

COMMENTARY

The engineering of the giant dragonflies of the Permian: revised body mass, power, air supply, thermoregulation and the role of air density

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ABSTRACT

An engineering examination of allometric and analogical data on the flight of giant Permian insects (Protodonata, *Meganeura* or griffinflies) indicates that previous estimates of the body mass of these insects are too low and that the largest of these insects (wingspan of 70 cm or more) would have had a mass of 100–150 g, several times greater than previously thought. Here, the power needed to generate lift and fly at the speeds typical of modern large dragonflies is examined together with the metabolic rate and subsequent heat generated by the thoracic muscles. This evaluation agrees with previous work suggesting that the larger specimens would rapidly overheat in the high ambient temperatures assumed in the Permian. Various extant mechanisms of thermoregulation are modelled and quantified, including behaviour, radiation and the constraints on convective respiration and evaporation imposed by air flow through spiracles. However, the effects of these on cooling an overheated insect are found to be limited. Instead, an examination of the heat budget in the flight medium indicates that, at about 1.6 bar (160 kPa), thermoregulation supply enters into equilibrium and, even at high ambient temperatures, overheating can be avoided and enough oxygen sourced. This approach indicates how fossil biology can be used to examine past atmospheres.

KEY WORDS: Protodonata, Flight, Meganeura, Atmospheric density

Introduction

It has long been considered that increased oxygen atmospheric concentrations removed a constraint on the increasing body size of the giant dragonflies of the Permian, the concept being that the limits to insect body size imposed by tracheal diffusion can rise as oxygen partial pressure increases (Dudley, 1998). This engineering review analyses body mass, power, respiration and thermoregulation of Protodonata (*Meganeura*) in order to re-examine their giant size in relation to modern species and proposes a possible relationship between the atmospheric composition and pressure in which they lived.

Meganeura were not slender creatures. Fig. 1, a mould from an original fossil in the Musée National d'Histoire Naturelle, Toulouse, France, of a *Meganeura monyi* with an estimated wingspan of 35 cm, clearly shows the thick body parts of the thorax and abdomen. *Namurotypus*, of which one German specimen with an estimated wingspan of 32 cm is partially preserved in semi-transparent rock, also shows a thorax similar in width to the

abdomen as well as spiny and surprisingly robust legs. Illustrations of *M. monyi* and a female *Meganeurula selysii* (Shear and Kukalova-Peck, 1990) also indicate creatures with strong mouth parts, well-developed pincers and strong long thick legs. In both drawings, the abdomen is similar in diameter to the thorax, unlike the structure of most modern dragonflies, which have much more slender abdomens. This large size – and consequently high mass – has attracted attention for over a hundred years as there are no extant insects of this size and their physiology in terms of power generation and thermoregulation is not understood. This Commentary examines the questions of mass, power generation to fly and hover, respiration and possible forms of thermoregulation of the largest of these creatures, including the effects of a higher atmospheric pressure in this era.

Body mass: allotropy and analogy

A review of the allometric scaling of body volume and wing length for Odonoptera, Orthoptera and Neuroptera (Clapham and Karr, 2012) shows that the best-fit major axis regression lines for extinct fossil Odonata is: $\log(\text{body volume}) = 2.661 \log(\text{wing length})^{-1.108}$, where body volume is in mm^3 and wing length is in mm.

This regression line is shown in Fig. 2, along with data for the extant species of Odonata shown in Table 1 (May, 1982, 1991; Jongerius and Lentink, 2010), including the largest petaltail petularid, allocated a mass of 2 g (considered to be a 'rather reasonable' value for *Petalura ingentissima* by G. Theischinger, personal communication). As Odonoptera have maintained their body shape (and even basic DNA) since the early Jurassic or before (May, 1982; Kohli et al., 2016; Bybee et al., 2016), this relationship appears to be still valid for a wide range of body masses for extant species and thus can also be used to estimate the volume of *Meganeura*. The wing length of *M. monyi*, 350 mm (Table 1), is taken from the span of 700 mm quoted by Clapham and Karr (2012) and 710 mm for *Meganeuropsis permiana* (Vermeij, 2016); the wing length of *Namurotypus* is based on the average span for the two German fossils.

The ratio of mass/volume follows that of most insects – smaller species having a higher density as trachea volume is reduced (Harrison et al., 2010). Using a deliberately low specific density of 0.3 for *Meganeura*, the volume estimate for *M. monyi* from this regression line results in a mass of 138 g, equivalent to the volume of a cylinder 40 mm in diameter and 350 mm in length, (body length = wing length, with similar diameter for thorax and abdomen).

