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The early Middle Triassic 'Grès à Voltzia' Formation of eastern France: a model of environmental refugium

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Abstract

The biotic recovery that succeeded the end-Permian life crisis event lasted a long period, estimated at ca 8 to 10 Myr, even 14 Myr. It is thought that it essentially proceeded from refugia whose geographic location can never be established. Their existence can nevertheless be inferred from the surprising stability exhibited by some fossil communities between the Late Palaeozoic and the Triassic. It is the case of the biocoenoses from the 'Grès à Voltzia' Formation (Upper Buntsandstein) of eastern France, which consist of Palaeozoic survivors (crustaceans, amphibians, insects, plants), taxa that announce the modern faunas (crustaceans, spiders, scorpions, insects), living fossils (lingulids, the panchronic species *Triops cancriformis*) as well as pioneering species which invaded rapidly the disturbed ecospaces (the herbaceous conifer *Aethophyllum*). The 'Grès à Voltzia' is Early Anisian in age and was deposited in a deltaic area, an environment transitional from nearshore to terrestrial, where locally less arid climatic conditions favoured the survival of plants and animals. The 'Grès à Voltzia' represents a model of the type of environment that may have acted as a refugium for terrestrial communities during the end-Permian mass extinction and its Triassic aftermath. *To cite this article: J.-C. Gall, L. Grauvogel-Stamm, C. R. Palevol 4 (2005)*.

Résumé

Le Grès à Voltzia (début du Trias moyen) de l'Est de la France, un modèle d'environnement refuge. La restauration de la biosphère qui a succédé à la crise biologique de la fin du Permien s'est échelonnée sur un intervalle de temps considérable, estimé entre 8 et 10 Ma, voire 14 Ma. Il est généralement admis qu'elle a essentiellement progressé à partir de refuges dont la localisation géographique n'a encore jamais pu être établie. Leur existence peut cependant être rattachée à l'étonnante stabilité dont firent preuve certaines communautés biologiques entre le Paléozoïque supérieur et le Trias. Il en est ainsi des biocoenoses de la formation du Grès à Voltzia (Buntsandstein supérieur) de l'Est de la France, qui comportent à la fois des formes héritées de l'ère primaire (crustacés, amphibiens, insectes, végétaux), des genres annonçant les faunes modernes (crustacés, araignées,

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scorpions, insectes), des « fossiles vivants » (lingules, l'espèce panchronique *Triops cancriformis*), ainsi que des espèces pionnières du repeuplement des espaces décimés lors de la crise (le conifère herbacé *Aethophyllum*). Le Grès à Voltzia, d'âge Anisien inférieur, s'est déposé dans un environnement deltaïque, un milieu de transition entre la mer et les terres émergées, où des conditions climatiques localement moins arides ont permis la survie des peuplements, tant en milieu aquatique que sur le continent. La formation du Grès à Voltzia propose un modèle d'environnement ayant joué, pour les peuplements des terres émergées, un rôle de refuge lors de la crise de la fin du Permien et de ses répercussions au début du Trias. ***Pour citer cet article : J.-C. Gall, L. Grauvogel-Stamm, C. R. Palevol 4 (2005)***.

1. Introduction

For evaluating the rate and patterns of the biological recovery that occurred after the dramatic end-Permian mass extinction, a significant amount of data on the Early Triassic faunas and floras is needed. Thanks to intensive biostratigraphic collecting, detailed study of well exposed outcrops and discovery of new fossiliferous localities throughout the world, the repopulation of the marine realm is becoming better and better known (see this issue). In contrast, data on the reconstruction of the continental ecosystems are rare and concern usually single taxonomic groups such as vertebrates or plants [1,2,4]. Furthermore, although the Triassic is widely distributed on all the continents, it is often represented by redbeds that are usually poorly fossiliferous.

From this point of view, the 'Grès à Voltzia' Formation from Eastern France, which belongs to the Upper Buntsandstein, is an exception as it provides interesting data about fossil communities on land at the dawn of the Mesozoic. This formation, which also consists of redbeds, originated in a fluvial environment that included a network of channels and overbank flats. Marine fossils in the formation testify to the close proximity of the sea and indicate that the 'Grès à Voltzia' Formation is part of a marine influenced delta [14]. It is one of the rare formations from the continental Triassic that is known to contain rich faunistic and floristic assemblages, including plants as well as terrestrial and aquatic animals. Their state of preservation is remarkable, as it includes mineralized tissues and soft-bodied organisms [17,18,39].

Although the 'Grès à Voltzia' belongs to the Buntsandstein, which is traditionally considered to be Lower Triassic, it is Early Anisian in age, i.e. ca. 8 Myr after the Permian–Triassic boundary [40], according to the biostratigraphic correlations between the Germanic Buntsandstein and the Alpine Triassic units [35,36]. Evidences of a Lower Anisian age of the 'Grès à Voltzia' are given by the conchostracans and the foraminiferal assemblages, but also by the occurrence of the bivalve *Myophoria vulgaris,* a typical Early Anisian species, and the lack of a closely related taxon, *Costatoria costata*, which is common in the Alpine Lower Triassic.

2. The geological setting

The 'Grès à Voltzia', which spans the transition from the continental formations of the Buntsandstein to the marine sedimentation of the Muschelkalk, was deposited on the western margin of the Germanic Basin, a broad depression extending over a large part of Central Europe and including a great part of Germany. Current directions indicate a sediment supply from west to east, i.e. from uplands in the position of the present Paris Basin towards the Tethys [14,16,17].

The 'Grès à Voltzia' is about 20 m thick on average and consists of two distinct units: the 'Grès à meules' and the overlying 'Grès argileux'. The 'Grès argileux' marks the beginning of the Muschelkalk sea transgression, while the 'Grès à meules' represents the last stage of the fluviatile facies that prevailed during the Buntsandstein. The fossiliferous horizons described here belong to the latter unit.

