

Leaf whorls of Cupressaceae from the Miocene FASTERHOLT flora, Denmark

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Leaf whorls referred to the fossil species *Hellia salicornioides* are found together with fruits, seeds and megaspores from the Middle Miocene FASTERHOLT flora, Jylland, Denmark. The external and internal morphology together with the epidermal structure have been investigated using the light microscope and scanning electron microscope. The well-preserved fossil specimens afford increased knowledge of the anatomy of this plant. Living species of Cupressaceae have been studied. Although *Hellia salicornioides* cannot be referred to any living genus the investigation clearly indicates that the fossil species may be placed in the family Cupressaceae, closely related to *Tetraclinis articulata*.

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Branchlets of Cupressaceae were found together with other small sized plant remains from the FASTERHOLT flora. The flora was sieved out from a fine grained sand bed in the browncoal pit of Carl Nielsen Ltd. near FASTERHOLT, Jylland, Denmark. It is considered to be of Middle Miocene age, placed in the Odderup Formation established by Rasmussen (1961).

The FASTERHOLT flora, comprising fruits, seeds, twigs, thorns, megaspores and fungi, is being studied by B. Eske Koch and W. L. Friedrich (Friedrich & Koch 1970, 1972, Koch & Friedrich 1970, 1971) and by the present author (Friis 1974, 1975, 1976).

Methods and material

The branchlets were prepared for light microscope studies of the epidermal structure in a concentrated nitric acid for 30–60 minutes followed by a 20 per cent solution of sodium hydroxide for 2–5 minutes. The material was then washed in water, dehydrated and mounted in euparal. Sections of the branchlets were cut with a “Jung Hartschnittmikrotom K” after the material was embedded in durcopan or in paraffin. The thickness of the sections is 10–15 microns. The sections were mounted in euparal. Branchlets for scanning electron microscope were attached on the stubs with colloidal silver and coated with

gold. The electron micrographs were taken on a Cambridge Stereoscan 600.

Herbarium specimens of living Cupressaceae were obtained from Rijksherbarium, Leiden:

Heyderia formosana (Florin) Li.

Papuacedrus arfakensis (Gibbs) Li.

Papuacedrus papuana (F. Muell) Li.

Papuacedrus torricellensis (Schlechter ex Lauterbach) Li.

Department of Botany, University of Aarhus:

Heyderia macrolepis (Kurz) Li.

Libocedrus bidwilli Hook.

Papuacedrus papuana (F. Muell) Li.

Forsthaven, Århus:

Heyderia decurrens (Torr.) K. Koch.

The Arboretum, Hørsholm:

Austrocedrus chilensis (D. Don) Florin.

Geological Department, University of Aarhus:

Tetraclinis articulata (Vahl) Masters.

Fossil specimens of *Hellia salicornioides* Unger from Wackersdorf, Germany (Gregor 1975) were sent to me by Dipl. Geol. J. Gregor, München.

At the Botanical Institute, PAN, Cracow, the following specimens of fossil Cupressaceae have been studied: *Tetraclinis carpatica* Maślankiewiczowa (1953) from Krościenko, *Tetraclinis wandae* Zablocki from Wieliczka, *Libocedrus salicornioides* (Unger) Heer from Stare Gliwice and from Sońnica.

