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Parameters in leaf and cuticle morphology

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ABSTRACT

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Consistent and variable factors in leaf and cuticle morphology are being discussed, in the light of fossil higher plant species described exclusively on the basis of leaf characters.

Key-words—Morphology, cuticle.

पत्तियों एवं उपचर्मों के आकृति विज्ञान के मापदण्ड

योहाना एच.ए. फ़ान कोनिनेबर्ग-फ़ान सिटर्ट

सारांश

पत्तियों एवं उपचर्मों के आकृति विज्ञान में संगत एवं परिवर्ती कारकों की चर्चा प्रस्तुत शोध पत्र में की गयी है, जिन्हें पत्तियों के अभिलक्षणों के आधार पर उच्चतर पादपाश्म प्रजातियों के प्रकाश में विशिष्ट रूप से अध्ययन हेतु लिया गया है.

संकेत शब्द—आकृति विज्ञान, उपचर्म.

INTRODUCTION

LEAVES are the most common type of higher plant fossils that have been recorded. Innumerable species have been described based only on leaf characters and/or cuticle characters. Many species have been established that differ from others only in one or a few small details. The aim of this paper is to discuss which characters in leaf and cuticle morphology are consistent, and are, therefore, acceptable as diagnostic features, and which are variable and are thus, at least on their own, useless as discriminating characters. This latter group of characters may have diagnostic value, however, only in combination with other characters.

LEAF MORPHOLOGY

Basic leaf architecture

The general outline of a leaf is, usually, a consistent parameter. A leaf is either simple or compound; if it is simple, it can be linear (Fig. 1a), lanceolate (Fig. 1b), elliptical (Fig. 1c), round, ovate (Fig. 1d), obovate (Fig. 1e) or fan-shaped (Fig. 1f) in outline and also bifurcate (Fig. 2c) and bipartite (Fig. 2d) leaves occur (Boersma, 1972); if it is compound it can be palmate (Fig. 2a) or pinnate (Fig. 2b) etc. (see e.g., Dilcher, 1974; Hickey, 1978).

The size of a leaf can be very variable: on one axis basal and apical leaves are usually smaller than the leaves in the middle part of the shoot. For instance, Weber (1968) figures a

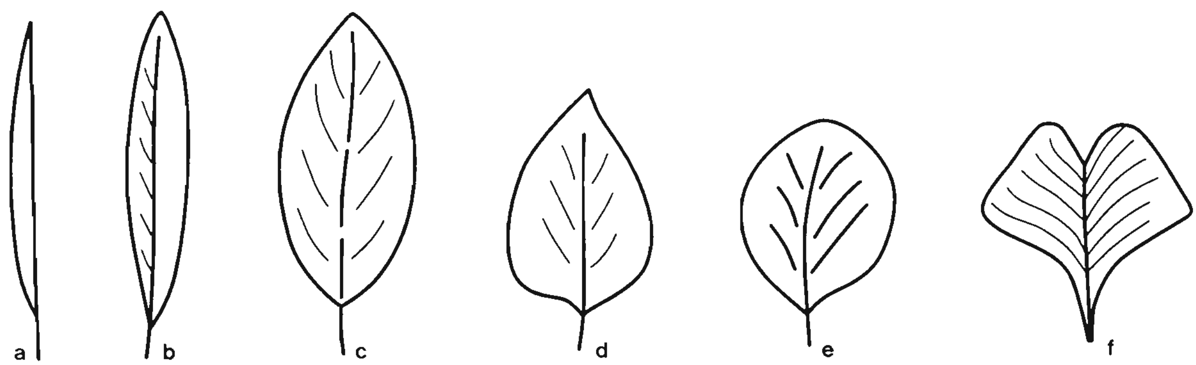


Fig. 1 — Some simple-leaf outlines; **a.** linear; **b.** lanceolate; **c.** elliptical; **d.** ovate; **e.** obovate; **f.** fan-shaped.

