

On flying insect size and Phanerozoic atmospheric oxygen

In a recent article in PNAS, Clapham and Karr (1) related the maximum wing length (MWL) of different Odonoptera and Orthoptera species to Phanerozoic atmospheric oxygen partial pressure (pO_2) as predicted by the GEOCARBSULF model (2). They argued that the MWL data assigned to 10-Myr periods is well correlated with elevated Paleozoic pO_2 levels, but that the correlation weakens and is ultimately decoupled during the Mesozoic and Cenozoic. To explain the correlation, they assumed that maximum insect size is constrained by a tracheal oxygen supply limit. To explain the decoupling, they referred to the notion that insect size increase results in reduction of flight maneuverability and increased aerial predation by birds (among others), i.e., a selective pressure against size increase also operates. This convenient mixed hypothesis deserves scrutiny.

First, the correlation presented (1) has several prominent exceptions that are not explained. For example, the large prothopteran, *Clathrotitan sculli* (*Cs*), from Australian Anisian beds (243–238 Myr), coincides with the bottom of the first pO_2 trough predicted by GEOCARBSULF after the late Permian oxygen crisis (Fig. 1).

Second, if a good correlation between MWL and Paleozoic pO_2 is accepted, an alternative explanation is offered by consideration of the dependence of insect flight power on atmospheric density. Using simple flight mechanics theory, minimum hover and cruise power vary with the inverse square root of density, i.e., hyperbaric atmospheric conditions permit reduced flight energy expenditure (3).

Third, in the absence of aerial predation, the emergence of the gigantic Meganisoptera during the Carboniferous and Permian does not necessarily require elevated pO_2 levels when it is assumed that these ancient Odonoptera were weak fliers with relatively low specific maximum power outputs compared with extant Anisoptera (Odonata).

Fourth, extant Anisoptera are capable of lifting loads exceeding their own weight during hover (4), indicating substantial power reserves. Large extant aeshnids have also been recorded flying at more than 2,500 m altitude above sea level (5). Therefore, at low altitude, extant Anisoptera must have wide oxygen supply margins when operating in their usual aerobic flight modes. Following Clapham and Karr (1), the hypothetical removal of aerial predation would result in evolving size increase. However, at the present pO_2 level, scale-up by one order

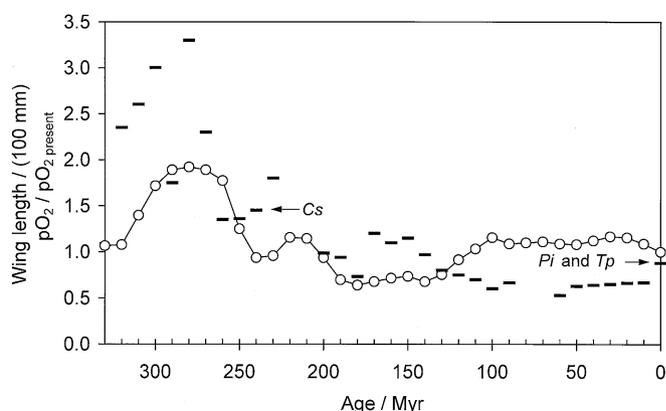


Fig. 1. Phanerozoic pO_2 (white circles) as predicted by Berner (2) and MWLs (black horizontal lines) based on data from Clapham and Karr (1), including *C. sculli* (*Cs*), with additional values for two extant species, *P. ingentissima* (*Pi*) and *T. plagiata* (*Tp*). Hind-wing lengths of these extant species (84–86 mm) were established by using specimens stored in the Natural History Museum (London, United Kingdom) and the Davies Collection held at the University of Cambridge (Cambridge, United Kingdom).

of magnitude would be permissible before the tracheal surface area constrains maximum feasible size.

Fifth, there is no evidence that the evasive maneuver capability of extant Anisoptera reduces as body size increases. Territorial dogfights among conspecific males tend to select larger individuals with good maneuverability and higher maximum flight speeds (5).

Finally, the MWL history presented (1) is reproduced in Fig. 1 with an important difference: two anisopteran species (5), *Petalura ingentissima* (*Pi*) and *Tetracanthagyna plagiata* (*Tp*), have been included. There is no evidence that these large extant species evolved during any relaxation of aerial predation over the past 10 Myr. A more credible proposition is that the fossil record represented in Fig. 1 is incomplete. The correlation reported by Clapham and Karr (1) would then be premature.

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