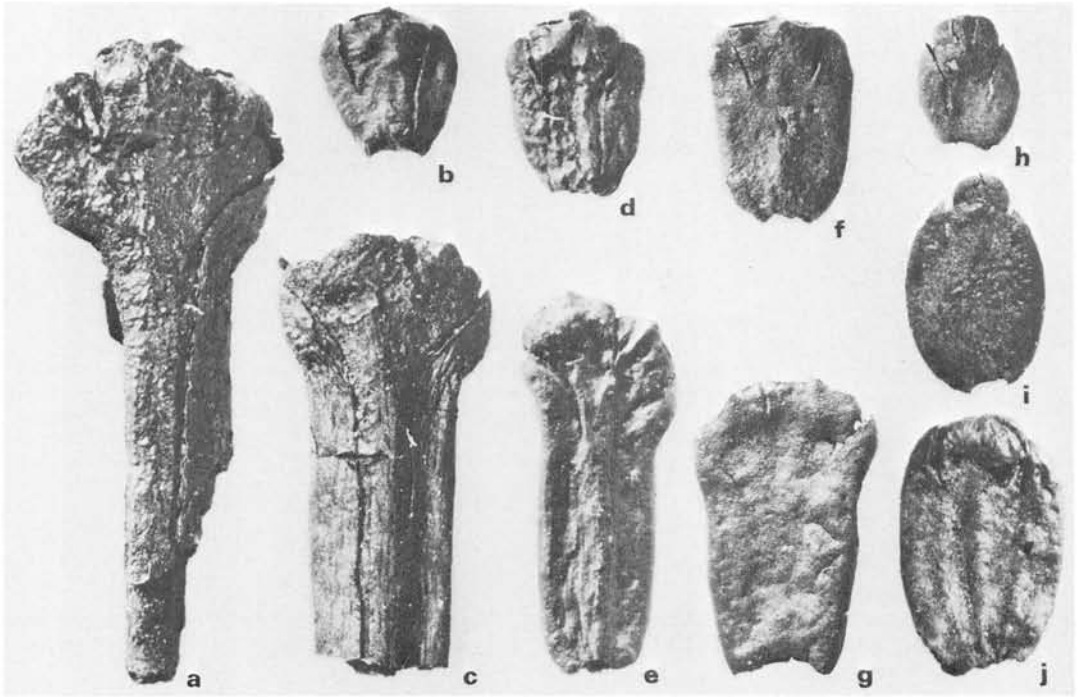


Fig. 1. *Hellia salicornioides*. a, c, e, larger leaf whorls showing branching system. b, d, leaf whorls with one marginal leaf free to the base of the axis. f, g, leaf whorls with small regular marginal leaves. h, i, j, terminal parts of the shoots. $\times 10$.

Material of *Hellia salicornioides* from Kreuzau described by Ferguson (1971) was sent to me by Dr. van der Burgh, Utrecht, the following specimens being studied: 3644, 3648, 3649, 3651, 3653, 3654, 3656 (see Ferguson 1971).

Systematic description

In the systematic description the terminology used by Florin & Boutelje (1954) is mainly followed.

Family: Cupressaceae.

Genus: *Hellia* Unger.

Hellia salicornioides Unger.

1840. *Hellia salicornioides* Unger – Unger p. 375.

1847. *Thuytes salicornioides* (Unger) Unger – Unger p. 11, Pl. 2, figs 1–4,7.

1847. *Libocedrites salicornioides* (Unger) Endlicher – Endlicher p. 275.

1855. *Libocedrus salicornioides* (Unger) Heer – Heer p. 47, Pl. 21, fig. 2.

1920. *Libocedrus salicornioides* (Unger) Heer – Kräusel p. 354–355, pl. 19, figs 4–6, Pl. 20, figs 1–3, text fig. 8.

1928. *Tetraclinis wandae* Zabłocki – Zabłocki p. 188, Pl. 8, figs 10–17a.

1961. *Tetraclinis articulata* (Vahl) Masters – Szafer p. 28, Pl. 7, figs 7–8.

External morphology. The branchlets are distinctly flattened and isolateral with dimorphic leaves. The branchlets preserved are 1.2–8.8 mm long and 1.3–3.8 mm broad and consist mostly of one, or occasionally two, leaf whorls (figs 1, 2). Smaller terminal parts of the shoots are mostly preserved.

The leaves are decussate, scale-like and differentiated into facial and marginal leaves. The

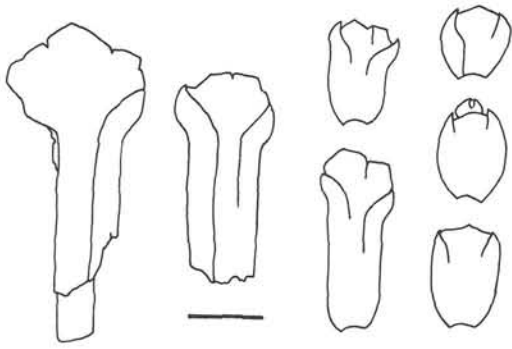


Fig. 2. *Hellia salicornioides*. Diagram showing different leaf whorls, scale = 2 mm.



Fig. 3. *Hellia salicornioides*. Transection of stomatal apparatus, $\times 500$.

two type of leaves are arranged apparently in a whorl. The facial leaves are opposite, the free parts being very short, triangular, and with obtuse apices. The marginal leaves are longer than the facial leaves; they are opposite, bilaterally compressed, and boatshaped with incurved apices. The free blade is 0.3–2.3 mm long. The marginal leaves are almost entirely fused to the facial leaves, but in some specimens they are free to the base of the whorl (fig. 1b, d). Both leaf types have a serrate and scarriose margin (figs 7b, 8, 10).

Internal morphology. The structure of the branchlets has been studied in transections and longisections (figs 3–6). The epidermis is composed of one layer of cells. Each cell is 12–20 μm long and 8–10 μm high. The epidermis on the exposed surface is covered with a cuticle 4–6 μm

thick. The stomata are sunken below the surface. The guard cells are usually badly preserved or not preserved at all. The subsidiary cells have papillae 5–6 μm high surrounding the external air-chamber. No internal air-chamber have been observed.

The mesophyll is differentiated into palisade parenchyma and an inner tissue. The former consists of one or two rows of cells ca. 40 μm high. This tissue occurs on both sides of the branchlets (figs 5, 6). The inner tissue consists of nearly isodiametric-polygonal cells, 25–40 μm in diameter. The innermost cells of the branchlets are usually much compressed and badly preserved. This tissue surrounds one median vascular bundle and two smaller lateral bundles supplying the marginal leaves. Near the base of the free facial leaves two median bundles separate to supply the facial leaves.

