

The Damgaard flora: A new Middle Miocene flora from Denmark

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A new fossil flora consisting of fruits and seeds has been recovered from a sand bed of Middle Miocene age at the exposure »Damgaard S« in the Søby-Fasterholt area, Denmark. 36 species have been recorded; the results of the floristic-climatic analyses indicate that the Damgaard flora is an arcotertiary flora that has grown under warm temperate to subtropical conditions. The most significant fossils in the Damgaard flora are the endocarps of *Comptonia*, assigned to a new species *C. srodoniowae*. Fruits and seeds of *Arctostaphyloides menzelii*, *Empetrum* sp., *Proserpinaca brevicarpa*, *Rhus* cf. *toxicodendron* and *Visnea* sp. have been recorded from Tertiary deposits of Denmark for the first time.

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During the summer of 1971 an exposure at the abandoned brown coal pit »Damgaard S« in the Søby-Fasterholt area (figs 1,2) was studied as part of a sedimentological training project. The present author attended the project and collected samples for carpological studies. The investiga-

tion was conducted by G. Larsen and H. Friis, Department of Geology, the University of Aarhus. A preliminary note on this work was given by Larsen & Friis (1973). Examinations of trace fossils from the brown coal pit were carried out by Asgaard & Bromley (1974). The locality

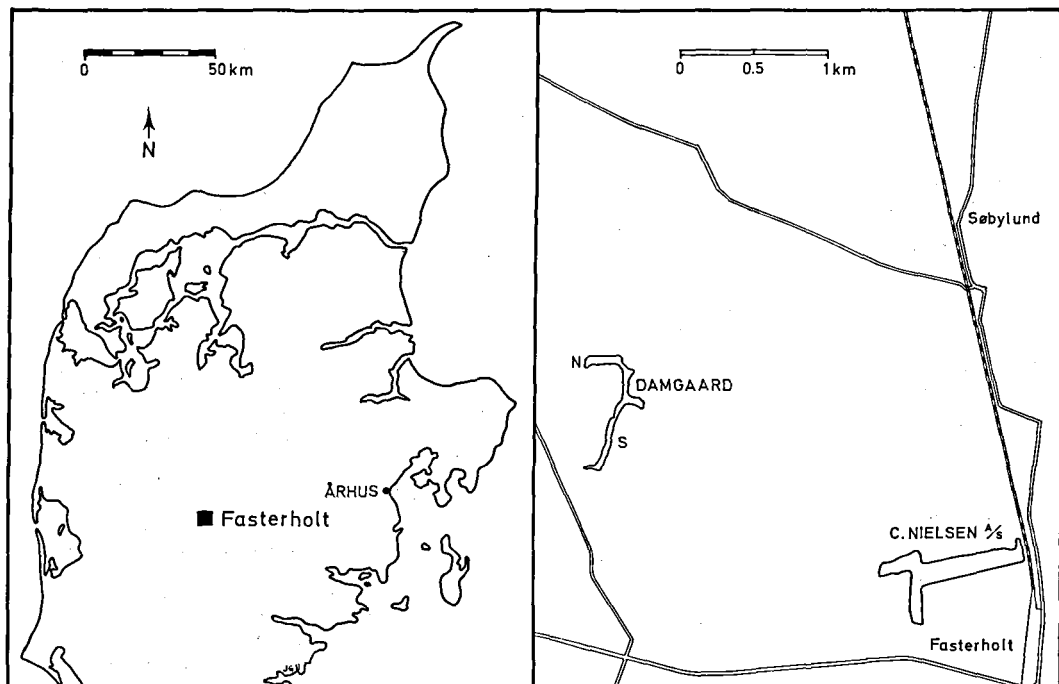


Fig. 1. Map showing main localities with plant macrofossils in the Søby-Fasterholt area. Damgaard N – Søby flora, Damgaard S – Damgaard flora, C. Nielsen A/S – Fasterholt flora.

was also briefly mentioned by Koch et al. (1973) in the outline of the geology of the Søby-Fasterholt area.

Locality and stratigraphy

The brown coal pit »Damgaard S« is situated in the Søby-Fasterholt area, Jylland, Denmark (fig. 1). The pit is abandoned and partly water-logged and the brown coal seams are totally submerged. The exposed section is composed of a 6–8 m thick series of Tertiary deposits overlain by 1.5–4 m of Quaternary deposits (figs 2, 3).

The Tertiary sequence consists of light cross-bedded sand discordantly overlain by up to 5 m of black, micaceous clay, which in the basal part is gravelly. Larsen & Friis (1973) referred the sand to the continental Odderup Formation (Middle Miocene) and the clay to the Marine Hodde Formation (uppermost Middle Miocene). According to S. Piasecki (personal communication 1978), who studied the dinoflagellate assemblages from the Hodde and Gram Formation, the entire Hodde Formation should be referred to the Upper Miocene. *Ophiomorpha* burrows which penetrate the sand from the basal gravel layer indicate that this facies was deposited in a littoral environment (Asgaard & Bromley 1974). Where the clay sequence is thickest there is a gradual change from the dark Hodde clay into dark, glauconitic clay which belongs to the basal part of the marine Gram Formation (Upper Miocene). The above mentioned formations were defined by Rasmussen (1961).

Samples for carpological studies were collected from the light cross-bedded sand and the fossils were washed out in water in the laboratory. The fossil material consists predominantly of rounded

pieces of wood, but in a few horizons fruits and seeds occur abundantly; these horizons numbered as: Dam 1, Dam 2, Dam 3, Dam 4, Dam 5 are indicated on figure 2. The thick cross-bedded units constitute lateral successions (fig. 2); the sand sequence is thought to have been deposited during a rather short period, consequently the plant remains are treated collectively. There is no definite evidence for the depositional environment of the sand bed, and as the plant fossils are rather worn, probably caused by transportation, they cannot contribute to the understanding of the environment.

Silicified lower Palaeozoic fossils have also been found in the cross-bedded sand. They are similar to those described by Spjeldnæs (in Koch & Friedrich 1970), and they are probably derived from the central part of the Baltic area (Spjeldnæs 1975).

The Damgaard flora

The plant remains collected in the brown coal pit Damgaard S are considered as one flora: the Damgaard flora. It comprises 36 species of fruits and seeds, and a few twigs (table 1). The preservation of the plant remains is variable, some fruits are badly worn while others have more fragile parts preserved, but they all give indication of a rather rough transportation. The preservation of the fruits and seeds does not allow detailed anatomical studies. The majority of species in the flora are represented by very few specimens; only a few species are well represented and allow more detailed descriptions and discussion.

The distribution of species throughout the profile is shown in table 1. Endocarps of *Comptonia srodoniowae* sp. nov. are the most common fos-

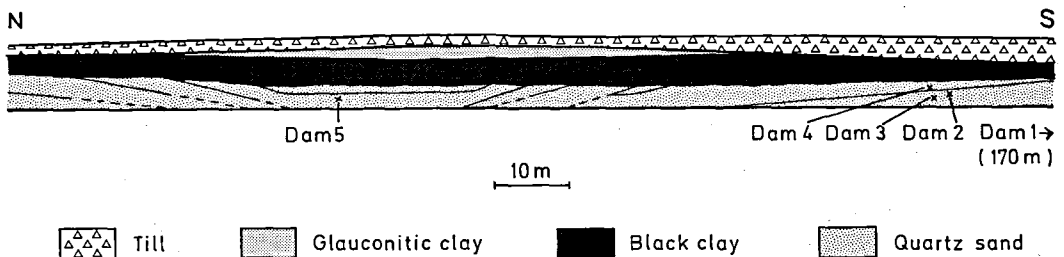


Fig. 2. Sketch of the exposure at Damgaard S. The numbers indicate horizons where fruits and seeds occur abundantly.



Fig. 3. View of the exposure at the brown coal pit Damgaard S. a = Quaternary, b = glauconitic clay, c = dark clay, d = Quartz sand. (Photo K. Raunsgaard Pedersen).

sils in the Damgaard flora and they are found in all samples together with the endocarps of *Myrica cf. ceriferiformis*. Leaf whorls of *Hellia salicornioides* are found in four samples; all other species were found in less than four samples (table 1).

Climatic interpretation of the Damgaard flora is based on analyses of three different groupings of flora-elements: 1. Arctotertiary – palaeotropical elements. 2. Herbaceous – arborescent elements (growth form). 3. Native – exotic elements (generic composition). Friis (1975), when applying these analyses to the Middle Miocene Fæstervold flora, gave a discussion of the methods.

The correlation between the content of palaeotropical species and the climate was discussed in detail by Mai (1965, 1967). The percentage of palaeotropical species is thought to increase with increasing temperature. Fossil floras dominated by the palaeotropical element are referred to as mastixioidean floras, and fossil floras dominated

by the arctotertiary element are referred to as arctotertiary floras (Mai 1965). The Damgaard flora is an arctotertiary flora with 65% of the species referred to the arctotertiary element and 35% to the palaeotropical element. This percentage composition is regarded as an indication of warm temperate to subtropical conditions (Mai 1965).

The relationship between growth form and climate was studied by Bailey & Sinnott (1916), and analyses of growth form have been applied to fossil floras by Reid & Chandler (1933) and Szafer (1946, 1954, 1961). Generally the percentage of arborescent species increases with increasing temperature when considering the dicotyledones. In the Damgaard flora the woody dicotyledonous species make up about 54% of all angiosperm species and 75% of all dicotyledonous species, which indicates tropical conditions. The high percentage of woody species may, in part at least, be a result of rough transportation with the loss of

Table 1. Fossil species identified from the brown coal pit »Damgaard S«

Species	Dam	Dam	Dam	Dam	Dam
	1	2	3	4	5
<i>Pinus</i> sp.			x		
<i>Taxodium dubium</i>			x	x	
<i>Hellia salicornioides</i>	x	x	x	x	
<i>Brasenia</i> cf. <i>tenuicostata</i>	x		x	x	
<i>Comptonia srodoniowae</i>	x	x	x	x	x
<i>Myrica</i> cf. <i>ceriferiformis</i>	x	x	x	x	x
<i>Myrica</i> cf. <i>minima</i>	x	x	x		
<i>Myrica</i> cf. <i>suppanii</i>	x		x		
<i>Pterocarya</i> sp.	x				
<i>Eurya stigmosa</i>	x	x			
<i>Visnea</i> sp.	x				
<i>Arctostaphyloides menzelii</i>	x		x		
<i>Epacridicarpum</i> sp.			x		
Ericaceae gen.?			x		
<i>Empetrum</i> sp.			x		
<i>Halesia crassa</i>	x				
<i>Intratropollenites instructus</i>			x		
<i>Aldrovanda praevesiculosa</i>					x
<i>Cecodon gibbosus</i>			x		
<i>Proserpinaca brevicarpa</i>			x		
<i>Rhus</i> cf. <i>toxicodendron</i>			x		
<i>Palirus</i> sp.			x		
<i>Vitis</i> cf. <i>silvestris</i>			x	x	
Alismataceae gen.?			x		x
<i>Potamogeton heinkei</i>				x	
<i>Cladium reidiorum</i>				x	
<i>Cladium</i> cf. <i>crassum</i>		x		x	
<i>Scirpus ragozinii</i>		x	x		x
<i>Scirpus</i> ? sp.			x		
Cyperaceae gen.? sp. 1			x		
Cyperaceae gen.? sp. 2			x		
<i>Sparganium camenzianum</i>		x	x		
<i>Carpolithus</i> sp. 1				x	
<i>Carpolithus</i> sp. 2			x		
<i>Carpolithus</i> sp. 3	x				
<i>Carpolithus</i> sp. 4			x		

the more delicate seeds of the herbaceous plants. It should be noted that the statistical basis is rather unreliable as only 16 dicotyledonous species have been considered.

