brazil's high plateau, reared to adult. Aside from *Pantala* (p. 52) these are the subfamily's only members to reach the New World.



DIVERSITY

101 species of (often forested) running waters in the global tropics

TAXONOMY

Genera *Archaeophlebia* (1 species), *Atoconeura* (6), *Bironides* (5), *Celebophlebia* (2), *Celebothemis* (2), *Elasmothermis* (8), *Eleuthemis* (5), *Huonia* (15), *Lanthanusa* (7),

Malgassophlebia (5), *Microtrigonia* (5), *Nannophlebia* (26), *Olpogastra* (1), *Onychothemis* (7), *Orionothemis* (1), and *Zygonoides* (4) included here, but position of *Risiophlebia* (2) is uncertain



In Africa and Madagascar, the riverkings (*Zygonoidea*; photo p. 35) and Bottletail (*Olpogastra lugubris*) fill this niche (**blue on map**). With its yellow-studded black body and narrow but swollen-based abdomen, the latter is almost identical to *Celebothemis delectollei* from Sulawesi. The gap between them may seem surprising but fits the distribution of the many smaller stream-dwellers.

While *Celebophlebia* is also confined to Sulawesi, that genus appears related to the archtails (*Nannophlebia*) that occur from there to Australia, mostly on New Guinea (**blue and purple on map**). These tiny black-and-yellow species, moreover, seem close to another 32 limited to New Guinea, the adjacent Moluccas, and the extreme north of Australia, placed in *Bironides*, *Huonia*, *Lanthanusa*, and *Microtrigonia*. The highlanders (*Atoconeura*) are limited largely to Africa's tropical uplands and three leaf-tippers (*Malgassophlebia*; photo p. 12) and firebellies (*Eleuthemis*) to the lowlands, while the Furbelly (*Archaeophlebia martini*) and another two leaf-tippers inhabit Madagascar.

ABOVE | The archtails (*Nannophlebia*), such as this male Common Archtail (*N. risi*) from Australia, perch with the slender abdomen held curved.

LEFT | The aggressive male of the Bottletail (*Olpogastra lugubris*) in Ghana.

RIGHT | A male of the Blushing Streamskimmer (*Elasmothemis rufa*) from Suriname.

In Asia (**dark pink on map**) only the potbellies (*Risioophlebia*) from the swamp forests of Sundaland and adjacent Indochina look similar, recalling *Nannophlebia* especially with their swollen abdomen bases and arched tails, but such an affinity is unproven. Nonetheless, the pantalines' distribution suggests they arose on Gondwana (p. 111) before Africa and Australia split from Antarctica and drifted toward Asia (compare pp. 171 and 199).

Probably, the ability to secure their eggs was instrumental in this subfamily's evolution. *Zygonyx* attach them to rocks in the splash zone of waterfalls (p. 54) and *Elasmothemis* in stringlike filaments to rootlets. Leaf-tippers glue the eggs to leaves above the water, while in flight, and firebellies stick clumps to leaves hanging in the current. Males defend such spots vigorously, flashing the bright orange or yellow undersides and white-pruinose backs of their abdomens.



SYLPHS, SETWINGS, AND KIN

BELOW | The abdominal club of this male White-tailed Sylph (*Macrothemis pseudimitans*) in Costa Rica may become covered entirely in white pruinosity.

With almost 140 species concentrated in the American tropics, this group seems like the New World's answer to Pantalinae (previous profiles): together, they make up about 35 percent of Libellulidae but over 70 percent of its flow-dependent species. Some *Dythemis* and *Brechmorhoga* adults are indeed uncannily like *Trithemis* and *Zygonyx*, the names setwing and dropwing referring to the same posture (p. 54).

No other libellulids, on the other hand, move quite as sylphs (*Macrothemis*) do. Contrary to what their scientific name suggests, they are rather small and slender, with males that skim rapidly over streams, landing close to the surface, usually flat on leaves, rocks, or sandbars. Away from water, they rest in an almost vertical position, their double-hooked claws recall those of other hanging (more distantly related) groups, notably *Macromia* (p. 80), hence their name.

With the similar little sylphs (*Gynothemis*), the larger and more consistently patrolling clubskimmers (*Brechmorhoga*), and the Antillean

Clubskimmer (*Scapania frontalis*), they form a group of over 60 tropical stream-dwellers.



