Acta Palaeobot. 41(2): 283–297, 2001

Changes in the leaves of Fagaceae during the Late Miocene and Pliocene in the Lower Rhine embayment*

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Received 29 March 2001; accepted for publication 27 September 2001

ABSTRACT. A biometrical study of leaf compressions-impressions from species of *Fagus* and *Quercus* from the Late Miocene and Pliocene deposits reveals a different pattern of behaviour of the species of these genera during the repeated changes of climate that took place during the period of deposition of the sediments. During the cooler periods the populations contracted to relict populations of small extension, during the warmer periods they expanded and filled the entire area. In *Fagus* these changes did not have any influence on the morphological variation of leaves. *Quercus pseudocastanea* shows great differences between the succeeding populations in this respect. These populations are as variable as the populations of recent *Q. petraea.* This variation in populations of *Quercus* is used for detailed stratigraphical differentiation.

KEY WORDS: leaf, biometry, Fagaceae, Lower Rhine embayment, Neogene

INTRODUCTION

The Oligo-Mio-Pliocene deposits of the Lower Rhine Basin were deposited under paralic circumstances. Lying between the “Rheinische Schiefergebirge” and the sea the region was a poorly drained lowland during highstands of the sea and was better drained during lowstands. In the periods of lowstands layers of sands were deposited, the clays and peats, and occasionally marine sediment represent the highstands. The result is a rhythmic series. In the Late Miocene the sand layers tend to be thick, in contrast to the clay layers which mostly are rather thin (personal observation). When during the Tertiary the influence of the climate on sea level and vegetation became more dominant, it is relevant to postulate these sand layers as representing cool periods and the clay layers and associated peat-browncoal layers as deposited during warm periods (see also Krutzsch 2000).

This alternate succession of sands and clays continues in the overlying uppermost Miocene and Pliocene. Generally it is considered to be the result of a rhythmic change of climate between subtropical conditions and cool temperate conditions, with a gradual overall decline in temperature during the entire period. This change in climate has been recorded to coincide with changes in the solar irradiation, as dictated by Milankovitch periodicities. At least in the mediterranean area this influence has been found back into the Pliocene and Late Miocene (Versteegh 1993, Santarelli 1997, Kloosterboer-Van Hoeve 2000). It is to be expected, that the same variability in irradiation also forced the rhythmic climatic change in Middle Europe.

It is to be hypothesized that as a result of changes in climate, the areal extend of various species of plants would expand or diminish.

* This publication is NSG (Netherland School of Sedimentary Geology) Paper No. 20020108.

Following a restriction in the distribution of a species, a sudden expansion occurred, but with similarly restricted morphological variability as in the small source population. Therefore, the stratigraphically successive populations of a species could differ markedly from one another. During such an expansion, the plants of a certain species could differ markedly from older or younger populations. This is demonstrated in two genera of the Fagaceae: *Quercus* and *Fagus* by means of a biometrical study of leaf impressions from the Neogene of the Lower Rhine embayment.

In addition to some sparsely occurring species such as *Quercus kubinyi* (Kovats ex Ettingshausen) Czeczott and *Q. gigas* Goeppert, *Q. pseudocastanea* Goeppert emend. Walther & Zastawniak was encountered throughout the entire series. In 1993 I combined *Q. roburoides* Gaudin into *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak. This was based mainly on the structure of the cuticle, which does not show any difference between these species. Moreover, it was identical to that of recent *Q. petraea* (Matt.) Lieblein (Van der Burgh 1993, Kürschner 1996). A further argument is the overall morphological comparability of both species with recent *Q. petraea* (Van der Burgh 1993). The study has been made using material of *Q. pseudocastanea;* some characters of which are noted and used but did not give a base for biometrical studies. For this study the populations of the Mio-Pliocene deposits and the Ealy Pliocene deposit are combined, as there are no differences between these two floras with respect to this species of *Quercus*

In the lower part of the Miocene deposits *Fagus menzelii* Kvaček & Walther is present (Pl. 2 figs 1, 2, 7), followed by *F. kraeuselii* Kvaček & Walther (Pl. 2 figs 3–6, 8, 9) in the younger Miocene and Pliocene deposits (cf. Kvaček & Walther 1991). These two leaf species are linked with each other through a common cupule-fruit species, *F. decurrens* Reid & Reid. They were formerly considered conspecificous and were described as *F. attenuata* Goeppert. The populations of the two closely related species of this genus are compared with each other irrespective of the species name attached to them.

Also studies by Denk and others make clear that it is extremely difficult to safely decide if one or two or more *Fagus* species are present in the European assemblages (T. Denk pers. comm.).

MATERIAL AND METHODS

During the last ten years collections were made in the quarry 'Hambach' near Düren, Lower Rhine embayment. For the stratigraphy the local interpretation of the stratigraphic division of the Neogene (Wutzler 2000) is followed. Part of these collections were made in the Late Miocene Inden Series. This consists roughly of three sequences, each characterized by a deposit of sands with a deposit of silty clays on top of it. Within these clays remains of warm-temperate to subtropical floras were found (leaf-floras 7B, 7D, 7F; Fig. 1).

Occasionally remains of impoverished cool-temperate floras were encountered in the top-layers of the clays. The Inden Series contains a browncoal seam, locally up to 17 m thick, in the west of the area. In the succeeding basal part of the Hauptkies Series also leaf remains were collected (leaf-flora 8A; Fig. 1).

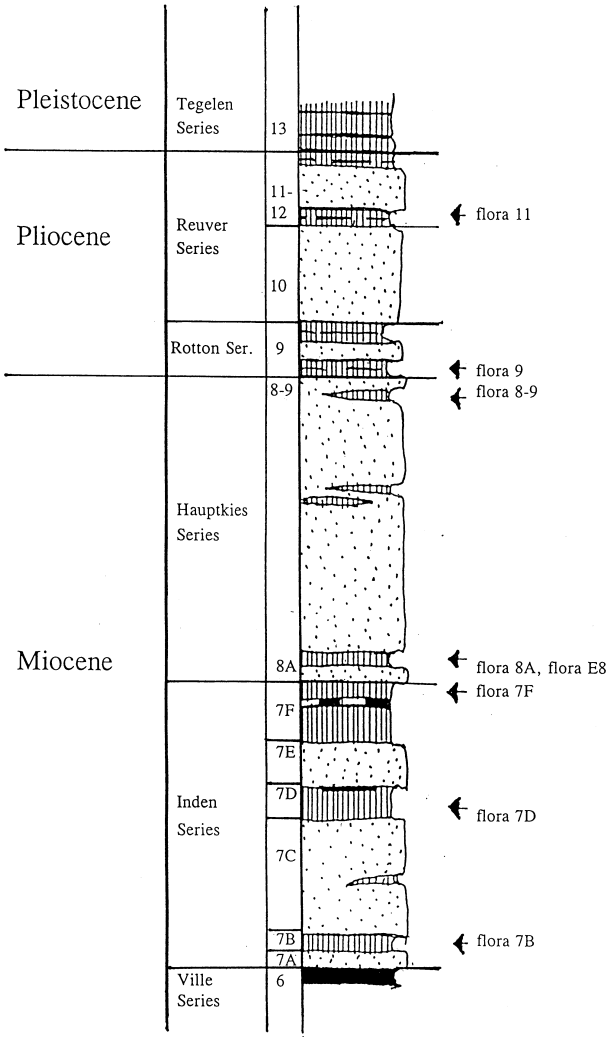

Fig. 1. Schematic profile of the Late Neogene of the Lower Rhine embayment indicating the levels of the studied floras. The numbers in the column represent the local interpretation of the Rheinbraun stratigraphic division (Wutzler 2000)

In the western part of the Lower Rhine embayment a clay was discovered and sampled near Heerlen (leaf flora 8–9; Fig. 1). This deposit belongs to the Hauptkies series, but locally it represents the latest, rather cool period of the Mio-Pliocene transition. This was directly followed by the rather warm Brunssum during which the Rotton series was deposited, a flora was collected from these deposits in Hambach (leaf flora 9; Fig. 1).

