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The first occurrence of the *Quercus* section *Cerris* Spach fruits in the Miocene of China

SHUYIN SONG[1], KATARZYNA KRAJEWSKA[2, *] and YUFEI WANG[1]

[1] Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, P.R. China,
e-mail: lics@public2.east.cn.net
[2] Museum of the Earth, Polish Academy of Sciences, 00-488 Warszawa, Al. Na Skarpie 27, Poland,
e-mail: mzpaleo@warman.com.pl

ABSTRACT. The carpological remain of *Quercus* L. section *Cerris* Spach from the Middle Miocene deposits in Shanwang, China, is described and compared with the European Tertiary taxa of *Quercus* and with extant species of *Quercus* sect. *Cerris* Spach from China. The comparison indicates that among fossil specimens the most morphologically related are fruits of *Q. cerrisaecarpa* Kol., and, of recent species – fruits of the deciduous *Q. acutissima* Carruth. and *Q. variabilis* Bl.

KEY WORDS: Fruit, *Quercus*, sect. *Cerris*, Tertiary, China

INTRODUCTION

Fossil remains of *Quercus* occur commonly in Tertiary floras of the northern hemisphere. The first believable records from Europe and North America origin from Middle Eocene (Bones 1979, Jones 1986, Kvaček & Walther 1989). The first macrofossils of *Quercus* L. in China were found in the Eocene sediments from Fushung, Liaoning (WGCPC 1978).

The history of the genus *Quercus* L. has been mainly studied on the basis of morphological and anatomical studies of leaves (Andreánszky 1959, Andreánszky & Kovács 1964, Iljinskaya 1980, Hummel 1983, Knobloch 1986, Kvaček & Walther 1989, Walther & Zastawniak 1991, Mai 1995). Records of well preserved fossil fruits of *Quercus* L., bearing important characters for tracing the evolutionary history of the taxa, are rather scanty found (Kvaček & Walther 1989, Zhou 1993).

In the fossil floras of China the section *Cerris* Spach has been so far represented only by leaf impressions (Hu & Chaney 1940, Zhou 1993). The carpological remain described here is the first fruit specimen of *Quercus* belonging to the sect. *Cerris* Spach from the Tertiary floras of China. This specimen comes from a new material collected in the 1990s from the Middle Miocene sediments of the Shanwang Formation, Shantung, eastern China. The Shanwang flora was discovered in 1935. In the diatomaceous deposits from this locality, besides numerous animal remains, unusually rich plant material was found. The flora was described for the first time by Hu and Chaney in 1940. Hu and Chaney (1940) recognized 2 species of *Quercus*: *Q. miovariabilis* Hu & Chaney and *Q. sinomiocenicum* Hu & Chaney, both belonging to the sect. *Cerris* Spach. *Q. dissimifolia* Geng was reported later from the same locality (WGCPC 1978). All of the above fossil species of *Quercus* are based on leaf remains. Apart from typical temperate families, i.e., Betulaceae, Aceraceae, Ulmaceae, Juglandaceae occurring in the Shanwang flora, subtropical and tropical genera like: *Lindera*, *Litsea* (Lauraceae), *Ficus* (Moraceae), *Meliosma*

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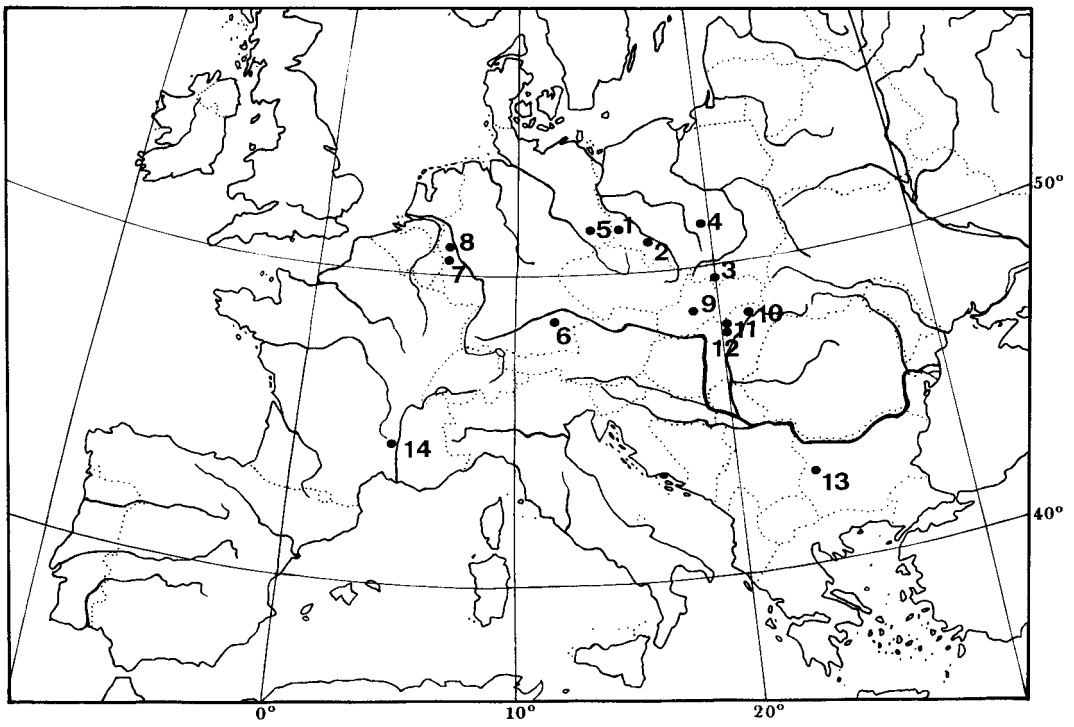