DIVERSITY

138 species in most standing and (especially) running waters in the New World's warmer reaches

TAXONOMY

Genera *Argyrothemis* (1 species), *Brechmorhoga* (16), *Dythemis* (7), *Edonis* (1), *Elga* (2), *Fylgia* (1), *Gynothemis* (4), *Macrothemis* (42),

Micrathyria (48), *Nephepeltia* (6), *Pachydiplax* (1), *Paltothemis* (3), *Scapania* (1), and *Zenithoptera* (4), but placement of *Nothodiplax* (1) uncertain





ABOVE | Checkered Setwing (*Dythemis fugax*) female in Texas, with its wings “set” to speed off.

BELOW | Red Rockskimmer (*Paltothermis lineatipes*) male in Arizona.



All feed over clearings and roads, multiple species often swarming together with females, which frequently have orange- or brown-marked wings, standing out.

As in many “stream-dragons” (pp. 74 and 92), the male’s slender abdomen can be expanded near its tip, forming a club with a pale mark at its base. While both club and mark (typically located on the abdomen’s seventh segment) are less frequent in libellulids than in other dragonflies, they are present in most dythemistines.

With black-checked bodies infused with red (or dark blue pruinosity) and a tendency to perch vertically on rocks and walls, Middle America’s rockskimmers (*Paltothermis*) recall *Bradinopyga* from Africa and Asia (p. 45). Their patrols over small streams and sustained feeding flights confirm they are affiliated to the sylphs, however.

While the subfamily forms the Neotropics' main libellulid radiation in running water, with *Erythrodiplax* their counterpart in more open stagnant sites there (p. 46), another nearly 60 dythemistines dominate well-vegetated or sheltered ponds and swamps. Most are recognized instantly by their glowing (blue-)green eyes, white face, and posture whereby they perch near the water with slender abdomen raised to show the tail-light and club, with wings drooped forward.

The species are mostly classified as Neotropical dashers (*Micrathyria*), but the Blue Dasher (*Pachydiplax longipennis*)—maybe

North America's most numerous dragonfly—and minute dryads (*Nephepeltia*) belong here too. Brazil's Mantled Dasher (*Edonis helenae*) and the barely known Canopy Skimmer (*Nothodiplax dendrophila*) from the Guianas may do too.

Other genera stand more on their own. The setwings (*Dythemis*) have a mixed habit, preferring streams but often breeding in standing waters too. Accordingly, they look like oversized dashers or, rather, like clubskimmers that perch with the abdomen up and wings down, thus “set” to take off again.

Named for Old Norse spirit guides *fylgia*, the Pearleye (*Fylgia amazonica*) is spritely indeed. Black with bright red tail and ghostly white eyes, the tiny males guard leaf-littered

pools in the Amazon rainforest. The Silverspot (*Argyrothemis argentea*) lights up shady streams in these tropical lowlands with its white-pruinose thorax as do the fairies (*Elga*) with their brilliant blue eyes.

Sapphirowings (*Zenithoptera*), which breed in forest-rimmed marsh and ponds, are also called morpho dragonflies. While smaller than *Morpho* butterflies, they too seem entirely dark with the wings shut, startling the observer when the blue-metallic (often white-banded) upperside is revealed! Except for Australia's *Cordulephya* (p. 84), no other dragonflies perch with closed wings when mature, although sapphirowings often droop them (or just the front pair) down as they relax, sitting high up in the trees.



ABOVE | Piebald Sapphirowing (*Zenithoptera viola*) female in French Guyana. The blue-metallic reflections are startling to us but may actually provide camouflage against a backdrop of glistening water.

MEADOWHAWKS, FLUTTERERS, AND KIN

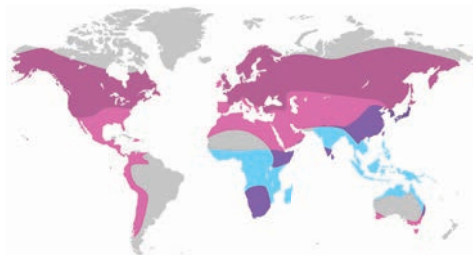


odonates can react quickly to environmental change (p. 6). Few have amazed observers more, however, than the whitefaces (*Leucorrhinia*) from the cooler parts of Eurasia and North America (**dark pink on map**). Once the boreal realm warms up in spring, these small dragonflies will soon dash over still water, their bright snouts and wingtip veins standing out against their dark bodies.