The estimated volume of *Namurotypus*, $60,000 \text{ mm}^3$, based on a wing length of 165 mm, equivalent to the volume of a cylinder of 22 mm in diameter and 150 mm in length, results in a mass of 18 g based on the same density. The legs of *Namurotypus*, 50 mm in length (as seen in the rock) and taken as 3 mm tubes of exoskeleton and muscle, could account for around 2 g, given that exoskeletal

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Glossary**Black body**

A black body is a theoretically ideal radiator and absorber of energy at all electromagnetic wavelengths. The term comes from the fact that a cold black body appears visually black. The energy emitted is called black body radiation.

GEOCARBSULF model

This is a model for the combined long-term cycles of carbon and sulfur that combines all the factors modifying weathering and degassing, a revised model of atmospheric CO₂ over Phanerozoic time and an isotope mass balance model for O₂, thus allowing atmospheric O₂ to be estimated over Phanerozoic time.

Hypobaric

A hypobaric chamber is used to simulate the effects of altitude, especially hypoxia (low oxygen) and hypobaria (low ambient air pressure).

Normobaric

Atmospheric pressure at sea level.

P_{O₂}

Partial pressure of oxygen. In a mixture of gases, each gas has a partial pressure which is the notional pressure of that gas if it alone occupied the entire volume of the original mixture at the same temperature. The partial pressure of a gas is a measure of thermodynamic activity of the gas's molecules; gases dissolve, diffuse and react according to their partial pressures, and not according to their concentrations in gas mixtures or liquids. This general property of gases is also true in chemical reactions of gases in biology.

Specific enthalpy

Specific enthalpy is the total energy in a system due to pressure and temperature per unit of mass in that system. Specific enthalpy is used in thermodynamic equations when one wants to know the energy for a given single unit mass of a substance. The SI units for specific enthalpy are kJ kg⁻¹.

Spiracle

An external respiratory opening on the body of an insect.

Stefan–Boltzmann law

The Stefan–Boltzmann law describes the power radiated from a black body in terms of its temperature. Specifically, this law states that the total energy radiated per unit surface area of a black body across all wavelengths per unit time (also known as the black body radiant emittance) is directly proportional to the fourth power of the black body's thermodynamic temperature.

Tracheae

The trachea are part of the respiratory system of insects. Air enters the insect's body via the spiracle to the trachea, which are tubes strengthened by rings of cuticle. From the trachea, the air moves into smaller tubes called tracheoles that spread throughout the body of the insect and allow oxygen to be delivered to the various parts of the body.

Viscosity

Informally, viscosity is the quantity that describes a fluid's resistance to flow. Fluids resist the relative motion of immersed objects through them as well as the motion of layers with differing velocities within them.

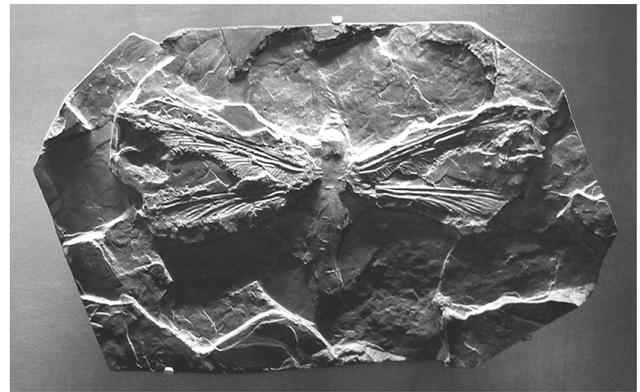


Fig. 1. Mould of a fossil Protodonata with a 35 cm wingspan. Late Carboniferous; Commentry, Allier, France. Musée d'Histoire Naturelle, Toulouse (photo credit: A.E.R.C.).

more primitive flying insects, Protodonata probably also had abdomens nearly as long as or longer than the wings (as indicated in Shear and Kukalova-Peck, 1990). However, despite showing that Protodonata wings are statistically indistinguishable from those of extant Anisoptera, May (1982) then makes the assumption that the wings of Protodonata were substantially larger relative to their bodies than in Odonata. By scaling up the thoracic data and assuming a short total body length, he thus makes a very conservative estimate of the mass of a 70 cm Protodonata at 17.8 g.

May (1982) was aware that this procedure might underestimate mass, as in Anisoptera subcuticular air spaces comprise 35–60% of the thoracic volume and provide thermal insulation of the flight muscles, as well as being important in ventilation of the tracheae (see Glossary).

