Fossil Magnoliaceae: a review of literature

By RICHARD S. PEIGLER

The family Magnoliaceae is fairly well represented in the fossil record of the Tertiary and Quaternary Periods of the Cenozoic Era (see Fig. 1). Some questionable records have been ascribed to the Cretaceous Period of the Mesozoic Era. The botanists and horticulturists who have developed the classification of Magnoliaceae have done so almost entirely by studying living (extant) species, largely ignoring the fossil record. Currently, paleobotanists are re-evaluating fossils assigned to Magnoliaceae; in fact, the literature all through the past century has examples of where fossil names have been transferred into or out of the Magnoliaceae. For the extant species, there likewise has been a certain amount of transfer of species from one genus to another and a refinement of the family concept: e.g. genera such as *Illicium, Kadsura,* and *Schisandra,* formerly considered to be magnoliaceous, have been placed under separate families. I am not certain if the generic boundaries defined by Dandy (1971) or intrageneric classification of two subgenera and eleven sections within *Magnolia* as outlined by Seitner (1968) are yet stable and widely accepted. The taxonomic debates in *Magnolia* literature at the levels of species, subspecies, varieties, and putative hybrids will continue long into the future, and I doubt that fossil data will have any value at these lower taxonomic levels.

Acceptable classifications of extant plants and animals can be reached by studies of morphology, chromosome numbers, biochemical analyses, use of cladistic methods, etc. in groups where little or no fossil record is available. However, we would know comparatively little about a group such as the redwoods and sequoias (Taxodiaceae), containing only three extant relict species, if we did not study the abundant fossil material which shows the group to have been widespread in the Northern Hemisphere in past ages. For the Magnoliaceae, new finds of fossils coupled with more reliable and sophisticated evaluation (Spicer 1986, Thomas 1986) of these and earlier finds ensure that this data base on phylogeny of the plant family will be increasingly useful to those working on taxonomy of living Magnoliaceae.

The current distribution of Magnoliaceae is restricted largely to eastern Asia, eastern North America, and Mesoamerica. The past distribution included Europe, western Asia, western North America, and Greenland. These past and present ranges are shared by other familiar plants: *Liquidamber, Sassafras,* and *Lindera,* to name a few. Genera currently restricted to eastern Asia such as *Ailanthus* (tree of heaven), *Cinnamomum* (camphor and cinnamon), and *Zelkova* were formerly present in western North America, Europe, and western Asia (Zhilin 1984 and others). In general, extinction

among the fauna and flora of these latter regions was caused by cooling and drying of the climates through the Tertiary followed by episodes of glaciation (Ice Ages) during the Pleistocene (Tidwell 1975, Tiffney 1977, Wolfe 1978, 1980, etc.).

This is a review article based mainly on historical and current literature, and it contains no original research.

Plant fragments as fossils

Leaves. Many leaf fossils were assigned to the wrong genus or even the wrong family by early workers. I cannot say whether the figured specimen of *Magnolia florissanticola* (Fig. 2) is correctly placed. Such re-evaluation would be better left to a trained paleobotanist. Tidwell (1975) gave the following characteristics to identify fossil *Magnolia* leaves: unlobed, entire (unserrated) margins; midvein tapering from thick near base to thinner toward apex, 4 - 15 secondary veins of alternate to subopposite ones curving apically near margins often connecting to ones above; tertiary veins at right angles to secondaries. Kvacek (1978) said that leaves of Magnoliaceae have "internal secretory bodies, paracytic stomata with guard cells slightly elevated above subsidiary cells, uniseriate trichomes." He went on to describe the leaf hairs and to discuss how to distinguish the various genera within Magnoliaceae (see Figs. 3-4).

