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# Plant remains from the Vellerat Formation (Oxfordian) of the Swiss Jura mountains

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*Key words:* Late Jurassic, Oxfordian, Northern Switzerland, Bennettitales, Araucariaceae conifers, Cheirolepidiaceae conifers, pollen

## ABSTRACT

The Natica Member of the Vellerat Formation (Late Oxfordian) has yielded a small florula in the quarry La Charuque (Péry-Reuchenette) in the Swiss Jura mountains. Four taxa have been found: the bennettitalean leaf *Zamites* cf. *feneonis*, the araucariaceous conifer *Brachyphyllum* cf. *thuioides* and the cone-scale *Araucarites* cf. *moreauana* and the cheirolepidiacean conifer *Pagiophyllum araucarinum* as well as male cones of the genus *Masculostrobus* that are thought to belong to the latter species. The size of the plant remains and the association with seeds and cones points to a parautochthonous assemblage. The palynological analysis indicates a small plant community growing near the coast.

## ZUSAMMENFASSUNG

Die Natica-Schichten der Vellerat Formation (Spätes Oxfordium) enthalten im Steinbruch La Charuque (Péry – Reuchenette) im schweizerischen Jura eine kleine fossile Flora. Unter den nachgewiesenen Arten befinden sich die Bennettitee *Zamites* cf. *feneonis*, die araucaroiden Koniferen *Brachyphyllum* cf. *thuioides* und *Araucarites* cf. *moreauana*, die Cheirolepidiacee *Pagiophyllum araucarinum* und deren männliche Zapfen der Gattung *Masculostrobus*. Die Grösse der Reste, ihre Einbettung und ihre Assoziation mit Samen und Zapfen deuten auf eine parautochthone Gemeinschaft. Die palynologische Analyse spricht für eine kleine Pflanzengemeinschaft, die an der nahen Küste wuchs.

## 1. Introduction

Although plant debris forms part of many sedimentary complexes, well preserved plants are rare or almost absent from Late Jurassic sediments of the Swiss Jura mountains. The purpose of the present contribution is to describe recently discovered specimens, to comment on previously found material and to discuss the paleogeographical significance of terrestrial fossils in the Late Jurassic of Switzerland.

Four species of the bennettitalean leaf genus *Zamites* have been figured by Heer (1877). *Zamites feneonis* (Pomel) has been reported from the Late Oxfordian Villigen Formation. One specimen comes from the Geissberg Member near Aarburg and two others have been collected in the Crenularis Member near Olten/Trimbach and Däniken (see Moesch in Heer [1877], p. 130). Another specimen comes from the Terrain-à-chailles

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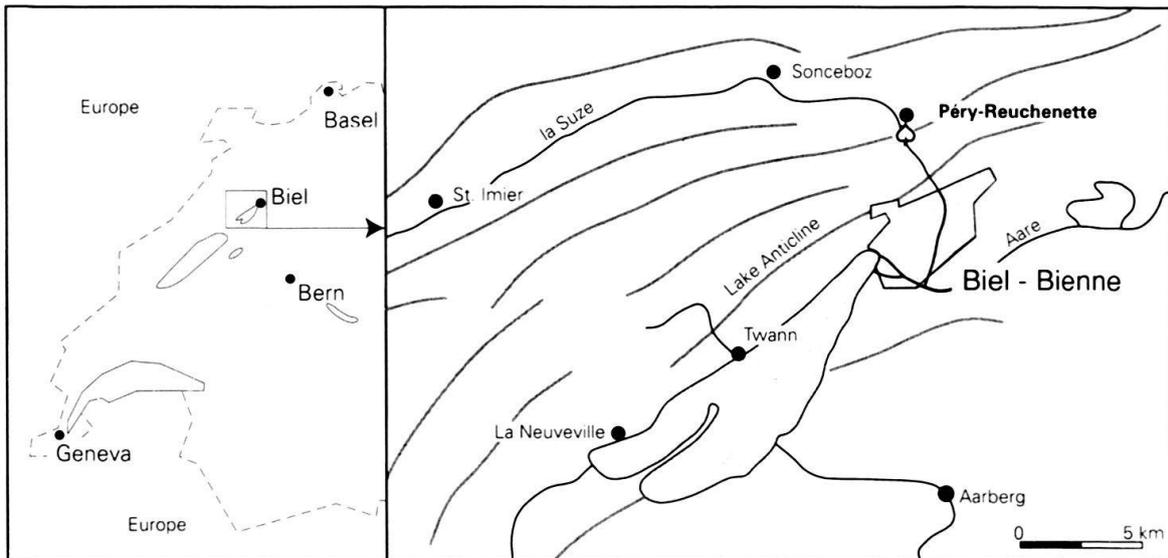


Fig. 1. Geological setting of the locality

Member (Bärschwil Formation) of St. Sulpice (see Jaccard in Heer [1877], p. 131). *Zamites formosus* Heer has been found in Kimmeridgian sediments of Mount Risoux (Vallée de Joux; see Renevier in Heer [1877], p. 131), while *Zamites renevieri* Heer is known from the Kimmeridgian of Vuargny (see Renevier in Heer [1877], p. 131) and *Zamites gracilis* Kurr from the Liassic of Blumenstein (see Fischer-Ooster in Heer [1877], p. 132). The latter will not be discussed here as it is of older age.

The Effingen Member of the Wildegg Formation has yielded a well preserved specimen of the conifer *Pachyphyllum* (= *Pagiophyllum*) *meriani* Heer near Bubendorf (BL). Reichel (1928) described a reasonably well preserved specimen of *Pagiophyllum araucarinum* (Saporta) from the Couches à ciment (Oxfordian) of St. Sulpice and Pümpin (1965) figures an imprint of a Bennettitalean leaf from the chalky limestones of the St. Ursanne Formation (see Fig. 3). Recently Phillippe (1995) reported *Agathoxylon desnoyersii* remains from the Kimmeridgian Reuchenette Formation near Solothurn. Meyer (1994a) also mentioned *Agathoxylon* sp. and badly preserved imprints of Equisetales (Meyer 1994b).

## 2. Material and Geological Setting

In 1993, the amateur collectors A. & H. Zbinden (Ipsach) discovered well preserved leaves and cones in the Late Jurassic Natica Member (Oxfordian) in the La Charuque quarry close to Péry-Reuchenette (see Gygi 1982 and Fig. 1, 2). Some of these specimens are now in the collection of the Naturmuseum Solothurn.

The quarry La Charuque displays one of the most complete Late Jurassic outcrops in the Swiss Jura Mountains where strata are continuously exposed from the Middle Jurassic Hauptrogenstein Formation (Bathonian) up to the Twannbach Formation (Portlandian).

