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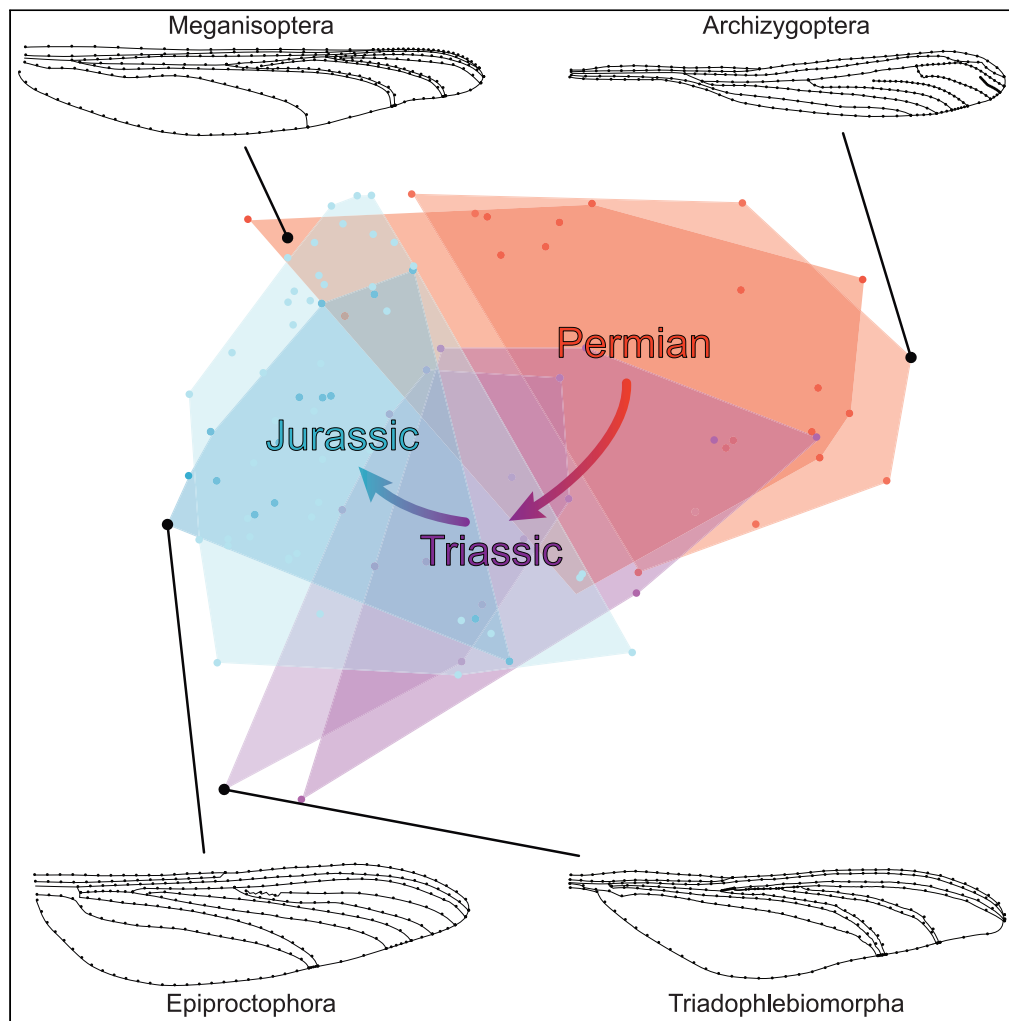
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## Article

## Disparification and extinction trade-offs shaped the evolution of Permian to Jurassic Odonata



Isabelle  
Deregnacourt,  
J r mie Bardin,  
Loic Villier,  
Romain Julliard,  
Olivier B thoux

deregnacourt.isa@gmail.com

**Highlights**

In 150 million years early dragonflies steadily lost morphological diversity

Permian-Triassic and Triassic-Jurassic transitions witnessed major restructurings

In both cases selective extinction of iconic groups was balanced by disparification

Early representatives of Odonata continuously evolved new shapes

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## Article

## Disparification and extinction trade-offs shaped the evolution of Permian to Jurassic Odonata

Isabelle Deregnaucourt,<sup>1,2,3,\*</sup> Jérémie Bardin,<sup>1</sup> Loïc Villier,<sup>1</sup> Romain Julliard,<sup>2</sup> and Olivier Béthoux<sup>1</sup>

## SUMMARY

Owing to their prevalence in nowadays terrestrial ecosystems, insects are a relevant group to assess the impact of mass extinctions on emerged land. However, limitations of the insect fossil record make it difficult to assess the impact of such events based on taxonomic diversity alone. Therefore, we documented trends in morphological diversity, i.e., disparity, using wings of Permian to Jurassic Odonata as model. Our results show a decreasing trend in disparity while species richness increased. Both the Permian-Triassic and Triassic-Jurassic transitions are revealed as important events, associated with strong morphospace restructuring due to selective extinction. In each case, a recovery was assured by the diversification of new forms compensating the loss of others. Early representatives of Odonata continuously evolved new shapes, a pattern contrasting with the classical assertion of a morphospace fulfilled early and followed by selective extinctions and specialization within it.

## INTRODUCTION

The onset of biodiversity in marine environments predated that of the emerged lands. It is commonly assumed that terrestrial biodiversity followed an increasing diversification from the Ordovician onward.<sup>1</sup> The five episodes of mass extinctions documented in the fossil record are thought to have been more severe in the oceans than on lands. Although evidence has been found of an impact of the end-Permian, Triassic-Jurassic, and Cretaceous-Paleogene extinctions on terrestrial vertebrates evolution,<sup>2,3</sup> the severity of these events on the overall terrestrial life, and to which particular extinction pattern they conformed, is not obvious. Besides plants, the fossil record of insects is a primary target to address this question. Most studies on the past diversity of the group recognize an important event contemporaneous to the end-Permian mass extinction, affecting taxonomic composition and/or richness,<sup>4–8</sup> and leading to the distinction of a Late Palaeozoic fauna on one hand, and a more modern Post-Palaeozoic one on the other.<sup>9</sup> However, because of limitations in temporal and geographic resolution of the fossil record, it cannot be ruled out that this event was a gradual turnover rather than a short-lived crisis.<sup>10</sup> It may also have been the outcome of multiple, successive events.<sup>8</sup> Nonetheless, changes observed during this interval are unparalleled in insect evolutionary history. Interestingly, other major events highlighted as having potentially impacted insect evolution (during the Late Pennsylvanian, Late Jurassic, and later Early Cretaceous)<sup>10</sup> do not overlap with the five mass extinctions of the marine realm.<sup>11</sup> In summary, the main drivers of biodiversity dynamics on emerged lands, and for insects in particular, remain inadequately explored in the deep time because of a lack of resolution and, to some extent, a dearth of taxonomic expertise.<sup>10</sup>

The fossil record of insects has essentially been investigated using diversity metrics, resting on units based on taxonomic rank, usually the genus, whose attribution is subjective. Moreover, inaccurate identification of stem-groups can have deterring effects on such metrics.<sup>12,13</sup> This issue applies vividly to Late Palaeozoic insect faunas, the affinities of some of their major constituents being yet debated. Approaching global taxonomic diversity dynamics using species abundance per locality can be a useful, alternative endeavor,<sup>10,14</sup> but inconsistent species delimitations, due to a yet limited knowledge on intra-specific variability,<sup>15</sup> may impair its outcomes. Moreover, because of the unparalleled diversity of the group and a shortage of investigators, only a handful of localities could be investigated for its insect content with suitable resolution.

