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# Recovery of the Triassic land flora from the end-Permian life crisis

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## Abstract

The recovery of the Triassic land flora after the end-Permian biotic crisis has not been studied in detail except in North China where examination of a complete sequence of Permian–Triassic strata containing fossil plants revealed that the recovery lasted until the end of the Middle Triassic. Our analysis of the Triassic floras of Europe shows that their recovery began, as in North China, with the proliferation of the lycopsid *Pleuromeia* during the Early Triassic and that it proceeded with the resurgence of the conifers in the early Middle Triassic (Early Anisian), the return of the cycadophytes and the pteridosperms in the Late Anisian and the progressive evolutionary modernization of the subsequent. This study shows that the climate played an essential role and that the temperature gradient from the equator to the poles was low. The fact that *Pleuromeia* was the most distinctive feature of the Early Triassic all over Eurasia and in the southern continents suggests that this lycopsid was an opportunistic pioneer plant which took advantage of the post-crisis vacuity of the environment to proliferate, preparing sites for recolonization with the plants having survived in refugia. ***To cite this article: L. Grauvogel-Stamm, S.R. Ash, C. R. Palevol 4 (2005).***

## Résumé

**Renaissance de la flore triasique après la crise de la fin du Permien.** La renaissance de la flore terrestre au Trias, après la crise biologique de la fin du Permien, n'a pas été étudiée en détail, sauf dans le Nord de la Chine, où l'examen d'une série permo-triasique complète contenant des plantes fossiles a révélé qu'elle a duré jusqu'à la fin du Trias moyen. Notre analyse des flores triasiques d'Europe montre que leur renaissance a commencé, comme dans le Nord de la Chine, avec la prolifération de la lycophyte *Pleuromeia* durant le Trias inférieur et qu'elle s'est poursuivie par la résurgence des conifères au début du Trias moyen (Anisien inférieur), la réapparition des cycadophytes et des ptéridospermes à l'Anisien supérieur et la modernisation évolutive progressive des flores suivantes. Cette étude montre que le climat a joué un rôle important et que le gradient thermique entre l'équateur et les pôles était faible. Le fait que *Pleuromeia* ait été l'élément le plus caractéristique au début du Trias dans toute l'Eurasie et dans l'hémisphère sud suggère que cette lycophyte était une plante pionnière et qu'elle a profité de la vacuité

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de l'environnement après la crise pour proliférer, préparant ainsi le terrain pour la recolonisation par des plantes ayant survécu dans des refuges. ***Pour citer cet article : L. Grauvogel-Stamm, S.R. Ash, C. R. Palevol 4 (2005)***.

*Keywords:* End-Permian life crisis; Palaeogeography; Palaeoclimate; Palaeoecology; Triassic land-plant recovery; China; Euramerica; Gondwanaland; Survival and recovery strategies; Refugia

*Mots clés :* Crise biologique de la fin du Permien ; Paléogéographie ; Paléoclimat, Paléoécologie ; Renaissance floristique du Trias ; Chine ; Euramérie ; Gondwana ; Stratégies de survie et de renaissance ; Refuges

## 1. Introduction

The Early Triassic biotic recovery has become a subject of increasing scientific interest and has resulted in two international projects: the Global Changes Program [73] and the IGCP Project 335 *Biotic recoveries from mass extinctions* [23,40,41]. However, because interest in recoveries has been less than in the crisis events themselves, the recuperation intervals have been only superficially examined and therefore are poorly understood [24]. This is particularly true of the Triassic recovery interval. Furthermore, most studies concern only marine invertebrates [24]. Although land plants are known to be particularly sensitive to environments and palaeoclimate [13,78,79] and therefore very likely to be instructive for evaluating the patterns and processes of biotic recovery, they have been rarely analysed in detail from this perspective. According to Erwin [21], Triassic land flora is equivocal. Indeed, opinions of the palaeobotanists about the response of the land flora to the end-Permian life crisis are very contrasting.

For most palaeobotanists (e.g., [86]), the Permian–Triassic interval was a long period of turnover and "replacement of higher-level taxa" since, unlike the faunal record, the plant megafossil record does not show clear evidence of any mass extinction at the end of the Permian. Recently, Kerp [46] noted that there is hardly any evidence for the extinction of major groups of plants at this boundary and that evidences for floral changes relies almost exclusively on palynological data. Dobruskina [18], who studied thoroughly the evolution of the floras across the Permian–Triassic boundary, never mentioned an end-Permian mass extinction event affecting the floras and therefore never referred to a Triassic land-plant recovery.

In contrast, some other palaeobotanists noted that the land floras have been severely affected by the end-Permian life crisis and that the number of families of higher land plants has drastically declined. Only six out of the 20 families of pteridophytes and four of the 20 families of gymnosperms known to have existed during the Permian persisted into the Triassic [14,15]. Retallack [70,71] also reported that the Early Triassic lowlands were an ecological wasteland. To our knowledge, Wang [81–83] is the first palaeobotanist who has thoroughly studied the land-plant recovery and noted its decimation at the Permian–Triassic transition and its subsequent recovery. Looy et al. [51], who analysed the Triassic land-plant recovery on the basis of palynological data, also noted that the end-Permian flora, particularly the conifers, have been decimated, and showed that the most suitable fossils for such studies are pollen and spores, because of their unique fossilization potential.

The purpose of the present paper is to tentatively review the state of our knowledge of the response of land plants to the end-Permian life-crisis and, where it is possible, to analyse their recuperation from this event.

## 2. The Permian–Triassic world: palaeogeographic and palaeoclimatic setting

Since the land plants are very sensitive to climatic change [13,78,79] and since it is one of the major extrinsic abiotic stress having modified the terrestrial vegetation [17], it is essential to analyse the evolution of the Permian–Triassic land floras in their palaeoclimatic and palaeogeographic context and to study the palaeofloras that succeeded one another under similar palaeolatitudes. Moreover, it is essential to consider palaeoecology for studying the major evolutionary transitions in continental biotas [16]. Such studies are rare since most palaeobotanical studies do not take into account these parameters.

Recently, Rees [67] presented an analysis of the evolution of the land-plant diversity at the Permian–

Triassic transition in different regions in a palaeogeographic context. He noted that a marked decrease in land floras is generally apparent at the Permian–Triassic boundary and that the flora diversity shows the effects of the northward motion of Pangea. However, he noticed that the scale and timing of these effects varied markedly between the regions and he concluded that they are best explained by differences in palaeogeography, palaeoclimate and fossil preservation than by catastrophic mechanisms.

It is worth to note, in this context, that the Permo-Triassic world, which consisted of the large supercontinent Pangea, was characterised by warming and oxygen decline [48] that lead to large seasonality and high aridity in the continental interiors [90]. Parrish [61] suggested moreover that Pangea was governed by an extreme monsoonal climate with sharp contrast between an extremely dry season and a rainy season. The warming, which is considered to have begun at the end of the Permian and to have continued across the Permo-Triassic boundary in the Scythian, is considered to have played a key role in causing the end-Permian extinction which devastated both marine and terrestrial ecosystems [48].