The relationship between the native and exotic elements in a fossil flora and the palaeoclimate was discussed by Wolfe & Barghoorn (1960). The percentage of exotic elements are thought to increase with increasing temperature. In the Damgaard flora 53% of the species may be included in the native element and 47% in the exotic element, which also indicates a warm climate. The native element here includes fossil species referred to extant genera now living in parts of the Middle European flora region (cf. Friis 1975). The exotic element includes fossil

species referred to genera, which are not represented in this area today.

The majority of species of the Damgaard flora have been compared to extant species, which are distributed within the warm temperate and subtropical regions of the world, and although the statistical foundation, on which the climatic analyses are based is slender, it may be concluded that the climatic conditions which prevailed in the Søby-Fasterholt area when the Damgaard flora existed were warm temperate to subtropical.

Two Middle Miocene floras have previously been described from the Søby-Fasterholt area: The Fasterholt flora and the Søby flora (fig. 1). The stratigraphic relationship between the three floras is shown in figure 4.

The Søby flora was discovered in the abandoned brown coal pit »Damgaard N« (fig. 1) by E. Fjeldsø Christensen, who recognised 16 species of leaves and fruits preserved in a brownish clay; parts of the taxonomic study of the Søby flora are already published (Christensen 1975, 1976). Samples of the plant bearing clay were separated by wet sieving for carpological studies and about 15 species of fruits and seeds were found. Geographically and stratigraphically the Søby flora is very close to the Damgaard flora (figs 1, 4). However, the two floras differ in many respects, which may be attributed to the difference in depositional environments and in the nature of the fossils. The Søby flora, which is deposited in clay, is thought to represent the vegetation of a restricted area, and the plant material has not been subjected to long transportation (leaves usually well preserved). The Damgaard flora, however, is deposited in sand and is thought to contain representatives of various local and regional vegetation; the plant material has been subjected to rather rough transportation (fruits and seeds usually worn). In spite of the difference in the depositional environment and the nature of the fossils, the Søby flora and the Damgaard flora also show some similarity. The most common fossils in the Damgaard flora are the endocarps of *Comptonia srodoniowae* sp. nov. *Comptonia* is also very common in the Søby flora, where it is represented by leaves of *C. acutiloba* (Christensen 1975) and endocarps of *C. srodoniowae* sp. nov. The endocarps of *Comptonia* from the two localities are very similar in size and shape. Conifers referred to *Pinus*, *Taxodium*

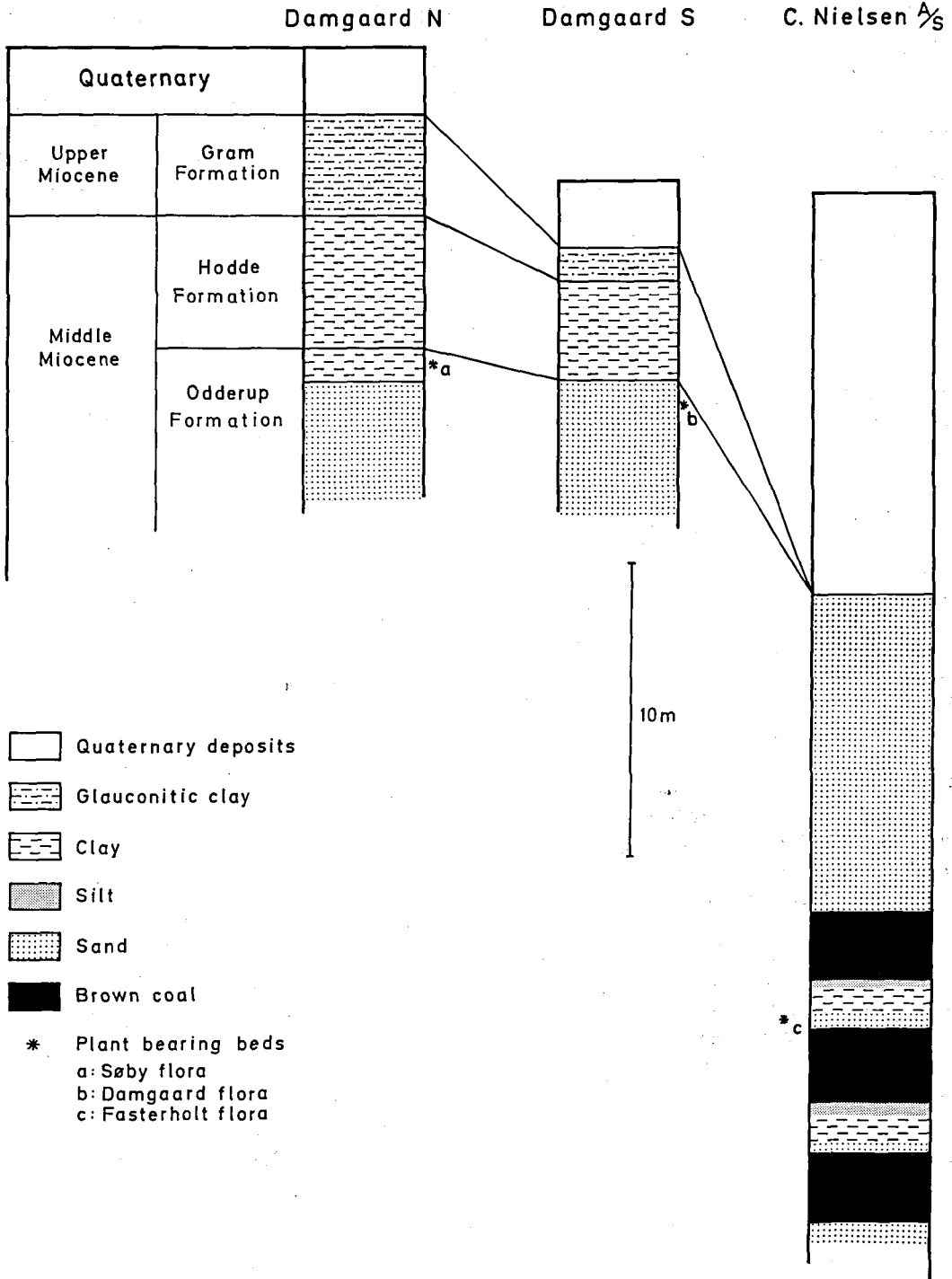


Fig. 4. Stratigraphical correlation of exposures with plant macrofossils in the Søby-Fåsterholt area (compiled from Larsen & Friis 1973, Christensen 1975).

and *Hellia salicornioides* are also found in both floras, together with fruits and seeds of *Myrica*, *Halesia*, *Proserpinaca*, Alismataceae, *Sparganium*, *Potamogeton* and *Scirpus*. In the Damgaard flora the palaeotropical element constitutes 35% of the species, whereas only one species from the Søby flora can be referred to this element.

The Fasterholt flora was discovered in the brown coal pit »C. Nielsen A/S« near Fasterholt (fig. 1) (Koch & Friedrich 1970, Koch et al. 1973). The flora is very rich and comprises more than 150 species of fruits, seeds, megaspores and leafy shoots. The preservation of the plant material is usually excellent and allows detailed morphological and anatomical studies, which was demonstrated by Koch & Friedrich (1971) and Friis (1977a, 1977b). The Fasterholt flora is accumulated in a fine grained sand bed intercalated between the two uppermost brown coal layers; it is thought to represent various plant communities from a rather local flora, and generally the fossils show no evidence of long transportation. The Damgaard flora has many species in common with the Fasterholt flora, but some species have not been recorded in the Fasterholt flora: *Arctostaphyloides menzelii*, *Empetrum* sp., *Halesia crassa*, *Intratropollenites instructus*, *Proserpinaca brevicarpa*, *Rhus* cf. *toxicodendron* and *Visnea* sp. *Intratropollenites instructus* is represented in the Damgaard flora by pollen-sacs with pollen. Similar dispersed pollen grains were also found in the lignite from the brown coal pit »C. Nielsen A/S« (Friis & Pedersen in prep.). Floristic-climatic analyses based on the small sized plant remains show that the Fasterholt flora is an arctotertiary flora in which about 60% of the species may be referred to the arctotertiary element (Friis 1975). The climatic conditions of the Damgaard flora and the Fasterholt flora are thought to have been rather similar.

Systematic description

Division: Gymnospermae
Class: Coniferopsida
Family: Abietaceae
Genus: *Pinus* Linné

Pinus sp.
Fig. 5A

Material: One seed
Occurrence: Dam 3.

Remarks. Macrofossils ascribed to *Pinus* occur rather seldom in the Tertiary deposits of Denmark. One dwarf shoot of *Pinus palaeostrobis* was described from the fossiliferous clay at Fasterholt by Mathiesen (1970) and few seeds of *Pinus* were also recorded from the Fasterholt flora (Friis 1975). Cones ascribed to *P. thomasi-anum* were found in the Søby flora by Christensen (1975) and at Sønderskov, Jylland, by Hartz (1909).

The extant species of *Pinus* are very difficult to distinguish on seed-characters. No fossil species of *Pinus* is based only on seeds and the present specimen is referred to *Pinus* sp.

Family: Taxodiaceae
Genus: *Taxodium* Richard

Taxodium dubium (Sternberg) Heer

1823. *Phyllites dubius* Sternberg – Sternberg p. 37, pl. 36:3.

1853. *Taxodium dubium* Heer – Heer p. 49, pl. 17:5–15.

Material: 6 seeds and about 60 fragments of seeds, 1 fragment of cone-scale.

Occurrence: Dam 3, Dam 4.

Remarks. Plant remains ascribed to *Taxodium* are very common in the plant-bearing Miocene deposits of Jylland. Mathiesen (1970) described well-preserved seeds, foliage twigs and cone scales of *T. dubium* from the lignitic clay at Moselund. From the Søby flora seeds of *T. dubium* were likewise described together with shoots and cones (Christensen 1975). Twigs, cones and seeds of *Taxodium* are among the most numerous fossils in the Fasterholt flora (Koch et al. 1973). The seeds from the Damgaard flora are in complete agreement with other seeds of *T. dubium* previously described from the Tertiary of Denmark.

Family: Cupressaceae
Genus: *Hellia* Unger

Hellia salicornioides Unger
Figs 5B, C.

