A Revision of the Genus Quercus L. Subgen. Cyclobalanopsis (Oersted) Schneider* in Malesia

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SUMMARY

Quercus L. is here compared with and regarded as a separate genus from *Lithocarpus* Bl., differing from the latter by its inflorescence, flower and pollen characters. The genus is subdivided into two subgenera, viz. subgen. *Quercus* (=subgen. *Eu-Quercus* A. Camus) and *Cyclobalanopsis* (Oersted) Schneider. The cupule in the former is beset with imbricate scales, and the male flowers are solitary along the rachis. In the subgen. *Cyclobalanopsis* the cupule is lamellate, and the male flowers are in 4-1-flowered dichasial clusters. The generic splits in *Quercus* proposed by Oersted (1867, 1871), Schottky (1912), and Schwarz (1936 a, b) are not accepted.

Quercus subgen. *Cyclobalanopsis* extends from Japan (Kanto Prov., C. Honshu) south- and westwards to Korea, China, Formosa, Indo-China (Vietnam, Laos, Cambodia), Thailand, Burma, N.E. India, and Western Malesia, with Indo-China as the centre. In Malesia the distribution does not extend further East than Borneo nor further North than Palawan. The centre of distribution in Malesia is in Borneo, from where 17 of the 19 species have been recorded.

Q. kerangasensis and *kinabaluensis* are described for the first time. *Q. valdinervosa* is a new species based on *Q. mespilifolia* Wall. ex A.DC. var. *borneensis* Heine.

The characters in the group, in particular the nature of the cupule in various genera, are extensively discussed. The questions on the identity of several species are explained. Keys, synonyms, and descriptions are given.

INTRODUCTION

This paper is the first contribution towards a revision of the *Fagaceae* in Malesia, represented by five of the seven genera currently recognized in the family. These five genera are *Castanopsis* Spach, *Lithocarpus* Bl., *Nothofagus* Bl., *Quercus* L. and *Trigonobalanus* Forman. Of these five genera no less than 200 species have been attributed to Malesia.

Quercus is the largest and the most widely distributed genus. In 1938, A. Camus monographed the genus, recognizing no less than 500 species. She followed Schneider (1906) by dividing the genus into two different subgenera, viz. *Eu-Quercus* and *Cyclobalanopsis*; in the former the cupule is armored with imbricate scales, whilst in the latter the cupule is lamellate. In her monograph, and also in 1948, A. Camus credited 17 species to Malesia. Of these only 11 are here acknowledged. In April 1966 I described five new species, and in the present paper I have added two and have proposed a new name which make the total number of species known from Malesia amount to 19. According to Schneider's circumscription all of these species belong to the subgen. *Cyclobalanopsis*.

* In April 1966, I erroneously referred to this subgenus under the name *Quercus* L. subgen. *Cyclobalanopsis* (Oersted) A. Camus.

The major point of interest in the genus *Quercus* lies in the controversy over its clear difference from the genus *Lithocarpus*, and also over the question on the generic splits as proposed by Oersted (1867, 1871), Schottky (1912), and Schwarz (1936 a, b).

A. DeCandolle (1863, 1964), Miquel (1863), Oudemans (1865), Baillon (1877), Bentham & Hooker f. (1880), Wenzig (1886), Hooker f. (1888), Koorders & Valeton (1904), O. von Seemen (1906), Brandis (1906), Hosseus (1911), Merrill (1908, 1921, 1923), Burkill (1935), Corner (1939, 1940), and Backer & Bakhuizen van den Brink Jr. (1965) were of the opinion that the genera *Quercus* (incl. *Cyclobalanopsis*, *Macrobalanus*, and *Erythrobalanus*) and *Lithocarpus* (incl. *Pasania*, *Cyclobalanus*, and *Synaedrys*) should be regarded as a single genus, namely *Quercus*, as these genera possess a similar type of cupule.

The opposite view was introduced by Oersted in 1867, in which *Quercus* was treated as a distinct genus, differing from *Lithocarpus* by its inflorescence and flower characters. This view was accepted by Prantl (1887, 1894), Schneider (1906), Dalla Torre & Harms (1900–1907), Schottky (1912), Gamble (1915), Koidzumi (1916), Rehder & Wilson (1916), Rehder (1919, 1929), Ridley (1924), Markgraf (1924), Henderson (1930), Lemée (1932, 1934, 1939), Schwarz (1936 a, b), Camus (1938, 1954), Barnett (1943, 1944), Hjelmqvist (1948), Brett (1964), Forman (1964), Melchior (1964), and many others.