Moreover, during the Triassic, Pangea moved about 10° northward so that the landmass was symmetric with respect to the equator by the Late Triassic [90]. Some authors noted that the temperature gradient between the equator and the poles was well-developed [67,90], whereas others indicated that it was small relative to those of today [48]. The comparative study of the Early Triassic floras of Russia (Siberia and Upper Volga), Europe and North China, in a palaeogeographic context, also suggests that it was small (see the section about Siberia). Indeed, the similarities shown by these floras cannot be explained if the palaeotemperature gradient that was developed since Siberia was situated at a palaeolatitude of ca. 60°N and North China, Germany and Upper Volga were at ca. 30°N. The palynological data for the Early Triassic of Eurasia also led to the same conclusion [89].

## 3. The Triassic land-flora recovery: some examples

Detailed studies of the Triassic land-flora recovery are very scarce since plant fossil records from the Lower Triassic interval are typically rare. Indeed, although Triassic strata are widespread on all the continents, they often consist only of red beds which, contrary to many believes, have no particular palaeoclimate significance [20], but in which fossils are usually rare or poorly preserved, if present.

The Permo-Triassic sequence of North China is an exception, since it consists of about 2000-m-thick continental Permo-Triassic red beds that contain a complete sequence of plant assemblage. Thus, owing to the numerous specimens collected from 16 areas and 4 provinces of North China, Wang [81–83] could make a detailed study of the land-plant evolution across the Permian–Triassic boundary, including a taphonomic and palaeoecologic analysis. He could follow step by step the evolution of the plant communities that succeeded one another during the Permian–Triassic interval and thus could analyse the post-crisis land-plant recovery. To our knowledge, it is the only place in the world where a complete sequence of fossil plants across the Permian–Triassic has been investigated with such detail and from this perspective. Therefore, since it is also the first study of that kind, it is here considered a model for studies on the Triassic land-plant recovery. However, the analysis of the Triassic land floras from other areas also revealed interesting within the framework of the Triassic land-plant recovery (Fig. 1).

### *3.1. The Triassic land-plant recovery in North China: a model*

Wang [81–83] pointed out that in North China, the end-Permian life crisis was caused by increasing desertification, which wiped out up to 75% of the land flora at the genera level and 98% at the species level, including most of the typical Palaeozoic species. Wang [81] showed that the total species number passed from 146 taxa in the lower Upper Permian (Tianlongsi Formation) to 54 taxa in the late Upper Permian (Sunjiagou F.), 16 taxa in the early Lower Triassic (Liujiagou F. = Induan) and 58 taxa in the late Lower Triassic (Heshangou F. = Olenekian) where it began again to increase, showing that the end- Permian life crisis was a long process that began well before the end of the Permian, and that the subsequent Triassic recovery was also a long process lasting until the end of the Middle Triassic. Moreover, outstanding reconstructions illustrate the landscape, flora composition and climatic evo-

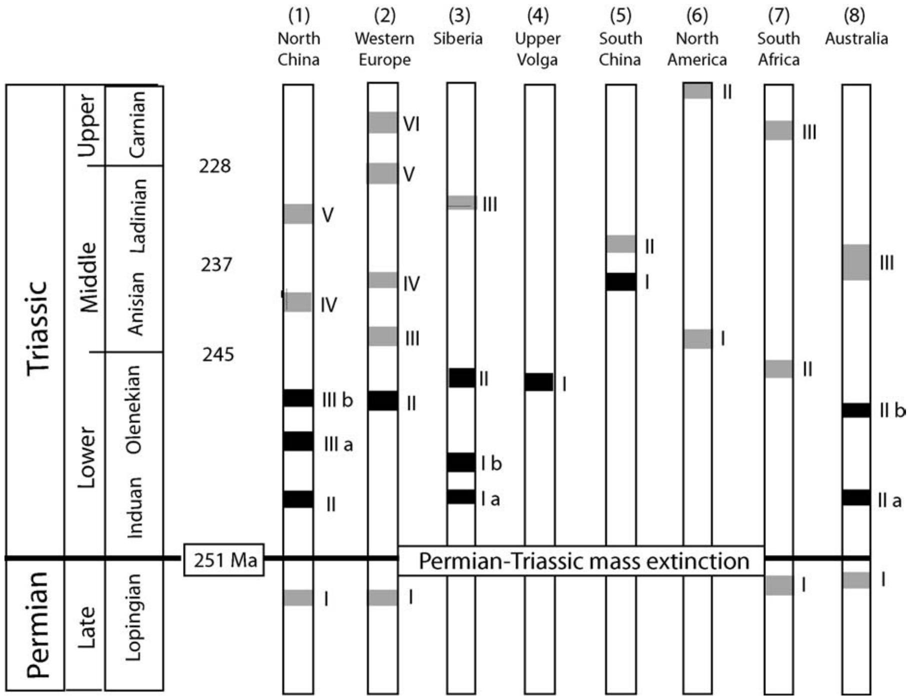

Fig. 1. Tentative simplified correlation table showing the distribution of the end-Permian and Triassic floras in different regions of the world: black = *Pleuromeia* or lycopsid-dominated floras; grey = more or less diversified floras. Please note that the columns and the plant-bearing beds are not at scale; stratigraphy after [60]. For the source data, see the references in the relevant sections. **(1) North China**: I –Late Permian (Sunjiakou Formation): *Ullmannia* zone; II–III: Induan–Olenekian: *Pleuromeia*-dominated floras (II – Induan: Liujiakou Fm. = *P. jiaochengensis* subzone; III – Olenekian: Heshangou Fm.; III a = *P. epicharis* subzone; III b: *P. sternbergii* subzone); IV – Anisian (Ermaying Fm.): *Tongchuanophyllum* zone including the *Isoetes* subzone at the base and the *Scytophyllum* subzone above; V – Ladinian (Tongchuan Fm.) with *Danaeopsis*. **(2) Western Europe:** I – Late Permian (Lopingian): Zechstein flora, Val Gardena flora, N. Italy = conifer-dominated floras; II – Olenekian (Middle Buntsandstein), Germany = *Pleuromeia*-dominated flora; III – Early Anisian ('Grès à *Voltzia*' Fm., Upper Buntsandstein), NE France: conifer-dominated flora; IV – Upper Anisian (Dont Fm.), N Italy: conifer/cycadophyte/fern-dominated flora; V - Late Ladinian (Lower Keuper), Germany = sphenopsid-dominated flora (Wengen Fm.), N. Italy = *Voltzia*-dominated flora; VI – Middle Carnian (Schilfsandstein), Germany = sphenopsid-dominated flora. **(3) Siberia (Russia):** I a, I b – Induan: *Pleuromeia* and *Tomiostrobus* (sub-genus of *Annalepis*) dominated-flora; II – Upper Olenekian: *Pleuromeia*-dominated flora, Taymyr, Verkoyanye ; III – Ladinian flora. **(4) Upper Volga (Russia):** I – Olenekian (Rybinsk Fm.): *Pleuromeia*-dominated flora. **(5) South China:** I – Anisian (Lower Badong Fm.): *Pleuromeia-Annalepis*-dominated flora; II – Ladinian (Upper Badong Fm.): *Annalepis*-dominated flora. **(6) North America:** I – Early Anisian (Moenkopi Fm.): flora with *Donwelliacaulis*; II – Late Carnian flora (Chinle Fm. with the Shinarump Member at the base and the overlying Petrified Forest Member, which is Late Carnian–Early Norian). **(7) South Africa (Gondwana):** I – Late Permian: *Glossopteris*-dominated flora; II – Late Olenekian (Burgersdorp Fm.): diversified flora; III – Early–Middle Carnian (Molteno Fm.): rich and diversified flora. **(8) Australia (Gondwana):** I – Late Permian: *Glossopteris*-dominated flora; II a, II b – Induan + Olenekian: lycopsid-dominated floras; III – Middle Triassic, (Basin Creek Fm. in the Nymboida Coal Measures, Clarence–Morton basin).

