Angiosperm Fruits and Seeds from the Middle Miocene of Jutland (Denmark)

By ELSE MARIE FRIIS

Det Kongelige Danske Videnskaberne Selskab
Biologiske Skrifter **24**:3

1742

Kommissionær: Munksgaard
København 1985

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Synopsis

Small carbonaceous angiosperm fruits and seeds are described from Middle Miocene strata of western Denmark. Most of the fossils were collected from the C. Nielsen A/S lignite quarry near Fasterholt, Central Jutland (Fasterholt flora). Additional samples were obtained from two horizons in the Damgaard lignite quarry near Fasterholt (Damgaard flora and Søby flora) and from two 120 m boreholes in the Fasterholt area (Lavsbjerg Øst and Fasterholt Plantage).

The fossil floras are basically of the arctotertiary type with a rather high content of palaeotropical species. They are all characterized by a high content of East Asian-North American genera and also by a high proportion of cosmopolitan and relictual genera. The proportion of tropical/subtropical genera ranges between 10 and 17 per cent. Vegetational analyses indicate that the original floras grew in environments corresponding to wetland communities of the Atlantic Coastal Plain of North America, under warm temperate to subtropical conditions.

In floristic composition the fossil floras from Denmark show great similarity with other late Oligocene and Miocene floras in Europe and Asia, especialy with floras characterized as warm temperate to subtropical. There is only a low correlation with floras younger than the Miocene and older than the Middle Oligocene.

About 120 species are recognized, most of them angiosperms. 75 angiosperm genera including about 110 species are studied. The Myricaceae, Ericaceae, Rosaceae, Lythraceae, and the Cyperaceae are the most diverge families, each with from 5 to 16 species. Among these, 42 have previously been recorded from other European and Asian Tertiary floras, while the remaining taxa are described for the first time. Fruits and seeds of *Clethra, Lyonia, Zenobia, Myrtus,* and *Pistia* are recorded for the first time from European fossil floras, and 15 new species are established: *Myrica kirchheimeri, Hypericum danicum, H. holyi, Clethra cimbrica, Lyonia danica, Zenobia fasterholtensis, Epacridicarpum chandlerae, Ludwigia corneri, L. collinsoniae, Myrtus palaeocommunis, Weigela srodoniowae, Cephalanthus pusillus, Carpolithes dorofeevii, C. nikitinii,* and *C. tiffneyi.* Two new combinations, *Myrica johnstrupii* (Hartz) and *Cladium bicorne* (Saporta), are proposed.

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Printed in Denmark by Bianco Lunos Bogtrykkeri A/S
ISSN 0366-3612 . ISBN 87-7304-150-5

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Fig. 1. Occurrence of Miocene deposits in Denmark (from Sorgenfrei & Bertelsen, 1954).

Introduction

During the late Tertiary extensive peat deposits were formed by the deciduous mixed forests and swamp forests which occupied the coastal regions of Central and Northern Europe (Kirchheimer, 1957; Teichmüller, 1958; Mai, 1964). A northern extension of these forests covered the lowlands of western Denmark adjacent to the transgressive Miocene sea (Koch & Friedrich, 1970; Koch, Friedrich, Christensen & Friis, 1974). This paper describes small angiosperm megafossils from the Middle Miocene strata of Jutland which together with other plant megafossils provide evidence of climate, ecology, and vegetation of the region at this time and contribute valuable information to our knowledge of the fossil record of flowering plants.

The earliest investigation of fossil plant remains from the Tertiary of Denmark was by Hartz (1909) who described several species of fruits and seeds from outcrops in Central Jutland. Subsequent studies by Mathiesen (1965, 1969, 1970, 1975) concentrated on leaf and wood remains collected from exposures in the Silkeborg and Fasterholt areas between 1917–1920. In 1968 renewed collecting in the Fasterholt area was initiated by B. E. Koch, and led to several palaeobotanical studies of leaf architecture (Christensen, 1975, 1976, 1978; Friis, 1977a), megaspore morphology (Friis, 1977b), fungi (Friis, 1976), wood anatomy (Wagner & Koch, 1974) and structure of fruits and seeds. The larger fruit and seed fossils (generally exceeding two millimetres in length) are currently under investigation by Koch and Friedrich (Friedrich & Koch, 1970, 1972; Koch & Friedrich, 1970, 1971), while studies of the smaller fruits and seeds have been carried out by the author (Friis, 1974, 1975, 1979, 1980).

This paper is based mainly on fossil fruits and seeds collected from the C. Nielsen A/S lignite quarry near Fasterholt, Central Jutland (Fasterholt flora). Additional samples were obtained from two horizons in the Damgaard lignite quarry near Fasterholt (Damgaard flora and Søby flora) and from two 120 m deep boreholes in the Fasterholt area (Lavsbjerg Øst and Fasterholt Plantage).

Geological setting

Miocene strata in Denmark are restricted to mid and southern Jutland (Fig. 1). They are unconformably overlain by Quaternary deposits of variable thickness, and have been exposed by fluvial and glacial erosion as well as excavations for lignite, quartz sand and clay. The total Miocene sequence in the Fasterholt area is at least 200 m thick and consists of interfingering marine and non-marine deposits grouped into a number of formations (Sorgenfrei, 1958; Rasmussen, 1961a, b, 1966). The samples discussed here are from the youngest Miocene formations, mainly the non-marine Odderup Formation of late Middle Miocene age. The non-marine strata have been dated primarily on the basis of their position relative to the marine strata.

The Odderup Formation consists mainly of coarse quartz sand with subordinate clay and lignite horizons deposited in fluvio-deltaic environments (Rasmussen, 1961a; H. Friis, 1978). The exposure at the C. Nielsen A/S lignite quarry shows about 17 m of sediments referred to the Odderup Formation comprising a lower lignite unit with three lignite beds alternating with layers of sand, silt and clay, and an upper unit of cross-bedded quartz sand unconformably overlain by Quaternary deposits (Koch & Friedrich, 1970; Koch et al., 1974). Plant megafossils have been collected from several horizons in the quarry, the most important being the "Fasterholt flora" extracted from the sands intercalated between the two uppermost lignite beds (Fig. 2).

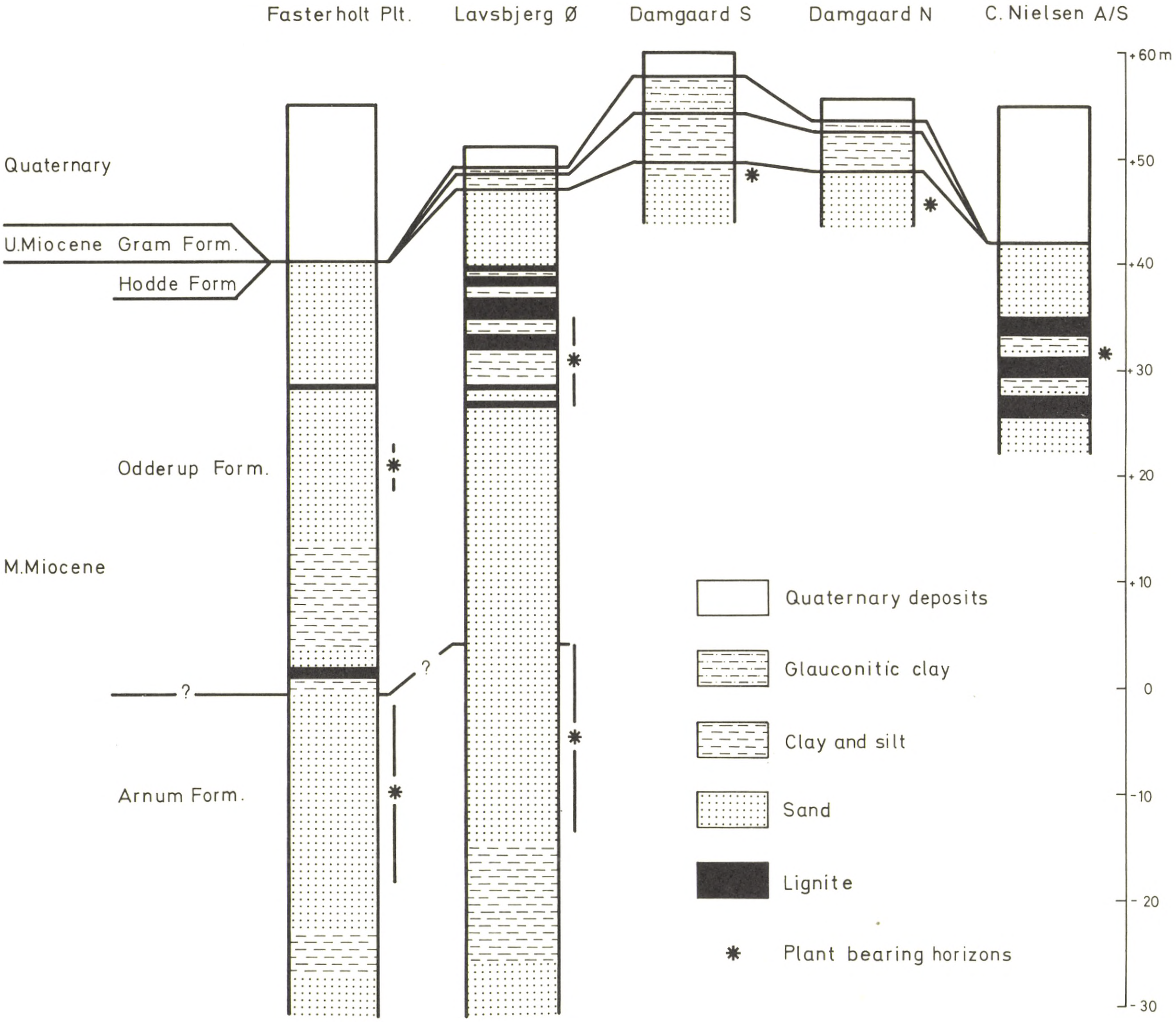


Fig. 2. Lithology and stratigraphy of the investigated sections in the Fasterholt area.

The Damgaard lignite quarry was abandoned and partly flooded at the time of collecting and the lower lignite unit was completely submerged. However, in the southern part of the quarry the exposed Odderup Formation consists of about three metres of cross-bedded quartz sand unconformably overlain by the marine Hodde end Gram Formations (Fig. 2) (Larsen & H. Friis, 1973; Friis, 1979). The plant megafossils which occur frequently throughout the sand sequence comprise the "Damgaard flora" (Friis, 1979). In the northern part of the quarry about three metres of the Odderup Formation is exposed and consists of finely laminated sands and clays grading into a more compact clay bed containing the "Søby flora" (Christensen, 1975). These clays are unconformably overlain by the marine Hodde Formation (Fig. 2).

The Lavsbjerg Øst borehole is situated about 1 km west of the C. Nielsen A/S lignite quarry. It penetrates about 120 m of Miocene strata which consist chiefly of sands and silts with several lignite beds in the upper part and with a clayey interval from 66–76 m below the surface (Fig. 2). Based on sedimentological and palaeontological evidence the lower 75 m of the sequence are considered to represent the marine Arnum Formation of Middle Miocene age. The upper part of the sequence including the lignite beds has been referred to the non-marine Odderup Formation. It is overlain by two metres of marine clays belonging to the Hodde and Gram Formations and subsequently by a thin cover of Quaternary deposits (H. Friis, Nielsen, Friis & Balme, 1980). Plant megafossils occur throughout the Miocene sequence, but are most abundant in the intervals 16.0–25.0 m and 47.0–64.5 m below the surface (Fig. 2).

The Fasterholt Plantage borehole is situated about 4 km west of the Lavsbjerg Øst borehole. It is 120 m deep. Only a few samples were available from the upper 46 m and the generalized lithological section shown in figure 2 is based exclusively on the driller's log. The Quaternary cover is about 16 m and overlays a Miocene sequence of fine grained sand and silt with several clays and lignite beds. Plant megafossils have been recovered from several levels throughout the Miocene sequence but are most abundant in the intervals 32.0–36.0 and 56.5–74.0 m below the surface. The presence of rebedded Mesozoic megaspores and similarity in floral assemblages suggest that the lower part of the sequence may be correlated with the Arnum Formation of the Lavsbjerg Øst borehole. The upper part containing lignite beds probably belongs to the Odderup Formation (Fig. 2).

Materials and methods

The fossils were extracted from the unconsolidated sediments by washing on a 125 um sieve. Mica which occurred abundantly in the borehole samples was removed from the fossil material by gravity separation in $ZnCl_2$ s.g. 1.90. Residual mineral matrix was removed from some of the fossils with HF. The fossils are all carbonaceous and generally well preserved. Specimens obtained from the sandy sediments are three-dimensionally preserved and usually somewhat abraded, while those extracted from the clays are preserved as compressions frequently with the epidermis intact. The fossils were studied using Cambridge S–2 scanning electron microscope.

Identification of the fossil material was based on comparison with modern as well as fossil fruits and seeds. Comparative modern material was primarily obtained from the collections of the Geology and Botany Departments, University of Aarhus, and from the Botanical Museum, University of Copenhagen. Further material was obtained from Dr. J. Ingram, Bailey Hortorium, Ithaca, New York; Dr. H. Sleumer, Rijksherbarium, Leiden; Dr. S. Graham, Kent State University; Dr. J. Gregor, Staatliches Museum für Naturkunde, Stuttgart; Dr. M.E. Collinson, University of London; Dr. S. Ødum, the Arboretum, Hørsholm. Information on seed morphology and anatomy was also obtained from illustrated handbooks (Netolitzky, 1926; Bertsch, 1941; Beijerinck, 1949; Katz, Katz & Kipiani, 1965; Corner, 1976). Comparative fossil material was studied during visits to Narodni Museum, Praha; Botany Department, PAN, Cracow; Muzeum Ziemi, Warsaw; Geology Department, Warsaw; Botany Department, AN, Leningrad; British Museum of Natural History, London; Muséum d'Histoire Naturelle, Paris.

Floristic composition

The fossil floras of the Fasterholt area show considerable similarities in floristic composition, the majority of species recorded in the Damgaard and Søby floras and the boreholes also occurring in the Fasterholt flora. However, a few species have not been recognized in the Fasterholt flora and are in central Jutland apparently confined to a lower or higher stratigraphical level. *Halesia crassa* and *Proserpinaca brevicarpa* are restricted to the Damgaard and Søby floras of the upper level, while *Actinidia* sp. and *Sambucus pulchella* are restricted to the lower levels of the boreholes.

Fasterholt flora

The plant megafossils of the Fasterholt flora, obtained from the C. Nielsen A/S lignite quarry, represent the most diverse fossil assemblage in the Fasterholt area. The flora comprises more than 150 species of three-dimensionally preserved reproductive and vegetative organs including fruits, seeds, anthers and twigs of angiosperms, cones, seeds and twigs of conifers, fern sporangia, megaspores of water ferns, and spore-bearing organs of fungi. The following genera have been identified based on the study of the larger plant fossils: *Equisetum, Pinus, Sequoia, Taxodium, Glyptostrobus, Tetraclinis, Magnolia, Liquidambar, Planera, Quercus, Pterocarya, Cyclocarya, Symplocos, Sphenotheca, Prunus, Trapa, Nyssa, Mastixia, Ganitrocera, Paliurus, Vitis, Tetrastigma, Phellodendron, Stratiotes, Spirematospermum,* and *Spondiaecarpum.* They are currently under investigation by Koch and Friedrich (Koch & Friedrich, 1970, 1971; Friedrich & Koch, 1970, 1972; Koch et al., 1974). Species identified among the smaller fossils are listed below.

PTERIDOPHYTA
  Lycopsida
    Selaginella pliocenica (1 megaspore)
  Pteropsida
    Salvinia cerebrata (650 megaspores and microsporangia)
    Salvinia sp. (25 megaspores)
    Azolla nikitinii (50 megaspores)
    Azolla ventricosa (85 megaspores)
    Azolla tuganensis (3 megaspores with massulae)

GYMNOSPERMAE
  Coniferopsida
    Pinus sp. (3 seeds)
    Sequoia sp. (more than 1000 seeds)
    Taxodium dubium (numerous fragments of seeds)
    Glyptostrobus europaeus (more than 1000 seeds)
    Hellia salicornioides (95 leaf whorls)

ANGIOSPERMAE
  Dicotyledones
    Liriodendron sp. (4 fruitlets, 70 seeds)
    Saururus bilobatus (30 fruitlets, 42 seeds)
    Brasenia cf. *tenuicostata* (154 seeds)
    Nuphar sp. (1 seed)
    Nymphaea sp. 1 (2 seeds)
    Nymphaea sp. 2 (1 seed)
    Liquidambar sp. (55 aborted seeds)
    Platanus neptuni (250 fruitlets)
    Ulmaceae genus? (few anthers)
    Alnus sp. (few anthers)
    Tubela cf. *baltica* (1200 fruits, 25 bract scales)
    Myrica wiesaensis (120 endocarps)
    Myrica stoppii (7 endocarps)
    Myrica kirchheimeri (25 endocarps)
    Myrica sp. (more than 2500 endocarps)
    Comptonia srodoniowae (40 endocarps)
    Rumex sp. (17 fruits)
    Eurya stigmosa (30 seeds and fragments)
    Hypericum holyi (50 seeds)

Hypericum danicum (85 seeds)
Poliothyrsis eurorimosa (21 seeds)
Clethra cimbrica (4 fruits, 25 seeds)
Lyonia danica (37 fruits)
Zenobia fasterholtensis (10 fruits)
Eubotrys sp. (1 fruit)
?*Enkianthus* sp. (1 fruit)
Epacridicarpum chandlerae (more than 3000 fruitlets)
Arctostaphyloides globula (1 fruit)
Arctostaphyloides menzelii (24 fruits and fragments)
Lysimachia sp. (6 seeds and fragments)
Potentilla pliocenica (1 fruitlet)
Potentilla sp. (1 fruitlet)
Rubus sp. 1 (550 endocarps and many fragments)
Rubus sp. 2 (10 endocarps)
Pyracantha acuticarpa (140 fruits, 1200 fruitlets)
Aldrovanda praevesiculosa (3 seeds)
Decodon gibbosus (118 seeds and many fragments)
Decodon vectensis (15 seeds)
Decodon sp. (10 seeds)
Mneme menzelii (10 seeds)
Microdiptera parva (23 seeds)
Microdiptera sp. (2 seeds)
Ludwigia corneri (105 seeds)
Ludwigia collinsoniae (75 seeds)
Myrtus palaeocommunis (250 seeds and many fragments)
Swida gorbunovii (120 endocarps and fragments)
Swida sp. (1 endocarp)
Aralia pusilla (60 endocarps and fragments)
Ilex saxonica (18 endocarps)
Paliurus sp. (65 seeds)
Weigela srodoniowae (4 fragments of fruits, 15 seeds)
Cephalanthus pusillus (23 mericarps)
Teucrium sp. 1 (3 nutlets)

Monocotyledones
Caldesia sp. 1 (2 fruits)
Alismataceae genus? sp. 1 (26 seeds)
Potamogeton heinkei (3 endocarps)
Potamogeton sp. (8 endocarps)
Najas sp. (1 seed)
Orchidaceae genus? sp. (1 seed)
Juncus sp. (5 seeds and few fragments)
Scirpus ragozinii (530 fruits)
Dulichium marginatum (1 fruit)
Cyperus sp. (100 fruits)
Cladium reidiorum (4 endocarps)
Cladium bicorne (6 endocarps)
Cladium sp. (1 endocarp)
Carex sp. 1 (30 fruits)
Carex sp. 2 (14 fruits)
?*Eriophorum* sp. 1 (1 fruit)
?*Eriophorum* sp. 2 (4 fruits)
Caricoidea jugata (6 fruits)
Cladiocarya europaea (310 endocarps)
Cladiocarya trebovensis (180 endocarps)
Cyperaceae genus? sp. (3 fruits)
Poaceae div. genera (14 specimens)
?*Epipremnum crassum* (3 seeds)
Pistia sibirica (350 seeds)
Lemna sp. (1 seed)
Typha sp. 1 (115 seeds)
Typha sp. 2 (200 seeds)
Typha sp. 3 (110 seeds)
Sparganium pusilloides (100 endocarps)
Sparganium multiloculare (1 endocarp)
Sparganium cf. *simplex* (19 endocarps)

Incertae sedis
Aracispermum canaliculatum (9 seeds)
Carpolithes natans (70 seeds)
Carpolithes dorofeevii (44 seeds)
Carpolithes nikitinii (115 seeds)
Carpolithes cf. *nikitinii* (11 seeds)
Carpolithes tiffneyi (90 seeds)
Carpolithes sp. 5 (11 seeds)
Carpolithes sp. 6 (60 seeds)
Carpolithes sp. 7 (1 seed)
Carpolithes sp. 8 (6 fruits)
Rhamnospermum bilobatum (44 specimens)

This list of the smaller fossils is based on a study of more than 14,000 specimens, most of which were angiosperms. About one third of the taxa were referred to fossil species previously described from other Tertiary floras of Europe, but the remaining fossils could not be accommodated in any known species, either due to inadequate material or to the fact that they had not previously been described. The fossil fruits and seeds of *Rubus,* Alismataceae, *Carex,* and *Typha* may be identical to material described from other fossil floras. However, difficulties in distinguishing modern species of these genera on the basis of fruit and seed characters have prevented an exact determination of these taxa. Fruits and seeds of *Clethra, Lyonia, Zenobia, Eubotrys, Myrtus,* and *Pistia* have for the first time been described from the fossil floras of Europa, and 15 new species have been established: *Myrica kirchheimeri, Hypericum danicum, H. holyi, Clethra cimbrica, Lyonia danica, Zenobia fasterholtensis, Epacridicarpum chandlerae, Ludwigia corneri, L. collinsoniae, Myrtus palaeocommunis, Weigela srodoniowae, Cephalanthus pusillus, Carpolithes dorofeevii, C. nikitinii,* and *C. tiffneyi.*

The most abundant fossils are fruits of *Epacridicarpum chandlerae* which constitute more than 20 per cent of all smaller angiosperm fossils of the Fasterholt flora. The various species of *Myrica* make up about 20 per cent of the specimens, and the Rosaceae, primarily represened by *Pyracantha acuticarpa,* constitute 14 per cent of the fossils. The Betulaceae and the Cyperaceae each includes about nine per cent of the angiosperm specimens, while each of the remaining taxa makes up less than three per cent of the fossils.

Damgaard flora

The plant megafossils of the Damgaard flora were collected from the southern part of the Damgaard lignite quarry and have already been described (Friis, 1979). The fossils are generally much abraded and give indication of rather rough transportation. The following species were identified:

GYMNOSPERMAE
- Coniferopsida
  - *Pinus* sp. (1 seed)
  - *Taxodium dubium* (6 seeds and many fragments)
  - *Hellia salicornioides* (8 fragments of leaf whorls)

ANGIOSPERMAE
- Dicotyledones
  - *Brasenia* cf. *tenuicostata* (22 seeds and fragments)
  - *Myrica* sp. (23 endocarps and many fragments)
  - *Comptonia srodoniowae* (100 endocarps and fragments)
  - *Pterocarya* sp. (1 endocarp)
  - *Eurya stigmosa* (2 seeds)
  - *Visnea* sp. (4 seeds)
  - *Epacridicarpum chandlerae* (5 fragments of fruits)
  - *Arctostaphyloides menzelii* (5 fruits, 16 fragments)
  - Ericaceae genus? sp. (1 fragment of fruit)
  - *Empetrum* sp. (1 endocarp)
  - *Halesia crassa* (1 endocarp)
  - *Intratriporopollenites instructus* (1 cluster of anthers)
  - *Aldrovanda praevesiculosa* (1 fragment of seed)
  - *Decodon gibbosus* (2 seeds)
  - *Proserpinaca brevicarpa* (2 endocarps)
  - *Paliurus* sp. (1 fruit, 1 fragment of fruit)
  - *Vitus* cf. *silvestris* (1 seed, 3 fragments)
- Monocotyledones
  - Alismataceae genus? sp. 1 (7 seeds)
  - *Potamogeton heinkei* (2 endocarps)
  - *Scirpus ragozinii* (12 fruits, 8 fragments)
  - *Cladium reidiorum* (1 endocarp, 1 fragment)
  - *Cladium* cf. *crassum* (2 endocarps)
  - ?*Eriophorum* sp. 2 (1 fruit)
  - *Cladiocarya europaea* (1 endocarp)
  - *Cladiocarya trebovensis* (2 endocarps)
  - *Sparganium pusilloides* (1 endocarp)
  - *Sparganium* cf. *simplex* (1 endocarp)
- Incertae sedis
  - *Carpolithes* sp. 1–4 (1 fruit of each species)

The material includes about 280 specimens of which about 95 per cent are angiosperms. Fruits of the Myricaceae (*Myrica* sp. and *Comptonia srodoniowae)* make up more than half of all the fossil specimens. Fruits related to the Ericaceae and the Cyperaceae, and seeds of the Cabombaceae are also well-represented in the fossil flora, while the remaining taxa each includes only a few specimens.

Søby flora

The Søby flora was collected from the northern part of the Damgaard lignite quarry. The fossils include leaf compressions as well as compressed cones, fruits and seeds. Fossil leaves of *Taxodium, Magnolia, Liquidambar, Ulmus, Castanea, Alnus, Comptonia, Juglans, Salix, Acer, Fraxinus,* and *Smilax* have been described along with reproductive organs of *Pinus, Taxodium, Halesia, Diospyros,* and *Leguminocarpon* (Christensen, 1975, 1976, 1978). Sieving of the leaf-bearing clay yielded numerous small fruits and seeds as well as twigs listed below together with the other reproductive organs of the Søby flora.

GYMNOSPERMAE
- Coniferopsida
  - *Pinus* sp. (1 seed, few cones; Christensen, 1975)
  - *Taxodium dubium* (many seeds, cones, leaves; Christensen, 1975)
  - *Hellia salicornioides* (3 leaf whorls)

ANGIOSPERMAE
- Dicotyledones
  - *Saururus bilobatus* (6 seeds)
  - *Platanus neptuni* (1 fruiting head)
  - *Myrica* sp. (1 endocarp)
  - *Comptonia srodoniowae* (9 endocarps, fragments)
  - *Hypericum danicum* (5 seeds, fragments)
  - *Poliothyrsis eurorimosus* (2 seeds)
  - *Halesia crassa* (many fruits; Christensen, 1978)
  - *Symplocos gothanii* (1 fragment of endocarp)
  - *Lysimachia* sp. (1 seed)
  - *Leguminocarpon* sp. (several fruits; Christensen, 1978)
  - *Microdiptera* sp. (1 seed)
  - *Ludwigia corneri* (1 seed)
  - *Proserpinaca brevicarpa* (2 fruits)
  - *Cephalanthus pusillus* (16 mericarps)
  - *Teucrium* sp. 2 (8 nutlets)
- Monocotyledones
  - Alismataceae genus? sp. 1 (44 seeds)
  - *Potamogeton heinkei* (1 endocarp)
  - *Scirpus ragozinii* (7 fruits)
  - *Dulichium marginatum* (13 fruits)
  - *Carex* sp. 2 (11 fruits)
  - *Carex* sp. 3 (2 fruits)
  - *Cladiocarya europaea* (3 fruits, fragments)
  - *Cladiocarya trebovensis* (40 fruits)
- Incertae sedis
  - *Carpolithes dorofeevii* (62 seeds)

There is almost no correlation between the fossil leaves and the reproductive organs recovered from the plant bearing clay, *Comptonia* and *Taxodium* being the only genera recognized both among the fossil leaves and among the reproductive organs. Among the fossil fruits and seeds, several species were probably herbaceous and would not be expected to have been preserved in a fossil leaf flora. Fruits and seeds referred to the Cyperaceae and Alismataceae constitute about half of the specimens studied, while seeds of *Carpolithes dorofeevii* of unknown affinity make up about one fourth of the specimens.

Lavsbjerg Øst

Plant megafossils were recovered throughout the Miocene sequence of the Lavsbjerg Øst borehole, although they were fragmentary, sparse and poorly preserved. In two horizons, however, fossils were more abundant. The following species were identified from the interval 16.0–25.0 m below surface based on the examination of about 35 specimens.

PTERIDOPHYTA
- Pteropsida
  - *Salvinia cerebrata* (1 megaspore)

GYMNOSPERMAE
- Coniferopsidae
  - *Sequoia* sp. (1 seed)

ANGIOSPERMAE
- Dicotyledones
  - *Saururus bilobatus* (1 seed)
  - *Brasenia* cf. *tenuicostata* (2 fragments of seeds)
  - *Eurya stigmosa* (1 seed)
  - *Epacridicarpum chandlerae* (2 fragments of fruits)
  - *Aldrovanda praevesiculosa* (8 fragments of seeds)
- Monocotyledones
  - *Alismataceae genus?* sp. 1 (1 seed)
  - *Cladiocarya europaea* (1 endocarp)
  - *Typha* sp. 2 (7 seeds)
  - *Typha* sp. 3 (6 seeds)
- Incertae sedis
  - *Carpolithes* cf. *nikitinii* (2 seeds)

The plant bearing horizons of the interval 47.0–64.5 m included a considerable number of fruits and seeds as well as megaspores. Species identified from this interval are listed below.

PTERIDOPHYTA
- Pteropsida
  - *Salvinia cerebrata* (145 megaspores, 110 microsporangia)
  - *Azolla nikitinii* (1 megaspore)
  - *Azolla ventricosa* (2 megaspores)
  - *Azolla* cf. *ventricosa* (170 megaspores)

GYMNOSPERMAE
- Coniferopsida
  - *Sequoia* sp. (1 fragment of seed)

ANGIOSPERMAE
- Dicotyledones
  - *Liriodendron* sp. (numerous fragments of seeds)
  - *Saururus bilobatus* (29 seeds)
  - *Brasenia* cf. *tenuicostata* (1 seed)
  - *Tubela* cf. *baltica* (1 fruit)
  - *Myrica* sp. (1 fragment of endocarp)
  - *Hypericum danicum* (9 seeds, 1 fragment)
  - *Actinidia* sp. (few fragments of seeds)
  - *Epacridicarpum chandlerae* (75 parts of fruits)
  - *Lysimachia* sp. (2 fragments of seeds)
  - *Pyracantha acuticarpa* (1 fragment of fruit)
  - *Rubus* sp. 2 (1 endocarp, 1 fragment)
  - *Aldrovanda praevesiculosa* (1 fragment of seed)
  - *Decodon vectensis* (6 seeds, 2 fragments)
  - *Microdiptera parva* (1 seed)
  - *Ludwigia corneri* (2 seeds)
  - *Sambucus pulchella* (1 fragment of endocarp)
- Monocotyledones
  - *Caldesia* sp. 2 (11 seeds)
  - Alismataceae genus? sp. 1 (18 seeds)
  - Alismataceae genus? sp. 2 (8 seeds)
  - ?*Limnocarpus* sp. (2 fragments of endocarps)
  - *Scirpus ragozinii* (5 fruits)
  - *Cladium* sp. (1 endocarp)
  - *Typha* sp. 2 (13 seeds)
  - *Typha* sp. 3 (33 seeds)
- Incertae sedis
  - *Carpolithes dorofeevii* (1 seed, 2 fragments)
  - *Rhamnospermum bilobatum* (5 specimens)

These identifications are based on an examination of about 660 specimens. Megaspores and microsporangia of Salviniaceae constitute about 65 per cent of all specimens. Fruits of *Epacridicarpum* and seeds of *Saururus, Alismataceae* and *Typha* make up the majority of the angiosperm fossils. In addition to the listed Tertiary plant fossils this level yielded several rebedded Palaeozoic and Mesozoic megaspores (H. Friis et al., 1980).

Fasterholt Plantage

Scattered plant megafossils were obtained from several horizons in the Miocene sequence of the Fasterholt Plantage borehole, but were most abundant at two levels. The following species were identified from the interval 32.0–36.0 m below surface based on the study of about 50 specimens.

GYMNOSPERMAE
- Coniferopsida
  - *Sequoia* sp. (6 fragments of seeds)
  - *Taxodium dubium* (1 fragment of seed)
  - *Glyptostrobus europaeus* (2 fragments of seeds)

ANGIOSPERMAE
  Dicotyledones
    Liriodendron sp. (13 fragments of seeds)
    Saururus bilobatus (3 seeds)
    Tubela cf. *baltica* (2 fruits)
    Myrica sp. (1 fragment of endocarp)
    Actinidia sp. (1 fragment of seed)
    Epacridicarpum chandlerae (5 fragments of fruits)
    Decodon vectensis (1 seed)
    Aralia pusilla (1 endocarp)
    Paliurus sp. (1 fragment of fruit)
    Sambucus pulchella (1 seed)
    Cephalanthus pusillus (1 fragment of mericarp)
  Monocotyledones
    Caldesia sp. 2 (1 seed)
    Alismataceae genus? sp. 1 (7 seeds)
    Cladium reidiorum (2 endocarps)

The interval 56.5–74.0 m yielded the following species:

PTERIDOPHYTA
  Pteropsida
    Salvinia cerebrata (7 megaspores, 5 microsporangia)
    Azolla nikitinii (10 megaspores)
    Azolla ventricosa (3 megaspores)

GYMNOSPERMAE
  Coniferopsida
    Sequoia sp. (2 seeds, 2 fragments)
    Taxodium dubium (1 seed)

ANGIOSPERMAE
  Dicotyledones
    Saururus bilobatus (21 seeds)
    Myrica sp. (1 endocarp)
    Comptonia srodoniowae (1 endocarp, 1 fragment)
    Hypericum danicum (1 seed)
    Actinidia sp. (2 seeds, 40 fragments)
    Epacridicarpum chandlerae (1 fragment of fruit)
    Pyracantha acuticarpa (10 fruitlets, 5 fragments)
    Rubus sp. 1 (1 endocarp, 1 fragment)
    Aldrovanda praevesiculosa (2 fragments of seeds)
    Decodon vectensis (6 seeds)
    Vitis sp. (8 fragments of seeds)
  Monocotyledones
    Caldesia sp. 2 (2 fruits, 1 fragment)
    Alismataceae genus? sp. 1 (35 seeds)
    Alismataceae genus? sp. 2 (20 seeds)
    Potamogeton sp. (3 endocarps)
    Caricoidea jugata (1 fragment of endocarp)
    ?*Epipremnum* sp. (1 abraded seed)
    Sparganium pusilloides (1 endocarp)
    Typha sp. 1 (5 seeds)
    Typha sp. 2 (23 seeds)
    Typha sp. 3 (22 seeds)
  Incertae sedis
    Aracispermum canaliculatum (1 fragment of seed)

The material collected from this level comprises about 260 specimens of which angiosperms constitute about 84 per cent and the Salviniaceae about 14 per cent. Seeds of Saururaceae, Alismataceae and Typhaceae constitute the majority of angiosperm fossils. In addition to the Tertiary fossils listed above several rebedded Mesozoic megaspores were collected from this interval.

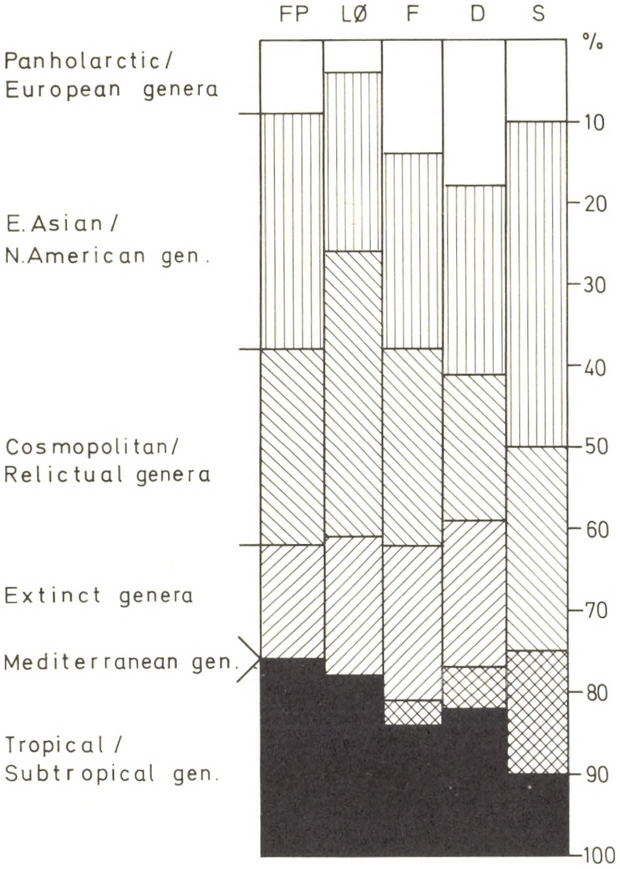
Vegetational analysis

Patterns of dispersal and processes during sedimentation and fossilization may have influenced the composition of the fossil plant assemblages considerably (Spicer, 1980; Collinson, 1983a,b). The fossil floras do, however, provide a rough picture of the original vegetation and criteria for comparison whith other fossil floras of similar preservation (Mai, 1965a, 1967; Friis, 1975). In the following discussion, megafossil floras with more than 25 species have been considered: Fasterholt flora, Damgaard flora, Søby flora, Lavsbjerg Øst (47.0–64.5 m), and Fasterholt Plantage (56.5–74.0 m).

Growth habit

The growth habits of the fossil species were estimated based on comparison with allied extant plants. A correlation between climate and the growth habit of extant dicotyledons has been pointed out by Bailey & Sinnott (1916), who demonstrated an increase of arborescent dicotyledons with increasing temperatures. In tropical lowland vegetation they found that more than 65 per cent of the species were arborescent while in warm temperate to subtropical lowland vegetation the arborescent dicotyledons constituted 25–65 per cent of the species. In temperate and polar regions less than 25 per cent of the dicotyledons exhibit a woody habit. In the fossil floras, species assumed to represent trees, shrubs, or vines constitute 40–50 per cent of all the fossil species. Species referred to the Salviniaceae and to the monocotyledons were probably all herbs, while all conifer species were probably arborescent. Among the dicotyledons, arborescent species predominate in the Fasterholt flora constituting about 70 per cent of the species. In the Søby flora and the two boreholes the woody species make up 50–60 per cent of the dicotyledons. Although herbaceous species are probably underrepresented in the fossil floras (Szafer, 1954; Friis, 1975), the content of woody species in the original vegetation must have been relatively high, falling within values stated for extant vegetation in warm temperate to subtropical regions.

Fig. 3. Phytogeographic composition of the investigated floral assemblages. FP = Fasterholt Plantage borehole (56.5–74.0 m), LØ = Lavsbjerg Øst borehole (47.0–64.5 m), F = Fasterholt flora, D = Damgaard flora, S = Søby flora.



Phytogeographic relationships

Two major floral elements, the palaeotropical and the arctotertiary, have been recognized in the Tertiary floras of Europe (Mai, 1965a, 1967, 1981). Fossil floras dominated by the palaeotropical element are referred to as mastixioid, while those dominated by the arctotertiary element are referred to as arctotertiary floras. The fossil floras of the Fasterholt area are all arctotertiary floras. The percentage of palaeotropical species varies from about 20 in the Søby flora to about 35–40 in the remaining four floral assemblages.

Based on distribution patterns in allied extant genera the fossils have been grouped into six phytogeographical elements (Fig. 3) following the classification proposed by Mai (1967). Data on modern plants were obtained mainly from Good (1964), Mai (1964) and Willis (1973).

1. Panholarctic/European genera: *Pinus, Nuphar, Liquidambar, Platanus, Quercus, Alnus, Pterocarya, Pyracantha, Swida, Vitis, Stratiotes*, and *Sparganium*.
2. East Asian/North American genera: *Taxodium, Glyptostrobus, Sequoia, Liriodendron, Saururus, Planera, Comptonia, Cyclocarya, Poliothyrsis, Actinidia, Eubotrys, Lyonia, Zenobia, Halesia, Decodon, Proserpinaca, Phellodendron, Nyssa, Aralia, Cephalanthus, Weigela*, and *Dulichium*. Several of these genera are now restricted to eastern North America:

Taxodium, Planera, Comptonia, Eubotrys, Zenobia, Decodon, Proserpinaca, and *Dulichium.* Others are now restricted to eastern Asia: *Glyptostrobus, Cyclocarya, Poliothyrsis, Actinidia, Phellodendron,* and *Weigela.*

3. Cosmopolitan genera and relicts: *Nymphaea, Rumex, Visnea, Hypericum, Clethra, Lysimachia, Potentilla, Rubus, Ludwigia, Ilex, Sambucus, Teucrium, Potamogeton, Najas, Juncus, Scirpus, Cyperus, Cladium, Carex, Lemna,* and *Typha.*
4. Mediterranean genera: *Tetraclinis* and *Paliurus.*
5. Tropical/subtropical genera: *Salvinia, Azolla, Magnolia, Brasenia, Myrica, Eurya, Symplocos, Aldrovanda, Myrtus, Mastixia, Tetrastigma, Caldesia,* and *Pistia.*
6. Extinct genera: *Hellia, Tubela, Epacridicarpum, Arctostaphyloides, Sphenotheca, Mneme, Microdiptera, Ganitrocera, Spondiaecarpum, ?Limnocarpus, Caricoidea, Cladiocarya, Aracispermum, Spirematospermum,* and *Rhamnospermum.* A number of species of unknown affinity has been accommodated in the form genus *Carpolithes.*

The fossil floral assemblages of the Fasterholt area show great similarity in phytogeographic composition (Fig. 3), and all have a high component of East Asian/North American genera, cosmopolitan genera, and relicts. Among the subtropical/tropical genera, several are now characteristic of mountain forests of Southeast Asia. The native element comprising species referable to genera now living in northern Europe (Friis, 1975), makes up 50–60 per cent of the fossil plant assemblages. None of the fossils have been referred to Recent species.

Ecology

An outline of the palaeoecology of the Fasterholt flora based primarily on studies of the smaller fossils, was presented in a previous work (Friis, 1975). Several major plant communities were recognized including swamp and hardwood forests, shrub bogs, fresh water marshes, and open water areas comparable to Recent plant communities of the Atlantic Coastal Plain of North America. The fossil species of the Damgaard and Søby floras, and from the two boreholes indicate that they were derived from similar environments. This is in accordance with results obtained from environmental studies of other Miocene lignite bearing strata of Europe (Kirchheimer, 1957; Teichmüller, 1958; Jux, 1968).

Among the assumed woody species several were referred to modern genera of wetland environments. The fossil species of *Taxodium, Glyptostrobus,* and *Nyssa* probably grew in inundated swamps and along sluggish streams. Extant species of *Taxodium* and *Nyssa* occur as dominant trees of the swamp forests of eastern North America. Species of *Pinus, Magnolia, Liquidambar, Alnus,* and *Ilex* may have occupied the more elevated areas of the swamps or they may have grown on the edge of the swamps in rich woods and along streams together with trees of *Liriodendron, Platanus, Quercus, Halesia,* and *Symplocos.* Extant representatives of these genera are also common in the wetland communities of eastern North America.

The shrubby vegetation is represented in the fossil floras by species of *Myrica, Comptonia, Eurya, Clethra, Lyonia, Zenobia, Eubotrys, Rubus, Pyracantha, Myrtus, Swida, Paliurus, Weigela,* and *Cephalanthus.* Some of these probably occurred in wet areas along swamp borders and along streams forming dense thickets. Allied extant species such as *Myrica cerifera, Lyonia ligustrina, Eubotrys racemosa,* and *Cephalanthus occidentalis* occur abundantly in a variety of wetland habitats of the Atlantic coastal Plain in bogs and along the borders of swamps, along stream banks and in thickets on the edge of lakes (Correll & Correll, 1972).

The majority of the assumed herbaceous species were referred to modern genera of aquatic or wetland environments representing a variety of habitats from open water areas to muddy soils. Free floating aquatics of shallow ponds, lakes and sluggish streams are represented in the fossil floras by species of *Azolla, Salvinia, Aldrovanda, Stratiotes, Pistia,* and *Lemna.* Extant *Salvinia* and *Pistia* are floating plants with sessile leaves in stoloniferous rosettes which commonly occur as pests in the tropics and completely cover the water surface (Hutchinson, 1975). They are represented in the Fasterholt flora by numerous specimens and may well have had a similar importance in the Miocene vegetation. The open-water areas are also represented by a number of rooted plants including species of *Brasenia, Nymphaea, Nuphar, Trapa, Najas,* and *Potamogeton.* Extant members of these genera occur commonly in shallow lakes and ponds and in slow streams. They have floating leaves or in *Najas,* and some species of *Potamogeton,* submerged leaves. *Nymphaea* and *Nuphar* often grow on the fringe of open-waters forming the outer line of the vegetation (Beaven & Oosting, 1939; Cohen & Spackman, 1974). Except for *Brasenia,* these rooted plants of the open-water are very rare in the Danish fossil floras, each represented by a few specimens only.

Rooted plants with emergent leaves and flowers are represented by species of *Caldesia,* Alismataceae, *Cladium, Dulichium, Scirpus, Carex, Cyperus, Juncus, Sparganium,* and *Typha.* Extant related genera constitute important elements of modern marsh vegetation and inner margins of shallow waters. Another group of bottom rooted water plants with leaf-bearing stems that emerge well above the water surface is represented by species of *Saururus, Proserpinaca,* and *Lysimachia.* The extant *Saururus cernuus* occurs abundantly in shallow water or on muddy soils of swamps, lakes and streams in the non-tidal swamp vegetation of the Atlantic Coastal Plain (Beaven & Oosting, 1939). Extant species of *Proserpinaca* are now restricted to eastern North America, also occurring in shallow water, along shores of lakes and streams.

Rooted plants with floating stems include species of *Decodon* and *Ludwigia.* Fossils referred to these genera occur abundantly in the fossil floras. The extant *D. verticillatus* forms an important constituent of the swamp and marsh vegetation of eastern North America. It roots along borders of ponds and streams and forms dense mats on the water surface in which other aquatics may root (Muencher, 1944; Hutchinson, 1975). The extant *Ludwigia palustris,* which is closely related to the fossil *L. collinsoniae,* also occur in the wetland areas of eastern North America. It may be completely submerged in swift streams or root on muddy banks forming carpet-like mats (Muencher, 1944).

Among the assumed wetland and aquatic herbs, species thought to represent fresh-water marsh plants constitute 50–60 per cent. Species thought to represent open water plants make up about 25–35 per cent of the herbs in the Fasterholt and Damgaard floras and the two boreholes. Surprisingly, the Søby flora thought to be deposited in lacustrine environments (Christensen, 1975) yielded only a single specimen referable to open-water plants (1 endocarp of *Potamogeton).*

Climate

The geographical and ecological distribution of related extant taxa, and assumed growth habit of the fossils, indicates that the fossil plants may have grown under warm temperate to subtropical conditions with abundant precipitation (cf. Friis, 1975). Most of the allied extant genera are distributed in temperate to subtropical regions of the Northern Hemisphere, the greatest common areas lying within 30°–45° N latitude, chiefly centered in eastern North America, East and Southeast Asia, and the Mediterranean regions. Related modern plant communities occur in the wetlands along the east coast of North America. The swamps and marshes of the Atlantic Coastal Plain and Florida are rather uniform in composition, but show some floristic divergence from north to south. The vegetation of the southern areas may be distinguished from the fossil assemblages by a higher content of tropical genera and families and by the presence of palms. The northernmost extension of several species related to the fossil taxa (e.g. *Saururus cernuus, Myrica cerifera, Eubotrys racemosa)* is in the Pocomoke swamp of Maryland at about 40° N latitude (Beaven & Oosting, 1939). The mean annual temperature for this area is about 15°C (mean July: 25°C, mean

February: 4°C). The mean annual precipitation is about 1250 mm (Beaven & Oosting, 1939).

Further evidence of the climate is provided by morphological features of *Brasenia* seeds. In extant *Brasenia schreberi* the seed surface bears small rounded or spiny protrusions of variable density, and according to H. Koch (1931) there is a marked correlation between surface ornamentation and the prevailing climate. In tropical regions the seeds develop spiny protrusions all over the surface, while in warm temperate and subtropical regions protrusions are developed at the basal part of the seed only, or are not developed at all. In the fossil seeds of the Fasterholt area protrusions are scattered on the basal part of the seed and suggest a warm temperate to subtropical climate.

Stratigraphy and comparison with other European and Asian fossil floras

Based mainly on geological context the fossil floras of the Fasterholt area have been referred to the Odderup Formation (Fasterholt flora, Damgaard flora, Søby flora, Lavsbjerg Øst 16.0–25.0 m, Fasterholt Plantage 32.0–36.0m) and Arnum Formation (Lavsbjerg Øst 47.0–64.5 m, Fasterholt Plantage 56.5–74.0 m) of Middle Miocene age. The Middle Miocene age is substantiated by comparison with other fossil floras of Europe (see below). A similar conclusion has been reached by Knobloch (1980) who estimated the Fasterholt and Damgaard floras to be of Badenian age, and the Søby (leaf) flora of Karpathian-Badenian age.

The majority of Tertiary floras described from Europe and Asia have been recovered from freshwater deposits and their age has primarily been established on the basis of intercalations with marine strata. Independent biostratigraphic systems for detailed stratigraphic resolution in continental strata have not so far been established, except for systems of strictly local value (cf. Brelie, 1967; Mai, 1967). Due to the lack of marine control in many areas and to the use of various non-correlative stratigraphical systems in different regions the correlation of Tertiary floras is problematic.

In the following comparisons which are based on floras with similar preservation states the occurrence of individual fossil species in the floras as well as the general composition of the floras have been considered. To simplify the comparison of the fossil floras four groups of phytogeographical elements have been considered. These are a) Panholartic, European, cosmopolitan and relict genera, b) East Asian and North American genera, c) Mediterranean and tropical/subtropical genera, d) Extinct genera. The similarity in the phytogeographical composition between the fossil floras of the Fasterholt area and other fossil floras is expressed by the index of affinity calculated according to the method of Sanders (1960).

Stratigraphic range of the fossil species

Among the smaller fossils of the Fasterholt area, 40 have been referred to species previously recorded from other European fossil floras. Due to the uncertain dating of many of these floras the stratigraphic ranges have been considered only in terms of major stratigraphic units (Table 1). With the exception of *Rhamnospermum bilobatum* and *Actinidia* sp. the fossil species have all been recorded from Miocene strata, some appearing in older strata as well as others extending into younger strata (Table 1). 11 of the fossil species are restricted to Miocene deposits, while *Rhamnospermum bilobatum* was previously recorded only from Paleogene floras and seeds similar to *Actinidia* sp. were recorded only from the Pliocene. If the more detailed dates suggested for some of the fossil floras are accepted it appears that the fossil floras of the Fasterholt area share the largest number of species with other Middle Miocene floras.

Several of the fossil species listed in table 1 have also been recorded from Tertiary deposits in Kazakhstan and Siberia. They seem to occur somewhat earlier in Asia than in Europe, and this may indicate a migration from east to west during the Oligocene-Pliocene (Dorofeev, 1963a; Mai, 1981). Two fossil species recorded from the Fasterholt area, *Azolla tuganensis* and *Aralia pusilla,* were previously known only from Tertiary deposits of Western Siberia.

Comparison with Paleocene and Eocene floras

The major Upper Paleocene-Lower Oligocene fruit and seed floras in Europe have been described from southern England (E.M. Reid & Chandler, 1926, 1933; Chandler, 1925–1978; Collinson, 1978a, b, 1980a, b; 1983a,b,c). However, rich megafossil assemblages, including fruits and seeds, have also been recorded from the Eocene lignite at Geiseltal, GDR (Mai, 1976a) and from the Eocene oil shales at Messel, GFR (Collinson, 1982a).

The late Paleocene-Eocene floras of Europe are clearly distinguished from younger floras by their tropical/subtropical character (Mai, 1981). Extant as well as extinct genera attributed to families such as the Annonaceae, Lauraceae, Menispermaceae, Icacinaceae, Bombacaceae, and Palmae occur abundantly in these floras, while in younger Tertiary strata they are scarce. Comparisons between selected Eocene floras and those of the Fasterholt area show low degrees of similarity in general composition (indeces of affinity: 35–45).

Among the fossil species of the Fasterholt area, few have previously been recorded from the Paleocene and Eocene (Table 1). One species, *Rhamnospermum bilobatum,* was previously known only from the Lower Tertiary.

Comparison with Pliocene floras

Pliocene fruit and seed floras have been recovered from numerous sites in Europe, from France in the West, to the Voronezh Region, USSR, in the East (C. Reid & E.M. Reid, 1915; E.M. Reid, 1920a, b; Szafer, 1946, 1947, 1954; Nikitin, 1957; Mai, 1965b, 1973; Maj, Majewski & Unger, 1963; Burgh, 1978, 1983).

The progressive cooling of the Pliocene which lead ultimately to the Pleistocene glaciation is reflected in the composition of these floras, which are generally characterized by a high content of Panholarctic-European and Cosmopolitan genera.

TABLE 1. Known stratigraphic range in Europe of fossil species from the Fasterholt area.

Fossil species	Paleocene	Eocene	Oligocene	Miocene	Pliocene
Eurya stigmosa	+	+	+	+	
Rhamnospermum bilobatum		+	+		
Decodon vectensis		+	+	+	
Microdiptera parva		+	+	+	
Cladiocarya trebovensis		+	+	+	
Glyptostrobus europaeus		+	+	+	+
Saururus bilobatus		+	+	+	+
Decodon gibbosus		+	+	+	+
Cladiocarya europaea		+	+	+	+
Platanus neptuni			+	+	
Poliothyrsis eurorimosa			+	+	
Swida gorbunovii			+	+	
Sparganium pusilloides			+	+	
Sparganium multiloculare			+	+	
Hellia salicornioides			+	+	+
Taxodium dubium			+	+	+
Pyracantha acuticarpa			+	+	+
Dulichium marginatum			+	+	+
Caricoidea jugata			+	+	+
Carpolithes natans			+	+	+
Azolla ventricosa				+	
Azolla nikitinii				+	
Salvinia cerebrata				+	
Myrica wiesaensis				+	
Myrica stoppii				+	
Arctostaphyloides globula				+	
Ilex saxonica				+	
Scirpus ragozinii				+	
Cladium reidiorum				+	
Cladium bicorne				+	
Pistia sibirica				+	
Aracispermum canaliculatum				+	+
Arctostaphyloides menzelii				+	+
Halesia crassa				+	+
Aldrovanda praevesiculosa				+	+
Mneme menzelii				+	+
Sambucus pulchella				+	+
Potamogeton heinkei				+	+
?*Epipremnum crassum*				+	+
Actinidia sp.					+
Total 40 species	1	9	20	38	19

Comparisons between the fossil floras of the Fasterholt area and Pliocene floras reveal little similarity in general composition, the indeces of affinity varying from about 70 for early Pliocene floras to about 50 for late Pliocene floras.

An important character distinguishing the Pliocene floras from those of older strata is the higher proportion of extant species in the floras. According to studies by E.M. Reid (1920b) the percentage of extant European species increases from about 5 per cent in the early Pliocene to about 85 per cent in the early Pleistocene floras. In the late Pliocene 60–70 per cent of the species were thought to represent extant species (Szafer, 1954; Mai et al., 1963).

Comparison with Oligocene and Miocene floras

The main occurrence of Oligocene and Miocene floras in Europe is within West and East Germany, central and southern Poland, Czechoslovakia, and southwestern USSR. Middle Oligocene-Upper Miocene floras are generally characterized by a high proportion of arctotertiary genera, and the dominance of swamp forest dominated by *Nyssa* and *Taxodium* (Mai, 1981). Species attributed to families such as Myricaceae, Theaceae, Ericaceae, Symplocaceae, Rosaceae and Mastixiaceae are important constituents in many of the European floras.

The best studied fruit and seed floras of the younger Tertiary are probably those of the Lausitz area, GDR. Detailed investigations of these floras were carried out by Kirchheimer (1935a, b, 1938a, 1939a, 1940a, b, 1941a, b, 1942a, b, 1943) and later by Mai (1960, 1963, 1964, 1967, 1970a, b, c, 1971, 1975a, b). The fossil fruits and seeds studied by Mai were obtained from late Oligocene to late Miocene strata in numerous outcrops and boreholes. Mai demonstrated considerable variation in floristic composition in fossil floras from different stratigraphic levels and attributed this variation to climatic fluctuations (Mai, 1967). Based on this variation, Mai (1967) distinguished 13 biostratigraphical zones (floral zones I–XIII) corresponding to 13 interchanging climatic phases. According to Ahrens & Lotsch (1967) the stratigraphical relation between the various plant bearing horizons was determined primarily on the assumption that the rate of sedimentation was the same within the whole area and was not interrupted at any time. This assumption may explain some of the inconsistency in floristic composition within floras referred to the same floral zone, especially within zone V. A provisional stratigraphical correlation of the deposits in the Lausitz area with those of the North Sea Region was proposed by Lotsch (1968), who correlated the floral zones I–V with the Chattian-Vierlandian, VI–VIII with Hemmoorian, and IX–XIII with Reinbekian-Lower Gramian.

Comparison of the floras from the Fasterholt area with those of the Lausitz area reveals considerable similarity in general composition with the floras characterized by Mai (1967) as warm temperate to subtropical (included in floral zones I, IV, VII, IX, XI), and less similarity with those classified as subtropical (II, VI, VIII, X, XII), or temperate (V, XIII).

Several fossil species of the Fasterholt area have also been recorded from the Lausitz area, the highest number in floral zones IV, VI, X and XI.

Important contributions to the knowledge of the late Tertiary fruit and seed floras of Western Germany were given by Menzel (1906, 1913) and Kirchheimer (1935a, 1936a, b, c, 1937a, 1939b, 1957). Recently detailed investigations have been carried out by Gregor (1975–1983), primarily concentrated on the fossil floras of the Oberpfalz lignites. These floras were characterized by Gregor (1978a) as mastixioid with a high content of palaeotropical genera. Among the 140 species described from the sandy interbeds, only 8 have been recorded among the smaller fossils of the Fasterholt area.

Several fruit and seed floras have been described from the Miocene of Poland, but due to lack of marine control the ages of those floras are also uncertain. The plant bearing strata of western

Poland, including the Konin and Turow floras, have been correlated with the floral zones of the Lausitz area, principally on the basis of palynological studies supported by lithological correlations (Raniecka-Bobrowska, 1970; Ziembińska-Tworzydło, 1974; Dyjor & Sadowska, 1977; Sadowska, 1977). The Miocene strata of central and southern Poland, including the fossil floras of Rypin, Wieliczka, the Gdow Bay, and Nowy Sącz Basin, could not be correlated with the deposits of western Poland and Germany.

The study of the Tertiary fruit and seed floras of Poland has chiefly been carried out by Szafer (1946, 1947, 1954, 1961), Łańcucka-Środoniowa (1957–1984), and Raniecka-Bobrowska (1957, 1959). Except for the Turow flora, the Polish Miocene floras may be classified as arctotertiary. Of these, the fossil flora of Stare Gliwice shows the greatest similarity to those of the Fasterholt area, but it also includes several taxa referred to extant species and thus may have been younger than the Danish floras.

The fossil floras of the European USSR were described by Dorofeev (1955a, b, 1959a, 1960a, 1966a, 1967a, b, 1968a, 1969a, 1970a, 1971, 1973a, 1976a, b, 1977a), Nikitin (1957), and Negru (1968, 1969, 1970, 1972). According to Dorofeev the ages of the floras range from Lower Oligocene to Pliocene, most being of Miocene age. The Miocene floras of the Odessa and Rostov regions are characterized by a very high content of herbaceous species, and Dorofeev (1959a) interpreted these floras as being derived from savannah-like vegetation. The Moldavian and Byelorussian floras are more related to the Middle Oligocene-Miocene arctotertiary floras of Central and Northern Europe, but they have only a few species in common.

Abundant fruit and seed fossils have been recovered from early Oligocene to late Miocene strata of Western Siberia (Nikitin, 1935, 1948, 1965; Dorofeev, 1955c, d, 1957, 1958a, b, 1959b, c, 1960b, 1961, 1962, 1963a, 1966b). They are distinguished from the Oligocene-Pliocene floras of Europe mainly by the absence of certain genera or families which are abundant in many of the European fossil floras, including fruits of *Myrica,* Symplocaceae and Mastixiaceae and seeds of Theaceae. In floristic composition they are generally similar to the arctotertiary floras of Europa, although Mediterranean genera have been recorded from only a few of the Siberian floras. Comparison with the fossil floras of the Fasterholt area shows high similarity, the indeces of affinity varying from 81 to 96. The majority of the fossil species described from Western Siberia are endemic to that region, but there are also many species in common with the European fossil floras. About 20 of the fossil species from the Fasterholt area have also been recorded in the Siberian floras.

Floristic and stratigraphic conclusions

The fossil floras of the Fasterholt area are basically arctotertiary floras with a rather high content of palaeotropical species. About 120 species have been recognized, most of them angiosperms. 75 angiosperm genera including about 110 species are described. The Myricaceae, Ericaceae, Rosaceae, Lythraceae, and the Cyperaceae are the largest families, each with from 5 to 16 species. The fossil floras of the different stratigraphical levels in the Fasterholt area show great similarity in floristic composition. They are all characterized by a high content of East Asian-North American genera and also by a high content of cosmopolitans and relictual genera. The proportion of tropical/subtropical genera ranges between 10 and 17 per cent. Vegetation analyses suggest that the original floras grew in environments corresponding to wetland communities of the Atlantic Coastal Plain of North America, under warm temperate to subtropical conditions, with abundant precipitation.

The fossil floras of the Fasterholt area have been compared with other Tertiary floras of Europe and Asia on the basis of the individual species as well as the general floristic composition. 42 of the fossil species recovered from the Danish fossil floras were previously recorded from other fossil floras, the largest number being described from Miocene floras of Europe. In floristic composition the fossil floras from Denmark show great similarity with late Oligocene and Miocene floras of Europe and Asia, especially with floras characterized as warm temperate to subtropical. There is only a low correlation with floras younger than the Miocene and older than the Middle Oligocene.

Systematics: Division Angiospermae

In this systematic study only the angiosperm fossils are considered. The megaspores and microsporangia of *Salvinia* and *Azolla* from the Fasterholt flora and the leaf whorls of *Hellia salicornioides*, have already been described (Friis, 1977a, b). The remaining conifer fossils and other larger fossils of the Fasterholt flora are under investigation by B.E. Koch and W.L. Friedrich.

The angiosperm families have been arranged according to the classification of flowering plants established by Takhtajan (1969, 1980). Morphological and anatomical features of modern seeds and fruits considered important for the identification of comparable fossils are briefly summarized for each family. All fossil material is deposited in the Department of Geology, University of Aarhus.

CLASS DICOTYLEDONES

Magnoliales

Magnoliaceae

The Magnoliaceae are represented in the Fasterholt flora by numerous seeds of *Magnolia* L. and *Liriodendron* L. Leaves probably assignable to *Magnolia* were described from the Søby flora (Christensen, 1978). Seed fragments of *Liriodendron* occur commonly in the Lavsbjerg Øst and Fasterholt Plantage boreholes.

The fruits of extant Magnoliaceae are generally apocarpous cone-like, and composed of spirally arranged follicles or samaras. Each fruitlet contains one to many seeds. The seeds are anatropous, bitegmic, exarillate, and endotestal with the mechanical layer in the inner epidermis of testa (Corner, 1976). The testa is differentiated into a sarcotesta and a woody endotesta. The endotesta consists of few (e.g. *Liriodendron)* to many (e.g. *Magnolia)* layers of lignified crystal cells. The endotestal cells are generally thin-walled but with internal fibrous lignifications. Each cell contains one, rarely more, angular crystals. The endotesta forms a marked heteropyle round the chalaza. The outer surface of endotesta is almost smooth in *Magnolia,* ofte with remnants of inner sarcotestal layers forming a fine "fingerprint" pattern (Tiffney, 1977). In *Liriodendron* the outer surface of endotesta bears irregular tubercles formed by lignified crystal cells.

Liriodendron L.
Liriodendron sp.
Plate 1, figs 1–7.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 47.0–47.5 m; 50.5–52.5 m; 53.0–57.5 m; 58.0–59.5 m; 60.0–61.0 m; 63.0–63.5 m; 110.5–111.0 m; Fasterholt Plt.: 33.0–33.5 m; 34.5–35.0 m; 36.0–36.5 m; 44.5–45.0 m.

Material. – 4 fruitlets, 70 seeds and many seed fragments (1001.01–33; 2001.01–05; SEM–50,–304,–305).

Description and remarks. – The fruitlets are unilocular samaras, laterally flattened with remnants of a dorsi-ventrally flattened wing. The dorsal margin is semi-circular and ventral margin straight or slightly convex. The lateral faces are convex with a distinct transverse ridge extending from ventral margin to base of dorsal wing. The fruit wall is woody, about 0.1 mm thick, composed of an inner layer of longitudinally aligned elongated sclereids and an outer layer of small equiaxial sclerenchyma.

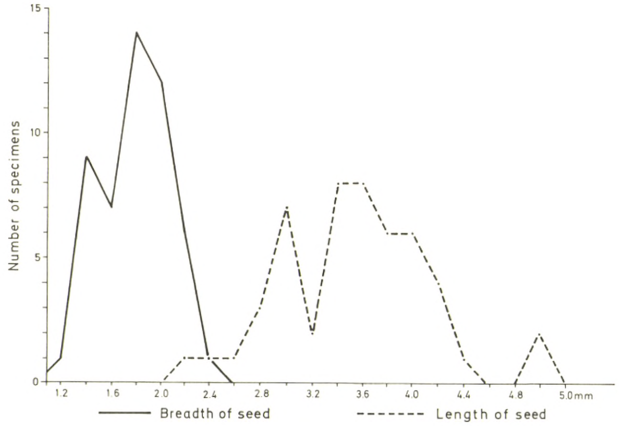


Fig. 4. Size distribution in fossil *Liriodendron* sp. from the Fasterholt flora.

Length of fruitlets: 2.8–4.7 mm; breadth: 2.2–3.0 mm. Each fruitlet contains one or two pendant seeds.

The seeds are 2.2(3.48)5.0 mm long and 1.2(1.75)2.4 mm broad; 50 seeds were measured (Fig. 4). The seeds are anatropous, ovate to elliptical in outline and dorsi-ventrally flattened with straight or curved longitudinal axes (Pl. 1, figs 1–3). The apex is constricted into a short funicular stalk (Pl. 1, fig. 4), which is sometimes broken exposing a small micropylar aperture, about 0.15 mm in diameter. The base of the seed is rounded or elongated into a short neck with a ventral chalaza marked by a distinct heteropyle, 0.2–0.3 mm in diameter (Pl. 1, figs 1–2, 5).

