ISSN (print): 1698-6180. ISSN (online): 1886-7995
www.ucm.es/info/estratig/journal.htm

Journal of Iberian Geology 34 (1) 2008: 57-72

Journal of Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

Floras from red beds of the Permian Basin of Lodève (Southern France)

Floras en las capas rojas de la cuenca pérmica de Lodève (Sur de Francia)

J. Galtier [1], J. Broutin [2]

[1]AMAP, UMR 5120 CNRS, CIRAD, TA A-51/PS2, Boulevard de la Lironde, 34398 Montpellier Cedex 05, France
e-mail: jean.galtier@cirad.fr
[2]UMR CNRS 5143 Paléobiodiversité et paléoenvironnements, Paléobotanique – Paléoécologie / Paléodiversité, Systématique et Evolution des Embryophytes, Université Paris 6, case courrier 1201, 12 rue Cuvier, 75005 Paris, France

Received:18/02/07/ Accepted:12/08/07

Abstract

The fossil plants from the red beds of the Lodève Basin are generally rare and of poor preservation in comparison to the well known "grey Autunian" flora. According to previous work by Doubinger and following a reinvestigation of available collections with new data, we propose lists of the floras from the red beds of the "transition zone", from the Rabejac Formation and, for the first time, from the Salagou Formation. *Callipteris* cf. *uralensis* and *Supaia* are two significant taxa; the first appears with the red beds whilst *Supaia* is only known from the Rabejac Formation. This genus, formerly considered to be endemic of Arizona, has been reported in Russia, Spain and China, in addition to the Lodève basin where its occurrence may be suggestive of a Late Artinskian to Kungurian age for this basal section of the former "Saxonian group". Of interest also, some conifers from Rabejac and the overlying Salagou Formations show either succulent leaves and /or cones similar to those of some Triassic conifers that certainly represent an important change in the flora in response to increasing dryness. Due to unfavourable conditions of fossilisation and considering the importance of animal life in the playas ecosystems of the Salagou Formation, the rare plants are interpreted as the impoverished reflect of an originally much more diverse vegetation perhaps dominated by arborescent conifers.

Keywords: macrofloras, Permian, red beds, Lodève, France

Resumen

Las plantas fósiles de las capas rojas de la cuenca de Lodève son generalmente escasas y su estado de conservación es relativamente pobre comparada a la flora del "Autuniense gris". De acuerdo con los trabajos previos de Doubinger y tras una reevaluación de las colecciones disponibles gracias a nuevos datos, son propuestas unas listas de las floras de las "capas rojas" de la "zona de transición" de la Formación de Rabejac y, por primera vez, de la Formación de Salagou. *Callipteris* cf. *uralensis* y *Supaia* representan dos taxones significativos; el primero aparece en las capas rojas mientras que *Supaia* solamente es conocido en la Formación de Rabejac. Este género, previamente considerado endémico de Arizona, ha sido citado como presente en Rusia, España y China, además de la cuenca de Lodève, en la que su presencia podría indicar una edad Artinskiana tardía a Kunguriana para esta sección

basal de lo que se conocía como "grupo Saxoniano". También es interesante el hecho de que algunas coníferas de Rabejac y de la Formación de Salagou, más reciente, muestran conos y/o hojas suculentas, similares a los de algunas coníferas Triásicas, lo que con toda certeza representa un cambio importante en la flora como respuesta a un clima progresivamente más seco. Debido a las condiciones desfavorables de fosilización y teniendo en cuenta la importancia de la actividad animal en los ecosistemas de playa de la Formación de Salagou, estas plantas poco frecuentes son interpretadas como los restos de una vegetación originalmente mucho más diversificada, posiblemente dominada por coníferas arborescentes.

Palabras clave: macrofloras, Pérmico, capas rojas, Lodève, Francia

1. Introduction

In the Lodève Basin, the Permian sedimentation started with fluviatile clastics and lacustrine black shales of the Usclas-Saint Privat and the Tuilières-Loiras Formations. These sediments (formerly named "Grey Autunian") were deposited under a warm and humid climate indicated by laminated lake sediments which yielded a rich and well-known flora dominated by conifers but where callipterids show a remarkable diversity (Grand'Eury, 1877; Zeiller, 1898; Florin, 1938-1945; Doubinger, 1956). Higher up, in the transition zone of the Upper Tuilières Loiras to Lower Viala Formations, the facies changed from grey to red and from fluvio-lacustrine to dominant fluvial. In grey sediments, the plant assemblage is equally dominated by callipterids and conifers but with the remarkable co-occurrence of calamites (Doubinger, 1963; Galtier and Broutin, 1995; indicated as macroflora B on Fig. 1, Lopez *et al*., 2008). From the Upper part of the Viala Formation onwards, the definitively red facies have been deposited under semi-arid conditions. Red beds of the transition zone contain a small plant assemblage which was described (Doubinger and Kruseman, 1965) at the same time, and partly confused, with the flora from the overlying Rabejac Formation. Above a major unconformity, the second sedimentation cycle (formerly named "Saxonian Group") starts with fanglomeratic deposits of the Rabejac Formation. This facies yielded a small flora (= flora C, Fig. 1, Lopez *et al*., 2008) with the remarkable first record of *Supaia* for the Lodève Basin (Doubinger and Heyler, 1975). Deposition also took place in an alluvial/flood plain environment with periodically water-filled ponds, however, in the top of the Rabejac Formation there is a fluent transition into the playa sediments of the overlying Salagou Formation (Körner *et al*., 2005). The occurrence of fossil plants in all red pelites is rare and their preservation is rather mediocre. The objective of this paper is a review of the available data concerning the floras from the red beds of the Lodève Basin. This study includes the re-investigation of plants from red beds ranging from the Transition Zone of the Tuilières-Loiras to Viala formations up to the Rabejac Formation, presently kept in diverse collections (Université Montpellier 2, Muséum National d'Histoire naturelle Paris, Université Lyon 1, Musée Fleury Lodève), and the first description of plants recently collected from fossiliferous rills and other levels from the Salagou Formation (floras D-E, Fig. 1, Lopez *et al*., 2008).

2. Techniques and studied material

The fossil plants are preserved as impressions or casts without organic matter. They are generally more or less preserved in three dimensions. This concerns stems which kept their cylindrical volume as well as compound leaves showing pinnules lying in different planes however no anatomical detail is preserved. As a result, the dégagement technique (Fairon-Demaret *et al*., 1999) has been used in some cases, for example to reveal the three-dimensional organisation of leaves. The general method of study is a combination of camera-lucida drawings and of photography under reflected light.

Material studied:

1) Specimens from the Rabejac Formation:

- *"Callipteris conferta*" and "*C. martinsii*" (figured by Doubinger and Kruseman 1965, Pl. XII, fig. 1; pl. XIII, figs 1 and 5), "*Callipteris uralensis*" (figured by Doubinger and Heyler 1959), *Supaia* sp., cf.*Walchia*, *Taeniopteris* sp., cf. *Crassinervia* (collections Université Montpellier 2, referred to as UM2LOD).
- *"Callipteris*" sp., *Supaia* sp., cf. *Walchia* (collections Musée Fleury, Lodève, referred to as MULOD).
- *"Callipteris"* cf. *uralensis* figured by Doubinger and Kruseman (1965, Pl. 13, fig. 2): specimen Fr. 62, coll. Université Lyon 1.
- *"Callipteris »* cf. *uralensis, Supaia sp.* (figured by Doubinger and Heyler 1975, Pl. 1, figs. 1-3): collections Muséum National Histoire Naturelle Paris, referred to as MNHNP.

2) Specimens from unspecified origin (ranging from the Tuilières-Loiras transition zone up to the Rabejac Formation): ?? *Calamites* sp*., Rhachiphyllum* sp., *Walchia* sp., *Taeniopteris* sp. (collections in Lodève and Montpellier).

3) Specimens from the Viala Formation: *Rhachiphyllum* sp. (collection Univ. Montpellier).

4) Specimens from the Salagou Formation:

-Unnamed specimens of branched stems and leaves, conifer twigs, cone, small taeniopterid leaf, collected by J. Lapeyrie from several rills at Bouisset, Dio, La Prade, Le Deves, Rieupeyre-La Boutine (see Garric, 2001).

-*Dichophyllum*-like specimen from Arièges, collected by J. Schneider.

-Unnamed specimens of stems and almond-like organs, collected near La Lieude by G. Gand, J. Schneider and colleagues in 2004 (all material in collections Univ. Montpellier).

3. Historical survey

3.1. Macroflora from the red beds of the Transition Zone

Doubinger (1963) first described a plant assemblage (13 taxa) from grey to yellow to red pelites exposed near the Mas d'Alary but unfortunately she did not provide any illustrations and we have not been able to locate this material. Later, Galtier and Broutin (1995) described and illustrated a similar flora from grey sediments of the same zone exposed in the former uranium mine. Both assemblages are characterized by the remarkable co-occurrence of calamites with callipterids and conifers. In contrast, the plants described by Doubinger and Kruseman (1965) from the transition zone, near St Alban and St Martin du Bosc, are preserved in red pelites. The small assemblage: *"Callipteris" conferta*, *"C." martinsii*, *"C."* cf. *uralensis*, *Schuetzia* sp., *Walchia* sp., *W. hypnoides*, cf. *Ullmannia*, consists only of callipterids and conifers. Some have been illustrated (cf. Table 1) but all plant fossils are fragmentary, sometimes "blurred" and their identification is doubtful. The most interesting taxa are *"C." martensii* and "*C." uralensis* elsewhere known in the Late Permian of England, Germany and Russia and not occurring in underlying deposits of the Lodève Basin.