From the Late Pliocene Reuver clay the flora, described by Laurent and Marty (1923) was studied (leaf flora 11; Fig. 1).

In the period 1972–1979, a leaf impression flora was also collected in the Quarry "Zukunft West" near Eschweiler in a horizon that was supposed to be the uppermost clay of the Inden Series. As will be pointed out below, this clay has to be dated as belonging to the younger Hauptkies Series (leaf flora E8; Fig. 1).

From the collected leaf-floras genera and species were compared with one another. For *Quercus* and *Fagus* some of the results are presented here. From these genera several hundreds of leaf impressions were studied (Tab. 1).

Table 1. Number of measured specimens of *Quercus* and *Fagus* per studied flora

Stratigraphic unity	Number of specimens	
	Quercus	*Fagus*
Late Pliocene, Reuver (11)	32	29
Early Pliocene, Hambach (9)	–	54
Mio-Pliocene, Brunssum (8–9)	86	211
Late Miocene, Hambach (8A)	27	54
Late Miocene, Eschweiler (E8)	59	136
Late Miocene, Hambach (7F)	17	46
Late Miocene, Hambach (7D)	62	48
Late Miocene, Hambach (7B)	17	28
Total	300	606

In addition a number of leaves of *Quercus petraea* (Matt.) Lieblein from the Utrecht herbarium, originating from localities all over Europe were analysed.

For this study, the following leaf characters were studied for both *Quercus* and *Fagus*: a) the relative position of the broadest part of the leaf, b) the relative length of the leaf, c) the number of secondaries and d) (only for *Quercus*) the relative length of the lobes. The number of secondaries was counted on both sides of the midrib; the relative length of the leaf (L/B) was calculated by the length (L) divided by the breadth (B). The relative length of the lobe was measured along the line between the tip of the lobe and the base of the innerving secondary. It was found by dividing the distance between the tip of the lobe and the crossing of the line between the adjoining sinuses (B-C), through the distance between the tip of the lobe and the base of the innerving secondary (A-B; Fig. 2). The position of the broadest part of the leaf is found by dividing the distance between the base and the axis of the greatest breadth (D-F) through the entire length (D-E; Fig. 2). The leaf characters used are as defined by Dilcher (1974).

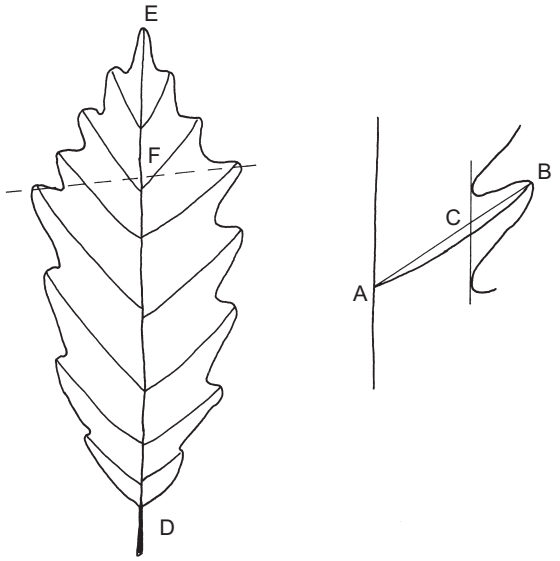

Fig. 2. Method of defining the relative position of greatest breadth and length of lobes; relative position of greatest breadth: D-F/D-E; length of lobes: B-C/A-B

The significance of the differences between the populations of the two genera has been tested by an independant sample T-test ($P<0.05$).

Furthermore a count was done on several regularly occurring species in the floras of the Inden Series and the Hauptkies Series, with the aim of establishing changes in the representation of species with time.

For the representation of the stratigraphy in the source area of the material, current nomenclature along with the Rheinbraun numbering of the strata (Wutzler 2000), has been used (Fig. 1).

The material used is stored in the collections of Naturalis (Leiden) and the Laboratory of Palaeobotany and Palynology (Utrecht) under the mentioned numbers.

MORPHOLOGICAL VARIATION

Quercus pseudocastanea Goepp. emend. Walther & Zastawniak

Number of secondaries. The number of secondaries is variable (between 8 and 32, average 18; Fig 5, Tab. 2, 3). It is stable in the Late Miocene Inden Series and "Hauptkies" Series (flora 7B,D,F, E8, 8A), but decreases sharply at the Miocene-Pliocene transition (flora 8–9, 9), with a scatter of between 8 to 22, average 11. The Late Pliocene (flora 11) gives a much higher average (15), with values between 12 to 26. Before comparing this with the herbarium material of recent populations, it

Table 2. Results from an independent sample T-test (P <0.05) of four characters in seven different populations of *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak

Character: / Population	number of secondaries	relative length	relative position of greatest breadth	relative length of lobes
L. Plioc. 11 – Mio/Plioc. 8, 8–9.	0.000	0.094	0.000	0.000
Mio-Plioc. 8–9 – L. Mioc. 8A.	0.000	0.000	0.878	0.000
L. Mioc. 8A – L. Mioc. E8	0.091	0.155	0.015	0.098
L. Mioc. E – L. Mioc. 7F	0.139	0.047	0.000	0.002
L. Mioc. 7F – L. Mioc. 7D	0.350	0.095	0.000	0.536
L. Mioc. 7D – L. Mioc. 7B	0.771	0.394	0.336	0.056

Table 3. The minimum-maximum and mean values of leaf characters for the different populations of *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak from the Late Miocene and Pliocene deposits

Leaf characters	Late Miocene	Early Pliocene	Late Pliocene
	7B – 8A	8–9,9	11
Number of secondaries	18 (10–32)	11 (8–22)	15 (12–26)
Relative leaf length	2.4 (1.0–4.1)	1.9 (1.3–2.5)	2.0 (1.4–2.6)
Greatest breadth of leaves	0.52 (0.15–0.75)	0.51 (0.32–0.73)	0.65 (0.54–1.04)
Relative length of lobes	0.26 (0.11–0.59)	0.63 (0.27–1.39)	0.36 (0.17–0.71)

Table 4. Variation of leaf characters in several regional populations of *Quercus petraea* (Matt.) Lieblein used in this study. The figures shown are the means of 3–7 counts or measurements (data collected from Utrecht Herbarium sheets)