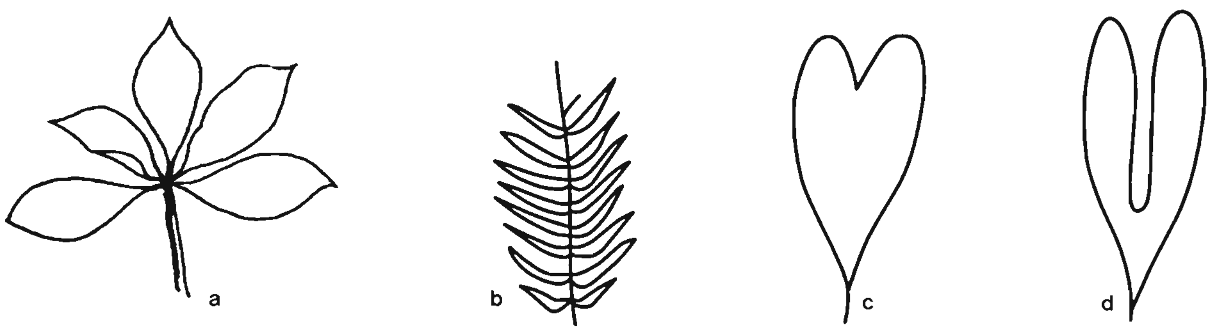


Fig. 2 — Some compound-leaf and simple-leaf outlines. **a.** palmate; **b.** pinnate; **c.** bifurcate; **d.** bipartite.

Podozamites lanceolatus shoot in which the leaves, when found dispersed, should probably been assigned to different species because of their different sizes. Also environmental circumstances influence the size of leaves. Everyone will be familiar with the differences between light and shadow leaves. Therefore, size alone can never be a diagnostic character.

Most fossil compound leaves are pinnate (e.g., ferns, cycads, Bennettitales, etc.) and it is usually a specific character if a plant is once, twice or even three times pinnate. But one has to be careful and consider that in modern ferns, plants that have usually pinnate leaves, can have bipinnate leaves when they tend to become large. In the same way bipinnate leaves may become tripinnate. This has been demonstrated for fossil pteridosperms (e.g., Kerp, 1988; Rees & Cleal, 1993). The last two authors even demonstrated in their paper that in the Triassic pteridosperm *Archangelskya furcata* 6 species could be combined that originally even belonged to 4 genera! This demonstrates how careful one should be with this type of leaves.

Leaf base

The presence or absence of a petiole is a diagnostic feature, but there may be a variation in size. The shape of the base, e.g., truncate (Fig. 3a), sagittate (Fig. 3b), cordate (Fig. 3c), etc., is a consistent parameter, but the size of those parts may vary along with the size of the leaf. Another constant factor is the mode of attachment of the leaf to the axis: decurrent, straight or with a restricted base etc. However, the angle under which a leaf or pinna is attached to the axis may vary considerably: one often sees that in a shoot the angle of attachment is smaller near the apex than in the middle part of the leaf or at the base.

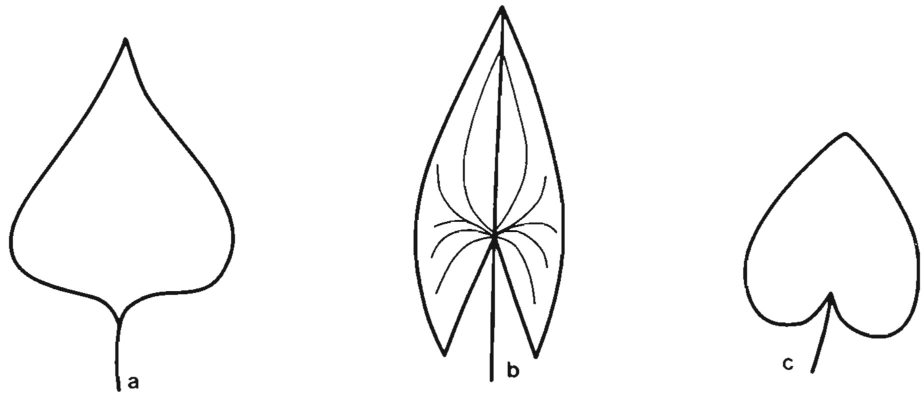


Fig. 3 — Various shapes of leaf bases and apices. **a.** leaf with a truncate base and an acuminate apex; **b.** leaf with a sagittate base and an acute apex; **c.** leaf with a cordate base and an obtuse apex.

