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Induced Power Scaling Alone Cannot Explain Griffenfly Gigantism

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Abstract

Paleozoic skies were ruled by extinct odonatopteran insects called "griffenflies", some with wingspans three times that of the largest extant dragonflies and ten times that of common extant dragonflies. Previous studies suggested that flight was possible for larger fliers because of higher atmospheric oxygen levels that would have increased air density. We use actuator disk theory to evaluate this hypothesis. Actuator disk theory gives similar estimates of induced power as has been estimated for micro-air vehicles based on insect flight. We calculate that for a given mass of griffenfly, and assuming isometry, a higher density atmosphere would only have reduced the induced power required to hover by 11%, which would have supported a flyer 3% larger in linear dimensions. Steady level forward flight would have further reduced induced power but could only account for a flier 5% larger in linear dimensions. Further accounting for the higher power available due to high oxygen air, and assuming isometry, we calculate that the largest flyer hovering would have been only 1.19 times longer than extant dragonflies. We also consider known allometry in dragonflies and estimated allometry in extinct griffenflies. But such allometry only increases flyer size to 1.22 times longer while hovering. We also consider profile and parasite power, but both would have been higher in denser air and thus would not have enhanced the flyability of larger griffenflies. The largest meganeurid griffenflies might have adjusted flight behaviors to reduce power required. Alternatively, the scaling of flight muscle power may have been sufficient to support the power demands of large griffenflies. In literature estimates, mass-specific power output scales as mass$^{0.24}$ in extant dragonflies. We need only more conservatively assume that mass-specific muscle power scales with mass^{0}, when combined with higher oxygen concentrations and induced power reductions in higher density air to explain griffenflies 3.4 times larger than extant odonates. Experimental measurement of flight muscle power scaling in odonates is necessary to test this hypothesis.

Key words: griffenfly, power, allometry, scaling, flight, Meganeura

Introduction

Before there were birds or pterosaurs, the largest flying animals were giant, dragonfly-like insects called *griffenflies.* These apex predators and their close relatives formed the group Meganisoptera, which persisted from the early Late Carboniferous to at least the end of the Middle Permian period, and included the largest insects ever to live on the Earth (Wootton et al., 1998; Nel et al., 2009; Polet, 2011). Griffenflies reached a maximum wingspan of 71 cm (Carpenter, 1939; Kukalová-Peck, 2009; Nel et al., 2018), dwarfing the largest modern dragonflies (*Petalura ingentissima*, wingspan 16 cm (Tillyard, 1908)) and damselflies (*Megaloprepus caerulatus*, wingspan 19 cm (Zhang et al., 2013)) by more than three-fold (Fig. 1). However, despite an extensive literature, the major causes of griffenfly gigantism remain obscure.

Meganisoptera and their kin are a part of the superorder Odonatoptera, with extant representatives being odonates (modern dragonflies, damsel-dragonflies and damselflies). Meganisopterans arose in the Carboniferous (Davis et al., 2010; Prokop and Nel, 2010) with their first recorded appearance in the Namurian B division (Brauckmann and Zessin, 1989) about 318–315 Myr ago (Dusar, 2006). The earliest known griffenfly, *Namurotypus sippeli*, had a wingspan of 32 cm (Brauckmann and Zessin, 1989), and the group later radiated into several large- and small-bodied forms (Ren et al., 2008). The largest representatives of the clade arose in the Upper Carboniferous (*Meganeura monyi*) and Lower Permian periods (*Meganeuropsis permiana*) (Ren et al., 2008; Wootton and Kukalová-Peck, 2000). These were aerial apex predators in late Paleozoic communities, and likely specialized in hunting large herbivorous winged insects in moist forested habitats near rivers, lakes, or marshes (Kukalová-Peck, 2009). However, despite their great diversity throughout the latter 60 Myr of the Paleozoic, the Meganisoptera went extinct at some time during the Late Permian as they are unknown in the Triassic (Nel et al., 2008). Subsequent odonatopterans would never again reach griffenfly size (Okajima, 2008).

To explain the great scale of these insects, and their eventual decline, previous studies have emphasized the role of changing atmospheric oxygen levels (Wootton and Kukalová-Peck, 2000; Graham et al., 1995; Dudley, 1998; Berner, 1999; Gans et al., 1999; Berner et al., 2000; Berner, 2005; Kaiser et al., 2007). Following the spread of ligniferous vascular plants some 375 Mya (Berner, 1999), atmospheric oxygen rose dramatically in the Carboniferous, and stayed high through much of the Permian, before declining with reduced rates of organic carbon burial and the drying of the continents (Berner, 2005; Berner and Canfield, 1989). Though specific estimates of late Paleozoic oxygen levels vary widely, most agree that oxygen rose to as much as 30% during the later Carboniferous (Cannell et al., 2022; Cannell and Nel, 2023; Wade et al., 2019), and declined substantially by the end of the Permian (Wade et al., 2019; Brand et al., 2021). By some estimates, with increased atmospheric oxygen, air density would have been up to 21% higher by the later Carboniferous, facilitating the evolution of larger body sizes by increasing the lift generated by flight surfaces (Graham et al., 1995). Larger body size may have also helped to mitigate oxygen toxicity for insect larvae in hyperoxic environments (Verberk and Bilton, 2011), or resulted from an increase in the rate of oxygen transport to flight systems (Polet, 2011). Insects have a tracheal respiratory system that relies heavily on the diffusion of oxygen into tissues during flight (Kaiser et al., 2007; Harrison and Lighton, 1998). Diffusion rate is proportional to tracheal surface area, which is proportional to length squared, while the total amount of oxygen the insect requires is proportional to its volume, which is proportional to length cubed (Polet, 2011). As a result, beyond a certain size, an insect can no longer supply its tissues with the oxygen required to support aerobic metabolism during flight. Higher atmospheric oxygen in the Paleozoic would have raised the concentration gradient of oxygen between the insect's tissues and the surrounding air, increasing the diffusion rate of oxygen into flight muscles, and raising the physiological cap on maximum size (Polet, 2011). Indeed, dragonflies observed in hyperoxic conditions readily supply more oxygen to flight muscles (Harrison and Lighton, 1998). In addition, several (though not all) flying insects reared under high-oxygen develop larger body sizes, either individually or across multiple generations (Harrison et al., 2006, 2010; Klok et al., 2009). As a result, oxygen should be a critical factor influencing insect size in deep time.