In Europe, two species favor peat bogs and acidic fens, two like lakes, often with abundant vegetation such as lily pads, and a fifth has intermediate tastes, such as for lushly grown ditches. As humans transformed the landscape, all five suffered. By the late twentieth century, the lake species had been virtually wiped out in the west, while the bog-dwellers, though largely confined to protected areas, were still quite abundant.

Within the last quarter-century, however, fortunes have turned completely. Numbers of the bog species are collapsing, notably at their southern limit, while the lake ones have become locally common again, even at isolated sites. The fifth species has made gains in many places, but losses elsewhere.

As summers get hotter, bogs are drying out. Climate change, moreover, affects wind patterns, and the persistent easterlies in the spring of 2018



DIVERSITY

108 species found almost worldwide at mostly standing waters that, especially in cooler regions, are often comparatively warm

TAXONOMY

Genera *Austrothemis* (1 species), *Celithemis* (8), *Leucorrhinia* (14), *Nannophyopsis* (2), *Nesogonia* (1), *Rhyothemis* (23), *Sympetrum* (56), and *Tyriobapta* (3)

ABOVE | A male Lilypad Whiteface (*Leucorrhinia caudalis*) in Switzerland, uncharacteristically not perching on floating plants.

brought all five species to western locations where they had never been seen before. Water and landscape management also improved, restoring and creating habitats.

The advance of southern species (p. 46) must have mattered too, as may the interactions between the five relatives themselves and with their predators. The bog species' short-spined nymphs appear more vulnerable to fish than the long-spined lake species, for example.

Leucorrhinia is the most boreal genus of the family's largest temperate radiation, with about 80 species in three genera. While whitefaces merely have black marks at the wing bases, the closely related small pennants (*Celithemis*) of eastern North America's marshy ponds and lakes have colored faces and often elaborate wing patterns in brown, red, and gold, like painted glass. Resting atop vertical perches, they brandish these wings like pennants (pp. 65 and 67);



LEFT | Pair of Variegated Meadowhawks (*Sympetrum corruptum*) laying eggs in Montana, USA.

UPPER RIGHT | Emerald Bijou (*Nannophyopsis clara*) male in Hong Kong.



LEFT | The spectacular Picturewing Flutterer (*Rhyothemis variegata*) must be among South Asia's most photographed dragonflies.

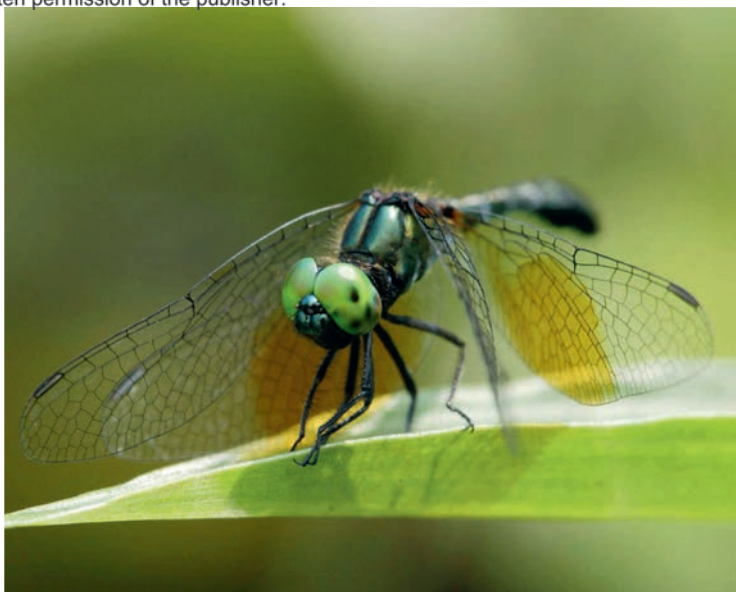
LOWER RIGHT | North America's Halloween Pennant (*Celithemis eponina*) strongly recalls some of its distant tropical relatives, notably Australia's Graphic Flutterer (*Rhyothemis graphiptera*).

Celithemis translates as “stained-libellulid” (p. 38).

With 56 known species—called darters in the Old World and meadowhawks in the New—*Sympetrum* is the most successful odonate genus in the temperate north: their cold- and drought-resistant eggs let them benefit from the many standing or flowing microhabitats there that warm up quickly but can cool down or dry out just as fast. Females have very varied spout-like nozzles to place them, therefore, one Asian species even being called *S. cordulegaster* for its spiketail-like apparatus (compare p. 86).

