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On a small flora with Araucariaceous conifers from the Röschenz Beds of Court, Jura Mountains, Switzerland

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Key words: Oxfordian, Jura Mountains, Araucariaceous conifers, new species, *in situ* pollen

ABSTRACT

Within the Röschenz Beds of the Vellerat Formation (Middle to Late Oxfordian; Jura Mountains of Switzerland) a small flora containing three taxa has been found: the araucariaceous conifer *Pagiophyllum cirinicum*, the female cone scale *Araucarites falsanii* and the male cone *Masculostrobus graiterensis* sp. nov. with *in situ* pollen that are thought to belong to the species as well. The size of the plant remains and the association with the cones implies a parautochthonous assemblage. The deposits from which the flora was collected are situated in a facies transition from the Günsberg to Röschenz Beds. The *in situ* pollen indicate a short transport distance which has paleogeographic implications.

ZUSAMMENFASSUNG

Innerhalb der Röschenz-Schichten der Vellerat Formation (mittleres bis spätes Oxfordium des schweizerischen Juragebirges) wurde eine kleine, aus drei Taxa bestehende Flora gefunden: die araucaroide Konifere *Pagiophyllum cirinicum*, die weibliche Samenschuppe *Araucarites falsanii* und der männliche Zapfen *Masculostrobus graiterensis* sp. nov. mit *in situ* Pollen, die vermutlich zu dieser Spezies gehören. Die Grösse der Pflanzenreste sowie die Assoziation mit den Zapfen deuten auf eine parautochthone Vergesellschaftung hin. Das beschriebene Material stammt aus einer Übergangsfazies zwischen den Günsberg- und Röschenz-Schichten. Die *in situ* Pollen deuten auf einen kurzen Transportweg, was von paleogeographischer Bedeutungen ist.

1. Introduction

This paper provides a further look into the paleobotany of the Middle Oxfordian in the Jura Mountains. Recently, van Konijnenburg-van Cittert & Meyer (1996) described a flora from the Röschenz Beds (formerly Natica Beds (Gygi 1995)) of the Vellerat Formation in the La Charuque quarry near Péry-Reuchenette (Canton Bern, Switzerland). They also discussed in detail a historic overview of Late Jurassic plant fossils in the Swiss Jura Mountains.

The purpose of the present work is to describe and discuss a new flora, again from the Röschenz Beds, consisting of three araucariaceous species (leaves and fructifications). Like the La Charuque flora, this flora also originated in a coastal environment. Thus further evidence is provided that supratidal environments may have covered significant areas of at least parts of the Jura Mountains during the Middle Oxfordian.

Moreover, palynological samples from the material were studied to see if traces from a larger flora could be detected.

2. Geological setting and material

The outcrop from which the small flora was recovered lies on the Graitery anticline on the eastern side of the Gorge de Court (Fig. 1). This locality has not been studied previously. Samples were taken for both paleontological and sedimentological examination, while care was taken to avoid contamination of the samples used for the palynological analysis. Thin sections of sediments were stained for carbonates. The deposits are entirely marine with mainly oolites and pellets in the lower half of the section and marly, lagoonal limestones, containing red oncolites and bioclasts (mainly large gastropods) in the upper half (Fig. 2). Two successive layers of reworked coral heads lie in the lagoonal deposits. They are interpreted as having been washed in from a nearby reef. Patch reefs are common in strata of the same age in nearby outcrops. The oolite bars indicate a water depth in the range of 5–10 m.

The plant material appears to have been deposited after a storm or tidal event. Large plant debris (logs with diameters of

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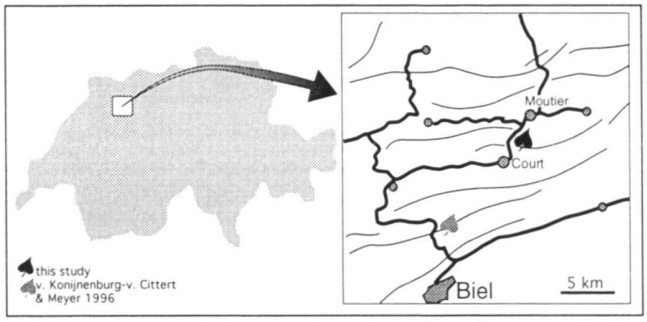


Fig. 1. Map showing the location of the outcrop (593.980 / 234.440). The locality lies between the villages of Court and Moutier. Anticlines are figured as thin lines, roads as thick lines.

up to 20 cm) are oriented in an east-west direction. A predominantly easterly paleo-current direction is deduced from the foresets within the oolite bars below the plant bearing beds. In one cluster of smaller plant debris, such as shoots, leaves and cones, the debris is aligned with a north-south orientation and is accumulated in an erosive depression formed by a minor channel on an oolite bar. Further clusters were found a few centimeters upsection in a marly oolite.