However, recent studies have challenged the central role of oxygen in this story (Polet, 2011; Okajima, 2008; Harrison et al., 2010; Henry and Harrison, 2014). Several Middle Permian, Triassic and Late Jurassic odonatopterans greatly outsized the largest modern dragonflies (Zhang et al., 2013; Nel et al., 2008), despite the fact that many atmospheric oxygen level estimates are lower than modern during these intervals (Berner and Canfield, 1989; Wade et al., 2019). Moreover, several modern insects employ compensatory, non-diffusive mechanisms of oxygen transport during flight, and large griffenflies may have used similar mechanisms to evade physiological constraints (Polet, 2011). As a result, previous studies have offered alternative explanations for griffenfly gigantism—usually invoking the size of their herbivorous insect prey (Wootton and Kukalová-Peck, 2000; Harrison et al., 2010) or the absence of maneuverable vertebrate flyers (Clapham and Karr, 2012; Nel et al., 2008; Okajima, 2008). Many researchers continue to believe that oxygen played a critical role in controlling Paleozoic insect body size (Polet, 2011; Zhang et al., 2013; Okajima, 2008; Harrison et al., 2010), but little has been done to quantify its contribution in relation to competing theories.

Ironically, recent modeling work to this effect has supported the role of oxygen in promoting early griffenfly gigantism. Allometric scaling relationships between wing length and tracheal size parameters were used to model maximum expected body sizes at historical oxygen concentrations (Okajima, 2008). Ultimately, this model overestimated the maximum body sizes of post-Paleozoic species. Likewise, using the largest compiled dataset of fossil Odonatoptera on record, a significant association was found (Clapham and Karr, 2012) between insect size and atmospheric pO2 until the Early Cretaceous, after which point they became decoupled. The authors suggest that this decoupling resulted from the appearance of maneuverable theropod flyers (enantiornithines and crown Aves), in line with previous suggestions (Nel et al., 2008; Okajima, 2008). Alternatively, Dorrington (2016) suggests that this decoupling resulted from the evolution of secondary genitalia (and the subsequent adoption of in-flight wheel copulation) in Lower Permian odonatopterans. Modeling flight power as a function of air density, Dorrington argues that the loads associated with mate carriage would have placed a major aerodynamic constraint on post-Paleozoic griffenflies. Carboniferous and Permian meganisopterans, free from this constraint, would have been able to achieve a greater size range (Dorrington, 2016). Likewise, Cannell (2018) argues that higher atmospheric oxygen concentrations would have increased air density, facilitating thrust generation in Permian meganeurids. As a result, despite recent challenges to the oxygen hypothesis, the modern consensus seems to suggest that changing atmospheric conditions suffice to explain Paleozoic griffenfly gigantism in the absence of volant theropods.

In this study, we use actuator disk theory to calculate how much bigger odonatopterans could have been given the higher density and higher fuel level afforded by the presumed end-Carboniferous atmosphere. For the sake of argument, we will use the atmospheric levels of oxygen and density given in Graham et al. (1995) (present day: 21% oxygen and 1.29 $\mathrm{kg\,m^{-3}}$ density; Upper Carboniferous: 35% oxygen and 1.56 $\mathrm{kg\,m^{-3}}$ density), but other values can be substituted in the formulas we give to allow assessment of the effects of alternative hypotheses of ancient and modern atmosphere comparisons. By estimating the ratio of induced flight power required in the end-Carboniferous to induced flight power required now under a variety of other assumptions, we calculate the effect on relative size of griffenflies relative to modern dragonflies. In doing so, we demonstrate that Paleozoic oxygen levels alone would have failed to lift the aerodynamic constraints associated with massive size in Meganisoptera.

Theory and Results

Actuator disk theory gives a formula for the induced power required for flight. We calculate the ratio of the induced power required by an end-Carboniferous flyer relative to a modern flyer. For a given mass and area swept out by the wings, this power ratio depends only on the densities of the air in