Fig. 1. Occurrences of fossil fruits of *Quercus* sect. *Cerris* in the Neogene floras of Europe. **1** – Ruszów, **2** – Sośnica, **3** – Domański Wierch, **4** – Bełchatów, **5** – Wischgrund, **6** – Achldorf, **7** – Kreuzau, **8** – Frimmersdorf, **9** – Močiar, **10** – Füzérradvány, **11** – Bánfalva, **12** – Felsötárkany, **13** – Kurilo, **14** – Rochessauve

(Sabiaceae), *Tetrastigma* (Vitaceae), *Eriobotrya* (Rosaceae) are present as well (Hu & Chaney 1940, Wgcpc 1978). The palaeo-climate indicated by the Shanwang flora is warm temperate to subtropical (WGCPC 1978). Leaf remains reported from two other localities of the Younnan Province and described as *Q. acutissima* Seem from the Mio-Pliocene flora Lincang and *Q.* cf. *aegilops* L. from the Pliocene flora of Yongping (Zhou 1993), belong probably to the sect. *Cerris* as well.

The sect. *Cerris* Spach is represented in the European and south-western Asian fossil floras begining from the Neogene (Fig. 1) while in the Early Tertiary floras oak remains from the sect. *Rubrae*, *Phellos* and subgenus *Cyclobalanopsis* prevail. Leaf and carpological records of *Quercus* sect. *Cerris* have been reported from numerous Miocene and Pliocene localities, e.g., Germany, Hungary, Poland, Slovakia, Bulgaria, France, Georgia, Moldavia, Abkhasia (Menzel et al. 1933, Weyland 1934, Stefanoff & Jordanoff 1935, Pimenova 1954, Yakubovskaya 1955, Grangeon 1958, Kilpper 1959, Andreánszky 1959, 1963, 1964, Kolakovsky 1964, Kolakovsky & Shakryl 1976, Zastawniak 1972, Sitár 1973, Hummel 1983, Knobloch 1986, Gregor 1986, Kovar-Eder 1988, Stuchlik et al. 1990, Walther & Zastawniak 1991). Among fossil fruits of *Quercus* sect. *Cerris*, mainly preserved as impressions or compressions, several taxa have been distinguished. The most common species are: *Q. cerrisaecarpa* Kol., *Q. sapperi* (Menzel) Mai ex Hummel and *Q. microcerrisaecarpa* Kol. Leaves of oaks of the sect. *Cerris* representing important elements of the Neogene floras of Europe, belong to *Q. gigas* Goepp. emend. Walther & Zastawniak, *Q. czeczottiae* Hummel and *Q. pseudocastanea* Goepp.

The fossil fruit designated as *Quercus* cf. *cerrisaecarpa* Kol. add a new taxon to the Shanwang flora and make it possible to follow the relationships between the European and Chinese Tertiary floras.

MATERIALS AND METHODS

Two specimens were collected from Shanwang diatomite open cast mine in Xie jie He Village (36°54'N, 118°20'E), Linqu County, Shandong Province, dated as Middle Miocene, 15 to 17,5 million years B. P. (Liu & Leopold 1992, Yang & Yang 1994, Li 1981). One of the specimens was extracted mechanically. It was isolated in hydrofluoric acid (38%) and then washed in water. The cleaned material was studied under scanning

electron microscope (SEM). The other specimen (No. CBP-SW-97-1) is housed in the Department of Palaeobotany, Institute of Botany, Chinese Academy of Sciences, in Beijing. The terminology for the fruit description follows Berggren (1981).

MORPHOLOGICAL DESCRIPTION

Quercus cf. ***cerrisaecarpa*** Kol.

Pl. 1 figs 1, 2, Pl. 2 figs 1–3, Fig. 2

Description. The fossil remain is preserved as a compression of an acorn with its well preserved basal part. The acorn has dimensions 14 × 21 mm, and about 13 mm in height. The scar of the acorn is circular and 10 mm in diameter. Only imbricate scales of the cupule are visible. The scales are linear with an attenuate apex, 4–7 mm long and 0.6–1.0 mm in diameter, triangular in cross section, covered with appressed straight trichomes 111.5–117.9 μm long and 6.4–7.6 μm in diameter. The height of the cupule and the shape of scales over the whole surface of the cupule are not visible.