They are good dispersers, some species migrating in great numbers. While most inhabit northeast Asia and North America, the genus has expanded south too, particularly in the Andes (**pink and purple on map p. 61, excepting Australia**). Eurasia’s vagile Red-veined Darter (*S. fonscolombii*) extends across the higher and drier parts of Africa and has even established outposts on high islands such as Sri Lanka and Réunion.

Its large relative, *S. dilatatum*, occurred on the mid-Atlantic island of St. Helena, but was last seen in 1963, probably extirpated by introduced frogs. The Hawaiian Streamhawk (*Nesogonia blackburni*) has similarly adapted to island streams. While looking so distinct that it was placed in a separate genus, genetics show it originated from within *Sympetrum*. The evidence, moreover, suggests that this temperate radiation originally came from the Old World tropics.



RIGHT | Male of the Obsidian Flutterer (*Rhyothemis plutonia*) in Thailand. Translating to the inapt “stream-libellulid,” the genus name may refer to rhyolite, a multicolored igneous rock.

Flutterers (*Rhyothemis*), formerly given their own subfamily Rhyothemistinae, are found at still waters with plenty of sun and vegetation (**blue and purple on map on p. 61**). They are the butterflies of the dragonfly world, with greatly expanded wings with extravagant dark markings. These, often interspersed with transparent windows and translucent amber, have strong blue, purple, and copper reflections, inspiring names such as Bronze, Iridescent, Obsidian, and Sapphire Flutterer.

Often abundant, these dragonflies clearly aim to be seen, sitting atop exposed perches, tilting their big wings from side to side in the breeze, like a funambulist on a tightrope, or weirdly angling their dark surface away from the sun. Aggregating to feed, they flutter about leisurely over clearings or shrubbery, often at some height. While seeming lackadaisical and weak, their flight can be very fast, and some species are strong migrants.

Treehuggers (*Tyriobapta*), by contrast, are restricted to Borneo, Sumatra, and the Malay Peninsula. They characteristically perch horizontally on tree trunks or rocks, camouflaged in blotched black and beige, like *Bradinopyga* (p. 45). Males become dark-glossy covered with bright pruinosity and fiercely defend small waterbodies in swamp forest. While two species have (almost) clear



wings, the third has extensively dark hind wings with purple reflections.

The bijoux (*Nannophyopsis*) of Southeast Asia have gleaming copper bodies and emerald eyes. Like the distantly related *Nannophya* (p. 49), from which their name derives, they are among the smallest dragons (down to $\frac{5}{8}$ in / 16 mm long). Perching deep inside weedy borders of ponds and lakes, with their yellow wings pressed forward and strongly clubbed abdomen curved down, they look almost like wasps.

Superficially, Australia's black-spotted red Swamp Flattail (*Austrothemis nigrescens*) is very distinct from its dark-metallic tropical cousins (**also pink on map p. 61**). Indeed, it is more like a temperate *Sympetrum*! The swampy pond and lake habitat, adult's paddle-shaped abdomen, and nymph's strange side-pointed eyes recall the bijoux, however.

LIBELLULIDAE—UROTHEMISTINAE

BASKERS AND KIN

Most insects cannot survive high concentrations of dissolved ions, but the closely related Black (*Selysiothemis nigra*) and Marl Pennants (*Macrodiplax balteata*), found along the Mediterranean and Caribbean coasts and in deserts nearby, fare well in brackish or alkaline waters. Their mature males' densely melanized skin (under a thin layer of reflective pruinosity) may help absorb intense heat and ultraviolet radiation, protecting the body beneath.

Like other so-called pennants (pp. 62 and 67), they sit atop exposed perches with legs thrust forward and wings raised, twisting in the breeze. The red Coastal Pennant (*M. cora*) breeds in lagoons in the Indo-Pacific, alongside 15 relatives known as baskers (*Urothemis*) and adjutants (*Aethriamanta*). These blue-pruinose or red species also inhabit warm and open sites, but favor richly vegetated standing freshwaters. The eggs of urothemistines can be bright green or blue and are often deposited on floating plants.

While *Urothemis* species are large and *Aethriamanta* small, this division may not hold up to closer scrutiny. *Selysiothemis* might best be sunk into *Macrodiplax*, thus losing a genus honoring the nineteenth-century founder of odonate taxonomy, the Belgian baron Edmond de Selys Longchamps.



