

The controlling factors limiting maximum body size of insects

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The purpose of this study is to consider the controlling factors limiting maximum body size of insects. For this analysis, we set up and quantitatively verify the following working hypothesis: insect body sizes can be explained only by the historical changes in the oxygen supply. The present study focuses on the body size of the Protodonata and Odonata. The amount of oxygen needed and that of oxygen entering the insect body was calculated using allometric equations. The theoretical maximum sizes at each geologic time were estimated from palaeo-atmospheric oxygen partial pressure and compared with the maximum size of known fossilized insects. The historical change in fossilized insect sizes was much larger than that in theoretical sizes. Additionally, from the Jurassic, despite an increase in the partial pressure of oxygen, which would theoretically increase maximum size, the maximum size of fossilized insects became smaller. These findings are inconsistent with the expectations of the working hypothesis. Oxygen supply is likely to partially limit the maximum size of insects with additional factors. □ *Allometry, body size, fossil, insect, Odonata, oxygen, Protodonata.*

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The maximum body size of living insects is limited, despite their morphological diversity and the presence of Palaeozoic gigantism. The wing length of the largest insect through the Phanerozoic period, Permian Protodonata (*Meganeuropsis permiana*), is 330×10^{-3} m (Carpenter 1939), whereas the wing length of the largest living dragonfly, *Petalura ingentissima*, is only 81×10^{-3} m (Silsby 2001). Several studies have been conducted to clarify the limiting factors in this phenomenon. Weis-Fogh (1964) insisted that body size limits were imposed by respiratory systems dependent on diffusion, i.e. the tracheal systems, which are different from mammalian respiratory systems. In insects, the main sources of oxygen in tissues are air-filled cuticular tubes called tracheoles, which branch from larger tubes called tracheae. The tracheae interface with the atmosphere through paired, valved openings called spiracles. This system may limit the body size of insects because the net rate of oxygen mass transport by diffusion is inversely proportional to the distance of diffusion. Graham *et al.* (1995) and Dudley (1998) showed that Palaeozoic insect gigantism and extant insect sizes can be qualitatively explained together by adding the elevation of atmospheric oxygen to Weis-Fogh's hypothesis. 'An increased global oxygen supply during the Mid-Devonian to late Carboniferous period would have enhanced diffusion-dependent processes such as respiration. Accordingly, certain organisms could attain a larger body size.'

This famous hypothesis has been supported by some experimental studies. Harrison & Lighton (1998) provided evidence for oxygen limitation of flight metabolism in a free-flying insect. This suggests that atmospheric hyperoxia could facilitate insect gigantism. Moreover, Berner *et al.* (2003) showed that the body mass of fruit flies (*Drosophila melanogaster*) increased following five generations of growth in chronic hyperoxia and hyperbaria.

On the other hand, some results negating the effect of oxygen diffusion on insect size also have been reported. Loudon (1989) showed the plasticity of insect tracheae in response to changes in oxygen concentration. Larval *Tenebrio molitor* (Insecta) were reared in different levels of oxygen (10.5, 15, 21%, all at 101.3 kPa total pressure) and the main tracheae (branching off from the spiracular tracheae) had a greater cross-sectional area at a lower concentration of ambient oxygen. The magnitude of the hypertrophy is consistent with maintenance of a fixed rate of oxygen delivery by diffusion. The plasticity can decrease or even cancel oxygen restrictions on insect body size. Moreover, the unknown mechanism of insect respiration observed by Westneat *et al.* (2003) showed the necessity to reappraise the importance of diffusion in insect respiratory systems. The new mechanism exhibited rapid cycles of tracheal compression and expansion in the head and thorax, and it could not be accounted for by any other known

Table 1. List of abbreviations.

