Phylogeny and biogeography of the Platystictidae (Odonata)

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Introduction

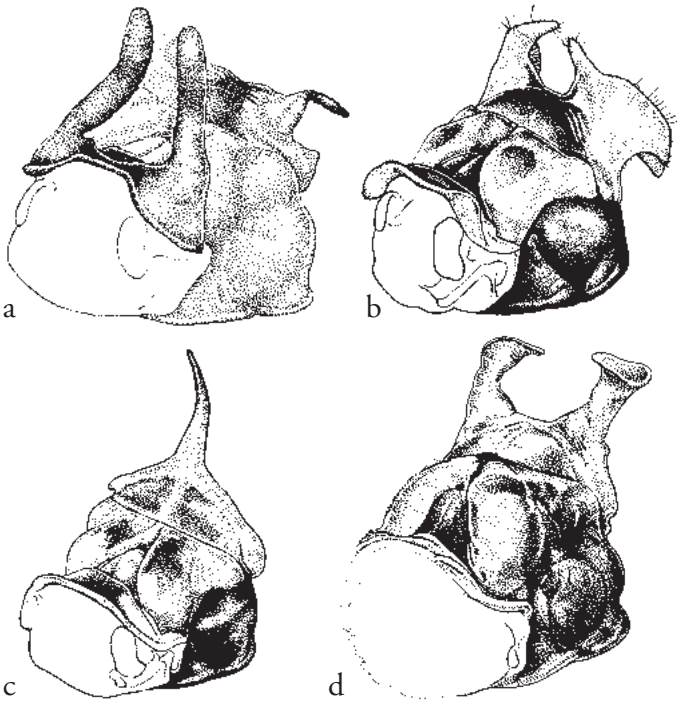
Tropical odonates are well-known for their brilliant colours, their size and conspicuous behaviour. Indeed, the scarlet abdomen, or the iridescent colours in the wings of some dragonflies and damselflies attract the attention of even the general naturalist when visiting a tropical lake or stream. The eye-catching display and agonistic behaviour of tropical calopterygoids and other damselflies also contribute to this general notion.

The species of the family Platystictidae, also known as forest damselflies or shadowdamsels, the subject of this publication, differ in nearly all aspects from this general impression of tropical odonates. Although platystictids are restricted to the tropics, they are dull-coloured, small insects with elusive behaviour. In the larval stage, they typically live in seepages or small streams deep in dark forest, while the imagos seem to hang all day from the tips of branches or leaves of trees and shrubs in gullies or along streams. The adults are poor flyers, and take the wing only when they are disturbed, to catch a prey, or are attracted by the opposite sex. They are underrepresented in many entomological collections, since they are simply not noticed by the general insect collector.

The family Platystictidae is known from southeast Asia (Sri Lanka and India eastwards to the Papuan region) and from Central and the northern part of South America. Most species are island endemics, or are even confined to parts of these islands only. The overall similar general appearance of dull brownish species with a blue tip of the abdomen conceals the huge variation in such structures as the pronotum, male anal appendages and secondary genitalia. This combination of characters makes the family Platystictidae a group of choice for a contribution to our understanding of the history of the aquatic biotas of the tropics. This thesis focuses on the following research questions:

(a) what is the diversity of the family Platystictidae at the species level, especially in southeast Asia, and what is the distribution of each species?
(b) which morphological and molecular characters can be used to reconstruct the phylogeny of this group of odonates?
(c) is the family Platystictidae a monophyletic group, and what are the relationships to other families of Zygoptera?
(d) what are the phylogenetic relationships of the species of the Platystictidae, based on the analysis of both morphological and molecular characters?
(e) which areas of endemism can be recognized based on the distributions of the species of Platystictidae?
(f) what are the relationships of the areas of endemism as defined by the distributions and phylogenetic relationships of the species of Platystictidae, and what is the relation to area cladograms based on other taxa?
(g) how did the present distributional pattern of the Platystictidae evolve, *e.g.*, in relation to the palaeogeography and palaeoclimatology?

Research questions (a) and (b) are treated in the second part (chapters 3 to 8) of this publication. This part includes several regional revisions of Platystictidae, including descriptions of 46 species new to science. Special attention was paid to the species of the Philippines, Sulawesi, and the Moluccas. A smaller paper was devoted to the fauna of Vietnam. These revisions were based on a significant amount of new material available in the National Museum of Natural History Naturalis, which was partly collected by myself



Platystictidae show bizarre variation in subtle structural details. Pronotum of Philippine *Drepanosticta* species. (a) *D. trachelocele* van Tol (Samar); (b) *D. centrosaurus* van Tol (Mindanao); (c) *D. ceratophora* Lieftinck (Balabac); (d) *D. myzouris* van Tol (Luzon) [not to scale].
For details, see Chapter 5 (Illustrations by E.J. Bosch and I.M. van Noortwijk).

during fieldwork in Vietnam and Indonesia. It was, for instance, exciting to study the bizarre variation in the processes of the pronotum of the species of *Drepanosticta* Laidlaw in the Philippines (this page and chapter 5). In other parts of the range, species mainly differ in the anal appendages of the male, e.g. in the genus *Protosticta* Selys of Sulawesi (chapter 6). These taxonomic papers also include discussions of characters.

The full variation of this family was taken into account for a reconstruction of the phylogeny and the historical biogeography of this family (Part 1, chapter 1). Chapter 2 reviews present knowledge of the zoogeography of freshwater invertebrates of southeast Asia, with special attention to Odonata. It also includes a rather extensive summary of the regional palaeogeography of the region during the Cenozoic. Unfortunately, well-founded phylogenetic reconstructions of aquatic insects of southeast Asia are still scarce, while such reconstructions are a prerequisite for biogeographical analyses.

The present biogeographical reconstruction based on Platystictidae is one of the first based on extensive taxon sampling and character analysis, and thus contributes to our understanding of the evolution of the aquatic biotas of southeast Asia. Platystictidae occur in Central and northern South America (subfamily Palaemnematinae), and the Oriental and Papuan regions (subfamilies Platystictinae and Sinostictinae). The reconstruction of the phylogeny of 53 species is based on morphological characters, while a preliminary analysis based on molecular characters (16S and 28S rDNA) is restricted to 55 samples of 44 species, including 22 samples representing 16 species of Platystictidae. The reconstruction of the phylogeny is used for an analysis of the historical biogeography of this family. The sister-group relationships at the base of the tree suggest that the New World and Old World taxa diversified already early during their evolution, presumably before the end of the Cretaceous (65 Ma). It is further concluded that the group may have evolved in Africa, that a tropical Europe during the Eocene has played a remarkable role as a pathway for forest damselflies to the New World, and that the taxa of southeast Asia all have evolved from a centre at the border of the Indian plate and Laurasia.

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