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Abstract. The limits and difficulties related to the tools currently in use for palaeosynecological comparisons of faunas or floras of different geological periods are discussed. The new method of the Wagner parsimony Applied to Palaeosynecology Using Morphology (WAPUM method), is defined and tested on morphological characters gathered from two insect groups Odonatoptera and Thripida. The difficulties related to the monophyly of the taxonomic groups used in the more traditional approaches are no longer a problem when using the WAPUM method. In the WAPUM a character is 'presence versus absence of species bearing a morphological structure'. The results obtained from use of the WAPUM minimize the number of changes among character states. Application of the WAPUM could reveal signals to confirm or object the currently available scenarios for the global changes in the evolution of past diversity and disparity of organisms (major changes or global crises of diversity).

Résumé. La parcimonie de Wagner sur base de caractères morphologiques : une nouvelle méthode pour les études paléosynécologiques. Les limites et difficultés inhérentes aux outils actuellement utilisés dans les comparaisons paléosynécologiques de faunes ou de flores de différentes périodes géologiques sont discutées. La nouvelle méthode de la parcimonie de Wagner appliquée à la paléosynécologie sur la base de caractères morphologiques (méthode WAPUM), est définie et testée à partir des caractères morphologiques de deux groupes d'insectes, les Odonatoptera et les Thripida. Les difficultés liées à la monophylie des groupes taxonomiques utilisés dans les approches plus traditionnelles disparaissent avec la méthode WAPUM. Dans l'approche WAPUM, un caractère est 'présence/absence d'une espèce portant une structure morphologique'. Les résultats obtenus à partir de la méthode WAPUM minimisent le nombre de changements d'état de caractères. Cet outil permet de tester les scénarios actuellement disponibles pour les changements globaux dans l'évolution de la diversité et de la disparité passée des organismes (changements majeurs ou crises globales de la diversité).

Keywords: Fossil record, Insecta, Odonatoptera, Thripida, cladistics, phylogeny.

The analysis of global, planetary, faunistic and floristic changes during the Phanerozoic eon is very important to define the stratigraphic divisions and the major crises of biodiversity. The only available tools to study and estimate these changes are 'typological' techniques, characterizing the different geological periods by the presence/absence of fossils that are supposed to be *a priori* characteristic of each of them.

The scope of this paper is to define a new tool to study palaeontological changes by means of compari-

sons and classification of sets of geological periods (global analyses) or sets of fossil assemblages after the comparison of their faunas and/or floras.

Current comparisons of the faunas or floras of different geological periods (for estimations of global crises) are based on variations of percentages extracted from lists of presences versus absences of taxa (orders, families). Only a few works concern insects, or more generally terrestrial arthropods, while these constitute the most diverse groups of animals since the Late Carboniferous. Jarzembowski & Ross (1996), Labandeira & Sepkoski (1993), Labandeira & Elbe (2001), Labandeira (2005), and Shcherbakov (2008a, b) proposed such analyses on the past diversity of insects. These authors considered that it is possible to use paraphyletic

groups, on the basis of a statistical analysis performed by Sepkoski & Kendrick (1993), who showed that for some artificially generated cases, it is possible that paraphyletic 'groups' can restore their 'a priori' known 'history of life' from which they are extracted. Nel (1998) and Gall et al. (1998) have already considered that the use of artificial, paraphyletic 'groups' poses a great risk of bias in the analyses. In the real concrete situation of the actual history of life, it is not possible to test the approach of Sepkoski & Kendrick (1993), if the paraphyletic 'groups' really restore correctly the 'history of life' simply because this 'history' is a priori unknown. Thus it is better to avoid using them.

The problem is specially acute for the Palaeozoic insects among which the paraphyletic or polyphyletic 'groups' are very numerous, with many fossils, some of which are related to major extant clades. The best well-known and obvious example of such para- and/or polyphyletic groups is the Paleozoic 'order' Protorthoptera, which comprises very numerous fossils and is one of the major 'orders' that is supposed to have disappeared at the end of the Permian [see list of attributed families in Carpenter (1992) except for Triassic Chaulioditidae (= Tomiidae sensu Aristov 2004)]. It 'contains', in fact, taxa of the 'orthopteroid', 'grylloblattid', and paraneopteran clades, among others, which survived after the Permian to the Recent period, introducing biases in the analyses cited above. There are many other possible paraphyletic or polyphyletic Palaeozoic major 'orders' (with numerous fossils), viz. the Grylloblattodea ('paraphyletic state of the order in respect to other perlideans' after Storozhenko 2002), the Hypoperlida (paraphyletic with respect to the Paraneoptera after Rasnitsyn 2002), etc. The solution of these problems of paraphyly and polyphyly is not to use these groups without precaution but to solve their phylogenetic relationships before using them for the analyses of palaeobiodiversity. It is possible to do so, as demonstrated by the recent works on the 'orthopteroid' insects (Béthoux & Nel 2002, among others).

The impact of taphonomic and palaeoecological biases in the various deposits can be also very important, as shown by the following example: Shcherbakov (2008b: 27) suggested that 'the most ancient dragonflies are considered to have essentially been hunters of paleodictyopteroids, and this is supported by their simultaneous decline in diversity'. Such an assumption is not obvious because the most recent fauna of Meganisoptera from the Guadalupian (Middle Permian) of Lodève (France) is also the most diverse (Nel et al. 2009), while the same deposits at Lodève have yielded only two species of Palaeodictyoptera. Thus this fauna would not support a simultaneous decline in diversity for both groups. This kind of relationships between taxa is very delicate to establish because of: - the lack of significant samples of both Palaeodictyoptera and Meganisoptera in the Lopingian (Upper Permian); - the taphonomic and palaeoecological biases can be very important and sometimes difficult to evaluate. In the case of the Lodève basin, the disproportion between the species records of Palaeodictyoptera and Odonatoptera could well be related to such biases: the Odonatoptera are predators with carnivorous aquatic larvae, while the adults and larvae of Palaeodictyoptera were terrestrial and phytophagous. Interestingly very few terrestrial plants have been found in these sediments.

The Wagner Parsimony Applied to Palaeo-synecology Using Morphology (WAPUM)

The general use of the Wagner Parsimony method of classification in synecology, as defined by Nel et al. (1998), can be applied to the classification of geological periods and/or palaeontological localities. Coiffard et al. (2004, 2008) have already tested this approach for classifying Cretaceous plant assemblages with some success. Petrulevicius (2001) discussed the method in some Upper Palaeocene localities of the same basin in North West Argentina and concluded that the localities should be grouped by their taphonomical similarities and arranged by groups of elements with similar taphonomical functionality (= taphons sensu Fernández-López 2000), i.e., surface/density of the body, degree of sclerotization of the body, etc. This is possible in some cases but we could found also same taxa in two localities and representing two different taphons, i.e., isolated wing in locality A and complete body in locality B.

The method of parsimony (sensu Crisci 1982) is 'a rule instructing the scientist to choose the simplest of several empirically equivalent hypotheses' but not a principle that would be based on an 'assumption about the simplicity of nature'. Unlike its application in the cladistic method, the general method of the Wagner Parsimony is independent of all ideas of phylogenetic sequence. The classification of a set of objects is based on a hierarchical system of shared characters, depending on their state compared to the states present in reference object(s), the outgroup(s). It allows: 1) to connect objects, with one (or several) most parsimonious or minimal tree(s) of classification, rooted or not, in order to minimise the total number of transformations; 2) to establish the character states at each node of the tree(s); 3) to trace the changes of state for each character in the most parsimonious trees;

4) to compare the trees, on the basis of various indices (length, consistency index, etc.); 5) to translate and synthesise the palaeontological data using the minimum *ad hoc* supplementary hypotheses, these hypotheses being clearly identified (choice of out-group(s), equally weighting of characters); 6) to estimate the impact of each datum on the construction of the minimal tree(s). The resulting minimal trees are **not** supposed to fit a phylogenetic analysis of the studied objects.

A. Which sets of objects to classify?

The current analyses are global or supposed to be so (comparisons of World faunas or floras at different stratigraphic levels) (Labandeira 2005). They do not make allowance for: - the incompleteness of the global fossil record, related to the lack of deposits (i.e. there are only a few Russian outcrops with insects around the boundary between the Permian and the Triassic that could hardly represent the World diversity) (Shcherbakov 2008a,b); - the incomplete fieldwork at some levels and lack of taxonomic studies for some 'difficult' groups (e.g. fossil Coleoptera, Hemiptera, and Lepidoptera are clearly understudied). Shcherbakov (2008b) proposed a curve representing the number of families of Odonatoptera for the Permian and Triassic, but no species are described for the uppermost Permian and lowermost Triassic. He also figured a maximum of diversity for the Triassic Ladinian that corresponds to the exceptional outcrop of Madygen (Kyrgyzstan). Several of these 'families' are suspected of paraphyly. The recent discoveries of Odonatoptera in the Permian Guadalupian of Lodève (southern France) have also greatly increased the record for the Middle Permian. This example shows that such curves are very sensitive to the presence of 'Konservat Lagerstätte' and descriptive work.