The seed wall is composed of a thick testa and a thin tegmen. Typically only the endotesta is preserved. It is 0.045–0.095 mm thick, and formed of two layers of columnar sclereids. The cells of the endotesta are thin-walled, infilled with fibrous lignifications, and each shows the imprint of a single angular crystal (Pl. 1, figs 6–7). In surface view the cells are polygonal and equiaxial. The outer surface of the endotesta is characterized by irregular tubercles formed from one or two layers of sclereids, also with internal fibrous lignifications and imprints of angular crystal. The exotesta (sarcotesta) is composed of an inner layer of transversely elongated thin-walled cells, 0.15 mm × 0.02 mm, arranged in distinct longitudinal rows, and an outer layer of elongated lignified cells. The inner epidermis of the testa has small narrow cells arranged in longitudinal rows. The tegmen is thin and composed of small cuboidal cells.

The presence of a heteropyle and endotestal crystal cells with fibrous lignifications clearly indicate relationship with modern Magnoliaceae, and based on the structure of the fruitlets and the endotestal tubercles the fossil may be placed in the extant genus *Liriodendron*. The fossil seeds differ mainly from those of the two living species (*L. chinensis* (Hemsl.) Sarg. and *L. tulipifera* L.) in their smaller size and thinner seed wall. In *L. tulipifera* the seeds are about 4.6–6.6 mm long and 1.9–3.4 mm broad and the seed wall about 0.2 mm thick.

The two extant species of *Liriodendron* occur today in China *(L. chinensis)* and southeastern North America *(L. tulipifera)*. The genus is widespread in fossil floras of the northern hemisphere, first appearing during the Upper Cretaceous. Fossil seeds of *Liriodendron* have been recovered from Oligocene and Miocene floras in Asia and Europe. Seven fossil species have been described. They have been separated based mainly on the seed size and shape and the structure of the endotesta. The seeds of *L. regulare* Dorofeev (1970b), described from the Oligocene of Western Siberia, are similar to the Danish seeds in size, shape and internal anatomy, but differ in the more regular spacing of the endotesta tubercles. The seeds of *L. uralensis* Dorofeev (1970b) are also quite similar to the Danish seeds, but have a slightly thicker seed wall. In most of the figured specimens the chalazal area is elongated into a short distinct neck. In the Danish seeds, a chalazal neck is present in about half of the specimens. The seeds of *L. balticum* Dorofeev (1970b) and *L. aptera* C. & E.M. Reid (1915) are generally smaller than the Fasterholt seeds, while those of *L. geminata* Kirchheimer (1957) and *L. krystofovichii* Dorofeev (1983) are larger. There is no information on wall structure in *L. aptera*. In *L. balticum* and *L.*

geminata the endotesta is somewhat thicker than in the Danish seeds. The seeds of *L. manykinii* Dorofeev (1983) differ from other species of *Liriodendron* in having three layers of almost isodiametric sclereids. Thus, the features of the Danish seeds do not conform completely to any of the previously described species. The differences are, however, slight, and as no information on seed variability in extant *Liriodendron* is available, it is considered inappropriate to establish a new fossil species for the Fasterholt material.

Piperales

Saururaceae

The Saururaceae are now restricted to Asia and North America and are represented in the Miocene strata of Denmark by fruits and seeds of *Saururus* L.

In extant Saururaceae the fruits are formed from three to five carpels. In *Saururus* the carpels are united only at the base, while in the other genera of the family the fruits are syncarpous. The fruitlets of *Saururus* contain one seed each (Wood, 1971). The seeds are small, hemi-orthotropous, and bitegmic with the mechanical layer of the seed coat in the tegmen. The testa is composed of thin-walled cells, that are usually crushed. The cells of exotegmen and endotegmen are cuboidal with very thick walls (Corner, 1976).

Saururus L.

Saururus bilobatus (Nikitin ex Dorofeev) Mai
Plate 2, figs 1–6.

1963a *Carpolithus bilobatus* Nikitin – Dorofeev, p. 227.
1965 *Carpolithus bilobatus* Nikitin sp. nov. – Nikitin, p. 92, Pl. 18:12–13, Pl. 19:1–2.
1978 *Saururus bilobatus* (Nikitin) Mai nov. comb. – Mai & Walther, p. 45, Pl. 25:1–2.
1959 *Heliotropium* sp. – Raniecka-Bobrowska, p. 198, Pl. 23:4–10.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 16.0–16.5 m; 47.0–48.0 m; 54.5–57.5 m; 59.0–60.5 m; 95.0–95.5 m. Fasterholt Plt.: 32.0 m; 34.5–35.5 m; 63.0–63.5 m; 65.0–66.5 m; 69.0–69.5 m; 74.0–74.5 m.

Material. – 1 entire fruit, 30 fruitlets, and 70 dispersed seeds. (1002.01–03; SEM-102,–114,–310).

Description and remarks. – The fruit is composed of four fruitlets, fused together at the bases. Each fruitlet with remnants of an outwardly curved style with decurrent papillate stigma. The fruitlets are small with a convex dorsal face, slightly flattened lateral faces and a split along the ventral margin (Pl. 2, figs 1–2). Length of fruitlets: 0.9(1.22)1.5 mm; breadth: 0.6 (1.08)1.3 mm; 21 fruitlets were measured. The outer surface is wrinkled with irregular tubercles (Pl. 2, figs 1, 4). The fruit wall is 0.05–0.25 mm thick and is thickest laterally. It is composed of polyhedral and isodiametric parenchyma cells with slightly thickened and strongly pitted secondary cell walls. Connections between the cells are limited to small areas and large intercellular spaces separate the cells (Pl. 2, fig. 5). Remains of staminal filaments have been observed fused with the basal part of the fruitlet in some specimens. Each fruitlet contains one erect seed.

The seeds are hemi-orthotropous and bitegmic, ovoid in shape, slightly pointed at the apical micropyle and rounded at the base (Pl. 2, fig. 3). Chalaza is sub-basal and ventral. Length of seed: 0.7(0.85)1.1 mm; breadth: 0.6(0.72)0.9 mm; 20 specimens were measured. The seed wall is about 0.045 mm thick. Testa is composed of an outer epidermis of thin-walled, equiaxial cells and an inner layer of transversely elongate thin-walled cells, arranged in distinct longitudinal rows. Tegmen consists of about three layers of thick-walled cells. The testa is often abraded exposing the shining surface of tegmen which shows imprints of the transverse testal cells (Pl. 2, fig. 3).

The characters of the fossil fruits and seeds are those of modern *Saururus* (Pl. 2, figs 7–9). The genus includes two extant species of bog plants, *S. chinensis* Hort. ex Loud. from eastern Asia and *S. cernuus* L.

from eastern North America. The fossil seeds differ, however, from those of the living species in having a testa with larger and more regularly arranged transverse cells.

The genus *Saururus* was first recognized in the fossil record by Mai (Mai & Walther, 1978), one fossil species, *S. bilobatus,* being described. The known stratigraphic range of the species in Europe is from the Upper Eocene to Pliocene. In Western Siberia the species has been recorded from Oligocene strata, forming an important constituent of the lignite facies (Dorofeev, 1963a; Nikitin, 1965). According to Raniecka-Bobrowska (personal communication, 1976) the fossil fruits from the Miocene flora of Konin described as *Heliotropium* sp. (Raniecka-Bobrowska, 1959) are identical with *Saururus bilobatus*.

Nymphaeales

The Nymphaeales are represented in the fossil floras of the Fasterholt area by seeds referred to the Cabombaceae *(Brasenia* Schreber) and the Nymphaeaceae (*Nymphaea* L., *Nuphar* Smith). The seeds of extant members in these two families have many features in common and their separation may be difficult to justify on the basis of seed characters alone (Collinson, 1980a). The seeds are all anatropous, bitegmic, exotestal and operculate. In the Cabombaceae and the subfamily Nymphaeoideae the exotestal sclereids have characteristic stellate-undulate cell walls. The seeds of the Nymphaeoideae are arillate while the other members of the order have exarillate seeds (Corner, 1976; Collinson, 1980a). The position of the hilum and micropyle in relation to the operculum has been used to distinguish nymphaealean genera (Dorofeev in Takhtajan, 1974; Collinson, 1980a). In *Brasenia,* the hilum and micropyle are close together at the top of the operculum while in *Nymphaea* they are separate. Several extinct genera have been described of which *Braseniella* Dorofeev (1973b) and *Sabrenia* Collinson (1980a) are intermediate forms between the Cabombaceae and the Nymphaeaceae.

Cabombaceae

Brasenia Schreber

Brasenia cf. *tenuicostata* Nikitin

Plate 3, figs 1–6.

1979 *Brasenia* cf. *tenuicostata* Nikitin – Friis, p. 123, figs 5D–G.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Lavsbjerg Øst: 16.0–16.5 m; 24.5–25.0 m; 55.5–56.0 m.

Material. – 140 seeds and few fragments of seeds. (1003.01–19; 2003.01–04; 3003.01–07; SEM–26,–53,–305).

Description and remarks. – The seeds are anatropous, bitegmic and exarillate, ellipsoidal in outline and with a distinct operculum (Pl. 3, fig. 1). Length of seed without operculum: 1.5–2.8 mm; breadth: 0.9–2.0 mm, the seeds of the Damgaard flora being slightly larger than those of the Fasterholt flora (Damgaard flora: length: 1.5(2.4)2.8 mm; breadth: 1.1(1.6)2.0 mm; 10 seeds were measured. Fasterholt flora: length: 1.5(1.78)2.5 mm; breadth; 0.9(1.25)1.6 mm; 50 seeds were measured). The operculum is conical, 0.1–0.2 mm high and 0.4 mm in diameter, built of columnar sclereids with non-undulate anticlinal walls. The micropyle is at the top of the operculum with hilum marked by a circular scar immediately below the micropyle.

The testa is 0.14–0.19 mm thick formed from an outer layer of columnar sclereids and an inner layer of parenchyma. The columnar cells are 0.14–0.18 mm high and 0.075–0.1 mm wide, with pitted and strongly thickened walls (Pl. 3, figs 4–5). The anticlinal walls are stellate-undulate generally with four to five digitations (Pl. 3, figs 2–3). The basal part of the seed is smooth or with small rounded tubercles. Tegmen is thin and membranous and its cellular structure is indistinct, except for the apical part, which has transverse cells with raised, strongly undulate, anticlinal walls (Pl. 3, fig. 6). The tegmen separates easily from testa and has been found dispersed in the sieved sediment samples. Similar dispersed tegmen were described by Weyland, Berendt & Peters (1960) from the Miocene as unknown microfossil Form E.

The position of micropyle and hilum at the top of the operculum, the stellate columnar cells of the exotesta and the lack of hairs place the fossils in the genus *Brasenia*. The genus includes one modern species, *B. schreberi* Gmel., the seeds of which are distinguished from the fossils in their larger size and thicker wall. *B. schreberi* is an aquatic herb with rooted stem and floating leaves. It is widely distributed in warm temperate to tropical regions.

Fossil seeds of *Brasenia* occur commonly in the Tertiary floras of Europe and Asia, and about 30 fossil species have been described, most of them from the Tertiary of the USSR (Dorofeev & Veličkevič, 1971; Dorofeev, in Takhtajan, 1974; Dorofeev, 1984). The first appearance of the genus is in the Middle Eocene (Mai, 1976a) and the greatest diversity of species is in the Miocene. The Danish seeds are distinguished from most other fossil species of *Brasenia* in having a rather thin seed wall. *B. bashirica* Dorofeev (in Takhtajan, 1974), *B. orientalis* V. Nikitin (1976), *B. sibirica* Dorofeev (1963a), *B. tenuicostata* Nikitin (1965), and *B. ucrainica* Dorofeev (1970a) also have rather thin seed walls ($\leq$0.2 mm thick), but none of them are identical to the Danish seeds. The greatest similarity is with the seeds of *B. tenuicostata*, but these are slightly larger than the Danish fossils (2.0–3.6 mm × 1.7–2.0 mm).

Nymphaeaceae

Nymphaea L.

Nymphaea sp. 1
Plate 3, figs 7–9.

Occurrence. – C. Nielsen A/S (Fasterholt Flora).
Material. – 2 seeds (SEM-54).
Description and remarks. – The seeds are crushed, 1.2–1.7 mm long and 0.8–1.2 mm broad, ellipsoidal in outline with rounded apex and base (Pl. 3, fig. 7). Hilum and micropyle are adjacent at the apical operculum. The seed wall is about 0.02 mm. Testa has one layer of cuboidal sclerenchyma cells with undulate anticlinal walls, the facets showing 8–14 rounded, regular digitations per cell (Pl. 3, fig. 9). The cells are transversely elongate 0.09–0.1 mm × 0.04–0.06 mm, aligned in distinct longitudinal rows (Pl. 3, fig. 8). Remnants of hairy protrusions from the cell margins form indistinct longitudinal ridges, apparently placed at two cell row intervals (Pl. 3, fig. 8).

Based on the features of operculum and testa the fossil seeds have been referred to the genus *Nymphaea*. The genus includes about 50 extant species of aquatic herbs with floating leaves widespread in temperate to tropical regions.

Fossil seeds of *Nymphaea* have been recorded from several fossil floras of Europe and Asia, but only few small forms comparable to the Danish fossils have been described, among these are *N.* cf. *coerulea* Sav. from the Miocene of Moldavia (Negru, 1972). *N. alba* L. foss. from the Miocene of Rypin (Łańcucka-Środoniowa, 1957), and *N. pusilla* Dorofeev (1971) from the Pliocene of Byelorussia. They all differ slightly from the Danish seeds either in shape or size.

Nymphaea sp. 2
Plate 4, figs 1–3.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed (SEM-54).
Description and remarks. – The seed is ellipsoidal, 1.5 mm long and 0.8 mm broad, slightly pointed at the base and apex (Pl. 4, fig. 1). The sclereids of exotesta are transversely elongate or nearly equiaxial, about 0.7–0.9 mm × 0.6–0.7 mm, aligned in distinct rows. They have undulate anticlinal walls with 8–12 digitations which may be forked at the tips (Pl. 4, figs 2–3). There are no trace of hairs.

The seed is distinguished from those of *Nymphaea* sp. 1 in its more elongate shape, in the shape of the sclerenchyma cells and in the absence of hairs. It shows considerable similarity with seeds of living *N. alba* L. in wall structure, but differs in its much smaller size.

Nuphar Smith

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed (SEM–54).
Description and remarks. – The seed is 4.6 mm long and 3.3 mm broad, obovate in outline with a distinct ridge along the raphe. An apical, ovate aperture indicates the position of operculum. Hilum is indicated by a slightly raised, narrow elliptical scar below the apical aperture. The seed wall is about 0.13 mm thick composed of a thick testa and a thin membranous tegmen. The testa consists of an outer layer of columnar sclereids and an inner layer of parenchyma cells. The facets of the sclereids are isodiametric and polygonal.

The genus *Nuphar* includes about 25 extant and 12 extinct species. Based on seed characters Dorofeev (in Takhtajan, 1974) separated the genus into two sections. The features of the fossil seed from the Fasterholt flora are those of the section *Nupharella* characterized by having an ovate operculum. The hilar scar is elongate placed partly on the operculum and partly below. The sclereid cells of testa are columnar. In the seeds of the section *Nuphar* the operculum is ovate or elongate, the hilar scar is circular placed close to the micropyle, usually on the operculum. The sclereids of the testa are cuboidal. The section *Nupharella* includes only fossil species principally from early and middle Tertiary strata, whereas the section *Nuphar* includes both fossil and modern species with the earliest occurrence in the Pliocene (Dorofeev in Takhtajan, 1974).

Hamamelidales

Hamamelidaceae

Plant remains of the Hamamelidaceae occur abundantly in the Miocene deposits of Denmark. Fruiting heads assignable to *Liquidambar* L. are among the most numerous fossils in the Fasterholt flora (Koch et al., 1973) and small fossils resembling aborted seeds of *Liquidambar* have also been recovered. Leaves of *Liquidambar* have been described from the Søby flora (Christensen, 1976) and Mathiesen (1975) recorded leaves of *Liquidambar* and *Parrotia* C.A. Mey. from the lignitic clay of Moselund. Among the larger fossils of the Fasterholt flora there are two-loculed fruits resembling those of *Corylopsis* Sieb. & Zucc., but these remain to be studied in detail.

The seeds of living Hamamelidaceae show considerable diversity in structure (Melikian, 1973). They are anatropous, bitegmic and mesotestal. In several genera (e.g. *Corylopsis, Disanthus* Maxim., *Hamamelis* L., *Trichocladus* Pers., the testa is massive, composed of many layers of small isodiametric sclereids, while in other genera (e.g. *Altingia* Nor., *Liquidambar)* testa is rather thin formed from a few layers of sclereids (Melikian, 1973; Corner, 1976). Winged seeds occur in *Liquidambar, Rhodoleia* Champ. ex Hook., *Exbucklandia* R.W. Brown, and others.

Liquidambar L.

Liquidambar sp.

Plate 4, figs 4–6.

Occurence. – C. Nielsen A/S (Fasterholt flora).
Material. – 55 specimens (1007.01; SEM–67, –124,–310).
Description and remarks. – The seeds are irregular in outline, 1.0–1.3 mm long and 0.8–1.1 mm broad and slightly flattened (Pl. 4, figs 4–5). The seed wall is about 0.15 mm thick composed of an outer layer of thin-walled columnar cells with equiaxial and polygonal facets, a middle layer of thin-walled cuboidal cells and an inner membranous layer (Pl. 4, fig. 6). Hilum is marked by an elongated aperture, about 0.2 mm long.

The fossils are very similar to aborted seeds of extant *Liquidambar* both in their irregular shape and in the structure of the seed wall (Pl. 4, fig. 7). The mature seeds differ in being regular in outline with a short distal wing and in having a thinner wall, the outer cells of testa being cuboidal. The lack of mature seeds among the plant fossils may be due to the more delicate nature of the seed wall. Among the larger plant fossils of the Fasterholt flora infructescenses of *Liquidambar* are abundant, and may include two different species, but they remain to be studied in detail. Fossil seeds of *Liquidambar* have not been described from other Eurasian fossil floras.

Platanaceae

Numerous infructescences and male inflorescenses of *Platanus* L. have been recovered from the Fasterholt flora along with many dispersed fruitlets. A single *Platanus* fruiting head was also recovered from the Søby flora.

The family includes a single extant genus, *Platanus,* of large trees with exfoliating bark. The flowers are unisexual borne in compressed heads. The pistillate flowers have five to nine free carpels in two or three whorls. They are surrounded by a number of staminodia and in some species by distinct sepals. The staminate flowers are composed of three to four stamens surrounded by free or fused sepals. The fruitlets are one-seeded, woody nuts with closely spaces trichomes. The seeds are hemi-orthotropous and bitegmic with a very thin seed coat similar in structure to that of *Liquidambar* (Melikian, 1973; Corner, 1976).

Platanus L.

Platanus neptuni (Ettingshausen) Bůžek, Holý & Kvaček.

Plate 4, figs 8–9, Plate 5, figs 1–5.

1867 *Sparganium Neptuni* Ettingsh. – Ettingshausen, p. 107, Pl. 7:9–15.
1967 *Platanus neptuni* (Ettingshausen 1866) comb. nov. – Bůžek, Holý & Kvaček, p. 205, Pl. 2:5–8, Pl. 3:1–9.
1973 *Platanus* sp. – Koch et al., p. 41, Pl.1:12.
1973 *Aracistrobus* sp. – Koch et al., p. 41, Pl. 2:21.

Occurence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora).

Material. – About 250 infructescence-axes, a few with fruitlets still attached, 250 dispersed fruitlets, 10 staminate-axes. (1008.01–42; 2008.01–07; SEM–17,–18,–79,–107).

Description and remarks. – The infructescence-axes are elongate ellipsoidal or ovoidal in outline, borne terminally on a thick peduncle (Koch et al., 1973, Pl. 2, fig. 21). Remnants of the flowers form a coarse reticulum on the surface of the axes. The lumina are four to eight sided, about 1.0–2.0 mm in diameter. The receptacle is slightly raised and bears four to eight fruitlets. In a few specimens fruitlets are still attached to the axis, but in the majority of fossils fruitlets are detached leaving more or less distinct scars on the receptacle. Length of axis: 7.0(9.2)12.0 mm; breadth: 3.7(5.8)8.0 mm; 25 specimens were measured. The peduncle is 1.9–4.0 mm wide and up to 15 mm long. There is a distinct joint between the peduncle and fruiting head. The epidermis of the peduncle is strongly cutinized and with distinct striations. It is composed of slightly transversely elongate epidermal cell with closely spaced hair bases. The epidermal cells are about 0.025 mm × 0.010 mm in size with straight and strongly thickened anticlinal walls. The hair bases are almost circular, about 0.025 mm in diameter, usually formed from one heavily cutinized cell.

The fruitlets are one-loculed nuts, narrowly triangular or obovate in outline, apically tapering into a persistent and slightly curved style (Pl. 4, fig. 8). A longitudinal split running from the top of the style to about 1.5 mm below the style base indicates that the carpel was not completely closed. In some cases the fruitlets are split along the ventral margin. Length of fruit without style: 6.0(7.04)8.5 mm; maximum breadth of fruit: 1.3(1.73)2.0 mm; breadth at style base: 0.6(0.72)0.9 mm; 10 specimens were measured.

The locule occupies the lower two thirds of the fruitlet. It is lined by a layer of transversely elongate sclereids and the outer wall of the fruitlet is composed of narrow, longitudinally aligned sclereids with finely pitted walls. The fruit wall above the apex of the locule is formed from thin-walled and isodiametric cells. A number of vascular bundles run from the base to the style. In the lower part of the fruitlets the bundles occur in the outer sclereid layer, while in the upper part they are bent inwards. The outer epidermis is about 0.015 mm thick composed of thin-walled, tabular cells with closely spaces hair bases (Pl. 5, fig. 9). The epidermal cells are equiaxial or longitudinally elongate, 0.020–0.120 mm long, arranged in distinct longitudinal rows. The anticlinal walls are straight and finely pitted. The hair bases are simple and composed of one to four slightly enlarged cells with thickened walls (Pl. 5, fig. 9). There are about 5 hair bases per 0.1 mm^2. The hairs are usually broken near the base leaving a circular scar about 0.015 mm in diameter.

There is a single seed in each fruitlet, 3.5–4.5 mm long and 0.8–1.0 mm broad. The seeds are hemiorthotropous, pendant, elongate obovate in outline and slightly flattened laterally with a distinct ventral ridge. The chalazal area is rounded and the micropylar area pointed. The seed coat is about 0.05 mm thick and composed of several layers. The outer epidermis is formed from small, equiaxial cells. The underlying layer has narrow, longitudinally elongate and thick-walled cells with slightly undulate anticlinal walls.

The staminate axes are elongate ellipsoidal, 1.5–6.5 mm long and 0.9–3.3 mm wide, and borne on a thick peduncle, 1.4–3.0 mm broad (Pl. 5, fig. 1). Its epidermal structure is similar to that of the fruiting axes. The inflorescences are abraded and no anthers have been observed attached to the axes. Remnants of flowers show in the center five to eight small protrusions, probably representing reduced carpels (Pl. 5, figs 2–3). They are surrounded by six to seven elongate scars, which probably represent the stamens. These are surrounded by numerous membranes which appear to be the remains of perianth parts. Pollen grains occur abundantly on the inflorescenses (Pl. 5, figs 4–5). They are prolate and tricolpate with short, broad colpi. Length of pollen about 20 um; equatorial diameter about 15 um. The pollen grains are semitectate and perreticulate, the muri being about 0.8 um wide and lumina 0.4–1.2 um in diameter. The surface of the colpi has irregularly spaced granae (Pl. 5, fig. 5).

The fossil material was compared to reproductive organs of modern *Platanus occidentalis* L., *P. orientalis* L., *P. racemosa* Nutt., and *P.* x *hybrida* Brot. There is considerable agreement in general structure, but the fossils differ from the extant species in the more elongate fruiting axes and the much thicker peduncle. The epidermal cells of the peduncle are longitudinally elongate in modern species, while transverse in the fossils, and the internal sclereids of the fruitlets are longitudinally aligned in modern *Platanus* and transverse in the fossils.

The fossil material from the Fasterholt area is closely related to the fossil species *Platanus neptuni* in having elongated fruiting axes borne terminally on a thick peduncle with transversely elongate epidermal cells and thick cuticle with distinct striations.

Platanus neptuni was originally described by Ettingshausen (1867) as *Sparganium neptuni* based on fruiting heads from the Tertiary of North Bohemia. It was later referred to the genus *Platanus* by Bůžek, Holý & Kvaček (1967), who included infructescenses, staminate heads as well as leaves in a single species, linking the three different organs together by similarity in epidermal structure. The leaves have pinnate venation, which only occur in one modern species, *P. kerrii* Gagnepai. The fossil leaves differ, however, from this species in epidermal structure, and Kvaček (1970) concluded that *P. neptuni* is distinct from extant *P. kerrii*.

Leaves and reproductive organs of *P. neptuni* have been reported from many Tertiary floras of Central Europe ranging in age from Middle Oligocene to Middle Miocene (Bůžek et al., 1967, 1976; Mai, 1963; Kvaček, 1970; Walther, 1974; Mai & Walther, 1978).

Urticales

Two families of the Urticales, the Ulmaceae and the Moraceae, have been recorded from the Miocene strata of Denmark. The Moraceae is represented by leaves of *Ficus* L. described by Mathiesen (1975) from the lignitic clay of Moselund. The Ulmaceae is represented in the Fasterholt flora by a few fruits of *Planera* Gmelin and several anthers with pollen grains similar to those of *Ulmus*. Leaves of *Ulmus* L. were described from the Søby flora by Christensen (1976).

The anthers containing the ulmaceous pollen grains are about 6.5 mm long and 5.5 mm wide opening by longitudinal slits. The pollen grains are stephanoporate, oblate and plano-convex with an equatorial diameter ranging from 19–23 um. The equatorial amb is circular. The grains are heteropolar and tectate, coarsely rugulate on the convex face and granulate on the concave face (Pl. 5, figs 6–7). This type of pollen is very common in the Tertiary strata of Europe, and generally assigned to the form genus *Polyporopollenites* Pflug. The fossils were compared to extant *Ulmus glabra* Huds., *U. laevis* Pall., and *U. minor* Miller. They differ from these modern species mainly in the smaller size of the anthers and pollen grains.

Betulales

Betulaceae

Fossil fruits, fruiting cones, bract scales, anthers, and leaves of the Betulaceae occur frequently in the Tertiary floras of Denmark. The Fasterholt flora contains numerous small fruits and bract scales assigned to the form genus *Tubela* Dorofeev, as well as fruiting cones and anthers related to extant *Alnus* Miller. In some of the anthers the pollen grains have five pores, while others contain pollen grains with four pores (Pl. 4, figs 8–9). Leaves and fruiting cones of *Alnus* were described from the fossil flora of Moselund (Mathiesen, 1975) and from the Søby flora, and leaves assigned to *Betula* L. were recovered from the Moselund flora (Mathiesen, 1975).

The flowers of extant Betulaceae are unisexual borne singly or in groups of two or three in catkins. The flowers are subtended by bracts, which in the tribe Coryleae *(Carpinus* L., *Corylus* L., *Ostrya* Scop., and *Ostryopsis* Decne.) are leaf-like and fused to form an involucre partly, or fully, enclosing the fruit. In the tribe Betuleae (*Alnus* and *Betula)* the bracts are woody and fused to form a three-lobed *(Betula)* or five-lobed *(Alnus)* bract scale (Abbe, 1974). Each fruit usually contains a single suspended, anatropous and unitegmic seed with a membranous and vascularized seed coat (Corner, 1976).

Three fossil genera of the Betulaceae have been described on the basis of fruits and bracts. *Corylocarpinus* Straus (1969) and *Palaeocarpinus* Crane (1981) are both related to the Coryleae, while *Tubela* Dorofeev (in Takhtajan, 1982) belongs to the Betuleae.

The genus *Tubela* was established to accommodate fossil fruits combining characters of modern *Betula* and *Alnus* (including *Duschenkia* Opiz). The fruits are cordate to elliptical in outline with a coriaceous pericarp forming narrow lateral wings. In general morphology they closely resemble fruits of extant *Alnus,* but differ in the internal structure of the fruit wall. According to Dorofeev (in Takhtajan, 1982) the species of *Tubela* may be grouped into three sections: *Tubela, Alnaria,* and *Itelmenia* which are linked by a few transitional forms. The species included in the section *Tubela* are closely related to the East Asian *Betula schmidtii* Regel and a few other East Asian species of *Betula,* which have broad fruits with narrow, coriaceous wings and thick bracts with three indistinct lobes. They are unlike most other extant *Betula* which have narrow fruits with membranous wings and distinctly tri-lobed bracts. Species included in the section *Alnaria* are most comparable to extant *Alnus.* The species of the section *Itelmenia* combine characters of modern *Alnus* and *Betula.* Bracts associated with the fruits of the section *Alnaria* and *Itelmenia* have not so far been recovered (Dorofeev, in Takhtajan, 1982). Although some of the fossil species may actually belong to *Alnus* or *Betula,* the establishment of the fossil genus *Tubela* seems justified by the presence of transitional forms within the group and by the difficulty in distinguishing fruits of extant *Alnus* from those of a few Asian species of *Betula.*

Tubela Dorofeev

Tubela cf. *baltica* (Dorofeev) Dorofeev
Plate 5, figs 10–11, plate 6, figs 1–3.
1973 *Alnus* sp. – Koch et al., Pl. 1:14.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 57.0–57.5 m.

Material. – About 1200 fruits and fragments of fruits, 25 bract scales (1009.01–11; 1010.01–04; 2009.01; SEM–68,–316).

Description and remarks. – The fruit is a winged nut, irregularly elliptic to circular in outline, and dorsiventrally flattened (Pl. 6, figs 1–2). The abaxial face is slightly convex and the adaxial face concave. Remnants of the two styles are usually present at the apex of the fruit (Pl. 6, fig. 3). There is a basal, sub-circular to angular attachment scar, about 0.1 mm in diameter. The lateral wings are thick and narrow. Length of fruit without styles: 1.0(1.5)2.0 mm; breadth: 1.0(1.34)1.65 mm; 40 specimens were measured. The fruit wall is formed from equiaxial or slightly elongated sclereids. The outer epidermal cells are cuboidal with equiaxial or slightly elongated facets, aligned in indistinct longitudinal rows. The cuticle is about 0.01 mm thick, and the surface darkbrown and shiny.

The locule is narrowly elliptic, 0.8–1.0 mm broad, often marked on the fruit by two longitudinal furrows (Pl. 6, fig. 1). In some fruits two small, anatropous ovules have been observed. The seeds are usually crushed.

One fruit attached to a bract has been observed, but the bract is abraded and yields no information of the lobes. Other bracts from the Fasterholt flora with lobes preserved, but with no fruits attached, are probably referable to the same species. They are fan-shaped and three-lobed (Pl. 5, figs 10–11), 1.8 (2.36)3.0 mm long, 2.1(2.82)3.3 mm broad near the apex, and 0.8(1.27)1.5 mm broad near the base; 15 specimens were measured. The median lobe is rather broad, about 0.8–1.5 mm, the margins being covered by the lateral lobes at the adaxial side (Pl. 5, fig. 11). The abaxial side of the bract is bulging with a strongly wrinkled surface (Pl. 5, fig. 10).

The features of the fossil fruits and bracts from the Fasterholt flora are clearly those of the genus *Tubela* section *Tubela*. They are most similar to *Tubela baltica* both in structure of fruits and bracts, but they differ in being slightly smaller. The species was first described by Dorofeev (1967c) as *Betula baltica* and was later transferred to the fossil genus *Tubela* (Dorofeev, in Takhtajan, 1982). The species of the section *Tubela* are very similar in general appearance, but the fruits of *T. baltica* may be distinguished by their more angular shape and their convexity on only one surface.

Myricales

Myricaceae

Fossil Myricaceae are abundantly represented in the Miocene strata of Denmark by endocarps and leaves of *Myrica* L. and *Comptonia* L'Héritier ex Ait. Endocarps of *Myrica* and *Comptonia* constitute more than half of the fossil specimens in the Damgaard flora and about one fifth of all smaller fossils in the Fasterholt flora. In the Søby flora leaves of *Comptonia* are a conspicuous element (Christensen, 1975). From the Silkeborg area leaves of *Myrica* were described by Mathiesen (1975), and several endocarps of *Myrica* were described by Hartz (1909) as *Carpolithes johnstrupii*.

The flowers of extant Myricaceae are small, simple, generally unisexual and borne in catkins. The fruits are small drupes with a very thick endocarp. They are one-loculed with no secondary locular partitions, and dehisce into two equal valves. The exocarp of some *Myrica* species, e.g. *M. cerifera* L., carries waxy emergences (Elias, 1971). Each fruit has a single erect and orthotropous seed. The seed wall is thin, membranous and formed from a single integument with about 9 postchalazal vascular bundles reaching almost to the micropyle (Corner, 1976).

Myrica L.

Myrica johnstrupii (Hartz) Friis nov. comb.
Plate 6, fig. 4.

1909 *Carpolithes Johnstrupii* m – Hartz, p. 58, Pl. 3:11a–c.

Emended diagnosis. – Endocarp bivalved, unilocular, subcircular to ovate in outline with rounded base and rounded or slightly acuminate apex. Margins not flattened. Locule ovoid, tapering apically into a short stylar canal, rounded at the base with non-protruding placenta. Endocarp wall thick. Thickness of endocarp wall in the plane of dehiscence varies from 0.25–0.4 mm near the base to 0.4–0.6 mm near the apex. Outer surface of endocarp almost smooth. Locule surface with small indictinct cells. Length of endocarp: 1.5(2.0)2.7 mm; breadth: 1.5(2.12)2.6 mm.
Lectotype. – Pl. 6, fig. 4 (Hartz, 1909, Pl. 3, fig. 11 a–c).
Type locality. – Sønderskov near Silkeborg, Jutland, Denmark.
Type stratum. – Micaceous gyttja clay, underlying lignitic bed.
Age. – Probably Miocene.
Occurence. – Sønderskov near Silkeborg.
Material. – About 40 specimens.
Remarks. – The following characterization was given by Hartz (1909) for the fossil species *Carpolithes johnstrupii:* "Under this name I bring together a group of small black, carbonized, bivalved spherical or elongated-pointed carpolithes with thick testa, all of which have in common that their inner cavity is pear-shaped, lighter-coloured and prolonged upwards into a quite thin canal, which seems to reach right through the testa of the carpolithe; they are common in the lignites".

The assignment of these fruits to the genus *Myrica* was first recognized by Kirchheimer (1937, 1938a), who placed some of the specimens in the fossil species *M. suppanii* Kirchheimer (1938b), while the remaining endocarps were tentatively referred to the fossil *M. wiesaensis* Kirchheimer (1938b).

Reexamination of *Carpolithes johnstrupii* supports Kirchheimer's view that more than one species is present in the original material described by Hartz (1909). The original material included a number of endocarps from the Tertiary strata of Sønderskov near Silkeborg together with reworked endocarps extracted from Pleistocene deposits. All the specimens from Sønderskov and a few of the reworked specimens may be accommodated in the reestablished fossil species *Myrica johnstrupii*. The remaining reworked endocarps are referable to the fossil species *M. wiesaensis*. A few unlabled specimens are related to endocarps from the Fasterholt flora described as *Myrica* sp.

The endocarps of *M. johnstrupii* closely resemble those of *M. suppanii,* but they differ in their smaller size and the non-protruding placenta.

The fossils described by Nikitin (1957) from the Pliocene of the Voronezh region as *Aracites johnstrupii* (Hartz) Nikitin and later by Dorofeev (1963a) as *Aracispermum johnstrupii* (Hartz) Nikitin differ from *Myrica johnstrupii* in their general structure, and are probably seeds.

Endocarps of *M. johnstrupii* have so far not been recovered from the Fasterholt area.

Myrica wiesaensis Kirchheimer
Plate 6, figs 5–6.

1938b *Myrica wiesaensis* nov. spec. – Kirchheimer, p. 328, Pl. 4:1–2.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 120 endocarps (1012.01–03; 2012.01–12; SEM–98).
Description and remarks. – The endocarps are ovate to elliptical in outline with acute apex and base (Pl. 6, figs 5–6). They are bisymmetric and formed from two equal valves. Dehiscense is along a marginal suture in the plane of symmetry. The endocarps are usually slightly compressed at the margins and near the apex. The locule is guttiform and the placenta does not protrude into the locule (Pl. 6, fig. 5). Length of endocarp: 2.4(3.24)4.1 mm; breadth: 2.0(2.34)3.3 mm; 53 specimens were measured.

The endocarp wall is 0.25–0.4 mm thick in the plane of dehiscence, thickest near the middle of the endocarp wall and thinner towards the base and apex. A few specimens have a much thicker wall varying from 0.4–0.7 mm. The outer surface of the endocarp is smooth or slightly rugose. The surface of locule shows small equiaxial or slightly elongate cells, arranged in longitudinal rows.

The fossil endocarps are clearly assignable to *Myrica wiesaensis* described by Kirchheimer (1938b) from Wiesa in Oberlausitz. They are distinguished from most other fossil *Myrica* by their fusiform shape, the flattened margins and the non-protruding placenta. Mai & Walther (1978) included the species in *M. boveyana* (Heer) Chandler (1957) stating that there is a gradual change from the typical *M. wiesaensis*-type to the *M. boveyana*-type. However, the Danish material has been compared to endocarps of *M. boveyana* described by Chandler (1957, 1961a, 1963a) from the Lower and Upper Headon Beds and from the Bovey Tracey Beds (specimens V. 33865–68, V. 42102–03, V. 43831–33) and they show considerable differences, the English endocarps being larger with a much thicker endocarp wall.

Endocarps of *Myrica wiesaensis* have been recorded from the Miocene of the Lausitz region, occurring in the floral zones IV, VI, VIII, X–XI (Kirchheimer, 1938b; Mai, 1967).

Myrica stoppii Kirchheimer

1942a *Myrica stoppii* n. sp. – Kirchheimer, p. 430, fig. 8.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 7 endocarps.
Remarks. – These very characteristic, large and rugose endocarps of *M. stoppii* were identified by Dr. J. Gregor, Stuttgart, from among the larger fossils of the Fasterholt flora. The species was previously recorded from the Middle Miocene floras of Wiesa in Oberlausitz (Kirchheimer, 1942a; Mai, 1964), Oder and Brüchelholz in Oberpfalz (Gregor, 1975, 1978a) and from the Upper Miocene flora of Rittsteig at Passau (Gregor, 1978a).

The endocarps of *M. stoppii* are closely related to those of the extant *M. rubra* (Lour.)Sieb. & Zucc. of eastern Asia considered to be a primitive member of the Myricaceae (Kirchheimer, 1957; Takhtajan, 1969).

Myrica kirchheimeri Friis sp. nov.
Plate 6, figs 14–15.

Derivation of name. – In honour of Professor F. Kirchheimer.
Specific diagnosis. – Endocarp bivalved, unilocular, elongate ovoid, with rounded base and acuminate apex. Margins not flattened. Locule elongate guttiform, tapering apically into a short stylar canal, rounded at the base with slightly protruding placenta. Endocarp wall thick. Thickness of endocarp wall in the plane of dehiscence varies from 0.25–0.5 mm near the base to 0.5–0.9 near the apex. Outer surface of endocarp almost smooth, locule surface showing small equiaxial cells with undulating cell walls, aligned in indistinct longitudinal rows. Length of endocarp: 3.7(4.29)4.9 mm; breadth: 2.1(2.65)3.3 mm.
Holotype. – Pl. 6, fig. 14 (2012.13).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 25 specimens (2012.13–16; SEM-98).
Remarks. – In general appearance the fossil endocarps are most similar to those of extant *M. californica* Cham., but they may be distinguished from the modern endocarps by their larger size.

Among the fossil endocarps of *Myrica* described from the Tertiary of Europe, those of *M. altenburgensis* Kirchheimer (1938b) show some similarity with the Danish endocarps, but differ in their broader shape and in being distinctly flattened.

Myrica sp.
Plate 6, figs 7–13.

1979 *Myrica* cf. *ceriferiformis* Kownas – Friis, p. 127, fig. 8A.
1979 *Myrica* cf. *minima* Negru – Friis, p. 128, fig. 8B.
1979 *Myrica* cf. *suppanii* Kirchheimer – Friis, p. 128, figs 8C–D.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora). Lavsbjerg Øst: 54.5–55.0 m. Fasterholt Plt.: 33.5–34.0 m; 69.0–69.5 m.

Material. – More than 2500 endocarps (1012.04–35; 2012.17–50; 3012.01–11; SEM–50).

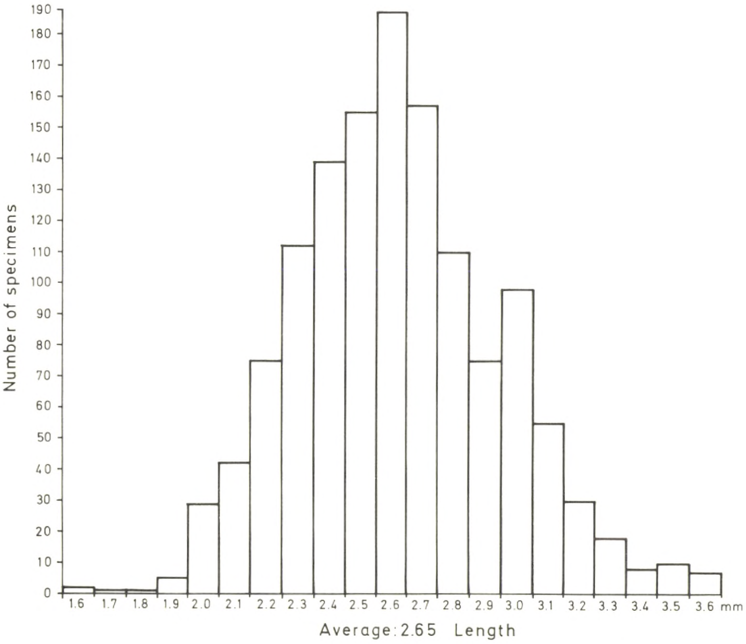


Fig. 5. Size distribution of fossil *Myrica* sp. from the Fasterholt flora (length).

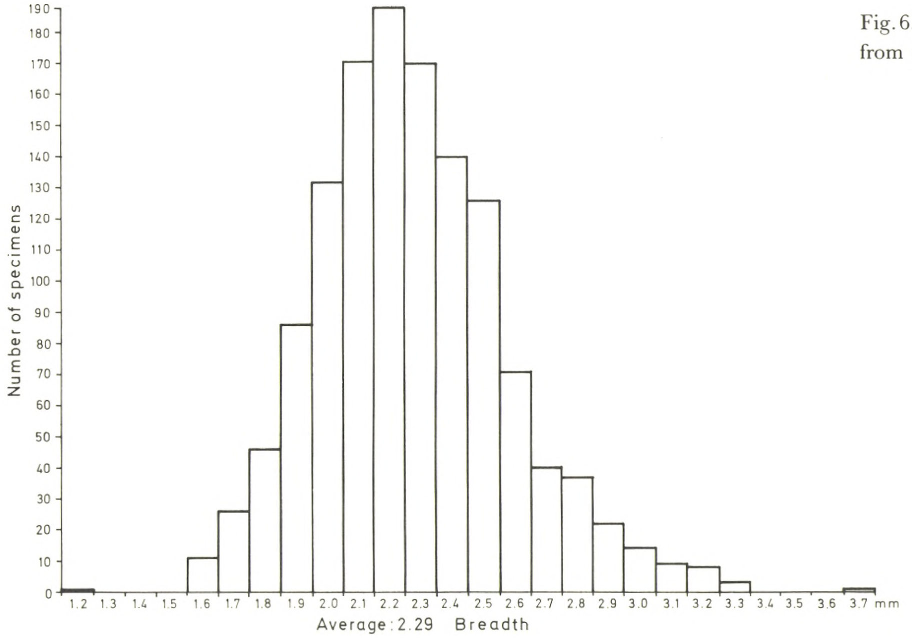
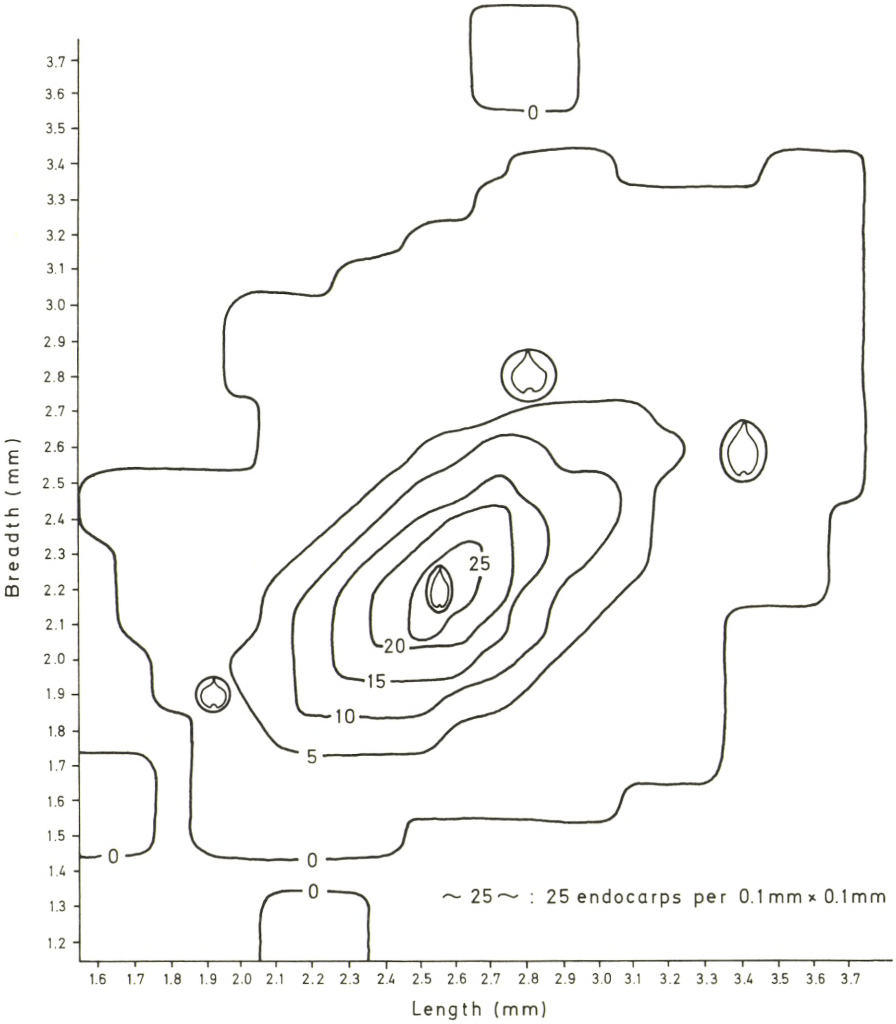


Fig. 6. Size distribution of fossil *Myrica* sp. from the Fasterholt flora (breadth).

Fig. 7. Size distributed of fossil *Myrica* sp. from the Fasterholt flora represented on the basis of average values.



Description and remarks. – The endocarps described here show a considerable variation in size and shape, varying from fusiform to almost circular in outline with rounded or acuminate apex and base. The margins of the endocarps are not flattened. The placenta is raised, and protrudes into the locule, which varies in shape from elongate guttiform to a broad inverted heart-shape (Pl. 6, figs 8–13). Length of endocarp: 1.6(2.65)3.6 mm; breadth: 1.4(2.29)3.7 mm; about 1300 specimens were measured (Figs 5–7).

The endocarp wall is formed from isodiametric sclereids with undulate and strongly thickened cell walls. In the plane of dehiscence the wall is generally thinner (0.15–0.4 mm) near the base of the endocap, and thickens towards the apex (0.2–0.7 mm). The exocarp is preserved in a few specimens. It consists of a thin inner parenchyma layer and an outer layer of warty emergences (Pl. 6, fig. 7).

Several fossil species of *Myrica* with non-flattened endocarp margins and a raised placenta have been described from Tertiary strata of Europe. Within the Danish material endocarps similar to *M. suppanii* Kirchheimer (1938b), *M. ceriferiformis* Kownas (1955), and *Myrica minima* Negru (in Dorofeev & Negru, 1970) are present. These species are primarily distinguished by their size and shape. Measurements of more than 1300 endocarps from the Fasterholt flora show, however, that transitions between the different forms are gradual in every respect (Figs 5–7) and differentiation into more than one species is not possible for the Danish material.

The fossil endocarps are closely related to those of extant *M. cerifera* L. and *M. pensylvanica* Loisel. which both occur in peat bogs and swamps of eastern North America. The endocarps of these two modern species are variable in size and shape and difficult to distinguish.

Comptonia L'Héritier ex Ait.

Comptonia srodoniowae Friis

1974 *Comptonia longistyla* (Nikitin) Dorofeev – Friis, p. 265 figs 1g–i.

1979 *Comptonia srodoniowae* sp. nov. – Friis, p. 124, figs 6A–L.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora). Fasterholt Plt.: 67.0–67.5 m; 69.0–69.5m.
Material. – 145 endocarps and fragments of endocarps. (1011.01–09; 2011.01–02; 3011.01–34; SEM-98).
Remarks. – A discussion of the species was given together with the description of the fossils of the Damgaard flora (Friis, 1979).

Juglandales
Juglandaceae

Numerous endocarps of *Pterocarya* Kunth and *Cyclocarya* Iljinskaya have been recovered among the larger fossils of the Fasterholt flora (Koch et al., 1973). A single poorly preserved endocarp of *Pterocarya* was also extracted from the Damgaard flora (Friis, 1979). Leaves assigned to the genus *Juglans* L. occur commonly in the Søby flora (Christensen, 1976).

Polygonales
Polygonaceae

This family is represented in the Tertiary deposits of Denmark by a few fruits of *Rumex* L. recovered from the Fasterholt flora.

The fruits of the Polygonaceae are small one-seeded nuts, generally triangular in outline, more rarely two-sided, and often surrounded by enlarged, persistent sepals. The seeds are orthotropous and basal. The seed wall is membranous and formed from one or two integuments (Corner, 1976). The outer epidermis of the fruit wall in *Rumex* and *Polygonum* L. is formed from cuboidal or columnar sclereids with strongly thickened and often undulate walls. In *Polygonum* the facets of the sclereids are often equiaxial, while in *Rumex* they are elongated (Marek, 1954).

Rumex L.

Rumex sp.

Plate 7, figs 1–3.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 17 fruits (1046.01; SEM-26,-67,-312).
Description and remarks. – The nuts are fusiform in outline and triangular in transection with sharp edges and slightly concave faces. The apex and base are pointed (Pl. 7, fig. 1). Length: 0.83(0.9)0.97 mm; breadth: 0.27(0.34)0.39 mm; 10 specimens were measured. The surface is light brown and shiny. The fruit wall is 0.013 mm thick, apparently comprised of two layers of cells. The cells of the outer layer have strongly undulate anticlinal walls. On the angles they are longitudinally elongated, while on the sides they are transversely elongated (Pl. 7, figs 2–3).

In wall structure and general morphology the fossil fruits are closely similar to those of extant *Rumex*, but they differ from most modern species in their smaller size and the thinner cell walls of the outer epidermis. Small fruits with cell structure comparable to that of the fossils have been observed in extant *R. maritimus* L. and *R. ucrainicus* Fisch.

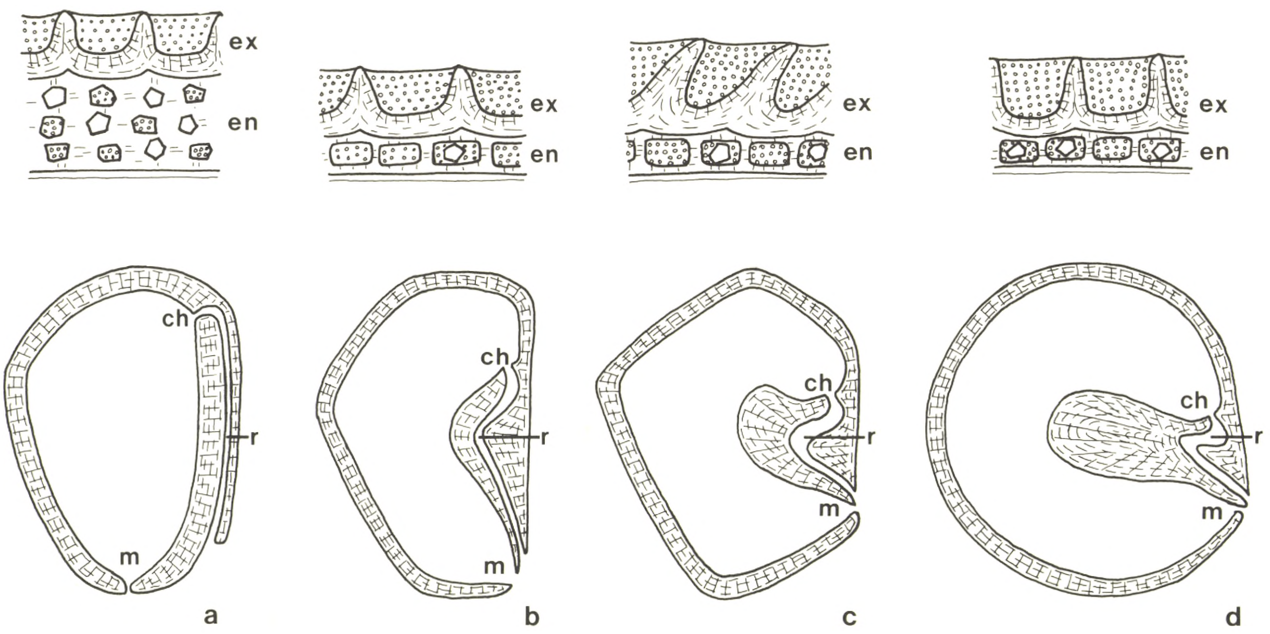


Fig. 8. Schematical sections of seeds of extant *Freziera* (a), *Adinandra* (b), *Eurya* (c), and *Cleyera* (d). ch = chalaza, en = endotesta, ex = exotesta, m = micropyle, r = raphe.

Fossil fruits of *Rumex* have been observed from several younger Tertiary floras of Europe and Asia, and are most abundant in the Pliocene floras (E.M. Reid, 1920c; Szafer, 1954; Nikitin, 1957). They are all distinguished from the Fasterholt fossil fruits by their larger size.

Theales

Theaceae

The Theaceae are represented in the fossil floras of the Fasterholt area by seeds of *Eurya* Thunberg recovered from the Fasterholt and Damgaard floras and from the Lavsbjerg Øst borehole, and a few seeds of *Visnea* L. fil. from the Damgaard flora. Seeds probably assignable to *Ternstroemia* Mutis ex L. fil. also occur among the larger fossils of the Fasterholt flora, but they still remain to be studied.

The fruits of extant Theaceae are three- to five-loculed capsules, berries or achenes. The seeds are anatropous or more commonly campylotropous. They are bitegmic and testal. The outer epidermis of testa is composed of cuboidal or columnar cells with strongly pitted and often strongly thickened inner walls. The mesotesta is formed from one to several layers of more or less isodiametric sclerotic crystal cells. Tegmen is unspecialized and membranous (Corner, 1976). Seeds of 20 extant species of *Eurya* have been studied. They are all slightly campylotropous, or more rarely anatropous. The cells of outer epidermis of the testa usually have a funnel-shaped cell lumina with strongly thickened inner walls. There is usually one or two layers of crystal cells with rather thin cell walls (Fig. 8c; Pl. 7, figs 10–12). The seeds of the related genera *Adinandra* W. Jack, *Cleyera* Thunberg, and *Freziera* Willd. have many features in common with those of *Eurya*, but may be distinguished by the structure of the seed wall. The seeds of *Adinandra* (7 species studied) are slightly campylotropous. The outer cells of testa are not funnel-shaped, the cell walls being of equal thickness. There is one to several layers of crystal cells often with thick cell walls (Fig. 8b). In *Freziera* (8 species studied) the seeds are usually anatropous or slightly campylotropous. The cells of outer testa are not funnel-shaped, the cell walls being of equal thickness. There are several layers of crystal cells, the cell walls being strongly thickened (Fig. 8a). The seeds of *Cleyera* are strongly campylotropous, and usually larger than those of the other three genera. The cells of outer testa are not funnel-shaped, the cell walls being of equal thickness. There is usually one layer of crystal cells (Fig. 8d).

Eurya Thunberg

Eurya stigmosa (Ludwig) Mai

Plate 7, figs 4–9.

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

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

1979 *Eurya stigmosa* (Ludwig) Mai – Friis, p. 130, fig. 8E.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Lavsbjerg Øst: 22.5–23.0 m.

Material. – 16 seeds and 18 fragments of seeds (1013.01–02; 3013.01–02; SEM–38,–313).

Description and remarks. – The seeds are campylotropous, laterally flattened and angular to almost circular in outline (Pl. 7, figs 4–7). They split into two equal valves revealing a horseshoe-shaped embryo cavity which curves around the condyle. The chalazal and micropylar limb are almost equal in size (Pl. 7, fig. 7). The raphe is internal, slightly curved, and marked by a hollow space in the condyle. The seeds are 0.9–2.0 mm long and 0.9–1.9 mm broad.

The seed wall is 0.05–0.15 mm thick composed of a thick sclerotic testa and a thin membranous tegmen. The outer epidermis of the testa is formed from columnar cells with strongly thickened and finely pitted inner periclinal and anticlinal walls (Pl. 7, figs 8–9). They are 0.05–0.12 mm high and 0.05–0.1 mm wide with polygonal facets arranged in about 9 rows around the condyle. Cells overlying the condyle are generally smaller and more elongate than the other cells. The lumen of the cells gradually narrow towards the base to form the characteristic funnel-shaped cavities on the seed surface (Pl. 7, fig. 8). The inner layer of the testa is formed from one to few layers of isodiametric sclereids. The tegmen is thin and rarely preserved.

The features of the fossil seeds indicate a close relationship with extant members of the genus *Eurya,* and in the shape of the seeds, shape of embryo cavity, and position of raphe and hilar scar they are most closely related to modern *E. chinensis* R. Br.

The genus is now distributed in Asia and Central America, and was first recognized in the fossil record by Dorofeev (in Kolakowsky, 1958). Several fossil species of *Eurya* have been described from fossil floras of Europe, the oldest reliable record being from the late Cretaceous (Knobloch & Mai, 1983). The fossil seeds from Denmark are similar to those of the fossil species *E. stigmosa* known in several fossil floras of Europe ranging from the Paleocene to Miocene (Mai, 1960, 1964, 1970b, 1971; Bůžek & Holý, 1964; Łańcucka-Środoniowa, 1966; Palamarev, 1971; Gregor, 1975, 1978a; Collinson, 1978a).

Hypericaceae

This family is represented in the Tertiary strata of Denmark by seeds of *Hypericum* L. recovered from the Fasterholt and Søby floras and from the two boreholes. They have been attributed to two new fossil species of the genus. Another group of small seeds similar to the fossil species *Hypericum tertiaerum* Nikitin and *H. septestum* Nikitin ex Dorofeev have been recovered from the Fasterholt and Søby floras and from the two boreholes. They are very similar to seeds of extant *Hypericum* in size and shape, but differ in the internal structure of the seed wall and therefore should not be assigned to this genus. As no other comparable genus has been recognized so far, the fossils have been placed in the form genus *Carpolithes* Brogniart (see p. 90).

The seeds of extant members of the Hypericaceae are anatropous, bitegmic and exotegmic with the mechanical layer in the outer epidermis of tegmen. The outer epidermal cells of testa are enlarged with slightly thickened anticlinal walls that form a distinct reticulum on the seed surface. The exotegmen is formed from columnar cells with thickened and finely pitted walls and with stellate-undulate anticlinal walls (Corner, 1976).

Hypericum L.

Hypericum holyi Friis sp. nov.
Plate 8, figs 1–7.

Derivation of name. – In honour of the palaeobotanist Dr. F. Holý.
Specific diagnosis. – Seeds anatropous and bitegmic, elongate ellipsoidal with straight or slightly curved axis and a mucronate apex and base. Raphe inconspicuous. Testa formed from transversely elongate cells which are thickened laterally. Tegmen composed of an inner layer of small, thin cells and an outer layer of cuboidal cells with thickened and strongly pitted walls and stellate-undulate anticlinal walls. The cell margins are raised and form a distinct reticulum with 16–20 longitudinal ridges on the tegmen surface. Length of seed: 0.96(1.07)1.23 mm; breadth: 0.35(0.47)0.55 mm.
Holotype. – Pl. 8, fig. 1 (SEM-121).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurence. – C. Nielsen A/S (Fasterholt flora).
Material. – 50 seeds (1047.01–02; SEM– 69,–121,–313).
Description and remarks. – The seeds are elongate, ellipsoidal with mucronate apex and base and it may be difficult to distinguish the micropylar and chalazal ends (Pl. 8, figs 1–3). The raphe is marked on the testa by a thin vascular strand running from base to apex. The testa is 0.03–0.05 mm thick and composed of an outer black layer of transversely elongate cells. The lateral walls are enlarged and form 16–20 distinct longitudinal ridges (Pl. 8, fig. 5). The testa is usually abraded exposing the inner brownish layer of tegmen which is formed from cuboidal cells with thickened, strongly pitted walls and stellately undulate facets (Pl. 8, figs 4, 6–7). The surface of tegmen is characterized by about 16 irregular longitudinal ridges connected by transverse ridges to form a reticulum.

The structure of the seed wall indicates a close relationship with seeds of extant *Hypericum.* Among the 30 modern species studied, those of *H. scabrum* L. from West Asia seem to be most similar to the fossils, but they differ in having less distinct longitudinal ridges and thinner walls of the testal cells.

Fossil seeds assigned to *Hypericum* have been recorded from several Eurasian Tertiary floras, most of them from the Pliocene. However, many of these show only superficially similarities with seeds of modern *Hypericum.* Thus the seeds described by Nikitin (1957, 1965) and Dorofeev (1959a, 1960a, 1963a, 1966a, 1968a, 1969b) as *Hypericum coriaceum* Nikitin and *H.*e.gr. *coriaceum* Nikitin are related to modern *Ludwigia* of the Onagraceae and the seeds of the two species *H. tertiaerum* Nikitin and *H. septestum* Nikitin ex Dorofeev are also distinguished from modern *Hypericum* by their internal structure. The seeds of the fossil *H. bornensis* Mai (in Mai & Walther, 1978) described from the Oligocene of GDR are very similar to the Danish fossils, but they differ in their smaller size.

Hypericum danicum Friis sp. nov.
Plate 8, figs 8–13.

Derivation of name. – From Denmark.
Specific diagnosis. – Seeds anatropous, bitegmic, broadly ellipsoidal, straight or slightly curved and with mucronate apex and base. Raphe inconspicuous. Testa formed from transversely elongate cells. Tegmen composed of an inner layer of small, thin cells and an outer layer of cuboidal cells with thickened and strongly pitted walls and stellate-undulate anticlinal walls. The cell margins are raised and form a distinct reticulum with 14 nodose

longitudinal ridges on the tegmen surface. Length of seed: 0.45(0.50)0.59 mm; breadth: 0.29 (0.33)0.40 mm.

Holotype. – Pl. 8, fig. 8 (SEM–122).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 55.5–57.5 m; 62.0–62.5 m. Fasterholt Plt.: 73.5–74.0 m; 81.0–81.5 m.

Material. – 85 seeds (1048.01; SEM–69,–122,–312).

Description and remarks. – The seeds are broadly ellipsoidal in outline and straight or slightly curved (Pl. 8, figs 8–9). The seed coat is black or dark brown, 0.025 mm thick. Remnants of testa are preserved in only a few specimens. The tegmen is formed from an outer layer of cuboidal sclereids with thickened and strongly pitted walls, the facets being stellately undulate (Pl. 8, figs 10–13). The tegmen surface is sculptured with about 14 longitudinal nodose ridges connected by transverse ridges to form a reticulum.

The fossil seeds are distinguished from those of *H. holyi* in their smaller size, the broader shape and in having less distinct longitudinal ridges. They are closely related to *H. bornense* Mai (in Mai & Walther, 1978), but differ in their smaller size (dimensions of *H. bornense*: 0.7 mm × 0.5 mm; number of longitudinal ridges: 8–12).

Violales

Flacourtiaceae

Fossil seeds of *Poliothyrsis* D. Oliver. (Flacourtiaceae) have been extracted from the Fasterholt and Søby floras and from Lavsbjerg Øst borehole.

The seeds of extant members of this family exhibit a great variety of forms being anatropous or orthotropous, bitegmic, arillate and alate, or exarillate. In the *Flacourtia* group the seeds have a fibrous exotegmen, while in the *Hydnocarpus* group tegmen is undifferentiated (Corner, 1976).

Poliothyrsis D. Oliver.

Poliothyrsis eurorimosa Mai

Plate 9, figs 1–4.

1980 *Poliothyrsis eurorimosa* sp. nov. – Mai, p. 289, Abb. 112, figs 1–8.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 88.0–88.5 m.

Material. – 23 seeds (1087.01; SEM–71,–312).

Description and remarks. – The seeds are ovoid with rounded base and pointed apex, 1.0–1.5 mm long and 0.7–0.8 mm broad (Pl. 9, figs 1–2). The chalaza is marked by a slight circular protrusion, about 0.4 mm in diameter. The raphe has not been observed. The seed wall is about 0.05 mm thick with three distinct layers; an outer layer of cuboidal cells with polygonal and almost isodiametric facets (Pl. 9, fig. 3), a middle layer of longitudinally elongated sclereids (Pl. 9, fig. 4) and an inner layer of thin-walled cuboidal cells. The seed wall is characterized by longitudinal cracks or ruptures running from apex to the chalazal area (Pl. 9, figs 1–2).

The genus *Poliothyrsis,* now restricted to China, was first recognized in the Tertiary strata of Europe and Asia by Mai (1980). Five fossil species have been described, and are mainly distinguished by the shape of chalaza, structure of surface cells and size of the seeds. The Danish seeds are identical to *P. eurorimosa* described from Upper Oligocene to Middle Miocene strata of Central Europe. This species is also very similar to *P. rimosa* (Nikitin ex Dorofeev) Mai (1980) previously assigned to the genus *Viola* L. (Dorofeev, 1963a; Nikitin, 1965), but differs in the slightly smaller size of the seeds. None of the fossil seeds have the characteristic wing of the extant *Poliothyrsis* preserved.

Ericales

Actinidiaceae

The Actinidiaceae are represented in the fossil floras of Denmark by remains of *Actinidia* Lindl.

recovered from the two boreholes Lavsbjerg Øst and Fasterholt Plantage.

