Climatic implications of microcarpological analyses of the Miocene Fasterholt flora, Denmark

ELSE MARIE FRIIS

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The Fasterholt flora has been sieved out from a fine grained sand bed intercalated in the two uppermost browncoal seams in the browncoal pit of Carl Nielsen Ltd. near Fasterholt, Jylland, Denmark. Climatic and floristic analyses are made chiefly on the basis of the small plant remains. The results of the analyses indicate that the Fasterholt flora is an arctotertiary flora that has grown under warm temperate to subtropical climatic conditions on a coastal plain on the border of a large delta. Some of the floristic-climatic analyses applied to the Fasterholt flora have been tested on several fossil floras described from western Siberia and northern Europe and the results show considerable accordance.

E. M. Friis, Geologisk Institut, Aarhus Universitet, DK-8000 Århus C, Denmark. June 27th, 1975.

The present study is part of the geological-palaeobotanical project undertaken by the Geological Institute of the University of Aarhus, Denmark, in the browncoal pit of Carl Nielsen Ltd. near Fasterholt, Jylland (fig. 1) (Koch & Friedrich 1970; Koch et al. 1973).

The browncoal deposits at Fasterholt are considered to belong to the Middle Miocene Odderup Formation as defined by Rasmussen (1961) (Koch & Friedrich 1970; Koch et al. 1973).

The Fasterholt flora has been sieved out from a fine grained sandy bed intercalated in the two uppermost browncoal seams of the browncoal pit and consists mainly of fruits and seeds, although twigs, thorns, megaspores and fungi have also been found.

The coarser fraction of fruits and seeds of the Fasterholt flora is under examination by B. Eske Koch and W. L. Friedrich (Friedrich & Koch 1970, 1972; Koch & Friedrich 1970, 1971). The small diaspores of the Fasterholt flora, comprising plant remains less than about 2 mm – in the following referred to as the Fasterholt microflora – have been examined by the present author.

About 125 species have so far been found in the Fasterholt microflora and about two thirds of the species have been described (table 1). More than 10000 specimens have been examined. The abundance expressed in per cent of each individual species of the Fasterholt microflora is shown in table 1.

In addition to the diaspores included in table 1 the Fasterholt microflora comprises remains of different fungi (table 2) and the twigs of *Hellia salicornioides* Unger.

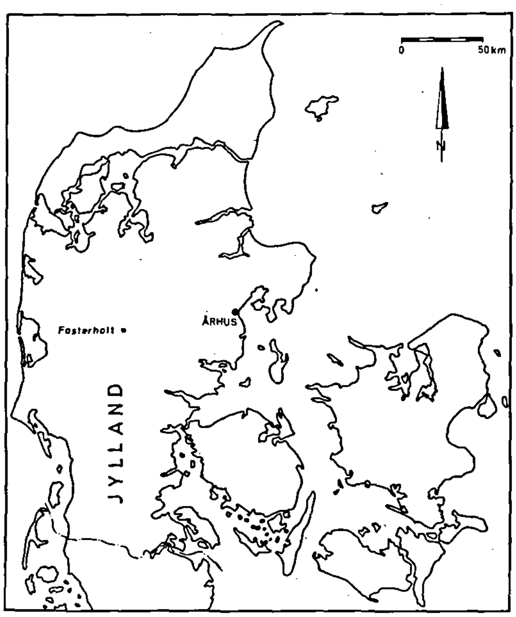

Fig. 1. Location map.

Table 1. Species represented in the Fasterholt microflora.

	Number of Specimens	%
Selaginella pliocenica Dorofeev	1	–
Salvinia cerebrata Nikitin	88	0.9
Salvinia cf. *cerebrata* Nikitin	20	0.2
Salvinia sp. 1	1	–
Salvinia sp. 2	1	–
Azolla nikitinii Dorofeev	10	0.1
Azolla sp.	2	–
Pinus sp.	2	–
Sequoia sp.	950	9.6
Glyptostrobus europaeus (Brogn.) Heer	660	6.7
Liriodendron sp.	49	0.5
Brasenia tenuicostata Nikitin	130	1.3
Liquidambar sp.	5	–
Platanus sp.	223	2.3
Urtica cf. *dioica* L.	2	–
Laportea sp.	5	–
Alnus decipiens (Nikitin) Dorofeev	880	8.9
Comptonia longistyla (Nikitin) Dorofeev	25	0.3
Myrica wiesaensis Kirchheimer	29	0.3
Myrica cf. *ceriferiformis* Kownas	310	3.1
Myrica cf. *suppanii* Kirchheimer	103	1.0
Myrica sp.	26	0.3
Eurya stigmosa (Ludw.) Mai	14	0.1
Hypericum sp. 1	25	0.3
Hypericum sp. 2	22	0.2
Hypericum sp. 3	25	0.3
Hypericum sp. 4	49	0.5
Hypericum sp. 5	30	0.3
Clethra sp.	3	–
Lyonia sp.	2	–
Erica sp.	7	0.1
Epacridicarpum mudense Chandler	3015	30.6
Rubus laticostatus Kirchheimer	350	3.5
Rubus cf. *laticostatus* Kirchheimer	7	0.1
Pyracantha acutiformis (C et E. M. Reid) Szafer	663	6.9
Aldrovanda praevesiculosa Kirchheimer	2	–
Decodon gibbosus (E. M. Reid) E. M. Reid	51	0.5
Decodon vectensis Chandler	4	–
Decodon sp.	8	0.1
Diclidocarya menzelii E. M. Reid	7	0.1
Microdiptera parva Chandler	20	0.2
Cornus gorbunovii Dorofeev	30	0.3
Aralia pusilla Dorofeev	60	0.6
Ilex saxonica Mai	12	0.1
Paliurus favonii Unger	53	0.5
Cephalanthus kireevskianus (Dorofeev) Ra.-Bobrowska	22	0.2
Scrophulariaceae gen. et sp. 1	34	0.3
Scrophulariaceae gen. et sp. 2	6	0.1
Orobanche sp.	33	0.3
Teucrium sibiricum Dorofeev	3	–
Caldesia proventitia Nikitin	2	–
Potamogeton cf. *wiesaensis* Kirchheimer	8	0.1
Scirpus ragozinii Dorofeev	380	3.8
Scirpus (?) sp. 1	1	–
Scirpus (?) sp. 2	2	–
Cladium reidiorum Nikitin	3	–
Cladium sp.	3	–
Carex (?) sp. 1	42	0.4
Carex (?) sp. 2	11	0.1
Carex (?) sp. 3	21	0.2
Carex (?) sp. 4	2	–
Cyperaceae gen. et sp. 1	225	2.3
Cyperaceae gen. et sp. 2	1	–
Cyperaceae gen. et sp. 3	140	1.4
Epipremnum sp. 1	3	–
Epipremnum sp. 2	300	3.0
Pistia sibirica Dorofeev	300	3.0
Aracispermum canaliculatum Nikitin	5	–
Aracispermum cf. *jugatum* Nikitin	4	–
Sparganium camenzianum Kirchheimer	28	0.3
Sparganium cf. *simplex* Huds.	13	0.1
Typha sp.	300	3.0
Rhamnospermum bilobatum Chandler	22	0.2
Carpolithes sp. 1	71	0.7

Table 2. Fungi represented in the Fasterholt microflora.

