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## The Triassic radiation of the entomofauna

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### Abstract

Assessing the insect evolution around the Permian/Triassic boundary faces various pitfalls. The taxonomic and phylogenetic frames are not consensually established, and diverse evidences suggest that the record is incomplete. Nevertheless, extensive studies in progress on the super-ordinal clades Archaeorthoptera and Odonatoptera reveal common trends. Several important lineages get extinct, and groups underrepresented or absent in Late Permian became major components of the entomofauna in Middle Triassic. In addition, the radiation of the Diptera and the diversification of the Coleoptera in the Triassic also support the hypothesis of an important renewal of the entomofauna at the Permian/Triassic boundary. *To cite this article: O. Béthoux et al., C. R. Palevol 4 (2005).*

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### Résumé

**La radiation de l'entomofaune au Trias.** Apprécier l'évolution des insectes au passage Permien–Trias se heurte à différents écueils. Les bases taxonomiques et phylogénétiques ne sont pas établies de manière consensuelle, et des preuves diverses montrent que le registre est incomplet. Néanmoins, les études approfondies en cours sur les clades super-ordinaires Archaeorthoptera et Odonatoptera révèlent des tendances communes. Plusieurs lignées importantes s'éteignent, et des groupes sous-représentés ou encore inconnus au Permien supérieur deviennent des composants majeurs de l'entomofaune du Trias moyen. Par ailleurs, la radiation des Diptera et la diversification des Coleoptera au Trias prouvent aussi qu'un important renouvellement de l'entomofaune a eu lieu au passage Permien/Trias. *Pour citer cet article : O. Béthoux et al., C. R. Palevol 4 (2005).*

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## Version française abrégée

### Introduction

L'évolution de la vie sur terre a été principalement étudiée d'après le registre fossile marin [3]. Cependant, les insectes constituent également un groupe majeur pour l'étude de l'évolution des écosystèmes continentaux, en raison de la diversité actuelle et passée de ce groupe [41]. Malgré l'absence de résultats consensuels sur l'évolution des insectes, il est généralement admis que le Permien est une période clé, avec la coexistence d'ordres typiquement paléozoïques et d'ordres modernes [30,33]. Les quinze millions d'années autour de la limite Permien–Trias sont marqués par l'extinction de plusieurs ordres et l'apparition d'une entomofaune « moderne ». Avant de discuter des effets de la crise biologique de la fin du Permien sur l'entomofaune et sur sa radiation apparente au Trias, il est nécessaire de présenter un état des lieux de notre connaissance des insectes du Paléozoïque supérieur au Mésozoïque inférieur.

### Limites des données actuelles

#### Bases taxonomiques

L'étude de la diversité taxonomique des insectes est basée sur une méthode consistant à dénombrer des unités taxonomiques, au sein de taxons de rang plus élevé. L'unité unanimement préférée jusqu'à présent est la famille [22,33,34,41]. Mais, dans le cas des insectes du Paléozoïque particulièrement, plusieurs facteurs montrent que cette unité n'est pas adéquate.

La source principale des données utilisées par Labandeira et Sepkoski [41], Jarzembowski et Ross [34] et Jarzembowski [33] est la compilation pré-cladistique de Carpenter [18], dont les diagnoses des familles se sont avérées imparfaites (voir [56] pour les familles de l'ordre des Caloneurodea; voir aussi [9]). Les attributions ordinales de plusieurs familles sont également discutables [9,14], de même que l'apport de Dmitriev et Ponomarenko [22], car ces auteurs tolèrent et utilisent abondamment des groupements paraphylétiques, provoquant des distorsions dans les analyses de paléobiodiversité.

L'hypothèse d'équivalence phylogénétique des familles est aussi critiquable. La pratique taxonomique

révèle que les taxons de rang élevé sont souvent créés sur la base d'un critère de disparité morphologique (voir [37] pour la création de l'ordre Mantophasmatodea). En conséquence, l'unité taxonomique de rang familial est plus un indicateur subjectif de disparité morphologique qu'un indicateur objectif de diversité taxonomique.

#### Parenté entre les ordres fossiles et modernes

Il n'existe pas actuellement de phylogénie consensuelle des insectes incluant les ordres fossiles. Les principales hypothèses [2,30,40] sont conflictuelles et impliquent des histoires évolutives différentes au passage Permien–Trias. Le cas du groupe « Protoperlaria » est particulièrement significatif.

#### La qualité du registre fossile des insectes

Les découvertes récentes faites dans le bassin permien de Lodève (Hérault, France) [12,50,51] et dans le « Grès à Voltzia » des Vosges, France [39,45,46,54,55], le plus ancien gisement triasique (Anisien inférieur) à avoir livré une entomofaune diversifiée, ont significativement modifié nos connaissances. Elles montrent, par conséquent, que les données disponibles sont encore très incomplètes. Aussi, quelques exemples d'inférences de date de cladogenèse d'après les données phylogénétiques montrent que de larges lacunes caractérisent le registre fossile connu, couvrant l'ensemble du Permien dans certains cas [28,35].

#### L'échantillonnage paléogéographique

Historiquement, le Permien supérieur a été étudié dans la région de Perm (Russie), le centre de l'Amérique du Nord et la Moravie (République tchèque). Quant au Trias, il a été surtout étudié en France, Asie centrale, Australie, Afrique du Sud et en Amérique du Nord. Ces échantillonnages ne peuvent prétendre représenter l'entomofaune ancienne mondiale.