The 'Grès à meules' consists of thick lenses of a fine-grained, grey or pink to red coloured sandstone, containing 20% to 30% potash feldspar. Remains of frag-

mentary plants and stegocephalian bones are found in the basal part. Sandstones are separated by thin layers of green or red shales commonly exhibiting a fine lamination, each lamina being a few millimetres thick. They contain beautifully preserved fossils including skeletons, shells and soft-bodied organisms that are concentrated at the top of the graded laminae. Rare intercalations of calcareous sandstones or sandy dolomites containing a sparse marine fauna of foraminifera, ostracods and molluscs, are related to marine influences. Evidences from the sedimentary structures and from palaeoecological data indicate a deltaic environment. The sandstone lenses correspond to deposits in meandering channels. During flooding, the plants and the amphibians living on land were dragged and dropped downstream. The shale layers originate from overbank deposits in abandoned channels or in depressions of the flood plain. Thus the quiet water bodies harbour a rich fauna and offer particularly favourable circumstances for the fossilisation of aquatic as well as terrestrial organisms. The frequency of mud cracks and plant roots in growth position indicates that, with time, the pools dried out. Moreover, from time to time, the delta area was briefly invaded by the sea during storms.

3. The climatic setting

The geological and biological events of the Permian–Triassic interval were controlled by the existence of the supercontinent Pangaea [42]. During this interval of time, very dry climatic conditions prevailed over large areas of the supercontinent [63]. Simulations of climate suggest very hot summers and cold winters [26]. Other authors conclude that a monsoonal climate, with alternate extremely dry and rainy seasons, must have existed [10,47]. In any case, the weathering of the Hercynian uplifts supplied large quantities of brightly coloured sediments, including pebbles, sands and clays, which were transported by rivers and wind into lowlands where they formed the widespread terrestrial redbeds that are so typical for this period. These conditions prevailed for a long interval of time, particularly in southwestern Gondwana where the Karoo Formation extended from the Permo-Carboniferous to the Early Jurassic, and also in northern areas like Europe, China and the United States.

In the western part of the Germanic Basin, the climate of the Lower and Middle Buntsandstein is assessed as being arid to semi-arid, considering the lack of soils and the occurrence of wind-faceted gravel [8]. An extensive development of calcrete palaeosols ('violet horizons') characterizes the Upper Buntsandstein. They indicate that growth of vegetation was possible and that the climate became less arid. During the deposition of the 'Grès à Voltzia', more humid conditions prevailed in relation to the vicinity of the advancing sea [17]. Water bodies became less ephemeral and favoured the settlement of plants and aquatic, as well as terrestrial, faunas.

4. The ecological setting

As a consequence of the increasing aridity that occurred in Europe during the Late Permian and Early Triassic, biotic communities became confined to fragmented habitats, near the most humid areas, for instance along floodplains, a distribution which may explain the scarcity of fossiliferous localities in this interval [33,64].

During half a century, an extensive palaeoecological sampling of numerous shale lenses of the 'Grès à Voltzia' was pursued, lamina by lamina, in the northern part of the Vosges mountains (northeastern France), an area covering about 30 × 30 km, in order to make an inventory of the fossil assemblages. Among the numerous lenses that have been investigated, less than 10 % were fossiliferous. Despite a similar lithology, the others are azoic. In addition, the biological assemblages differ slightly from place to place [14]. This observation evokes a mosaic of ponds harbouring local biological communities. Similarly, in the Permian of the Lodève Basin (Massif Central, France), Gand et al. [19] described fossil assemblages comprising bivalves, crustacean and insects, intercalated in a thick succession of azoic redbeds. In the Buntsandstein of the Germanic Basin, Jörg [28] also recorded crustacean and fishes from rare shale lenses. Such isolated localities similarly evoke small, ephemeral populations having survived in hostile environments, such as oases. It is very likely that the parcelling up of the terrestrial ecosystems favoured small vicariant populations that find shelter in isolated places. It is also the case for the 'Grès à Voltzia' biological communities, which were established in a deltaic plain where the climate was not as dry as the inner part of the continent because of its proximity to the Tethys. As described below, the fossils from

this formation originated from different biotopes [14,16].

4.1. The fluvial channel assemblages

Palaeocurrent directions deduced from cross bedding, erosional structures and channel shape, indicate a dominant transport of the sediments from west to east [14]. Lenses of red or grey sandstones can be several metres thick. Their lateral extent varies from a few metres to more than a hundred metres. The lower, erosive surface, of the sandstones exhibits an assemblage of flute casts, groove casts, prod and bounce marks. The upper surface is covered with ripple-marks. The sandstone is built up of a succession of laminae with well-developed parting lineation and crescent-shaped scour marks. The vertical distribution of the sedimentary structures indicates a decrease in strength of the current with time. Sandstones resulted from sediments deposited at times of flood [14,17]. They contain plant debris derived from equisetales, ferns and conifers and amphibian bones (stegocephalids). The fossils which are disarticulated and broken, usually are intersecting the bedding plane and are jumbled together. Obviously, they have undergone prolonged transport and reworking before accumulating downstream in the watercourses. Thus these assemblages provide valuable data about the communities that lived upstream from where the fossils are found. In particular, amphibians are never found in the more distal area of the 'Grès à Voltzia' delta.

4.2. The temporary pools communities

Lenses of green or red silty clay represent overbank deposits laid down by the overspilling of flood water from river channels onto adjacent lowlands. In the resulting temporary ponds and pools, a rich aquatic fauna flourished and their margins were colonised by a variety of plants that were themselves inhabited by many arthropods. The occurrence of *Lingula* in some shale lenses indicates that some pools were supplied with brackish water. It is likely that the delta platform was scattered with a set of water bodies from more fresh upstream to brackish downstream. The fossil assemblages represent biocoenoses, as indicated by the preservation of animals in life position, such as the brachiopod *Lingula,* and by the fossilisation of in situ root systems as well as by the occurrence of trails of limulids and clutches of insect and fish eggs.