Because it is primarily specimen based, quantifying morphological diversity (hereafter disparity) is an effective surrogate to detect extinction and radiation events, and analyze their properties. Disparity metrics can be

<sup>1</sup>Centre de Recherche en Paléontologie – Paris (CR2P), Sorbonne Université, MNHN, CNRS, 57 rue Cuvier, CP38, F-75005 Paris, France

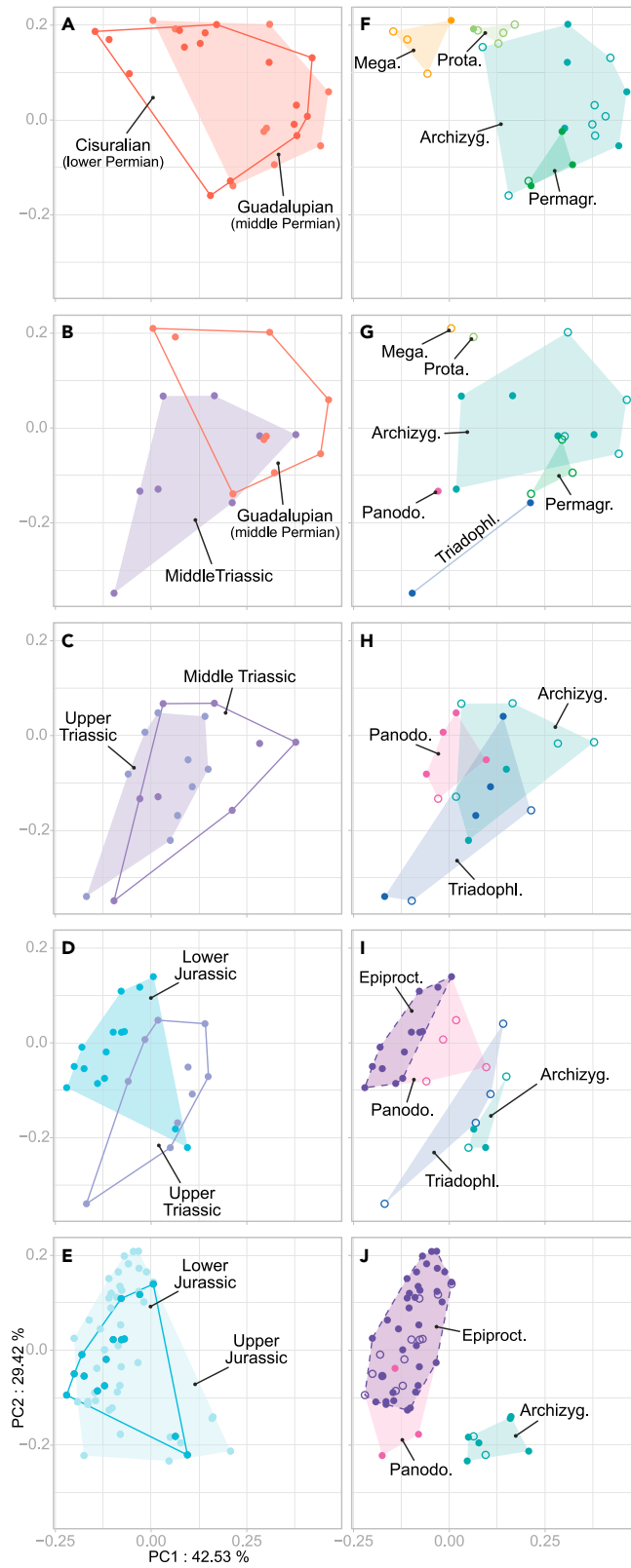
<sup>2</sup>Centre d'Ecologie et des Sciences de la Conservation (CESCO), Sorbonne Université, MNHN, CNRS, 43 rue Buffon, 75005 Paris, France

<sup>3</sup>Lead contact

\*Correspondence: [deregnaucourt.isa@gmail.com](mailto:deregnaucourt.isa@gmail.com)

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**Figure 1. Odonata morphospace occupation from the Cisuralian (lower Permian) to the Upper Jurassic**

(A–E) Temporal changes between consecutive epochs; on each plot, the outlined convex hull (without infilling) corresponds to the oldest epoch of the two, that filled (and without outline) to the youngest. Dots represent species and are color-coded according to the epoch they lived in.

(F–J) Temporal changes by the different clades; on each plot, empty circles correspond to species sampled in the oldest epoch of the two, dots to the youngest; convex hulls plotted for major clades, with constituent species color-coded accordingly. Mega., Meganisoptera; Prota., Protanisoptera; Permagr., Permagrionidae; Archizyg., Archizygoptera; Triadopl., Triadophlebiomorpha; Panodo., Panodonata; Epiproct., Epiproctophora.

gathered into three categories, depending on whether they describe the size of the occupied morphospace, the density of observations (i.e., individual shapes), or their position in this morphospace.<sup>16–18</sup> Considered altogether, within a theoretical framework initiated by Foote<sup>16</sup> (Figure S1), they allow a fine-tuned characterization of global morphospace occupation dynamics. Gould<sup>19</sup> canonized the model of an early burst of disparity followed by a gradual decrease throughout clade history. He also introduced the idea of a decoupling between species richness and the disparity of a group which became a major avenue of research.<sup>20,21</sup> Disparity metrics provide, to some extent, indications on the evolution of ecological and functional diversity of a given taxon.<sup>22–24</sup> For example, an increase in morphospace volume coupled with a position shift is believed to reflect the exploration of a new niche. The re-colonization of ecological niches left empty after extinction events, or the creation of new niches by acquisition of new, adaptive morphological traits, can be differentiated.<sup>21,25</sup> Eventually, further insights on macroevolutionary questions can be obtained by contrasting dynamics derived from both taxonomic diversity and disparity-based metrics.<sup>16,19,26–29</sup>

Despite its potential, disparity has seldom been applied to insects. Insect mouthparts distribution revealed that the last three major crises (Permian-Triassic, Triassic-Jurassic, and Cretaceous-Cenozoic) had no depletion effect on disparity.<sup>30,31</sup> Instead, the number of mouthparts classes steadily increased from the Devonian onwards. However, even though mouthparts bear crucial information on insect feeding strategies, their documentation in the pre-amber fossil record rests on rare, well-exposed fossils. Compared to mouthparts, wings are far more abundant as fossils and easier to document. Moreover, they are a privileged item to compute landmark-based morphometrics analyses<sup>32–36</sup> and to elaborate a dataset exploitable with a focus on disparity.