Before deciding which of these two opposite views should be adopted here, I have carried out a comparative study on the morphology of the inflorescence, flower, cupule, and pollen grains, and also on the anatomical structure of the cupule and the fruit wall of both genera. The main conclusions should be drawn here are as follows:

(1) I fully agree with Oersted and others in separating *Lithocarpus* from *Quercus*. These two genera may be distinguished from one another by the following characters:

Quercus	*Lithocarpus*
a. Inflorescence unisexual.	... Inflorescence usually androgynous or mixed.
b. Male inflorescence flexuous, pendent.	... Male inflorescence rigid, thick or slender, erect.
c. Male flower normally with 6 stamens and without a pistillode.	... Male flower normally with 12 stamens, and always with a pistillode.
d. Anthers basifixed, c. 0.5–1 mm long.	... Anthers dorsifixed, c. 0.20–0.25 mm long.
e. Female flower mostly without staminodes.	... Female flower with 12 staminodes.
f. Styles flattened, bearing broad stigmatic surface, or cylindrical and grooved with capitate stigmas.	... Styles terete, bearing minute, terminal, punctiform stigmas.

Quercus	*Lithocarpus*
g. Pollen grains prolate-spheroidal, c. 30 × 20 μ, mostly 3-colpate, rarely 3-colporate; exine more or less scabrate.	... Pollen grains prolate-perprolate, c. 18 × 10 μ, always 3-colporate; exine relatively smooth (seen under light-microscope).
h. Cupule normally solitary along the rachis.	... Cupule solitary or aggregated in dichasial clusters along the rachis.

(2) In its general form and also in its anatomical structure, the cupule of *Quercus* is exactly the same as that of *Lithocarpus*. The similarity even extends to the type of external emergences (scales or lamellae) covering the cupule. The cupule of these two genera represents a distinct type and differs from the other type recognized in the *Fagaceae*, viz. *Fagus-Castanea*-type, by being open, cup- or saucer-shaped or completely covering the solitary fruit, indehiscent, not spiny but covered with imbricate scales or concentric lamellae. I do not think, however, that the characters of the cupule alone are sufficient to merge *Lithocarpus* with *Quercus*.

(3) Three different types of anatomical structure of the fruit wall in the *Fagaceae* are distinguished, viz. Quercoid-type (*Quercus, Castanea, Castanopsis, Lithocarpus*), Fagoid-type (*Fagus, Trigonobalanus*), and Nothofagoid-type (*Nothofagus*). The descriptions of these anatomical structures are given on p. 369 and figured in Plates 3–5.

(4) With respect to the generic splits in *Quercus*, it may be pointed out here that Oersted (1867) was the first who suggested splitting the genus into two smaller genera, viz. *Quercus* and *Cyclobalanopsis*. Amongst the later authors who accepted this subdivision are: Schottky (1912), Markgraf (1924), Kudo & Masamune (1930), Nakai (1939), Hjelmqvist (1948), Li (1953, 1963), and Brett (1964). In 1936 Schwarz even proposed subdividing the genus into four genera, namely *Quercus* s.s., *Macrobalanus, Erythrobalanus*, and *Cyclobalanopsis*. No subsequent author has accepted this suggestion.

The characters used by the above mentioned authors, to distinguish the two or four smaller genera, are that of the cupule, abortive ovules, male inflorescence and flower, and the styles. In the present study however it was found that except for the presence of a lamellate cupule in *Cyclobalanopsis*, all the differing characters are too inconsistent to be regarded as generically important. There are too many intermediate characters which obscure a clear distinction between those smaller genera. Therefore, I am of the opinion that it is not worthwhile to split the genus *Quercus* into two or four smaller genera. Amongst the previous authors who have accepted this idea are: Gamble (1915), Koidzumi (1916), Rehder & Wilson (1916), Ridley (1924), Trelease (1924), Handel-Mazzetti (1929), A. Camus (1938), Lemée (1939), Rehder (1940), Müller (1942 a, b), Barnett (1943, 1944), Hutchinson (1959), Forman (1964), Ohwi (1965), and many others.

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CHARACTERS

Habit: in Malesia species of *Quercus* are trees of medium to large size. Under favourable conditions an individual tree may reach c. 40 m in height and 1.20 m in diameter. In each species there is a general tendency for the plant to attain a smaller size at a higher elevation. This is probably due to the more favourable ecological conditions in the lowland forests. The ecological variation also extends to the size, texture and indumentum of the leaves. In *Q. elmeri, gemelliflora, lineata, lowii, subsericea,* and *valdinervosa,* for example, the leaves of the plant growing at lower altitude are larger, thinner and less pubescent than those of a tree inhabiting a higher altitude. The trunk is usually straight, very rarely stunted. In most species buttresses are absent, but in *Q. argentata, elmeri, gemelliflora, percoriacea, pseudo-verticillata,* and *treubiana,* it may reach c. 1–3 m in height. The crown is usually dense, spreading, and makes up about one third or one half of the total height of the tree.