#### La transition P/T chez les insectes d'après une sélection de groupes

Après ce constat, il s'avère que l'approche la plus sensée est de se concentrer sur des groupes dont la monophylie est établie, et dont la taxonomie est remise à jour. C'est le cas des clades super-ordinaux des Archaeorthoptera (sauterelles, grillons) et des Odonoptera (demoiselles, libellules), dont les études systématiques sont en cours.

### *Les Archaeorthoptera*

Plusieurs changements importants caractérisent le passage Permien–Trias chez les Archaeorthoptera (Fig. 1). En premier lieu, l'ordre des Caloneurodea disparaît, alors qu'il représentait 20% des espèces d'Archaeorthoptera connues au Permien [6]. La perte en disparité morphologique est aussi significative, puisque cet ordre présente des types morpho-fonctionnels uniques (type de vol et appareil de stridulation), différents de ceux du Trias. En revanche, le sous-ordre Ensifera (grillons) qui représentait environ 5% des espèces au Permien, atteint 25% des espèces d'Archaeorthoptera au Trias. L'acquisition d'un appareil de stridulation semble avoir favorisé la diversification du groupe, qui a eu lieu pendant les quinze millions d'années qui séparent notre dernier enregistrement permien du premier enregistrement triasique.

### *Les Odonoptera*

Au Permien, les Odonoptera comprennent six clades principaux (Meganisoptera, Protanisoptera, Lapeyriidae, Protozygoptera, Triadophlebiomorpha, Panodonata), dont seulement trois existent au Trias (Protozygoptera, Triadophlebiomorpha, Panodonata – Fig. 3). Le groupe des Triadophlebiomorpha, faiblement représenté au Permien, est très diversifié au Trias. C'est aussi le cas du clade des Panodonata qui inclut tous les représentants actuels des Odonoptera. Les Meganisoptera permo-carbonifères sont encore très diversifiés au Permien supérieur. Les époques d'extinction exactes de ces clades anciens demeurent inconnues, se situant aussi probablement pendant la lacune d'enregistrement du passage Permien–Trias.

### *Autres groupes significatifs*

Les Coleoptera, présents au Permien seulement dans certains gisements, sont abondants dans tous les gisements triasiques, et constituent la composante majeure des entomofaunes modernes [41]. L'ordre des Diptera est inconnu au Permien mais, dès son premier enregistrement au Trias, il est composé de groupes « phylogénétiquement » distants [38,39]. Le groupe s'est apparemment diversifié en quinze millions d'années.

### *Discussion*

Malgré un registre fossile incomplet, il est possible de mettre en évidence des tendances communes chez

les Archaeorthoptera et les Odonoptera entre le Permien et le Trias. Après l'apparition et la diversification de certains groupes au passage Carbonifère–Permien, certains d'entre eux s'éteignent au passage Permien–Trias et sont relayés, au Trias, par d'autres groupes, sous-représentés auparavant. Le cas des Coleoptera et des Diptera est comparable. Comme la même dynamique évolutive se retrouve chez des clades phylogénétiquement et écologiquement distants, il est vraisemblable qu'un ou plusieurs facteur(s) extrinsèque(s) ai(en)t affecté leur évolution d'une manière similaire. La crise biologique permo-triasique représente peut-être un de ces facteurs.

Ces modifications ont eu lieu dans l'intervalle de 15 Ma qui sépare les enregistrements les plus proches du passage P/T. Leur contemporanéité et/ou leur soudaineté ne peuvent être démontrées, en raison de lacunes dans le registre fossile.

Une approche basée sur les concepts de diversité écologique pourrait permettre d'aborder la question de la restauration des écosystèmes après le passage P/T. L'entomofaune du Grès à Voltzia serait particulièrement intéressante dans cette perspective, car c'est la plus proche du passage P/T qui soit suffisamment riche et diversifiée. Cependant, l'analyse taphonomique proposée par Gall [26], qui permettrait de corriger le biais inhérent à l'échantillonnage fossile, n'a pas concerné les insectes de ces gisements. Aucun gisement permien qui pourrait servir de référence n'a été étudié dans cette perspective. De sérieuses avancées sont encore nécessaires dans ce domaine.

### *Conclusion*

Bien que l'enregistrement fossile des insectes au Permien et au Trias soit incomplet, certains groupes permettent néanmoins de mettre en évidence des dynamiques évolutives comparables, au passage Permien–Trias. Chez tous les groupes étudiés, des clades inconnus ou sous-représentés dans les gisements connus du Permien supérieur se sont certainement rapidement diversifiés au Trias inférieur ou à la fin du Permien, au vu de leur importante diversité au Trias moyen. De toute évidence, l'importance relative de ce renouvellement reste à tester. Il est indéniable que la lacune paléontologique des quinze millions d'années autour du passage Permien–Trias constitue une période majeure dans l'histoire des insectes. Mais il serait

important de s'assurer que le passage Carbonifère–Permien, par exemple, n'a pas été aussi important dans l'histoire du groupe.