The family includes three extant genera, *Actinidia, Clematoclethra* (Franchet) Maxim., and *Saurauia* Willd., with about 320 species chiefly distributed in tropical and subtropical Asia and America. The family is related to several families of the Dilleniales, Ericales and Theales (Engler, 1964; Takhtajan, 1969; Cronquist, 1981). The fruits are capsules or berries. The seeds are anatropous and unitegmic, arillate or exarillate. The outer epidermis of the tegmen is composed of large cuboid cells with strongly thickened inner walls and hexagonal facets (Corner, 1976).

Actinidia Lindl.

Actinidia sp.

Plate 9, figs 5–6.

1947 *Actinidia polygama* Maxim fossilis – Szafer, p. 106, Pl. 9:15–17.

1947 *Actinidia* sp. – Szafer, p. 107, Pl. 9:18–19.

1954 *Actinidia polygama* Maxim foss. – Szafer, p. 35, Pl. 7:16–17.

Occurrence. – Lavsbjerg Øst: 54.5–57.0 m; 59.0–59.5 m; 64.0–64.5 m. Fasterholt Plt.: 33.0–33.5 m; 35.5–36.5 m; 56.5–57.0 m; 64.0–64.5 m; 65.0–65.5 m; 67.0–68.0 m; 68.5–71.0 m; 73.0–73.5 m.

Material. – 1 seed and numerous fragments of seeds.

Description and remarks. – The seed is anatropous, elongated elliptic, slightly compressed laterally, 2.1 mm long and 1.0 mm broad. The apex is rounded and base slightly pointed at the micropyle. The hilum is adjacent to micropyle, and marked by an elliptical scar, about 0.2 mm long (Pl. 9, fig. 5). The raphe is marked by an inconspicuous crest with smaller cells than elsewhere on the seed surface. The seed wall is 0.05–0.1 mm thick with a single layer of cells. The inner cell walls are strongly thickened and finely pitted, the facets being polygonal and isodiametric (Pl. 9, fig. 6), 0.07–0.1 mm in diameter on the lateral faces of the seed, and about 0,04 mm in diameter on the raphe. The cells are arranged in about 15 irregular longitudinal rows on each side. The inner surface of the seed has a polygonal pattern with slight depressions indicating the position of the anticlinal walls.

The characteristic seed surface in extant *Actinidia* with the strongly thickened inner walls and hexagonal facets (Pl. 9, figs 7–8) permits identifications of even very small seed fragments. The seed structure of the related *Saurauia* is similar, but differs in the presence of thickened protrusions of various length at the junctions of the anticlinal walls (Corner, 1976).

Fossil seeds of *Actinidia* have been reported from several Eurasian fossil floras. In Europe the genus ranges from the late Eocene to the early Quaternary (Chandler, 1963b; Mai, Majewski & Unger, 1963; Tralau, 1963) and in Western Siberia from Oligocene to Miocene (Dorofeev, 1963a). Five fossil species of *Actinidia* have been described. Two fossil species of *Actinidia (A. poolensis, A. crassisperma)* described by Chandler (1926, 1963b) from the Paleocene of southern England were later transferred to the genus *Saurauia* by Mai (1970c). The species of *Actinidia* may be distinguished on the basis of size, shape and number of cell rows. The Danish material cannot be referred to any of the established species. They are similar to fossil seeds described from the younger Tertiary of southern Poland as *Actinidia polygama* Maxim foss. (Szafer, 1947, 1954). The Polish material was subsequently referred by Kirchheimer (1957) to the fossil species *A. faveolata* C. Reid & E.M. Reid (1915). However, seeds of *A. faveolata* from the type locality are larger than the Danish and the Polish material and clearly distinguished by having a larger number of cells rows (20 – 22 × 2) (see also Łáncucka-Środoniowa, 1966).

Clethraceae

The Clethraceae are represented in the Tertiary strata of Denmark by fruits and seeds of *Clethra* recovered from the Fasterholt flora.

The family includes one genus, *Clethra* L., with about 64 extant species of evergreen or deciduous shrubs or trees, with a discontinuous tropical and subtropical distribution. Most species occur in tropical America and Asia; two species occur in temperate North America (Hu, 1960; Sleumer, 1967a).

The fruits of extant *Clethra* are subglobular and trilocular bearing simple hairs either singly or in fascicles. The seeds are irregular with or without serrate winged margins (Pl. 10, figs 6–8). The extant species may be grouped into two sections (Sleumer, 1967a). The section *Clethra* includes 25 species distributed in North America, and Asia. They have irregular angular seeds without marginal wings (Pl. 10, figs 7–8). The seeds of the section *Cuellaria* are flattened with a distinct wing. Two subsections were recognized by Sleumer (1967a), subsection *Cuellaria* including 38 species in Central and South America, and subsection *Pseudocuellaria* comprising a single species, *C. arborea* Ait., from Madeira. The seeds of subsection *Cuellaria* have a distinct wing surrounding the seed body (Pl. 10, fig. 6), while in the seeds of *C. arborea* the wing is most pronounced apically and basally (Pl. 10, fig. 5). According to Hu (1960) *C. arborea* is most closely related to species of the section *Clethra*.

Clethra L.

Clethra cimbrica Friis sp. nov.
Plate 9, figs 9–11, Plate 10, figs 1–4.

Derivation of name. – From the Cimbrian peninsula (Jutland).
Specific diagnosis. – Capsule three-loculed, subglobose and slightly three-lobed, pubescent. Placentation subapical, central and axile, seeds numerous. Style one, arising from a slight cavity in the apex of capsule. Dehiscence loculicidal. Calyx persistent, five-lobed, and longer than capsule, five-nerved at maturity. Seeds anatropous, dorsi-ventrally flattened, irregularly elliptical with a distinct serrate, winged margin, the wing being most pronounced apically and at the base. Seed coat formed from a layer of shallow cells with polygonal facets; outer periclinal walls thin usually not preserved; inner periclinal and anticlinal walls thickened and strongly pitted, forming a distinct reticulum. Marginal cells elongated to form a serrate wing surrounding the seed. Cells of ventral face radiating from chalaza, narrowly elongated and arranged in longitudinal rows in the central part of the seed. Cells of dorsal face polygonal, irregularly arranged. Length of capsule: 2.5–3.1 mm; breadth: 2.5–3.1 mm. Length of seed: 1.0(1.4)1.8 mm; breadth: 0.6(0.9)1.3 mm; 10 specimens were measured.
Holotype. – Pl. 9, figs 9–10, Pl. 10, fig. 1 (1015.01).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 4 fruits and fragments of fruits; many seeds, enclosed in the fruits as well as dispersed (1015.01–03; SEM–28,–46,–83,–306).
Description and remarks. – The fruit is a three-loculed, subglobular capsule with loculicidal dehiscence (Pl. 9, figs 9–10). The style preserved in a presumed immature fruit is slender, about 0.9 mm long and triangular in cross-section arising from a slight cavity in the apex of the calyx. The stigma is not preserved. The placentation is subapical and axile, the position of placenta being marked with a small elongate scar near the apex of the fruit (Pl. 9, fig. 10).

The fruit wall is about 0.1 mm thick, formed from an outer layer of small isodiametric cells and an inner layer of elongated sclereids diverging from the placenta. The outer surface of the fruit has remnants of simple, stiff hairs, about 0.03 mm wide. They are usually abraded and the total length is unknown.

The fruit bears a persistent, coriaceous calyx of five imbricate sepals. In the mature fruits the calyx-lobes show five distinct vascular bundles, the median more prominent than the lateral.

The seeds are anatropous, dorsi-ventrally flattened, elliptical or irregular in outline with a serrate and winged margin (Pl. 10, figs 1–4). The seed wall is composed of an outer layer of shallow cells forming a coarse reticulum. On the dorsal face of the seed the cells are isodiametric, about 0.1–0.15 mm in diameter, and irregularly arranged. Ventrally the cells diverge from chalaza, which is marked on the seed as a plug of minute cells or a short slit, about 0.1 mm long. The outer periclinal walls are thin and membranous, rarely preserved. The inner periclinal and the anticlinal walls are strongly pitted, the apertures of the pits being about 0.01 mm in diameter (Pl. 9, fig. 11). The marginal cells are usually elongated, 0.1–0.3 mm long, and form a serrate wing.

The features of the fossils clearly indicate a relationship to extant *Clethra*, the greatest similarity being with fruits and seeds of extant *C. arborea* (Pl. 10, fig. 5). In this species the calyx lobes usually have five distinct bundles, while other species studied have one to three bundles. The seeds of *C. arborea* are similar to the fossil in general morphology, but differ in having slightly larger surface cells.

Fossil leaves, fruits and seeds ascribed to the genus *Clethra* have been recorded from several European fossil floras, but according to Sleumer (1967b) there is no certainty whether any of these fossils really belong to the genus. The fossil fruits of *Clethra berendtii* (Goeppert) Caspary (1881) first described as *Carpantholithus berendtii* (Goeppert, 1836; Goeppert & Berendt, 1845) from the Baltic amber have very small calyx-lobes unlike those of extant *Clethra* (Conwentz, 1886) and the species should probably be excluded from this genus. The fossil species *C. hantonensis* Chandler (1963b) was described from the Lower Tertiary of southern England based on a single seed. The seed is irregular in shape with non-serrate margin. The arrangement of the surface cells seems to differ from that observed in extant *Clethra*, and the assignment to this genus is therefore uncertain. The fruits of *Clethracarpum asepalum* Menzel (1913), according to Mai (1971) should be included in the fossil species *Visnea germanicum* Menzel.

Seeds clearly assignable to *Clethra* have been recovered from Miocene deposits of southern Poland (Łańcucka-Środoniowa, personal communication, 1976). They are similar to the North American *C. alnifolia* L., and differ from the Danish seeds in having a non-serrate and unwinged margin. Thus the genus *Clethra* was presented by two different lineages in Europe at least from the Miocene.

Ericaceae

Fossils related to the Ericaceae occur abundantly in the Miocene strata of Denmark and are represented by fruits and seeds assignable to the extant genera *Eubotrys* Nutt., *Lyonia* Nutt., *Zenobia* D. Don, and possibly also *Enkianthus* Lour., and to the fossil genera *Arctostaphyloides* Kirchheimer and *Epacridicarpum* Chandler.

The seeds of extant Ericaceae are generally small and unitegmic with the mechanical layer in the outer epidermis of tegmen. Alate seeds occur in several genera (Corner, 1976; Collinson & Crane, 1978). The fruits are berries, drupes or capsules. Five-loculed, loculicidal capsules comparable to some of the fossil fruits occur in many genera of the subfamily Arbutoideae (e.g. *Andromeda* L., *Cassiope* D. Don, *Chamaedaphne* Moench, *Enkianthus, Epigaea* L., *Eubotrys, Leucothoe* D. Don, *Lyonia, Oxydendrum* DC., *Pieris* D. Don, and *Zenobia)*. Five-loculed capsules are also present in genera of the subfamily Rhododendroideae (e.g. *Kalmia* L., *Ledum* L., *Phyllodoce* Salisb., and *Rhododendron* L.), but they differ from those of the Arbutoideae in having septicidal dehiscence.

The genera of the Arbutoideae show great similarity in fruit morphology, but may be distinguished on the basis of combined fruit and seed characters. The fruits of *Lyonia* differ from those of other genera in having strongly thickened and lignified dorsal margins. The seeds are narrowly oblong with longitudinally elongated outer cells of tegmen (Pl. 11, fig. 7). Oblong ovoid or elliptic capsules occur in *Enkianthus, Oxydendrum,* and some species of *Lyonia,* in other members of the subfamily the capsules are usually subglobose. In *Enkianthus,* ovules are few and the seeds large, wingless (Pl. 12, fig. 15) or alate, while *Oxydendrum* has numerous ovules and small, thread-like seeds. The seeds of *Andromeda* are elliptic in outline, laterally flattened with rounded faces and margins. The surface of the seeds is smooth and shiny and the outer cells of tegmen minute. The seeds of *Chamaedaphne* are irregular ovoid, angular and laterally flattened, almost smooth with delineations of slightly elongated cells forming the outer tegmen. *Epigea* has hirsute capsules with many ovules. The seeds are ovoid, somewhat angular and with indistinct surface cells. The seeds of *Eubotrys* are irregular, angular and laterally flattened, often with straight ventral margin and acute apex (Pl. 12, fig. 11). The cells of outer tegmen are equiaxial with thickened and finely pitted anticlinal walls. The seeds of *Leucothoe* show some diversity in shape, those of the South American species generally being narrowly oblong with elongated surface cells, while those of the North American and some Asian species have irregular and angular seeds, equiaxial surface cells and indistinct marginal wing. The seeds of the Asian species, *L. grayana* Maxim., are oblong, flattened with elongated surface cells and with basal and apical wing. The seeds of *Pieris* are narrowly oblong with acute apex and base. In *Zenobia,* the seeds are irregular ovoid and angular, not flattened (Pl. 12, fig. 7). The outer cells of testa have thickened and finely pitted anticlinal walls and equiaxial facets.

Lyonia Nutt.

Lyonia danica Friis sp. nov.
Plate 12, figs 1–6; Fig. 9.

Derivation of name. – From Denmark.

Diagnosis. – Capsule five-loculed, subglobose and slightly five-lobed. Placentation subapical, central and axile, placentae reniform protruding into the locule. Ovules many. Style one, about 0.5 mm in diameter. Dehiscence loculicidal. Dorsal sutures strongly thickened and lignified. Calyx persistent, five-lobed, lobes short and broadly triangular with rounded apices. The joint between calyx and pedicel is distinct. Seeds anatropous, many in each locule, narrowly oblong, more or less sickle-shaped. Seed coat apparently formed from two layers, the inner layer crushed and outer layer formed from longitudinally elongated cells. The cell walls are thin and finely pitted, anticlinal walls not raised. Length of capsule without calyx: 2.2(2.4)2.8 mm; diameter of capsule: 2.8(3.2)3.6 mm; length of seed: 0.6–0.8; breadth of seed: 0.15–0.25.

Holotype. – Pl. 11, fig. 1 (1017.01).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora).

Material. – 37 fruits, many seeds enclosed in the fruits (1017.01–03; 2017.01–05; SEM–23,–83,–104).

Description and remarks. – The fruit is a five-loculed loculicidal capsule, subglobose and slightly five-lobed in outline (Pl. 11, figs 1–3). The style rounded or five-angled, about 0.5 mm in diameter and arises from a slight cavity in the apex of the capsule. At dehiscence the valves split from the central axis. The placentation is subapical and axile. The placentae are projecting, reniform, about 0.8 mm long and 0.3–0.5 mm broad (Fig. 9).

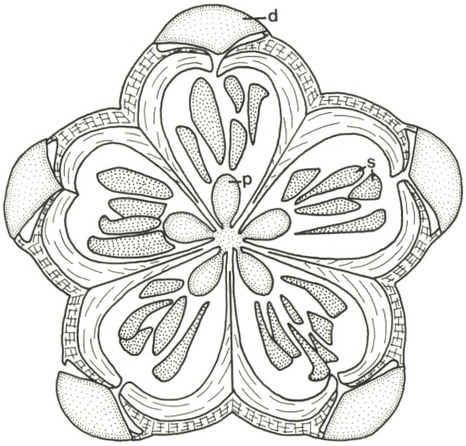


Fig. 9. Fossil *Lyonia danica* Friis sp. nov. Schematical section of fruit.
d = dorsal thickening, p = placenta, s = seed.

The dorsal sutures are strongly thickened forming rounded narrow ridges that usually break off at dehiscence leaving a more or less distinct scar at the margins of the valves (Pl. 11, figs 1–4). The dorsal thickenings are slightly triangular in transection, composed of isodiametric sclereids with thickened and lignified walls with simple pits (Pl. 11, fig. 4).

The fruit wall is about 0.2 mm thick, formed from two distinct layers (Pl. 11, fig. 4). The outer layer is about 0.06 mm thick, dark brown composed of equiaxial cells. The inner layer is about 0.14 mm thick consisting of transversely aligned elongated sclereids dorsally or longitudinally aligned sclereids at the septae. The epidermis is formed from one layer of cuboid cells with equiaxial facets. The external surface of the capsule is lustreless, smooth, sometimes slightly wrinkled.

There is a persistent five-lobed coriaceous calyx (Pl. 11, fig. 3). The calyx-lobes are broadly triangular with rounded apices and wrinkled surface. The length of the sepals is about one third of the total length of the capsule. The joint between calyx and pedicel is distinct.

Each locule contains numerous narrowly oblong seeds (Pl. 11, figs 5–6). The outer layer of tegmen is composed of elongated cells, 0.02 mm × 0.08–0.13 mm, aligned in longitudinal rows. The anticlinal walls are thin and finely pitted.

The presence of dorsal thickenings on the capsule clearly place the fossils in the extant genus *Lyonia*. The genus comprises about 35 extant species of shrubs occurring predominantly in North America and the West Indies but with a few species in East Asia (Gleason, 1968). Features of the capsule and calyx distinguish the different species of the genus, whereas seed characters seem to be of less importance. The fossil fruits closely resemble those of the North American *L. ligustrina* (L.) DC. which have subglobose capsules, about 2.5 mm long and 3.5 mm in diameter, and short, broadly triangular calyx-lobes, about one third the length of the capsule. Other extant species with fruits of similar size and shape can be distinguished from the fossils in having larger sepals.

Fossil fruit of Ericaceae with loculicidal dehiscence have been described from several Tertiary floras in Europe and Asia, and been assigned to the extant genera *Andromeda, Gaultheria, Leucothoe, Oxydendrum,* and *Pieris*. The generic position of many of these fossils is, however, uncertain, due to inadequate information. They all differ from the Danish fruits in the lack of dorsal thickenings and most are also considerably larger. A new fossil species, *Lyonia danica,* has therefore been established to accommodate the Fasterholt fossils. The genus was previously recorded from the Tertiary of Europe on the basis of leaf impression described as *Xolisma* spec. aff. *X. (Andromeda) ferruginea* (Stefanoff & Jordanoff, 1935).

Zenobia D. Don

Zenobia fasterholtensis Friis sp. nov.
Plate 12, figs 1–6.

Derivation of name. – From the village Fasterholt, Denmark.

Specific diagnosis. – Capsule five-loculed, subglobose and slightly five-lobed. Placentation subapical, central and axile, seeds many in each locule. Style one, arising from a deep cavity in the apex of capsule. Dehiscence loculicidal, dorsal sutures not thickened. Calyx persistent with five lobes longer than half the length of capsule. Joint between calyx and pedicel distinct. Seeds anatropous, angular ovoid in outline with flattened ventral face. Hilar scar elongated. Seed coat 0.03 mm thick comprising an outer layer of equiaxial cuboidal cells with polygonal facets and an inner layer of crushed cells. Length of capsule without calyx: 2.2–2.8 mm, diameter: 2.7–3.0 mm. Length of seed: 0.5–1.0 mm; breadth: 0.3–0.6 mm.

Holotype. – Pl. 12, fig. 1 (2018.01)

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora).

Material. – 10 fruits with many seeds, fragments of fruits and a few dispersed seeds (2018.01–02; SEM-81).

Description and remarks. – The fruits are subglobular five-loculed capsules with loculicidal dehiscence (Pl. 12, figs 1–2). The style arises from a deep cavity in the apex of the capsule. The dorsal sutures are not thickened. The placentation is subapical, central and axile, the axis being cone-shaped and five-angular.

The fruit wall is about 0.2 mm thick and composed of an inner brownish layer of elongated sclereids and an outer black layer of isodiametric parenchyma. The outer surface of the fruit is lustreless and wrinkled. The calyx is persistent, coriaceous and five-lobed. The calyx-lobes are not intact in any specimens, but they were certainly longer than half the length of the fruit. The joint between pedicel and calyx is distinct.

Each locule contains many, small anatropous seeds, irregularly ovoid and angular in outline (Pl. 12, figs 3–4). The seed coat is 0.030 mm thick formed from an outer layer of cuboidal cells with thickened and finely pitted anticlinal walls, and an inner membranous layer of crushed cells (Pl. 12, fig. 6). The cells of outer layer have polygonal and isodiametric facets, 0.006–0.025 mm in diameter, arranged in indistinct longitudinal rows (Pl. 12, fig. 5).

The fossil capsules are very similar to those of extant *Andromeda, Chamaedaphne, Eubotrys, Leucothoe, Pieris,* and *Zenobia* and the assignment to the genus *Zenobia* is based mainly on the characteristical seeds enclosed in the capsules. The genus includes one living species, *Z. pulverulenta* (Bartr.) Pollard, a deciduous-leaved shrub occurring in wet woods of the Atlantic Coastal Plain of North America (Gleason & Cronquist, 1963).

The fossil capsules are very similar to those of the fossil *Lyonia danica* in size and shape, but they differ in the lack of dorsal thickenings. The seeds of the two species also differ considerably, those of *L. danica* being oblong with elongated surface cells, while those of *Z. fasterholtensis* are ovoid and angular with equiaxial surface cells.

This is the first record of the genus in Europe. The fossil fruits and seeds of *Zenobia* differ from most other Eurasian fossil Ericaceae mainly in their smaller size. The fruits from Hartau, Merka, and Wiesa recorded by Mai (1960, 1964) as *Leucothoe narbonensis* (Saporta) are similar to the Danish fossils in size, but differ in shape. The seeds enclosed in the fruits are ovoid and seem to be more similar to those of *Pieris* in shape and cell structure. The type material of *Andromeda (Leucothoe) narbonensis* Saporta (1865) includes fruits and leaves from the Aquitanian of Armissian. The fruits are mostly preserved as impressions and little organic material remains. They are distinguished from the Danish fruits in their larger size (3.8–4.0 × 3.5 mm) and their truncate-ovoid shape. (No. 12785, 12801 were studied at the Museum National d'Histoire Naturelle, Paris).

Eubotrys Nutt.

Eubotrys sp.

Plate 12, figs 8–10.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 fruit with many seeds (2016.01; SEM-81).
Description and remarks. – The fruit is a subglobose, five-loculed, loculicidal capsule with style arising from a deep cavity in the apex of the capsule (Pl. 12, fig. 8). The dorsal sutures are not thickened. The placentation is subapical, placentae being angular and projecting with longitudinal ridges. The calyx is not preserved. The fruit is 1.5 mm long and 2.1 mm in diameter. The fruit wall is composed of an outer black layer of parenchyma cells and an inner brownish layer of sclerenchyma cells. The outer surface of the capsule is wrinkled.

There are many seeds in each locule, the seeds being anatropous, laterally flattened, with straight or concave ventral margins and semi-circular dorsal margins. The apex of the seed is acuminate and slightly bent (Pl. 12, figs 9–10). Length of seed: 0.65–0.75 mm; breadth of seed: 0.3–0.4 mm. The seed coat is formed from an outer layer of cuboidal cells with equiaxial facets and thickened and finely pitted anticlinal walls.

The characters of the fossil fruit and seeds are those of extant *Eubotrys,* which includes two species of eastern North American deciduous shrubs. The fossils are most similar to *E. racemosa* (L.) Nutt., which has more or less regular seeds with straight or slightly curved ventral margin (Pl. 12, fig. 11), while the seeds of *E. recurva* (Buckl.) Britt. are more irregular in shape. *E. racemosa* grows in woods and barrens in moist acid soil on the Atlantic Coastal Plain (Gleason & Cronquist, 1963).

Ericaceae?

Enkianthus Lour.

?Enkianthus sp.
Plate 12, figs 12–14.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 fruit with a single seed (2019.01; SEM–55).
Description and remarks. – The fruit is a five-loculed, loculicidal capsule, ellipsoidal in outline and five-lobed in transection (Pl. 12, fig. 12). Placentae have not been observed. The fruit wall is about 0.1 mm thick, formed from an inner layer of elongated sclereids and an outer layer of parenchyma cells. The outer epidermis has been abraded away. The fruit bears a persistent, coriaceous calyx, the calyx-lobes are not preserved. Length of capsule without calyx: 2.7 mm; diameter: 2.0 mm.

A single seed has been observed in the fruit. It is anatropous, ellipsoidal in outline, slightly curved, 1.6 mm long and 0.75 mm broad and pointed at the micropyle (Pl. 12, fig. 13). The outer epidermal cells of the seed coat shows polygonal and isodiametric facets, 0.03–0.06 mm in diameter, the anticlinal walls being thickened and finely pitted (Pl. 12, fig. 14).

The fossil specimen is comparable to extant *Enkianthus* in having ellipsoidal fruits and rather large seeds, but the fossil seed differs from those of most extant *Enkianthus* species in lacking a wing. Unwinged seeds do occur in *Enkianthus subsessilis* (Miq.) Makino (Pl. 12, fig. 15), but they are different from the fossil seed in having much larger and more regularly spaced outer epidermal cells. Together with the poor preservation of calyx and outer fruit wall this makes the assignment of the fossil to the genus *Enkianthus* uncertain.

The fossil fruit and seed differ from other Tertiary Eurasian fossil Ericaceae in size and shape. The genus *Enkianthus* has not been reported from other fossil floras.

Epacridicarpum Chandler
Epacridicarpum chandlerae Friis sp. nov.
Plate 13, figs 1–6.

1979 *Epacridicarpum* sp. – Friis, p. 131.

Derivation of name. – In the honour of the late palaeobotanist, Miss M. E. J. Chandler.
Specific diagnosis. – Fruit subglobose, five-loculed with a short style and five-lobed stigma. Placentation subbasal and axile. Fruit wall comprised of three distinct layers, a thin outer layer of small cuboidal cells with polygonal facets, a middle layer of small isodiametric parenchyma cells and an inner layer of elongated sclereids, 0.1 mm long and 0.005 mm wide, diverging from placenta. Length of fruit: 0.9(1.1)1.5 mm; diameter: 1.1(1.3)1.5 mm.
Holotype. – Pl. 13, fig. 1 (SEM–325).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Lavsbjerg Øst: 22.5–23.0 m; 27.5–28.0 m; 47.0–48.0 m; 50.5–51.0 m; 52.5–53.0 m; 53.5–54.0 m; 54.5–60.5 m; 63.0–63.5 m. Fasterholt Plt.: 32.0–33.0 m; 34.5–35.0 m; 35.5–36.0 m; 64.0–64.5 m.
Material. – More than 3000 fruits and fruitlets (1020.01–07; 3020.01; SEM–29,–103,–325,–326).
Description and remarks. – The fruit is a subglobose, five-loculed drupe (or capsule) which split easily

along the septa, and sometimes also along the dorsal sutures (Pl. 13, figs 1–4). It is subtended by a five-lobed, hypogynous calyx, preserved only in a few specimens (Pl. 13, fig. 1). One specimen has remnants of a five-lobed stigma (Pl. 13, fig. 2). The exocarp is thin, black, and rarely preserved. It is composed of small cuboidal cells with polygonal facets and aligned in longitudinal rows. The mesocarp is brownish, up to 0.2 mm thick, formed from small thin-walled isodiametric cells, about 0.040 mm in diameter (Pl. 13, figs 4–5). The endocarp is black, about 0.06 mm thick composed of elongated sclereids, 0.1 mm long and 0.005 mm wide, diverging from the placentae (Pl. 13, figs 1, 6). No seeds have been observed in the fruits.

The features of the fossil fruits are clearly those of the genus *Epacridicarpum* Chandler (1960) established to accomodate fossil fruits of uncertain generic position, but probably related to the Epacridaceae (Ericales). The investigation of the well-preserved Danish fruits indicates that they are probably drupes comparable but much smaller than those of extant *Arctostaphylos* Adans. (Ericaceae). Small drupes resembling the fossil fruits are also present in the genera of the Empetraceae, but they all differ in the number of endocarps and in the structure of the mesocarp. Mai (1976a) suggested a possibly relationship to the Cyrillaceae (Ericales), but none of the studied modern species seems to conform with the fossils. The fruits of *Cliftonia* Banks ex Gaertn. are larger than the fossils and have three wings, and the fruits of *Cyrilla* Garden ex L. are two-celled and have a much thicker mesocarp with considerable variation in cell size.

Three species were established based on fossil fruits from the Lower Tertiary of southern England (Chandler, 1960, 1961a, 1963). The Danish fruits are most similar to those of *E. mudense* Chandler (1960) and *E. headonense* Chandler (1961a), but in the English material the alignment of the sclereids at the surface of locule is more undulate and generally more distinct than in the Danish fruits, and the fruit wall is slightly thicker. The fruits of *E. colwellense* Chandler (1963a) are more angular in outline than other species of *Epacridicarpum*. They may represent abraded forms of *E. mudense* or *E. headonense*.

Fossil fruits of *Epacridicarpum* have also been recorded from the Middle Eocene flora of Geiseltal, GDR (Mai, 1976a), and from Middle Oligocene strata of the Weisselster-Becken, GDR (Mai & Walther, 1978). Fossil fruits from the Miocene of the Gdow Bay, southern Poland, assigned by Łańcucka-Środoniowa (1966) to *Epacridicarpum* cf. *mudense* should be attributed according to more recent studies to the fossil genus *Arctostaphyloides* (Łańcucka-Środoniowa, personal communication, 1978).

Arctostaphyloides Kirchheimer

Arctostaphyloides globula (Menzel) Kirchheimer

1906 *Elaeocarpus globulus* sp. nov. – Menzel, p. 142, Pl. 7:5–12.
1909 *Elaeocarpus globulus* Menzel – Hartz, p. 124, Pl. 5:2–5.
1936a *Arctostaphyloides globula* (Menzel) – Kirchheimer, p. 117, Pl. 12:12a–g.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 fruit (1021.02).
Remarks. – The fossil genus *Arctostaphyloides* was established by Kirchheimer (1936a) to accommodate fossil fruits of unknown generic position related to extant *Arctostaphylos* Adans. The fruits of *Arctostaphyloides globula* differ from those of *A. menzelii* Kirchheimer (1936a) in their globular shape and larger size.

Arctostaphyloides menzelii Kirchheimer

1913 *Elaeocarpus globulus* Menzel – Menzel, p. 47, Pl. 5:1–3.
1936a *Arctostaphyloides menzelii* n. sp. – Kirchheimer, p. 117, Pl. 12:13a–e.
1979 *Arctostaphyloides menzelii* Kirchheimer – Friis, p. 130, fig. 8b.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora).

Material. – 6 fruits and 18 fragments of fruits. (1021.01; 3021.01–05).
Remarks. – The fruits of *Arctostaphyloides menzelii* from the Damgaard flora were described previously (Friis, 1979). A few additional fruits have also been recovered from the Fasterholt flora.

Empetraceae

Empetrum L.
Empetrum sp.

Occurrence. – Damgaard S (Damgaard flora).
Material. – 1 endocarp (3022.01).
Remarks. – Only a single specimen of *Empetrum* has been recorded from the Tertiary deposits of Denmark. It was briefly described together with the other fossils of the Damgaard flora (Friis, 1979).

Ebenales

Three families of the Ebenales, the Styracaceae, the Symplocaceae, and the Ebenaceae, are represented in the Danish Tertiary floras. The Symplocaceae are chiefly represented by numerous endocarps of *Symplocos* Jacquin, among the larger fossils of the Fasterholt flora and by few specimens assigned to the fossil genus *Sphenotheca* Kirchheimer (Koch et al., 1973). Endocarps of *Halesia* Ellis ex L. (Styracaceae) have been recorded from the Søby and Damgaard floras (Christensen, 1978; Friis, 1979), and few calyces of *Diospyros* L. (Ebenaceae) were found in the Søby flora (Christensen, 1978).

Primulales
Primulaceae

A few seeds and fragments of seeds of *Lysimachia* (Primulaceae) have been extracted from the Fasterholt and Søby floras and from the Lavsbjerg Øst borehole.

The family comprises mainly herbaceous species. The fruits are unilocular capsules formed from five carpels. The seeds are anatropous and bitegmic or in some genera campylotropous and unitegmic. The outer epidermal cells of the testa are often large and projecting with thickened walls. The inner epidermis of the tegmen may be formed from a layer of crystal cells (e.g. *Lysimachia* L.) or crystal may be absent (e.g. *Androsace* L.) (Corner, 1976).

Lysimachia L.
Lysimachia sp.
Plate 13, figs 7–10.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 55.0–55.5 m; 56.0–56.5 m.
Material. – 5 seeds and 4 fragments of seeds (1023.01; SEM–71).
Description and remarks. – The seeds are hemi-anatropous, elliptic or slightly angular in outline (Pl. 13, figs 7–8), 1.1–1.4 mm long and 0.8–1.1 mm broad. The hilum is marked by a narrow, elongated scar on the ventral crest. The seed wall is about 0.065 mm thick. The outer layer is formed from light brown strongly projecting columnar cells with irregularly thickened cell walls (Pl. 13, figs 9–10). The inner layer is black, shiny and formed of one layer of cuboidal crystal cells with strongly thickened anticlinal and inner periclinal walls. Each cell has an imprint of a single crystal (Pl. 13, fig. 9).

The seed characters are clearly those of the Primulaceae and the fossils are particularly similar to extant *Lysimachia vulgaris* L. (Pl. 13, fig. 11) which have large projecting outer testal cells and crystal cells with strongly thickened cell walls and a single crystal. The seeds of *L. vulgaris* differ, however, in their more angular shape.

Fossil seeds of the Primulaceae have been recorded from several other fossil floras in Europe and Asia, the oldest occurrence being from the Oligocene (Chandler, 1957; Dorofeev, 1963a). The seeds of *L. angulata* Dorofeev (1963a) are similar to the Danish seeds in general appearance, but they differ in their larger size and more angular shape. The seeds of *L. boveyana* Chandler (1957) are smaller than the Danish material.

Rosales
Rosaceae

Fossil fruits assignable to the Rosaceae occur abundantly in the Tertiary of the Fasterholt area and include species of *Potentilla* L., *Rubus* L., *Pyracantha* Roemer, and *Prunus* L. in the Fasterholt flora. A few fruits of *Pyracantha* and *Rubus* were also recovered from the Lavsbjerg Øst and Fasterholt Plantage boreholes.

The fruits of the Rosaceae are diverse and form the basis for a subdivision of the family (Engler, 1964). The fruits of the subfamily Spiraeoideae are apocarpous or pseudosyncarpous formed from 1–8 carpels, the fruitlets being dry, and predominantly follicles. In the subfamily Rosoideae the fruits are generally apocarpous formed from many carpels, the fruitlets being drupes or nutlets. The fruits of the Prunoideae are drupes formed from a single carpel. In the Maloideae the fruits are apocarpous or syncarpous formed from 1–5 carpels, usually partly fused with the concave receptacle to form a pome.

The seeds of the Rosaceae are anatropous, unitegmic or bitegmic, the seed coat exhibiting great variation in structure (Corner, 1976).

Potentilla L.

Potentilla pliocenica E.M. Reid

Plate 13, figs 12–13.

1920c *Potentilla pliocenica* sp. nov. – E.M. Reid, p. 127, Pl. 8:31, 33.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 fruitlet (SEM–88).
Description and remarks. – The fruitlet is 0.9 mm long and 0.65 mm broad, laterally flattened with semicircular dorsal margin and a ventral margin which is curved and slightly concave near the apex (Pl. 13, fig. 12). The fruitlet is split along the ventral and dorsal margin. The outer surface is almost smooth with outlines of small, equiaxial sclereids (Pl. 13, fig. 13).

The fruitlet is similar to those of some extant *Potentilla* species. The genus includes about 300 living species of herbs or small shrubs which are widely distributed in temperate regions of the Northern Hemisphere. Fruitlets of *Potentilla* have been described from several younger Tertiary floras of Europa and Western Siberia, the earliest record being from Miocene strata (Dorofeev, 1963a; Mai, 1967). Three fossil species of *Potentilla* have been established based on fruitlets. The specimen from the Fasterholt flora is closely related to *P. pliocenica* E.M. Reid (1920c) described from the Pliocene flora of Castle Eden. This species has been recorded from several other fossil floras of Europe and Asia (E.M. Reid, 1920c; Dorofeev, 1963a; Mai, 1965b, 1967; Palamarev, 1970), and in the Lausitz area the species occurs in floral zones XI and XIII (Mai, 1967). The two other fossil species of *Potentilla, P. proanserina* Nikitin (1965) and *P. tomskiana* Nikitin (1965) described from Western Siberia, are distinct in having surface sculpture of irregular ridges.

Potentilla sp.

Plate 13, fig. 14.

Occurrence. – C. Nielsen A/S (Fasterholt flora)
Material. – 1 fruitlet (SEM-88).
Description and remarks. – The fruitlet is 1.2 mm long and 0.9 mm broad, slightly flattened laterally. The dorsal margin is semi-circular and the ventral margin slightly convex (Pl. 13, fig. 14). The surface is almost smooth with fine outlines of small equiaxial sclereids.

The general morphology and wall structure of the fruitlet is similar to *Potentilla pliocenica,* but differs in its larger size and in being less compressed. The fruitlet has some similarity to extant *Potentilla palustris* (L.) Scop., but is smaller.

Rubus L.

Rubus sp. 1.

Plate 14, figs 1–2, 4–6.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 47.5–48.0 m; 55.0–55.5 m; Fasterholt Plt.: 67.5–68.0 m; 68.5–69.0 m.

Material. – About 550 endocarps and many fragments of endocarps. (1027.01–13; 2027.01; SEM–76,–322).

Description and remarks. – The endocarp is laterally flattened, elliptic or ovate in outline with semicircular dorsal margin forming a sharp keel. The ventral margin is straight or slightly convex (Pl. 14, figs 1–2). The base of endocarp is rounded and the apex slightly acuminate or rounded. Length of endocarp: 1.4(1.73)2.0 mm; breadth: 0.6(1.02)1.3 mm; 105 specimens were measured (Fig. 10). The endocarp is broadest at or below the middle. The outer surface is characterized by anastomosing ridges which form a coarse reticulum (Pl. 14, fig. 4). Lumina are of various shapes and sizes, usually more or less equiaxial with a diameter ranging from 0.1–0.4 mm. Traces of vascular bundles are marked on the top of the ridges by narrow furrows. The endocarp wall is 0.1–0.12 mm thick built of elongated sclereids arranged in two distinct layers. The inner layer is dark brown with transversely aligned sclereids, and the outer layer is light brown with longitudinally aligned sclereids (Pl. 14, figs 5–6). The sclereids have thickened secondary walls with scattered simple pits. They are 0.08–0.16 mm long and 0.004–0.008 mm in diameter. Remains of the exocarp and mesocarp have been observed in a few specimens as a thin shiny layer of thin-walled, equiaxial cells.

The endocarp is one-loculed containing a single pendulous and anatropous seed on a subapical placenta. The seed is elliptic in outline, slightly pointed at the micropylar end and rounded at the chalaza. The raphe is ventral. The seed wall is thin and usually crushed, the outer epidermis being formed from cuboidal cells with isodiametric facets.

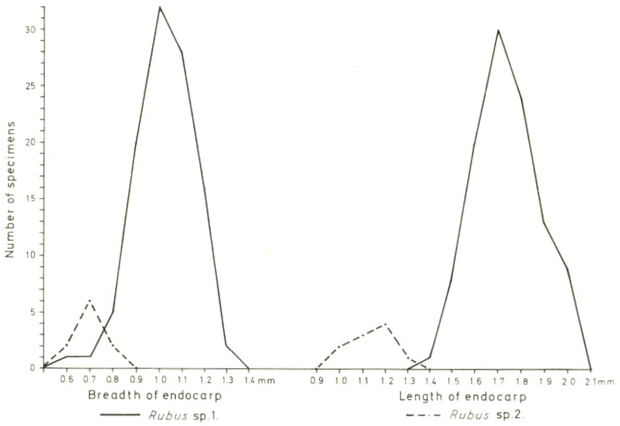


Fig. 10. Size distribution of fossil *Rubus* sp. 1 and *Rubus* sp. 2 from the Fasterholt flora.

The general appearance and wall structure of the fossil fruitlets shows complete agreement with fruitlets of extant *Rubus*. The genus includes a large number of species of shrubs and herbs (2000 apomictic species of the subgenus *Rubus* have been described). They are distributed in most parts of the world, particular in temperate regions (Good, 1964). Some species may be distinguished by the size and shape of endocarp and by the form of the reticulum, while other species have very similar endocarps. Thus, it cannot be excluded that the fossil material comprises more than one species. However, the small size range (Fig. 10) and the uniformity in surface ornamentation suggests that the endocarps were derived from a single species.

Fossil endocarps of *Rubus* are widespread in the Eurasian Tertiary and 12 fossil species have been established (C. Reid & E.M. Reid, 1910; Chandler, 1925; Kirchheimer, 1942a; Dorofeev, 1963a, 1969b, 1970b, 1977b; V. Nikitin, 1976), the earliest record being from the Lower Tertiary of southern England (Chandler, 1925). The specific characters of many of the fossil species are vague, and although the Danish endocarps do not agree completely with any of them, the establishment of a new fossil species cannot currently be justified.

Rubus sp. 2

Plate 14, fig. 3

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 10 endocarps (1028.01; SEM–81).
Description and remarks. – The endocarp is elliptic or ovate in outline and laterally flattened. The ventral margin is distinctly concave near the apex (Pl. 14, fig. 3). Length of endocarp: 1.0(1.15)1.3 mm; breadth: 0.6(0.7)0.8 mm; 10 specimens were measured (Fig. 10). The endocarp wall is comprised of two distinct layers of elongated sclereids perpendicular to each other, the outer surface showing a coarse reticulum of anastomosing ridges.

In general morphology and wall structure the endocarps are similar to those described above (*Rubus* sp. 1), but differ in their smaller size (Fig. 10) and the distinct ventral concavity. There is no gradual change in size from one type to the other suggesting that they represent two different species. The endocarps of *Rubus* sp. 2 differ from those of other fossil *Rubus* in their shape and smaller size.

Pyracantha Roemer

Pyracantha acuticarpa (C. Reid & E.M. Reid) Szafer
Plate 14, figs 7–9.

1915 *Cotoneaster acuticarpa* sp. nov. – C. Reid & E.M. Reid, p. 98, Pl. 9:1–2.
1920b *Crataegus acuticarpa Reid (=Cotoneaster acuticarpa* Reid) – E.M. Reid, p. 125, Pl. 8:23.
1961 *Pyracantha acuticarpa* Reid (= *Cotoneaster acuticarpa* Reid 1915) – Szafer, p. 64, Pl. 16:13.
1920b *Crataegus microcarpa* sp. nov. – E.M. Reid, p. 126, Pl. 8: 26–28.
1920b *Crataegus nodulosa* sp. nov. – E.M. Reid, p. 126, Pl. 8:25.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 56.0–56.5 m. Fasterholt Plt.: 64.0–64.5 m; 65.0–65.5 m; 67.5–68.0 m; 68.5–70.5 m.
Material. – 140 complete fruits and more than 1200 fruitlets (1026.01–28; 2026.01–05; SEM–84,–318).
Description and remarks. – The fruit is subglobular slightly truncate apically and retuse at the stylar area, pseudosyncarpous and formed from five nutlets which are fused basally and free apically. The nutlets are enclosed and partly fused with the concave receptacle (Pl. 14, fig. 7). Length of fruit: 2.5(3.02)3.5 mm; diameter: 2.8(3.23)4.1 mm; 25 specimens were measured. The apical part of the receptacle bears remnants of five coriaceous sepals.

The fruitlet is one-loculed with straight ventral margin and semi-circular dorsal margin. It is slightly pointed at the base and usually retuse at the base of the style. In crosssection the fruitlet is almost triangular with flattened lateral faces and rounded dorsal face. An indistinct longitudinal concavity overlies the dorsal margin. The free parts of the fruitlets are covered by a shiny cuticle constituting about one half to two thirds of the lateral faces (Pl. 14, fig. 8). Length of fruitlet: 2.1(2.58)3.0 mm; breadth: 1.2(1.6)2.0 mm; 25 specimens were measured.

The fruit wall is 0.2–0.5 mm thick, and thickest along the ventral margin. It is composed of equiaxial or slightly elongate sclereids. A conspicuous bundle supplying the ovule enters near the base of ventral face. The placentation is subapical with one seed in each locule. Remnants of an aborted second ovule have been observed in a few specimens.

The seed is anatropous and ascending with a ventral raphe. It is obovoid in outline with slightly concave ventral margin and semi-circular dorsal margin. The seed coat is thin and formed from two layers. The outer epidermis is built of cuboid cells with equiaxial facets (Pl. 14, fig. 9). The inner layer is membranous with indistinct cell structure.

The fossil fruits and nutlets are clearly assignable to the genus *Pyracantha,* which includes about 10 species of evergreen shurbs distributed in temperate and subtropical regions from southeastern Europe to Taiwan, the majority occurring in China (Li, 1963). The greatest similarity is with fruits of extant *Pyracantha coccinea* Roemer, a plant of dry habitats in S. Europe to Caucasus (Good, 1964; Negru, 1972).

The fruits of *Pyracantha* are very similar to those of *Crataegus* L. and *Cotoneaster* Medicus, but differ in a few details. In *Crataegus* the fruits are formed from 1–3 (5) almost completely fused carpels. In *Cotonea-*

ster the fruits are formed from 2–3 (5) almost entirely free carpels. The fruits of *Pyracantha* are formed from 5 partly fused carpels.

Fossil fruits attributed to *Crataegus, Cotoneaster,* and *Pyracantha* have been recorded from many Tertiary floras of Europe and several fossil species have been established, the oldest record being in the Middle Oligocene (Mai & Walther, 1969; Walther, 1980).

The fossil fruits from the Fasterholt area are assignable to the fossil species *Pyracantha acuticarpa.* The fossil fruits of *Crataegus microcarpus* E.M. Reid (1920b) and *C. nodulosa* E.M. Reid (1920b) described from the Pliocene of Castle Eden are similar to those of *P. acuticarpa* in size and shape and should be assigned to the same species. A similar fruitlet was also recorded from the Miocene strata of Moldavia described as *P.* cf. *coccinea* (Negru, 1972).

Fruits of *P. acuticarpa* have been recorded from several European fossil floras ranging from Middle Oligocene to Pliocene (C. Reid & E.M. Reid, 1915; E.M. Reid, 1920b; Szafer, 1961; Mai & Walther, 1969; Gregor, 1975, 1978a; Burgh, 1978; Walther, 1980). It is recorded from the floral zones III–VI, X, XII–XIII (Mai, 1967). Fossil leaves associated with fruits of *P. acuticarpa* were described by Walther (1980) from the Middle Oligocene of GDR as *Pyracantha krauselii.* They were compared to extant *P. coccinea, P. crenulata* (Roxb.) Roemer, and *P. crenato-serrata* (Hance) Rehder, and the fossil leaves and fruits are thought to represent a single species (Walther, 1980).

Nepenthales

Droseraceae

The family is represented in the fossil floras of Denmark by a few seeds of *Aldrovanda* extracted from the Fasterholt flora and fragments of seeds recovered from the Damgaard flora and the Lavsbjerg Øst and Fasterholt Plantage boreholes. Seeds of *Aldrovanda* have also been recorded from the Pleistocene of Denmark as *Hydrocharis morsus-ranae* L. (Hartz, 1909).

The fruits of extant Droseraceae are one-loculed capsules with parietal or central placentation. The seeds are anatropous, bitegmic and exotestal with the mechanical layer in outer epidermis of testa, except possibly for *Drosophyllum* Link. In the seeds of *Aldrovanda* L. the outer epidermis of testa is formed from columnar cells with thickened outer walls and inner epidermis of columnar cells with slightly thickened walls (Corner, 1976).

Aldrovanda L.

Aldrovanda praevesiculosa Kirchheimer
Plate 15, figs 1–3.

1935b *Aldrovanda vesiculosa* L. foss. – Kirchheimer, p. 28, figs 5–7.
1941a *Aldrovanda praevesiculosa* n. sp. – Kirchheimer, p. 309, fig. 1.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Lavsbjerg Øst: 22.5–23.0 m; 24.5–25.0 m; 47.0–47.5 m. Fasterholt Plt.: 68.5–69.5 m.

Material. – 3 seeds and fragments of seeds (1029.01; 3029.01; SEM-88).

Description and remarks. – The seeds are anatropous, and ovoid in outline with a short neck at the micropylar end and a slightly pointed chalaza (Pl. 15, fig. 1). The raphe is marked by a slightly raised longitudinal ridge. The micropylar aperture is circular, about 0.2 mm in diameter. The seed is 1.1–1.3 mm long and 0.8–1.0 mm broad. The seed wall is about 0.15 mm thick. The outer epidermis is black and formed from a layer of columnar sclereids, about 0.05 mm high with polygonal and equiaxial facets, about 0.015 mm in diameter. The outer periclinal and anticlinal walls are strongly thickened, while the inner periclinal walls are very thin (Pl. 15, fig. 2). The inner epidermis of testa is brownish formed from a layer of thin-walled columnar cells, about 0.1 mm high (Pl. 15, fig. 3). The tegmen is thin with indistinct cellular structure. The surface of the seed is black and shiny with indistinct outlines of polygonal facets of the outer palisade layer.

The seed characters are clearly those of *Aldrovan-*

da. The genus includes a single living species, *A. vesiculosa* L., a rootless aquatic herb distributed in shallow waters in tropical and subtropical regions. Eight fossil species have been established based on fossil seeds from Tertiary and Quaternary strata of Europe and Asia, seven of these being restricted to the Tertiary, with the earliest record from Late Eocene strata. Based on seed morphology Dorofeev (1968b) grouped the species of *Aldrovanda* into three sections. Section *Aldrovanda* comprises ellipsoidal, symmetrical seeds *(A. intermedia* E.M. Reid & Chandler, 1926, *A. eleanora* Nikitin, 1957, *A. vesiculosa* L.). Section *Obliqua* includes obovate or ellipsoidal, asymmetric seeds *(A. ovata* (Chandler) E.M. Reid & Chandler, 1926, *A. praevesiculosa, A. sobolevii,* Dorofeev, 1968b, A. *dokturovskyi* Dorofeev, 1963b). The third section, *Clavatae,* comprises relatively small, obovate or claviform seeds (*A. nana* Dorofeev, 1960a, *A. clavata* Dorofeev, 1963a). The distinction between some of the fossil species is, however, problematic and based primarily on variation in size. The evolutionary lineages proposed by Dorofeev (1968b) for the genus are therefore questionable.

The fossil seeds from Denmark are assignable to *A. praevesiculosa* described from the Miocene of Senftenberg, GFR (Kirchheimer, 1941a). They are also very similar to the seeds of *A. nana* and *A. sobolevii* described from the Tertiary of USSR (Dorofeev, 1960a, 1968b) and the specific distinction between these species is unclear.

Fossil seeds of *A. praevesiculosa* have been recovered from a few European Miocene floras (Kirchheimer, 1941a; Nötzold, 1961; Mai, 1967; Raniecka-Bobrowska, 1959) and from a single Pliocene flora (Palamarev, 1970). It occurs in the floral zones IV, VI, VIII, and XI. The seeds described by Nötzold (1963) as *A. praevesiculosa* should be attributed to the fossil species *Carpolithes nitidus* Nikitin ex Dorofeev (1963a).

Myrtales

Lythraceae

The Myrtales are represented in the fossil floras of Denmark by numerous seeds referred to the Lythraceae, Onagraceae, and Myrtaceae, and a few fruits referred to Trapa L. (Trapaceae). The fossil seeds of *Carpolithes natans* Nikitin show features occuring in modern Myrtales (see p. 88), and should probably be referred to that order. They are particularly similar to the seeds of modern *Sonneratia* L. fil. (Sonneratiaceae).

The fossil Lythraceae of the Danish Miocene floras include three species referable to the extant *Decodon* Gmelin, and three species referable to the fossil *Microdiptera* Chandler and *Mneme* Eyde.

The seeds of extant Lythraceae are small and anatropous, often angular, obpyramidal. They are bitegmic and exotegmic with a fibrous tegmen and in some genera with a crystalliferous endotesta. In some genera the mesotesta is expanded laterally or over the raphe to form a thick wing (Corner, 1976). A distinct germination valve has been observed in *Decodon,* and is apparently present in other genera as well. Four fossil genera related to the Lythraceae have been described on the basis of fossil seeds. *Alatospermum* Chandler (1962), *Microdiptera,* and *Mneme* all include small, slightly flattened seeds with a narrow germination valve on the antiraphe-side, and usually with thick lateral wings. In *Alatospermum* the germination valve extends over the whole length of the seed body, while in *Microdiptera* and *Mneme* it occupies only the lower half or two thirds of the length. The cells of the germination valve are minute in *Mneme* and arranged in about 20 longitudinal rows, while in *Microdiptera* they are large and distinct, arranged in about 10 longitudinal rows. The seeds of *Palaeolythrum* Chandler (1960) have a marginal wing, but no germination valve. Four further fossil genera *(Cranmeria, Minsterocarpum, Pachyspermum,* and *Tamesicarpum)* possibly related to the Lythraceae were described from the Eocene of southern England based mainly on fossil fruits (E.M. Reid & Chandler, 1933), and one genus, *Enigmocarpon* Sahni (in Sahni & Rode, 1937), was described from the Lower Tertiary of India.

Decodon Gmelin

Decodon gibbosus (E.M. Reid) E.M. Reid
Plate 15, figs 4–9.

1920b *Diclidocarya gibbosa* n. sp. – E.M. Reid, p. 32, Pl. 4:23,25.

1929 *Decodon gibbosus* E.M. Reid – E.M. Reid, in Nikitin, p. 37, Pl. 589:9.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora).
Material. – 120 seeds and many fragments (1030.01–08; 2030.01–03; 3030.01; SEM-91).
Description and remarks. – The seeds are irregular obpyramidal, usually with rounded corners. The ventral face is obtriangular, straight or slightly concave, occupied almost entirely by the germination valve. The dorsal face is convex and rounded and the lateral faces straight or slightly convex (Pl. 15, figs 4–6). The micropyle is a small circular aperture at the base of the germination valve. The hilar scar is circular, 0.2–0.5 mm in diameter, placed close to the micropyle. Length of seed: 0.8(1.11) 1.5 mm; breadth (dorsi-ventrally): 0.9(1.09)1.5 mm; breadth (laterally): 0.6(0.83)1.2 mm; 20 specimens were measured.

The embryo cavity is obovate and occupies one third to two thirds of the seed (Pl. 15, fig. 6). The raphe is internal and dorsally embedded in the thick mesotestal tissue. Five distinct tissues of the seed coat have been observed. The outer epidermis is heavily cutinized, formed from one layer of shallow lignified cells with isodiametric facets. The mesotesta is strongly developed dorsally and consists of polyhedral and isodiametric cells, about 0.02 mm in diameter, with slightly thickened and finely pitted walls (Pl. 15, figs 6–7). The endotesta is formed from cuboidal to columnar sclereids infilled with spongy lignifications and with imprints of angular crystals (Pl. 15, fig. 8). The exotegmen is formed from narrow, elongate fibres with strongly lignified walls (Pl. 15, fig. 9). The inner epidermis of tegmen is thin with indistinct cell structure.

The fossil seeds are similar to those of modern *Decodon* (Pl. 15, figs 10–12), but are smaller and have a thicker dorsal tissue. The genus includes one living species, *D. verticillatus* (L.)Ell., an aquatic shurb restricted to eastern North America.

Fossil seeds of *Decodon* occur abundantly in Eurasian Tertiary floras and about 13 fossil species have been described. The genus first appeared in the Eocene and had its maximum distribution in the Miocene. It disappeared from Europe in the Lower Quaternary (Mai et al., 1963; Dorofeev, 1977c; Tiffney, 1981). The Danish seeds are identical to those of the fossil *D. gibbosus*. They differ from other fossil species of *Decodon* mainly in their thick dorsal tissue. The species was first ascribed to the fossil genus *Diclidocarya* E.M. Reid (1920a) and later reassigned to the extant genus *Decodon* (E.M. Reid, in Nikitin, 1929). *D. gibbosus* ranges from the Eocene to Pliocene and is especially abundant in Oligocene and Miocene strata of Europe and Asia (Dorofeev, 1977c).

Decodon vectensis Chandler
Plate 16, figs 1–3.

1963a *Decodon vectensis* n. sp. – Chandler, p. 37, Pl. 30:86–90; Pl. 31:91–98.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 55.5–57.5 m; 58.0–58.5 m. Fasterholt Plt.: 35.5–36.0 m; 56.5–57.0 m; 64.0–64.5 m; 65.5–66.0 m; 69.0–69.5 m.
Material. – 29 seeds (1030.09–12; SEM–91,–333).
Description and remarks. – The general structure of the fossil seeds resembles that of *D. gibbosus,* but *D. vectensis* is more regular in shape with angular, and often protruding corners and rather thin dorsal mesotestal tissue (Pl. 16, figs 1–3). At the apex of the germination valve there are one to three narrow ridges. The surface of the valve shows imprints of angular crystals. Length of seed: 0.9(1.29)1.4 mm; breadth (dorsi-ventrally): 0.6(0.77)0.9 mm; breadth (laterally): 0.7(0.93)1.2 mm; 10 specimens were measured.

The fossil seeds are identical to those of *D. vectensis* described from the Eocene of Colwell Bay. Two other fossil species of *Decodon* with more or less straight edges and distinct corners were described by Dorofeev (1977c) from the Tertiary of the USSR.

The seeds of *D. tavdensis* are smaller and narrower, while the seeds of *D. antiquus* are very similar to *D. vectensis* and should possibly be included in this species. According to Dorofeev *D. antiquus* differs from *D. vectensis* in its broader shape, but broad specimens also occur among the original material from southern England (e.g. V.43879).

Decodon vectensis has also been recorded from Oligocene and Miocene deposits of Germany in the floral zones I–IV, VII, X–XIII (Mai, 1967).

Decodon sp.
Plate 16, fig. 4.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 14 seeds (1030.12–13; SEM–91,–333).
Description and remarks. – The seeds are similar in general structure to those of *D. gibbosus* and *D. vectensis,* but are smaller and with large surface cells on the germination valve. The ventral face is narrowly obtriangular (Pl. 16, fig. 4) and the lateral faces straight. The dorsal tissue is poorly developed and the embryo cavity occupies about three quarters of the seed. The germination valve has rectangular cells aligned in longitudinal rows. Length of seed: 1.1–1.3 mm; breadth of seed (dorsi-ventrally): 0.6–0.8 mm; breadth of seed (laterally): 0.6–0.8 mm.

The fossil seeds resemble those of the fossil *D. tavdensis* Dorofeev (1977c) described from the Oligocene of the Sverdlovsk Region, but they differ from the typical *D. tavdensis* seeds in having more prominent apical corners.

?Lythraceae

Microdiptera Chandler

Microdiptera parva Chandler
Plate 16, figs 5–7, 9–11; Fig. 11a.
1957 *Microdiptera parva* n. sp. – Chandler, p. 107, Pl. 15: 133–149, text-fig. 2.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 56.0–56.5 m.
Material. – 24 seeds (1032.01–02; SEM–93,–333).
Description and remarks. – The seeds are anatropous and bitegmic, irregular, obtriangular or obtrullate in outline and somewhat flattened. The seed cavity is elliptic in outline and flanked by two lateral wings (Pl. 16, figs 5–7, 9). The antiraphe-side is convex with a narrow, elliptic germination valve, which covers the lower half of the seed body. The surface of the germination valve shows large isodiametric cells arranged in about 10 longitudinal rows (Pl. 16, figs 5–6). The raphe-side is almost flat and the seed cavity is flanked by two lateral, longitudinal furrows (Pl. 16, figs 7, 9). Length of seed: 0.9(1.21)1.6 mm; breadth of seed: 0.8(1.03)1.4 mm; 20 specimens were measured.

The seed coat is thick and consists of five distinct layers, apparently representing exo-, meso-, and endotesta, and exo- and endotegmen. The exotesta is thin, formed from one layer of thin cells, which are thin-walled and isodiametric over the germination valve or may be elongate and lignified. The mesotesta consists of equiaxial and polyhedral cells with slightly thickened and finely pitted walls. It is strongly developed laterally to form two thick wings (Pl. 16, figs 9–10; Fig. 11). The endotesta is formed from cuboidal or columnar sclereids with spongy lignifications (Pl. 16, figs 10–11). The lignifications are more dense over the germination valve and the endotestal cells are here apparently crystalliferous. The exotegmen comprises a layer of narrow longitudinal cells with thickened and strongly pitted walls (Pl. 16, fig. 11). The endotegmen is thin, formed from one layer of thin-walled, longitudinal cells.

The fossil seeds are similar to those of the fossil genus *Microdiptera* Chandler (1957) first described from the Lower Tertiary of southern England. The genus was established to accommodate small, winged seeds related to the Lythraceae, but of unknown generic affinity. The Danish seeds have been compared to a number of extant genera of the Lythraceae. They are in general structure very similar to seeds of modern *Pemphis* J.R. & J.G.A. Forst., which

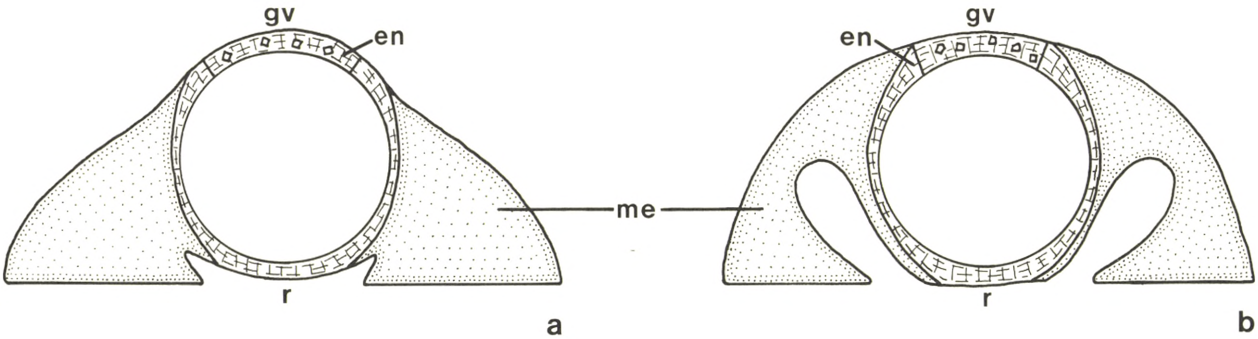


Fig. 11. Schematical sections of fossil *Microdiptera* (a) and *Mneme* (b). en = endotesta, me = mesotesta, r = raphe.

includes two species of tropical shrubs or small trees distributed from Africa and Madagascar to the Pacific. Like the fossil seeds, those of *Pemphis* have lateral wings formed from the expanded mesotestal tissue (Pl. 16, figs 12–13) and apparently a narrow germination valve on the antiraphe-side (dorsal side) with large, isodiametric epidermal cells in about 10 longitudinal rows. The cells of endotesta have strongly thickened walls, and are crystalliferous over the germination valve (Pl. 16, fig. 14). The exotegmen is formed from one layer of narrow, longitudinal cells with thickened and strongly pitted walls. The fossil seeds differ, however, from those of *Pemphis* in having elongate, lignified cells of exotesta and spongy lignifications of endotesta. These details may be insignificant, but for the present the fossils have been retained in the fossil genus *Microdiptera*.

Two fossil species of *Microdiptera* were described from the Lower Tertiary of southern England (*M. parva* and *M. major* Chandler, 1963b), one species (*M. donata* (Holý) Tiffney, 1981) from the Miocene of Czechoslovakia, and two species were described from the Oligocene of the USSR (*M. elongata* (Dorofeev) Dorofeev, 1968b, and *M. tavdensis* Dorofeev, 1968b). The fossil seeds described from the Miocene of the Urals as *Mneme uralensis* (Dorofeev) Eyde (1972) resemble those of *Microdiptera* in the structure of the germination valve and should possibly also be referred to this genus.

The Danish seeds are identical to those of *Microdiptera parva* described from the Oligocene Bovey Tracey flora (Chandler, 1957). The species has been recorded from several other European fossil floras (Chandler, 1961a, 1963b; Mai & Walther, 1978; Palamarev, 1971) and occurs in floral zones II–IV, VI and X (Mai, 1967). The species also occurs in the presumed Oligocene Brandon lignite, eastern North America (Tiffney, 1981).

Microdiptera sp.
Plate 16, fig. 8.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora).
Material. – 3 seeds (1032.03; SEM–97).
Description and remarks. – The seeds resemble those of *Microdiptera parva,* but are laterally flattened and without lateral wings (Pl. 16, fig. 8). They are 0.9–1.2 mm long and 0.5–0.8 mm broad.

Mneme Eyde

Mneme menzelii (E.M. Reid) Eyde
Plate 17, figs 1–6; Fig. 11b.

1927 *Diclidocarya Menzelii* sp.nov. – E.M. Reid, p. 3, Pl. 580: 1–7.
1972 *Mneme menzelii* (E.M. Reid) Eyde, comb. nov. – Eyde, p. 114.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 10 seeds (1031.01–02; SEM–93,–97).

Description and remarks. – The seeds are anatropous and bitegmic, sub-circular in outline and slightly compressed. The antiraphe-side is convex with a narrow, elliptic germination valve that occupies one half to two thirds of the length of the seed (Pl. 17, figs 1–2). The surface cells of the valve are small, indistinct and arranged in about 20 longitudinal rows. The seed cavity is flanked by thick lateral wings formed from the expanded mesotesta (Pl. 17, fig. 4; Fig. 11). The raphe-side of the seed is almost flat with two deep grooves along the edges of the seed body (Pl. 17, figs 3–4; Fig. 11). Length of seed: 1.0(1.2)1.7 mm; breadth: 1.1(1.26) 1.4 mm; 7 specimens were measured.

The structure of the seed coat is very similar to that of *Microdiptera parva* with five distinct layers. The outer epidermis is comprised by elongate lignified cells that curve around the germination valve. The epidermal cells of the germination valve are small and thin-walled. The mesotestal cells are isodiametric and polyhedral with thickened and finely pitted walls (Pl. 17, fig. 5). The endotestal cells are well-developed at the antiraphe-side, densely infilled with spongy lignifications and with imprints of crystals. The exotegmen is formed from a layer of narrow, longitudinal cells with thickened and strongly pitted walls (Pl. 17, fig. 6). The cells of endotegmen are thin-walled and longitudinal.

The fossil genus *Mneme* Eyde (1972) is typified by *M. menzelii,* which was previously assigned to the now rejected fossil genus *Diclidocarya* (E.M. Reid, 1920a, 1927; E.M. Reid, in Nikitin, 1929). The seeds of *Mneme* are closely similar to those of *Microdiptera,* but have much smaller surface cells at the germination valve and two deep furrows flanking the seed body at the raphe-side of the seed (Fig. 11). The genus includes three fossil species, *M. menzelii* (E.M. Reid) Eyde (1972), *M. minor* (Chandler)Eyde (1972), and *M. sibirica* (Nikitin ex Dorofeev)Eyde (1972).