The site lies in a facies transition from the Günsberg to Röschenz Beds. To the east outcrops of the Günsberg Beds are found while in the Gorge de Court to the west the Röschenz Beds crop out.

The fossil material described here was obtained from one bed especially rich in plant detritus (arrow in Fig. 2).

Figured and described specimens are stored in the collection of the Natur Museum Solothurn (samples are numbered with the prefix "NMS"), the sedimentological samples from the section studied (Fig. 2) are stored at the Geological Institute of the University of Basel.

3. Methods

The fossils were studied under a dissecting microscope and, whenever possible, cuticle and pollen preparations were made to confirm the determinations. Cuticles and in situ pollen were prepared by macerating in Schultze's reagent (a saturated mixture of KClO3 and 33% HNO3), followed by neutralization in 5% ammonia. After rinsing thoroughly in water, the upper and lower cuticles were separated with needles and transferred to slides (mounted in glycerin jelly and sealed with paraffin). For the pollen preparations, complete pollen sacs were macerated in the same way as the cuticles. After a thorough rinse in water, the pollen mass was transferred to a slide and the pollen grains (mounted in glycerine) were then gently separated with needles. Finally the slide was sealed with paraffin. The slides were studied and photographed with a Leitz Ortholux microscope. The palynological samples were treated with heavy

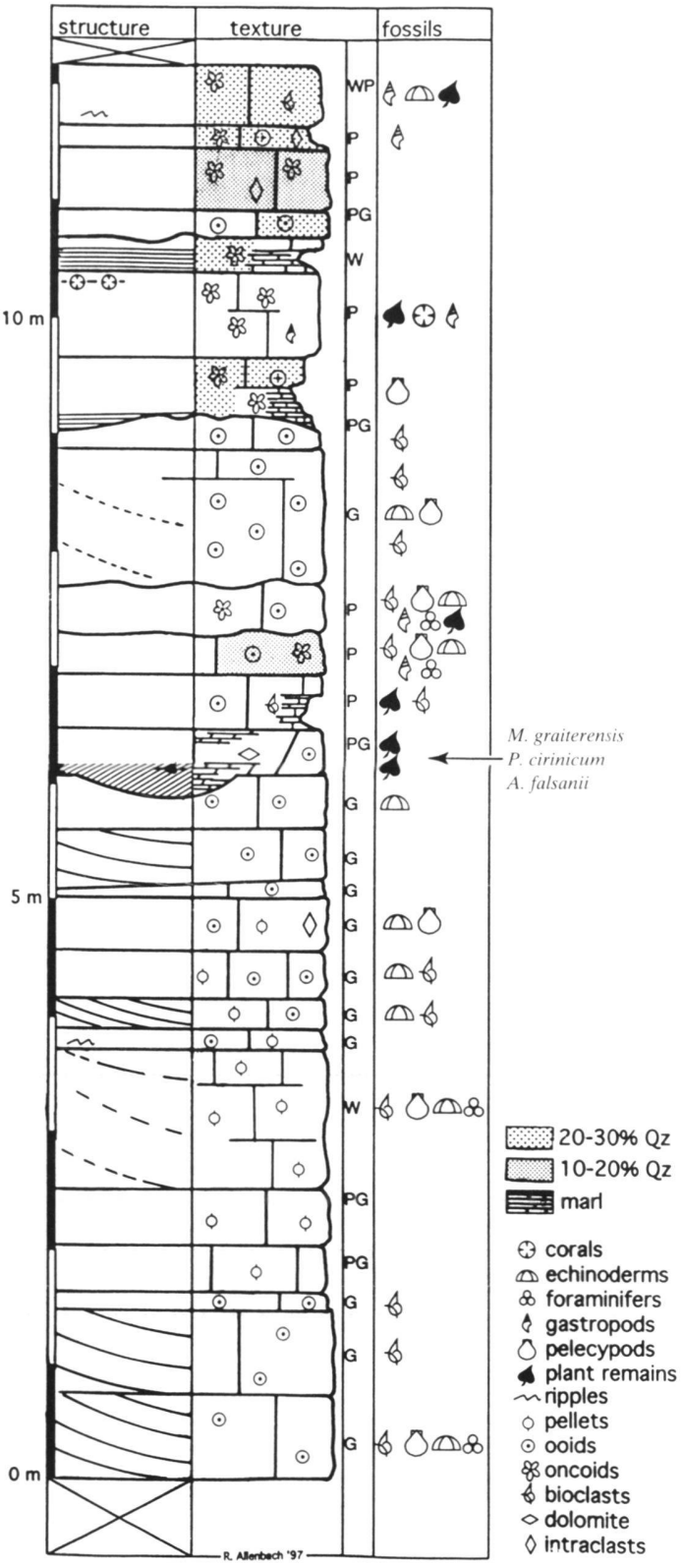


Fig. 2. Stratigraphic column of the Röschenz Beds at the Court locality.

liquid separation ($ZnBr_2$) and the sample residues were sieved using an 18 µm metal precision sieve. Some of the samples were treated with 3% KOH and the remainder with Schultze's reagent to bleach the palynomorphs. For the slides glycerin jelly was used as a mounting medium. It should be noted that heating of the samples resulted in an immediate dissolution into tiny, amorphous fragments.