## 1. Introduction

The evolution of life on Earth has been mainly investigated from the well-studied marine record. One of the major challenges of modern systematic palaeontology is to compare the observed trends with those pictured from the continental ecosystems [3]. Two groups are of particular interest in this regard, plants and insects, because they are among the major structuring components of the terrestrial communities. The plant record has received considerable attention (see for example [21,57,59,71]) in regard to the insects. Focusing on the later group would be meaningful in considering its outstanding fossil and modern diversity [41]. This contrasts with the current paucity of detailed and consensual results about its phylogeny and evolution. Comprehensive taxonomic and phylogenetic backgrounds of ordinal-ranked groups based on modern methods are commonly missing.

One opinion is nevertheless consensual: the Permian is a key-period in the evolution of insects, with the contemporaneous occurrence of typical Late Palaeozoic orders as well as modern ones [30,33]. The Permian–Triassic boundary is the only period in insect evolution when several insect orders became extinct concurrently. After the Permian–Triassic boundary, the composition of the insect class generally matches that of the modern fauna. Outlining the differences between the Permian and Triassic entomofaunas would determine if a radiation event accompanied this origin of the modern fauna.

## 2. Limits of the current dataset

### 2.1. Taxonomic background

Our current knowledge of patterns of insect diversity through time is based on the enumeration of taxonomic units within the class as a whole, or within super-ordinal or ordinal groups. The most widely used unit in such compilations has been the family [22,33,34,41], but a number of factors make the use of family level

data unsatisfactory, particularly in the investigation of patterns of insect biodiversity during the Palaeozoic.

The main source of family data has been the volumes of the *Treatise on Invertebrate Paleontology* [18]. This treatment pre-dates the widespread use of cladistics and, even though it involved the lifetime work of a single author, does not apply the concept of a family uniformly throughout. Some *Treatise* families date to 1885 [16], when taxonomic practices differed from those today. Consequently, a number of these taxa are synonyms or paraphyletic, possibly causing problems in the analysis of palaeobiodiversity [61]. The proportion of data that is unreliable is unknown, but it was significant enough to support the abandonment of the previous familial frame (see [13,56] on families of the order Caloneuroidea; [9] for 'Protorthoptera'). In other words, the fundamentals of our current understanding may be biased by an analytically incorrect database.

A good example of the familial definition issue is provided by Dmitriev and Ponomarenko [22]. They synonymised 212 of the 1261 insect families recognized by previous authors, a reduction of nearly 20%. But they did not discuss the basis for their taxonomic decisions, and they continued to use paraphyletic taxa (at familial, super-familial, ordinal, and super-ordinal levels). Thus, their new taxonomic scheme may not be a significantly better basis for investigating trends in biodiversity.

A more fundamental issue concerns the assumption of the comparability of the families. Taxa of familial and higher taxonomic ranks are usually established based on morphological 'difference'. A recent example is provided by the order Mantophasmatodea [37]. It is based on a unique combination of morphological traits, but contains just 12 genera [24,37]. Thus, the rank attributed to this taxon does not reflect its taxonomic diversity but morphological distance between it and previously erected orders. Hence, the family rank unit is not strictly related to the taxonomic diversity, but is rather a subjective index of morphological disparity. Since the two components of biodiversity, the taxonomic diversity and the morphological disparity, can provide very different signals [25,49], new approaches should be developed and applied in order to better discriminate between them.

From this point, one can suggest that instead of attempting to cover the evolution of the whole class across the Permian/Triassic boundary, it would be more

meaningful to extensively review significant monophyletic groups.

## 2.2. Relationships of extinct and modern orders

There is no consensual phylogeny of the insect class including the fossil orders. The proposals of Kukalová-Peck [40], Grimaldi [30], and of the Russian team [2] are strongly conflicting (see also [33]). Consequently, the exact relationships of several fossil orders in respect of modern orders are yet a matter of debate. Even the validity of several orders is argued. For example, there is no consensus on the exact relationships of the non-archaeorthopterid ‘Protorthoptera’, i.e. *Protoperlaria sensu* Tillyard [65], i.e. *Grylloblattida sensu* Storozhenko [64]. The group might include – or be included in – the orders Plecoptera (stoneflies) [30,65], *Grylloblattaria* [64], and/or Embioptera (webspinners) [66] (see also a discussion in [14]). Each of these hypotheses implies a different evolutionary history during the Late Palaeozoic and the Early Mesozoic. Since the group represents 20% of the species recognized in the Permian Wellington Formation (Kansas, USA; see <http://www.windsofkansas.com/elmodiv2.html>), the lack of consensual data on its relationships is an important issue.

## 2.3. The fossil record of insects

Although measurements of the quality of the fossil record of insects are still missing (but see [70]), there is some evidence that it could be improved. The faunas newly investigated are suitable empirical tests of the quality of our knowledge.

The Permian fauna of the Lodève Basin (Hérault, France; Permian) has been systematically studied for some years [50]. Three discoveries show that our current record of Permian insects is patchy. Among the Odonoptera, the family Lapeyriidae represents the closest sister group of the lineage of Nodialata and the more inclusive lineage of Odonoptera having developed a true nodus [50]. The family Saxonagrionidae is the oldest representative of the Panodonata, viz. the stem group of the Recent Odonata, e.g., damselflies and dragonflies [51]. Among the clade Archaeorthoptera (e.g., related to grasshoppers and crickets), the family Permostridulidae is the only known stridulating member of the order Caloneurodeia and, incidentally, the old-

est evidence of an insect sound production [12]. Béthoux et al. [13] demonstrated that this family, among the Caloneurodeia, has very primitive traits in wing venation, apart from the stridulatory apparatus. Since more derived members are recorded in Late Carboniferous, it implies that the most basal representatives are, up to now, unknown. This gap is related to the lack of Early Carboniferous entomofaunas, when insect basal cladogenesis events likely occurred [5], or had already occurred [23].