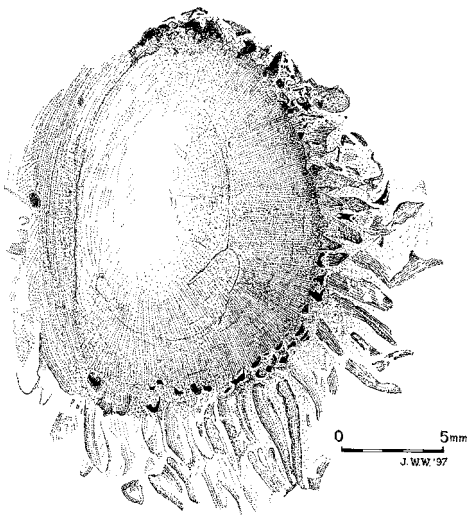

Fig. 2. The fruit of fossil oak from the flora of Shanwang, No. CBP-SW-97-1, drawn by J. Wieser

COMPARISON WITH FRUITS OF *QUERCUS* FROM EUROPEAN TERTIARY

The comparison with fossil *Quercus* taxa occurring in the European floras (Fig. 1) indicates that morphologically the fruits of *Q. cerrisaecarpa* Kol. are the most closely related to the specimen from the Shanwang flora (Tab. 1). *Q. cerrisaecarpa* Kol. has been quite often found in the Neogene floras of Europe and south-western Asia. This taxon was described for the first time from the Late Miocene flora of the Kodor valley (Kolakovsky 1964). Cupules from this locality attain 5–6 mm in height and 15–23 mm in diameter, they are covered by narrow linear scales with acute ends. These scales reach 0.5–1.2 mm in width, like scales of the cupule from Shanwang, but they are somewhat longer, exceed 10–13 mm in the length. Unlike scales of the cupule described from Shanwang they are recurved. Very similar to the specimen from Shanwang are cupules of *Q. cerrisaecarpa* reported from the Pliocene flora of Ruszów (Hummel 1983). They are 18–35 mm in diameter; their margin is bordered by a ring of straight scales similar in length and width to the scales of the cupule found in Shanwang: up to 8.0 mm × 0.7–1.0 mm. The scar is 8–12 (14) mm in diameter. Closely similar specimens occur also in the Miocene flora of Močiar, Slovakia (Sitár 1973) as well as in the Pliocene flora of Bulgaria, from where they were described as *Q. drymeja* Ung. (Stefanoff & Jordanoff 1935). Two types of scales are preserved on the cupules of *Q. drymeja* sensu Stefanoff and Jordanoff: upper lanceolate-acuminate, slightly reflexed and lower, shorter than upper, triangular in outline and straight.

The cupules of another fossil species *Q. sapperi* (Menzel) Mai ex Hummel, often occurring in the Neogene floras of Europe are bigger than the specimen from Shanwang; their diameter can reach: 3.0–5.0 cm (Achldorf, Miocene, Gregor 1982), 4.0–4.5 cm (Kreuzau, Miocene, Weyland 1934), or 3.5 cm (Domański Wierch, Pliocene, Zastawniak 1972). They are covered by much wider and longer scales. In *Q. sapperi* ssp. *latisquamosa* Hummel they are triangular in shape, 2.0–3.5 mm wide in the specimens from Ruszów (Hummel 1983), and in the specimen from Domański Wierch they reach 3.0 mm (Zastawniak 1972). The scar is bigger than in specimen from the flora of Shanwang, 12–15 mm in diameter (Hummel 1983). In *Q. sapperi* ssp. *sapperi* scales are lanceolate in outline, straight or slightly curved, up to 15 mm long and 1.0–2.0 mm wide; the scar is 10–12 (14) mm in diameter (Hummel 1983).

Comparing the fruits of another rarely reported species *Q. microcerrisaecarpa* we can

Table 1. Comparison of the fossil fruit of *Quercus* from the flora of Shanwang with selected fossil species of *Quercus* from the Neogene floras of Europe and south-western Asia