4. Systematic descriptions

Coniferopsida
Order Coniferales
Family Araucariaceae

Genus *Pagiophyllum* HEER
Pagiophyllum cirinicum (SAPORTA) HEER emend. Barale
(Fig. 3–4)

Description

Within the examined material numerous stem and shoot fragments of various sizes were found. The largest stem fragment has an overall length of 9 cm and is 1.2–1.5 cm wide (Fig. 3a). No further details could be seen.

Among the shoot fragments a specimen of probably penultimate order with an axis approximately 5 mm wide was found, along with some remnants of leaves (Fig. 3b). This is the best preserved specimen. The free part of those leaves is around 3–4 mm long. Small ultimate shoot fragments are quite common; e.g., a fragment 5.5 cm long, with spirally arranged leaves around a 1.5 mm wide axis (Fig. 3a) and leaves approximately 5–6 mm long. The leaf base cushions are 2–2.5 mm high and the free parts of the leaves are 3–5 mm in length. Leaves are thick and slightly falcate.

Only small fragments of cuticle could be recovered; normal epidermal cells between the stomata are rectangular to almost isodiametric. The stomata themselves appear to be arranged in bands, and within the individual bands in short longitudinal files (Fig. 4a). Within these bands the stomata are densely clustered, separated by only 1–4 epidermal cells. Stomata are longitudinally oriented and incompletely dicyclic. Guard cells are only slightly sunken, surrounded by 4–6 subsidiary cells and an irregular and often incomplete ring of encircling cells (Fig. 4b). No papillae are present, on the subsidiary cells or on the normal epidermal cells.

Discussion

Barale (1981) gives a detailed description of *Pagiophyllum cirinicum* which was originally described from Kimmeridgian sediments in Portugal and France (Saporta 1879, Heer 1881). The species has also been recorded from Oxfordian sediments in Germany (Salfeld 1909) and Kimmeridgian deposits in Spain (Amor 1951, Ferrer 1951). Barale (1989), however, demonstrated that *P. cirinicum* was not present in Spain.

The specimens described here agree in all macromorphological aspects with Barale's emended diagnosis. Since we only have small cuticle fragments, we cannot be sure if stomata are present on both the upper and lower cuticle (amphistomatic cuticle) as in *P. cirinicum*. In the largest fragment, the stomata appear to be arranged in a band (Fig. 4a). Barale (1981) stated that on the upper cuticle the stomata were arranged in short files with stomata occurring occasionally outside the files. On the lower cuticle two broad stomatal bands with marginal and median stomata-free zones were described. Within the bands the stomata were arranged in files, but with stomata occurring frequently outside the files. The stomata were usually imperfectly dicyclic and occasionally perfectly dicyclic (around the guard cells a ring of subsidiary cells plus a more or less complete ring of encircling cells was seen).

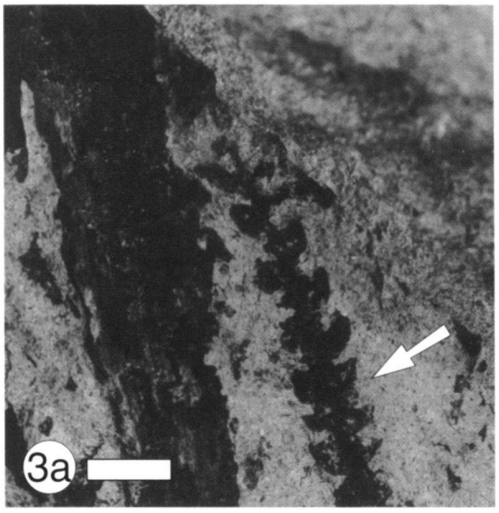
Although we only have small cuticle fragments, the material matches the descriptions made by Barale (1981). The fact that these are found in association with the female cone scale further supports the attribution of these specimens to *P. cirinicum*.

P. cirinicum is attributed to the conifer family Araucariaceae[3] mainly because of its female cone scales (Barale 1981). The general shoot morphology and cuticle anatomy support this classification. Stomata with a more or less complete ring of encircling cells and subsidiary cells (as well as normal epidermal cells) without papillae are typical for the Araucariaceae. Despite their being small, our cuticle fragments agree with this description and we do not hesitate to attribute our material to this species, moreover, because the female cone is associated as well.