The specimen of *Namurotypus* in semi-transparent rock exhibits a thorax that is comparable in diameter to the initial section of the abdomen and perhaps slightly longer than in extant species, and, in Shear and Kukalova-Peck (1990), body length can be seen to be similar to wing length, so these assumptions appear not to hold true.

Wings are made of dense cuticle with a relative density of 1.2 and are a structural element in which wing loading is a function of area – width (W) and length (L) – moment in engineering terms is a function of load \times length, and shear strength a function of width \times thickness (T). Thus:

$$\text{Moment} = f(L \times L \times W) \quad (1)$$

and

$$\text{Shear strength} = f(W \times T); \quad (2)$$

T therefore is a function of L^2W/W , or L^2 .

The total mass of *Sympetrum vulgatum* wings, as measured by Jongerius and Lentink (2010), was found to be 3.4 mg for an average wing length of 27 mm (fore and hind). Wing thickness to supply rigidity under loading should thus increase at a higher rate than wing length. However, if wings are taken to factor equally in all dimensions (L , W and T) and using the scale factor of chitin to body mass (Lease and Wolf, 2010), the mass of a 350 mm wing can be estimated using the cube of the ratio $350/27=12.96$. Thus, total wing mass of both pairs of the similar shaped wings of a Protodonata with wing length of 350 mm would have been $3.4 \times 12.963=7.5$ g. Wing to body mass ratios have usually been found to be between 0.5% and

chitin mass scales isometrically with dry body mass across the Insecta as well as for Odonata in particular (Lease and Wolf, 2010), and that both chitin and muscle have a relative density greater than 1 (Ellington, 1985). The mass predicted by May (1982) for *M. monyi* for a 350 mm wing length, however, results in a volume similar to that of *Namurotypus*, which when plotted on the log scale of Fig. 2 lies far below the allometric line for Odonatoptera.

In his examination of heat exchange in Meganeuridae, May (1982) makes it clear that his conclusions on their estimated mass are based on extrapolation from extant organisms, considering the evident close taxonomic and morphological relationship of protodonates to living dragonflies. May (1982) also considers that, as a long abdomen provides aerial stability and is the rule among the

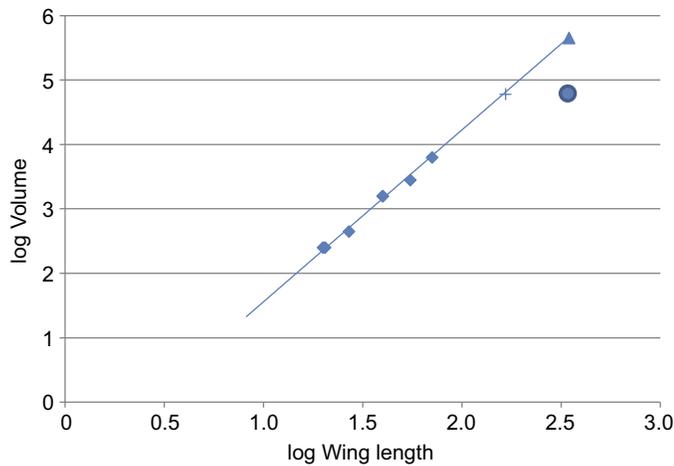


Fig. 2. Chart showing log–log plot of wing length and volume for the extant dragonflies given in Table 1 (diamonds). The regression line is the equation for extinct Odonata (Clapham and Karr, 2012), including calculated values for *Namurotypus* (plus sign) and *Meganeura monyi* (triangle). The value estimated by May (1982) is shown as a circle. Extant dragonfly data fit the regression line for the extinct species, suggesting that this relationship would be valid for the giant species.

5% of body mass (Ellington, 1985); taking the higher value of 5% as a constraint, total body mass for 7.5 g of wing cuticle would therefore be 150 g. Lease and Wolf (2010) also document that the isometric pattern found between chitin and body mass indicates that exoskeletal investment may not be the primary limit on insect body size. In other words, the existence of an exoskeleton is not a precondition for the present small size of insects.

A study of the flight of insects found that their design is very close to isometric over a 100,000-fold body mass (*m*) range, with wing area being proportional to $m^{0.667}$ on average; wingbeat frequency also increases as size decreases, scaling as $m^{-0.25}$ (Dudley, 2000). Hence, the wing area of the *M. monyi* reconstruction gives an estimated total mass of about 100 g when scaled to *A. junius*.