The Danish seeds are identical to those of *M. menzelii.* The species is common in the Miocene and Pliocene floras of Europe (E.M. Reid, 1927; Kirchheimer, 1935a; Łańcucka-Środoniowa, 1956; Dorofeev, 1959a, 1967b; Raniecka-Bobrowska, 1959; Mai, 1964; Palamarev, 1970) and in Miocene floras of Asia (Dorofeev, 1963a, 1969b). It was referred by Mai (1967) to the arctotertiary floral element and recorded in the floral zones IV–V, VII, IX–XIII reaching its maximum abundance in zones XI–XII.

Onagraceae

This family is represented in the Miocene floras of Denmark by numerous seeds assignable to the extant genus *Ludwigia* L. extracted from the Fasterholt and Søby floras and from the Lavsbjerg Øst borehole. They are described as two new fossil species of the genus.

The seeds of extant Onagraceae are small, anatropous, bitegmic, and often have a prominent raphe. In some genera the seeds are exotegmic with a fibrous exotegmen while in others they are endotestal with lignified, crystalliferous cells of endotesta and exotegmic fibres. The seeds of *Ludwigia* have characteristic crystalliferous endotestal cells with undulate cell walls, and often with a large central crystal surrounded by several smaller crystals (Corner, 1976; Eyde, 1978). The raphe is usually about one fifth to half as wide as the seed body, but in some species (e.g. in section *Macrocarpon)* it is as wide as the seed body and serves as a float. The seed wall is fused with the fruit wall in some species of *Ludwigia* (Eyde, 1978).

One fossil genus, *Palaeeucharidium* E.M. Reid & Chandler (1933) probably related to the Onagraceae, has been established based on fruits and seeds from the Lower Eocene London Clay flora.

Ludwigia L.

Ludwigia corneri Friis sp. nov.

Plate 18, figs 1–7.

Derivation of name. – In honour of Professor E. J. H. Corner.

Specific diagnosis. – Seeds anatropous, elongate ellipsoid with mucronate micropyle. Raphe-tissue strongly developed, about as wide as the seed body. Seed coat about 0.02 mm thick. Outer epidermis composed of transversely elongate cells arranged in about 14 longitudinal rows; the cell walls are thin and finely pitted. Endotesta consists of one layer of crystal cells with strongly thickened and stellate-undulate anticlinal walls. Exotegmen formed from one layer of narrow, longitudinal cells. Endotegmen consists of slightly elongate, thin-walled cells. Length of seed: 0.7(0.93)1.0 mm; breadth of seed body: 0.3(0.34)0.4 mm; breadth of seed with raphe: 0.42(0.58)0.6 mm; 10 specimens were measured.

Holotype. – Pl. 18, fig. 1 (SEM-339).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 51.5–52.0 m; 56.0–56.5 m.

Material. – About 110 seeds (1043.01–02; SEM–69,–111,–339).

Description and remarks. – The seeds are anatropous with an elongate ellipsoid seed body and a very prominent raphe, which in most specimens has been abraded (Pl. 18, figs 1–3). The seed coat is 0.02 mm thick and comprised of four distinct layers. The outer epidermal cells are shallow, transversely elongate, about 0.05 × 0.017 mm, with thin and finely pitted cell walls (Pl. 18, fig. 5). They are arranged in about 14 longitudinal rows. Over the raphe the epidermal cells are longitudinally elongated and irregularly arranged. The outer epidermis is usually abraded away to reveal the surface of the endotesta. The endotesta is formed from a layer of crystal cells, which have strongly thickened anticlinal and inner periclinal walls. They are almost isodiametric with a diameter of about 0.023 mm, the cell lumen is angular, about 0.009 mm in diameter, with undulate anticlinal walls (Pl. 18, figs 4, 6–7). The endotestal cells are arranged in about 30 longitudinal rows. The outer epidermis of the tegmen comprises a layer of longitudinally aligned fibres with rather large pits. The inner epidermis of the tegmen is formed from a layer of longitudinally elongate cells, about 0.015 × 0.003 mm, with strongly pitted cell walls (Pl. 18, fig. 4).

The fossil seeds are in complete agreement with those of modern *Ludwigia*. The genus includes about 75 species of herbs and small shrubs, widely distributed in aquatic and wetland environments in temperate to tropical regions. Most species are known from tropical America (Raven, 1963). One species, *L. palustris* (L.) Ell., occurs in Europe. Seeds with a large raphe comparable to that of the fossil seeds have been observed in *L. lagunae* (Morong) Hara, *L. suffruticosa* Walt., and *L. longifolia* (DC.) Hara. All other species studied have a less prominent raphe.

Fossil seeds of *Ludwigia* have been described from a few fossil floras of Europe, and one fossil species, *L. krauselii* Mai (in Mai & Walther, 1978), has been established based on seeds from the Oligocene flora of Haselback, GDR. Fossil seeds of *Ludwigia* from the Pliocene flora of Rippersroda in Thuringia were attributed to the extant species *L. palustris* (Mai et al., 1963). The fossil seeds described by Dorofeev from Tertiary floras of Europe and Asia as *Hypericum coriaceum* Nikitin and *H.* e.gr. *coriaceum* Nikitin should probably also be referred to *Ludwigia*, but due to inadequate information on the seed coat structure the assignment of these fossils to *Ludwigia* is uncertain. They differ from the Danish fossils in their smaller size. The Danish seeds resemble those of *L. krauselii* in size and general structure, but they are more narrow and with a smaller number of cell rows in the endotesta. A new fossil species, *L. corneri*, has been established to accommodate the Danish fossils.

Ludwigia collinsoniae Friis sp. nov.
Plate 18, figs 8–13.

Derivation of name. – In honour of the palaeobotanist Dr. M.E. Collinson.

Specific diagnosis. – Seeds anatropous, elongate ovoid, slightly compressed laterally and slightly curved. Raphe distinct, but rather thin. Seed coat 0.01–0.03 mm thick. Outer epidermis of testa composed of transversely elongate cells arranged in about 10 longitudinal rows; the cell walls are thin and finely pitted. Endotesta formed from a layer of crystal cells with strongly thickened and undulate anticlinal walls. Exotegmen formed from narrow, longitudinal fibres. Endotegmen comprised of slightly elongate, thin-walled cells. Length of seed: 0.45(0.48)0.6 mm; breadth: 0.25(0.28)0.3 mm; 25 specimens were measured.

Holotype. – Plate 18, fig. 8 (SEM-340).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora).

Material. – About 75 seeds (1035.01–02; SEM-109,–110,–340).

Description and remarks. – The seeds are small, anatropous and elongate ovoid, slightly curved, with pointed micropyle and chalaza (Pl. 18, figs 8–10). They are slightly compressed laterally and with a thin, distinct raphe (Pl. 18, figs 8–9). The outer epidermis of the testa is formed from narrow, transversely elongate cells, 0.07 × 0.009 mm, with thin and finely pitted walls (Pl. 18, fig. 12). They are arranged in about 10 longitudinal rows. The epidermal cells over the raphe are longitudinal. The endotesta is composed of a layer of crystal cells with undulate and strongly thickened walls and a small angular lumen (Pl. 18, fig. 13). They are arranged in about 30 longitudinal rows. The depth of the endotestal cells vary from about 0.01 mm near the micropyle and chalaza to about 0.03 mm at the middle of the seed (Pl. 18, fig. 11). The exotegmen is formed from narrow, longitudinally elongated cells with strongly thickened and finely pitted walls. The endotegmen is formed from thin-walled, narrow cells.

The fossil seeds are very similar to those of modern *Ludwigia palustris,* which are also small, with a thin raphe, and with variable depth of the endotestal cells, but the fossil seeds are slightly smaller. A similar variation in size of the crystal cells has not been observed in other extant species of *Ludwigia*. The fossil seeds from the Pliocene flora of Rippersroda assigned to *L. palustris* (Mai et al., 1963) are very similar to the Danish fossils, but they apparently have a more prominent raphe. The seeds of *Hypericum coriaceum* Nikitin, *H.* e.gr. *coriaceum* Nikitin, and *Ludwigia krauselii* (see p. 60) are all larger than the Danish seeds, and a new fossil species, *L. collinsoniae*, is therefore established for the Danish fossils. In general structure they resemble those of *L. corneri,* but are smaller, have a less prominent raphe, narrower epidermal cells of testa and more variable depth of the endotestal cells.

Myrtaceae

This family is represented in the Miocene of Denmark by numerous seeds assignable to the extant genus *Myrtus* L. recovered from the Fasterholt flora.

The Myrtaceae is a large family and exhibits a great variety in fruit and seed structure. The seeds are anatropous, hemitropous, or campylotropous, unitegmic or bitegmic with the mechanical layer in the exo-, meso-, or endotesta. The endotestal cells are crystalliferous in some genera. The tegmen is generally unspecialized sometimes with a layer of tannin-cells. The seeds are commonly wingless, but in some genera they are alate. The genera of the subfamily Leptospermoideae have a capsule or nutlike fruit usually with anatropous and endotestal seeds. The seeds of *Eucalyptus* L'Herit. vary greatly from anatropous, hemitropous to campylotropous. In the genera of the subfamily Myrtoideae the fruits are berries or more rarely drupes with anatropous or campylotropous seeds. In the tribe Myrteae the seeds are campylotropous and exotestal (mesotestal) with an endotestal plug at the micropyle (Corner, 1976).

The fossil genus *Myrtospermum* Chandler (1957) was established to include fossil seeds related to extant species of the section Myrtinae. Subsequent studies by Chandler (1960, 1961a, 1964) proved that most of the species referred to *Myrtospermum* actually belonged to the Theaceae. A single species, *M. cooperi* Chandler (1961b) should probably be retained in the Myrtaceae. The fossil genus *Palaeorhodomyrtus* E.M. Reid & Chandler (1933) includes fruits and seeds from the Lower Eocene London Clay flora. It was first compared to modern *Rhodomyrtus* (DC.) Reichenb. (E.M. Reid & Chandler, 1933) and later to the modern *Myrtus* (Quiévreux & Reid, 1937). The fruits were, however, described as five-loculed capsules, and thus differ from the berries of *Rhodomyrtus* and *Myrtus*. Possibly these fossils should also be referred to the Theaceae.

Myrtus L.

Myrtus palaeocommunis Friis sp. nov.
Plate 17, figs 7–12; Fig. 12.

Derivation of name. – From the related extant species, *Myrtus communis* L.
Specific diagnosis. – Seeds campylotropous, bitegmic, slightly compressed laterally and irregularly reniform in outline. Micropyle truncate with a subcircular aperture, 0.5–0.7 mm in diameter, in a few specimens closed by a slightly convex operculum. Chalaza inwardly curved. Basal and central concavity between the limbs with remnants of median septum and raphe. Embryo cavity strongly curved, sub-circular in transection. Seed coat 0.05–0.2 mm thick formed from a thick testa of one to several layers of slightly elongate sclerenchyma cells, and a thin tegmen of small, narrow elongate cells arranged parallel to the curvature of the seed. Seed surface smooth and shiny. Length of seed: 1.4(2.45)2.7 mm; breadth: 1.8(2.59)3.3 mm; thickness: 0.7(1.17)1.8 mm.
Holotype. – Pl. 17, fig. 7 (SEM–342).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – About 250 seeds and numerous seed fragments. (1033.01–20; 2033.01–11; SEM–75,–317,–341,–342).
Description and remarks. – The seeds are bitegmic, campylotropous and strongly curved with an irregular, horseshoe-shaped outline, usually flattened at one side and convex at the other (Pl. 17, figs 7–10). The micropylar limb is truncate at the base and has a central, sub-circular aperture, 0.5–0.7 mm in diameter, which in a few specimens is closed by a slightly convex operculum. The chalazal limb is inwardly curved and the chalaza faces the central cavity (Fig. 12). Along the concave margin of the seed there is a low ridge, which runs from chalaza to micropyle (Pl. 17, fig. 11; Fig. 12). Remnants of the raphe are preserved in several specimens as thorn-like protrusions from the chalaza (Pl. 17, figs 7–8).

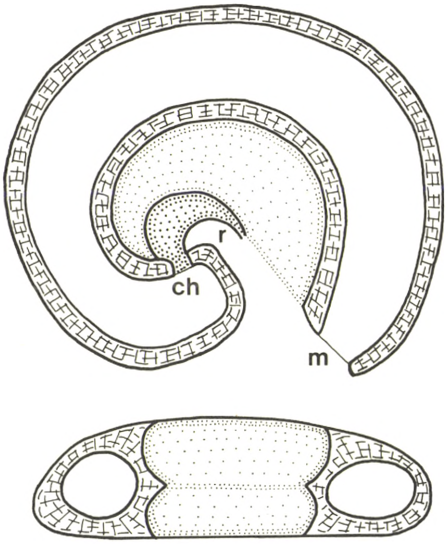


Fig. 12. Fossil *Myrtus palaeocommunis* Friis sp. nov. Schematical section of seed.
ch = chalaza, m = micropyle, r = raphe.

The seed wall is 0.05–0.2 mm thick and formed from two distinct layers. The testa is composed by cuboidal to columnar cells arranged perpendicular to the surface of the seed body. The cell walls are slightly thickened and finely pitted (Pl. 17, figs 11–12). The tegmen is thin and black, and composed of narrow, elongate cells, aligned parallel to the curvature of the seed.

The fossil seeds are almost identical to those of extant *Myrtus communis* L. in general morphology and structure of the seed coat, but they differ in the presence of the median ridge along the inner margin of the seed.

The genus *Myrtus* includes about 100 species of shrubs and trees distributed in subtropical and temperate regions, mainly in America. *M. communis* is probably native to West Asia and has long been naturalized in the Mediterranean region occupying an important constituent of the xeromorphic maquis vegetation (Willis, 1973).

There are no unambiguous records of *Myrtus*-seeds in the fossil floras of Europe or Asia. Seeds from the Lower Oligocene Kali deposits of Alsace described as Myrtaceae genre 3 sp. (cf. *Myrtus* sp. or *Rhodomyrtus* sp.) by Quiévreux and E.M. Reid (1937) resemble the Danish seeds in general appearance, but differ in the shape of raphal and chalazal area. According to Quiévreux and E.M. Reid (1937) similar seeds have also been recovered from other Lower Tertiary sediments in France and southern England. Fruits of *Myrtus* were reported from the Middle Miocene flora of Wieliczka (Łańcucka-Środoniowa, 1963), but they have not been described. There are no other records of these characteristic seeds and a new fossil species, *M. palaeocommunis,* has been established to accommodate the Danish fossil seeds, closely related to extant *M. communis.*

Hippuridales

Haloragaceae

A few fruits referable to the extant genus *Proserpinaca* L. were recorded from the Damgaard and Søby floras.

The fruits of the Haloragaceae are one to four loculed drupes or nuts with a single pendant and anatropous ovule in each locule. The seeds are bitegmic with very thin unspecialized seed coat (Corner, 1976).

Proserpinaca L.

Proserpinaca brevicarpa Dorofeev
Plate 18, fig. 14.

1976a *Proserpinaca brevicarpa* Dorofeev sp. nov. – Dorofeev, p. 1037, fig. 1:1–14.
1979 *Proserpinaca brevicarpa* Dorofeev – Friis, p. 134, fig. 8 I.

Occurrence. – Damgaard S (Damgaard flora). Damgaard N (Søby flora).
Material. – 4 fruits (3036.01–02; SEM–327).
Remarks. – The fruits were previously described with the fossils of the Damgaard flora (Friis, 1979). The species has been recorded from Oligocene and Miocene floras in Central and eastern Europe (Dorofeev, 1976a; Mai & Walther, 1978).

Cornales

Cornaceae

Numerous endocarps assignable to the Cornales have been recovered from the Miocene strata of Denmark. They represent four families, the Cornaceae, Mastixiaceae, Nyssaceae, and Araliaceae. Endocarps of *Nyssa* L. are among the most common fossils of the Fasterholt flora and are being studied in detail by Friedrich and Koch. Endocarps of *Nyssa* have also been recorded from the lignitic clay at Moselund (Mathiesen, 1975), and from Salten and Sønderskov *(Carpolithes nyssoides* Hartz, 1909). Pollen of *Nyssa* was described by Ingwersen (1954). The Mastixiaceae is represented by few endocarps of *Mastixia* Blume and *Ganitrocera* Kirchheimer. They are being studied together with the larger fossils of the Fasterholt flora. The Cornaceae is represented by two species of *Swida* Opiz (often included in the genus *Cornus* L.) recovered from the Fasterholt Flora.

The Cornaceae includes about 100 species of small trees, shrubs and herbs. The fruits are 1–4 loculed drupes or berries with a single anatropous seed in each locule. The seeds are unitegmic with thin-walled seedcoat (Corner, 1976).

Swida Opiz

Swida gorbunovii (Dorofeev) Negru

Plate 19, figs 1–3.

1955a *Cornus gorbunovii* Dorofeev sp. nov. – Dorofeev, p. 137, Pl. 6:13–16.
1959 *Cornus* aff. *stolonifera* Michx. – Raniecka-Bobrowska, p. 192, Pl. 22:3–7.
1972 *Swida gorbunovii* Dorof. – Negru, p. 146.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 120 endocarps and fragments of endocarps. (1038.01–05; 2038.01–05; SEM–95,–319).
Description and remarks. – The endocarps are two-loculed, more or less bilaterally symmetrical with a median septum in the plane of symmetry. The shape of the endocarp varies from ovate to obliquely elliptical (Pl. 19, figs 1–2). The apex is slightly pointed and the base usually rounded. A narrow median depression overlies the septum and encircles the endocarp. The outer surface of the endocarp is almost smooth with about eight groups of vascular bundles running from base to apex, three on each side and two in the septal furrow. The endocarp splits along the septum starting at the base. Length of endocarp: 1.9(2.49)3.0 mm; breadth: 2.2(2.8)3.4 mm; 25 specimens were measured.

The endocarp wall is about 0.1 mm thick and composed of an outer layer of equiaxial, polyhedral sclereids with thickened and strongly pitted walls and an inner layer of slightly elongate, rectangular sclereids (Pl. 19, fig. 3). Remains of exocarp have been observed in a few specimens as a thin shiny layer. Each locule contains a single anatropous seed with thin membranous seed coat in which the cellular structure is unclear.

A key to fossil and extant genera related to *Cornus* was given by Mai (1976b). The Danish fossils are in general structure comparable to fruits of the extant genus *Swida*. The genus comprises about 36 modern species of small trees or shrubs predominantly distributed in southeastern Asia and North America, occurring mainly in wet woods and on stream banks. Two main types of endocarps have been recognized among modern species of *Swida*, some are almost globular while others are slightly compressed and often elliptical in outline. The fossil endocarps are related to the latter type, especially *S. stolonifera* (Michx.) Opiz, but they are smaller than all modern species studied.

Several fossil species of *Swida* and *Cornus* have been described from Eurasian Tertiary floras. The Danish material is referable to the fossil species *S. gorbunovii* described from the Odessa area. The species has been recorded from several other European and Asian fossil floras ranging in age from the Oligocene to Miocene (Dorofeev, 1955a, 1963a, 1966c, 1967a; Mai, 1964) including the floral zones I, IV, VI–VII, IX–XIII in the GDR (Mai, 1967).

Swida sp.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 endocarp (2038.06).
Description and remarks. – The endocarp is bilocular, almost globular and only slightly pointed apically. The surface is almost smooth with remnants of vascular bundles. There is no median depression as in *S. gorbunovii*. The diameter of the endocarp is about 2.8 mm and the endocarp wall 0.1 mm thick.

The endocarp is very similar to the fossil species *S. bessarabica* Negru (1972) described from Sarmatian strata of Moldavia, but it differs in having less marked median line and a more regular shape. The fossil endocarp differs from those of modern *Swida* in its smaller size and the absence of longitudinal ridges on the endocarp surface.

Araliaceae

This family is represented in the Tertiary strata of Denmark by endocarps of *Aralia* L. recovered from the Fasterholt flora. A single *Aralia* endocarp was also recovered from the Fasterholt Plantage borehole.

The fruits of modern Araliaceae are drupes with five endocarps each containing a single seed. The seeds are anatropous and unitegmic with a thin, usually crushed seed coat (Corner, 1976).

Aralia L.

Aralia pusilla Dorofeev

Plate 19, figs 4–7.

1963a *Aralia pusilla* Dorofeev sp. nov. – Dorofeev, p. 248, Pl. 48:7–9.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Fasterholt Plt.: 35.5–36.0 m.
Material. – 61 endocarps and a few fragments of endocarps. (1039.01–06; SEM–90,–322).
Description and remarks. – The endocarp is laterally flattened often with a longitudinal concavity in the middle of the lateral faces. The dorsal margin is semi-circular and the ventral margin straight, sometimes with a minor apical concavity. The base of endocarp is rounded and the apex slightly pointed (Pl. 19, figs 4–5). Length of endocarp: 1.8(2.14)2.35 mm; breadth: 1.0(1.09)1.2 mm; 25 specimens were measured.

The endocarp wall is about 0.15 mm thick, and formed from about 6 layers of transversely aligned sclereids, approximately 0.020 mm long and 0.005 mm in diameter (Pl. 19, figs 6–7). The outer surface of the endocarp is slightly rugose and generally lustreless. A few specimens have remnants of exocarp and mesocarp preserved as a thin shiny layer. The seed coat is thin, usually crushed and with an indistinct cell structure.

The genus *Aralia* includes about 30 extant species of herbs, shrubs, or trees, predominantly distributed in temperate and subtropical regions of eastern North America and East Asia (Good, 1964). Small endocarps comparable to the fossil material have been observed in *A. chinensis* L., *A. mandshurica* Rupr., and *A. racemosa* L., but the fossil endocarps are generally more slender in outline.

Fossil endocarps of *Aralia* have been described from many European and Asian Tertiary floras ranging in age from the Oligocene to Pliocene, 12 fossil species have been established, most of them based on fossil material from eastern and western Asia (Dorofeev, 1963a, 1969b; V. Nikitin, 1976). Some Pliocene forms were attributed to modern species of *Aralia* (C. Reid & E.M. Reid, 1915; E.M. Reid, 1920c, 1924). The fossil endocarps from the Fasterholt area are similar in size and shape to those of *A. pusilla* described from the Oligocene of Western Siberia. They differ from most other fossil *Aralia* in their slender shape and rather smooth endocarp surface. This is the first record of the species in Europe.

Celastrales

Aquifoliaceae

In the Tertiary strata of the Fasterholt area the Aquifoliaceae are represented by endocarps and clusters of pollen grains assignable to the genus *Ilex* L. Pollen of *Ilex* was also reported from palynological studies of lignites in the Fasterholt area (Ingwersen, 1954).

The family includes about 450 species of trees and shrubs distributed mainly in tropical and subtropical regions of the world. The fruits are drupes with several endocarps. Each endocarp contains a single anatropous and unitegmic seed. The outer epidermis of the seed coat is formed from cuboid cells with lignified anticlinal and inner periclinal walls (Corner, 1976).

Ilex L.

Ilex saxonica Mai

Plate 19, figs 8–11.

1964 *Ilex saxonica* sp. n. – Mai, p. 33, Pl. 2:19–21; Pl. 6:7–8.

1970a *Ilex saxonica* Mai – Mai, p. 461, Pl. 60:10; Pl. 61:14–18.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 19 endocarps (1040.01–07; 2040.01–02; SEM–95,–317).
Description and remarks. – The endocarps are elongate elliptic in outline with sub-circular dorsal face and

straight ventral margin. In transection they are almost triangular with flattened lateral faces and a convex dorsal face. The lateral faces join at the ventral margin to form an acute angle. The surface has four to six longitudinal and sometimes anastomosing ridges with traces of vascular bundles occurring on dorsal as well as lateral faces (Pl. 19, figs 8–9). Length of endocarp: 3.2(3.9)5.4 mm; breadth (dorsi-ventrally): 1.2(1.38)1.7 mm; breadth (laterally): 1.2(1.87)1.9 mm; 15 specimens were measured.

The endocarp wall is 0.10–0.15 mm thick and formed from elongated sclereids, the outer sclereids are arranged diagonally and the inner are transversely aligned (Pl. 19, fig. 10).

The endocarp is one-loculed containing a single anatropous seed with a thin seed coat and one layer of cuboidal cells with polygonal and isodiametric facets. The anticlinal walls and inner periclinal walls are thickened (Pl. 19, fig. 11).

Fossil endocarps assigned to the genus *Ilex* have been recovered from several younger Tertiary floras in Europe, and 19 fossil species have been established (E.M. Reid, 1924; Mai, 1964, 1970a; Gregor, 1975, 1978a; Burgh, 1978). A detailed survey of fossil endocarps of *Ilex* was given by Mai (1970a, b) together with a key to the fossil species. Distinguishing features are primarily the number, shape and arrangement of ridges, endocarp size, and the angle between the lateral faces. The features of the Danish endocarps are clearly those of *I. saxonica* described from the Miocene of Wiesa and Hartau, GDR. They are closely similar in general appearance to endocarps of the fossil species *I. ahrensii* Mai (1970a), both species having prominent wing-like ridges, but they differ in their larger size, smaller number of ridges, and smaller angle between the lateral faces. *I. saxonica* has been recorded from Lower to Upper Miocene floras of Central Europe (Mai, 1964, 1970a; Gregor, 1975, 1978a) and is represented in floral zones IV, VI–VII, X–XII. It is particularly abundant in floral zone VI (Mai, 1967).

Ilex saxonica is closely related to extant *I. perado* Ait. distributed in the Macronesian Region and the Azores.

Rhamnales

Rhamnaceae

The Rhamnales is represented in the Tertiary strata of Denmark by numerous fruits and seeds of the Rhamnaceae *(Paliurus* Mill.) and the Vitaceae (*Vitis* L., *Tetrastigma* (Miq.) Planch.), most of them extracted from the Fasterholt flora.

The fruits of the Rhamnaceae are generally two- or three-loculed, drupes, berries or dry fruits. There is a single seed in each locule. The seeds are anatropous, bitegmic and exotestal with the mechanical layer in the outer epidermis of testa. The outer epidermis is formed from columnar cells often with thickened walls and reduced lumen. The other layers of the seed coat are generally unspecialized (Corner, 1976).

Paliurus Mill.

Paliurus sp.

Plate 19, figs 12–15; Plate 20, fig. 1.

1979 *Paliurus* sp. – Friis, p. 135.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Fasterholt Plt.: 32.0 m.

Material. – 65 dispersed seeds (1041.01–02; 2041.01; 3041.01; SEM–88,–316).

Description and remarks. – The seeds are flattened, 1.1(1.74)2.4 mm long and 1.1(1.46)2.4 mm broad. The smaller seeds are irregularly elliptical in outline, while the larger seeds are sub-circular (Pl. 19, figs 12–14). The seeds are brownish with a shiny surface. The smaller seeds are usually smooth near base and apex and strongly wrinkled in the middle. The larger seeds are smooth or only slightly wrinkled. The seed coat is composed of a thick outer layer of palisade cells with thickened walls, undulate facets and a thin, crushed, inner layer (Pl. 19, fig. 15; Pl. 20, fig. 1).

The features of the fossil seeds are identical to those of extant *Paliurus* (Pl. 20, fig. 2). The smaller seed corresponds to extant immature or aborted seeds, while the larger fossils are similar to mature seeds.

Fossil fruits of *Paliurus* occur abundantly among the larger plant fossils of the Fasterholt flora (Koch et al., 1973). They contain seeds similar to the dispersed seeds and were probably derived from the same species. Pairs of stipule thorns with one thorn straight and the other recurved, probably also representing the same species have also been recovered from the Fasterholt flora. The characters of the various fossil organs indicate a close relationship with extant *P. spina-christi* Mill. occurring in the Mediterranean region.

Fossil fruits of *Paliurus* have been described from several European and Asian fossil floras, the oldest record being in the Oligocene (Kirchheimer, 1957; Dorofeev, 1963a). A few fossil species have been established on the basis of fruit characters and dispersed seeds have not previously been described. Specific determination of the Fasterholt material will therefore depend on the future studies of the fruits.

Dipsacales

Caprifoliaceae

Two genera of the Caprifoliaceae have been recovered from the Tertiary strata of Denmark, *Sambucus* L. represented by a single seed and few fragments from the Lavsbjerg Øst and Fasterholt Plantage boreholes, and *Weigela* Thunberg represented by seeds and a few fruit fragments in the Fasterholt flora.

The fruits of extant Caprifoliaceae are drupes, berries or capsules usually with many seeds. The seeds are anatropous and unitegmic with the mechanical layer in the outer tegmen. The structure of outer epidermis varies between the different species, thickened outer cell walls occurring in *Sambucus*, while several other genera have thin outer walls and thickened and pitted anticlinal and inner walls (Corner, 1976).

The seeds of *Weigela* are alate or without wing, and extant species of *Weigela* may be grouped into three sections based on their seed characters (Krüssmann, 1962). Section *Utsugia* includes species with a thin marginal wing of elongated cells developed on three sides of the seed (Pl. 20, fig. 10). The seeds of species included in section *Calysphyrum* are wingless or have a weakly developed marginal wing. In section *Weigelastrum* the seeds are alate, generally with a distinct wing formed from equiaxial cells. The seeds of *W. maximowiczii* (S. Moore) Rehd. are distinguished from the other species of the section in having a marginal wing formed from elongated cells as those of section *Utsugia*. The seeds of extant *Diervilla* Mill. resemble those of *Weigela* but are wingless, thicker and have larger surface cells.

Sambucus L.

Sambucus pulchella C. Reid & E.M. Reid
Plate 20, figs 3–4.

1915 *Sambucus pulchella* sp. nov. – C. Reid & E.M. Reid, p. 135, Pl. 17:7–10.

Occurrence. – Lavsbjerg Øst: 59.0–59.5 m; 101.0–101.5 m. Fasterholt Plt.: 33.0–35.5 m.
Material. – 1 seed and few fragments of seeds (SEM-64).
Description and remarks. – The seed is obovate in outline and dorsi-ventrally flattened, about 2.1 mm long and 1.0 mm broad. The micropyle is marked by a small circular aperture near the base. The seed surface is characterized by irregular, nodular and transverse ridges (Pl. 20, fig. 3). The seed coat is about 0.05 mm thick and composed of two layers. The outer layer is black formed from thick-walled cells with rectangular or polygonal facets aligned in longitudinal rows. The anticlinal walls are slightly undulate (Pl. 20, fig. 4). The inner layer of seed coat is brownish and formed from transversely aligned, elongated sclereids.

In general morphology and wall structure the fossil seeds are similar to those of extant *Sambucus*, but only the seeds of *S. canadensis* L. agree with the fossil specimen in their small size.

Sambucus seeds have been described from several Eurasian fossil floras, and nine fossil species have been established, the earliest record being from the Eocene. The Danish seed is in complete agreement with those of *S. pulchella* described from the Pliocene of Reuver, Swalmen, and Brunssum. The seeds of *S. bashkirica* Dorofeev (1977b), *S. colwellensis* Chandler (1963a), *S. pusilla* Dorofeev (1977b), *S. jacutica* V. Nikitin (1976), *S. lucida* Dorofeev (1963a), and *S. mudensis* Chandler (1963a) are related to *S. pulchella* in size and shape, but differ in having more distinct and rugose surface sculpture.

A detailed description of *S. pulchella* was given by Kirchheimer (1942b). The species has been recovered from Miocene and Pliocene strata of Europe and Western Siberia (C. Reid & E.M. Reid, 1915a; E.M. Reid, 1920a; Kirchheimer, 1942b; Dorofeev, 1963a; Nikitin, 1965; Palamarev, 1970).

Weigela Thunberg

Weigela srodoniowae Friis sp. nov.
Plate 20, figs 5–9.

Derivation of name. – In honour of the palaeobotanist Dr. M. Łańcucka-Środoniowa.
Specific diagnosis. – Seeds alate, laterally flattened and irregularly elliptic in outline with a marginal wing surrounding about two thirds of the seed. Inner layer of seed coat thin, cell structure unclear, outer layer formed from cuboid cells with isodiametric and polygonal facets arranged in about 2 × 20 longitudinal rows, the outer cell walls membranous, the anticlinal and inner walls thickened and strongly pitted. Marginal cells of wing thin-walled and elongated. Length of seed with wing: 1.6 mm; breadth: 0.75 mm; length of seed without wing: 1.0–1.2 mm; breadth: 0.5–0.7 mm.
Holotype. – Pl. 20, fig. 5 (SEM–338).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 4 fragments of fruits containing seeds and 16 dispersed seeds (1043.01–02; SEM–46, –90,–112,–306,–338).
Description and remarks. – The seeds are irregularly elliptic in outline and laterally flattened, slightly pointed at the base and rounded at the apex. Winged specimens have been recovered enclosed in small fragments of fruits, but in dispersed seeds the wing has usually been abraded (Pl. 20, figs 5–8). The wing is marginal and membranous formed from elongated and thin-walled cells. It surrounds about two thirds of the seed, being most strongly developed apically. The outer margin of the wing is almost entire (Pl. 20, figs 5–6).

The outer epidermis of seed coat is composed of flattened cells with isodiametric and polygonal facets, 0.02–0.05 mm in diameter, arranged in 2 × 20 longitudinal rows. The outer periclinal walls are membranous, rarely preserved. The inner periclinal and anticlinal walls are thickened and strongly pitted, the pits being circular and irregularly spaced (Pl. 20, fig. 9). The inner layer of seed coat is thin without distinct cellular structure.

The fossil seeds of *Weigela* are comparable to those of extant species included in the section *Utsugia* and *W. maximowiczii* (S. Moore) Rehd. which all have a thin membranous marginal wing formed from elongated thin-walled cells. In general morphology they are most related to seeds of extant *W. hortensis* (Sieb. & Zucc.) C.A. Mey. (Pl. 20, figs 10–11), but the fossils differ in having much thinner cell walls.

The genus is now restricted to East Asia. It has been recorded from Miocene and Pliocene floras of Poland, two species, *W. szaferi* and *W. oraviensis*, being established by Łańcucka-Środoniowa (1967). In Asian fossil floras the genus is represented by four fossil species, *W. biskeana*, *W. plana*, and *W. pulchella* being described by V. Nikitin (1976) from the Miocene of the Mammoth Mountain, East Asia, and *W. krystofovichiana* described by Dorofeev (1957, 1963a) from the Oligocene and Miocene of Western Siberia. The fossil species may be distinguished by the shape and size of the seeds, the size of outer cells, and number of cell rows. None of the previously described fossil species are identical to the Danish seeds, and a new fossil species, *W. srodoniowae,* has been established to accommodate these fossils.

Gentianales

Rubiaceae

The Gentianales are represented in Tertiary strata of Denmark by seeds of *Menyanthes* L. (Menyanthaceae) reported from the lignitic clay at Moselund (Mathiesen, 1975), and fruits of *Cephalanthus* L. (Rubiaceae) from the Fasterholt and Søby floras and from the Fasterholt Plantage borehole.

The fruits of extant Rubiaceae are drupes, berries, capsules or schizocarps. The seeds are anatropous and unitegmic with seed coat usually reduced to the outer epidermis (Corner, 1976). In several genera a funicular outgrowth, a strophiole, is present. This structure was first described for the Rubiaceae by Lloyd (1902) for seeds of *Diodia* L. A placental outgrowth resembling a strophiole was described by Perisamy and Parameswaran (1962) for seeds of *Tarenna* Gaert. and *Randia* L.

Cephalanthus L.

Cephalanthus pusillus Friis sp. nov.

Plate 21, figs 1–7.

Derivation of name. – From the small size of the fruit.

Specific diagnosis. – Fruit a schizocarp, composed by two one-seeded mericarps. Mericarp obovoid, slightly dorsi-ventrally flattened. Ventral face flat with a shallow median furrow. Dorsal face convex, apically truncate. Placentation apical, germination valve semi-circular constituting the upper third of ventral face. Fruit wall about 0.04 mm thick formed from elongate sclereids. Seed strophiolate, apotropous pendulous, obovoid, slightly dorsi-ventrally flattened. Strophiole apical, sickle-shaped. Hilum dorsal, marked by a narrow slit. Raphe dorsal, indistinct. Outer cells of seed coat with polygonal, isodiametric cells with slightly raised anticlinal walls. Length of mericarp: 1.4–2.9 mm; breadth: 0.7–1.1 mm. Length of seed: 1.2–1.4 mm; breadth: 0.5–0.8 mm.

Holotype. – Pl. 21, fig. 1 (1044.01).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Fasterholt Plt.: 35.5–36.0 m.

Material. – 37 mericarps, 10 fragments of mericarps, 1 dispersed seed (1044.01–09; SEM–44).

Description and remarks. – Only separate mericarps were recovered from the Fasterholt flora (Pl. 21, figs 1–3), while in the Søby flora a single entire fruit was found (Pl. 21, fig. 4). The mericarps are elongate to broadly obovoid with a flattened ventral face and convex dorsal face. On the ventral face an indistinct longitudinal furrow indicates the position of the ovular bundle. The germination valve is ventral and apical. It splits along the lateral margins of the mericarps and remain attached to it (Pl. 21, fig. 5). A shallow incision at the apex of the germination valve indicates the position of the placenta.

The fruit wall is about 0.04 mm thick composed of elongate sclereids transversely aligned at the ventral side of the mericarp and irregularly orientated at the dorsal side to form a "fingerprint"-like pattern.

The seeds are obovoid and slightly compressed (Pl. 21, fig. 7). There is an apical sickle-shaped strophiole surrounding the seed at the upper part of dorsal side and at the apex (Pl. 21, fig. 6). The strophiole is formed from small thin-walled cells, about 0.01 mm in diameter. The hilum is dorsal, marked by a narrow slit, about 0.25 mm long. Raphe is dorsal and indistinct.

The seed coat is thin and composed of one layer of cells with polygonal and isodiametric or slightly elongate facets, 0.02–0.04 mm in diameter, arranged in irregular, longitudinal rows. The anticlinal walls are slightly raised forming a fine reticulum on the seed surface (Pl. 21, figs 6–7).

In general structure the fossil fruits and seeds are similar to those of extant *Cephalanthus* (Pl. 21, figs 8–10), but they differ from the modern material examined in their smaller size.

The genus was first recognized in the fossil record by Raniecka-Bobrowska (1959) who described *C.* aff. *occidentalis* L. from the Upper Miocene flora of Konin, Poland, and assigned *Carpolithus radiatus* Heer (1869) from Cłapowo (Rixhöft) to the same species. Similar fruits were described by Szafer (1961) from Stare Gliwice. The Polish material was subsequently included in the fossil species *Cephalanthus kireevskianus* (Dorofeev) Dorofeev described from the Oligocene and Miocene of Western Siberia (Dorofeev, 1960b, 1963a). These fossils are all larger than the Danish fossil and a new fossil species, *C. pusillus,* has been established for the Danish material.

Fruits resembling *Cephalanthus* were also described by Chandler (1962) from the Lower Tertiary of southern England *(Carpolithus* sp., p. 152, Pl. 26, figs 1–2 and *Carpolithus* sp., p. 154, Pl. 26, figs 11–12), but according to Collinson (personal communication, 1979) the preservation of these fossils is not adequate for certain determination.

Lamiales
Lamiaceae

In the Tertiary deposits of Denmark the Labiatae is represented by few fruitlets of *Teucrium* L. extracted from the Fasterholt and Søby floras.

The fruits of the Lamiaceae are four-loculed schizocarps composed of four nutlets and generally with gynobasic style, the members of the subfamily Ajugoideae being distinguished in having apical style. The seeds are anatropous and unitegmic with reduced seed coat (Corner, 1976).

Teucrium L.

Teucrium sp. 1

Plate 22, figs 1–2.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 3 fruitlets (1045.01; SEM–124).
Description and remarks. – The fruitlets are elliptic in outline and slightly dorsi-ventrally compressed. Only separate fruitlets have been recovered, but their form suggests that they were derived from groups of four, attached to each other in the lower half of the fruitlet. The contact area is large, almost circular and smooth (Pl. 22, fig. 1). The position of style is marked by a small protrusion in the upper half of the contact area. The fruitlet is a one-loculed nut, 0.9–1.1 mm long, and 0.6–0.8 mm broad. No seeds have been observed. The fruit wall is about 0.03 mm thick. The outer surface is characterized by narrow anastomosing ridges, which are mainly longitudinally aligned with a few transverse ridges on the dorsal side near the apex. On the ventral side they form an irregular reticulum with lumina varying from 0.1–0.2 mm in diameter. The outer cells of fruit wall have equiaxial facets and slightly undulate anticlinal walls (Pl. 22, fig. 2).

The characters of the fruitlets are those of the subfamily Ajugoideae. In surface sculpture the fossils are most similar to fruitlets of extant *Teucrium.* The genus includes about 300 living species of herbs and underscrubs.

Five fossil species of *Teucrium* have been described from Tertiary strata of the USSR. Two modern species were recorded from the Tegelen, the Netherlands (C. Reid & E.M. Reid, 1907, 1910). The Danish fruitlets are most related to those of the fossil *T. sibiricum* Dorofeev (1963a) and *T. tatianae* Nikitin (1957), but due to inadequate information on the wall structure of these species the Danish material has not been referred to any of the established fossil species.

Teucrium sp. 2
Plate 22, figs 3–4.

Occurrence. – Damgaard N (Søby flora).
Material. – 8 fruitlets (SEM–124,–327).

Remarks. – The fruitlets are similar to those of *Teucrium* sp. 1 in size, shape and general morphology (Pl. 22, fig. 3), but they differ in having smaller cells of outer fruit wall and straight anticlinal cell walls (Pl. 22, fig. 4).

CLASS MONOCOTYLEDONES

Alismatales

Alismataceae

A few fruitlets and many abraded seeds of the Alismataceae have been recovered from the Tertiary strata of Denmark, most of the specimens being extracted from the Lavsbjerg Øst and Fasterholt Plantage boreholes. The fruitlets are referable to the extant genus *Caldesia* Parl. The seeds resemble those of extant *Sagittaria* L. and *Alisma* L., but their generic position is uncertain due to inadequate preservation.

The fruits of extant Alismataceae are apocarpous formed from three to many nutlets, generally with a single curved seed. The nutlets are laterally compressed, and thin-walled forms often have a marginal wing. The seeds are campylotropous and strongly recurved. They show some variation in structure of outer epidermis and in size and shape of micropylar and chalazal limb, but it is difficult to distinguish members of the extant genera on seed characters only.

Two fossil genera of Alismataceae have been described based on fruits and seeds. *Sagisma* Nikitin (1965) comprises wingless fruits with a single recurved seed. In fruit character it is similar to extant *Limnophyton* Miq., while in seed characters it is most similar to *Caldesia* and *Sagittaria* (Dorofeev, 1963a). *Alismaticarpum* M. E. Collinson (1983a) includes fruits with a thin marginal wing and a single recurved seed. The general features of the fossils are those of the Alismataceae, but they are not closely comparable to any extant genus (Collinson, 1983a).

Caldesia Parl.

Caldesia sp. 1
Plate 22, figs 5–7.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 2 fruits (1052.01; SEM–113,–331).
Description and remarks. – The fruitlet is one-loculed and laterally flattened with straight or slightly convex ventral margin and semi-circular dorsal margin (Pl. 22, fig. 5), 1.6–1.7 mm long and 0.9–1.1 mm wide. The style is ventral and almost apical. The surface of the fruitlet has a few indistinct longitudinal ridges. The fruit wall is 0.1 mm thick and composed of columnar sclereids with nodose thickenings of the cell walls (Pl. 22, fig. 7). There is a single seed with a strongly curved embryo. It is about 1.4 mm long and 0.8 mm broad. No complete seed has been observed and the relation between dorsal and ventral limbs is therefor unknown (Pl. 22, fig. 6). The cell structure of the seed coat is indistinct.

The fossil fruits are very similar to extant *Caldesia* in general morphology and structure of fruit wall (Pl. 22, fig. 8), but they differ in their smaller size.

Eight fossil species of *Caldesia* have been established based on material from the USSR (Dorofeev, 1960a, 1963a, 1969a, 1972, 1977a; Niktin, 1965) and one species, *C. cylindrica* (E.M. Reid) Dorofeev was established based on material from western Europe (E.M. Reid, 1920a; Dorofeev, 1963a). In size and shape the Danish fruits are most similar to the fossil *C. proventitia* Nikitin ex Dorofeev described from the Oligocene and Miocene of Western Siberia (Dorofeev, 1963a; Nikitin, 1965), but the Danish fruits are more smooth.

Caldesia sp. 2
Plate 22, figs 9–10.

Occurrence. – Fasterholt Plt.: 65.0–66.0 m; 70.0–70.5 m.

Material. – 3 fruits and 1 fruit fragment (SEM-113).

Description and remarks. – The fruitlets are 1.5 mm long and 0.7–0.75 mm broad, one-loculed with an almost straight or slightly concave ventral margin and a semi-circular dorsal margin (Pl. 22, fig. 9). The style is ventral and almost apical. The surface of fruitlet has a few indistinct longitudinal ridges connected by irregular transverse ridges. The fruit wall is about 0.05 mm thick and formed from columnar sclereids with strongly thickened walls and isodiametric facets.

The seed is 1.3 mm long and 0.5 mm wide. The limbs are slightly acuminate towards the base, the ventral (chalazal) limb being narrower, and about 0.2 mm shorter, than the dorsal (micropylar) limb (Pl. 22, fig. 10).

The fruits are distinguished from those of *Caldesia* sp. 1 by their more slender shape and in having transversely arranged ridges. They are closely resembling fruits of the fossil *Caldesia antiqua* Dorofeev (1977a) described from the Oligocene of Byelorussia, but differ in having thicker transverse ridges.

A few dispersed seeds closely related to those of *Caldesia* sp. 2 have been recovered from the Lavsbjerg Øst (47.0–47.5 m; 55.5–56.0; 56.5–57.5 m; 58.5–59.0 m; 60.0–60.5 m; 63.0–63.5 m), and Fasterholt Plantage boreholes (35.5 m; 65.0–65.5 m) and are probably attributable to the same species.

Alismataceae genus? sp. 1
Plate 22, fig. 11

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora). Lavsbjerg Øst: 16.0–16.5 m; 42.5–43.0 m; 47.0–47.5 m; 51.5–52.0 m; 54.5–55.0 m; 55.5–56.5 m; 57.0–58.0 m; 58.5–59.0 m; 85.5–86.0 m; 90.5–91.0 m. Fasterholt Plt.: 34.5 m; 36.0 m; 44.5–45.0 m; 52.5–53.0 m; 56.5–57.0 m; 63.0–63.5 m; 64.0–64.5 m; 65.0–65.5 m; 67.0–67.5 m; 68.5–69.5 m; 70.0–71.0 m; 72.0–72.5 m; 73.0–74.0 m; 78.5–79.5 m.

Material. – 150 seeds (1054.01; 3054.01–02; SEM–337).

Description and remarks. – The seeds are strongly recurved, laterally flattened, with a slightly concave ventral margin and a semi-circular dorsal margin. They are 0.9–1.4 mm long and 0.6–0.8 mm wide, the chalazal limb being slightly shorter than the micropylar limb (Pl. 22, fig. 11). The preservation of the seeds is variable, and generally only the inner membranous seed coat is preserved. It is yellowish or light brown with a shiny surface and indistinct cell structure. A few specimens show longitudinal striations.

Similar seed morphology has been observed in extant species of *Sagittaria* and some *Caldesia* as well as in fossil *Sagisma*. The greatest similarity seems to be with seeds of *Sagittaria*, but as none of the seeds occur in the fruits, generic delimitation of the material has not been possible.

Alismataceae genus? sp. 2
Plate 22, fig. 12.

Occurrence. – Lavsbjerg Øst: 47.0–47.5 m; 49.5–50.0 m; 54.5–55.0 m; 55.5–56.0 m; 57.5–58.0 m; 60.0–60.5 m; 84.0–84.5 m. Fasterholt Plt.: 63.0–63.5 m; 65.0–65.5 m; 66.0–66.5 m; 67.5–68.0 m; 68.5–71.0 m; 75.0–75.5 m; 76.0–76.5 m; 81.0–81.5 m; 91.0–91.5 m.

Material. – 39 seeds (SEM-337).

Description and remarks. – The seeds are strongly curved and laterally flattened with a straight ventral margin and a slightly convex dorsal margin, 0.8–0.9 mm long and 0.6–0.75 mm broad. The two limbs are of equal length. The breadth of chalazal limb is about half the breadth of micropylar limb

(Pl. 22, fig. 12). The outer cells of the seed coat are usually abraded. The inner layer of the seed coat is membranous and yellowish with indistinct cell structure or with longitudinal striations.

Similar seeds with a very broad micropylar limb are found in *Alisma, Echinodorus* Rich. ex Engelmann, *Damasonium* Mill. (Alismataceae) and *Limnocharis* Kunth (Limnocharitaceae). The seeds of *Damasonium* and *Limnocharis* are sculptured with distinct transverse ridges and those of *Echinodorus* have strongly thickened outer epidermal cell walls, which most likely would be preserved in the fossil state. Thus the fossil seeds seem to be most comparable with seeds of *Alisma,* but due to the inadequate preservation they cannot be referred to this genus with certainty.

Najadales

Potamogetonaceae

The family is represented in the Tertiary strata of Denmark by endocarps of *Potamogeton* L., two species being recognized. Two endocarp fragments similar to the fossil genus *Limnocarpus* C. Reid were recovered from the Lavsbjerg Øst borehole. The endocarps of this genus show intermediate characters between *Potamogeton* and *Ruppia* L. (C. Reid, 1898; E.M. Reid & Chandler, 1926; Collinson, 1982b).

The Potamogetonaceae includes about 100 species of aquatic herbs widely distributed in fresh or brackish water. The fruits are usually apocarpous formed from one to four drupes, or more rarely nutlets. The endocarps are laterally flattened and characterized by a dorsal germination valve and a more or less central depression on each lateral face. There is a single campylotropous seed in each fruitlet curved around a prominent condyle. The micropylar and chalazal limbs are of almost equal thickness. The seed coat is thin and membranous (Aalto, 1970; Collinson, 1982b).

Seven fossil genera related to *Potamogeton* and *Ruppia* have been established based on fossil fruits (Collinson, 1982b). They all have endocarps with dorsal germination valve and a lateral depression and may be distinguished by the structure of fruit wall and germination valve, the position of condyle, seed shape, the extent of the germination valve and several other features (Collinson, 1982b).

Potamogeton L.

Potamogeton heinkei Mai

Plate 22, figs 13–14.

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

1979 *Potamogeton heinkei* Mai – Friis, p. 136, figs 10F–G.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora).

Material. – 6 endocarps (1055.01; 3055.01; SEM–100,–336).

Description and remarks. – The endocarps are obovate in outline, laterally flattened, 1.3–1.7 mm long and 1.0–1.1 mm broad. The ventral margin is slightly convex, the dorsal margin rounded and the lateral faces flattened with a marked central depression (Pl. 22, fig. 13). There is a dorsal germination valve extending from base almost to the apex. It is composed of several layers of elongated sclereids and has no keel (Pl. 22, fig. 14). The endocarp is one-loculed with a strongly curved seed cavity. The fruit wall is composed of a thin outer layer of thin-walled cells with equiaxial cell outlines and a thick inner layer of elongated sclereids running parallel to the curve of the seed cavity.

The fossil endocarps are in general structure similar to those of extant *Potamogeton* especially to species of the subsection *Colorati* (Graebm.) Hagstr., but they are smaller than those of all modern species.

Fossil endocarps of *Potamogeton* are common in the Tertiary floras of Europe and Asia, the earliest record being from the late early Eocene of southern England (Chandler, 1963b; Collinson, 1982b). More than 30 fossil species have been established, but most of them differ from the Danish endocarps by their larger size. The endocarps of *P. heinkei* and *P. wiesaensis* Kirchheimer (1942a) are comparable to the Danish fossils in size and shape, but *P. wiesaensis* differs in having a marked keel on the germination valve. *P. heinkei* has previously been recorded from Miocene strata of GDR. (Mai, 1960, 1967).

Potamogeton sp.
Plate 22, figs 15–16.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Fasterholt Plt.: 65.5–66.0 m; 69.0–69.5 m.
Material. – 11 endocarps and few fragments of endocarps (1055.02–03; SEM–100,–336).
Description and remarks. – The endocarps are similar to those of *P. heinkei* in general structure, but they differ in their slightly smaller size (length 0.9–1.2 mm; breadth: 0.75–0.9 mm) and in the structure of germination valve (Pl. 22, fig. 15). The valve is built of two cell layers of elongated sclereids except at the median part where several layers of sclereids form a distinct keel (Pl. 22, fig. 16).

Potamogetonaceae or Ruppiaceae

Limnocarpus C. Reid
?*Limnocarpus* sp.
Fig. 13.

Occurrence. – Lavsbjerg Øst: 53.5–54.0 m; 56.0–56.5 m.
Material. – 2 fragments of endocarps.
Description and remarks. – The endocarp is 1.6 mm long and 1.1 mm wide, broadly ovate in outline and laterally flattened. The ventral margin is concave near the apex and convex at the base. The dorsal margin is semi-circular. A lateral depression indicating the position of the condyle occurs near the ventral margin in the upper third of the endocarp (Fig. 13). The seed cavity is curved around the condyle, the basal limb being much wider than the apical limb. The position of the style is marked by an indistinct apical mucro. A distinct spine is placed apically on the lateral face close to ventral margin (Fig. 13). Only two half specimens of poor preservation were recovered and the material yields no information on the germination valve.

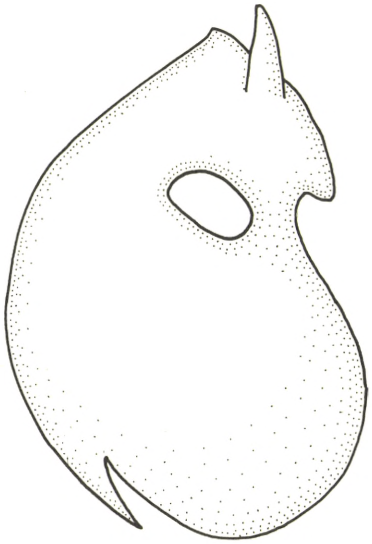


Fig. 13. Fossil ?*Limnocarpus* sp. Endocarp from the Lavsbjerg Øst borehole (56.0–56.5 m), x 40.

The position of condyle and shape of seed cavity indicate close relationship with the fossil genus *Limnocarpus*, but due to the lack of important diagnostic characters the fossil cannot with certainty be referred to this or any of the related genera described by Collinson (1982b).

Najadaceae

A single seed assignable to the extant genus *Najas* L. was recovered from the Fasterholt flora.

The family includes one genus of aquatic herbs widely distributed in fresh water habitats. The fruits of extant *Najas* are one-loculed nuts containing a single anatropous seed. The seeds are composed of an outer layer of thick-walled cells and an inner membranous layer.

Najas L.

Najas sp.

Plate 23, figs 1–2.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed (SEM–114).
Description and remarks. – The seed is 2.2 mm long and 0.7 mm broad. It is flattened and narrowly obovate in outline, narrowing into a short stalk at the base (Pl. 23, fig. 1). The seed coat is composed of an outer layer of thick-walled cells with equiaxial or slightly longitudinally elongate facets, arranged in about 15 × 2 longitudinal rows, and an inner membranous layer composed of thin-walled longitudinally elongated cells (Pl. 23, fig. 2). The micropyle is apical, marked on the inner layer of seed coat by a short mucro (Pl. 23, fig. 2).

Fossil seeds and fruits of *Najas* have been recorded from many European and Asian fossil floras, the earliest record being from the Oligocene. 17 fossil species have been established, most of them based on material from Tertiary deposits of the USSR. Among these, five species, *N. oligocenica* E.M. Reid & Chandler (1926), *N. irtyshensis* Dorofeev (1963a), *N. reticulata* Dorofeev (1963a), *N. pliocenica* Dorofeev (1966a), and *N. maeotica* Dorofeev (1969a) comprise small seeds with distinct, reticulate surface structure comparable to that in the Fasterholt flora. In the arrangement of the surface cells the Danish seed is most similar to *N. irtyshensis* from the Miocene of Western Siberia, but the Siberian fruits are more elliptic. According to Dorofeev (1963a) *N. irtyshensis* is most closely related to the extant *N. graminea* Del. distributed in atlantic and southern Europe, North Africa, Middle and Southeast Asia and Australia.

?Orchidales

?Orchidaceae

A single seed with structure resembling that in some modern orchids was recovered from the Fasterholt flora.

The fruits of extant Orchidaceae are generally one-loculed capsules with a great number of minute seeds often with much reduced seed coat and embryo. The surface structure of seeds varies considerably (Rauh, Barthlott & Ehler, 1975).

Orchidaceae genus?

Plate 23, figs 3–4.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed (SEM–114).
Description and remarks. – The seed is small, ellipsoidal with obtuse apex and slightly pointed base, 0.55 mm long and 0.25 mm wide. The outer epidermis of the seed coat is characterized by rather large, longitudinally elongate and slightly spirally arranged cells with strongly thickened anticlinal and inner periclinal walls, the thickenings of the inner walls being fibrous (Pl. 23, figs 3–4). The outer periclinal walls are thin, membranous, and rarely preserved.

Small seeds with large conspicuous outer epidermal cells occur in many families, e.g. the Pyrolaceae, Gesneriaceae, Burmanniaceae, Philydraceae, and the Orchidaceae. In these families fibrous thickenings of the inner periclinal walls have only been observed in seeds of the Orchidaceae (e.g. *Gongora truncata* Lindl. illustrated by Rauh et al., 1975) and the fossil seed has tentatively been referred to this family. The family comprises about 17,000 species in 735 genera and no attempt has been made to place the fossil in one of the extant genera. Fossil seeds assigned to the Orchidaceae have not been recorded from other Tertiary floras.

Juncales

Juncaceae

This family is represented in the fossil floras of Denmark by a few seeds of *Juncus* L. from the Fasterholt flora.

The fruits of modern Juncaceae are one- or three-loculed capsules formed from three carpels. They contain numerous *(Juncus)* or few *(Luzula* DC.) small, anatropous seeds. In *Juncus* the seed coat is usually thin with rather large outer epidermal cells arranged in about 10–20 longitudinal rows. A key to subfossil seeds of *Juncus* was given by Körber-Grohne (1964).

Juncus L.

Juncus sp.

Plate 23, figs 5–6.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 5 seeds and few fragments of seeds. (1058.01; SEM–114).
Description and remarks. – The seeds are small, 0.45–0.6 mm long and 0.18–0.22 mm broad, elongate ellipsoidal and slightly curved. The chalazal end is rounded and the micropylar end pointed (Pl. 23, fig. 5). The seed coat is thin and composed of two cell layers. The cells of outer epidermis are slightly transversely elongated, 0.02 × 0.04 mm, and arranged in about 12 longitudinal rows. The anticlinal walls are thickened and form a conspicuous reticulum on the seed surface. The inner cells are narrow and transversely aligned with thickened anticlinal walls (Pl. 23, fig. 6).

The features of the fossil seeds are clearly those of extant *Juncus* (Pl. 23, figs 7–8). The genus is cosmopolitan with about 300 living species of herbaceous plants, most abundant in wet places of temperate and arctic regions.

Possibly as a result of the small size of the seeds and the delicate nature of the seed coat, fossil seeds of *Juncus* have been recovered from only a few fossil floras, the earliest record being seeds of the fossil species *J. vectensis* M.E. Collinson (1983a) from the Lower Oligocene of southern England. This species is distinguished from the Danish seeds by its smaller size and larger number of cell rows on the outer epidermis. Fossil seeds of *Juncus* have also been described from the Miocene of southern Poland (Łańcucka-Środoniowa, 1966), northern Bohemia (Rudolph, 1935), and Moldavia (Negru, 1972). None of these seeds are identical to the Danish fossils.

Cyperales

Cyperaceae

Fossil fruits of the Cyperaceae occur abundantly in the fossil floras of the Fasterholt area and are represented by species referable to the extant genera *Scirpus* L., *Dulichium* Persoon, *Cyperus* L., *Cladium* P.Br., *Carex* L., and possibly *Eriophorum* L., and to the fossil genera *Caricoidea* Chandler and *Cladiocarya* E.M. Reid & Chandler.

The Cyperaceae is a large family of herbs widely distributed all over the world frequently in wetland environments. It includes about 4000 species in 90 genera. The fruits are one-loculed nuts, free or enclosed by the utricle. They show a considerable diversity in shape and structure of the fruit wall. Fruit morphology and anatomy of some European Cyperaceae were described by Kowal (1958) and Marek (1958). The ultrastructure of the fruit epidermis of the Cyperaceae has provided taxonomically useful information (Schuyler, 1971; Walter, 1975; Toivonen & Timonen, 1976). The fruits contain a single basal seed with a thin membranous seed coat.

Three fossil genera related to the Cyperaceae have been established based on fossil fruits from the Lower Tertiary of southern England (*Caricoidea* Chandler, 1957, *Cladiocarya* E.M. Reid & Chandler, 1926, *Scleriocarya* Chandler, 1963b). *Scleriocarya* comprises a single species, *S. tribracteata* Chandler (1963b), and is distinguished from the two other genera in having the fruits partly enclosed by three thick bracts. *Caricoidea* is a heterogenous genus including tricarpellate forms with thick outer parenchymatous layer and thick inner sclerenchyma as well as bicarpellate forms with a thin outer layer. The type species of *Caricoidea, C. nitens* (Heer) Chandler (1957) is apparently tricarpellate with thick outer and inner layers, and in the revision of the genus Mai (in Mai & Walther, 1978) excluded the bicarpellate forms from *Caricoidea* assigning them to *Cladiocarya*. The type species of *Cladiocarya, C. foveolata* E.M. Reid & Chandler (1926) comprises bicarpellate endocarps with a truncate neck and coarse longitudinal ridges on the endocarp surface. Mai (in Mai & Walther, 1978) also included bicarpellate forms with a smooth endocarp surface in *Cladiocarya,* and in the present work the concept of Mai have been accepted. The species of the two genera have been compared to extant *Chorizandra* R.Br., *Cladium, Diplasia* Persoon, and *Mapania* Aubl. (Mai & Walther, 1978).

Scirpus L. *sensu lato*

Scirpus ragozinii Dorofeev

Plate 23, figs 9–12.

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

1979 *Scirpus ragozinii* Dorofeev – Friis, p. 137, figs 10L–N.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora). Lavsbjerg Øst: 47.5–48.0 m; 53.5–54.0 m; 56.0–56.5 m; 57.5–58.0 m.

Material. – About 550 fruits (1059.01–03; 3059.01–03; SEM–26,–125,–336).

Description and remarks. – The fruits are one-loculed nuts, obovate in outline and broadly triangular in crosssection with flattened or slightly concave faces (Pl. 23, figs 9–10). The fruits are 1.15(1.40)1.62 mm long excluding the style and 0.49(0.63)0.71 mm broad; 50 specimens were measured. The apex is mucronate, sometimes with remnants of the apical style, which may be up to 0.17 mm long. The base is cuneate with remains of a persistent perianth composed of six thin bristles. In well preserved specimens the bristles extend the full length of the fruit. The fruit wall is about 0.02 mm thick. The outer surface is black with indistinct, undulate transverse ridges. The outer epidermis of the fruit wall show narrow, longitudinally aligned cells with strongly pitted and slightly undulate anticlinal walls (Pl. 23, figs 11–12).

The fossil fruits are comparable to those of living *Scirpus* L. *sensu lato* (including *Schoenoplectus* (Reichenb.) Palla and *Trichophorum* Persoon). The genus includes about 300 extant species mainly distributed in wet habitats. The species exhibit a great variation in the structure of fruit wall, some having a well developed mesocarp and endocarp, while others have a thin fruit wall. The epidermis cells are usually polygonal and isodiametric, but some species have transversely or longitudinally elongated surface cells (Marek, 1958; Schuyler, 1971). The wall structure of the fossil fruits is closely similar to that of extant *S. mucronatus* L. which also has longitudinally elongated epidermal cells and undulate transverse ridges. However, the fossil fruits are more slender than those of the Recent species.

Fossil fruits attributed to *Scirpus* occur abundantly in the Tertiary floras of Europe and Asia, the earliest record being from the Lower Eocene (Chandler, 1960). 12 fossil species have been established and many fossils were assigned to modern species. The characters of the Danish fossils are almost identical to those of *S. ragozinii* Dorofeev (1963a) although the Danish material includes slightly longer specimens. The species has been recorded from Oligocene and Miocene deposits of Western Siberia (Dorofeev, 1963a) and from GDR, floral zones III–V, VII, X–XI (Mai, 1967).

Dulichium Persoon

Dulichium marginatum (C. Reid & E.M. Reid) Dorofeev

Plate 24, figs 1–2.

1915 *Dulichium spathaceum* var. *marginatum* var. nov. – C. Reid & E.M. Reid, p. 66, Pl. 3:5–6.

1915 *Dulichium spathaceum* var. *ellipticum* var. nov. – C. Reid & E.M. Reid, p. 66, Pl. 3:7.

1963a *Dulichium marginatum* (C. & E.M. Reid) Dorofeev comb. nov. – Dorofeev, p. 117, Pl. 13:17–23.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora).
Material. – 15 fruits. (1062.01; SEM–100,–327).
Description and remarks. – The fruits are flattened and elongated elliptic in outline with an acuminate to mucronate apex (Pl. 24, fig. 1). In a few specimens remnants of a slender style are preserved. The fruit narrows at the base into a short, usually distinct stalk. Length of fruit excluding the style: 1.8–2.5 mm (length with style up to 3.3 mm); breadth: 0.82–0.9 mm. The fruit wall is thin. The outer cells of the pericarp show polygonal and equiaxial facets, 0.015–0.020 mm in diameter, arranged in about 2 × 40 longitudinal rows (Pl. 24, fig. 2).

The characters of the fossil fruits agree with those of extant *Dulichium*. The genus includes a single living species, *D. arundinaceum* (L.) Britton, now restricted to North America. The genus was first recognized in the fossil record of Europe by Hartz (1904) who recorded fruits resembling extant *D. arundinaceum* from interglacial deposits of Denmark. Later, fruits of *Dulichium* have been described from many Tertiary and Quaternary floras in Europe and Asia, the oldest record being from the Oligocene (Dorofeev, 1963a; Mai & Walther, 1978). Several fossil species of *Dulichium* have been described, although specific limitation is difficult (Kirchheimer, 1957; Truchanowiczowna, 1973). The Danish fruits are identical to those of *D. marginatum* which occurs in Oligocene and Miocene strata of Western Siberia (Dorofeev, 1963a) and in Upper Oligocene to Pliocene strata of Europe (Dorofeev, 1963a; Mai, 1967; Mai & Walther, 1978).