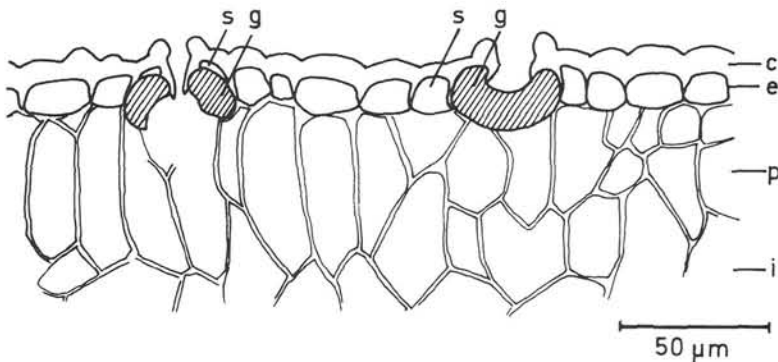


Fig. 3. Diagrammatic transection of a leaf of *Hellia salicornioides*. c = cuticle, g = guard cell, i = inner tissue, p = palisade tissue, s = subsidiary cell.

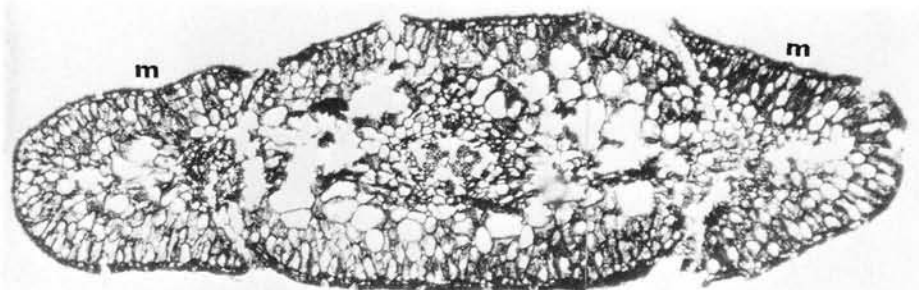


Fig. 5. *Hellia salicornioides*. Transsection of leaf whorl showing central axis and marginal leaves (m), $\times 60$.

The median bundle is lentiform in transection, about $180 \mu\text{m}$ long and $70 \mu\text{m}$ wide. Only primary xylem has been observed. In longisections tracheary cells with bordered pits have been observed.

One resin canal occurs near the dorsal margin of the marginal leaf (fig. 6a) and one occurs on the dorsal side of the facial leaf bundle (fig. 6b).

Epidermal structure. The leaves are amphistomatic. The underside of the facial leaves has two small stomatal bands at the basal margin of the free blade. Under the free blade a broad stomatal band covering the median region extends to the base of the axis (figs 7a, 8). The upper side of the

facial leaves bears few irregularly arranged stomata (fig. 9).

The marginal leaves have the stomata in two broad bands arranged parallel to the margins starting about 0.2–0.4 mm from the apex and running to the base of the axis. Below the free blades these bands are united with the stomatal bands of the facial leaves. The median zone of the marginal leaves are non-stomatal. The upper side of the marginal leaves bears a few, scattered stomata.

The distribution of the stomata is shown in figs 7a & 8. Within the stomatal bands the stomatal apparatuses are irregularly arranged in diffuse longitudinal rows with diverse orientation.

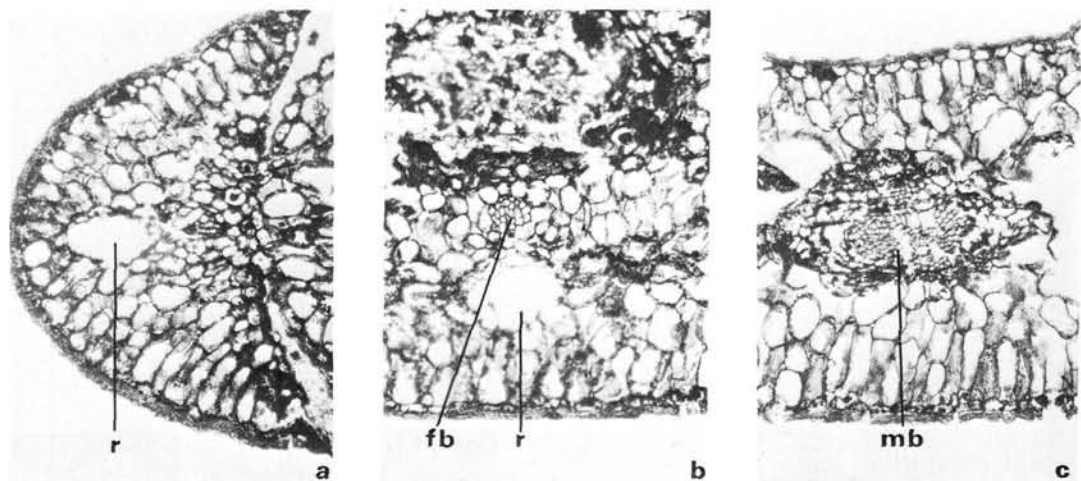


Fig. 6. Transsections of leaf whorl of *Hellia salicornioides*. a, marginal leaf. b, facial leaf. c, axis below the free blades. fb = facial leaf bundle. mb = median bundle. r = resin canal, $\times 120$.