The water bodies were harsh environments. Indeed, the fossiliferous lenses of shale correspond to pools of small lateral extent, perhaps on the sites of abandoned channels, which dried out relatively quickly, resulting in mass mortality among the aquatic fauna. As one goes upwards investigating a single shale lens, a diverse aquatic fauna is gradually replaced by terrestrial vegetation, sometimes with the root systems preserved in situ, and desiccation cracks appear at the top. Similarly, trace element content of the clay minerals, especially boron, increases and indicates that the salinity of the pool rose over time. The occurrence of pyrite testifies that the water body became oxygen depleted. All these observations confirm that the pools decreased in size and dried out. Concerning the gymnosperms for instance, a 60-cm-thick shale lens exhibits only one cycle from the immature reproductive organs to the dispersed seeds, showing that it corresponds to a short period of time [14]. It is evident that the organisms must have suffered great variations in temperature, oxygenation and salinity as time passed. Indeed, some palaeoecological characters can be considered as responses of the fauna to harsh environmental conditions, such as the sheaths of mucilage that protected the insect eggs from desiccation [18], and the very short life cycle, a couple of weeks, of the estheriids that allows these crustaceans to survive long enough to reproduce in ephemeral ponds [12,34].

5. The fossil assemblages of the 'Grès à Voltzia'

The fossil assemblages of the 'Grès à Voltzia', including plants and animals, exhibit a low diversity of species and often a high abundance of individuals (Table 1). They comprise less than twenty species of plants and about fifty species of animals, insects excluded. Detailed quantitative data from different shale lenses are available in figures 28 and 29 of [14]. The most abundant group concerns the arthropods, especially the crustaceans (18 species) and the insects (about 200 species). The estheriids represent the dominant crustaceans. Thousands of their carapaces can be found at the surface of the laminae. Smaller species, such as *Schimperella* or *Palaega*, are more abundant than bigger ones, such as *Clytiopsis* or *Anhelkocephalon*. As

Table 1
The 'Grès à Voltzia' fossil record
Tableau 1
Inventaire paléontologique du Grès à Voltzia

Fresh and brackish water fauna	
Limnomedusids	*Progonionemus vogesiacus* Grauv. & Gall
Annelids	*Eunicites triasicus* Gall & Grauv.
	Homaphrodite speciosa Gall & Grauv.
	Spirorbis cf. pusillus (Martin)
	Triadonereis sp.
Brachiopods	*Lingula tenuissima* Bronn
Bivalves	*Myophoria vulgaris* (Schlotheim)
	Homomya impressa (Alberti)
Limulids	*Limulitella bronni* (Schimper)
Crustacea	
Branchiopoda	*Triops cancriformis* (Schaeffer)
	Isaura minuta (Zieten)
	Isaura sp.
	Palaeolimnadia alsatica Reible
	Palaeolimnadiopsis dictyonata Reible
	Praeleaia sp.
Ostracoda	*Triassinella* aff. *tsorfatia* (Sohn)
	Cytheracea undet.
Euthycarcinoidea	*Euthycarcinus kessleri* Handlirsch
Halicyna	*Halicyne ornata* Trümpy
Malacostraca	*Triasocaris peachi* Bill
	Schimperella beneckei Bill
	Schimperella kessleri Bill
	Palaega pumila Gall & Grauv.
	Anhelkoceplalon handlirschi Bill
	Diaphanosoma rare Bill
	Antrimpos atavus (Bill)
	Clytiopsis argentoratensis Bill
Fishes	*Saurichthys daubreei* Firtion
	Dipteronotus aculeatus (Jörg)
	Dorsolepis virgatus Jörg
	Pericentrophorus minimus Jörg
	Coelacanthoidea undet.
Terrestrial fauna	
Spiders	*Rosamygale grauvogeli* Selden & Gall
Scorpions	*Protobuthus elegans* Lourenço & Gall
	Gallioscorpio voltzi Lourenço & Gall
Millipedes	Coelochaeta undet.
Insects	
Ephemeroptera	*Triassodotes vogesiacus* Sinitshenkova & Papier
	Toxodotes coloratus Sinitshenkova & Papier
	Triassoephemera punctata Sinitshenkova & Papier
	Voltziaephemera fossoria Sinitshenkova & Papier
	Triassomanthus parvulus Sinitshenkova & Papier
	Mesoplectopteron longipes Handlirsch
	Triassonurus doliiformis Sinitshenkova & Papier
	Minorella virgata Sinitshenkova & Papier
	Vogesonympha ludovici Sinitshenkova & Papier

Table 1
(continued)

