Structural diversity and functional morphology of the damselfly ligula: implications for taxonomy, systematics and evolutionary biology

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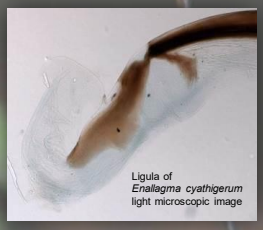
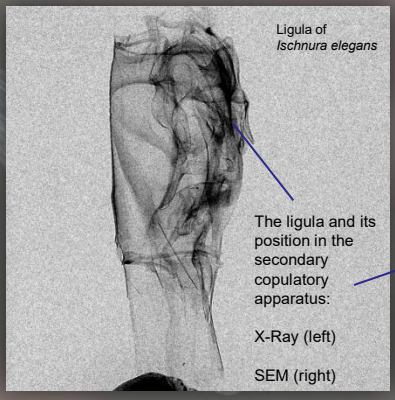
Diversity and evolution of animal genitalia have intrigued systematic and evolutionary biologists for a long time. Particularly in arthropods, male genitalia often provide the only reliable diagnostic characters available for distinguishing species suggesting that they evolve much more rapidly than other morphological characters.

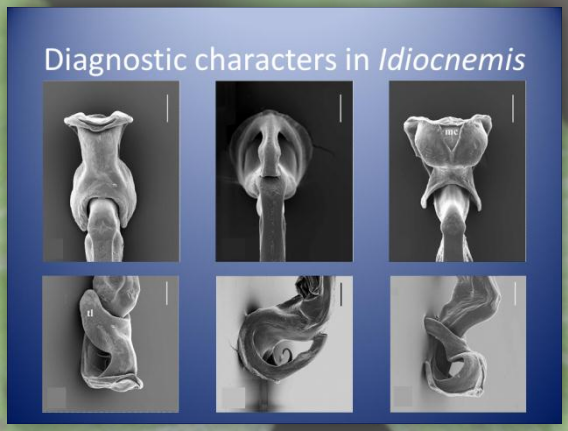
The **ligula or secondary penis** of the male damselfly (Odonata: Zygoptera) is a multifunctional structure primarily designed for sperm transfer and supposedly - in many species – for sperm removal (Cordero-Rivera, 2010). Since Waage (1979), for the first time, had provided evidence for the occurrence of sperm competition in calopterygid damselflies, several further cases and mechanisms of sperm competition in Odonata have become known. However, the diversity and variation of these functional morphological traits is largely unknown for many groups of Zygoptera, and the underlying mechanisms are poorly understood.

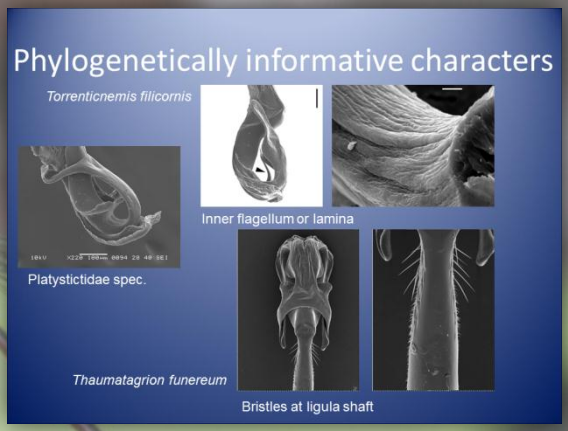
In the course of phylogenetic-taxonomic projects on damselflies, scanning electron microscopic (SEM) studies of the male secondary copulatory apparatus in the damselfly families Coenagrionidae, Platycnemididae, Platystictidae and Argiolestidae and others were performed, providing new insights with regard to the amazing structural diversity of the zygopteran ligula.