Phylogenies of major fossil insect clades are generally unknown. Hence, it is impossible to provide a global measurement of the quality of the fossil record of insects using appropriate indices [4]. However, some examples are significant. Wills [70] reported several ordinal ghost ranges exceeding 100 Myr. Recent hypotheses on the phylogenetic relationships within the clade Archaeorthoptera suggest that the family Geraridae and the order Titanoptera are sister-groups [6,28]. This implies a gap covering the Permian period (but new material remains to be described, see below). In Odonoptera, the discovery of *Bechlya ericrobinsoni* Jarzembowski and Nel, 2002, the oldest representative of the Protozygoptera, in the Late Carboniferous (Westphalian) of England, implies a significant gap in the record of Nodialata covering all the Stephanian and Early Permian [35].

## 2.4. Palaeogeographic sampling

Historically, the Late Permian deposits that have been the most intensively studied are located in the region of Perm (Russia), Central North America, Moravia. Those from the Triassic are from France, Central Asia, Australia, Southern Africa, and North America. Very wide areas are still poorly known (China, India, South America, main part of Africa, etc.). Due to this sampling bias, the fossil insect record cannot adequately represent the world insect diversity for these periods.

## 3. The P/T transition of selected insect clades

At this point of the discussion, it is necessary that we proceed with caution on global interpretations. We must focus on well-known monophyletic groups, or on very deep changes in the importance of major groups. Two major taxa ranging from Late Palaeozoic to Recent

are currently studied using modern phylogenetic methods and are partly taxonomically updated: the superordinal clades Archaeorthoptera (crickets, grasshoppers and fossil taxa) and Odonatoptera (damselflies, dragonflies and fossil taxa). Although they are incompletely investigated, some evolutionary trends can be outlined after the current data, which will be tested further.

### 3.1. Archaeorthoptera

The clade Archaeorthoptera belongs to the Polyneoptera, i.e. is more or less related with the Dictyoptera (cockroaches, mantises, termites), the Plecoptera (stoneflies), the Dermaptera (earwigs), the Phasmida (stick insects), and some more cryptic orders [68,69]. As currently known, it includes mainly the extant order Orthoptera (grasshoppers, crickets) and the extinct orders Caloneurodeia and Titanoptera [8]. The assignment of the order Caloneurodeia to the Archaeorthoptera has been recently ascertained [10,13]. Besides the recognized orders cited above, the clade encompasses a part of the ‘Protorthoptera’ group (see [9] for a recent update). Membership of Archaeorthoptera is established based on complex characters of the wing venation [7,8].

Although the phylogeny of the Archaeorthoptera will require additional taxonomic investigations, several Permian and Triassic groups are commonly considered as monophyletic, i.e. the extinct orders Caloneurodeia and Titanoptera, and the order Orthoptera. Within Orthoptera, the sub-order Ensifera (crickets) is well circumscribed and rooted [11]. The composition of the clade Panelcanida [8], present essentially in the Triassic, e.g. in the ‘Grès à Voltzia’ in northeastern France, requires further investigations and its trends will not be discussed herein.

Considering the Permian as a whole, the Archaeorthoptera clade is roughly composed of 70% of species belonging to the Orthoptera, 20% of species belonging to the Caloneurodeia, 10% belonging to remnants of Carboniferous groups (including an inferred species of Titanoptera) ([6]; total of 66 species recognized). The Triassic profile of the Archaeorthoptera is clearly different (mainly compiled from the deposit of Madygen, Russia; total of 51 species recognized): the order Caloneurodeia is missing, and the Titanoptera encompasses about 25% of the species. No major changes affect the

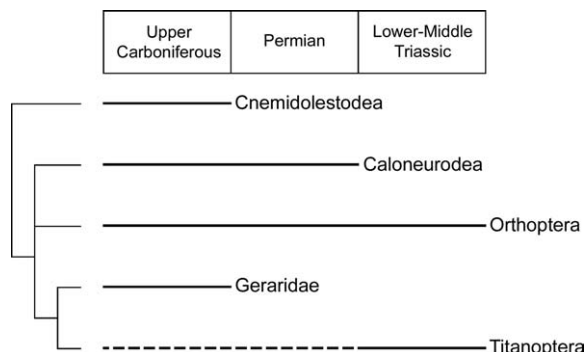


Fig. 1. Phylogenetic relationships and geological occurrence of major of Archaeorthoptera currently recognized.

Relations phylogénétiques et distributions stratigraphiques des clades majeurs d’Archaeorthoptera actuellement reconnus.

order Orthoptera as a whole, which encompasses 75% of the species (70% in Permian) (but see below its inner composition – Fig. 1).

The extinction of the order Caloneurodeia, though apparently not critical in terms of global taxonomic diversity because of its low diversity, is very significant in terms of morphological disparity: its flight mode was unique within Archaeorthoptera. Its representatives possessed two pairs of identical slender wings, which are typical of a bimotorist flight mode. Moreover, at least one Permian family acquired a stridulatory apparatus [12]. All these features depict insects that are very different from other Archaeorthoptera.