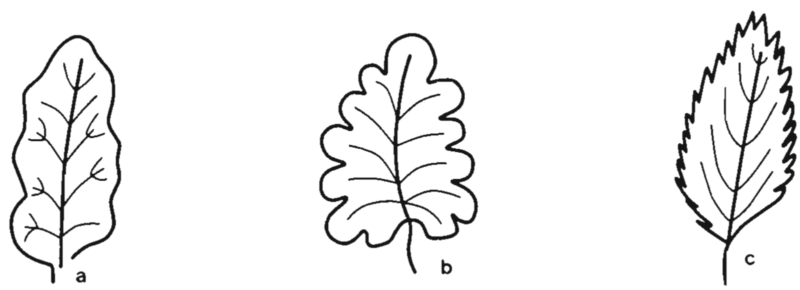


Fig. 4 — Forms of leaf margin. **a.** lobed; **b.** crenate; **c.** dentate.

Leaf apex

As in the other leaf morphology parameters, the shape of the apex is usually a constant character: the apex may be acute (Fig. 3b), obtuse (Fig. 3c), acuminate (Fig. 3a), truncate, etc. One sometimes sees that, under certain circumstances, a leaf apex may divide into two or even three apices in living plants. This has also been demonstrated for fossil plants, see e.g. Kerp (1988). Daber (1980) discusses leaf overtopping in Carboniferous and Permian plants in detail.

Leaf margin

A leaf margin may be entire (integer) or more or less lobed (Fig. 4a) or incised such as crenate (Fig. 4b), dentate (Fig. 4c), etc. The general character is usually consistent, but again the size of the lobes, teeth etc. may vary considerably within one species or even one plant. As a rule one can say that teeth or lobes etc. are larger in large leaves or pinnae than in smaller leaves or pinnae from the same species. The shape of the leaf margin is also influenced by climatic circumstances. Chaloner and Creber (1990) point out that leaves with entire margins occur more in tropical rainforests, while leaves with a non-entire margin are more often found in temperate, deciduous forest trees.

Leaf thickness

The thickness of a leaf can vary between herbaceous (or even membranous) and coriaceous. Usually this is a constant character, but small variations may be caused by environmental circumstances. In general, one can say that thin-cuticled leaves with a soft texture are more often found in temperate regions, while tough, coriaceous leaves (usually with a thick cuticle) occur mostly in tropical rain forests (Chaloner &

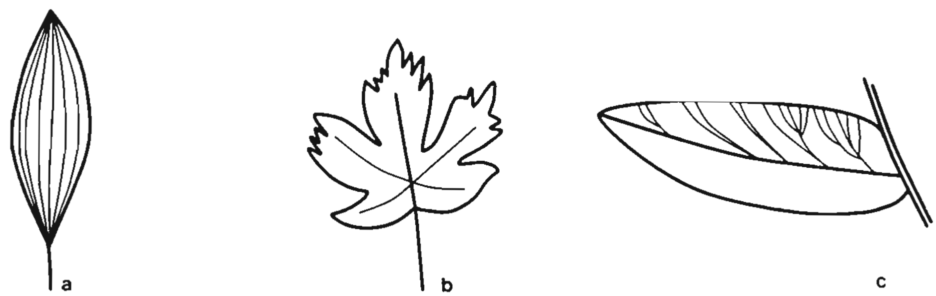


Fig. 5 — Leaf venation patterns: **a.** parallel venation; **b.** palmate venation; **c.** pinnate venation with secondary veins that are once - three times forked.

Fig. 6 — Leaf venation patterns. **a.** anastomoses between veins; **b.** net venation; **c.** veins that run straight to the margin; **d.** veins that end before the margin, giving off small lateral veins; **e.** flexuous midrib with unforked secondary veins.

Creber, 1990). This is true for extant plants, and there is no reason to believe that it should be different in fossil leaves.

Venation

The general venation pattern is a consistent character in leaf morphology. Leaves can have parallel (Fig. 5a), palmate (Fig. 5b) or pinnate (Fig. 5c) venation. In the latter case, there is a midrib with secondary veins. These secondary veins can be simple or once, twice or even three times forked or branched (Fig. 5c). Usually the secondary veins in larger leaves are more often branched than in smaller leaves of the same plant, because veins are only conducting canals, and in a larger leaf more veins are necessary than in a smaller leaf. Thus, the number of secondary vein-branching is a variable character, often depending on the size of the leaf.