Localities	Number of secondaries	Relative leaf length	Relative position of greatest breadth	Length of lobes
Amersfoort, Netherlands	17	1.74	0.53	0.46
Aserbaijan	20	1.93	0.52	0.33
Burgenland, Austria	15	1.89	0.52	0.38
Ciscaucasius	18	1.95	0.57	0.73
Gulpen, Netherlands	13	1.60	0.63	0.30
Killarney, Ireland	13	1.98	0.63	0.49
Hinzweiler, Germany	15	1.58	0.57	0.48
Limberg, Germany	14	1.93	0.60	0.64
Loire Atlantique, France	14	1.87	0.61	0.44
Lynmouth, Gr. Brittain	14	1.80	0.54	0.38
Macedonia	13	2.42	0.45	0.44
Malcante, Switzerland	16	1.81	0.60	0.53
Montenegro	13	1.70	0.52	0.61
Mottskogen, Norway	13	2.05	0.55	0.47
Odebro, Sweden	11	1.87	0.64	0.59
Opgrimby, Belgium	14	1.87	0.66	0.58
Ross island, Ireland	13	1.72	0.58	0.42
Stauffenberg, France	15	1.79	0.50	0.39
Wiener Wald, Austria	12	1.47	0.55	0.38
Variation of populations	11–20	1.47–2.42	0.50–0.68	0.30–0.73
Variation of individual leaves	9–22	0.90–3.00	0.31–0.79	0.22–1.01

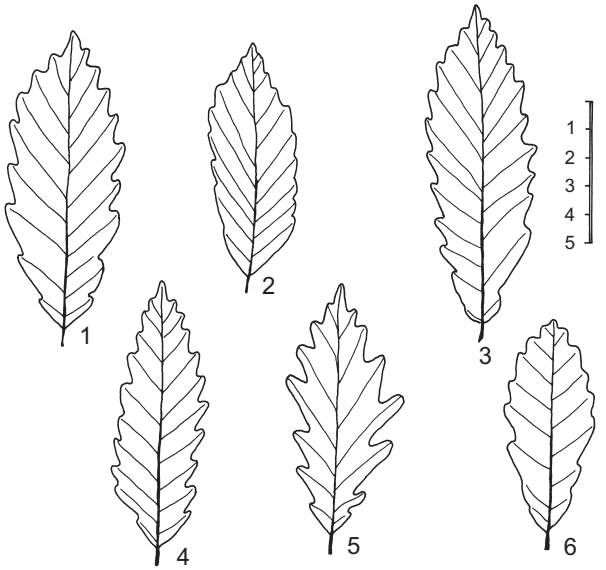

Fig. 3. Drawings of leaves of *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak; the scale bar 5 cm. **1** – specimen No. U 18624, flora 7B, Late Miocene, Hambach; **2** – specimen No. U 19266, flora 7D, Late Miocene, Hambach; **3** – specimen No. U P1619, flora 8E, Late Miocene, Eschweiler; **4 –** specimen No. U 18209, flora 8A, Late Miocene, Hambach; **5** – specimen No. U 09941, flora 8–9, Mio-Pliocene, Brunssum; **6** – after Laurent & Marty (1923), Pl. 7 fig. 2, Late Pliocene, Reuver

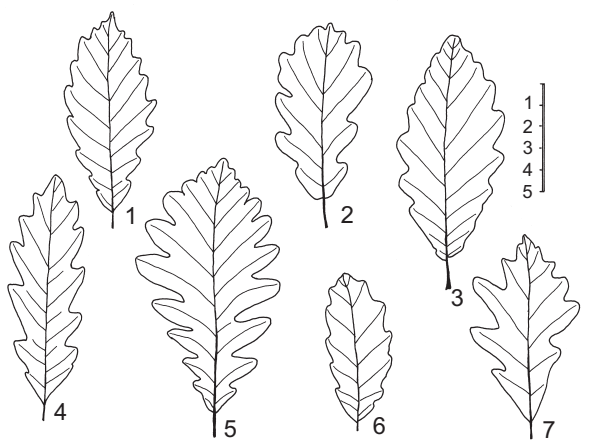

Fig. 4. Drawings of leaves of different populations of *Quercus petraea* (Matt.) Lieblein; the scale bar 5 cm. **1** – Utrecht Herbarium No. 300229 B; Burgenland, Austria; **2** – Utrecht Herbarium No. 93353; Loire Atlantique, France; **3** – Utrecht Herbarium No. 323759 B; Aserbaijan; **4** – Utrecht Herbarium No. 313077 B, Macedonia; **5** – Utrecht Herbarium No. 223756 B; Ciscaucasius; **6** – Utrecht Herbarium No. 8343 B; Mottskogen, Norway; **7** – Utrecht Herbarium No. 256351; Opgrimby, Belgium

has to be realized that they are a summary of several populations all over Europe. They can only be used for establishing the presence or absence as well as the variation of a leaf character. Therefore no histograms of the used characters were made. In the recent species *Quercus petraea* (Matt.) Lieblein the variability lies between 9 to 22 secondaries (Tab. 4). Therefore, it is clear that the most important change during the Tertiary history of the species is the sharp decrease in the latest Miocene. This population however was replaced at the end of the Early Pliocene by a population characterized by a higher number of secondaries (Fig. 5, Tab. 3).

Relative length. (Fig. 6, Tab. 3). Its values decrease slightly during the period of deposition of the Inden Series and Hauptkies Series (flora 7B,D, E8, 8A; Fig. 3: 1–4, Pl. 1 figs 1–3, 5, 6), but decreases sharply at the Late Miocene-Early Pliocene transition (flora 8–9, 9, Fig. 3: 5, Pl. 1 fig. 7). Once again, the population of the Late Pliocene (flora 11) has a longer relative length (Fig. 3: 6, Pl. 1 fig. 4). The recent populations vary from almost

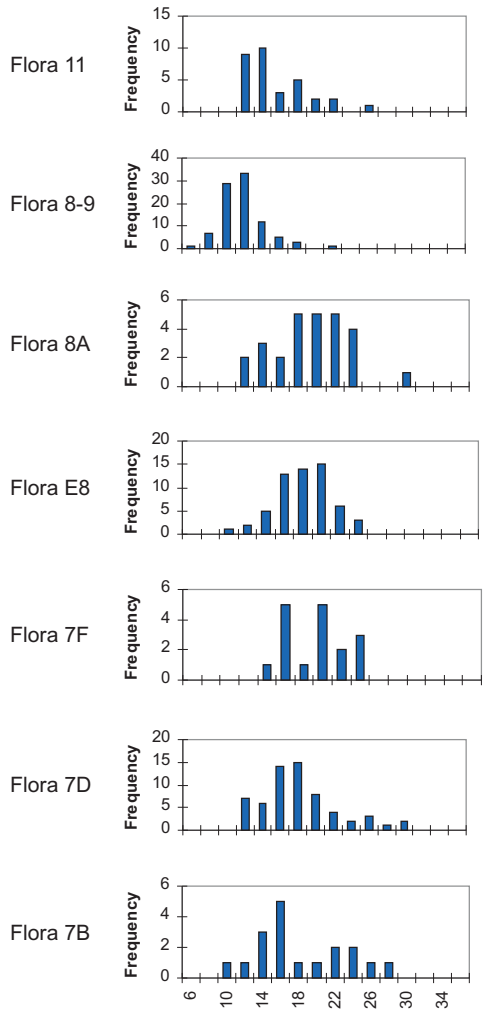

Fig. 5. *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak, histograms of number of secondaries of leaves in the succeeding populations