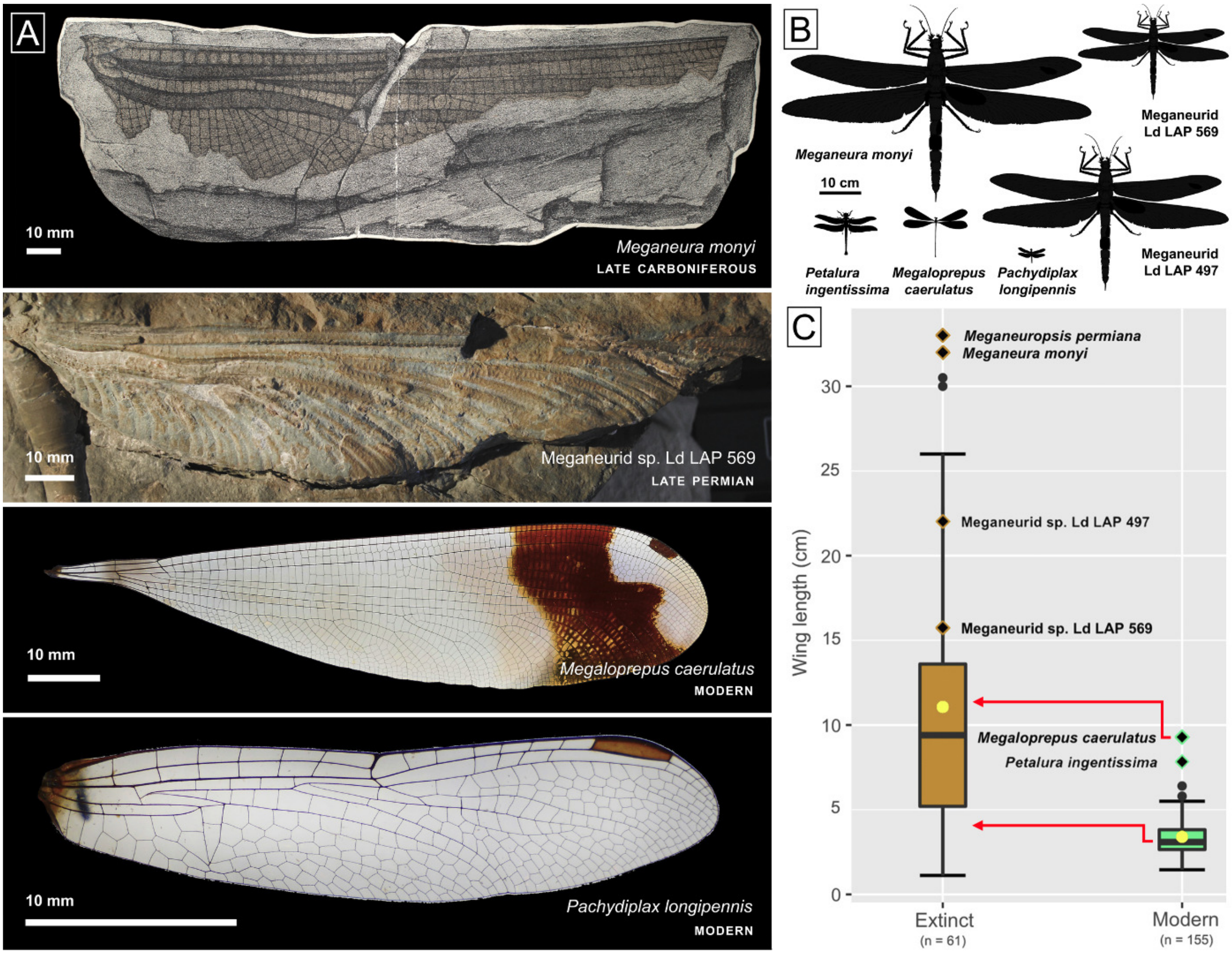

Fig. 1. Extinct odonatopterans dwarfed the largest modern species. (A) Specimen photographs of wing fragments from two fossil meganeurids (MNHN F R53003 and Ld LAP 569), the largest modern odonate (YPM ENT 585229), and a common modern North American dragonfly species (YPM ENT 145400) with a wing length close to the mean. (B) Whole-body silhouettes illustrate rough size differences between highlighted taxa. (C) Box plots comparing wing length distributions in pre-Cenozoic and modern species. MNHN photographs were taken by Gaîl Doitteau (e-recolnat Project, MNHN) and provided by André Nel. Musée de Lodéve photographs were taken by Jean Lapeyrie and provided by Stephane Fouché. Silhouettes were adapted from previous reconstructions—by Kukalová-Peck (2009) (Fig. 4; *Meganisoptera* spp.) and Pettigrew (1873) (*Petalura ingentissima*)—or original photographs of YPM specimens (*Pachydiplax longipennis*, *Megaloprepus caerulatus*). Wing length data for boxplots is provided in Table S1. Red arrows indicate greatest change in size of median and largest modern species due to reductions in induced power due to high ancient atmospheric density, high oxygen and allometry combined (see Results below). The size of many stem-group odonatopterans cannot be explained by these factors alone.

the two periods. This ratio can be further used with various assumptions of scaling, fuel availability, and flight similarity, to calculate how much larger a flyer could have been in the higher density end-Carboniferous atmosphere than in the lower density modern atmosphere.

We will use an actuator disk model to consider flight in extinct Odonatoptera. Actuator wing disk theory gives the induced power P_i for atmospheric density ρ, and thrust T, with ϕ being the angle swept out by a wing and r being wing length:

$$P_\mathrm{i} = \sqrt{\frac{T^3}{2\rho\phi r^2}}. \tag{1}$$

This expression is formula 5.10 derived in Chapter 5 of Van Kuik (2022) adjusted for the area swept out by the wings. During stationary hovering, thrust produced is just equal and opposite to weight with $T = mg$ where m is mass and g is gravitational acceleration. Gravitational acceleration is taken as constant since the earth radius has changed less than 0.8% during the last 400 million years (McElhinny et al., 1978). Thus, equation (1) shows that for a given flying mass, the induced power required to keep the mass in the air is lower if air density is higher. We can write two versions of this equation to reflect the induced power required during the modern and Carboniferous times. The induced power required to keep a flyer hovering (see Vogel (1994)) is:

$$\begin{aligned} P_\mathrm{i,m} &= \sqrt{\frac{(m_\mathrm{m} g)^3}{2\rho_\mathrm{m}\phi_\mathrm{m} r_\mathrm{m}^2}} \\ P_\mathrm{i,c} &= \sqrt{\frac{(m_\mathrm{c} g)^3}{2\rho_\mathrm{c}\phi_\mathrm{c} r_\mathrm{c}^2}} \end{aligned} \tag{2}$$

where the subscripts m and c refer to modern and Carboniferous flyers. For two flyers of equal mass and equal wing disk area, we can use equation (2) to calculate the ratio of induced power

Table 1. Symbols and Subscripts

Symbols	Definition
ϕ	Angle swept out by wing
ρ	Atmospheric (air) density
μ	Viscosity
AR	Aspect ratio
C_d	Coefficient of drag
C_l	Coefficient of lift
g	Gravitational acceleration
l	Length dimension
m	Mass
n	Wing beat frequency
P	Power
r	Wing length
s	Surface area
T	Thrust
V	Volume
v	Airspeed relative to the body

Subscripts	
avail	available from muscles
c	Carboniferous atmosphere
E	Ellington
H	High
i	induced
isa	international standard atmosphere
L	Low
m	modern atmosphere
mm	mm or mm^3
M	meganeurid
par	parasite
pro	profile
si	SI units

required in the Upper Carboniferous atmosphere $P_{\mathrm{i,c}}$ relative to induced power required in the modern atmosphere $P_{\mathrm{i,m}}$:

$$\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}} = \sqrt{\frac{\rho_{\mathrm{m}}}{\rho_{\mathrm{c}}}} = \sqrt{\frac{1.29}{1.56}} = 0.91 \tag{3}$$

with atmospheric densities:

$$\begin{aligned} \rho_{\mathrm{m}} &= 1.29 \\ \rho_{\mathrm{c}} &= 1.56 \end{aligned} \tag{4}$$

both with units of $\mathrm{kg\,m^{-3}}$, are the assumed densities of the modern and Upper Carboniferous atmospheres. Thus, the induced power required to keep a given mass of odonatopteran in the air is expected to have been 91% as much during the Carboniferous, due to the effects of density on induced power.

We can use the power formulas (2) with various assumptions of scaling and power available to calculate how much larger a flyer could be in the Carboniferous than in modern times. First, assume isometry:

$$\begin{aligned} m &\propto l^3 \\ \phi r^2 &\propto l^2 \end{aligned} \tag{5}$$

where the constants of proportionality are the same in the Carboniferous and the modern. Further assume that some ratio of induced power is available in the Carboniferous relative to modern times. Then using equations (5) and (2):

$$\frac{P_{\mathrm{i,m}}}{P_{\mathrm{i,c}}} = \frac{\sqrt{\frac{(l_{\mathrm{m}}^3 g)^3}{2\rho_{\mathrm{m}} l_{\mathrm{m}}^2}}}{\sqrt{\frac{(l_{\mathrm{c}}^3 g)^3}{2\rho_{\mathrm{c}} l_{\mathrm{c}}^2}}}. \tag{6}$$

This equation (6) can be rearranged such that:

$$l_{\mathrm{c}} = l_{\mathrm{m}} \left(\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}}\right)^{\frac{2}{7}} \left(\frac{\rho_{\mathrm{c}}}{\rho_{\mathrm{m}}}\right)^{\frac{1}{7}}. \tag{7}$$

If we assume that the induced power available was the same in the Carboniferous flyer as in a modern one then, using equation (7) and our model density assumption (4) we get:

$$l_{\mathrm{c}} = (1)^{\frac{2}{7}} \left(\frac{1.56}{1.29}\right)^{\frac{1}{7}} l_{\mathrm{m}} = 1.03 l_{\mathrm{m}}. \tag{8}$$

Thus, in the case of equal available energy, a hovering Carboniferous flyer could have been 3% larger than a modern flyer based solely on the greater induced power due to the denser air in the Carboniferous. This effect is graphically illustrated in Fig. 2.