Fig. 1. Tableau de corrélation simplifié, montrant la distribution des gisements à flore de la fin du Permien et au Trias dans les différentes régions discutées dans le texte ; les gisements à *Pleuromeia* ou à lycopsides de type *Pleuromeia* sont indiqués en noir. Échelle stratigraphique d'après [59]. Noter que les colonnes et les niveaux à plantes ne sont pas à l'échelle.

lution [82 (Fig. 1), 83 (Fig. 2)] and show that immediately after the end-Permian life crisis, the landscapes looked like deserts. As shown in palaeogeographic reconstructions, in the Early Triassic, North China was at latitude of ca. 30°N, latitude which is characterized by arid climates [90].

Wang [83] recognized two stages in the land-plant recovery: the first was the Early Triassic *Pleuromeia* stage with three sub-zones, which was dominated by the lycopsid *Pleuromeia* (Fig. 1, 1.II–III) and the second was the Middle Triassic *Tongchuanophyllum* stage with two sub-zones (the *Isoetes* sub-zone and the *Scy-*

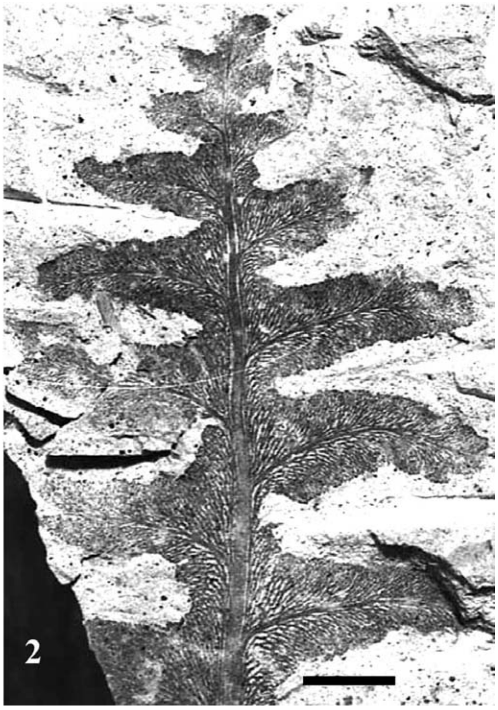

Fig. 2. Cf. *Tongchuanophyllum sp.*, frond with netvenation, 'Grès à *Voltzia*', Vosges (northeastern France). Scale bar = 1 cm.

Fig. 2. Cf. *Tongchuanophyllum sp.*, fronde avec nervation réticulée, Grès à *Voltzia*, Vosges, Nord-Est de la France. Barre d'échelle = 1 cm.

*tophyllum* sub-zone), which is characterized by the broad-leaved pteridosperm *Tongchuanophyllum* and the sphenopsids *Equisetites* and *Neocalamites* (Fig. 1, 1.IV–V). He also noted that six plant-communities succeeded during this interval.

In the very Early Triassic, the climate in North China was said [83] to have been an arid–hyperarid Sahara type, and the area was a vast sandy plain crossed by dry washes devoid of any vegetation. Small ephemeral depressions formed on the plain around which plants were able to grow. These depressions resembled oases found today in the Sahara Desert [83]. The appearance of this environment marks the start of the Triassic plant recovery. Indeed, monotypic populations of three species of the lycopsid *Pleuromeia (P. jiaochengensis, P. epicharis, P. sternbergii*) inhabited these depressions and succeeded one another during the Early Triassic. It is worth noting that *P. jiaochengensis* [84], which appeared the first, shortly after the end-Permian life crisis, when the living conditions were the worst, is very small (usually 20–30 cm tall) compared to the species that evolved later, *P. epicharis* and *P. sternbergii* (respectively 1 m and 2 m tall). Some other plants, such as ferns (*Crematopteris, Anomopteris)* and sphenopsid (*Neocalamites)*, are sometimes associated with *Pleuromeia* or formed monospecific populations alongside the lycopsid on the edge of the depressions. It is noteworthy that most of these plants are preserved in life position, indicating that they were part of typical biocoenoses and that they were buried very rapidly, e.g. by sheet floods, such as those which occasionally occur in desert environments. Other plants commonly found in the *Pleuromeia* stage of North China, include *Phyllotheca*, *Peltaspermum*, *Scytophyllum, Neuropteridium, Schizoneura, Voltzia*, *Yuccites* and *Willsiostrobus*. Some of them *(Anomopteris, Neuropteridium, Schizoneura, Voltzia, Yuccites)* are also sporadically present in the Early Triassic Buntsandstein of western Europe and more common in the early Middle Triassic 'Grès à *Voltzia*' flora of northeastern France [25,30]. According to Wang [83], the end of the Early Triassic was characterized by the spread of what had been patchy vegetation into adjacent areas.

In contrast, during the Middle Triassic, rainfalls increased and the lakes and streams became permanent waterbodies since the climate had become less arid [83]. In the Anisian, *Pleuromeia* was no longer present because the growth conditions are said to have become unfavourable for that plant. The broad-leaved pteridosperm *Tongchuanophyllum* became the dominant plant together with the sphenopsids (*Equisetites, Neocalamites*). Dense horsetail-marshes grew around the waterbodies while *Isoetes* populations colonized small ephemeral ponds. In the Ladinian, new ferns, such as *Cladophlebis, Todites* and *Danaeopsis* appeared which show that the recovery progressed. Pteridosperm colonies containing *Tongchuanophyllum, Scytophyllum* etc. were still present on the river banks. As noted by Wang [83], although each stage and sub-zone is characterized by a dominant plant, none of the genera cited above is strictly confined to a given stage or sub-zone.

### *3.2. The Triassic land-plant recovery in Europe: a discontinuous story*

Kerp [46] recently pointed out that the plant megafossil record from the Permian through the lower Middle Triassic of Europe is poorly known, and seems to preclude study of the Triassic land-plant recovery in this area. Similarly Meyen [57] had recognized that a detailed reconstruction of the Permian–Triassic transition was impossible. However, a new analysis by us, of the principal oldest Triassic floras known in Europe has given a good impression of the Triassic land-plant recovery in this region and shows that there are many similarities with North China. In fact, according to palaeogeographic maps [90], both areas were approximately at the same latitude, i.e. ca 30°N, in the Early Triassic, which would explain that both have had a similar land plant evolution.

