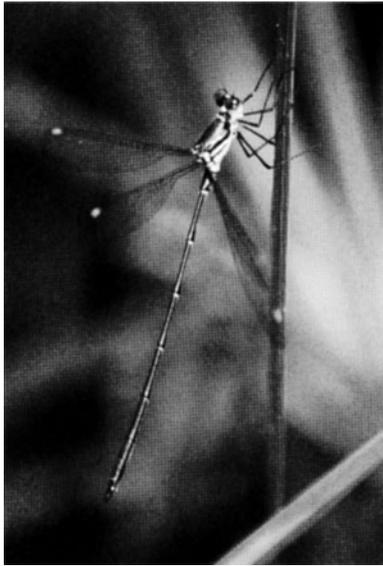


## Forum:

### Openwing perching in Zygoptera

K. Reinhardt: Open questions in the evolution of openwing perching in the Zygoptera (Odonata): a comment on Dennis Paulson — 103-109

D. R. Paulson: Openwing perching in some Zygoptera (Odonata): a response to Klaus Reinhardt — 111-118



One of the robust metallic green synlestids, *Synlestes weyersii*, is common on eastern Australian streams. Victoria, Eurobin Creek; 11 January 2003; photo by Netta Smith.

## Open questions in the evolution of opening perching in the Zygoptera (Odonata): a comment on Dennis Paulson

Klaus Reinhardt

Department of Animal and Plant Sciences, University of Sheffield,  
Sheffield S10 2TN, UK.  
<k.reinhardt@sheffield.ac.uk>

Key words: Odonata, dragonfly, foraging, perching, thermoregulation.

### ABSTRACT

In a recent paper D.R. Paulson (2004; IJO 7: 505-515) presented five hypotheses concerning the way wings are held in the Zygoptera during perching. A critical examination suggests that most of them have substantial flaws that prevent their testing. Based on Bechly's phylogeny (1998; <<http://www.bechly.de/system.htm>>) I suggest that the wing perching mode in the Odonata has changed five or six times, depending on whether the ancestral situation in the Odonata was closed-wing or opening perching, respectively. Combining parts of Paulson's hypotheses into a more plastic cost-benefit framework is suggested as an alternative approach, such as the investigation of possible trade-offs between thermoregulatory and foraging benefits and costly predation risk.

### INTRODUCTION

Paulson (2004), hereafter Paulson, directed attention to the opening perching behaviour (OWP) by some Zygoptera. Paulson summarised several observations and suggestions by previous authors and awarded them formally the rank of hypotheses. I will argue here that many of these may require additional observations, experimental manipulations, a phylogenetic approach and a more thorough treatment of the literature (see below).

Paulson (p. 506) defined OWP as follows: the species must perch with wings spread nearly or completely to the horizontal, at least some of the time. Therefore, the observation of a single individual with one incidental opening posture (such as in *Calopteryx*) will be classified as OWP (although it is unclear whether Paulson did classify the opening roosting by calopterygids as OWP in his paper). In the Coenagrionidae it is very difficult to decide whether a wing position is open or half-open (Sternberg & Buchwald 1999: 248, 272, 369, 370; see also p. 380 for an example of the Lestidae). Excluding such wing positions is problematic because some of the functions related to OWP, such as thermoregulation, will favour plasticity in wing posture.

Perching is more difficult to define than the wing posture itself. It may be applied to a behaviour of individuals sitting on a landmark in order to wait for prey or for mates. Wing posture during behaviours that Paulson later discussed under opening or closedwing 'resting' (e.g. p. 512) such as individuals inflating their wings with hemolymph after emergence, open wings during underwater oviposition or of dying individuals (p. 512) do not appear to fall under the category 'perching'. I conclude that erecting and testing hypotheses regarding the origin and maintenance of OWP requires tighter definitions than those provided by Paulson.

However, even when excluding the latter types of openwing postures from further discussion a number of questions remain as to the validity of erecting and testing Paulson's hypotheses. I will deal with each of them separately before suggesting that parts of them can be combined into a framework that is open to rigorous testing.