The higher oxygen content in the Carboniferous potentially means that more energy can be delivered to the flight muscles. If we assume that all the additional oxygen can be used to power flight then $35\%/21\% = 5/3 \approx 1.7$ times as much power is available. The combined effect of higher density and higher power availability can be used in equation (7):

$$l_{\mathrm{c}} = \left(\frac{35}{21}\right)^{\frac{2}{7}} \left(\frac{1.56}{1.29}\right)^{\frac{1}{7}} l_{\mathrm{m}} = 1.19 l_{\mathrm{m}}. \tag{9}$$

Thus the combined effects of density and oxygen concentration would have made it possible to have a hovering flyer that was 19% larger in the Carboniferous and this can be graphically represented as in Fig. 2.

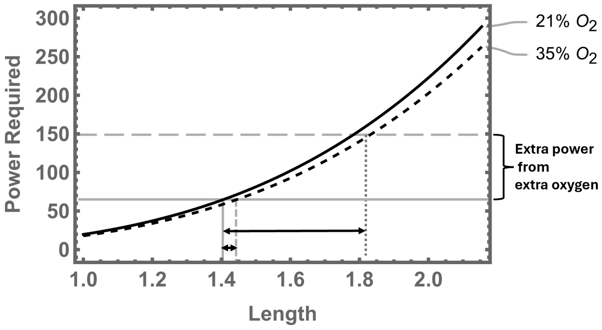

Fig. 2. Power required by a hovering dragonfly-like animal at each length in the presumed 21% O_2 atmosphere (black line) and 35% O_2 atmosphere (dashed line). A flyer in a higher-density medium requires less induced power to support its weight. Increases in length (short horizontal double-headed arrow) at a given available level of power (solid horizontal gray line) are made possible by the higher flight power due to the higher density atmosphere stipulated in the end-Carboniferous relative to the modern atmosphere. More O_2 in the end-Carboniferous made possible a greater delivery of power (curly bracket) and the two effects together made possible a greater length (long horizontal double-headed arrow). Note that the units in this graph are arbitrary. The mathematical argument gives proportions. Thus, the increased atmospheric density allows a 3% increase in length and that effect plus the increased energy content of the air allows a 19% increase in lengths.

Thus far we have assumed isometry for dragonfly-like flyers. Next we will consider whether allometric changes could help to explain the larger size of observed griffenfly fossils when taken together with the aerodynamic and energetic effects of a higher-oxygen atmosphere. First we must establish the allometric scaling relationships for wing length among odonatopterans. For the allometry of odonatopterans we will rely on fitted scaling relationships from Clapham and Karr (2012) in which fossil data was used to model the length-volume scaling of extinct odonatopterans. Meganisopteran body width as a function of wing length has a similar scaling as does extinct odonatopteran body width (Clapham and Karr, 2012) supporting the use of the extinct odonatopteran allometry to consider meganeurid allometry. Furthermore, according to calculations of Cannell (2018), two extinct meganeurid species have volume V in mm^3 predicted by the relationship given by Clapham and Karr (2012):

$$V_{\mathrm{mm}} = 10^{-1.108} r_{\mathrm{mm}}^{2.661}, \tag{10}$$

where r_{mm} is wing length in mm and V_{mm} is volume in mm^3. We now substitute the exponent of wing length, 2.661, into equation (6) instead of the 3rd power of length in that isometric equation; then further assume that wing area scales isometrically, and solve and substitute as before:

$$\begin{aligned} l_{\mathrm{c}} &= l_{\mathrm{m}} \left(\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}}\right)^{\frac{2}{3*2.661-2}} \left(\frac{\rho_{\mathrm{c}}}{\rho_{\mathrm{m}}}\right)^{\frac{1}{3*2.661-2}} \\ &= \left(\frac{35}{21}\right)^{\frac{2}{5.983}} \left(\frac{1.56}{1.29}\right)^{\frac{1}{5.983}} l_{\mathrm{m}} \\ &= 1.22\, l_{\mathrm{m}} \end{aligned} \tag{11}$$

from which we conclude that, when accounting for estimated allometry of odonatopteran mass as a function of wing length, a Carboniferous flyer could have been 22% larger.

The scaling relationship we used Clapham and Karr (2012) estimated volume but we are interested in further refining calculations to take into account an estimated mass of the meganeurids. We will also use the volume vs wing length relationship (10) with the assumption that the density of odonatopterans and meganeurids was $\rho_{\mathrm{M}} = 0.3\ \mathrm{g\,cm^{-3}}$ to estimate the mass of meganeurids and to compare the scaling of extinct odonatopterans to extant dragonflies. Densities of 0.3 or 0.4 $\mathrm{g\,cm^{-3}}$ were considered by Cannell (2018) and this body density is also supported by extensive measurements and extrapolations in Greenlee et al. (2009) for orthopterans as they hypothetically approach the size of meganeurids. With appropriate unit conversions, the equation for the presumed mass of meganeurids is thus:

$$m_{\mathrm{si}} = 0.3 \times 10^{-6} \times 10^{-1.108} (1000\, r_{\mathrm{si}})^{2.661} \tag{12}$$

with mass m_{si} and wing length r_{si} in SI units of kg and m, respectively.

The fitted relationships for four families of extant dragonflies and for the overall sample of all four families of extant dragonflies are shown in Fig. 3. The scaling of extinct odonatoperans is very similar to the extrapolated scaling of extant dragonflies. Thus the presumed allometric scaling is suitable to calculate induced power requirements for meganeurid-sized odonatopteran flyers in the ancient atmosphere based on extrapolations from extant dragonfly scaling.