Whatever method is employed ('traditional' as those of Labandeira or Jarzembowski, or Wagner Parsimony); these analyses are based on two primary hypotheses: - the known fossil record more or less reflects past biodiversity; - the bias of incompleteness of the fossil record is the same for all periods, or nearly so. This assumption is probably true for the Late Carboniferous to the Present, although some periods are favoured by the presence of very rich 'Konservat Lagerstätte' (e.g. Eocene Baltic amber) while others clearly have not enough outcrops (e.g. the Lopingian and the Lower Triassic). The situation is even worse for the Mississipian (Lower Carboniferous) in which insects are still unknown or nearly so, probably because very little fieldwork has been done until now to find fossil insects (Prokop *et al.* 2005). It should be possible to test these hypotheses through the comparison and degree of congruence between different Wagner Parsimony analyses

undertaken on the basis of different sets of taxa.

Another problem is the definition of the stratigraphic units to be compared: is it significant to compare periods (Carboniferous to Permian, Triassic, etc.), or to compare subdivisions of these periods (subperiods, epochs and stages)? A limitation occurs with the richness of the available information for each unit: e.g. we have significant information on the World insect fauna for the Lower, Middle, and Upper Permian, but we lack information if we want to compare the insect faunas of the subdivisions of these three subperiods. A different approach for solving these problems would be to compare actual fossil localities (corresponding to different stratigraphic units), instead of their units (Coiffard *et al.*, 2004, 2008). This option would allow better analyses because other data available in actual localities or fossil associations could be tested after the preliminary analysis, i.e. the taphonomic and palaeoecological biases. This option implies comparison of localities with similar taphonomic biases. For example, in fossil insect analyses, comparing amber assemblages with lacustrine assemblages is of less use than the comparison of amber assemblages alone. It is probably more difficult to compare lacustrine assemblages because the taphonomic biases can be very different, greatly affecting the faunistic composition of the compared assemblages (e.g. the Playa palaeoenvironment of the Permian of Lodève is strikingly different from the estuarine palaeoenvironment of the Middle Triassic of Grès des Vosges) (Gall 1971; Lopez *et al.* 2008).

It is then necessary to define the characters used for the comparison of the geological intervals or the palaeontological assemblages, the weighting of the characters, and out-group(s).

B. The characters

A character is the 'presence' versus 'absence' of something (taxon, species with a particular morphological structure). It is under the state 'present' in at least a part of the set of objects we want to classify (here studied geological intervals or palaeontological localities). In synecological analyses, a character is the 'presence versus absence of a taxon' (Nel *et al.* 1998).

Taxa as characters?

For synecological analyses, the best suited taxa are species because different species can have very different biology, chorology, and ecology. Thus the use of species will give the most precise synecological results. The difficulties in using species in recent synecological analyses are often related to the time-consuming process of identification of the samples.

For palaeocological analyses, the fossil record of taxa lower than the family level (genera and species) is too incomplete to be used (at least for insects). Therefore the analyses are to be based on families and/or taxa of higher rank.

Nevertheless, fossil or extant families or supra-familial taxa are more or less artificial sets of species. Some are considered as monophyletic, because they share synapomorphies (more precisely characters that are currently considered as so). Thus the palaeosynecological analysis will depend on the changes in the status of the taxa that are used to perform it. A taxon can be found monophyletic in a first phylogenetic analysis and para- or polyphyletic later. Even for monophyletic taxa, the limits of 'genus', 'family' or other groups of higher rank can also depend on the author (a fossil can be considered either as the sister group of a extant family or be included in the family). Because of this situation of possible paraphyly or polyphyly, and fluctuating limits of what is a family, counting the number of families of a given period has little sense (see for example the family diversity curve proposed by Shcherbakov 2008b: fig. 1).

Furthermore, the monophyly of numerous fossil groups of high rank is not supported by any apomorphy. For example, there is still no known apomorphy that supports the monophyly of the well known Meganisoptera ('giant griffenflies'), while it is the most diverse Palaeozoic odonatopteran group (Nel *et al.* 2009). Yet the presence of this group during the Permian and its absence during the Triassic must reflect some change in the World ecosystems. The use of groups or clades in palaeosynecological analyses cause problems.

An alternative: using morphological characters instead of taxa

Instead of using taxa that may not reflect exactly ecological or morpho-functional characters, we propose to develop a different approach we call here 'Wagner parsimony Applied to Palaeosynecology Using Morphology' (the WAPUM method), based on characters defined as the 'presence versus absence of species having a morphological character'.

A first option would be to use only the morphological characters that define the apomorphies supporting the taxa (genera, families, or any clades of different ranks) as characters. But there is no special reason to restrict the set of characters to apomorphies. A more complete option is to use any morphological structures in our characters, **without** considering their polarization as plesiomorphies and apomorphies in the available phylogenetic analyses. For example, for an analysis based on the Odonatoptera, a possible character will be 'absence versus presence of species having wings with-out nodus', while a different character will be 'absence versus presence of species having wings with a nodus'. The two characters shall be under the state 'present' for the Permian, while the first one must be under the state 'absent' for the Triassic. The presence of Odonatoptera without nodus during the Palaeozoic and their absence during the Triassic are both informative because these structures are certainly related to the flight of these predatory insects (Wootton *et al.* 1998), and thus should be linked to their prey's capture capacity, to the absence or relative rarity of flying vertebrates, and *in fine* to adaptations to the Palaeozoic terrestrial ecosystems.

This approach allows including information that is present in 'groups' that are suspected of paraphyly or polyphyly (viz. the Meganisoptera). Otherwise the information coming from such taxa is to be rejected in palaeosynecological analyses based on taxa as characters.

When a phylogenetic analysis of the concerned clade is available, some morphological structures can be homoplastic, and their treatment needs a discussion: for example, the character 'absence versus presence of a species without sclerotized pterostigma' is under that state 'present' for the Carboniferous and Permian, because of the Meganisoptera, but also in the Triassic for the Triadophlebiomorpha, in the Jurassic and Early Cretaceous for some Anisoptera: Aeschnidiidae, and in the Cenozoic to Recent for some Calopterygidae. The absence of a pterostigma is clearly a plesiomorphy for the Meganisoptera and Triadophlebiomorpha, but it is a reversion in some Aeschnidiidae and Calopterygidae. Thus such a character will obviously be a homoplasy in the palaeosynecological Wagner Parsimony analysis. Two options are then possible: make the analysis with or without such characters. If they are removed *a priori* from the analysis, it is always possible to use them as attributes to determine if their presence could be correlated to environmental attributes.

Labandeira (1997, 2006) proposed a rather similar approach with a direct analysis of the evolution of the mouthpart structures of the insects, independently of the taxa themselves, but he did not apply the characters he obtained (the 'functional feeding groups') to a Wagner Parsimony analysis. It would be interesting to treat these data in a Wagner Parsimony approach.

Presence versus absence of a palaeosynecological character

The presence

Three options are available to define the presence of a character (a taxon or a 'species bearing a morphological structure') in a geological period or a palaeontological locality:

a) the direct evidence based on the presence of the concerned character. Using only the strict fossil record, the more hypothetical presences obtained by indirect evidences, are to be considered as dubious and considered as missing data (coded '?' in Wagner matrices).

b) the indirect palaeoentological evidence based on the presence of the character during a period with no direct available record but for which it can be inferred by its presence in adjacent periods (just before and after). Such gaps in the fossil record can be filled based on the assumption that there is no difficulty in the determination of the fossil taxa, which is not always obvious. These gaps between two records could be treated either as real presences or as missing data. This latter approach is based on the preliminary choice to have as few *a priori* as possible. Using this choice of treatment, more precise parsimonious inferences on the context of the missing data can be made after the Wagner analysis has been performed.

c) Indirect evidence: the presence of the character during a period can be inferred after the biogeographical reconstructions and/or the sister groups relationships of the concerned taxon have been determined. The presence versus absence of some structures during a particular period can be inferred after the phylogenetic analysis of the corresponding clade. For example, in the clade Thripida (thrips and relatives), the presence of the thysanopteran-type of arolia and modified mouthparts can be inferred in all their representatives since the Permian on the basis of their presence in two Jurassic species of one subclade and in all the Recent and Cretaceous Thysanoptera of the other subclade (Nel *et al.* 2007, 2010 this issue, submitted).