Previous data	Red beds of the Transition zone	Rabejac Formation	Proposed list for the Rabejac Formation
Pecopteris cyathea *P. cyathea* var. *major*		DK 1965, pl. 12, fig. 3 DK 1965 not figured	? *Pecopteris cyathea*
Callipteris conferta	DK 1965, pl.12, fig. 2	DK 1965, pl.12, fig.1	*Autunia conferta* *Rhachiphyllum* sp.
Callipteris uralensis *C.* cf. *uralensis*	DK 1965, pl.12, fig. 4	DH 1959, pl. 15, figs 1-3 DK 1965, pl.12, fig. 5	cf. *Supaia*
Callipteris martinsii	DK 1965 not figured	DK 1965, pl.13, figs 1,5	cf. *Peltaspermum martinsii*
Schuetzia sp.	DK 1965 not figured		
cf. *Pseudoctenis middrigensis*		DK 1965 not figured	cf. *Pseudoctenis middrigensis*
Supaia sp.		DH 1975, pl.1, figs 1-3 And new data	*Supaia* sp. aff. *thinnfeldioides*
Walchia sp.	DK 1965, pl. 13, fig.3	DK 1965 not figured	*Walchia* sp
Culmitzchia cf. *hirmeri*	DK 1965, pl. 13, fig.4	DK 1965 not figured	*Culmitzchia* cf. *hirmeri*
Ernestiodendron filiciforme		DK 1965 not figured	*Ernestiodendron filiciforme*
cf. *Ullmannia*	DK 1965 not figured		
		New data	? *Calamites* *Taeniopteris* sp. 1,2 cf. *Lepeophyllum* cf. *Pagiophyllum*

Table 1.- Plants known from red beds of the Transition Zone and of the Rabejac Formation according to previous studies by Doubinger and Heyler 1959 (=DH1959), Doubinger and Kruseman 1965 (=DK 1965) and Doubinger and Heyler 1975 (=DH1975).

Table 1.- Plantas conocidas de la Zona de Transición de la Formación Rabejac según los estudios previos de Doubinger y Heyler (1959) (=DH1959), Doubinger y Kruseman (1965) (=DK1965) and Doubinger and Heyler (1975) (=DH1975).

3.2. Flora from the Viala Formation

Previous studies by Doubinger and collaborators did not record any macroflora from the red pelites of the Viala Formation. In this paper we report the rare evidence of plants from this level. Interestingly, a microflora (Odin *et al.,* 1986) was obtained from a single bed at the base of the Upper Viala Formation and this indicated a dominance of bissacate pollens and the appearance of *Lueckisporites*.

3.3. Macroflora from the Rabejac Formation

Doubinger and Heyler (1959), Doubinger and Kruseman (1965), Doubinger and Heyler (1975) described plants preserved as impressions from the Rabejac Formation. The plants are difficult to identify at the specific level due to relatively poor preservation. The flora includes nine taxa, either figured or not, as listed on Table 1.

It is significant that five of these taxa (*"Callipteris" conferta*, "*Callipteris" uralensis*, *"Callipteris" martinsii*, *Walchia* sp. and *Culmitzchia* cf. *hirmeri*) have been described, at the same time by Doubinger and Kruseman (1965), as co-occurring in an underlying horizon of the "Transition Zone". Of the four remaining taxa, *Ernestiodendron filiciforme* occurs in the Early Permian, Usclas-Saint Privat Formation, of the same Basin whilst *Pecopteris cyathea* is a species both common in the Late Pennsylvanian and in the Rotliegend of Germany (Holotype from Manebach). As a result of previous studies, the Rabejac Formation is characterized by the first record of *Supaia* and *Pseudoctenis*. Unfortunately the last taxon has not been illustrated and we have not been able to find the specimen mentioned by Doubinger and Kruseman (1965). In contrast, a number of specimens assignable to *Supaia* have been recognized and are described in this paper along with a reconsideration of the occurrence of uncommon taxa like "*Callipteris" uralensis* and *"Callipteris" martinsii.*

4. Results

4.1. Macroflora from the Rabejac Formation and underlying red beds

The plants essentially belong to callipterid pteridosperms and conifers; in addition, possible cycads and problematic specimens of calamites and ferns must be mentioned.

4.1.1. Sphenopsids

Previous authors did not mention any representatives of the sphenopsids in red sediments of the Lodève Basin. A single specimen (LOD 1007, collections University of Montpellier) seems to represent the pith cast of a calamitean trunk. The specimen is 9 cm in diameter and shows one node and closely spaced verticals ribs suggestive of *Calamites cistii*. This specimen being of unspecified origin may be from the red beds of the "Transition Zone". This would not be surprising, considering that calamiteans have been reported from the grey sediments of the same zone by Doubinger (1963) and Galtier and Broutin (1995).

4.1.2. Ferns

Doubinger and Kruseman (1965) described and illustrated *Pecopteris cyathea* and *P. cyathea* var. *major* from the Rabejac Formation, however, we have not been able to find these specimens and no other example of this fern has been recognised during our re-investigation of the collections.

4.1.3. Callipterid pteridosperms

Callipterids represent the majority of fossil plants preserved in the red sediments from the Rabejac Formation.

Rhachiphyllum sp.

A 20 cm long compression of a frond from the Rabejac formation was attributed to *"Callipteris conferta*" by Doubinger and Kruseman (1965, Pl; 12, fig.1) on the basis of the overall morphology, size and pinnule shape and despite the indistinct venation. Re-investigation of this specimen (Fig.1) reveals a number of features (pinnae arranged at wide angles of about 90°, pinnules with indistinct midvein , apparent multiple venation on the primary rachis) which are not in accordance with *Autunia conferta* as it has been re-defined by Kerp (1988). The three-dimensional preservation of the frond shows that along each pinna the pinnules are directed towards the abaxial side of the frond (i.e. opposite the exposed side). The pinnules are vaulted, obliquely inserted and decurrent with their tips embedded in the sediment; as a result they appear round-ovate, less than 10 mm long and 5 mm wide. Intercalary pinnules are inserted laterally on the primary rachis but do not cover its adaxial side. Due to the thickness of the lamina, the pinnule midvein is not visible whilst the pinna rachis shows only a faint midvein and the primary rachis shows several parallel and branched veins (Fig. 1). According to the re-evaluation of the classification of callipterid pteridophylls by Kerp (1988) and

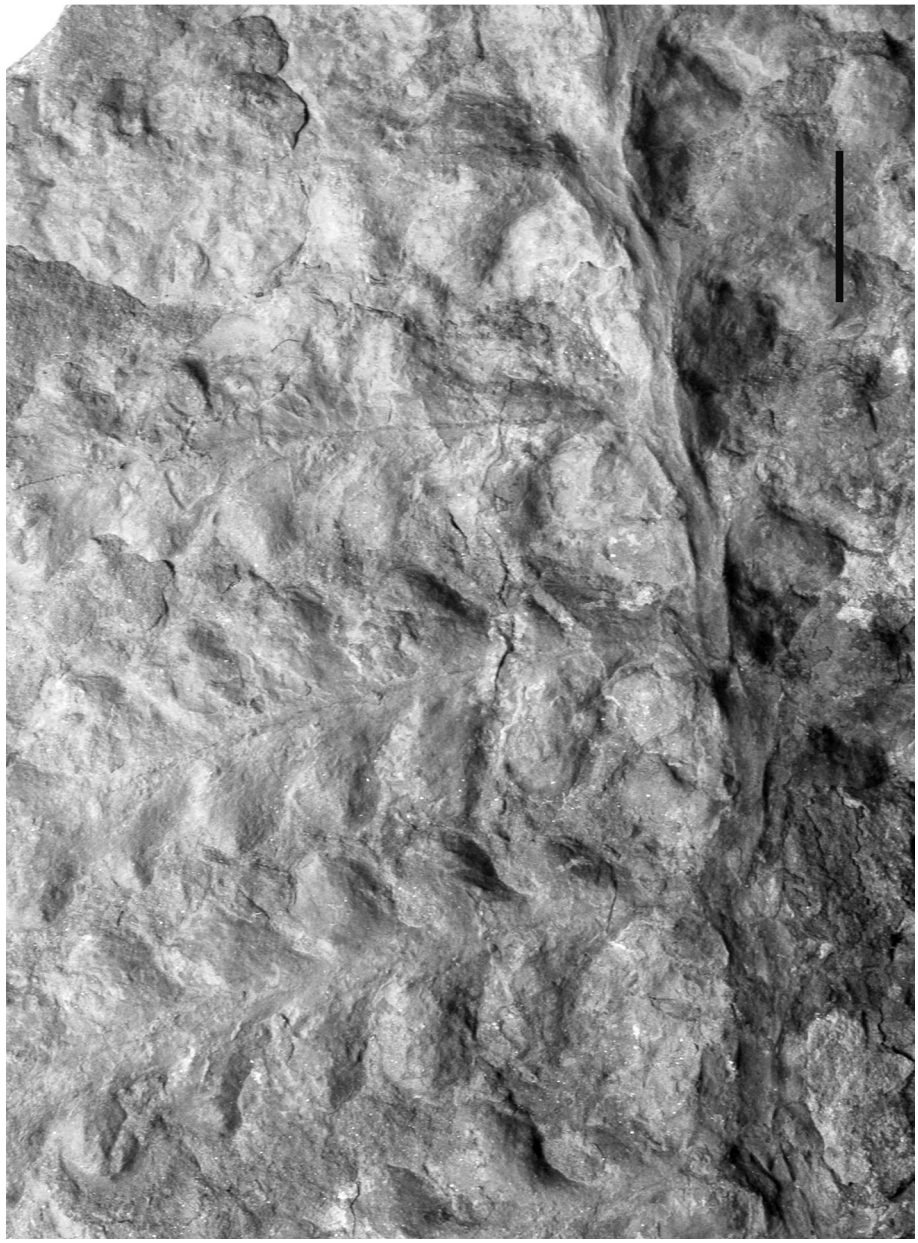

Fig. 1.- *Rhachiphyllum* sp. Specimen previously illustrated as "*Callipteris conferta*" by Doubinger and Kruseman (1965, Pl. XII, 1), showing the pinnae arranged at wide angles, pinnules with indistinct midvein and multiple venation on the primary rachis. LOD 1021. Rabejac Fm. Scale bar = 10 mm.