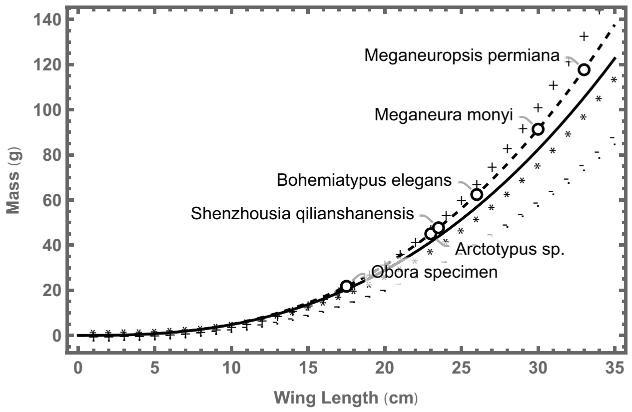

Fig. 3. Scaling of extinct odonatopterans and anisopterans. The scaling of mass as a function of length for extinct odonatopterans appears to be very similar to that of modern anisopterans. Symbols: + is Aeshnidae,* is Libelluidae,- is Gomphidae,. is Corduliidae, black line is fitted function from all measured anisopteran families (May, 1981) and dashed line is calculated from extinct odonatatopterans (Clapham and Karr, 2012) with the assumption that body density is 0.3 $\mathrm{g\,mL^{-3}}$. Individual open dots are specific meganisopteran fossil masses calculated assuming the extinct odonatopteran mass scaling and using fossil wing lengths from the supplement to Clapham and Karr (2012).

Now we are in a position to estimate specific numbers for the mass and induced power of dragonflies and griffenflies and we will compare the calculations from actuator disk theory with a theoretical framework developed by Ellington (1999) to calculate power required by micro-air vehicles but based on insights from insect flight. Actuator disc theory gives induced power using equation (1) with $T = mg$, and we take $\phi = 2\pi/3 = 120°$ as our base case, as does Ellington (1999). For the mass in equation (1) we use the scaling relationship from equation (12), and for the wing length r we use SI units as well. The calculations of Ellington (1999) use more variables, including the wing beat frequency n, the coefficient of lift C_{l}, and the wing aspect ratio $\mathcal{R}$. To compare the predictions of Ellington (1999) to those of equation (1) we rearrange an equation for supported mass as a function of several variables, equation 6 of Ellington (1999), so that the wing beat frequency is a function of supported mass. We substitute this formula for wing beat frequency into an equation for induced power per mass, equation 7 from Ellington (1999), and multiply that equation by mass to get an expression for induced power:

$$P_{\mathrm{i,E}} = \frac{22 m^{\frac{3}{2}}}{r\sqrt{\phi}}. \tag{13}$$

An astute observer will note that the units in the above equation (13) do not work; some unit adjustment must be occurring in the coefficient and Ellington (1999) does note that several unspecified ‘minor variables’ are incorporated in constants, including in particular an unspecified value for air density. We substitute equation (12) for the mass m in equation (13) and use SI units for r to compare actuator disk theory to the induced power calculated from the formula in Ellington (1999). The predictions of the two theories - actuator disk and micro-air vehicle - are quite similar (Fig. 4A); this similarity should not be surprising since the two theories purport to describe similar flight phenomena. Furthermore all of the information about wingbeat frequency, aspect ratio, and lift coefficients has been removed from the more complete theory to make the comparison. These same variables that have been removed are likely variables that could be changing systematically to allow larger griffenflies to hover. Thus paleontologists could look for evidence of systematic changes in combinations of parameters in equation 7 of Ellington (1999) that would result in greater induced power per mass and that might have enabled larger griffenflies to fly. Those changes would be increases in wing beat frequency, angle swept by the wings, coefficient of lift, wing length and aspect ratio. An investigation of systematic changes in flight-relevant morphology with size, some of which has already been considered by Dorrington (2016) is warranted.

The above considerations have been entirely theoretical. But experiments with altered atmospheres have been conducted with modern dragonflies. Specifically, Henry and Harrison (2014) compared power consumption during flight of dragonflies in heliox and nitrox gas mixtures that have densities of 0.5 and 1.25 $\mathrm{kg\,m^{-3}}$. In this case the ratio of power required is:

$$\frac{P_{\mathrm{i,H}}}{P_{\mathrm{i,L}}} = \sqrt{\frac{\rho_{\mathrm{L}}}{\rho_{\mathrm{H}}}} = \sqrt{\frac{0.5}{1.25}} = 0.63. \tag{14}$$

However, this experimentally measured reduction was only about 10% in CO2 emission rate, which should correspond to power consumed by dragonflies flown in the higher density nitrox atmosphere. The fact that this experiment showed less reduction in power consumed suggests that our actuator disk model overestimates the reduction of power due to air density alone or that the modern dragonflies are otherwise compensating for or failing to use all the available power in the artificially changed atmosphere of the experiment. In any case, this experiment confirms that a higher atmospheric density reduces the power required to fly. Indeed, the experimentally measured effect on energy consumed seems to be bigger for the treatments in which dragonflies were flown at different oxygen concentrations, suggesting that, if anything, our model overestimates the role of oxygen in facilitating griffenfly gigantism (Henry and Harrison, 2014).

Experiments have also been conducted with euglossine bees flying in low (Heliox) versus normal density atmospheres but with normal concentrations of oxygen (Dudley, 1995). The heliox and normal air densities were 0.44 and 1.2 $\mathrm{kg\,m^{-3}}$ and thus the predicted induced power ratio using equation (14) in air versus heliox is 0.6. The experimentally observed ratio of induced power in that experiment for two of the three species tested was 0.67 and 0.7, in fairly good agreement with predictions; results for a third species appear anomalous. Changes in flight parameters such as wing beat amplitude and lift coefficient as well as higher muscle power output were also observed as correlates of the lower induced power required during hovering in higher density air.

We have extensively discussed how a higher density atmosphere would have reduced induced power during hovering, although this reduction would not have been enough to account for hovering in the largest griffenflies. Next we expand our analysis to induced power during level, steady forward flight and also consider other components of power, specifically parasite power and profile power. Parasite power is the power required to overcome the drag on the griffenfly body during flight. Drag is often represented empirically as a function of the square of air speed v and the surface area s of the projection of the body on a plane perpendicular to air speed; thus the parasite power may be described by:

$$P_{\mathrm{par}} = 0.5\rho v^3 s C_{\mathrm{d}}, \tag{15}$$

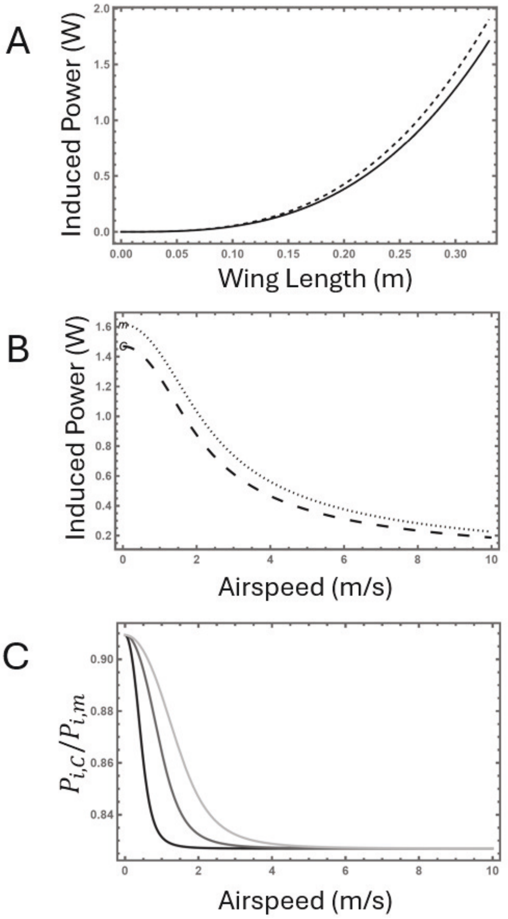

Fig. 4. A. Dashed line shows the scaling of induced power in real units as predicted using formulas from Ellington (1999) rearranged to eliminate variables: lift coefficient, aspect ratio, and wing beat frequency. This induced power prediction from Ellington (1999) is quite similar to that predicted by the actuator disk theory (black line), but is 11% higher, in accord with the typical 15% higher indicated in Ellington (1999, 1984). For purposes of the comparison of the predictions of the two theories, atmospheric density was set to $\rho_{\mathrm{isa}} = 1.2250$ in accordance with the International Standard Atmosphere. B. Induced power during flapping, level flight as a function of forward speed at Carboniferous (dashed line) and modern (dotted line) density atmospheres. Symbols "c" and "m" show the induced power for hovering, i.e. zero airspeed. The calculation uses equation (18) and assumes $T = m_{\mathrm{si}}g, \phi = 2\pi/3, g = 9.8$ $\mathrm{m\,s^{-2}}$, $r = r_{\mathrm{si}}$ and is calculated with a wing length representing that of *Meganeuropsis permiana* with $r_{\mathrm{si}} = 0.33$ m . C. Induced power in level flapping flight, equation (18), was used to calculate the ratio of powers in the Carboniferous and modern air density $P_{\mathrm{i,c}}/P_{\mathrm{i,m}}$ with three different ratios of $(T/(\phi r^2))^2 = 0.25, 5, 25\ \mathrm{kg^2\,m^{-2}\,s^{-4}}$ (black, dark gray, and light gray lines, respectively) which corresponds to wing lengths $r_{\mathrm{si}} = 0.01, 0.1, 0.33$ m using equation (12) to calculate mass m_{si} from r_{si} to calculate thrust $T = mg$. These example lines span the range from the smallest extant dragonfly, *Nannophya pygmaea* to the largest griffenfly, *Meganeuropsis permiana*. All the ratios start at the same point during hovering and asymptote to the same ratio at high speed. Thus, bounds (20) and (21) can be established for the effect of air density on induced power at all forward flight speeds.

where ρ is the air density, v is the airspeed relative to the body and C_{d} is the coefficient of drag of the body, which may itself depend on Reynolds number. Thus, higher air density could be expected to increase parasite power unless mitigated by a corresponding decrease in the speed. The goal here is not to estimate the relative contributions of each of these effects but rather to note that the effects of higher air density would have raised parasite drag and thus not have favored larger flyers.

Profile power is the aerodynamic power required to flap the wings. Similar to parasite power, profile power is also a function of air density multiplied by several other variables as given in equation 29 of Ellington (1984). Since Sane and Dickinson (2001) found that equations 8 and 9 in Ellington (1999) for profile power give underestimates, we will use the simpler equation 10 in Ellington (1999), which gives considerably higher values, to estimate profile power. By comparing that equation 29 with equation 10 in Ellington (1999), we infer an approximate air density adjustment term ρ/ρ_{isa} where we reference density to the international standard atmosphere, ρ_{isa}; then rearranging equation 6 in Ellington (1999) to solve for frequency and substituting in equation 10 of Ellington (1999), profile power is:

$$P_{\mathrm{pro}} = 17\frac{\rho}{\rho_{\mathrm{isa}}}\frac{\sqrt{\mathcal{R}}}{\sqrt{C_l}}\frac{m^{3/2}}{r}. \tag{16}$$

Because the density term is in the numerator, the profile power will also have been higher during the Carboniferous unless griffenflies used compensating changes in the other flight variables. Thus neither profile power nor parasite power will have tended to make flight easier in the Carboniferous. Conventionally, profile power is taken to be independent of speed. If we use the scaling relation (12) to substitute for mass in equation (16) and use the following assumptions: $C_{\mathrm{l}} = 1$, $\mathcal{R} = 10$ with the Carboniferous air density and use the reported wing length for *Meganeuropsis permiana* of $r_{\mathrm{si}} = 0.33$ m then equation (16) gives a profile power of $P_{\mathrm{pro}} = 3.4$ W. For comparison, the induced power from equation (13) is $P_{\mathrm{i,c}} = 1.9$ W. In fruit flies, aerodynamic power is dominated by profile power (Sane and Dickinson, 2001). Similarly, in an example closer in size to griffenflies, a flapping robot (Lee et al., 2022) with 0.14 m wings had measured aerodynamic power and implied induced power in a 5:1 ratio. A study of damselfly and dragonfly flight (Wakeling and Ellington, 1997) measured equal profile and induced powers with both powers increasing with increasing airspeed. The implication here is that profile power may be as large or larger than induced power. Inspection of equations (13) and (16) shows that profile power increases faster with increasing air density than does induced power. Thus, during the Carboniferous the lower power afforded by the reduced induced power might have been offset by the larger profile power.

To complete the picture of aerodynamic power, we next develop equations for induced power during level flapping forward flight. The classical analysis of level flight at speed v has the actuator disc at a small angle below the horizontal and then the thrust is:

$$T = 2\rho\phi r^2 v_{\mathrm{i}}\sqrt{v^2 + v_{\mathrm{i}}^2}, \tag{17}$$

where ϕr^2 is the area swept out by the wings and v_{i} is the induced velocity. Rearrange equation (17) to find v_{i} and substitute in equation (18) to find induced power:

$$P_{\mathrm{i}} = Tv_{\mathrm{i}} = \frac{T}{\sqrt{2}}\sqrt{-v^2 + \sqrt{\left(\frac{T}{\rho\phi r^2}\right)^2 + v^4}}. \tag{18}$$

This induced power formula becomes the standard hovering equation (1) when v is zero and the induced power declines in the classic fashion as v increases; induced power required to generate a given thrust is greater in modern than in Carboniferous atmospheres at all speeds (Fig. 4B). We can use equation (18) to calculate the ratio of induced power in a Carboniferous flyer to induced power in a modern flyer $P_{\mathrm{i,c}}/P_{\mathrm{i,m}}$ by making substitutions for the observed scaling of mass with wing length (12) and substitutions for the relevant densities (4). Fig. 4C shows that ratio as a function of flight speed for flyers with the observed scaling of mass and wing length with three wing lengths spanning the range from the smallest dragonfly to the largest griffenfly. The ratio is larger at a given speed for larger flyers but is bounded at an airspeed of zero and at high air speeds.