Cyperus L.
Cyperus sp.
Plate 24, figs 3–4.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – About 100 fruits. (1063.01–02; SEM–26,–96).
Description and remarks. – The fruits are elliptic or obovate in outline and slightly triangular in transection with mucronulate apex and slightly pointed base (Pl. 24, fig. 3). Length of fruits: 0.62(0.73)0.79 mm; breadth: 0.33(0.38)0.42 mm; 25 specimens were measured. The surface of the fruit is light brown and shiny with distinctly delimited epidermal cells arranged in longitudinal rows. The fruit wall is about 0.02 mm thick formed from an inner layer of narrow longitudinally elongated sclereids, and an outer layer of cuboid cells with isodiametric facets and finely undulate anticlinal walls (Pl. 24, fig. 4).

The structure of the fruit wall is closely similar to that of fruits of extant *Cyperus,* which have an inner layer of narrow sclereids and an outer layer of cuboid cells with equiaxial facets and finely undulate anticlinal walls (Marek, 1958). The genus includes about 500 extant species predominantly distributed in tropical to warm temperate regions. One species, *C. fuscus* L., is native to Europe. The genus has been recorded from a few younger Tertiary and Quaternary floras of Europe and Asia (Łańcucka-Środoniowa, 1966).

Cladium P. Br.
Cladium reidiorum Nikitin ex Dorofeev.
Plate 25, fig. 1.

1948 *Cladium reidiorum* (m.m.) (nomen nudum) – Nikitin, p. 1103.
1963a *Cladium reidiorum* Nikitin – Dorofeev, p. 119, Pl. 14: 35–41, fig. 18:20–24.
1965 *Cladium reidiorum* Nikitin sp. nov. – Nikitin, p. 62, Pl. 6:10–16, 19.
1979 *Cladium reidiorum* Nikitin – Friis, p. 137, figs 10H–I.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Fasterholt Plt.: 35.5 m.
Material. – 6 endocarps and few fragments of endocarps (1067.01; 3067.01; SEM–103).
Description and remarks. – The endocarps are one-loculed, obovate in outline and sub-circular in transection with a mucronate apex and a short

basal neck (Pl. 25, fig. 1). In some specimens remnants of a three-lobed basal extension have been preserved. The endocarp is 1.03–1.3 mm long and 0.7–0.9 mm broad. The endocarp wall is black, 0.05–0.08 mm thick, composed of an outer layer of isodiametric sclereids with strongly thickened and pitted cell walls and an inner layer of transversely elongated sclereids.

The features of the endocarps are those of *Cladium* which includes 50–60 extant species mainly distributed in fresh water and brackish marsh communities of subtropical and tropical regions.

Eight fossil species of *Cladium* have been described from Oligocene and younger Tertiary floras in Europe and Asia. The Danish material agrees with the fossil *C. reidiorum* described from Oligocene and Miocene floras of Western Siberia and from Miocene floras of Europe, occurring in the floral zones IV, VII and X of GDR (Dorofeev, 1963a; Nikitin, 1965; Mai, 1967).

Cladium bicorne (Saporta) Friis comb. nov.
Plate 25, figs 2–3.

1873 *Aralia bicornis* – Saporta, p. 82, Pl. 12:17.
1888 *Carex cornuta* – Saporta, p. 76, Pl. 5:19.
?1889 *Spermites hians* – Saporta, p. 143, Pl. 20: 12–17.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 6 endocarps (1066.01–04; 2066.01; SEM–103,–337).
Description and remarks. – The endocarps are one-loculed and one-seeded with a central and basal germination aperture, about 0.3–0.4 mm in diameter. Three distinct longitudinal ridges extend from base to apex indicating the presence of three carpels. The endocarp is obovate in outline, subcircular in transection with a rounded to mucronate apex and a short, basal neck with a complex basal extension, formed from three flattened protrusions supporting a triangular collar, about 0.1 mm thick and 1.7 mm wide (Pl. 25, figs 2–3). The endocarp is 2.3–2.5 mm long and 1.5–1.8 mm wide. The endocarp wall is black, about 0.17 mm thick, composed of a thick outer layer of isodiametric sclereids with strongly thickened cell walls, and an inner layer of transversely aligned, thick-walled cells with striate inner cell walls.

The characters of the fossil fruits are very similar to those of extant *Cladium*. The Danish material is identical in size and shape of the endocarps and the structure of the basal extension to moulds of endocarps described from the Tertiary of southern France as *Aralia bicornis* and *Carex cornuta* (No. 11673 type V6 and No. 13965 were studied at the Muséum National d'Histoire Naturelle, Paris). Although these fossils are preserved only as impressions there is no doubt that they should also be referred to the genus *Cladium*, and a new combination, *C. bicorne* (Saporta) Friis is proposed. The fossils described by Saporta (1889) as *Spermites hians* should likewise be assigned to *Cladium*. Material of this species was not available for study, but the illustrated specimens are similar to those of *C. bicorne*.

The endocarps of *C. bicorne* are of similar size and shape as *C. macrocarpum* Dorofeev (1960a) described from Lower to Middle Miocene strata of Byelorussia, but they are distinguished by the shape of the basal extension.

Cladium cf. *crassum* Negru

1979 *Cladium* cf. *crassum* Negru – Friis, p. 137, figs 10J–K.

Occurrence. – Damgaard S (Damgaard flora).
Material. – 2 endocarps (3068.01–02).
Remarks. – The endocarps were described together with the other fossils of the Damgaard flora (Friis, 1979). They are similar in shape to the endocarps of *C. bicorne*, but differs in their smaller size.

Cladium sp.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 47.5–48.0 m.

Material. – 3 endocarps and few fragments of endocarps (1069.01; SEM–103).

Description and remarks. – The endocarps are subcircular in outline and slightly flattened with rounded apex and short, indistinct basal neck. The germination aperture is about 0.25 mm in diameter. There are no remnants of a basal extension. Length of endocarp: 1.35–1.55 mm; breadth: 1.1–1.35 mm. The surface of the endocarp is characterized by four to five longitudinal grooves extending from base to apex. The endocarp wall is dark brown formed from an outer layer of thick-walled isodiametric sclereids and an inner layer of transversely elongated sclereids.

The fossils are distinguished from the other *Cladium* endocarps from the Fasterholt area in having grooves and no ridges on the endocarp surface. They are closely similar to extant *C. germanicum* Schrader and *C. mariscus* (L.) R.Br. in the morphology of the endocarps, but differ in their smaller size.

Carex L.

Carex sp. 1
Plate 24, figs 5–8.

Occurrence. – C. Nielsen A/S (Fasterholt flora).

Material. – 30 fruits (1064.01; SEM–26,–96,–336).

Description and remarks. – The fruits are one-loculed nuts, elliptic or slightly obovate in outline and triangular in transection with flattened or slightly convex faces (Pl. 24, figs 5, 7). The apex is mucronulate with a small circular stylar scar, about 0.07 mm in diameter. The style is not preserved in any of the specimens studied. The base is acuminate into a short stalk. Length of fruit: 0.95(1.03)1.27 mm; breadth: 0.55(0.62)0.80 mm; 15 specimens were measured. The fruit wall is about 0.025 mm thick. The outer cells of the sclerenchyma layer are cuboid with regular hexagonal facets. Each cell has remnants of a central structure resembling silica cones of extant Cyperaceae (Pl. 24, fig. 8). In some specimens remnants of an outer layer of thin-walled, equiaxial cells are preserved and possibly representing the tissue of an enclosing utricle (Pl. 24, figs 5–6).

Among the fruits of extant Cyperaceae, which have been studied, comparable wall structure has only been observed in species of *Carex*. The genus includes 1200 living species. The fruits of extant *Carex* are enclosed by a modified glume forming a closed sac, the utricle. Although a few utricles have been recovered from the Fasterholt flora, none of them contain fruits.

Numerous fossil fruits of *Carex* have been described from the Tertiary floras of Europe and Asia, the earliest record being from the Upper Eocene (Chandler, 1963a). Most of the fossil fruits were ascribed to extant species and only a few fossil species have been established.

Carex sp. 2
Plate 24, figs 9–10.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora).

Material. – 25 fruits (1065.01; SEM–26,–96).

Description and remarks. – The fruits are broadly fusiform in outline and triangular in transection, the faces being flattened or concave (Pl. 24, fig. 9). The apex is acuminate into a slender, triangular style, 0.1 mm wide and up to 0.3 mm long. Length of fruit without style: 1.55(1.73)1.98 mm; breadth: 0.7(0.99)1.3 mm; 15 specimens were measured. The fruit wall is about 0.025 mm thick. The outer cells of the sclerenchyma layer are cuboid with hexagonal facets, finely pitted anticlinal walls and possibly remnants of a central silica cone (Pl. 24, fig. 10). The inner cells of the sclerenchyma layer are transversely elongate. In some specimens remnants of an outer parenchyma layer have been preserved.

The fruits are in general morphology and wall structure closely related to extant *Carex*. They are distinguished from the fossil fruits of *Carex* sp. 1 in their larger size and in the shape of the fruit.

Carex sp. 3

Occurrence. – Damgaard N (Søby flora).
Material. – 2 fruits.
Remarks. – The fruits closely resemble those of *Carex* sp. 2 from the Fasterholt and Søby floras in shape and wall structure, but they are distinguished by their larger size (length without style: 2.4–2.8 mm; breadth of fruit: 1.5–1.7 mm). They are similar in size and shape to the fruits of the fossil *C. antiqua* Dorofeev (1970b) described from the Middle Miocene of the Sverdlovsk Region, but due to inadequate information on wall structure in the Ural-specimens the Danish material cannot be referred to this species with certainty.

Eriophorum L.

?*Eriophorum* sp. 1
Plate 24, fig. 11.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 fruit (SEM-125).
Description and remarks. – The fruit is obovate in outline, 1.92 mm long and 0.9 mm broad, and triangular in transection with flattened faces. The apex is mucronate with remnants of the style. The base is acute with remnants of three bristles (Pl. 24, fig. 11). The fruit wall is about 0.03 mm thick with a darkbrown and shiny surface showing delineations of small, narrow, longitudinally aligned cells.

The wall structure of the fossil fruit is comparable to that of *Eriophorum,* but the fossils differ from all modern species studied in their smaller size. Fossils similar to the Danish fruit were described from the Pliocene flora of Fortuna Garsdorf as *E. angustifolium* Honckeny (Burgh, 1978), but they are much smaller than modern fruits of the species.

?*Eriophorum* sp. 2
Plate 24, fig. 12.
1979 *Scirpus* (?) sp. – Friis, p. 137, fig. 10.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora).
Material. – 5 fruits (1061–01; 3061–01; SEM–125).
Description and remarks. – The fruits are obovate in outline and triangular in transection with flattened or slightly concave faces (Pl. 24, fig. 12). The apex is mucronulate and base acute. In a single specimen the base shows the remnants of bristles. Length of fruits without style: 1.5–1.7 mm; breadth: 0.7–1.0 mm. The fruit wall is dark brown, about 0.04 mm thick. The surface is shiny with longitudinally elongated cell outlines with slightly undulate anticlinal walls. The inner cells of fruit wall are transversely elongated, and arranged in longitudinal rows.

The fossil fruits are comparable to fruits of living *Eriophorum* in structure of the fruit wall, but they differ from the extant species in their smaller size.

Caricoidea Chandler

Caricoidea jugata (Nikitin ex Dorofeev) Mai
Plate 25, figs 4–5; Fig. 14a

1963a *Aracispermum jugatum* Nikitin – Dorofeev, p. 133, Pl. 17:44–47.
1965 *Aracispermum jugatum* Nikitin sp. nov. – Nikitin, p. 66, Pl. 8:7–8.
1978 *Caricoidea jugata* (Nikitin) Mai nov. comb. – Mai & Walther, p. 141, Pl. 48:35–36.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Fasterholt Plt.: 69.0–69.5 m; 70.5–71.0 m.
Material. – 8 specimens (1072.01–02; 2072.01; SEM–124).
Description and remarks. – The fossils are one-loculed fruits, obovate in outline and triangular or rhombic in transection (Pl. 25, fig. 4). There is an apical depression and a truncate base with a central aperture. The fruits are 1.7–2.45 mm long and 1.3–1.6 mm broad, built of two distinct layers (Fig. 14a). The outer layer (utricle or exocarp?) is 0.15–0.5 mm thick formed from small polyhedral and equiaxial cells with thickened and pitted walls. The outer epidermis is black and shiny, composed of minute narrow cells (Pl. 25, fig. 5). The inner layer (pericarp or endocarp?) is 0.1 mm thick,

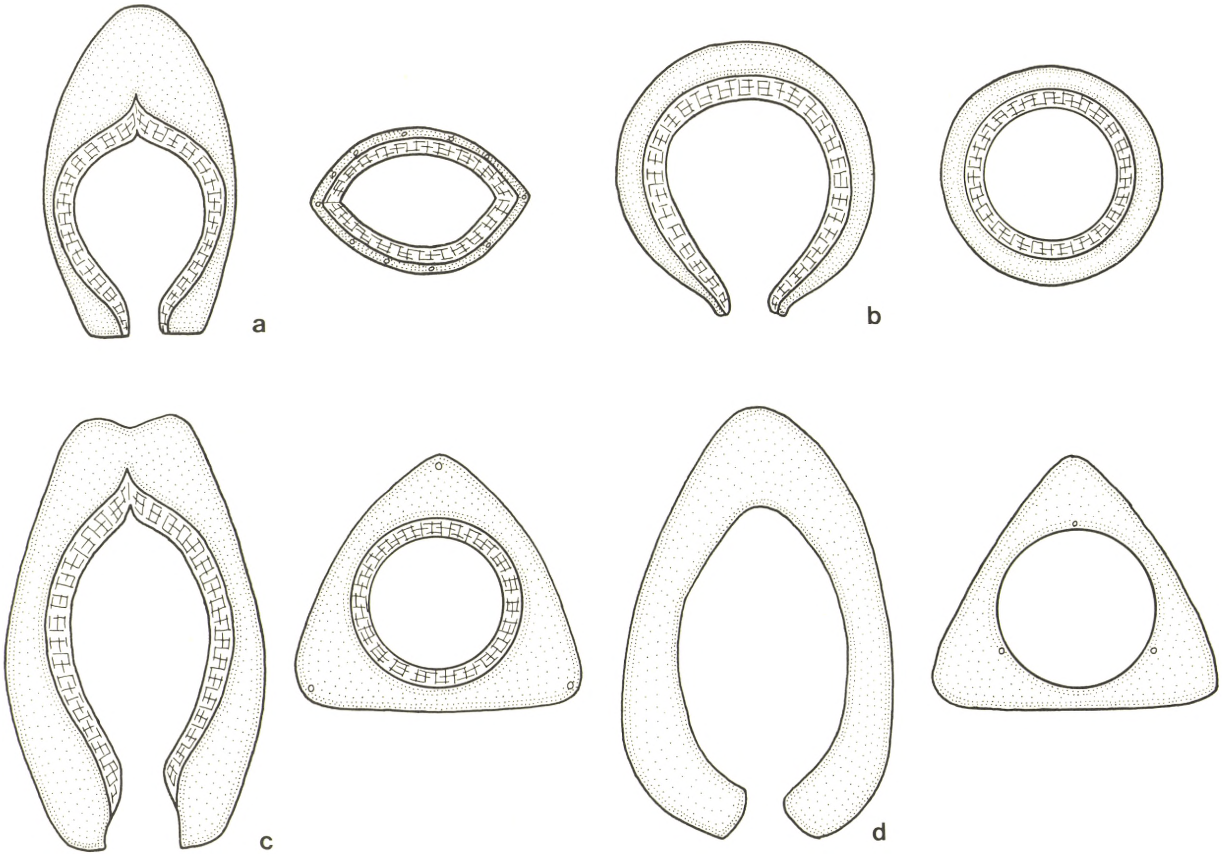


Fig. 14. Fossil fruits of Cyperaceae from the Fasterholt area. *Cladiocarya europaea* (a), *Cladiocarya trebovensis* (b), *Caricoidea jugata* (c), and *Cyperaceae genus*? sp. (d).

composed of sclereids with strongly thickened cell walls. Three to four vascular bundles extend from base to apex in the outer layer close to the surface (Fig. 14a).

The features of the fossil fruits are those of the fossil genus *Caricoidea* Chandler (1957), and in general structure are comparable to some extant members of the tribe Hypolytreae (Mapanieae). About 10 fossil species of *Caricoidea* have been established (Mai & Walther, 1978). The Danish fruits show complete agreement with the fruits of *Caricoidea jugata* described from the Oligocene and Miocene of Western Siberia (Dorofeev, 1963a; Nikitin, 1965). The species has also been recorded from Oligocene to Pliocene floras of Europe (Mai, 1964; Mai & Walther, 1978; Burgh, 1978).

Cladiocarya E.M. Reid & Chandler

Cladiocarya europaea Mai

Plate 26, figs 1–3, Fig. 14b.

1978 *Cladiocarya europaea* (Dorofeev) Mai nov. comb. – Mai & Walther, p. 143, Pl. 1:9; Pl. 48:37–38.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora). Lavsbjerg Øst: 22.0–22.5 m.

Material. – About 300 specimens (1070.01–04; 3070.01; SEM–105,–331).

Description and remarks. – The fossils are one-loculed, bisymmetric and composed of an inner sclerenchyma layer and an outer parenchyma layer (Fig. 14b). A single specimen with outer tissue completely preserved has been recovered. It is 1.5 mm long and 0.95 mm broad, ovate in outline with a broad truncate base and acute apex (Pl. 26, fig. 1). The outer epidermis has closely spaced verrucae resembling silica cones of extant Cyperaceae (Pl. 26, fig. 3). In most specimens the outer tissue has been worn off. These specimens are 0.7(0.89)1.2 mm long and 0.62(0.78)1.0 mm broad, obovate in outline with mucronulate apex and a short, usually distinct basal neck (Pl. 26, fig. 2). The surface has five to eight indistinct and sometimes anastomosing ridges indicating the position of the vascular bundles.

The fossils are similar to material from the Oligocene Haselbacher Serie, GDR, described by Mai (in Mai & Walther, 1978) as *Cladiocarya europaea*. The species was based on unpublished material from the USSR studied by Dorofeev (Mai & Walther, 1978). The stratigraphical range of the species is from the Middle Eocene to Pliocene.

Cladiocarya trebovensis (Bůžek) Mai
Plate 26, figs 4–6; Fig. 14c

1963 *Sparganium trebovense* n. sp. – Bůžek p. 126, Pl. 11–13.
1964 *Sparganium chomutovense* n. sp. – Bůžek & Holý, p. 127, Pl. 8:5–9; fig. 2:7 a–b.
1978 *Cladiocarya trebovensis* (Bůžek) Mai nov. comb. – Mai & Walther, p. 144, Pl. 1:9, Pl. 48:39–41.
1979 Cyperaceae Genus? sp. 1 – Friis, p. 138, fig. 10P.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora).

Material. – About 120 specimens (1071.01–05; 3071.01; SEM–105,–331).

Description and remarks. – The fossils are one-loculed and bisymmetric, varying in shape from ovoid with an acute apex and truncate base to almost spherical (Pl. 26, figs 4–5). The fossils are 0.9(1.14)1.4 mm long and 0.82(1.02)1.15 mm broad; 25 specimens were measured. The fruit wall consists of an inner tissue of thick-walled sclereids and an outer layer of parenchyma cells with thin and finely pitted cell walls (Pl. 26, fig. 6; Fig. 14c).

The wall structure of the fossils is similar to that of extant *Cladium jamaicense* Crantz, but the fossils differ in being bisymmetrical and formed from two carpels, while the fruits of *C. jamaicense* are radially symmetrical and formed from three carpels. Some modern species of *Cladium* are, however, bisymmetric, but none of these are similar to the fossils.

The fossils are identical to fruits of *Cladiocarya trebovensis* previously recorded from Lower to Middle Miocene strata of Bohemia (Bůžek, 1963) and from Upper Eocene to Middle Miocene strata of GDR (Mai & Walther, 1978).

Cyperaceae genus? sp.
Plate 25, figs 7–9; Fig. 14d.

Occurrence. – C. Nielsen A/S (Fasterholt flora).

Material. – 3 fruits and few fragments of fruits (1073.01; SEM–108).

Description and remarks. – The fruits are one-loculed, ovoid in outline and triangular in transection (Pl. 25, figs 7, 9), 2.1 mm long and 1.5 mm broad. They are composed of a thick outer parenchyma tissue and a thin inner layer of small, isodiametric sclereids (Fig. 14d). The outer epidermal cells are regular hexagonal and in some places with distinct verrucae (Pl. 25, fig. 8) resembling silica cones of some modern Cyperaceae. Three vascular bundles extend from base to apex near the inner margin of the parenchyma tissue (Fig. 14d).

The fossils are similar to extant Cyperaceae in general morphology and wall structure, but it has not been possible to include them in any modern genera. Although comparable to the fruits of *Cari-*

coidea jugata in size and shape, they differ in having a poorly developed sclerenchyma layer and in the position of the vascular bundles.

Poales

Small fossils resembling caryopses of grasses have been recorded from the Fasterholt flora, probably representing several genera. The material is poorly preserved and not described here.

Arales

Araceae

The Araceae is represented in the Tertiary strata of the Fasterholt area by numerous seeds of *Pistia* L. and a few seeds possibly related to the genus *Epipremnum* Schott.

The Araceae is a large family including about 2000 species in 115 genera predominantly distributed in tropical areas. The fruits of extant Araceae are generally berries with one to many locules. The seeds are anatropous, campylotropous or orthotropous, one to many in each locule. The seeds are bitegmic usually with well-developed testa and many genera have raphide sacs. A survey of seed morphology of extant Monstereae and related fossils was given by Madison & Tiffney (1976).

Pistia L.

Pistia sibirica Dorofeev

Plate 27, figs 1–7.

1955c *Pistia sibirica* m. (nomen nudum) – Dorofeev, p. 941, Fig. 1:8–9.

1958b *Pistia sibirica* Dorof. – Dorofeev, p. 543, Fig. 1:16–17.

1963a *Pistia sibirica* Dorofeev sp. nov. – Dorofeev, p. 130, Pl. 17:21–25.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – About 350 seeds (1076.01–35; 2076.01; SEM–27,–96,–332).
Description and remarks. – The seeds are orthotropous and bitegmic, cylindrical or ellipsoidal in outline with truncate apex and base. They are circular or slightly angular in transection, the longitudinal axis is straight or slightly curved (Pl. 27, figs 1–2, 7), and they are 1.5(1.7)2.1 mm long and 0.65(0.9)1.1 mm wide; 50 specimens were measured. The surface of the seed is characterized by irregular longitudinal ridges. The outer epidermis is wrinkled and often loosened from the testa. The epidermal cells show almost equiaxial facets (Pl. 27, fig. 5). The testa is 0.075–0.3 mm thick composed of isodiametric and polyhedral cells with slightly thickened and finely pitted walls (Pl. 27, figs 4–7). Spherical intercellular spaces, apparently of lysigenous origin are scattered in the testal tissue, particularly in the outer layer of the testa, where they occur between the irregular ridges (Pl. 27, figs 2, 6–7). The tegmen is thin, comprising an inner membranous layer and an outer layer of small transversely aligned cells. It is ovoid in outline with a rounded base and slightly pointed apex, about 1.2 mm long and 0.7 mm wide (Pl. 27, fig. 3). The chalaza is marked on the testa by a rather large, circular or slightly angular basal aperture, and on the tegmen by a thickened circular area. The micropyle is apical, forming a rather wide funnel-shaped aperture in the testa and a small apical plug in the tegmen (Pl. 27, figs 3–4).

In general morphology and wall structure the fossil seeds closely resemble modern seeds of the monotypic *Pistia,* and differ only in their slightly smaller size. The intercellular spaces of the fossil seeds are comparable to the raphide sacs of the modern seeds, and they probably also contained crystals. The living *P. stratiotes* L. is widely distributed in tropical and subtropical regions occurring in sluggish streams, ponds and lakes, often as a pest (Hutchinson, 1975).

One fossil species of *Pistia, P. sibirica* Dorofeev (1955c, 1958b, 1963a), has been described from the Oligocene and Miocene of Western Siberia. Although the Siberian seeds are typically wider than the Danish seeds, occasional more slender specimens occur among the Siberian material. The species was also recorded from the Miocene of GDR by Mai and Walther (1983).

Epipremnum Schott

?*Epipremnum crassum* C. Reid & E.M. Reid
Plate 26, fig. 7.

1915 *Epipremnum crassum* sp. nov. – C. Reid & E.M. Reid, p. 71, Pl. 4:1–9.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 3 seeds and 1 isolated tegmen (1075.01; SEM–113,–328).
Remarks. – The fossil seeds are in complete agreement with seeds assigned to the fossil species *Epipremnum crassum*. This species has been reported from the Oligocene and Miocene of Western Siberia (Dorofeev, 1963a) and from the Miocene and Pliocene of Europe (C. Reid & E.M. Reid, 1915; Łańcucka-Środoniowa, personal communication, 1976). It is distinguished from seeds of extant *Epipremnum* by the structure of the seed wall and the position of the raphe. It is possible that the fossils should be excluded from the genus, but until more extant species have been studied a detailed revision of the fossil species is not possible.

Lemnaceae

A single seed referable to the Lemnaceae has been recovered from the Fasterholt flora.

The family includes 6 genera and 30 species of minute, free-floating or submerged aquatic herbs of world wide distribution. The fruits of the Lemnaceae are utricles with one to several anatropous or orthotropous seeds. The seeds are bitegmic with a membranous tegmen and a thick testa bearing longitudinal ridges. The fossil genus *Lemnospermum* V. Nikitin (1976) was established to accommodate ribbed fossil seeds related to the Lemnaceae, but of uncertain generic position.

Lemna L.

Lemna sp.
Plate 26, figs 8–9.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed and 1 fragment of seed (SEM–97).
Description and remarks. – The seed is broadly ellipsoidal, 0.6 mm long and 0.4 mm broad with a rounded base and apex, and 20 indistinct longitudinal ridges (Pl. 26, fig. 8). The seed coat is about 0.05 mm thick comprising a thick testa of small polyhedral cells with slightly thickened walls and a thin membranous tegmen. The cells of outer epidermis show polygonal and almost equiaxial outlines (Pl. 26, fig. 9).

The structure of the seed indicate a close relationship with extant *Lemna*, and in cell structure and number of longitudinal ridges the fossil is very similar to seeds of *L. triscula* L. It differs only in its smaller size. The seeds of living *L. perpusilla* Torrey and *L. paucicostata* Hegelmaier illustrated by Kandeler & Hügel (1974) differ from the fossil seed in having larger outer epidermal cells.

Fossil seeds of *Lemna* have been described from a number of Eurasian Tertiary floras, the earliest record being in the Oligocene (Dorofeev, 1963a; Łańcucka-Środoniowa, 1966; Mai & Walther, 1978). A single fossil species, *L. tertiaria* Dorofeev (1963a) was established based on fossil seeds from Western Siberia. They differ from the Danish seeds in their larger size and the smaller number of ribs.

Typhales

Typhaceae

Fossil seeds assignable to the extant genus *Typha* L. occur abundantly in the Miocene floras of Denmark represented by at least three species.

The family comprises a single genus with about 15 species of aquatic herbs. The flowers of the Typhaceae are reduced and crowded in a cylindrical spike. The fruits are small achenes with a single, pendant and anatropous seed. The seeds of the various species are rather uniform, but some species may be distinguished based on variations in seed shape and size.

Typha L.

Typha sp. 1

Plate 27, figs 8–9.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Fasterholt Plt.: 65.0–65.5 m; 70.0–70.5 m; 73.0–73.5 m.

Material. – About 120 seeds (1083.01; SEM–100).

Description and remarks. – The seeds are elongated ellipsoidal with truncate apex and cuneate base, with straight or slightly curved longitudinal axis (Pl. 27, figs 8–9). They are 1.0(1.13)1.35 mm long and 0.27(0.34)0.41 mm broad; 42 specimens were measured. The maximum breadth is at, or below, the middle of the seed. There is an apical operculum with a short hilar stalk. The diameter of operculum is one third to one fourth the maximum breadth of seed. The seed coat is thin, formed from a dark outer layer of transversely elongated cells arranged in indistinct longitudinal rows, and an inner yellowish membranous layer with indistinct cell structure.

The fossil seeds are clearly assignable to the genus *Typha* and their size and shape is comparable to seeds of living *T. latifolia* L.

Fossil seeds of *Typha* have been described from many Eurasian Tertiary floras. About 25 fossil species have been established based on material from the Tertiary of the USSR (Dorofeev, 1963b, 1966b, 1969a, 1971, 1982; Negru, 1972). They are distinguished mainly by variation in size and shape. The Danish seeds are most similar to those of the fossil *T. tanaitica* Dorofeev (1982) described from the Miocene of the Rostov region, but have a smaller operculum.

Typha sp. 2

Plate 27, figs 10–11.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 16.0–16.5 m; 24.5–25.0; 27.0–27.5 m; 41.0–41.5 m; 47.0–48.0 m; 53.5–55.0 m; 55.5–56.5 m; 88.0–88.5 m. Fasterholt Plt.: 56.5–57.0 m; 63.0–63.5 m; 65.0–65.5 m; 72.0–72.5 m; 73.0–73.5 m; 78.5–79.0 m; 81.0–81.5 m; 91.0–91.5 m.

Material. – About 250 seeds (1082.01; SEM–114).

Description and remarks. – The seeds are 0.87(0.95)1.02 mm long and 0.24(0.29)0.33 mm broad with maximum breadth at the middle of seed; 40 specimens were measured (Pl. 27, figs 10–12). The diameter of operculum is one half to one third the maximum breadth of seed. The wall structure is similar to that of *Typha* sp. 1.

In size and shape the fossil seeds are comparable to those of modern *T. angustifolia* L. Similar fossil seeds were described from the Miocene of the Charkow Region as *T. pulchella* Dorofeev (1982), but these seeds are slightly broader and have a smaller operculum.

Typha sp. 3

Plate 27, figs 12–13.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 16.0–16.5 m; 47.0–47.5 m; 51.5–53.0 m; 54.5–58.5 m; 59.0–60.0 m; 86.0–86.5 m. Fasterholt Plt.: 56.5–57.0 m; 64.0–64.5 m; 65.0–65.5 m; 66.0–66.5 m; 68.5–69.0 m; 70.0–71.0 m; 78.5–79.0 m.

Material. – About 175 seeds (1081.01; SEM–114).

Description and remarks. – The seeds are 0.55(0.72)0.86 mm long and 0.25(0.30)0.37 mm broad with maximum breadth at the middle of the seed; 40 specimens were measured (Pl. 27, figs 12–13). The diameter of operculum is half to one third the maximum breadth of seed. The wall structure is similar to that of *Typha* sp. 1.

The fossil seeds are comparable to those of living *T. shuttleworthii* Kock & Sonder in size and shape. The Danish seeds are most similar to the fossil *T. ovalis* Dorofeev (1982) described from the Miocene of the Tambov Region, but due to the lack of cellular details in the Russian material, an assignment of the Danish seeds to the species is not possible. Similar fossil seeds were also described from the Oligocene of Kazachstan as *T. pusilla* Dorofeev (1963b), but these have a narrower apex than the Danish seeds.

Sparganiaceae

This family is represented in the fossil floras of the Fasterholt area by endocarps of *Sparganium* L. assigned to three different species.

The Sparganiaceae includes about 15 living species in one genus. They have small reduced flowers crowded in globose heads. The fruits are drupes with a one-loculed endocarp and a single anatropous seed.

Sparganium L.

Sparganium pusilloides Mai
Plate 28, figs 1–2.

1978 *Sparganium pusilloides* Mai nov. sp. – Mai & Walther, p. 149, Pl. 48:19–26.
1979 *Sparganium camenzianum* Kirchheimer – Friis, p. 138, Figs 10R–S.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora). Damgaard N (Søby flora).
Material. – About 100 endocarps and few seeds (1078.01–07; 3078.01; SEM–114).
Description and remarks. – The endocarps are one-loculed, elongated fusiform to broadly elliptical in outline and slightly angular in transection with rounded or pointed base. The endocarps narrow apically into a short neck with oblique apex and a subcircular germination aperture (Pl. 28, figs 1–2). The endocarps are 1.0(1.54)2.2 mm long and 0.6(0.76)1.0 mm broad; 54 specimens were measured. The endocarp wall is about 0.1 mm thick and composed of large sclereids with thickened and pitted cell walls. The inner cells of endocarp are narrow and longitudinally aligned. Remnants of exocarp show longitudinally elongated cells with thin and finely pitted walls. A few vascular bundles extend from base to apex on the outer surface of endocarp.

The fossils are similar to those of *Sparganium pussiloides* described from the Middle Oligocene Haselbacher clay (Mai & Walther, 1978). The species is related to the fossil *S. camenzianum* Kirchheimer (1941b), but differs in the more slender shape of the fruits and the less distinct apical neck. It is distinguished from most other fossil *Sparganium* by its smaller size. The species has been recorded from Middle Oligocene to Middle Miocene floras of Central Europe (Mai & Walther, 1978).

Sparganium cf. *simplex* Huds.
Plate 28, figs 3–4.

1979 *Sparganium camenzianum* Kirchheimer – Friis, p. 138, Figs. 10T–U.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard S (Damgaard flora).
Material. – 20 endocarps. (1079.01–02; 2079.01;3079.01; SEM–100,–118,–328).
Description and remarks. – The endocarps are one-loculed or rarely two-loculed, broadly fusiform in outline, narrow apically into a short oblique neck with a subcircular germination aperture (Pl. 28, figs 3–4). They are 2.1(2.77)4.2 mm long and 1.1(1.59)2.1 mm broad. The endocarp wall is about 0.2 mm thick, composed of an inner sclerenchyma layer of transversely elongate cells with thickened and strongly pitted walls, and an outer layer of equiaxial cells with slightly thickened walls. About 10 distinct vascular bundles extend from base to apex.

The endocarps differ from those of *Sparganium pusilloides* in their larger size, broader shape and much thicker endocarp wall. They are similar in size and shape to the fossil *S. camenzianum,* but differ in the thicker wall.

Sparganium multiloculare E.M. Reid & Chandler

1926 *Sparganium multiloculare* n. sp. – E.M. Reid & Chandler, p. 63, Pl. 3:12–18.

1909 *Sparganium ramosum* – Hartz, p. 126, Pl. 5:14–16.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 endocarp (SEM–118).
Description and remarks. – The endocarp is four-loculed, 3.2 mm long and 2.0–4.2 mm broad with a few prominent longitudinal ridges. In general structure it is similar to endocarps of *Sparganium multiloculare* described from the Oligocene of southern England. The species has also been recorded from Oligocene and Miocene floras of Central Europe and Western Siberia (Mai, 1967; Dorofeev, 1963a).

Incertae sedis

Aracispermum Nikitin ex Dorofeev

Aracispermum canaliculatum Nikitin ex Dorofeev
Plate 28, figs 5–6.

1963a *Aracispermum canaliculatum* Nikitin – Dorofeev, p. 134, Pl. 17:40–43.
1965 *Aracispermum canaliculatum* Nikitin sp. nov. – Nikitin, p. 66, Pl. 8:1–4.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 10 seeds (1085.01; SEM–77,–125,–330).
Description and remarks. – The seeds are anatropous, narrowly obovate in outline with slightly pointed base and oblique truncate apex with a subcircular aperture, about 0.6 mm in diameter (Pl. 28, figs 5–6). They are 2.7–3.4 mm long and 0.9–1.4 mm broad. The seed wall is thick and comprises three distinct layers. The outer epidermal cells are almost rectangular and longitudinally aligned. The middle layer is thick and formed from isodiametric sclereids with thickened and strongly pitted walls. This layer is most strongly developed along the raphe, which extends from the base to the apex and is delimited by two distinct longitudinal furrows (Pl. 28, figs 5–6). The inner seed wall is formed from one layer of transversely aligned cells with strongly thickened and pitted walls.

The fossil genus *Aracispermum* was established by Nikitin (1965) to accommodate small, smooth seeds with a large micropylar aperture, related to the Araceae, but of unknown generic position. Although the genus was not formally established until 1965, species of *Aracispermum* were described in previous publications (Dorofeev, 1960a, 1963a; Chandler, 1962). The species included in the genus show considerable diversity and they probably represent a number of different genera. According to Mai (in Mai & Walther, 1978) *A. hippuriformis* Nikitin (1965) is closely related to extant *Alpinia Roxb*. of the Zingiberaceae.

The features of the Danish seeds are in complete agreement with those of *A. canaliculatum,* first illustrated by Dorofeev (1955c, 1958b) and described in a later work (Dorofeev, 1963a). The formal establishment of the species was presented by Nikitin (1965). The species has been recorded from the Oligocene and Miocene of Western Siberia, from the Oligocene of Transural and from the Miocene of Europe (Dorofeev, 1955c, 1958b, 1960a, 1963a, 1966c; Nikitin, 1965; Łańcucka-Środoniowa, 1966; Mai, 1967; Gregor, 1978a). The fossil seeds described by Chandler (1963b) as *Carpolithus* sp. (p. 152, Pl. 24: 25–26) from the Lower Tertiary of southern England are similar to *A. canaliculatum* in general appearance and should possibly be referred to this species.

Carpolithes Brogniart

Carpolithes natans Nikitin ex Dorofeev
Plate 28, fig. 7; Fig. 15.

1963a *Carpolithus natans* Nikitin – Dorofeev, p. 277, Pl. 49: 13–15.
1965 *Carpolithus natans* Nikitin – Nikitin, p. 95, Pl. 20:10–15.
1978 *Punica natans* (Nikitin) Gregor – Mai & Walther, p. 105, Pl. 41:1–3.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – About 70 seeds (1086.01–02; 2086.01–03; SEM–101,–328).
Description and remarks. – The seeds are anatropous or slightly campylotropous, irregular in shape and

with angular faces. There is an obtriangular to obovate germination valve in the lower half of the seed (Pl. 28, fig. 7). The seeds are 2.8(3.99)5.0 mm long and 1.4(1.86)2.9 mm broad. The hilum is marked by an angular scar at the base of the seed. The embryo cavity is elongated and more or less curved. The raphe is placed opposite to the germination valve and enclosed in a hollow, irregular chamber, generally larger than the embryo cavity (Fig. 15). The seed coat overlying the raphal chamber is thin and often abraded. The seed coat surrounding the embryo is 0.2–0.3 mm thick, composed of a thick sclerotic outer layer and a thin membranous inner layer.

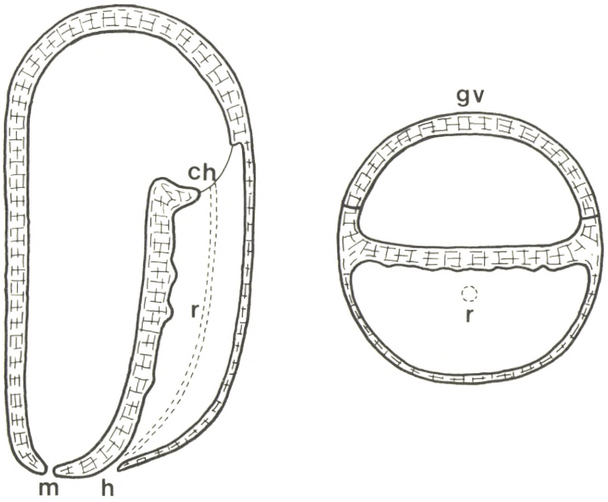


Fig. 15. Schematical section of fossil *Carpolithes natans* from the Fasterholt flora. ch = chalaza, gv = germination valve, h = hilum, m = micropyle, r = raphe.

Carpolithes natans was first proposed for seeds of unknown botanical affinity from the Oligocene of Western Siberia (Dorofeev, 1963a; Nikitin, 1965). The species was later assigned to the extant genus *Punica* L. of the Punicaceae (Gregor, in Mai & Walther, 1978). There are, however, important differences between the fossil seeds and those of extant *Punica,* which make the assignment of the fossils to this genus dubious. The seeds of *Punica* have a marked heteropyle at the top of the germination valve, while in the fossils no heteropyle has been observed. Further, the seeds of *Punica* have no raphal chamber and the raphe overlies the germination valve. In the fossil seeds there is a distinct raphal chamber placed on the opposite side of the germination valve. A raphal chamber comparable to that of the fossil seeds is present in extant *Sonneratia* of the Sonneratiaceae, and there is considerable similarity between these seeds and the fossils. However, the seeds of the Sonneratiaceae and many other Myrtales have a fibrous tegmen, which has not been observed in the fossil seeds, and the generic position of the fossils is still uncertain.

Carpolithes natans has been recorded from several European and Asian Middle Oligocene to Upper Miocene floras and is often found in association with fruits and seeds of *Saururus bilobatus* (Dorofeev, 1963a; Nikitin, 1965; Mai, 1967; Stachurska, Dyjor, Kordysz & Sadowska, 1971; Mai & Walther, 1978; Burgh, 1978).

Carpolithes dorofeevii Friis sp. nov.
Plate 29, figs 1–7.

Derivation of name. – In honour of the palaeobotanist Dr. P. I. Dorofeev.

Specific diagnosis. – Seeds anatropous and narrowly ellipsoidal with an indistinct raphe and a small apical operculum. Seed coat 0.03–0.06 mm thick formed from an outer layer of shallow, thin-walled cells with polygonal and isodiametric facets, arranged in about 18 longitudinal rows, and an inner layer of sclereids with slightly thickened and finely pitted walls. Sclereids columnar with straight anticlinal walls, or near the micropyle and chalaza thin with deeply stellate-undulate anticlinal walls. Length of seed: 0.72(1.01)1.25 mm; breadth: 0.32(0.43)0.56 mm.

Holotype. – Plate 29, fig. 1 (SEM–69).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middle Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Damgaard N (Søby flora). Lavsbjerg Øst: 51.5–52.0 m; 56.0–56.5 m.

Material. – 107 seeds (1088.01–02; SEM–69,–109).

Description and remarks. – The seeds are narrowly ellipsoidal, rounded at the chalaza and slightly pointed at the micropyle, which is marked by a small conical operculum (Pl. 29, figs 1–3, 5). The seed coat is 0.03–0.06 mm thick formed from two layers of cells. The outer epidermis is rarely preserved. It is formed from shallow, thin-walled cells with polygonal and isodiametric facets, arranged in about 18 longitudinal rows (Pl. 29, fig. 1). The inner seed coat is formed from one layer of sclereids with slightly thickened and finely pitted walls (Pl. 29, figs 6–7). Typically the sclereids are columnar, but in the basal and apical parts of the seed they are thin (Pl. 29, figs 3–4). Except for the cells near the micropyle the sclereids have straight anticlinal walls and regular hexagonal cell outlines (Pl. 29, fig. 7). Around the micropyle the sclereids have deeply stellate-undulate anticlinal walls (Pl. 29, fig. 5).

The fossil seeds resemble those of modern *Hypericum* L. in size and shape, but differ in the structure of the seed coat. In the seeds of *Hypericum* the sclereids are of equal size and shape, all with strongly thickened and stellate-undulate anticlinal walls. Sclereids with straight anticlinal walls were not observed in any of the species studied. It has not been possible in the present study to identify any other extant genus with seed characters similar to those of the fossil and they are provisionally assigned to the fossil genus *Carpolithes*.

In general appearance and wall structure the fossil seeds are closely similar to seeds of *Hypericum septestum* Nikitin (var. *sibiricum* Nikitin) described from the Tertiary of Western Siberia (Dorofeev, 1963a; Nikitin, 1965), but differ in being smaller and narrower. The seeds of the fossil species *Hypericum tertiaerum* Nikitin (= *H. septestum* Nikitin var. *typicum* Nikitin) described from the Pliocene of the Voronezh Region are also closely similar to the Danish seeds, but are smaller with higher sclereid cells. They probably all belong to the same natural group. Another species probably related to this group, *Carpolithes nikitinii*, is described below.

Carpolithes nikitinii Friis sp. nov.
Plate 29, figs 9–14.

Derivation of name. – In honour of the late palaeobotanist Dr. P. A. Nikitin.

Specific diagnosis. – Seeds anatropous, ellipsoidal to broadly ellipsoidal with indistinct raphe and a small apical operculum. Seed coat 0.02–0.08 mm thick formed from an outer layer of shallow, thin-walled cells with polygonal and isodiametric facets and an inner layer of sclereids with slightly thickened and finely pitted walls. Sclereids columnar with straight anticlinal walls, or near the micropyle and chalaza thin with deeply stellate-undulate anticlinal walls. Length of seed: 0.55(0.72)0.83 mm; breadth: 0.44(0.53)0.63 mm.

Holotype. – Plate 29, fig. 8 (SEM–109).

Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.

Type stratum. – Odderup Formation.

Age. – Middel Miocene.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 16.0–16.5 m.

Material. – 115 seeds (1090.01–02; SEM–109).

Description and remarks. – The general features of the fossil seeds are those of *Carpolithes dorofeevii*, but can be distinguished by their smaller size, more rounded shape (Pl. 29, figs 8–10) and the size of the sclereids (Pl. 29, fig. 11). In *C. nikitinii*, the sclereids vary in depth from 0.02–0.08 mm, gradually becoming higher towards the middle of the seed (Pl. 29, fig. 10). The facets of the sclereids are typically hexagonal with straight anticlinal walls (Pl. 29, figs 11, 14). Close to the micropyle, the anticlinal walls are deeply stellate-undulate (Pl. 29, figs 12–13).

The fossil seeds are similar to those of the fossil *Hypericum tertiaerum* Nikitin in the size and shape of the sclereids, but differ in their smaller size and more rounded shape.

Carpolithes cf. *nikitinii* Friis

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 11 seeds (1089.01).
Remarks. – The fossil seeds are closely comparable to those of *Carpolithes nikitinii*, but differ in their larger size, more narrow shape and in having a slightly thicker seed coat. Length of seed: 0.87(0.96)1.07 mm; breadth: 0.54(0.59)0.65 mm; thickness of seed coat: 0.02–0.10 mm.

In size and shape the seeds are very similar to those of the fossil *Hypericum tertiaerum* Nikitin (= *H. septestum* Nikitin var. *typicum* Nikitin) from the Pliocene of the Voronezh Region (Nikitin, 1957, 1965). They may belong to the same species, but due to inadequate information on the Voronezh material a definite specific determination of the Danish fossils has not been possible.

Carpolithes tiffneyi Friis sp. nov.
Plate 28, figs 8–10.

Derivation of name. – In honour of the palaeobotanist Dr. B.H. Tiffney.
Specific diagnosis. – Seeds anatropous, unitegmic, irregular ovoid to ellipsoidal with rounded or angular faces. Hilum and micropyle marked by an elongated split near the apex. Seed coat 0.01 mm thick formed from one layer of thin cells with polygonal and equiaxial or elongate cell outlines. Outer periclinal walls membranous, anticlinal and inner periclinal walls thickened and strongly pitted. Length of seed: 0.42(0.53)0.66 mm; breadth of seed: 0.21(0.37)0.49 mm.
Holotype. – Pl. 28, fig. 8 (SEM–123).
Type locality. – C. Nielsen A/S lignite quarry at Fasterholt, Denmark.
Type stratum. – Odderup Formation.
Age. – Middle Miocene.
Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 4 fragments of fruits and 90 seeds (1091.01–02; SEM–25,–120,–123).
Description and remarks. – The structure of the fruits are not clear, as only fragments have been found, but they are apparently bilocular with central and axile placentation and many seeds in each locule. The length of the fruit is about 1.2 mm and the diameter about 1 mm. The seeds are anatropous and probably unitegmic, irregular ovoid to ellipsoidal in outline with angular or rounded faces (Pl. 28, figs 8–9). The seed coat is formed from a single layer of rather large, thin cells with polygonal facets forming a distinct reticulum. The cells are equiaxial or slightly elongate, varying in length from 0.05–0.2 mm. The outer periclinal walls are thin, membranous, and generally not preserved. The inner periclinal and anticlinal walls are thickened and strongly pitted (Pl. 28, fig. 10).

Similar small reticulate and unitegmic seeds occur in many families (e.g. the Ericaceae, Orobanchaceae, Lentibulariaceae, Gentianaceae, Scrophulariaceae). The structure of the fossil fruits may suggest a relationship with members of the Asteridae, but sufficient comparative material has not been available for the present study and the fossils are therefore provisionally assigned to the genus *Carpolithes*.

Carpolithes spp. 1–4

1979 *Carpolithus* sp. 1, sp. 2, sp. 3, sp. 4 – Friis, p. 138–139, figs 11A–F.

Occurrence. – Damgaard S (Damgaard flora).
Material. – Each species contains a single specimen (3106.01–04).
Remarks. – The fruits were described previously (Friis, 1979). No additional material has been recovered.

Carpolithes sp. 5
Plate 30, figs 1–2.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 11 seeds (1096.01; SEM–25,–124).
Description and remarks. – The seeds are ellipsoidal

with oblique base and mucronulate apex (Pl. 30, fig. 1). The micropyle is apical and the basal chalaza is indicated by a circular aperture, about 0.1 mm in diameter. Length of seed: 0.5(0.63)0.75 mm; breadth: 0.37(0.5)0.65 mm; 10 specimens were measured. The seed wall is thin with about 15 distinct nodose ridges extending from base to apex on the outer surface. The cells of the outer seed wall are narrow and transversely elongated, 0.04 mm × 0.005 mm, arranged in longitudinal rows with two rows between the ridges (Pl. 30, fig. 2).

Small ellipsoidal seeds with longitudinal ridges and transversely elongated surface cells have been observed in several families (e.g. the Pontederiaceae and Scrophulariaceae). However, none of the modern species studied are in complete agreement with the fossil seeds. The seeds of the Pontederiaceae usually have a smaller number of ridges (8–10) and the ridges are generally thin easily abraded. The surface cells are much larger than in the fossils with only a single row of cells between two ridges.

Carpolithes sp. 6
Plate 30, figs 4–6.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – About 60 seeds (1097.01; 2097.01; SEM–97).
Description and remarks. – The seeds are narrowly ovate in outline and flattened with mucronate apex and rounded base (Pl. 30, figs 4–5). Length of seed: 1.3(1.49)1.8 mm; breadth: 0.45(0.59)0.7 mm; 25 specimens were measured. The seed coat is thin formed from an outer layer of thick-walled cells resembling osteosclereids, and an inner layer of longitudinally elongated cells with straigh transverse anticlinal walls and undulate longitudinal anticlinal walls (Pl. 30, fig. 6).

The seeds show some similarity to those of the fossil *Vallisneria ovalis* Mai (in Mai & Walther, 1978) described from the Oligocene of GDR, but differ in their smaller size. There is no information on cell structure. No comparative material of modern *Vallisneria* have been available for the present study.

Carpolithes sp. 7
Plate 30, fig. 3.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 1 seed (SEM–97).
Description and remarks. – The seed is anatropous, 1.2 mm long and 0.7 mm wide, elliptic in outline and slightly compressed laterally with a distinct raised raphe (Pl. 30, fig. 3). The micropyle is apical marked by a circular aperture, about 0.1 mm in diameter. The hilum is marked by an elongated scar below the micropyle. The seed coat is about 0.01 mm thick. The cells of the outer epidermis are narrow, transversely elongated and arranged in about 16 longitudinal rows. At the micropylar area and at the raphe the cells are almost isodiametric.

The seeds show some similarity with those of the Nymphaeaceae, but no modern equivalent has yet been found. In general appearance *Carpolithus* sp. 4 (Mai, 1964; Mai & Walther, 1978) from the Oligocene and Miocene of Central Europe is similar to the Danish seed, but differs in its larger size.

Carpolithes sp. 8
Plate 30, fig. 7.

Occurrence. – C. Nielsen A/S (Fasterholt flora).
Material. – 6 fruits (1103.01; SEM–81).
Description and remarks. – The fruits are 1.0–1.1 mm long and 0.75–0.82 mm broad, one-loculed, laterally flattened and irregular ovate in outline with subcircular dorsal margin and slightly convex ventral margin (Pl. 30, fig. 7). The base of style is slightly hook-shaped and curved forward. The outer surface has an indistinct ridge which parallels the margin of the fruit and a number of small protrusions at the middle of the fruit (Pl. 30, fig. 7). The fruit wall is about 0.02 mm thick formed from an inner layer of transversely elongate sclereids and an outer layer of isodiametric sclereids with polygonal facets.

The fossil fruits are similar in general appearance to fruits of modern *Laportea* Gaudich. (Urticaceae) and some *Ranunculus* L. (Ranunculaceae), but none of them show complete agreement with the fossil material.

Rhamnospermum Chandler

Rhamnospermum bilobatum Chandler
Plate 30, figs 8–10.

1925 *Rhamnospermum bilobatum,* n. gen. et sp. – Chandler, p. 30, Pl. 5: la–c, Fig. 13.

Occurrence. – C. Nielsen A/S (Fasterholt flora). Lavsbjerg Øst: 47.5–48.0 m; 54.5–55.0 m; 55.5–56.5 m; 57.5–58.0 m.
Material. – About 48 specimens (1101.01–02; 2101.01; SEM–41).
Description and remarks. – The fossils are sub-circular in outline and bilobed, the lobes being separated by a deep grove which in the middle has a circular aperture, about 0.5 mm in diameter (Pl. 30, fig. 8). On the other side of the fossil there is another circular aperture which is usually covered by a small conical operculum (Pl. 30, fig. 9). The wall is thin and membranous formed from two layers. The outer layer is black and lustreless, sculptured by anastomosing ridges forming a reticulum of polygonal lumina arranged in longitudinal rows radiating from the apertures. The surface of lumina is ornamented by small, closely spaced protrusions (Pl. 30, fig. 10). The inner layer of the wall is black, shiny and sculptured with sharp ridges forming a regular reticulum.

The fossils are in complete agreement with those of *Rhamnospermum bilobatum* described from the Lower Tertiary of southern England. They were originally described as seeds related to modern *Rhamnus* L. (Chandler, 1925). Later Chandler (1960a, 1962) expressed some doubt as to the nature of the fossils.

The wall structure of the fossils is unlike the structure observed in other plant remains and it is possible that the fossils have been derived from some kind of animal.

Acknowledgements

This paper is an abbreviated revision of my licentiate dissertation completed at the University of Aarhus, 1980. I am grateful to Dr. F. Holý, Narodní Museum, Praha, who introduced me to the study of fossil fruits and seeds, and to Dr. M. Łańcucka-Środoniowa, Botanical Institute PAN, Cracow, for valuable guidance during the early part of this study. I am greatly indebted to Dr. M.E. Collinson, University of London, Dr. P.R. Crane, Field Museum, Chicago, and Dr. B.H. Tiffney, Yale University, New Haven, for valuable critism of the manuscript and for improving the English text. Thanks are also due to Dr. C. Blanc, Muséum National d'Historie Naturelle, Paris, Dr. J.D. Brisson, National Research Council, Canada, Dr. P.I. Dorofeev, Botanical Institute, AN, Leningrad, Dr. G.F. Elliot, British Museum (Nat.Hist.), London, Dr. H. Friis, University of Aarhus, Dr. S. Graham, Kent State University, Dr. J. Gregor, University of Munich, Dr. J. Ingram, Cornell University, Dr. D.H. Mai, Humboldt University, Berlin, Dr. K. Raunsgaard Pedersen, University of Aarhus, Dr. J. Raniecka-Bobrowska, Geological Institute, Warsaw, and Dr. H. Sleumer, Rijksherbarium, Leiden, for valuable help and material. Dr. B. Hansen, University of Copenhagen, and Dr. K. Larsen, University of Aarhus are thanked for the permission to study modern fruits and seeds at their institutions. Dr. H.J. Hansen, University of Copenhagen, is thanked for the permission to use the scanning electron microscope at the Geology Department. I also thank M. Dybdahl, L. Eklund-Jürgensen, L. Jans, J. Gissel Nielsen, and J. Sommer for valuable help in preparing typescript and illustrations. The study is part of the "Søby-Fasterholt project" conducted by B.E. Koch, who provided some of the material. The study was supported by the Danish Natural Science Research Council. I gratefully acknowledge the receipt of a Niels Bohr Fellowship which has enabled me to prepare this paper.

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Indleveret til Selskabet maj 1984.
Færdig fra trykkeriet april 1985.

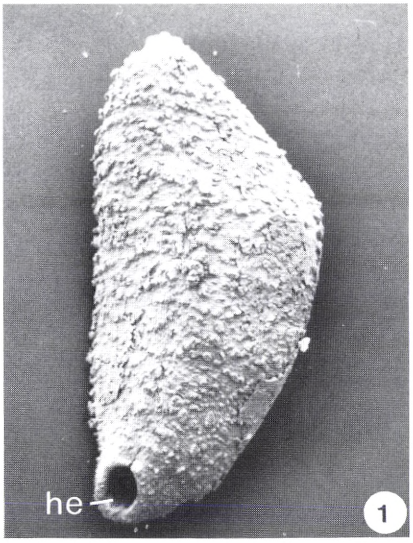
Plate 1–30

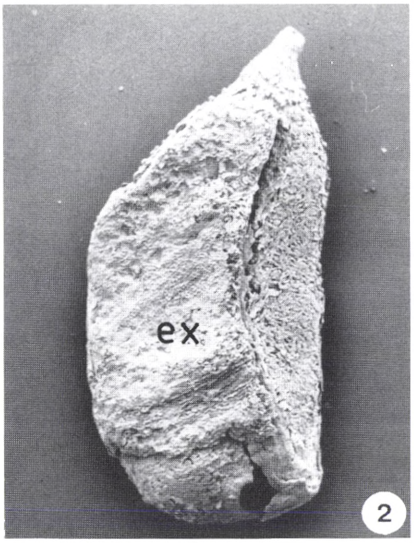
PLATE 1

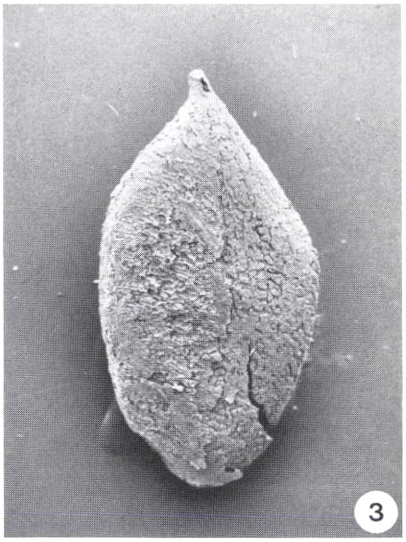
Fossil *Liriodendron* sp. from the Middle Miocene Fasterholt flora.

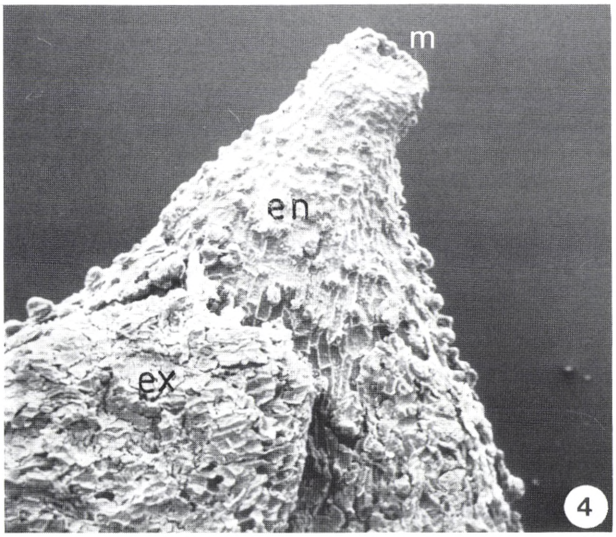
1. Ventral view of seed showing surface of endotesta and a marked basal heteropyle (SEM–304_1, ×20).
2. Ventral view of seed with remnants of exotesta (SEM–304_2, ×20).
3. Dorsal view of seed with remnants of exotesta (SEM–304_3, ×20).
4. Apical part of seed with micropyle (same specimen as in fig. 2, SEM–304_2, ×80).
5. Basal part of seed with heteropyle (SEM–50_3, ×80).
6. Section of seed wall showing endotestal cells with fibrous lignifications (SEM–305_1, ×850).
7. Section of seed wall showing endotestal cells with fibrous lignifications and imprints of crystals (1001.31, ×500).

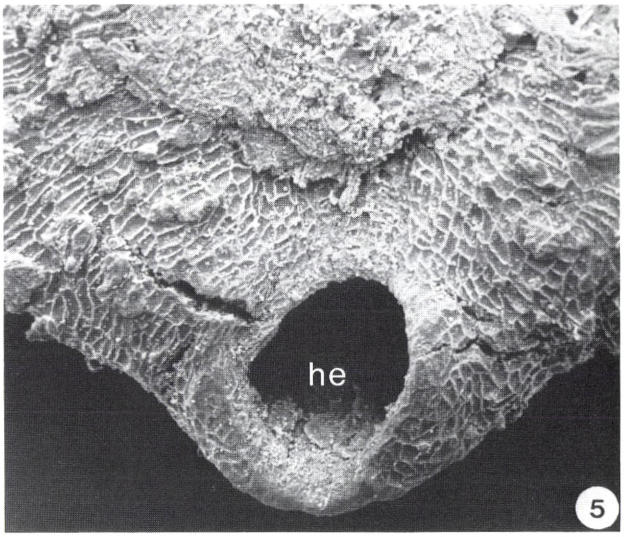
All figures SEM except fig. 7 which is transmitted light micrograph.
en = endotesta, ex = exotesta, he = heteropyle, c = imprint of crystal, m = micropyle.

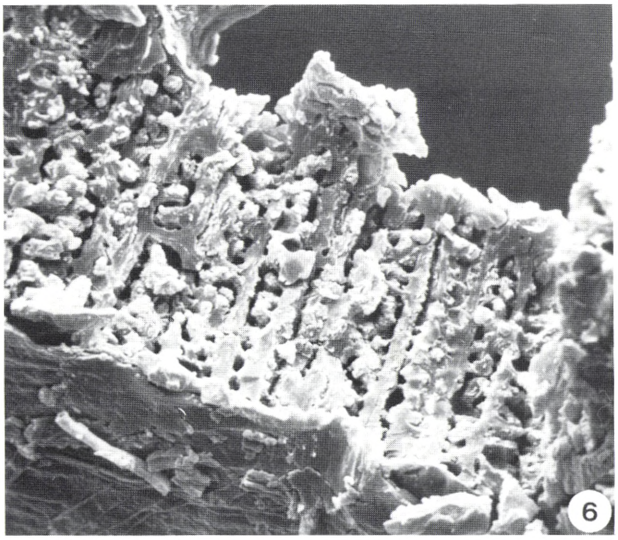












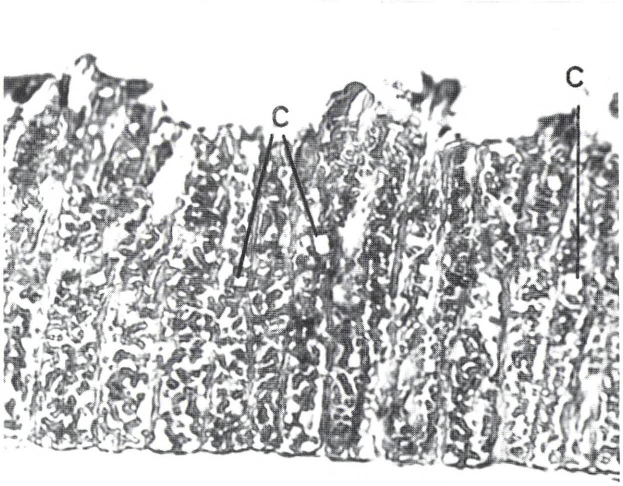


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PLATE 2

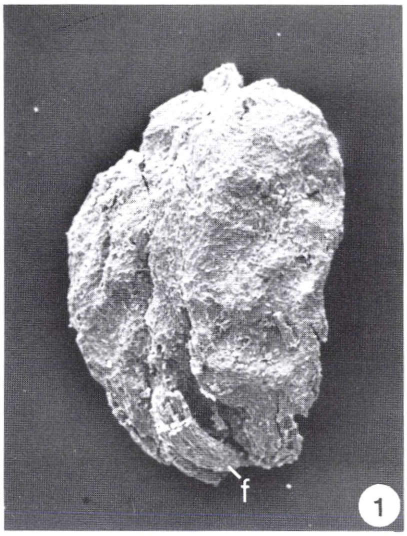
Fossil *Saururus bilobatus* (Nikitin ex Dorofeev) Mai from the Middle Miocene Fasterholt flora (figs 1–6).

1. Dorsal face of fruitlet with remnant of filament (SEM–114_8, ×55).
2. Ventral face of fruitlet (SEM–102_1, ×38).
3. Seed showing transversely elongated testal cells and sub-basal chalaza (SEM–310_3, ×75).
4. Surface of fruitlet with irregular tubercles (SEM–102_3, ×150).
5. Section of fruit wall showing strongly pitted cells and large intercellular spaces (SEM–102_4, ×750).
6. Section of seed wall showing thin-walled testal cells and strongly thickened cells of tegmen (SEM–102_5, ×750).

Extant *Saururus cernuus* L. from eastern North America (figs 7–9).

7. Dorsal face of fruitlet with irregular tubercles (SEM–311_1, ×30).
8. Section of fruit wall showing strongly pitted cells and large intercellular spaces (SEM–311_3, ×375).
9. Seed showing transversely elongated testal cells and sub-basal chalaza (SEM–311_2, ×55).