The Natica Member (Ziegler 1962) comprises the highly variable sedimentary units

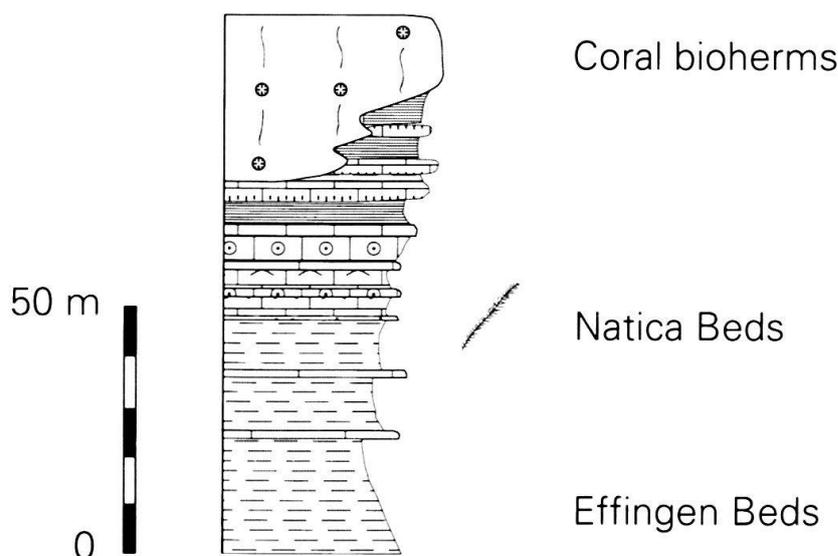


Fig. 2. Overall section of the Röschenz beds.

between the Vorbourg Member at the base and the Hauptmumienbank at the top (Fig. 3). This plant yielding member forms part of the Vellerat Formation (Bolliger & Burri 1967) and Gygi (1995) recently introduced the new term Röschenz Schichten for this well established term. The average thickness of the Natica Member is about 35 m (Gygi & Persoz 1986). The upper part consists of marls and limestones, stromatolites with mud cracks, black pebble conglomerates and small tidal channels that have been formed in the intertidal and supratidal part of a large tidal complex (Gygi & Persoz 1986; Hauser 1994). Above these peritidal carbonates the marls and limestones contain remains of decapod crustaceans, jaws of pycnodontid fishes, gastropods („*Natica*“) and well preserved cups of the crinoid *Apiocrinus meriani* (oral comm. A. & H. Zbinden).

### 3. Methods

The fossils were studied under the binocular and, if possible, cuticle preparations were made to confirm the determinations. Cuticles were prepared by macerating in Schulze's reagent, a mixture of  $\text{KClO}_3$  and 33%  $\text{HNO}_3$ , followed by a treatment in 5% ammonia for neutralizing. After rinsing thoroughly in water, the upper and lower cuticle were separated with needles and transferred to slides (mounted in glycerine jelly, sealed with paraffin). The slides were studied and photographed with a Leitz Ortholux microscope.

The palynological samples were treated with heavy liquid separation ( $\text{ZnBr}_2$ ) and the sample residues were sieved using a 15  $\mu\text{m}$  metal precision sieve. For the slides, glycerine jelly was used as a mounting medium.

All the material described here is stored in the Naturmuseum Solothurn, and numbered with the prefix NMS.





Fig. 4. *Zamites* cf. *Z. feneonis* from La Charuque quarry (NMS 20'400; scale bar 1 cm).

#### 4. Systematic descriptions

Cycadophyta  
Bennettitales

Genus *Zamites* BRONGNIART  
*Zamites* sp. cf. *Z. feneonis* (POMEL) ETTINGHAUSEN  
(Fig. 4, 5)

##### *Description*

One leaf fragment (NMS 20'400) was found in the Swiss material that can provisionally be attributed to this species. It consists of an axis with first three pinnae on one side, then seven on the other side, and apically again two on the first side (Fig. 4). The length of the pinnae varies between 10 and 17 mm, their width between 3 and 5 mm. They arise at an angle of ca. 80° from the axis, and show bases constricted on two sides which is typical for the genus *Zamites*. Their apex is pointly obtuse. Venation is parallel with a concentration of c. 25 per cm.

The upper cuticle consists of epidermal cells with sinuous walls; the lower cuticle shows a median stomatal zone and two non-stomatal marginal zones with sinuous epider-

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Fig. 3. Time frame of the Oxfordian sediments of Switzerland with indication of plant remains discussed in the text (adapted from Gygi 1995).

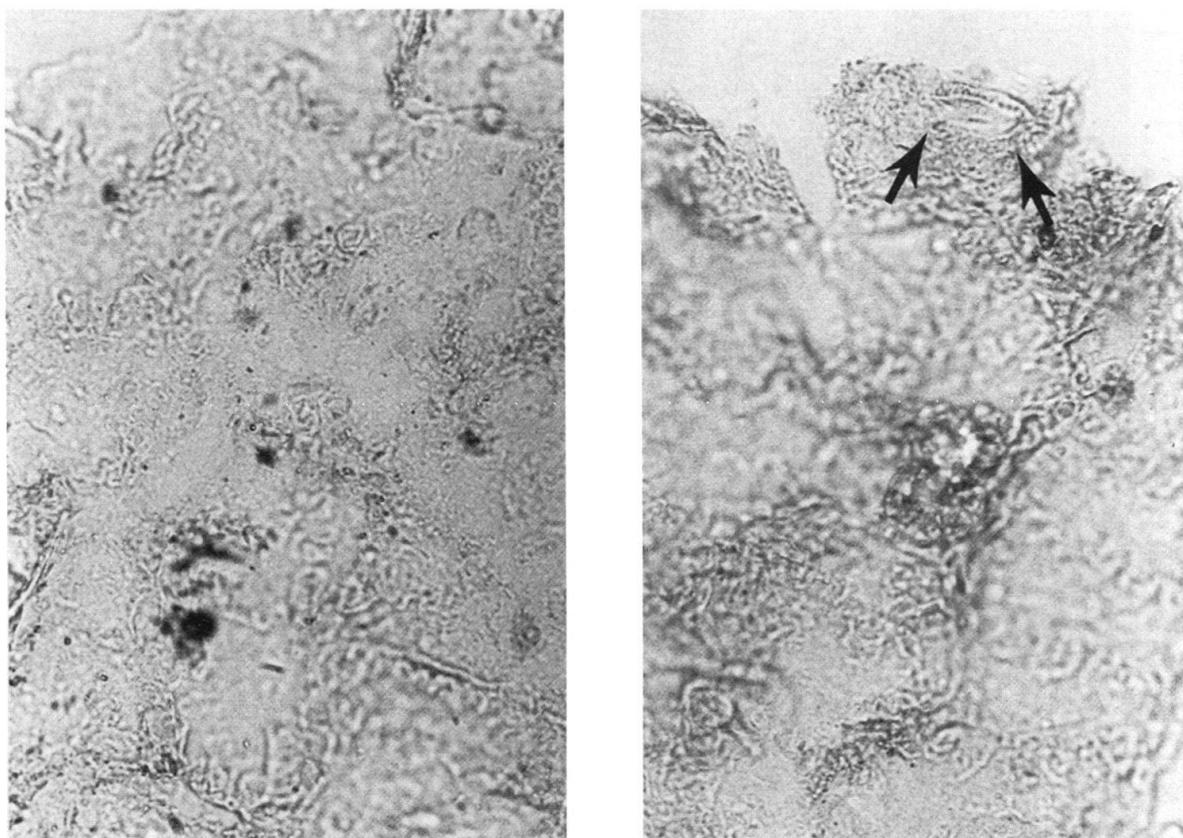


Fig. 5. *Zamites* cf. *Z. feneonis* cuticle. a) upper cuticle, b) lower cuticle, stoma near arrow ( $\times 400$ ).

mal cells. Stomata arranged in short files, syndetocheilic. No hair bases or papillae observed (Fig. 5).