Fig. 1.- *Rhachiphyllum* sp. Specimen previously illustrated as "*Callipteris conferta*" by Doubinger and Kruseman (1965, Pl. XII, 1), mostrando la disposición pinacea con ángulos grandes, pínulas con indiferenciadas venas medias y múltiples venas en el rachis primario. LOD 1021. Formación Rebejac. Barra de escala = 10 mm.

Kerp and Haubold (1988) we suggest to refer this type of frond to the morphogenus *Rhachiphyllum* Kerp. Additional material, kept in the collections of Montpellier University and collected in the Viala Formation, consists of two smaller fronds with the same habit (pinnae inserted at wide angle and small rounded pinnules). The preservation is relatively poor and does not allow a more precise taxonomic description of this type of frond.

Autunia conferta (Sternb.) Kerp

Doubinger and Kruseman (1965, pl. 12, fig.2) illustrated a pinna fragment with three pinnules clearly showing the venation characteristic of the species. This specimen, not yet located in the collections, comes from the Transition Zone where *A. conferta* is very common in the grey facies. However, several fragments of bipinnate fronds from the Rabejac Formation may be attributed to *A. conferta* despite a relatively poor preservation; they show pinnae inserted at angles of 30 to 60° and pinnules with a strong midvein (Fig. 2A).

cf. *Peltaspermum martinsii* (Germar) Poort and Kerp.

Two fragments of small bipinnate fronds showing small "shrivelled" pinnules have been attributed to *"Callipteris martinsi"* by Doubinger and Kruseman (1965, Pl.13, figs. 1, 5) who emphasized the contrast between this species and the other associated callipterids with broad pinnules. The two figured specimens, kept in the collections of Montpellier, have been studied together with a third one of same origin (i.e. Rabejac Formation) showing only

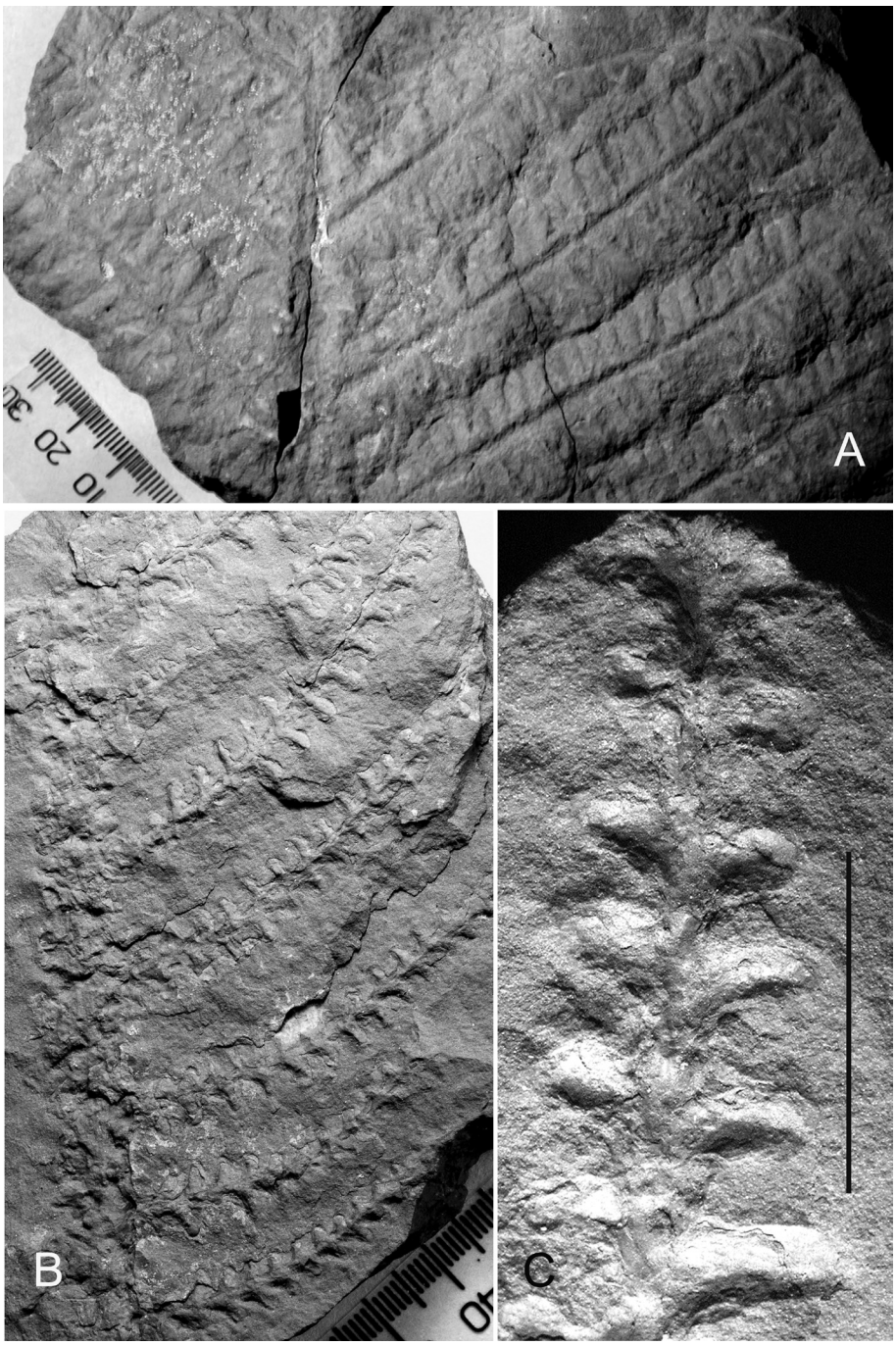

Fig. 2.- A. *Autunia conferta.* Fragment of bipinnate frond with pinnae at angles of about 60° and pinnules with marked midvein. LOD 1014. Rabejac Fm. B-C. cf. *Peltaspermum martinsii.* Bipinnate frond (B) illustrated by Douginger and Kruseman (1965, Pl. XIII, 1) and detail of the same (C) showing the short alethopteroid, distantly spaced pinnules with indistinct venation. LOD 1022. Rabejac Fm. Scale bar in C = 10 mm.

Fig.2.- A. *Autunia conferta.* Fragmento de fronde bipinado con ángulos de unos 60º y pínulas con marcadas venas centrales. LOD 1014. Formación Rebejac. B-C. cf. *Peltaspermum martinsii*. Fronde bipinado (B) ilustrado por Doubinger y Kruseman (1965, PL. XIII, 1) y de talle del mismo (C) mostrando el corto alethopteroide, las pínulas distanciadas con venas indiferenciadas. LOD 1022. Formación Rebejac. Barra de escala en C = 10 mm.

portions of pinnae. This plant is characterized by small (2.5 - 4.5 mm long, 1.5 – 2.4 mm wide), alethopteroid, entire-margined pinnules, certainly coriaceous with thick lamina and indistinct venation (Fig. 2B-C). The pinnules are more or less regularly spaced (at 3 to 4.8 mm intervals) along the pinna rachis. Pinnae are subopositely attached to the primary rachis; they are slender, up to 70 mm long, showing a distal decrease of pinnule length (Fig. 2B). Intercalary pinnules, similar to other pinnules, are obscuring the primary rachis (Fig. 2B). The attribution of these specimens to *Lepidopteris* (*C.) martinsii* has been questioned by Kerp (2000) who suggested that they are most probably conifers. Despite relatively poor preservation, present evidence supports the interpretation of the ultimate axes as pinnae bearing alternately small pinnules rather than ultimate branches bearing spirally arranged needle-like conifer leaves. *Lepidopteris* is a morphogenus based on foliar morphology and the combination *L. martinsii* is preferred by Kerp and Haubold (1988) for such specimens. However, *Peltaspermum* has been redefined by Poort and Kerp (1990) as a natural genus including sterile foliage and ovuliferous organs for the species

P. martinsii. The foliage from Lodève is incomplete however the pinnae are slender and the pinnules are similar to those in specimens of *Peltaspermum martinsii* illustrated by Poort and Kerp (1990) and Visscher *et al.* (2001). The Lodève specimens look almost identical, in pinna and pinnule organisation, to the "*Callipteris martinsi*" described by Stoneley (1958, fig. 5 a,d) from the Upper Permian of England, however, slightly lobed pinnules have been illustrated in one English specimen, a feature unknown in our material. Therefore, we propose that the Lodève specimen be referred to as cf. *Lepidopteris martinsii*.

cf. *Supaia* (=*Callipteris uralensis* Doubinger and Heyler).