Bats have also evolved to hover and catch insects, and bat wingbeat frequency has been found to be a function of ($m^{-0.24}$), valid for a range of 1 g to 1 kg and very similar to the wingbeat scaling of insects (Norberg and Norberg, 2012). The relationship between mass and wingspan was also found to be strongly correlated: wingspan=1.295 $m^{0.334}$ (Norberg and Rayner, 1987).

Table 2 shows the corresponding mass and wingspan/2 for this relationship. The 5 cm wing lengths of *A. junius* and *M. taeniolata* (at approximately 1 g) and *Petalura ingentissima* at 2 g and wingspan of 14 cm closely match the bat data, suggesting that creatures obeying similar laws of flight have similar overall mass and size. With a wing length of 16.5 cm, *Namurotypus* could therefore be expected to have a mass of the order of 10 g, and a mass of 150 g would be compatible for *M. monyi*.

In summary, the allometric and analogical mass values for *Meganeura* with a wingspan of 70–71 cm are: (1) log wing length volume: 138 g (Clapham and Karr, 2012); (2) wing mass (5% of total mass constraint): 150 g; (3) wing area/ $m^{0.667}$ ratio: 100 g (Dudley, 2000); (4) bats (equivalent mass by wingspan): 150 g.

These values are much higher than the estimate of 17.8 g made by May (1982), yet, despite the stated reservations, this value for the largest *Meganeura* has ‘stuck’ and is often quoted in the literature (Heinrich, 1993) or in the low mass values reflected in the suggested wing loadings for *N. sippelorum* (Wootton and Kukalova-Peck, 2000), which are shown to be higher in larger Odonata (Worthen and Jones, 2006). This strange disparity can only be imagined as a very cautious and conservative effort to obtain a low mass, as trained biologists would already be aware that much heavier values contradict the physics and physiology of flying insects (see below).

As a final check on these estimates, a volume estimate for *M. monyi* can be made based on the illustrations made by Shear and Kukalova-Peck (1990). These show no insulating air sacs on the thorax and suggest a long wide and thick abdomen. When scaled for a wing length of 350 mm, this volume is similar to a cylinder 360 mm in length and 35 mm in diameter: 346 cm³. Taking the low density estimate of 0.3, this gives a mass of 104 g to which the mass of the wings can be added, giving a total body mass of 111.5 g; a density value of 0.4 gives a mass close to 150 g; and using the average measured density of *A. junius* of 0.63 (Table 1) gives a mass of 218 g, or 225.5 g plus wings. Thus, the value of 150 g can still be considered conservative, especially considering Plate 1 of Nel et al. (2009), in which large fossil *Meganeura* abdomens are shown to be materially substantial enough for the original shape to be preserved.

Flight and power

Based on the relationship between wing length and wingbeat frequency for insects, which scales to $m^{-0.25}$ (Dudley, 2000), the expected wingbeat frequency in hertz for several species of Odonata can be estimated as shown in Table 3. This table also shows the wingbeat needed to support a given mass for a given wing length

Table 1. Comparison of mass, wingspan and volume data for extant Odonata and extinct Protodonata

Species	Mass (g)	Wingspan (mm)	Wing length (mm)	log Wing length	log Volume	Volume (mm ³)	Mass/volume
Odonata							
<i>Epithea cynosura</i>	0.18	40	20	1.301	2.4	250	0.720
<i>Micrathyrta atra</i>	0.2	41	20.5	1.311	2.4	250	0.800
<i>Sympetrum vulgatum</i>	0.23	55	27	1.43	2.65	450	0.511
<i>Anax junius</i>	0.8	80	40	1.6	3.2	1400	0.571
<i>Anax junius</i>	1.04	80	40	1.6	3.2	1500	0.693
<i>Macromia taeniolata</i>	1.18	110	55	1.74	3.45	2700	0.437
<i>Namurotypus</i>	18	330	165	2.22	4.78	60,000	0.300
<i>Petalura ingentissima</i>	2	140	70	1.85	3.8	6000	0.333
Protodonata							
<i>Meganeura monyi</i> May (1982)	17.8	700	350	2.54	4.78	60,000	0.300
<i>Meganeura monyi</i> (this Commentary)	138	700	350	2.54	5.66	460,000	0.300

Data were obtained from May (1982, 1991) and Jongerius and Lentink (2010). Bold text indicates data from this Commentary based on the regression data.

Table 2. Relationship between mass and wingspan for a range of bats

Mass (g)	Wingspan/2 (cm)
1	5.0
2	13.5
10	17.5
30	20.1
100	30.0
150	34.4
300	43.3
500	51.4

Data were derived from Norberg and Rayner (1987).