#### Discussion

*Zamites feneonis* has been described in detail by Barale (1981, p. 96). It is known from the Oxfordian and Kimmeridgian of France and has also been recorded from the Oxfordian of Switzerland (St. Sulpice and Däniken: Heer 1877). The present material can be provisionally identified with the above species, although the pinnules are quite small for a normal *Zamites feneonis* and the apices of the pinnules are more or less obtuse while they are acute in typical *Z. feneonis*. Therefore, we hesitate to make a definitive species assignment.

*Zamites pumilio*, also known from the Oxfordian and Kimmeridgian of France (Barale 1981) has a size similar to our leaf fragment. However, the pinnae in our specimen arise at an angle of about  $80^\circ$  just as in *Z. feneonis*, while the angle of the arising pinnae in *Zamites pumilio* is  $45$  to  $60^\circ$ ; furthermore, the number of veins per cm is approximately 23 in *Z. feneonis*, while it is up to 100 in *Zamites pumilio*. Finally the ordinary epidermal cells in *Z. feneonis* are quite sinous as in our material, while they are only very slightly sinous in *Zamites pumilio*. Therefore we assign our material provisionally to *Z. feneonis* despite the small size of its pinnules and the slightly obtuse pinnule apices.



Fig. 6. *Brachyphyllum* cf. *B. thuioides* with *Araucarites* cf. *moreauana* (near arrow) (NMS 20'402;  $\times 2.5$ ).

Apart from the material of this species recorded by Heer (1877) from St. Sulpice and Däniken, Pümpin (1965, Fig. 21) figured a Bennettitalean leaf from the St. Ursanne Formation of the Central Jura mountains. This leaf fragment is ca. 12 cm long and 9 cm wide; the pinnules arise at ca.  $70^\circ$  and are ca. 5 cm long and 1 cm wide. The low quality of the figure does not allow to count the concentration of the parallel veins. It may well belong to *Zamites feneonis* as the specimen fits in size and overall morphology.

Heer (1877) also describes the species *Zamites formosus* from the Kimmeridgian of Mount Risoux (Vallée de Joux). This species was based on one specimen only, differing from *Z. feneonis* in the place where the pinnules show their greatest width, near the base in *Z. feneonis* and just below the middle in *Z. formosus*. The same species has also been recorded together with *Z. feneonis* by Saporta (1891) from Châtelneuf (French Jura). We believe that the slight differences between these two species are due to variation and that they are conspecific. This view is also supported by Contini (1972) who reported material of *Zamites* from the Late Oxfordian of Haute-Saône (France) and by Barale (1981) who synonymized *Z. formosus* with *Z. feneonis*.

*Zamites renevieri* Heer from the Kimmeridgian of Vuargny (see Renevier in Heer [1877], p. 131) differs from the present material in the much larger size of its leaves and pinnules (the total leaf must have been up to 1 m long and 20 cm wide), while *Z. feneonis* never reached more than a length of 25 cm and a width of 14 cm (see Barale 1981).

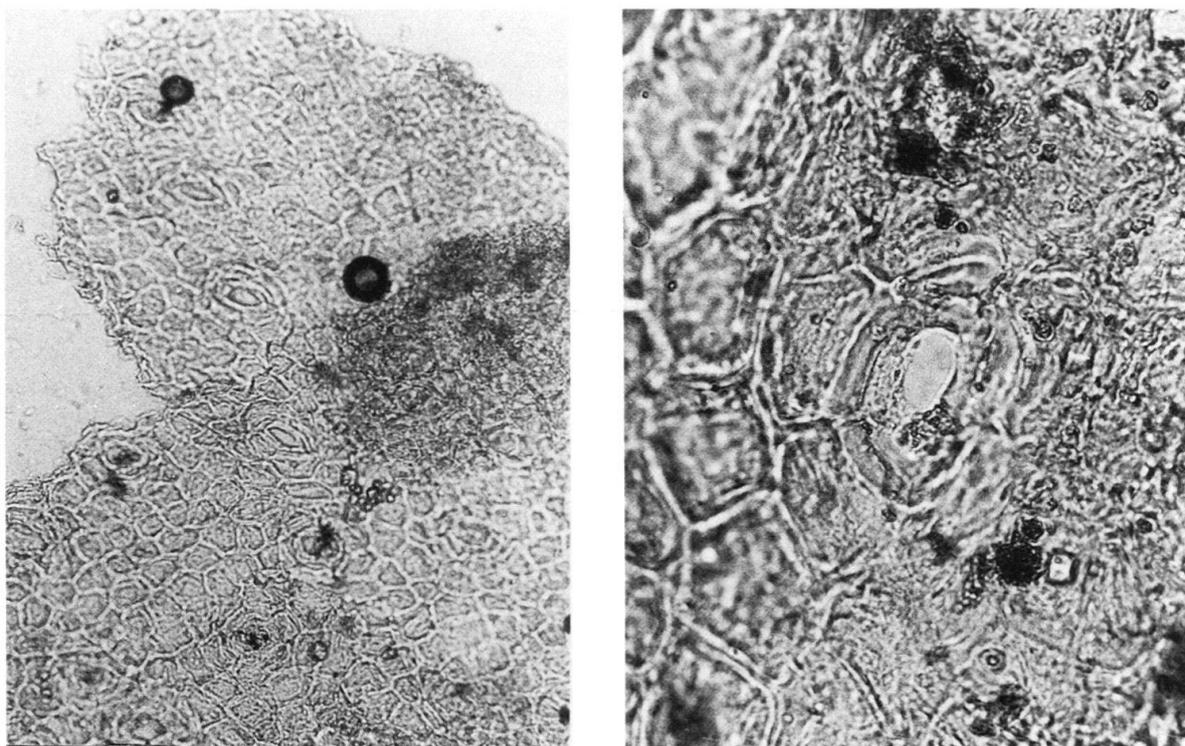


Fig. 7. *Brachyphyllum* cf. *B. thuioides* a) cuticle ( $\times 100$ ); b) stoma ( $\times 400$ ).

Coniferopsida  
 Order Coniferales  
 Family Araucariaceae

Genus *Brachyphyllum* LINDLEY & HUTTON  
*Brachyphyllum* sp. cf. *B. thuioides* (POMEL) SAPORTA  
 (Fig. 6, 7)

### *Description*

Two specimens of *Brachyphyllum* were observed (NMS 20'401, NMS 20'402). The material consists only of small leafy shoots; they are ca. 3 mm wide and covered with spirally arranged leaves that are 2–3 mm long and 2 mm wide (Fig. 6).

