Dragonflies of the Golfo Dulce Region, Costa Rica

Piedras Blancas National Park
"Regenwald der Österreicher"

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Introduction

Visitors to the La Gamba Research Station will find a rich array of tropical life. As well as an overwhelming diversity of plants, they will see birds and butterflies, two of the most popular and conspicuous groups of animals. Hummingbirds, noisy toucans, and brilliant butterflies like the iridescent *Morpho* or the spectacular *Heliconius* are well known throughout the world. But there are many other groups which are just as recognisable yet not as widely known. Unfortunately there is often a dearth of knowledge about such organisms, and access to the relevant literature is difficult. Sometimes, however, we just need a little help to find them. Dragonflies are skilled fliers, fearless predators, and passionate lovers, and once you notice them, you will find them fascinating.

The ecology and behaviour of the Central American dragonfly fauna has been laid out in detail in the specialist literature (see references), and more interested readers are invited to consult these sources. This booklet is designed as a pocket guide to the identification of the most frequently observed species around La Gamba. The descriptions of characteristics and differences between the species are limited to essential information. Although identification can be difficult, and for some species beyond the scope of this booklet, it should be possible to recognise most of the common species present in the region. For the interested observer, this booklet will serve as an introduction to the diversity of a fascinating group of animals. We hope it will raise awareness of the diversity of dragonflies, but also of how urgently we need to work for their conservation.

History and diversity of dragonflies

The first fossil records of a group called Protodonata, closely resembling today's dragonflies and thought to represent their ancestral form, date from the Upper Carboniferous period 325 million years ago. With a wingspan of 70 cm, *Meganeura monyi* was one of the largest insects ever to have lived on the planet. Today's dragonflies are considerably smaller, but these ancient insects still have a valuable place in the ecosystem. Today the order Odonata (dragonflies) is divided into three suborders, the most common being the smaller Zygoptera (also known as damselflies) and the larger Anisoptera. A third suborder, the Anisozygoptera, which combines characteristics of the other two groups, is represented by two species in Nepal and Japan.

Approximately 5700 species have been described so far, with almost equal numbers in Zygoptera and Anisoptera. Because larval growth responds positively to temperature, dragonflies are assumed to have developed in a warm climate. Today the greatest diversity is found in tropical regions, declining towards higher latitudes. Areas of the highest diversty are found in South America and South East Asia, especially in montane regions where examples of previously unknown species are often reported.

Adults and larvae

Zygoptera and Anisoptera can be easily identified as adults and larvae. Adult Zygoptera are usually finely built insects with slender abdomens. The eyes are separated and situated laterally on the head. Their fore wings and hind wings are fairly similar in shape and venation, and are held over the abdomen when resting. In flight they are less acrobatic than Anisoptera, and are often found patrolling in dense vegetation near the water's edge. The larvae of Zygoptera are small and slender, this shape often appearing pronounced by the presence of three flattened, elongated and highly tracheate caudal appendages that serve as respiratory organs. Three tropical families form the exception, showing either lateral gills on the abdomen (Euphaeidae and Polythoridae), or gill tufts at the end of the abdomen (Amphipterygidae).

Adult Anisoptera are built robustly, with a long or stout abdomen. Their large eyes cover almost the whole head and meet on top of the head, or they can be slightly separated as in the family Gomphidae. The wings differ in shape and venation and are held open when resting. Anisoptera can be observed perching on exposed structures along banks, or patrolling for hours over the

water surface. The larvae are stout and have three strong spines instead of lamellate appendages. They breathe by 'rectal ventilation', pumping water through the rectum, where a tracheate organ serves for gas exchange. Water can be expelled from the rectum very forcefully, so that the larva swims forward. This 'jet propulsion' is also used to escape predators.

Larvae and adults are predators and fairly opportunistic in their choice for prey, although specialisation does occur (see Pseudostigmatidae). Both developmental stages are perfectly adapted to this lifestyle. Larvae actively search out or ambush their prey, detecting it visually or by touch, and capture it by the rapid protraction of the modified lower lip (or 'labium') which forms the so-called 'mask'. Adults detect prey with their large eyes. In flight, they can turn quickly, hover, and even fly backwards, since the flight muscles insert directly on the wing base, allowing them to move each pair of wings independently. Even fast-flying prey such as other dragonflies can be captured by their acrobatic manoeuvres, held by their legs, and then manipulated with their sharp mandibles.