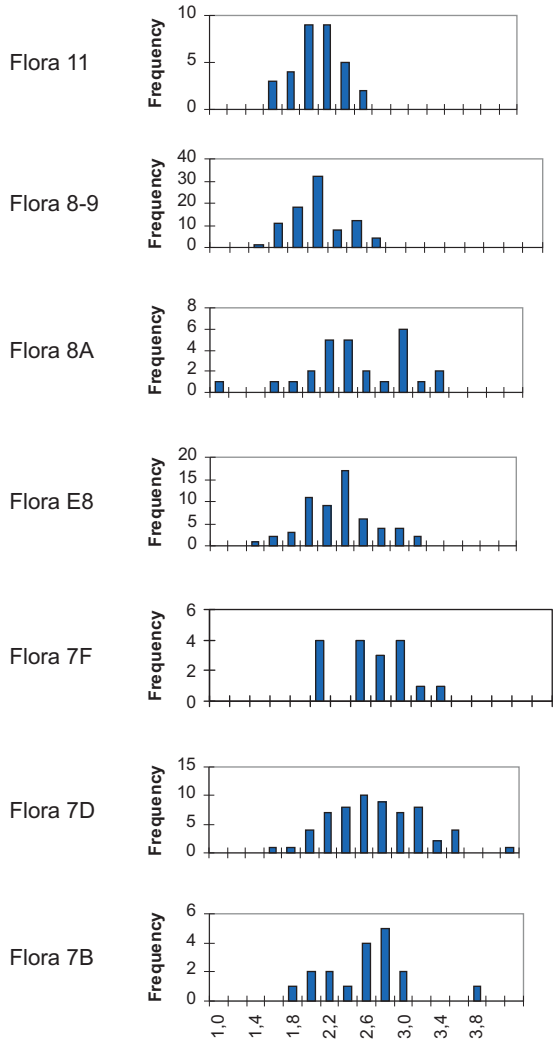

Fig. 6. *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak, histograms of relative length of leaves in the succeeding populations

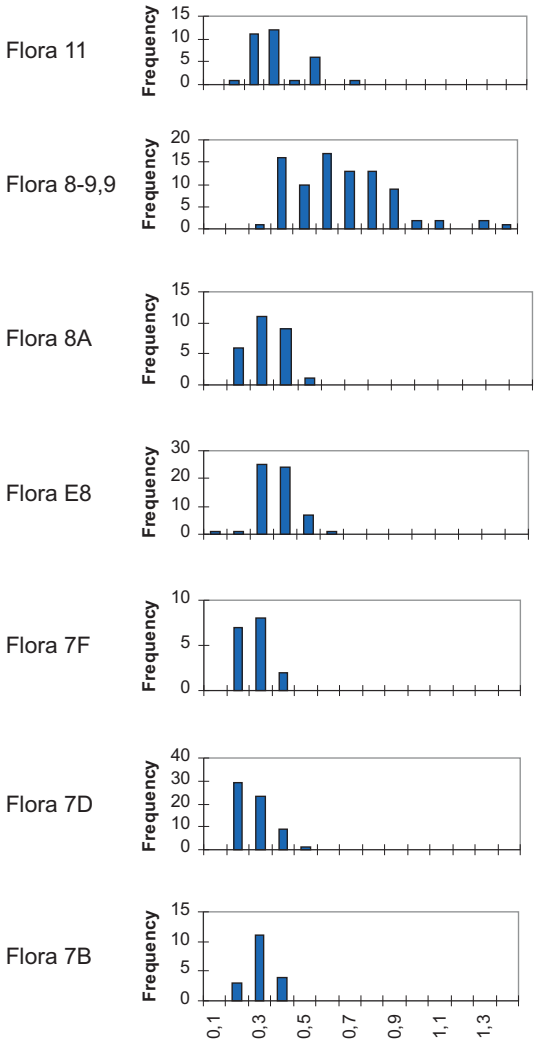

Fig. 7. *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak, histograms of relative length of lobes of leaves in the succeeding populations

rounded to oblong: the L/B varies from 0.9–3.0 (Tab. 4).

Relative length of lobes also varies with time. In the lower part of the Inden Series (flora 7B) the lobes were variable in length, then became very short in the middle and upper part of the Inden Series (flora 7 D,F), slightly longer in the Hauptkies Series (flora E8, 8A) and long in the Mio-Pliocene and Early Pliocene (flora 8–9, 9; Fig. 7, Tab. 3). The Late Pliocene population (flora 11) has short lobes. The material of recent populations of *Q. petraea* is very diverse. Nearly all measured lengths of past populations are represented in it, but rather long lobes prevail (Tab. 4).

Relative location of broadest part of the leaf does not show a strong variation: The leaves were almost elliptical to obovate (average 0.6–0.7) in the Late Miocene and Early Pliocene populations (flora 7B,D,F, E8, 8A, 8–9, 9) and changed abruptly to strongly obovate in the Late Pliocene population (flora 11; Fig. 8, Tab. 3). As the relative length of the leaf varies from 1.0–4.1, the relative location of the broadest part of the leaf indicates the shape of the leaf which ranges from ovate through elliptic to obovate, but also some oblong leaves were present. The recent populations of *Q. petraea* show mostly an obovate shape, but also elliptical populations are present.

In conclusion, the material from the Inden Series (flora 7B,D,F) is very uniform (Fig. 3: 1, 2). The lobing is slight and the number of secondaries is high (Fig. 3, Tab. 3). In the Late Miocene Hauptkies Series there is a slight difference with more elongated leaves, while also part of them show an auriculate base (flora E8, 8A; Fig. 3: 3, 4). In the Miocene-Pliocene