The amphistomatic cuticle is ca. 3  $\mu\text{m}$  thick and fragile. Stomata are arranged in short files on both surfaces but the stomatal density on the adaxial surface is less than on the abaxial surface. There are narrow stomatal free marginal zones. The epidermal cells between the stomatal files are isodiametric, thick-walled and more or less arranged in files (Fig. 7a). The stomata are amphicyclic and irregularly orientated. The two guard cells are surrounded by a ring of subsidiary cells and a ring of encircling cells. The number of the subsidiary cells (and of encircling cells) is usually five, but varies between four and six. No papillae have been observed on the subsidiary cells nor on the ordinary epidermal cells. The inner walls of the subsidiary cells form a ring around the stomatal pit (Fig. 7b).



Fig. 8. *Araucarites* cf. *A. moreauana* (NMS 20'403;  $\times 4$ ).

### *Discussion*

The small leafy shoots described here cannot be assigned with certainty to *B. thuioides* known from the Oxfordian and Kimmeridgian of France and Turkey. The leaves are smaller than the usual size of *B. thuioides* (6–7 x 5–6 mm; see Barale 1981, p. 140) but it agrees quite well with a specimen of this species described by Barale & Flaman (1982, p. 257), also from the Oxfordian of France, which shows much smaller leaves (3 x 2 mm). *Brachyphyllum moreauana* has been described numerous times from Oxfordian and Kimmeridgian deposits of France; this species has been synonymized with *B. thuioides* by Barale (1981). In the French material this species is associated with the cone-scale *Araucarites moreauana*. In our material a similar cone-scale is present; therefore, we conclude that the leafy shoot figured here might be assigned to *Brachyphyllum thuioides*. If this assignment is correct, then the cuticle of the species has been recognized for the first time.

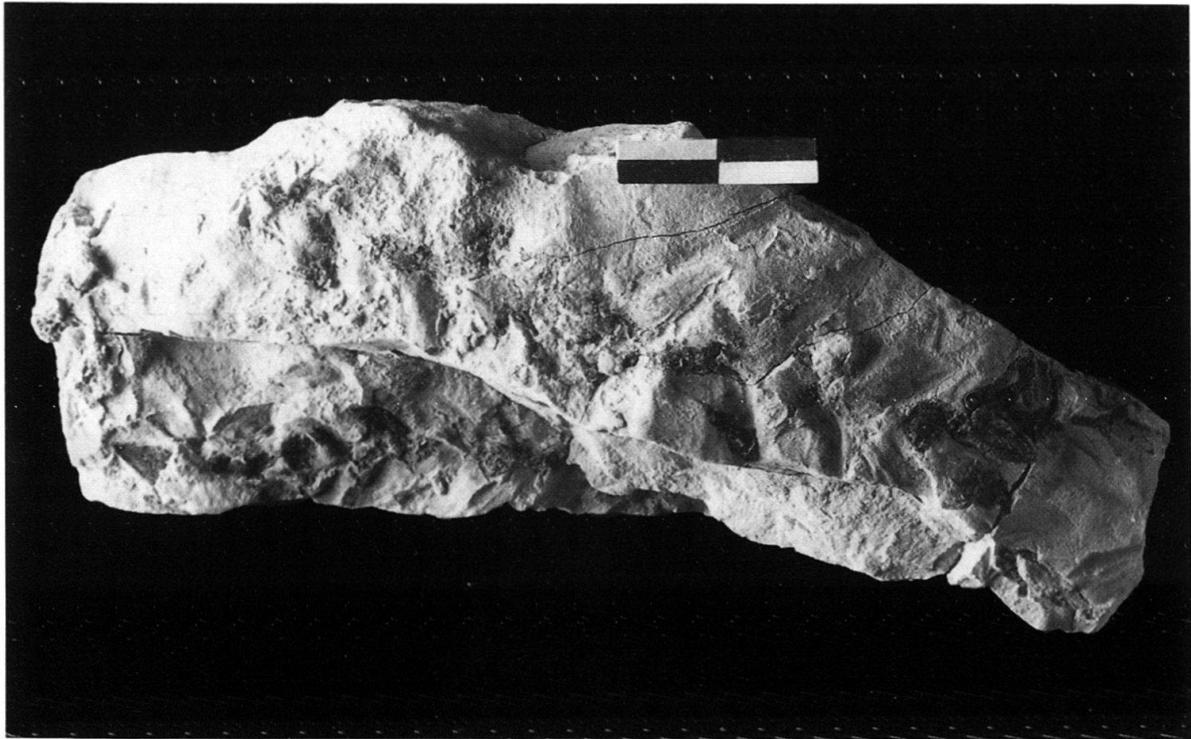


Fig. 9. *Pagiophyllum araucarinum* (NMS 20'384; scale bar 2 cm).

Another species that compares quite well with our material is *Brachyphyllum speciosa* (Pomel) Saporta. The leaves of this species are only slightly smaller (2 mm long, 1 mm wide; see Barale, 1981) than in our material, the stomata are also arranged in short files but they are only monocyclic (surrounded by a ring of subsidiary cells) and not amphicyclic (surrounded by a ring of subsidiary cells and a ring of encircling cells) as in our material.

Genus *Araucarites* PRESL

*Araucarites* sp. cf. *A. moreauana* (SAPORTA) SEWARD

(Fig. 6, 8)

*Description*

There is one specimen of a rather badly preserved *Araucarites* cone-scale, 2.4 cm long and 1.7 cm wide (NMS 20'403; Fig. 8). Its counterpart is only partly preserved but the imprint of the seed is much clearer (12 mm long, 6 mm wide). The typical triangular apex of an *Araucarites* scale can not be observed. Specimen NMS 20'402 also shows an imprint of an *Araucarites* cone-scale in close association with *Brachyphyllum* cf. *thuioides* (Fig. 6).

*Discussion*

The specimens fit *A. moreauana* as described by Barale (1981, p. 179) as to size and general outline. However, as the typical triangular apex has not been preserved, we cannot



Fig. 10. *Pagiophyllum araucarinum* (NMS 20'383;  $\times 2$ ).

make a definite assignment. *A. moreauana* is believed to be the female cone scale of *Brachyphyllum thuioides* (see Barale 1981), which is in agreement with the probable presence of this species in the Natica Member.

Family Cheirolepidiaceae

Genus *Pagiophyllum* HEER

*Pagiophyllum araucarinum* (SAPORTA) POMEL

(Fig. 9–13)

#### *Description*

Almost every slab in the collection shows at least a few leaves of this species. Well preserved shoots can be found on NMS 20'383 and NMS 20'384. The longest shoots can be found on NMS 20'384 (Fig. 9); this specimen shows two parallel shoots, one is 9 cm long, the other 6 cm, both are up to 2 cm wide. The leaves are spirally arranged around a broad axis (3 mm) and are rather widely spaced. This specimen also shows the largest leaves, they can reach 15 mm in length (free part 10 mm long) and 6 mm in width. The apex is acute. NMS 20'383 also shows two shoots next to each other (Fig. 10); they are 30 and 35 mm long, up to 15 mm wide and consist of 8 and 10 leaves respectively along the axis. The leaves are 1 cm long and 4 mm wide; they show an acute apex.