### PHYLOGENETIC INERTIA HYPOTHESIS

Paulson rejects this hypothesis because OWP and closedwing perching (CWP) are scattered across the Zygoptera and OWP presumably arose independently in more than one of the three zygopteran superfamilies. This, however, is not contrary to the notion that it might be phylogenetically constrained (i.e. phylogenetic 'inert'). I suggest that the lack of a phylogenetic approach and a lack of testable predictions makes Paulson's rejection of this hypothesis invalid. In fact, using the examples mentioned by Paulson and mapping them on Bechly's (1998) phylogenetic tree (Fig. 1) results in two evolutionary scenarios. Given that the sister group of extant Odonata, the Ephemeroptera, keep their wings folded when perched (e.g. Dettner & Peters 1999: 777), OWP might be the derived situation. If OWP is an apomorphy in the Odonata, CWP must have evolved five times – in the Chlorocyphidae, Calopterygidae, *Hemiphlebia*, Sympecmatinae, and the Coenagrionomorpha (nomenclature sensu Bechly 1998). If one assumes that the ancestral Odonata showed CWP, six events require explanation: the evolution of OWP in the Amphipterygida, Euphaeidae, Lestida, Megapodagrionidae and Anisoptera, as well as the rise of CWP (or reduction of OWP) in the Sympecmatinae. If the opening posture of *Calopteryx* represents OWP, one additional loss of OWP would have to be explained in its sister taxon *Hetaerina*. Furthermore, if Tillyard's (1917) observation of closedwing posture in *Lestes* is a case of CWP and the questionable observation of OWP in the Megalestinae holds true, the reduction of OWP might have taken place at an earlier stage (cf. Fig. 1). The ancestral state of wing holding will not be easy to reconstruct as the common ancestor of the Ephemeroptera and the Odonata, the Palaeodictyopteroidea, are extinct.

Phylogenies better resolved than that by Bechly (1998) will doubtless alter our understanding in this area, such as when adopting the view of an Anisoptera + Lestoidea clade (e.g. Saux et al. 2003). However, a comparison of the costs and benefits of OWP in the sister taxa Sympecmatinae + Lestinae, as well as the Euphaeidae + *Hetaerina* (and *Calopteryx*) may be a fruitful start for addressing phylogenetic constraints on OWP, because it is lost once under any scenario.

## WING DISPLAY HYPOTHESIS

The suggestion that OWP is related to wing display requires that wing display does occur from a perch. This assumption was not tested. However, most wing displays in the Zygotera, and indeed in the insect world, take place on the wing (see the many examples on *Calopteryx*; Ruppell et al. 2005) rather than from a perch. Unless display is shown to take place from a perch at all (H. Wildermuth [pers. comm.] mentions to me an example in *Calopteryx splendens* [Harris]) it remains irrelevant to the relationship between wing display and perch posture that wings are broader in families with coloured wings (p. 506) (see also Ruppell et al. 2005: 89 for a similar suggestion), and that “no openwing zygoteran with uncolored wings ... uses its wings for display” (p. 508). It is clearly a difficulty to definitely assign any observed pattern to the perching posture. For example, Ruppell et al. (2005: 89) clearly point out that many selection pressures will act on the wing colour and form. These are, however, not necessarily related to perch posture.

In his Wing Display Hypothesis it is also unclear whether Paulson considered the UV pattern on the wings (Hilton 1986) as “colourful” wings given the ability of Zygotera or Odonata to perceive UV light.

## QUICK TAKEOFF HYPOTHESIS

Paulson ascribes an advantage of OWP to the Zygotera because “almost all Anisoptera utilize it” (p. 507). This argument is not compelling because OWP in the Anisoptera is likely to originate from a single evolutionary event (Fig. 1). It is, therefore, more parsimonious to assume that OWP in the Anisoptera is maintained by (phylo)genetic constraints rather than by repeated selective benefits. Paulson makes two predictions concerning the foraging behaviour: (1) in OWP Zygotera there is a faster takeoff and/or a faster adjustment of the flight direction than in CWP Zygotera. Therefore (2) OWP species will typically forage by sallying, CWP species by gleaning. The latter prediction has a number of problems. First, it rests on support for the first prediction. Second, a faster takeoff by OWP zygoterans does, in my opinion, not predict that gleaning species perform CWP. Finally, and most importantly, I suggest that the prediction is the reverse from Paulson’s prediction. If OWP is suggested to provide a benefit to sallying then one would predict that sallying species should perform OWP more often than gleaners but not necessarily that OWP species sally more often than CWP.