Rosellinites areolatus (Fresenius et v. Meyer) Kirchheimer
Trematospharites lignitum (Heer) Meschinelli
Diatrype cf. *disciformis* (Hoffman ex Fries) Fries
Hysterographium (?) sp.
Sclerotiniaceae gen.(?)

The fossils are very well preserved. There has been no deformation of the material during fossilization as can be seen from the outline of the cells in the fruit walls and testa. Comparison of the testa of closely related living and fossil species indicates that the intercellular spaces of the fossil have retained their original form and size. The material has apparently only been submitted to slight physical influence during tranportation from the habitat to the place of deposition. None of the diaspores are unduly worn and many of the seeds and fruits still retain the epidermis and cuticle. The preservation of the fossil diaspores tends to indicate that the content of fossil fruits and seeds probably represents a rather local flora.

With the intention of making a floristic and climatic interpretation of the Fasterholt flora different methods of taxonomic analysis have been used. The taxonomic methods are based on comparison of the fossil plants with related living genera.

The methods include (1) vegetation analyses and (2) phytogeographical analyses. The analyses are fundamentally qualitative, but the quantitative aspect has also been considered.

Vegetation analyses

In vegetation analyses the habitat and growth form of the fossil plants are estimated on the basis of the physiological requirements of the related living genera.

Ecology

The Fasterholt microflora is divided into 3 groups on the basis of comparison with living genera and their ecology: dryland plants, wetland plants, and aquatic plants. The great majority of the fossil flora are plants from the aquatic and wetland environments.

Fossil species making up 16% of the Fasterholt microflora can be referred to living genera from aquatic environments, among them species of *Salvinia, Azolla, Brasenia, Aldrovanda, Potamogeton* and *Pistia.* 57% of the fossil species are referred to living genera from wetland environments.

The wetland plants are species of *Selaginella, Glyptostrobus, Liquidambar, Alnus, Myrica, Hypericum, Clethra, Lyonia, Erica, Decodon, Cornus, Cephalanthus, Teucrium, Caldesia, Scirpus, Cladium, Carex, Sparganium* and *Typha.*

The dryland plants include species of *Pinus, Sequoia, Liriodendron, Platanus, Urtica, Laportea, Comptonia, Eurya, Rubus, Pyracantha, Aralia, Ilex, Paliurus* and *Epipremnum.* However, several of these dryland genera have representatives in the wetland environments, e. g. *Pinus, Rubus, Aralia* and *Ilex.*

Important for the ecological considerations of the Fasterholt flora are the plant remains from the coarser fraction determined by B. Eske Koch and W. L. Friedrich (table 2 in Koch et al. 1973). These genera are: *Taxodium, Tetraclinis, Magnolia, Mastixia, Nyssa, Planera, Prunus, Pterocarya, Quercus, Symplocos, Vitis* and *Stratiotes.*

Many of the genera suggest that the flora has grown in swampy, coastal environments bordering a sizable delta. This assumption is supported by the local as well as the regional geology (Rasmussen 1966; Koch et al. 1973).

Comparisons with recent vegetations show that the Atlantic Coastal Plain of the eastern and southeastern United States is of interest for the interpretation of the environments of the Fasterholt flora. The plant communities of the Mississippi Delta marshlands of southeastern Louisiana have been studied by Penfound & Hathaway (1938) and Hall & Penfound (1939). These authors recognized different associations. The *Quercus* association on the drier habitat includes several species of *Quercus.* This genus is rare in the Fasterholt flora (Koch et al. 1973). It is represented by a few cupulae but no fruits are found. Generally, fruits of *Quercus* are seldom found in fossil floras, probably because of rapid decomposition (Takhtajan 1969). The *Taxodium-Nyssa* association (the cypress-gum swamps) occupies the lower elevations. The swamp is dominated by *Nyssa* and *Taxodium.* These two genera are amongst the most common fossils in the Fasterholt flora (Koch et al. 1973).

Hall & Penfound (1939) listed 22 species in the *Taxodium-Nyssa* association of which 45 % are represented by genera in the Fasterholt flora. Penfound & Hathaway (1938) listed 110 species in this association. Of these 14 % are represented by genera also found in the Fasterholt flora.

The plant communities of the Coastal Plain of North Carolina have been studied by Wells (1928, 1942) who recognized 13 different associations. From the xeric dune community and the xeric salt marsh community only few genera have been found in the Fasterholt flora. In the hydric freshwater marsh that follows, *Typha* and *Scirpus* are dominant. These two genera are also common in the Fasterholt flora. Among the subdominants in the hydric freshwater marsh *Cladium* and *Carex* are mentioned and these two genera were also found in the Fasterholt flora.

The *Nyssa-Taxodium-Chamaecyperis* association of North Carolina is very much like the cypress-gum association in southeastern Louisiana. This association is succeeded by the xeric shrub bog community. Many of the shrub plants belong to genera also found in the Fasterholt flora: *Ilex, Myrica, Magnolia, Liquidambar, Clethra* and *Lyonia* (= *Xolisma*).

From the Coastal Plain of North Carolina 285 species are recorded by Wells (1928) and

15% of these species are referred to genera also found in the Fasterholt flora.

The Pocomoke Swamp on the eastern shore of Maryland is considered as the northernmost occurrence of the cypress swamp vegetation of the Atlantic Coastal Plain. It has been studied by Beaven & Oosting (1939). Among the 285 species recorded from the different associations in the Pocomoke Swamp 20 % are referred to genera also found in the Fasterholt flora.