Life cycle

Dragonflies are hemimetabolic insects, exhibiting incomplete metamorphosis and lacking a pupal stage like that in butterflies; the adult develops during the last larval stage. Their life cycle comprises three phases: egg, several larval stages, and adult. The larvae live predominantly in fresh water, inhabiting lakes, streams, bogs, and ephemeral water bodies. Only a handful of species are known to develop in the brackish water of marine marshes, or to have terrestrial larvae. Many species are generalists, capable of inhabiting a wide spectrum of freshwater systems. Some species, however, have narrow breeding site requirements and are thus sensitive to disturbances and habitat destruction. Many of these specialists are rare, but they can be used for the assessment of ecological freshwater status.

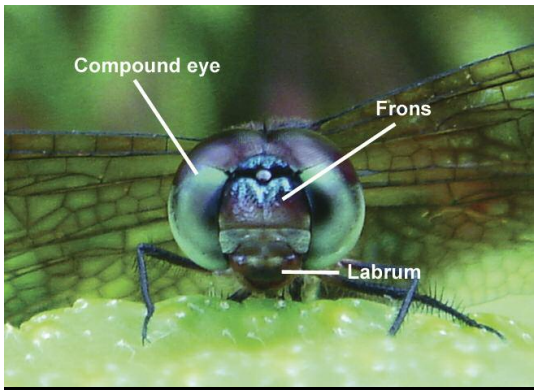
After mating, the female lays fertilised eggs either on the water (exophytic), or into (sometimes submerged) plants (endophytic). Before oviposition, suitable habitats for development are selected by the adults. During this selection they orientate on environmental factors like the reflection of the aquatic surface, and the vegetation structure. After one or more weeks the embryo will have completely developed, and the first larva (prolarva) will be ready to hatch from the egg. Subsequently, having reached the water (in the case of endophytic eggs), the prolarva starts to moult (i.e. to leave the old cuticula), in a process called 'ecdysis'. During the larval phase, which can last from a few weeks up to several years, up to 15 ecdyses are completed, separated by periods of foraging behaviour and growth. In temperate regions, eggs or larvae can display a diapause, a reduction of metabolism and growth during winter.

The final larval stage, at which an adult is contained within the larval skin, sees the larva leaving the water for emergence. This spectacular scene usually takes place shortly before dawn. The larva climbs up a suitable structure, often a piece of aquatic vegetation, and searches for a firm grip with its legs. The larval skin then bursts at pre-formed points, and the young adult leaves the skin. After a short rest the adult unfolds its wings and abdomen by pumping in haemolymph. After emergence, the smooth and shimmering skin first has to harden. Then the dragonfly sets off on its maiden flight, leaving the site of emergence.

Young adults spend their first days on the side of the water in order to build up fat reserves, and to avoid interference from mature and territorial dragonflies. The sexual organs are not yet fully developed, and they start to mature during this period. In some tropical species, when breeding habitats have dried out, this pre-reproductive time can be prolonged for months until the beginning of the next wet season. When the sexual organs have fully developed, the adults turn to suitable water bodies for reproduction.

Males spend many days at reproductive sites, where they establish temporary territories that are defended against other males. Females are often dispersed around other habitats and only visit the water bodies for copulation and oviposition. When a female enters a territory, the male flies up and tries to grasp her with the caudal appendages, on the female's thorax in the case of Zygoptera, and on her head in Anisoptera. The male then bends its abdomen forward to transfer

sperm from its sexual organs to its copulation organ. Finally, the female bends her abdomen forward to bring her genitals into contact with the copulation organ of the male, forming the 'wheel of love' (see *Libellula herculea*). With its copulation organ, the male is able to remove sperm from previous copulations with other males and transfer its own sperm into the female. Copulation can take place while airborne or resting, and may take anything from a few seconds to many minutes. The female can start to lay eggs immediately after copulation. Males often guard the female during oviposition, either still attached or hovering next to her, to avoid other males attempting to copulate.