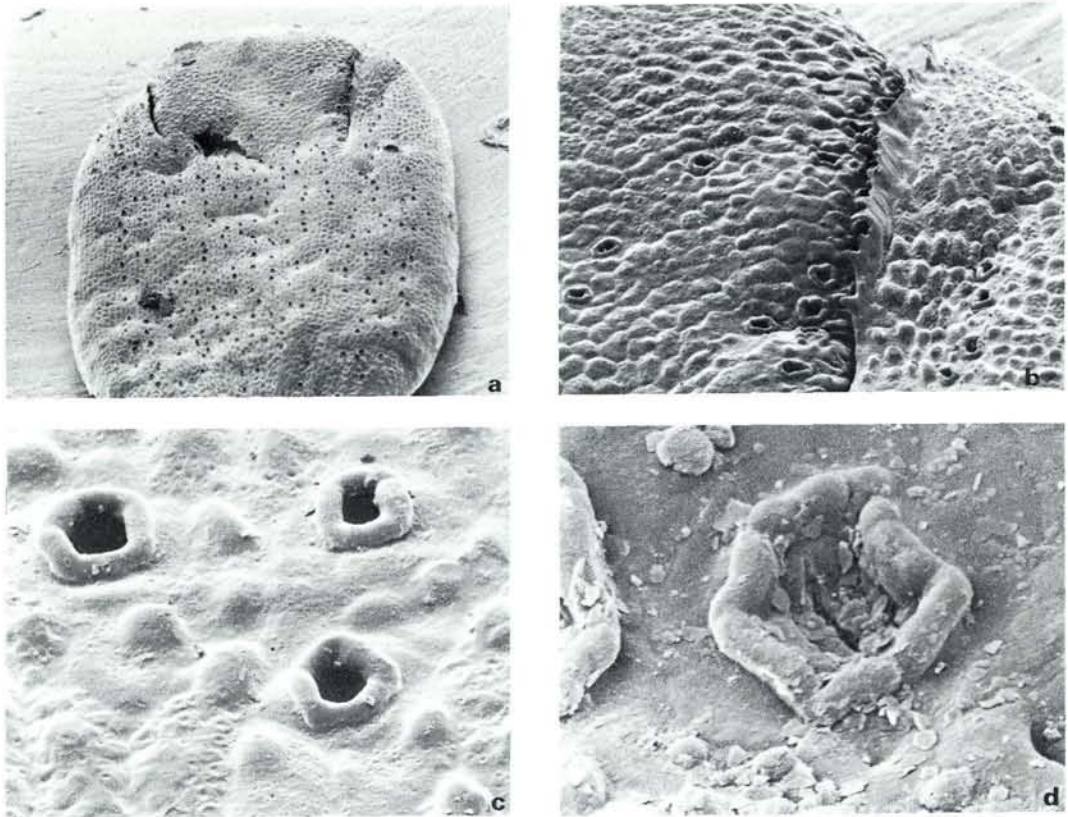


Fig. 7. Scanning electron micrographs of *Helleia salicornioides*. a, leaf whorl with stomata, $\times 37.5$. b, marginal leaf, $\times 150$. c, surface of axis showing verrucate papillae and stomata surrounded by oblong papillae, $\times 750$. d, stomatal apparatus of the upper side of facial leaf, $\times 1500$.

The stomatal apparatuses are monocyclic or incompletely amphicyclic with 4–6 subsidiary cells, usually arranged with two polar cells and the others lateral. The proximal part of the subsidiary cells bears an oblong papilla which forms a marked wall around the external air-chamber (figs 7b, c, 11). The stomata are slightly depressed, the shape of the external air-chamber being rectangular or oval and 12–20 μm long. The guard cells are usually not preserved on the exposed surface of the leaves, but some specimens have very well preserved stomatal apparatuses on the upper side of the facial leaf with distinct T-shaped pieces (fig. 9) and distinct stomatal slit (fig. 7d).

The non-stomatal regions have about 90 epi-

dermal cells per 0.1 mm^2 . The outline of the cells is isodiametric-polygonal or rectangular. They are arranged in diffuse longitudinal rows. The cell walls are about 2 μm thick, sometimes strongly pitted. In most specimens the cell walls are straight, but in the older ones they are slightly undulated.

The external wall of the epidermal cell may be furnished with 1–4 cuticular papillae which are circular and verrucate in shape, sometimes laterally fused. The diameter is about 10 μm and the height is about 5 μm (figs 7c, 11). The papillae are usually found near the base of the leaf whorl and near the base of the free blade. Usually the subsidiary cells have very few verrucate papillae or none.