Several fragments of pinnae bearing subopposite relatively long pinnules have been first attributed to *Callipteris uralensis* by Doubinger and Heyler (1959), then to *C.* cf. *uralensis* by Doubinger and Kruseman (1965). They are from the Rabejac Formation with the exception of one specimen from the Transition Zone (cf. Table 1). Two specimens, kept in Montpellier, originally illustrated by Doubinger and Heyler (1959) and another kept in Lyon, illustrated by Doubinger and Kruseman (1965, Pl. 13, fig 2), have been reinvestigated as well as a dozen of specimens referable to this taxon from collections in Montpellier, Paris and Lodève. Doubinger and Heyler (1959) emphasized the biconvex shape of the pinnules with a lamina "more or less inclined as a roof", i.e. inverted V-shaped in section with the midrib forming the top. This feature is well visible (Fig. 3A) on all the specimens but it is more pronounced in the most proximal region of the pinnule. The midvein is generally prominent and basally decurrent whilst the oblique lateral veins are very narrow and closely spaced. All the observed specimens are incomplete pinnae ranging from 4 to 26 cm long, pinna rachis being 2 to 4 mm broad, subopposite pinnules ranging from 20 to 60 mm long and 5 to 11 mm broad. This exceeds the length values (20 to 38 mm long) given by previous authors who noted the alethopteroid-type pinnules, basally confluent, and resulting in a 3-5 mm lamina fringe along the rachis. The interval between pinnule midveins ranges from 7 to 15 mm and the pinnule lamina generally overlap a little (Fig. 3A). Doubinger and Heyler (1959) justified the attribution to *Callipteris uralensis* by the large size of the pinnules, their decurrent base along the rachis and their "roof-shape". However, the specimens of *C. uralensis* figured by Zalessky (1927) and Neuburg (1948) show broad pinnules with a smaller ratio (pinnule length/width), i.e. the pinnules in the Lodève specimens appear more slender. The venation of the pinnules is more similar to that observed in *Supaia* (see below) than to the type material of *C. uralensis* described by Zalessky. Another difference is the pronounced "roof-shaped" aspect of the pinnules in Lodève specimens (Fig. 3A) which may be explained by a thicker lamina and the three-dimensional morphology of the pinnules preserved in a coarser-grained sediment. These specimens have thick and biconvex pinnules very similar to some of the *Supaia* material from the Hermit Shale described by White (1929): see for example *Supaia sturdevantii* or *Supaia* sp. (White 1929, Plate 18, fig. 2a or Plate 32, fig. 2). Moreover in some examples two pinnae lying side by side are diverging from a point that certainly represents a bifurcation of the rachis, a feature demonstrated in the fronds of *Supaia* that are discussed below. This may explain why Doubinger and Heyler (1975) finally questioned the possible attribution of their specimens of *C. uralensis* to the genus *Supaia*. Seven specimens in Paris and most in Montpellier are from the Rabejac Formation (Cartels locality). However, of some others the origin is unknown and we cannot exclude that they are from the red beds of the Tuilières Loiras Formation. Considering the differences and uncertainties mentioned above, the attribution of this material to *C. uralensis* is very dubious. Awaiting a revision of the type material of Zalessky, *C. uralensis* has been classified as "Species dubiae" by Kerp and Haubold (1988). Therefore, considering the probable bifurcation of the rachis, we propose to follow Doubinger and Heyler (1975) final questioning and to designate these callipterid specimens from the Tuilières-Loiras and Rabejac Formations as cf. *Supaia* instead of *Callipteris* cf. *uralensis*.

Supaia sp., aff. *thinnfeldioides.*

The first report of the genus *Supaia* in Europe was based on two specimens from the Rabejac Formation, now kept in the Muséum National d'Histoire Naturelle Paris, nicely illustrated by Doubinger and Heyler (1975, Pl. 1, figs 1-3). The first specimen consists of two fragments of pinnae 12 and 15 cm long, lying side by side, and interpreted as one portion of a bifurcate frond just distal to the fork. The pinnules are elongated, up to 53 mm long and 7 to 9 mm wide, of alethopteroid-type with decurrent and confluent bases. The second specimen (Fig. 3B) shows excellent preservation of the pinnules with fine venation. There is also evidence that the pinnule laminae do not overlap and the pinnules do not show the pronounced biconvex ("roof shape") morphology described above in cf. *Supaia* ("*Callipteris* cf. *uralensis")* (Fig. 3A).

A dozen of other specimens, kept in the collections of Lodève and Montpellier, can also be attributed to the genus *Supaia*. Two specimens correspond to nearly complete fronds showing a primary rachis bifurcating, at an angle of about 30°, into two pinnae rachises 20 to 26 cm long. This suggests that the entire fronds were up to 34

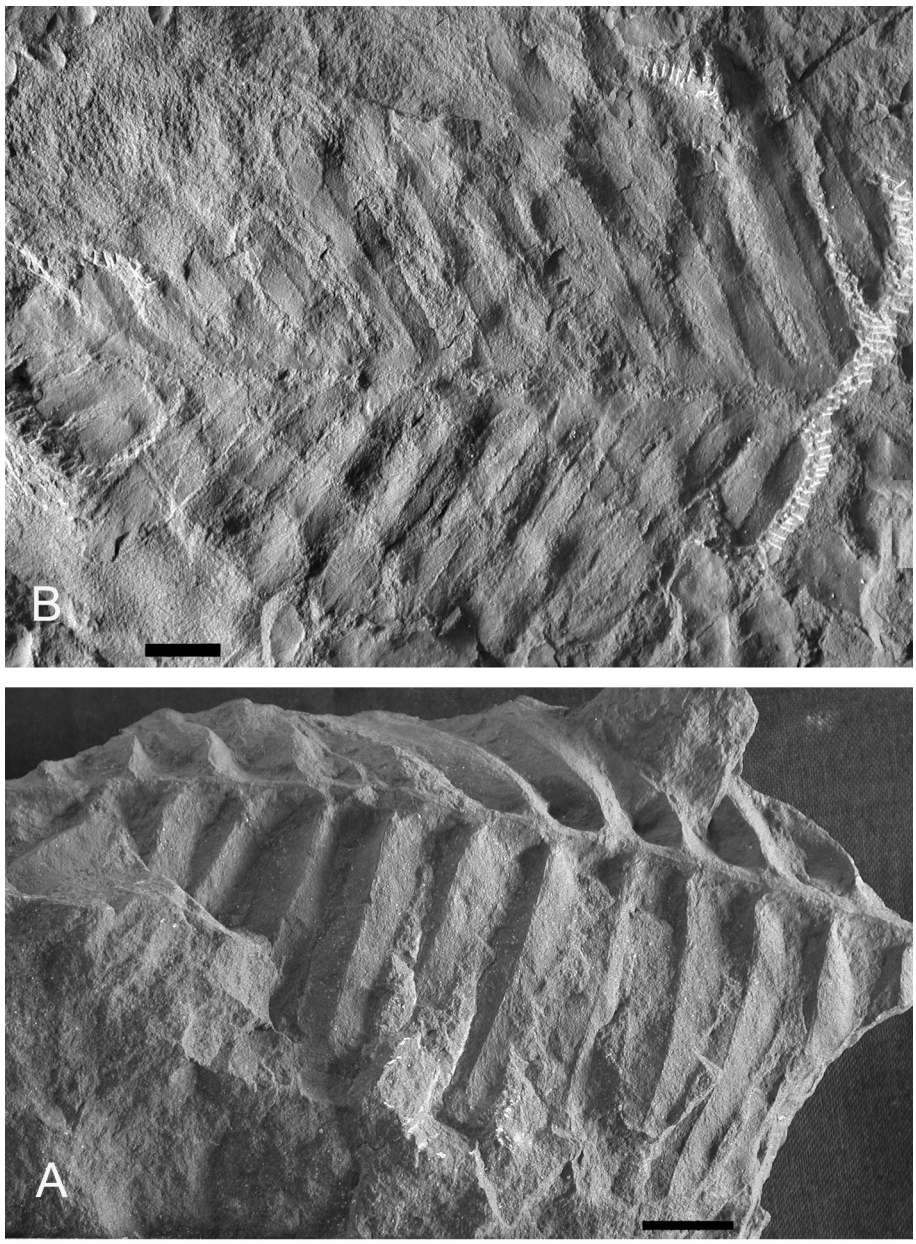

Fig. 3.- *A.* cf. *Supaia.* Specimen illustrated as "*Callipteris uralensis"* by Doubinger and Heyler (1959, Pl. XV, 2), showing the strongly biconvex pinnules. LOD 1020. Rabejac Fm. Scale bar = 10 mm. B. *Supaia* sp. aff. *thinnfeldioides*. Specimen illustrated by Doubinger and Heyler (1975, fig. 2) showing elongated alethopteroid, non overlapping pinnules. MNHNP xx . Rabejac Fm. Scale bar = 10 mm.