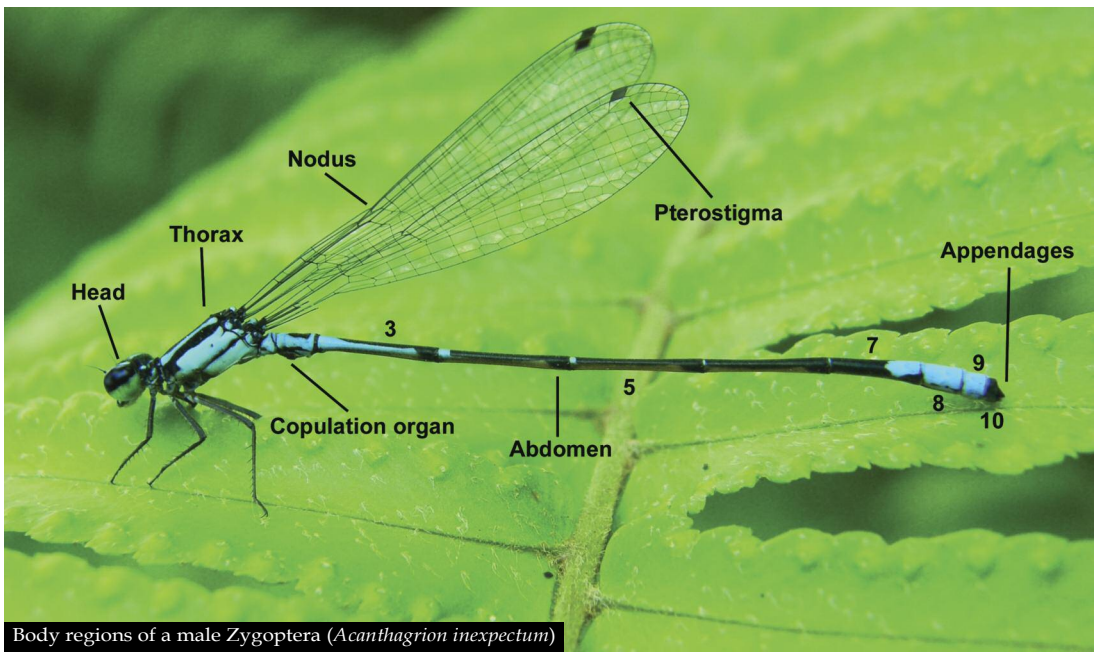


Front view of the head of an Anisoptera (*Macrothemis* sp. Libellulidae)

Morphology of the adult

The body of a dragonfly is separated into head, thorax and abdomen. The head bears two large compound eyes, three median ocelli, and two short antennae. Between the eyes, the 'frons' forms the frontal part of the head. Below the frons, the labrum covers the mouthparts, which handle prey. The colouration of eyes, frons, and labrum can be important characteristics for identification. The thorax consists of three segments, each with a pair of legs. The first segment (prothorax) is short. The second and third segments are fused and dorsally inclined backwards, and each has a pair of wings. The wings have five major veins and numerous crossveins. The front margin of the wing is formed by a vein called the 'costa'. Details of venation are variable, but two conspicuous structures are present in all species. The 'nodus' is a strong crossvein, inserted at the front edge of the wing approximately half way along its length. The 'pterostigma' is a dark cell at the distal part of the wing on the costal side. The base of the wing can be narrow for the length of several cells (petiolate), extended, or neither. The colouration and markings on the wings can be helpful characteristics for identification.

The abdomen consists of ten segments of variable length. The first two segments are short, segments 3–7 are long, and segments



Body regions of a male Zygoptera (*Acanthagrion inexpectum*)

8–10 become shorter again. In males, segments 2 and 3 bear the copulation organ ventrally. Females have ovipositors at the ventral side of segment 8, sometimes extending to the tip of the abdomen, or a small vulvar lamina. At the end of the abdomen are the appendages, two upper and two lower in Zygoptera males, and two upper and one lower in Anisoptera.