a_1	–	Exponent
a_2	–	Exponent
a_3	–	Exponent
A_t	$[m^2]$	The summed cross-sectional area of tracheal system
C_0	$[mW(Pa)^{-1}(kg)^{-\frac{2}{3}}]$	Constant proportionality
C_1	$[mol(sW)^{-1}]$	Constant proportionality
C_2	$[mol(sPam)^{-1}]$	Constant proportionality
C_3	–	Constant proportionality
C_4	$[(m)^2(kg)^{-\frac{2}{3}}]$	Constant proportionality
C_5	$[m^{(1-a_1)}]$	Constant proportionality
C_6	$[kg(m)^{-a_2}]$	Constant proportionality
C_7	$[W(kg)^{-a_3}]$	Constant proportionality
D_t	$[m]$	The thoracic diameter
L_t	$[m]$	The mean length of tracheal system
L_w	$[m]$	The maximum length of single wing
M_b	$[kg]$	The total body mass
M_f	$[W]$	The flying metabolic rate
O_2e	$[mol/s]$	The net rate of oxygen mass entering insect body
O_2n	$[mol/s]$	The net rate of oxygen mass needed by insect
ΔP_{O_2}	$[Pa]$	The total difference in oxygen partial pressure

mechanisms, such as abdominal pumping, autoventilation and circulatory fluid motion. Other studies suggested additional limiting factors for insect size. One possible explanation is that the gigantism of insects could be caused by an ‘arms race’ between predator and prey, and that this process was ended by the emergence of other much larger predators – larger vertebrates (Vermeij 1987; Shear & Kukulová 1990). Atmospheric temperature and density are also possible factors that could affect body size (Dudley 1998; Makarieva *et al.* 2005). However, no studies have been carried out to quantitatively verify each of these hypotheses as ‘whether historical changes in fossilized insect sizes can be explained by these factors’. These factors can compositely work on insect size, and it makes revealing the limiting factor for insect size more difficult. It is therefore necessary to test first the presence of each factor’s effect and to determine its magnitude.

Then, this study set up and was performed to theoretically and quantitatively verify the following working hypothesis: insect body sizes can be explained only by a historical change in the oxygen supply. The theoretical maximum size at each geologic time are estimated from palaeo-atmospheric oxygen partial pressure and compared with the maximum size of known fossilized insects. If actual patterns in fossil records are in good agreement with theoretical patterns, the preceding working hypothesis is supported. In

contrast, if these show incongruence, the hypothesis is contradicted and other factors should be considered.

The model

General expressions of theoretical body size

All abbreviations used in this study are listed in Table 1. The present study focuses on Protodonata and Odonata. Protodonata is an extinct group which have the all-time largest insect and Odonata is the nearest extant group of it. In this study, they are treated as a single group because little is known about the Protodonata.

Let us consider the net rate of oxygen mass entering the insect body and the net rate of oxygen mass needed by the insect. The former is denoted by O_2e (mol/s) and the latter is denoted by O_2n (mol/s). Although there are few studies investigating the allometric relationship between O_2n and other traits, the metabolic rate is known to have an allometric relationship with O_2n . Because the metabolic rate is measured by oxygen consumption (e.g. May 1979), O_2n is given by equation (1):

$$O_2n = C_1 M_f \quad (1)$$

where C_1 is the constant of proportionality and M_f (W) is the metabolic rate during flight. Second, let us

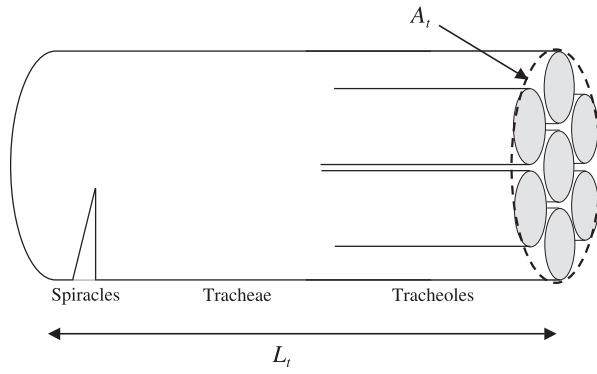


Fig. 1. Schematic diagram of the insect tracheal system. A_t is the summed cross-sectional area (m^2) and L_t is the mean length (m) of tracheal system. It was drawn by modifying fig. 1 in Loudon (1989).

