

Supporting Information

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SI Text

Insect Size Database. The database consists of more than 10,500 measured insect specimens, ranging in age from Serpukhovian (latest Mississippian, Namurian A) to latest Miocene. Modern insects were not included because the extant fauna is known considerably better than any fossil assemblage. All specimens were preserved as compression fossils; amber preservation was not included because of the strong temporal bias (only post-Jurassic) and bias toward small size. The largest insect from each 10-Myr bin is listed in Table S1. Bins with fewer than 50 specimens (70, 80, 210, and 220 Ma) were excluded from analyses.

The age of each insect locality was resolved to the finest possible stratigraphic level. Some localities could be dated precisely by radiometric dating of co-occurring volcanic units, particularly for Cenozoic volcanic maar lakes or volcanic-dammed lakes, such as Florissant, or through marine ammonite biostratigraphy in many Jurassic localities from Europe. Others, such as Mesozoic nonmarine localities in central Asia (e.g., Madygen, Shurab, and Karatau), are less finely resolved and were assigned to the midpoint of published age determinations. Localities were then assigned to 10-Myr-long bins (e.g., 145–155 Ma) for correlation with published atmospheric environmental oxygen concentration (pO_2) (1, 2) proxy records.

There is some uncertainty inherent in comparing the three records, each of which were obtained independently and based on slightly different timescales. The largest bias is during the Triassic because of the drastic lengthening of the Norian (3); we use a 228-Ma age for the Carnian-Norian boundary instead of 216.5 Ma in the timescale used in the GEOCARBSULF model (2). The result of this is to offset the maximum insect size about 10 Myr earlier than the oxygen peak.

The length of the wing, tegmen (Orthoptera and relatives, Blattodea and relatives, some Hemiptera), elytron (Coleoptera), or hemelytron (some Hemiptera) was recorded, along with the wing width and, if preserved, body length and body width. In groups with two pairs of wings (fore and hind wings), the larger of the two pairs was used. Sizes were taken from measurements directly reported in the systematic description or were measured from published illustrations if no size was given in the text. Many fossil wings are incomplete because of taphonomic degradation following the death of the insect, especially in the largest insects. Estimates of the original wing length were taken from the published description when provided, or extrapolated by us using wing length:width ratios from related taxa. All but one (undescribed Odonata IGM 8826) of the largest recorded insects from each time interval were either complete or had an estimated length provided by the taxon's author.

Allometric Scaling of Body Width and Volume. Because the distance over which oxygen must be transported is the key constraint, body radius, not wing length, is the physiologically relevant dimension. Wing length is a reasonable proxy for body size because it is highly correlated to body length ($r = 0.905$, $P < <0.001$) and body width ($r = 0.64$, $P < <0.001$). Although wing length is less precise than more physiologically relevant measurements, like body size, it is also less subject to distortion during compression and fossilization. Furthermore, body length and width are less commonly preserved, particularly in Paleozoic and Triassic fossils, which are predominantly isolated wings. We used allometric scaling equations calculated from complete fossil specimens to estimate body width (Fig. S1) and body volume (Fig. S2) for the majority of specimens preserved only as isolated wings. This approach

only works on groups that have an approximately cylindrical body geometry, as the dorso-ventral thickness of the body cannot be measured or estimated from 2D compression fossils. Nevertheless, there is a consistent decrease from larger width for a given wing length (Orthoptera) to narrower body width (Neuroptera), reminiscent of the insect physiognomy categories of Wheeler (4).

Sample Size Effects. Because the largest insects are uncommon, the fact that our dataset contains substantially more data in some Permo-Carboniferous bins than in many Meso-Cenozoic intervals could bias the record toward larger size. The presence of very large insects, larger than any Jurassic-Recent taxa, in the moderately or sparsely sampled 320-, 310-, and 290-Ma bins implies that observed size trends are solely an artifact of sample size variation. Potential effects of sample size differences were assessed in two ways: first, by randomly subsampling each bin at a quota of 100 specimens to achieve uniform sampling; and second, by randomly subsampling the same size distribution at the actual levels of each interval.