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

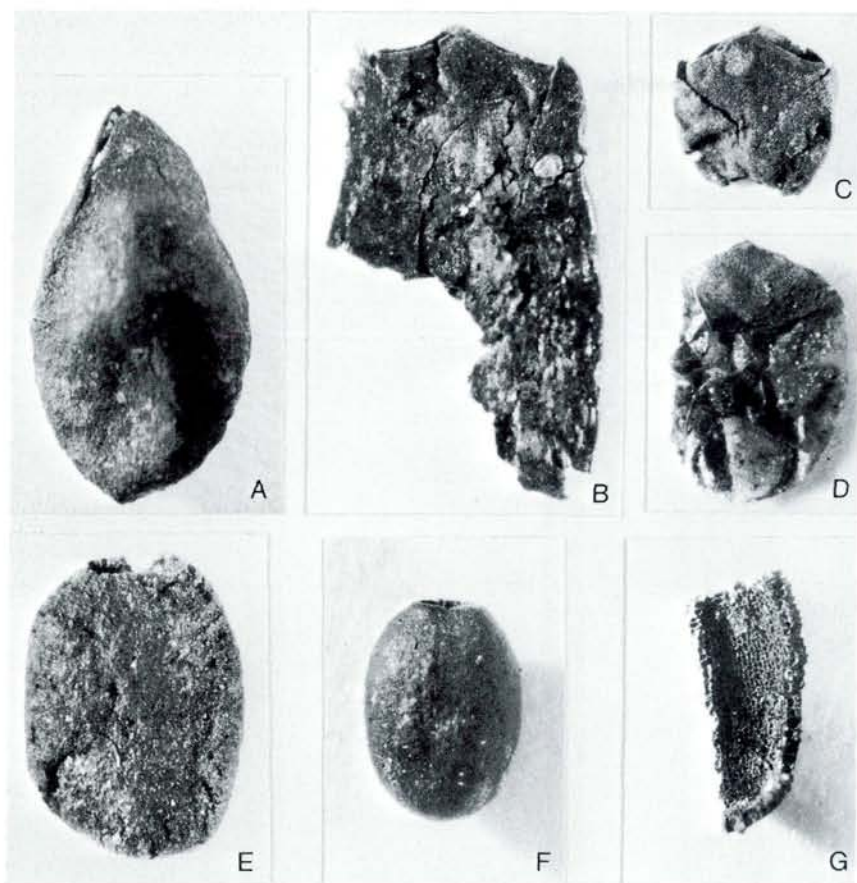


Fig. 5. A, *Pinus* sp., seed. B–C, *Hellia salicornioides*, leaf whorls. D–G, *Brasenia* cf. *tenuicostata*. D, inner integument.

E–F, seeds. G, inner surface of outer integument showing digitate sclereids. $\times 15$.

1847. *Thuytes salicornioides* Ung. – Unger p. 11, pl. 2: 1–4, 7.

1977a. *Hellia salicornioides* Unger – Friis p. 104, figs 1–13.

Material: 8 fragments of leaf whorls.

Occurrence: Dam 1, Dam 2, Dam 3, Dam 4.

Remarks. The present material is similar in both morphological features and epidermal structure to those described from the fossil flora of Fæstervold (Friis 1977a). Fragments of *H. salicornioides* were also found in the transitional bed of alternating sand and clay below the plant-bearing bed at the locality Damgaard N. Twigs of *H. salicornioides* are very common in younger Tertiary plant-bearing beds of Europe; it belongs to an extinct genus *Hellia*, which is closely related to the extant *Tetraclinis* (Friis 1977a).

Division: Angiospermae

Class: Dicotyledones

Family: Cabombaceae

Genus: *Brasenia* Schreber

Brasenia cf. *tenuicostata* Nikitin

Figs 5D–G.

Material: 10 seeds, 6 fragments of seeds, 6 inner integuments.

Occurrence: Dam 1, Dam 3, Dam 4.

Description. Seeds anatropous, elongated elliptical, 1.5–2.8 mm long, average = 2.4 mm, 1.1–2.0 mm in diameter, average = 1.6 mm, 10 specimens measured. Seed wall consists of two distinct layers. Outer integument 0.15–0.19 mm thick, built of palisade-shaped sclereids with strongly pitted anticlinal walls. The inner integument is

very thin, membranous and yellowish, with a conspicuous, circular and thickened chalaza at the base and a pointed micropylar part at the apex (fig. 5D). The outer surface of the seed is granular, black and with inconspicuous pattern of the strongly digitate sclereids. Hilum and micropyle are placed close together on a conical structure at the apex of the seed.

Remarks. Fossil seeds of Nymphaeales have been classified primarily on the basis of position of hilum and micropyle and the wall structure (Dorofeev in Dorofeev et al. 1974). The seeds from Damgaard are similar to those from FASTERHOLT assigned to *Brasenia tenuicostata* (Friis 1975). They correspond exactly with modern *Brasenia* in the features of the hilum and micropyle as well as wall structure. About 20 fossil species of *Brasenia* have previously been described from the Tertiary of Europe and Asia. In regard to external features the Danish seeds agree with those of *Brasenia tenuicostata* described by Nikitin (1965) from the Tertiary of western Siberia, but they differ in having a slightly thicker seed wall. They also resemble the seeds of *B. teumeri* Kirchheimer (1935), but they differ from this species in having a much thinner seed wall. According to M. Collinson (personal communication 1978) *B. teumeri* differs from modern *Brasenia* in the position of hilum and micropyle. Seeds of Nymphaeales from the Eocene of Geiseltal, GDR, described as *B. cf. teumeri* by Mai (1976) differ from *B. teumeri* in having a thinner seed wall; they will be described as a new species by Mai in a coming paper. The Danish specimens seems to be related to the Geiseltal material both in regard to internal and external features.

Brasenia is a monotypic genus of aquatic plants

which is widely distributed in tropical and subtropical regions of the world. According to Koch (1931), who studied a large amount of extant *B. purpurea* (= *B. schreberi*) seeds, the surface ornamentation varies considerably from smooth to completely spiny specimens; the variation found in the extant species is possibly the result of climatic conditions as spiny specimens were found in tropical regions of Africa and India, whereas smooth or slightly spiny specimens were found in the extra-tropical regions of North America, Japan and Australia (Koch 1931).

Family: Myricaceae

Genus: *Comptonia* Banks

Comptonia srodoniowae sp. nov.

Figs 6A-L.

1974. *Comptonia longistyla* (Nikitin) Dorofeev – Friis p. 267, figs 1g-i.

1975. *Comptonia longistyla* (Nikitin) Dorofeev – Friis p. 180.

Diagnosis. Endocarps elongated ovoid, fusiform or guttiform, apex acuminate into style base. Endocarp one-loculed, two-valved with dehiscence along a marginal suture. External surface with one to nine conspicuous, usually high longitudinal ribs, extending from the base to the middle of the endocarp. Locule guttiform, tapering into a long apical stylar canal. Surface of locule smooth with small equiaxial cells. Endocarp wall consists of small, isodiametric stone cells; thickness of wall at dehiscence plane about 0.3 mm.

Length of endocarp: 2.0–4.4 mm

Breadth of endocarp: 0.8–2.1 mm

Table 2. Measurements of *Comptonia srodoniowae* sp. nov. from Denmark: Length of endocarps.

	Length (mm):	2,01-2,4	2,41-2,8	2,81-3,2	3,21-3,6	3,61-4,0	4,01-4,4
Damgaard	number of specimens	1	4	9	17	9	4
	%	2,3	9,1	20,4	38,7	20,4	9,1
Fasterholt	number of specimens	4	11	9	5	3	1
	%	12,1	33,4	27,3	15,1	9,1	3

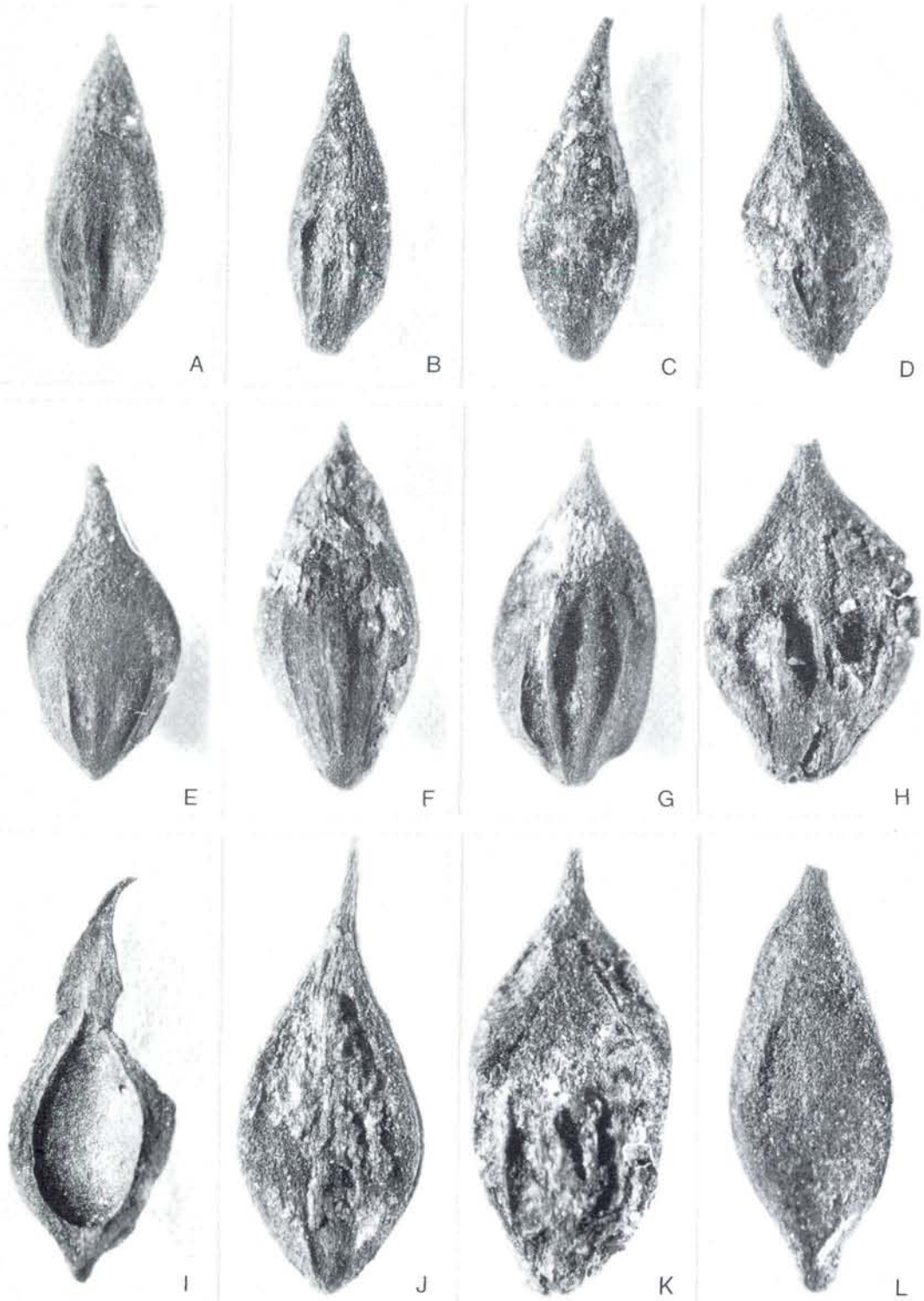


Fig. 6. *Comptonia srodoniowae* sp. nov., endocarps. G, Holotype. $\times 15$.

Holotype: Fig. 6G.

Type locality: Brown coal pit »Damgaard S«, Fæsterholt, Denmark.

Type stratum: Odderup Formation. Middle Miocene.

Derivation of name: Dr. M. Łańcucka-Środoniowa, Polish palaeobotanist.

Material: 44 endocarps and 56 fragments of endocarps.

Occurrence: Dam 1, Dam 2, Dam 3, Dam 4, Dam 5.

Description. The endocarps are very variable in size and shape, bisymmetric and one-loculed. The dehiscence is along a marginal suture in the plane of symmetry and the endocarps split into two equal valves (figs 6I–J). They are elongated ovoid, guttiform or fusiform in outline, usually somewhat flattened at the margins of the valves and at the apical part of the endocarps. The apex

is acuminate, often into a long mucronate style base, which is sometimes slightly curved (figs 6C–D). The endocarps are somewhat pointed at the base. The length of the endocarps: 2.0–4.4 mm, average = 3.7 mm (fig. 7, table 2). Breadth: 0.8–2.1 mm, average = 1.6 mm (fig. 7, table 3).