Stems. Although Tidwell (1975) provided photographs of many fossil species of xylem, none are for Magnoliaceae. Taylor (1981: 87) illustrated a "scalariform pitted vessel of *Magnolia*" with a 275X magnification. The detailed stem structure of Magnoliaceae is undoubtedly useful taxonomically as seen in the study by Page (1984). She described a new fossil genus of plant judged to likely be Magnoliaceae from the Upper Cretaceous of California. Comparisons of cambium, secretory cells, primary and secondary xylem, etc. were made to those of living *Magnolia, Liriodendron,* and *Michelia* as well as to *Magnoliaceoxylon panochensis* (Page)Wheeler, Scott, & Barghoorn. The Miocene *Magnolioxylon scandens* Schönf. was also described from a species of petrified wood (Nemejc 1975: 96). Plant fossil genera based on fragments of wood or stem have traditionally ended with the suffix *-oxylon.* Comparisons between wood fossils must be made with caution because certain features of wood anatomy are thought to represent evolutionary grades, rather than clades.

Pollen and Flowers. Pollen of Magnoliaceae may have useful taxonomic characters. Huang (year?) provided detailed descriptions of the pollen grains of *Magnolia coco* (Lour.)DC., *Michelia alba* DC., *Michelia formosana* (Kanehira) Masam., and *Micheliopsis kachirachirai* (Kanehira & Yam.)H. Keng. Unfortunately, as Tiffney (1977) pointed out, pollen of Magnoliaceae is quite susceptible to chemical and biological degradation, so fossil pollen of this family is virtually non-existent. Baghai (1988) mentioned reports of *Liriodendron* fossil pollen.

I found no figures or descriptions of *Magnolia* flowers in the literature. Although magnoliaceous flowers readily shatter with tepals falling to the ground, fossilization of entire flowers seems possible since branchlets bearing intact flowers are often blown to the ground during storms. In their diagrams of the proposed reconstruction of their

Fig. 1 GEOLOGIC TIME CHART

ERA	PERIOD	EPOCH	Millions of Years	
			Start	Duration
Cenozoic	Quaternary	Holocene = Recent		
		Pleistocene	1.8	1.8
	Tertiary	Pliocene	11	10
		Miocene	25	14
		Oligocene	40	15
		Eocene	60	20
		Paleocene	70	10
Mesozoic	Cretaceous	(Last period of "Age of Reptiles" following Triassic and Jurassic)	135	65

Note: Ages given are approximate. The Holocene is equal to the last 10,000 years.

extinct magnoliaceous genus *Archaeanthus* Dilcher & Crane (1984) showed leaves, stems, flower, and mature aggregate fruit. This remarkable plant may represent a species of Magnoliaceae which existed prior to the divergence of the two tribes (*sensu* Dandy 1971) of the family.

Cones. Fruits of *Magnolia* and allied genera are found in fossil deposits and are generally more readily identified as belonging to this family than are the fossils of other parts of the plant. Because cones of *Liriodendron* shatter into separate seeds when ripe, generally these samaras are known as fossils for that genus. Some species described from remains of cones are *Magnoliaestrobus noszkyi* (Jabl.) Rásky, *Magnoliaestrobus hungaricus* Rásky (both cited from Hungary by Hably 1985), *Magnoliaestrobus gilmourii* Seward & Conway from Cretaceous of Greenland, and *Magnolia volhynica* Stanilovsky from the Eocene of the Ukraine (P. Dorofeev & N. Imchanitzkaja *in* Takhtajan 1974). Figures of these latter two were given by Nemejc (1975). Also from Greenland are fossil cones of *Magnolia inglefieldii* Heer (L. Rüffle, personal communication). The "*Magnolia* sp. fructus" described and figured by Shvaryeva (1983) appears to be a few separate carpels on fragments of stone. Cones of cycads and conifers (*Pinus,*

Metasequoia, etc.) are well known from the fossil record, many of which are beautifully preserved (Tidwell 1975, Taylor 1981, Mai 1987a, etc.).