That bound can be mathematically demonstrated by recasting the ratio in isometric terms and taking limits as speed goes to zero and infinity. That ratio of induced power of a Carboniferous flyer to induced power in a modern flyer with substitutions to model isometric scaling is:

$$\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}} = \frac{l_{\mathrm{c}}^3 g\sqrt{-v^2 + \sqrt{\left(\frac{l_{\mathrm{c}}^3 g}{\rho_{\mathrm{c}} l_{\mathrm{c}}^2}\right)^2 + v^4}}}{l_{\mathrm{m}}^3 g\sqrt{-v^2 + \sqrt{\left(\frac{l_{\mathrm{m}}^3 g}{\rho_{\mathrm{m}} l_{\mathrm{m}}^2}\right)^2 + v^4}}}. \tag{19}$$

This ratio decreases with increasing v, and is higher with greater thrust per swept wing disc area ($T/(\phi r^2)$; Fig. 4C). The limits of this ratio at the speed extremes, evaluated at our model air densities, are:

$$\lim_{v\to 0}\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}} = \frac{l_{\mathrm{c}}^{7/2}\rho_{\mathrm{m}}^{1/2}}{l_{\mathrm{m}}^{7/2}\rho_{\mathrm{c}}^{1/2}} = 0.91\frac{l_{\mathrm{c}}^{7/2}}{l_{\mathrm{m}}^{7/2}} \tag{20}$$

$$\lim_{v\to\infty}\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}} = \frac{l_{\mathrm{c}}^{4}\rho_{\mathrm{m}}}{l_{\mathrm{m}}^{4}\rho_{\mathrm{c}}} = 0.83\frac{l_{\mathrm{c}}^{4}}{l_{\mathrm{m}}^{4}} \tag{21}$$

where (20) is the same as the power ratio for hovering in (7). Equations (20) and (21) give upper and lower bounds for the ratio of induced power for hovering as well as power across a range of flying speeds in arbitrary units during the Carboniferous and modern times. By setting these power ratios, as we did previously in equations (8) and (9) and solving for l_{c} we can similarly estimate how much larger a flyer could be for a given ratio of induced powers. For a rapid flyer, benefiting from maximum reduction in induced power due to their airspeed (21) we find:

$$l_{\mathrm{c}} = l_{\mathrm{m}}\left(\frac{P_{\mathrm{i,c}}}{P_{\mathrm{i,m}}}\right)^{1/4}\left(\frac{\rho_{\mathrm{c}}}{\rho_{\mathrm{m}}}\right)^{1/4} = l_{\mathrm{m}}(1)^{1/4}\left(\frac{1.56}{1.29}\right)^{1/4} = 1.05 l_{\mathrm{m}}. \tag{22}$$

Therefore, the increase in linear size due to the reduction in induced power in higher density air is maximally about 5% at speed in level flight.

We have thus far used ratios of power to determine how much larger an odonatopteran flyer could be in the Carboniferous than in the modern atmosphere either assuming equal power available in the Carboniferous and modern flyer (e.g. equations (8) and (22)); alternatively we assumed an ratio of available power based on the ratio of oxygen in the atmosphere (e.g. equations (9) and (11)). But a larger flyer might be expected to have room for a larger wing muscle system that might deliver more power. Now we will assume a scaling in the available power from flight muscle. There is some variability in assumptions about how such power availability from muscles scales. One conventional prediction of scaling derives from the assumption that energy is proportional to muscle mass and that the rate of muscle contraction is proportional to wingbeat frequency. Assuming isometry, $m \propto l^3$ and assuming frequency, $f \propto l^{-1/2}$, then the available power is $P_{\mathrm{avail}} \propto mf \propto l^{5/2}$ (e.g. Pennycuick (1989, 1992)). Then, assuming energy proportional to oxygen concentration and with density assumptions (4),

$$l_{\mathrm{c}} = l_m \left(\frac{35}{21} \frac{l_{\mathrm{c}}^{5/2}}{l_{\mathrm{m}}^{5/2}} \right)^{2/7} \left(\frac{\rho_{\mathrm{c}}}{\rho_{\mathrm{m}}} \right)^{1/7} = 1.8\, l_{\mathrm{m}}. \tag{23}$$

But a higher possible scaling with muscle-mass specific scaling of 0.24 has been reported (Schilder and Marden, 2004) in a study using several species of dragonflies, which, assuming muscle mass scales isometrically with flyer mass, would suggest an available power scaling of $P_{\mathrm{avail}} \propto m^{1.24}$. Similarly, $P_{\mathrm{avail}} \propto m^{4/3}$ has been suggested and $P_{\mathrm{avail}} \propto m^{1.13}$ has been interpreted from data from a range of flying animals (Ellington, 1991). More conservatively, assuming simply that power scales with flyer mass, $P_{\mathrm{avail}} \propto m \propto l^3$, and density assumptions (4), predicted length of griffenflies relative to extant odonates is:

$$l_{\mathrm{c}} = l_m \left(\frac{35}{21} \frac{l_{\mathrm{c}}^{3}}{l_{\mathrm{m}}^{3}} \right)^{2/7} \left(\frac{\rho_{\mathrm{c}}}{\rho_{\mathrm{m}}} \right)^{1/7} = 3.4\, l_{\mathrm{m}} \tag{24}$$

Note that this last equation would predict the actual sizes of the largest griffenflies relative to the largest extant odonates, but requires muscle power production to scale with mass. It will be imperative to test whether such scaling can be observed in extant odonates. It is also noteworthy that the analysis is highly sensitive to this last assumption about the scaling of muscle power. The reason for this sensitivity is that the scaling of muscle power with flyer mass may be nearly of the same order as the scaling of induced power (scaling with $m^{3/2}$, as in equations (2) or (13)) during hovering and to profile power as in equation (16). When scaling laws are nearly of the same order, small changes in the scaling will predict large changes in relative size. If the scaling of available muscle power is as high as Schilder and Marden (2004) and Ellington (1991) suggest, there might be no implied calculable limit to the size of griffenflies. Measuring the relevant scalings of muscle and flight powers is imperative and may allow reconstruction of the likely flight habits of griffenflies.