Besides the extinction of the Caloneurodeia, the most striking modification is the new proportion raised by the sub-order Ensifera, with 25% of the total Triassic archaeorthopterid species (5% in Permian). This ratio is conservative, since several of the Triassic ensiferan species described by Gorochov [27], from the deposit of Madygen, are herein considered as synonyms, because the effect of post-depositional deformation was overlooked by this author (O.B., pers. obs.).

The cladogenesis events that led to the diversity of the Ensifera can be dated with the best possible resolution around the P/T boundary. The first known true Ensifera is *Raphogla rubra* Béthoux et al., 2002 (Fig. 2a), from the Lodève basin, i.e. one of the Latest Permian deposits that yielded Archaeorthoptera [11], the precise age of which is ranging from Ufimian to Tatarian according to Schneider and Roscher, 2001, <http://www.geo.tu-freiberg.de/palaeo/>. The Earliest Triassic Ensifera is *Galliagryllavus vogesiacus* Marchal-Papier et al., 2000, from the ‘Grès à Voltzia’ Early Ani-

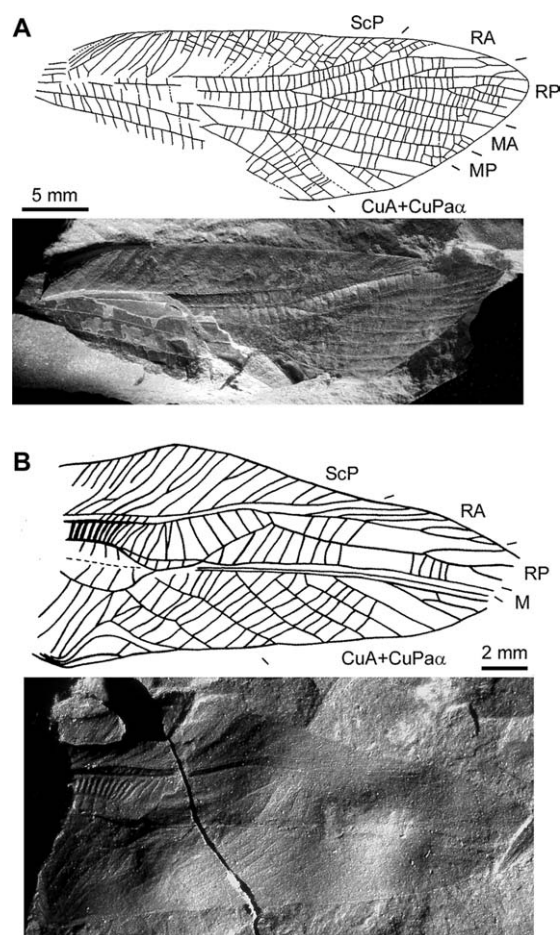


Fig. 2. Representatives of the sub-order Orthoptera: Ensifera (crickets). (a) *Raphogla rubra* Béthoux et al., 2002, the oldest recorded cricket, sister-group of all other Ensifera; Upper Permian, Lodève basin (Hérault, France) (modified from [11]); (b) *Gallia gryllavus vogesiacus* Marchal-Papier et al., 2000, the Earliest Mesozoic cricket, belonging to a derived clade within Ensifera; Lower–Middle Triassic, ‘Grès à Voltzia’ (Vosges, France) (modified from [46]). Wing venation nomenclature: ScP, posterior subcosta; RA, anterior radius; RP, posterior radius; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuPa $\alpha$ , most anterior branch of the posterior cubitus [7,8].

Fig. 2. Représentants du sous-ordre Orthoptera : Ensifera (criquets). (a) *Raphogla rubra* Béthoux et al., 2002, le plus ancien criquet connu, groupe-frère de tous les autres Ensifera; Permien supérieur, bassin de Lodève (Hérault, France) (modifié d’après [11]). (b) *Gallia gryllavus vogesiacus* Marchal-Papier et al., 2000, le plus jeune criquet mésozoïque, appartenant à un clade dérivé au sein des Ensifera; Trias inférieur/moyen, « Grès à Voltzia » (Vosges, France) (modifié d’après [46]). Nomenclature de nervation alaire : ScP, subcosta postérieure ; RA, radius antérieur ; RP, radius postérieur ; MA, media antérieure ; MP, media postérieure ; CuA, cubitus antérieur ; CuPa $\alpha$ , branche la plus antérieure du cubitus postérieur [7,8].

sian (France) [46] (Fig. 2b), i.e. the earliest known Triassic deposit that yielded Archaeorthoptera. Unfortunately, the two deposits are separated by at least 15 Myr. No more precise resolution can be currently reached. Since the Triassic *Gallia gryllavus* belongs to the derived clade Gryllida [8], it implies that the most basal cladogenesis events within the Ensifera occurred previously. Although 15 Myr separates *Gallia gryllavus* from *Raphogla*, we can at least state that a group that constituted about 25% of the Triassic archaeorthopterid species evolved during this gap. Naming this event a ‘radiation’ is a matter of scale.

The order Titanoptera deserves a special mention. It is recorded in only two Triassic deposits (Madygen, Russia; New South Wales, Australia), but two fragmentary specimens, one from the Late Permian of South France and the other from the Triassic of the Vosges (France) remain to be described. The order is very rare in the fossil record and might have narrow palaeoenvironmental preferences. It is rooted in the Carboniferous and is practically unknown during the Permian. Finally, despite an apparent rather high diversity in the Triassic, any attempt to draw ‘titanopterid’ evolutive trends is clearly premature.