Fig. 3.- *A.* cf. *Supaia*. Specimen ilustrado como "*Callipteris uralensis*" by Doubinger and Heyler (1959, Pl XV, 2) mostrando las robustas pínnulas biconvexas. LOD. 1022. Formación Rabejac. Escala de la barra = 10 mm. B. *Supaia* sp. aff. *thinnfeldioides*. Espécimen ilustrado en Doubinger y Heyler (1975, fig. 2) mostrando largos alethopteroides y pínnulas no sobreimpuestas. MNHNP xx. Formación Rebejac. Barra de escala = 10 mm.

cm long and about 15 cm wide (Fig.4). Pinnules were borne along the rachises and as well as shortly below the bifurcation of the rachis. Even if pinnules are partly hidden in the sediment their gross morphology is the same as in the *Supaia* specimen (Fig. 3B) originally illustrated by Doubinger and Heyler (1975). There is no evidence of a marked asymmetry in the size of the pinnules borne on the exterior and on the interior of the forked rachises. In some specimens completely preserved pinnules are up to 75 mm long and 12 mm wide, exceeding the values given by Doubinger and Heyler (1975). Therefore, pinnules are typically elongate, with a large length/width ratio (generally above 6) and they are generally positioned subopposite and densely spaced along the rachis (at intervals of 8 to 15 mm). We agree with previous authors who compared the Lodève *Supaia* with the American species *S. thinnfeldioides*. Comparison with the illustrations provided by White (1929) shows that, amongst the six American species, *S. thinnfeldioides* is the most similar with regard to the size and morphology of the pinnules, differing mainly in pinnule spacing. *Supaia* has been recently described from the Permian of China (Wang, 1997) and Spain (Gand *et al.,* 1997) but in both cases the pinnule morphology (and ratio pinnule length/width) was different and the fronds were significantly smaller than in the specimens from Lodève. Additional information is needed about pinnule nervation and frond variability before a systematic decision is made concerning the Lodève specimens which are designated provisionally as *Supaia* sp. aff. *thinnfeldioides*.

Fig. 4.- *Supaia* sp. aff. *thinnfeldioides*. Specimen showing an entire frond with the characteristic basal bifurcation. MULOD 514. Scale bar = 10 cm.

Fig. 4.- *Supaia* sp. aff. *thinnfeldioides*. Especimen mostrando el fronde entero con características de bifurcación basal. MULOD 514. Barra de escala = 10 mm.

4.1.4. ?Cycads

Taeniopteris sp.1

One specimen (Fig. 5A) in the Montpellier collections comes from the Rabejac Formation; it corresponds to a fragment of distorted leaf, being more than 15 cm long, but neither the base nor the top are preserved. The leaf is characterized by a prominent straight midrib, 6 (basally) to 4-5 mm thick, surrounded by lamina with parallel veins. The maximum width of the lamina, in the supposed median region of the leaf, is 60 mm but there is an apparent gradual diminution towards the basal region. The surface of the midrib is either smooth or longitudinally striated. Secondary veins appear to dichotomize at their very base, then they maintain an angle of 70-80° throughout the lamina; they are about 12 to 15 veins per cm at the leaf margin. There is no evidence of marginal dentation. The identification of this leaf is difficult due to incomplete preservation. We suggest similarities with *Taeniopteris multinervia* and *T. fallax*. The two species possess a strong midrib and a comparably broad lamina. However, some *T. multinervia* have been shown to possess marginal dentation and transferred to the species *T. doubingeri* Remy and Remy (1975). *T. fallax* is interpreted by

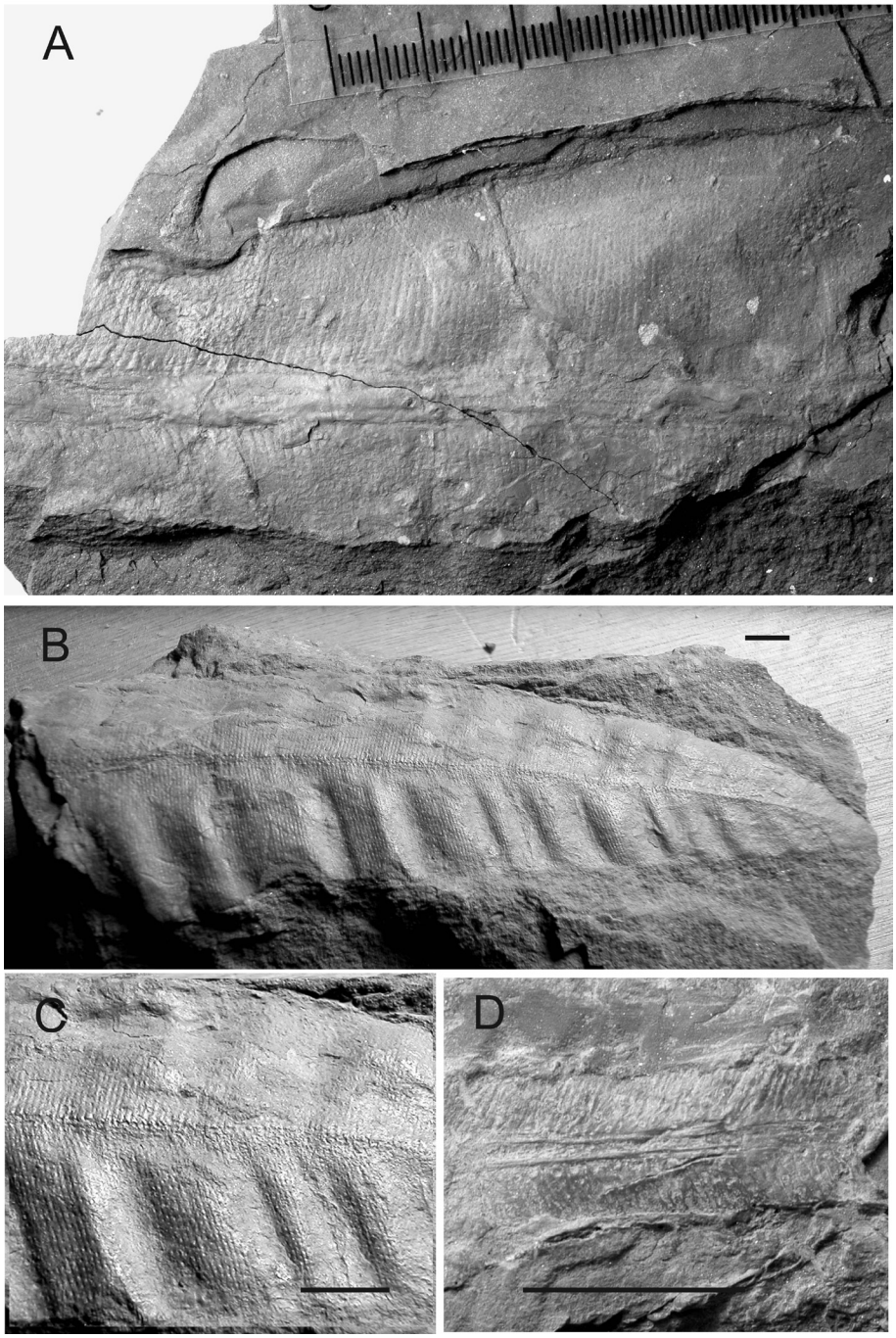

Fig. 5.- A. *Taeniopteris* sp. 1. Specimen with a characteristic strong midrib. LOD 1018. Rabejac Fm. B-C. *Taeniopteris* sp. 2. Leaf with intact apical region and narrow midrib; detail of midrib and venation are shown on (C). MULOD 1236. Scale bar = 10 mm. D. Portion of narrow taeniopterid-like leaf or leaflet with well marked mid vein (aff. *Taeniopteris coriacea*) . LOD 1038, Bouisset, Salagou Fm. Scale bar = 10 mm.

Fig. 5.- A *Taeniopteris* sp. 1. Especimen con una característica robusta vena central. LOD 1018. Formación Rabejac. B-C. Taeniopteri sp. 2. Hoja con region apical intacta y una estrecha vena central. La disposición de las venas (C). MULOD 1236. Escala de la barra = 10mm. D. Porción de una estrecha hoja tipo taeniopterid con una vena media bien marcada (aff.*Taeniopteris coriacea*). LOD 1038, Bouisset Formación Salagou. Barra de escala 10mm.

Doubinger (1956) as spatulate-shaped instead of fusiform as suggested by the present specimen. Another difference concerns the vein density which is at least twice lower in the present specimen than in *T. doubingeri, T. multinervia* and *T. fallax*.

Taeniopteris sp. 2

A nicely preserved leaf, 17 cm long, with its intact apical region (Fig. 5B) is kept in the Lodève Museum Collections. It is interpreted as the median and upper half of an originally very elongated-lanceolate leaf. The main difference with the specimen described above (Fig. 5A) concerns the narrow and rather indistinct midrib from which veins depart at an angle of 70 to 80° (Fig. 5C). Gentle undulations of the lamina have been preserved suggesting a rather quick taphonomic process. The maximum width of the lamina is of 60 to 70 mm, the vein density is of 14 to 17 veins per cm and there is no evidence of marginal dentations, all these features are similar to those of our first specimen. Due to its narrow midrib combined with a broad lamina, this specimen could be attributed to the species *T. abnormis,* a species sometimes considered