(Ellington, 1999) for a modelled hovering insect, which in turn enables the power output in mW g^{-1} to be estimated.

Measured wingbeat frequency scaled with $m^{-0.25}$ corresponds closely to the predicted wingbeat to support a given mass for modelled hovering flight. The power output at this frequency per wing length is also fairly constant, ranging from around 30 mW g^{-1} for the smallest species to 40 mW g^{-1} . This model estimates that a 150 g *Meganeura* would thus develop 6 W of mechanical power for 40 mW g^{-1} . From the allometric data of muscle per body mass (40%), one can estimate that the mass of muscle giving this power is 40% of 150 g , i.e. 60 g , which, for muscle that can develop a power output of 100 W kg^{-1} (May, 1991), results in 6 W of mechanical power – thus, power estimates from the model and muscle mass are similar.

Respiration as a constraint on size

Insects in flight have the highest mass-specific metabolic rate of the animal kingdom and deliver oxygen in the gas phase through the tracheal system (Dudley, 2000). Gas exchange in insects occurs primarily through tracheae leading from spiracles (see Glossary) in the exoskeleton. These penetrate organs and tissues and eventually terminate as blind-ending tubules or tracheoles. Insect respiratory and cardiac systems thus deliver oxygen from air to cells by either diffusive or convective mechanisms driven by relatively low pressure (Harrison et al., 2013).

The GEOCARBSULF model (see Glossary; Berner, 2006) estimates atmospheric CO_2 and O_2 levels by reconstructing the important long-term sources and sinks through time. This model predicts a higher mass of atmospheric oxygen for the Carboniferous–Permian, about 50% higher than present values. This difference (and subsequent assumed increase of 10% in air pressure) is often taken as a cue for the removal of a constraint on insect size in this period. However, experiments with extant

dragonflies of varying size, flying in different levels of oxygen, found that atmospheric oxygen can be dropped to 25% while incurring relatively minor changes in flight metabolic rate (Henry and Harrison, 2014). This study also found that air density did not greatly affect dragonfly flight metabolism: in the helium–oxygen gas mixture known as ‘heliox’ (which is 50% less dense than air at sea level), wingbeat frequency increased and there were significant linear effects of body mass on the number and duration of flights, but overall physiology remained the same.

An updated reconstruction of atmospheric oxygen also questions the interpretation of Carboniferous/Permian insect body size being largely determined by the diffusional limits of atmospheric oxygen, as the supposed maximum oxygen concentration during this period does not occur in updated datasets (Schachat et al., 2018). As soon as winged insects appear in the fossil record, insect fossils become far more abundant than arachnids, but Schachat and colleagues (2018) note that no link can be made between the sudden development of winged insects and any change in P_{O_2} (see Glossary); thus, oxygen levels might not have been the driver for evolution of the very large insects of this period.

A further constraint on respiration in large *Meganeura* is the number and size of the spiracles. The fossils shown in Nel et al. (2009), clearly show pairs of small spiracles of about 1 mm in diameter on each segment. Adding a pair of thoracic spiracles (as in extant petalurids) gives nine pairs. Assuming some valve mechanism for operating half of these spiracles for intake and half for outflow (as in locusts and blowflies; Groenewald et al., 2012; Wasserthal and Fröhlich, 2017), a pressure gradient would be needed to operate these valves and optimize flow. The highest pressure difference in locust respiration was found to be about 1% (Groenewald et al., 2012), which allows for an estimate to be made of maximum airflow through an orifice at different pressure gradients (www.tlv.com/global/TI/calculator/air-flow-rate-through-orifice.html).

Thus, for nine, say, 2 mm diameter spiracles operating at a pressure gradient of 1% at 1 bar (where 1 bar is 100 kPa) and 40°C , the air flow is only 180 mm^3 per direction. As shown below, this air flow supplies only 5% of the oxygen for flying metabolic rate of large *Meganeura* (considering an atmosphere of 30% oxygen). At higher ambient pressures, e.g. 1.6 bar , this flow increases to around 260 mm^3 for the same 1% pressure difference. In terms of moles of O_2 entering the animal, however, the difference would be: flow increase \times pressure; thus, at higher air pressure or density, where less power is needed to fly, oxygen supply (air intake) is 17% of the