Terrestrial fauna (continued)	
Odonatoptera	*Voltzialestes triasicus* Nel, Papier, Grauv.-Stamm & Gall
	Triadotypus guillaumei Grauv. & Laurentiaux
Plecoptera	undetermined
Orthoptera	*Triassophyllum leopardii* Papier, Nel, Grauv.-Stamm & Gall
	Galliagryllavus vogesiacus Papier, Nel & Grauv.-Stamm
	Triassoparacyrtophyllites bifurcatus Papier, Nel & Grauv.-Stamm
	Voltziahagla pseudoveinosa Papier, Nel & Grauv.-Stamm
Blattodea	*Voltziablatta intercalata* Papier & Grauv.-Stamm
	Voltziablatta grauvogeli Papier & Grauv.Stamm
	Transitoblatta reticulata Papier, Nel & Grauv.-Stamm
	Scleroblatta densa Papier, Nel & Grauv.-Stamm
	Subioblatta undulata Papier, Grauv.-Stamm & Nel
Phasmatodea	*Palaeochresmoda grauvogeli* Nel, Papier, Bethoux & Gall
Hemiptera	*Gallodunstania grauvogeli* Lefevre, Nel, Papier, Grauv.Stamm & Gall
	Ipsviciidae undet.
	Hylicellidae undet.
Neuroptera	undetermined
Mecoptera	*Pseudopolycentropus triasicus* Papier, Nel & Grauv.Stamm
	Prochoristella pilosa Papier, Nel & Grauv.-Stamm
	Laurentiptera gallica (Laurentiaux & Grauv.)
Trichoptera	undetermined
Diptera	*Grauvogelia arzvilleriana* Krzeminski, Krzeminska & Papier
	Louisa nova Krzeminski & Krzeminska
	Tanus triassicus Krzeminski & Krzeminska
	Archilimonia vogesiana Krzeminski & Krzeminska
	Vymrhyphus blagoderovi Krzeminski & Krzeminska
	Gallia alsatica Krzeminski & Krzeminska
Coleoptera	30 species
Amphibians	*Eocyclotosaurus lehmani* (Heyler)
	Odontosaurus voltzii Meyer
Reptiles	undetermined.
Plant megafossils	
Lycopsids	*Pleuromeia* sp.
	Bustia ludovici Grauv.-Stamm
Sphenopsids	*Schizoneura-Echinostachys paradoxa* (Schimper & Mougeot)
	Echinostachys oblonga Brongniart : fructification of *S. paradoxa*
	E. cylindrica Schimper & Mougeot : fructification of *S. paradoxa*
	Equisetites sp.
	Equisetostachys verticillata Grauv.-Stamm: fructification of *Equisetites*
Ferns	*Anomopteris mougeotii* Brongniart
	Neuropteridium Schimper
	Crematopteris typica Schimper & Mougeot: fertile frond of Neuropteridium
Cycads	*Zamites vogesiacus* Schimper & Mougeot
Ginkgophytes	*Baiera* sp.
Conifers	*Voltzia walchiaeformis* Schimper & Mougeot
	Voltzia heterophylla Brongniart
	Voltzia sp.

Table 1
(continued)

Plant megafossils (continued)	
Conifers	*Albertia* sp.
	Yuccites vogesiacus Schimper & Mougeot
	Aethophyllum stipulare (Brongniart)
	Cycadocarpidium pilosum Grauv.-Stamm
	Willsiostrobus rhomboidalis (Grauv.-Stamm) : male cone of *Yuccites*
	Willsiostrobus cordiformis (Grauv.-Stamm)
	Willsiostrobus denticulatus (Grauv.-Stamm)
	Willsiostrobus acuminatus (Grauv.-Stamm): male cone of *Aethophyllum stipulare*
	Darneya peltata (Schaarschmidt & Maubeuge): male cone of *Albertia* sp.
	Darneya mougeotii Grauv.-Stamm
	Darneya dentata Grauv.-Stamm
	Sertostrobus laxus Grauv.-Stamm: male cone of *Voltzia* sp.
PALYNOMORPHS	
Spores	*Aulisporites* (Leschik) Klaus: spore from *Bustia ludovici*
	Calamospora tener (Leschik) Mädler : spore from *Equisetostachys verticillata*
	Calamospora keuperiana Mädler: spore from *Echinostachys oblonga* and *E. cylindrica*
	Retusotriletes mesozoicus Klaus
	Punctatisporites fissus Leschik: spore from *Anomopteris* mougeotii
	Cyclogranisporites cf. *congestus* Leschik
	Osmundacidites senectus Balme: spore from *Anomopteris mougeotii*
	Microreticulatisporites galli Adloff & Doubinger
	Verrucosisporites applanatus Mädler
	V. remyanus (Mädler) Adloff & Doubinger
	V.cf. *contactus* Clarke
	Duplicisporites granulatus Leschik
Pollen	*Triadispora staplini* (Jansonius) Klaus : pollen from *Sertostrobus laxus*
	T. facata Klaus : pollen from *Darneya peltata*
	T. plicata Klaus
	T. epigona Klaus
	Illinites kosankei Klaus: pollen from *Willsiostrobus acuminatus*
	I. chitonoides Klaus
	Angustisulcites klausii Freudenthal
	Microcachryidites fastidioides (Jansonius) Klaus
	M. doubingeri Klaus
	Voltziaceaesporites heteromorphus Klaus: pollen from *Willsiostrobus rhomboidalis*
	Alisporites circulicorpus Clarke: pollen from *Willsiostrobus denticulatus*
	A. grauvogeli Klaus: pollen from *Willsiostrobus bromsgrovensis*
	A. toralis (Leschik) Clarke: pollen from *Willsiostrobus cordiformis*
	Hexasaccites muelleri Reinhardt & Schmitz: pollen from *Willsiostrobus hexasacciphorus*
	Cycadopites subgranulosus (Couper) Clarke
	C. carpentieri (Delcourt & Sprumont) Adloff & Doubinger
	Camerosporites secatus Leschik
Marine fauna	
Foraminifera	*Glomospirella oscillens* Koehn-Zaninetti, Brönnimann & Gall
	Glomospirella aff. *spirillinoides* (Grozdilova & Glebovskaia)
	Glomospira sp.
	Agathammina aff. *austroalpina* Kristan-Tollmann & Tollmann
	Lagenidae undet.

Table 1
(continued)

Marine fauna (continued)	
Gastropods	*Naticopsis gaillardoti* Lefroy
	Loxonema obsoletum (Zieten)
Bivalves	*Entolium discites* (Schlotheim)
	Hoernesia sp.
Ichnocoenoses	
Trace fossils	*Rhizocorallium commune* Schmid
	Isopodichnus problematicum Schindewolf
	Kouphichnium gracilis Linck
	Planolites montanus Richter
	Taenidium sp.
	Chirotherium sp.
Eggs	*Palaeoxyris regularis* Brongniart
	Monilipartus tenuis Gall & Grauvogel
	Clavapartus latus Gall & Grauvogel
	Furcapartus exilis Gall & Grauvogel

far as the entomofauna is concerned, the dominant groups, related to the number of collected specimens, are the Blattodea (41%), the Ephemeroptera (15%) and the Coleoptera (12%) [39]. The flora is widely dominated by the conifer *Voltzia*, the fern *Anomopteris* and the horsetail *Equisetites*.