consider the entering oxygen (O_2e). Although insect respiration includes not only passive gas diffusion but also active convection, only diffusional O_2e is estimated in this study. It is impossible to estimate the convective O_2e , because there is little information about the magnitude and mechanism of convection during insect respiration. If the insect tracheal system is treated as a conglomerate circular cross-section cylinder which has the summed cross-sectional area A_t (m^2) and the mean length L_t (m) (Fig. 1), then O_2e is described by Fick's law as (Loudon 1989):

$$O_2e = C_2 \Delta P_{O_2} \frac{A_t}{L_t} \quad (2)$$

where C_2 is the constant of proportionality and ΔP_{O_2} (Pa) is the total difference in oxygen partial pressure between the ambient and mitochondria. If the partial pressure of oxygen at the mitochondria is taken to be zero (Jones *et al.* 1985), then $\Delta P_{O_2} = P_{O_2,ambient} - P_{O_2,mitochondria} \cong P_{O_2,ambient}$ (Loudon 1989). The diffusion coefficient is approximated to be constant, and thus it can be included as a constant of proportionality (C_2). The diffusion coefficient for oxygen will actually be positively associated with atmospheric density and negatively with temperature, but our understanding of palaeo-atmospheric density and temperature is too limited to express them numerically. Similarly, palaeo-atmospheric total pressure is unknown, and thus there is no choice but to assume that total pressure has been constant and equal to the modern value of one: 100 kPa (see Discussion).

Next, we rewrite equations (1) and (2) as scaling laws (allometric equations) by insect body size. Since insect bodies are hardly preserved as fossils with the exception of their wings, throughout this study the maximum length of a single wing (L_w (m)) was used as an indication of body size.

The length and cross-sectional area of the tracheal system is largely unknown. Therefore, I introduce the following assumptions with considering dimensionally homogeneous:

$$L_t = C_3 D_t \quad (3)$$

$$A_t = C_4 M_b^{\frac{2}{3}} \quad (4)$$

where C_3 and C_4 are constants of proportionality, D_t (m) is the thoracic diameter and M_b (kg) is the insect body mass. Because the gas exchange apparatus of insects is distributed along their length, thoracic diameter may be crucial for oxygen availability in insects of variable shape.

Equations to calculate D_t , M_b and M_f are as follows:

$$D_t = C_5 L_w^{a_1} \quad (5)$$

$$M_b = C_6 L_w^{a_2} \quad (6)$$

$$M_f = C_7 M_b^{a_3} \quad (7)$$

where C_5 , C_6 and C_7 are constants of proportionality, and a_1 , a_2 and a_3 are exponents (see equations 11, 12 and 13). Inserting these equations into equations (1) and (2), we obtain the general expressions by L_w for O_2n and O_2e :

$$O_2n = C_1 C_7 (C_6 L_w^{a_2})^{a_3} \quad (8)$$

$$O_2e = \frac{C_2 C_4 (C_6 L_w^{a_2})^{\frac{2}{3}}}{C_3 C_5 L_w^{a_1}} P_{O_2,ambient} \quad (9)$$

Finally, the theoretical maximum size is expressed by equation (10), combining equations (8) and (9); it is the size at which O_2e becomes equal to O_2n .

$$L_w = \left(\frac{C_2 C_4}{C_1 C_3} \left(C_5 C_6^{a_3 - \frac{2}{3}} C_7 \right)^{-1} P_{O_2,ambient} \right)^{\frac{1}{\left(a_2 \left(a_3 \frac{2}{3} \right) + a_1 \right)}} \quad (10)$$

Allometric equations

The parameters C_5 , C_6 , C_7 , a_1 , a_2 and a_3 were computed by regression analyses using empirical data from modern Anisoptera (May 1979, 1981) (Table 2). The units of measurement in May (1979) were M_f (W) and M_b (kg), and that in May (1981) were D_t (cm), L_w (cm) and M_b (g). If these are altered into D_t (m), L_w (m), M_b (kg) and M_f (W), we get following equations.

$$D_t = 0.2125 L_w^{1.063} \quad (11)$$

Table 2. Data used to estimate tracheal diameter, body mass and flying metabolic rate (equations 11, 12 and 13).