The female cone scale of *P. cirinicum* is known from both Portugal and France as *Araucarites falsanii* (SAPORTA) BARALE, although a complete cone has never been found. So far, one female cone scale has been found in our material which is described in the next paragraph.

Male cones of *P. cirinicum* are not yet known from either Portugal or France, although Barale (1981) described two male cones with araucariaceous pollen grains from the Creys locality (France) where *P. cirinicum* is common. His *Masculostrobus* sp. A (BARALE) is a small cone that yielded relatively small inaperturate pollen grains (mean diameter 38 µm). He compared this cone to that of *Brachyphyllum thuioides* (POMEL) BARALE. The second species, *Masculostrobus* sp. F (BARALE) will be discussed in more detail in the next paragraph since it is comparable to the male cones found in our material.

[3] *Pagiophyllum* as a whole is a foliage genus and therefore it can not be assigned to a family when based on reproductive characteristics only. However, attribution to a family is possible at species level which is the common procedure.



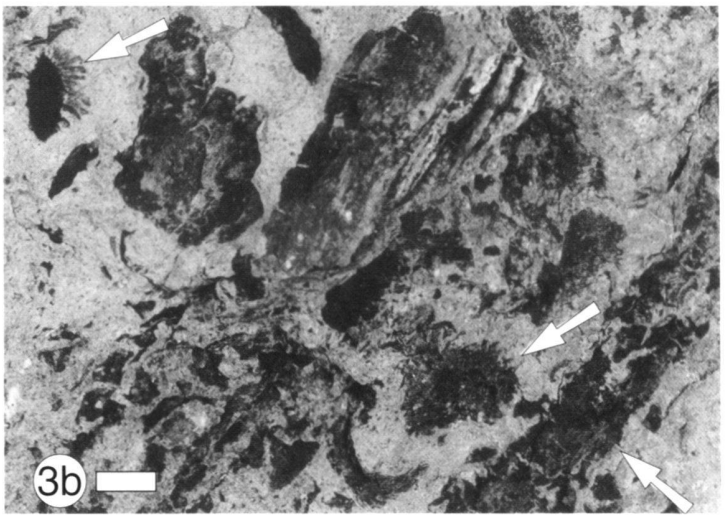


Fig. 3. *Pagiophyllum cirinicum* (SAPORTA) BARALE.
a. One of the numerous stem fragments plus a fragment of an ultimate shoot (arrow); bar = 5 mm. NMS 20882
b. Fossil assemblage with an Araucarian shoot fragment (right arrow), oblique view of a male cone (center arrow) and a further male cone (left arrow); bar = 5 mm. NMS 20882

Fig. 4. *Pagiophyllum cirinicum* (SAPORTA) BARALE.
a. part of a stomatal band; bar = 40 µm
b. stomata; bar = 25 µm

Genus *Araucarites* PRESL
Araucarites falsanii (SAPORTA) BARALE
(Fig. 5)

Description

Only one female cone scale was found (see Fig. 5) in our material. The length of the scale itself is 13 mm, with an additional acute apical tip 3 mm in length. The maximum width of the scale is 11 mm wide. A faint imprint of a seed can be observed which is 9 mm long and 3 mm wide. A cuticle could not be obtained from the specimen as it was only an imprint.

Discussion

The species has been described in detail by Barale (1981) but to date complete cones of this species have not been found. In length the cone scales vary between 12 and 23 mm, and between 11 and 13 mm in width. The base is approximately 5 mm wide. Apically, the scales end in a long acute tip which is normally about half the length of the cone scales. These scales carry one large, oval, median seed.

In its general morphology the Röschenz Beds cone scale matches with this description, and although the apical tip is not as long as in some of Barale's specimens, it is clearly present and corresponds well with the specimens figured by Barale in his plate 52 figures 1 and 3.

Genus *Masculostrobus* SEWARD
Masculostrobus graiterensis sp. nov.
(Fig. 6–8)

Holotype: NMS 20877 (Fig. 6a)

Derivatio nominis: From the Montagne du Graitery (Graitery anticline) where the locality is situated.

Repository

The *Masculostrobus graiterensis* holotype, additional cones (including the female scale *Araucarites falsanii*) and pollen samples are stored at the Natur Museum Solothurn, Switzerland.

Diagnosis

Male conifer cones, around 10 mm long and 6–8 mm wide at the middle. Microsporophylls are spirally arranged, consisting of a short stalk approximately 2 mm long, and a rhomboidal head about 2 mm high. The number of pollen sacs is unknown; they are, however, elongated. Cuticle of the microsporophyll head is delicate, showing rectangular to isodiametric epidermal cells. The stomata are probably scattered and of the same type as those of *P. cirinicum.* Pollen is inaperturate and circular to oval in shape with a diameter of 61 µm (extremes were found to be 54 and 68 µm). The exine is 1–2 µm thick, usually folded and finely granulate.