Seeds. The magnoliaceous seed of the tribe Magnoliaceae has a brightly colored fleshy outer layer (sarcotesta) on a stony interior portion (sclerotesta), the latter of which is abundantly preserved in fossil deposits in many locales of the Northern Hemisphere. Tiffney (1977) has reviewed the literature and drawn many new conclusions pertaining to the relationships between earlier fossil finds and extant taxa within Magnoliaceae. Another significant discussion which relied mainly on seed fossils was by Tralau (1963: 37-40). Seminal remains are apparently reliably identifiable to the generic level. Several paleobotanists confine their studies primarily to fossil seeds (e.g. Mai 1971, 1975, 1987a, b). Many diagrams and photographs of magnoliaceous seeds are given in the references cited above in this paragraph as well as by Nemejc (1975) and Takhtajan (1974). Figure 5 shows a fossil seed of *Magnolia gliwicensis* Szafer (1961) from the Miocene of Poland. Seventeen species of *Magnolia* based on seeds from the London clay (Eocene) deposits were listed by Chandler (1964), although Tiffney (1977) suggested that several of these names may be synonymized after new information he developed on seeds of *Magnolia* is applied to these specimens.

Fossils of Magnolia

Records of *Magnolia* from the Cretaceous of North America are doubtful (J. Wolfe, G. Upchurch, pers. comm.). The family may have arisen that early, but probably not the genus itself. Z. Kvacek (pers. comm.) considers the so-called Upper Cretaceous *Magnolia* species of Europe such as *M. speciosa* Heer and *M. amplifolia* Heer to be doubtful. LaMotte (1952) cited several records for the genus from the Paleocene and Eocene, but these will require re-confirmation in future studies. Reports from Oligocene, Miocene, and later epochs (refer to Fig. 1) are plentiful and most of these are likely valid. Tiffney (1971: 311) wrote: "Although *Magnolia* seeds are common throughout the European Tertiary, forms comparable to modern species do not become prevalent until the Late Miocene, when they supplant earlier, now extinct, forms."

A fossil plant from North America named *Magnolia obovata* Newberry is considered to be a junior synonym of the fossil *Nyssa vetusta* Newberry (Hollick *in* Newberry 1898). Interestingly, this name is also a junior primary homonym of *Magnolia obovata* Thunberg, which in turn is considered a subjective junior synonym of the extant Japanese *M. hypoleuca* Siebold & Zuccarini. Hably (1985) compared certain fossil finds to *M. obovata*, but he was referring to the modern Japanese species, not the North American fossil name.

Another nomenclatural error is found in Andreánszky (1966). He compared some Hungarian fossils to the living *M. grandiflora* L., *M. acuminata* L., and *M. punduana* Wallich with no problem (although the latter is now considered to be a species of *Michelia).* However, in the same paper he compared another leaf imprint to the "Japanese *M. dealbata* Zucc.", and yet *M. dealbata* is a living Mexican species. Based on the name,