The endocarp wall is at the dehiscence plane about 0.3 mm thick. The cell structure is inconspicuous. The locule is guttiform and tapers into a long apical styler canal. At the base there is a straight vascular canal, about 0.4 mm long. The surface of the locule is smooth and shows small equiaxial cells, about 0.02 mm in diameter.

The external surface shows one to nine conspicuous longitudinal ribs or crests extending from the base to the middle of the endocarp or very seldom to the apex; the shape and length of the ribs are very variable (figs 6A–L), but they are usually acute-edged and sometimes rather high near the middle of the endocarp (fig. 6G). In a

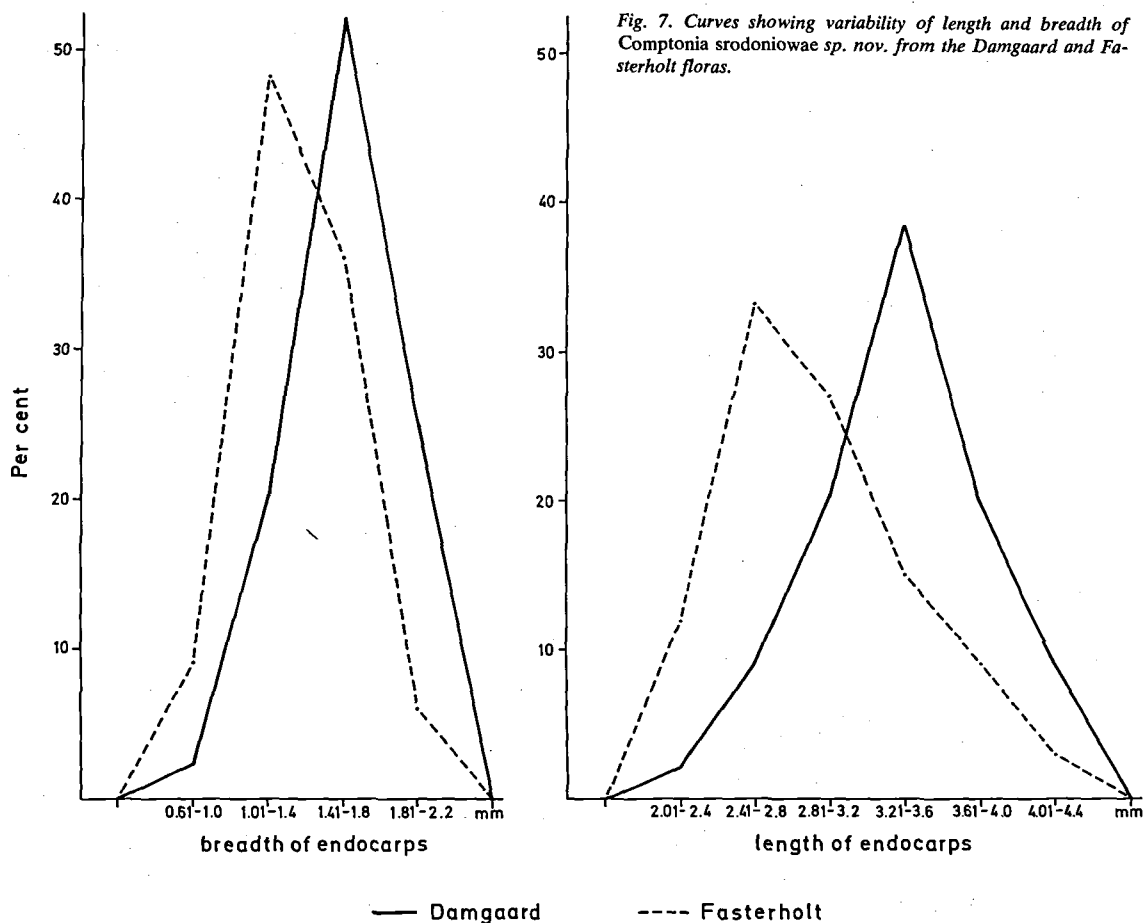


Table 3. Measurements of *Comptonia srodoniowae* sp. nov. from Denmark: Breadth of endocarps.

		Breadth (mm):			
		0,61-1,0	1,01-1,4	1,41-1,8	1,81-2,2
Damgaard	number of specimens	1	9	23	11
	%	2,3	20,4	52,3	25
Fasterholt	number of specimens	3	16	12	2
	%	9,1	48,5	36,4	6,0

few specimens remains of a thin exocarp are preserved.

Remarks. The above described endocarps are referred to the genus *Comptonia*. The genus includes only one extant species, *C. perigrina*, that is restricted to the eastern North America (Small 1972). In the Tertiary, however, the genus was widely distributed in the fossil floras of Europe, Asia and North America. The fossil record of *Comptonia* extends from the Upper Cretaceous to Miocene in Asia and from Eocene to Miocene in Europe; in North America *Comptonia* is known from the Upper Cretaceous to the present (Budancev & Gladkova 1963). The genus was very common in the Lower Tertiary floras of North America, but during the Neogene the occurrence decreased in North America, and *Comptonia* was much more abundant in Asia than in America (Chaney 1967). Gladkova (1965) distinguished 11 species of *Comptonia* from Western Siberia based on palynological studies. The characteristic, deeply lobed leaves of *Comptonia* are also widespread in the fossil floras of Asia and Europe (Budancev & Gladkova 1963, Zhilin 1974, Ruffle 1976). Based on studies of endocarps 9 fossil species of *Comptonia* were established from Tertiary deposits of the USSR (table 5).

Endocarps of *Comptonia* are also known from the Fasterholt flora (Friis 1974). They are very closely related to the endocarps from the Damgaard flora as regards their shape and surface ornamentation, but the endocarps from Fasterholt are generally smaller than those from Damgaard (table 3, 4). To facilitate the comparison of the material from the two localities, the percentage distributions of the measurements were calculat-

ed and expressed in figure 7. They are regarded as belonging to the same species and the variation in size may be attributed to difference in environmental conditions. The endocarps from Fasterholt were previously assigned to *C. longistyla*, but with this rich find of *Comptonia*-endocarps in the Damgaard flora, the Danish material shows a greater variation in size and shape than is known for *C. longistyla* (table 5); they also differ from *C. longistyla* by having generally shorter and higher ribs; a new species, *C. srodoniowae* is therefore established for the Danish material. Few specimens from the Damgaard flora are also related to *C. tymensis* (e.g. figs 6H, K), but there is a gradual change from one type to another.

Leaves of *Comptonia acutiloba* were recorded from the nearby Søby flora (Christensen 1975) as well as a few fruits clearly assignably to *C. srodoniowae*. It is very likely that the endocarps of *C. srodoniowae* and the leaves of *C. acutiloba* come from the same plant, but they have not been found in organic connection. According to Ruffle (1976) *C. acutiloba* is conspecific with *C. difformis*.

Genus: *Myrica* Linné

Myrica cf. *ceriferiformis* Kownas
Fig. 8A.

Material: 15 endocarps, 27 fragments of endocarps.

Occurrence: Dam 1, Dam 2, Dam 3, Dam 4, Dam 5.

Description. Endocarps one-loculed, ovate and bisymmetric, at dehiscence splitting into two valves. Length 2.1–2.7 mm; breadth 1.5–2.2 mm. Locule ovate, apically tapering into a short stylar

Table 4. Fruit characters of fossil and extant *Comptonia*

Species	Author	Length mm	Breadth mm	Shape of endocarp and ribs
<i>C.aldanensis</i>	Dorofeev 1966	2.8-4.6	1.3-2.6	elliptic ribs many, conspicuous
<i>C.baranovae</i>	V. Nikitin 1976	1.9-2.5	1.1-1.4	elliptic ribs conspicuous
<i>C.costata</i>	Dorofeev 1966	4.0-5.0	2.2-3.0	ovate ribs many, conspicuous
<i>C.crassa</i>	Dorofeev 1966	3.9-4.9	2.6-3.2	elliptic no ribs
<i>C.debilis</i>	V. Nikitin 1976	1.5-2.0	0.8-1.0	fusiform or guttiform ribs inconspicuous
<i>C.gorbunovii</i>	Dorofeev 1966	3.2-5.2	1.9-4.6	ovate ribs many, conspicuous
<i>C.longistyla</i>	P. A. Nikitin 1965 Dorofeev 1966	2.0-3.2	1.6-2.7	guttiform to fusiform ribs conspicuous, not high
<i>C.tiulinae</i>	Dorofeev 1966	1.9-4.2	1.0-2.5	elliptic ribs thin
<i>C.tymensis</i>	Dorofeev 1966	3.3-5.0	1.82.3	broadly ovate ribs conspicuous
<i>C.srodoniowae</i>	Friis sp. nov.	2.0-4.4	0.8-2.1	guttiform to fusiform ribs conspicuous, often high
<i>C.perigrina</i>	Linné Coulter	3.1-4.8	2.1-3.0	ovate ribs inconspicuous

canal, and with a slightly projecting placenta at the base. Surface of locule with small equiaxial cells. Endocarp wall about 0.2 mm thick. In some specimens parts of exocarp are preserved (fig. 8A). It consists of closely spaced, nearly isodiametric warts, about 0.2 mm in diameter, that form a honey-combed shaped pattern on the surface.

Remarks. The endocarps from the Damgaard flora closely resemble those of *M. ceriferiformis* described from the Tertiary of Poland by Kownas (1955), but they are slightly smaller. They were compared to the extant *M. cerifera* and *M. caroliniana* from eastern North America. Endocarps assigned to *M. cf. ceriferiformis* are among the most numerous fossils in the FASTERHOLT flora.

Myrica cf. minima Negru
Fig. 8B.

Material: 3 endocarps, 6 fragments of endocarps.
Occurrence: Dam 1, Dam 2, Dam 3.
Description. Endocarps subglobular, slightly pointed at the apex. Length 1.3–1.6 mm; breadth 1.3–1.7 mm. Endocarp wall about 0.2 mm thick.

Remarks. The above described endocarps are closely related to those of *M. cf. ceriferiformis*,

but they differ in the more globular shape and the smaller size. In regard to shape and size they agree with those of *M. minima* described from the Miocene of Moldavia, USSR, by Negru (Dorofeev & Negru 1970), but there is no information on the shape of the locule, for which reason the Danish material could not be referred to this species with certainty.

Myrica cf. suppanii Kirchheimer
Figs 8C–D.

Material: 5 endocarps.

Occurrence: Dam 1, Dam 3.

Description. Endocarp elliptical to subcircular, 2.6–3.2 mm long and 2.0–2.5 mm broad. Endocarp wall 0.2–0.45 mm thick at the plane of dehiscence; in the median region it is up to 0.8 mm thick.

Remarks. The endocarps are closely related to those of *M. suppanii* described from Wiesa by Kirchheimer (1938a) and from RAGEWITZ and MERKA (1939), but they are generally slightly smaller and more ovate in shape than other endocarps ascribed to *M. suppanii*. They differ from the endocarps of *M. cf. ceriferiformis* and *M. cf. minima* in their larger size and thicker endocarp wall.