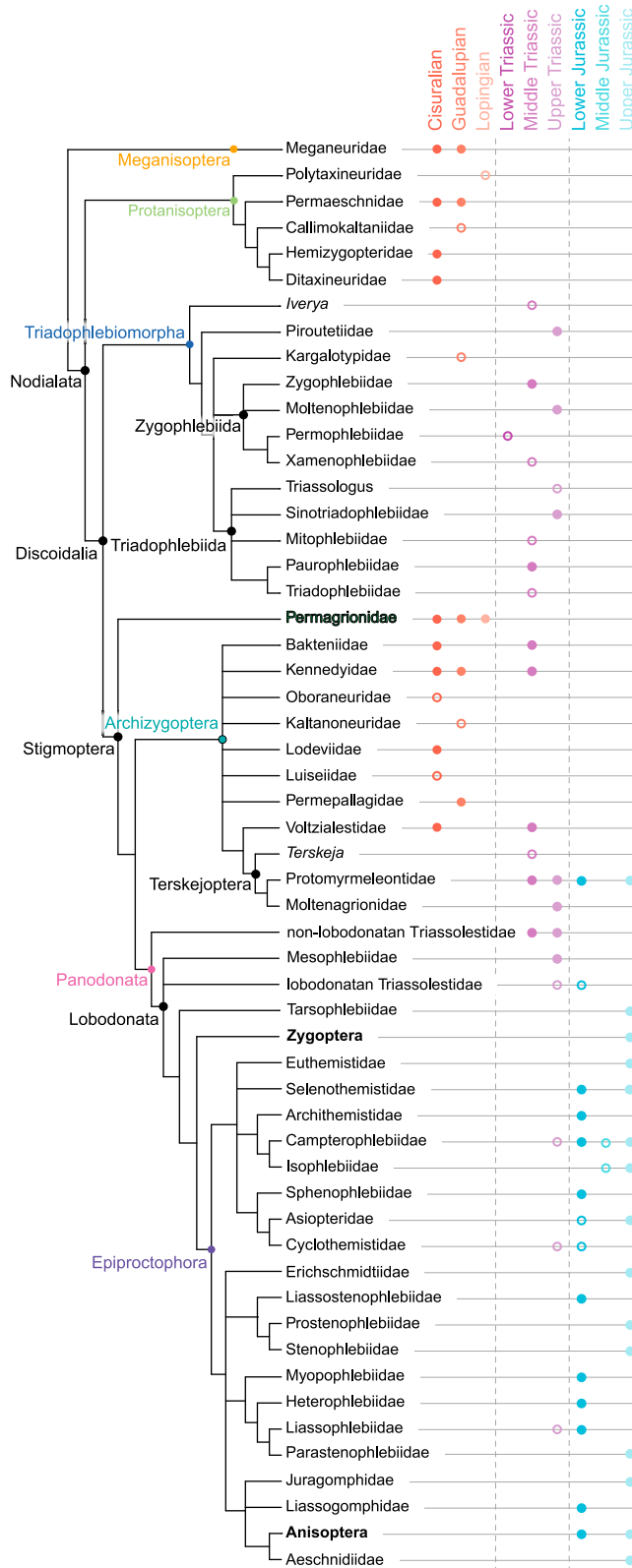
Although a general pattern of insect wing venation homologies is widely accepted,<sup>37</sup> consensus is still lacking on how it applies on some insect groups. Concurrently, applying a given set of landmarks along a vein being simple vs. branched is conceptually impossible. Given these limitations, the Odonata (dragon- and damselflies and stem-relatives) appear ideally suited. Wing venation homologies of Odonata are complex but have been securely identified,<sup>38–40</sup> providing a large number of landmarks and a variety of configurations suitable for morphometric analyses. Moreover the group has been in existence for 320 million years,<sup>41–43</sup> a period covering three of the five main historical extinctions, and has a rich fossil record, with about a thousand described fossil species,<sup>44</sup> mainly known from wings. Last but not least, the main groups of fossil odonates have been recovered from distant localities,<sup>45,46</sup> suggesting data derived from their fossil record are less likely to be impacted by biases relating to sampling or spatial distribution.

In order to identify the putative signature of two of the main historical extinctions, the end-Permian and the end-Triassic events, on Odonata evolution, we collected data on wing shape of Early Permian to the Upper Jurassic representatives and derived disparity metrics. The outcome was compared with taxonomic diversity metrics.

## RESULTS

### Structure of the Odonata wing morphospace

The morphospace obtained for Odonata wings is summarized as a principal-component analysis (PCA) of output data from geometric morphometric analyses. The first two axes (PC1, PC2) account for a substantial amount of shape variation (72%), complemented by the third axis (PC3, 9%; Figures 1 and S2; interactive 3D plot Data S2). Wing structure and venation (Figure S4 and Table S1) can be related to observed variations. Those explained by PC1 are concentrated in the postero-median area of the wing. Low PC1 scores indicate a wide postero-basal area, while high scores indicate a petiolated wing (i.e., a very reduced postero-basal area). This axis also indicates that both the anterior median vein (MA) and the posterior median vein (MP) end basally and that the most postero-basal outline section (O10) is short (high score) vs. long MA, MP, and O10 section (low scores). Concurrently, the origins of branches



**Figure 2. Consensual phylogeny of Odonata families from the Cisuralian (lower Permian) to the Upper Jurassic**

Circles indicate the occurrence of a given taxon at a particular epoch; full circles indicate that at least one species was considered for disparity analysis, while empty circles indicate that none of the known fossil material proved complete enough.

from the posterior radial vein (RP; and of their associated intercalary veins) are located apically (high scores) vs. more basally (low scores). The second axis differentiates wings with a nodus in a basal (low scores) vs. more distal position (high scores). Concurrently, the end of MP is in a more apical (low scores) vs. basal position (high scores). The third axis differentiates wings which are slender and whose veins are parallel and close together until their end, at wing apex (low scores), from wings with the posterior-most branch of RP (RP3+4), MA, and MP ending more basally and with their respective endings more distant from each other (high scores).

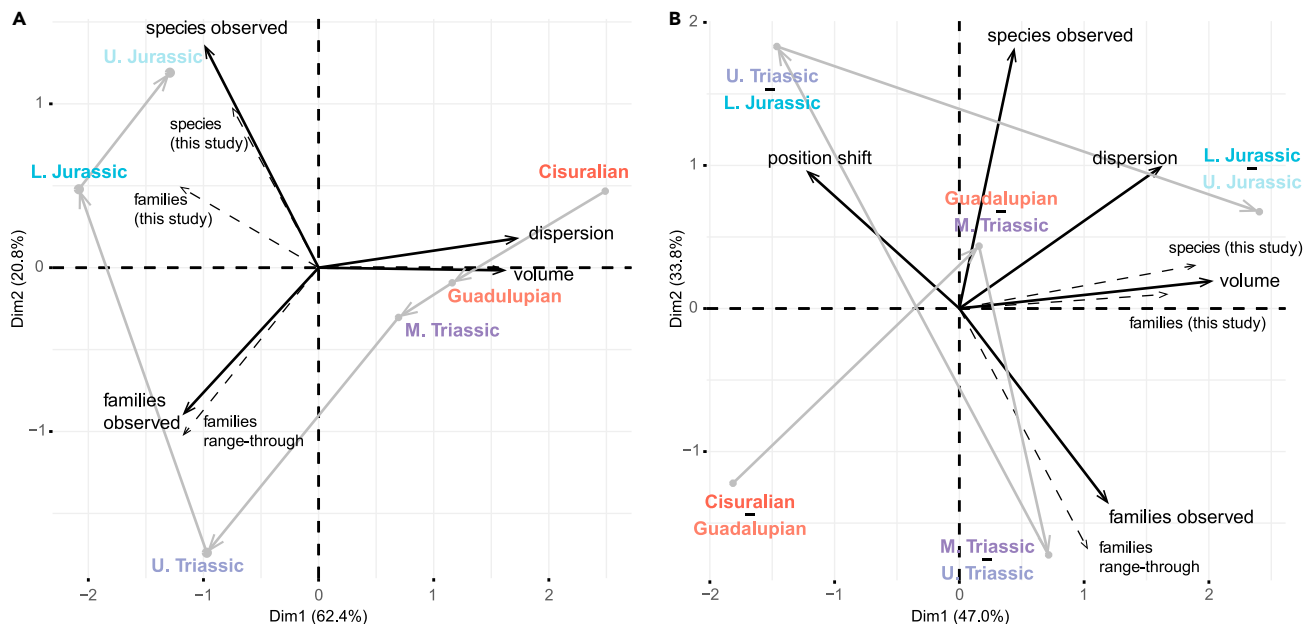
There is limited overlap in morphospace area occupied by the main taxa (Figures 1F–1J and 2; Data S2). The griffenflies (Meganisoptera; restricted to the Permian in our analysis) occupy a distinct area (low scores on PC1 and PC3 and high scores on PC2) indicating wings with a wide postero-basal area, a long posterior subcostal vein (ScP), and a wide MA-MP area. In their vicinity, but yet distinct from them, the Protanisoptera occupy an area with intermediate scores on PC1 and PC3 and very high scores on PC2, also indicating a rather long ScP and a wide MA-MP area but coupled with some degree of vein parallelism.