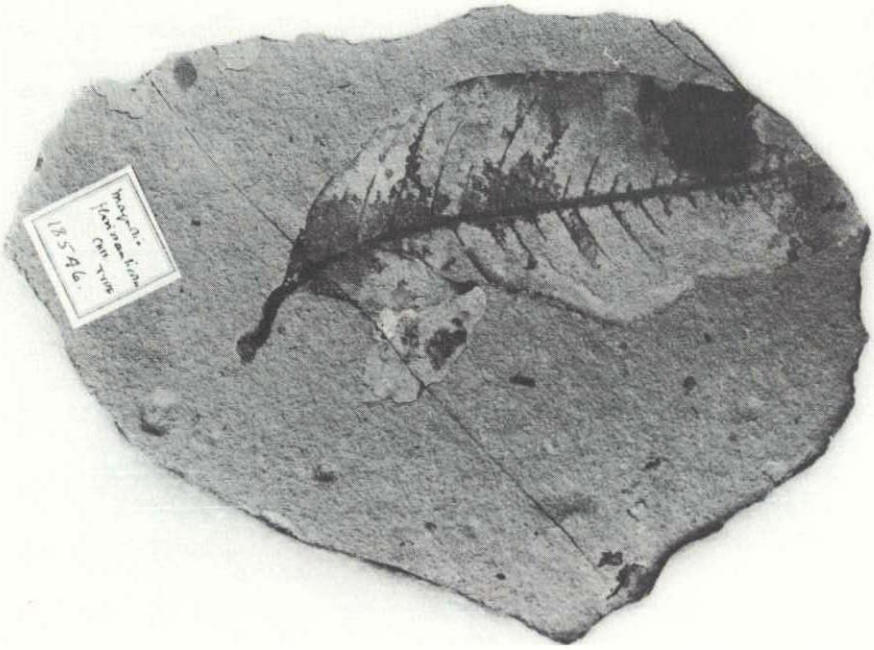

Fig. 2. Holotype of Magnolia florissanticola *Cockerell. From Florissant, Teller Co., Colorado. Upper Miocene. Specimen in Univ. Colo. Museum, Boulder.*

we might guess that Andreánszky meant *M. denudata* Desr., a synonym of *M. heptapeta* (Buc'hoz)Dandy. However, the fossil leaf is about 20 centimeters long and 10 wide, comparable to the Mexican *M. dealbata.* Hably (1985: 19) again cited the fossil material as "*M.* cf. *dealbata* Sieb. & Zucc." in his catalog.

A detailed analysis of fossils from Eurasia was considered to represent the extant Japanese *M. kobus* DC. by Tralau (1963). He listed numerous literature references of *M. cor* Ludwig, *M. ultima* Kirchheimer, and *M. kobus,* all under the synonymy of *M. kobus.* All these fossils were considered to be referable to *M. kobus* itself or taxa that were virtually indistinguishable from it. They included records from the Lower Pleistocene in The Netherlands; Upper Miocene, Miocene, Upper Pliocene, Pliocene of Poland; Pliocene of France, Germany, and Japan; and Miocene and Oligocene of the USSR. Tralau's map 9 proposed a past distribution of *M. kobus* across Europe and Asia. Therefore, it seems likely that representatives of the section *Buergeria* of the genus were widespread and common in Eurasia for the past 35 million years, becoming extinct only during the last 1 1/2 million years except in the Far East.

The excellent work by Tiffney (1977) is the most comprehensive and insightful paper I have found on fossil Magnoliaceae, the detailed discussions of which are not indicated by the title of the article. He described two new species of *Magnolia* from the Brandon Lignite (Middle Oligocene?) of Vermont, based on seeds. His *Magnolia septentrionalis* is perhaps nearest to

M. grandiflora, but he went on to explain why none of the European comparisons to *M. grandiflora* are valid. *Magnolia waltonii* Tiffney shares characteristics of the seeds of section *Theorhodon* (particularly the Mexican *M. schiediana* Schlechtendal) and section *Tulipastrum* such as *M. acuminata* and *M. quinquepeta* (Buc'hoz)Dandy. Tiffney proposed various hypotheses of relationships of his two new species to other fossil and extant species. The affinities between the various Eurasian fossils called *M. ultima, M. cor,* and *M. kobus* were discussed in greater detail than was given by Tralau (1963), and new comparisons were made to well known living species. A final paragraph deals with separation of the North American and European floras which were apparently connected by a land bridge during Early Eocene (see also Wolfe 1978, 1980).