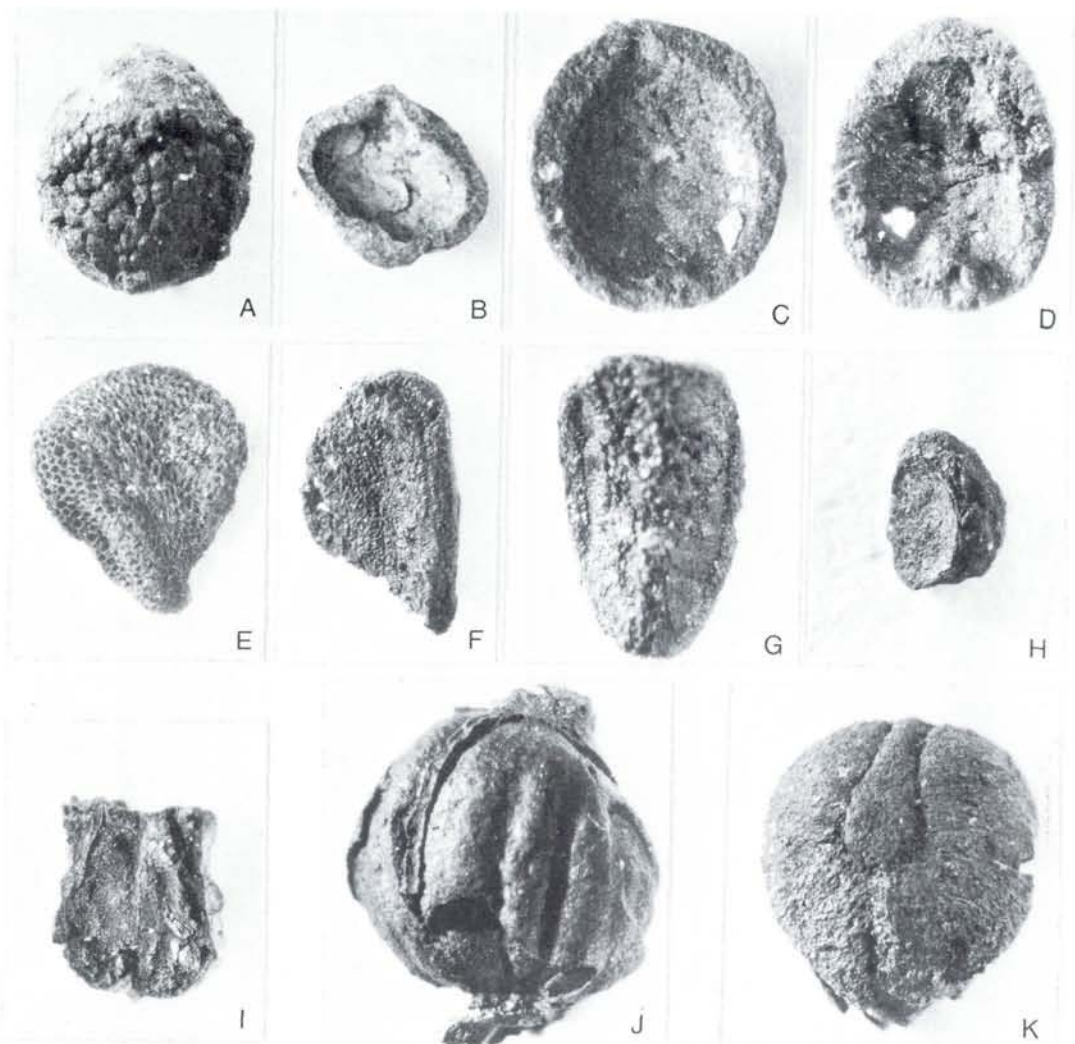


Fig. 8. A, *Myrica* cf. *ceriferiformis*, endocarp with parts of exocarp preserved, $\times 15$. B, *Myrica* cf. *minima*, endocarp, $\times 15$. C-D, *Myrica* cf. *suppanii*, endocarps, $\times 15$. E, *Eurya stigmosa*, seed, $\times 15$. F, *Visnea* sp., seed, $\times 10$. G, *Arctostaphyloides*

menzelii, part of fruit, $\times 15$. H, *Empetrum* sp., endocarp, $\times 15$. I, *Rhus* cf. *toxicodendron*, fruit, $\times 10$. J, *Vitis* cf. *silvestris*, seed, $\times 10$.

Plant remains assigned to *Myrica* are rather common in the Tertiary deposits of Denmark. From the lignitic clay at Silkeborg Vesterskov Mathiesen (1975) described a new species *M. cimbrica* based on the leaf remains. From Sønderkov and Salten Hartz (1909) described the endocarps of *Carpolithes johnstrupii*, which probably includes more species of *Myrica*. A few endocarps of *Myrica* were also found in the plant-bearing clay at the Søby flora locality. In the Fæsterholt flora endocarps of *Myrica* are very common (Friis 1975) and four species have been re-

cognised: *M. cf. ceriferiformis*, *M. cf. minima*, *M. cf. suppanii* and *M. wiesaensis*; a more detailed description and discussion of the *Myrica* endocarps will be given in the taxonomic treatment of the Fæsterholt flora.

Family: Juglandaceae

Genus: *Pterocarya* Kunth

Pterocarya sp.

Material: One valve of endocarp.

Occurrence: Dam 1.

Remarks. Endocarps of *Pterocarya* are very common in the Fasterholt flora (Koch et al. 1973); they differ from the present specimens by having distinct longitudinal ridges on the surface of the endocarp. The lack of ridges on the Damgaard specimen might be due to the preservation. The endocarps of *Pterocarya* are closely related to those of *Cyclocarya* Iljinskaja and *Sphaerocarya* Dorofeev (Dorofeev 1970, Gregor 1975). The endocarp from Damgaard seems to be most related to *Pterocarya limburgensis* C. et E. M. Reid (1915), but due to the bad preservation the exact determination is not possible.

Family: Theaceae

Genus: *Eurya* Thunberg

Eurya stigmosa (Ludwig) Mai

Fig. 8E.

1860. *Potamogeton stigmosus* Ludwig – Ludwig p. 60, pl. 8: 13.

1960. *Eurya stigmosa* (Ludw.) nov.comb. – Mai p. 79, pl. 4: 8–17.

Material: 2 seeds

Occurrence: Dam 1, Dam 2.

Description. Seeds campylotropous, irregular ovoid. Dimensions of the two seeds: 2.0 × 1.9 mm and 0.9 × 0.9 mm. At dehiscence the seeds split into two equal valves. Seed wall about 0.15 mm thick. Seed-cavity curved, the limbs being of unequal length, separated by a condyle. Surface of seed-cavity smooth. The external surface is ornamented with conspicuous honey-comb shaped cells arranged in concentric rows parallel to the margin. The cells that overlie the condyle are elongated.

Remarks. *Eurya stigmosa* is widely distributed in the Tertiary floras of Europe (Mai 1960, 1971). The species was also found in the Fasterholt flora, but the seeds are all much smaller than the big specimen from Damgaard. *Eurya stigmosa* was compared to the extant *E. japonica* that occurs in temperate and subtropical regions of south-eastern Asia. The species occurs in mountains in the tropical regions of Asia (Mai 1960, 1971).

Genus: *Visnea* Linné

Visnea sp.

Fig. 8F.

Material: 4 seeds.

Occurrence: Dam 1.

Description. Length of seed 2.5–3.6 mm; breadth 2.2–2.5 mm. Seeds campylotropous, ovoid. Seed wall thick and consisting of two layers. Seed-cavity curved, limbs of unequal length, separated by the condyle composed of large cells. External cells of testa radially elongated and rectangular, about 0.1 × 0.05 mm, arranged in concentric rows parallel to the margin.

Remarks. The seeds from the Damgaard flora are related to those of *Campylospermum hordwellense* described by Chandler (1925, 1961) from the Eocene flora of Hordle, England (V.20034–35, V.42169–72 studied at the British Museum N.H.). The fossils were compared by Chandler (1961) to extant species of *Ternstroemia* and *Anneslea* (Theaceae). In a later study Mai (1971) referred the fossil species to the genus *Visnea* (Theaceae). The seeds from Damgaard differ from the English material mainly by being less flattened, possibly due to a smaller number of seeds in the fruits of the Danish material. As only single seeds were found in the Damgaard flora, the exact number of seeds per fruit is not known. *Visnea hordwellensis* (Chandler) Mai has 5–8 seeds per fruit and *V. germanica* Menzel (1913) has 3–5 seeds per fruit (Mai 1971) and probably the Danish material is most closely related to the German species.

The genus *Visnea* includes only one extant species *Visnea mocanera*. It is an evergreen shrub or small tree that occurs in woods in the mountains of the Canaries and Madeira (Melchior 1925).

Family: Ericaceae

Genus: *Arctostaphyloides* Kirchheimer

Arctostaphyloides menzelii Kirchheimer

Fig. 8G.

1936. *Arctostaphyloides menzelii* n.sp. – Kirchheimer p. 117, pl. 12: 13.

Material: 5 fruits and 16 fragments of fruits.

Occurrence: Dam 1, Dam 3.

Description. Fruits elliptic and somewhat flattened, 2.6–4.2 mm long and 2.1–3.4 mm in diameter, built of about 5 segments. Fruit wall very

thick and occupying most of the fruit obscuring the seed-cavity. The cells are »fleshy« parenchymatous and isodiametric or slightly elongated, about 0.1 mm in diameter. The axis is fibrous.

Remarks. The fruits from the Damgaard flora were compared to fruits of *Arctostaphyloides menzelii* in the collections of the Botanical Institute, PAN, Cracow, and they were in complete agreement with the smaller, possibly undeveloped fruits of this species. The fossils were compared to living species of *Arctostaphylos* (Kirchheimer 1936), but the generic position of the fossil fruit is still unclear.

Genus: *Epacridicarpum* Chandler

Epacridicarpum sp.

Material: 5 valves of fruits.

Occurrence: Dam 3.

Description. Only the valves of the fruit are represented. They are about 0.9 mm long and 0.6 mm broad. They come from a drupe with 5 endocarps. The fruit wall is composed of two principal layers. The outer layer is brownish and consists of small isodiametric cells; it is only preserved in two specimens. The inner layer, the endocarp, is black and consists of elongated sclereids. The surface of the locule is shining and composed of elongated cells that diverge from the placenta.

Remarks. The fossil genus *Epacridicarpum* was established by Chandler (1960) and includes fruits comparable to fruits of Epacridaceae, of which the closer relationship is unknown. Chandler (1960, 1963) described the fruits of *Epacridicarpum* as capsules. Fruits of *Epacridicarpum* are the most numerous fossil in the Fæsterholt flora and the studies of this material have shown that the fruits are drupes related to the extant *Arctostaphylos*, but they differ from this genus in being much smaller. Mai (1976) suggested a relationship to the Cyrillaceae, but this suggestion is still unproved and until now the generic relationship is uncertain. The Danish material is very similar to *E. mudense* Chandler (1960) and *E. headonense* Chandler (1960), but differs in the length and shape of the sclereids. The species will be described in detail in the taxonomic treatment of the Fæsterholt flora.

Genus? Tribe Andromedeae?

Material: 1 fragment of fruit.

Occurrence: Dam 3.

Description. One fragment of a five-loculed capsule with loculicidal dehiscence. The fragment consists of two carpels united by the septum. It is 1.2 mm long and about 0.9 mm broad. The segment is slightly incurved at the apex. Fruit wall about 0.5 mm thick; the external surface wrinkled.