The uniform subsampling test was repeated 1,000 times for each 10-Myr bin and the mean size of the largest wing was calculated from the 1,000 trials. The subsampled sizes are substantially smaller than the raw data in the Paleozoic and Triassic, slightly smaller in the Jurassic, and virtually unchanged in the Cenozoic (Fig. S4). This pattern is partially the result of greater sampling in some Permo-Carboniferous bins but results more from the sparse number of very large insects. In the Cenozoic, many insects are close to the maximum size limit; in contrast, the largest Permo-Carboniferous wings are often 20–80 mm larger than the next biggest specimen.

Although uniform subsampling indicates that sample size effects do not bias the pattern, imposing a uniform quota exaggerates their impact and is not the most appropriate technique because it assumes that the original sampling was random. Our sampling was targeted to document the largest insects, not to achieve random coverage of all insect sizes, so is focused on large-bodied groups, such as Odonatoptera, Panorthoptera, and Neuroptera. Cenozoic bins could contain substantially more taxa by including more of the extremely diverse record of small-bodied Diptera, Hemiptera, Coleoptera, and Hymenoptera. Heavily sampled bins therefore reflect increased reporting of small- to medium-sized taxa, not more intense sampling overall, and the targeted sampling of the raw record is a closer approximation of true size trends than expected from simple random sampling of all insect fossils.

The size distribution of insect wing lengths is a broadly log-normal distribution, although truncated at small sizes because of intrinsic size limitations and taphonomic or collecting bias against the smallest taxa (<5 mm). We used maximum-likelihood estimation to calculate the mean and SD of the size-frequency distribution that best fit nearly 1,500 insect sizes in the 270- and 280-Ma bins, two of the most completely sampled intervals (Fig. S5). Fossil size data are not perfectly described by a log-normal distribution because the right tail, encompassing large insects, is relatively heavy, a pattern common among many animal groups (5). As such, random samples from this distribution will, on average, underestimate the actual maximum-recorded insect size. Nevertheless, comparison of relative differences in the maximum sizes subsampled from a single distribution with the observed pattern of maximum sizes can indicate whether observed maximum sizes reflect different levels of sampling of the same distribution.

Because actual size distributions are heavy-tailed compared with a log-normal distribution, the subsampled sizes underestimate the expected size at a given sampling quorum. Regardless, the pronounced changes in recorded size are substantially larger than the relatively flat results expected from subsampling the same distribution at different levels (Fig. S6). In particular, the largest Cenozoic insects are much smaller than expected from random sampling the same distribution that yielded giant Paleozoic insects.

Maximum-Likelihood Model Fitting. Models describing trends in wing length were fit using maximum-likelihood estimation using the package *bbmle* (6) in the statistical programming environment R (7). Maximum-likelihood methods simultaneously estimate the best-fit parameters of each model and compare multiple models using the bias-corrected Akaike information criterion (AICc) (8). The AICc value quantifies the degree of support for each model by balancing the goodness-of-fit (log-likelihood) against model complexity (the number of parameters), with the smallest value indicating the best fit. Values are reported here as ΔAICc , the difference between each model and the best-supported model. The AICc values can be converted into Akaike weights, which sum to one and indicate the relative degree of support for each model.

Three basic models were compared. Model 1 (“oxygen”) explains wing length as a function of atmospheric $p\text{O}_2$ throughout the entire history of insects, fitting the best slope and intercept to the wing length:oxygen relationship. Model 2 (“oxygen/140 Ma break”) fits the best slope and intercept only for the Carboniferous-Jurassic (320- to 140-Ma bins) and holds the slope constant at zero and fits the intercept for the Cretaceous-Recent.

This model enforces size stasis but allows a best-fit estimate of the wing length during that interval. Model 3 (“oxygen/140 Ma/90 Ma breaks”) fits slope and intercept for the Carboniferous-Jurassic (320- to 140-Ma bins) and enforces size stasis (slope = 0) but with different best-fit sizes (intercepts) for the Cretaceous and Cenozoic. Model 4 (“oxygen/200 Ma/140 Ma/90 Ma breaks”) adds an additional break between 230 and 200 Ma (Late Triassic) and allows the intercept to vary with constant zero slope for the Jurassic, Cretaceous, and Cenozoic separately. These four basic models were supplemented by four others (models 1a, 2a, 3a, and 4a) that use the same conditions but make use of multiple regression with a separate best-fit slope and intercept for the wing length:paleolatitude relationship (using the absolute value of paleolatitude). The best-fit paleolatitude slope and intercept is applied to the entire Carboniferous-Recent dataset.