All figures SEM.
ch = chalaza, f = filament, ta = testa, tn = tegmen.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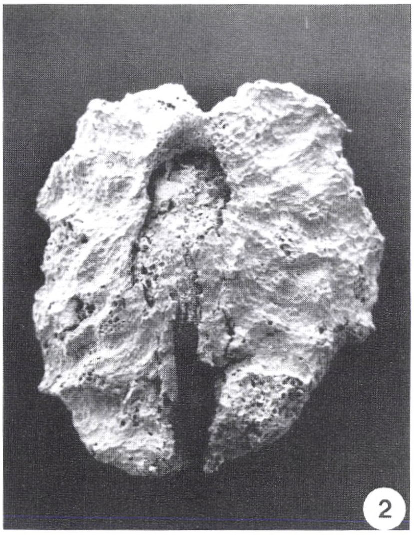
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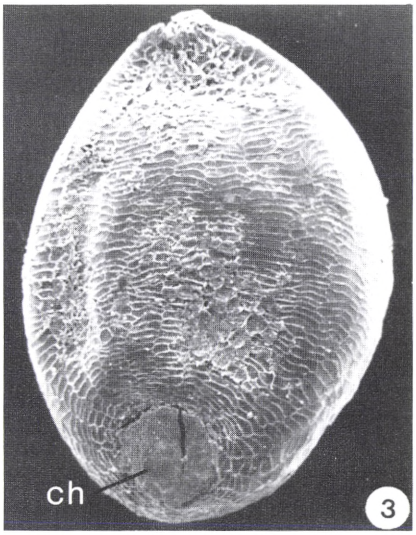
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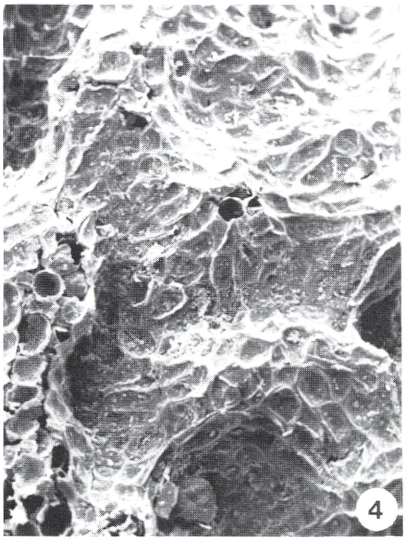
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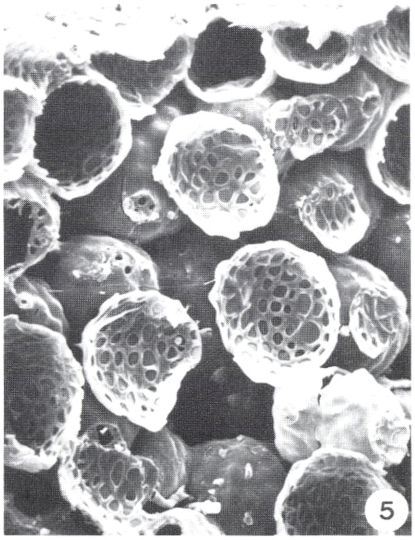
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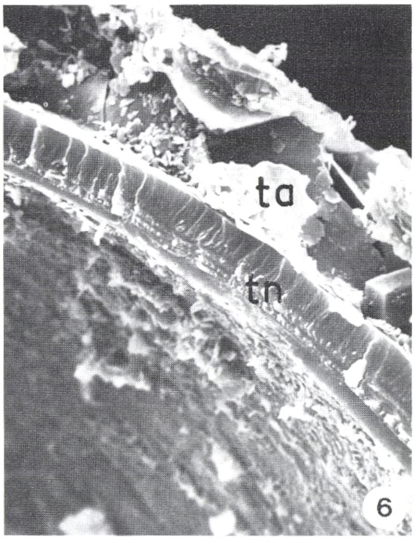
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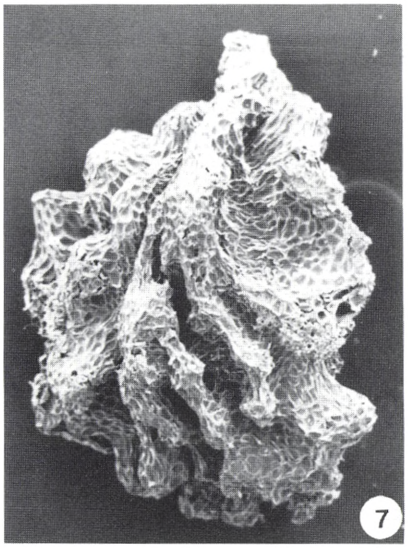
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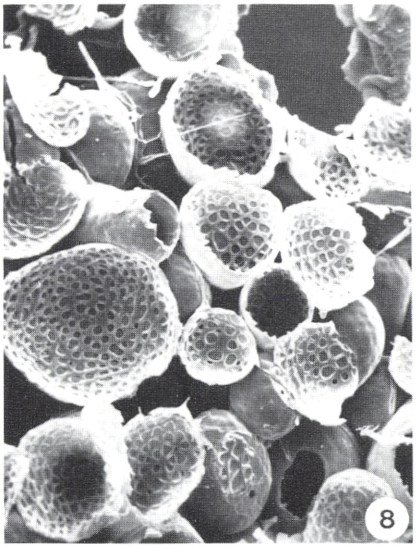
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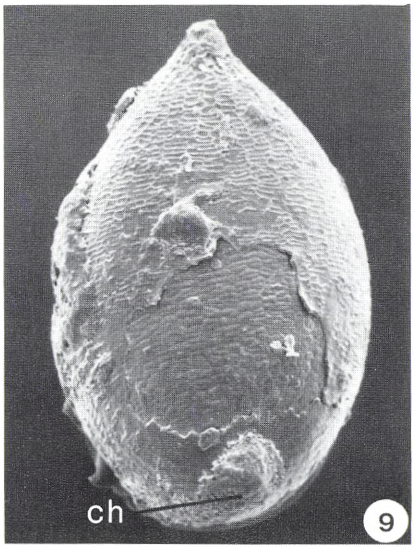
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PLATE 3

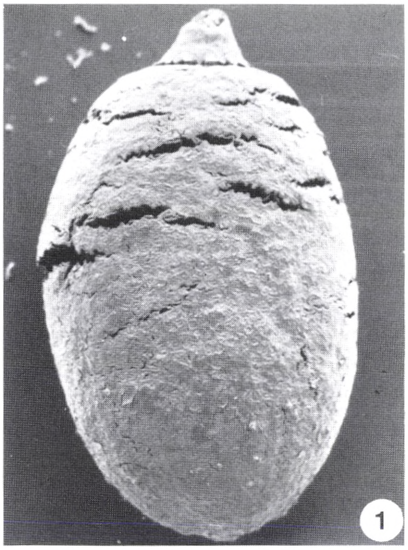
Fossil *Brasenia* cf. *tenuicostata* Nikitin from the Middle Miocene Fasterholt flora (figs 1–6).

1. Seed with the apical operculum preserved (SEM–305_4, ×40).
2. Detail of fig. 1 showing surface of seed with stellate-undulate anticlinal walls of sclereids (SEM–305_4, ×470).
3. Detail of fig. 1 showing basal tubercle (SEM–305_4, ×935).
4. Section of seed showing columnar cells of testa (SEM–305_5, ×40).
5. Detail of testa showing pitted walls of sclereids (SEM–305_5, ×400).
6. Apical part of tegmen showing micropyle and cells with undulate anticlinal walls (1003.14, × 100).

Fossil *Nymphaea* sp. 1 from the Middle Miocene Fasterholt flora (figs 7–9).

7. Seed with remnants of hairs (SEM–54_1, ×50).
8. Surface detail of seed with stellate-undulate sclereids and remnants of hairs (SEM–54_1, ×350).
9. Surface of sclereids with stellate-undulate anticlinal walls (SEM–54_1, ×700).

All figures SEM except fig. 6 which is transmitted light micrograph.
ha = hair, m = micropyle, ta = testa, tn = tegmen.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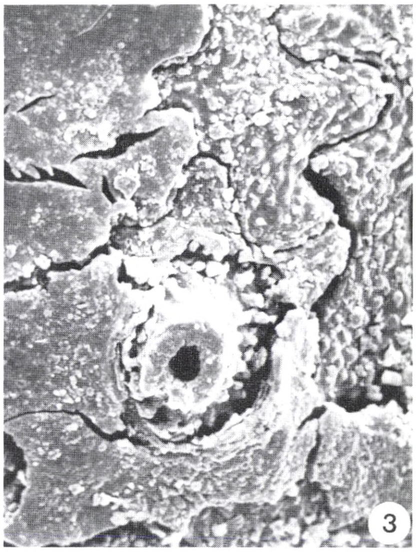
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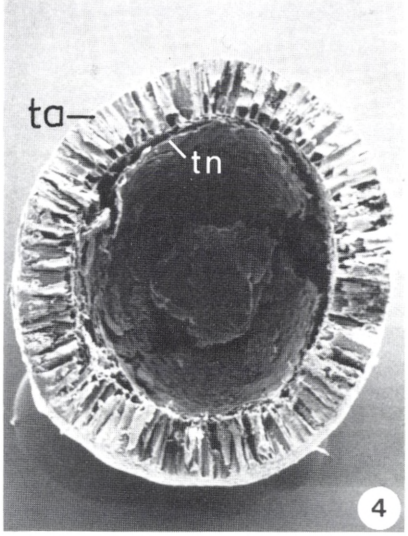
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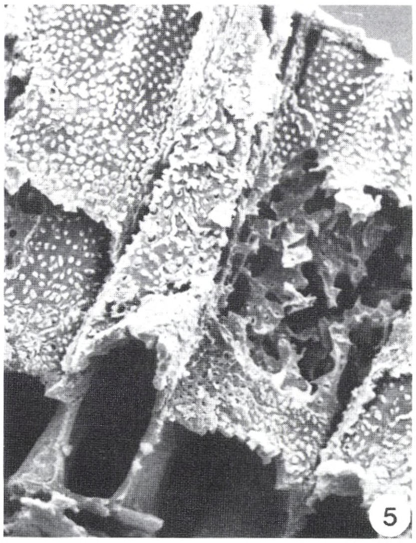
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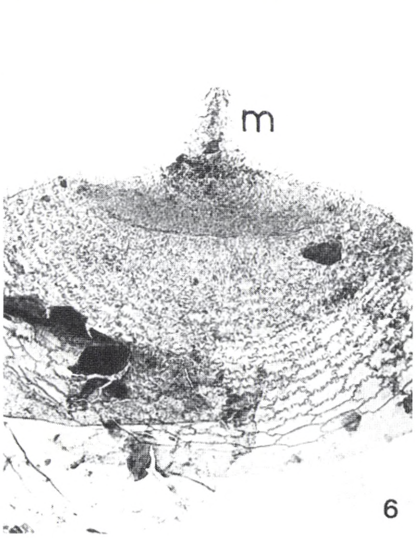
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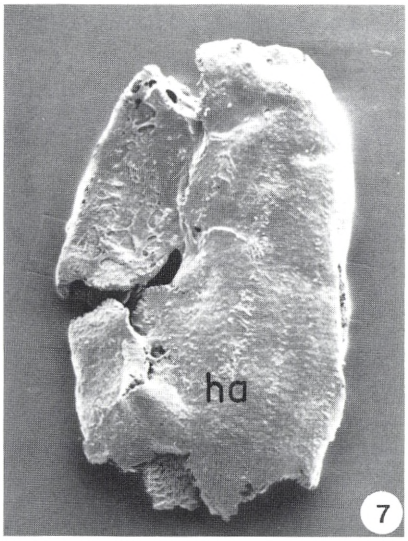
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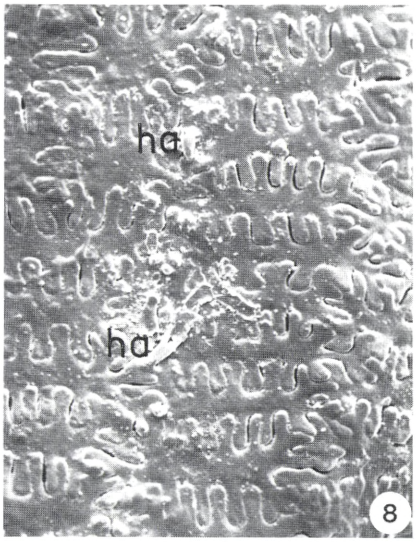

ha
ha
8


9

PLATE 4

Fossil *Nymphaea* sp. 2 from the Middle Miocene Fasterholt flora (figs 1–3).

1. Seed (SEM–54_3, ×50).
2. Surface detail of seed showing stellate-undulate walls of sclereids (SEM–54_3, ×350).
3. Surface of sclereid with stellate-undulate anticlinal walls (SEM–54_3, ×700).

Fossil *Liquidambar* sp. from the Middle Miocene Fasterholt flora (figs 4–6).

4. Seed with marked hilar scar (SEM–310_4, ×55).
5. Seed (SEM–124_8, ×38).
6. Section of seed showing columnar testal cells (SEM–124_9, ×75).

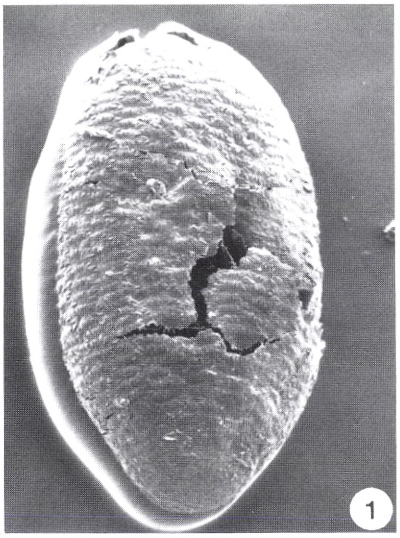
Extant *Liquidambar styraciflua* L. from North America (fig. 7).

7. Section through aborted seed showing columnar testal cells (SEM–67_7, ×150).

Fossil *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček from the Middle Miocene Fasterholt flora (figs 8–9).

8. Fruitlet with remnants of style and distinct apical split (1008.01, ×8).
9. Cuticle of fruitlet showing structure of epidermis with hair bases (1008.12, ×100).

All figures SEM except fig. 8 which is reflected light micrograph and fig. 9 which is transmitted light micrograph.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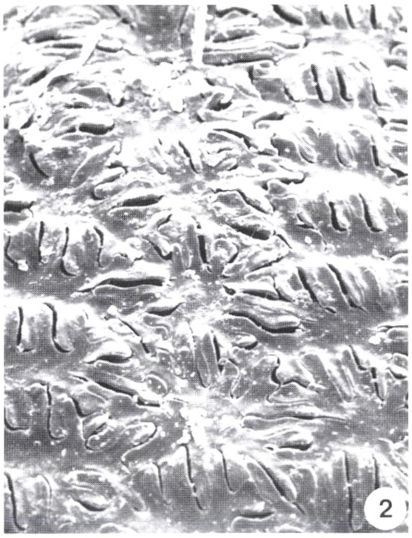
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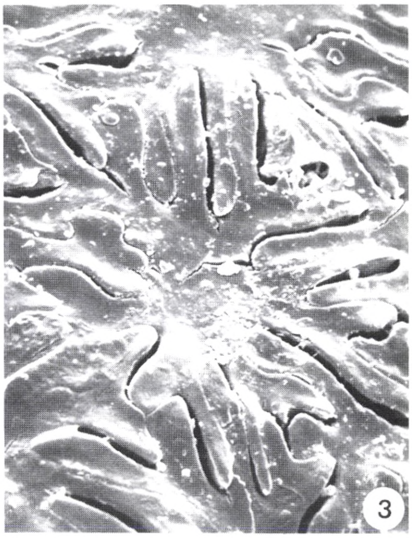
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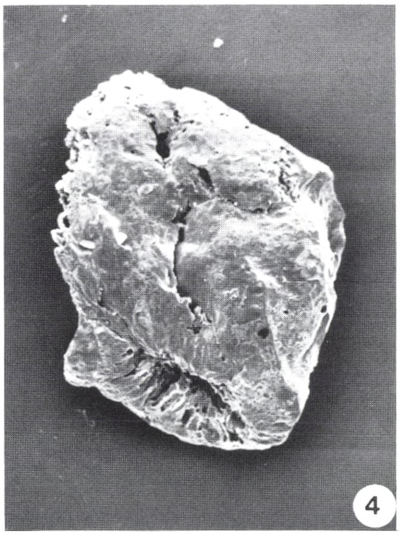
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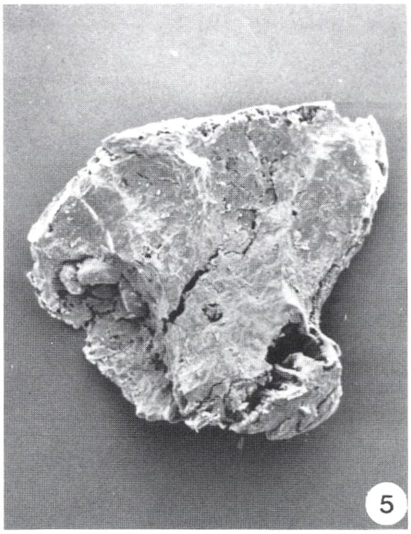
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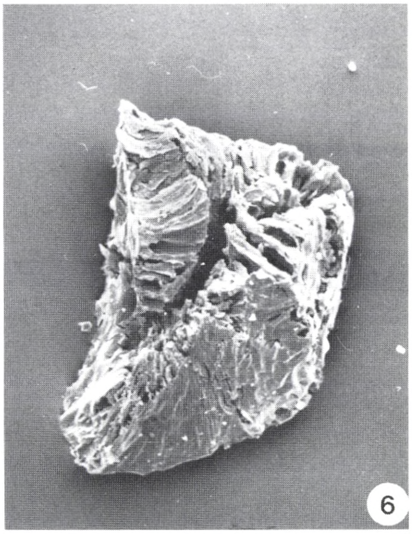
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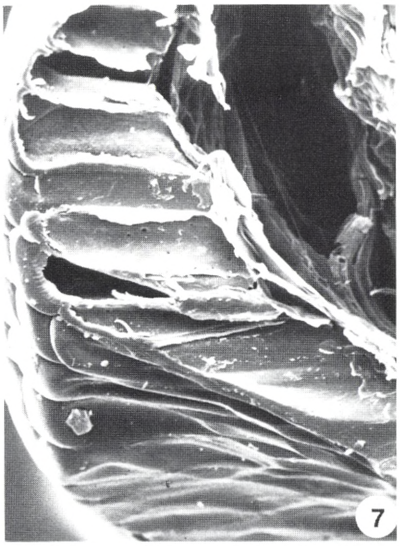
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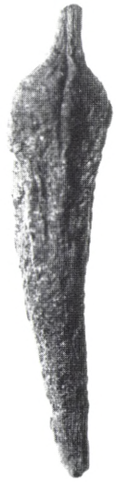
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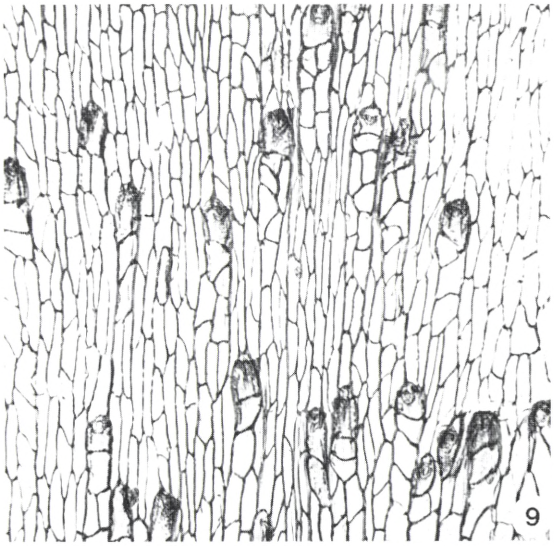
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PLATE 5

Fossil *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček from the Middle Miocene Fasterholt flora (figs 1–5).

1. Staminate axis borne on a thick peduncle and with remnants of flowers (SEM–107, ×15).
2. Detail of staminate axis showing remnants of flowers (SEM–107, ×60).
3. Detail of flower showing eight central protrusions (reduced carpels?) surrounded by seven elongated structures (scars from stamens?) (SEM–107, ×90).
4. Tricolpate pollen grains from surface of staminate axis (SEM–107, ×1200).
5. Tricolpate pollen grains from staminate axis showing granulate surface of colpi (SEM–107, ×1800).

Fossil pollen of Ulmaceae from the Middle Miocene Fasterholt flora (figs 6–7).

6. Pollen grains in anther (SEM–86, ×750).
7. Single pollen grain from same anther as fig. 6 (SEM–86, ×1500).

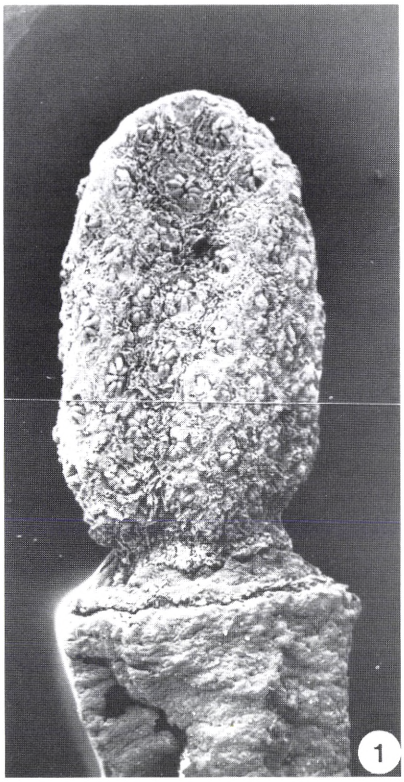
Fossil pollen of *Alnus* from the Middle Miocene Fasterholt flora (figs 8–9).

8. Anther with tetraporate pollen grains (SEM–66, ×300).
9. Single pollen grain from same anther as fig. 8 (SEM–66, ×2400).

Fossil *Tubela* cf. *baltica* (Dorofeev) Dorofeev from the Middle Miocene Fasterholt flora (figs 10–11).

10. Dorsal side of bract scale (SEM–316_1, ×18).
11. Ventral side of same bract scale as fig. 10 (×15).

All figures SEM except fig. 11 which is reflected light micropgraph.



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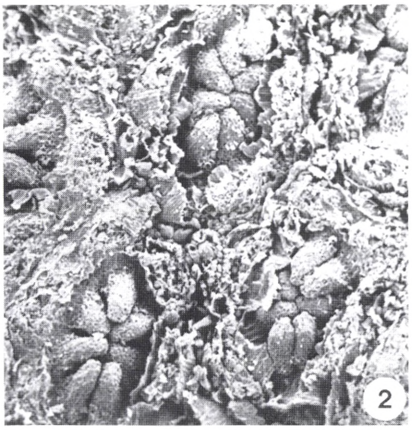

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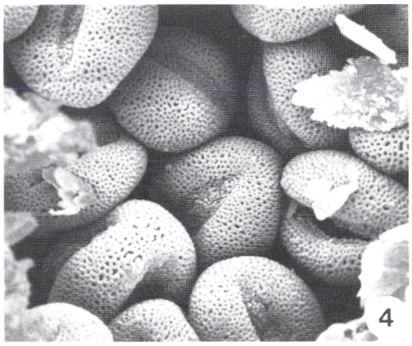

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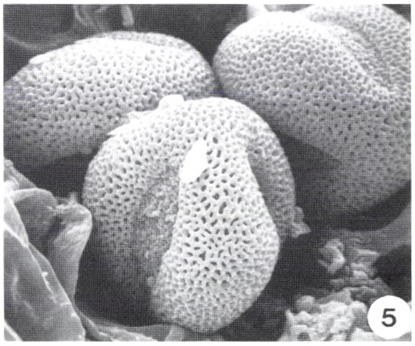

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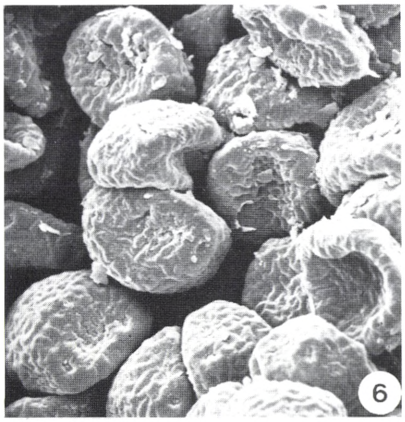

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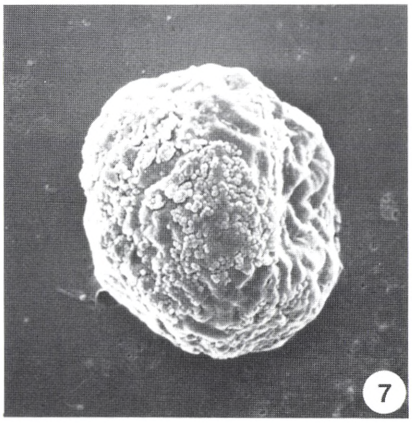

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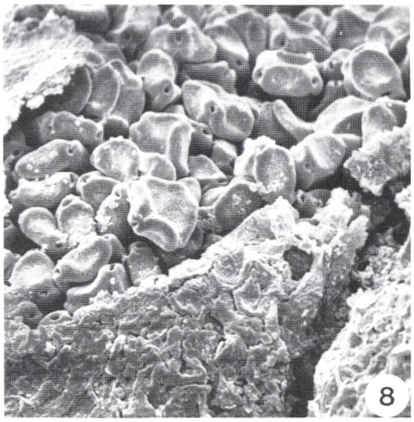

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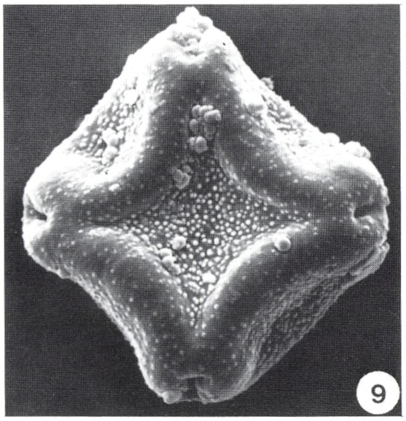

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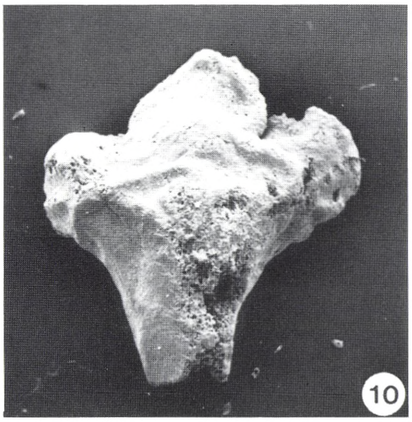

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PLATE 6

Fossil *Tubela* cf. *baltica* Dorofeev from the Middle Miocene Fasterholt flora (figs 1–3).

1. Fruit with remnants of two styles (SEM–68_2, ×25).
2. Fruit with remnants of two styles and with basal attachment scar (SEM–316_2, ×35).
3. Detail of fig. 2 showing apical part of fruit with styles and outlines of epidermal cells (SEM–316_2, ×140).

Fossil endocarps of *Myrica* from Sønderskov near Silkeborg (fig. 4) and from the Fasterholt flora (figs 5–15).

4. *Myrica johnstrupii* (Hartz) Friis comb. nov. Lectotype. Valve of endocarp showing internal morphology of fruit (Coll. Hartz, D.G.U., Copenhagen, ×12.5).

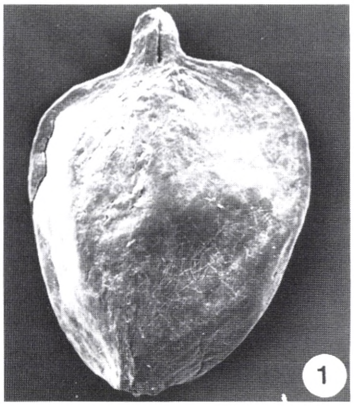
5–6. *Myrica wiesaensis* Kirchheimer. Internal view of endocarps (2012.01–03, ×12.5).

7. *Myrica* sp. Outer surface of fruit with warty emergences of exocarp (1012.09, ×12.5).

8–13. *Myrica* sp. Internal view of endocarps showing variation in size and shape (2012.26–34, ×12.5).

14. *Myrica kirchheimeri* Friis sp. nov. Holotype. Internal view of endocarp (2012.13, ×12.5).
15. *Myrica kirchheimeri* Friis sp. nov. Internal view of endocarp (2012.14, ×12.5).

All figures reflected light micrographs except figs 1–3 which are SEM.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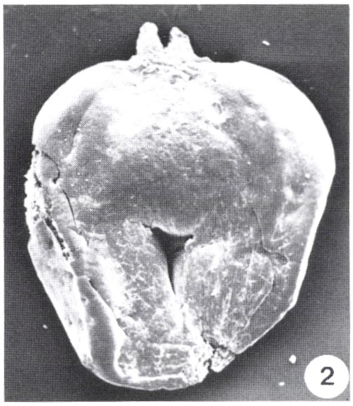
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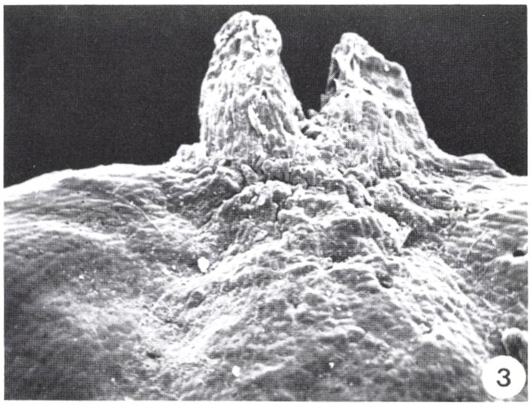
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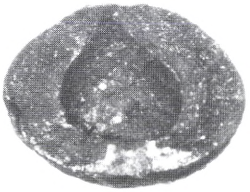
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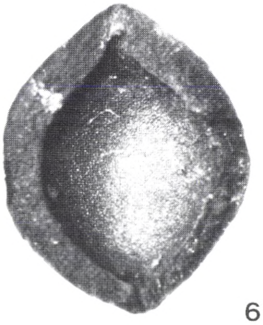
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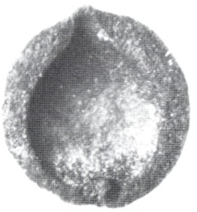
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PLATE 7

Fossil *Rumex* sp. from the Middle Miocene Fasterholt flora (figs 1–3).

1. Fruit (SEM–312_6, ×55).
2. Detail of fruit surface showing longitudinally aligned marginal cells and transversely aligned cells (SEM–312_6, ×650).
3. Cell surface showing undulate anticlinal walls (SEM–312_6, ×1300).

Fossil *Eurya stigmosa* (Ludwig) Mai from the Middle Miocene Fasterholt flora (figs 4–9).

4. External view of seed (SEM–313_1, ×35).
5. External view of seed (SEM–38_2, ×35).
6. External view of seed (SEM–38_3, ×35).
7. Internal view of seed showing condyle, raphe, and seed wall (SEM–38_1, ×35).
8. Detail of seed surface showing funnel shaped testal cells with finely pitted walls (SEM–313_3, ×300).
9. Section of seed wall showing large cells of exotesta and small endotestal cells (SEM–38_1, ×350).

Extant *Eurya* from East Asia (figs 10–12).

10. *Eurya chinensis* R. Br. Internal view of seed showing condyle, raphe, and seed wall (SEM–99_1, ×35).
11. *Eurya chinensis* R. Br. Detail of seed surface showing funnel shaped testal cells with finely pitted walls (SEM–99_2, ×300).
12. *Eurya japonica* Thunb. Section of seed wall showing large cells of exotesta and small endotestal cells with crystals (SEM–39_3, ×350).

All figures SEM.
ch = chalaza, m = micropyle, r = raphe.


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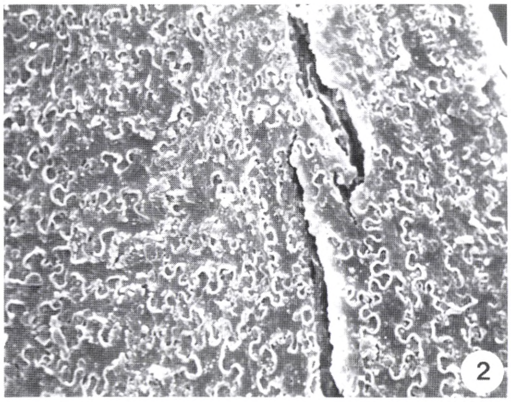
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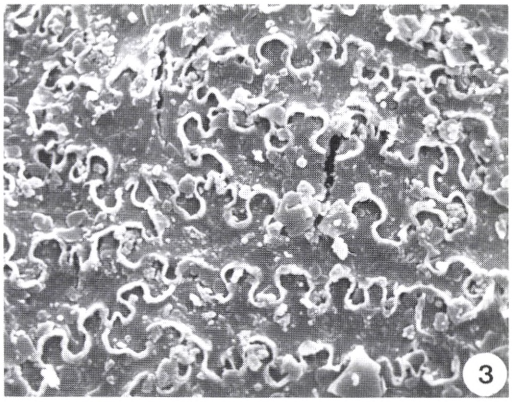
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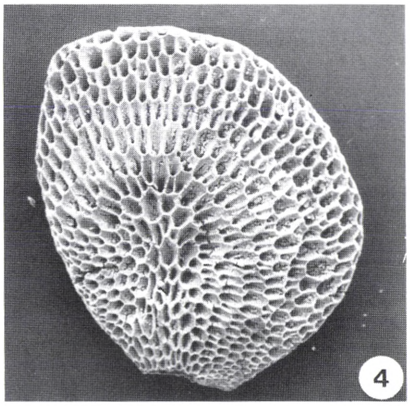
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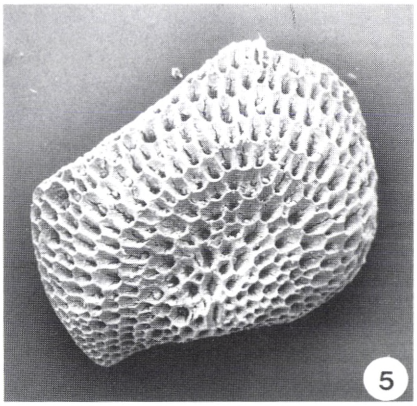
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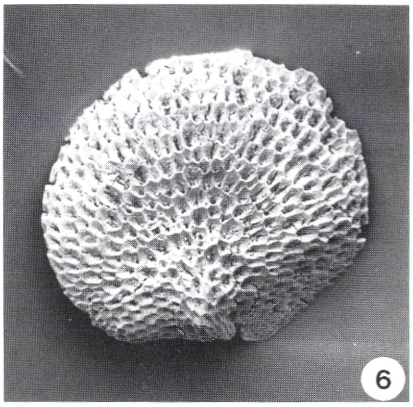
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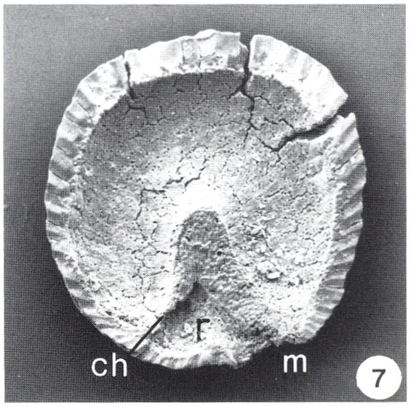

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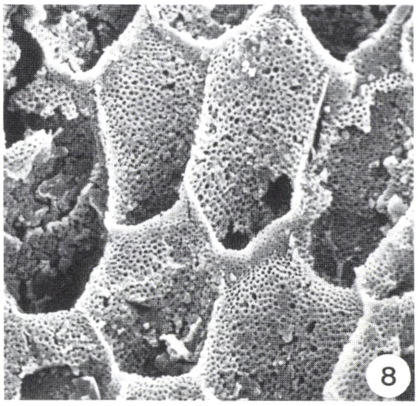
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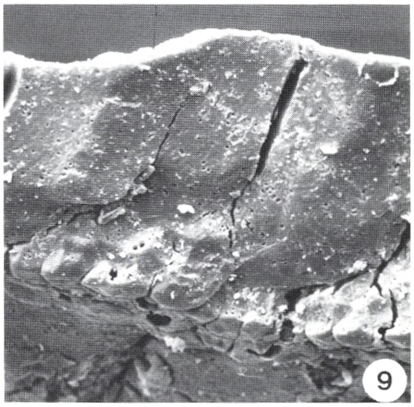
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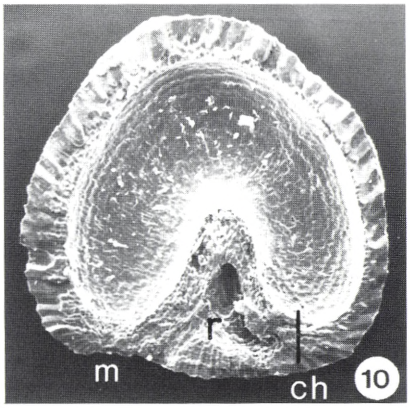

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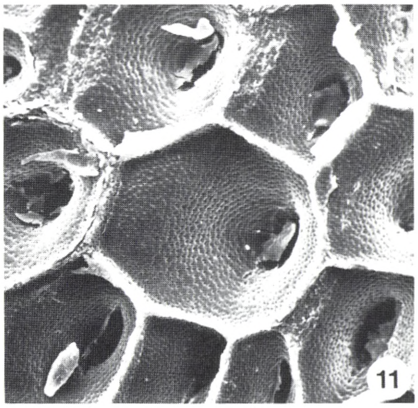
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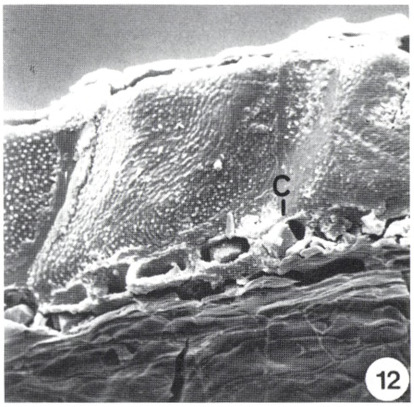

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PLATE 8

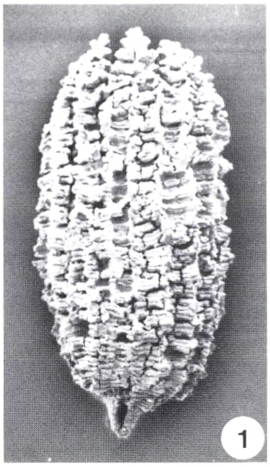
Fossil *Hypericum holyi* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–7).

1. Holotype. Seed with testa preserved (SEM–121, ×50).
2. Seed with remnants of testa (SEM–313_6, ×55).
3. Seed showing surface of tegmen (SEM–313_5, ×55).
4. Apical part of seed showing cells of tegmen with undulate anticlinal walls and remnants of testa (SEM–121, ×130).
5. Detail of seed surface showing narrow cells of testa (SEM–69_4, ×325).
6. Detail of seed showing surface of tegmen with imprints of narrow testal cells (SEM–313_5, ×325).
7. Detail of seed showing surface of tegmen with stellate-undulate and raised anticlinal walls (SEM–313_7, ×350).

Fossil *Hypericum danicum* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 8–13).

8. Holotype. Seed showing reticulate surface of tegmen (SEM–122, ×100).
9. Seed (SEM–312_4, ×100).
10. Detail of seed near apex showing outline of tegmen cells with strongly undulate anticlinal walls (SEM–69_5, ×650).
11. Detail of seed showing surface of tegmen (SEM–69_5, ×650).
12. Detail of tegmen showing strongly pitted and undulate walls (SEM–69_5, ×1300).
13. Section of seed wall showing thickened and pitted walls of tegmen cell (SEM–312_5, ×700).

All figures SEM.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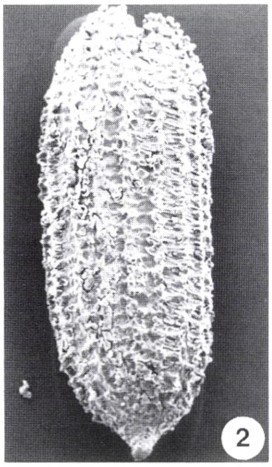
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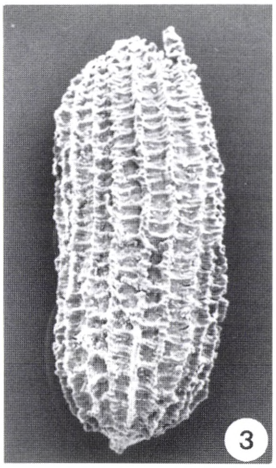
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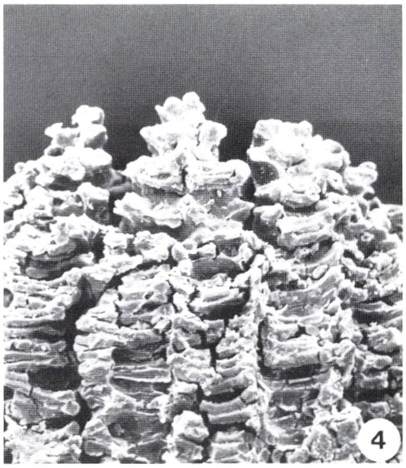
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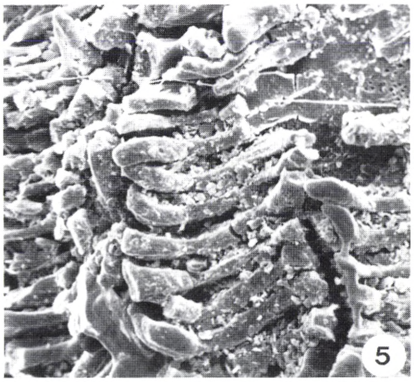
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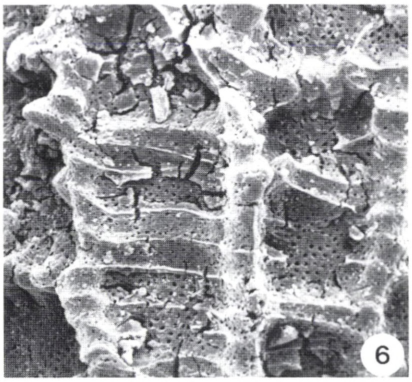
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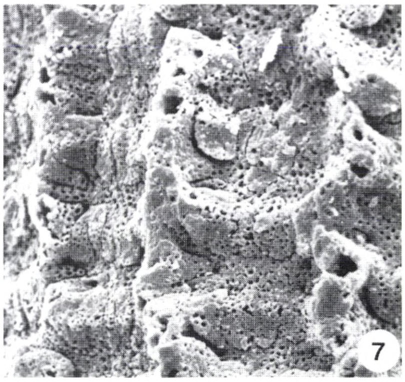
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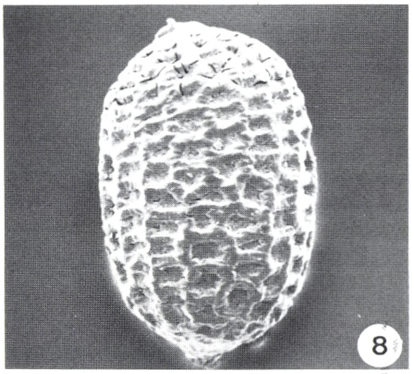
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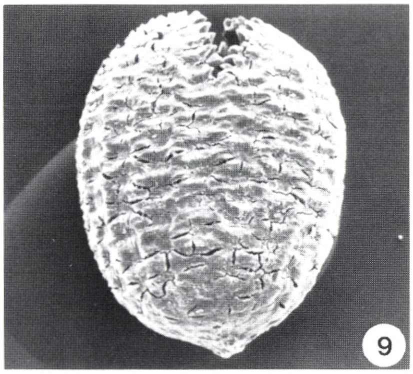
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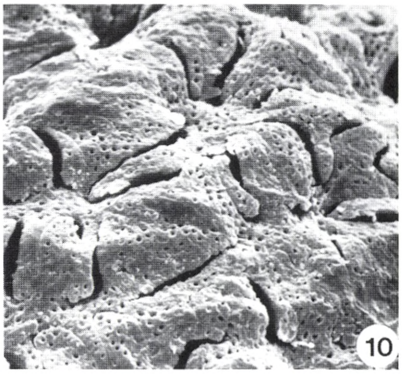
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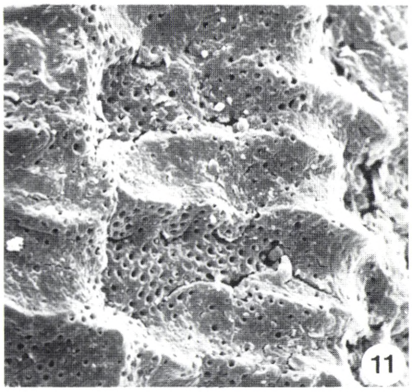
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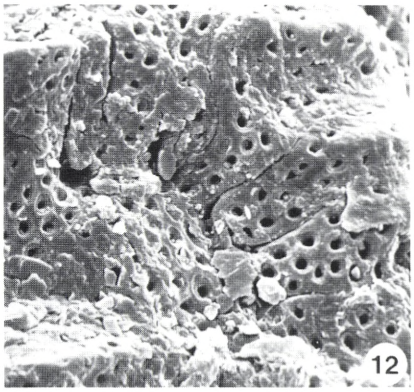
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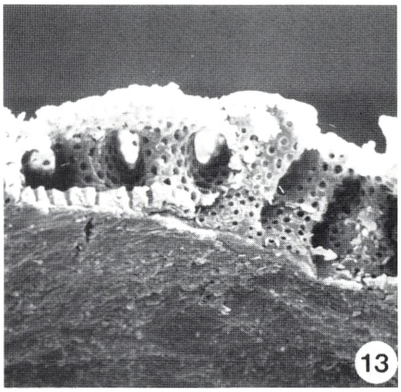
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PLATE 9

Fossil *Poliothyrsis eurorimosa* Mai from the Middle Miocene Fasterholt flora (figs 1–4).

1. Seed with raised chalaza (SEM–71_4, ×50).
2. Seed with longitudinal cracks (SEM–71_5, ×50).
3. Detail of seed surface showing outer epidermis (SEM–312_3, ×350).
4. Section of seed showing longitudinally elongated sclereids (SEM–312_2, ×350).

Fossil *Actinidia* sp. from the Fasterholt Plantage borehole (67.5–68.0 m) (figs 5–6).

5. Seed (SEM–58_1, ×33).
6. Detail of seed surface showing thickened and finely pitted anticlinal and inner walls (SEM–58_1, ×235).

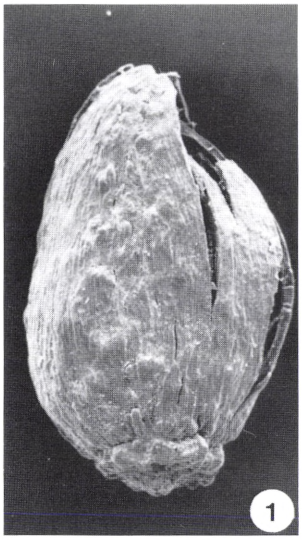
Extant *Actinidia arguta* Franch. & Sav. from East Asia (figs 7–8)

7. Seed (SEM–59_1, ×23).
8. Detail of seed surface showing inner and anticlinal walls (SEM–59_1, ×110).

Fossil *Clethra cimbrica* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 9–11).

9. Holotype. Fruit with seeds (1015.01, ×15).
10. Holotype. One locule has been removed showing position of placenta (1015.01, ×15).
11. Seed with strongly pitted cell walls and serrate margin (1015.04, ×55).

All figures SEM except figs 9–10 which are reflected light micrographs and fig. 11 which is transmitted light micrograph.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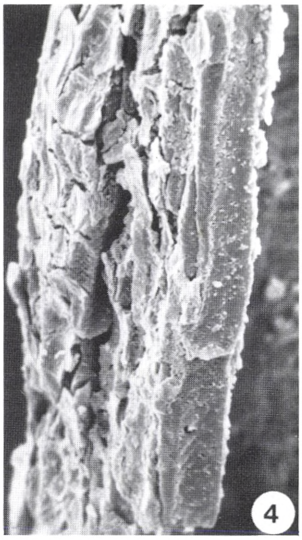
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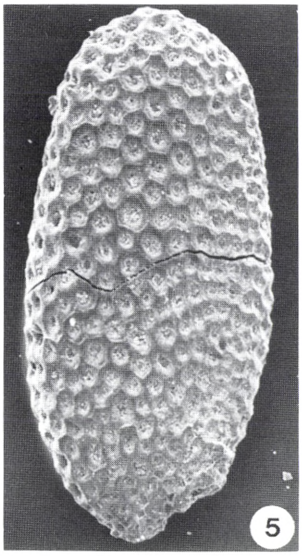
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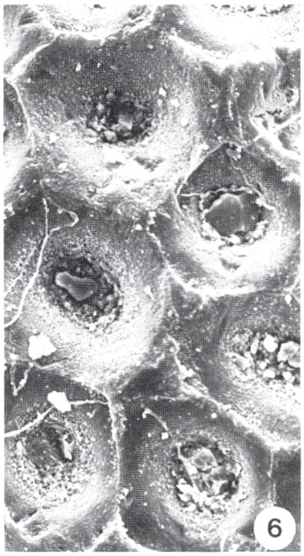
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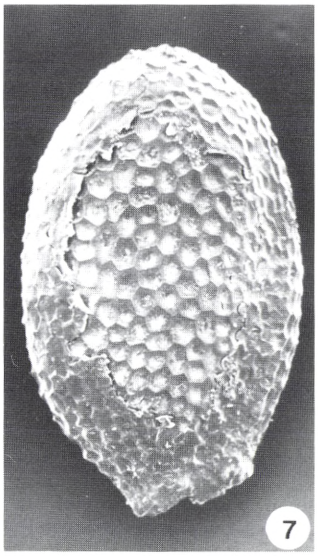
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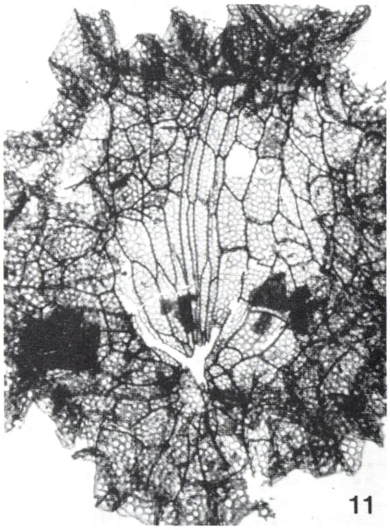
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PLATE 10

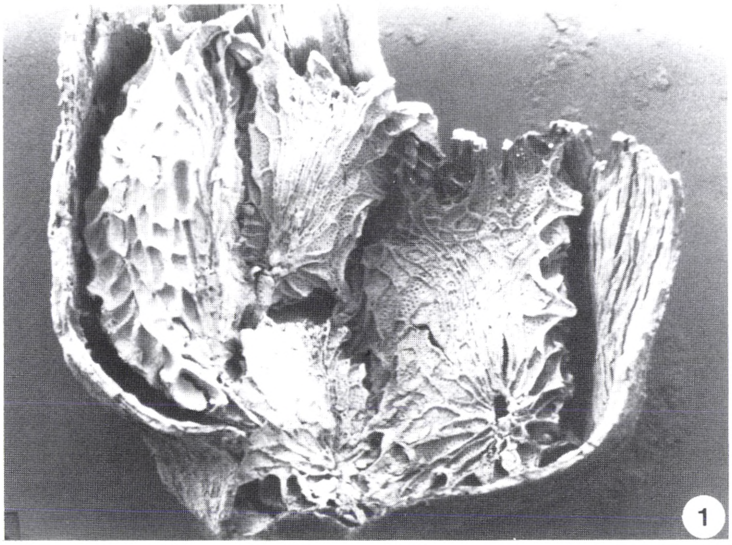
Fossil *Clethra cimbrica* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–4).

1. Fragment of holotype with seeds (SEM–28_1, ×38).
2. Seed with strongly serrate margin (SEM–306_5, ×40).
3. Seed with strongly pitted inner and anticlinal walls (SEM–306_4, ×45).
4. Seed from holotype (SEM–83_4, ×40).

Seeds of extant *Clethra* (figs 5–8).

5. *Clethra arborea* Ait. from Maidera (SEM–315_2, ×40).
6. *Clethra macrophylla* Mart. & Gal. from S. America (SEM–315_4, ×40).
7. *Clethra barbinervis* Sieb. & Zucc. from East Asia (SEM–315_3, ×40).
8. *Clethra alnifolia* L. from eastern North America (SEM–315_5, ×40).

All figures SEM.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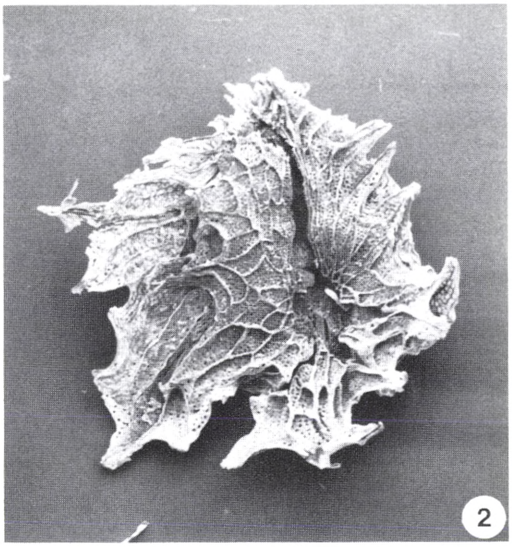
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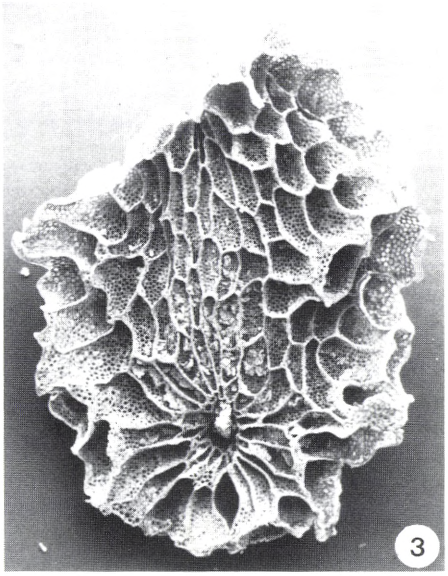
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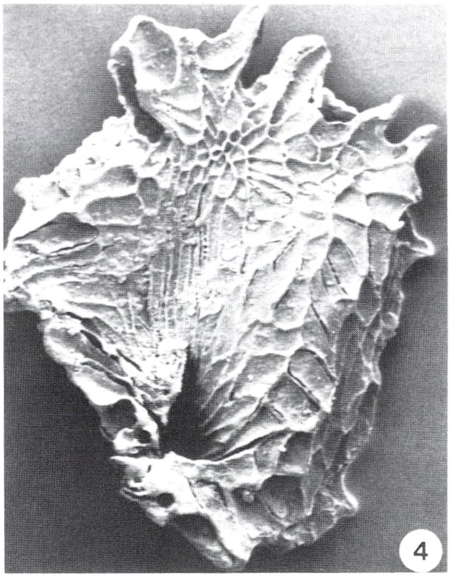
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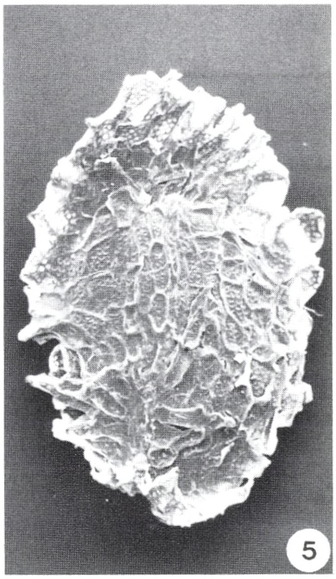
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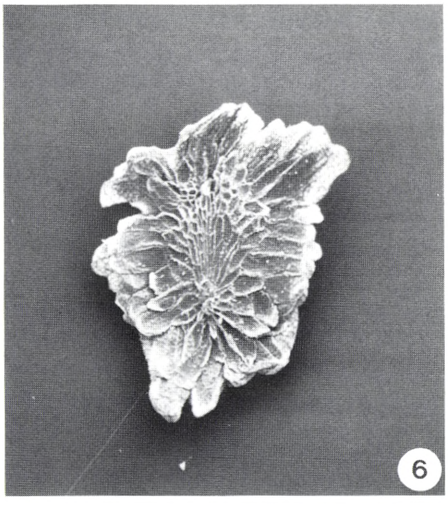
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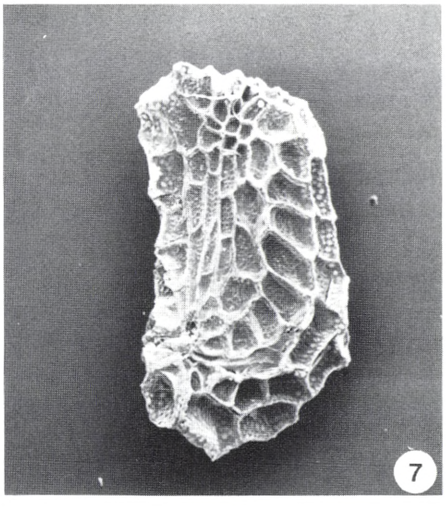
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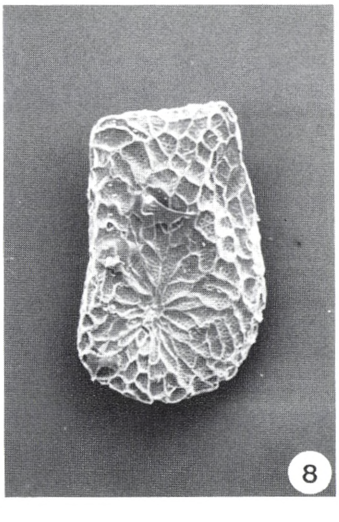
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PLATE 11

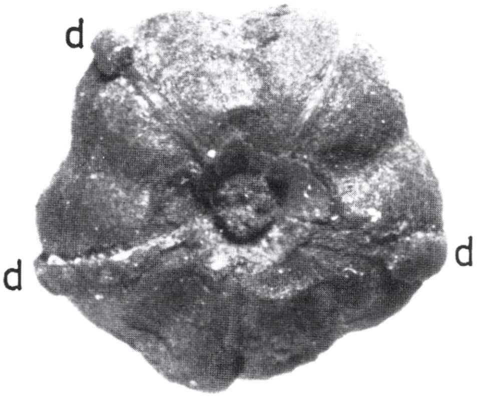
Fossil *Lyonia danica* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–6).

1. Holotype. Apical view of fruit with dorsal thickenings preserved (1017.01, ×15).
2. Apical view of fruit (2017.01, ×15).
3. Lateral view of fruits with remnants of calyx and dorsal thickenings (1017.02, ×15).
4. Section of fruit showing fruit wall with a triangular dorsal thickening and locules with many seeds (1017.08, ×45).
5. Fragment of fruit showing placentae with elongated seeds (SEM–104_1, ×25).
6. Seeds from fruit (SEM–104_2, ×70).

Seed of extant *Lyonia mariana* (L.) D. Don from eastern North America (fig. 7).

7. Seed (SEM–314, ×70).

Figs 1–3 reflected light micrographs, fig. 4 transmitted light micrograph, and figs 5–7 SEM.
d = dorsal thickening, p = placenta, s = seed.



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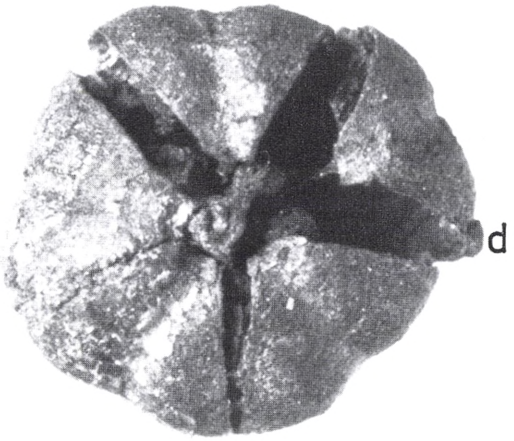

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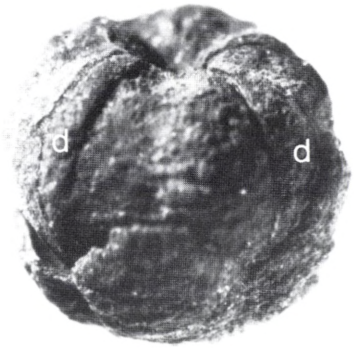

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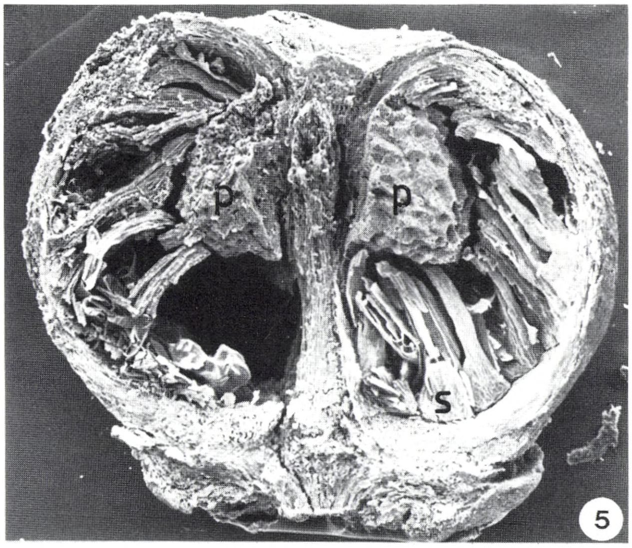

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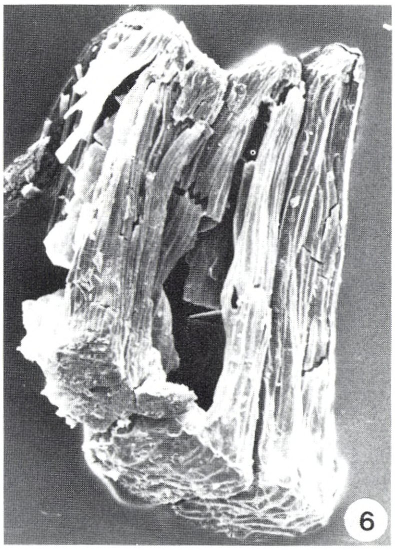

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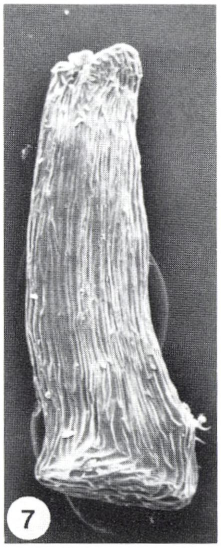

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PLATE 12

Fossil *Zenobia fasterholtensis* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–6).

1. Holotype. Lateral view of fruit with calyx preserved (2018.01, ×15).
2. Lateral view of fruit with calyx preserved (2018.02, ×15).
3. Fragment of fruit with seeds (from holotype, SEM–81_7, ×60).
4. Seeds from fruit fragment (SEM–81_7, ×100).
5. Surface detail of seed (SEM–81_7, ×500).
6. Section of seed showing one layer of cuboidal cells (SEM–81_8, ×600).

Seed of extant *Zenobia pulverulenta* (Bart.) Pollard from eastern North America (fig. 7).

7. Seed (SEM–311_5, ×38).

Fossil *Eubotrys* sp. from the Middle Miocene Fasterholt flora (figs 8–10).

8. Fruit (2016.01, ×15).

9–10. Seeds from fruit (SEM–$81_{5–6}$, ×50).

Seed of extant *Eubotrys racemosa* (L.) Nutt. from eastern North America (fig. 11).

11. Seed (SEM–314_1, ×50).

Fossil ?*Enkianthus* sp. from the Middle Miocene Fasterholt flora (figs 12–14).

12. Fruit (2019.01, ×15).
13. Seed from fruit (SEM–55_1, ×30).
14. Detail of seed surface (SEM–55_1, ×600).

Seed of extant *Enkianthus subsessilis* (Miq.) Makino from East Asia (fig. 15).

15. Seed (SEM–55_2, ×25).

Figs 1–2, 8, and 12 reflected light micrographs, all other figures SEM.


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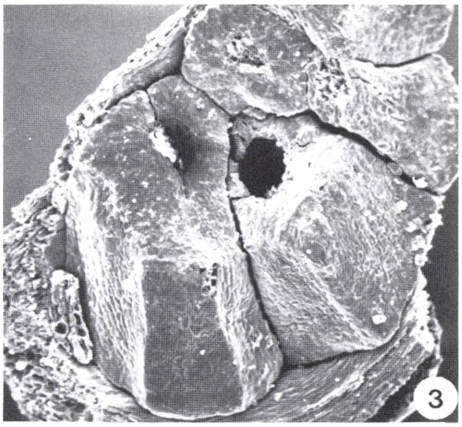
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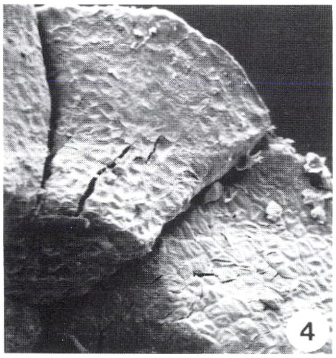
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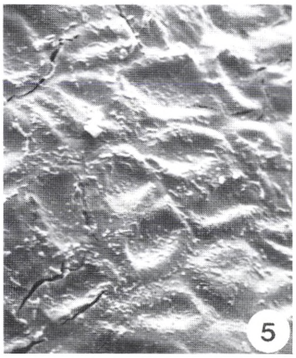
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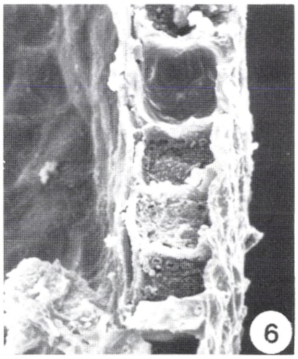
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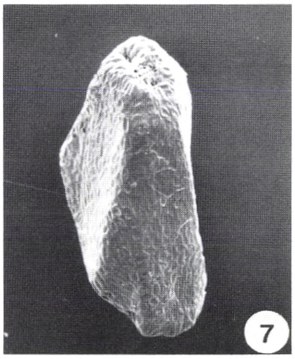
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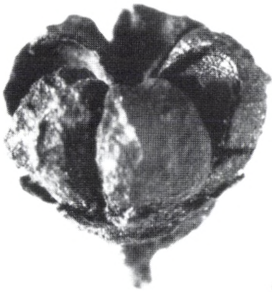
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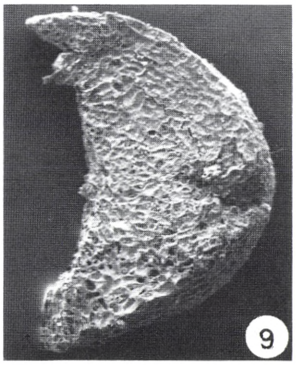
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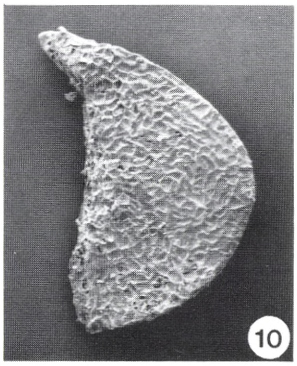
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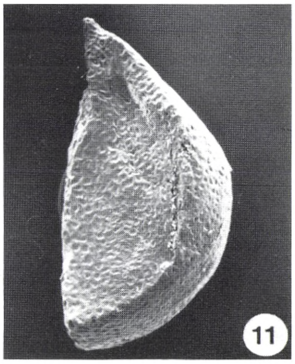
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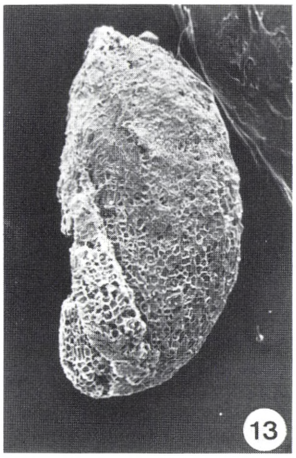
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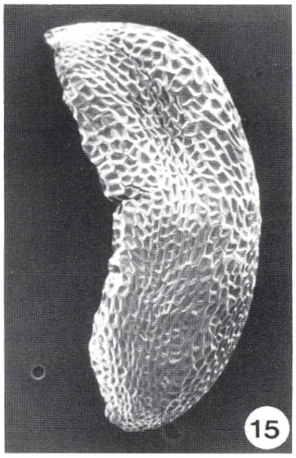
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PLATE 13

Fossil *Epacridicarpum chandlerae* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–6).