Among the Discoidalina, the Triadophlebiomorpha, a large group of mostly Triassic species, are somewhat spread along PC1 and PC2. The group splits into two main sets of shapes closely matching the recognized subgroups. One, the Zygophlebiida, occupy an area with the lowest PC2 scores and low PC1 scores. They are characterized by a complex set of veins fusions involving the second posterior branch of RP (RP2) and nearby intercalary veins.<sup>47,48</sup> Their position reflects a distinctive combination of a wide area between MP and the posterior wing margin, a basal position of the end of ScP (i.e., of the nodus), and an unusually long anterior-most intercalary vein. The second group, the Triadophlebiida, occupy a more central position.

Turning to the large group of odonates possessing a pterostigma (namely, the Stigmoptera), species composing the Permigrionoidea are clustered in a small area characterized by rather high scores on PC1, low scores on PC3, and intermediate scores on PC2. This position reflects slender and petiolate wings. Also, within Stigmoptera, the Archizygoptera, the only group to cover the complete temporal range of our analysis, occupy a very large area of the morphospace. Notably, Permian representatives occupy the area with the highest values of PC1, reflecting, among other traits, very petiolate wings. Within Archizygoptera, species belonging to the genus *Progoneura* are remarkable in that their location is characterized by extremely high scores on all PCs, indicating an extremely reduced MP in conjunction with a distal position of RP branches and of the associated intercalaries. Another Permian archizygopteran occupying an extreme position is *Lodevia longialata*, with a very low score on PC3, owing to a very strong parallelism of RP branches, the associated intercalaries, and MP, in relation with a distal location of their respective endings.

The Terskejoptera is a major lineage of Archizygoptera in terms of both temporal range (from the Triassic to the Cretaceous; Figure 2) and morphological distinctiveness. Its main constituents are the Protomyrmeleontoidea. They occupy a comparatively small area and are characterized by intermediate scores on PC1, rather low scores on PC2, and the highest scores on PC3, clearly distinguishing them from other Archizygoptera. Indeed, there is nearly no overlap between Terskejoptera and other Archizygoptera, in particular with respect to Permian forms.

Most of the Panodonata, the taxon including all extant species, occupy a particular area characterized by negative scores on PC1, and spreading from a pole characterized by rather high scores on PC3 and extremely high scores on PC2 to a pole characterized by extremely low scores of PC3 and rather low scores on PC2. This range reflects shapes spreading from (i) wide wings with distant veins endings and a long ScP (i.e., with a nodus situated near the half of the wing) to (ii) petiolate, slender wings with veins parallel and close to each other, and a short ScP (i.e., with nodus in the first half of the wing). However, the few Panodonata which do not belong to the Lobodonata, and which are all from the Triassic, are located aside from their Jurassic relatives, in a central position, at the edge of the “archizygopteran area” (Figures 1B, 1C, 1G, and 1H). Ultimately, Jurassic dragonflies (Anisoptera) and their closest stem-relatives (namely, the Aeschniidae) on one hand, and damselflies (Zygoptera) on the other, are gathered in two distinct areas, each at one pole of the “panodonatan area” (high scores of PC2 and PC3 for the former; low scores of PC2 and PC3 for the latter).



**Figure 3. Principal-component analysis of diversity and disparity metrics**

(A) Analysis made on raw values.

(B) Analysis computed on net differences between successive epochs. Black arrows, metrics used to compute PCA, including disparity (volume, as sum of ranges on each individual PC; dispersion, as median pairwise distances between species of a given time interval; position shift, relevant in B only, as shift in centroid position of two consecutive temporal subsamples) and diversity metrics (all known species/families); dashed arrows, diversity metrics plotted onto PCA, including species/families selected for disparity analysis (“this study”) and range-through for families; gray arrows, temporal trajectory.

### Respective inputs from disparity and diversity metrics

We computed a PCA to assess whether diversity and disparity metrics are correlated (Figures 3 and S3). Volume of morphospace occupation and dispersion among taxa covary but are not significantly correlated to taxonomic richness (Figures 3A and 4). In other words, taxonomic diversity and disparity are complementary, each metric accounting for distinct aspects of the fossil record (Figure 3A). Dispersion decreases through time, recalling a bottom-heavy disparity pattern,<sup>21</sup> with few but morphologically distinct early taxa and a progressive filling of the morphospace. To a lesser extent, volume follows the same general trend, with an initial, large morphospace gradually reducing over time.

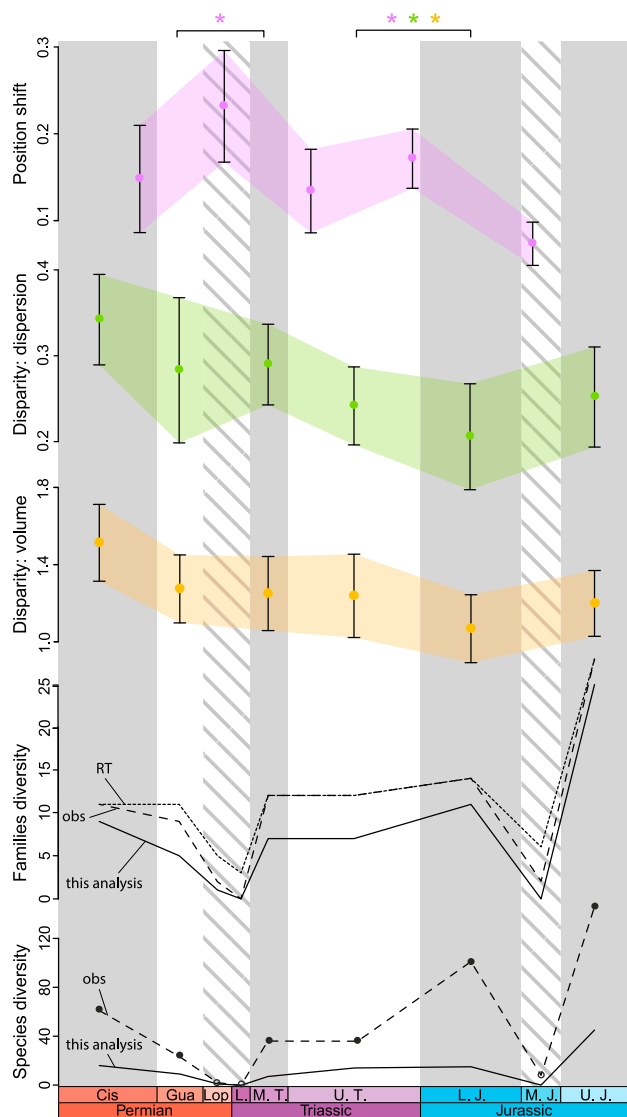
The PCA based on differentiated values (Figure 3B; i.e., where the amount of change from one temporal interval to another is quantified as the net difference between time interval values) reveals that shifts in diversity metrics and in occupied areas do not have a constant relationship. Major shifts occur synchronously at the Permian-Triassic and Triassic-Jurassic transitions (the two covered mass extinctions).