The gathering of these three types of direct and indirect evidence can be qualified as part of the character's total evidence. It adds information to the data matrix, but it also increases the chances to add errors or not well-founded information.

The absence

In comparisons of stratigraphical levels, the non-discovery of a fossil taxon in the geological periods that have followed its youngest fossil record does not mean that it was not present as a Lazarus taxon. There are several examples of such taxa, viz. the presence of the damselfly family Hemiphlebiidae in the Lower Cretaceous, represented in the modern fauna by only one Australian species, with no Cenozoic record (Lak *et al.* 2009). Consequently, in no way does the direct evidence of the youngest-known fossil record of a taxon demonstrate that it was not present in younger periods. As there is no way to determine the exact

times of extinction of a taxon after its youngest record, it is just possible to record as an absence the available data of non-discovery. In this case, an assumption of absence can be proposed as a primary hypothesis, to be discussed on the basis of the resulting most parsimonious trees.

In order to distinguish the possible situations covered by an 'absence', a character can be coded as follows: - not yet appeared: 0; present in fossil record: 1; extinct: 2; - not yet appeared: 0; present in fossil record: 1; lazarus (no longer present in fossil record but present in modern record): 2.

The situation slightly differs for comparisons of palaeontological localities because the palaeoecological information becomes more important than in the comparisons of different levels; thus one can assume that rare, Lazarus taxa are not very important for the analyses and the reconstructions of the palaeoenvironments, certainly less important than the relatively frequent taxa. Thus, in a palaeoenvironmental perspective, it is possible to consider such taxa as missing data.

To summarize

- The presence of a character can be considered as unambiguous if the concerned taxon (or structure) have been discovered as fossils (but also in the case of a taxon if it is supposed to be monophyletic, and if the identifications were correctly made).

- The absence of a character in the fossil record is fundamentally more ambiguous.

Independence of the characters

The problem of the independence of the characters is difficult. Some structures are present in a unique clade (for example those supporting the monophyly of a family). One could argue that they are not strictly independent. Only the discovery of fossils bearing only some of these characters would demonstrate their independence. But this problem also occurs in nearly all the phylogenetic analyses, especially for those based on molecular data. Thus the characters can be considered as primarily independent, and be re-analysed after the search for the most parsimonious trees. Furthermore, it is of interest to use all the morphological structures that occur and support one clade because they better translate the 'degree' of specialization of the concerned clade, which could be related to the particular ecosystems of the periods during which this clade was present. For example, the odonatopteran families Aeschnidiidae and Cymatophlebiidae are present during the Jurassic, but the former is characterised by no less than six 'major', unique morphological structures, while species of the latter bear only one known structure that

cannot be found in the other odonatopteran groups. In a palaeosynecological analysis based on the presence versus absence of taxa, these two families have the same weight, while the Aeschnidiidae are certainly much more 'significant' than the Cymatophlebiidae in the characterisation of the Upper Jurassic palaeobiotas for their numerous, particular morphological structures that did not cross the end of the Lower Cretaceous. The palaeosynecological analyses based on the taxa as characters ignore this dimension, because different family names could correspond to very different degrees of specialisation.

Treatment of the characters

The characters have to be treated as equally weighted, reversible, and unordered, in order to avoid as many *a priori* considerations a possible (Nel *et al.* 1998). We have to take into account that, although we use equally weighted characters, we are still choosing what characters we are using, as in all cladistic analyses.

'Keystone' and rare taxa for morphological structures

The fossil record is clearly incomplete. Fossil are generally remains of organisms that were very frequent, frequent enough at least during a significant period, and living in some palaeoenvironment as to have a 'chance' to be fossilised. In many cases, the fossil lineages are known through a uniquely oldest representative, with a subsequent diversification and more fossils in more recent periods. As an example, the Upper Carboniferous Holometabola are known through very few fossils while the clade diversified during the Permian, Triassic and in more recent periods (Nel *et al.* 2007; Béthoux 2009). Nevertheless these 'apparently rare' oldest-known Holometabola demonstrate the presence of this clade and of the morphological structures related to it in at least some of the ecosystems of the Moscovian. Such 'rare' fossils certainly correspond to organisms that were already frequent when they were living. They are therefore important in the palaeoecological analyses.

C. The outgroup(s)

For the primary polarisation of the characters/taxa, it is necessary to define or choose one or more object(s) of comparison, the outgroup(s).

In synecological analyses, Lambshead & Paterson (1986) and Bellan-Santini *et al.* (1994) suggested using an outgroup consisting of a hypothetical locality containing no species. Nel *et al.* (1998) have already discussed and dismissed this option.

In the special case of a palaeoecological perspective, it is possible to use real outgroup(s). As the scope is to analyse the evolution of the palaeobiotas, the oldest studied period or locality can be chosen as a real outgroup. With this choice, the presence of an 'ancient' taxon or morphological structure, present in this outgroup, is considered as primarily 'plesiocenotic', and the presence of a 'more recent' taxon or morphological structure as primarily 'apocenotic' or 'derived' (*sensu* Nel *et al.* 1998). Several outgroups (periods or localities older than the studied set of objects) can be applied alternatively or simultaneously and their impact on the analysis tested.

This approach is problematic because considering the presence of the most 'ancient' taxa or morphological structures as plesiocenotic does not take into account the fact that these taxa or structures were adapted to the life in the oldest studied period. It is more logical to use a theoretical empty period, so that each period or group of periods is characterized by apocenotic presences of characters (taxa or morphological structures). Using this choice of an empty outgroup, a character being the 'absence versus presence of a species bearing a structure', the absence will be considered as primarily plesiocenotic and the presence as primarily apocenotic.

D. Analysis of the results

The most parsimonious trees can be summarized through their strict consensus tree. If there is a grade in the resulting tree that follows the succession of the studied objects through time, then no clear hiatus between subsets of levels appears. If some subsets of objects appear as separate groups, not corresponding to their succession through time (absence of congruence between the timing and the tree topology), then it is possible to define an important hiatus that could correspond to faunistic (or floristic) breaks in time.

Furthermore, if the tree is replaced by a 'phylogram' indicating the number of changes on the branches, it is possible to visualize the global changes between the various levels and thus to identify the crucial periods of change. The treatment of the missing data (coded as '?') can be achieved in the same way as in the current cladistic analyses, i.e. by parsimonious inferences on the final tree(s). It allows estimates of possible correlations between the distributions of the different characters.