6. The recovery patterns

The richness and the state of preservation of the 'Grès à Voltzia' fossil assemblages are remarkable and very unusual for Triassic redbed formations. In addition, their ecological implications provide further insights into the patterns of the post-crisis recovery.

6.1. The coexistence of Palaeozoic and 'modern' taxa

As far as the systematic attributions are reliable, Table 2 shows that the marine fauna is composed of a greater proportion of holdover taxa than the freshwater/brackish fauna, which in turn is composed of more holdover taxa than the terrestrial fauna. This may imply that extinction intensity was greatest amongst terrestrial faunal communities and lowest in the marine ones. Indeed, the terrestrial fauna from the 'Grès à Voltzia' is represented by new genera and new families, whereas the marine organisms still resemble the Palaeozoic ones. The land vegetation partly resembles the Late Permian flora, from which it is con-

sidered to be descended [9]. Moreover, the 'Grès à Voltzia' fossil record confirms the statement that the replacement of the Palaeozoic taxa by the Mesozoic ones was not an abrupt or a complete event. For instance, a comparison of the faunas from the 'Grès à Voltzia' and the middle Pennsylvanian Mazon Creek (Illinois, USA) shows that they have 2 genera and 12 families in common [7].

The crustaceans, which are the dominant group among the aquatic fauna, provide good examples of this statement. They include the family Euthycarcinidae, which has representatives in both Carboniferous and Triassic faunas, and the superfamily Cycloidea, which comprises the Carboniferous genus *Cyclus* and the Triassic genus *Halicyne* (Fig. 4). The latter survived until the end of the Triassic [50]. In the 'Grès à Voltzia', they coexist with more evolved Malacostraca, such as the isopods *Palaega* and *Anhelkocephalon* and the decapods assigned to the recent families Penaeidae (*Antrimpos*) (Fig. 3) and Erymidae (*Clytiopsis*). It was recently suggested that the crustaceans were amongst the final groups of organisms to reappear in the marine realm [58]. From this point of view, environments such as the 'Grès à Voltzia' delta may have acted as a refugium for these arthropods during the Permian ocean anoxia, unless they invaded later from some other unknown refugia.

The arachnomorphs of the 'Grès à Voltzia' also show a similar mixture of Mesozoic and Palaeozoic representatives. The scorpions comprise two genera, one of which belongs to the recent super-family Buthoidea

Table 2

Estimation of the Palaeozoic holdover taxa present in the 'Grès à Voltzia' biotas (calculated after [3,41])

Tableau 2.

Estimation des taxons survivants du Paléozoïque, présents dans les biocœnoses du Grès à Voltzia

|	Groups represented in the 'Grès à Voltzia' biotas	Number of genera	Genera originating in the Palaeozoic (%)	Number of families	Families originating in the Palaeozoic (%)
Marine fauna	Foraminifera	3	100	3	100
	Brachiopods	1	100	1	100
	Molluscs	6	30	6	80
Fresh water & brackish water fauna	Medusids	1	0	1	0
	Annelids	4	50	3	100
	Limulids	1	0	1	0
	Crustacea	15	40	14	70
	Fishes	4	0	4	20
Terrestrial fauna	Spiders	1	0	1	0
	Scorpions	2	0	2	50
	Insects	30*	0	29*	0
	Amphibians	2	0	2	0
Plants	Lycopsids	2	0	2	0
	Sphenopsids	2	100	2	100
	Ferns	2	0	**	
	Pteridosperms	1	0	1	0
	Gingkophytes	1	100	1	100
	Cycadophytes	1	0	1	0
	Conifers	4	50	4	50
Ichnofossils		6	80		

* Incomplete data. ** Systematic position under discussion.

(*Protobuthus*), whereas the other (*Gallioscorpio*) exhibits several features inherited from Palaeozoic lineages [38]. In contrast, the only spider described from the Buntsandstein belongs to the living mygalomorph Hexathelidae [54].

The rich entomofauna of the 'Grès à Voltzia' needs more extensive investigations. Fossil insects systematic of family level remains unsatisfactory [5]. Considering the ordinal rank, among the 15 orders which are present, 13 were present in the Palaeozoic. The order Blattodea, for instance, comprises genera having Palaeozoic features (*Transitoblatta*) and genera with features of modern cockroaches (*Voltziablatta, Scleroblatta*) [39]. The Odonatoptera and the Ephemeroptera reveal the same story (Figs. 1 and 2). Concerning the Odonatoptera, one taxon (*Voltzialestes*), which belongs to an undetermined family of the Protozygoptera, announces the modern Odonata, whereas another taxon (*Triadotypus guillaumei*), which belongs to the family Triadotypidae, is close to some Palaeozoic representatives [39]. As to the Ephemeroptera, one of the isolated wings (*Triassodotes*) shows affinities with those of the

Permian family Misthodotidae, whereas a larva, assigned to the genus *Triassonurus,* is similar to those of the living family Siphlonuridae (Marchal-Papier, oral com.)