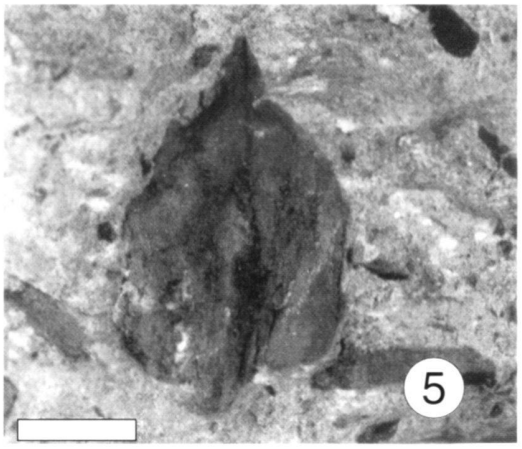


Fig. 5. The only female cone scale, *Araucarites falsanii* (SAPORTA), so far associated with *Pagiophyllum cirinicum* (SAPORTA) BARALE and *Masculostrobus graiterensis* sp. nov. in the Graitery assemblage; bar = 5 mm. NMS 20878

Description

A number of male cones in differing states of preservation were recovered from the Court locality (Fig. 6). These were found to vary only insignificantly in size. The smallest cone measures 8 mm in length and 6 mm in width (Fig. 6b), while the largest is 14.5 mm in length and 10 mm in width (Fig. 6c). The holotype (Fig. 6a) is 12 mm long and 8 mm wide. *M. graiterensis* sp. nov. shares the same basic cone morphology with other araucariaceous cones. The microsporophylls are spirally arranged around the central axis which is 1–2 mm wide. The exact number of pollen sacs could not be determined, but in comparison with other male araucariaceous cones, 2 or 3 pollen sacs per microsporophyll is likely.

The cuticle fragment from the microsporophyll head contains only more or less rectangular epidermal cells with rather thick walls, as were also found in e.g. the male cone of the araucariaceous conifer *Brachyphyllum mamillare* (Harris 1979). No complete stomata could be observed, but in several cases cavities indicate the positioning of the stomata, and in one case remains of subsidiary and encircling cells are still present (Fig. 7). These look exactly like those found in the leaves of *P. cirinicum.*

The pollen (Fig. 8) is of the general type found in araucariaceous plants (both living and fossil; see van Konijnenburg-van Cittert 1971, Harris 1979, Barale 1981, Balme 1995). The exine consists of two layers: nexine (smooth inner layer) and sexine (granulate outer layer). Usually the nexine and sexine are attached to each other (Figs. 8a–c), but in some grains the nexine is separated from the sexine forming an 'inner cavity' (Fig. 8d). This feature is known from both extant araucariaceous pollen grains as well as from fossil ones (van Konijnenburg-van Cittert 1971).