	Q. cerrisaecarpa			*Q. microcerrisaecarpa*		*Q. sapperi*			*Q. sapperi* ssp. *latisquamosa*		*Q. sapperi* ssp. *sapperi*	*Q. variabiliformis*	*Q.* cf. *cerrisaecarpa*
	KODOR	RUSZÓW	MOČIAR	KODOR	SOŚNICA	ACHLDORF	KREUZAU	SOŚNICA	RUSZÓW	DOMAŃSKI WIERCH	RUSZÓW	RUSZÓW	SHANWANG
cupule diameter (mm)	15–23	18–35	18–30	8–13	10	30–50	40–45	20	(6)30	35	(10)20–40	30	22
acorn height (mm)	15			13									
acorn diameter (mm)				14									
scar diameter (mm)		8–12 (14)							12–15		10–12 (14)		10
scale shape	linear, curved	straight		linear, curved	ensi-form, bent		linear, lan-ceolate	lanceola-te-mu-cronate	straight or curved, triangular	narrow triangular, acute	lanceolate straight or curved	flat	linear
scale length (mm)	10–13	to 8.0	5.0–6.0	13–15	10.0	7.0–8.0	7.0–8.0	7.0	10.0	10.0	to 15.0	10.0	4.0–7.0
scale width (mm)	0.5–1.2	0.7–1.0		1.0	0.8	1.0–2.0		1.5–2.0	2.0–3.5	3.0	1.0–2.0	1.5	0.6–1.0

notice that they are much smaller than fruit found in Shanwang; the diameter of cupules reaching 8–13 mm in the specimens from the Kodor valley (Kolakovsky 1964) or 10 mm in the specimen from Sośnica (Walther & Zastawniak 1991). Scales surrounding margins of the cupules are slightly bent in the upper part, longer and somewhat wider than the scales of the specimen from the flora of Shanwang, in the specimens from the Kodor valley they are 13–15 mm long and 1.0 mm wide (Kolakovski 1964), in the cupule from Sośnica – 10 mm × 0.8 mm (Walther & Zastawniak 1991).

Another fossil species described from the Pliocene flora of Ruszów – *Q. variabiliformis* Hummel, has characteristic flat, quite wide (1.5 mm at the base) and up 10 mm long upper scales. These scales are wider and longer that the scales of specimen from Shanwang. Middle scales are 2 mm wide, C-shaped or/and S-shaped with distinctly narrowed ends; lower scales reach about 2 mm in width (Hummel 1983).

COMPARISON WITH RECENT SPECIES OF *QUERCUS*

The fossil fruits of *Quercus* from the flora of Shanwang show a close affinity to the sect. *Cerris* Spach. Three extant species, *Q. acutissima* Carruth., *Q. chenii* Nakai and *Q. variabilis* Bl. in China have been chosen from among Chinese representatives of the section (Pl. 1 figs 3–8). Thirty fruits of each of the above species have been measured in the aim of comparison. The specimens were taken from the herbarium of the Institute of Botany Academy Sinica in Beijing (PE). Based on the comparison between the extant and fossil specimens, two recent species, *Q. acutissima* and *Q. variabilis*, are similar to the specimen from the flora of Shanwang (Tab. 2). The similarity is expressed in size of the fruits and scar diameter. The cupules in the studied extant and fossil specimens are covered by scales. The upper scales surrounding the margin of cupules in *Q. acutissima* and *Q. variabilis* are somewhat different in shape.They are subulate while in the fossil species they are linear. The scales in *Q. variabilis* (Pl. 1 figs 3–4, Pl. 2 figs 4–5) reach a similar length but they are much wider than in the fossil specimen, their width amounts 1.5–2.0 mm. In *Q. acutissima* the scales (Pl. 1 figs 5–6, Pl. 2 figs 7–8) are longer and somewhat wider (8–10 × 1.0–1.5 mm) than

Table 2. Comparison of the fossil fruits of *Quercus* from the flora of Shanwang and recent species of *Quercus* sect. *Cerris* Spach. occurring today in China

Species/ Character	*Q. acutissima* Carruth.	*Q. chenii* Nakai	*Q. variabilis* Blume	*Q.* cf. *cerrisaecarpa* Kol. (fossil)
Fruit diameter (mm)	20–40	14–16	25–40	22
Ratio of cupule covering acorn	1/2	1/3	2/3	?
Cupule height (mm)	10–50	7–9	14–16	?
Acorn shape	ovate	elliptic	globose or broadly ovate	?
Acorn height (mm)	17–22	15–25	14–16	?
Acorn diameter (mm)	15–20	13–15	14–16	?
Scar diameter (mm)	8–12	3–6	7–12	10
Scale shape	subulate	linear, reflexed	subulate, reflexed	linear
Scale length (mm)	8–10	2–3	5–7	4–7
Scale width (mm)	1.0–1.5	0.8–1.2	1.5–2.0	0.6–1.0
Cross-section of scale	v-shaped	obtriangular	elliptic	?
Hair shape	straight, tip reflexed	straight, tip reflexed	curved, tip reflexed	straight
Hair length (μm)	173.5–196.4	158.7–173.8	78.2–88.0	111.5–117.9
Hair diameter (μm)	7.6–8.0	7.6–8.0	5.9–6.5	6.4–7.6

in the specimen from Shanwang. On the scales in the examined recent species of *Quercus*, as well as in the fossil specimen, there occur trichomes (Pl. 2 figs 3, 6, 9, 12). In *Q. acutissima* they are similar in shape and approximately 7.6–8.0 μm wide, but much longer (173.5–196.4 μm) than those of the fossil specimen from Shanwang (111.5–117.9 μm). In *Q. variabilis* trichomes reach a similar width but they are shorter (78.2–88.0 μm long), and 5.9–6.5 μm wide; apart from this they are curved unlike the trichomes in the fossil specimen.