Two further significant works on fossil *Magnolia* must be mentioned. These are the study by Mai (1975) and the 14 species of *Magnolia* treated by Dorofeev & Imchanitzkaja (*in* Takhtajan 1974). Here one can find complete synonymies, original descriptions, redescriptions, and good figures. Pneva (1986) has since added the Upper Oligocene *Magnolia takhtajanii* to the list of Asian fossil magnolias. This species had large leaves and was compared by Pneva to modern Asian and American representatives of the section *Rytidospermum.*

Fossils of Liriodendron

Remains of this genus are known from leaf and seed compressions. As mentioned earlier, individual samaras are generally fossilized because ripe cones shatter. LaMotte (1952) cited four species in his catalog of North American fossil species: *L. hesperia* Berry from the Miocene of Washington State; *L. psilopites* Wodehouse from the Eocene of Garfield County, Colorado; *L. tulipifera* L. from the Holocene and Pleistocene of Maryland, Alabama, North Carolina, and Louisiana; and the European *L. procaccinii* Unger from Paleocene localities of Greenland and Iceland. Nemejc (1975) listed *L. islandiana* Sap. also from Iceland and Greenland. Baghai (1988) compared *L. hesperia* to the two extant species in considerable detail; her work appears to be the most current and reliable for fossils of this genus.

Arnold (1947) stated that *Liriodendron* in Europe was terminated by Pleistocene glaciation, but "up to that time a species indistinguishable from the American *L. tulipifera* existed in the lowlands of western Europe." Some of these fossil finds of France, Poland, and Germany have been called *L. tulipifera fossilis* Reid (Nemejc 1975). Mai (1987a) described *L. fragilis* based on material from various German Miocene locales. A well known European tuliptree is *L. procaccinii* (mentioned above from Greenland). It is cited by Hably (1985) from deposits in Hungary and by Givulescu (pers. comm.) from Romania. A junior synonym is *L. helveticum* Heer from Switzerland. Kirchheimer named *L. geminata* from seeds from Pliocene in Poland (E. Zastawniak, pers. comm.). The Oligocene *L. haueri* Ettingshausen was described in 1869 from Czechoslovakia (Z. Kvacek, pers. comm.). Two further Oligocene species were named by Dorofeev (*in* Takhtajan 1974): *L. balticum* and *L. uralense.*

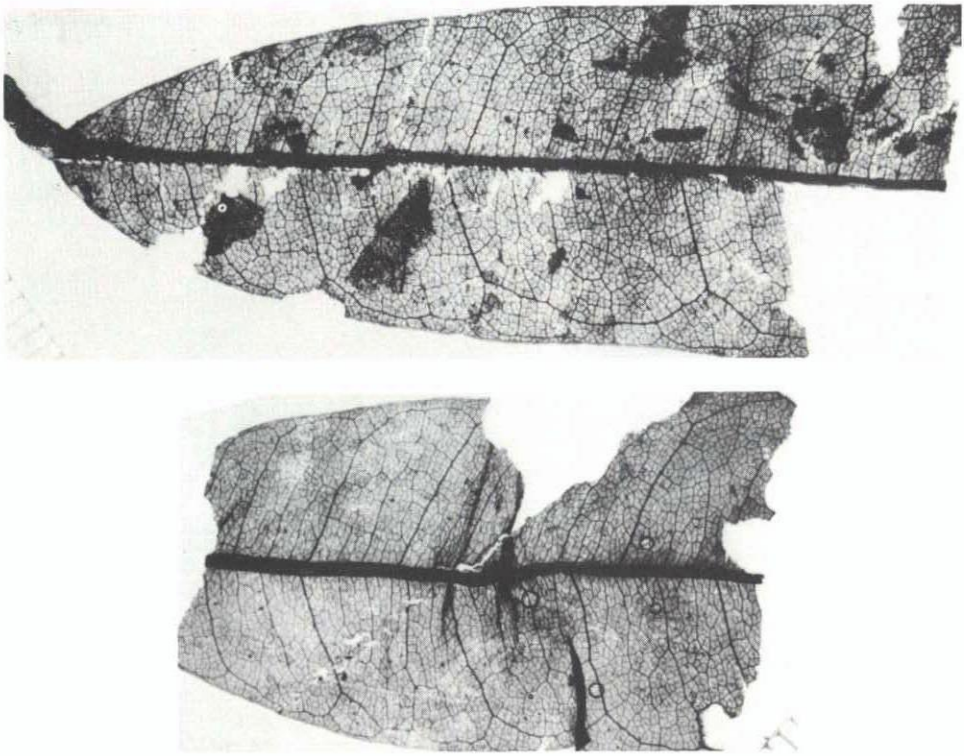

Fig. 3. Fossil leaf transfers of Magnolia kristinae *Knobloch & Kvacek. From Wackersdorf, Bavaria, Germany. Lower Miocene. Specimen with petiole is the holotype. Photos from Dr. Z. Kvacek.*