Paulson suggests he found evidence for his hypothesis in the lack of robust evidence against it. In order to test its first prediction he cited a third investigator showing that two species differing in wing holding posture on the perch had different takeoff times. However, it was not shown how the takeoff time – that is the time between the prey signal input to the brain and the takeoff response – was measured. Perhaps more relevant is the time between takeoff and actual prey capture; note that this prey pursuit time was suggested by Miller (1995: 25) to be related to thermoregulation – see Thermoregulation Hypothesis. The two species cited by Paulson to differ in takeoff times (a coenagrionid and a lestid) are phylogenetically quite distant and will differ in many biological aspects in addition to wing holding.

In my opinion, this poor support for his first prediction would preclude testing its follow-up prediction. By testing the second prediction nevertheless, Paulson finds that among 36 genera OWP and gleaning are less often associated than expected by chance (though his table 2 only shows 35 genera – perhaps *Pseudagrion* was included in two categories?). I have three objections to his conclusion. First, 39% of the genera are from a single family, the Coenagrionidae, for which OWP likely represents only one evolutionary event (Fig. 1) and thus pseudoreplications. Second, I suggest the strong support to be reconsidered. Twenty out of 35 genera refer to Paulson's own unpublished observations (Paulson's table 2), 16 of which support his Quick Takeoff Hypothesis (openwing perchers sallying, closedwing perchers gleaning). These unpublished examples agree with published observation in three out of five cases (*Ischnura*: Parr & Parr 1996; *Enallagma*: van den Berg 1993; *Hetaerina*: Dunkle 1990: 31) but disagree in one, perhaps two: lestids are reported to both sally and glean (Jödicke 1997). The opening posture of calopterygids (see examples cited in Ruppell et al. 2005: 43-44) is discussed several times (e.g. Paulson, pp. 507, 510) but not included in his table 3 – so it remains unclear whether calopterygids were included as OWP by Paulson. Third, during a rather superficial search I found two further examples, all counter to Paulson's observations: *Mortonagrion* and *Platycnemis* employ midair foraging (Corbet 1999: 356) but show CWP (e.g. Wilson 1995: 90-91; Martens 1996: pl. 1). Both disagreeing examples are from sources cited by him earlier (Wilson 1995; Corbet 1999). Taken together I suggest that Paulson's Quick Takeoff Hypothesis needs reconsideration before erecting it and derive testable predictions.

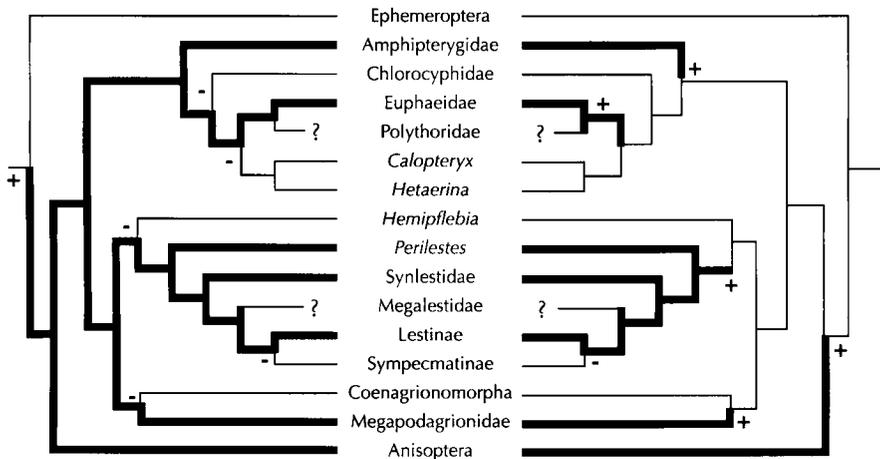


Figure 1: Phylogenetic distribution of openwing perching in the Odonata — thick lines indicate the presence of the trait, thin lines its absence, '+' refers to a presumed evolutionary novelty, '-' to an evolutionary loss of openwing perching (or the occurrence of CWP). See text for further explanations.