Several other specimens (registered as sample NMS 20'394) show short shoots of the same species (usually 3 to 5 cm long). The leaves are always spirally arranged around a rather broad axis and are widely spaced. The leaves arise at angles of 60–90°, and vary in length between 10 and 12 mm, their width lies between 4 and 5 mm. The apex is always acute and a keel is present in some of the leaves. One exception is a possible young shoot (NMS 20'404), 5 cm long and 15 mm wide, in which the spirally arranged leaves are quite

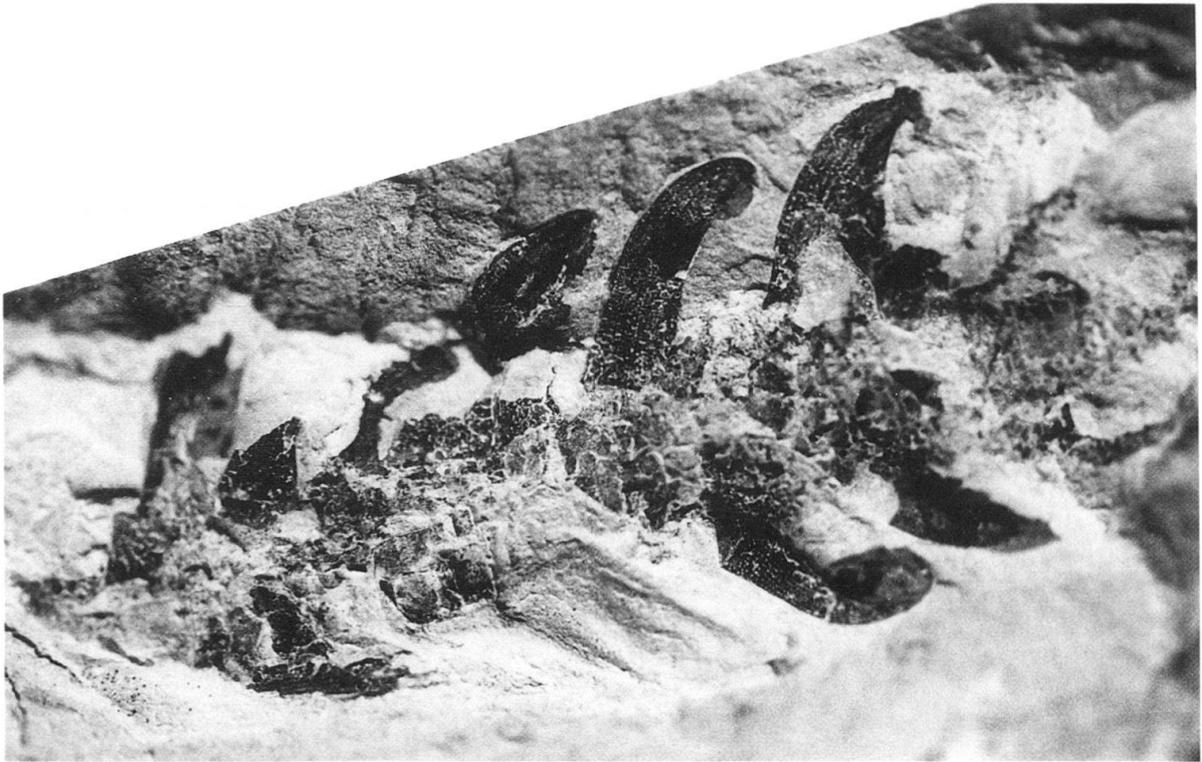


Fig. 11. *Pagiophyllum araucarinum* (NMS 20'404;  $\times 3.5$ ).

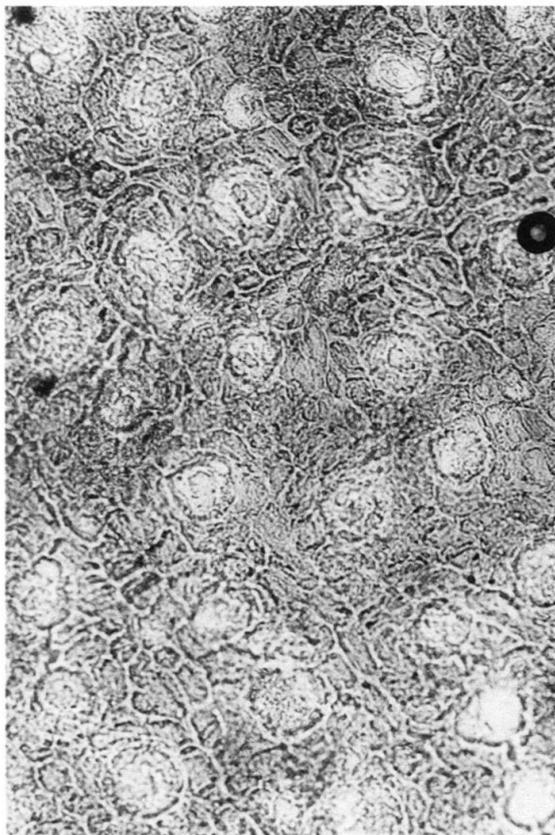


Fig. 12. *Pagiophyllum araucarinum* a) cuticle ( $\times 100$ ), b) stoma with papillae on the subsidiary cells ( $\times 400$ ).