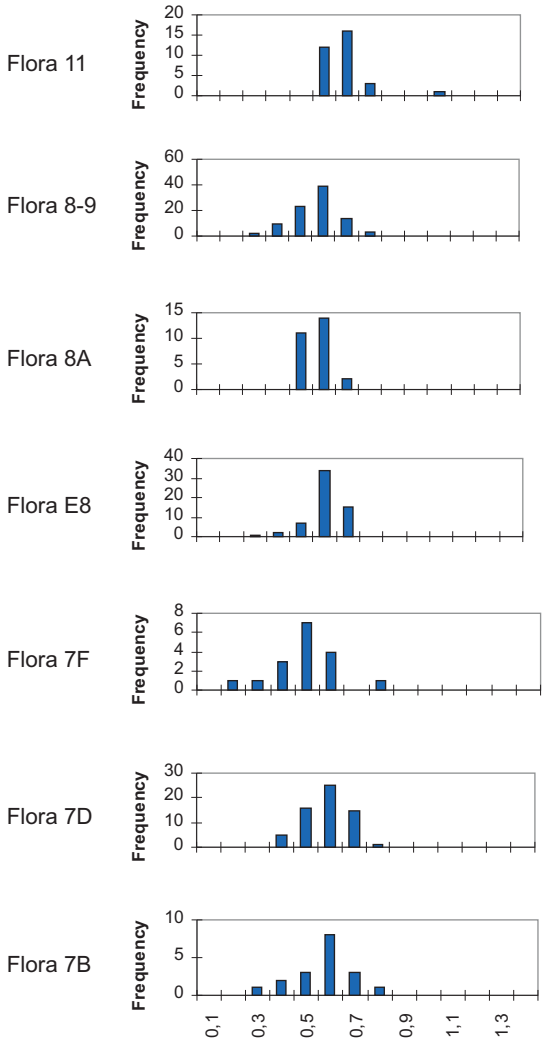

Fig. 8. *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak, histograms of relative position of greatest breadth of leaves in the succeeding populations

and Early Pliocene deposits *Quercus* is represented by the so called "*Q. roburoides*" form, and is characterized by a lower number of secondaries, a rather irregular shape and long lobes (flora 8–9, 9; Fig. 3: 5).

From the Late Pliocene clays an already somewhat impoverished flora (flora 11) was studied. The leaf impressions of *Quercus* are again different, being more comparable with the Miocene types rather than with the Early Pliocene type: more regular in shape and shorter lobes (Fig. 3: 6).

The analysis of leaves of recent *Q. petraea* (Matt.) Lieblein shows that the variability of each character, expressed in the fossil populations of *Q. pseudocastanea* Goeppert emend. Walther & Zastawniak is also found in the recent species. However, the combination of characters is consistently different (Fig. 4), except in one case: *Q. petraea* from Opgrimby, Belgium, is exactly comparable with the material originally ascribed to *Q. roburoides* Gaudin (Fig. 4: 7). Even the rounded to auriculate base of the Late Miocene Hauptkies Series population of *Q. pseudocastanea* is present in a recent population (Western Ireland) of *Q. petraea* and in British populations of this species (Cousens 1963, Wigston 1975).

The results of a T-test of the significance in the differences between the populations are depicted in Table 2. From this table it is clear, that there are significant differences between the populations of the Inden Series in Hambach (flora 7B,D,F) and that in Eschweiler (flora E8; 3 characters). There is only a slight difference between the latter and the population of the Hauptkies Series (flora 8A; 1 character). The Early Pliocene population (flora 8–9, 9) is different from both the Hauptkies Series population and the Late Pliocene population (flora 11; 3 characters in both cases).

Our first conclusion of this biometrical study of the successive populations of *Q. pseudocastanea* Goeppert emend. Walther & Zastawniak is that it is a single but variable species. All the populations even the often separated "*Q. roburoides*" type are entirely comparable with the highly variable recent *Q. petraea* (Matt.) Lieblein.

Fagus

The results of a T-test of the significance in the differences between the populations are depicted in Table 5. From this table, it is clear that the oldest population (*Fagus menzelii* Kvaček & Walther) is different (3 characters) from the following two populations, which themselves are not particularly different (Pl. 2 figs 1, 2, 7). There are significant differences between the populations of the Inden Series (flora 7B,D,F) in Hambach and that in Eschweiler (flora E8; 2 characters). But there is also a clear difference between this population and that of the Hauptkies Series (flora 8A; 2 characters). Again there is a clear difference between this population and that of the Mio-Pliocene (flora 8–9) and Early Pliocene deposits (flora 9), which themselves are not different (Pl. 2, figs 5, 6, 8, 9). The population of the Early Pliocene and that of the Late Pliocene (flora 11) show only a slight difference (1 character).

Table 5. Results from an independent sample T-test (P <0.05) of three characters in eight different populations of *Fagus* (*Fagus menzelii* Kvaček & Walther and *Fagus kraeuselii* Kvaček & Walther combined)

Character: / Population	number of secondaries	relative length of leaf	relative position of greatest breadth
L. Plioc. 11 – E. Plioc. 9	0.000	0.212	0.383
E. Plioc. 9 – L. Mioc. 8–9	0.185	0.594	0.290
L. Mioc. 8–9 – L. Mioc. 8A	0.000	0.000	0.394
L. Mioc. 8A – L. Mioc. E8	0.000	0.000	0.647
L. Mioc. E – L. Mioc. 7F	0.000	0.000	0.837
L. Mioc. 7F – L. Mioc. 7D	0.300	0.183	0.498
L. Mioc. 7D – L. Mioc. 7B	0.011	0.011	0.005

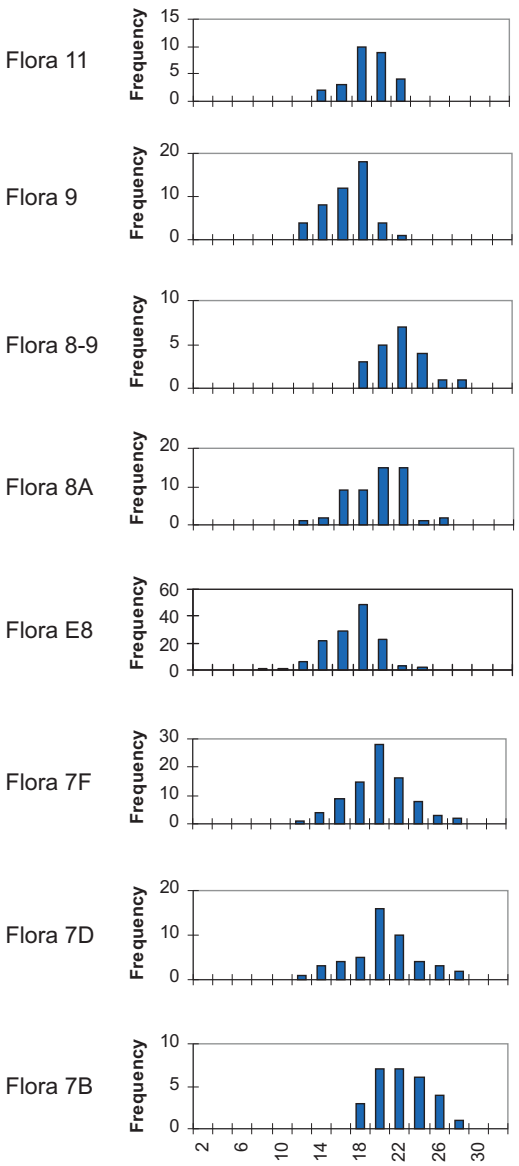

Fig. 9. *Fagus menzelii* Kvaček & Walther (7A-F) and *F. kraeuselii* Kvaček & Walther (E8–11); histograms of number of secondaries of leaves in the succeeding populations