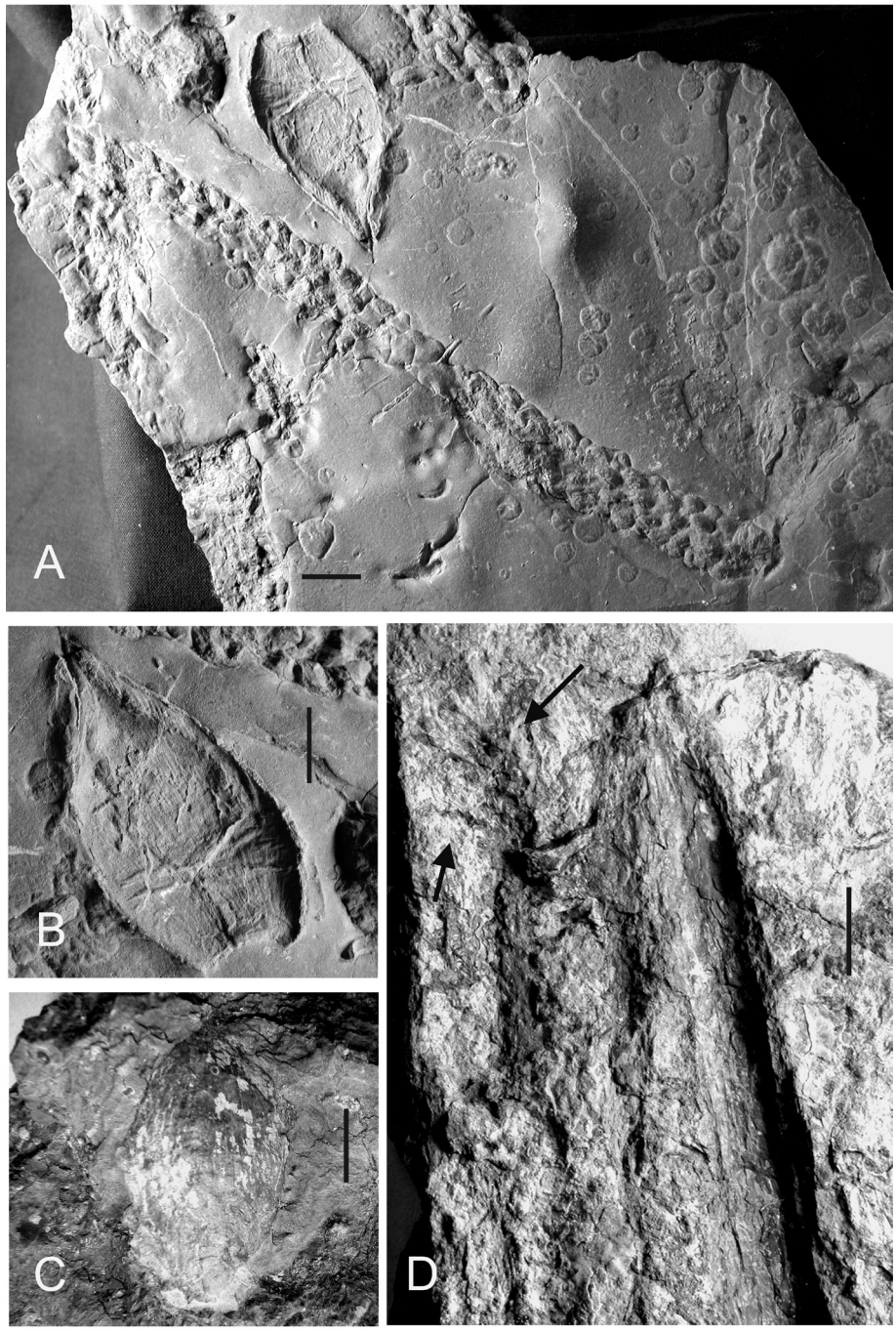

Fig. 6.- A. Probable conifer twig of *Pagiophyllum*-type with short, broad, apparently succulent, leaves. LOD 1019. Rabejac Fm. Scale bar = 10 mm. B. *Lepeophyllum*-like, isolated lanceolate leaf or bract with parallel veins and sharp apex. LOD 1019. Rabejac Fm. Scale bar = 10 mm. C. Problematic almond-like organ . LOD 1027, La Lieude, Salagou Fm. Scale bar = 10 mm. D. Woody axes and possible conifer twigs with attached linear leaves (arrows). LOD 1036, La Lieude, Salagou Fm. Scale bar = 10 mm.

Fig. 6.- A. Probable rama pequeña tipo *Pagiophyllum* con cortos, anchos y aparentemente suculentas hojas. LOD 1019. Formación Rabejac. Escala de barra= 10mm. B. Tipo *Lepeophyllum*, hoja pequeña aislada y lanceolada con venas paralelas y apex afilado. LOD 1019. Formación Rabejac. Barra de escala = 10mm. D. Ejes leñosos y posible rama pequeña de conífera con hojas incluidas (flechas). LOD 1036. La Lieude, Salagou Fm. Barra de escala = 10mm.

as a synonym of *T. multinervia* (see discussion in Doubinger, 1956). Unfortunately, the origin of this specimen is not known.

It is interesting to note that the three species mentioned above (*T. fallax, T. multinervia* and *T. abnormis*) have been recorded by Doubinger (1956) from the Tuilières flora of the Usclas-Saint Privat Formation of the same basin. However, it is the first time that *Taeniopteris* is recorded from red sediments, and the genus occurs up into the Rabejac Formation.

4.1.5. Cordaites and Conifers

Doubinger and Kruseman (1965) mentioned the frequency of very fragmentary remains of walchian conifers occurring both in the Rabejac Formation and in the underlying Transition Zone but only a few specimens have been illustrated and/or identified at the specific level (Table 1): *Otovicia hypnoides* (only from the Transition Zone), *Ernestiodendron filiciforme* and *Culmitzschia hirmeri* (both from the Transition Zone and the Rabejac Formation). Revision of the available collections provided little new

data except one specimen from Rabejac, collected by J. Garric, showing a branched twig, about 12 mm diameter, with short and broad leaves (Fig. 6A). Morphologically these leaves appear succulent and resembling mesozoic conifers like *Pagiophyllum* or *Cyparissidium*. It is of particular interest, that this twig is associated with an isolated lanceolate leaf or bract of about 5 cm long and 2.5 cm wide, with a broad base, a sharp apex and a dense system of parallel veins (Fig. 6B). This is comparable to scaly leaves attributed to the cordaitean genera *Crassinervia* or *Lepeophyllum* (Neuburg 1965) from the Permian of Angara. A second specimen from Rabejac suggests the attachment of two similar scaly leaves to an axis.

5. Macroflora from the Salagou Formation

We present here, for the first time, information on plants from the Salagou Formation thanks to the intensive collecting of J. Lapeyrie in diverse fossiliferous rills and of additional collections of J. Schneider and colleagues from the Arièges and La Lieude localities (see suggested stratigraphy of these horizons in Garric, 2001).

During an excavation at La Lieude locality (site F 17 G) the red pelites have yielded a number of small stems partially preserved three-dimensionally but without anatomy, up to 30 cm long, with a diameter of 1 to 5 cm. These fragments cannot be identified but they may be interpreted as branches of woody plants. In association with these axes, a large number of almond-like organs (Fig. 6C) have been found; they range from 4 to 7 cm long and 2 to 4 cm wide and their surface is always striated. These problematic fossils are very difficult to interpret and their exact nature (? plants or invertebrates) is questioned. If they were plants, they certainly were deciduous organs (? seeds or buds of scaly leaves). It may be interesting to compare them to the possible cordaitean scaly leaves described above (Fig. 6B) from the Rabejac Formation which show a similar morphology.

The red pelites from the Arièges locality have yielded small repeatedly branched axes (2 mm diameter), terminating in narrow ultimate segments up to 40 mm long with a central vascular strand (Fig. 7A). They are interpreted as portions of fronds where the laminae are dichotomously or pinnate dichotomously divided as described in *Dichophyllum moorei* (Andrews, 1941, figs. 11-18; Meyen, 1987, fig. 48f).

The fossiliferous rills of the Salagou Formation have been discovered by J. Lapeyrie, in which he found new well preserved fossils (mainly crustaceoans and insects). These rills are silt bodies formed of fine siltites with a colour varying from grey-green to red; some fossils plants have been found in association with, but less commonly than, animals. Among the plants are cylindrical axes (Fig. 7B), certainly fragments of woody branches, that cannot be identified, as well as twigs with attached incomplete linear leaves (Fig. 6D, arrow) that may represent voltzialean conifers. Of more interest is a small cone 1.6 mm diameter, three-dimensionally preserved but exposed in median longitudinal section (Fig. 7D). It is interpreted as a male cone composed of peltate microsporophylls, the elongate sporangia being attached to the heel of the microsporophyll and parallel to the stalk. Pollen sacs are visible near the top of the cone and one is lying obliquely (arrows, Fig. 7E). This pollen cone is similar in size and organization to Triassic cones referred to as *Masculostrobus* or *Willsiostrobus* (Grauvogel- Stamm and Schaarschmidt, 1978, 1979). Several examples of narrow, dichotomously branched axes have been found in fossiliferous rills (Fig. 7C). They are reminiscent of leaves of *Sphenobaiera digitata* (Meyen 1987, fig. 48h) or even of the Mesozoic genus *Czekanowskia* (Florin, 1936, Pl. 32, figs 7-10). Finally, one small taeniopterid-like leaf (Fig. 5D), only 7 mm wide, is considerably smaller than the taeniopterids from the Rabejac Formation; however, the well-marked main vein and branched lateral veins are well preserved and this specimen certainly belonged to a pinnate taeniopterid leaf with narrow pinnules like *Taeniopteris coriacea*.

6. Discussion

The present reinvestigation of the fossil plant assemblages from the Permian red beds of the Lodève Basin revealed a marked decrease in plant diversity by comparison with the older flora from the "grey Autunian" which comprises 46 taxa (Doubinger, 1956). In the Tuilières-Loiras Formation, 22 taxa have been recorded, including those from the Transition Zone, with 18 taxa found in grey sediments (Doubinger, 1963; Galtier and Broutin, 1995) and only 8 in red sediments (Doubinger and Kruseman 1965). For the overlying Viala Formation, which yielded a microflora (association LO3 of Doubinger *et al.,* 1987), we found a single specimen that we identified as *Rhachiphyllum* sp. However the Rabejac Formation yielded a dozen of taxa whilst only a pair of specimens were identifiable from the Salagou Formation. The unfavourable conditions of fossilisation in these red sediments evidently account for the small number of well preserved and taxonomically identifiable specimens.