Table 3. Dragonfly and Protodonata wingbeat and power allometric data

Species	L (mm)*	m (g)*	Wingbeat (Hz)*	$m^{-0.25\ddagger}$	Wingbeat for constant $m^{-0.25\times L\ddagger}$	Power (mW g^{-1}) [§]
Odonata						
<i>Epithea cynosura</i>	20	0.175	43	0.8694	43	30
<i>Micrathyria atra</i>	20.5	0.214	39	0.8268	41	30
<i>Anax junius</i>	40	0.804	29	0.5939	29	40
<i>Anax junius</i>	40	1.038	29	0.5571	28	40
<i>Macromia taeniolata</i>	55	1.18	31	0.5395	27	40
<i>Namurotypus</i>	165	18 [¶]	10 [§]	0.273	14	40
<i>Petalura ingentissima</i>	70	2.0	18 [§]	0.4729	23	40
Protodonata						
<i>Meganeura monyi</i>	350	138 ^{¶¶}	3 [§]	0.1607	8	40

L, wing length; m, mass.

*L, m and wingbeat data are from May (1991) unless indicated otherwise; †m and wingbeat from constant $m^{-0.25\times L}$ data are from Dudley (2000); §power data and wingbeat data are from Ellington (1999); ¶m is from Clapham and Karr (2012); bold values are from this Commentary.

metabolic rate (similar to the 25% found by Henry and Harrison, 2014) and is less constrained.

Metabolic rate, overheating and thermoregulation

According to Heinrich (1993), all insects over 1 g (approximate mass of, for example, the green darner, *A. junius*) use some form of thermoregulation. This is essential because physiological performance degrades for most insects at ambient temperatures of between 40 and 46°C; thus, excessive rates of heat production associated with large body size could impose an upper limit to the elevation of body temperature, as overheating during flight and solar heat loads cannot be offset by convective cooling (Dudley, 2000).

May (1995) measured the metabolic rates of several individual *A. junius* during crepuscular feeding flights and estimated a generation of about 0.3–0.4 W g⁻¹ of body mass (inversely proportional to temperature), with similar rates of heat loss at the same ambient temperatures (22–27°C). Wingbeat frequency dropped and time spent gliding increased during warmer weather and in sunlight.

The maximum muscle mass-specific (mechanical) power for a dragonfly has been estimated at 156 W kg⁻¹ for *S. sanguineum*, with measurements of heat production immediately after flight indicating a mechanical efficiency of 13%, i.e. 87% of the metabolism was generated as heat (Wakeling and Ellington, 1997). Taking 40% of the body mass as muscle, this relationship gives a similar result to the value found by May (1995) for *A. junius*: 0.156 W g⁻¹ × (87%/13%) × 40% = 0.39 W g⁻¹.

This raises the question of how metabolic rate would scale in Protodonata. Henry and Harrison (2014) found that the oxygen sensitivity of CO₂ emission rates and flight behaviours of larger dragonflies were not significantly related to body mass in either normobaric or hypobaric (see Glossary) atmospheres for mass in the range 0.1–1.2 g. By contrast, the metabolic rate (MR) of large flying insects has been found to scale with mass as $m^{0.87}$ (Niven and Scharlemann, 2005), where:

$$\text{FMR} = k130m^{0.87}, \quad (3)$$

$$\text{RMR} = k4.14m^{0.66}, \quad (4)$$

where FMR is flying MR, RMR is resting MR, m is mass in g and the constant k of 0.0031 transforms these equations from MR (mm³ O₂ h⁻¹) to W, calibrated to give a FMR rate of 0.4 W for a 1 g dragonfly (as found by May, 1995) and similar to the value found by Polcyn (1988) of 0.48 W. Thus, a 150 g *Meganeura* would produce 31.5 W ($k \times 130 \times 150^{0.87}$) or 0.21 W g⁻¹.

May (1982) estimated a heat production value for an uninsulated *Meganeura* of about 4 W, with a total MR (including 13% of mechanical energy) of 4.6 W for a body mass of 17.8 g, or 0.26 W g⁻¹.

Thus, a *Meganeura* of 150 g would be expected to develop: (1) a FMR of 31.5 W, according to the power function of Niven and Scharlemann (2005); (2) a FMR of 33.7 W, according to May (1982), at a MR of 0.26 W g⁻¹; or (3) total power of about 46 W considering both the modelled mechanical energy to hover and available muscle mass (6 W), which represent 13% of total metabolism.

Based on these different approaches, a reasonable assumption can thus be made that the FMR of a *Meganeura* with a 70 cm wingspan would have been around 32 W, of which 13% would be mechanical energy and 87% heat, or about 28 W.