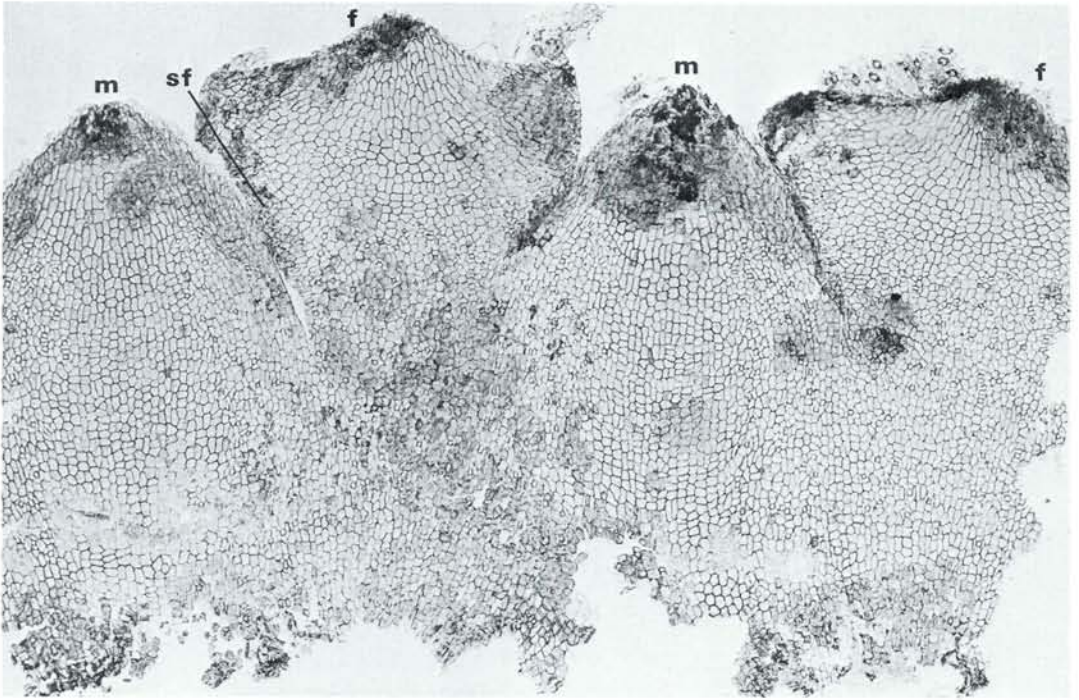


Fig. 8. Epidermis structure of *Hellia salicornioides*. *f* = facial leaf. *m*. = marginal leaf. *sf*. = stomatal band of facial leaf. $\times 40$.

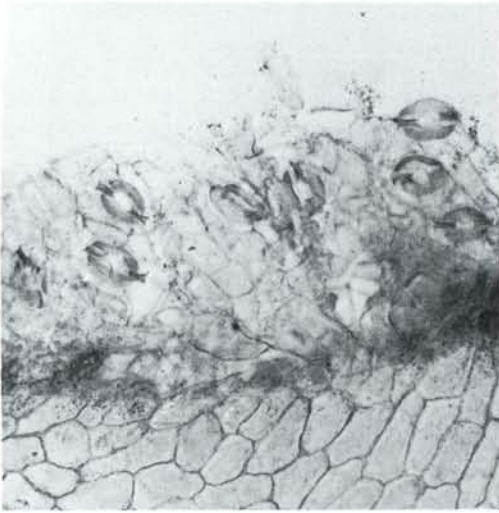


Fig. 9. *Hellia salicornioides*. Stomata of upper side of facial leaf, $\times 200$.

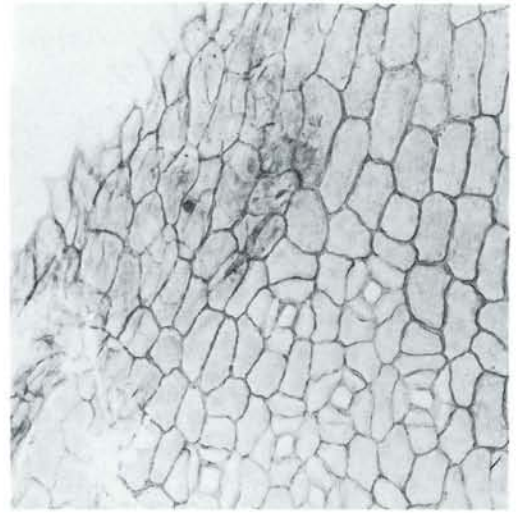


Fig. 10. *Hellia salicornioides*. Serrate and scarriose margin of marginal leaf, $\times 200$.

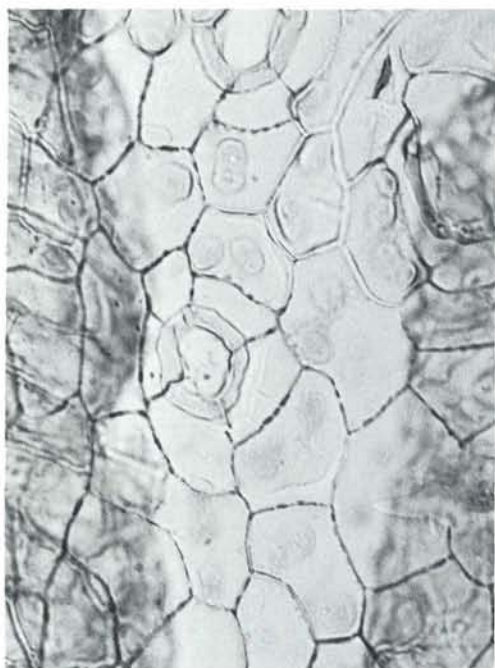


Fig. 11. *Hellia salicornioides*. Epidermis structure of exposed surface with verrucate papillae and oblong papillae surrounding the stomata, $\times 500$.