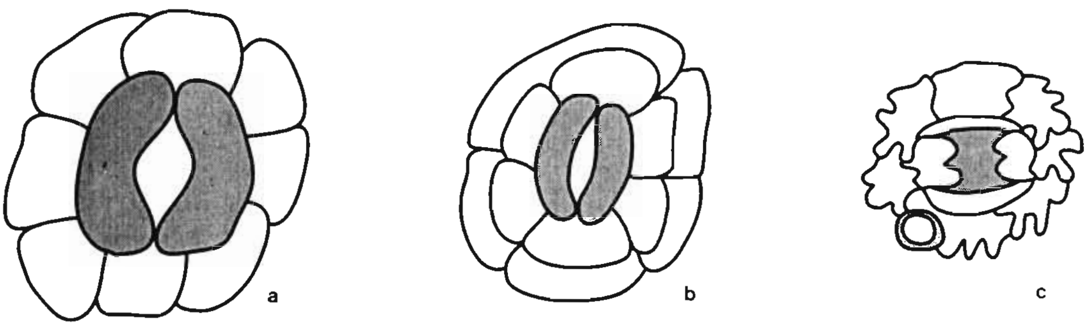
The number of veins per cm is a character often used in species diagnosis (e.g., Harris, 1964, 1969). This is a useful character. However, caution is still necessary because e.g., in apical leafs and pinnae the vein may change considerably, and this character should never be used as the only discriminating character for a species.

The number of veins entering a pinnule can also be a diagnostic feature. If more than one vein enters the pinnule, it is of importance which part of the pinnule is served by one or more "minor" veins.

The presence of anastomoses (Fig. 6a) between vein branches is a constant character, but the number of those anastomoses is variable. In extreme cases there is a net venation (a very consistent character; Fig. 6b).

The continuation of the (mid)vein, and the course of the veins (e.g. straight (Fig. 6c), flexuous (Fig. 6e), etc. may be consistent characters.

The place where veins end is also a fairly consistent feature: veins can run straight to the margin (Fig. 6c) - or in case of parallel venation to the apex. They can also end before the margin, usually giving off small lateral veins (Fig. 6d). The angle under which the veins reach the margin can, just as the angle of branching from the midrib, be a diagnostic feature.



a b c

Fig 7 — Various types of stomata. **a.** haplocheilic stomata apparatus consisting of stomatal aperture, two guard cells (dotted) and a ring of subsidiary cells; **b.** haplocheilic stoma with a ring of encircling cells around the subsidiary cells; **c.** syndetocheilic stoma, accompanied by a trichome base (also dotted).

Some general morphological characters

The presence and nature of hairs, trichomes, etc. on leaves can be a very consistent character, not only in extant plants but also in fossils (e.g., the Carboniferous *Neuropteris scheuchzeri*) but the number of these organs is often dependent on environmental circumstances. The nature of these organs is always a diagnostic feature (see e.g., Krings & Kerp, 1998). Glands and hydatodes (water excretion organs) may also be present on leaves and/or stems and are diagnostic features.

CUTICLE MORPHOLOGY

A cuticle is a thin, extracellular layer which overlies the epidermis and protects the plant against drought and moisture loss. The cuticle forms a cast of the epidermis, and epidermal features are recognisable in cuticles. Cuticles, contrary to epidermis, are usually very resistant and are easily fossilised. Most plant species have their own characteristic epidermal pattern which is displayed in the overlying cuticle. Hence the interest of cuticles in the study of fossil plants.

Kerp (1990) in his study of fossil gymnosperms by means of cuticular analysis, gave a brief review of characters used in cuticular analysis. That paper is an ideal basis for a short discussion of the consistency and variability of cuticular characters. Characters to be used include the differentiation between lower and upper cuticle, the shape and arrangement of the epidermal cells and stomata, and the presence of cuticular ornamentation. Some of these features reflect the epidermal pattern, others are cuticular characters. A combination of characters can have taxonomic value. However, the variability of characters can be considerable and should be tested for each species by the analysis of a number of specimens.