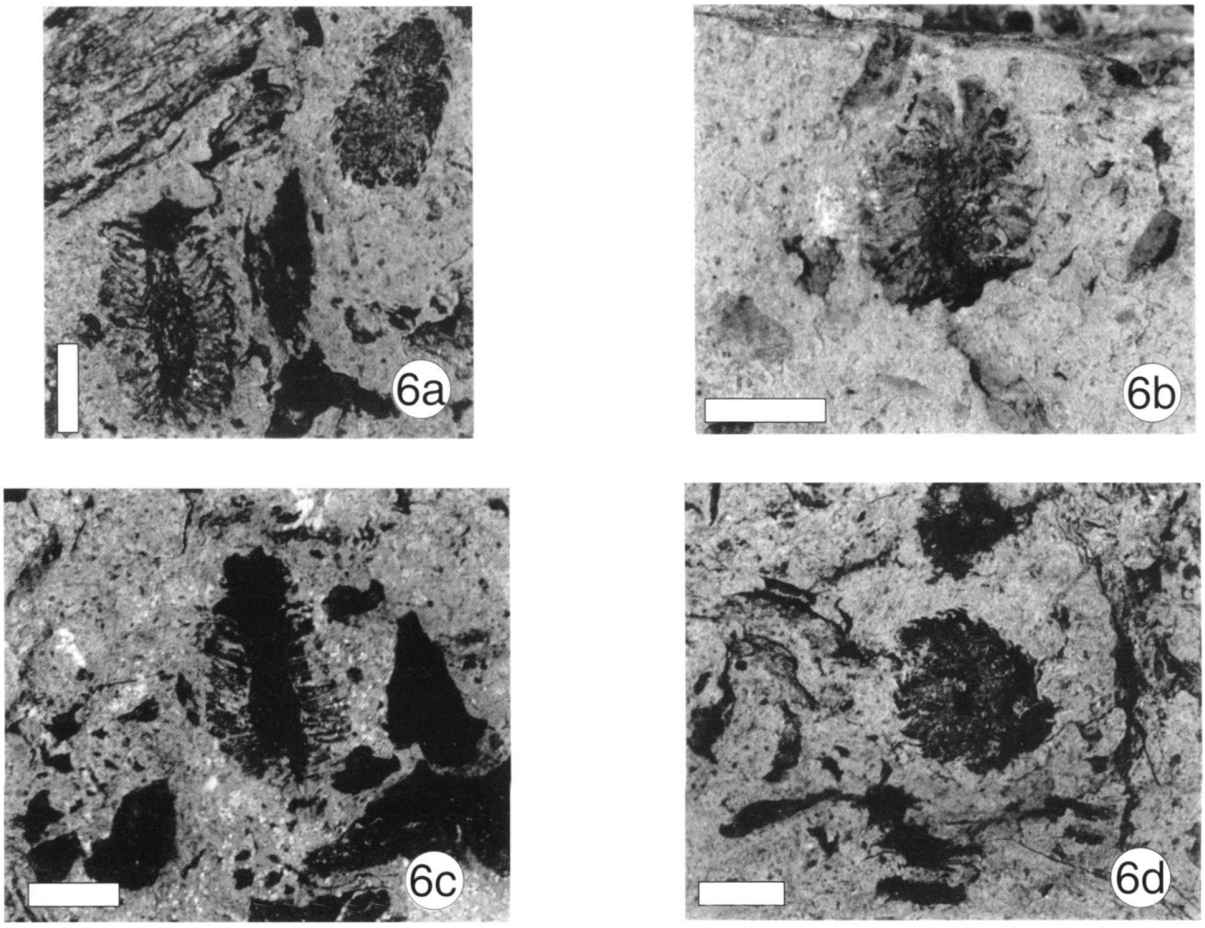


Fig. 6. *Masculostrobus graiterensis* sp. nov.
a. Two specimens of *Masculostrobus graiterensis* sp. nov. with the holotype to the left; bar = 5 mm. NMS 20877
b. The smallest specimen with partially preserved central axis; bar = 5 mm. NMS 20879
c. The largest specimen, approximately 14 mm in length. Note the preservation of the fine sporophylls; bar = 5 mm. NMS 20880
d. Basal view of a compacted cone; bar = 5 mm. NMS 20881

Discussion

Male cones of this kind yielding araucariaceous pollen, fall within the genus *Masculostrobus* when found separated from the coniferous shoots to which they were originally attached. Most araucariaceous pollen cones have usually been found attached to shoots of *Brachyphyllum;* e.g. from the Jurassic *Brachyphyllum lorchii, B. mamillare, B. mirandai* and *B. speciosa* (Harris 1979, Balme 1995). Occasionally detached cones have been described as belonging to *Masculostrobus* species, e.g. *Masculostrobus dorchensis* which possibly belongs to *Brachyphyllum desnoyersii* (Barale 1981).

Based on its pollen, *Masculostrobus graiterensis* sp. nov. certainly has araucariaceous affinities. The cones are attributed to *P. ciricinum* based on the association with the shoots (*P. ciricinum* is the only macrofossil present in the association) and the conformity in cuticular features.

Masculostrobus graiterensis sp. nov. differs from *M. dorchensis* from the Kimmeridgian of Orbagnoux (France) mainly because of its smaller size (*M. dorchensis* is 20 x 9 mm). The pollen is of the same size, but according to Barale (1981) the pollen in *M. dorchensis* is of the *Callialasporites* type, as the nexine is always separated from the sexine.

Barale (1981) also described *Masculostrobus* sp. F from Creys (Kimmeridgian of France), a locality in which *Pagiophyllum cirinicum* is quite common but from where he only had one cone of this type (15 mm long and 5–6 mm wide). The microsporophyll heads were quite large (4–5 mm in height). The cone itself is not figured; only the pollen and a cuticle fragment from the microsporophyll head. However, Barale's *Masculostrobus* sp. F is probably conspecific with *Masculostrobus graiterensis,* as its pollen corresponds in every detail with the pollen found in *Masculostrobus graiterensis.* The same applies