### Temporal variations

There are no significant changes in morphospace occupation between the Cisuralian (lower Permian) and the Guadalupian (middle Permian; Figure 4). Indeed, the two corresponding morphospace areas largely overlap (Figure 1A), with the main odonate lineages being identical in both epochs (Figures 1B and 2). Volume and dispersion metrics are slightly decreasing from the Cisuralian to Guadalupian but not significantly (Figure 4 and Table 1). There is a slight shift in position that can be related to the occurrence of marginal morphologies (at the periphery of the morphospace) within the Kennedyidae (Achizygoptera) during the Guadalupian. In summary, the Permian is characterized by a relative stability in both diversity and disparity.

Volume and dispersion metrics have roughly similar values from the Guadalupian to the Middle Triassic. However, there is a significant shift in position. Such pattern suggests that peculiar shapes got lost but were compensated by the emergence of new ones.





**Figure 4. Temporal changes in disparity and diversity of Odonata from the Cisuralian (lower Permian) to the Upper Jurassic**

Disparity trends derived from volume (sum of ranges; orange), dispersion (median pairwise distances; green) and shift in centroid position between two consecutive epochs (purple) (data are represented as mean values of bootstrapped subsamples  $\pm$  SD; asterisks indicate significant differences in these metrics between epochs obtained from permutation tests); and diversity trends derived from taxonomic richness (Paleobiology Database<sup>44</sup>; continuous line [“this study”], species/families selected for disparity analysis; dashed line [“obs”], all known species/families; and dotted line [“RT”] range-through for families).

The transition from Middle to the Upper Triassic is overly similar to the Cisuralian-Guadalupian one, with morphospace occupation metrics not differing significantly, and a taxonomic composition remaining essentially unchanged. The number of families reaches its highest point during the Upper Triassic, which can be explained by the appearance of several early members of the Eiproctophora (Figure 2). However, the corresponding fossils could not be included in our shape analysis because of material incompleteness. Considering the area occupied by their known Jurassic relatives, volume and position metrics may prove somewhat underestimated for the Upper Triassic. The Triassic-Jurassic transition is the only interval with significant differences in all disparity metrics (Figure 4). The Upper Triassic odonate fauna occupies a morphospace volume larger than that of the Lower Jurassic one. Similarly, dispersion decreases during the interval. This configuration can be possibly explained by an aggregation of species into distinct clusters. In

**Table 1. Disparity metrics for each epoch and p values obtained by a permutation test**

	Volume	Dispersion	Position
<b>Disparity</b>			
Cisuralian	1.51	0.34	–
Guadalupian	1.27	0.28	–
Middle Triassic	1.25	0.29	–
Upper Triassic	1.24	0.24	–
Lower Jurassic	1.07	0.20	–
Upper Jurassic	1.20	0.25	–
<b>p values</b>			
Cisuralian/Guadalupian	0.14	0.13	0.05
Cisuralian/Middle Triassic	0.52	0.51	0
Middle Triassic/Upper Triassic	0.32	0.34	0.14
Upper Triassic/Lower Jurassic	<b>0.04</b>	<b>0.04</b>	<b>0</b>
Lower Jurassic/Upper Jurassic	0.57	0.58	1

Values correspond to the mean of 1,000 bootstrap replications, significant p values in bold.

addition, the observed shift in position points toward an extinction and appearance of morphologies occupying distant areas of the morphospace (Figure 1D).

Finally, no major changes in morphospace occupation were observed from the Lower to the Upper Jurassic (Figure 1E): volume and dispersion metrics show a slight increase (though not significant) and position remains unchanged (Figure 4). Concurrently, taxonomic diversity increases. Such combination is consistent with the diversification of Lobodonta, including, among other aspects, the appearance of the first Zygoptera.

## DISCUSSION

Dynamics of disparity for arthropods have been among the most scrutinized in the literature. An important controversy opposes the bottom-heavy pattern<sup>19,49,50</sup> to a model of nearly constant disparity throughout their history.<sup>51–54</sup> The debate stems from disputed interpretations of the relationships between Cambrian and extant faunas. Looking at a broad scale, Hughes et al.<sup>21</sup> showed in a meta-analysis focused on Metazoa that clades are basically bottom heavy and that top-heavy clades can occur when facing major extinction events. As for plant taxa, the bottom-heavy pattern is the most widespread, but with exceptions.<sup>55</sup> Benson et al.<sup>56</sup> suggested that even if the early burst model can be supported at the scale of the main animal clades and throughout the entire Phanerozoic, a more gradual pattern may be the rule for smaller subsets and at finer temporal scale. Studies on such cases within arthropods, such as trilobites,<sup>57</sup> Late Palaeozoic to Recent insects,<sup>6</sup> and crustaceans<sup>58</sup> demonstrated that maximum disparity can be delayed during diversification. Our analysis, focusing on diversity and disparity dynamics in Odonata as whole, and of its constituent clades over 150 million years of evolution, provides a new case relevant to the debate.

Considered globally, volume and dispersion disparity metrics slightly decreased throughout the considered period, a pattern which can be interpreted as a bottom-heavy profile, while specific diversity increased. In other words, the Cisuralian was populated by few but morphologically distinct species, while Jurassic ones were more numerous but more uniform. However, the seemingly monotonous long-term trend does not withstand scrutiny at a lower scale. Indeed, two impactful short-term events were detected by our analysis. The first one encompasses the Permian-Triassic transition. Guadalupian and Middle Triassic Odonata communities display similar diversity values at both species and family levels (Figure 4). Concurrently, a significant taxonomic turnover took place (Figures 1F–1H). These data are consistent with a high level of extinction followed by a fast recovery. This interpretation is corroborated by the changes in morphospace occupation. This interval witnessed the disappearance of the Meganisoptera (griffenflies), a strictly Palaeozoic group of odonates including, among others, the iconic *Meganeura*. Although they represent a recurring component of Pennsylvanian and Permian insect faunas,<sup>59,60</sup> a small subset only could be taken into account as most representatives are large-sized

and therefore are often recovered as fragmentary remains. Yet, the comparatively reduced sample allowed demonstrating the high morphological distinctiveness of these insects (Figures 1F and 1G) and, therefore, the incidence their extinction had. The less common Protanisoptera, another group of strictly Palaeozoic Odonata, are nested in a similar area of the morphospace. The disappearance of these two groups complies with the model of the side-specific extinction model (Figure S1E; which, in our case, can also be regarded clade specific), clearly evidenced by the shift in position (also contributed by the disappearance of some distinctive Archizygoptera, such as *Progoneura*). Concurrently, during the Triassic, the rise of the Triadophlebiomorpha,<sup>48,61,62</sup> a group characterized by their petiolate wing base and unique development of particular areas of the wing, further dragged the morphospace toward a fringe opposite to that occupied by the Meganisoptera (Figure 1H). The steady dispersion and volume metrics (Figure 4) across the temporal interval are therefore due to a trade-off. In summary, the Permian-Triassic transition witnessed selective extinctions compensated by the rise of new groups representing new shapes. This deep reconfiguration took place during an interval of about 15 million years. The precise timing cannot be investigated in a period of scanty fossil record. To some extent, a similar pattern was found in beetles,<sup>63</sup> with a decrease in both taxonomic diversity and morphospace occupation in the Lower Triassic followed by a recovery of both metrics to a pre-crisis level as early as in the Middle Triassic.