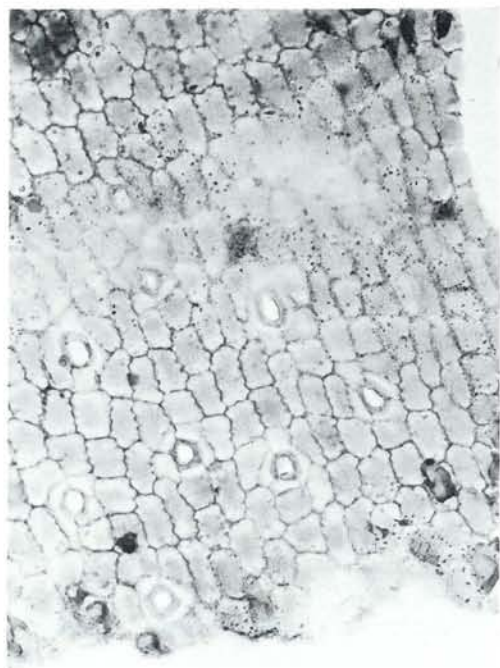


Fig. 12. Epidermis structure of exposed surface of *Hellia salicornioides* with slightly undulated cell walls, $\times 200$.

Discussion. The leaf whorls from FASTERHOLT closely resemble *Hellia salicornioides* Unger (1840) from Radoboj. The species was described by Unger (1847) as *Thuytes salicornioides*. According to Unger it is closely related to the fossil species *Thuytes callitrina* Unger. Both species were compared to the living *Thuja articulata* Desf. (= *Tetraclinis articulata* (Vahl) Masters) (Unger 1847).

Fossil plants ascribed to *Hellia salicornioides* are widely distributed in the Tertiary floras of Europe (Zalewska 1961, Givulescu 1962a). The Danish material comprises small sized, slender leaf whorls with almost parallel margins. Big fan-shaped leaf whorls as described from many leaf-floras have not been found in the FASTERHOLT flora. Studies of *Hellia salicornioides* from KREUZAU indicate a huge diversity in shape and size of the leaf whorls and big fan-shaped whorls are found in organic connection with the small slender type (fig. 13). In respect to the epidermal structure there is a close resemblance between the Danish material and *Hellia salicornioides*

described from other fossil floras of Europe (Kräusel 1920a, b; Mai 1963, Walther 1964; Ferguson 1971; Givulescu 1975a, b).

In their external morphology and size the branchlets from FASTERHOLT closely resemble *Hellia salicornioides* and *Tetraclinis wandae* found in diaspor floras from Poland (Zablocki 1928, 1930a, b; Szafer 1961; Łańcucka-Środoniowa 1966). The epidermal structure has not been described for this material.

Hellia salicornioides is closely related to the Cupressaceae. The fossil species was compared with species of *Libocedrus*, s. lat. (*Libocedrites salicornioides* (Unger) Endlicher 1847, *Libocedrus salicornioides* (Unger) Heer 1855). The following species of *Libocedrus*, s. lat. have previously been considered: *L. decurrens* (= *Heyderia decurrens*), *L. macrolepis* (= *Heyderia macrolepis*), and *L. chilensis* (= *Austrocedrus chilensis*) (Endlicher 1847, Heer 1855, Kräusel 1920a, Raniecka-Bobrowska 1962, Mai 1963, Ferguson 1971).