Liriodendron meeki Heer from the Cretaceous of Nebraska has been demonstrated to be a leaf imprint belonging to the legume genus *Dalbergia* according to Arnold (1974); Cretaceous specimens from Greenland, Kansas, and Nebraska were cited as *Dalbergites simplex* (Newberry)Sew. & Con. (Fabaceae) which had also been ascribed to *Liriodendron* by the original author (Nemejc 1975). These fossils are now believed to be plants which are not legumes either (G. Upchurch, pers. comm.). *Menispermophyllum celakovskii* (Velenovsky) Velenovsky was originally called a *Liriodendron* (Z. Kvacek, pers. comm.). *Liriodendron trilobata* Chaney is now considered to be a specimen of the fossil maple *Acer minutifolium* Chaney (Wolfe & Tanai 1987). Obviously unrelated plant groups may share the peculiar leaf shape seen in true *Liriodendron.* Thus, none of the species mentioned in this paragraph are true Magnoliaceae.

Fossils of Talauma, Manglietia, and Michelia

The present-day distributions of the genera *Michelia* and *Manglietia* are restricted to southeastern Asia, whereas extant species of *Talauma* grow in tropical America and Asia (Dandy 1971, Nemejc 1975). Like *Magnolia* and *Liriodendron,* these three genera ranged in other parts of the world during the Tertiary. Fossil and extant

seeds of these genera can be identified by reference to the distinguishing characters outlined by Tiffney (1977). The extinct magnoliaceous genus *Magnoliaespermum* Kirchheimer, based on Upper Oligocene seeds from Poland and Germany, has certain characters like the seeds of *Talauma* and others more like *Manglietia* (Tiffney 1977). Leaf fossils of *Talauma* and *Manglietia* can be identified by the characteristic hairs and epidermis described by Kvacek (1978).

Chandler (1964) described *Talauma wilkinsonii* from the London Clay flora (Eocene) of southern England, based on seeds. *Talauma egerensis* Andreánszky (1955), described from fossil leaves from Hungary, was likened to the extant *T. pubescens* Merrill from the Philippines. Another leaf fossil from Hungary assigned to this genus was cited by Hably (1985: 22).

Mai (1971, 1987b) described three new fossil species of *Manglietia* and transferred *Carpolithus zinkeisenii* to the genus. These descriptions are based on seeds from Germany as follows: *Manglietia hercynica* Mai (1971), Middle Paleocene, likened to the living *M. kwangtungensis* (Merr.)Dandy of China; *M. zinkeisenii* (Geinitz)Mai (1971), Lower Oligocene; *M. germanica* Mai (1971), Miocene, considered to resemble the extant *M. glauca* Blume from Java; and *M. multicostata* Mai (1987b), Upper Paleocene. Other fossil finds from USSR have been classified under *Manglietia* (Shakryl 1987: 118). Some of the many species of *Magnolia* described from fossil seeds from the London Clay (Chandler 1964) may be found to actually belong under *Manglietia* after being re-examined (Tiffney 1977).

The genus *Michelia* was possibly present in Japan during the Holocene and Bulgaria during the Eocene (Tiffney 1977). I have been unable to obtain the original references for the very few finds of this genus in the fossil record, but they are cited in Tiffney's bibliography.