Among the other examined recent species *Q. chenii* is morphologically related to the fossil taxon also (Tab. 2). The fruits of *Q. chenii* are smaller and the scar diameter is twice smaller (Pl. 1 figs 7–8). The scales surrounding margins of the cupules (Pl. 1 figs 7–8, Pl. 2 figs 10–11) are much shorter, their length reaching 2–3 mm; only their width and shape are similar. The trichomes covering the scales in *Q. chenii* (Pl. 2 fig. 12) are much longer (158.7–173.8 μm).

Quercus acutissima Carruth. occurs now in China, between 60–2200 m alt., also in Korea, Japan, Vietnam and India (Fig. 3); it grows on clayey and sandy, mostly dry habitats, at foothills, along mountain slopes and sea coasts. *Q. variabilis* Bl. is at present distributed in the northern part of China, along southern mountain slopes below 800 m alt. In the southwestern China it grows from the sea-level up to elevations of 3000 m alt., on dry, sandy and rocky habitats; it also occurs in Japan and Korea (Camus 1936–1939, Wang 1961, Chun & Huang 1998) (Fig. 3).

Q. acutissima is a dominant element in the warm temperate deciduous broad-leaved forest of the northern part of China with accessory of *Quercus variabilis* and various species of *Quercus*: *Q. mongolica*, *Q. aliena*, *Q. dentata* as well as *Pinus koraiensis*, *Acer mono*, *Phellodendron amurense*, *Tilia amurensis*, *Betula dahurica*, *Alnus japonica*, *Vaccinium buergeri*, *Neillia vekii*, *Kalopanax septemlobus*, *Clerodendron trichotomum*, *Alangium platanifolium*, *Symplocos paniculata*, *Styrax obassia* and with *Zanthoxylum schinifolium*, *Lespedeza bicolor*, *Weigela praecox*, *Indigofera kirilowii* etc. in the shrub layer. *Quercus acutissima* is also the main element in the warm-temperate deciduous broad-leaved forests of central China where it occurs together with accessory *Q. variabilis* as well as with *Q. serrata*, *Q. mongolica*, *Q. dentata*, *Zelkova serrata*, *Acer* sp. div., *Pterocarya stenoptera*, *Paulownia* sp., *Tilia mongolica*, *Evonymus patens*, *Sapium japonica*, *Ulmus parvifolia*, *Fraxinus chinensis*, *F. bungeana*, *Celtis bungeana*, *Ulmus macrocarpa*, *Ailanthus altissima* (Wu 1980).

Quercus acutissima and *Q. variabilis* are dominant elements of the forests spread in the northern region of the subtropical part of China: in the subtropical evergreen forests, in the deciduous broad-leaved forests and in the mixed mesophytic forests. They occur together