Model inputs included wing length, estimated body volume, or estimated body width, compared against paleo- $p\text{O}_2$ proxies from the GEOCARBSULF model (2) and the COPSE model (1) (although data-model comparison using COPSE model output, particularly in the early Mesozoic, implies that it is less reliable than GEOCARBSULF output). The additional results for body width, body volume, and using the COPSE $p\text{O}_2$ model are presented in Table S4. None of the six data-model combinations was best explained by oxygen over the entire history of insects and all identified the Early Cretaceous (140 Ma) as an important break in the history of insect size. An additional breakpoint at 230–200 Ma was supported by the COPSE models and by body volume, potentially indicating the importance of pterosaurs as flying vertebrate competitors or predatory.

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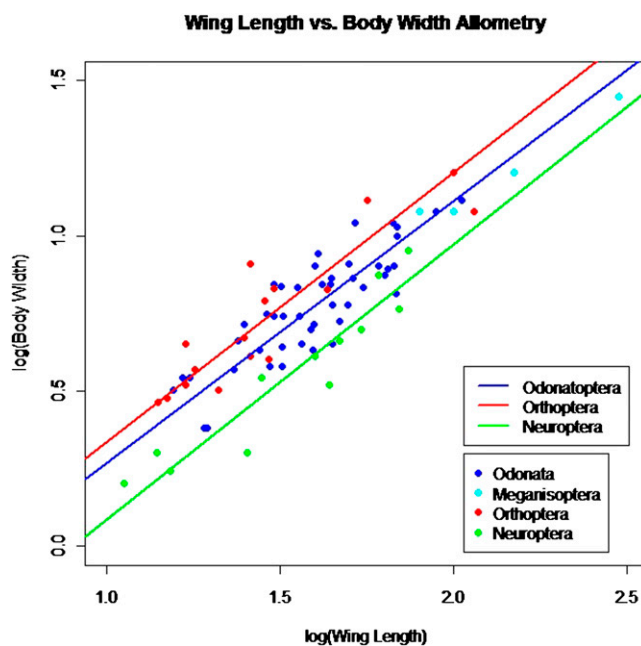


Fig. S1. Allometric scaling of body width and wing length for Odonoptera, Orthoptera, and Neuroptera. Best-fit major axis regression lines for each group are: Odonoptera: $\log(\text{body width}) = 0.898\log(\text{wing length}) - 0.661$; Orthoptera: $\log(\text{body width}) = 0.953\log(\text{wing length}) - 0.642$; and Neuroptera: $\log(\text{body width}) = 0.889\log(\text{wing length}) - 0.805$. All equations use base 10 logarithms.

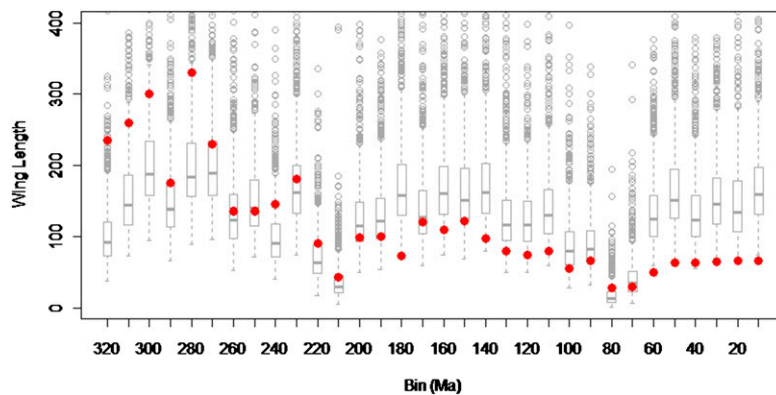


Fig. S6. Box-and-whisker plot showing maximum wing length recorded in 1,000 trials, with each trial sampling the same number of specimens from a constant log-normal distribution (on a log scale, mean = 1.1017, SD = 0.3776). Red dots show maximum recorded size from each time bin.