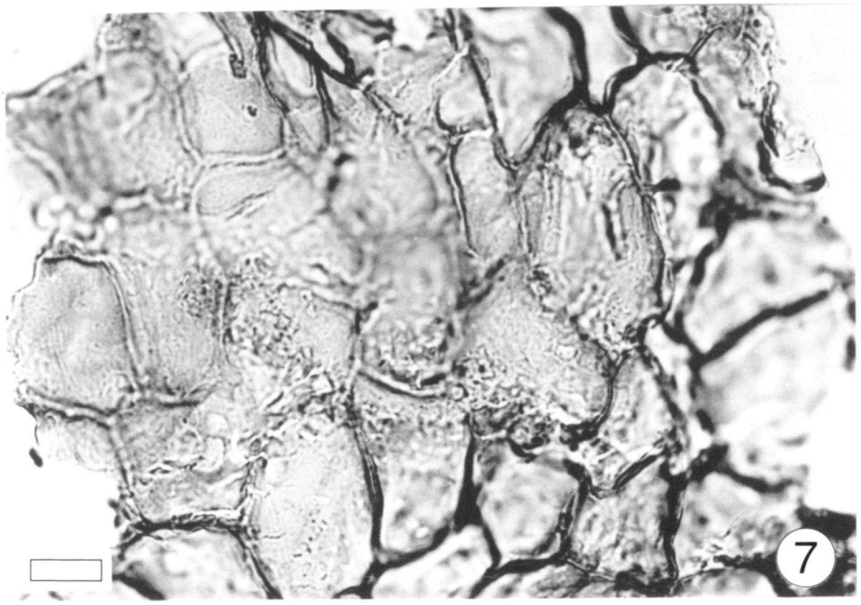


Fig. 7. *Masculostrobus graiterensis* sp. nov., cuticle from microsporophyll head; bar = 20 µm.

for the cuticle fragment of the microsporophyll head from the Creys locality, despite the fact that the size of the microsporophyll head appears to be larger than in the cones presented here. This latter feature, however, could not be verified.

Comparison of the pollen found in the *Masculostrobus graiterensis* sp. nov. cones with dispersed pollen of about the same age reveals that *Araucarites australis* COOKSON bears the closest resemblance (van Konijnenburg-van Cittert 1971, Balme 1995), although some authors assign such pollen to the genus *Inaperturopollenites* PFLUG (Barale 1981). Pollen grains in which the nexine is separated from the sexine would fall within the genus *Callialasporites* SUKH-DEV.

5. Palynology

Samples from the coal bearing beds of the Court locality were also examined for palynomorphs. Over 90% of the pollen is from the types *Araucariacites* and *Callialasporites* that clearly originated from the cones described above (over 350 grains of these types were counted). A few other sporomorphs were found, albeit in very low numbers; 25 *Spheripollenites* grains which may originate from various taxa; 15 smooth trilete more or less triangular fern spores, 6 trilete spherical fern spores and two spores of the Middle Jurassic fern genus *Klukisporites;* 20 bisaccate grains that may have originated from either conifers or pteridosperms; 5 grains of *Perinopollenites* sp. originating from the conifer family Taxodiaceae; 2 [*Classopollis*] *Circulina* grains (conifer family Cheirolepidiaceae) and one *Monosulcites* grain (either from the Cycadales, Bennettitales or Ginkgoales).

Moreover, one specimen of *Botryococcus* was found, an algae that lives in fresh or brackish water. Palynological evidence for a marine influence, in the form of dinoflagellate cysts, was not found.

6. Discussion

In general the Röschenz Member reflects a period of shallow water with emergent areas while the Günsberg Beds, with their patch-reefs and oolite bars, are fully marine. These facies changes are interpreted as the effect of a pronounced sea-floor topography formed in part by synsedimentary tectonics (Allenbach 1997). The lateral extent of emergent areas has not been reconstructed so far. Direct evidence for emergence is the existence of *in situ* in plant roots and mud cracks (Gygi & Persoz 1986). Ziegler (1990), however, does not indicate any emergent areas in the Jura Mountains in his paleogeographic map covering the Oxfordian. When the amount of plant material found in numerous localities as well as the distribution of limnic ostracods (Ziegler 1962) is taken into account, it appears that substantial areas were subaerially exposed during parts of the Oxfordian (see also Pittet 1996). Also the presence of detrital quartz in the deposits of the Röschenz Beds in general indicates emergent areas to the north of the area examined. Detrital quartz grains can only be deposited after erosion of a crystalline rock (i.e. basement) or after reworking of a quartz-bearing sediments. Measured paleocurrents (obtained from oriented samples of tempestites from the Effingen Member) are from the north-west to the south-east (Allenbach 1997) and thus, it becomes evident that the quartz source lies to the north-west of the central Jura Mountains; in all probability in the general area of the present Vosges and Ardennes Massifs.

Since female cone scales and male cones containing *in situ* pollen are interpreted as being parautochthonous, the data