A total of 37 % of the Fasterholt genera are known in the Pocomoke Swamp, 28 % are known in the Coastal Plain of North Carolina and 23 % can be found in the swamps of southeastern Louisiana.

From this knowledge of recent plant communities of the Atlantic Coastal Plain and from the local geological investigations it is reasonable to assume that the Fasterholt flora grew on a similar coastal plain with only slight elevations. The following reconstruction of the environments of the Fasterholt flora may be made: In the areas with the water table at or above the soil surface for long periods of the year there has been freshwater marsh dominated by *Typha* and cyperaceae. A swamp forest dominated by *Nyssa*, *Taxodium* and *Glyptostrobus* occupied areas covered with shallow water for long periods. Subdominants in the swamp forest were species of *Cephalanthus, Clethra, Cornus, Ilex, Magnolia, Myrica* and *Rubus*. The herbaceous plants were dominated by *Scirpus* and *Carex*. Areas with the water table temporarily at the surface were occupied by a shrub bog with species of *Myrica, Clethra, Erica, Lyonia, Ilex* and *Magnolia*. The bordering forest on the better drained soil was a mixed mesophytic forest with species of *Alnus, Aralia, Juglans, Liquidambar, Liriodendron, Magnolia, Myrica, Nyssa, Paliurus* and *Pterocarya*. The scrubby growth was dominated by species of *Pyracantha, Rubus* and *Eurya*. *Epipremnum* and *Vitis* were important vines.

This interpretation is supported by comparison with the mixed mesophytic forest of southern China which has also a great deal of genera in common with the Fasterholt flora. The following genera known from the Fasterholt flora have been recorded from the Lower Yangtze: *Alnus, Aralia, Cornus, Clethra, Epipremnum, Eurya, Ilex, Juglans, Liquidambar, Liriodendron, Magnolia, Myrica, Nyssa, Paliurus, Pinus, Prunus, Pterocarya, Quercus, Rubus, Symplocos* and *Vitis* (Wang, 1961).

In ponds and lakes species of *Azolla, Salvinia, Brasenia, Aldrovanda, Potamogeton, Stratiotes* and *Pistia* have grown. Streams and lakes have been bordered by species of *Decodon, Hypericum* and cyperaceae. Hartz (1909) also referred to the 'dismal swamps' of the southeastern United States as a possible similar environment for the formation of the Tertiary browncoal of Jylland. For the Miocene browncoal of Die Niederrheinische Bucht a similar interpretation has been given by Teichmüller (1958).

Growth form

Studies by Bailey & Sinnott (1916) showed that in recent vegetation there is a marked correlation between environment and growth form. The results of their investigations indicated in general that the percentage of arborescent dicotyledonous species decreases with increasing latitude. In tropical and subtropical environments woody dicotyledons are preponderant and towards higher latitudes the proportion of herbaceous dicotyledonous species increases (table 3).

This correlation between environment and growth form was used by Reid & Chandler

Table 3. Percentage distribution of arborescent and herbaceous species in selected living floras (after Bailey & Sinnott 1916) and the Fasterholt microflora.

	Arborescent %	Herbaceous %
Ellesmereland	9	91
N. E. Siberia	14	86
England	13	87
N. E. Germany	14	86
E. C. North America	23	77
S. E. United States	24	76
Florida Keys	45	55
Hongkong	59	41
Ceylon	64	36
Malay States	83	17
Brazil	83	17
Fasterholt microflora	63	37

(1933) in the interpretation of the London Clay flora. About 97 % of the London Clay species are considered as arborescent plants, which suggests that the London Clay flora was tropical. These authors have also shown that the percentage of woody plants in European Cenozoic floras decreases with decreasing age which indicates climatic cooling during the Cenozoic (Reid & Chandler 1933). The authors recorded the following percentages for woody species in selected Tertiary and Quaternary floras of Europe: London Clay flora, Eocene, 97 %; Hordle flora, Eocene, 85 %; Bembridge flora, Oligocene (Miocene?, Mai 1964), 57%; Pont-de-Gail flora, Pliocene, 51%; Reuver flora, Pliocene, 57%; Tegelen flora, Quaternary, 28%; Cromer flora, Quaternary, 22% (Reid & Chandler 1933). In the climatic interpretations of the Tertiary and Quaternary floras of Poland Szafer (1946, 1954, 1961) also utilizes the relation between woody and herbaceous dicotyledonous species.

In the Fasterholt microflora the arborescent dicotyledonous species make up 63 % of the total number of dicotyledonous species and 42% of the total number of angiosperm species of the microflora. This is not considered to be an exact figure for the relation between woody and herbaceous species of the original flora because fruits and seeds of woody plants are normally better suited for preservation than fruits and seeds of herbaceous plants (Szafer 1954). The proportion of woody dicotyledonous species of the Fasterholt flora increases when the larger fruits and seeds of the flora are considered as nearly all of them derive from woody plants (Koch et al. 1973).

Although the percentages do not give the exact figures for the compositions of the flora, they indicate a relatively warm climate.

The percentage distribution of arborescent dicotyledonous species has also been calculated for a number of Cenozoic diaspore floras described from western Siberia (Dorofeev 1963), Poland (Szafer 1946, 1954, 1961; Raniecka-Bobrowska 1959; Mai 1964) and from DDR (Mai 1967). The percentages calculated for DDR are based on the fossil species given in the flora zone diagram presented by Mai in 1967 (p. 64).

The results have been plotted in a diagram (fig. 2) and from the curve it is seen that the proportion of arborescent dicotyledonous species in the European fossil floras decreased from Oligocene to Pleistocene with some fluctuations. It is presumed that the fluctuations in the diagram reflect climatic fluctuations. The very high content of arborescent species in the Miocene flora of Wieliczka may be due to the preparation process as only material retained on the 1 mm sieve was included in the investigation (Zabłocki 1928).

In western Siberia a pronounced change occurred from Oligocene to Miocene. This may be an expression of a climatic deterioration caused by the regression of the Chegan Sea (Dorofeev 1963).

Phytogeographical analyses

In these analyses the fossil plants are compared with living genera and the geographical and climatic ranges of the living genera are used in the climatic interpretation of the fossil floras.