Palynological studies have shown that in Europe the Triassic land-plant recovery spanned the Early Triassic and went through two stages, a survival interval in the Early Triassic dominated by the lycopsid *Pleuromeia* and the recovery interval itself at the end of this period characterized by the resurgence of the conifers, with both intervals representing the repopulation period [51]. Our analysis of the Triassic floras led to a similar scenario but clear evidences of the recovery interval itself are only from the Early Anisian, i.e. the early Middle Triassic. Moreover, it shows that the recovery extended into the Middle Triassic and it also illustrates how it developed.

Before analysing the Triassic land-plant recovery, it is essential to consider the characteristics of the floras which existed at the end of the Permian and of which the Triassic conifer-dominated flora is considered to be descended [18]. These floras which are represented by the Val Gardena flora in the southern Alps and the Zechstein flora [76] (Fig. 1, 2.I) also were dominated by conifers showing all adaptations to an arid climate [45]. The Walchiaceae which is the most common group of the Latest Carboniferous and Permian in Europe became extinct at the Permian–Triassic transition [45,46]. It is worth to note that the conifers also were the dominant plants in the Late Permian flora of North China (Fig. 1, 1.I), with the genus *Ullmannia* being the most common taxon [82].

### 3.2.1. The Early Triassic Pleuromeia flora of Germany or the opportunistic pioneer lycopsid-dominated flora

The *Pleuromeia* flora is the oldest Triassic land flora represented in Europe (Fig. 1, 2.II) and is found in Germany in the Middle Buntsandstein of Early Triassic age [25,31,43,52]. Since it mostly consists of the lycopsid *Pleuromeia*, it differs very much from the Late Permian conifer-dominated flora described above. As in North China, *Pleuromeia* is often the only fossil plant which is present. The high density of their stems that are often preserved in life position, suggests that they formed dense monotypic populations around abandoned channels and temporary pools. The wide expansion of these lycopsids all over Eurasia and in the southern continents is considered the most distinctive feature of the Early Triassic [18]. This overwhelming occurrence of *Pleuromeia* suggests that it was an opportunistic pioneer plant that took advantage of the post-crisis vacuity of the environment to proliferate. Besides, in present-day ecosystems, lycopsids are also considered to be pioneer plants that take over disturbed sites [64] but like the living *Isoetes*, they compete poorly with other plants [65].

In Lammersdorf (Germany), as in North China, the fern *Anomopteris* is associated with the lycopsid populations [25] and similarly is represented by reduced pinnae (15–30 cm long and 3–5 cm wide) compared to those of *Anomopteris* (1–2 m long and 30–50 cm wide) which occurred later in the 'Grès à *Voltzia*' of northeastern France, during the second stage [30,32]. It is difficult to determine if the species are the same since the specimens from the Middle Buntsandstein of Germany are preserved in coarse sandstone and therefore too poorly preserved to allow an accurate identification. Their smaller size may indicate either that it represents another species or that growth conditions were poor or that the plants have been fossilized before they reached their full size. Only very few other plants have been reported from the Lower Triassic and from the older literature it is often difficult to identify these plants exactly and it is unclear how they are associated. Moreover, often only their occurrence is reported. These plants are *Schizoneura, Neuropteridium, Voltzia, Yuccites*, all of which are also typically found in the Early Triassic *Pleuromeia* stage of North China [83] and in the Early Anisian flora of northeastern France [30].

The *Pleuromeia*-dominated flora of Germany (Fig. 1, 2.II) closely resembles the *Pleuromeia* flora of North China, particularly that of the third sub-zone which is also characterized by *P. sternbergii* (Fig. 1, 1.IIIb), and therefore it can be similarly considered to represent the first stage of the Triassic land-plant recovery in Europe. The *P. jiaochengensis* and *P. epicharis* sub-zones that have been recognized in North China (Fig. 1, 1.II, IIIa) have not been found in the Lower Triassic of Europe (Fig. 1, 1.II), although the palynological data show that they also probably existed here too [34,51].

In the Triassic land-plant recovery worked out by Looy et al. [51], the *Pleuromeia*-dominated flora corresponds to the survival interval, i.e. an interval during which "populations expand, although with very limited diversification among surviving lineages" [22,41]. This definition seems to suit since the lycopsid *Pleuromeia* is considered to be a survivor from the Palaeozoic. According to Meyen [57], it is related to the Carboniferous taxon *Chaloneria* and the Permian taxa *Viatschevslavia* and *Signacularia*. However, the fact that the ancestors have not been recognized precisely may be explained by the morphological changes that may have occurred at the Permian–Triassic transition in response to the rapid environmental changes [10].

### *3.2.2. The Early Anisian or early Middle Triassic 'Grès à Voltzia' flora of northeastern France: a conifer-dominated flora*

The conifer-dominated flora which appears to have succeeded the *Pleuromeia* flora is represented by the flora found in the 'Grès à *Voltzia*' Formation of northeastern France (Fig. 1, 2.III) [30]. This flora is richer and more diversified than the *Pleuromeia* flora although the number of taxa still remains low. It is considered to be xeromorphic [53] and closely related to the Late Permian Zechstein flora, which is also dominated by the conifers [18,46,76].

*3.2.2.1. Geological setting.* The 'Grès à *Voltzia*' Formation, which also consists of red beds, represents the youngest part of the Upper Buntsandstein and has been dated as Early Anisian, i.e. the very beginning of the Middle Triassic [26]. Comprehensive sedimentological studies have shown that it was deposited in a deltaic environment along the western border of the German Basin and that it contains two facies corresponding to two biotopes: fluvial channels and temporary pools on the floodplain [26–28]. It is worth noting that such facies and ecospaces also existed in the Triassic in North China [83]. The silty clay lenses that correspond to sediments deposited in the more or less ephemeral ponds scattered on the floodplain, between the channels, provided most of the well preserved plant remains that have been described, as well as the aquatic and terrestrial animals, including numerous associated insects, and give an impressive insight into the ecosystems and landscapes of the early Middle Triassic [26–28,30,54]. The fact that the 'Grès à *Voltzia*' is one of the oldest Triassic continental formations that is known to contain such a rich and well-preserved biotic assemblage and the nearest known to the end-Permian life crisis, led to regard it as representing a period of biotic recovery [29]. In the present issue (see Gall & Grauvogel-Stamm) it is considered a model of environment that has acted as a refugium for terrestrial communities during the end-Permian life crisis and its Triassic aftermath.