Table S1. Largest insect in each 10-Myr bin

Bin	Oxygen	COPSE	<i>n</i>	Species name	Order	Length (mm)	Paleolat	Locality name	Age	Ref.
10	21.6	1.15	394	<i>Mediaeschna lucida</i>	Odonata	66.7	36.3	Shanwang, Shandong	Middle Miocene	(1)
20	22.6	1.27	253	<i>Merlax bohemicus</i>	Odonata	66.5	50.5	Bilina mine	Early Miocene	(2)
30	22.7	1.38	614	" <i>Orthacanthacris</i> " <i>lineata</i>	Orthoptera	65	43.6	Celas Gard	Early Oligocene	(3)
40	22.1	1.45	222	<i>Triaeschna gossi</i>	Odonata	64	48.5	Bagshot beds, Bournemouth	Late Eocene	(4)
50	21.4	1.46	458	<i>Pseudotettigonia amoena</i>	Orthoptera	63	52.7	Jutland	Early Eocene	(5)
60	21.5	1.45	197	<i>Arctolocusta groenlandica</i>	Orthoptera	53	62.3	Atanekrdluk, Greenland	Middle Paleocene	(6)
70	21.7	1.48	5	Odonata IGM 8826	Odonata	29	32.4	Saltillo, Coahuila	Late Campanian	(7)
80	21.9	1.51	1	<i>Stantoniella cretacea</i>	Blattodea	28	54.4	Willow Creek	Campanian	(8)
90	21.7	1.54	51	<i>Paraliupanshania torvaldsi</i>	Odonata	66.6	43.8	Kzyl-Zhar	Turonian	(9)
100	21.5	1.55	54	<i>Ptiloteuthis foliatus</i>	Blattodea	79	41.5	Cottonwood Creek	Cenomanian	(10)
110	20.8	1.49	265	<i>Colossocossus giganticus</i>	Hemiptera	80	-7.5	Ararape Basin, Crato	L. Aptian-E. Albian	(11)
120	18.8	1.39	348	<i>Sinaeschnidia cancellosa</i>	Odonata	75	44.2	Liaoning Province	Barremian-E. Aptian	(12)
130	16	1.26	282	<i>Gigantoeschnidium ibericus</i>	Odonata	80	29.7	Las Hoyas	Late Barremian	(12)
140	14.5	1.21	565	<i>Prohoyaeschna milleri</i>	Odonata	97	41.5	Durlston Bay, Swanage	Late Berriasian	(9)
150	15.7	1.23	386	<i>Kalligramma haeckeli</i>	Neuroptera	122	40.2	Solnhofen	Tithonian	(13)
160	15.3	1.21	582	<i>Cymatophlebia suevica</i>	Odonata	110	39.3	Schalksburg-Schule	Topmost Oxfordian	(9)
170	14.5	1.15	361	<i>Hemerobioides giganteus</i>	Odonata	120	42.4	Stonesfield	Bathonian	(14)
180	14	1.12	847	<i>Campterochlebia elegans</i>	Odonata	73.1	41.5	Schandelah, Braunschweig	Toarcian	(15)
190	14.8	1.07	256	<i>Pteropteron mirabile</i>	Odonata	94	42.1	Shurab 3, Sai-Sagul	Pliensbachian	(16)
200	19	1.05	152	<i>Sogdophlebia singularis</i>	Odonata	98.5	49.7	Shurab (Middle area)	Rhaetian	(16)
210	22.5	1.04	26	<i>Italomyrmeleon bergomensis</i>	Stem-Odonata	42.4	32.6	Ponte Giurino village	Late Norian-Rhaetian	(17)
220	22.6	1.02	21	<i>Triadotypus nana</i>	Stem-Odonata	90.7	8.5	Dent de Villard, Vanoise	Carnian-Norian	(18)
230	19.6	1.02	554	<i>Gigatitan similis</i>	Titanoptera	180	36.5	Madygen	Ladinian-Carnian	(19)
240	19.2	1.08	183	<i>Clathrotitan scullyi</i>	Titanoptera	145	-61.2	Beacon Hill	Anisian	(20)
250	24	1.17	354	<i>Triadotypus guillaumei</i>	Stem-Odonata	136	14.4	Bust, Grès a Volzia	Early Anisian	(21)
260	31	1.14	184	<i>Kargalotypus kargalensis</i>	Stem-Odonata	135	29.2	Kargala	L. Word-E. Capitan	(22)
270	32.2	1.15	761	<i>Arctotypus sp. A</i>	Meganisoptera	230	6.9	Lodève Basin F36	Roadian-Wordian	(23)
280	32.7	1.26	864	<i>Meganeuropsis permiana</i>	Meganisoptera	330	5.4	Elmo	Late Artinskian	(24)
290	32.4	1.39	254	Obora Specimen (large)	Meganisoptera	175	10.4	Obora	Sakmarian	(25)
300	30.4	1.33	764	<i>Meganeura monyi</i>	Meganisoptera	300	-1.9	Commentry	Stephanian B-C	(26)
310	26.2	1.29	419	<i>Bohemiatypus elegans</i>	Meganisoptera	260	3.9	Otvovice	Westphalian C	(27)
320	21.4	1.26	97	<i>Shenzhousia qilianshanensis</i>	Meganisoptera	235	11.6	Xiaheyuan, Ningxia	Namurian B-C	(28)