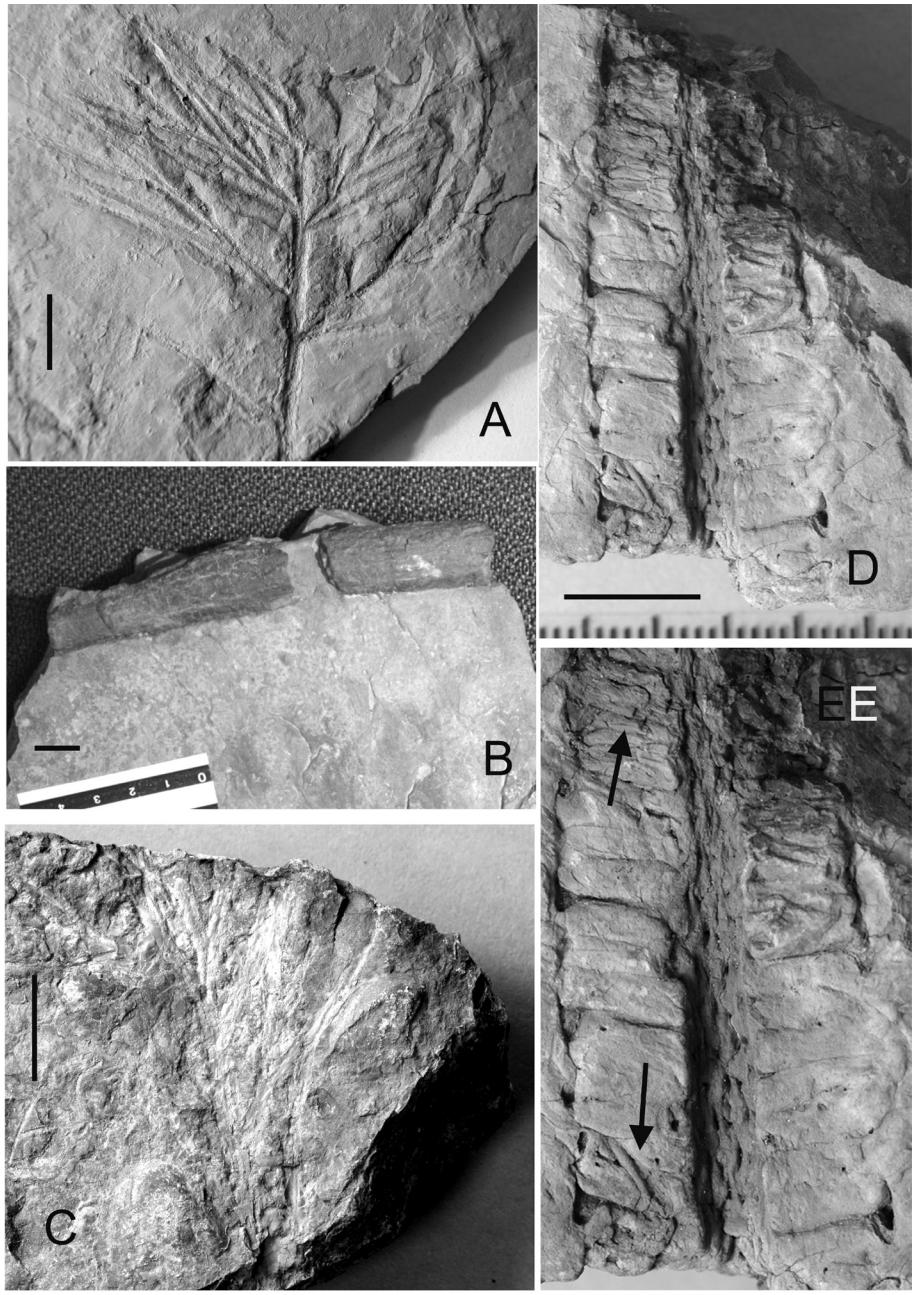

Fig. 7.- A. Fragment of branched leaf similar to *Dichophyllum moorei*. LOD 1030, Arièges, Salagou Fm. B. Portion of large cylindrical stem. LOD 1035, Rieupeyre, Salagou Fm. Scale bar = 10 mm. C. *Sphenobaiera*-like leaf. LOD 1032, Le Deves, Salagou Fm. D-E. Male conifer cone similar to *Willsiostrobus* showing peltate bracts. Elongate pollen sacs are visible (arrows). LOD 1037, Dio, Salagou Fm.

Fig. 7.- Fragmento de hoja ramificada de *Dichophyllum moorei*. LOD 1030, Ariéges, Formación Salagou. B. Parte de un tallo largo y cilíndrico. LOD 1035, Rieupeyre, Formación Salagou. Escala de barra = 10 mm. C. Hoja tipo *Sphenobaiera*. LOD 1032, Le Deves, Formación Salagou. D-E. Cono macho de conífera de *Willsiostribus* mostrando pequeñas hojas protegidas. Son visibles los sacos alargados de polen (flechas). LOD 1037, Dio, Formación Salagou.

According to previous work by Doubinger and collaborators and to the present investigation, we propose the following lists of plant assemblages from the successive red beds in the Lodève Basin. (N.B. The taxa inside brackets have not been found again or never illustrated and they are considered as very doubtful):

1) Red beds from the Transition Zone (Tuilières –Loiras Formation): *Autunia conferta, cf. Supaia =“Callipteris* cf. *uralensis”, cf. Peltaspermum martinsii, Walchia sp., Culmitzchia* cf. *hirmeri, Otovicia hypnoides,* (*Schuetzia* sp., cf. *Ullmannia*)

2) Viala Formation: *Rhachiphyllum* sp.

3) Rabejac Formation: *Autunia conferta, Rhachiphyllum* sp., cf. *Peltaspermum martinsii, cf. Supaia =”Callipteris* cf. *uralensis”, Supaia* sp. aff. *thinnfeldioides*, *Taeniopteris* sp.1 et sp. 2, cf. *Lepeophyllum*, *Walchia* sp., *Culmitzchia* cf. *hirmeri, Ernestiodendron filiciforme*, *Pagiophyllum*-like leafy twigs, (*Pecopteris cyathea*, cf. *Pseudoctenis middrigensis*).

4) Salagou Formation: cf. *Willsiostrobus, Taeniopteris* sp. aff. *coriacea*, *Sphenobaiera* sp., *Dichophyllum* aff. *moorei* (? n. sp), diverse leafy conifer twigs and small branched axes, probable seeds and roots, all taxonomically unidentifiable even at the generic level.

Some remarks have to be made concerning these lists of plant assemblages:

- We only took in consideration the specimens with an undisputable mention of origin, this means that several ten specimens in the collections of Montpellier and Lodève have been identified but not listed, they all correspond to known taxa.

- In the list of plants from the Transition Zone, we are very sceptical with regard to *Schuetzia* and *Ullmanni*a, two taxa not illustrated and just mentioned with strong reservations by Doubinger and Kruseman (1965).

- Similarly in the Rabejac list, the unique specimen attributed to *Pseudoctenis* has not been located and the short description provided by Doubinger and Kruseman could apply to many specimens of "*Callipteris* cf. *uralensis"* = cf. *Supaia*. We are also sceptical with regard to the identification of *Pecopteris cyathea*, of which the figured specimen could not be located.

The comparison of the floras from the red beds with those from the grey sediments reveals differences that are certainly ecologically significant; this is particularly evident if we consider the probably contemporaneous floras from the grey versus the red beds of the Transition zone. The sphenopsids (*Annularia spicata, Calamites cistii, C. cruciatus, C. gigas, Sphenophyllum thonii*) are very diversified in the first but absent in the red sediments; similarly the callipterids with small pinnules (*Arnhardtia mouretii, Gracilopteris strigosa, Rhachiphyllum schenkii*), but also *Odontopteris subcrenulata, Cordaites borassifolius* and *Poacordaites* which were extending from the basal Autunian into the grey sediments of the Transition zone become absent in the red sediments. The changes in environment (increased dryness) which were certainly responsible for these differences, did not affect the conifers and some callipterids so abruptly; *Autunia conferta* seems to persist up to the Rabejac Formation whilst callipterids (*Supaia*) with large and thick pinnules were certainly better adapted to the dry environment. Interestingly also, some broad-laminate taxa like *Taeniopteris* , already present in Late Carboniferous coal swamp environment and in the basal "Autunian", reappear in the Rabejac Formation and apparently extend up into the Salagou Formation. Some new data, for example the possible occurrence of cordaiteans with scaly leaves of *Lepeophyllum* or *Crassinervia* type, previously known from the Permian of Angara, the occurrence of *Dichophyllum*-like leaves and the conifers with broad, possibly succulent, leaves and small cones of *Willsiostrobus* type similar to Triassic conifers, may represent new transitional forms to the Mesozoic flora. This needs to be confirmed by additional collecting and observations.

7. Comparison with other contemporaneous floras and conclusions

Considering the plant species diversity in the "red beds" of the Transition zone and the Rabejac Formation, the Lodève Basin must be considered as the second in taxa richness after the Hermit Shale (Grand Canyon, Colorado, USA) with regard to this type of facies. This is particularly spectacular concerning the abundance of fronds belonging to *Supaia*, a genus only known, except the Hermit Shales, in Shanxi, China and in the Cantabrian Mountains, Spain. Therefore one may suggest that these localities (at least the euramerican ones) are approximately contemporaneous. In fact, a correlation of the Pena Segra locality (Cantabrian mountains) with the "zone 4" of the Rajejac Formation has been already proposed (Gand *et al.,* 1997) based on ichnofossil biozones.