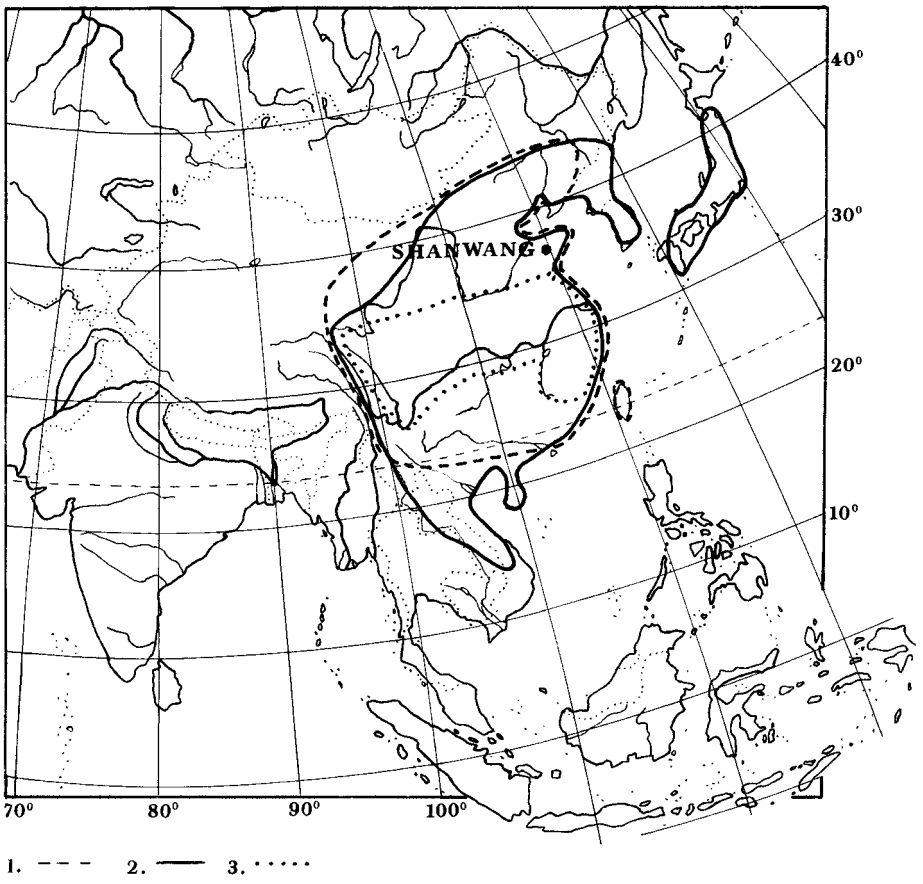

Fig. 3. Geographic distribution of: **1** – *Quercus variabilis* Blume, **2** – *Q. acutissima* Carruth., **3** – *Q. chenii* Nakai

with *Q. fabri, Q. glandulifera, Q. aliena, Q. chenii, Q. engleriana, Castanea sequinii, Liquidambar formosana, Platycarya strobilacea, Albizzia kalkora, Dalbergia hupeana, Rhus chinensis, Pistacia chinensis, Carpinus fargesii, Bothrocaryum controversum, Tilia henryana, Diospyros kaki, Sassafras tzumu, Castanopsis sclerophylla, Cyclobalanopsis glauca, C. gracilis, C. myrsinaefolia, Lithocarpus glaber, L. henryi, Ilex chinensis, I. cornuta, Cinnamomum camphora, Phoebe shaereri* (Wu 1980). Trees of *Quercus acutissima* also form pure forests (Chun & Huang 1998). On mountain slopes at elevations of 2600–3000 m above the sea level they grow together with *Abies fargesii, Abies chinensis, Larix chinensis, Rhododendron shanii* (Wu 1980).

The geographic distribution of *Q. chenii* Nakai (*Q. acutissima* ssp. *chenii* Camus) is restricted to central and eastern China (Fig. 3); it grows from the sea-level to elevations of 600 m (Chun & Huang 1998). *Quercus chenii* forms pure forests and also occurs in the deciduous broad-leaves forests in hilly landscape (Chun & Huang 1998).

CONCLUSIONS

1. Fossil fruit specimen of *Quercus* sect. *Cerris* Spach – *Q.* cf. *cerrisaecarpa* Kol., originating from Middle Miocene of China has been described for the first time. It is interesting to note that in Europe, as well as in Eastern Asia, some Tertiary plants occur with a very great degree of affinity.

2. The most morphologically related species to the fossil specimen from the flora of Shanwang are actually growing in China *Q. acutissima* Carruth. and *Q. variabilis* Bl. of the sect. *Cerris*.

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PLATES

Plate 1

Quercus cf. *cerrisaecarpa* Kol., Shanwang, No. CBP-SW-97-1

1. The acorn surrounded by scales, × 2
2. Scales of acorn, ca × 5.5

Quercus variabilis Blume

3. The fruit and the cupule, top view, × 2
4. The scar of the acorn, × 2

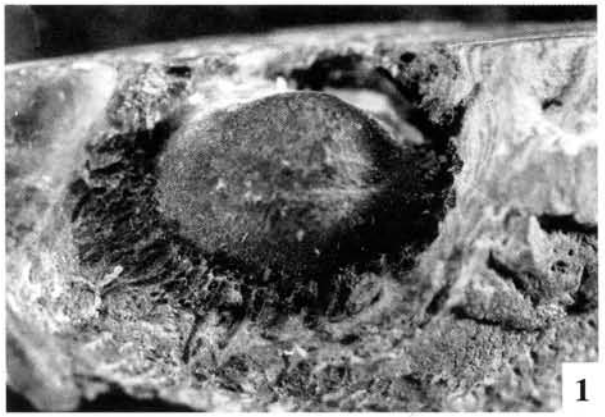
Quercus acutissima Carruth.