1. Holotype. Half of fruit split along the dorsal sutures and with remnants of calyx (SEM–325, ×30).
2. Fruit with five lobed style (SEM–326_2, ×33).
3. Apical view of fruit showing five segments (SEM–326_1, ×30).
4. Half of fruit split along the ventral sutures (SEM–326_5, ×33).
5. Section of fruit wall showing endocarp of narrow sclereids and mesocarp of thin-walled cells (SEM–325, ×300).
6. Surface detail of locule showing sclereids (SEM–325, ×600).

Fossil *Lysimachia* sp. from the Middle Miocene Fasterholt flora (figs 7–10).

7. Seed (SEM–71_6, ×38).
8. Slightly abraded seed (SEM–71_7, ×38).
9. Surface detail of seed showing outer layer of columnar cells and inner layer of crystal cells (SEM–71_7, ×330).
10. Section of seed showing columnar cells of outer layer (SEM–71_8, ×300).

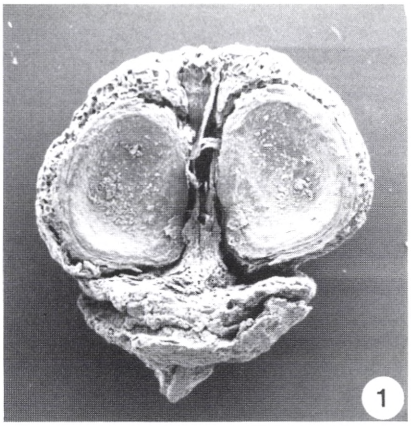
Extant *Lysimachia vulgaris* L. (fig. 11).

11. Seed (SEM–73_2, ×35).

Fossil *Potentilla* from the Middle Miocene Fasterholt flora (figs 12–14).

12. *Potentilla* sp. 1. Fruitlet (SEM–88_3, ×38).
13. *Potentilla* sp. 1. Surface detail of fruitlet (SEM–88_3, ×600).
14. *Potentilla* sp. 2. Fruitlet (SEM–88_4, ×38).

All figures SEM.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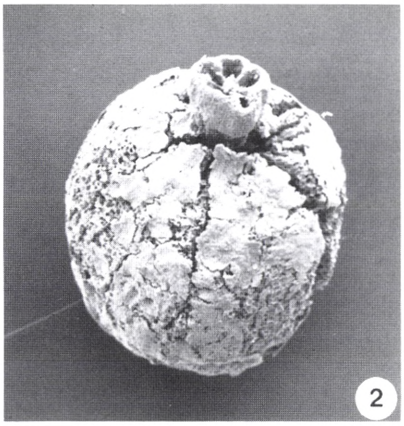
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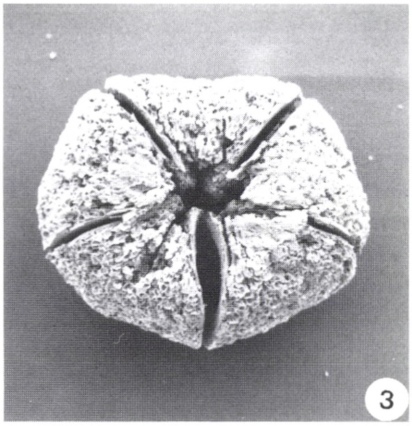
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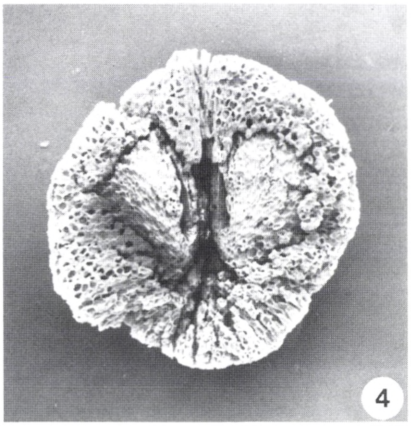
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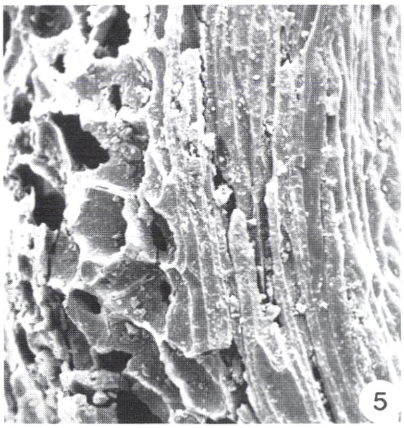
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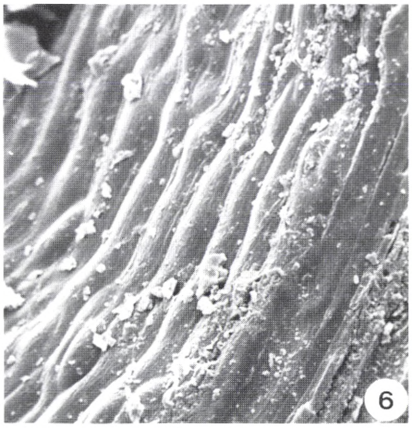
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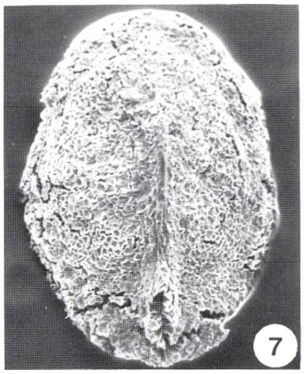
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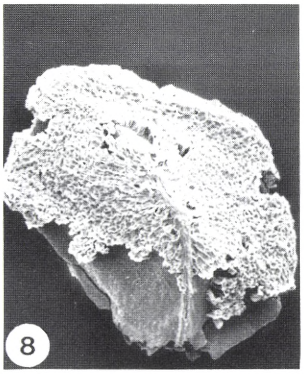
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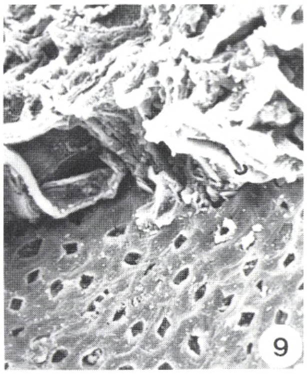
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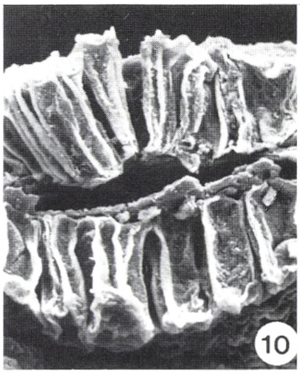
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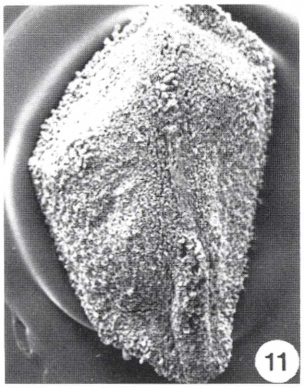
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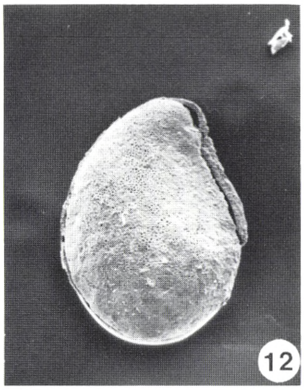
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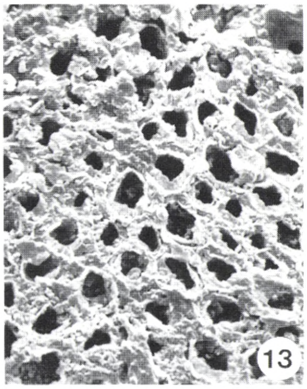
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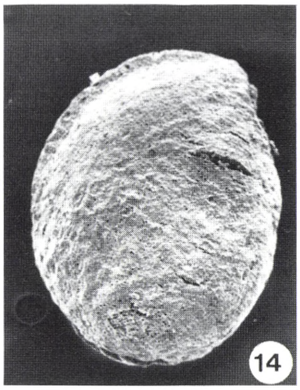
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PLATE 14

Fossil *Rubus* from the Middle Miocene Fasterholt flora (figs 1–6).

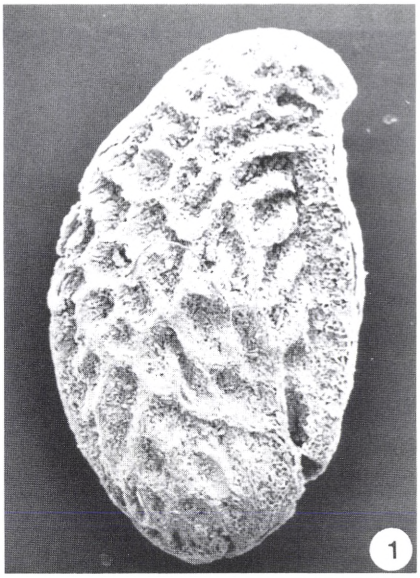
1–2. ***Rubus*** sp. 1. Endocarps (SEM–322_{1-2}, ×38).

3. ***Rubus*** sp. 2. Endocarp (SEM–81_4, ×38).
4. ***Rubus*** sp. 1. Surface detail of endocarp showing reticulum and narrow sclereids (SEM–322_1, ×150).
5. ***Rubus*** sp. 1. Crosssection of endocarp wall showing inner layer of transversely elongated sclereids and outer layer of longitudinally aligned sclereids (SEM–76_8, ×350).
6. ***Rubus*** sp. 1. Longitudinal section of endocarp (SEM–76_7, ×350).

Fossil *Pyracantha acuticarpa* (C. Reid & E.M. Reid) Szafer from the Middle Miocene Fasterholt flora (figs 7–9).

7. Fruit with five partly fused nutlets (SEM–318_2, ×20).
8. Part of fruit with three nutlets (SEM–318_1, ×20).
9. Fragment of fruit showing section of fruit wall and seed surface (SEM–84_3, ×140).

All figures SEM.
fw = fruit wall, s = seed.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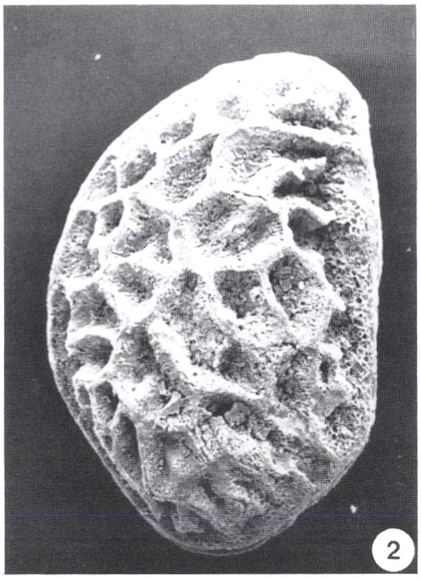
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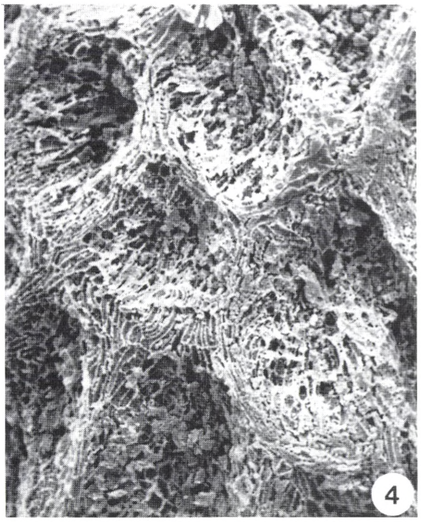
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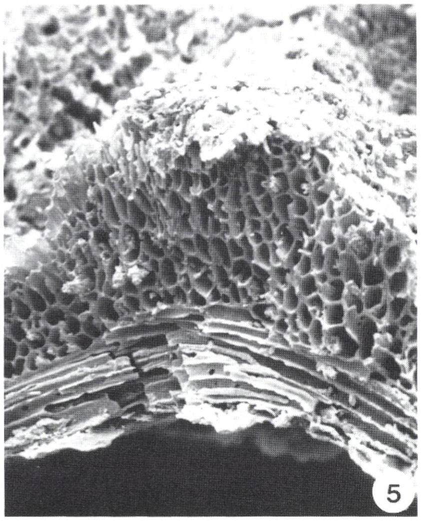
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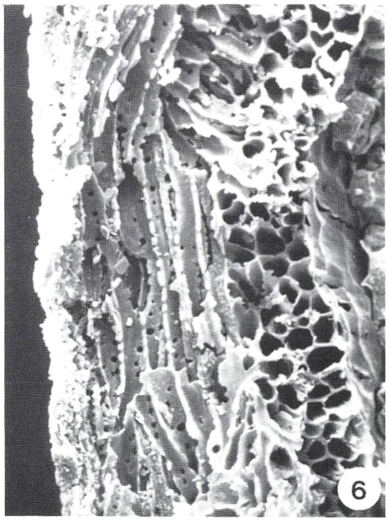
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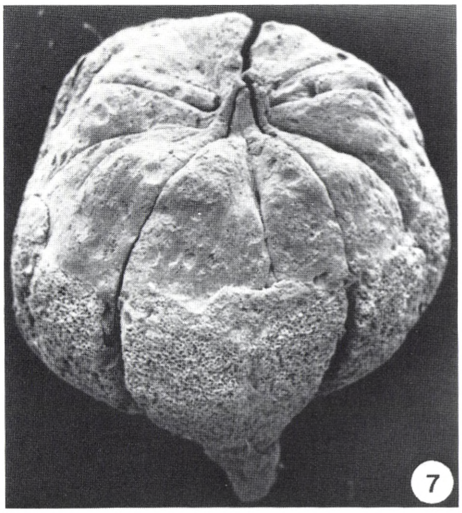
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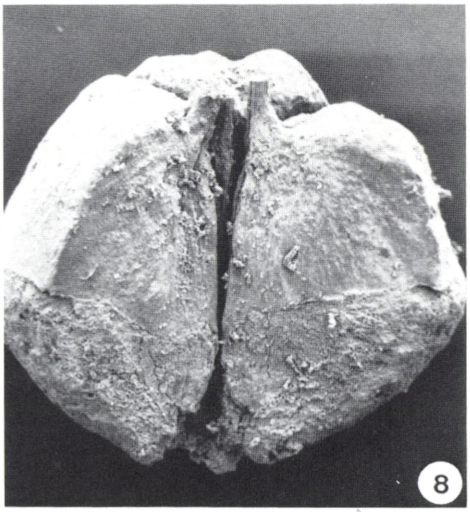
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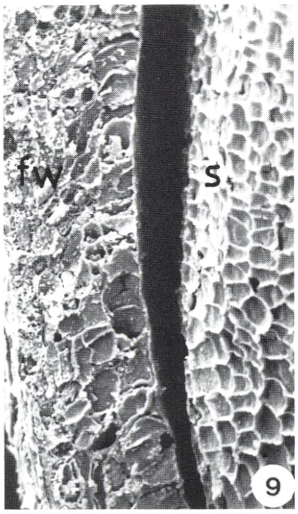
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PLATE 15

Fossil *Aldrovanda praevesiculosa* Kirchheimer from the Middle Miocene Fasterholt flora (figs 1–3).

1. Seed (SEM–71_1, ×45).
2. Fragment of seed showing outer epidermis of testa with strongly thickened outer and anticlinal walls (SEM–88_1, ×350).
3. Fragment of seed showing inner epidermis of testa with thin-walled cells (SEM–88_1, ×700).

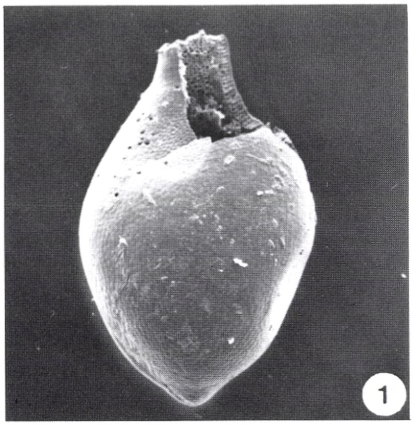
Fossil *Decodon gibbosus* (E.M. Reid) E.M. Reid from the Middle Miocene Fasterholt flora (figs 4–9).

4. Seed with slightly developed dorsal tissue (SEM–91_4, ×35).
5. Seed with strongly developed dorsal tissue (SEM–91_2, ×35).
6. Section of seed showing position of hilum, raphe, chalaza, and micropyle, and thick dorsal mesotesta (SEM–91_5, ×35).
7. Finely pitted cells of mesotesta (SEM–91_5, ×1400).
8. Endotesta at the germination valve with imprints of crystals (SEM–91_5, ×350).
9. Surface of locule showing elongated cells of tegmen (SEM–91_5, ×700).

Seeds of extant *Decodon verticillatus* (L.) Ell. from eastern North America (figs 10–12).

10. Ventral view of seed with germination valve (SEM–334_2, ×30).
11. Section of seed showing position of hilum, raphe, chalaza, and micropyle (SEM–334_1, ×30).
12. Detail of meso- and endotesta (SEM–334_1, ×600).

All figures SEM.
c = imprint of crystal, ch = chalaza, h = hilum, m = micropyle, r = raphe.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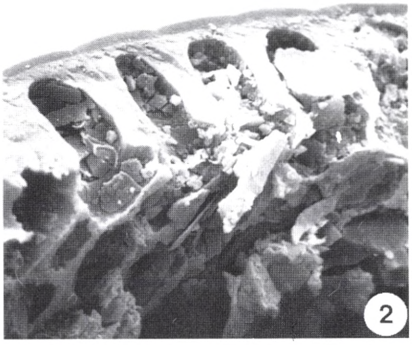
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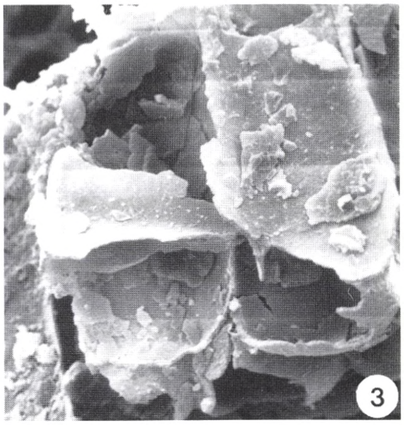
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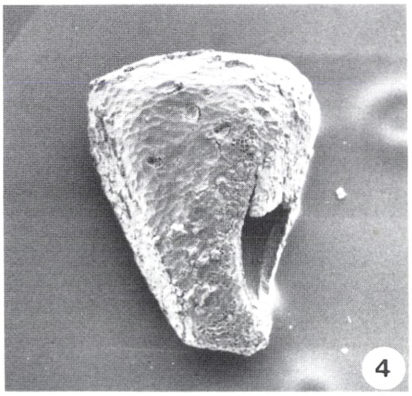
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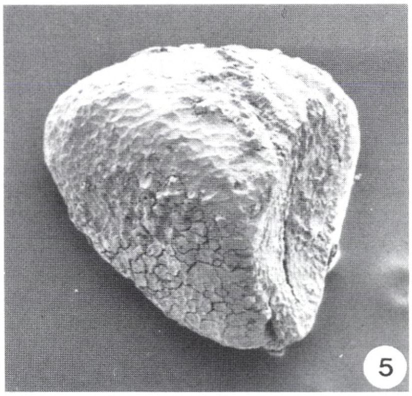
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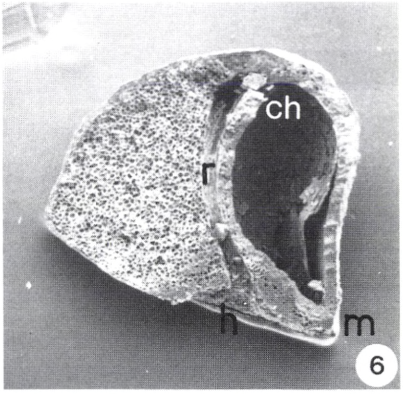
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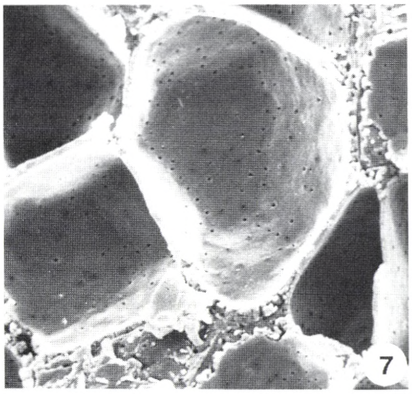
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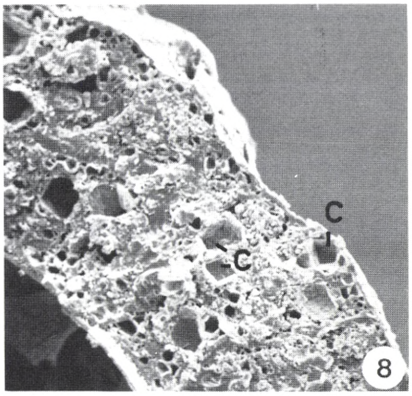
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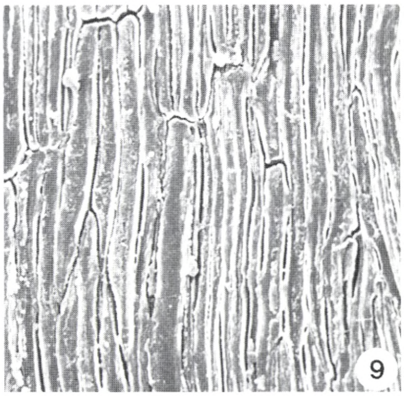
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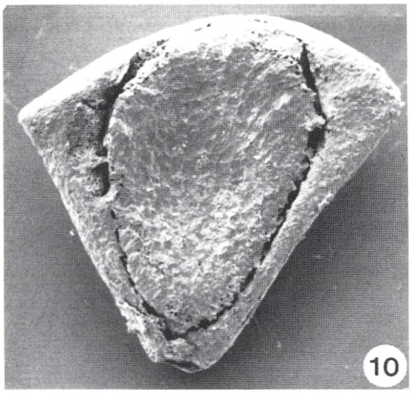
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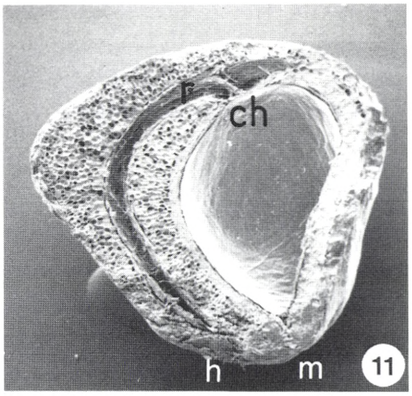
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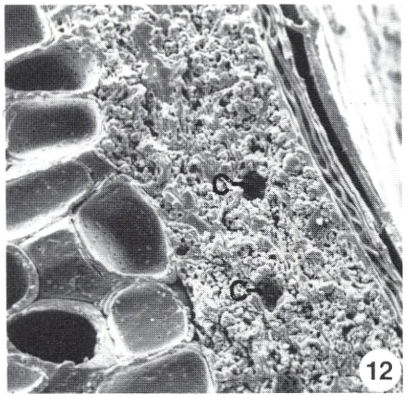
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PLATE 16

Fossil *Decodon vectensis* Chandler from the Middle Miocene Fasterholt flora (figs 1–3).
1. Ventral view of seed with germination valve (SEM–333_1, ×35).
2. Lateral view of seed (SEM–91_{10}, ×35).
3. Section of seed showing slightly developed dorsal tissue (SEM–91_{12}, ×35).

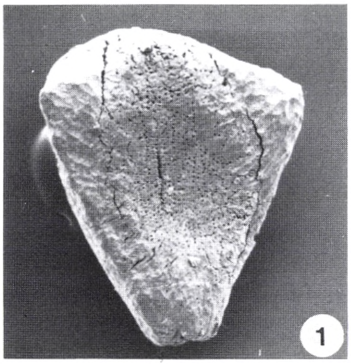
Fossil *Decodon* sp. from the Middle Miocene Fasterholt flora (fig. 4).
4. Ventral view of seed (SEM–333_2, ×35).

Fossil *Microdiptera parva* Chandler from the Middle Miocene Fasterholt flora (figs 5–7, 9–11).
5–6. Antiraphe-side of seeds with germination valve (SEM–93_{1-2}, ×35).
7. Raphe-side of seed (SEM–93_3, ×35).
9. Section of seed showing central embryo cavity and lateral wings (SEM–333_3, ×70).
10. Detail of seed wall showing thin-walled and finely pitted cells of mesotesta and endotesta with fibrous lignifications (SEM–93_4, ×700).
11. Detail of endotesta at the germination valve (SEM–93_4, ×700).

Fossil *Microdiptera* sp. from the Middle Miocene Søby flora (fig. 8).
8. Lateral view of seed (SEM–97_3, ×35).

Extant *Pemphis madagascariensis* (Baker) Koehne (figs 12–14).
12. Section of seed showing central embryo cavity and lateral wings (SEM–334_3, ×30).
13. Detail of seed wall showing finely pitted mesotestal cells, endotestal cells with crystals and strongly thickened walls, and tegmen (SEM–334_4, ×600).
14. Detail of seed wall near valve showing endotestal cells with crystals (SEM–334_4, ×300).

All figures SEM.
c = crystal, en = endotesta, me = mesotesta, tn = tegmen.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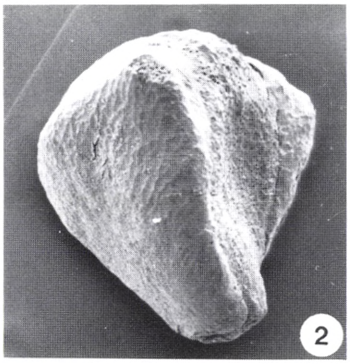
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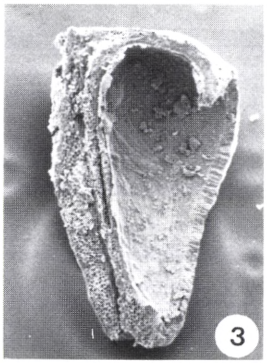
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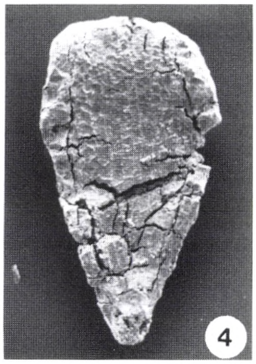
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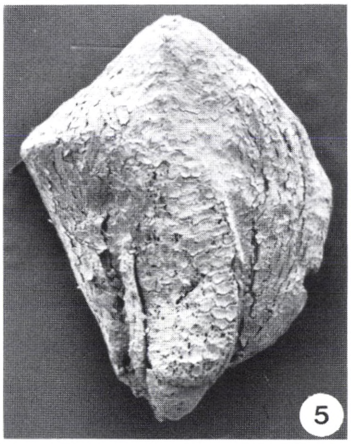
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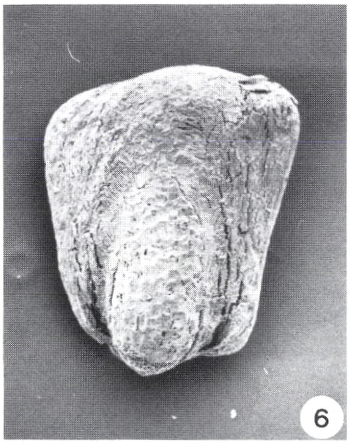
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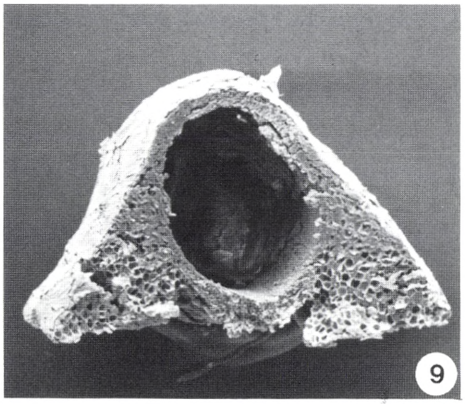
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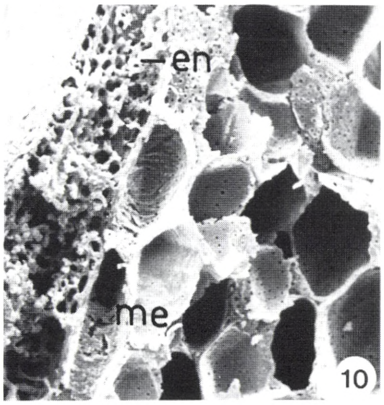

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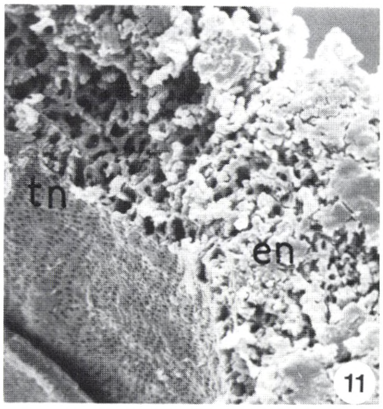

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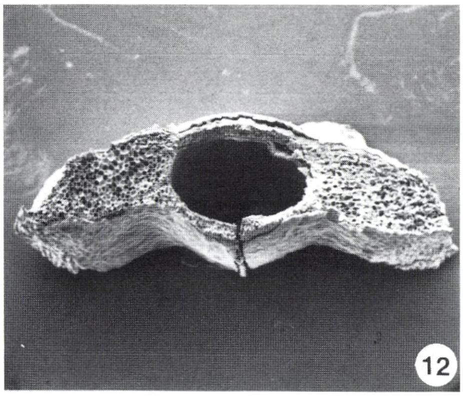
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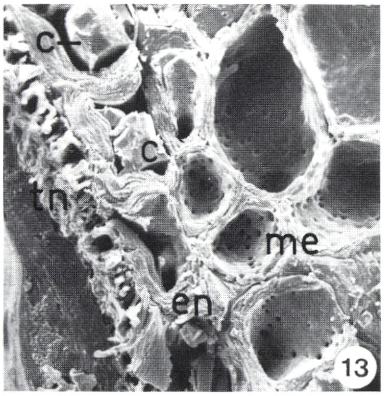

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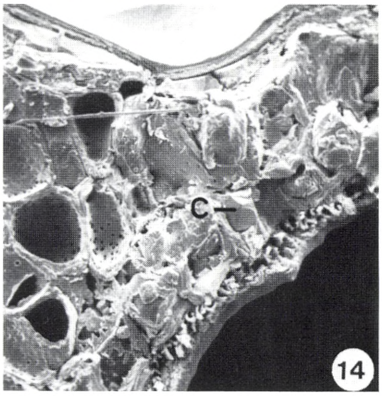

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PLATE 17

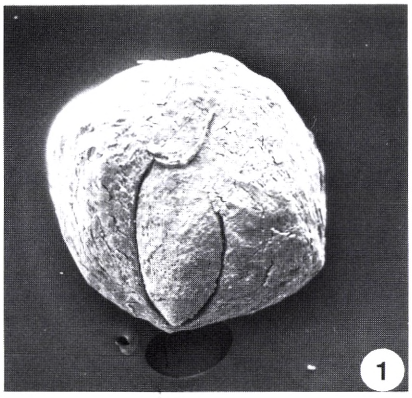
Fossil *Mneme menzelii* (E.M. Reid) Eyde from the Middle Miocene Fasterholt flora (figs 1–6).

1. Antiraphe-side of seed with germination valve (SEM-93_7, ×35).
2. Antiraphe-side of seed. The germination valve has been lost (SEM–93_8, ×35).
3. Raphe-side of seed (SEM–97_1, ×35).
4. Section of seed showing thick lateral wings (SEM–93_9, ×70).
5. Detail of mesotesta (SEM–93_9, ×1400).
6. Surface of locule showing cells of tegmen (SEM–93_9, ×3500).

Fossil *Myrtus palaeocommunis* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 7–12).

7. Holotype. Seed with remnant of raphe (SEM–342, ×18).
8. Seed (SEM–341_1, ×18).
9. Seed (SEM–317_3, ×18).
10. Seed (SEM–75_1, ×18).
11. Section of seed (SEM–75_5, ×50).
12. Detail of seed wall showing finely pitted testal cells (SEM–75_5, ×600).

All figures SEM.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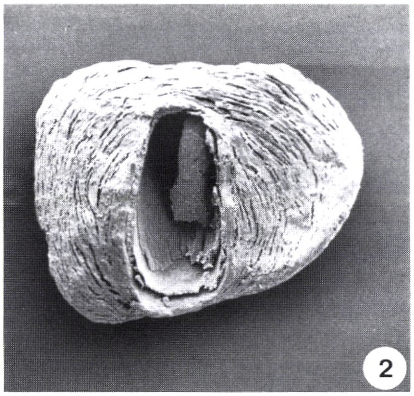
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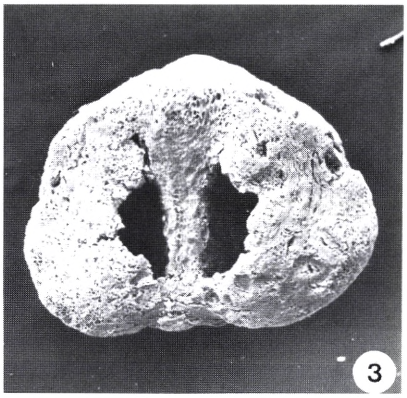
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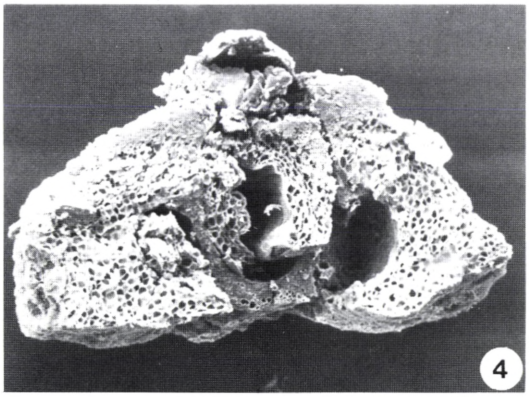
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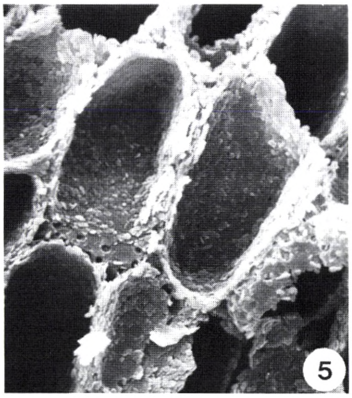
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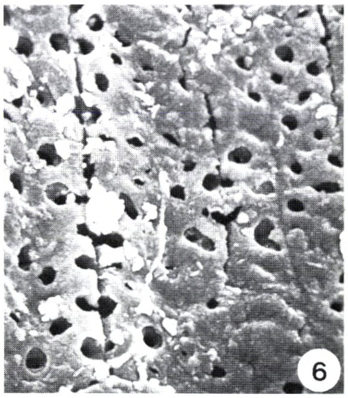
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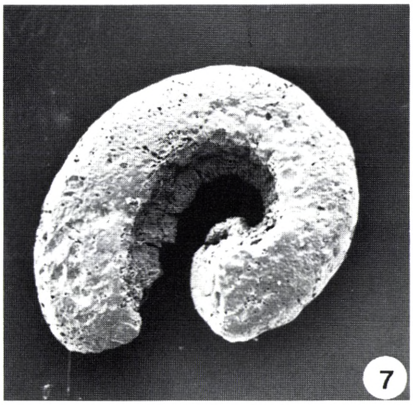
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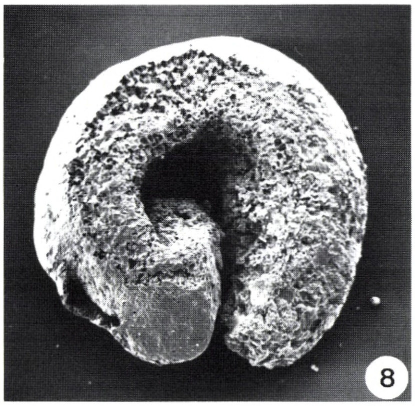
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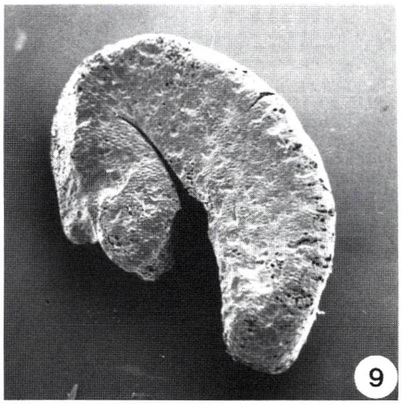
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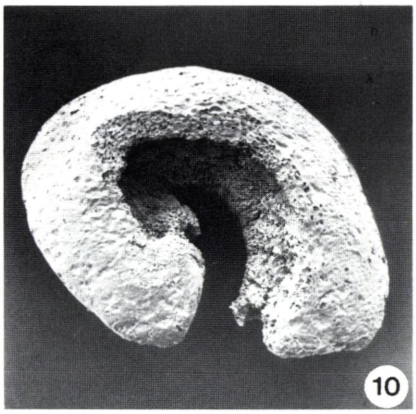
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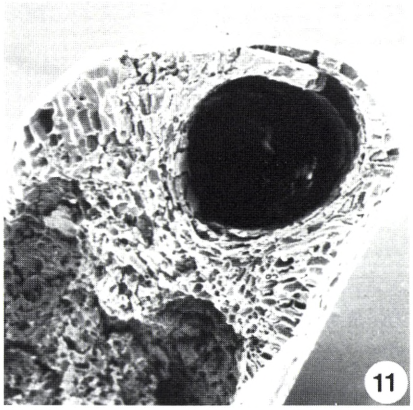
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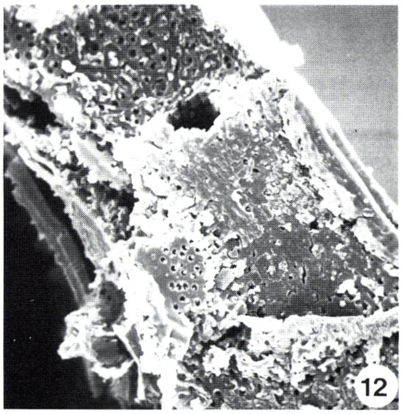
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PLATE 18

Fossil *Ludwigia corneri* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–7).

1. Holotype. Seed with prominent raphe (SEM–339, ×65).
2. Seed with part of raphe preserved (SEM–69_{14}, ×65).
3. Seed with raphe abraded (SEM–69_{10}, ×65).
4. Inner surface of seed showing narrow cells of tegmen (SEM–69_{13}, ×600).
5. Surface detail of seed with transversely elongated cells of exotesta (SEM–69_{12}, ×600).
6. Surface detail of abraded seed showing crystal cells of endotesta (SEM–69_{11}, ×210).
7. Detail of crystal cells showing undulate anticlinal walls and imprints of a large central crystal surrounded by many smaller crystals (SEM–69_{11}, ×1050).

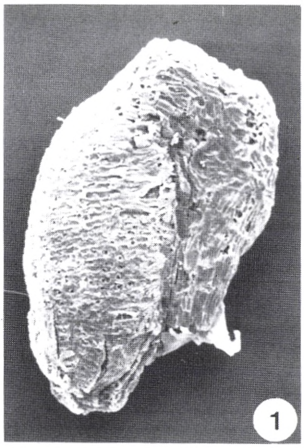
Fossil *Ludwigia collinsoniae* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 8–13).

8. Holotype. Seed with remnants of raphe (SEM–340, ×75).
9. Seed with exotesta preserved (SEM–109_{11}, ×75).
10. Longitudinal section of seed showing variability in size of endotestal cells (SEM–109_{13}, ×100).
11. Detail of seed wall showing strongly thickened endotestal cells and narrow cells of tegmen (SEM–109_{13}, ×1400).
12. Detail of seed surface showing endotestal cells with imprints of crystals (SEM–109_{12}, ×700).
13. Detail of seed surface showing transversely elongated cells of exotesta (SEM–111, ×350).

Fossil *Proserpinaca brevicarpa* Dorofeev from the Middle Miocene Søby flora (fig. 14).

14. Endocarp (SEM–327_3, ×20).

All figures SEM.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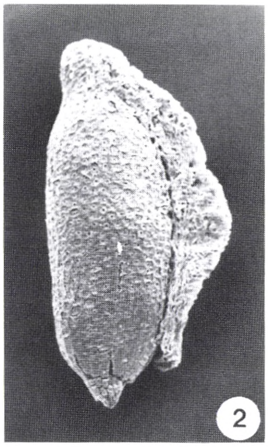
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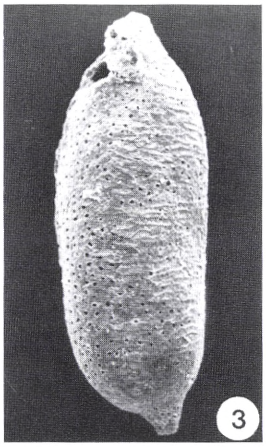
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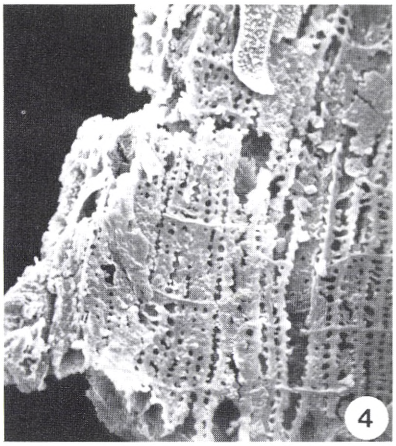
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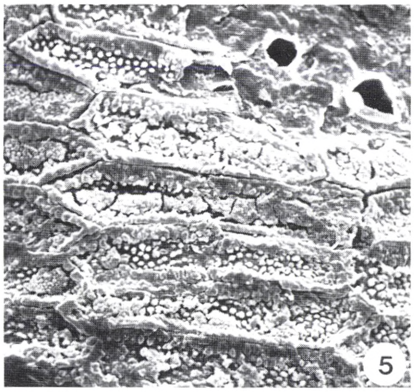
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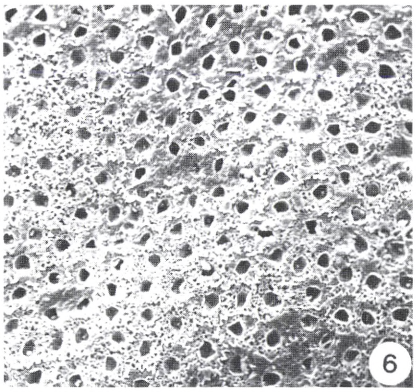
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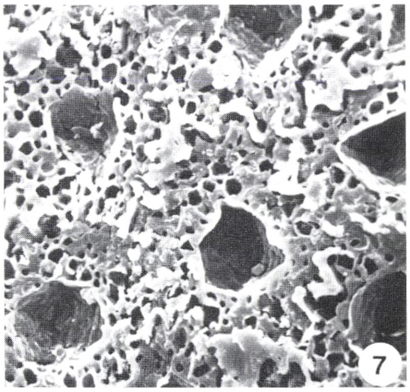
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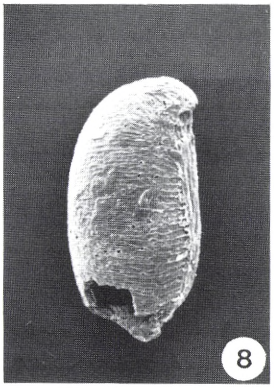
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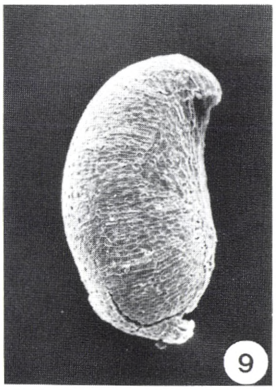
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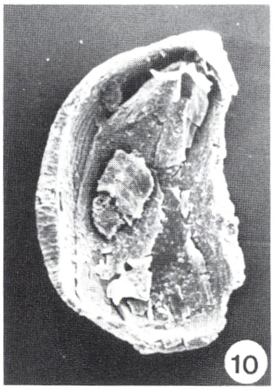
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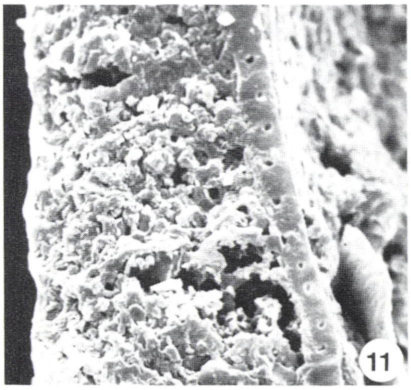
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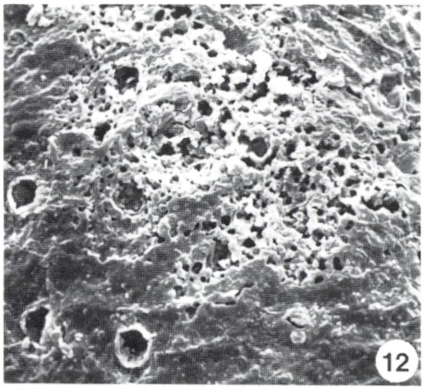
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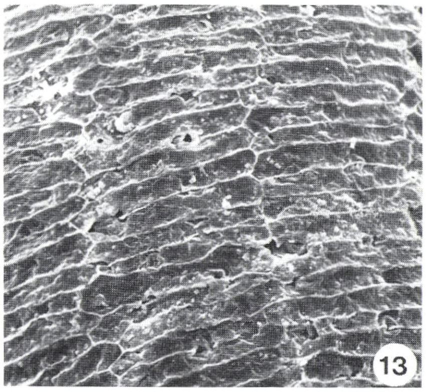
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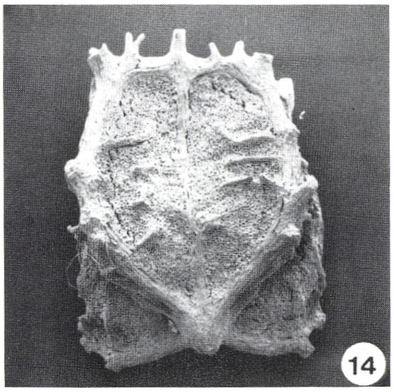
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PLATE 19

Fossil *Swida gorbunovii* (Dorofeev) Negru from the Middle Miocene Fasterholt flora (figs 1–3).

1. Endocarp with median depression and eight groups of vascular bundles (SEM–319_1, ×18).
2. Endocarp with median depression and indistinct vascular bundles (SEM–319_2, ×18).
3. Section of endocarp wall showing equiaxial sclereids (SEM–319_3, ×300).

Fossil *Aralia pusilla* Dorofeev from the Middle Miocene Fasterholt flora (figs 4–7).

4–5. Endocarps (SEM–322_{3-4}, ×22).
6. Surface detail of endocarp showing transversely elongated sclereids (SEM–322_4, ×300).
7. Longitudinal section of endocarp showing sclereids (SEM–90_6, ×400).

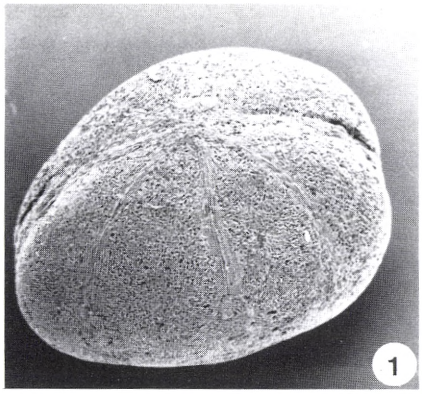
Fossil *Ilex saxonica* Mai from the Middle Miocene Fasterholt flora (figs 8–11).

8. Ventral view of endocarp (SEM–317_2, ×13).
9. Lateral view of endocarp (SEM–317_1, ×13).
10. Longitudinal section of endocarp wall showing inner layer of transversely elongated sclereids and outer layer of diagonally arranged sclereids (SEM–95_2, ×350).
11. Surface detail of seed (SEM–95_2, ×700).

Fossil *Paliurus* sp. from the Middle Miocene Fasterholt flora (figs 12–15).

12. Small seed (SEM–316_4, ×25).
13. Small seed with wrinkled surface (SEM–88_7, ×25).
14. Seed with abraded outer layer (SEM–88_8, ×20).
15. Surface detail of abraded seed showing columnar cells of outer layer (SEM–88_8, ×60).

All figures SEM.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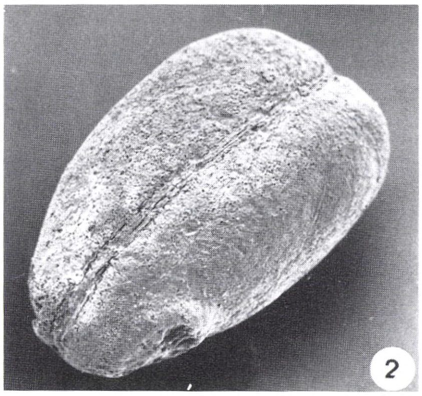
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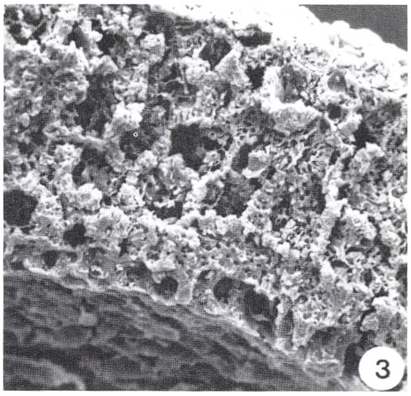
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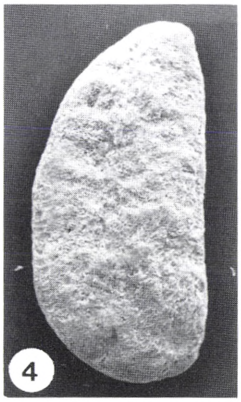
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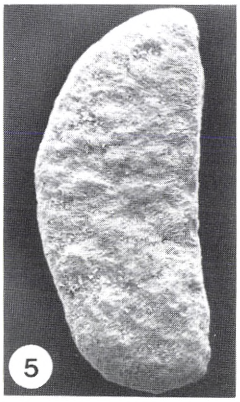
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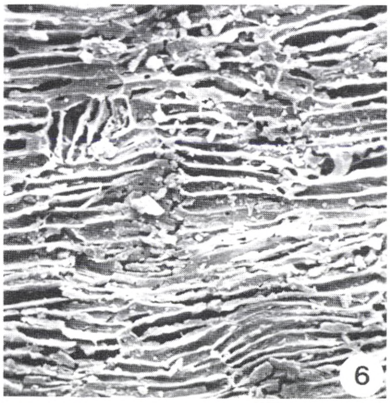
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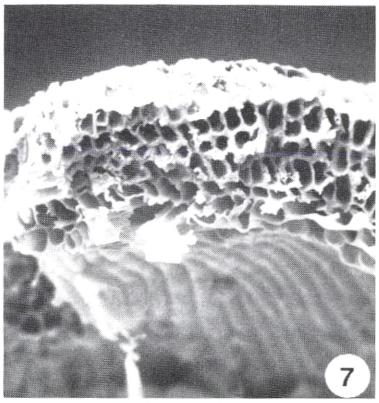
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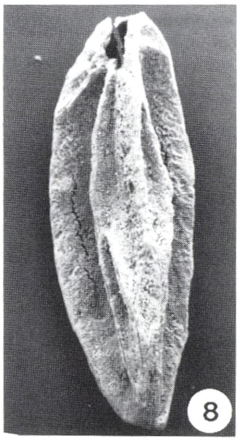
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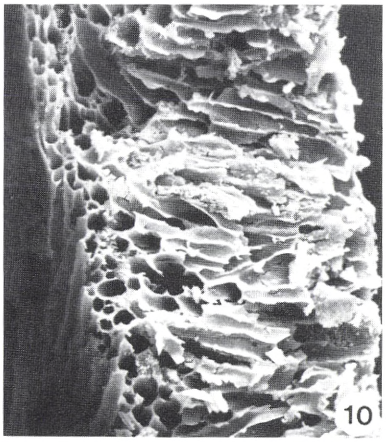
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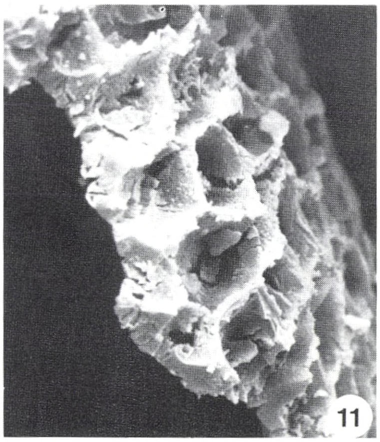
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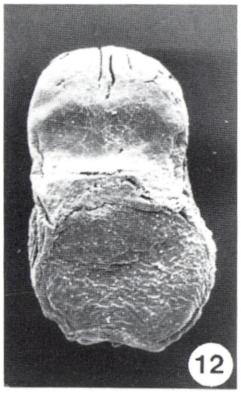
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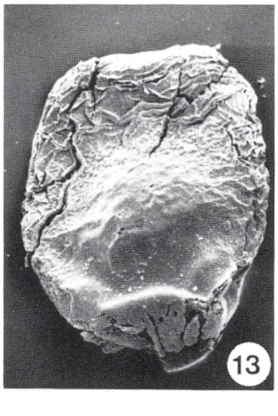
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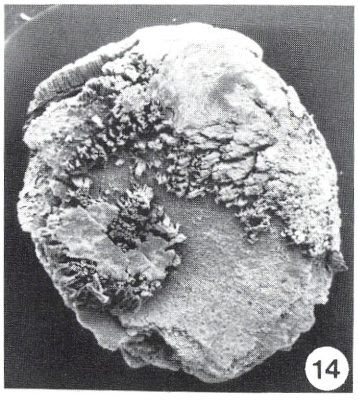
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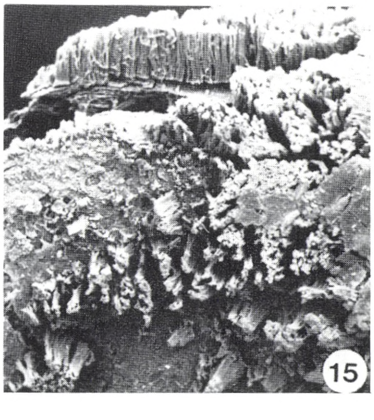
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PLATE 20

Fossil *Paliurus* sp. from the Middle Miocene Fasterholt flora (fig. 1).

1. Detail of columnar sclereids of outer layer (SEM–88_8, ×350).

Extant *Paliurus spina-christi* Mill. from southern Europe (fig. 2).

2. Section of seed showing outer layer of columnar cells (SEM–89_8, ×350).

Fossil *Sambucus pulchella* C. Reid & E.M. Reid from the Lavsbjerg Øst borehole (33.0–33.5 m) (figs 3–4).

3. Seed (SEM–64_1, ×30).
4. Surface detail of seed (SEM–64_1, ×400).

Fossil *Weigela srodoniowae* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 5–9).

5. Holotype. Seed with wing preserved (SEM–339, ×35).
6. Seed with wing preserved (SEM–306_6, ×35).
7. Seed with wing partly preserved (SEM–90_1, ×35).
8. Seed with wing abraded (SEM–306_7, ×35).
9. Surface detail of seed showing thickened and pitted inner and anticlinal walls and remnants of thin outer walls (SEM–46_7, ×540).

Extant *Weigela hortensis* (Sieb. & Zucc.) C.A. Mey. from East Asia (figs 10–11).

10. Seed with wing (SEM–89_5, ×35).
11. Surface detail of seed showing strongly thickened anticlinal walls (SEM–89_5, ×700).

All figures SEM.


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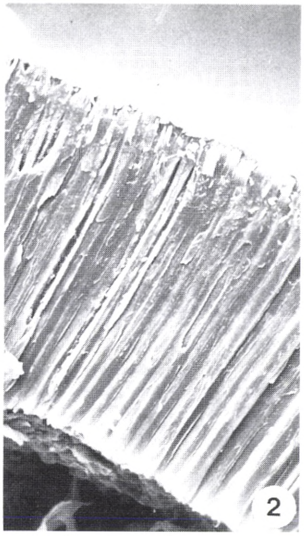
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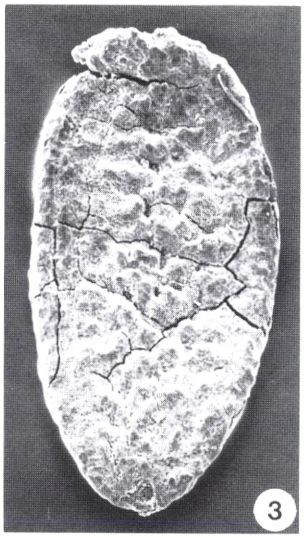
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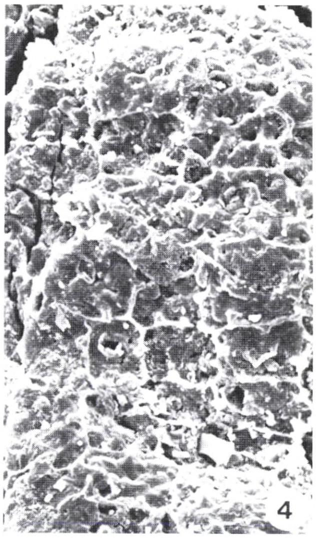
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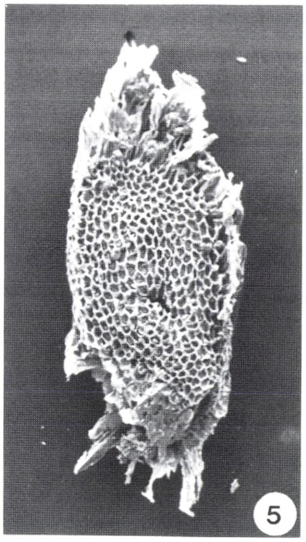
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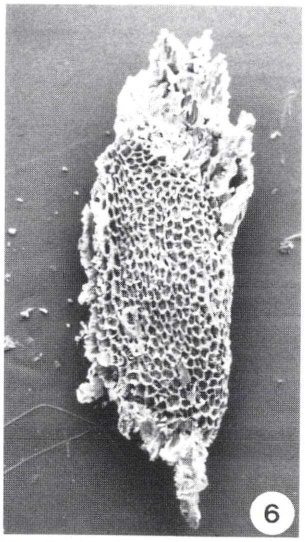
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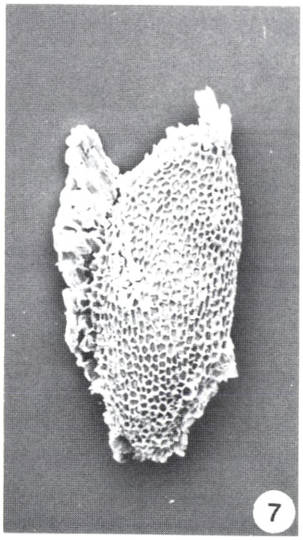
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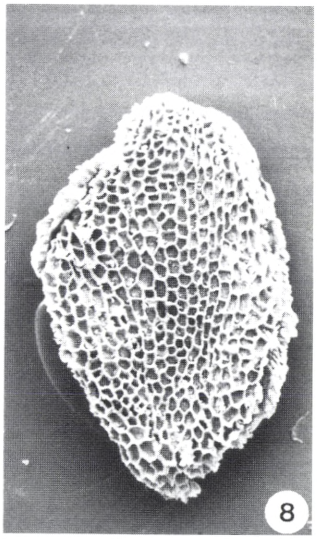
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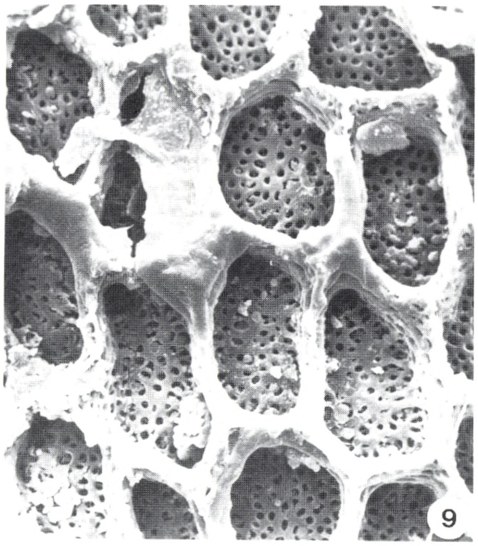
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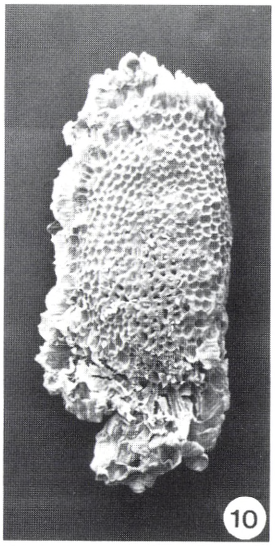
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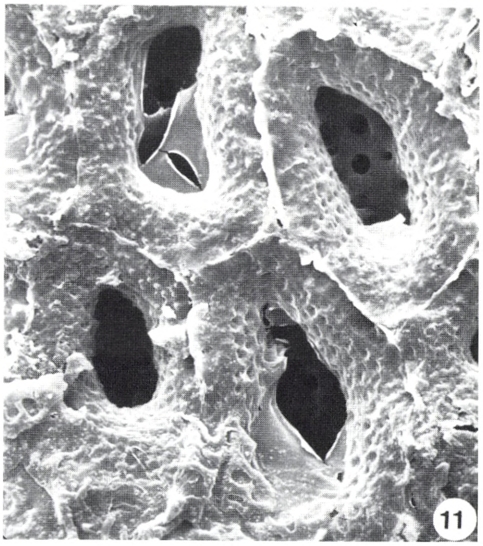
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PLATE 21

Fossil *Cephalanthus pusillus* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–3, 5–7) and Søby flora (fig. 4).

1. Holotype. Mericarp with germination valve attached (1044.01, ×25).

2–3. Mericarps with germination valve attached (SEM–44_{4-5}, ×30).

4. Fruit with two mericarps (×25).

5. Apical part of mericarp with germination valve (SEM–44_{2}, ×70).

6. Apical part of mericarp with germination valve detached showing strophiole and seed (SEM–44_{2}, ×70).

7. Seed from mericarp (SEM–44_{3}, ×35).

Extant *Cephalanthus occidentalis* L. from North America (figs 8–9).

8. Apical part of mericarp with germination valve (SEM–45, ×35).

9. Apical part of mericarp with germination valve detached showing strophiole and seed (SEM–45,×20).

Extant *Cephalanthus glabratus* K. Schum. from South America (fig. 10).

10. Seed (SEM–45, ×20).

All figures SEM except figs 1 and 4 which are reflected light micrographs.
s = seed, st = strophiole.