With regard to the flora from the 'Grès à Voltzia', it shows many similarities with the Permian flora and therefore it is considered to have been descended from it [9]. Indeed most of its taxa seem to be inherited from the Palaeozoic, such as the horsetail *Schizoneura paradoxa*, the fern *Anomopteris mougeoti* [22], the lycopsid *Pleuromeia* [21], a descendant from the widespread Carboniferous taxon *Chaloneria* [24], and the conifer *Yuccites*, a possible survivor of the Palaeozoic cordaites [19].The fern genus *Neuropteridium,* the foliage of which resembles that of *Neuropteris*, similarly may be a descendant of this Carboniferous genus. Likewise the conifer genus *Voltzia,* which is the most characteristic fossil of the 'Grès à Voltzia', already existed in the Middle Permian of Germany [53]. The regular branching pattern shown by the species *V. walchiaeformis* from the 'Grès à Voltzia' quite resembles that of the Permian *Walchia*. Moreover, it is worth noting that
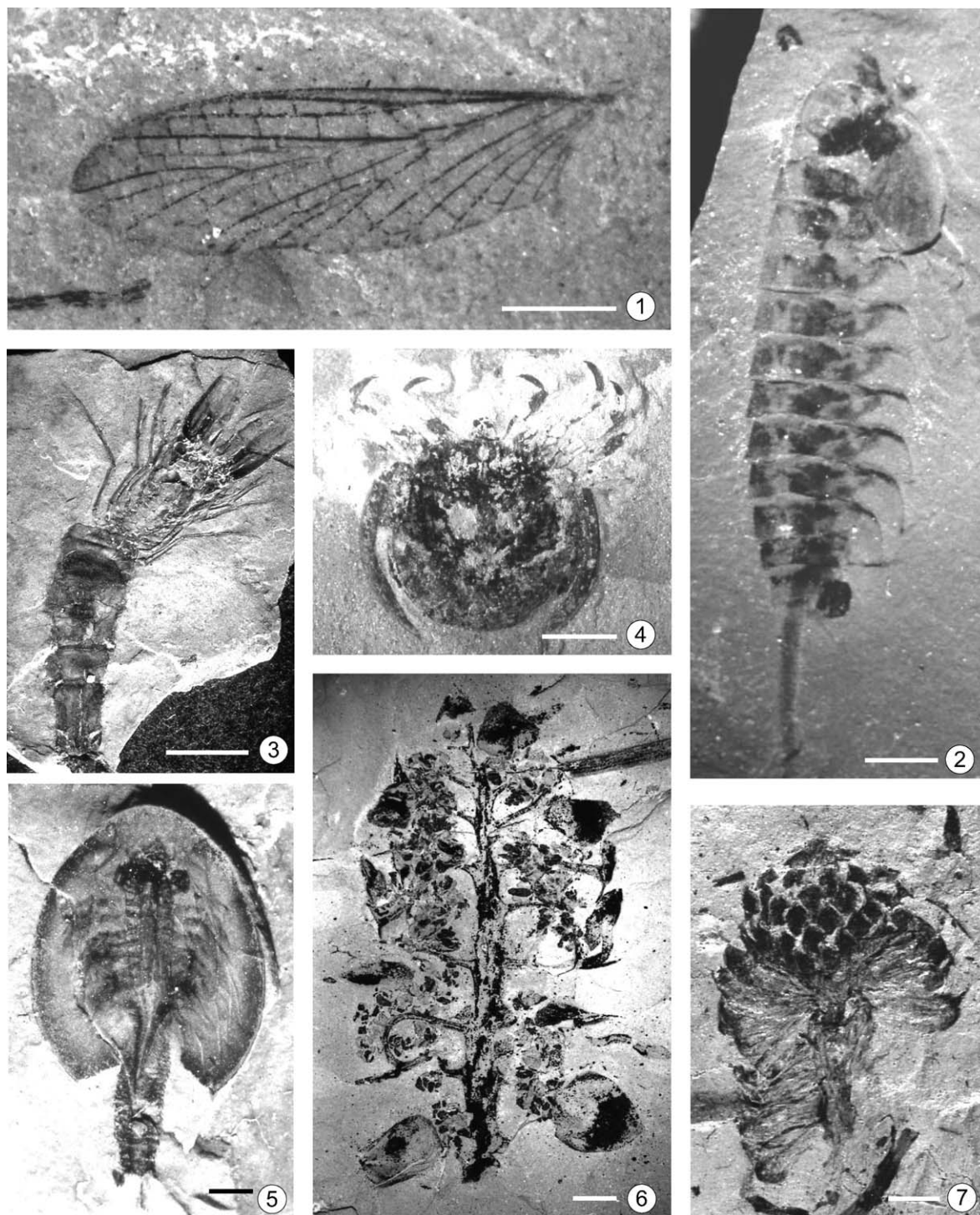
Figs. 1–7. Fauna and flora from the 'Grès à Voltzia' Formation. Taxa with Palaeozoic features: (**1**) Wing of Ephemeroptera : *Triassodotes vogesiacus* Sinitshenkova & Papier (scale = 1 mm); (**4**) Crustacea : *Halicyne ornata* Trümpy (scale = 5 mm); (**6**) Pollen cone of *Darneya peltata*

the pollen cones from the 'Grès à Voltzia' (*Darneya* and *Willsiostrobus*) show two kinds of organisation, of which only the type represented by *Willsiostrobus* (Fig. 7), with a structure similar to cones of the extant Araucariaceae [20,23], survived beyond the Middle Triassic. In contrast, those assigned to *Darneya* show archaic features and do not seem to have survived the Anisian. Indeed, *Darneya* (Fig. 6) resembles the pollen cones of some Permian cordaites and some Permian conifers, particularly *Voltzia hexagona* [23,32,53]. Moreover, it is likely that the conifer foliage of the 'Grès à Voltzia' attributed to *Albertia* existed in the Permian, where it is called *Archaeopodocarpus germanicus*, *Ullmannia bronni* or *Culmitszia florini* ([20] and unpublished observations). These observations show that *Albertia* already existed in the Palaeozoic. A Permian refugium where arboreous forests from the Carboniferous still persisted has already been described in China [65].

According to this analysis of the Triassic floras and their interpretation in the light of the generalized model of biotic recovery proposed by Kauffmann and Erwin [30], the 'Grès à Voltzia' flora would represent the first stage of the recovery interval. The Early Triassic *Pleuromeia* flora would correspond to the preceding survival interval [24].

In brief, the end-Permian extinction corresponds to a step-wise, graded mass extinction rather than to a catastrophic extinction, which implies that the crisis was interrupted by more or less long intervals during which new species can appear [25].