Palaeotropical and arctotertiary elements

In his study of the younger Tertiary floras of DDR Mai (1964, 1965, 1967) used two phytogeographical elements in the climatic and stratigraphical interpretations of the floras: The arctotertiary element and the palaeotropical element. They are defined by Engler (1882) as follows:

"Das arcto-Tertiäre Element, ausgezeichnet durch zahlreichen Coniferen und die zahlreichen Gattungen von Bäumen und Sträuchern, welche jetzt in Nordamerika oder in dem extratropischen Ostasien und in Europa herrschen" (Engler 1882, p. 327).

"Das paläotropische Element, ausgezeichnet durch die in den Tropen der alten Welt dominierenden Familien und Unterfamilien, namentlich aber auch durch Fehlen einzelner im arcto-tertiären Gebiet verbreiteter Pflanzenfamilien, Gruppen und Gattungen" (Engler 1882, p. 328).

Fossil floras characterized by the preponderance of the arctotertiary element are called arctotertiary floras. Fossil floras characterized

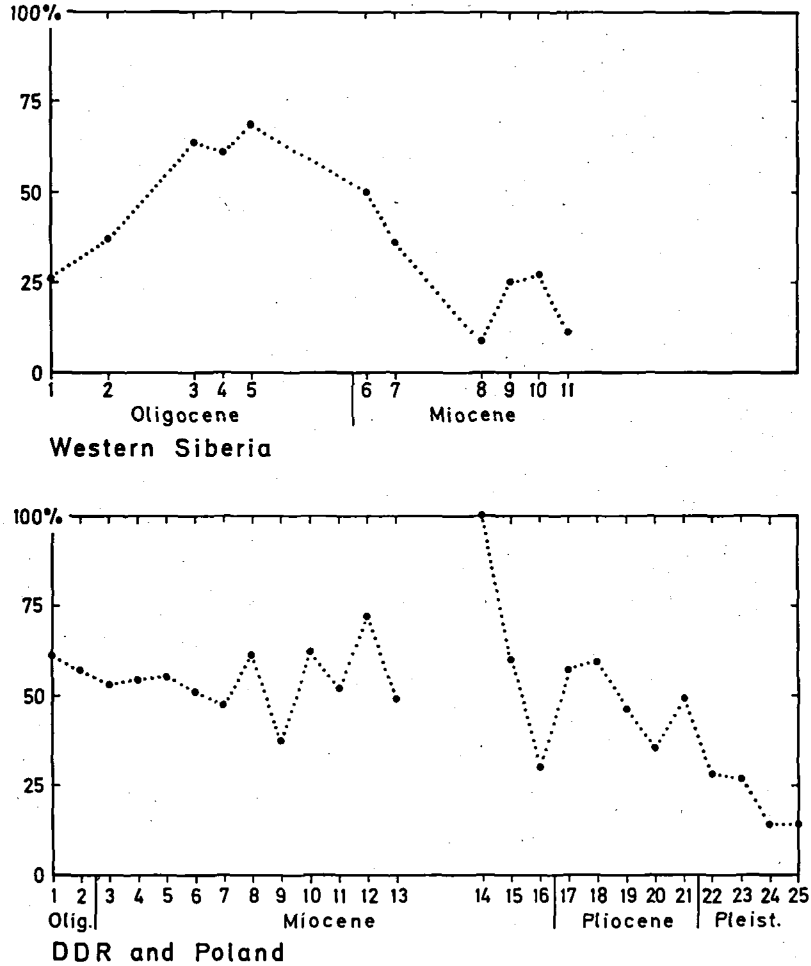

Fig. 2. Distribution of arborescent dicotyledonous species in fossil floras from western Siberia and Europe. Western Siberia: *1. Byeloyarka on the Tavda river, 2. Vasskovo on the Tavda river, 3. Rezhenka on the river Bolshaya Kirgizka, 4. Kompassky Bor on the Tym river, 5. Kozyulino on the Tom river, 6. Kireevskoye on the Ob river, 7. Novonikolskoye on the Irtysh river, 8. Chernoluchye on the Irtysh river, 9. Lezhanka on the Irtysh river, 10. Isakova on the Irtysh river (from Dorofeev, 1963).* DDR: *1–13. flora zones I–XIII (from Mai 1967).* Poland: *14. Wieliczka (from Mai 1964), 15. Stare Gliwice (from Szafer 1961), 16. Konin (from Raniecka-Bobrowska 1959), 17. Krościenko (from Szafer 1946), 18. Huba, 19. Mizerna I, 20. Mizerna I/II, 21. Mizerna II, 22. Mizerna II/III, 23. Mizerna III, 24. Mizerna III/IV, 25. Mizerna IV (from Szafer 1954).*

by the predominance of the palaeotropical element are called mastixioidean floras (Mai 1965). The concept of mastixioidean floras was first introduced by Kirchheimer (1938) for fossil floras with a content of species referred to the family Mastixiaceae.

The two types of floras interchanged with each other as result of rhythmic climatic fluctuations during the Oligocene and Miocene in DDR (Mai 1965, 1967). On the basis of this interchange Mai (1967) established 13 biostratigraphical zones.

The method has some limitations as can be seen from the following examples. *Myrica ceriferiformis* has been referred to the arctotertiary element and *Myrica suppanii* to the palaeotropical element (Mai 1967). According to Bůžek & Holý (1964) these two species of *Myrica* may be identical and allied to the living species *Myrica cerifera* of North America. In his analysis Mai also included species of extinct genera. Species of the genus *Microdiptera* Chandler are referred to the palaeotropical element whereas species of the genus *Diclidocarya* E. M. Reid are referred to the arctotertiary element. However, both genera are compared with the living genus *Decodon* Gmel. which is referred to the arctotertiary element.

Despite these limitations the analysis is considered to be a useful biostratigraphical method as applied by Mai for the younger Tertiary floras of DDR (Mai 1965, 1967).

In the analysis of the Fasterholt microflora species of extinct or organ genera have only been considered if they were classified by Mai as palaeotropical or arctotertiary.