Equation numbers	Taxa	Sample size	R^2	Reference
11	Odonata (Anisoptera)	109 (29 species)	0.918	May (1981)
12	Odonata (Anisoptera)	111 (29 species)	0.917	May (1981)
13	Odonata (Anisoptera)	15 (15 species)	0.91	May (1979)

The units of measurement in May (1979) were $Mf(W)$ and Mb (kg), and that in May (1981) were Dt (cm), Lw (cm) and Mb (g). Let these units be altered into Dt (m), Lw (m), Mb (kg) and Mf (W), we get equations (11), (12) and (13).

$$M_b = 1.853L_w^{2.586} \quad (12)$$

$$M_f = 166M_b^{1.01} \quad (13)$$

Equation (11) was obtained from 109 data for males of 29 species of Anisoptera ($R^2 = 0.918$) and (12) was obtained from 111 data for them ($R^2 = 0.917$) (May 1981). Equation (13) was obtained from 15 data for 15 species of dragonflies ($R^2 = 0.91$) (May 1979).

Theoretical body size and fossil records

By substituting equations (11), (12) and (13) into equation (10), and by representing unknown coefficients C_1 , C_2 , C_3 and C_4 as a single coefficient C_0 , we have equation (14):

$$L_w = (2.294 \cdot 10^{-2} \times C_0 P_{O_2, ambient})^{0.5126} \quad (14)$$

Since the value of C_0 cannot be estimated, the difference in L_w is expressed not by an absolute value, but by relative values of two standards: the C_0 value calculated from *M. permiana* (all-time largest) and that from *P. ingentissima* (modern largest). Several attempts have been made to estimate the $P_{O_2, ambient}$ through the Phanerozoic period (e.g. Lasaga 1989; Berner 2001). This study obtained the value of $P_{O_2, ambient}$ per 10 million years from Berner (2003) summarizing previous works. When *M. permiana* was used as a standard, $C_0 = 1.4 \times 10^{-1}$ was obtained by substituting $P_{O_2, ambient} = 35$ and $L_w = 330 \times 10^{-3}$ into the equation (14). Namely, the value for C_0 is determined by assuming the size of *M. permiana* ($L_w = 330 \times 10^{-3}$) is the upper limit of the Permian atmosphere ($P_{O_2, ambient} = 35$) allowed and C_0 is constant through the Phanerozoic period. When *P. ingentissima* was used as a standard, $C_0 = 1.5 \times 10^{-2}$ was obtained by substituting $P_{O_2, ambient} = 21$ and $L_w = 81 \times 10^{-3}$ into the equation (14). Finally, the theoretical upper limits (L_w) and the temporal changes in these values were obtained by substituting the C_0 and $P_{O_2, ambient}$ (Curves 1 and 2) (Fig. 2).

The 95% confidence interval of L_w was obtained by the bootstrapping procedure. Data were randomly selected from the original dataset without avoiding