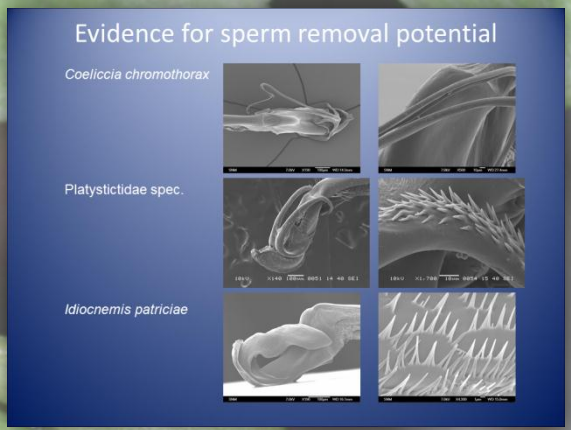




In many groups of damselflies, the ligula provides **diagnostic and taxonomic characters** that may be used to recognize and distinguish between different species. Often the species of those groups are rather similar with regard to secondary sexual characters such as the male posterior appendages, or to colouration. In contrast, species that have uniform ligulae usually are more diverse in other character complexes, suggesting that different selective forces are in effect among zygopteran genera and families, or that there is selection pressure on different character complexes. Different ligula types within a group of closely related species have also been referred to different mating systems (Robinson & Novak, 1997). The evolution of different mechanisms of sperm competition even within allopatric populations of the same species may be an important factor triggering speciation (Cordero-Rivera et al., 2004). The ligula also provides **phylogenetically informative characters**. In platystictid damselflies, the morphological and presumably functional diversity is high, but the ligula may be fairly constant at species-group level. In Platycnemididae, the inner flagellum of the ligula head is a particular structure characterizing a large clade of Papuan representatives of this family. The lack of spines on the ligula shaft is an autapomorphy of Platycnemidiae (Gassmann, 2005).







Sperm competition may be considered widespread in the Zygoptera. Sperm removal potential can be derived from several kinds of morphological structures, the most 'obvious' of them being the comb-like arrangements of micro-spines found on different parts of the ligula (Gassmann, 2007). But also hollowed flagellae, spoon-shaped lobes and other structures may be suitable for males to remove the sperm of competitors from the female spermathecae. **Sexual conflict**, i.e. the battle between the sexes over the control of fertilization, is largely held responsible for divergence in genital structures. Several candidate structures were identified in damselflies. Males of diverse groups in the superfamily Megapodagrionidea have the ligula armed with fields or arrays of seemingly robust spines. Some Coenagrionidae possess knife-shaped structures that may be considered harmful for the female genital tract and therefore suitable for preventing other males from successfully inseminating the female after the first copulation.

Research perspectives from studying the diversity of structures of the odonate secondary copulatory apparatus touch the areas of taxonomy, systematics, evolutionary biology, functional morphology and even biomechanics. The correspondence between the ligula structure and other sexual characters with particular mating systems might prove rewarding for estimating the behavioral ecology of a species. The study of (functional) diversity contributes to our understanding of speciation processes in the Odonata, and the apparently passive movability of the ligula is subject to current functional-morphological and biomechanical research (ongoing research in cooperation with the Functional Morphology and Biomechanics Group at Kiel University, Germany).

References
Cordero-Rivera, A., Andre, J.A., Cordoba-Aguilar, A. & Utzeri, C. (2004). Postmating sexual selection: allopatric evolution of sperm competition mechanisms and genital morphology in calopterygid damselflies (Insecta: Odonata). *Evolution*, 58(2), pp. 349–359.
Cordero-Rivera, A. & Cordoba-Aguilar, A. (2010). Selective forces propelling genitalic evolution in Odonata. In: Leonard, J. & Cordoba-Aguilar, A. (eds): The evolution of primary sexual characters in animals. Oxford University Press. Eberhard, W.G. Evolution of genitalia: theories, evidence and new directions. *Genetica* 138: 5-18.
Gassmann, D. (2007). Die Ligula der Kleinlibellen im Rasterelektronenmikroskop--Morphologische Strukturen und evolutionsbiologische Bedeutung. *Mikrokosmos*, 96(3), 183-187.
Gassmann, D. (2005): The phylogeny of Southeast Asian and Indo-Pacific Calicnemiinae (Odonata:Platycnemididae). *Bonner Zoologische Beiträge* 53(1/2): 37-80.
Robinson, J.V. & Novak, K.L. (1997). The relationship between mating system and penis morphology in ischnuran damselflies. *Biological Journal of the Linnean Society* 60: 187-200.
Waage, J.K. (1979). Dual function of the damselfly penis: sperm removal and transfer. *Science* 203: 916-918.