## SHINY WING HYPOTHESIS

Paulson “hypothesize[s] that wings, although transparent, are likely to reflect sunlight and therefore, make their bearer more conspicuous to predators” (p. 507). He (p. 508) additionally assumes that predation risk is larger for smaller species and that larger bodied species more often employ OWP (although his supporting table 1 does not contain measurements of wing or body size). Because Zygoptera are generally smaller than Anisoptera, Paulson suggests the Zygoptera to attract a greater diversity of predators. This suggestion needs additional explanation as well as rigorous testing given (1) that the shiny area of wings was not obviously correlated to body size across species (e.g. Hilton 1986) and (2) there is no obvious theoretical reason why predation risk should be related to the number of predator species.

Paulson states that “zygopterans that are conspicuous because of wing position may be at greater risk from aerial predators than are anisopterans that are conspicuous for the same reasons” (p. 508) because Anisoptera “have a greater chance of escaping a predation attempt” (p. 508). This is reasonable only if predators are avoided by escape flight rather than, as later mentioned by Paulson, by closing the wings, or remaining motionless, as seen in *Calopteryx maculata* (Beauvois) upon the arrival of the aerial predator *Hagenius brevistylus* Selys (Dunkle 1990: 22). In his supportive evidence Paulson then neglects his predicted relationship between conspicuousness and wing holding within the Zygoptera because he compares all Zygoptera against all Anisoptera, not just their OPW representatives: “odonate collectors know that Anisoptera are harder to catch than Zygoptera” (p. 508). In addition, human collectors are a very poor representative of the visual spectra and foraging speed of odonate hunting falcons, swallows, bee-eaters and odonates.

The Shiny Wing Hypothesis predicts the opposite of the Wing Display Hypothesis, namely that large, colourfully winged species more often employ CWP (p. 511). It is unclear, then, how larger-winged species are more successful in distracting predators. Other supportive observations by Paulson are irrelevant to the Shiny Wing Hypothesis: the avoidance of male sexual approaches by females (see Corbet 1999: 471-472 for an extensive discussion), the wing transparency of two Anisoptera with CWP, the relationship between OWP and the maturation period (p. 512) or whether the abdomen is held below or between the wings.

## THERMOREGULATION HYPOTHESIS

Jacobs (1955) observed that anisopterans lower their wings when perching at high temperatures. Her suggestion that this behaviour serves to shade their thorax, i.e. lower thorax temperatures, was not supported experimentally in a libellulid (May 1976). Paulson used the latter study to reject the Thermoregulation Hypothesis but did not consider Miller’s (1995: 25) suggestion that warm air trapped under the lowered wings may keep the thorax temperature high and thus allow rapid flight. In any case, the relationship between wing lowering in the Anisoptera and OWP in the Zygoptera should be addressed before rejecting the Thermoregulation Hypothesis for OWP in the Zygoptera. For example, heat gain by OWP in the Zygoptera at cool temperatures would be the opposite effect of body cooling (if any) by thorax shading as found in the Anisoptera. In sun-perchers CWP may assist in avoiding

overheating and this may indeed be of thermoregulatory significance. By contrast, Paulson suggests that “if open wings were involved in thermoregulation, they should occur in zygopterans that normally perch in the sun” (p. 510).

I propose that OWP functions suggested to be related to the Shiny Wing and Quick Takeoff Hypotheses should be tested for their thermoregulatory significance in the Zygoptera. At several places, Corbet (1999) provides substantial evidence for it. Paulson predicted that because sunlight reflection makes wings more conspicuous “zygopterans that usually perch in the shade are more likely to use the openwing position than those usually perching in the sun” (p. 508). This statement, opposite to his other hypotheses (pp. 510, 512), does, in my but not in Paulson’s opinion, indicate a thermoregulatory function of OWP.