In conclusion, the Triassic Archaeorthoptera differ significantly from the Permian ones by the absence of the order Caloneurodeia and the apparent sudden rise of the sub-order Ensifera.

### 3.2. Odonatoptera

Before the recent discovery of the oldest Nodialata in the Late Carboniferous [35], it was supposed that the Carboniferous and Early Permian Odonatoptera belonged to basal ‘pre-nodialatan’ groups (Meganisoptera), and that the diversification of the group occurred later during the Late Permian. The presence of *Bechlyia* in the Carboniferous implies that the most basal cladogenesis events within the Odonatoptera are yet unrecorded (probably occurring during the Early Carboniferous – Fig. 3), but also that the rise and diversification of the Nodialata cannot be reliably correlated with a Late Permian–Early Triassic event.

Several other recent discoveries demonstrated that the diversity of the clade Odonatoptera was very important during the Permian. The ‘old’ famous group of Meganeuridae (commonly referred to ‘giant dragonflies’) was flourishing, even more than in the Carbon-

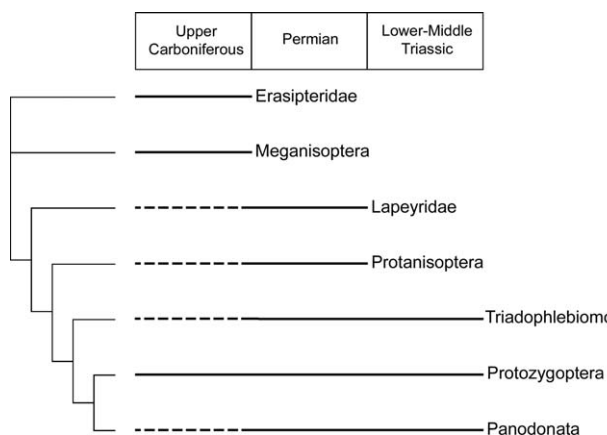


Fig. 3. Phylogenetic relationships and geological occurrence of major clades of Odonatoptera currently recognizes.

Fig. 3 Relations phylogénétiques et distribution stratigraphiques des clades majeurs d'Odonatoptera actuellement reconnus.

iferous, with no less than four species in the Late Permian of Lodève, which have a wing size ranging between 4 and 30 cm (A.N., pers. obs.; Fig. 4a). This morphological disparity corresponds to a wide range of habitats. The highly specialized group of Protanisoptera is still strictly known from the Permian, with

numerous families and genera, and wide morphological disparity [32]. Interestingly, this group is still unknown in the Late Permian of Lodève, while it is present in the localities of nearly the same age and close palaeogeographic location (North America), perhaps due to palaeoenvironmental preferences of the group. The Protozygoptera were present and very diverse during the Permian and Triassic (Madygen, Kirghisistan, Grès des Vosges, Northern France), with no decrease in diversity or morphological disparity around the boundary between the two periods. Until recently, the very wide group of the Triadophlebiomorpha was only known from Triassic deposits (Madygen Formation and 'Grès des Vosges'), but a recent discovery demonstrated their presence in the Late Permian [52] (Fig. 4b). The first representatives of the modern clade Odonata (zygopteran and anisopteran lineages) are known from the Late Triassic but, as they belong to already very advanced subgroups, the group is certainly older and probably appeared during the Permian, as the oldest Panodonata (a clade including the Odonata and its closest sister-groups) is Late Permian [51]. Nevertheless, the Panodonata and Odonata were certainly less diver-

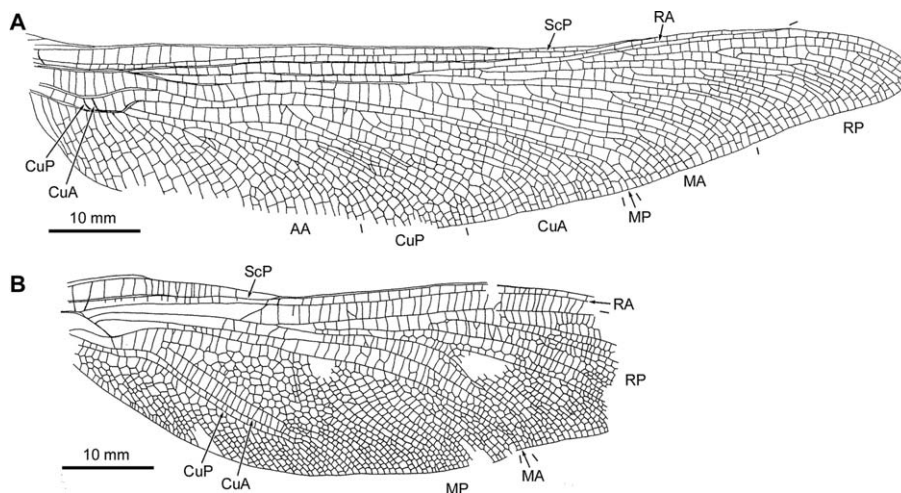


Fig. 4. Representatives of the super-ordinal clade Odonatoptera (dragonflies, damselflies). (a) Undetermined Meganeuridae (Tupinae), belonging to a Carboniferous 'lineage' extinct at the Permian–Triassic boundary; Upper Permian, Lodève Basin (Hérault, France; specimen Ld LAP 156, Lapeyrie Collection). (b) *Permophlebia uralica* Nel et al., 2001, a Permian representative of the Triadophlebiomorpha, a clade flourishing in the Triassic; Upper Permian, Vorkuta basin (North Ural, Russia) (modified after [52]). Wing venation nomenclature as in Fig. 2 and: CuP, posterior cubitus; AA, anterior analis.