A similar pattern was observed during the Upper Triassic-Lower Jurassic interval. Whereas diversity metrics remain roughly constant, the Odonata morphospace experienced a major restructuring. The event is partly driven by the extinction of taxa characterized by marginal morphologies, such as the Triadophlebiomorpha. The gracile, damselfly-like Archizygoptera experienced the most severe loss of their history: during the Jurassic, the remaining representatives of this group all belong to the Protomyrmeleontoidea and form a restricted cluster. The Panodonata, including all extant forms and their closest fossil relatives, populated a large, previously unoccupied morphospace area early in the Jurassic. A consequence of these dynamics is that the Lower Jurassic morphospace is split into two, comparatively dense, distinct clusters, both located aside the area occupied during the Upper Triassic. The decrease in both dispersion and volume metrics complies with an extinction affecting forms similar to the ancestral shape (Figure S1G) and favoring survival of the marginal forms, qualifying a disruptive selection. Such a major event, involving selective extinction and recovery at the Triassic-Jurassic transition, is detected here for the first time for insects. Neither disparity data derived from mouthparts morphology<sup>30,31</sup> nor taxonomic richness<sup>4,9,64</sup> provided evidence of such impactful event on insect faunas during this interval. Its consequences on Odonata were at least as severe as those which occurred during the Permian-Triassic transition.

In both cases, selective extinction affected entire clades occupying marginal positions, while new forms experienced a disparification in previously unoccupied areas. Rather than volume and dispersion metrics, pointing toward a deceptive continuous trend, position shift proved essential to characterize these two critical events. Morphospace occupation closely matching the recognized Odonata taxa, position shifts could be readily associated with extinction of particular groups and the disparification of new ones, and their significance assessed.

Besides the particular impact of short-term events on the observed, global trends, it is worth scrutinizing the dynamics of some subgroups in particular as they may display idiosyncratic dynamics. The Panodonata do not conform a bottom-heavy pattern. Instead, the group shows a continuous, slight increase in both volume and dispersion (Figures 1G–1J) from Middle Triassic to the Upper Jurassic. Interestingly, the area occupied by early forms, in the Triassic, was totally abandoned during the Triassic-Jurassic transition (Figure 1I). The observed rise in disparity is concurrent with a similar trend in species richness. By the end of the Jurassic, the Panodonata are mainly composed of crown-group representatives. The Panodonata therefore stand out in the early history of Odonata, with a diversification concurrent with a disparification. Incidentally, the evolution of Panodonata contradicts the view that the Permian-Triassic remodeling led to a post-Palaeozoic modern insect fauna.<sup>9,10</sup> Even though they are expected to be present as early as the Cisuralian,<sup>65</sup> crown-group representatives do not contribute significantly to odonate diversity before the Jurassic.

There is undoubtedly a link between morphological diversity and adaptation. Documenting changes in disparity is therefore likely to provide insights on ecological pressures to which extinct organisms were subjected. Odonates being both aerial predators and preys, flight performances are of major importance in their success at foraging and predator avoidance.<sup>66</sup> It is therefore tantalizing to relate the observed dynamics with particular elements of wing morphology, such as the nodus (characterizing the Nodialata), the pons (Discoialia), the pterostigma (Stigmoptera), and the petiole. These structures play an important role in flight performance<sup>67</sup> and were acquired during the period of interest (Figure 2). However, the main shape variations

accounted for by the first two PCs are not linked to these specific structures but instead reflect changes affecting several veins concurrently, in distinct areas of the wing. To some extent, this is in line with the view that odonate wings are highly integrated structures.<sup>33</sup> Moreover, besides wing venation and shape, the distribution of resilin joints along veins has a global impact on flight performance,<sup>68</sup> but this aspect is virtually impossible to take into consideration for early stem-group taxa. Nonetheless, it is striking that, once acquired, the nodus, the pons, and the pterostigma were never lost, with the exception of the pterostigma in helicopter damselflies and jewelwings. Additionally, all taxa lacking nodus and pons disappeared during the Permian-Triassic transition. The same applies to taxa lacking a pterostigma at the Triassic-Jurassic transition. As for the petiole, it is associated with a specific area of the morphospace, where several groups co-occur, indicating some degree of homoplasy. In summary, it is yet uneasy to closely relate the observed shape variations with flight performance and ecological niche. The successive acquisition of key apomorphies, yet to be identified, may partly explain the repeated pattern of clade-specific morphospace remodeling.

Considered globally, from the Permian to the Jurassic, the early evolutionary dynamics of Odonata conform the hypothesis predicting a partial decoupling of morphological and taxonomic diversity<sup>16</sup> (Figures 4 and S3). Such pattern has been documented for insects as a whole,<sup>30,31</sup> with a continuous increase in both parameters. However, in the case of Odonata, disparity metrics (volume and dispersion) decreased throughout the considered period, a trend indicative of a bottom-heavy disparity pattern, which is expected for a clade unaffected by a major crisis.<sup>21</sup> Further scrutiny reveals that the most striking patterns in early representatives of Odonata morphological evolution are severe shifts in occupied areas which occurred during mass extinction intervals. The Permian-Triassic and the Triassic-Jurassic transitions witnessed a depauperation of particular areas of the morphospace due to selective extinction, and the subsequent rise of new groups, representing new shapes and, potentially, new flight strategies. The Odonata morphospace was deeply restructured during these two events. This trade-off between extirpation and settlement of morphospace area contradicts the classical assertion of a morphospace fulfilled early and followed by subsequent selective extinctions and clustering within the initial area. Instead, the observed, recurring pattern recalls the single selective peaks model<sup>20</sup> as well as the model of rotation of occupied areas, documented in arthropods.<sup>53</sup>

### Limitations of the study

Representatives of each of the major taxa known within the studied time bins were included (Figure 2). Yet, because only complete wings could be taken into account in our study, the majority of the known species had to be discarded. This might have induced an under-representation of the past disparity of the group and might have particularly altered dispersion metrics. Although we sparingly resorted to retro-deformation and reconstruction of missing parts, the impact of these processes needs further validation tests. Because of a comparatively lower amount of undeformed fossil material during the Triassic, differences between Middle and Upper Triassic samples might have been underestimated (notably as a consequence of uniformization resulting from the retro-deformation process). Finally, a more exhaustive fossil record, in particular for the Lopingian and the Lower Triassic, and for Triassic representatives of Epiroctophora, might demonstrate that the observed significant variations were more gradual than currently appreciated.

### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
- **RESOURCE AVAILABILITY**
  - Lead contact
  - Materials availability
  - Data and code availability
- **METHOD DETAILS**
  - Species selection
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  - Morphometric data acquisition
  - Specimen retro-deformation and reconstruction
  - Testing the impact of missing fossils
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
  - Morphospace computation
  - Disparity metrics

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.107420>.