Differentiation between upper and lower leaf cuticle

In the majority of plants, the upper and lower leaf cuticles are different. Differences are in the thickness, the shape, arrangement and ornamentation of the epidermal cells and the presence of stomata. Leaves with stomata on the upper surface are called epistomatic (usually only floating water plants), those with stomata on the lower surface hypostomatic. Amphistomatic leaves have stomata on both surfaces, usually more on one surface than on the other.

Epidermal cells

The shape of epidermal cells is not very consistent: within one leaf they may vary from isodiametric/polygonal to elongate/rectangular. Usually these various forms are concentrated in groups of (sister) cells having the same shape and orientation, thus representing a special portion of the leaf.

Elongate, rectangular cells are often arranged in rows or bands. In, for instance, cycads and pteridosperms those elongated epidermal cell rows overlie the veins, while the epidermal cells between the veins are polygonal in outline (see Harris, 1964).

Anticlinal walls can be anything between straight and strongly sinuous (e.g., Bennettitales, Harris, 1969). They can also show fine microstructures or thickenings, especially in the corners (Kerp, 1990).

Periclinal walls often show thin areas or thickenings. Papillae are hollow or solid outward projections of the periclinal walls. They vary within a species in size and frequency, often due to environmental circumstances. Papillae, like hairs and trichomes, are believed to give the leaves protection. In fossils, multicellular hairs are rarely preserved. Often only the hair bases are present. Unicellular trichomes are more frequently encountered. They are common in cycads (especially Nilssoniales) and Bennettitales. In the latter group they often accompany a stoma (Harris, 1964, 1969; Fig.7c). Fine ornamentation of the periclinal walls is common; f.i. striae can be very characteristic. They often occur in the cycad genera *Pseudoctenis* and especially *Ctenis*.

Stomata

The stomatal apparatus consisting of an aperture and two reniform guard cells is well-known. Especially in gymnosperms (except for *Caytonia*, see Harris, 1964), they are surrounded by a number of cells that are different from normal epidermal cells and usually more strongly cutinized: the subsidiary cells (Fig. 7a). Sometimes a second or even a third ring of differently developed cells is present: the encircling cells (Fig. 7b). The whole complex consisting of the stomatal aperture, the guard cells, the subsidiary and the encircling cells (if present) is called the stomatal apparatus or complex. For details and for the difference between haplocheilic and syndetocheilic stomata, see Kerp, 1990.

The general arrangement of the stomata is a consistent parameter We saw already that the presence of stomata on the upper and/or lower surface is a specific feature. Also the arrangement in for instance rows or stomatal bands is a character that can be well used in a diagnosis. Rarely, stomata are randomly scattered over a leaf surface as in *Brachyphyllum crucis* (Harris, 1979). In cycads and pteridosperms, where the veins are marked by elongated epidermal cells, the stomata tend to avoid these areas. Stomata-free zones are also found near leaf margins.

Stomatal orientation is often a diagnostic feature: the orientation - longitudinal, oblique or transverse - can be used as a character even on generic level (Harris, 1979, used the difference in stomatal orientation to distinguish between the genera *Podozamites* and *Lindleycladus*).

Stomatal frequency has no taxonomic value. It can vary considerably even within a single specimen. Consider for instance the difference between sun and shade leaves (Kürschner, 1996; Barbacka & van Konijnenburg-van Cittert, 1998). The stomatal frequency tends to decrease with the increasing size of the epidermal cells. Therefore, the stomatal index was introduced: Stomatal Index = 100S / (E+S).

S= number of stomata per unit area; E = number of epidermal cells per unit area.

The stomatal index is a much more consistent factor but it may vary within one species with changes in atmospheric CO_2 level. Research on stomatal response to changes in palaeoatmospheric CO_2 level is progressing rapidly (see e.g. Kürschner, 1996).

The structure of the stomatal complex is a very constant feature in a species. The division into haplocheilic (Fig. 7a,b) and syndetocheilic (Fig. 7c) stomata is a good example (Florin, 1931, 1933). The total stomatal complex can be sunken, or the guard cells only; this feature is usually interpreted as being for protection, just as the presence of papillae on subsidiary cells that overhang the stomatal pit.

The presence and shape of the subsidiary and encircling cells can be very specific. The "rampart"-like thickening of the subsidiary cells of e.g., *Pagiophyllum maculosum* is one of the main diagnostic features of this species (van Konijnenburg-van Cittert, 1987). Striae present on the subsidiary cells of many Cheirolepidiaceous conifers are another example (Harris, 1969).