Fig. 4. Représentants du clade super-ordinal Odonatoptera (libellules, demoiselles). (a) Meganeuridae (Tupinae) indéterminé, appartenant à une « lignée » carbonifère éteinte au passage Permien–Trias ; Permien supérieur, bassin de Lodève (Hérault, France ; spécimen Ld LAP 156, collection Lapeyrie). (b) *Permophlebia uralica* Nel et al., 2001, un représentant permien des Triadophlebiomorpha, un clade florissant au Trias ; Permien supérieur, bassin de Vorkuta (Nord de l'Oural, Russie) (modifié d'après [52]). Nomenclature de nervation alaire comme sur la Fig. 2 ; CuP, cubitus postérieur ; AA, analis antérieure.



sified during the Late Permian and Early Triassic than in the Late Triassic.

In summary, the recent discoveries demonstrated that our knowledge of the Permo-Triassic fauna of Odonoptera is fragmentary, but some patterns can be reliably outlined. It appears that no less than six main clades were present in the Late Permian, but three of them were not found in the Triassic deposits (Meganisoptera, Protanisoptera, Lapeyriidae). Thus, the change in the fauna of Odonoptera is evident. However, the timing is poorly constrained as the fossil record is extremely scarce in the Late Permian and Early Triassic.

### 3.3. Other significant groups

The Coleoptera is a dominant order in terms of species richness in the Early–Middle Triassic of the Vosges, the oldest known formation that provided diversified Coleoptera, and in later periods [45,55]. This group is present in all the Triassic and more recent deposits. The most ancient Coleoptera are recorded from the Permian, though it has never been recorded in some Late Permian localities (e.g., Lodève Basin), where it was either absent or of minor importance [55]. Similarly, we could hypothesize that they were not yet adapted to some special Late Permian environments. On the contrary, this group has been widespread in all continental environments since the Mesozoic and Cenozoic, as the most important component of the entomofaunas. Its morphological and taxonomic diversification probably took place between the Late Permian and the Middle Triassic.

The Diptera are still not recorded during the Permian, but are diverse in the Early–Middle Triassic. In the deposit of the Grès à Voltzia, the order represents a diverse fauna with numerous families [38,39], phylogenetically distant (several ‘Nematoceran’ groups and Brachycera), even if these fossils are the first and oldest known representatives of this order. These discoveries demonstrate the great antiquity of the order Diptera, much older than the Early–Middle Triassic. Based on our current knowledge, it diversified during the gap of 15 Myr, as the Coleoptera.

## 4. Discussion

During preparation, this article turned out to be more a prospective paper rather than the publication of ascer-

tained data. Nevertheless, the evolution of the Archaeoptera and that of the Odonoptera show similarities during the Permian and the Triassic: (1) after the appearance and first diversification of major lineages during the Permo-Carboniferous, some of them get extinct between the Late Permian and the Middle Triassic, (2) an extinction event occurs between the Latest Permian and the Middle Triassic, and (3) in the Triassic, the previously underrepresented groups undergo an apparent sudden diversification. Even some groups that are absent or rare in the Permian record (Diptera, Coleoptera) show a surprising taxonomic diversity in the earliest known Triassic deposit with a significant entomofauna, i.e. the ‘Grès à Voltzia’. Since this pattern is recognized in clades that are phylogenetically and ecologically distant, one can assume that an extrinsic factor affected them in a similar way. Nevertheless, a gap of 15 Myr separates our Latest Permian record from the Earliest Triassic one. Therefore, no one can assume a scenario of sudden and contemporaneous extinctions or diversifications affecting these groups at the Permo-Triassic boundary.

The important diversifications that occurred during the ‘Permian–Triassic gap’ can be considered as a recovery in the Odonoptera, in which new taxa replaced the Permian ones in similar ‘niches’. For example, the ‘giant’ Meganeuridae of the Late Permian were replaced by very large Triadophlebiomorpha in the Middle and Late Triassic, which were already present, but less diverse than the former group in the Permian. But this process was not a recovery for the Coleoptera or the Diptera, which diversified in the Triassic, but were probably not affected by major extinction in the Latest Permian. They were probably minor groups in the Palaeozoic.

Before concluding, we wish to consider in this discussion another approach to assess a possible collapse and recovery of the entomofaunas during the P/T transition: comparing the ecological diversity of communities through time. It is generally admitted that diverse and mature insect communities possess more species, and relatively more uncommon ones. It will be demonstrated below that the current fossil data are insufficient to provide results, though methodological tools are newly available.

The species richness (i.e. the total number of species) and the evenness (i.e. the distribution of the individuals among the species) are suitable descriptors of

the ecological diversity of a community, especially if used together [44]. However, the numerous available evenness indices [62] show variable sensitivity to rare, median and dominant taxa [1,58], depending on concepts on which the indices are based. This is a serious issue for their general use. As pointed out by [58], those indices always result in a loss of information, which must be avoided as far as possible when describing multivariate data.