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## AUTHOR CONTRIBUTIONS

All authors conceived the project. I.D. wrote the initial manuscript with significant inputs from all other authors. I.D. generated the main dataset; I.D. and J.B. processed it. Figures were made by I.D. with significant inputs from J.B., L.V., and O.B.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
<b>Deposited data</b>		
Morphometric data sources	<a href="#">Data S1</a>	N/A
Landmark coordinate data	Mendeley Data: <a href="https://doi.org/10.17632/h9zbtrxsc.1">https://doi.org/10.17632/h9zbtrxsc.1</a>	N/A
R source code	Mendeley Data: <a href="https://doi.org/10.17632/h9zbtrxsc.1">https://doi.org/10.17632/h9zbtrxsc.1</a>	N/A
<b>Software and algorithms</b>		
R Studio v.4.1.2	R Core Team <sup>69</sup>	N/A

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Isabelle Deregnacourt ([deregnacourt.isa@gmail.com](mailto:deregnacourt.isa@gmail.com)).

#### Materials availability

This study did not generate new unique reagents.

#### Data and code availability

- Landmark dataset and vector-line drawings have been deposited at Mendeley and are publicly available as of the date of publication. The DOI is listed in the [key resources table](#).
- All original code has been deposited at Mendeley and is publicly available as of the date of publication. The DOI is listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

### METHOD DETAILS

#### Species selection

A list of fossil Odonata species, with their stratigraphic record, was extracted from the Paleobiology Database<sup>44</sup> from the Cisuralian (early Permian) to the Upper Jurassic. It was double-checked and complemented if necessary. A pattern of vein homologies that could be consistently applied to the entire selection of Odonata was then adopted (Figure S4). Because this pattern can only be applied on (sub-)complete, undeformed wings, only a subset of the known specimens could be used. The list of these specimens is provided in Data S1. As for the Permian, 16 Cisuralian (lower Permian) species, over 61 known, were considered; 9 over 23 for the Guadalupian (middle Permian). As for the Lopingian (upper Permian), the wing venation pattern could be applied to a single species only (over the two known); this epoch was therefore ignored, as computation of disparity metrics requires several observations, yet the corresponding species contributed the total morphospace.

No species is known in the Lower Triassic. Eight Middle Triassic species was selected (among 36). Among the 32 species known of the Upper Triassic, only 10 were considered sufficiently complete. The low ratio of Triassic odonates suitable for our analysis is essentially due to the fact that most of known fossils for that period have been found at Madygen, where specimens endured important tectonic deformation.<sup>70,71</sup> As a consequence, most specimens cannot be used in morphometric analyses, pending shape restoration (but see below).

More species are known in the Jurassic. For the Lower Jurassic, 15 species (over 101) were selected; and 44 (over 146) for the Upper Jurassic. There are only 8 species known for the Middle Jurassic and none of them proved sufficiently complete to be analyzed.



In order to maximize the number of known families represented for each epoch, and in particular for the Triassic, several specimens were retro-deformed and/or missing parts reconstructed using a standardized and repeatable method based on Thin Plate Spline<sup>48</sup> (see [star method](#) Details section).

### Phylogenetic and taxonomic background

We derived a consensual phylogeny and taxonomic framework by combining information from Bechly,<sup>72</sup> Nel et al.,<sup>47</sup> Nel et al.,<sup>46</sup> Tierney et al.,<sup>73</sup> Deregnaucourt et al.<sup>74</sup> and Nel & Piney<sup>75</sup> (Figure 2).

### Morphometric data acquisition

The adopted terminology for main veins follows Kukalová-Peck, 1991,<sup>37</sup> and Deregnaucourt et al.<sup>76</sup> was followed for intercalary veins of the radial area (Table S1). Homologies were assessed using consensual reviews<sup>38,39</sup> as well as more specific, recent accounts.<sup>46,48,74,77</sup> A subset of venation elements was selected to compose a single pattern applicable to the entire sample of Odonata species (Figure S4; Table S1). The corollary is that several elements were discarded, because they are not present in all selected species, such as the pons (absent in Meganisoptera and Protanisoptera), and CuA and CuP (strongly reduced, or even absent, in some Archizyoptera). Simple veins were represented by a single curve. The only bifurcating vein, namely RP, was split into 5 curves. The wing margin was divided in 10 sections, delimited by the ends of two successive main veins or intercalary veins (among those selected). When veins are divided into several branches in only a few species, such as RP3+4 within the Triadophlebiomorpha, only the most posterior branch was considered.

From an anatomical perspective, specialists usually recognize fusion of wing veins. For geometric morphometrics, sections involving veins fusion can be considered as composed of veins running aside each other, and therefore treated as two different, superimposed curves, or as a single, distinct object. The latter option was followed, as it allows the inclusion of species possessing, and species lacking, a given fusion. Each specimen was redrawn in vector line drawing under Adobe Illustrator (Adobe Systems, San Jose, CA, USA) based on published and/or new data (see details in Table S1). A specific RGB colour-coding was attributed to each vein or vein section. Colour-coding was inspired by colors used in the literature.<sup>40,76</sup>

Acquisition of homologous landmarks and geometric morphometrics analyses were conducted under R.<sup>69</sup> Landmarks of types I and II were automatically placed thanks to a dedicated script. Type I landmarks are placed at the start, and end, of each vein or vein section. Trajectories of each vein is captured using sliding semi-landmarks.

The number of semi-landmarks on each vein and vein section was calculated based on the mean length of the section (Table S1). Once semi-landmarks were distributed, a Procrustes superimposition was performed to correct for the effects of size, rotation and translation. During this step, semi-landmarks were treated as sliding landmarks by minimizing the bending energy.

### Specimen retro-deformation and reconstruction

To complement our dataset, and in particular for the Triassic, several specimens from the Madygen locality were retro-deformed. This approach best addresses pitfalls inherent in this material. The options are to either (i) remove deformed specimens from the dataset, (ii) include them uncorrected, or (iii) include them once retro-deformed. The pitfall of option (i) is that shapes expected to occupy critical areas of the morphospace will not be considered. This can have critical implications when comparing time bins. Conversely, adopting the option (ii) could introduce undue gain in morphospace volume by adding genuinely false shapes. As for option (iii), the potential pitfall is that the distinctiveness of particular taxa at a particular time bin could be under-estimated (if shapes from another time bin were used in the retro-deformation process). This last option is therefore best-suited to avoid unjustified over-estimation of disparity variations.

To compute retro-deformation, the set of landmarks, applied to a deformed wing, was submitted to 37 different rotations (over 180°) and 11 elongation factors (from 100% to 200%) to generate 407 retro-deformed shapes (landmark sets/wings). Each retro-deformed shape was compared to a chosen, reference shape, which was either a complete wing of the closest relative to the (retro-)deformed specimen, or a mean shape derived from several specimens belonging to species very closely related to it (see below and Data S1). Comparison was performed by a Procrustes superimposition, the selected

retro-deformed shape is the one minimising the Euclidean distances with the reference. We regard this shape as the best approximation of the initial shape, given our current knowledge, but also as the one adding the least disparity to the analysis.

In detail, the most recent members of the distinctive family Kennedyidae (Archizygoptera), *Kennedyia carpenteri* Pritykina, 1981<sup>61</sup> and *Kennedyia gracilis* Pritykina, 1981<sup>61</sup> are represented by complete but deformed wings from the Madygen locality. To consider the morphological information carried by these species we computed a retro-deformation using a consensus shape derived from known complete material of Permian *Kennedyia* spp.