Considering that its allometric dimensions can be considered to be 8 times bigger than those of *A. junius*, its surface area would be about 64 times larger (8²), and from May (1995), the heat loss from a flying *A. junius* is 0.23 W at 27°C and a flying speed of 10 m s⁻¹ (the closest to the assumed tropical environment of Protodonata); thus, total heat loss for a flying *Meganeura* would be 0.23 W × 64 = 14.7 W, i.e. half the heat production. The specific heat of dragonfly body tissue is approximately 3.3 J g⁻¹ C⁻¹ (May, 1982); hence, with an excess of about 17 W, the whole body would incur a rise from 30 to 40°C in about 99 s of flight. If preflight ‘shivering’ to heat the flight muscles to a higher and optimum temperature of 38°C was normal, overheating to 40°C would only take 20 s. Even taking into account a slightly higher acceptance of thoracic temperature, overheating of such a large creature in flight would be rapid.

May (1982) arrived at similar results, even with a much lower body mass – these results indicated that body temperature would be expected to vary from 42°C for a mid-sized *Meganeura* flying at 10 m s⁻¹ and with uninsulated thoracic air sacs to 104°C in *M. monyi* at 2.5 m s⁻¹ (insulated). May (1982) concludes by saying that *M. monyi* obviously did not operate at 104°C, but, for a heat production rate of ~4 W, he notes that even short powered flights would present the risk of overheating. May (1982) then raises some possibilities of dealing with heat: (1) crepuscular activity (not a viable option in tropical conditions as ambient temperatures remain high and a large-eyed predator relies on light); (2) extra time in gliding (although continuously powered flight is necessary during hunting and perhaps during aggressive or sexual encounters); and (3) increasing cooling through convective transfer of heat to expired air or evaporation.

Convective respiration is an important mechanism for thermoregulation; however, supposing the tracheal membrane thickness to be the same cellular thickness for all Odonata, if an insect is scaled by a linear factor of, say, 5, volume (L^3) would increase by 125 (5³), whereas trachea area (length and circumference of the trachea) and spiracle area can only increase by L^2 or 25. Thus, trachea area and volume would have to greatly increase with volume, limiting muscle mass and imposing a limit on insect size – unless the concentration of gases (in mol m⁻³) were also increased through a higher percentage of O₂ or higher air density.

The original formula of Niven and Scharlemann (2005) of $\text{FMR} = 130m^{0.87}$, where m is in mg and oxygen consumption is in mm³ per hour, gives a value of 1150 mm³ s⁻¹. Taking an atmospheric oxygen content of 30%, this results in an air flow of nearly 4000 mm³ s⁻¹. Taking the mass of a cubic meter of air at 25°C as 1.25 kg, this maximum FMR air flow represents a mass of 0.0048 g s⁻¹. A constraint on this heat loss can be found from the specific enthalpy (see Glossary) of dry air at 30°C (30.2 J g⁻¹) as compared with that of moist saturated air at 40°C (166.4 J g⁻¹) and assuming that all air exchange is from dry to saturated at these temperatures. The heat needed is thus mass × difference in specific enthalpy, or 0.65 W, representing a maximum constraint on this form of cooling. The Permian climate is assumed to be humid so any change in enthalpy would have been far lower. The constraint in spiracle air flow reduces the possibility of convective and evaporation cooling to less than the order of 0.1 W.

This agrees with Church (1960), who mentions that in flying insects little of the heat generated in flight is lost by evaporation. Grasshoppers have been found to reduce body heat in hot, dry desert conditions through evaporation, surviving for an hour at external temperatures of 48°C by increasing respiration rate (Prange, 1990). These experiments, however, were carried out in dry, desert-like conditions, and in humid, tropical conditions, Prange (1990)

suggests that this mechanism would be limited and slow in cooling large thoracic muscles. As mentioned by Heinrich (1989), insects lack capillaries, and have little blood, no sweat glands and generally little water to spare for evaporation.

The insects may have sought shade to cool off through resting. However, there are two additional factors that are problematic: the RMR of large flying insects and sun radiation. RMR is scaled to mass and, using the equation from Niven and Scharlemann (2005), the RMR for a 150 g *Meganeura* would be 0.4 W. This RMR implies an air flow of only $10 \text{ mm}^3 \text{ s}^{-1}$ (well within the spiracle air flow capacity rate), suggesting that these animals were perchers, developing short bursts of flight and oxygenating their tissues during rest. Tropical sunlight also has 137 mW cm^{-2} of energy and a cylinder equivalent to body volume with a plan area of 140 cm^2 would thus receive 19 W; even reflecting as much light and heat as fresh snow (80%), around 4 W would still be absorbed. The insects might have sought shade to avoid solar heating; however, the canopy of a tropical forest still allows the transmission of infrared and the radiation at lower canopy levels has been found to be enriched in the thermal near-infrared wavelengths (de Castro, 2000).