*3.2.2.2. Flora composition: basinal and extrabasinal taxa.* The 'Grès à *Voltzia*' flora is dominated by various conifers among which are the genera *Voltzia*, *Albertia, Yuccites, Aethophyllum* plus several types of reproductive organs. The other taxa which are present, such as the sphenopsids *Schizoneura, Equisetites,* the ferns *Neuropteridium, Crematopteris* and *Anomopteris* and the gingkophyte *Sphenobaiera,* also occur in the Triassic of North China [83]. The most common taxon of the formation is *Voltzia* and then *Equisetites* and *Anomopteris*. *Pleuromeia* seems to be missing or is extremely rare and there is no clear evidence of its presence in the palynomorph assemblages of the 'Grès à *Voltzia*'. It is worth to note that this flora contains typical wetland forms as well as elements from drier habitats. The remarkable herbaceous conifer, *Aethophyllum stipulare*, which was adapted to live in ruderal habitats [74], very likely omitted developmental stages in ontogeny in response to environmental stress [78]. The several entire 1–2-m-tall entire fertile plants that have been found together in a lens of green silty clays, i.e. in the basinal area, suggest that they formed dense populations around the temporary pools, like the living reeds, and that they have been transported by a sudden flood and apparently buried before they were moved very far [30]. The fact that some plants such as the casts of the thick *Equisetites* stems and the long, entire fronds of *Anomopteris mougeotii* only occur in sandstones beds suggests that they lived in drier habitats, along the channel banks, probably more upstream. Indeed, the isolated pinnae of the fern only occur in the silty clayey lenses [32]. It is worth to note that this flora also very likely contains several elements which seem to be extrabasinal ones and therefore usually not preserved in the fossil plant record [63]. Indeed, in spite of an intensive collecting, there are several taxa, yet undescribed, which are represented only by a single specimen, such as that, for example, which has been designed an 'undetermined fern' by Grauvogel-Stamm et al. [35 (Pl. 2, fig. 4)] and which is figured here (Fig. 2). According to Wang [83], it resembles the pteridosperm taxon *Tongchuanophyllum* which characterizes the Anisian in North China but it also may be related to *Pseudodanaeopsis aberi* from the Carnian of northern Italy [62]. The cycadophyte *Otozamites vogesiacus*, which was figured by Schimper and Mougeot [75 (pl. 18, Fig. 1) is also represented by a single specimen, which unfortunately is lost.

*3.2.2.3. Interpretations.* The 'Grès à *Voltzia*' flora represents the second stage of the Triassic land-plant recovery in Europe. It is an illustration of the beginning of the recovery interval itself and therefore represents an important step of this multistage process. This interpretation contrasts with that of Dobruskina [18], who considered that the *Pleuromeia* flora and the *Voltzia* flora were two distinct coeval floras that were confined to distinct areas, i.e. in coastal areas in the case of the *Pleuromeia* flora, and that they represent the first stage in the development of the Triassic flora in Eurasia and the last phase of the Palaeophytic. However, the palynological data clearly show that the *Voltzia* flora succeeded the *Pleuromeia* flora [51].

The 'Grès à *Voltzia*' flora clearly illustrates the resurgence of the gymnosperms, and particularly the conifers, having survived the end-Permian life crisis. Indeed, several taxa seem to be similar, such as *Voltzia* and *Pseudovoltzia*, which Schweitzer [77] considers to be synonymous, as well as the supposed compound pollen cones of *Darneya* and those found in the Permian of Germany [47] or those of *Voltzia hexagona* from the Middle Permian of Germany [77]. Moreover, *Darneya* and *Albertia* seem to be related to *Ullmannia bronni* and *Culmitzshia florini* (unpubl. obs.). The gingkophyte *Sphenobaiera* also occurs in the Late Permian and the 'Grès à *Voltzia*' floras, although in the latter this taxon is represented only by seedlings, indicating that the mother-plant lived in extrabasinal areas [33].

It is very likely that the plants of the 'Grès à *Voltzia*' that occur sporadically in the *Pleuromeia* flora are plants which very likely escaped the end-Permian life crisis and lived in refugia of extrabasinal areas. The replacement of the *Pleuromeia* flora by the conifer-dominated flora or *Voltzia* flora may be explained by a change in climatic and growth conditions enabling the *Voltzia* flora to invade basinal lowlands. Like in the transition from the Earlier to the Late Palaeozoic floras, the Triassic land-plant recovery appears to be a multistage process that involved the replacement of lowland forms by groups of species from more remote drier regions [16].

### *3.2.3. The Upper Anisian flora of northern Italy or the conifer/cycadophyte/fern-dominated flora*

The Upper Anisian flora of the Dont Formation in the northern Dolomites (Italy) (Fig. 1, 2.IV), which has been recently described [11,49,50] and which is slightly younger than the 'Grès à *Voltzia*' flora, is also dominated by the conifers. Besides, it contains high percentages of ferns and cycadophytes showing that this flora is by far richer and more diversified than the 'Grès à *Voltzia*' flora [30]. The fact that contains many of the characteristic Ladinian taxa, such as the cycadophytes *Dioonitocarpidium, Pterophyllum*, *Nilssonia,* the pteridosperms *Scytophyllum, Peltaspermum* and possibly *Sagenopteris*, indicates that this flora is closer to the Ladinian floras, i.e. the Lettenkohle flora of northeastern France, the Lower Keuper flora of Germany and the flora from the Wengen Formation in Italy [35,42,44,80] than to the 'Grès à *Voltzia*' flora. Thus this flora which contains new typical Mesozoic taxa and thus looks more modern, clearly indicates that the Triassic land-plant recovery made great progresses and that the climate improved and enabled new plants to settle. The climate, which in the 'Grès à *Voltzia*' is considered to have been warm alternately dry and humid, is said to be warm and humid in the case of the Upper Anisian flora of northern Italy [49,50].

The Ladinian floras (Fig. 1, 2.V) which succeeded show that the land-plant recovery made new progresses with the appearance of a new fern family, the Matoniaceae (*Phlebopteris*). However the progresses between the Upper Anisian and the Late Ladinian floras are far less marked than those which occurred between the Early and Upper Anisian floras. Indeed, the Ladinian floras do not fundamentally differ from the Upper Anisian flora, indicating that the Ladinian was a period of relative stasis in the recovery.

The differences observed between the different Ladinian floras are very likely related to the differences in palaeoenvironments. Thus, it appears that the Upper Anisian flora is closer to that of the Ladinian of northern Italy [80], which is also dominated by the conifers, particularly *Voltzia,* than to the Ladinian flora of southern Germany [42,44], which was deposited in the swamps of a delta, and is dominated by the sphenopsid *Equisetites arenaceus* and the lycopsid *Annalepis*.

However, it is worth to mention that the Upper Anisian flora as well as the Ladinian ones, still includes some of the taxa that characterize the 'Grès à *Voltzia*' flora, such as *Neuropteridium, Anomopteris mougeotii, Yuccites, Voltzia,* which illustrate the gradual and slow process of flora replacement.

### *3.2.4. Contribution of the palynological data for filling the gaps in our knowledge of the Triassic land-plant recovery in Europe*

Several studies have shown the value of palynomorphs for analysing patterns of land-plant recovery, and thus avoiding the difficulties related to the incompleteness of plant megafossil record [51,64]. Although palynological data may be a potential source of error in palaeoenvironmental reconstructions that are essential for analysing the major evolutionary transitions in continental biotas [16], those used by Looy et al. [51] revealed very instructive for studying the Triassic land-plant recovery and understanding it on the basis of the fossil plant records alone.

Indeed, the palynological studies clearly documented the vegetation change across the Permian–Triassic transition and confirmed that the end-Permian life crisis severely affected the Late Permian floras of Euramerica, because most of the conifers that had been the dominant plants disappeared at the Permian–Triassic boundary, among which the Walchiaceae [45,46]. Similarly, the dominance of the *Pleuromeia* spores in most of the Lower Triassic show that the recovery began with a dominance of this lycopsid in the Lower Triassic. The fact that *Endosporites papillatus,* the degradational form of the *Pleuromeia* microspores [35], spans the whole Lower Triassic shows that the dominance of this lycopsid extended through all the period in Europe after all, as in North China. Moreover, palynological studies clearly show that the period of lycopsid dominance was followed by a period of conifer dominance [51].