6.2. The occurrence of refugium taxa and 'living fossils'

Jablonski [27] introduced the concept 'Lazarus taxa' to refer to organisms that vanish from the stratigraphic record during the biotic crisis and reappear later. Schubert and Bottjer [51] used the term 'disaster forms' to identify opportunistic taxa that bloom during the aftermath of mass extinction events. 'Progenitor taxa' were defined by Kauffman and Harries [31] as species that evolved during the crisis and seeded the post-extinction recoveries, thus helping to rebuild the new ecosystems.

Living fossils refer to taxa with low evolutionary rates. They often possess wide environmental tolerance, e.g. to fluctuations of salinity and/or oxygen content, or survive in areas where predators and competitors are rare. The absence of those taxa during long stratigraphical intervals implies that unsampled refugia existed. In the 'Grès à Voltzia' Formation, living fossils are represented by the brachiopoda *Lingula tenuissima* BRONN, which is omnipresent in the different facies, as well as by the limulids and the coelacanth. But the most astonishing example of morphological stasis belongs certainly to the crustacea *Triops (Apus) cancriformis* (Schaeffer), a species fully identical to the living one (Fig. 5). The same taxon was described from the Permian of the French Massif Central [19]. Its re-appearance in the Middle Triassic, after apparently vanishing from the fossil record, is typical for a 'Lazarus taxon'.

The branchiopod crustacea estheriids *(Isaura, Palaeolimnadia, Palaeolimnadiopsis, Praeleaia)* are the most common animals in the 'Grès à Voltzia'. Thanks to their small body size, their short life history of only a few weeks and their rapid population growth, they may be considered as typical ecological opportunists adapted to colonise temporary water bodies. Their numerical dominance in the 'Grès à Voltzia' emphasizes the persistence of stressful environmental conditions during the Early Triassic.

6.3. Dwarfism or 'Lilliput' effect?

It is well known that the body size of organisms depends on the availability of resources and space. That is why animals from islands are often smaller than their representatives from nearby continents. The stressed, often brackish and fragmented habitats of the 'Grès à Voltzia' environment certainly affected the body size of the organisms. Indeed, small body size is widespread among the 'Grès à Voltzia' living communities. For instance, the body length of the spider *Rosamygale* does not exceed 6 mm [54]. The isopod crustacea *Palaega pumila* measures less than 7 mm. The insect fauna is mostly represented by isolated wings, the size of which varies from 2 to 20 mm, with an average of 5–6 mm. However, it is worth noting that it also contains a big dragonfly *Triadotypus guillaumei*, the span (27 cm) of which is half the span (about 60 cm) of the very large Carboniferous *Meganeura*, from which it is supposed to be descended. Likewise, the size of the bivalve *Myophoria vulgaris* (Schlot.) is half the size of the same species in the marine Middle Triassic (Muschelkalk Formation).

A similar tendency to body size reduction was documented by Urbanek [61] in his study on the recovery of graptoloids after the Silurian biotic crisis. He termed this the 'Lilliput' effect, and it is a phenotypic response to the unfavourable conditions that prevailed during the immediate aftermath of this biotic crisis [29,45]. A different interpretation of the body size reduction has been suggested by Twitchett [57]. According to him, the drop of primary productivity during the crisis involves a decrease in the biomass, which leads to a reduction either in abundance of the populations or in body size of the taxa. The latter have more chances to be preserved in the fossil record.

Size reduction is also documented in the flora, particularly by the conifer *Aethophyllum stipulare*. Indeed, whereas fossil and recent conifers are typically shrubby or arborescent, *Aethophyllum* is an herbaceous plant of only one or two metres high. Moreover, in very poor environmental conditions, its height can be even more reduced. Indeed, one of the entire specimens with root and ovulate cones is only 30-cm tall. This conifer is interpreted as a fast growing ruderal species rapidly invading vacant ecospaces thanks to a prolific production of small seeds [48].

6.4. The ecologic strategies of land recolonisation

It is commonly observed that after a disastrous event like a forest fire, the recovery of the devastated environments starts with fast growing herbaceous plant communities, such as weeds and grasses, and trees arrive later. Lycopsids and ferns are often pioneer species that take over disturbed sites. Indeed, spore-bearing vascular plants are superior to seed plants for preparing recolonisation sites [43]. The 'Grès à Voltzia' Formation contains some common ferns such as *Anomopteris*, proving that they found propitious environmental conditions to settle and grow. Fuchs et al. [13] showed that *Anomopteris* colonized the borders of ephemeral water bodies in the Middle Buntsandstein of the Eifel (Germany), together with the lycopsid *Pleuromeia*. This latter genus was an opportunistic pioneering plant in the Early Triassic, which took advantage of the vacuity of the environment to colonise the empty niches after the end-Permian life crisis. Indeed, it often is the only fossil plant in the Lower Triassic plant record, being represented by dense monospecific populations preserved in life position [21]. The same observation

has been made in the Lower Triassic of northern China, showing that it used the same ecologic strategies [64]. The conifer *Aethophyllum* also very likely used its fast growth to proliferate and occupy quickly wide areas. This also may explain why its pollen grains, *Illinites kosankei* Klaus, are widespread in many palynological assemblages from the Triassic of Europe and Asia [20].

Concerning the colonization of the ephemeral water bodies, the omnipresence of estherids crustacea in all fossiliferous localities of the 'Grès à Voltzia' may be interpreted as one of the first stages of the biological recovery of these biotopes, preceding the arrival of bigger predators.

7. The 'Grès à Voltzia' delta, an environmental refugium model ?

Many workers concluded that the biological recovery following a mass extinction event results from the immigration of taxa from refugia. The term refugium commonly refers to restricted habitats where organisms are protected against stressful conditions during times of environmental perturbations and thus can survive [57].