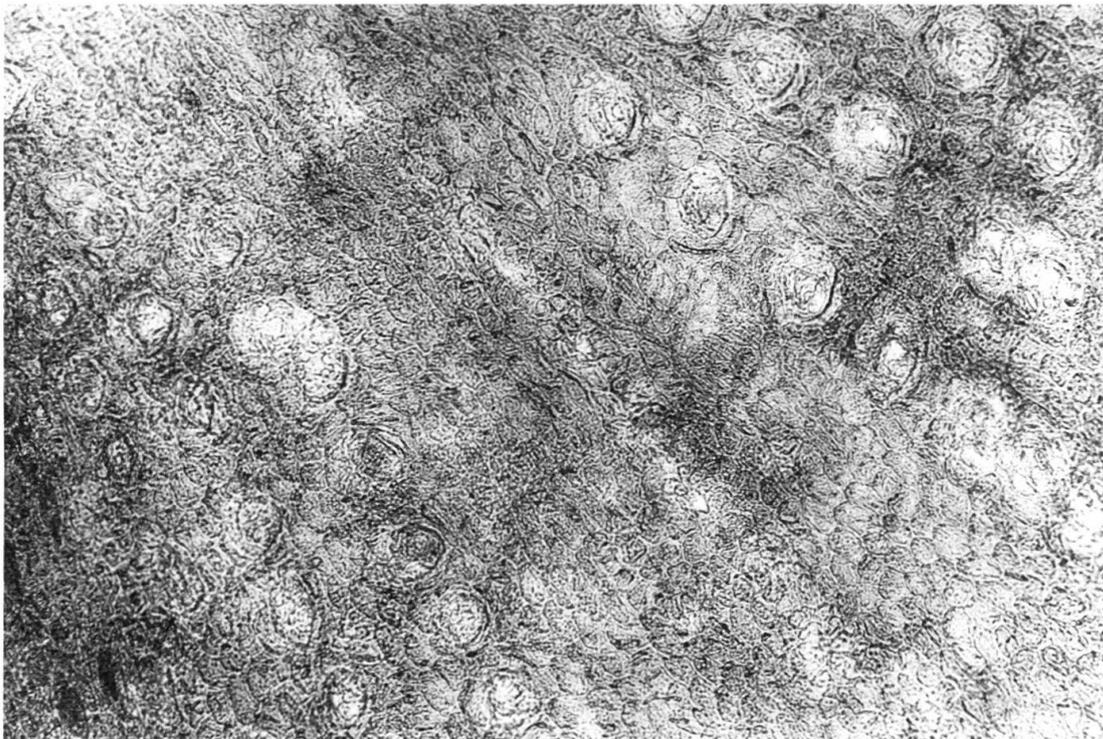


Fig. 13. *Pagiophyllum araucarinum* cuticle of large leaf with stomata-free central area ( $\times 100$ ).

close to each other and the apical part of the leaves is slightly bent (Fig. 11). The leaves show a normal size (10 mm long and 4 mm wide) but their apex is more or less obtuse.

The amphistomatic cuticle of all the specimens is more or less identical: The stomata are equally crowded on both sides and arranged in long files avoiding the margins, the leaf bases cushion and in large leaves avoiding the central area (Fig. 13). The stomatal files are only separated by one to three rows of ordinary epidermal cells. The stomata within a file are sometimes touching (never sharing their subsidiary cells) but are usually separated by one to four epidermal cells (Fig. 12a). The stomata are monocyclic, usually longitudinally oriented. The subsidiary cells form a ring around the sunken guard cells and bear papillae overlying the stomatal pit (Fig. 12b). The number of subsidiary cells is usually four or five, occasionally six. The ordinary epidermal cells are polygonal, isodiametric with rather thick cell walls and without papillae.

### Discussion

*Pagiophyllum araucarinum* has been described in great detail by Barale (1981, p. 172) who also included *P. kurrii* (Lower Jurassic of Germany), *P. connivens* (Lower and Middle Jurassic of England) and a part of *P. peregrinum* (Lower and Middle Jurassic of England and Germany). In France, this species is common in Middle and Late Jurassic deposits (last occurrence in the Oxfordian).

Our material can be attributed without any doubts to the above species as it agrees both in macromorphological and cuticular aspects.



Fig. 14. *Conites* sp. (NMS 20'396;  $\times 4$ ).

*P. araucarinum* has also been reported by Reichel (1928) from the Oxfordian of St. Sulpice (Switzerland). Heer (1877, p. 137) mentioned a well preserved specimen of *Pachyphyllum meriani* from the Oxfordian of Bubendorf. His figure (Plate LVI, Fig. 2) shows a shoot that looks identical to *P. araucarinum* in size and general morphology. Heer mentioned that the surface was covered with several rows of small dots: these are the rows of stomata that can also be seen in our material of *P. araucarinum* (Fig. 11, and in general in all well preserved specimens of this species).

#### Coniferalean Fructifications incertae sedis

Genus *Conites* STERNBERG

*Conites* sp.

(Fig. 14)

One conifer cone (NMS 20'396) with a length of 21 mm and a width of 14 mm shows a central axis with spirally arranged sporophylls around it. There are too few details visible, therefore a definite statement whether it is a female or male cone is problematical. However, it seems as if there are immature ovules attached to the cone (Fig. 14) implying that it might be a female cone.

Genus *Masculostrobus* SEWARD

*Masculostrobus* sp.

(Fig. 15a, 16)

One specimen (NMS 20'401) shows a male cone 8 mm long, 7 mm wide, consisting of an axis with spirally arranged microsporophylls (Fig. 15a). The microsporophylls are ca. 1 mm wide and 0.8 mm high, and show a cuticle with a few stomata in the central area (Fig. 16b). These stomata agree more or less with those of *Pagiophyllum araucarinum*;

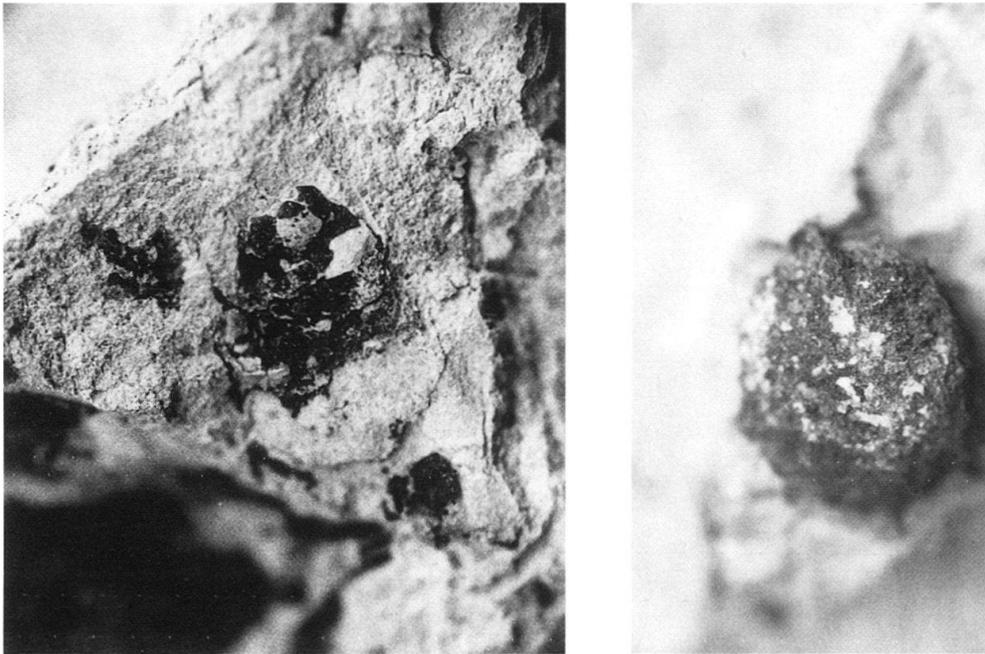


Fig. 15. a) *Masculotrobus* sp. (NMS 20'401;  $\times 3$ ). b) *Carpolithus* sp. (NMS 20'395;  $\times 5$ ).

furthermore, the margins of the microsporophylls is typically scarious (see Fig. 16a), a character that occurs in the Cheirolepidiaceae only. Therefore, this is probably a male cone belonging to *P. araucarinum*. However, the typical *Classopollis* pollen belonging to the Cheirolepidiaceae has not been found, rendering a definite assignment impossible. Barale (1981, p. 176) did not find any male cones of this species with pollen preserved, but he mentioned many pollen of the *Classopollis* type in the layers with *Pagiophyllum araucarinum*. The palynological study of our samples has also revealed many pollen of this type (*Corollina*).