Wagner Parsimony based on the characters of the type 'presence versus absence of species with particular structure' allows making analyses without considering the problem of the monophyly of all the concerned 'groups' within the studied clade. It also gives testable results as for those of the cladistic approach in phylogeny, unlike the scenarios currently proposed for the evolution of past biodiversity. Our
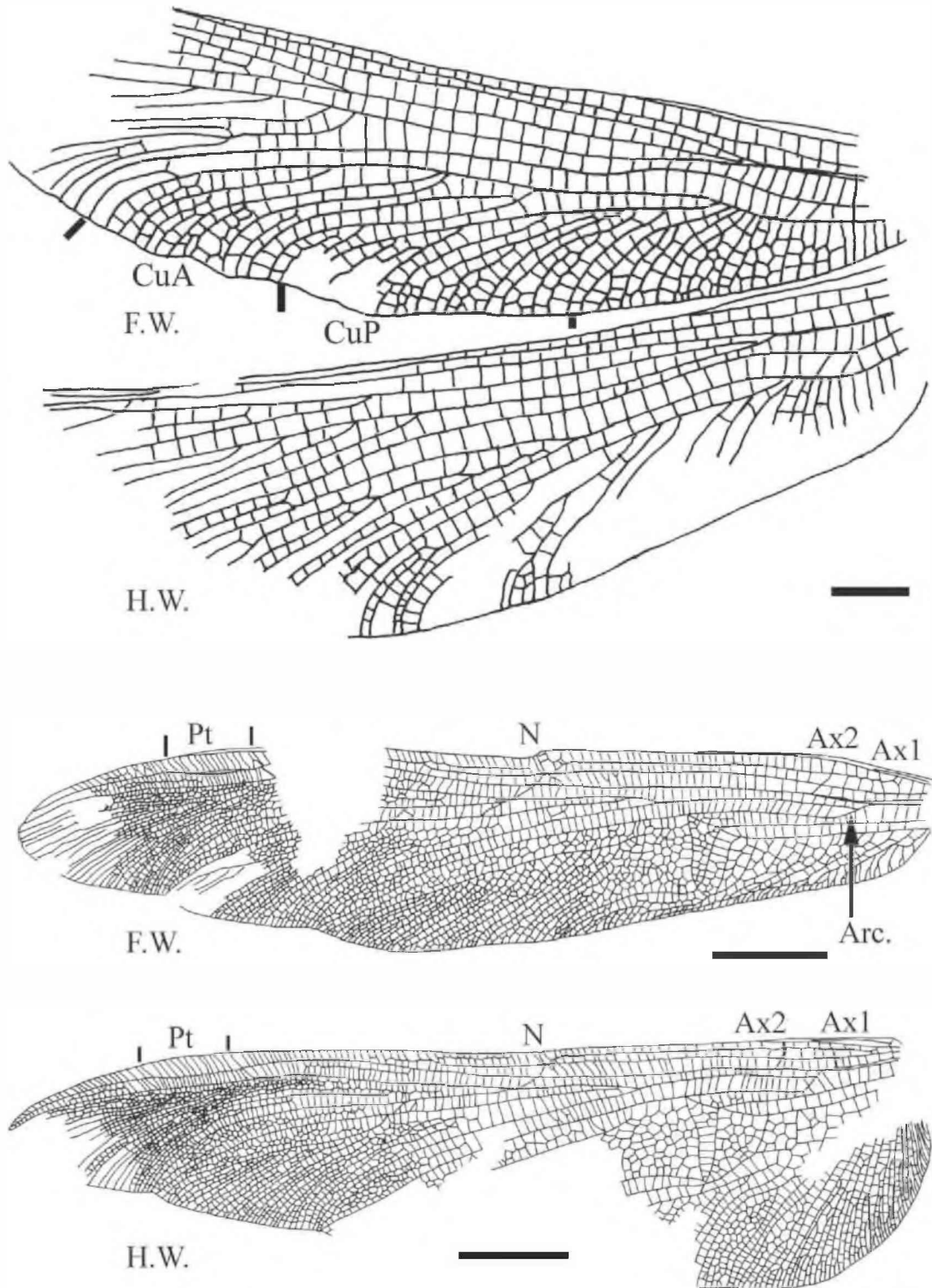
Figure 1
Examples of wings of Odonatoptera showing the major changes in the venation that have occurred between the Paleozoic (meganeurid *Tupus gallicus* Nel *et al.* 2009) and the Lower Cretaceous (aeschnidiid *Linaeschnidium sinensis* Huang *et al.* 2009): development of pterostigma Pt, nodus N, arculus Arc., primary antenodal crossveins Ax1 and Ax2, etc.

approach analyses the evolution and replacement of morphological structures through time in order to relate them to ecological changes that could have influenced them.

This approach does not pretend to analyse the evolution of the number of species, genera, or families in a group. But for the reasons of incompleteness of the fossil record, of the lack of taxonomic studies for numerous groups, of the great impact of the periods with 'Konservat Lagerstättes' versus periods lacking such rich outcrops, it seems that the analyses based on 'presence versus absence of taxa' are very uncertain, at least for insects.

Application to actual examples

We test the new method based on the Wagner Parsimony approach using presence versus absence of morphological structures as characters. We apply the method to the studies of the Palaeozoic, Mesozoic, and Cenozoic Odonatoptera and Thripida.

Characters are equally weighted and unordered. When a character is present in two stages but not recorded for the interval between them, we complete the matrix with the same state of the other two stages. The analysis performed with question marks '?' for such missing data has given the same trees. Exact solutions obtained via Branch and Bound (or implicit enumeration) searches of equally most parsimonious trees have been performed using Paup* 4.0b10 and TNT 1.1 (Goloboff *et al.* 2003). TNT was also used to calculate and display the synapomorphies of the trees.

A. Odonatoptera

This clade is chosen for the following reasons: - these insects are predators, and as so they should be sensitive to the major changes in the ecosystems through the changes occurring in their prey. They are also 'iconic' of the 'giant' Palaeozoic insects, which are supposed to become extinct at the end of the Permian; - the phylogeny of the Odonatoptera is relatively well understood, compared to groups like the Grylloblattodea or the waste basket taxon of 'Protorthoptera'; - its systematic study is based on wing venation structures, at least for the Palaeozoic taxa. These structures are rather well preserved in fossils; - its fossil record for the Palaeozoic was greatly improved recently with several important discoveries.

The data were obtained from Bechly (1996), Fleck *et al.* (1999, 2001), Bechly *et al.* (2001), Jarzembowski & Nel (2002), Huguet *et al.* (2002), Fleck & Nel (2003), Zessin (2008), Ren *et al.* (2008), Nel *et al.* (1999, 2001, 2008, 2009).

The chosen intervals are Lower, Middle, and Upper Late Carboniferous (Bashkirian, Moscovian, Upper Pennsylvanian), Lower, Middle, and Upper Permian (Cisuralian, Guadalupian, Lopingian), Lower-Middle Triassic, Upper Triassic, Lower Jurassic, Middle-Upper Jurassic, Lower Cretaceous, Upper Cretaceous, and Cenozoic. We grouped together the Lower and Middle Triassic and the Lower and Upper Jurassic because of the lack of information on the Lower Triassic and Middle Jurassic Odonatoptera.

Another difficulty emerges with the 'Meganisoptera': this well-known 'group' ('giant griffenflies') ranges from the Bashkirian to the Middle Permian, with the most recent species in the Guadalupian of the Lodève, Var, and Alpes Maritimes basins (red Permian of the South of France) (Nel *et al.* 2009). No Upper Permian Meganisoptera are described till now, but Shcherbakov (2008b) indicated the presence of 'dragonflies Meganeuridae in Aleksandrovka (Bashkir district)' (Upper Permian, Capitanian, Russia). This would be the youngest meganisopteran but it needs to be verified, as confusion is possible with the Triadotypidae that are superficially very similar to the Meganisoptera. Thus we consider that the Meganisoptera (and their morphological structures) are not recorded in the Upper Permian. Also our present knowledge on Mesozoic Zygoptera is very fragmentary, as this group is still unknown in the Upper Triassic and Lower Jurassic, while it should be present as the sister group of the Epiproctophora. Our choice of characters is based on their importance in the general morphology of the various groups of Odonatoptera (fig. 1). This analysis is not based on all the available characters of the known families and genera, as many of them are homoplastic.

The analysis, based on 121 characters (Appendix 1), gave three equally most parsimonious trees, with the following characteristics: length 161 steps; Consistency Index CI 0.75; CI excluding uninformative characters 0.73; Retention Index 0.91; Rescaled Consistency Index RC 0.69.

The strict consensus tree is given in fig. 2. There is no special grouping of any intervals (no grouping of the Permian stages or of the Carboniferous stages, or even of the Palaeozoic stages), except for a grouping of Middle-Upper Jurassic with Lower Cretaceous subperiods, and a grouping of the Upper Cretaceous with the Cenozoic stages. The grouping of stages after the Lower Late Carboniferous Bashkirian is supported by the states '1' for the characters '16', '19', '21', '26', '30', '32', '33' and '44', suggesting important changes in the odonatopteran morphology (and consequently ecology and biology) during the Middle Late

Carboniferous Moscovian. It seems that the ecological changes between the Upper Carboniferous and the Lower Permian did not affect the odonatopteran morphological structures. The absence of Permian or Palaeozoic groupings, separated from a grouping of the Triassic and Lower Jurassic, suggests that the Permian-Triassic crisis did not fundamentally affect the evolution of the morphology of the Odonatoptera, as the most important structures of these insects were acquired much earlier, during Moscovian-Upper Pennsylvanian and/or during the Lower Permian (Cisuralian).

Interestingly, Odonatoptera are predators that are greatly dependant on their prey. They should have been greatly affected by the alleged major changes in the entomofauna in relation to this crisis. It seems that this was not the case. At least at each transition (Carboniferous-Permian or Permian-Triassic), the clades that could replace the taxa that became extinct were already present.