Discussion

Our analysis of power during hovering and during level flapping flight suggest that Paleozoic air densities would have facilitated only slight size increases among extinct odonatopterans. Changing air densities would have failed to provide the power necessary to support extreme gigantism in the largest Carboniferous griffenflies. As a result, we conclude that the aerodynamic effects of higher Paleozoic oxygen levels would have been minimal. This calls into question the aerodynamic significance of atmospheric oxygen for insect gigantism. It also suggests that steady-state flapping flight may have been less energetically feasible for the largest griffenflies under the assumed scaling regimes, as higher air densities would have only slightly reduced the power required for meganeurids to stay aloft despite their mass.

This result may seem surprising, since air density has been shown to influence insect flight metabolism. Indeed, insects flown at low air densities expend more energy to maintain the same induced power during flight (Henry and Harrison, 2014). However, that study noted that dragonflies are less sensitive to this effect than bees, and speculated that perhaps this lesser sensitivity was due to the smaller wing beat frequencies, stroke amplitudes, and wing-loadings of the dragonflies. If larger meganisopterans, like *M. monyi*, had lower wing beat frequencies and stroke amplitudes than modern odonates, they might be even less sensitive to changing air densities—again challenging the aerodynamic significance of Paleozoic oxygen for griffenfly size.

In the absence of aerodynamic support from air density, Paleozoic meganeurids may have compensated for their large size by either increasing positive allometry in wing length, or employing different flight patterns than modern large odonates——i.e., flight patterns that require less power, perhaps with a greater reliance on gliding. This is consistent with their recent interpretation as less maneuverable aerial predators (Nel et al., 2018), along with earlier claims that they relied primarily on gliding (as discussed in Wootton and Kukalová-Peck (2000)). Indeed, meganeurids lacked many of the smart-wing features associated with versatile flight in modern odonates, including the wing nodus and arculus, which assist in bracing the wing against aerodynamic stresses and maintaining camber (Wootton and Kukalová-Peck, 2000). In addition, modern dragonflies flown in hypoxic conditions conserve energy by performing fewer and shorter flights (Henry and Harrison, 2014). Following previous interpretations, *M. monyi* may have compensated for its large size by gliding or otherwise adjusting its flight behavior, with little help from its denser flight medium. We encourage future studies to expand the present model to account for behavioral and anatomical modifications, such as gliding maneuvers, adjustments to stroke amplitude or wing beat frequency, and changes in wing aspect ratio, that might help to explain how the largest meganisopterans stayed airborne.

We emphasize that while the foregoing discussion questions the impact of oxygen on induced power during hovering and level flapping flight, it does nothing to challenge the potential physiological effects of elevated oxygen content (e.g., (Polet, 2011; Okajima, 2008; Verberk and Bilton, 2011)). Additional work is needed to model the impact of air density on physiological models examining oxygen transport and metabolic rate (Okajima, 2008), steady-state flapping flight, and non-steady effects in flapping flight (e.g., (Vogel, 1994; Freymuth, 2007)). Additional work placing changes in odonatopteran size, wing morphology, and induced power into a precise phylostratigraphic context with changing air density, temperature, and fossil occurrence data for pterosaurs and avialans could also help to disentangle the contributions of different biotic and abiotic factors to odonatopteran size.

Actuator disk model limitations

There are several limitations to this model. Firstly, we used an actuator disk model of flapping flight with a wing incline at 0° from horizontal (Wakeling and Ellington, 1997) during hovering and only a small angle below horizontal during level forward flight; in contrast, many sampled dragonflies have a stroke plane tilted downward 60° from the horizontal (body) axis (Freymuth, 2007; Norberg, 1975), although both the damselfly and the dragonfly in Wakeling and Ellington (1997) have stroke planes nearly perpendicular to the thrust vector similar to the assumptions in the present paper. Secondly, the model above, like classical propeller models, also assumes steady-state flight, in which induced power and lift remain essentially constant throughout the wing stroke cycle (Sane, 2003). However, in reality, most odonatopterans beat their fore and hindwings out of phase and change both their pitch and direction throughout the stroke cycle, leading to complex, unsteady flow patterns (Wootton and Kukalová-Peck, 2000; Vogel, 1994). These unsteady effects often delay wing circulation between strokes. As a result of these discrepancies, in both wing incline angle and wingbeat phase, steady-state actuator disk theory tends to overestimate lift coefficients (Freymuth, 2007). A more complete and specific aerodynamic model would be desirable to test the validity of our less-specific model of flight.

The models of scaling of induced power, profile power, and parasite power provide broad insight but there are some specific areas that bear further investigation. (1) We have only imprecise estimates of the relative size of induced, profile, or parasite power as functions of size and airspeed. Functions describing these parameters are needed to explore the parameter space to understand how griffenflies might have moved. (2) Our model does not consider how patterns of flapping might change the analysis; comparison between damselfly and dragonfly flight routines or trends of flight pattern with size might be informative. (3) Although we focused on the broad brush analyses available from actuator disc theory we supplemented with some analyses (Ellington, 1984, 1999) that include variables such as frequency and wing amplitude; but the current formulations of those formulas do not lead to predictions of how variables such as frequency and amplitude might covary. Such covariance merits investigation. (4) Our model of flight forces is based on a long-standing practice of dividing the flight power into components but the actual accounting based on the underlying Navier-Stokes equations has no such components. Modern computational methods allow more precise modeling of flow and an approach based on those equations might reveal more precise scaling relations. Examples of recent approaches to such calculations are: Bode-Oke et al. (2018); Bomphrey et al. (2016). (5) We have not considered heat generation by flight muscles and the potential problems of heat loss in large griffenflies.

Our calculations focused on the effects of air density on induced power during hovering or steady level flight. We showed that, even in combination with higher oxygen concentration and known allometry, higher air density could explain only slight size increases in griffenflies, i.e. $\approx 20\%$ (red arrows Fig. 1). Changes in flight patterns with size might reduce power required at the largest sizes, and muscle power scaling may have helped to support the largest griffenflies, but our current understanding of such power scaling in flight muscles is still incomplete and uncertain. In particular, it is unclear whether the muscle power scaling observed in extant dragonflies could be extrapolated to griffenflies given the possibly competing space requirements of the tracheal system. But our calculations suggest that muscle power scaling with $P_{\text{avail}} \propto m^1$, together with increased oxygen concentration and lower induced power requirements could be enough to explain the largest griffenflies. Future research on this problem would do well to determine whether such muscle power scaling is plausible.

Conflict of interest

There are no conflicts of interest inherent to this work.

Supplementary data

Supplementary data is available at Table S1

Author contributions

O.E., C.G., M.H. and A.K. conceived of the project and developed the mathematics. A.C. and A.N. contributed to the mechanical, geological, paleontological and phylogenetic context.

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