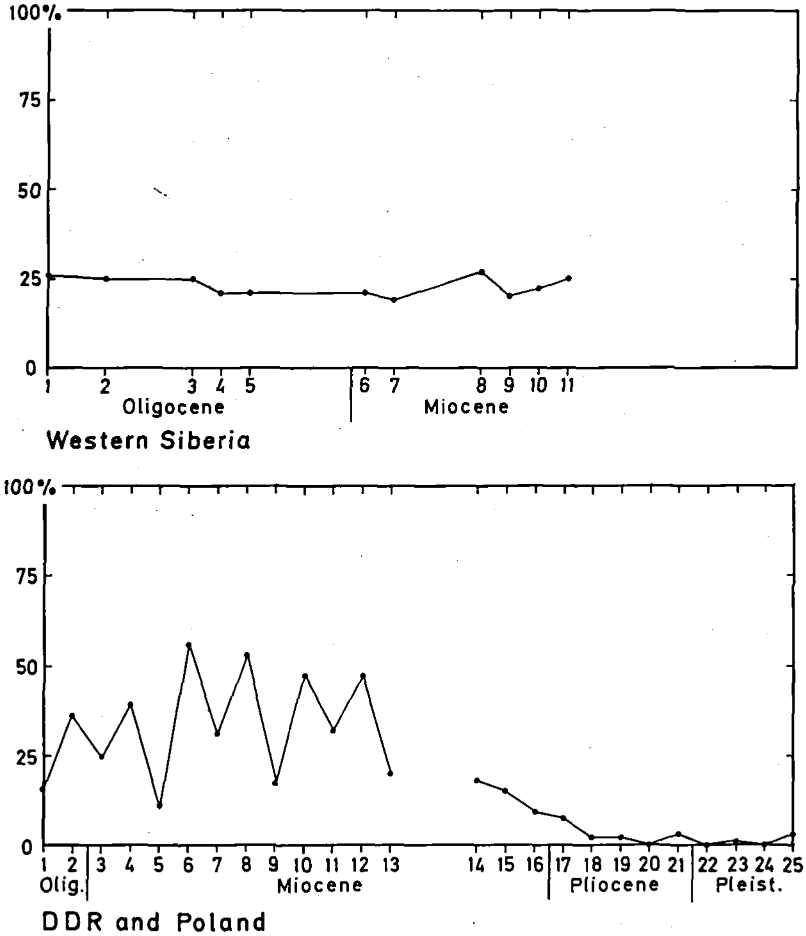

Fig. 3. Distribution of the palaeotropical element in fossil floras from Western Siberia and Europe. Western Siberia: *1. Byeloyarka on the Tavda river, 2. Vasskovo on the Tavda river, 3. Rezhenka on the river Bolshaya Kirgizka, 4. Kompassky Bor on the Tym river, 5. Kozyulino on the Tom river, 6. Kireevskoye on the Ob river, 7. Novonikolskoye on the Irtysh river, 8. Chernoluchye on the Irtysh river, 9. Lezhanka on the Irtysh river, 10. Isakovka on the Irtysh river (from Dorofeev 1963).* DDR: *1–13: flora zones I–XIII (from Mai 1967).* Poland: *14. Wieliczka (from Mai 1964), 15. Stare Gliwice (from Szafer 1961), 16. Konin (from Raniecka-Bobrowska 1959), 17. Krościenko (from Szafer 1946), 18. Huba, 19. Mizerna I, 20. Mizerna I/II, 21. Mizerna II, 22. Mizerna II/III, 23. Mizerna III, 24. Mizerna III/IV, 25. Mizerna IV (from Szafer 1954).*

The Fasterholt microflora is an arctotertiary flora as the arctotertiary element is dominant. A total of 61 % of the species are referred to the arctotertiary element and 39 % are referred to the palaeotropical element. The arctotertiary element is preponderant both quantitatively and qualitatively. In the microflora 12 species are represented by more than 2% each of all specimens considered (table 1). Of these, 8 species are referred to the arctotertiary element: *Sequoia* sp., *Glyptostrobus europaeus, Platanus* sp., *Alnus decipiens, Myrica* cf. *ceriferiformis, Rubus laticostatus, Pyracantha acuticarpa* and *Scirpus ragozinii.*

When considering the coarser fraction of fruits and seeds the relation between the two elements remains unchanged. In this fraction, too, the arctotertiary element is dominant (Koch et al. 1973). The relation between the arctotertiary and the palaeotropical elements of the Cenozoic floras from western Siberia and northern Europe mentioned above has also been analysed. The results of the analysis have been plotted against time in fig. 3.

In the western Siberian fossil floras the proportion of the palaeotropical element remains almost unchanged. No explanation of this has been found, but it can be mentioned that most of the palaeotropical species in this area belong to aquatic or extinct genera.

In northern Europe the proportion of the palaeotropical element decreases during the Neogene from about 50 % in the Miocene to about zero during the Pleistocene. In Pliocene and Pleistocene the palaeotropical element only makes up a minor part of the northern European fossil floras.

Mai has estimated the climatic conditions for the 13 flora zones of DDR. Floras with a high content of palaeotropical species are considered as warm temperate or subtropical floras, whereas floras with a lower content of this element are considered as temperate or cool temperate floras (Mai 1965, 1967).

Relationship between native and exotic elements

Reid (1920) has pointed out that there is a connection between the species composition of a fossil flora and the age of the flora. The studies of Reid were carried out on Pliocene and Pleistocene European floras. Reid indicated that the content of species in the fossil flora that can be referred to recent species now living in the geographical region of the fossil flora is diminishing with increasing age. Similar investigations of the species composition of European Tertiary floras were carried out by Mädler (1939) and Szafer (1946, 1954).

The method has also been applied by Barghoorn (1951) in a study of Upper Cretaceous and Tertiary floras of North America. Instead of using the species composition of the fossil floras the generic composition was considered. The fossil plants have been divided into 3 elements. The native element includes genera which now survive in the living flora of the region of the fossil deposit. The exotic element includes genera now exotic to the region of the fossil deposit. The third element includes extinct or organ genera. In a later study Wolfe & Barghoorn (1960) united the two last elements into one group: the "non-native" (in this study: exotic element).

The study of the generic composition of the North American Cenozoic floras indicates that there is a marked increase of the native element with decreasing age. A leaf-margin curve has been made for the same North American fossil floras and is related to the curve made for the generic composition of the floras (Wolfe & Barghoorn 1960). Climatic interpretations based on leaf-margin analysis (entire v. non-entire margined) are generally accepted as being valid for Cenozoic floras (Bailey & Sinnott 1916; Wolfe & Barghoorn 1960; Wolfe & Hopkins 1967; Dilcher 1973) and it is emphasized that the change in generic composition as well as the leaf-margin curve reflect climatic changes (Wolfe & Barghoorn 1960).