Remarks. The characters are those of the Ericaceae, probably the tribe Andromedeae, but the fruit-segment is too incompletely preserved to be referred to any living genus.

Family: Empetraceae

Genus: *Empetrum* Linné

Empetrum sp.

Fig. 8H.

Material: 1 endocarp.

Occurrence: Dam 3.

Description. Endocarp subcircular in outline, laterally compressed. Ventral margin straight and slightly incurved near the base, showing the position of the placenta; dorsal margin curved. Length 1.4 mm, breadth 1.0 mm.

Remarks. The endocarp has been compared to those of the extant *Empetrum nigrum* and they show considerable agreement. *Empetrum* has a discontinuous distribution in the temperate regions of the Northern hemisphere and in temperate South America (Good 1964).

Family: Styracaceae

Genus: *Halesia* Ellis

Halesia crassa (C. et E. M. Reid) Kirchheimer
Figs 9A–D.

1915. *Camptotheca crassa* sp. nov. – C. and E. M. Reid p. 121, pl. 14: 1a, b, 3–4.

1943. *Halesia crassa* (C. et E. M. Reid) – Kirchheimer, 505–515 pp.

Material: 1 endocarp.

Occurrence: Dam 1.

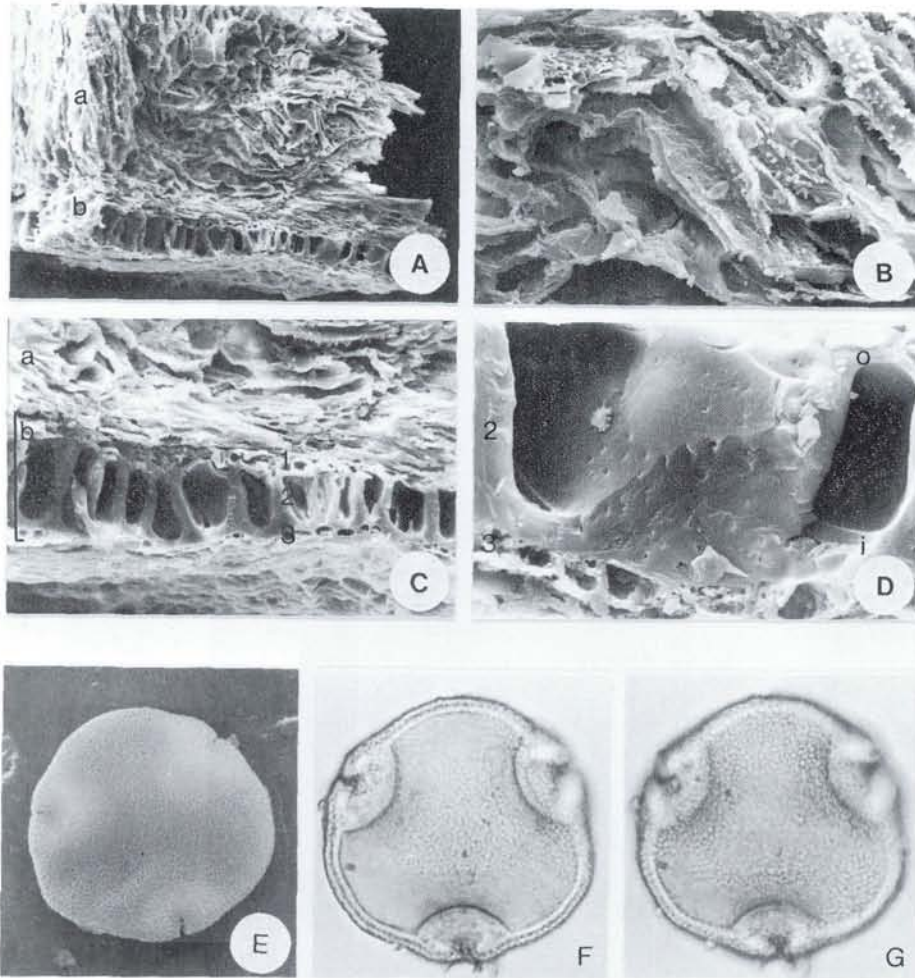


Fig. 9. A–D, *Halesia crassa*, SEM-micrographs of endocarp and seed wall. A, part of endocarp and seed wall, $\times 100$. B, sclereids of inner endocarp wall, $\times 500$. C, endocarp and seed wall, $\times 250$. D, seed wall, $\times 1000$. a = endocarp wall, b = seed wall, o = outer periclinal wall, i = inner periclinal wall, l = outer layer

of seed wall, 2 = middle layer of seed wall, 3 = inner layer of seed wall. E–G, *Intratriporollenites instructus*, pollen grains. E, SEM-micrograph of pollen grain, $\times 1000$. F–G, light microscope-micrograph of pollen grain, same grain, F, lower focus of G, $\times 1000$.

Description. Endocarp fusiform, 16 mm long and 6 mm wide, flattened. Apex somewhat acuminate, style not preserved. Surface of endocarp much abraded with indistinct longitudinal ridges. Endocarp 2-loculed (?), one locule being fertile, the other sterile. The endocarp wall is very thick, brownish and composed of two distinct layers. The outer layer is 0.5 mm thick, consisting of slightly elongated sclereids, regularly arranged. The inner layer is composed of elongated, irregularly arranged sclereids, it pierces the outer layer in a few places. The seed wall is black, 0.045–0.060 mm thick and consists of three lay-

ers (fig. 9C). The outer layer is 0.01–0.02 mm thick and built of parenchymatous cells in few rows, the cells are about 0.008 mm wide and 0.006 mm high, often compressed. The middle layer of the seed wall is uniseriate and composed of conspicuous columnar cells 0.035–0.045 mm high and 0.015–0.040 mm wide. The outer periclinal walls are about 0.002 mm thick and the inner about 0.008 mm. The anticlinal walls are about 0.005 mm thick, slightly pitted (fig. 9D). The inner layer of the seed wall is parenchymatous, 0.006–0.015 mm thick, built of one or few layers of strongly pitted cells (fig. 9D).

Remarks. The surface of the endocarp is much abraded and the identification of the fossil is based on the internal structure and size of the endocarp. It shows considerable agreement with the features of *Halesia crassa* from the Upper Miocene flora of Kausche, Niederlausitz, as stated by Kirchheimer (1943). The species was first described by Reid & Reid (1915) from the Pliocene flora of Swalmen, the Netherlands, as *Camptotheca crassa*. Later Kirchheimer (1943) assigned the species to *Halesia*, comparing it with extant *Halesia carolina* from eastern North America.

The genus *Halesia* includes four species of deciduous shrubs or trees. Three species are found in North America and one in China. They occur on wet soil in rich woods, along river banks and at the edge of swamps. The fruits are two- or four-winged drupes (Correll & Correll 1972).

Halesia is represented in only a few fossil floras of Europe ranging in age from Lower Miocene to Upper Pliocene (Mai 1965, Tralau 1965). In western Siberia *Halesia crassa* is recorded back in the Middle Oligocene (Novomichailovskaja) by Dorofeev (1963).

Halesia crassa is very common in the Søby flora, represented by endocarps and winged fruits. Investigation of the fruits show that they are four-winged (Christensen personal communication 1978). Winged fruits of *Halesia* from the Upper Pliocene of Weilerswist, Germany, were assigned to *Halesia* cf. *carolina* by Tralau (1965). He stated that the affinity of the winged fruits from Weilerswist with the endocarps of *Halesia crassa* is unclear. However, both the winged fruits of *H.* cf. *carolina* and the endocarps of *H. crassa* closely resemble *H. carolina* and they are clearly distinguished from *H. monticola* and *H. diptera* by their smaller size; *H. diptera* is also distinguished from *H. carolina* by having two-winged fruits (Kirchheimer 1943, Dorofeev 1963, Tralau 1965).

Endocarps from the Middle Miocene flora of Wackersdorf, Germany, described by Gregor (1975) as *Halesia* cf. *crassa* differ from the Danish specimen in their smaller size.

Family: Tiliaceae

Genus: *Intratripopollenites* Pflug et Thomson

Intratripopollenites instructus (R. Potonié) Thomson et Pflug
Figs 9E–G.

1931. *Tiliae-pollenites instructus* – R. Potonié p. 556, fig. 9.

1953. *Intratripopollenites instructus* (R. Pot. & Ven.) n. comb. – Thomson & Pflug p. 89, pl. 10: 14–23.

Material: One group of anthers with numerous pollen grains.

Occurrence: Dam 3.

Description. Anthers closely spaced and embedded in a brownish tissue. The group of anthers is a fragment of a larger, possibly globular cluster. More than 30 elongated and slightly curved pollen sacs were counted at the fragment. Each sac contains numerous pollen grains. The pollen grains are tri-colporate, oblate in equatorial view and inter-semi-angular or slightly inter-hexagonal in polar view (figs 9E–F). Greatest diameter 31–40 μm , average = 35 μm , 100 specimens being measured. The polar axis is 17–20 μm , only few specimens were measured. The grains are heteropolar, tectate and intrareticulate. The endexine is strongly thickened around the apertures, the shape of the aperture area being lenticular, 11–15 μm in diameter and 6–9 μm high.

Remarks. The pollen grains of *Intratripopollenites instructus* from the Damgaard flora were studied by the use of light microscope as well as SEM and TEM, and a detailed description of the species is given in a separate paper by Friis & Pedersen (in prep.).

Similar pollen grains were previously recorded from the Søby-Fasterholt area (Ingwersen 1954, Mai 1961).

The species ranges in age from the Upper Oligocene into the Lower Pliocene with culmination in the Middle Miocene (Mai 1961).

Family: Droseraceae

Genus: *Aldrovanda* Linné

Aldrovanda praevesiculosa Kirchheimer

1941a. *Aldrovanda praevesiculosa* n.sp. – Kirchheimer p. 309, fig. 1.

Material: 1 fragment of seed.

Occurrence: Dam 5.

Remarks. A small fragment, 0.8×0.5 mm, was found with part of the neck preserved. The external surface and the wall structure of *Aldrovanda* are so characteristic that even very small fragments can be determined. The fragment from Damgaard agrees in every respect with seeds of *Aldrovanda praevesiculosa* from the Fasteherholt flora. The genus *Aldrovanda* includes only one extant species *A. vesiculosa*. It is an aquatic plant that grows in shallow water. The geographical range is discontinuous within the subtropical and tropical regions of the world (Kirchheimer 1941a).

Family: Lythraceae

Genus: *Decodon* Gmelin

Decodon gibbosus (E. M. Reid) E. M. Reid

1920. *Diclidocarya gibbosa* n.sp. – E. M. Reid p. 83, pl. 4: 23, 25.

1929. *Decodon gibbosus* – E. M. Reid in P. A. Nikitin, s. 37, pl. 589: 7–9.

Material: 2 seeds.

Occurrence: Dam 3.

Remarks. The seeds agree in shape and size with those of *Decodon gibbosus*. The preservation of the seeds is rather bad and they cannot be studied in detail. The species is very common in the Fasteherholt flora. *Decodon* includes one extant species, *D. verticillatus*, that is restricted to eastern North America.

Family: Haloragaceae

Genus: *Proserpinaca* Linné

Proserpinaca brevicarpa Dorofeev

Fig. 8I

1976. *Proserpinaca brevicarpa* Dorof. sp.nov. – Dorofeev p. 1037, fig. 1: 1–4.

Material: 2 fruits.