The genus *Libocedrus* Endlicher has been

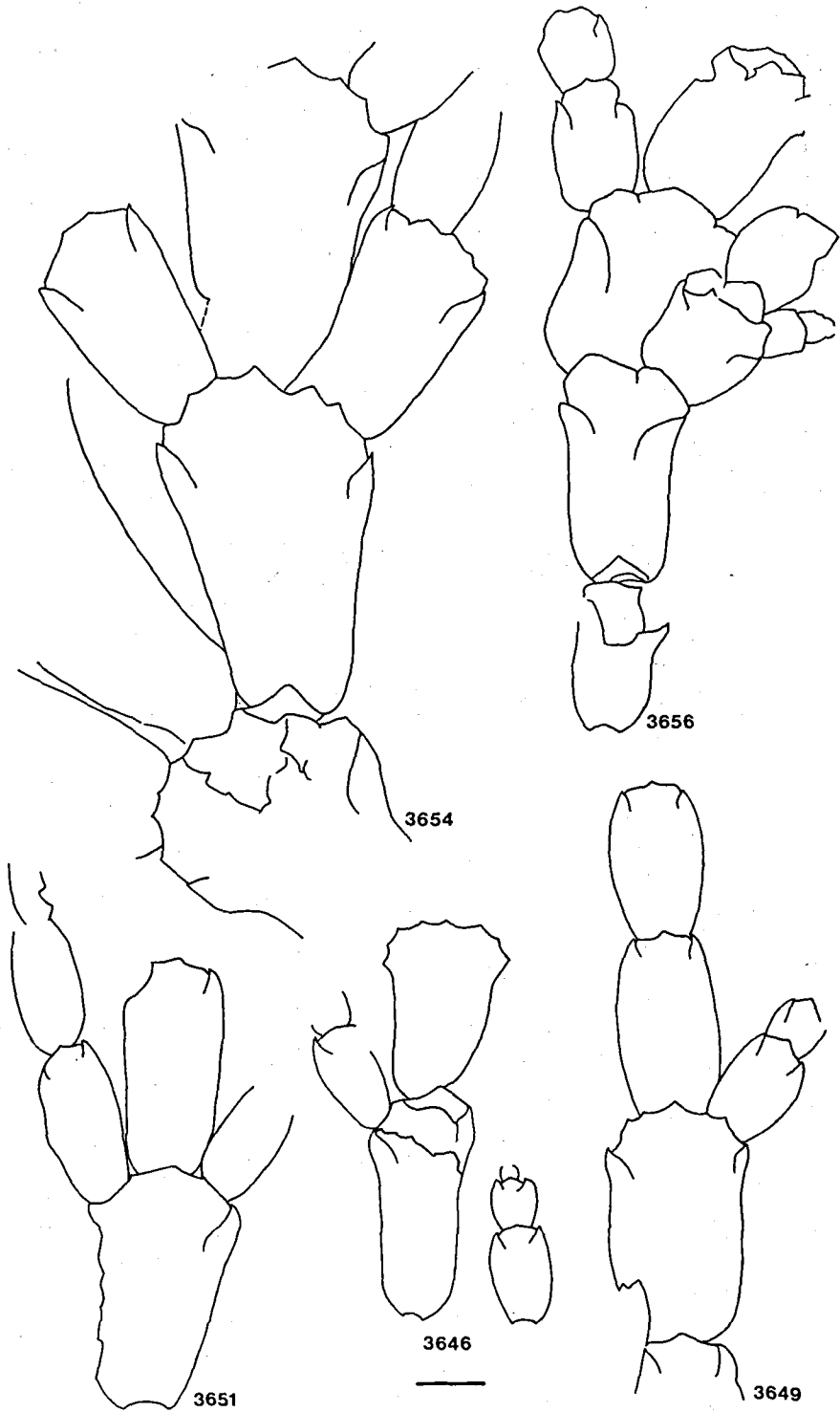


Fig. 13. *Hellia salicornioides* from Kreuzau showing a great diversity in shape and size of the leaf whorls. The numbers refer to museum-numbers of Laboratorium voor palaeobotanie en palynologie, Utrecht, scale = 2 mm.

subdivided by some authors into several genera: *Heyderia* K. Koch, *Libocedrus* Endlicher, s. str., *Papuacedrus* Li, *Austrocedrus* Florin & Boutelje, and *Pilgerodendron* Florin (Li 1953, Florin & Boutelje 1954). In the present study this subdivision has been followed.

The external morphology and the epidermal structure of leaves of the 5 genera were profoundly studied by Florin (1930a, b, 1931) and Florin & Boutelje (1954). On the basis of these studies the following specimens have been selected for further examinations: *Heyderia decurrens*, *Heyderia macrolepis*, *Heyderia formosana*, *Libocedrus bidwilli*, *Austrocedrus chilensis*, *Papuacedrus torricellensis*, *Papuacedrus arfakensis*, and *Papuacedrus papuana*. In addition leaves of *Tetraclinis articulata* have been examined (table 1).

In regard to their external morphology the species of *Heyderia*, *Austrocedrus* and *Tetraclinis* differ from *Hellia* by having the marginal leaves free to the base. This character, however, is also found in a few specimens of *Hellia*. In *Papuacedrus*, on the other hand, the marginal leaves are usually fused and in *Papuacedrus torricellensis* the marginal leaves are also fused to the facial leaves. In this respect the fossil are closely related to *Papuacedrus*, but the base of the facial leaves is much broader in *Hellia* than in *Papuacedrus*.

The dispersion of the stomatal apparatuses of the exposed surface of the leaves differs within the investigated species. *Heyderia* and *Austro-*

cedrus have, on the marginal leaf, two broad stomatal bands running parallel to the leaf margins. In *Papuacedrus* the stomatal bands of the marginal leaves are broad and the bands of the two marginal leaves are fused or nearly fused in the median part of the axis. The bands are subdivided into smaller bands.

In *Tetraclinis* the stomata are arranged in two depressed stomatal bands at the margin of the facial leaves separated by a broad non-stomatal band. The stomata are completely covered by the margins of the marginal leaves.