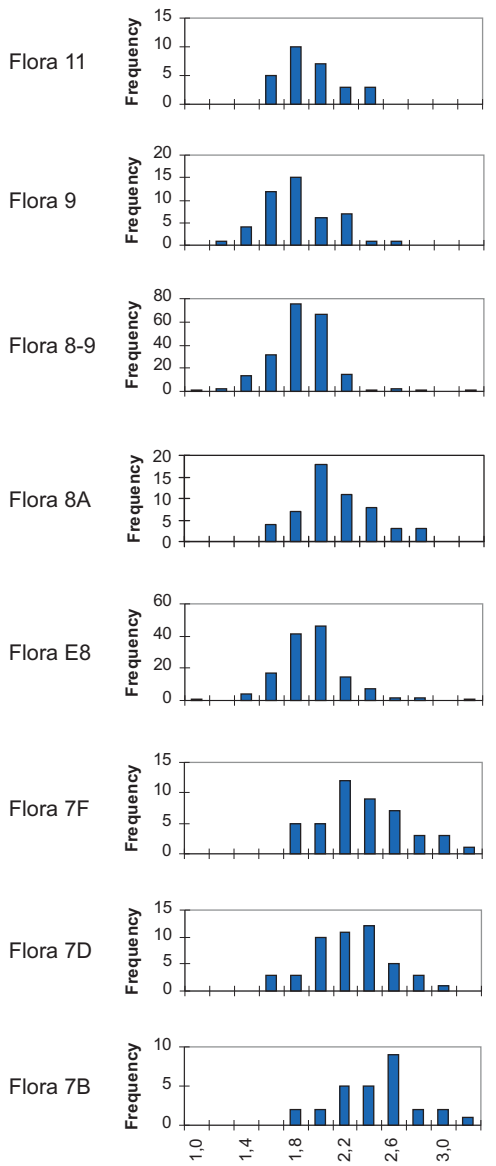

Fig. 10. *Fagus menzelii* Kvaček & Walther (7A-F) and *F. kraeuselii* Kvaček & Walther (E8–11); histograms of relative length of leaves in the succeeding populations

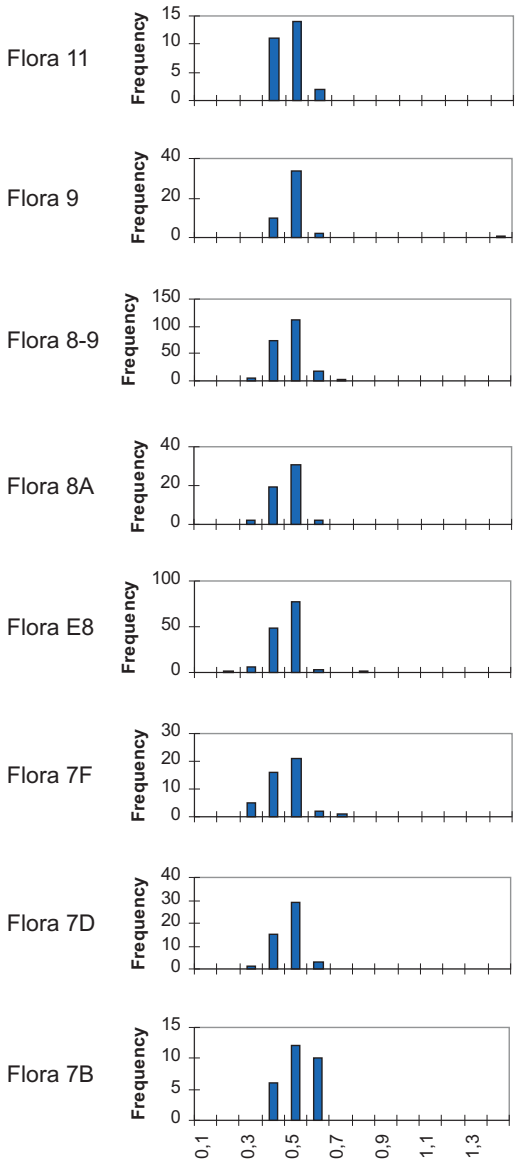

Fig. 11. *Fagus menzelii* Kvaček & Walther (7A-F) and *F. kraeuselii* Kvaček & Walther (E8–11); histograms of relative position of greatest breadth of leaves in the succeeding populations

The number of secondaries is reduced gradually from 18–28, mean 24 in the base of the Inden Series (flora 7B) to 12–22, mean 16 in the Pliocene deposits (flora 9, 11; Fig. 9). A reduction of the relative length of the leaves is observed, the mean value of L/B being reduced from 2.6 to 1.8 (Fig. 10). The relative position of the greatest breadth does not show much difference between the populations. Only in the lowermost population the position is generally in the upper halve of the leaf (Fig. 11). As the recent European species of *Fagus* differ markedly from both fossil species, the latter must be considered as extinct and no direct comparison can be made (T. Denk pers. comm.).

INTERPRETATION

The history of the younger Neogene vegetation in NW Europe is, as exemplified by that of the Lower Rhine embayment, a history of temporary retreat and expansion of vegetations, as a result of changes in climate. It is clear from other studies that climatic changes were different in severity. During the cold periods, the flora was supposedly reduced to small surviving populations, which in the following warmer period expanded swiftly, but retained the characters of small populations. So, the populations preserved in the clays are a testimony to changes during time, that were intensified in the small populations resulting from the retreat of vegetations during the cooler periods. For *Quercus pseudocastanea* Goeppert emend. Walther & Zastawniak this resulted in morphological differences between the oaks of the successive floras, but these differences were only fluctuations around the main characters of the species. For instance, the complete flora of the transitional period from the Late Miocene to Early Pliocene was cool-temperate. In the successive warm Early Pliocene flora the type of *Quercus* did not change.

The Late Miocene populations of *Q. pseudocastanea* are – generally speaking – almost identical, no significant difference could be found. The population during the transition to the Pliocene and the Early Pliocene population itself are quite different. They differ especially in the strong reduction of number of the secondaries, and the increase in the length of the lobes. Also, a marked increase in the percentage of irregular formed leaves is found. The Late Pliocene population represents a return to the older (Miocene) type: the lobes are smaller, the leaves are less irregular, and there is an increase in the number of secondaries.

Depending on the different populations some differences are present, and are probably dependant on ecological factors. Both *Quercus* and *Fagus* are relatively large in the younger Pliocene population, however, between the various populations there are no other significant differences.

The recent material, representing several populations of *Quercus petraea* (Matt.) Lieblein, displays a great variability in characters (Tab. 4): leaves with still a great number of secondaries are present (9–22 versus 10–32 in the Miocene populations), regular and irregu-

lar types are present next to one another, and types with non cuneate, but auriculate bases are to be found. These are frequently considered as hybrids with *Q. robur* L.. However, the presence of the character in Late Miocene populations from the Hauptkies Series, as well as in British populations (Cousens 1963, Wigston 1975) points to a greater variability within the species than hitherto assumed.

Fagus reacted quite differently on the repeated changes in environmental conditions. On the whole, the gradual change of characters was not disrupted, not even by the change in species from *F. menzelii* Kvaček & Walther to *F. kraeuselii* Kvaček & Walther. However, if we look at the numbers of specimens in the various populations there is a marked difference between *F. menzelii* and *F. kraeuselii*. The latter is always represented by a great number of leaves, which often dominate the leaf impression floras, while the former is not very numerous in any population; see Table 5 in which *Fagus* is represented by its percentage in the leaf flora.