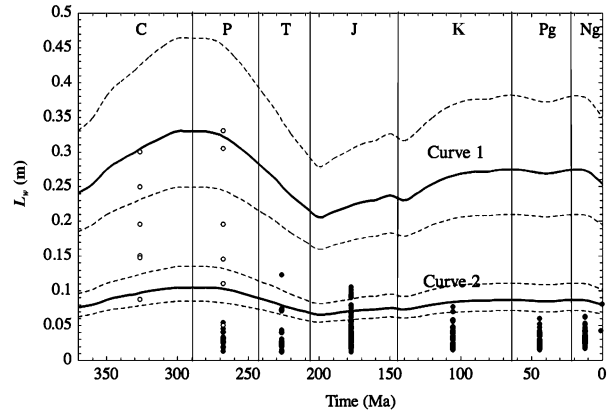


Fig. 2. Comparisons between theoretical and empirical maximum sizes in dragonflies. Solid curves show the upper limits of insect size (L_w) imposed by oxygen partial pressure, which is calculated from equation (14). Curve 1 is standardized on *M. permiana*, and Curve 2 is standardized on *Petalura ingentissima*. Dashed curves show 95% confidence intervals. Body size (wing length) of fossil Protodonata (\circ) and Odonata (\bullet) are plotted against geologic age; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; Ng, Neogene (not absolute age). Ma, millions of years before the present. The modern maximum dragonfly size (*P. ingentissima*, $L_w = 81 \times 10^{-3}$ m) is also plotted as a filled circle. The number of fossil Protodonata are 12 and the number of fossil Odonata are 240 (Bechly 2000a, b, 2001, 2003, 2005; Bechly & Ueda 2002; Bechly *et al.* 2003; Brauckmann & Zessin 1989; Brongniart 1884; Carle & Wighton 1990; Carpenter 1932, 1933, 1939, 1943, 1947, 1992; Fleck *et al.* 2001, 2004; Fraser 1955; Gentlini 1988, 1992; Gentlini & Peters 1993; Hagen 1858, 1861–1863, 1862, 1866; Hugué *et al.* 2002; Jarzembowski 1988, 1990, 1994; Jarzembowski & Nel 1996; Kennedy 1931; Martínez-Delclòs & Nel 1991; Martynov 1927, 1929; Needham 1907; Nel 1991, 1992; Nel & Brisac 1994; Nel & Escuille 1992, 1993, 1994; Nel & Henrotay 1992; Nel & Martínez-Delclòs 1993; Nel & Paicheler 1992, 1994a, b, c; Nel & Papazian 1990; Nel & Petrulėvičius 2005; Nel *et al.* 1993, 1996, 1998, 2001, 2005a, b, c; Papazian & Nel 1989; Petrulėvičius & Nel 2005; Pritykina 1968, 1970, 1977, 1981; Prokop & Nel 2002; Schmidt 1958; Schumann 1967; Scudder 1892; Sellards 1906; Tillyard 1922, 1924, 1925; Ueda *et al.* 2005; Whalley 1979, 1980; Zalessky 1955; Zessin 1983; Zhang *et al.* 2006; Zhang 1992).

duplication until the number of selected data became equal to the number in the original data set. Ten thousand replicates of the datasets were produced by repeating the above process 10 000 times. A regression analysis was carried out for each replicate. The values of C_5 , a_1 , C_6 and a_2 of the equations (5) and (6) were obtained and L_w were calculated by substituting these

values in equation (10) for each replicate. Note that the 95% confidence interval of L_w computed does not include errors in the calculation of M_f (equation 7), because the data set to calculate M_f has only 15 points, which is not enough to perform the bootstrapping method (see discussion). Empirical data showing historical changes in body size (wing length) in fossilized dragonflies were compared with that of theoretical L_w . The wing length of fossil data is the length of either the forewing or hindwing, because it is very rare to find both the forewing and hindwing of a single insect in the fossil record. However, the difference of the length between the forewing and hindwing was negligible as an index for body size. For the species for which both forewing and hindwing fossils exist, the average of their lengths was used as the indication of body size.

The values of theoretical L_w were compared with the maximum size of fossilized dragonflies (Fig. 2). When C_0 was determined using *M. permiana* (Curve 1), the theoretical values of the maximum size were much larger than the empirical values of the maximum size from the Mesozoic to modern periods. When C_0 was determined using *P. ingentissima* (Curve 2), the theoretical values of the maximum size were much smaller than the empirical values of the maximum size before the Jurassic. In all standards, the important findings in Figure 2 are as follows. The historical change in fossilized insect size is much larger than the theoretical one. Additionally, from the Jurassic, despite an increase in the partial pressure of oxygen and the corresponding increase in theoretical insect size, fossil sizes became smaller. These findings are inconsistent with the expectations of the working hypothesis.

Discussion

The present study suggests that historical changes in insect size cannot be explained by only historical changes in oxygen supply. This incongruence of the empirical patterns of changes in body size and expected patterns of that based on oxygen supply may be partially explained by the incompleteness of the fossil record of dragonflies. However, incongruence of the maximum size between the Palaeozoic fossilized Protodonata and the expected maximum size in the Palaeozoic (Curve 2) cannot be explained by the incompleteness of the fossil records, because it is estimated by body size distribution of modern dragonflies and oxygen supply in the Palaeozoic.