DIVERSITY AND OCCURRENCE

18 species of (mostly open) standing waters in warmer parts of the world, only one reaching the Americas

TAXONOMY

Closely related genera *Macrodiplax* (2 species) and *Selysiothemis* (1), **pink on map**; *Aethriamanta* (6) and *Urothemis* (9), **blue**

TOP | Coastal Pennant

(*Macrodiplax cora*) male, perching at the end of a stick like a fluttering banner. Sometimes called Macrodiplactinae or even awarded family rank, the subfamily has distinctly wide-spaced venation.

ABOVE | Black Pennant

(*Selysiothemis nigra*) male in Portugal.

AMBERWINGS, BLACKWINGS, AND POSSIBLE KIN



Entirely glossy black with deep red branding on the abdomen and sometimes face and wing bases, male blackwings (*Diastatops*) appear like glowing coals. They pursue each other in a rapid fluttery flight along the grassy verges of ponds and ditches in South America's tropical lowlands. At rest, the very broad and densely veined wings are often held at weird angles, possibly to prevent overheating, as males are known to abandon the waterside on hot afternoons.

If blackwings are smoldering embers, the tiny amberwings (*Perithemis*) are like flickering flames. The feisty males' wings and body appear entirely orange, run through with yellow to reddish veins and marked intricately with yellow and brown, like brooches of gold filigree. Female wings are more often clear, banded with amber and brown.

Like other compact libellulids with tinted wings, such as *Palpopleura* (p. 46) or *Zenithoptera* (p. 60), both sexes perch prominently and often high up, tilting one or both pairs of wings up or down, or waving them slowly. With a buzzy flight, they are easily mistaken for wasps or bees. All species favor smaller and often sheltered stagnant waters, like forest pools. Males typically perch in sunspots near the



DIVERSITY

62 species of richly vegetated standing and slow-flowing waters, mostly in the American tropics

TAXONOMY

Genera *Brachymesia* (3 species), *Diastatops* (8), *Idiataphe* (4), *Oligoclada* (25), *Perithemis* (12), and *Planiplax* (5), but inclusion *Chalybeothemis* (3) and *Trithetrum* (2) speculative (both blue on map)

TOP LEFT | Red-saddled Blackwing (*Diastatops pullata*) male in Ecuador. Greek for "divided eyes," the genus name refers to the wide-spaced eyes, unique in Libellulidae.

LOWER LEFT | Mexican Amberwing (*Perithemis intensa*) male in Arizona, USA.

surface, taking off frequently to drive intruders away or inspect their little kingdom in a low hovering flight.

While both genera have slim legs, those of their apparent relatives of open water, the spiderlegs (*Planiplax*) and tropical (*Brachymesia*) and metallic (*Idiataphe*) pennants, are longer still. Bigger with less color in the wings, but often bright red bodies, all favor larger ponds and lakes. These pennants (compare pp. 62 and 65) rest at the tip of stems, raising their wings like flags. The restless males perch far out over water, readily speeding off for long skimming flights.

The small and slender leafsitters (*Oligoclada*), by contrast, spread their spindly legs across the top of leaves to oversee swampy backwaters and sluggish streams. Their dark bodies' slight steely sheen and light pruinosity creates a dull-metal look, contrasting with often gleaming green eyes. Found at weedy borders of lakes and rivers in Southeast Asia, greeneyes (*Chalybeothemis*) are remarkably alike. Equatorial Africa's Fiery (*Trithetrum navasi*) and Sooty Darters (*T. congoense*) are ecologically and structurally close, the former recalling a red *Brachymesia*. Further study, however, must confirm whether their long-mysterious affinities are truly Neotropical.



TOP RIGHT | Common Greeneye (*Chalybeothemis fluviatilis*) male in southern Cambodia.



LOWER RIGHT | A male Guiana Spiderleg (*Planiplax phoenicura*) showing off its long limbs in Brazil.

SADDLEBAG GLIDERS AND KIN

BELOW | As all species in the genus, this male Carolina Saddlebags (*Tramea carolina*) in Canada is a strong migrant. *Trameare*, indeed, is Latin for “passing through.”