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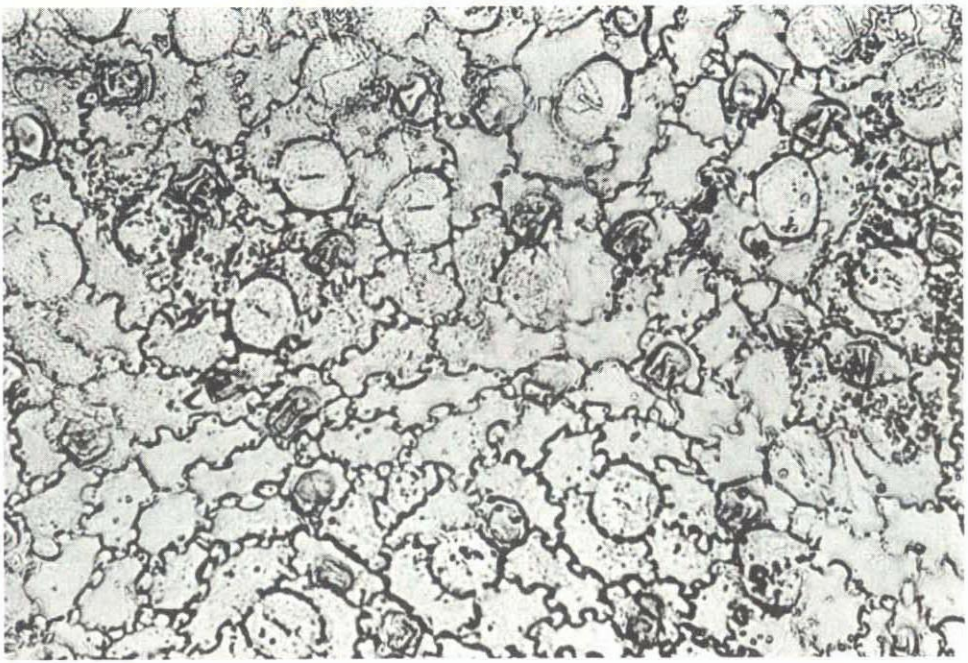

Fig. 4. Lower cuticle of leaf fossil of Magnolia liblarensis *(Kräusel & Weyland) Kvacek. From Liblar Mine near Cologne, Rhineland, Germany. Miocene. Photo from Dr. L. Rüffle.*

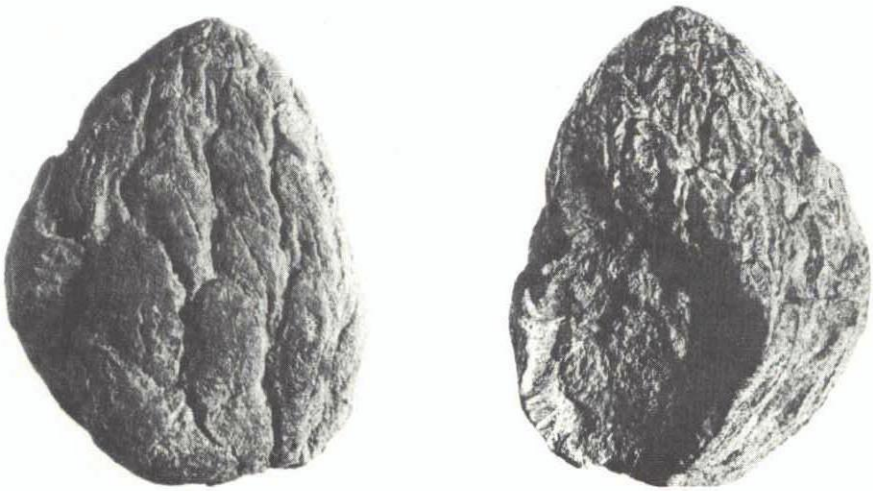

Fig. 5. Two views of holotype seed of Magnolia gliwicensis *Szafer. From Stare Gliwice, Upper Silesia, Poland. Middle Eocene. Photo from Dr. E. Zastawniak.*

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