The only odonatopteran clade restricted to the Permian is the Protanisoptera, with *Polytaxineura stanleyi* Tillyard 1935 as a unique youngest record
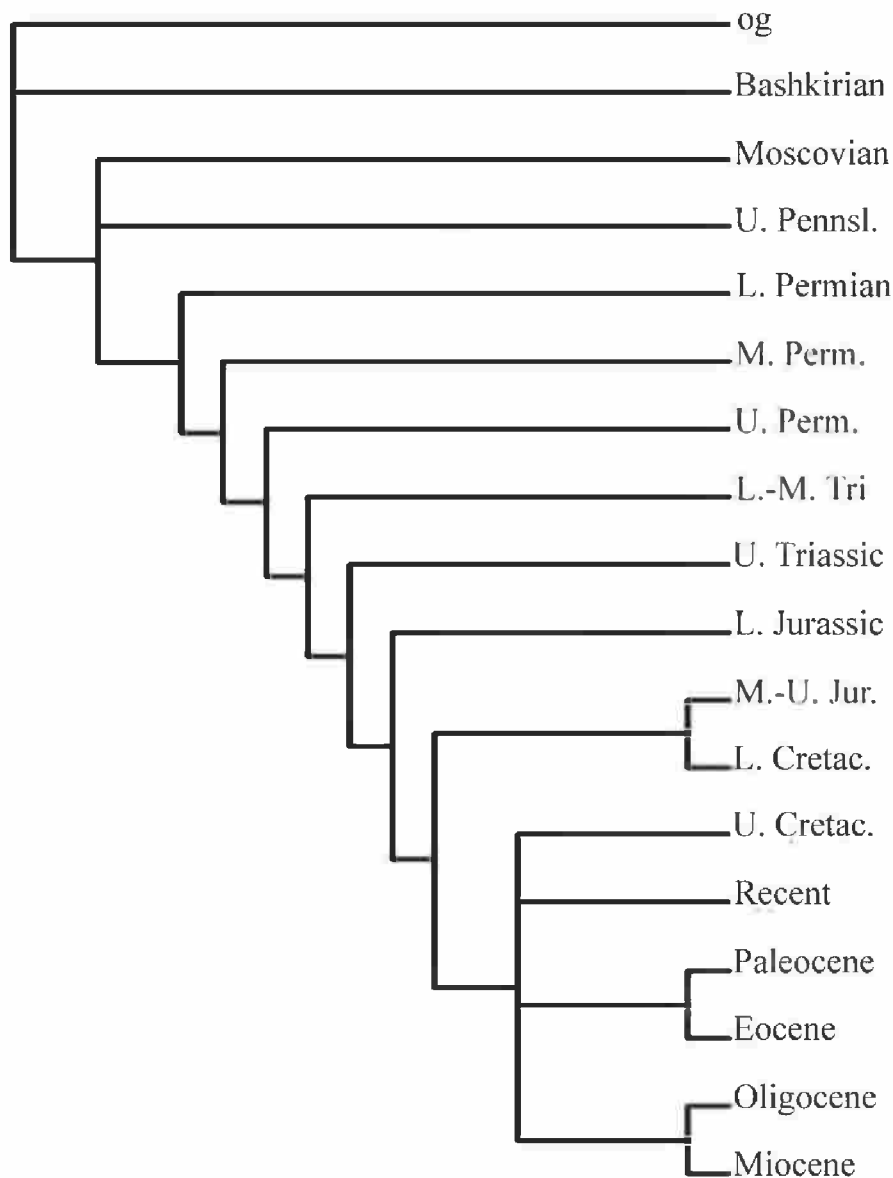

Figure 2
Strict consensus tree obtained after the Wagner parsimony analysis based on Odonatoptera.

from the Upper Permian of Australia. The other alleged Upper Permian protanisopteron is *Gondvanoptilon* Rösler *et al.* 1981 from the Irati Formation, Brazil, now dated from the Lower Permian (Santos *et al.* 2006). It seems that this Permian group, together with the Meganeuridae, were already declining (if not extinct) well before the end of the Permian.

The changes between the stratigraphic levels can also be detected through the quantity of strict synapocenosies supporting the grouping. For example the grouping (Upper Triassic and more recent levels) is supported by 15 characters. But these are of different types, viz. reversions or structures disappearing at this time ('25', '27', '43', '45', '46'), plus some synapocenosies (structures appearing at this time) ('37', '38', '39', '50', '56', '121'); also, some characters support this grouping such as '57', '58', '59', '60', 109', '110', but they are characters appearing during the Upper Triassic but disappearing later. This shows that great changes occurred in the odonatopteran morphology at least between the Middle and Upper Triassic. But we have to keep in mind that the odonatopteran faunas are rather badly known for the Lower and Middle Triassic. Thus these changes could have occurred earlier, during these stages.

Changes can also be detected through the topology of the tree itself, as for the Jurassic-Cretaceous. There is a grouping of the Middle-Upper Jurassic with the Lower Cretaceous, suggesting major changes among Odonatoptera at the boundary between the Lower and Upper Cretaceous. The grouping [Middle-Upper Jurassic, Lower Cretaceous] is supported by the state 1 for the characters 67, 68, 75 to 78, 112 to 115. The clade [Upper Cretaceous, Cenozoic] is supported by the state 1 for the characters 99, 100 and 104. These two clades correspond to several groups (Tarsophlebiidae, Aeschnidiidae, Isophlebioidea, etc.) with highly specialized structures proper to the Middle-Upper Jurassic and Lower Cretaceous, and to the appearance of several modern lineages during the Upper Cretaceous (Libellulidae, etc.). Lastly, the grouping (Paleocene, Eocene) is supported by one character of the Palaeomacromiidae, a family known in these stages, but may be older, and could have appeared during the Lower Cretaceous based on its palaeobiogeography (indicated by '?' in the matrix). The grouping (Oligocene, Miocene) is due to a character of the Sieblosiidae, a family proper to these stages. Several other families are known in the Eocene, but they could have been present in the Paleocene or even the Upper Cretaceous (Petrulevičius & Nel 2003, 2004, 2005, 2007). Further field researches shall be necessary in the future to precisely relate the two groupings (Paleocene,

Eocene) and (Oligocene, Miocene); nevertheless, they could be explained by the global climatic cooling during the Late Cenozoic.

The presence of several characters in some epochs is supported by only one 'key' fossil (viz. Moscovian *Bechlya*, Lopigian *Permophlebia*, Guadalupian *Saxonagrion*, Upper Cretaceous libellulid *Palaeolibellula* Fleck *et al.* 1999). This shows that these analyses are very sensitive to such discoveries. We have to keep in mind that the presence of a taxon in a given stage (i.e. the protozygopteran *Bechlya* in the Moscovian) demonstrates that this clade was probably already frequent then because fossil specimens are generally rare examples of actually frequent species.

The absence of significant changes in the odonatopteran morphology between the Upper Permian and Lower Triassic is rather surprising as the Permian-Triassic boundary is considered as the most important crisis of biodiversity. The more 'modern' lineages of Odonatoptera with the keystone new morphological structures (nodus, pterositgma, etc.) were already present during the Late Permian. But some 'ancient' morphological structures have also been retained in some Triassic taxa. This does not imply that numerous species, genera or families could have become extinct around the end of Permian (but with some uncertainty, see Gall *et al.* 1998). Nevertheless, the end-Permian crisis did not significantly affect the morphology of the Odonatoptera, which questions the impact of this crisis on the palaeoecology of this group of insects. By comparison, the important changes in the odonatan morphology during the Cenomanian (Lower-Upper Cretaceous boundary), with the disappearance of 'ancient' and development of 'modern' morphological structures, suggests important changes in the palaeoecology of the Odonata. These changes could be related to the changes in aquatic environments during the Cenomanian, in relation to the eutrophication of the water of lakes and ponds due to the proliferation of hydromacrophytes and to the greater input of organic matter produced by the newly dominant angiosperms (Kalugina 1974). This eutrophication is supposed to have affected the aquatic insects and consequently their predators, the larvae of Odonata.

B. Thripida

This clade is of interest because Nel *et al.* (submitted) proposed a new phylogenetic hypothesis after which it is possible to infer the presence of some characters (mouth part structures) in Palaeozoic taxa after their presence in the modern and Mesozoic Thysanoptera and in some Lower Cretaceous Moundthripidae (character 35).

The chosen stratigraphic divisions are Upper Carboniferous (Moscovian, Upper Pennsylvanian), Permian, Triassic, Lower Jurassic, Middle-Upper Jurassic, Lower Cretaceous, Upper Cretaceous, Cenozoic and Recent. We grouped together the Lower and Middle Triassic and the Lower and Upper Jurassic because of the lack of information on the Lower Triassic and Middle Jurassic Thripida.

The analysis is based on 35 characters (see appendix 2). It gave four equally most parsimonious trees with the following characteristics: length 45 steps; Consistency Index CI 0.75; CI excluding uninforma-

tive characters 0.69; Retention Index 0.80; Rescaled Consistency Index RC 0.61.