Schubert and Bottjer [52], studying the consequences of the end-Permian life crisis event on the Early Triassic invertebrate faunas in the western USA, concluded that the observed increase in taxonomic diversity originates from 'unknown refuges'. Erwin [11] suggested a 'nearshore refugium' for the Triassic gastropod genera that escaped the extinction and contributed to the subsequent recovery. Looy et al. [37] inferred from palynological data that the European Triassic gymnosperm taxa, particularly the genus *Yuccites*, migrated northward from a southern Gondwana 'refugium' or from North America. Harries et al. [25] develop a theoretical approach in order to make an inventory about the survival and repopulation patterns after the mass extinction events. They noted that, because of the short period of time involved, the recolonisation of damaged environments cannot solely be the result of an ecologic radiation. Kauffman and Harries [30] distinguish 'short-term refugium species', which rapidly return to their primary habitats after the crisis, and 'long-term refugium species', which undergo evolution and adaptation during a long interval of time. Perhaps, 'Lazarus taxa' may correspond to species that keep the ability to

reoccupy their primary habitats after the environmental normalization. In short, refugia act as reservoirs from where species were able to recolonise later the abandoned territories. But do refugia really exist as geographic entities? Some authors [66] reject this possibility, arguing that the missing taxa in previously sampled areas is just the result of inadequate collecting. The exceptional rich biotic communities of the 'Grès à Voltzia' Formation give a further opportunity to reconsider this debate about refugia.

It was established that a faunal continuum exists in environments transitional from nearshore to terrestrial in the Late Palaeozoic [49] and in the Mesozoic [7]. A comparison of the 'Grès à Voltzia' biotas with those of the Carboniferous 'Konservat-Lagerstätten', particularly that of Mazon Creek (USA), which also corresponds to transitional environments from nearshore to terrestrial, reveals an astonishing similarity in composition. Indeed, like in the 'Grès à Voltzia', the fossil content shows that the biological assemblages lived in widely fluctuating environments, such as shallow marine areas, marginal environments and deltaic plains, and display a remarkable stability and morphological stasis over long period of time [7,55]. Living communities develop adaptive responses to environmental factors. For instance, high fluctuating and stressful conditions maintain a great degree of stability among the biocoenoses [6,55]. Biodiversity is low in such environments and it is known that species-poor communities are more resilient and more stable than those with higher diversity [44]. Consequently, it may be expected that those marginal environments were more immune from the effects of the mass extinction events.

In this point of view, the 'Grès à Voltzia' crustaceans are significant. Indeed, they include 'archaic' taxa inherited from the Palaeozoic (*Euthycarcinus, Halicyne*), 'modern' taxa that announce the Mesozoic and the Cenozoic biotic world (*Antrimpos, Clytiopsis, Palaega...*) as well as 'living fossils' (*Triops,* estheriids). Some genera, such as *Halicyne* and *Schimperella*, were recorded from other Triassic localities around the world, but they are never associated with a crustacean fauna as diverse as in the 'Grès à Voltzia' Formation. Overall, the richness of the palaeontological record from the 'Grès à Voltzia', which includes plants as well as aquatic and terrestrial animals, is unique for Triassic redbeds. Most taxa such as those of limnomedusids, spiders, insects, herbaceous conifers etc., are only known from the 'Grès à Voltzia'. None of the other fossiliferous localities from this time exhibit such a biodiversity [15]. Why are the 'Grès à Voltzia' biotas so exceptional?

A possible interpretation lies in the fact that the 'Grès à Voltzia' environmental setting is unusual for Triassic Pangaea. Indeed, the transitional areas located between the terrestrial realm and a marine-influenced delta, form protected habitats away from the extensive marine anoxia of the Permian–Triassic interval [67], and created a favourable situation for aquatic organisms. They also maintained more humid climatic conditions, which stimulated the settlement of plants and terrestrial animals. Deltas always existed at the border of the Pangaea during Permian and Triassic time. It is therefore not surprising that such environments were settled by Palaeozoic survivors as well as by Lazarus taxa (*Lingula*, *Triops...*). Nevertheless, we still do not know if the 'modern' taxa like the spiders or the insects have originated and evolved in situ or if they invaded the deltaic area from other places. In other words, are they resident species or immigrants?

Anyway, despite its Lower Anisian age, the deltaic environment of the 'Grès à Voltzia Formation' seems to be a model of the type of refugium that allowed aquatic and terrestrial organisms to survive the stressful conditions of the long interval of time extending from the Late Permian through the Early Triassic. Less climatic aridity promoted, locally, a faster postextinction recovery of the terrestrial communities. Similarly, in some marine areas, the absence of anoxia favoured a more rapid faunal recovery [59]. Therefore, refugia have to be understood in an environmental sense rather than a geographic one [62,66].

8. Conclusion

The recovery that followed the end-Permian mass extinction took an abnormal long period of time, more than 5 Myr [47,60], and even 10–14 Myr for the land flora [24]. Such a long time shows that the ecosystems recovered very gradually, possibly because of an unusually long period of environmental degradation immediately after the crisis event. For instance, global oceanic anoxia spanned the Early Triassic [56,67], lasting as long as the worldwide extension of the redbed facies that occurred in the tropical regions of Pangaea. Simi-

larly, a long time was necessary to restore the salinity-driven circulation in the ocean, which was destroyed during the Late Permian [46]. The arid climatic conditions that prevailed on the continents resulted in habitat shrinkage that created a multitude of isolated geographic areas. Such conditions also prevailed in the 'Grès à Voltzia' deltaic environment, where a patchwork of small habitats harboured low diversity communities comprising Palaeozoic survivors, Lazarus taxa and 'modern' genera, an association that, until now, has never been described anywhere else in the world. Moreover, despite their Early Anisian age, these communities show a great similarity with those of the Carboniferous transitional environments, a support in favour of the astonishing stability through time of the communities living in such environments [6]. Indeed, most of the groups do not seem to have been much affected by the extinction crisis. The land flora also shows such a continuum, since the conifers were the dominant plants in the Late Permian and the early Middle Triassic floras, being just interrupted by a lycopsid-dominated interval in the Early Triassic [37].

All these observations may indicate that marginal environments, such as those of the 'Grès à Voltzia', may have acted as refugia during the life crises, i.e. protected areas that remain habitable in an otherwise inhospitable world.

Acknowledgements

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