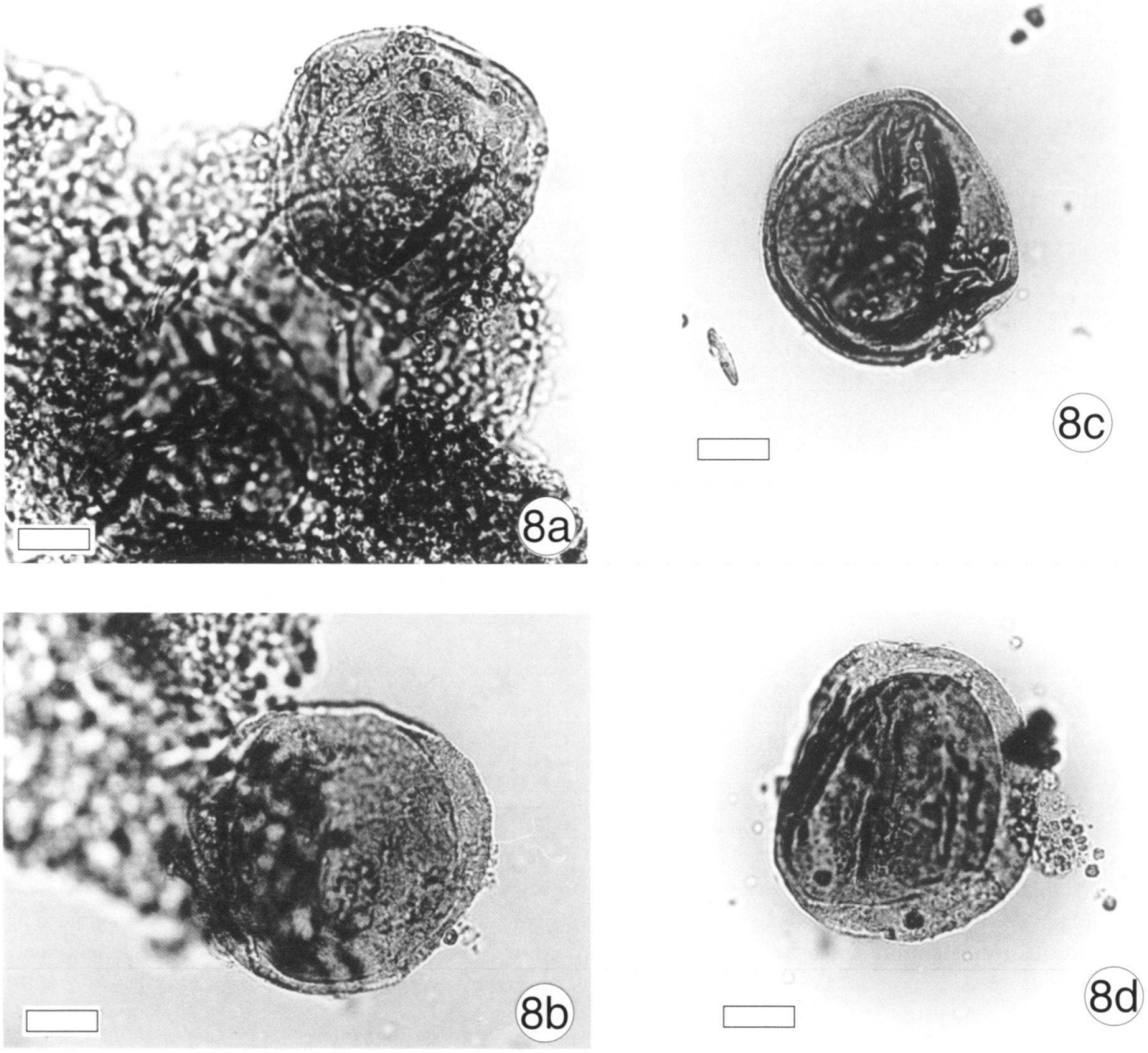


Fig. 8. *Masculostrobus graiterensis* sp. nov.
a. pollen partly still in a pollen sac; bar = 20 µm
b. one pollen grain sticking out from a pollen sac; bar = 20 µm
c. pollen grain of the *Araucariacites* type; bar = 20 µm
d. pollen grain of the *Callialasporites* type; bar = 20 µm

presented here provide further evidence for emergent areas in a very shallow marine environment. This is also the case in the La Charuque quarry, situated about 20 km to the south-west. Sediments resembling beach deposits, again containing leaves and seeds, as well as Pterosaur remains (Meyer et al. 1997) have been found in the La Charuque quarry near Reuchenette in strata younger than those discussed by van Konijnenburg-van Cittert & Meyer (1996). However, given the fact that the Court locality contains a lower species diversity which cannot be the result of sorting during transport, we assume that the fossil remains originated from a different source area than the ones of La Charuque. In turn this indicates widespread supratidal environments. The palynological analysis revealed that the material probably originated from a stand of Araucariaceous trees, which are believed to have lived in coastal environments, without being mixed with many other plants. Some undergrowth of ferns might have been present and the other (rare) gymnosperm grains were probably washed in by a stream. The accumulation and lineation of the plant fragments indicate a deposition caused by an event, in all probability a storm. Given the susceptibility to erosion and reworking of intertidal and supratidal deposits, it is not surprising that little direct evidence for supratidal environments has been found in the area. Analysis of paleocurrents in association with plant remains and facies patterns may allow an approximate reconstruction of emergent areas in the future.

Acknowledgments

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