The strict consensus tree is given in fig. 3. The polytomy affecting the Triassic, Lower Jurassic, and Middle-Upper Jurassic is due to the lack of information on the faunas of these periods. The set (Lower Cretaceous, Upper Cretaceous, Cenozoic, Recent) emerges due to the presence of well-preserved true Thysanoptera in the Lower Cretaceous Lebanese amber, while amber with Thripida remains unknown in the Jurassic and the Triassic. Nevertheless, the Mesozoic as a whole is separated from the Palaeozoic because of the
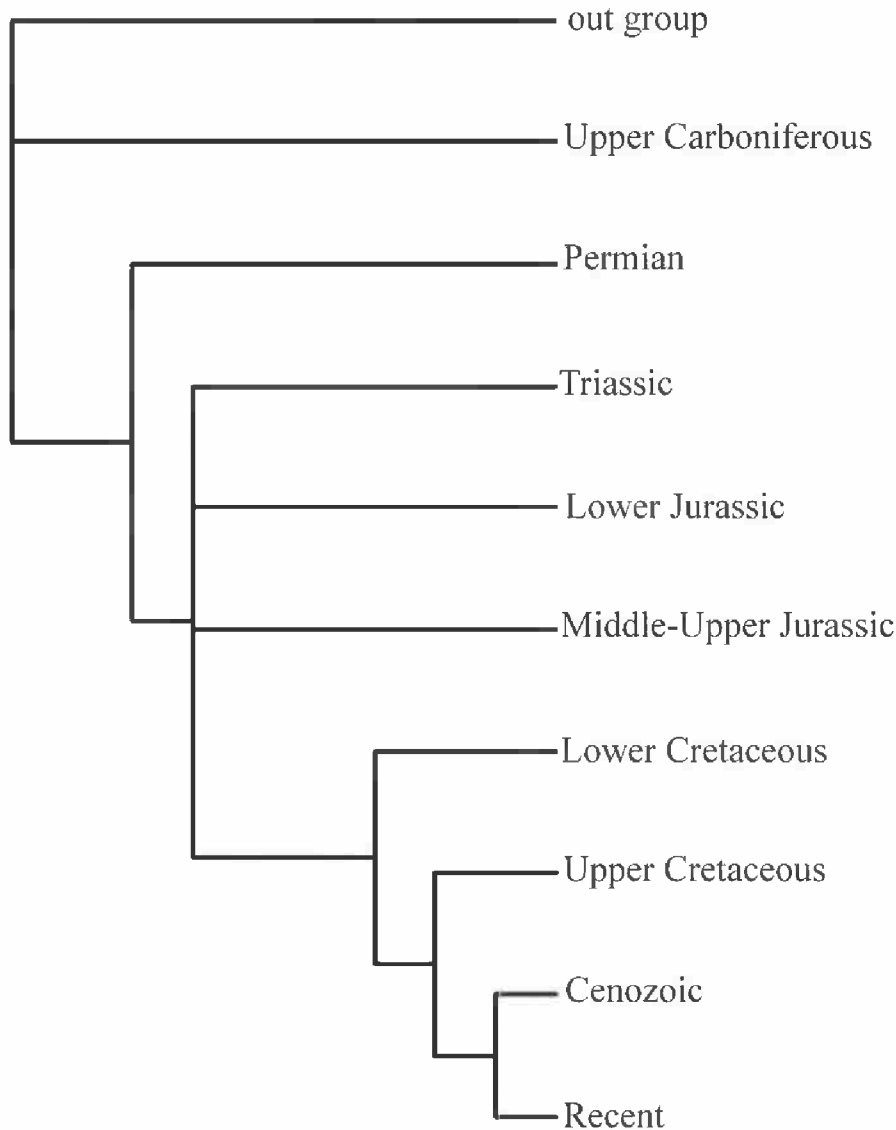

Figure 3
Strict consensus tree obtained after the Wagner parsimony analysis based on Thripida.

presence of Thysanoptera in the Upper Triassic, while this group remains unknown in the Middle or Lower Triassic and the Permian. This example shows that the incompleteness of the fossil record can introduce bias or uncertainty in the analysis. Nevertheless it seems that, in the present state of the art, the Upper Triassic Thripida are very different from those of the Permian, and that great changes also occurred during the Cretaceous. Both periods correspond to great changes in plants with the appearance and diversification of angiosperms or seed plants.

Conclusion

Our studies on the Odonatoptera and Thripida are preliminary, but they demonstrate the feasibility of the Wagner parsimony analyses based on morphological structures (WAPUM). They remain to be applied to the morphological structures of all groups of insects for the Phanerozoic. It is a considerable quantity of work but the analyses can be achieved despite of the lack of phylogenetic analyses to confirm or reject the monophyly of the 'groups' that are currently used in the more 'traditional' studies in the changes of past diversity. The basic requirement of such analyses is to increase our knowledge on the past diversity and disparity of the insects. Therefore every new description of new families or genera with original morphological structures requires, full morphological details, especially where the oldest or youngest records of a clade (e.g. Azar & Nel 2010; Vitali 2010; Peñalver & Grimaldi 2010; Petrulevičius *et al.* 2010), or a new clade (Azar *et al.* 2008, 2010; Kirejtshuk *et al.* 2010; Szwedo & Stroiński 2010) are concerned.

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Appendix 1.

List of characters with comments for the analysis based on the Odonatoptera

1. Species with MP branched: 0. absence; 1. presence
2. Species with MP unbranched: 0. absence; 1. presence; [Odonatoptera have MP unbranched, except in the Triadophlebiomorpha]
3. Species with CuP with a Z-like kink at the point of fusion with AA: 0. absence; 1. presence; [A character of the Odonatoptera]
4. Species with ScP fused with the costal margin distinctly basal of the wing apex: 0. absence; 1. presence; [A character of the Odonatoptera]
5. Species with prothoracic winglets: 0. absence; 1. presence; [prothoracic winglets are present in the Bashkirian *Eugeropteron lunatum* Riek & Kukalová-Peck 1984, *Erasipteroides valentini* (Brauckmann *et al.* 1985), plus maybe *Zessinella siope* Brauckmann 1988; their presence in the Moscovian Erasipteridae is problematic, so we code it with a '?']
6. Species without prothoracic winglets: 0. absence; 1. presence
7. Species with base of MA connected with medial stem: 0. absence; 1. presence

8. Species with base of MA not connected with medial stem, but fused with R: 0. absence; 1. presence; [connection of MA to radius is a character present in Meganeuromorpha and Nodialata; oldest Meganeuridae are known from the Chinese Bashkirian]
9. Species with large wing span of more than 300 mm: 0. absence; 1. presence; [species (in Namurotypidae and Meganeuridae) with very large wing spans are known from the Bashkirian to the Guadalupian (Middle Permian)]
10. Species with RA and RP not basally fused to a long double-barrel radial stem: 0. absence; 1. presence
11. Species with RA and RP basally fused to a long double-barrel radial stem: 0. absence; 1. presence
12. Species with median stem suppressed: 0. absence; 1. presence
13. Species with the 'paralogid pattern of anal and cubital veins', i.e. 'AA1 well developed; CuP with more than eight posterior branches, covering a very long area that is distinctly longer than that of CuA': 0. absence; 1. presence; [a character proper to the Moscovian to Autunian Paralogidae (Nel *et al.* 2009)]
14. Species with the 'kohlwaldiid pattern of anal and cubital veins', i.e. 'presence of numerous simple posterior branches emerging from a common stem AA+CuP+CuA': 0. absence; 1. presence; [a character proper to the Moscovian Kohlwaldiidae (Nel *et al.* 2009)]
15. Species without 'a characteristical oblique vein between RA and RP near the base of RP2 (subnodal vein)': 0. absence; 1. presence
16. Species with 'subnodal vein': 0. absence; 1. presence; [an oblique 'subnodal vein is present in the Meganeuridae (Moscovian to Guadalupian) and the Nodialata]
17. Species with a 'precostal field' distinctly elongated and widened in basal half of wing: 0. absence; 1. presence; [a meganeurine character]
18. Species without true 'odonatoid' nodus: 0. absence; 1. presence
19. Species with true 'odonatoid' nodus, with more or less oblique nodal and subnodal veinlets: 0. absence; 1. presence; [the oldest odonatopteran with a true nodus is the Moscovian protozygopteran *Bechlya* Jarzembowski & Nel 2002]
20. Species with MA branched: 0. absence; 1. presence
21. Species with MA unbranched: 0. absence; 1. presence; [the oldest odonatopteran with MA unbranched is the Moscovian protozygopteran *Bechlya*]
22. Species without pterostigma: 0. absence; 1. presence
23. Species with a 'protanisopteran' pterostigma: 0. absence; 1. presence
24. Species with an 'odonatan' pterostigma: 0. absence; 1. presence; [the pterostigmal area is not preserved in the unique type specimen of the Moscovian protozygopteran *Bechlya*, but an undescribed fossil, protozygopteran-like, with a sclerotized pterostigma is known from the Upper Pennsylvanian of Carrizo Arroyo, New Mexico (Kukalová-Peck pers. comm.), Protanisoptera with a true pterostigma are known in the Cisuralian (Lower Permian)]
25. Species without a 'characteristic oblique vein MAb between MA and MP that is developed as a secondary branch of MA': 0. absence; 1. presence
26. Species with a 'characteristic oblique vein MAb between MA and MP that is developed as a secondary branch of MA': 0. absence; 1. presence; [the oldest odonatopteran with MAb is the Moscovian protozygopteran *Bechlya*]
27. Species with CuA emerging from M+Cu close to the CuP-crossing and making a Z-like kink: 0. absence; 1. presence
28. Species with CuA emerging from M+Cu well distal to the CuP-crossing, but basal to MAb and with CuA long before its fusion with AA: 0. absence; 1. presence; [A protozygopteran and triadophlebiomorphan character known from the Moscovian to the Upper Triassic]
29. Species with CuA emerging from M+Cu opposite MAb, and CuA short before its fusion with AA: 0. absence; 1. presence; [a true odonatan character, known in the Guadalupian oldest odonatan *Saxonagrion minutus* Nel *et al.* 2000]