Occurrence: Dam 3.

Description. Fruits four-loculed, four-lobed nuts, nearly tetragonal and slightly narrowed near the apex. Length of fruits 1.7 mm, breadth 1.0–1.3 mm. External surface with 8 thin longitudinal

nerves (ribs), one that overlies each septum and one slightly winged, on the edges of the fruit, the latter has small thornlike projections. Between the longitudinal ribs smaller anastomosing ribs form a coarse reticulum. Apically thornlike remains of the calyx-veins have been preserved.

Remarks. Four fossil species of *Proserpinaca* have been described from the Tertiary and Quaternary of Europe and Asia. The Endocarps of *P. brevicarpa* Dorofeev (1976), *P. europaea* Dorofeev (1976) and *P. pterocarpa* (Dorofeev 1958) were compared to the extant *P. palustris*; they differ from the endocarps of *P. reticulata* C. et E. M. Reid (1915), comparable to the extant *P. pectinata*, by having more sharply angled ribs on the surface and by having more or less pronounced winglike projections on the edges of the fruits. Dorofeev (1976) emphasized that the Oligocene specimens of *Proserpinaca* have a wide wing, the Miocene fruits have a narrow wing and the Pliocene fruits are wingless. The Danish specimens are slightly winged and they are in agreement with the narrowly winged Miocene species *P. brevicarpa*, described from the Upper Miocene of Byelorussia by Dorofeev (1976). Two fruits of *Proserpinaca* from the plantbearing clay at the Søby flora locality are similar to the fruits from the Damgaard flora. The Byelorussian specimens of *P. brevicarpa* are all three-loculed, whereas the Danish fruits are four-loculed. However, four-loculed fruits of *Proserpinaca* have been found in fossil floras of Poland (Szafer 1954, Raniecka-Bobrowska 1959), Czechoslovakia (Bůžek & Holý 1964) and Western Siberia (Nikitin 1965). In Europe four-loculed fruits were recorded back in the Lower Miocene (Bůžek & Holý 1964), whereas three-loculed fruits were recorded back in the Upper Miocene, where they were found together with four-loculed specimens (Raniecka-Bobrowska 1959); in the Pleistocene flora of Mizerna III four-loculed fruits were also found together with three-loculed specimens (Szafer 1954). Table 5 shows the stratigraphic range and locule number of fossil *Proserpinaca*-fruits in Europe. The fruits of extant *Proserpinaca* are all three-loculed, and it is possible that a reduction from four to three locules have occurred in the Upper Miocene. This was also suggested by Bůžek & Holý (1964).

Proserpinaca includes two extant species of

Table 5. Number of locules in fossil *Proserpinaca*-fruits in Europe.

Age	Number of locules	Locality	Author
Pleistocene	3	Mizerna III/IV	Szafer 1954
	4 3	Mizerna III	
	3	Mizerna II/III	
U. Pliocene	3	Mizerna II	Szafer 1954
M. Pliocene	3	Mizerna I-I/II	Szafer 1954
	3	Baldero, Razlog	Palamarev 1970
L. Pliocene	3	Reuver, Swalmen, Brusum	C. & E. M. Reid 1915
	3	Kroszcienko, Huba	Szafer 1954
U. Miocene	3	Brestkoj Region	Dorofeev 1976
	4 3	Konin	Raniecka-Bobrowska 1959
M. Miocene	4	Søby-Fasterholt area	Present work
L. Miocene	4	Chomutov-Most-Templice Basin	Bůžek & Holy 1964
Recent	3	SE North America	Muencher 1944

aquatic plants, restricted to east and southeast North America (Muencher 1944).

Family: Anacardiaceae

Genus: *Rhus*

Rhus cf. *toxicodendron*

Fig. 8J.

Material: 1 fruit.

Occurrence: Dam 3.

Description. Fruit oval, slightly oblique and laterally flattened, bisymmetric and somewhat pointed at the apex. At the base there are remains of a coriaceous calyx. The fruit has about 12 longitudinal ridges running from apex to base. Length 4.8 mm, breadth (dorsiventrally) 4.0 mm, breadth (laterally) 2.5 mm. In some places the surface seems to be covered by a thin layer of inorganic material, or possibly resin.

Remarks. The fruit has been compared to several species of the Anacardiaceae and there is considerable agreement with the fruits of *Rhus toxicodendron*, but this differs from the fossil fruit by having more irregular longitudinal ridges. *Rhus toxicodendron* is restricted to the Atlantic North America Region (Good 1964).

Family: Rhamnaceae

Genus: *Paliurus* Miller

Paliurus sp.

Material: 1 fruit and 1 fragment of fruit with seed.

Occurrence: Dam 3.

Remarks. The preservation of the fruit does not allow any detailed description, and the material has not been referred to any species. Fruits of *Paliurus* are very common in the Fasterholt flora, and seeds of *Paliurus* similar to the seed from Damgaard were also found in the Fasterholt flora together with the small plant remains; they are thought to be immature because of their small size and wrinkled surface.

Paliurus includes eight extant species of shrubs and small trees that occur in the warm temperate and subtropical regions of Europe and Asia (Wettstein 1935).

Family: Vitaceae

Genus: *Vitis* Linné

Vitis cf. *silvestris* Gmelin

Fig. 8K.

Material: 1 seed and 3 fragments of seeds.

Occurrence: Dam 3, Dam 4.

Description. Seeds ovate, at the base narrowed to a short beak. Chalaza elongated or spatulate. There are no dorsal radiate markings. Ventral infolds about 2 mm long and up to 0.4 mm wide, parallel with smooth external margins. Raphe ridge not raised above main body of seed. The raphe is not fully preserved, but seems to be thread-like. Length 4.1 mm breadth 3.6 mm.

Remarks. The terms used in the description of the seeds are those used by Tiffney & Barghoorn (1976). The seeds are closely related to those of *Vitis* cf. *silvestris* figured by Kirchheimer (1938b) from Reuver and Hoogerheide, the Netherlands, and from Klettwitz, Germany. They are also related to the fossil species *V. teutonica*. As only few and badly preserved specimens were found, the material has not been referred to a fossil species. Seeds of *Vitis* are very common in the FASTERHOLT flora, where the genus is represented by more species.

Class: Monocotyledones

Family: Alismataceae

Genus: ?

Figs 10A–E.

Material: 7 seeds.

Occurrence: Dam 3, Dam 5.

Description. Seeds amphitropous, elongated, horseshoe-shaped and laterally flattened, 1.0–1.4 mm long and 0.6–0.7 mm wide. Longitudinal axis somewhat curved. Limbs of nearly equal length, the micropylar limb being about 0.5 mm longer than the chalazal limb, and also a little wider. Seeds yellow or brownish with a smooth and shining surface; the cell structure is inconspicuous.

Remarks. The seed characters are those of the Alismataceae. The material has been compared to seeds of *Alisma*, *Caldesia*, *Echinodorus* and *Sagitaria*. The fossils are most related to the seeds of *Alisma plantago-aquatica*, but the seeds of *Caldesia* are also similar; as the fruits were not

found it is not possible to refer the fossil seeds to any genus, but only to the family Alismataceae. Similar seeds were described by Dorofeev (1963) from the Tertiary of western Siberia as Alismataceae gen. 3 and by Negru (1972) from the Miocene flora of Moldavia as *Alisma* sp. Similar seeds were also found in the FASTERHOLT flora. Few fruits of *Caldesia* were likewise found in the FASTERHOLT flora.

Family: Potamogetonaceae

Genus: *Potamogeton* Linné

Potamogeton heinkei Mai

Figs 10F–G.

1960. *Potamogeton heinkei* sp. nov. – Mai p. 78, pl. 4: 1–6, fig. 3

Material: 2 endocarps.

Occurrence: Dam 4.

Description. Endocarps obovate and laterally flattened. Neither stalk nor style are preserved, and both apex and base are rounded. Dimensions of the two endocarps: 1.5 × 1.0 mm and 1.7 × 1.1 mm. Ventral area slightly convex, sides flat with a central depression, about 0.3 mm long and 0.15 mm wide; tissue of the central depression usually abraded. Dorsal area rounded, the germination valve is broken in both specimens, but a small fragment remains at the base showing a flattened roof-shaped profile. Valve not reaching base of style, but stops about 0.5 mm from the top. Lateral surface shows long, narrow cells, elongated parallel to the curve of the locule; an

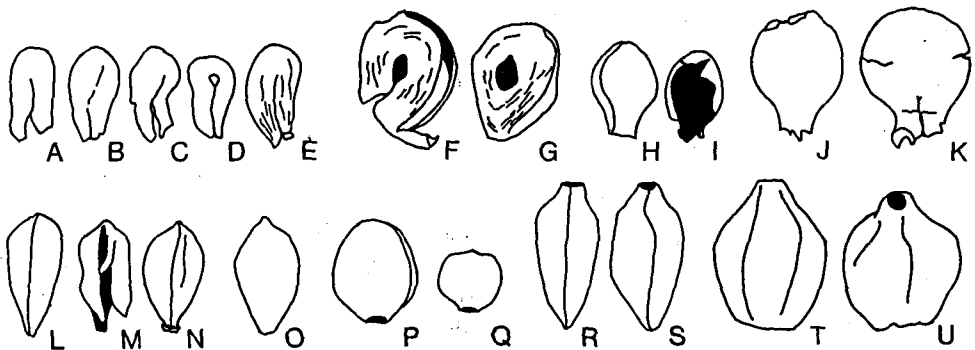


Fig. 10. A–E, Alismataceae, seeds. F–G, *Potamogeton heinkei*, endocarps. H–I, *Cladium reidiorum*, endocarps. J–K, *Cladium* cf. *crassum*, endocarps. L–N, *Scirpus ragozinii*, fruits. O, *Scirpus* (?) sp., fruit. P, *Cyperaceae* Genus ? sp. 1, endocarp. Q,

Cyperaceae Genus ? sp. 2, endocarp. R–U, *Sparganium camenzianum*, endocarps, R and S same specimen, T and U same specimen. × 10.

outer layer of small cells is sometimes preserved. Endocarp wall about 0.1 mm thick. Seed-cavity curved and has a shining surface showing long narrow cells aligned parallel to the curvature.

Remarks. The terms used in the description of the endocarps are mainly those used by Aalto (1970). The characters of the endocarps agree with those of the subsection *Colorati* (Graebn.) Hagstr. The fossils are closely related to *Potamogeton heinkei* described from the Lower Miocene (?) flora of Hartau, GDR (Mai 1960). They differ from the related *P. wiesaensis* by having a rounded valve without keel. Endocarps of *Potamogeton* were also found in the Fasterholt flora, two of these specimens are very close to the fruits from Damgaard; nine specimens differ by being smaller and by having a distinct keeled valve.

The genus *Potamogeton* has a cosmopolitan distribution; it includes about 100 species of aquatic plants (Good 1964).

Family: Cyperaceae
Genus: *Scirpus* Linné

Scirpus ragozinii Dorofeev
Figs 10L–N.

1963. *Scirpus ragozinii* Dorofeev sp.nov. – Dorofeev p. 123, pl. 13: 38–45, fig. 18: 1–6.

Material: 12 fruits and 8 fragments of fruits.
Occurrence: Dam 2, Dam 3, Dam 5.
Description. Fruits obovate, three-sided, apex narrowed to a short style-base, about 0.7 mm long and 1.2 mm wide. At the base the fruit has the remains of the bristles. Length of fruit: 1.4–1.6 mm, breadth: 0.6–0.8 mm. Surface black and shows longitudinally aligned, elongated cells; the cell walls also make a slightly transverse pattern. Fruit wall about 0.2 mm thick.