Grangeon (1951, 1958) has made similar analyses of the generic composition of European Tertiary floras. He indicated a gradual increase of the native element from 31 % in the Upper Eocene flora of Hordle, England, to 60 % in the Upper Miocene flora from Le Coiron, France (Grangeon 1958).

In objection to the method Axelrod (1957) pointed out that genera now found in the local flora may be represented by totally different species from those to be found in the fossil flora. From the Fasterholt microflora one such example can be mentioned. The genus *Myrica* is referred to the native element of the Fasterholt flora as *Myrica* is represented in the living European flora by the species *Myri-*

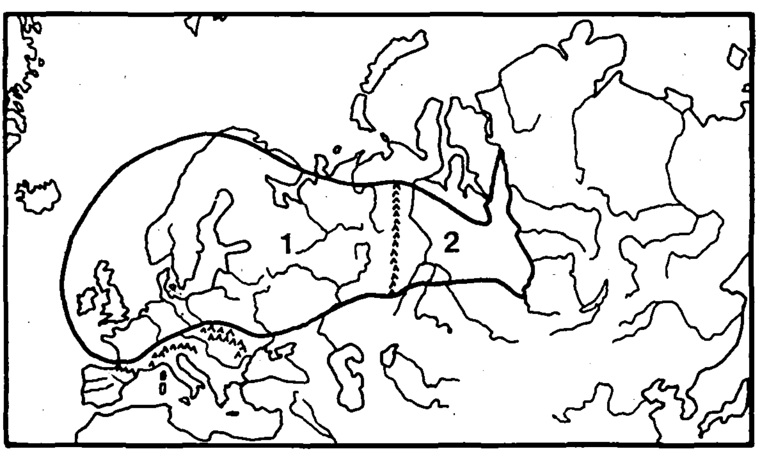

Fig. 4. Regional distribution of elements native to Tertiary and Quaternary floras of northern Europe (1) and Tertiary floras of western Siberia (1 & 2).

ca gale. However, the fossil *Myrica* fruits from the Fasterholt flora differ from those of *Myrica gale* and they are more closely related to the fruits of the living species *Myrica cerifera* and *Myrica pensylvanica* which are now restricted to North America. It should be mentioned that only few fossil species older than Pliocene can be referred to living species, whereas comparisons with living genera are more certain. In general, however, the analysis may give the outline of the climatic evolution of a region.

The analysis of the generic composition has been applied for the Fasterholt flora. Fossil species referred to genera now living in parts of the North European flora province and in parts of the middle European flora region are included in the native element. The following zones and provinces (after Engler 1882) have been included: *Picea vulgaris* zone, *Picea obovata* zone, the Atlantic province, the Subatlantic province, the Sarmatic province and the European Mittelgebirge province. The area thus includes a region in which the flora has evol-

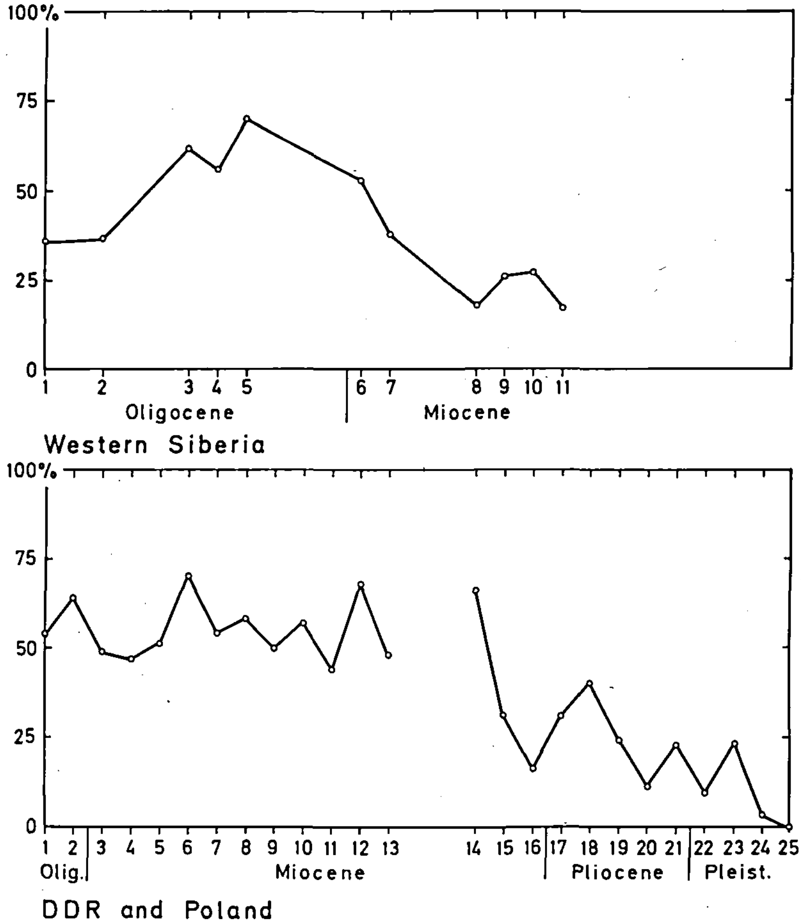

Fig. 5. Distribution of the exotic element in fossil floras from western Siberia and Europe. Western Siberia: *1. Byeloyarka on the Tavda river, 2. Vasskovo on the Tavda river, 3. Rezhenka on the river Bolshaya Kirgizka, 4. Kompassky Bor on the Tym river, 5. Kozyulino on the Tom river, 6. Kireevskoye on the Ob river, 7. Novonikolskoye on the Irtysh river, 8. Chernoluchye on the Irtysh river, 9. Lezhanka on the Irtysh river, 10. Isakovka on the Irtysh river (from Dorofeev 1963).* DDR: *1–13. flora zones I–XIII (from Mai 1967).* Poland: *14. Wieliczka (from Mai 1964), 15. Stare Gliwice (from Szafer 1961), 16. Konin (from Raniecka-Bobrowska 1959), 17. Krościenko (from Szafer 1946), 18. Huba, 19. Mizerna I, 20. Mizerna I/II, 21. Mizerna II, 22. Mizerna II/III, 23. Mizerna III, 24. Mizerna III/IV, 25. Mizerna IV (from Szafer 1954).*