## CONCLUSION

Paulson put forward several interesting ideas for the function and evolution of OWP. After the above examination of his examples I suggest, however, that the erection of most of his hypotheses is not justified, and neither are the derivation of many of his predictions. I also argue that several of his examples do not represent tests of his predictions. As a consequence, I suggest that researchers do, at present, not accept the hypotheses and do not consider his tests as valid rejections of previously existing ideas. A preliminary analysis suggests that the wing perching mode in the Odonata has changed several times in evolutionary times. However, a clear definition of perching, a more rigorous phylogenetic approach and experimental studies should be used to build up a sufficient empirical base that justify the generation and testing of hypotheses. I suggest that future experimental work simultaneously addressing the costs of OWP in the form of predation risk and overheating with the benefits of body temperature optimisation, predator distraction and foraging success may be a fruitful starting point of experimental work. A second area that I suggest for further investigation is to study how taxa differ in their relaxed wing position, i.e. the wing posture achieved without muscle power. For example, Sternberg & Buchwald (1999: 194) suggest that at cold temperatures muscle relaxation leads to an openwing position. Thus, any energy required to hold the wings open or closed on a perch may have to be included into cost-benefit considerations. Such studies may be a contribution to Paulson’s aim that “The variation in wing position in both closedwing and openwing species is worthy of further consideration” (p. 513).

## ACKNOWLEDGEMENTS

This paper has seen quite substantial changes. I wish to thank the reviewers Frank Suhling and Hansruedi Wildermuth for agreeing and disagreeing remarks and additional comments.

## REFERENCES

- Bechly, G., 1998. Phylogenetic systematics of Odonata.  
 <<http://www.bechly.de/system.htm>>.
- Corbet, P.S., 1999. Dragonflies: behaviour and ecology of Odonata. Harley Books, Colchester.
- Dettner, K. & W. Peters, 1999. Lehrbuch der Entomologie. Gustav Fischer, Stuttgart.
- Dunkle, S.W., 1990. Damselflies of Florida, Bermuda and the Bahamas.  
 Scientific Publishers, Gainesville.
- Heymer, A., 1975. Der stammesgeschichtliche Aussagewert des Verhaltens der Libelle *Epallage fatime* Charp. 1840. Zeitschrift für Tierpsychologie 37: 163-181.
- Hilton, D.F.J., 1986. A survey of some Odonata for ultraviolet patterns.  
 Odonatologica 15: 335-345.
- Jacobs, M.E., 1955. Studies on territorialism and sexual selection in dragonflies.  
 Ecology 36: 566-586.
- Jödicke, R., 1997. Die Binsenjungfern und Winterlibellen Europas. Lestidae.  
 Westarp, Magdeburg.
- Martens, A., 1996. Die Federlibellen Europas. Platycnemididae. Westarp, Magdeburg  
 & Spectrum, Heidelberg.
- May, M.L., 1976. Thermoregulation and adaptation to temperature in dragonflies  
 (Odonata: Anisoptera). Ecological Monographs 46: 1-32.
- Miller, P.L., 1995. Dragonflies. The Richmond Publishing, Slough.
- Parr, M.J. & M. Parr, 1996. Risky gleaning behaviour by *Ischnura elegans* (Vander L.)  
 (Zygoptera: Coenagrionidae). Notulae Odonatologicae 4: 124.
- Paulson, D.R., 2004. Why do some zygopterans (Odonata) perch with open wings?  
 International Journal of Odonatology 7: 505-515.
- Rüppell, G., D. Hilfert-Rüppell, G. Rehfeldt & C. Schütte, 2005. Die Prachtlibellen  
 Europas. Gattung Calopteryx. Westarp, Hohenwarsleben.
- Saux, C., C. Simon & G.S. Spicer, 2003. Phylogeny of the dragonfly and damselfly  
 order Odonata as inferred by mitochondrial 12S ribosomal RNA sequences.  
 Annals of the Entomological Society of America 96: 693-393.
- Sternberg, K. & R. Buchwald, 1999. Die Libellen Baden-Württembergs, Band 1.  
 Allgemeiner Teil; Kleinlibellen (Zygoptera). Ulmer, Stuttgart.
- Tillyard, R.J., 1917. The biology of dragonflies. Cambridge University Press, Cambridge, UK.
- van den Berg, M.A., 1993. *Enallagma glaucum* (Burmeister), a newly recorded predator of  
 the citrus psylla, *Trioza erytrae* (Del Guercio) (Zygoptera: Coenagrionidae; – Hemiptera:  
 Triozidae). Notulae Odonatologicae 4: 29-31.
- Wildermuth, H., 1994. Reproductive behaviour of *Diastatops intensa* Montgomery (Aniso-  
 ptera: Libellulidae). Odonatologica 23: 183-191.
- Wilson, K.D.P., 1995. Hong Kong dragonflies. Urban Council, Hong Kong.