Remarks. The fruits are closely related to those of *Scirpus ragozinii* described by Dorofeev (1963) from Oligocene deposits of western Siberia. It was compared to the extant *S. mucronatus*, *S. supinus* and *S. melanospermus* (Dorofeev 1963). Fruits ascribed to *S. ragozinii* are very common in the Fasterholt flora.

Scirpus (?) sp.
Fig. 10 O.

Material: 1 fruit.

Occurrence: Dam 3.

Description. Fruit obovate, two-sided with a short pointed stylebase. Surface dark-brownish and shows very narrow cells, longitudinally aligned; there is no transverse pattern. Length of fruit: 1.5 mm, breadth: 0.8 mm.

Remarks. As only one specimen of rather bad preservation was found the generic position of the fossil is unclear, but it is related to fruits of extant *Scirpus*.

Genus: *Cladium* Beauvois

Cladium reidiorum Nikitin
Figs 10H–I.

1948. *Cladium reidiorum* (m.m.) (Nomen nudum) – P. A. Nikitin p. 1103.

1965. *Cladium reidiorum* Nikitin sp.nov. – P. A. Nikitin p. 62, pl. 6: 10–16, 19.

Material: 1 endocarp and one fragment of endocarp.

Occurrence: Dam 4.

Description. Endocarp obovate, rounded in longitudinal section and slightly triangular in transection, 1.2 mm long and 0.8 mm broad. Fruit contracted at the base to a short neck, 0.2 mm long and 0.3 mm wide. At the edges of the neck there are remnants of the basal extension. Apex rounded with a very short mucronate style-base. Three inconspicuous longitudinal ridges extend from the apex. Endocarp wall about 0.05 mm thick.

Remarks. The endocarps from Damgaard are clearly assignable to *Cladium reidiorum* described from the Tertiary of western Siberia by Nikitin (1965). The species was also recorded in the Fasterholt flora.

Cladium cf. *crassum* Negru
Figs 10J–K.

Material: 2 endocarps.

Occurrence: Dam 2, Dam 4.

Description. Dimensions of the two endocarps: 1.8 × 1.4 mm and 1.4 × 1.2 mm. Basal neck about 0.4 mm long and 0.6 mm wide.

Remarks. The endocarps from Damgaard are related to *Cladium crassum* described by Negru (1972) from the Miocene of Moldavia, USSR, but they differ from the Moldavian material by being a little smaller. They differ from *C. reidiorum* by their larger size and broader neck.

Genus ? sp. 1.

Fig. 10P.

Material: 2 endocarps.

Occurrence: Dam 3.

Description. Endocarp 1.3–1.4 mm long and 1.2 mm broad, subglobular, two-sided, narrowed at the base to an inconspicuous short neck with a circular aperture, about 0.2 mm in diameter; apex slightly pointed. From apex two longitudinal furrows extend to the base, one at each side. Surface smooth, somewhat abraded with small equiaxial cells.

Remarks. The endocarps are related to the Cyperaceae, but the generic position is unclear. They are comparable with other fossil endocarps assigned to the Cyperaceae, e.g. *Caricoidea obscura* Chandler (1960), but as the exocarp has not been preserved the identification of the endocarp is not possible. Endocarps similar to the above were also found in the Fasterholt flora.

Genus? sp. 2.

Fig. 10Q.

Material: 1 endocarp.

Occurrence: Dam 3.

Description. Endocarp 0.8 mm long and 0.9 mm broad, two-sided and subglobular, at the base narrowed to a short neck.

Remarks. The endocarp is rather badly preserved; it is similar to endocarps ascribed to Cyperaceae from the Fasterholt flora, which are comparable with species of the fossil genus *Caricoidea* Chandler (1957). It differs from the other endocarps (Genus ? sp. 1) by its smaller size and a more distinct neck. The better preserved specimens from the Fasterholt flora also have indistinct longitudinal ridges.

Family: Sparganiaceae

Genus: *Sparganium* Linné

Sparganium camenzianum Kirchheimer
Figs 10R–U.

1941b. *Sparganium camenzianum* sp. nov. – Kirchheimer p. 225, fig. 18.

Material: 2 endocarps.

Occurrence: Dam 2, Dam 3.

Description. – Endocarps fusiform, one-loculed, irregular angled in cross-section, at the apex narrowed to a short neck with a subcircular aperture, about 0.2 mm in diameter. Outer surface somewhat abraded showing very small cells. One specimen has six longitudinal bundles running from base to apex; on the other specimens the bundles are obscure. Dimensions of the two endocarps: 2.0 × 1.0 mm and 2.1 × 1.5 mm.

Remarks. The endocarps from Damgaard were compared to material of *Sparganium camenzianum* from Wiesa, determined by Dr. Mai, Berlin, and they agree in both size and shape. Numerous endocarps ascribed to *S. camenzianum* were also recorded from the Fasterholt flora. They are usually narrow and 3-angled and generally smaller than the specimens from Damgaard.

Incertae Sedis

Genus: *Carpolithus* Linné

Carpolithus sp. 1.

Figs 11A–B.

Material: 1 fruit.

Occurrence: Dam 4.

Description. Fruit ovoid, three-sided and three-loculed, 1.5 mm long and 1.2 mm broad. Placenta basal, projecting and globular, about 0.2 mm in diameter. Surface of locule dull with slightly elongated cells, about 0.006 mm long, diverging from the placenta. Fruit wall 0.06 mm thick with inconspicuous cell-structure. Central axis 1.5 mm thick.

Remarks. The fruit has been compared to three-loculed fruits from several families (e.g. Droceraceae, Ericaceae, Euphorbiaceae, Theaceae, Violaceae), but the systematic position is still unknown.

Carpolithus sp. 2.

Fig. 11F.

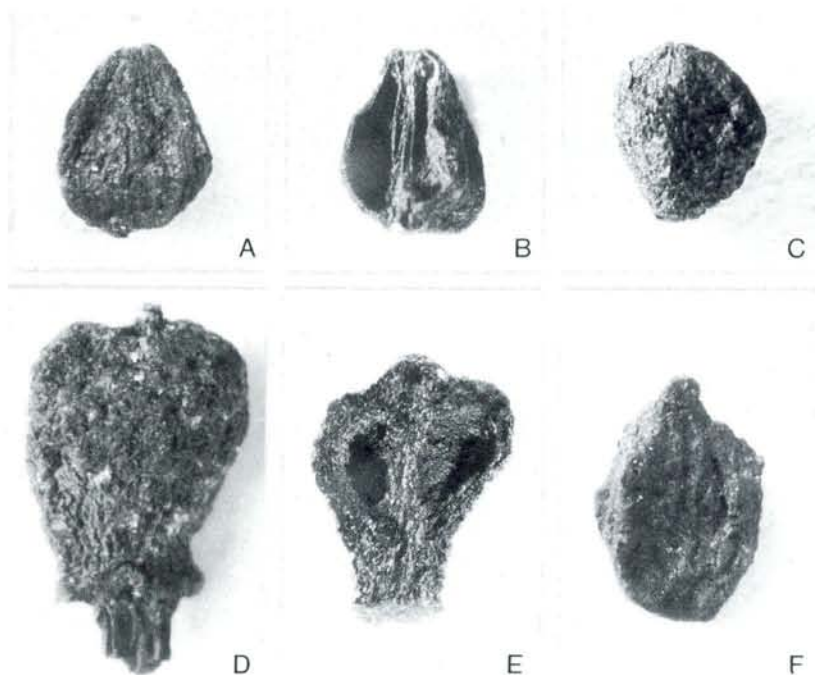


Fig. 11. A–B, *Carpolithus* sp. 1. A, external view of fruit. B, internal view of same specimen. C, *Carpolithus* sp. 3, fruit. D–E,

Carpolithus sp. 4. D, fruit with stalk. E, internal view of same specimen. F, *Carpolithus* sp. 2, fruit. $\times 15$.

Material: 1 fruit.

Occurrence: Dam 3.

Description. Fruit woody, three-sided and one-loculed, 2.2 mm long and 1.3 mm broad. Fruit wall 0.1 mm thick, consisting of small inconspicuous cells; outer epidermal layer black. Surface of fruit with irregular longitudinal ridges. No seeds were observed.

Remarks. The systematic relationship of the fruit is unknown.

Carpolithus sp. 3.

Fig. 11C.

Material: 1 fruit.

Occurrence: Dam 1.

Description. Fruit flattened, ovoid, 1.5 mm long and 1.2 mm wide. Surface almost smooth with small, nearly equiaxial cells.

Remarks. The systematic position of the fruit is unknown.

Carpolithus sp. 4.

Figs 11D–E.

Material: 1 fruit.

Occurrence: Dam 3.

Description. Fruit elongated obovoid, with a short stalk and remnants of a coriaceous calyx at the base. Apically remains of a short, apparently five-lobed style can be seen. Length of fruit with stalk: 3.2 mm, length without stalk: 2.2 mm; breadth: 1.7 mm. Fruit five-loculed, the locules being about 0.8 mm long and situated in the apical part of the fruit (fig. 11E). Placentation sub-apical; seeds have not been observed. Central axis about 0.2 mm broad. Fruit wall about 0.2 mm thick at the apical part, the cell-structure indistinct, but the cells appears to be »fleshy«. Bundles to the placentae and fruit wall diverge from the stalk. Surface wrinkled; epidermal cells very small, isodiametric. The ovary is superior and the fruit apparently a berry.

Remarks. The characters agree with those of the Ericaceae, possibly tribe Arbutaeae, but it has not

been possible to refer it with certainty to this family.

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Dansk sammendrag

En ny fossil flora, Damgaard floraen, beskrives fra den forladte brunkulgrav »Damgaard S« i Søby-Fasterholt området. Floraen, som overvejende består af frugter og frø, er udslemmet fra lyst skrålejret sand tilhørende den mellem miocæne Odderup formation; sandet overlægges af den marine Hodde Formation, som er henregnet til den øverste del af Mellem Miocæn. Prøver af det lyse sand blev indsamlet langs gravens østvæg. Fem af disse prøver indeholdt fossile frugter, frø, kviste og pollensække, som samlet beskrives som Damgaard floraen. Floraen, som omfatter 36 arter, er karakteriseret ved en rig forekomst af endokarpier af *Comptonia srodniowae* sp. nov. Frugter og frø af *Taxodium*, *Brasenia*, *Myrica*, *Arctostaphyloides* og *Scirpus* er ligeledes almindelige i floraen, mens de øvrige arter kun er repræsenteret ved få eksemplarer.

Floristisk-klimatiske undersøgelser viser, at Damgaard floraen er en arktotertiær flora, som har vokset under varmt tempererede til subtropiske forhold. Floraen har mange fælles træk med de to andre mellem miocæne floraer beskrevet fra Søby-Fasterholt området, Søby floraen og Fasterholt floraen. Forskellene mellem de tre floraer må først og fremmest søges i deres forskellige bevaringsform; Søby floraen er en bladflora fundet i et ler sediment, mens Damgaard og Fasterholt floraerne hovedsageligt består af frugter og frø aflejret i sand. Mens Damgaard floraen er ret artsfattig med planterester, som vidner om kraftig transportpåvirkning, er Fasterholt floraen meget rig, og fossilerne synes kun at have været udsat for ringe transport.

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