This scenario is quite well in harmony with the palaeobotanical analysis for western Europe. However, it is worth to note that the recovery scenario established on palynological data [51] has been interpreted in the light of the generalized model of biotic recovery established for terrestrial and marine ecosystems [40,41]. In spite of fundamental differences in the evolution of plant and animal kingdoms [78,79] and in the mechanics of the end-Permian event for terrestrial plants and marine invertebrates [16], the post-crisis recovery of these different communities followed similar patterns. Looy et al. [51] noted that "in general, the progress of terrestrial ecosystem recovery after the P–Tr crisis appears to be in harmony with the situation in the marine biosphere." Similar observations have been made for land and marine animals [78]. In fact, it appears that terrestrial and aquatic ecosystems have the same behaviour under extrinsic stress [66].

According to the generalized model of biotic recovery [40,41], the Early Triassic *Pleuromeia*-dominated flora represents the survival interval of the repopulation, and the early Middle Jurassic floras correspond to the recovery interval itself, with the early Anisian flora of northeasten France representing the first phase and the Upper Anisian of Italy corresponding to the second phase.

## *3.3. The Triassic land-plant recovery: limited stories*

In many other areas, the Uppermost Permian and Lower Triassic are represented by marine facies [46]. However, in some areas continental facies with fossil plants are intercalated with marine deposits making it possible to determine which of the recovery stages the plant record belongs to. In most areas discussed below (North America, Siberia, South China, South Africa and Australia), the recovery seems to have been completed during the Middle Triassic as well as in Europe and North China. Nevertheless, disagreements in identifications of fossil plants from stage to stage, from place to place, and from continent to continent are a further problem that makes it difficult to accurately compare fossil floras [42,44].

### *3.3.1. Russia*

*3.3.1.1. Siberia.* The Triassic of Siberia is represented by a nearly complete sequence of strata consisting of alternating marine and continental deposits, with the latter being rich in fossil plants [59]. The Early Triassic flora in this sequence consists of two assemblages that are said to occupy different niches. The Early Triassic flora of Taymyr, Verkhoyanye, which is dominated by the lycopsids *Pleuromeia* and *Tomiostrobus* = subgenus of *Annalepis* [19] in the Induan (Fig. 1, 3.Ia, Ib) and consists of only *Pleuromeia* in the Olenekian (Fig. 1, 3.II), is said to have been confined to the marine plain.

It resembles that of the Early Triassic of Germany. The Early Triassic flora of the Tunguska and the Kuznetsk basins (Korvunchana flora), dominated by conifers and ferns, is thought to have occupied intracontinental areas. Since the age of this flora is not clear [57], we do not take it into account in the correlation table. The Middle Triassic flora is represented in Taymyr and Verkhoyanye by a Ladinian flora only (Fig. 1, 3.III) that contains pteridosperms (*Scytophyllum, Vittaephyllum),* sphenopsids *(Neocalamites, Schizoneura*), ferns *(Cladophlebis*), cycads (*Taeniopteris*) and conifers *(Podozamites, Yuccites*) [59]. Although this Ladinian flora contains a limited number of taxa in this area, it shows some similarities with the Lower Keuper flora of Germany [42,44].

This floristic evolution shows that in Siberia as well as in Europe and North China the Triassic land-plant recovery began with a dominance of the lycopsids, particularly *Pleuromeia*. This similarity is surprising since in the Early Triassic, according to the palaeogeographical maps [90], these areas were not at all at the same latitude, with Siberia being approximately at 60°N and Europe and North China being at approximately 30°N, These observations would indicate that the temperature gradient from equator to pole was small, as stated by Kidder and Worsley [48] or that Siberia was not at the right place on the palaeogeographic reconstructions.

*3.3.1.2. The Upper Volga. Pleuromeia* has been recorded in many places in Russia [18], among which the richest locality is near Rybinsk, on the bank of the Volga River. It yielded several hundreds of *Pleuromeia* remains [58].

The Parshino beds of the Rybinsk Formation, which consist of lacustrine marls, are Olenekian in age [18] (Fig. 1, 4.I). The numerous *Pleuromeia* remains are represented by stems, 4-lobed rhizophores and reproductive organs [18,31], suggesting that this lycopsid formed very rich and dense monospecific population. They are associated with numerous amphibians, fishes and crustaceans. A reconstruction shows that these lycopsids grew on the banks of a lake, in a warm and humid climate [58].

### *3.3.2. South China*

In South China, Early and Middle Triassic strata are mostly marine, and only the Middle Triassic Badong Formation, which consists of red beds, contains plant fossils. That flora consists of two assemblages, with the lowermost being Anisian and the overlying being Ladinian [56 (and references cited therein)] (Fig. 1, 5.I, 5.II). The Anisian assemblage is dominated by the lycopsids *Pleuromeia* (many in life position) and *Annalepis*, but it also includes most of the taxa described in the 'Grès à *Voltzia*' flora of northeastern France and the Ermaying Formation of North China, which are both early Middle Triassic [30,83]. The Ladinian assemblage that includes mainly *Annalepis*, *Equisetites*, *Neocalamites*, *Scytophyllum*, *Voltzia*, *Taeniopteris* is said to resemble the upper part of the Ermaying Formation of North China [56]. However, it also resembles the Ladinian floras of Siberia and Germany. In contrast, the fact that *Pleuromeia* was still present in the Anisian in South China, whereas in North China and Europe it disappeared or is very rare, may be explained by differences in palaeogeography and climate. According to recent palaeogeographic reconstructions [90], South China was at the equator in the Early Triassic, whereas North China and Europe were close to the northern tropic at that time, latitude that is characterized by arid climates. South China reached the tropics only in the Middle Triassic which would explain why *Pleuromeia* proliferated only at that period.

### *3.3.3. North America*

The only continental Early and Middle Triassic strata in North America occur in the southwestern United States and are assigned to the Moenkopi Formation. They form a clastic wedge that thins eastward from Nevada and western Utah into western New Mexico and Colorado. A few plant fossils and a larger variety of other fossils occur in the Moenkopi, including marine invertebrates (pelecypods, gastropods, brachiopods, ammonites) and vertebrates (fish, amphibians and reptiles). Also tetrapod trackways and foot prints are found on the surface of some of the beds in the unit. Plant fossils found in the formation are mostly limited to poorly preserved impressions of giant sphenopsids, although the impression of a coniferous leafy shoot was reported by one of the early investigators. Other workers have noted the occurrence of plant impressions in the unit, but have not described or illustrated them. However, a small, unusual flora has been described from a lens of mudrock near the top of the formation in eastern Arizona, in the Middle Triassic (Early Anisian)

(Fig. 1, 6.I) [8]. This flora is dominated by large (up to 30 cm in diameter) fragments of the trunks of a tree fern (*Donwelliacaulis chlouberii*) that resembles *Lesangeana voltzii* from the early Middle Triassic 'Grès à *Voltzia*' flora of northeastern France [30,75]. In addition, there are casts of large sphenopsids (*Neocalamites*) and small fragments of gymnosperm wood. It appears that the environment the plants inhabited was similar to that of North China during this time and Europe when the Buntsandstein was deposited: a vast sandy flood plain crossed by braided river system with pools in between, ringed by populations of *Neocalamites* and *Donwelliacaulis* with unidentified conifers in the adjacent extrabasinal floras. Possibly, this area functioned as a refugium, because a tree fern that is closely related to the Moenkopi species occurs in the overlying Chinle Formation of Late Triassic age at a locality about 30 km east of this locality [8].

