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Micro-morphological adaptations of the wing nodus to flight behaviour in four dragonfly species from the family Libellulidae (Odonata: Anisoptera)

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ABSTRACT

Adult dragonflies can be divided into two major groups, perchers and fliers, exhibiting notably different flight behaviour. Previous studies have yielded conflicting results regarding the link between the wing macro-morphology and flight style in these two groups. In this study, we present the first systematic investigation of the micro-morphological differences of wings of percher and flier dragonflies in four closely related species from the family Libellulidae. Our results suggest that the shape and material composition of wing microstructural components and, in particular, the nodus are adapted to facilitate the specific wing functioning in fliers and perchers. The findings further indicate a decreasing trend in the area proportion of the soft resilin-dominated cuticle in the nodus in the series of species from typical perchers to typical fliers. Such a reduction in the resilin proportion in the nodus of fliers is associated with an increase in the wing aspect ratio. The knot-shaped protrusion at the nodus of perchers, which becomes notably smaller in that of strong fliers, is likely to act as a mechanical stopper, avoiding large wing displacements. This study aims to develop a novel framework for future research on the relationship between wing morphology and flight behaviour in dragonflies.

1. Introduction

Dragonflies are known for their impressive flight performance (Marden, 2008). These insects are capable of a variety of flight speeds (May, 1991), modes (Azuma and Watanabe, 1988) and manoeuvres (Rüppell, 1989), which make them superior to many other flying insects (Sun et al., 2016). On the basis of their flight behaviour, dragonflies can be divided into two major groups: "perchers" and "fliers" (Corbet, 1962). As may be inferred from the name, perchers are those that usually perch during active periods and fly over short distances. In contrast, fliers spend most of the time in flight and rest only for short periods of time.

Contradictory data can be found in the literature regarding the relationship between the wing morphology and flight behaviour of perchers and fliers. The pioneering study of May, (1981a) showed significant differences in macro-morphology of wings between these two groups. He reported a tendency in wings of flier species to become longer and narrower, compared to those of perchers with a similar size. However, Wakeling (1997) found no significant difference in wing macro-morphological characteristics between these two groups.

It has been suggested that the flight style of insects has a close relationship with the lift production capacity of their wings (Rajabi et al., 2016a). Not only in dragonflies, but also in many other flying insects, the aerodynamic lift generation is strongly influenced by wing deformability (Mountcastle and Combes, 2013; Nakata and Liu, 2011; Walker et al., 2009). Deformations experienced by dragonfly wings during flight are known to be essentially controlled by wing microstructural components (Newman, 1982; Wootton, 1981; Rajabi et al., 2016a–d). Hence, it is plausible to hypothesise that wing micro-components in dragonflies having different flight behaviour may be adapted in different ways to result in certain wing deformations.

Here, in order to assess the presence of such adaptations, we comparatively study the wing micro-morphology in percher and flier dragonflies. We utilize modern imaging techniques to investigate the microstructure and material composition of a specialized wing component, the nodus (Fig. 1). This microstructural element is known to contribute to the wing twisting and, consequently,

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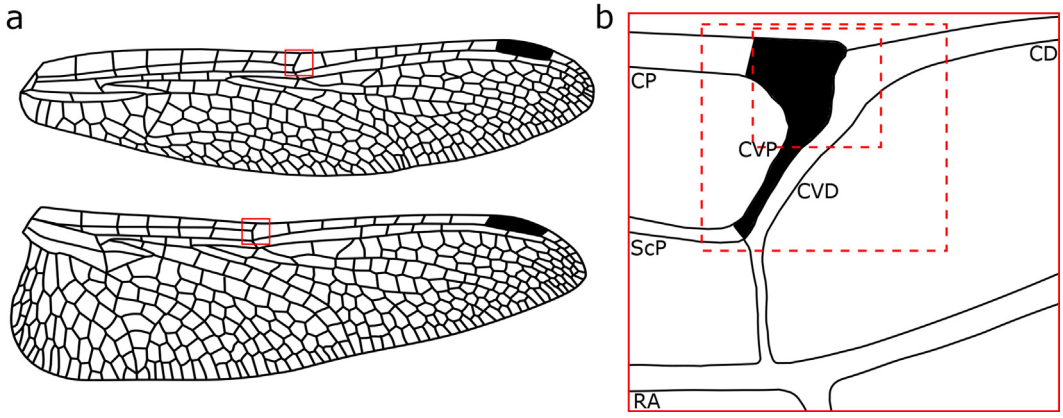