Oxygen is from refs. 29 and 30 (COPSE model, given as a ratio relative to modern pO_2). The number of measured specimens per bin is indicated in column "*n*." The paleolatitude (paleolat) of each locality was calculated using PointTracker (31). The ordinal placement of some Paleozoic-Triassic Odonatopterans (Odonata + Meganisoptera) is approximate because of the complex phylogeny of these stem-group taxa (18, 32).

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Table S2. Estimated body width for the widest insect in each 10-Myr bin

Bin	Species name	Order	Length (mm)	Width (mm)	Ref.
10	<i>Platycleis speciosa</i>	Orthoptera	54	10.21	(1)
20	<i>Terpandrus ikiensis</i>	Orthoptera	58	10.93	(2)
30	<i>“Orthacanthacris” lineata</i>	Orthoptera	65	12.18	(3)
40	<i>Triaeschna gossi</i>	Odonata	64	9.14	(4)
50	<i>Pseudotettigonia amoena</i>	Orthoptera	63	11.82	(5)
60	<i>Arctolocusta gronlandica</i>	Orthoptera	53	10.03	(1)
90	<i>Paraliupanshanian torvaldsi</i>	Odonata	66.6	9.47	(6)
100	<i>Paraliupanshanian rohdendorfi</i>	Odonata	60.3	8.66	(6)
110	<i>Cratostenophlebia schwickerti</i>	Odonata	70	9.91	(7)
120	<i>Allaboilus hani</i>	Orthoptera	60	11.28	(8)
130	<i>Pseudaboilus wealdensis</i>	Orthoptera	75	13.96	(9)
140	<i>Procyrtophyllites britannicus</i>	Orthoptera	95	17.49	(9)
150	<i>Pycnophlebia robusta</i>	Orthoptera	115	24.6	(10)
160	<i>Cymatophlebia suevica</i>	Odonata	110	14.87	(6)
170	<i>Scalpellaboilus angustus</i>	Orthoptera	95	17.49	(8)
180	<i>Campterochlebia elegans</i>	Odonata	73.1	10.3	(11)
190	<i>Pteropteron mirabile</i>	Odonata	94	12.91	(12)
200	<i>Sogdophlebia singularis</i>	Odonata	98.5	13.46	(12)
230	<i>Gigatitan similis</i>	Titanoptera	180	32.16	(13)
240	<i>Clathrotitan scullyi</i>	Titanoptera	145	26.17	(14)
250	<i>Triadotypus guillaumei</i>	Stem-Odonata	136	17.99	(15)
260	<i>Kargalotypus kargalensis</i>	Stem-Odonata	135	17.87	(16)
270	<i>Arctotypus</i> sp. A	Meganisoptera	230	28.83	(17)
280	<i>Meganeuroopsis permiana</i>	Meganisoptera	330	39.87	(18)
290	Obora Specimen (large)	Meganisoptera	175	22.56	(19)
300	<i>Meganeura monyi</i>	Meganisoptera	300	28	(20)
310	<i>Bohemiatupus elegans</i>	Meganisoptera	260	32.18	(21)
320	<i>Shenzhousia qilianshanensis</i>	Meganisoptera	235	29.39	(22)

Gray shaded rows indicate intervals where the specimen with the greatest estimated width differs from the specimen with the longest wing (in some cases because the longest wing belongs to a group where we cannot allometrically estimate body width). Numbers in red are actual measurements from the specimen.