Genus *Carpolithes* STERNBERG  
*Carpolithes* sp.  
 (Fig. 15b)

NMS 20'395 shows a three-dimensionally preserved seed, ca. 10 mm long and 8 mm wide with a strong apical keel (Fig. 15b). As no more details are preserved, no definitive assignment can be given.

## 5. Palynology

One sample from the locality has been investigated for palynomorphs. It yielded a well-preserved, low diversity sporomorph association. Sporomorphs proved to be the dominant palynomorph group. In addition, the palynological assemblage showed a poorly preserved, low diversity dinoflagellate cyst association. Based on the concurrent occurrences of *Acanthaulax venusta*, *Gonyaulacysta jurassica* and *Scrinodinium crystallinum*, an Oxfordian age can be assigned to the sample (see e.g. Feist-Burkhardt & Wille, 1992; Riding

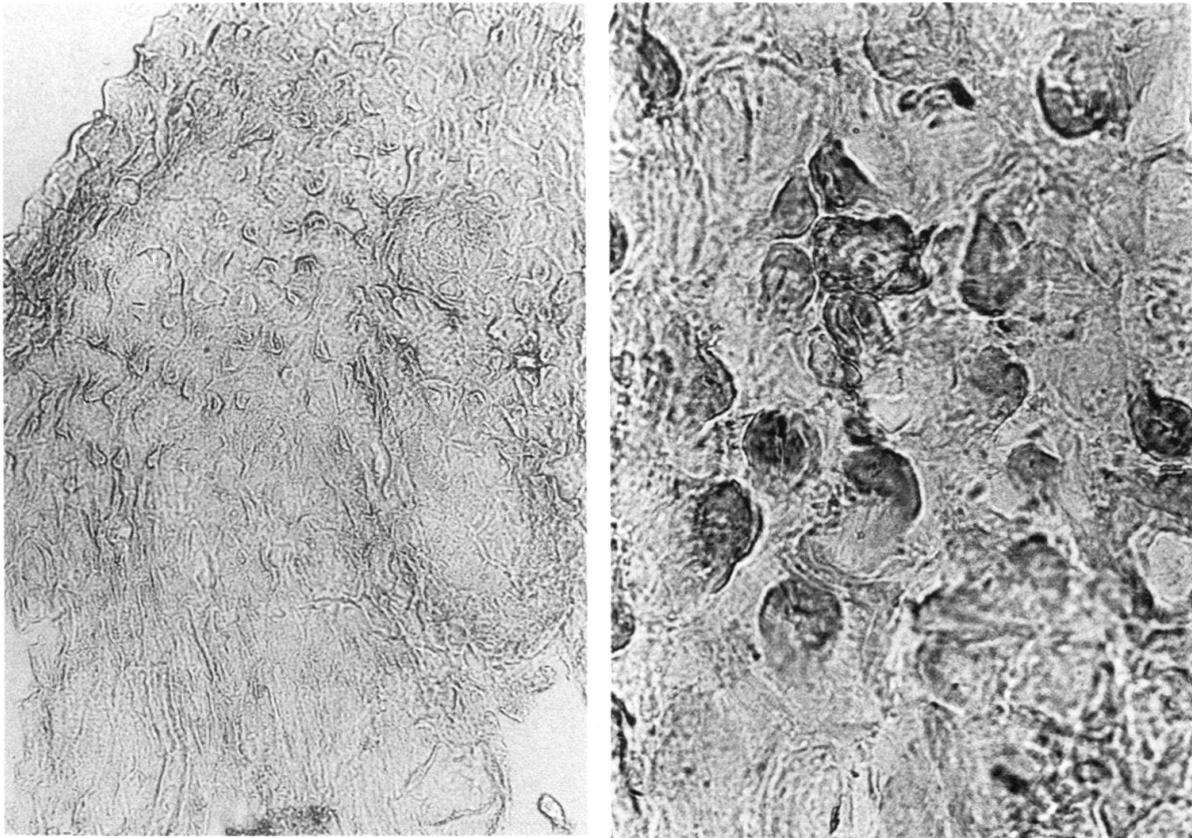


Fig. 16. *Masculostrobus* sp. a) cuticle of microsporophyll ( $\times 100$ ), b) stomata with papillae ( $\times 400$ ).

& Thomas, 1992). The main palynomorph groups and the pollen assemblage have been figured in pie diagrams in figure. 17. The spore contents of the sample are shown in table 1, and the dinoflagellate cysts in table 2.

Tab. 1. Spores

<i>Deltoidospora</i> spp.	7 %
<i>Concavisporites</i> spp.	< 1%
<i>Gleicheniidites senonicus</i>	< 1%
<i>Retitriletes austroclavatidites</i>	< 1%
<i>Stereisporites</i> spp.	< 1%

Tab. 2. Dinoflagellate cysts and acritarchs (all occurring in low percentages)

<i>Acanthaulax venusta</i>	<i>Scrinodinium crystallinum</i>
<i>Cribroperidinium</i> spp.	<i>Sentusidinium pilosum</i>
<i>Gonyaulacysta jurassica</i>	<i>Systematophora valensii</i>
<i>Korystocysta</i> spp.	<i>Systematophora</i> spp.
<i>Micrhystridium</i> spp.	<i>Valensiella ovulum</i>