Fig. 1. (a) The fore- and hindwing of the dragonfly *C. servilia*. The red boxes show the position of the nodus in the wings. (b) A magnified view illustrating the nodus and adjacent areas. The region painted black represents the area in which measurements were performed. The small and large dashed boxes show the regions examined in SEM and CLSM, respectively. CD, distal costal vein; CP, proximal costal vein; CVD, distal nodal cross vein; CVP, proximal nodal cross vein; RA, anterior radial vein; ScP, posterior subcostal vein. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

formation of a cambered section in flight (Rajabi et al., 2017; Wootton and Newman, 2008). Hence, considering the role that the nodus plays in wing aerodynamics, it is expected that differences in wings of perchers and fliers, if any, are also reflected in the micro-morphology of this element. Four members of the family Libellulidae (Odonata: Anisoptera) were chosen as model studies. The selected species are known to have different flight behaviour, ranging from a typical percher with very small territories to a strongly-specialized flier.

2. Materials and methods

2.1. Sample preparation

The dragonflies *Acisoma panorpoides*, *Brachythemis contaminata*, *Crocothemis servilia* and *Pantala flavescens*, all belonging to the family Libellulidae, were selected as model species (Fig. 2). The specimens were collected in Nanjing (China) in August 2015 and were euthanized using CO_2. For microscopy studies, three adult male individuals

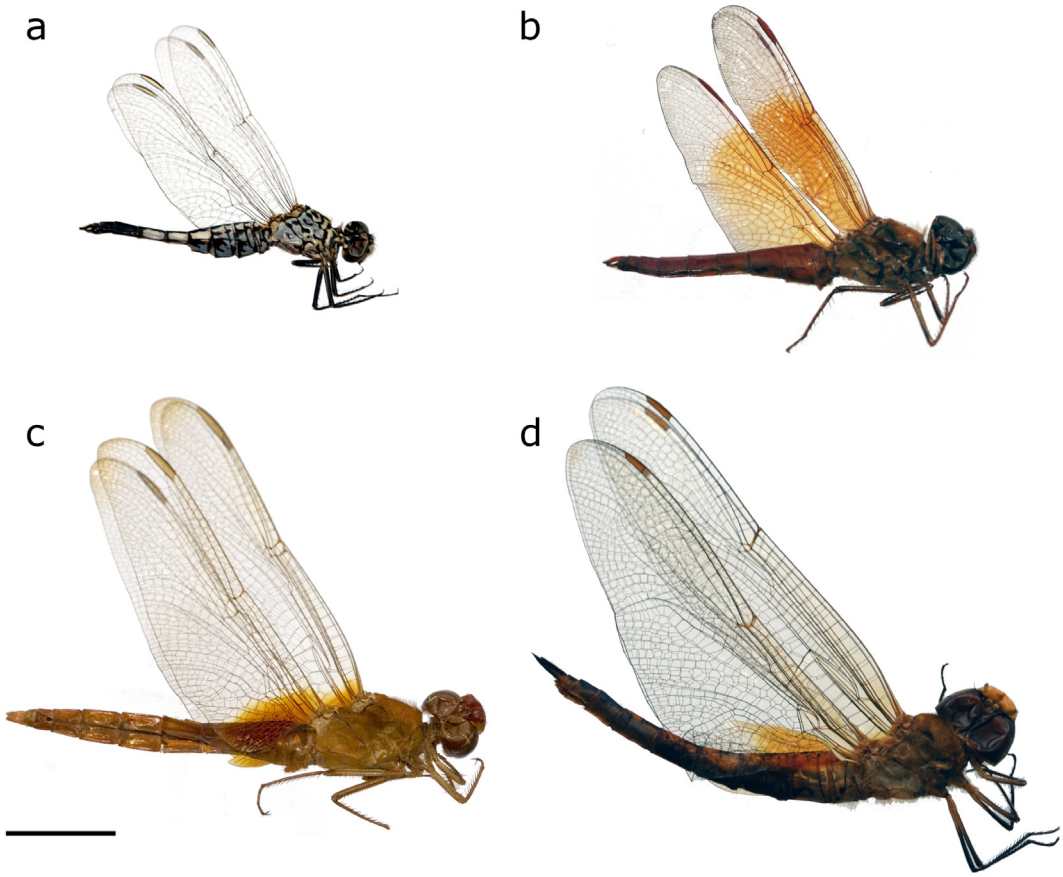

Fig. 2. Four members of the family Libellulidae selected for this study: (a) *A. panorpoides* is a typical percher showing a "temporal" territorial behaviour. (b) *B. contaminata* is an active percher. (c) *C. servilia* is a territorial percher, but under certain circumstances behaves as a flier. (d) *P. flavescens* is a typical flier. Scale bar: 1 cm.