5. The fruit and the cupule, top view, × 2
6. The scar of the acorn, × 2

Quercus chenii Nakai

7. The fruit and the cupule, side view, × 2
8. The scar of the acorn, × 2

phot. S. Song, L. Dwornik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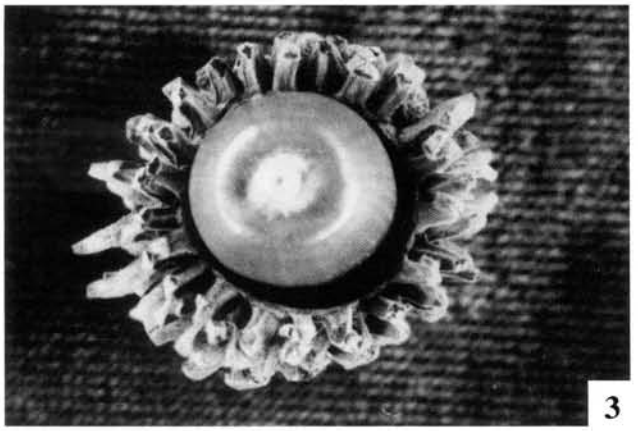
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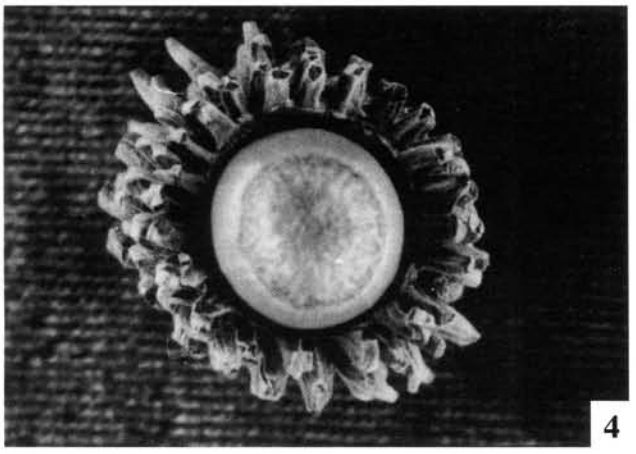
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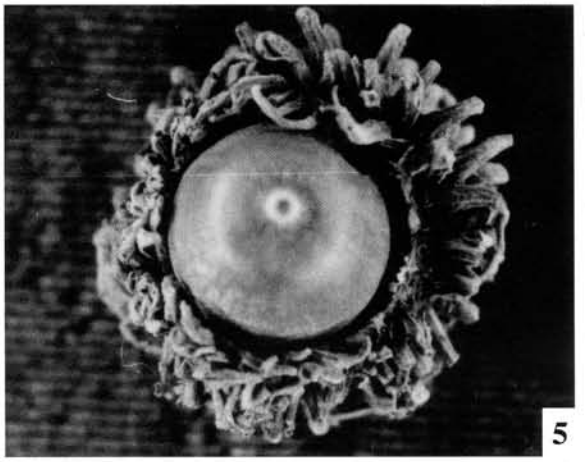
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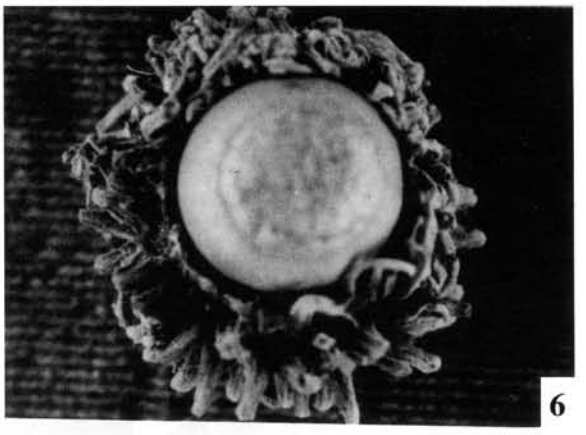
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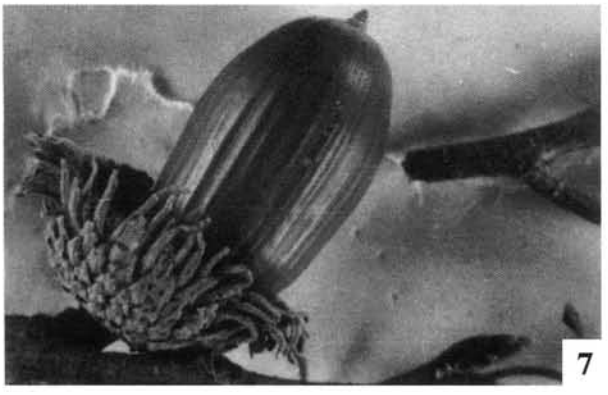
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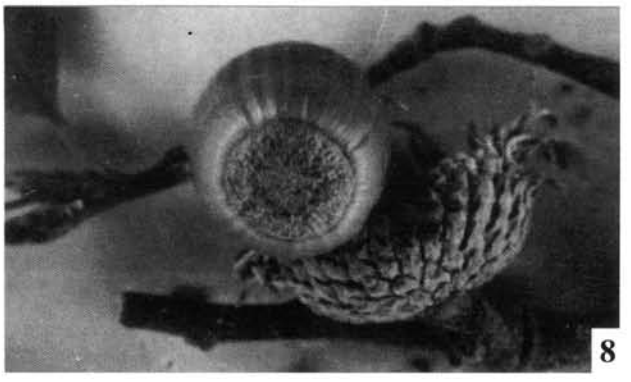
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Plate 2