30. Species with petiolated wings, formed by the long fusion of AA with AP: 0. absence; 1. presence; [the oldest odonatopteran with petiolated wings is the Moscovian protozygopteran *Bechlya*]

31. Species with petiolated wings, formed by the long fusion of M+Cu+A: 0. absence; 1. presence; [a triadophlebiomorphan character, known in the Thuringian *Permophlebia uralica* Nel *et al.* 2001]

32. Species with CuP as crossvein-like perpendicular veinlet (= CuP-crossing) between M+Cu and AA: 0. absence; 1. presence; [the oldest odonatopteran with CuP-crossing is the Moscovian protozygopteran *Bechlya*]

33. Species with oblique basal brace transformed into a transverse 'basal bracket' Ax0 looking like a primary antenodal: 0. absence; 1. presence; [the oldest odonatopteran with Ax0 is the Moscovian protozygopteran *Bechlya*]

34. Species with a protanisopteran vein IMA: 0. absence; 1. presence

35. Species without a secondary male apparatus on second abdominal segment: 0. absence; 1. presence; [the male genital apparatus is described for the Bashkirian *Namurotypus sippeli* Brauckmann & Zessin 1989 (Bechly *et al.* 2001), but very little is known about the male genitalia of the Moscovian to Guadalupian Meganeuridae and the Permian Protanisoptera (Huguet *et al.* 2002)]

36. Species with a secondary male apparatus on the second abdominal segment: 0. absence; 1. presence; [the presence of a secondary male apparatus is recorded in an undescribed protozygopteran from the Autunian of Russia, but still undetermined for *Bechlya* (Nel pers. obs.)]

37. Species with a pterostigmal brace: 0. absence; 1. presence

38. Species with a discoidal cell distally distinctly widened in the hindwing, correlated with a much less oblique MAb than in the forewing: 0. absence; 1. presence

39. Species with a distinct anal angle in male hindwings: 0. absence; 1. presence; [38 and 39 are epiproctophoran characters, clade known from the Upper Triassic to Recent]

40. Species without a pterostigmal brace: 0. absence; 1. presence

41. Species with RA with an apical secondary branch: 0. absence; 1. presence

42. Species with one of the postsubnodal crossveins midway between nodus and apex is developed as an oblique vein: 0. absence; 1. presence; [both characters 41 and 42 are protanisopteran]

43. Species without a simple CuA: 0. absence; 1. presence

44. Species with a simple CuA: 0. absence; 1. presence

45. Species with a CuP re-emerging distally from the anal vein: 0. absence; 1. presence

46. Species without two strong primary antenodal brackets Ax1 and Ax2: 0. absence; 1. presence

47. Species with two strong primary antenodal brackets Ax1 and Ax2: 0. absence; 1. presence

48. Species with a tracheated lestine oblique vein 'O' between RP2 and IR2: 0. absence; 1. presence

49. Species with a distinct nodal furrow: 0. absence; 1. presence

50. Species with vein MAb and origin of CuA on MP aligned and dorsally enforced by strong sclerotisation: 0. absence; 1. presence

51. Species with a pterostigmal brace: 0. absence; 1. presence

52. Species with subdiscoidal cell hypertrophied and developed as a 'pseudo discoidal cell' in hindwings: 0. absence; 1. presence; [a tarsophlebiid character]

53. Species with MAb & MP & CuA fused for a considerable distance before separation of MP and CuA in hindwings: 0. absence; 1. presence; [a tarsophlebiid character]

54. Species with five tarsomeres: 0. absence; 1. presence

55. Species with three tarsomeres: 0. absence; 1. presence

56. Species with secondary branching of CuA into an anterior longitudinal branch CuAa and a posterior transverse branch CuAb: 0. absence; 1. presence

57. Species with subdiscoidal cell enlarged and with a bulged posterior margin in hindwings: 0. absence; 1. presence

58. Species with [AA & CuP] and [MP & CuA] partly fused basal of arculus in hindwing: 0. absence; 1. presence; [a character of Triassolestidae]

59. Species with subdiscoidal cell posteriorly open in hindwing: 0. absence; 1. presence

60. Species with a very long and straight gaff (= basal CuA before its branching): 0. absence; 1. presence; [59 and 60 are characters of Isophlebioidea]

61. Species with three caudal gills of larvae secondarily absent and replaced by complex rectal gills: 0. absence; 1. presence

62. Species with larval epiproct and paraprocts strongly shortened and forming a so-called 'anal pyramid' together with cerci: 0. absence; 1. presence; [61 and 62 are euepiproctophoran characters (Epiophlebiidae and Anisoptera); presence inferred in Heterophlebioptera after the sister group relationships between Epiophlebiidae and Anisopteromorpha sensu Bechly (1996)]

63. Species with forewing discoidal cell very transverse and narrow: 0. absence; 1. presence

64. Species with unique unicellular anal loop lying beneath subdiscoidal cell and ventrally closed by CuAb that is parallel to AA and thus directed towards wing base instead of posterior wing margin: 0. absence; 1. presence; [63 and 64 are characters of Heterophlebioptera]

65. Species with hindwing discoidal cell divided into triangle and hypertriangle: 0. absence; 1. presence

66. Species with forewing discoidal cell divided into triangle and hypertriangle: 0. absence; 1. presence

67. Species with nodal and subnodal veinlet extremely oblique: 0. absence; 1. presence

68. Species with stenophlebiid oblique vein between RP1 and RP2: 0. absence; 1. presence; [67 and 68 are characters of Stenophlebiidae]

69. Species with secondary short pseudo-IR1 developed and arising as apparent branch on RP1 near distal side of pterostigma: 0. absence; 1. presence

70. Species with RP2 strictly aligned with subnodus: 0. absence; 1. presence

71. Species with distinct pseudo-anal vein PsA delimiting a subdiscoidal triangle in both pairs of wings: 0. absence; 1. presence

72. Species with adults resting with wings strictly horizontally outstretched: 0. absence; 1. presence; [70, 71, and 72 are characters of Pananisoptera]

73. Species with discoidal triangles strictly triangular in both pairs of wings (because the triangular vein which divides the discoidal cell into hypertriangle and discoidal triangle ends precisely at the distal angle of the discoidal triangle): 0. absence; 1. presence

74. Species with a second accessory oblique vein between RP2 and IR2 distal of 'lestine' oblique vein: 0. absence; 1. presence; [a neoanisopteran character]

75. Species with discoidal triangles strongly transverse in both pairs of wings, widely separated from arculus: 0. absence; 1. presence

76. Species with both pairs of wings with a characteristic row of several very distinct 'pseudo-anal-loops' beneath anal vein: 0. absence; 1. presence

77. Species with CuAb reduced to an 'oblique crossvein' between CuA and Aspl: 0. absence; 1. presence

78. Species with female ovipositor hypertrophied: 0. absence; 1. presence; [75 to 78 are aeschnidiid characters]

79. Species with hindwings with a well-defined anisopteran anal loop: 0. absence; 1. presence; [anisopteran character]

80. Species with pterostigmal brace vein shifted (in basal 3/4 of wing), midway between nodus and apex: 0. absence; 1. presence; [a petalurid character, convergently present in some Aeschnidiidae]