The flora that occurs in the overlying non-marine Chinle Formation of Late Triassic age and in the Newark Supergroup of Late Triassic and Early Jurassic age in eastern North America [7] resembles the coeval floras of Europe, although apparently much less diversified. The lowest member of the Chinle, the Shinarump Member, which is traditionally regarded Late Carnian in age (Fig. 1, 6.II) contains sphenopsids (*Equisetites*), ferns (*Phlebopteris*, *Cladophlebis*), cycadophytes (*Palaeocycas*, *Macrotaeniopteris*, *Zamites*, *Eoginkgoites*) and conifers (*Pagiophyllum, Pelourdea*). The overlying Petrified Forest Member of the Chinle, which is Late Carnian–Early Norian in age includes a species of *Sphenopteris*, the peculiar sphenopsid *Schizoneura* [5], a giant sphenopsid that is referred to *Neocalamites* [39] and large strap-like leaves strongly reminiscent of the Palaeozoic leaf *Cordaites* which are called *Pelourdea* [6] and that also resemble the *Yuccites* leaves from the 'Grès à *Voltzia*' of northeastern France [30]. It is worth to note that most of these taxa are also present in the coeval floras of Europe. *Sphenopteris* and *Neocalamites* have been both recorded from the Ladinian and Carnian of Germany [42,44]. Similarly, strap-like leaves occur in the Ladinian and/or Carnian of Germany where they are assigned to *Desmiophyllum* [44] and in the Ladinian flora of Italy, where they are assigned to *Yuccites* [80]. Concerning *Schizoneura* of which the type-species *S. paradoxa* was originally defined in the Anisian flora of northeastern France [30], it is also present in the Ladinian and Carnian floras of Germany [42,44]. However, in spite of similar foliage, it is not possible to ascertain whether the different species are related. In *S. gondwanensis* from the Permo-Carboniferous of South Africa, the reproductive organs are not known and in *S. manchuriensis* from the Late Permian of northeastern China, the structure of the reproductive organs differs from that of the type-species *S. paradoxa* [30].

The fact that *Phlebopteris, Palaeocycas* and *Eoginkgoites* are present in the Late Carnian Shinarump Member supports the identification of representatives of both the modern fern family Matoniaceae and the cycadophytes in the Ladinian and/or Carnian floras of Germany and indicates that the recovery reached the same stage at approximately the same time in both North America and Europe. Thus, it seems that recovery concomitantly followed similar stepwise patterns in both areas and that extinction of Palaeozoic forms continued stepwise into the Late Triassic, as in Europe. Unfortunately nothing is known about the beginning of the recovery, and particularly if the typical recovery taxon *Pleuromeia* existed there in the Early Triassic.

#### *3.3.4. Gondwanaland: two examples*

The recovery of the land flora in Gondwana after the end-Permian crisis seems to have generally paralleled that of the land flora in the northern continents with only a few species surviving the event and new forms gradually appearing at first [70,71]. According to Anderson et al. [3], the most significant extinction event associated with the crisis was the sudden loss of the glossopterids, which had been the dominant plants throughout Gondwana during the Permian (Fig. 1, 7.I, 8.I). The demise of glossopterid-dominated vegetation and its replacement by peltasperm-, lycophyte-, and corystosperm-dominated floras appear to be essentially synchronous across Gondwana [55]. However, according to some authors [1,9,36], *Glossopteris* apparently did not become completely extinct after the end-Permian biotic crisis as there are some records of Triassic floras in which *Dicroidium* and *Glossopteris* occur together. The sphenopsids (*Sphenophyllum, Annularia, Phyllotheca, Equisetites*) declined rather abruptly just before the end of the Permian and later in the Early Triassic some of them (*Equisetites, Phyllotheca)* recovered, whereas several new ones appeared (*Neocalamites, Schizoneura*) and sphenopsids again became dominant elements in the land flora of Gondwana during the Late Ladinian and Carnian. It is worth noting that in

Germany, the Lower Keuper and Schilfsandstein floras, which are respectively Ladinian and Carnian in age, are also dominated by the sphenopsids, suggesting comparable ecological conditions [42]. In contrast, the herbaceous lycopsids (*Cylostrobus*, *Skilliostrobus*), which had been only a small part of the Permian land flora in Gondwana, expanded suddenly with the advent of the Triassic and became dominant during the Early Triassic, but then declined and virtually disappeared by the end of the Period. The Voltzialean conifer *Voltziopsis* followed the general trend of the herbaceous lycopsids, although it was somewhat more common in the Late Permian. Indeed it became dominant in the Early Triassic land flora of Gondwana, after which it declined and became again common in the Late Triassic. The earliest occurrence of the conifer *Heidiphyllum* is Anisian. The other conifers (*Rissikia, Pagiophyllum*) had a rather erratic history, since they quickly became prominent members of the land flora during the Early Triassic, but then declined and became rare until near the end of the Triassic when they expanded rapidly once again. Another important group that arose after the end-Permian crisis was the corystosperms. That group, which includes *Dicroidium*, became common during the Early Triassic, but disappeared near the end of the Period. Several other groups appeared for the first time in Gondwana in the Early Triassic, including the cycads (*Pseudoctenis*, *Halleyoctenis*, *Ctenis*) and the bennettitaleans (*Zamites*, *Ptilophyllum*, *Nillsoniopteris*). It is worth noting that in Europe these groups did not appear until the Middle Triassic.

*3.3.4.1. South Africa.* Knowledge of the early stages of the recovery of the land flora in southern Africa is sparse and limited to the Burgersdorp Formation of late Early Triassic (Late Olenekian) age (Fig. 1, 7.II) [1]. This flora is rather small, comprising only 13 genera including the lycopsid *Gregicaulis*, the sphenopsid *Calamites*, the ferns *Asterotheca* and *Cladophlebis*, the peltasperms *Lepidopteris,* the corystosperm or umkomasialean *Dicroidium,* the conifer *Sewardistrobus* as well as the ginkgophytes *Ginkgoites* and *Sphenobaiera* and the cycads *Pseudoctenis* and *Nilssoniopteris.* The last two are the earliest representatives of the cycads in Gondwana, as noted above. On the other hand, a much richer and more diverse flora occurs in the Late Triassic (Carnian) Molteno Formation in South Africa (Fig. 1, 7.III). Ongoing research [2,4 and references cited therein] have demonstrated that the flora contains 92 genera, with 291 species. This large and diverse flora includes representatives of most major plant groups and demonstrates that the land-flora recovery is well advanced at the beginning of the Late Triassic.