Identification

Characteristics for unambiguous identification include wing venation and the structure of the male copulation organ or the ovipositor. Examination of these structures requires specialist knowledge and the ability to capture individuals. Colouration, however, can also be useful for identification, although species–level determination is not always possible. Any individuals observed should be compared with the photographs, sizes, and descriptions of details in this booklet.

Males can be recognised by the presence of a secondary copulation organ at the ventral side of segments 2 and 3 of the abdomen, which forms a small but prominent structure absent in females. Females may have a conspicuous ovipositor on the ventral side at the end of the abdomen. In Anisoptera, the ovipositor may be reduced to a small laminate structure arising from the end of segment 8, and projecting towards segment 9. Males are usually brightly coloured and often have conspicuous markings on the wings. Females are usually dark or brownish yellow and less colourful.

Body and wing measurements may help to distinguish between similarly coloured species of different sizes. The body and abdomen sizes given in this booklet include the caudal appendages. Values given are either means of several individuals, or measurements of single individuals. Individual variation in body proportions can be up to several millimetres, and this should be borne in mind when comparing observed dragonflies with the values given in the description. Measures of size and body parts account for both sexes if not indicated otherwise.

The abundances of species are given for the region around La Gamba, and do not apply to their frequencies in Costa Rica or Central America.

The most frequently observed forms of different species are illustrated in this booklet. If an observed individual does not fit any of the photographs, this may be for one of two reasons. Either the species is not included in the booklet, or the individual is of a different sex or age. The following caveats have to be kept in mind during identification: species of the same genus may be similarly coloured; colouration may differ between males and females of the same species; pre-reproductive males often resemble females and usually become darker before entering the reproductive period; the shallow colouration of recently emerged adults turns into their characteristic pattern after several hours, but wing markings may need longer to become fully developed. Descriptions of immature and mature forms, and males and females, are given in the text wherever they are available. Species closely resembling each other are also mentioned in the text.

The availability of aquatic habitats for larval development constrains reproduction in dragonflies, and consequently the rainy season marks the climax of the reproductive period for many species. Adults of some species may be absent during the dry season, either not yet emerged from their larval stage, or occupying alternative habitats. It is therefore possible that not all species present in the region may be observable during a short visit.

Tropical dragonflies

In both their ecology and behaviour, tropical dragonflies deviate in some ways from temperate species. In montane regions isolation processes have favoured speciation, and diversity in the tropics by far exceeds the number of species in temperate regions. In the tropics, manifold niches have enabled the development of specialised life strategies. The larvae of Neotropical Pseudostigmatidae and some other families, for example, inhabit 'phytotelmata' - water-filled cavities like tree holes or plant tanks. The long abdomen of Pseudostigmatidae females is useful for oviposition into such deep structures. The strategy of migrating species such as *Pantala flavescens* may be linked to the unstable and unpredictable availability of breeding waters in drier regions. This circumtropical species often forms swarms of hundreds of thou-

sands of individuals migrating over long distances in front of rain fronts. The eggs are laid in bodies of water that sometimes persist no longer than a month. This becomes possible due to the speed of embryonic and larval development. In tropical montane forests, turbulent and shaded streams harbour a rich dragonfly fauna. In temperate regions, in contrast, relatively few species are adapted to these special conditions.

The dragonfly fauna of Costa Rica is one of the best-studied in Central America, yet it is still not fully explored. In comparison with Austria (77 species) and Europe (125 species), Costa Rica is very rich in dragonflies, with 268 currently described species. Many of these dragonflies are part of the North and South American fauna, but a small but significant proportion of Costa Rican dragonflies are endemic to the region, which includes Nicaragua and Panama. *Cora semiopaca*, a species present in La Gamba, is endemic to Costa Rica. The Caribbean slope of the Cordillera seems to harbour more species.

Odonatological field trips around La Gamba

Although dragonflies are often seen flying or resting on vegetation beside water, the easiest way to observe them is at their breeding sites, usually streams or ponds. Odonatological field trips therefore concentrate on aquatic habitats, but these habitats are embedded in a matrix of landscapes that heavily influence the quality of breeding sites. Dragonfly distribution is greatly affected by the drastic difference between undisturbed forests and intensively used agricultural areas and their respective water bodies.