In the present estimation of L_w , errors due to variations in the relationship between body mass and flight metabolic rate (M_f , equation 13) are not

included, because the sample size used is too small to obtain the range of errors by the bootstrapping procedure. However, the error caused by the variations in this relationship is likely small, because body mass and metabolic rate are known to have a clear relationship, and the correlation coefficient obtained for the dragonflies samples is very high ($R^2 = 0.91$). Thus, the maximum size of insects is not determined only by the limitation of oxygen supply. Nevertheless, the possibility of the effect of oxygen supply on the sizes of fossil dragonflies cannot be entirely excluded, because there are some experimental studies that support the effect of oxygen on body size (Harrison & Lighton 1998; Berner *et al.* 2003), and because Curve 1 corresponds to the body sizes of the fossils from the Carboniferous to the Permian. Therefore, oxygen supply is likely to partially limit the maximum size of insects with additional factors.

Factors that can affect the maximum body size of dragonflies are (1) convection in insect respiratory systems; (2) atmospheric density and temperature; (3) the difference of body form between Odonata and Protodonata; and (4) influence of flying vertebrates.

Even if insect respiratory systems depend on oxygen convection, an increase in the partial pressure of oxygen can enhance the oxygen supply of insects, and it can make insect sizes larger. If the effect of oxygen convection is considered, the range of fluctuation in theoretical curves becomes smaller than in Figure 2.

The present analysis neglects the influence of density and temperature by assuming that they have been constant through time, due to the limitation in information regarding the palaeo-atmosphere. However, temperature and density can change the diffusion coefficient. For example, they can change C_2 in equation (2). Additionally, the flying metabolic rate of the dragonfly (*Anax junius*) decreases with increasing ambient temperature (May 1995), and body length for the largest terrestrial poikilotherms becomes larger with increasing ambient temperature (Makarieva *et al.* 2005).

While the exact values of the total palaeo-atmospheric pressure are still unknown, it likely increased with an increase in the partial pressure of oxygen because oxygen levels vary on top of a constant atmospheric nitrogen levels. Then, the actual range of fluctuation in oxygen partial pressure should be larger than the value used in this analysis. A hyper-dense atmosphere facilitates flying behaviour (Dudley 1998) and may decrease oxygen demand. Moreover, a hyper-dense atmosphere can enhance oxygen diffusion, and can increase the oxygen supply. In summary, the range of fluctuation in theoretical curves becomes larger by adding the effect of atmospheric density to the verification.

Additionally, it is important that bodies of Protodonata were considerably smaller in proportion to their wings than extant Odonata (May 1982; Brauckmann & Zessin 1989). Thus, it is likely that Protodonata had lower total oxygen demand than the estimated value in this study. Figure 2 showed all giant dragonflies in the Palaeozoic that belonged to Protodonata and the minimum size of Protodonata was equal to the maximum size of Odonata in the Permian. The maximum size of Odonata even increased after the extinction of Protodonata. These findings suggest that there was a difference in niche requirements between the Protodonata and Odonata. However, the aim of this paper was to find the pure effect of the limitation of oxygen supply on insect size by neglecting the differences between taxonomic groups. Hence, in the beginning, the effect of oxygen needed to be verified without consideration of taxonomic differences. In following studies, the effects of taxonomic difference should be considered. Unfortunately, the latter verification is impossible because limited knowledge about the Protodonata.

Although the above factors can make the range of fluctuation in theoretical curves either larger or smaller, these cannot dissolve the contradiction of the temporal pattern of change between empirical and theoretical values of maximum body size since the Jurassic: the theoretical maximum size increases, whereas fossil records show a decrease in the maximum size. The emergence of flying vertebrates is suggested as the reason why insect sizes become smaller from the Triassic, especially from the Jurassic. Only insects can fly in the Palaeozoic, but the oldest known pterosaurs emerged in the Triassic (e.g. *Preondactylus*, Wild 1984) and birds emerged in the Jurassic period (*Archaeopteryx*, Fountaine *et al.* 2005). The respiratory systems of vertebrates can supply more oxygen mass than the tracheal systems of insects when body sizes are larger. If advantageous use of the oxygen supply makes flying vertebrates exceed insects as a predator or a competitor, insect sizes are limited to be small by flying vertebrates. Interaction among groups with similar lifestyles would be crucial factors that limit body size.

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