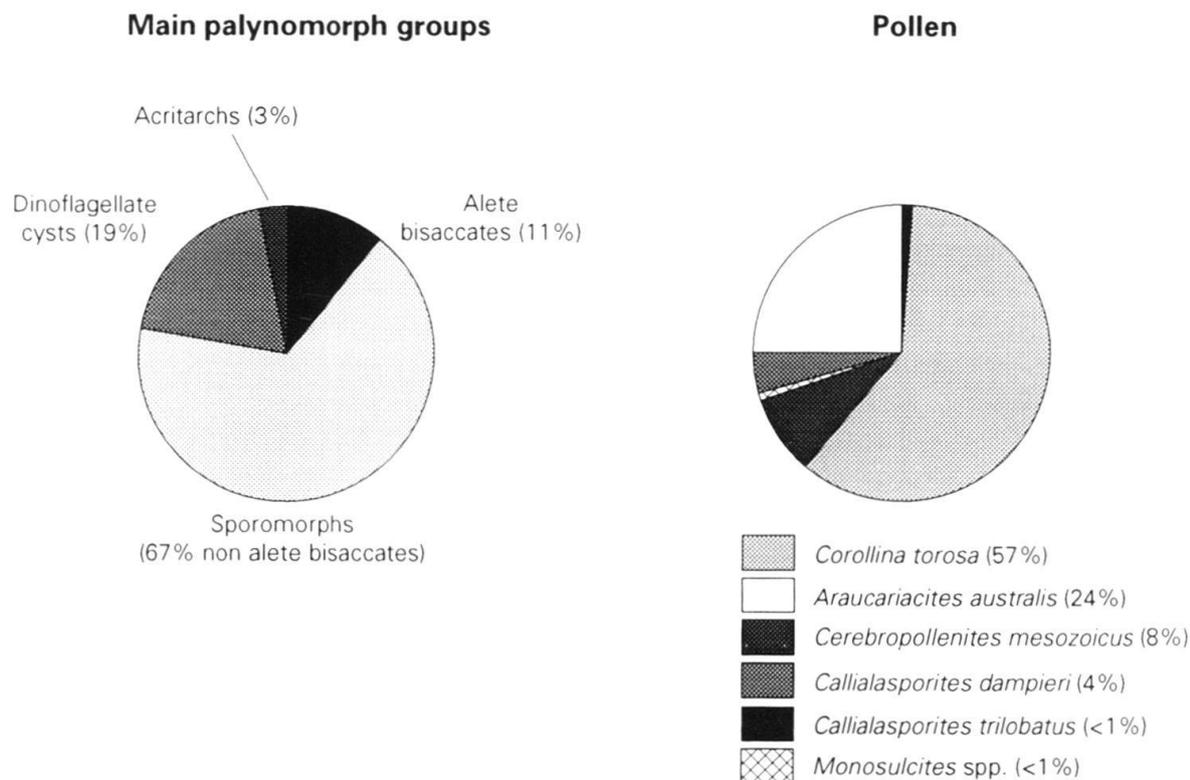


Fig. 17. Pie diagrams of main palynomorph groups and pollen.

Comparing palynological and paleobotanical results, we see that the most common sporomorph in the assemblage (*Corollina torosa*, a grain with affinities to the conifer family Cheirolepidiaceae) is in close agreement with the common occurrence of *Pagiophyllum araucarinum* in the macroflora. The other conifer, *Brachyphyllum* cf. *thuoides* in close association with the cone scale *Araucarites* cf. *moreauana* belongs to the Araucariaceae. The sporomorph assemblage contains three species with araucariaceous affinities: *Araucariacites australis*, *Callialasporites dampieri* and *Callialasporites trilobatus*. These three pollen taxa are so closely related that they can indeed be found within one species (van Konijnenburg-van Cittert 1971). The other pollen grain that regularly occurs in the assemblage is *Cerebropollenites mesozoicus*, a pollen with unknown affinities. It is remarkable that only very few *Monosulcites* grains have been found, as this type is shed by Bennettitalean plants such as *Zamites*, that has been found in the macroflora.

The fact that sporomorphs are the dominant palynomorph group but that dinoflagellates and acritarchs are present as well indicates that the assemblage comes from a small plant community that must have grown near the coast.

## 6. Discussion

Comparing the floras known from the Oxfordian/Kimmeridgian of Switzerland and France, we observe that the French floras are in general much more diverse than the small florules that have been recorded from Switzerland. The flora from the Kimmerid-

gian Calcaires lithographiques of Creys, Armailles and Orbagnoux (Dép. Jura) contains almost 60 taxa (Barale 1981), *Zamites feneonis* being by far the most common plant in these horizons. Almost every locality, even where only one or two species are present, has yielded this taxon. The Oxfordian sediments of France display a much less diversified flora. Barale (1981) recorded 11 taxa from 4 localities: One species of *Sphenopteris* (fern of unknown affinity), *Stachypteris* (Fam. Schizaceae), *Zamites feneonis* and *Z. pumilio* (both Bennettitales), *Brachyphyllum* sp., *Elatides williamsonii* (all conifers) and the seed *Carpolithes* sp. (see also Barale & Contini, 1976). All the species from the Swiss Oxfordian (Heer, 1877; Reichel, 1928; Pümpin, 1965 and this paper) have also been recorded from the French Oxfordian. Moreover, Contini (1972) described a florule from Haute-Saône with *Zamites feneonis* (including *Z. formosus* in it), *Brachyphyllum thuioides* and remains of Characeans (fresh water algae). The Natica Member of the Swiss and adjacent French Jura mountains, as well as our locality, has also yielded abundant characean remains (Oertli & Ziegler, 1958).

The specimens described here consist of plant fragments of ca. 10 cm, thus we think that they are not completely autochthonous but have not been transported over a long distance; in the case of an autochthonous deposit larger specimens might be expected. This is supported by the fact that next to the leaves and shoots cones and seeds were found. Transport over long distances would not produce such an assemblage. However, as we only have few specimens, we cannot draw any further conclusions.

The same applies to any climatic conclusions during the growth period of these plants. The fact that all specimens have a more or less tough cuticle (especially those of *Pagiophyllum araucarinum* are thick) is in agreement with the general view on European climate during Oxfordian times being relatively warm. Vakhrameev (1991) reports average annual temperatures of 17 to 22° C for northern Europe. Parallel to this recorded warming an aridization of the climate followed. To withstand this climate, plants needed, amongst other adaptations, thick cuticles, which can be seen in our florula. The composition of the European floras in Oxfordian times changed: Bennettitales became widespread while the diversity of ferns, Nilsoniales and Ginkgoales drastically reduced. Cheirolepidiaceous conifers (able to withstand drought conditions) increased in numbers, just as conifers belonging to the Araucariaceae (see Vakhrameev 1991). The taxa found in our material (Bennettitales, Araucariaceans and remains of Cheirolepidiaceans) all point to a dry and warm climate.

Indication of emergent facies has long been recognized in the adjacent French Oxfordian sediments (Enay, 1980). The partial skeleton of the sauropod genus *Bothriospondylus* as well as teeth of carnosaurs from the Oxfordian of Damparis (Lapparent 1943; Dép. Jura: Dôle) have been interpreted as *in situ* remains of terrestrial animals (Buffetaut, 1988). De Broin et al. (1991) point to numerous emergent areas during the Oxfordian and Kimmeridgian of the French Jura mountains.

Furthermore it has been shown that the Röschenz Beds (Natica Member) contain biogenic and sedimentary structures like stromatolitic horizons, black pebbles and mud cracks that indicate deposition in the uppermost inter- to supratidal part of an ancient tidal flat. The terrestrial plant remains from Péry-Reuchenette and coeval coal beds from Moutier (Laubscher & Pflirter 1984; Gygi & Persoz 1986) as well as fresh water characeans demonstrate that during the Late Oxfordian some parts of the Swiss Jura have been emergent areas. Recent discoveries of sauropod dinosaur tracks in the lowermost

part of the Kimmeridgian Reuchenette Formation near Moutier as well as the recognition of a megatracksite in the uppermost part of the same Formation (Meyer 1993) give further evidence of repeated emergence of large areas in the Swiss Jura mountains.

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Note added in proof:

Further evidence for coastal and continental deposits – now probably eroded – come from coeval outcrops in the La Charuque quarry and a locality further to the north. Low-angle cross-bedded silty sandstones yield large quantities of plant macroremains as well as skeletal elements of terrestrial reptiles. Equivalent rocks further north show silty calcareous layers with innumerable stem fragments of Equisetales and remains of tree trunks (R. Allenbach, Basel; pers. comm. and own observations).

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