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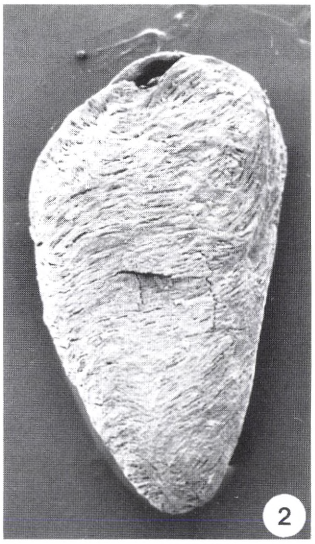
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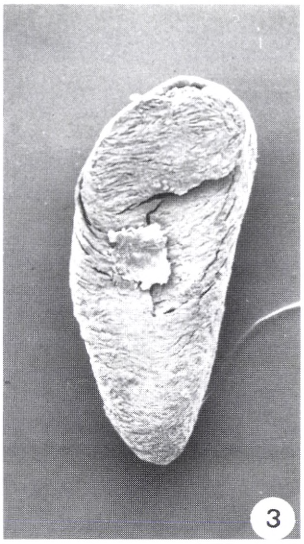
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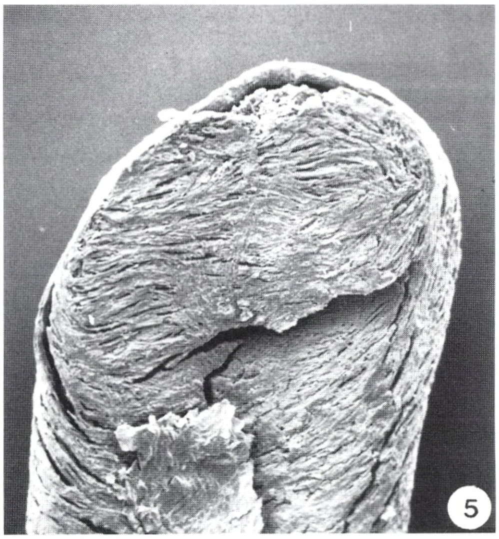
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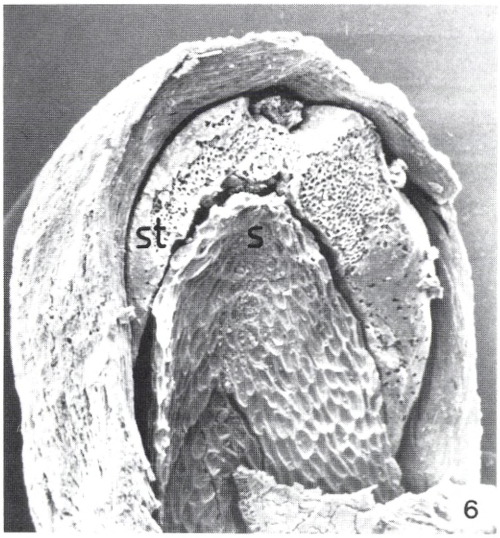

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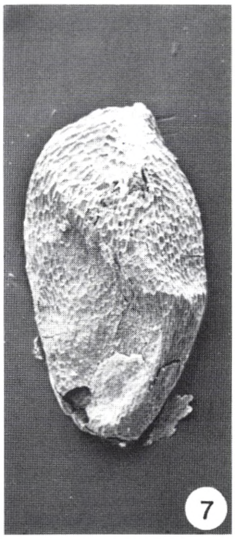
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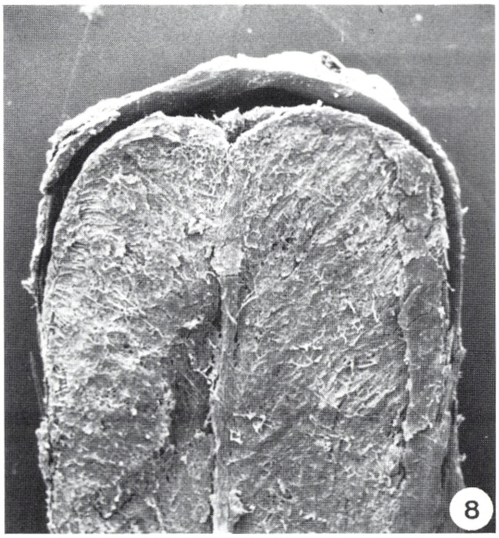
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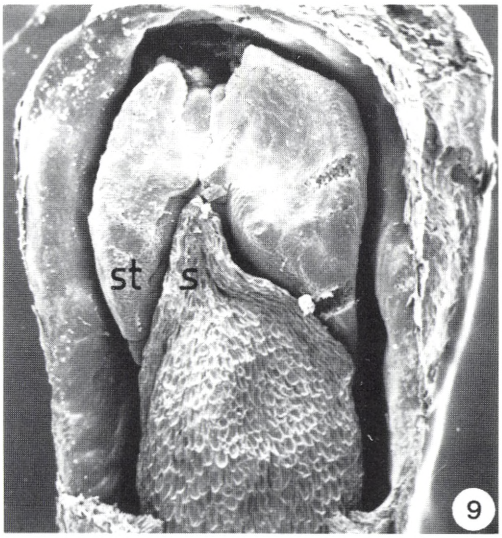

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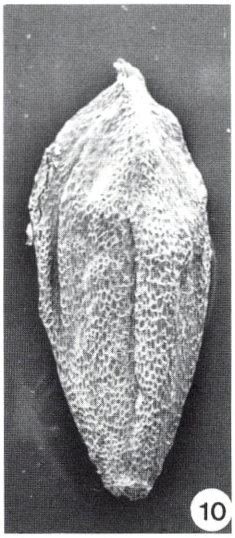
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PLATE 22

Fossil *Teucrium* sp. 1 from the Middle Miocene Fasterholt flora (figs 1–2).
1. Ventral view of nutlet (SEM–124_6, ×45).
2. Surface detail of nutlet showing undulate cell walls (SEM–124_6, ×250).

Fossil *Teucrium* sp. 2 from the Middle Miocene Søby flora (figs 3–4).
3. Ventral view of nutlet (SEM–327_5, ×45).
4. Dorsal view of nutlet (SEM–327_4, ×45).

Fossil *Caldesia* sp. 1 from the Middle Miocene Fasterholt flora (figs 5–7).
5. Fragment of fruit (SEM–113_6, ×35).
6. Seed from fruit (SEM–113_8, ×35).
7. Section of fruit showing nodose thickenings of sclereids (SEM–113_7, ×300).

Extant *Caldesia parnasifolia* Parl. (fig. 8).
8. Section of fruit showing nodose thickenings of sclereids (SEM–117_9, ×160).

Fossil *Caldesia* sp. 2. from the Fasterholt Plantage borehole (70.0–70.5 m) (figs 9–10).
9. Fruit (SEM–113_3, ×30).
10. Seed from fruit shown in fig. 9 (SEM–113_5, ×45).

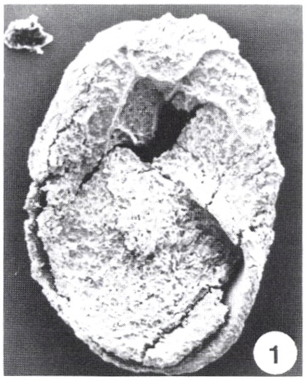
Fossil Alismataceae genus ? sp. 1 from the Middle Miocene Fasterholt flora (fig. 11).
11. Seed (SEM–337_2, ×38).

Fossil Alismataceae genus ? sp. 2 from the Middle Miocene Fasterholt flora (fig. 12).
12. Seed (SEM–337_3, ×38).

Fossil *Potamogeton heinkei* Mai from the Middle Miocene Fasterholt flora (figs 13–14).
13. Endocarp (SEM–100_2, ×35).
14. Section of germination valve (SEM–336_6, ×120).

Fossil *Potamogeton* sp. from the Middle Miocene Fasterholt flora (figs 15–16).
15. Endocarp (SEM–336_5, ×35).
16. Section of germination valve (SEM–113_9, ×250).

All figures SEM.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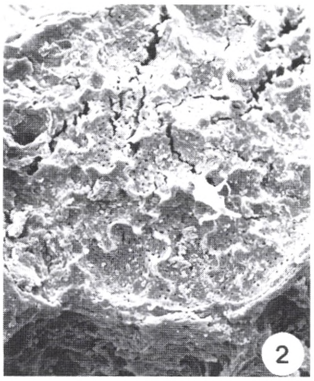
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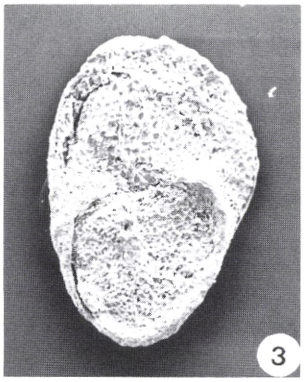
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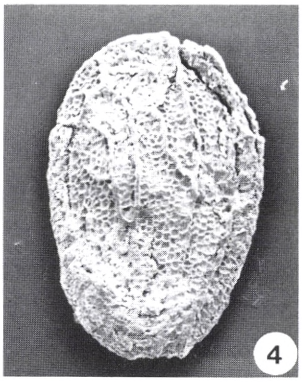
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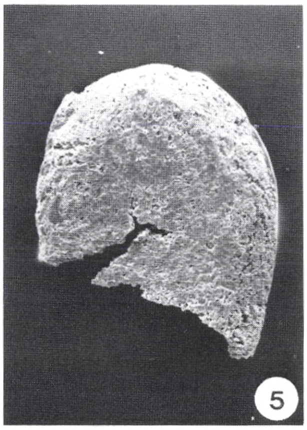
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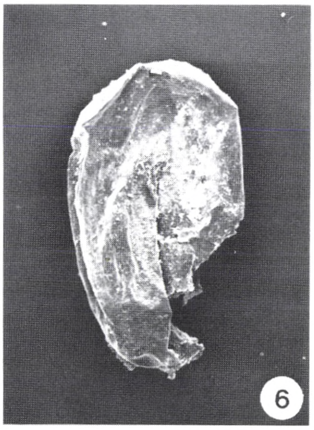
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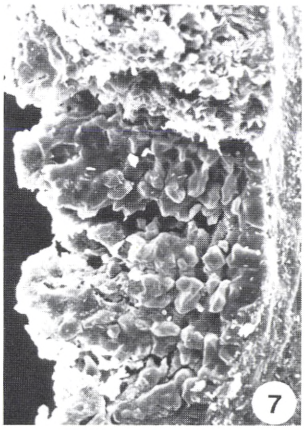
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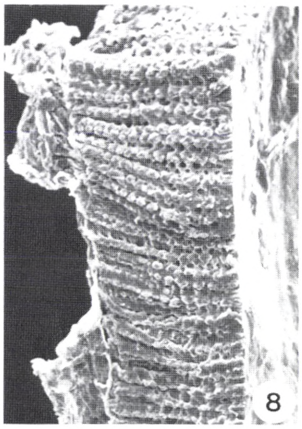
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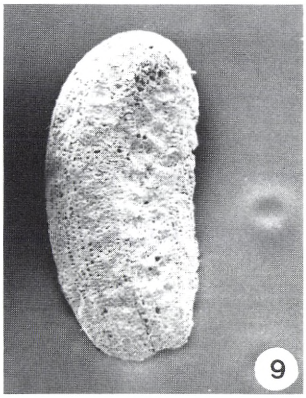
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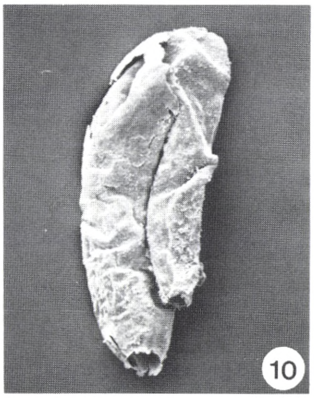
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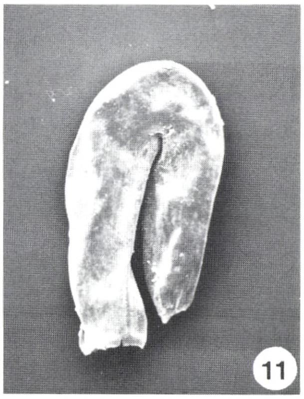
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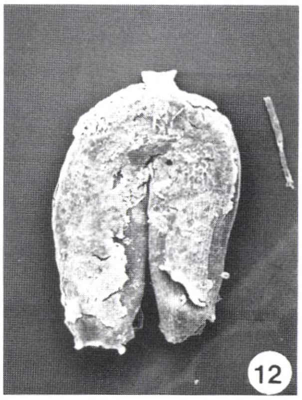
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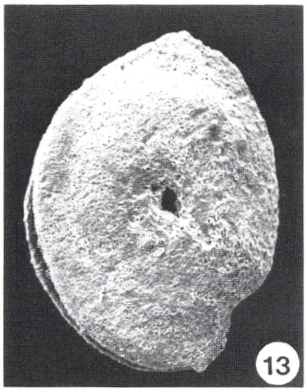
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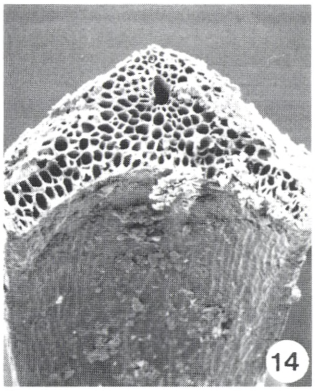
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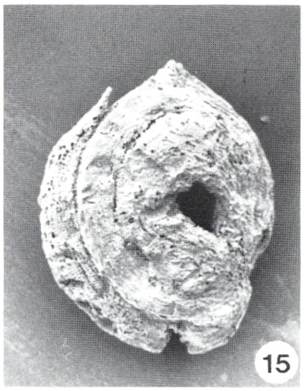
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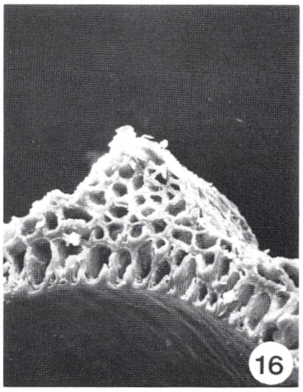
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PLATE 23

Fossil *Najas* sp. from the Middle Miocene Fasterholt flora (figs 1–2).

1. Seed (SEM–114_{10}, ×30).
2. Apical part of seed showing inner and outer layers of seed coat (SEM–114_{10}, ×70).

Fossil ?Orchidaceae from the Middle Miocene Fasterholt flora (figs 3–4).

3. Seed (SEM–114_{11}, ×100).
4. Surface detail of seed (SEM–114_{10}, ×350).

Fossil *Juncus* sp. from the Middle Miocene Fasterholt flora (figs 5–6).

5. Seed (SEM–114_{12}, ×100).
6. Surface detail of seed (SEM–114_{12}, ×525).

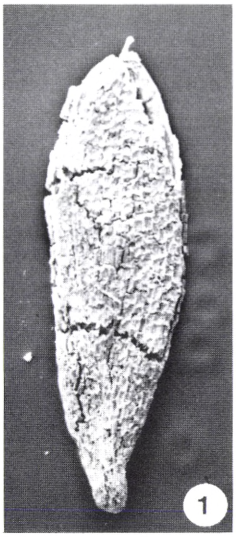
Extant *Juncus bulbosus* L. (figs 7–8).

7. Seed (SEM–116_{9}, ×100).
8. Surface detail of seed (SEM–116_{9}, ×525).

Fossil *Scirpus ragozinii* Dorofeev from the Middle Miocene Fasterholt flora (figs 9–12).

9. Fruit with remnants of bristles (SEM–125_{1}, ×40).
10. Fruit (SEM–125_{2}, ×40).
11. Surface detail of fruit showing longitudinal cells of outer epidermis (SEM–125_{1}, ×750).
12. Detail of epidermis cells showing pitted and slightly undulate anticlinal walls (SEM–125_{2}, ×1600).

All figures SEM.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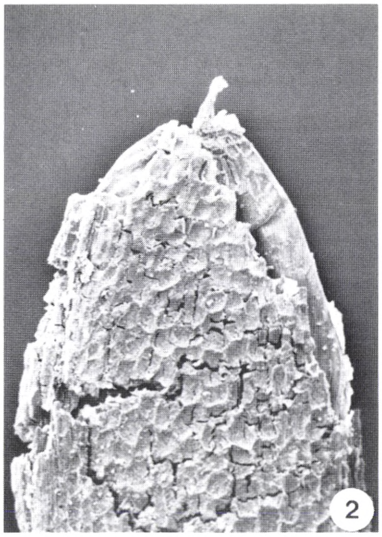
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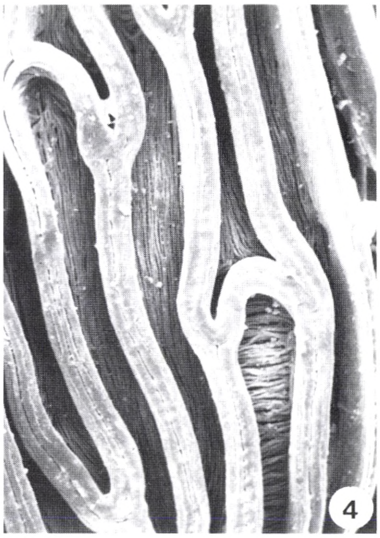
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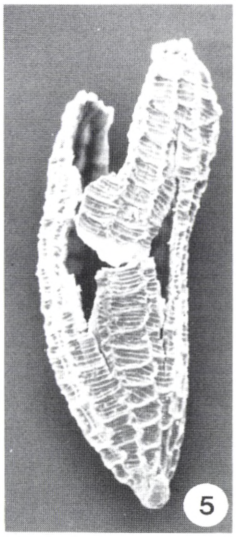
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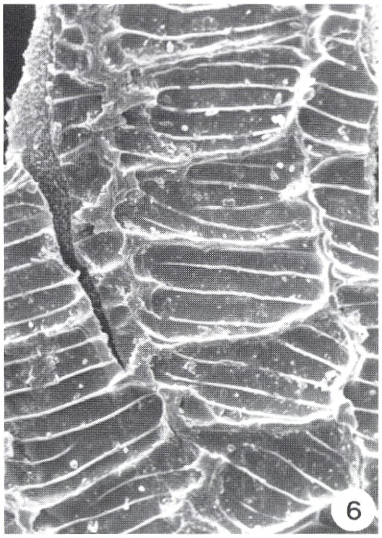
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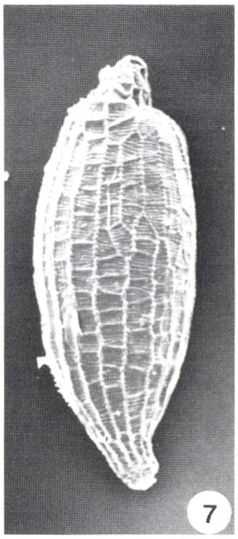
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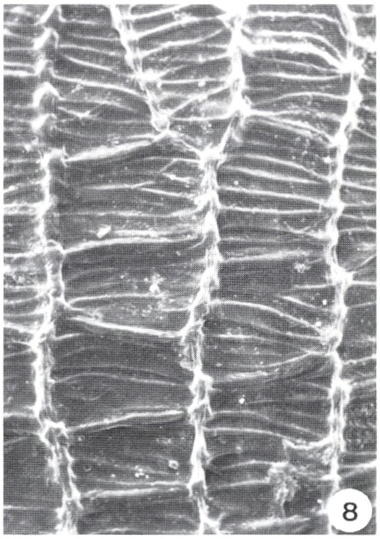
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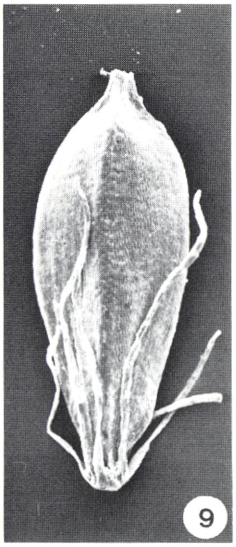
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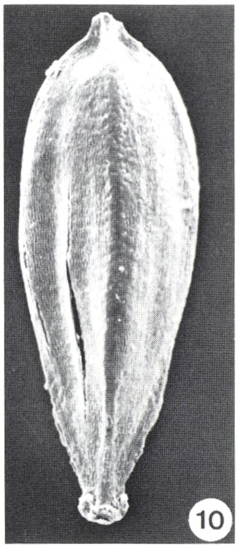
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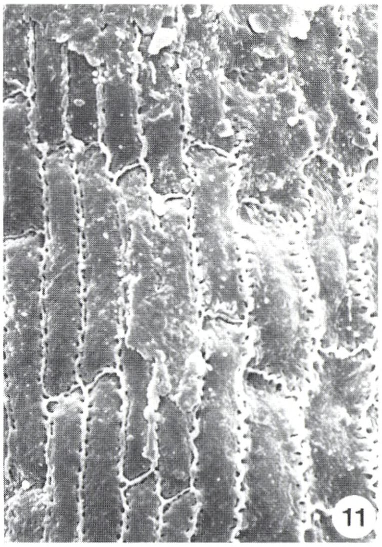
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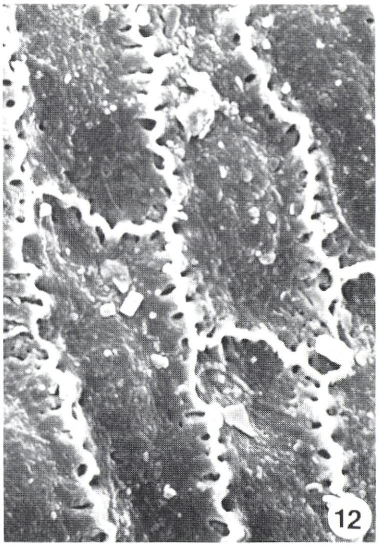
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PLATE 24

Fossil *Dulichium marginatum* (C. Reid & E.M. Reid) Dorofeev from the Middle Miocene Søby flora (figs 1–2).

1. Fruit with remnants of bristles (SEM–327_2, ×25).
2. Surface detail of fruit (SEM–327_2, ×700).

Fossil *Cyperus* sp. from the Middle Miocene Fasterholt flora (figs 3–4).

3. Fruit (SEM–96_6, ×100).
4. Surface detail of fruit showing finely undulate walls (SEM–96_6, ×700).

Fossil *Carex* sp. 1 from the Middle Miocene Fasterholt flora (figs 5–8).

5. Fruit with remnants of utricle (?) (SEM–96_{12}, ×53).
6. Surface detail of fruit (SEM–96_{12}, ×350).
7. Fruit (SEM–96_{13}, ×53).
8. Surface detail of fruit (SEM–96_{13}, ×700).

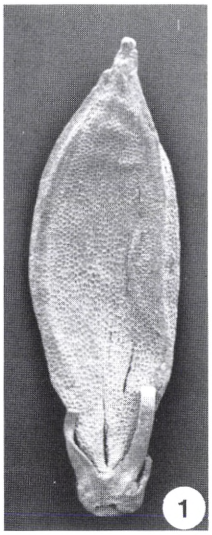
Fossil *Carex* sp. 2 from the Middle Miocene Fasterholt flora (figs 9–10).

9. Fruit (SEM–96_{10}, ×30).
10. Surface detail of fruit (SEM–96_{10}, ×350).

Fossil ?*Eriophorum* from the Middle Miocene Fasterholt flora (figs 11–12).

11. ?*Eriophorum* sp. 1. Fruit (SEM–125_4, ×30).
12. ?*Eriophorum* sp. 2. Fruit (SEM–125_5, ×30).

All figures SEM.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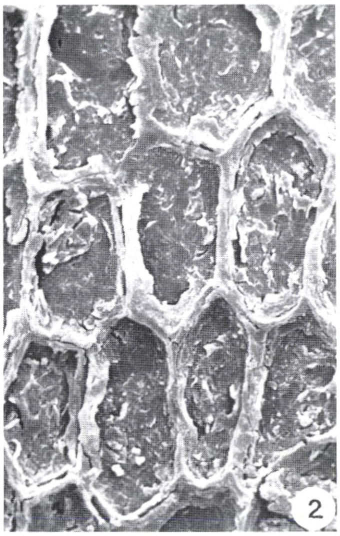
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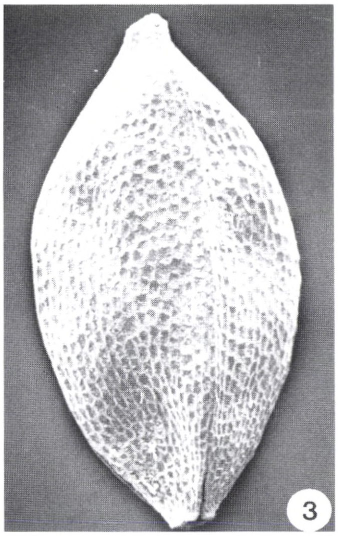
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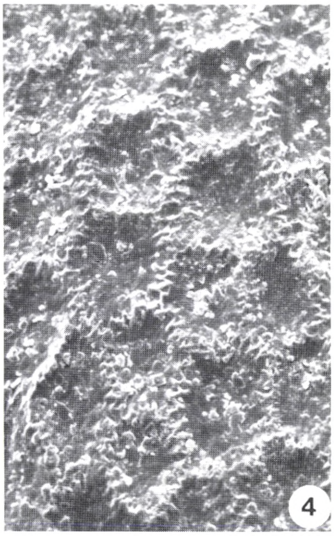
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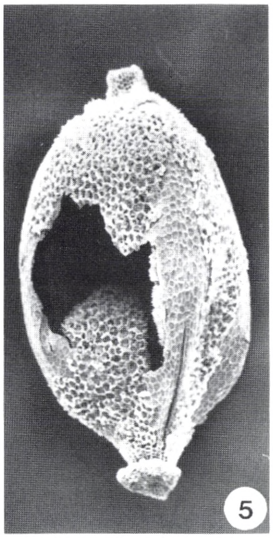
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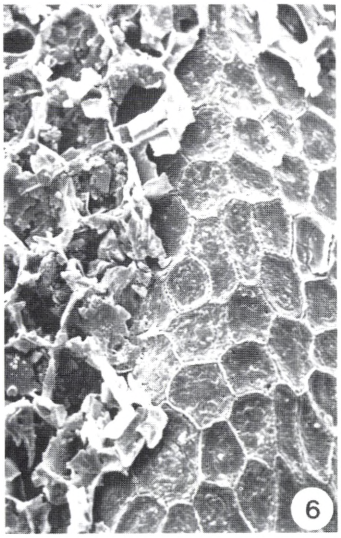
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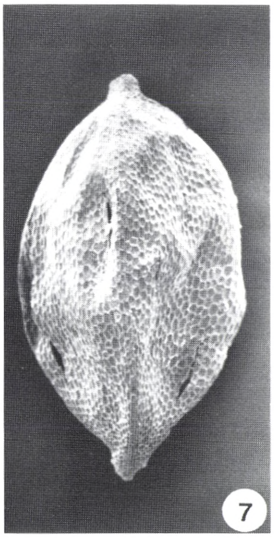
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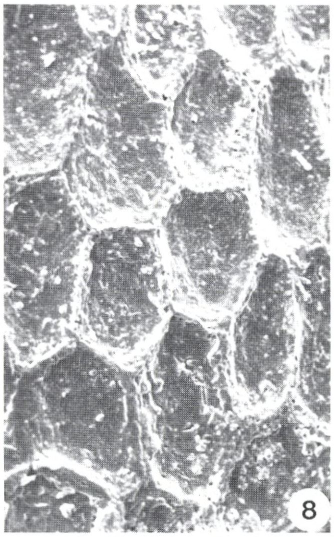
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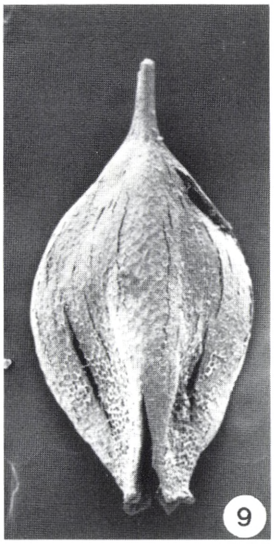
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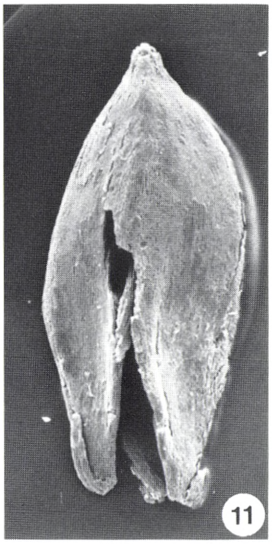
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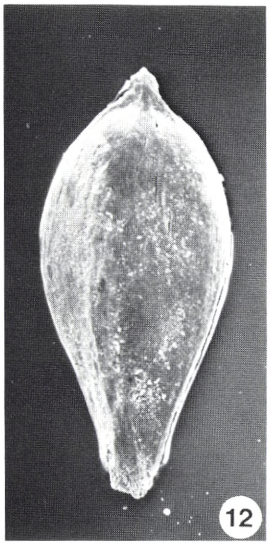
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PLATE 25

Fossil *Cladium reidiorum* Nikitin ex Dorofeev from the Middle Miocene Fasterholt flora (fig. 1).

1. Endocarp (SEM–103_6, ×50).

Fossil *Cladium bicorne* (Saporta) Friis comb. nov. from the Middle Miocene Fasterholt flora (figs 2–3).

2. Endocarp (SEM–337_1, ×20).
3. Basal view of endocarp showing basal extension (SEM–337_1, ×25).

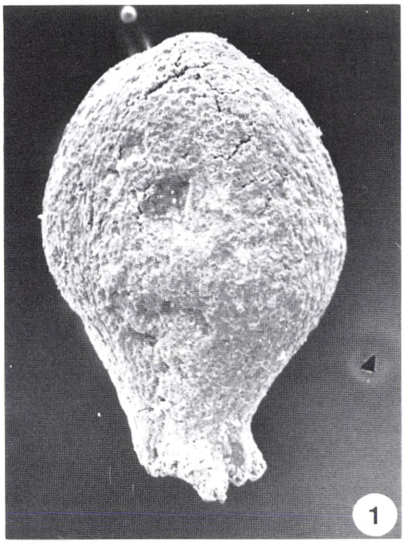
Fossil *Caricoidea jugata* (Nikitin ex Dorofeev) Mai from the Middle Miocene Fasterholt flora (figs 4–6).

4. Fruit (SEM–124_2, ×20).
5. Surface detail of fruit showing slightly undulate walls of outer epidermis (SEM–124_2, ×350).
6. Crosssection of fruit (SEM–124_5, ×35).

Fossil Cyperaceae genus ? from the Middle Miocene Fasterholt flora (figs 7–9).

7. Fruit (SEM–108_3, ×30).
8. Surface detail of fruit (SEM–108_3, ×700).
9. Crosssection of fruit (SEM–108_2, ×28).

All figures SEM.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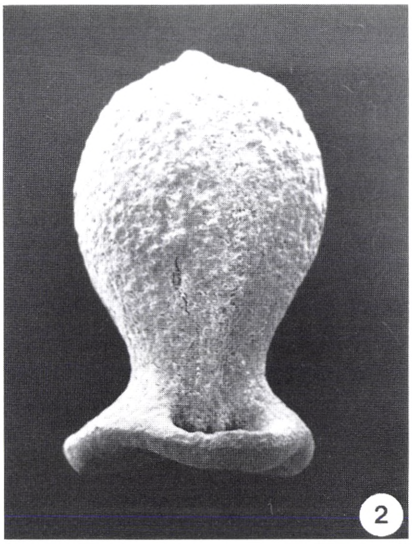
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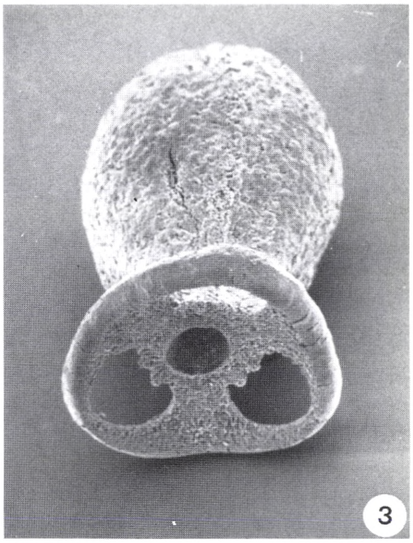
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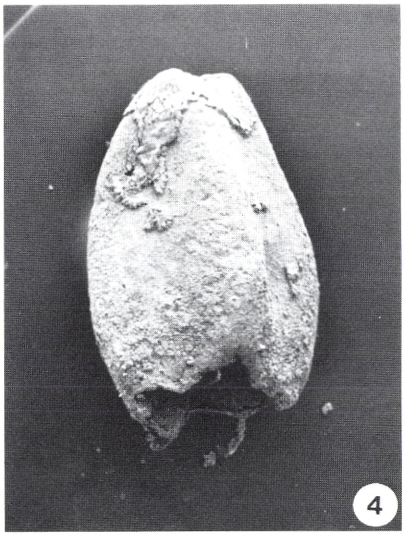
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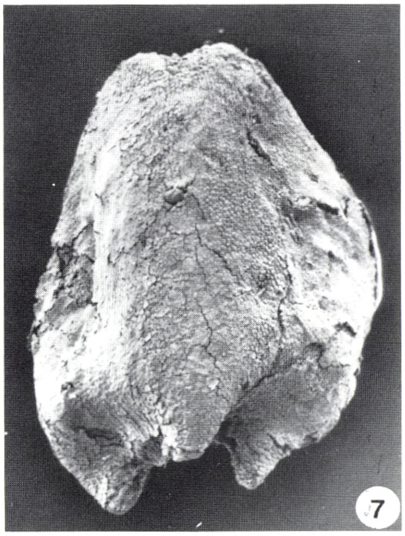
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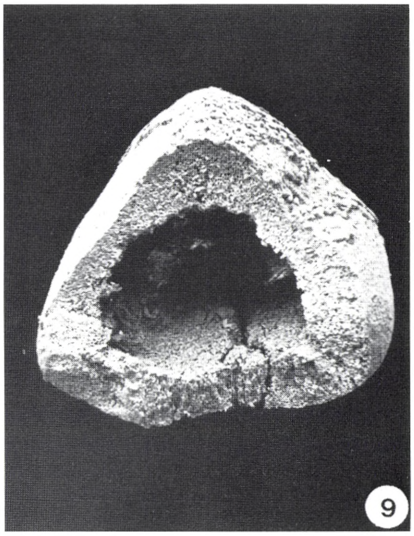
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PLATE 26

Fossil *Cladiocarya europaea* Mai from the Middle Miocene Fasterholt flora (figs 1–3).

1. Fruit with outer layer preserved (SEM–105_1, ×40).
2. Fruit with outer layer partly abraded (SEM–331_4, ×52).
3. Surface detail of fruit showing closely spaced verrucae (SEM–331_4, ×1400).

Fossil *Cladiocarya trebovensis* (Bůžek) Mai from the Middle Miocene Fasterholt flora (figs 4–6).

4. Basal view of fruit (SEM–331_1, ×52).
5. Fruit with indistinct basal neck (SEM–105_6, ×50).
6. Crosssection of fruit showing thin-walled cells of outer layer and strongly thickened cells of inner layer (SEM–105_8, ×350).

Fossil ?*Epipremnum crassum* C. Reid & E.M. Reid from the Middle Miocene Fasterholt flora (fig. 7).

7. Seed (SEM–328_3, ×20).

Fossil *Lemna* sp. from the Middle Miocene Fasterholt flora (figs 8–9).

8. Seed (SEM–97_{10}, ×70).
9. Surface detail of seed (SEM–97_{10}, ×1400).

All figures SEM.


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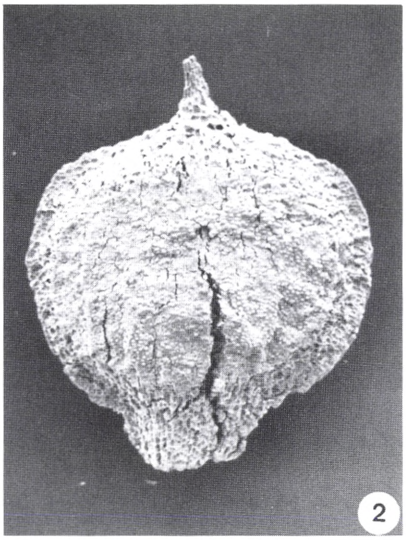
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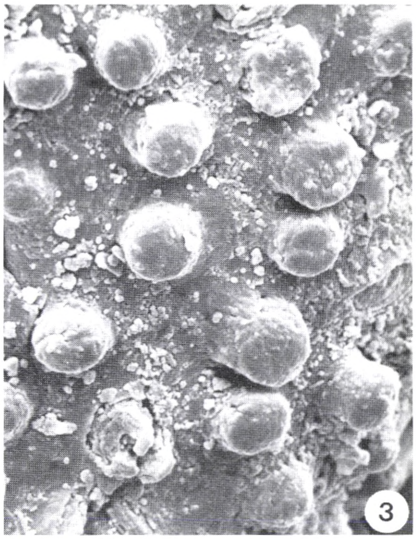
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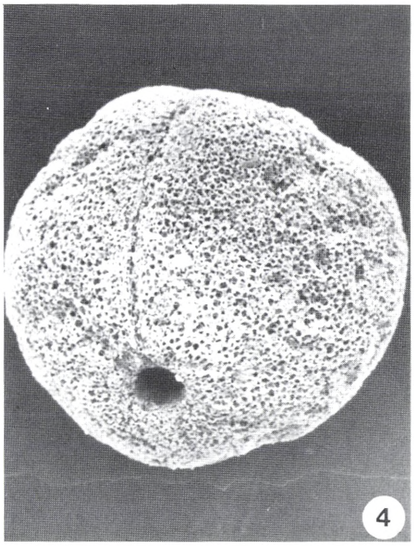
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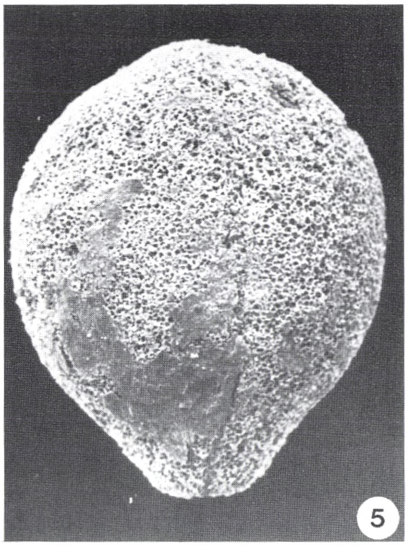
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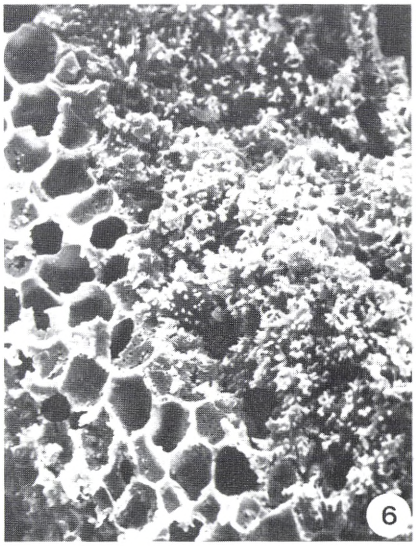
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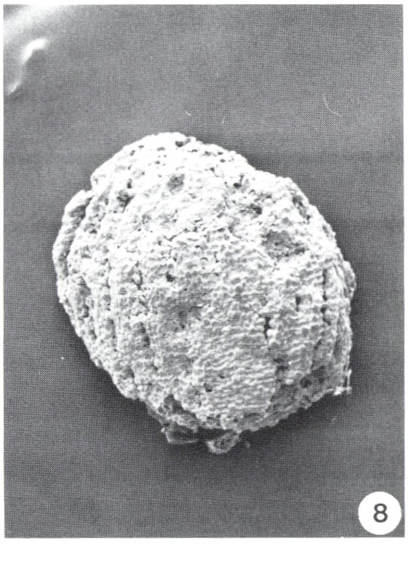
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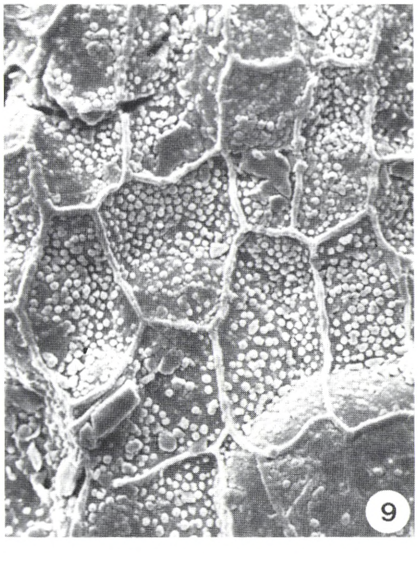
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PLATE 27

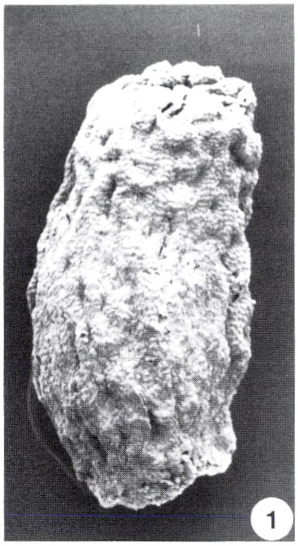
Fossil *Pistia sibirica* Dorofeev from the Middle Miocene Fasterholt flora (figs 1–7).

1. Seed with epidermis preserved (SEM–332_2, ×35).
2. Abraded seed showing intercellular spaces (SEM–332_3, ×35).
3. Tegmen showing chalaza and micropyle (SEM–96_5, ×32).
4. Longitudinal section of seed showing chalaza and micropyle (1076.05, ×45).
5. Detail of seed surface showing epidermis and depressed area over intercellular space (SEM–332_2, ×350).
6. Detail of abraded seed showing intercellular spaces (SEM–332_3, ×350).
7. Section of seed showing equiaxial and thin-walled cells of testa and intercellular spaces (1076.05, ×200).

Fossil *Typha* from the Middle Miocene Fasterholt flora (figs 8–13).

8– 9. *Typha* sp. 1 (SEM–100_{4-5}, ×50).
10–11. *Typha* sp. 2 (SEM 114_{1-2}, ×70).
12–13. *Typha* sp. 3 (SEM–114_{3-4}, ×70).

All figures SEM except figs 4 and 7 which are transmitted light micrographs.
ch = chalaza, m = micropyle.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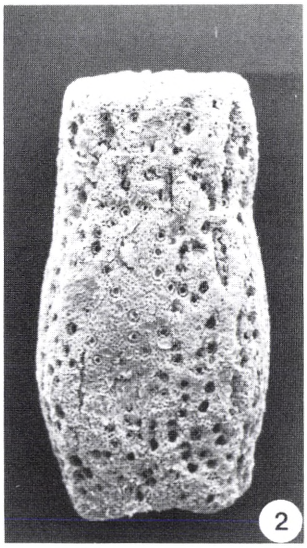
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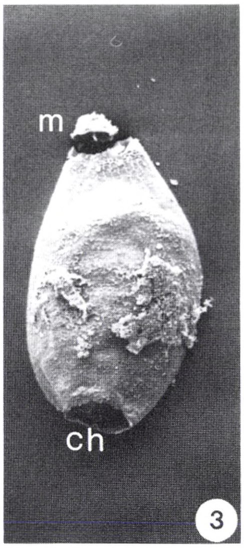
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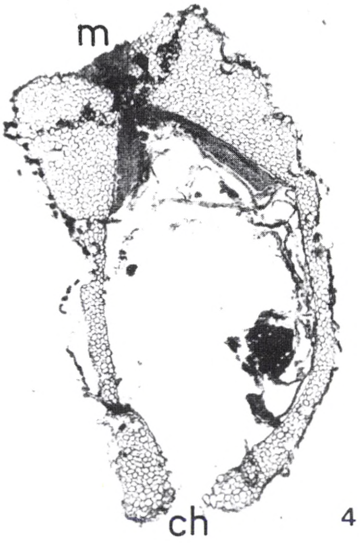
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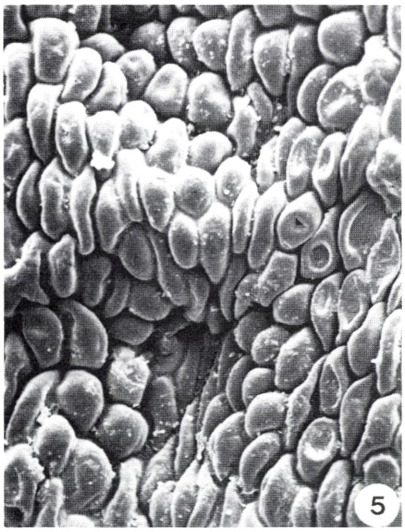
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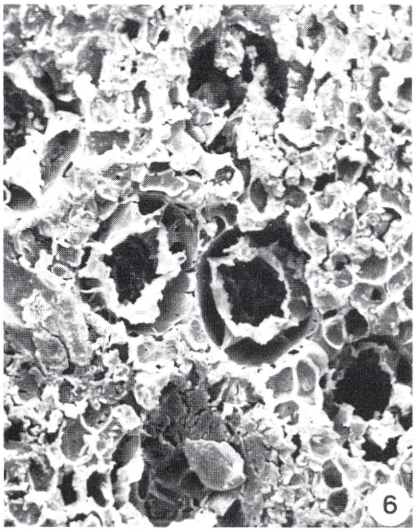
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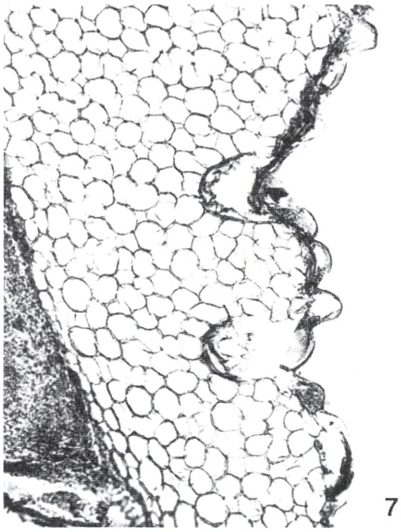
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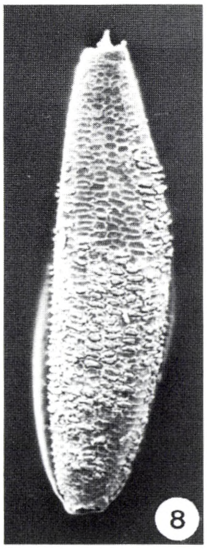
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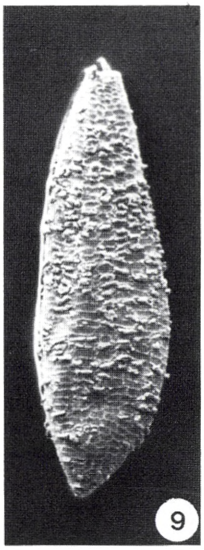
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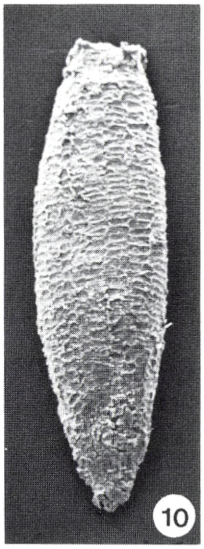
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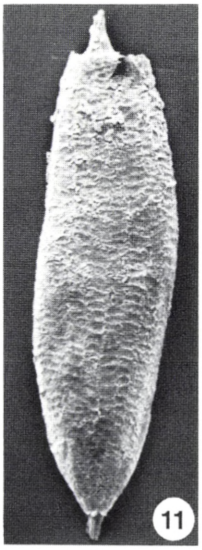
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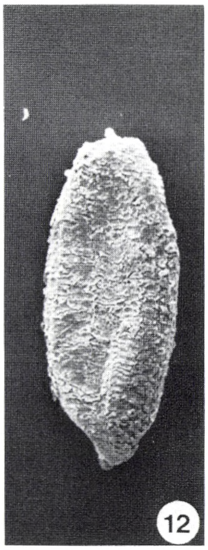
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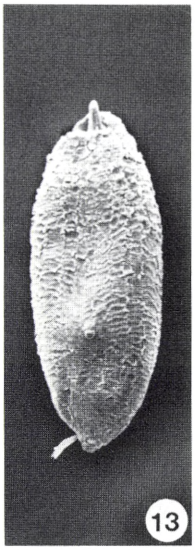
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PLATE 28

Fossil *Sparganium pusilloides* Mai from the Middle Miocene Fasterholt flora (figs 1–2).

1. Endocarp (SEM–100_7, ×35).
2. Endocarp (SEM–100_9, ×35).

Fossil *Sparganium* cf. *simplex* Huds. from the Middle Miocene Fasterholt flora (figs 3–4).

3. Endocarp (SEM–328_1, ×20).
4. Endocarp (SEM–328_2, ×20).

Fossil *Aracispermum canaliculatum* Nikitin ex Dorofeev from the Middle Miocene Fasterholt flora (figs 5–6).

5. Seed with prominent raphe and two lateral furrows (SEM–125_8, ×20).
6. Crosssection of seed showing strongly developed seed wall around the raphe (SEM–77_1, ×45).

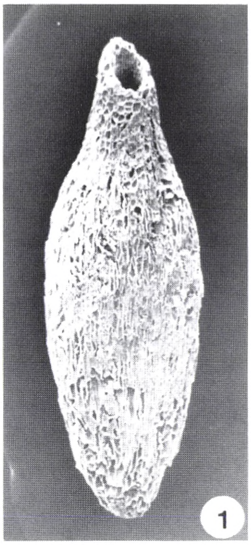
Fossil *Carpolithes natans* Nikitin ex Dorofeev from the Middle Miocene Fasterholt flora (fig. 7).

7. Seed with germination valve attached (SEM–328_1, ×15).

Fossil *Carpolithes tiffneyi* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 8–10.).

8. Holotype. Seed (SEM–123, ×100).
9. Seed (SEM–120_{10}, ×100).
10. Internal view of seed showing strongly pitted cell walls (SEM–25_7, ×400).

All figures SEM.
r = raphe.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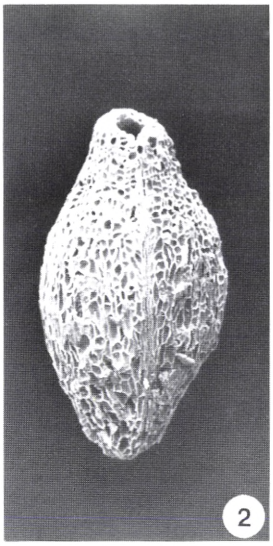
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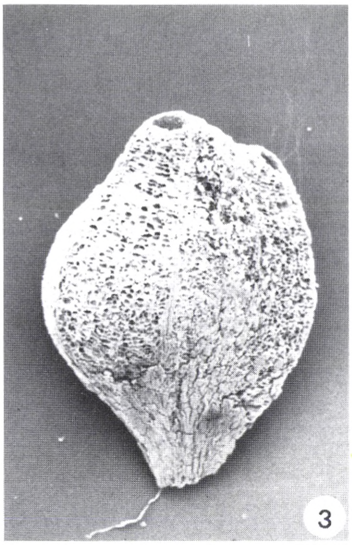
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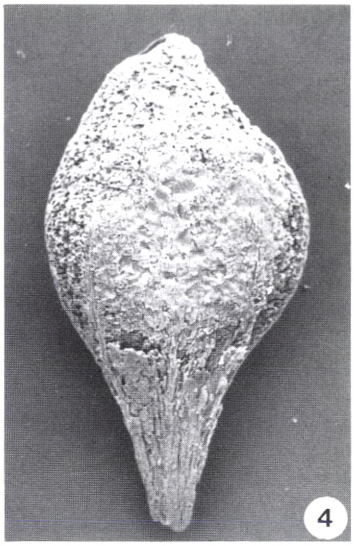
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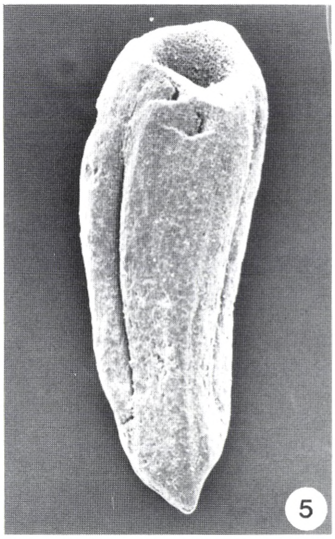
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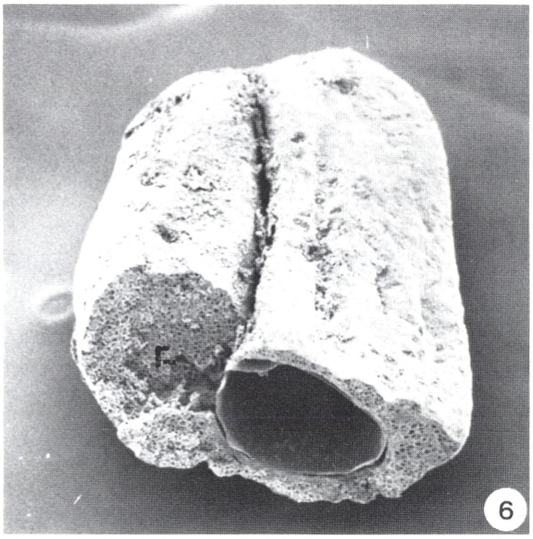
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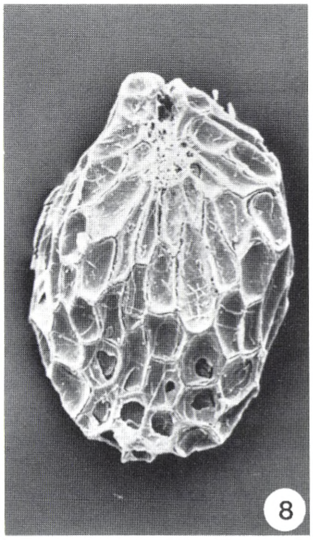
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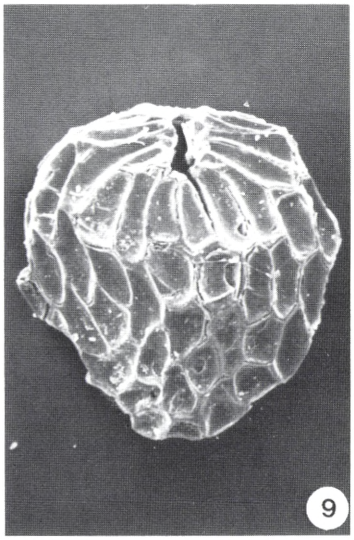
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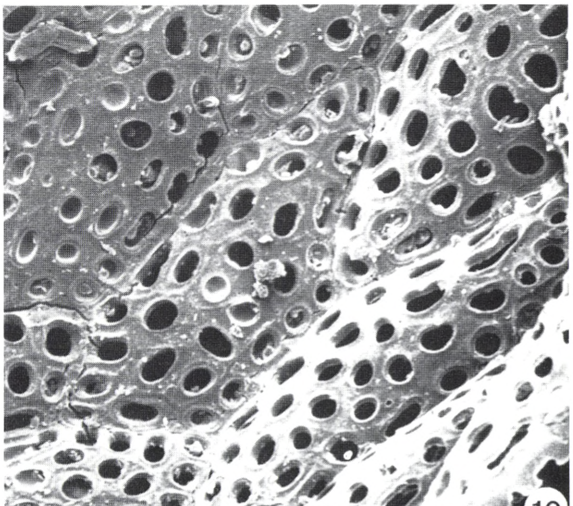
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PLATE 29

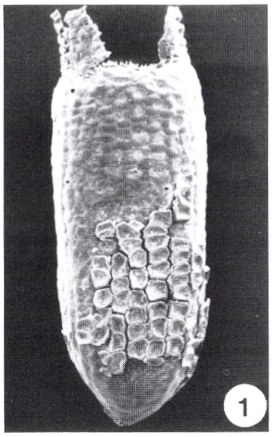
Fossil *Carpolithes dorofeevii* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 1–7).

1. Holotype. Seed with remnants of outer layer of seed coat (SEM–69_7, ×60).
2. Seed with remnants of raphe (SEM–69_8, ×60).
3. Longitudinal section of seed (SEM–109_3, ×60).
4. Crosssection of seed showing columnar cells of inner layer (SEM–109_1, ×120).
5. Apical part of seed showing stellate-undulate cell walls and apical operculum (SEM–109_2, ×300).
6. Crosssection of seed showing finely pitted walls of sclereids (SEM–109_1, ×600).
7. Surface of inner layer near middle of seed showing hexagonal cell outlines (SEM–69_9, ×600).

Fossil *Carpolithes nikitinii* Friis sp. nov. from the Middle Miocene Fasterholt flora (figs 8–10).

8. Holotype. Seed (SEM–109_4, ×60).
9. Seed with remnants of outer layer of seed coat (SEM–109_5, ×60).
10. Longitudinal section of seed (SEM–109_9, ×60).
11. Crosssection of seed showing columnar cells of inner layer (SEM–109_8, ×100).
12. Apical view of seed showing stellate-undulate cell walls (SEM–109_6, ×120).
13. Detail of apical cell showing strongly undulate walls (SEM–109_6, ×660).
14. Hexagonal cell outlines of columnar sclereids (SEM–109_6, ×660).

All figures SEM.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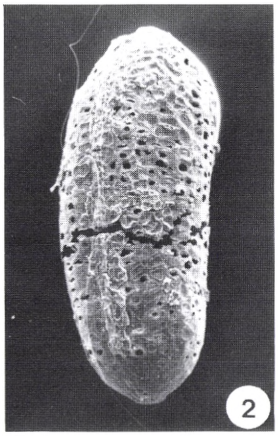
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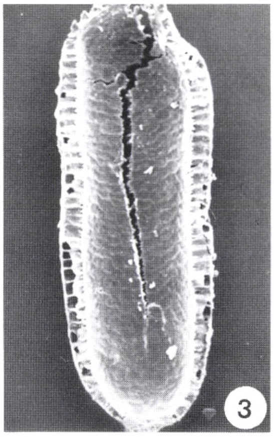
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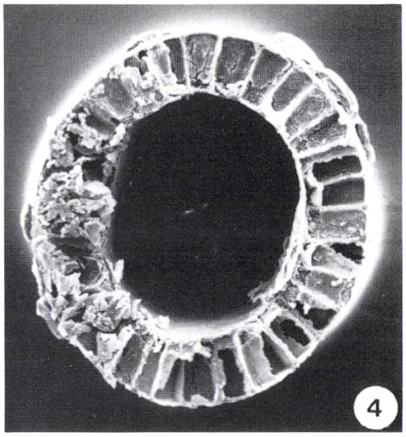
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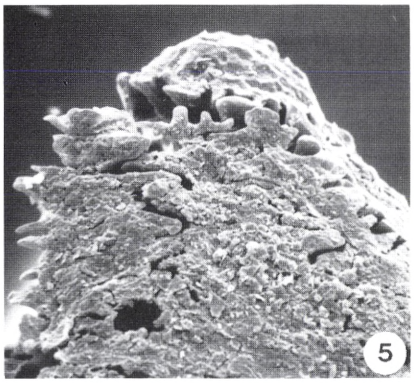
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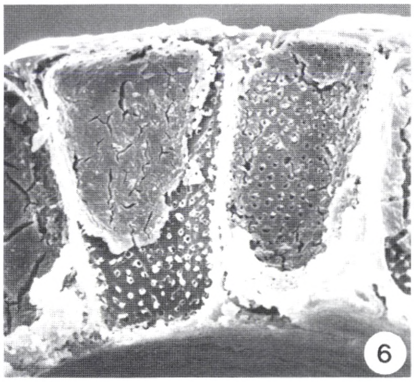
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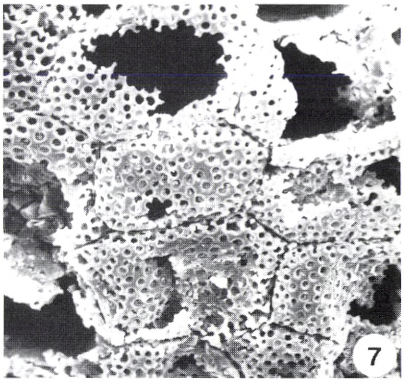
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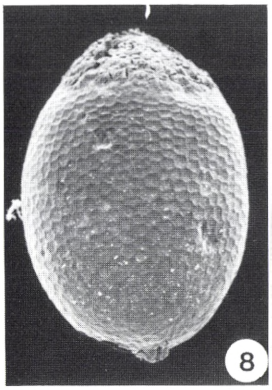
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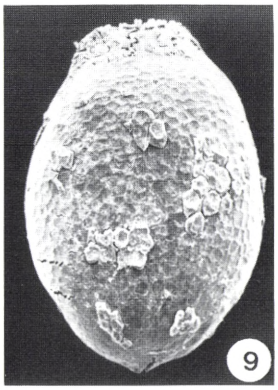
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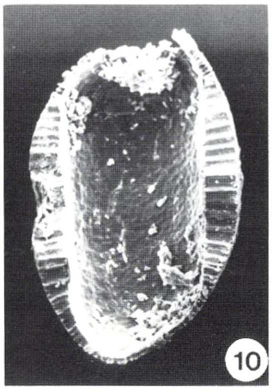
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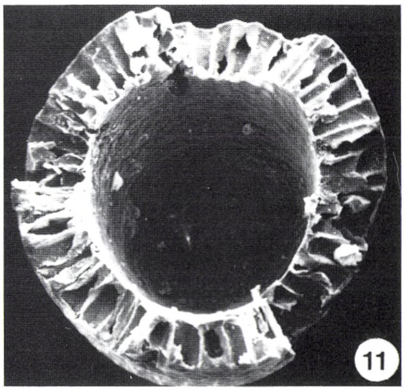
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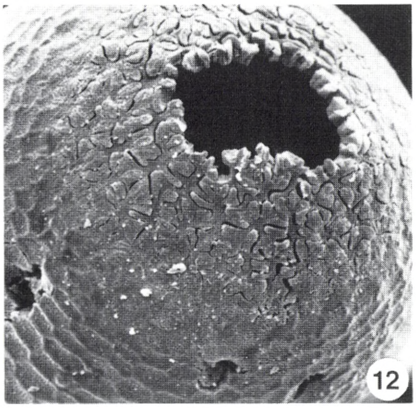
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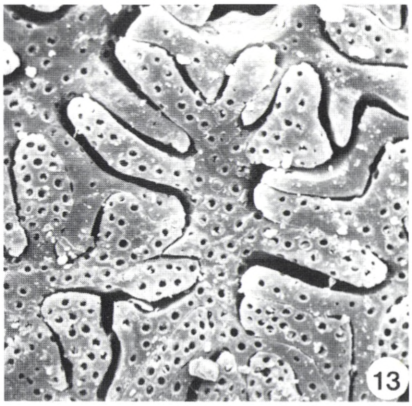
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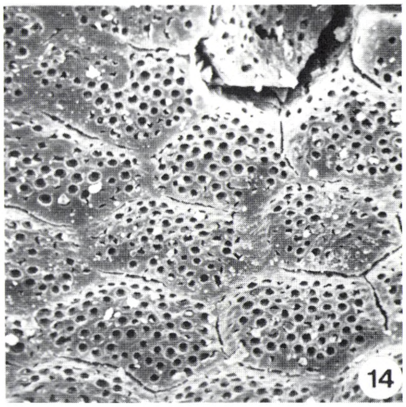
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PLATE 30

Fossil *Carpolithes* sp. 5 from the Middle Miocene Fasterholt flora (figs 1–2).
1. Seed (SEM–124_1, ×70).
2. Surface detail of seed (SEM–124_1, ×140).

Fossil *Carpolithes* sp. 7 from the Middle Miocene Fasterholt flora (fig. 3).
3. Seed (SEM–97_9, ×53).

Fossil *Carpolithes* sp. 6 from the Middle Miocene Fasterholt flora (figs 4–6).
4–5. Seeds (SEM–97_{5-6}, ×45).
6. Surface detail of seed showing undulate cells of inner layer (SEM–97_5, ×350).

Fossil *Carpolithes* sp. 8 from the Middle Miocene Fasterholt flora (fig. 7).
7. Fruit (SEM–81_2, ×53).

Fossil *Rhamnospermum bilobatum* Chandler from the Middle Miocene Fasterholt flora (figs 8–10).
8. Well-preserved specimen with central aperture (SEM–329_2, ×20).
9. Operculum (SEM–41_2, ×70).
10. Surface detail of fossil showing cells of outer layer (SEM–329_1, ×800).

All figures SEM.


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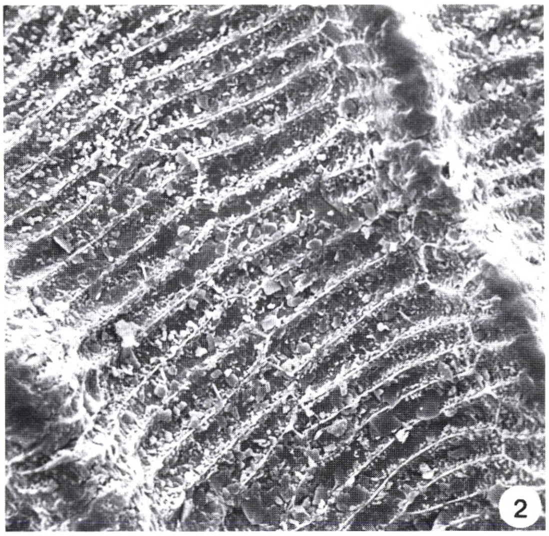
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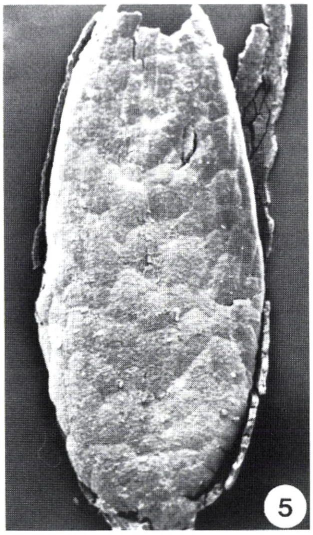
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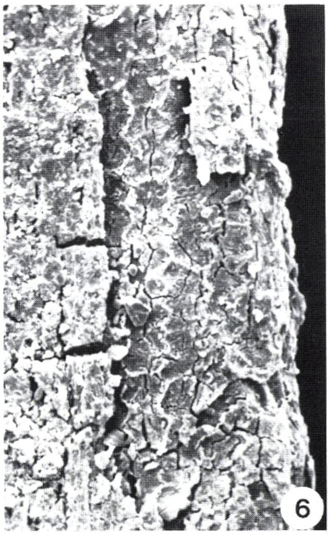
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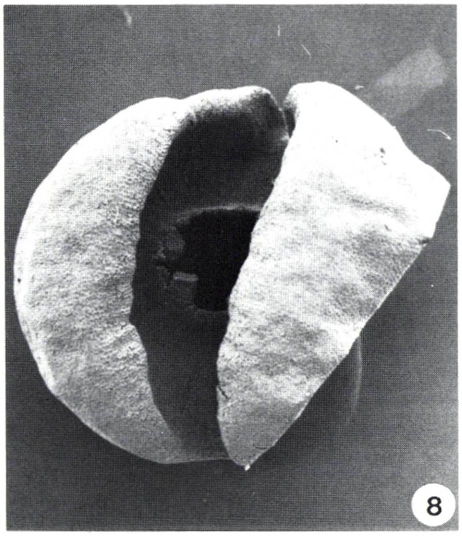
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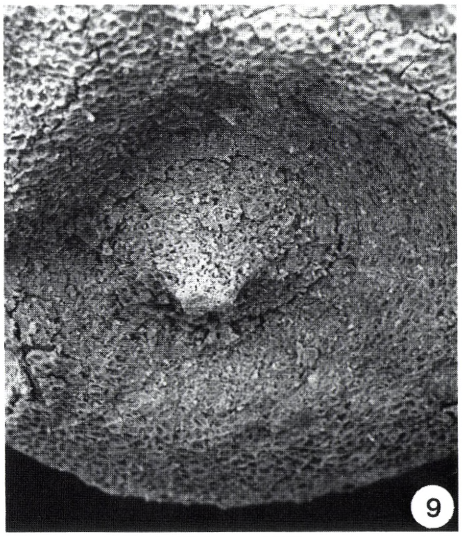
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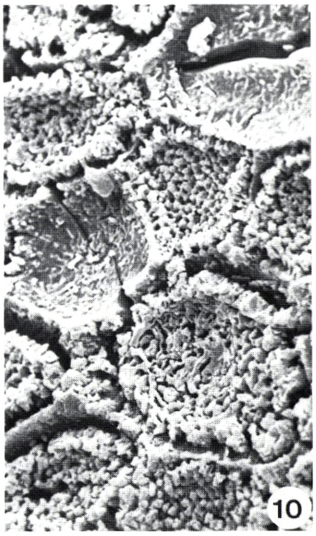
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Printed in Denmark by Bianco Lunos Bogtrykkeri A/S. ISSN 0366-3612. ISBN 87-7304-150-5