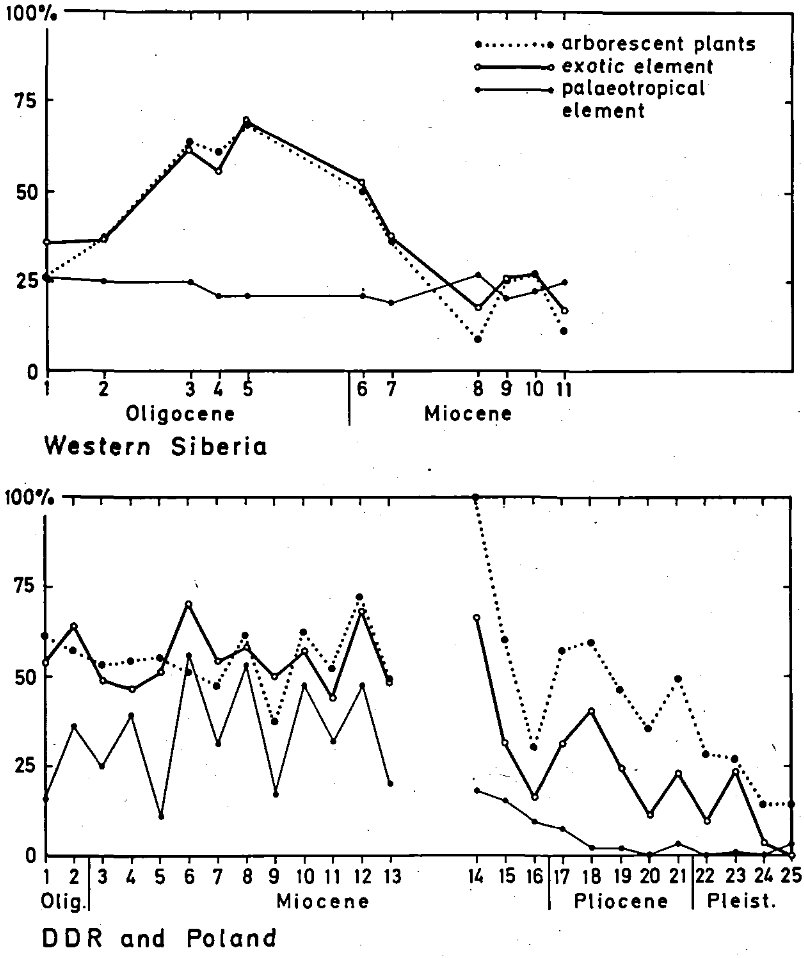

Fig. 6. Compilation of figures 3, 4 and 6. Western Siberia: 1. Byeloyarka on the Tavda river, 2. Vasskovo on the Tavda river, 3. Rezhenka on the river Bolshaya Kirgizka, 4. Kompasský Bor on the Tym river, 5. Kozyulino on the Tom river, 6. Kireevskoye on the Ob riber, 7. Novonikolskoye on the Irtysh river, 8. Chernoluchye on the Irtysh river, 9. Lezhanka on the Irtysh river, 10. Isakovka on the Irtysh river (from Dorofeev 1963). DDR: 1–13. flora zones I–XIII (from Mai, 1967). Poland: 14. Wieliczka (from Mai 1964), 15. Stare Gliwice (from Szafer 1961), 16. Konin (from Raniecka-Bobrowska 1959), 17. Krościenko (from Szafer 1946), 18. Huba, 19. Mizerna I, 20. Mizerna I/II, 21. Mizerna II, 22. Mizerna II/III, 23. Mizerna III, 24. Mizerna III/IV, 25. Mizerna IV, 25. Mizerna IV (from Szafer 1954).

ved under nearly the same external conditions (fig. 4).

In the Fasterholt microflora about 65 % of the species are referred to the native element and about 35% are referred to the exotic element. The proportion of the exotic element in the Fasterholt flora seems to increase when the coarser fraction of fruits and seeds of the Fasterholt flora is considered. Compared to the fossil floras of western Siberia and northern Europe (fig. 5) the percentage of the Fasterholt flora is high and indicates a warm climate.

The relation between the native and exotic elements has been examined for the same European and western Siberian fossil floras as mentioned above. The percentages of the exotic element in the fossil floras have been plotted against time in fig. 5.

Regarding the European fossil floras, the native element is defined in the same way as for the Fasterholt flora. Genera now living in the north and middle European region and in the west Siberian flora zone are included in the native element of the western Siberian fossil floras. The European region has been combined with the Siberian region because the Ural Mountains are not considered to have been a pronounced floristic barrier during the Tertiary. The Urals had been transformed into a peneplain during the period from the Upper Jurassic to Miocene, and only during the Pliocene and the Quaternary were the Ural Mountains reelevated (Nalivkin 1960).

The graphs for the arborescent plants (fig. 2), palaeotropical element (fig. 3), and exotic element (fig. 5) have been combined in fig. 6.

Examination of fig. 6 reveals that the three graphs are closely correlated for the European fossil floras, and it is assumed that they are all the results of the climatic evolution of the region under consideration. In Pliocene and Pleistocene the palaeotropical element only makes up a minor part of the European floras and the method does not seem applicable for these stages in Europe. For the Oligocene and Miocene floras of western Siberia only the analyses of the generic composition and the growth form seem to be valuable in the climatic interpretations of the fossil floras.

Geographical elements

In the Fasterholt microflora 62 species can be referred to living genera. On the basis of the phytogeographical distribution of the living genera the fossil species have been divided into 5 geographical elements.

1. The eastern North American/eastern Asiatic element comprises genera now living in the Atlantic part of North America or in eastern Asia or both. The following genera are included: *Glyptostrobus, Liriodendron, Liquidambar, Platanus, Comptonia, Eurya, Lyonia, Decodon, Aralia, Epipremnum.*
2. The Holarctic element includes genera that are widely distributed within the northern temperate or cool temperate zone. The following genera are included: *Pinus, Alnus, Cornus.*
3. The tropical/subtropical element includes genera now living in tropical or subtropical environments or both. Excluded are such genera that can be referred to the eastern North American/eastern Asiatic element. The following genera are included: *Selaginella, Salvinia, Azolla, Brasenia, Laportea, Clethra, Aldrovanda, Ilex, Paliurus, Cephalanthus, Caldesia, Pistia.*
4. The cosmopolitan element comprises genera with a worldwide distribution. The following genera are referred to this element: *Myrica, Hypericum, Rubus, Orobanche, Potamogeton, Scirpus, Cladium, Carex, Sparganium, Typha.*
5. The dispersed element contains genera with a dispersed distribution and genera that cannot be referred to one of the above mentioned elements. This element includes the following genera: *Sequoia, Urtica, Erica, Pyracantha, Teucrium.*

For other purposes a more detailed classification seems useful (Reid & Chandler 1933; Szafer 1946). However, 5 elements are considered to be adequate for the present study. Szafer (1961) also recommended dividing the fossil floras into the smallest number of elements as possible as a large number makes the division more complicated.