STRATIGRAPHICAL IMPLICATIONS

Quercus pseudocastanea Geoppert emend. Walther & Zastawniak from the Inden Series Top-clay of Eschweiler (E8) differs in some characters (relative length of the leaves, relative length of the lobes and relative position of the greatest breadth, Figs 6–8) from the population of this species in the Top-clay of the Inden Series in Hambach. For these characters there is more similarity with the population of the basal Hauptkies Series of Hambach. Also the Eschweiler population is characterized by the presence of auriculate leaf bases in many of the leaves (Fig. 3: 3, Pl. 1 figs 3, 6), which are absent in the population of this species in the Top-clay of the Inden Series in Hambach. These auriculate leaf bases are also documented in the basal Hauptkies Series of Hambach. Hence the Top-clay of the Inden Series in Eschweiler is supposed to be stratigraphically coeval to the basal part of the Hauptkies Series in Hambach.

This supposition is corroborated by the difference of species of *Fagus*: while in Hambach *Fagus menzelii* Kvaček & Walther was still present (Pl. 2 figs 2, 7), this species had been replaced by *F. kraeuselii* Kvaček & Walther in the nearby Eschweiler population (Pl. 2 figs 3, 4). It is unlikely that these two locations harboured two totally different species of *Fagus*, without a trace of the other species in the taphofloras derived from them. Belz (1992, Belz & Mosbrugger 1994) also reported the changeover from *F. menzelii* to *F. kraeuselii* at the beginning of the Hauptkies Series.

In addition, the results of counts of regularly occurring species endorse this: *Liquidambar europaeum* A. Braun is lacking in Eschweiler, *Acer tricuspidatum* Bronn and *Alnus* sp. div. are absent or only present in low percentages in the Eschweiler flora as well as in the basal Hauptkies Series flora; *Zelkova zelkovifolia* (Unger) Bůžek & Kotlaba is well-represented in Eschweiler and only present in low percentages in Hambach (Tab. 6). The floral composition of the Top-clay of the Inden Series of Hambach is comparable with a flora of a lower level, locally distinguished as 7D. In both floras *Alnus* sp. div. and *Liquidambar europaeum* are well-represented, *Acer tricuspidatum* reaches 10 and 22% in these respective floras, *Zelkova zelkovifolia* is sparse and in both floras *Fagus menzelii* is present with medium percentages (Tab. 6, Pl. 2 figs 1, 2, 7).

Hence, it is clear from a biostratigraphical

Table 6. Abundance of some taxa in part of the stratigraphical succession of floras (in percentages)

Species / Flora: / Age:	flora 7D L. Miocene	flora 7F L. Miocene	flora E8 L. Miocene	flora 8A L. Miocene	flora 8–9 Mio-Pliocene
Fagus kraeuselii	–	–	46.8	34.6	25
Fagus menzelii	13.5	18.4	–	–	–
Zelkova zelkovifolia	–	2	14.2	3.2	12
Acer tricuspidatum	22.2	10	0.8	2	0.4
Liquidambar europaeum	4.4	14.5	–	1.3	4.4
Alnus sp. div.	27	23.7	1.4	8.3	1.4

point of view, that several arguments can be mustered to compare the Top-clay of the Inden Series in Eschweiler with the basal clays of the Hauptkies Series in Hambach and not with the Top-clay of the Inden Series in that locality. In our opinion, the Top-clay of the Inden Series in Eschweiler is missing. The Inden sands overlying the upper seam are covered by a basal Hauptkies Series clay. In Hambach, however, both clays are present, with that of the Hauptkies Series often being eroded and more sandy than the almost continuous Inden clay.

CONCLUSIONS

From this biometrical study of leaf morphology we can see two different trends in species/genus behaviour:

a) *Fagus* is very uniform and the sequence of populations shows only continuous trends in leaf morphology, and an absence of great variability. From the fact that both related species have disappeared altogether we may infer a certain vulnerability of this type of evolution strategy against changing circumstances.

b) *Quercus pseudocastanea-Q.petraea* is notably variable in leaf morphology and isolated populations are very different, however, the number of genetically different populations is so great that the species as a whole does not change very quickly. The species is still viable and very vigorous.

c) The differences in shape of the leaves of a single species can be used for stratigraphy.

ACKNOWLEDGEMENTS

The author wishes to thank all who have enabled him to do this study, the Rheinbraun A.G (Köln) for permission to collect in their quarries, The management of Naturalis (Leiden) to make use of their collections, the colleagues at the Laboratory of Palaeobotany and Palynology, Utrecht, particularly Prof. dr. H. Visscher for help and discussion; especial thank is due to drs L. Kouwenberg for help with statistical computation and to Dr. J.H.A. van Konijnenburg-van Cittert (Laboratory of Palaeobotany and Palynology, Utrecht) as well as Dr. E. Crouch Msc. for correcting the English text.

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PLATES

Plate 1

Quercus pseudocastanea Goeppert emend. Walther & Zastawniak

1. Specimen No. U 18595, flora 7B, Late Miocene, Hambach
2. Specimen No. U 18741, flora 7D, Late Miocene, Hambach
3. Specimen No. U 12599, flora 8E, Late Miocene, Eschweiler
4. Sine numero, Naturalis, Leiden s.n., flora 11, Late Pliocene, Reuver
5. Specimen No. U 11785, flora 8A, Late Miocene, Hambach
6. Specimen No. U 12796, flora 8A, Late Miocene, Hambach
7. Specimen No. U 17349, flora B8–9, Mio-Pliocene, Brunssum