The number of subsidiary cells (and encircling cells) can vary considerably within one leaf and is thus not a reliable character. However, the average number of subsidiary cells in a species appears to be very consistent. This average number of subsidiary cells can be easily calculated when a significant number of stomata is counted (at least 100; if possible 300). Clement-Westerhof (1984) was the first to use this feature in diagnoses, and she was able to recognise different conifer species exclusively on the basis of bulk-macerated material.

CONCLUSIONS

In general, leaf outline, leaf thickness, base, apex and margin shape and the venation are consistent characters. But number and size are variable factors and are as a rule dependent of local or general environmental circumstances. So size or number on its own should never be used as a specific character, but if used, always in combination with other characters.

The same applies for cuticular features. Differences between upper and lower cuticle, the arrangement of the stomata, the structure of the stomatal complex are consistent characters. But stomatal frequency (contrary to the stomatal index), number of papillae etc. are variable.

REFERENCES

Barbacka M & van Konijnenburg-van Cittert JHA 1998. Sun and shade leaves in two Jurassic species of Pteridosperms. Review of Palaeobotany & Palynology 103 . 209-221.

Boersma M 1972. The heterogeneity of the Form Genus *Mariopteris* Zeiller; a comparative morphological study with special reference to the frond composition of west-European species. Elinkwijk, Utrecht. 172 pp.

Chaloner WG & Creber GT 1990. Do fossil plants give a climatic signal? Journal of Geological Society of London 147 : 343-350.

Clement - Westerhof JA 1984. Aspects of Permian Palaeobotany and

Palynology. IV. The Conifer *Ortiseia* Florin from the Val Gardena Formation of the Dolomites and the Vicentian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Goeppert)Schimper. Review of Palaeobotany & Palynology 41 : 51-166.

Daber R 1980. Zum Problem der Gabelwedelformen des Karbons und Perms - eine †bersicht. Schriftenr. Geol. Wiss. Berlin, 16 : 15-48.

Dilcher DL 1974. Approaches to the identification of Angiosperm leaf remains. The Botanical Review 40 : 1-157

Florin R 1931. Untersuchungen zur Stammesgechichte der Coniferales und Cordaitales. Kungl.Sv.Vet.Akad.Handl. (3), 10(1) : 1-588.

Florin R 1933. Studien Ÿber die Cycadales des Mesozoikums nebst Eršrterungen Ÿber die Spaltšffnungsapparate der Bennettitales. Kungl. Sv. Vet. Akad. Handl. (3). 12(5): 1-134.

Harris TM 1964. The Yorkshire Jurassic Flora. II. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History), London. 191 pp.

Harris TM 1969. The Yorkshire Jurassic Flora. III. Bennettitales. British Museum (Natural History), London. 186 pp.

Harris TM 1979. The Yorkshire Jurassic Flora. V. Coniferales. British Museum (Natural History), London. 166 pp.

Hickey LJ 1978. Origin of the major features of Angiosperm leaf architecture in the fossil record. Cour. Forsch.-Inst. Senckenberg 30 27-34.

Kerp JHF 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). Review of Palaeobotany & Palynology 54 : 249-360.

Kerp JHF, 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios 5 : 548-569.

Krings M & Kerp H 1998. Epidermal anatomy of *Barthelopteris germarii* from the Upper Carboniferous and Lower Permian of France and Germany. American Journal of Botany 85 (4) 553-562.

Kürschner WM 1996. Leaf stomata as biosensors of palaeoatmospheric CO_2 levels. LPP Contribution Series no. 5, 143 pp; Utrecht.

Rees P McA & Cleal CJ 1993. Marked polymorphism in *Archangelskya furcata*, a pteridospermous frond from the Jurassic of Antarctica. Special papers in Palaeontology 49 : 85-100.

van Konijnenburg - van Cittert JHA 1987. New data on *Pagiophyllum maculosum* Kendall and its male cone from the Jurassic of North Yorkshire. Review of Palaeobotany & Palynology 51 : 95-105.

Weber R 1968. Die fossile Flora der RhŠt-Lias-†bergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. Erlanger Geol. Abh. 59: 1-76.