The epidermis cells of the non-stomatal bands are more elongated in *Heyderia* and *Austrocedrus* than in *Papuacedrus*, *Tetraclinis* and *Hellia salicornioides*. In *Tetraclinis* the epidermal cells of the facial leaves are nearly isodiametric and closely resemble those of *Hellia salicornioides*. The epidermal structure of *Papuacedrus* also have some agreement with the fossil material.

The orientation of the stomatal apparatuses is mostly longitudinal in *Austrocedrus* and in *Papuacedrus*. In *Heyderia*, *Tetraclinis* and *Hellia* they are diversely orientated.

Hellia salicornioides is generally referred to the Cupressaceae. This point of view is supported by the present study. The objections of referring the fossils to this family expressed by Ferguson (1971) are here rejected. Reduced marginal leaves fused to the facial leaves are found within species of *Papuacedrus* and we also find large sized whorls here.

The fossil species is not identical with any of

Table 1. Comparisons of the investigated genera.

	Extern. morphology				Epidermal structure								
	Leaves in apparent whorls of four	Marginal and facial leaves fused	Leaves with serrate margins	Leaves amphistomatic	Monocyclic or incompletely amphicyclic stomata	Stomata in broad bands	Stomata in diffuse longitudinal rows	Stomata diversely orientated	Stomata not closely arranged	Epidermal cells relatively small	Number of subsidiary cells	Subsidiary cells lack distal papillae	
<i>Hellia</i>	+	+	+	+	+	+	+	+	+	+	4-6	(+)	
<i>Austrocedrus</i>					+						4-6	+	
<i>Heyderia</i>	+		+	+	+		+	+			4-8		
<i>Libocedrus</i>			+	+	+						4-7		
<i>Papuacedrus</i>		+		+	+	+		+		+	4-7	(+)	
<i>Tetraclinis</i>	+		+	+	+		+	+		+	4-6	(+)	

the examined living species, but there is some agreement in the epidermal structure, as well as in the external and internal structure, of *Tetraclinis articulata*. However, *Tetraclinis articulata* has markedly xeromorphic characters with deeply depressed stomatal bands.

A few cone-scales resembling *Tetraclinis* have been reported from the FASTERHOLT flora (Koch & Friedrich 1970, Koch et al. 1972), but until now no connection between the fructifications and the leaves can be established.

It is possible that *Tetraclinis* and *Hellia* have evolved from a common ancestor in the Tertiary of Europe and that *Tetraclinis* has survived in the Mediterranean vegetation by adaptation to xeromorphic conditions. Fossil leaves ascribed to *Tetraclinis* cf. *articulata* have been found together with leaves of *Hellia salicornioides* in the Upper Miocene floras from Romania (Givulescu 1962b, 1975a). Mai (1964, 1970) mentioned that more species from the humid Miocene floras of Europe are found strongly altered in the xeromorphic vegetation of southern Europe of today.

The geographic distribution of the investigated species also point to a connection between *Hellia salicornioides* and *Tetraclinis articulata*. This species is limited to Morocco, Algeria, Tunisia, southern Spain and Malta. *Papuacedrus* has three species all limited to New Guinea. *Austrocedrus* is found in southern Chile. The genus *Heyderia* has a disjunct range with one species in the Pacific North America, and two species in southeastern Asia. *Libocedrus* has a disjunct range in the southern hemisphere.

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Dansk sammendrag

Skud af *Hellia salicornioides* er fundet sammen med FASTERHOLT floraens mindre planterester. Floraen, som hovedsageligt består af frugter og frø, er udslemmet fra et sandlag mellem de to øverste brunkulslag i A/S C. Nielsens brunkulsglav ved

Fasterholt, Vestjylland. Brunkulsserien menes at tilhøre den Mellem Miocæne Odderup formation.

Hellia salicornioides har flade, isolaterale skud med skælformede modsatte blade, hvis frie del oftest er meget lille. De fleste skudrester omfatter kun enkelte led, mens andre består af de to yderste led. Marginalbladene er bådformede og indad-bøjede. Facialbladene er lavt triangulære. Bladene flar svagt takket kant. Epidermisstrukturen er undersøgt ved hjælp af lysmikroskopi og scanning elektron mikroskopi af den velbevarede kutikula. Læbeceller findes både på bladenes overside og underside. Facialbladene og marginalbladenes læbecelle bånd er smeltet sammen på akslen under de frie blade.

De fossile skud er sammenlignet med nulevende arter af Cupressaceae. Der er en vis overensstemmelse mellem *Hellia salicornioides* og *Tetraclinis articulata*. Imidlertid har *Tetraclinis* stærkt xeromorfe karakterer. Muligvis har de to arter udviklet sig fra en fælles stamform i Europas Tertiær, og *Tetraclinis* har overlevet i den mediterrane vegetation ved en tilpasning til xeromorfe forhold. *Hellia salicornioides* har ikke med sikkerhed kunnet henføres til nogen nulevende slægt, men undersøgelsen viser klart, at den fossile art bør henføres til familien Cupressaceae.

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