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Table S3. Estimated body volumes for the largest insect in each 10-Myr bin

Bin	Species name	Order	Length (mm)	Volume (mm ³)	Ref.
10	<i>Mediaeschna lucida</i>	Odonata	66.7	5,572	(1)
20	<i>Merlax bohemicus</i>	Odonata	66.5	5,527	(2)
30	<i>“Orthacanthacris” lineata</i>	Orthoptera	65	4,829	(3)
40	<i>Triaeschna gossi</i>	Odonata	64	4,992	(4)
50	<i>Pseudotettigonia amoena</i>	Orthoptera	63	4,453	(5)
60	<i>Arctolocusta groenlandica</i>	Odonata	53	2,845	(6)
90	<i>Paraliupanshania torvaldsi</i>	Odonata	66.6	5,550	(7)
100	<i>Paraliupanshania rohdendorfi</i>	Odonata	60.3	4,260	(7)
110	<i>Cratostenophlebia schwickerti</i>	Odonata	70	6,336	(8)
120	<i>Sinaeschnidia cancellosa</i>	Odonata	75	7,613	(9)
130	<i>Gigantoaeschnidium ibericus</i>	Odonata	80	9,039	(9)
140	<i>Prohoyaeschna milleri</i>	Odonata	97	15,094	(7)
150	<i>Pycnophlebia robusta</i>	Orthoptera	115	21,203	(10)
160	<i>Cymatophlebia suevica</i>	Odonata	110	21,093	(7)
170	<i>Hemerobioides giganteus</i>	Odonata	120	26,589	(11)
180	<i>Campterochlebia elegans</i>	Odonata	73.1	7,110	(12)
190	<i>Pteropteron mirabile</i>	Odonata	94	13,883	(13)
200	<i>Sogdophlebia singularis</i>	Odonata	98.5	15,723	(13)
230	<i>Gigatitan similis</i>	Titanoptera	180	67,752	(14)
240	<i>Clathrotitan scullyi</i>	Titanoptera	145	38,675	(15)
250	<i>Triadotypus guillaumei</i>	Stem-Odonata	136	37,098	(16)
260	<i>Kargalotypus kargalensis</i>	Stem-Odonata	135	36,376	(17)
270	<i>Arctotypus sp. A</i>	Meganisoptera	230	150,161	(18)
280	<i>Meganeuropsis permiana</i>	Meganisoptera	330	392,433	(19)
290	<i>Obora Specimen (large)</i>	Meganisoptera	175	72,564	(20)
300	<i>Meganeura monyi</i>	Meganisoptera	300	304,523	(21)
310	<i>Bohemiatupus elegans</i>	Meganisoptera	260	208,087	(22)
320	<i>Shenzhousia qilianshanensis</i>	Meganisoptera	235	159,005	(23)

Gray shaded rows indicate intervals where the specimen with a greater estimated volume differs from the specimen with the longest wing.

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Table S4. Maximum-likelihood model support for the four basic models (1–4) explained above using body width, body volume, and the alternative COPSE model for Phanerozoic pO₂, ordered from best-supported to least by Δ AICc

Model	Berner (2)/body width		Berner/body volume		COPSE (1)/wing length		COPSE/body width		COPSE/body volume	
	Δ AICc	Akaike wt	Δ AICc	Akaike wt	Δ AICc	Akaike wt	Δ AICc	Akaike wt	Δ AICc	Akaike wt
1	608.3	<0.001	561.5	<0.001	437.4	<0.001	419.0	<0.001	389.0	<0.001
2	0.0	0.767	2.0	0.192	16.0	<0.001	0.1	0.449	13.9	<0.001
3	3.2	0.152	1.3	0.279	8.8	0.012	3.3	0.089	13.2	0.001
4	4.5	0.081	0.0	0.529	0.0	0.988	0.0	0.462	0.0	0.998

Proportional model support is indicated by the Akaike weights (wt); the best-supported model is shown in red.