Olszewski [53] proposed to use taxon-sampling curves (commonly referred to as rarefaction or accumulation curves; [29]) as a unique descriptive figure of community diversity. The species richness can be estimated after the fitting of those curves with models [19,67], while the ecosystem evenness is described by the slope of the steepest segment of the rarefaction curve [53]. Indeed, several studies already demonstrated the usefulness of this approach for comparing arthropod and insect communities (e.g., [15,17,60]) as well as the efficiency of trapping methods [42,43], without explicit mention of the evenness. One can notice that the main interest of the method relies in its absence of information loss.

This method requires a dataset of abundances (number of specimens) per species, for one or several samples. Such data are available for a part of the entomofauna of the 'Grès à Voltzia' Formation, which is the oldest Triassic fossiliferous deposit rich in insects. This deposit of Anisian age, i.e. the beginning of the Middle Triassic, yielded more than 5300 specimens belonging to 17 orders [45]. The species inventory is partly published, but an individual-based rarefaction curve cannot yet be processed from the available data, because they are too patchy. The database of the rich Russian Permian and Triassic collections ([http://palaeoentomolog.ru/Collections/rus\\_loc.html](http://palaeoentomolog.ru/Collections/rus_loc.html)) provides the number of specimens per orders only, which is not suitable for our approach, because biological entities that are competing in communities are not orders, but species.

The next step, estimating the original community characteristics from a fossil insect collection, is yet a difficult issue. The taphonomic analysis proposed by Gall [26], which would have allowed a correction of the fossil sampling bias of the Grès à Voltzia, did not involve insects. Smith [63] demonstrated that the taphocoenotic beetle assemblage of shallow, subsurface sediment, along the shoreline of a recent ephemeral lake,

differs significantly from the original beetle assemblage. Not only the proportions between genera and families of the dead and living assemblages differ, but also the generic and family compositions. Smith's taphocoenotic vs. original relative abundances per size is the only measurement of bias applicable to fossils, whose habitats and feeding types are unknown. Supposedly, the original species richness could be estimated by this way. Smith [63] showed that species smaller than 5-mm long are over-represented in the taphocoenosis he studied. This is not the case for numerous Cenozoic outcrops (A.N. pers. obs.). Also, from the collection of the 'Grès à Voltzia', Papier et al. [55] indicated only one species based on a single entire specimen that belongs to this size group, among 584 specimens belonging to 32 species (most remains are isolated elytra). Several explanations are possible: (1) the size range of Cenozoic or Triassic Coleoptera was significantly different from that of Recent Coleoptera; (2) there is a significant bias from the taphocoenosis to the collection assemblage, with regard to species longer than 5 mm, i.e. the elytra smaller than 3 mm have not been collected, which is not the case in the Grès à Voltzia and in the Oligocene of Aix-en-Provence; (3) Smith's ephemeral lake ratios are not applicable to the palaeoenvironment of the Grès à Voltzia and several Cenozoic palaeolakes (Lubéron, Aix-en-Provence...). In conclusion, the Grès à Voltzia beetle collection abundance cannot yet be corrected after the available literature data on experiments on taphonomic bias.

Henwood [31], followed by McCobb et al. [48], compared fossil assemblages to human trap methods. This approach could be very fruitful. In the approach of Longino and Colwell [42], and Longino et al. [43], who compared the efficiency of various trapping methods, one could attempt to characterize fossil sampling efficiency based upon species accumulation curves. Then fossil collection accumulation curves could be corrected with appropriate ratios. However, it is obvious that this approach needs numerous new quantitative taphonomical studies (already advocated, see [20]), made feasible since processes involved in insect fossilisation are better understood [47].

Finally, we consider that the hypothesis of a post-crisis diverse entomofauna of the 'Grès à Voltzia' needs to be supported by further investigations, including measurement of fossil sampling bias and reference to

community structure. For example, 41% of the specimens belong to only nine species of Blattodea, with one species, *Voltziablatia grauvogeli* Papier and Grauvogel-Stamm, 1995 [54], which cumulates by itself 32%. These ratios are very likely due to a fossil sampling bias rather than to a low diversity of the original assemblage, but this is yet undemonstrated.

## 5. Conclusion

Recent works using modern methodologies focused on monophyletic groups and, on the basis of comprehensive taxonomical updates, show that evolutive dynamics can be outlined from the available record of Late Palaeozoic and Early Mesozoic entomofaunas. There is some evidence that the Permian and Triassic entomofaunas differ significantly, and that groups that are underrepresented during the Permian are contrastingly diversified in the Middle/Late Triassic. However, the role of extrinsic vs. intrinsic factors will have to be carefully discriminated in future works.

Obviously, those patterns will have to be refined and tested, by the discovery of deposits closer to the P/T boundary, and by a comparison with patterns observed in other groups of organisms. In addition, serious improvements are desirable in quantitative taphonomy of insects, in order to obtain better measurements of ecological diversity of ancient entomofaunas. Eventually, one might notice that another possible life crisis event must be used as a control, in order to assess the magnitude of the P/T renewal. The Carboniferous–Permian boundary is a good candidate, because a significant floral renewal happened during this period [36], as for the P/T transition.

This prospective paper shows that picturing the evolution of the insect class around the Permian/Triassic boundary is a difficult and long-term task. The main reason is the hyper-diversity of the group, and the relative lack of facilities involved in its study. Although large collections, deposits, and efficient tools are available, major questions on the evolution of insects are yet hard to address by the palaeoentomologists community, which has been historically under-represented.

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