In the Fasterholt microflora the cosmopolitan element is the most abundant with 40 % of the species. The eastern North American/eastern Asiatic element together with the tropical/subtropical element makes up 47 % of the fossil species which can be referred to living genera. Only 5 % of the fossil species can be referred to the holarctic element (table 4).

When considering the phytogeographical distribution of the living genera allied to the Fasterholt microflora it appears that the area in which the related living genera occur lies in the northern hemisphere between 30° and 45° latitude. A very great deal of the genera

Table 4. Phytogeographical elements of the Fasterholt microflora.

	Phytogeographical elements	Species	%	Genera	%
1	Eastern North American/ eastern Asiatic element	13	21	10	25
2	Holarctic element	3	5	3	7.5
3	Tropical/subtropical element	16	26	12	30
4	Cosmopolitan element	25	40	10	25
5	Dispersed element	5	8	5	12.5

can be found in the southeastern United States and in southeastern Asia.

From the geographical analysis it is assumed that the Fasterholt flora lived under warm temperate to subtropical climatic conditions. The annual rainfall is considered as having been very high, about 1000–2000 mm as stated for southeastern North America and eastern Asia by Walther (1973).

Conclusion

The results of the floristic-climatic analyses indicate that the Miocene Fasterholt flora is an arctotertiary flora with a relatively high content of palaeotropical species. Wetland and aquatic species are preponderant. Comparisons with different plant communities of the Atlantic Coastal Plain of North America show that there is a generic accordance between the plants of this region and the plants of the Fasterholt flora. The Fasterholt flora might have grown on a similar coastal plain on the border of a large delta. The Fasterholt flora has a high content of arborescent dicotyledonous species. This, together with the content of palaeotropical species and the generic composition of the flora, indicates a warm temperate or subtropical character of the flora.

Three of the floristic-climatic analyses applied to the Fasterholt flora have been tested on the fossil floras described from western Siberia, DDR and Poland, viz. the analyses of the growth form, the palaeotropical and arctotertiary elements, and the generic composition. The results of the analyses seem in general to reflect the climatic conditions under which the fossil floras have grown, but the applicability of the different methods seems to be dependant on time and place. Hence the analysis of the palaeotropical element does not seem applicable, either for the fossil floras of the western Siberian region or for the Pliocene and Pleistocene floras of northern Europe. For the Miocene floras of northern Europe all three analyses appear to be of equal validity and thus applicable in the climatic interpretations of the Fasterholt flora.

In this study the combined results of the analyses have been limited to the climatic interpretations of the Fasterholt flora, but it is beleived that the analyses also comprise a useful contribution to a stratigraphical evaluation of the fossil floras.

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Dansk sammendrag

En floristisk-klimatisk undersøgelse er udført for Fasterholt floraen på grundlag af floraens mindre plantefossiler. De mindre plantefossiler udgør en væsentlig del af hele Fasterholt floraen og omfatter ca. 85 beskrevne arter af frugter, frø, megasporer og fungi.

Fasterholt floraen er udslemmet af et finkornet sandlag mellem de to øverste brunkulslag i A/S Carl Nielsens brunkulsgrav ved Fasterholt, SØ for Herning. Den anses for at tilhøre den øverste del af den Miocene Odderup Formation (Koch & Friederich 1970; Koch et al. 1973).

Den økologiske analyse viser, at Fasterholt floraen har et væsentligt indhold af arter, som er knyttet til sumpet miljø. Sammenligninger med recente vegetationer synes at vise, at Fasterholt floraen kan have vokset i randen af et større delta på en kystslette af samme type som den Atlantiske Kystslette i Nord Amerika, hvilket også støttes af den lokale og regionale geologi.

Indholdet af træagtige dikotyledoner er meget højt, hvilket peger mod et varmt klima. Fasterholt floraen er en arktotertiær flora, idet det arktotertiære element er dominerende både kvantitativt og kvalitativt. Den slægtsmæssige sammensætning viser, at ca. en trediedel af mikrofloraens arter tilhører slægter, som ikke længere findes i det europæiske område. En geografisk analyse viser, at det kosmopolitiske floraelement er dominerende, og kun få af floraens arter kan henføres til det holarktiske floraelement. Ca. halvdelen af arterne er henført til det østlige Nordamerikanske/Sydøstasiatiske floraelement samt det tropisk/subtropiske element. Det største fælles areal for de tilsvarende recente slægters udbredelse ligger mellem 30° og 45° på den nordlige halvkugle, og en meget stor del af slægterne findes nu i det sydøstlige Nord Amerika og i det sydøstlige Asien.

Resultaterne af de floristiske og klimatiske analyser viser, at *Fasterholt-floraen har vokset under varmt* tempererede til subtropiske forhold.

For at belyse de anvendte metoder er tre af analyserne sammenlignet for en række Tertiære floraer beskrevet fra Europa og Vest Sibirien. Det drejer sig om analyser af vækstform, af det palæotropiske og

arktotertiære element og af den slægtsmæssige sammensætning. Der er på visse punkter stor overensstemmelse mellem resultaterne af de tre analyser, og de synes at afspejle de klimatiske betingelser, hvorunder de fossile floraer har vokset. Analysernes anvendelighed synes at være afhængige af tid og sted. Således er analysen af det palæotropiske element ikke anvendeligt for de fossile floraer i Vest Sibirien og heller ikke for de Pliocæne og Pleistocæne floraer i Nord Europa. I Miocæn synes alle tre metoder at være af samme værdi for de europæiske floraer og kan således benyttes i den klimatiske tolkning af Fasterholt floraen.

I dette arbejde er de forskellige analysemetoder kun anvendt i den floristisk-klimatiske vurdering af Fasterholt floraen, men en kombineret anvendelse af metoderne synes også at kunne yde et bidrag ved en stratigrafisk vurdering af Tertiære floraer.

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