*3.3.4.2. Australia.* In contrast to South Africa, the Late Permian to Middle Triassic plant fossil record in Australia is much more complete, with plant bearing units present on either side of the Palaeozoic–Mesozoic boundary (Fig. 1, 8.I, 8.II). Some of the earliest-known Triassic (Induan and Olenekian) floras in Australia were described from the Bowen Basin of Queensland (Fig. 1, 8.IIa and IIb) [12,88]. Although the floras are comparatively small, they are diverse and include mainly herbaceous lycopsids such as *Skilliostrobus*, *Cylostrobus* and the characteristic Early Triassic form *Pleuromeia* as well as several types of pleuromeid vegetative structures [87]. A few plant megafossils have also been identified from the basal Narrabeen Group of Early Triassic age at a few localities in the Sydney Basin [68,69]. They include sphenophytes (*Schizoneura*, *Equisetites*), a peltasperm (*Lepidopteris)* [72] and a conifer (*Voltziopsis)*. At one locality, some ferns have been recorded, but not identified [68]. Slightly higher the earliest representatives of the seed fern *Dicroidium* appeared and became very common in the late Early Triassic and most common in the Middle Triassic [70].

The late Early Triassic (Olenekian) flora that is described from the Lorne Basin in southeastern Australia (Fig. 1, 8.IIb) [38] is rather small, but it illustrates how rapidly the land flora recovered in this region after the end-Permian crisis. The flora is slightly younger than those just discussed and consists of 17 identifiable species as well as several unidentified forms. They include several lycopsids including the genus *Skilliostrobus* and an unnamed sphenophyte, possibly *Equisetites*. The ferns are represented in this flora by several taxa including *Coniopteris*, *Cladophlebis*, and *Microphyllopteris* and the seed ferns by *Dicroidium, Pteruchus*, and *Lepidopteris*. Also present are the cycadalean *Taeniopteris,* the holdover conifer *Voltziopsis*, and the ginkgoalean *Rhipidopsis*. Large diverse Middle Triassic floras occur at several localities in eastern Australia, particularly in the Basin Creek Formation in the Coal Measures, in the Clarence–Morton Basin (Fig. 1, 8.III), where they have been or are being studied by Holmes [37 and references cited therein].

These studies demonstrate that the land flora in this region had recovered in the Middle Triassic from the end-Permian crisis.

## 4. The duration of the Triassic land-plant recovery

The present analysis of the Triassic floras known in Europe, including the palynological data, shows that the Triassic land-plant recovery really began toward the end of the Early Triassic and that most of the progresses occured during the Anisian. Indeed, the progresses in diversification of the land flora are far much marked between the Early and Late Anisian than between the Late Anisian and Late Ladinian, in spite of a similar duration of each period, i.e. respectively 8 and 9 million years. Moreover, it shows that in western Europe the recovery began with the resurgence of the conifers having survived the end-Permian life crisis. Indeed, it is worth to note that the conifers were already the dominant plants of the Late Permian floras. Similarly, the reappearance in the Upper Anisian, when conditions improved, of the taxon *Dioonitocarpidium* that already existed in the Early Permian of Texas and North China [16,85], also seems to indicate that the growth conditions have considerably improved at that time [22]. Conversely it indicates that refugia must have existed where such taxa could survive during the biotic crisis. The whole recovery or repopulation process took about 14 million years, with the Early Triassic survival interval extending over about 5 million years, according to the most recent geochronological data [60].

In comparison to all the other major life crises in Earth History, the Triassic biotic recovery is considered to have proceeded exceptionally slowly. However, the most intriguing aspect is the long delay in the onset of the recovery in the Early Triassic, i.e. the 5 million years of the survival interval and of the lycopsid dominance, whereas recovery usually begins within 1–2 million years after the crisis [22,24]. This delay in the case of the Triassic land plant, and particularly in the resurgence of the conifer-dominated floras, may be explained by the considerable time required to re-diversify and favourably adapt to new environments [55] or by the persistence of harsh conditions.

## 5. Conclusions

Our review of the Triassic land-plant recovery shows that it followed a long stepwise process. The only place until now where it has been studied in detail, from its very beginning just after the end-Permian life crisis, is in North China. There, the recovery is shown to have lasted until the end of the Middle Triassic and to have consisted of two stages, with the first in the Early Triassic being overwhelmingly dominated by the lycopsid *Pleuromeia* and the second in the Middle Triassic characterized by the presence of the pteridosperm *Tongchuanophyllum*.

Our analysis, in a palaeogeographic and palaeoclimatic context, of the oldest principal Triassic floras that are known in Europe shows that the Triassic land-plant recovery also went through two stages: a long survival interval in the Early Triassic, similarly dominated by the lycopsid *Pleuromeia*, and the recovery interval itself in the early Middle Triassic, which is marked by the resurgence of the conifers having survived the end-Permian life crisis and the return of the cycadophytes and the pteridospersms in the Late Anisian. The beginning of this interval is illustrated by the Early Anisian flora of the 'Grès à *Voltzia*' Formation of northeastern France, and the second phase is represented by the Late Anisian flora of the Dont Formation of the Dolomites, in northern Italy. Both floras are dominated by the conifers, but the latter is richer, more diversified and closer to the Ladinian floras, showing that the recovery is much more advanced than in the 'Grès à *Voltzia*' flora. In contrast, in the Ladinian and Carnian, land-plant recovery seemed to have slowed down since far less new plant taxa seemed to have appeared. It is worth noting that the transition between the stages was gradual and that the newly evolved taxa coexisted temporarily with those of the previous stage.

These observations show that the recovery process lasted ca. 14 million years, with the survival interval reaching ca. 5 million years, according to the most recent geochronological data [60]. This long delay which is the longest documented for any mass extinction, is considered the most intriguing aspect of the process, since recovery usually begins within 1–2 million years after the crisis [22,24].

These results greatly contrast with those of Dobruskina [18], who considered that the Early Triassic and early Middle Triassic (Anisian) floras represented the last phase of the Palaeophytic and that the Ladinian and Carnian floras marked the beginning of the Mesophytic. They also contrast with those of Schweitzer [76], who considered that the Late Permian floras marked the beginning of the Mesozoic.

A comparative study of the land floras of other regions in the world, such as North America, Russia, South China, and Gondwanaland, only permitted to consider limited parts of the land-plant recovery since the Uppermost Permian and the Triassic in those areas are typically represented by marine facies. Most of the floras that are present also seem to show that the recovery was well advanced in the Middle Triassic and probably concomitantly followed a similar stepwise pattern. Comparison between the Early Triassic floras of western Europe, Siberia and North China also allowed us to show that the temperature gradient between the equator and the poles was small. In most of the areas where there are non-marine Lower Triassic strata, the lycopsids of the *Pleuromeia*-type were the dominant plants, suggesting that they were opportunistic pioneer plants having proliferated in the devastated lowlands, whereas the other surviving plants lived in extrabasinal refugia. It seems that the end-Permian life crisis has had a major devastating effect on the ecological organization of lowland vegetation, leaving Early Triassic floras species-poor and dominated largely by opportunists [70,71].

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