The Batkeniidae are also a distinctive family of Archizygoptera present during both the Permian and the Triassic. All Triassic representatives were recovered from the Madygen locality and are therefore known from deformed material. Whereas the material of *Paratriassoneura primitiva* (Pritykina, 1981)<sup>61</sup> is too incomplete, that of *Batkenia pusilla* Pritykina, 1981<sup>61</sup> proved well-suited, with the known material preserving two complete wings and one almost complete of a single individual. We retro-deformed the two complete wings using the Permian Batkeniidae *Engellestes cherkadensis* Nel et al., 2012<sup>46</sup> as reference shape, and then computed a mean shape.

The triassolestids that do not belong to the Lobodonata are important as they may represent an approximation of the ancestral shape of the entire Panodonata. To include as many of these species as possible, we retro-deformed the best-preserved wing of *Triassolestodes asiaticus* Pritykina, 1981<sup>61</sup> using the holotype of the Triassic species *Triassoneura andersoni* Riek, 1976<sup>78</sup> as reference shape.

The Triadophlebiomorpha are a prominent component of Triassic Odonata<sup>61</sup> but are mainly known from Madygen material. Among the known species, *Zygophlebia ramosa* Pritykina, 1981<sup>61</sup> could be retro-deformed, as a closely-related species, *Moltenophlebia lindae* Deregnaucourt et al., 2021,<sup>48</sup> could be used as reference shape.

In order to ensure a sampling of shapes as exhaustive as possible, we also endeavored to reconstruct some partly incomplete specimens. Missing parts were reconstructed based on complete reference specimens (chosen as for the retro-deformation method) and following Deregnaucourt et al.<sup>48</sup> (see [Data S1](#)). This process involved five species.

The Voltzialesitidae (Archizygoptera) are represented in the Cisuralian (lower Permian), with *Azaroneura permiana* Nel et al., 2012,<sup>46</sup> and the Middle Triassic, with *Voltzialesites triasicus* Nel et al., 1996.<sup>79</sup> However, each species is known based on a single wing lacking a part of its base. This area was reconstructed using a pool of known, complete (and undeformed) wings of Protomyrmeleontidae. That minimising the Euclidean distances with the known part of each wing was used as reference. The same procedure was used to complete the wing base of *Tillyardomyrmeleon petermilleri* Henrotay et al., 1997<sup>80</sup> and the wing base and apex of *Moltenagrion konningskroonensis* Deregnaucourt et al., 2021.<sup>74</sup> The wing venation of *Moltenophlebia lindae* (Triadophlebiomorpha), as reconstructed in Deregnaucourt et al.,<sup>48</sup> was added to the sample.

### Testing the impact of missing fossils

We considered the impact of the lack, in our sample, of particular groups known to occur at a given epoch but which known fossils were not suited for the morphometrics analysis. The Camptero-phlebiidae and the Liassophlebiidae are two families of Panodonata sampled for the Lower and Upper Jurassic in our analysis, but which have reported occurrences in the Triassic. As for the former family, *Sogdophlebia singularis* Pritykina, 1970<sup>81</sup> is known from a single specimen preserving the basal third of a wing, which is probably deformed. It is therefore too fragmentary to be reconstructed with confidence. Nevertheless, we tested the impact of adding a Camptero-phlebiidae to our Upper Triassic sample. To do so, a mean shape derived from the sampled Jurassic Camptero-phlebiidae was added to the Upper Triassic. The obtained results were similar to those obtained without this addition.

As for the Liassophlebiidae, several species of the genus *Liassophlebia* Tillyard, 1925 were found at the Strensham locality (Blue Lias Formation, Wilmcote Limestone Member; Worcestershire county, UK), first regarded as Lower Jurassic<sup>82,83</sup> and later as Upper Triassic.<sup>84</sup> However, these Triassic specimens are too fragmentary to be reconstructed with confidence and added to the sample. To test the impact of the presence

of Liassophlebiidae in the Upper Triassic, we used the only other representative of the genus in our sample, belonging to *Liassophlebia magnifica* Whalley, 1985,<sup>85</sup> from the Lower Jurassic. The specimen was duplicated in the Upper Triassic. The obtained results were similar with and without this addition.

The Triassic Triadophlebiomorpha exhibit a number of distinctive traits. It therefore appeared important to consider earlier forms. *Permophlebia uralica* Nel et al., 2001<sup>47</sup> is regarded as one of the two Permian representatives of the group. However, even though the corresponding material was collected in the area of the Vorkuta basin, it was actually retrieved from a drilling core, at a depth corresponding to the zonations T1cb1 or T1cb2 (V. Silantiev, pers. com. 2022). It can then be established that the corresponding strata belong to the Lower Triassic Charkabozh Formation<sup>86</sup> (A. Felker, pers. com. 2022). Besides age-related issues, the only known wing lacks both the base and apex, and no suitable reference could be identified with certainty, because the phylogenetic position of the species is unclear.<sup>47</sup> *Kargalotypus kargalensis* (Martyanov, 1932),<sup>87</sup> from the Kargala locality (Tatarian; Orenburg Region, Russia) is then the only Permian Triadophlebiomorpha. Unfortunately, it is known only from the distal half (maybe two-thirds) of a single wing. Because of uncertainties on its affinities within Triadophlebiomorpha on one hand,<sup>47</sup> and the wide range of morphologies exhibited by the Triassic members of this group, it proved impossible to derive a reliable surrogate to be added to the Permian sample.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Morphospace computation

A Principal component analysis (PCA) was performed for all the 136 fossil wings, representing 103 species. For the species represented by more than one wing, a mean shape was computed by taking the mean of the Principal Component (PC) scores of each specimen. Each species is thus represented by a single point in the morphospace. Extreme shapes corresponding to the minimum and maximum of the two first PC axes were generated to visualize shape variation (Figure S2).

### Disparity metrics

Disparity is the quantification of the diversity of morphologies.<sup>16,19</sup> The multidimensional space derived from a Principal Component Analysis is assumed to represent an empirical morphospace of wing shape diversity. Species coordinates on PC axes are used as raw variables to compute disparity measures. Several metrics are available that can be gathered into three categories, whether they describe size of the occupied morphospace, density of observations, and position of the observations within the morphospace.<sup>16–18</sup> These different types of metrics provide complementary information.<sup>16–18</sup> The size approximates the amount of space occupied, higher values indicating the occurrence of more extreme shape combinations. Dispersion metrics tend to become higher when observations are sparsely distributed, and lower when observations are densely distributed. The position metrics informs on changes in the location of the occupied areas within the morphospace.

Size of morphospace occupation was estimated by computing the sum of ranges of the PC scores; dispersion as the sum of variances of the PC scores; and position as the sum of distances between centroids of data subsets. The metrics were computed on the seven first PCs and rarefied to standardize sampling biases. A thousand bootstrap replicates were computed for eight species, which is the minimum number of species sampled in the analyzed time bins.

Significance of disparity changes between successive time bins was assessed using permutation tests. Each permutation run consists in attributing a random time bin to each species. Disparity metrics calculated in a thousand permutations provide a distribution corresponding to no difference between the two considered time bins (H0 hypothesis). A p value corresponds to the number of runs that have more extreme values compared to the raw measure.<sup>88</sup> The impact of the number of bootstrap replications on each p value was tested (Figure S5).