81. Species with RP1 and RP2 basally parallel up to pterostigma; thus area between these two veins basally is distinctly narrow with only one row of cells between them: 0. absence; 1. presence; [an aeshnopteran character]
82. Species with Rspl: 0. absence; 1. presence
83. Species with Mspl: 0. absence; 1. presence
84. Species with costal margin and RA thickened along pterostigma: 0. absence; 1. presence
85. Species with distal part of antesubnodal area free of crossveins ('cordulegastrid gap'): 0. absence; 1. presence
86. Species with larva with spoon-shaped (scoop-like) concave prehensile mask: 0. absence; 1. presence; [85 and 86 are two cavilabiatan characters]
87. Species with wings with a basal fork of IR2 basal of lestine oblique vein: 0. absence; 1. presence; [a cordulegastrid character]
88. Species with pterostigmata not parallel sided (distal side more oblique than basal side): 0. absence; 1. presence
89. Species with anal loop at least elongated and enlarged, with more than five cells: 0. absence; 1. presence
90. Species with gaff (= basal CuA before its branching) strongly prolonged and very straight in hindwing: 0. absence; 1. presence
91. Species with anal loop longitudinally elongated and broad (at least 7–9 cells large) and of pentagonal shape: 0. absence; 1. presence; [a character of Chlorogomphida]
92. Species with basal part of postsubnodal area free of crossveins ('libellulid gap'): 0. absence; 1. presence; [a character of the Paneurypalpidomorpha]
93. Species with elongated gaff (= basal CuA before its branching) sigmoidally curved in hindwing: 0. absence; 1. presence
94. Species with CuAa with only one or two posterior branches: 0. absence; 1. presence; [93 and 94 are characters of the Eurypalpidomorpha]
95. Species with sectors of arculus approximate, diverging from one point or even fused basally: 0. absence; 1. presence
96. Species with nearly all antenodal crossveins aligned in both pairs of wings: 0. absence; 1. presence
97. Species with a midrib in anal loop: 0. absence; 1. presence
98. Species with elongated and boot-shaped anal loop: 0. absence; 1. presence
99. Species with the two primary antenodal brackets Ax1 and Ax2 very indistinct in forewings and indistinguishable from secondaries in hindwings: 0. absence; 1. presence
100. Species with second crossvein between RP1 and RP2 developed as 'libellulid oblique vein': 0. absence; 1. presence
101. Species with 'steleopterid'-type structure of the cells in certain areas of the wings: 0. absence; 1. presence; [the Steleopteridae is a very specialised family which is only known in the Middle to Upper Jurassic, (Fleck et al. 2001)]
102. Species with midfork is recessed basally to a position between 12-26 % of wing length: 0. absence; 1. presence; [a calopteran character]
103. Species with nodus in a very basal position (at distinctly less than 40 % of wing length): 0. absence; 1. presence; [an amphipterygoid character]
104. Species with strong tendency towards a basal curving of RP1/2 arising on RP with a secondary insertion: 0. absence; 1. presence; [a character of Calopterygomorpha, probably Upper Cretaceous (Dumont et al. 2005; Lin et al. 2010)]
105. Species with derived type of 'star-shaped' microsculpture (micrasters) on the pterostigmata: 0. absence; 1. presence; [a lestomorphan character, known in a Lower Cretaceous fossil in Lebanese amber (Azar et al. 2010)]
106. Species with RP1 kinked at insertion of the pterostigmal brace vein: 0. absence; 1. presence
107. Species with tibial comb of fore legs degenerated: 0. absence; 1. presence; [106 and 107 are characters of Hemiphlebiidae, known in the Lower Cretaceous (Lak et al. 2009)]

108. Species with pterostigma rather short with only 2 (rarely 3) crossveins beneath it: 0. absence; 1. presence; [a character of Coenagrioniformia, known in the Lower Cretaceous (Jarzembowski et al. 1998)]
109. Species with IR1, RP2 and IR2 fused basally and with their common stalk originating on RP3/4: 0. absence; 1. presence
110. Species with RP3/4 secondarily forked into RP3/4a and RP3/4b: 0. absence; 1. presence; [109 and 110 are characters of Protomyrmeleontidae, ranging from Upper Triassic to Lower Cretaceous (Nel et al. 2005)]
111. Species with very long legs and tarsi: 0. absence; 1. presence; [a character of Tarsophlebiidae]
112. Species with larval paraprocts (not cerci) strongly hypertrophied and forcep-like: 0. absence; 1. presence
113. Species with ScP crossing through nodus and ending much distally: 0. absence; 1. presence; [112 and 113 are characters of Aeschnidiidae]
114. Species with unique shape of very elongate and narrow hindwing discoidal triangle (anterior side of discoidal triangle distally curved and ending on anterior side (MA) of hypertriangle; MAb strongly sigmoidally curved, with a very concave basal part and a strong angle in distal part): 0. absence; 1. presence; [a character of the aeshnopteran family Liupanshaniidae (Lin et al. 2002)]
115. Species with discoidal triangles of unique and similar shape in both pairs of wings (transversely elongate, narrow, and strictly triangular of stenophlebiid type): 0. absence; 1. presence
116. Species with male hindwing with very acute or even hook-like projecting anal angle: 0. absence; 1. presence; [a campterophlebiid character]
117. Species with area of 'anal triangle' in male hindwings hypertrophied and subdivided into numerous cells: 0. absence; 1. presence; [a character of the Isophlebioidea]
118. Species with a large elongated cell beneath submedian area: 0. absence; 1. presence; [a character of the Proterogomphidae]
119. Species with first postnodal 'palaeomacromiid' oblique vein: 0. absence; 1. presence; [a character of the Palaeomacromiidae, a family known from the Paleocene and Eocene, but could date from the Lower Cretaceous (Petrulevičius & Nel 2007)]
120. Species with ScP crossing through the nodus and extending not very far beyond it: 0. absence; 1. presence; [a character of the Sieblosiidae, a family known in the Oligocene and Miocene]
121. Species with brace CuP (between M+Cu and AA) distinctly curved: 0. absence; 1. presence; [a character of the Epiproctophora]

Appendix 2.
List of characters with comments for the analysis based on the Thripida

1. Species with fringe on wings: 0. absence; 1. presence
2. Species without fringe on wings: 0. absence; 1. presence
3. Species with CuP almost aligned with M: 0. absence; 1. presence
4. Species with CuP and M not aligned: 0. absence; 1. presence
5. Species without CuA: 0. absence; 1. presence
6. Species with CuA: 0. absence; 1. presence
7. Species with a stem CuA-M: 0. absence; 1. presence
8. Species without a stem CuA-M: 0. absence; 1. presence
9. Species with CuA emerging perpendicular to R and sigmoidal: 0. absence; 1. presence
10. Species with CuA not emerging perpendicular to R: 0. absence; 1. presence
11. Species with CuA emerging perpendicular to R but not sigmoidal: 0. absence; 1. presence
12. Species with a brace cup: 0. absence; 1. presence
13. Species without brace cup: 0. absence; 1. presence
14. Species with ScP: 0. absence; 1. presence

15. Species without ScP (or faint): 0. absence; 1. presence
16. Species with RA as crossvein: 0. absence; 1. presence
17. Species with RA normal: 0. absence; 1. presence
18. Species with M emerging after fork RA-RP: 0. absence; 1. presence
19. Species with M emerging before fork RA-RP: 0. absence; 1. presence
20. Species with distal part of CuP as crossvein or absent: 0. absence; 1. presence
21. Species with CuP long normal: 0. absence; 1. presence
22. Species with ovipositor pointed downwards: 0. absence; 1. presence
23. Species with ovipositor pointed upwards: 0. absence; 1. presence
24. Species with proximal part of CuP lacking: 0. absence; 1. presence
25. Species with entire CuP present: 0. absence; 1. presence
26. Species with tube-like 10th abdominal segment: 0. absence; 1. presence
27. Species without tube-like abdominal segment: 0. absence; 1. presence
28. Species with wings without venation: 0. absence; 1. presence
29. Species with wings with veins: 0. absence; 1. presence
30. Species without branches on R and M: 0. absence; 1. presence
31. Species with branches on R and M: 0. absence; 1. presence
32. Species with mouthcone prognathous: 0. absence; 1. presence
33. Species with mouthcone opistho- or hypognathous: 0. absence; 1. presence
34. Species with CuA simple: 0. absence; 1. presence
35. Species with right mandible absent: 0. absence; 1. presence

Appendix 3.

Matrix 1. Matrix of stratigraphic levels and characters based on Odonatoptera

Available as downlading material on the website http://ann.sef.free.fr/

Appendix 4.

Matrix 2. Matrix of stratigraphic levels and characters based on Thripida

Available as downlading material on the website http://ann.sef.free.fr/