Quercus cf. *cerrisaecarpa* Kol., Shanwang

1. Scales of cupule, SEM, ca × 15
2. Cross-section of a scale, SEM, ca × 80
3. Unicellular trichomes of the scale, SEM, ca × 140

Quercus variabilis Blume

4. Scales of the cupule, SEM, ca × 15
5. Cross-section of the scale, SEM, ca × 80
6. Unicellular trichomes of the scale, SEM, ca × 140

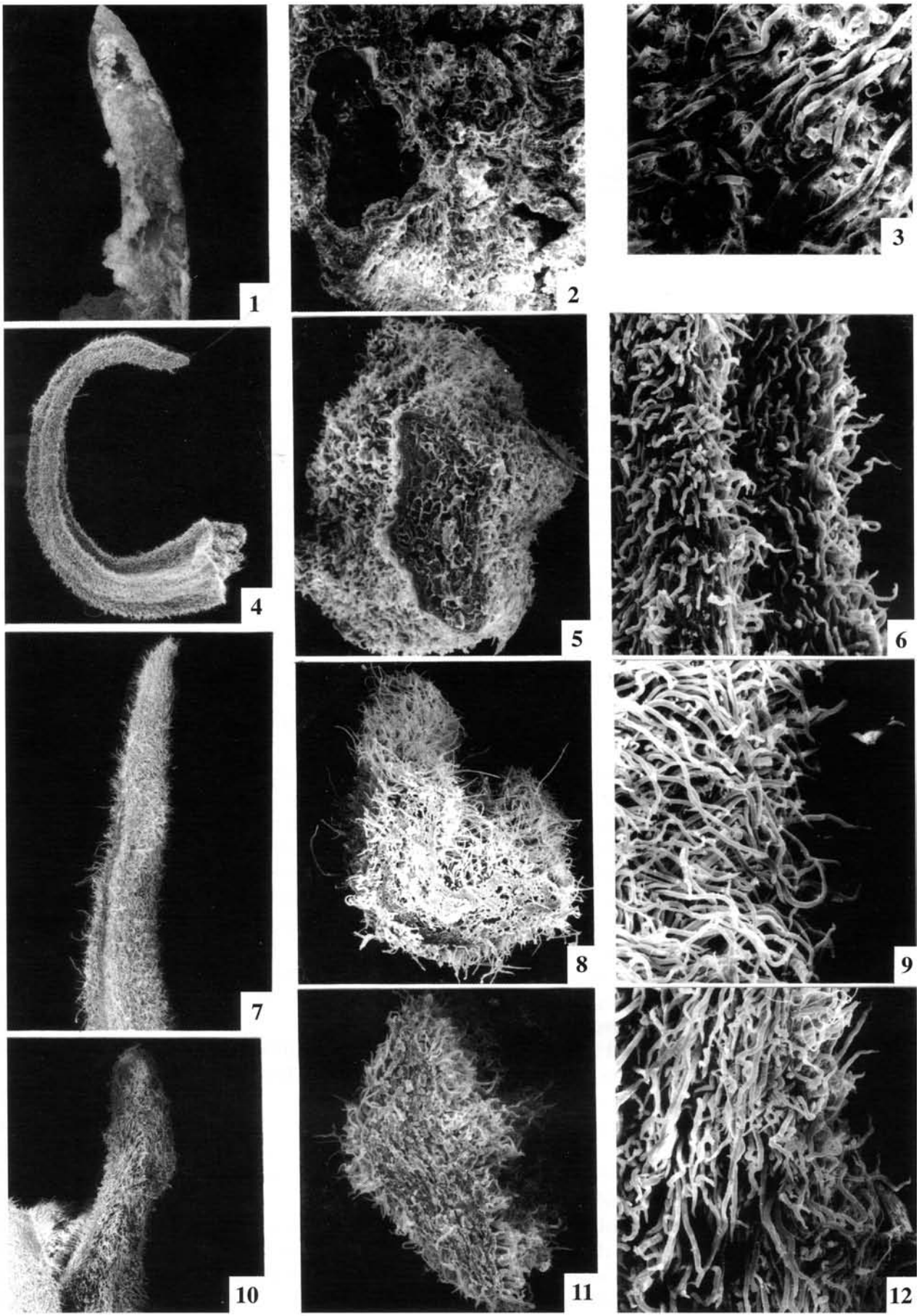
Quercus acutissima Carruth.

7. Scales of the cupule, SEM, ca × 15
8. Transection of the scale, SEM, ca × 50
9. Unicellular trichomes of the scale, SEM, ca × 140

Quercus chenii Nakai

10. Scales of the cupule, SEM, ca × 15
11. Cross-section of the scale, SEM, ca × 80
12. Unicellular trichomes of the scale, SEM, ca × 140

phot. S. Song, L. Dwornik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