In contrast, it is more difficult to compare the flora from the Salagou Formation with those from "red beds" of other west-European Permian Basins. Most of the red beds of other Basins such as Rodez, Saint-Affrique, or the Upper Rotliegendes Thuringia, are generally "aphytic" or contain plant associations comparable to that of Rabejac, even in the upper levels of the series: for example Gasberg locality, Rotterode beds, in Thuringia (Lützner, 1987).

The famous "thuringian" macrofloras reported in other basins such as Agay (Visscher, 1968), Toulon (Durand, 2006), etc., with *Ullmannia frumentaria*, *U. bronnii*, *Quadrocladus orobiformis*, *Pseudovoltzia liebeana*, *Sphenobaiera digitata* come from dark grey sediments, rich in organic matter (a facies that does not occur in Lodève-Saint-Affrique-Rodez), intercalated within the red beds deposits. However we found, in the Salagou Formation, some leafy twigs similar to *Ullmannia* or *Pseudovoltzia liebeana,* with rare cones suggestive of conifers known in the Triassic.

Comparisons of macrofloras and, a fortiori, biostratigraphic correlations, between the red beds of the different west European Permian basins remains difficult. An exhaustive re-investigation of the collections of specimens originating from the different localities and, eventually, new collecting in this "unpromising" facies, supposed late Permian ("Thuringian" s.l.) would be necessary for comparison with the Salagou paleoflora and for establishing an inter-calibration with the zonation based on ichnofossils.

Acknowledgements

We are greatly indebted to J. Lapeyrie, J. Garric, J. Schneider, G. Gand, P. Ellenberger and D. Heyler who collected a number of specimens used in this study. We thank also J. Dejax and D. de Franceschi, Muséum National Histoire Naturelle, Paris and M. Valles-Bled and S. Fouché, Musée Fleury, Lodève, for access to material kept in their Museum collections.

References

Andrews, H. N. (1941): *Dichophyllum moorei* and certain associated seeds. *Ann. Missouri Bot. Gard.,* 28: 375-384.

Doubinger, J. (1956): Contribution à l'étude des flores autuno-stéphaniennes. *Mém. Soc. géol. France*, N.S., 35: 1-180.

Doubinger, J. (1963): Nouvelles observations sur la flore fossile de l'Autunien de Lodève. *C.R. somm. Soc. géol. France*, 3: 74-75.

Doubinger, J., Heyler, D. (1959): Note paléontologique sur le Permien de Lodève et de Bourbon-l'Archambault. *Bull. Soc. géol. France*, 1: 304-311.

Doubinger, J., Heyler, D. (1975): Nouveaux fossiles dans le Permien français. *Bull. Soc. géol. France*, 17: 1176-1180.

Doubinger, J., Kruseman, G. P. (1965): Sur la flore du Permien de la région de Lodève (zone de transition et Saxonien inférieur). *Bull. Soc. géol. France*, 7: 541-548.

Doubinger, J., Odin, B., Conrad, G. (1987): Les associations sporopolliniques du permien continental du basin de Lodève (Hérault, France). Caractérisation de l'Autunien supérieur, du Saxonien et du Thuringien. *Ann. Soc. géol. Nord*, 106: 103-109.

Durand, M. (2006): The problem of the transition from the Permian to the Triassic Series in southern France: comparison with other Peritethyan regions. In: Lucas S. G., Cassinis, G., Schneider, J.W. (eds.), *Non Marine Permian Biostratigraphy and Biochronology*, Geological Society Special Publication, 265: 281-296.

Fairon-Demaret, M., Hilton, J., Berry, C.M. (1999): Surface preparation of macrofossils (dégagement). In: T.P. Jones, Rowe, N.P. (eds.), *Fossil Plants and Spores: modern techniques*: 33-35, Geological Soc., London.

Florin, R. (1936): Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen alters. *Palaeontographica* B, 81: 72-173.

Florin, R. (1938-1944): Die Koniferen des Oberkarbons und des unteren Perms. *Palaeontographica* B, 85: 1-729.

Galtier, J., Broutin, J. (1995): La flore de la Zone de transition de l'Autunien supérieur de Lodève. *Sci. Géol. Bull. Strasbourg*, 48: 83-93.

Gand, G., Kerp, H., Parsons, C., Martinez-Garcia, E. (1997): Palaeoenvironmental and stratigraphical aspects of animal traces and plant remains in Spanish Permian red beds (Pena Segra, Cantabrian Mountains, Spain). *Geobios*, 30: 295-318.

Garric, J. (2001): Les rigoles fossilifères du Saxonien du bassin de Lodève. *Bull. Soc. Hist. Nat. Autun*, 173: 7-48.

Grand'Eury, C. (1877): Flore carbonifère du département de la Loire. *Mémoires Acad. Sci. Paris,* 24: 1-624.

Grauvogel-Stamm, L., Schaarschmidt, F. (1978): Zur Nomenklatur von *Masculostrobus* Seward. *Sci. Géol. Bull. Strasbourg*, 31: 105-107.

Grauvogel-Stamm, L., Schaarschmidt, F. (1979): Zur Morphologie une Taxonomie von *Masculostrobus* Seward und anderen Formgattungen peltater männlicher Koniferenblüten. *Senckenbergiana lethaea,* 60: 1-37.

Kerp, J.H.F. (1988): Aspects of Permian palaeobotany and palynology. X. The West- and Central European species of the genus *Autunia* Krasser emend. Kerp (Peltaspermaceae) and the form-genus *Rhachiphyllum* Kerp (callipterid foliage). *Rev. Paleobot. Palynol*., 54: 249-360.

Kerp, H. (2000): The modernization of landscapes during the Late Paleozoic-Early Mesozoic. In: R.A. Gastaldo, W.A. DiMichele (eds.), *Phanerozoic Terrestrial Ecosystems*. The Paleontological Soc. Papers, 6: 79-111.

Kerp, J.H.F., Haubold, H. (1988): Aspects of Permian palaeobotany and palynology. VIII. On the reclassification of the West- and Central European species of the form-genus *Callipteris* Brongniart 1849. *Rev. Palaeobot. Palynol.,* 54: 135-150.

Körner, F., Schneider, J.W., Gand, G. (2005): Sedimentology and geochemistry of the Permian red beds of the Lodève Basin- implications for environment and climate. *Abstracts Permian and Triassic playas Symposium*, Montpellier: p. 17-18.

Lopez, M., Gand, G., Garric, J., Körner, F and Schneider, J. (2008). The playa environments of the Lodève Permian basin (Languedoc, France). *Journal of Iberian Geology,* 34 (1): 29-56.

Lützner, H. (1987). Sedimentary and Volcanic Rotliegendes of the Saale Depression, *Symposium on Rotliegendes in Central Europe, Erfurt, 1987: Excursion Guide Book*, 132p.

Meyen, S.V. (1987). *Fundamentals of Palaeobotany*. Chapman and Hall, London, 432p.

Neuburg, M. F. (1965): Permian Flora of Pechora Basin. Part II. Cordaiteans (Cordaitales), Vojnovskeans (Vojnovskyales), Gymnosperm seeds of an undetermined position (Semina Gymnospermarum incertae sedis). *Trans. Acad. Sc. USSR, Geol. Inst*., 116: 1- (in russian).

Odin, B., Doubinger, J., Conrad, G. (1986): Attribution des formations détritiques rouges du Permien du Sud de la France au Thuringien, d'après l'étude du bassin de Lodève: implications géologiques, paléontologiques et paléoclimatiques. *C. R. Acad. Sci. Paris*, 302: 1015-1020.

Poort, R.J., Kerp, J.H.F. (1990): Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of Western and Central Europe and a reclassification of species formerly included in *Peltaspermum* Harris. *Rev. Palaeobot. Palynol.* 63: 197-225.

Remy, W., Remy, R. (1975): Beiträge zur Kenntnis des morpho-genus *Taeniopteri*s Brongniart. *Argumenta Palaeobotanica*, 4: 31-37.

Stoneley, H.M.M. (1958): The Upper Permian Flora of England. *Bull. Brit. Mus (Nat. Hist) Geology*, 3: 293-337.

Visscher, H. (1968): On the Thuringian age of the Upper Palaeozoic sedimentary and volcanic deposits of the Estérel, Southern France. *Review of Palaeobotany and Palynology*, 6: 71- 83.

Visscher, H., Kerp, H., Clement-Westerhof, J.A., Looy, C.V. (2001): Permian floras of the soutern Alps. *Natura Bresciana Ann. Mus. Civ. Nat., Brescia,* Monograf. 25: 117-123.

Wang, Z.-Q. (1997): Permian *Supaia* fronds and an associated *Autunia* fructification from Shanxi, China. *Palaeontology,* 40: 245-277.

White, D. (1929): Flora of the Hermit Shale in the Grand Canyon, Arizona. *Carnegie Inst. Washington Publ.* 405: 1-221.

Zalessky, M.D. (1927): Flore permienne des limites ouraliennes d'Angaride. *Mémoires Comité géologique*, N.S. 176: 5-52.

Zeiller, R. (1898): Contribution à l'étude de la flore ptéridologique des schistes permiens de Lodève. *Bull. Mus. Hist. Nat. Marseille*, 1: 6-69.