All of natural size

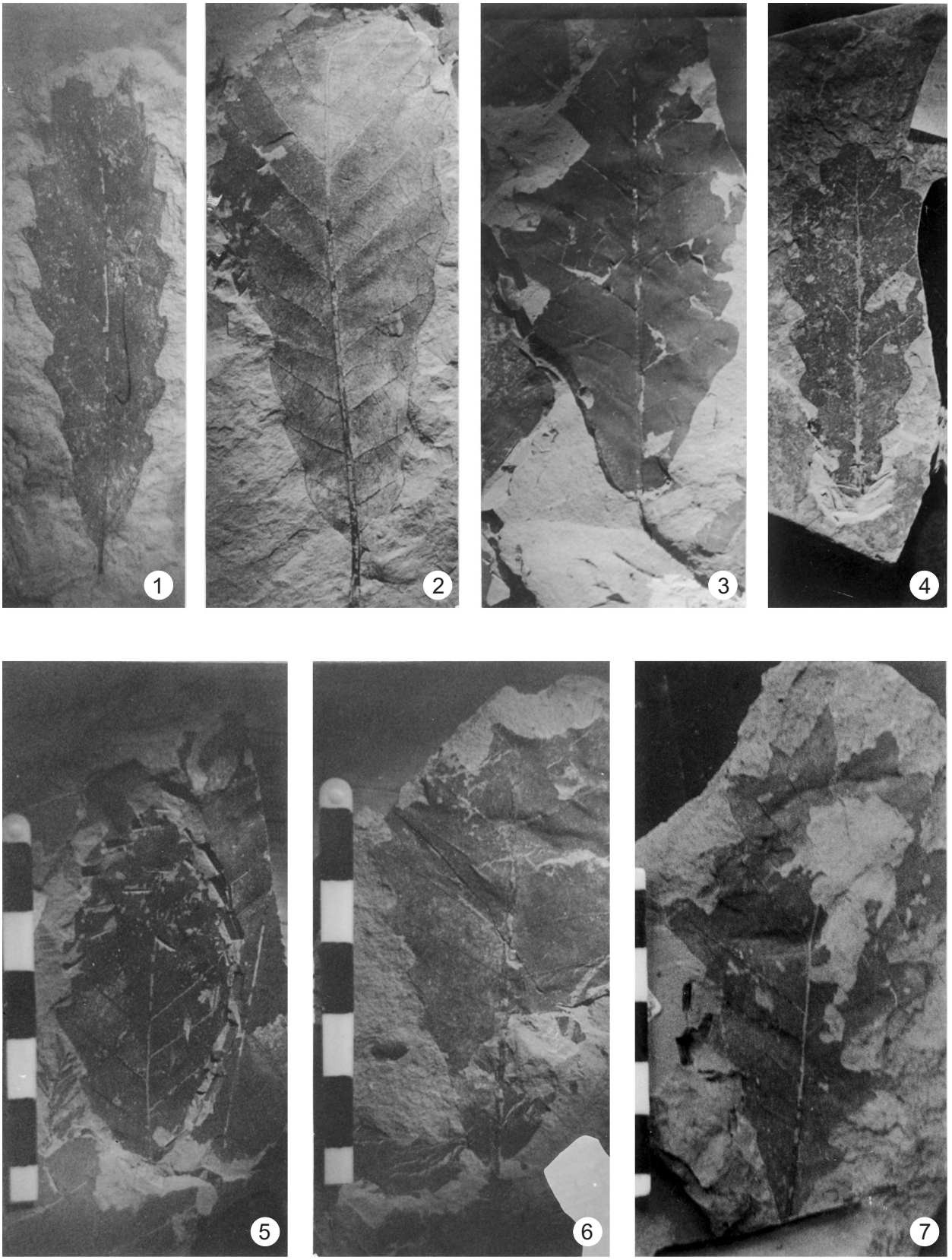
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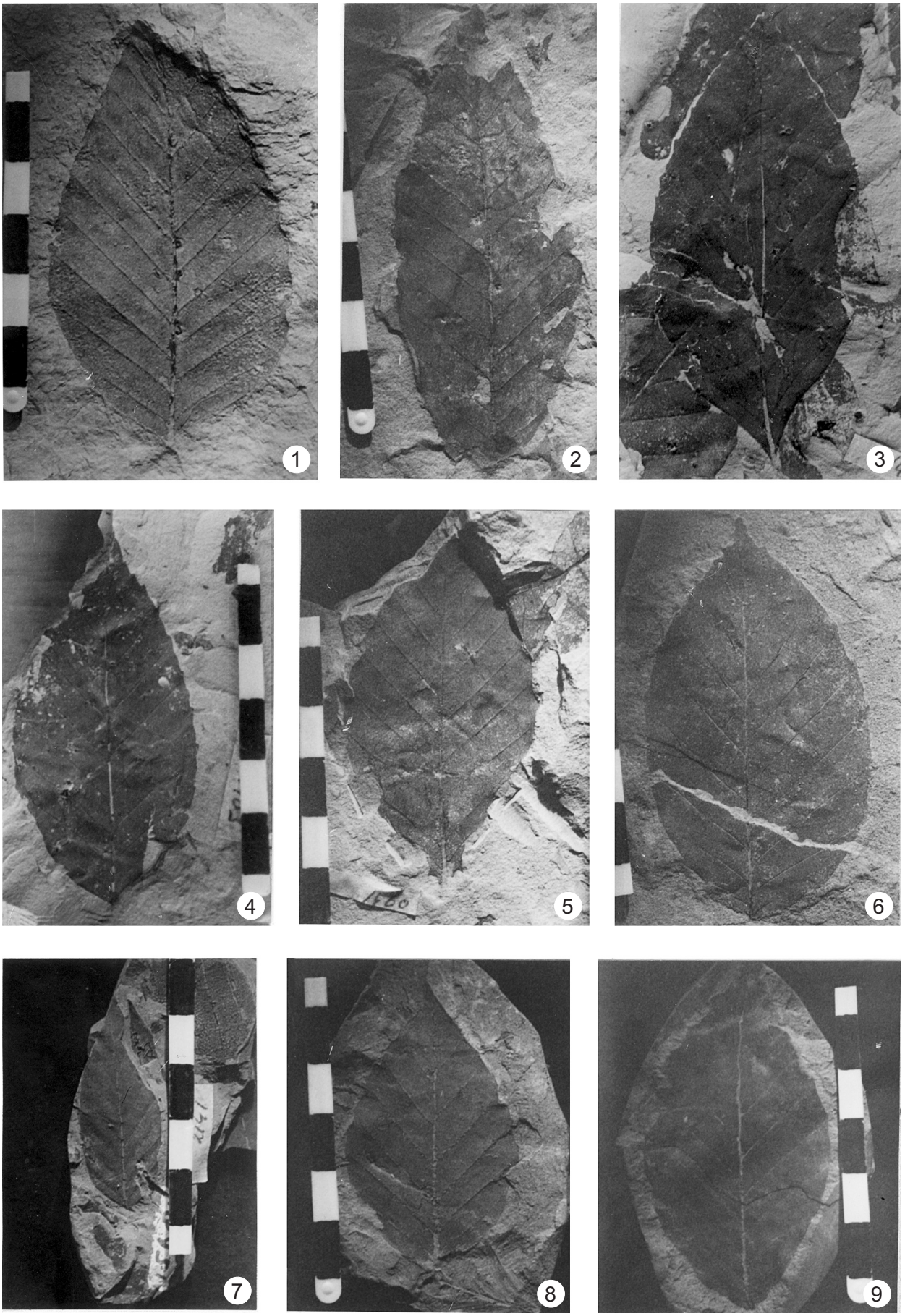
Plate 2

1. *Fagus menzelii* Kvaček & Walther, specimen No. U. 19168, flora 7D, Late Miocene, Hambach
2. *Fagus menzelii* Kvaček & Walther, specimen No. U. 12854, flora 7F, Late Miocene, Hambach
3,4. *Fagus kraeuselii* Kvaček & Walther, specimen No. U. 12522, flora 8E, Late Miocene, Eschweiler
5. *Fagus kraeuselii* Kvaček & Walther, specimen No. U. 10328, flora 9, Early Pliocene, Hambach
6. *Fagus kraeuselii* Kvaček & Walther, specimen No. U. 10140, flora 9, Early Pliocene, Hambach
7. *Fagus menzelii* Kvaček & Walther, specimen No. U. 15684, flora 7F, Late Miocene, Hambach
8. *Fagus kraeuselii* Kvaček & Walther, Naturalis, Leiden, s.n., flora 8–9, Mio-Pliocene, Brunssum
9. *Fagus kraeuselii* Kvaček & Walther, Naturalis, Leiden, s.n., flora 8–9, Mio-Pliocene, Brunssum

All of natural size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