Flocks of Wandering Gliders (*Pantala flavescens*; p. 52) often contain similar dragonflies with wing markings flanking the body like bags on a saddle. Called gliders in the Old World too, but saddlebags in the New, the genus *Tramea* is indeed much like *Pantala*. The hind pair of the long, pointed wings is similarly broad and triangular, with notably smaller stigmas than the front. The big nymphs are spindly and thin-skinned, with bulging eyes and toothy protruding palps to quickly see and grab their prey, the abdomen ending in long and slender spines.

Closer scrutiny and genetics show they are not closely related. Both are adapted to seasonal rains, growing rapidly by feeding ferociously in balmy water, then setting off to find fresh opportunities. Adults are built to fly long distances with minimal effort, tending to glide and hover as they patrol their breeding sites or feed, before resting with a hanging posture.

Tramea species favor more vegetated ponds and also often perch atop exposed lookouts with the abdomen held up or pressed down and wings raised to



DIVERSITY

39 species of mostly open standing waters in warmer parts of the world

TAXONOMY

Genera *Antidythemis* (2 species), *Atratothemis* (1), *Camacinia* (3), *Garrisonia* (1), *Hydrobasileus* (3), *Miathyria* (2), *Pseudotrimea* (1), *Tauriphila* (5), and *Tramea* (21)

TOP RIGHT | The tricolored male of the Blazing Sultan (*Camacinia harterti*) seems to be on fire: rarely seen, this Asian behemoth probably breeds only between the buttresses of giant rainforest trees.

LOWER RIGHT | Hyacinth Glider (*Miathyria marcella*) male in Florida, USA.

show their markings. While *Pantala* females usually oviposit alone, *Tramea* males release and recapture their mate each time she swoops down to hit the water, unique behavior facilitated by their very long and slender claspers.

Although not all affinities are confirmed, aside from *Tramea* (**pink and purple on map**), another 18 conspicuous patrollers of standing waters, which readily wander and mostly rest hanging, are included in the subfamily too (**purple only**). Besides half of *Tramea* species, eight gliders in the closely related *Garrisonia*, *Miathyria*, and *Tauriphila* are Neotropical. They often mix with saddlebags in foraging flights, but are smaller and more colorful and favor floating vegetation (water lettuce and hyacinth, especially), their nymphs living among the roots. Amazonia's poorly known velvet gliders (*Antidythemis*) have unusually large stigmas.

The remaining diversity ranges from tropical Asia to the Pacific, although two Asian *Tramea* are common in Africa too. *Hydrobasileus* gliders and sultans (*Camacinia*) sail majestically over lush ponds and lakes on colored wings. Largely carmine and ebony, the massive Red (*C. gigantea*; photo p. 34) and Black (*C. othello*) Sultans appear like hefty hyperactive *Neurothemis* (p. 45). Hardly known, the Swarthy Sultan (*Atratothemis reelsi*) from Indochina and adjacent China could be allied, while *Pseudotrimea prateri*, reported sparsely along the Himalaya, may just be a *Tramea* with smaller wing spots.



DUSKDARTERS AND KIN



Visit any urban pond in tropical Africa or Asia by nightfall and you may see numerous dragonflies skimming fast and low over the foul water. Initially red with dusky-stained wings, eventually only dark dashes with whirring white flashes are visible in the gloom. Some without bright flashes tap the floating debris with their tail-ends, veer up, swing around, and tap down again, twisting to-and-fro as in a trance.

Named for the rhythmic motion with which its eggs are laid, the Twister (*Tholymis tillarga*) is among the tropics' most tolerant (even inhabiting brackish water) and widespread odonates; the Evening Skimmer (*T. citrina*) is its American counterpart. Daylight reveals a brown smear in each hind wing, paired in Twister males by a patch of gleaming pruinosity that looks ever brighter as darkness falls.

Flying continuously at dusk and (if warm enough) dawn, and hanging in vegetation all day, these are the quintessential crepuscular dragonflies, with big eyes, plain bodies, and broad



DIVERSITY

19 species of standing and slow-flowing waters in warmer parts of the world, but with only one reaching the Americas

TAXONOMY

Genera *Brachythemis* (6 species), *Deielia* (1), *Parazyxomma* (1), *Pseudothemis* (2), *Tholymis* (2), and *Zyxomma* (6), but placement of *Zygonychidium* (1) tentative

TOP | Following humans and other animals to snatch up disturbed insects, this Southern Banded Groundling (*Brachythemis leucosticta*) is among Africa's most familiar dragonflies.

LOWER | Male of the Twister (*Tholymis tillarga*) resting at daytime, showing the wing markings that stand out at dusk.

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