Forests

Forests may originally have been the primary habitat of dragonflies in Costa Rica, and the prevailing conditions may have influenced the mixture of species living in them. Swamps and smaller streams can be completely shaded and flow can be very turbulent, which provides well oxygenated water, but with an increased risk of being carried away by the water. Polythoridae like *Cora semiopaca* prefer these conditions. The forest interior, where *Mecistogaster modesta*

A shaded stream in the forest interior

and *Megaloprepus cerulatus* can be found, is dark, and temperatures are lower than in open habitats, constraining the thermal requirements of adults. Many species living in the forest are shade–loving and are therefore not found in open areas. For a species like *Philogenia zeteki*, the dense understorey may additionally provide protection from predators. Such forest species are specialised to these circumstances, whereas many other species would not be able to survive. Forests have been hit hard by human activity, and the remaining islets surrounded by open landscape may be too small or isolated to sustain populations of forest dragonflies. In forests, on the other hand, degraded and open patches like those caused by tree falls or logging, as well as roads, resemble open landscapes and are often used by species like *Uracis imbuta* which are usually found in open habitats.

Cultivated landscapes

Cultivated landscapes are those artificially shaped by human land use. Bodies of water in these environments are usually exposed to the sun, leading to higher temperatures and lower oxygen levels. Pollution by the inflow of agrochemicals or domestic sewage can influence water quality. Embedded in a matrix of relatively uniform landscapes including plantations, crop fields and pastures, narrow strips of gallery forest often form the last remnants of primary vegetation. In this dramatically altered landscape, the dragonfly fauna is different, and generalist species like many Libellulidae, which are able to live under a wide range of environmental conditions, prevail. On a small spatial scale, species richness can increase in cultivated areas through the colonisation of these habitats by generalists. Mostly, however, generalist species like *Erythrodiplax* fusca are widespread and common and therefore, on a broader scale, overall richness may be reduced.

Forest margins

Aquatic habitats at forest margins can either resemble forests or open landscapes depending on the type and density of gallery vegetation. Running water along forest margins may be suitable for shade–loving species such as *Heteragrion erythrogastrum*. Artificial ponds can be exposed to the sun and may be colonised by generalist species like *Orthemis ferruginea*. In the garden of the Research Station, several small ponds and rivulets provide habitats for generalists, and some common species can frequently be observed there.

Stream with open canopy surrounded by cultivated areas

Zygoptera

Family Polythoridae
(polythorids, polytóridos)

They are medium–sized Zygoptera species with dense wing venation, many antenodal crossveins, and short legs. In contrast to members of the Calopterygidae, the bases of the wings in Polythoridae are petiolate, the wings are relatively narrow, and males lack red colouration at the base. Females are light to dark brown. Polythoridae are shade–loving dragonflies that live beside streams in undisturbed forests. The larvae have lateral gills on the abdomen.

Cora notoxantha
size: 39 mm, abdomen: 31 mm, fore wing: 25 mm

The thorax of the **male** is bright yellow or blue, with a thin black mid-dorsal line in some individuals. Blue coloured individuals may be confused with *Cora marina*, a species common in Central America, but in that species the abdomen is almost blue dorsally. The eyes are dark and the face is white. This species is known from Costa Rica and Panama.
We found this rare species beside a forest stream

Cora notoxantha male

Cora semiopaca

size: 35 mm, abdomen: 27 mm, fore wing: 27 mm

This stream–dwelling species is endemic to Costa Rica. The **male** has characteristic reflective zones on the wings, and dark bands on the distal parts of the wings. In the dark forest undestorey, the shimmering blue reflections may attract females that are searching for mating partners and suitable sites for oviposition. The face is white. The **female** in this photograph was not identified to the species level but is likely to be a female of *Cora semiopaca*; most females in the genus look similar. This stream–dwelling species may be threatened by disturbance due to its small range size.

We found this rare species beside a stream running through a shaded ravine.

Cora semiopaca male

Cora sp. female