A black body cylinder (see Glossary) equivalent to the estimated cylinder volume would radiate, using the Stefan–Boltzmann equation (see Glossary), 3 W of heat loss for a 40°C body in a 30°C environment. *Meganeura* were not perfect black bodies, but did have a larger surface area, so taking radiated heat loss at a conservative value of 3 W and considering the RMR of 0.4 W, total heat loss would be only 2.6 W in calm air – not considering the energy needed to devour and digest prey. Thus, to cool down the entire body by 10°C would take $150 \text{ (mass)} \times 3.3 \text{ (specific heat of dragonfly tissue)} \times 10^\circ\text{C} / 2.6 \text{ (heat loss in W)} = 1903 \text{ s}$, which is just over half an hour. This time is extremely long and if any direct or infrared solar heat is added, cooling starts to become impractical.

Thus, from the foregoing analysis, it is apparent that the main constraint for giant flying *Meganeura* was overheating in a relatively short flight period that required long periods of subsequent cooling. To illustrate the issue, a very simple experiment can be performed by placing a finger on the surface of a 25 W incandescent light bulb at room temperature and turning on the light. It takes about 15 s to become uncomfortably hot... Hence May's (1982) conclusion that large Protodonata probably had some unknown means of physiologically accelerating heat loss.

This unknown cooling mechanism could have been the flight medium itself. Aerodynamic lift (normal to the relative velocity) is directly proportional to air density, so large Protodonata could have flown with less power in an atmosphere of higher density. At higher densities, viscosity (see Glossary) becomes an issue, and it would be expected that, if air density were to increase over time, evolutionary pressure would favour larger sizes – as observed in the fossil record of the Permian (Schachat et al., 2018).

Taking the presumed oxygen content of the Permian atmosphere as 30% and the constant mass of N_2 assumed by the GEOCARBSULF model, the expected atmospheric pressure would be around 1.1 bar. Considering the linear relationship between air density and power as well as heat loss at a flight speed of 10 m s^{-1} , as pressure (or density) increases, it is possible to determine the point at which power, respiration and thermoregulation enter into equilibrium: this occurs at a pressure of approximately 1.5–1.6 bar. (1) Higher O_2 molecular density per trachea area requires less trachea volume (from 5 times the volume to around 2 times). (2) Higher density results in the need for less power (as lift is proportional to air density) and thus less generated heat and lower air intake. (3) Higher air flows through the spiracles

allow more oxygen to enter the animal. At 1.6 bar, this is estimated at the equivalent of $260 \text{ mm}^3 \text{ (air flow)} \times 1.6 \text{ (pressure)}$, or 17% of the FMR. (4) Higher pressure leads to additional convective heat loss (again proportional to density).

Conclusion

The Devonian fossil record of insects, which does not contain any direct evidence of wings, is followed by a 62-million-year 'Hexapod Gap' devoid of insect material that encompasses the Late Devonian (383–359 Ma) and Mississippian (359–323 Ma). The sudden appearance of wing-powered flight after this period may thus be related to air density as flight evolution presumably took place in favourable conditions.

This is not a new idea. Harlé and Harlé (1911) observed that the flight of large animals, such as the dragonflies of the Carboniferous, required higher air pressure to compensate for the extra weight. Dudley (1998) also touches on this, noting that not only hexapod insects but also a diversity of arthropod classes, as well as various amphibians, displayed gigantism during the Permian and that the end-Devonian origin of flight in insects also correlates well with an increasing air density in the late Paleozoic.

A review of the mass of the largest *Meganeura* results in an estimate of 150 g and the power needed for this animal to fly would certainly require thermoregulation to avoid rapid overheating. Of the mechanisms available for the cooling of very large insects, a higher density flight medium of around 1.5–1.6 bar offers the greatest scope for reaching thermal equilibrium and adequate oxygen supply. Other cooling options such as respiratory convection or evaporation appear to be constrained by available respiratory air flow.

Fossil biology of flight represents one of the few means of examining past atmospheric conditions. Future research of well-preserved large-winged fossils may indicate how any microstructures on the wing or leading edge are scaled in relation to present-day specimens and whether this bears any relation to the air density in which these insects lived.

Competing interests

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