Bark: in the nineteen species from Malesia, three different types of bark may be distinguished, viz. the smooth and lenticellate bark (*Q. argentata, kerangasensis, kinabaluensis, nivea, percoriacea,* and *valdinervosa*), the finely fissured bark (*Q. chrysotricha, lowii,* and *subsericea*), and the scaly bark which peels off profusely into rectangular pieces (*Q. oidocarpa, pseudo-verticillata,* and *treubiana*).The bark in *Q.gemelliflora* and *lineata* may be smooth and lenticellate or finely fissured. In all species the outer bark is usually thin and hard, and pale yellow to greyish-brown in colour; the inner bark is sometimes as thick as 2.5 cm, brittle, fibrous, ridged on its inner surface, and pale yellow to reddish-brown in colour. The tannin content may be up to 20 per cent of the dry weight.

Wood: from the available information it seems to be impossible to distinguish species of *Quercus* by the wood characters alone. According to Cutler (1964), the wood of some species of *Quercus* is almost indistinguishable from that of *Lithocarpus* and *Trigonobalanus.* The wood of these three genera differs from that of *Fagus, Nothofagus, Castanea* and *Castanopsis* by its dendritic distribution of the solitary vessels, uni- to multi-seriate rays, concentric bands of parenchyma, bordered pitting in the wall of vessels and ray-cells, and by its frequency of the libriform fibres. Cutler also mentioned however that the genera in the *Fagaceae* are not always clearly defined from one another by the wood characters alone. There are many overlapping characters between some species, not only of the same genus but also of different genera. In the Malesian species the wood is usually pale yellow to yellowish-brown in colour, moderately hard and heavy, but not durable, splitting very easily, and difficult to work with. The growth rings are indistinct, and the sapwood is not sharply defined from the heartwood.

Twigs: in the Malesian species the new shoots are as a rule conferted. Young twigs are densely covered with yellowish-brown, either simple or stellate-adpressed hairs. Older twigs are glabrous and densely or sparsely lenticellate. Though the twigs are terete, the pith is always star-shaped with 4–5 lobes in cross-section.

Vegetative buds: in most of the Malesian species the vegetative buds are not characteristic for a particular species, but usually small, c. 0.2–1 by 0.2–0.5 cm, ovoid-globose or ovoid-conical, with the scales ovate-acute and densely simple or stellate tomentellous. The arrangement of the scales is as a rule imbricate, but in *Q. valdinervosa* it is sometimes in four symmetrical rows. In *Q. subsericea* and *treubiana,* the vegetative buds are elongated, ovoid-ellipsoid, and the scales are linear-acute.

Stipules: in Malesia the stipules are extrapetiolar, caducous, linear-acute, c. 0.2–1 by 0.1–0.2 cm, with simple or stellate tomentum or with woolly or stiff pubescence. These characters are however not specific.

Leaves: the simple leaves are spirally arranged, usually crowded near the tip of the twig, or occasionally in a pseudo-whorled arrangement (*Q. pseudo-verticillata*); venation pinnate, with the midrib and lateral nerves usually flattened or impressed on the upper surface and more or less prominent on the lower surface. The petiole, whether it is long and slender or short and thick, is always thickened at the base; glabrous or more commonly densely or sparsely tomentose or densely stiff or woolly pubescent. In *Q. chrysotricha, merrillii, pseudo-verticillata,* and *steenisii,* the petiole is c. (0.1)–0.3–0.5–(1.0) cm long, whilst in the other fifteen species it is slender, c. (1.0)–2–3–(4.5) cm long. The adaxial side of the petiole in *Q. lowii, nivea, oidocarpa, percoriacea,* and *subsericea,* is deeply sulcate at least in the upper part near the leaf-base. In the other species the adaxial side of the petiole is either flattened or rounded. The petiole of the mature leaf may be completely glabrous (*Q. argentata, oidocarpa, percoriacea,* and *valdinervosa*), densely stellate tomentose (*Q. gaharuensis, lowii,* and *nivea*), densely sericeous (*Q. chrysotricha, gemelliflora, merrillii, pseudo-verticillata, subsericea,* and *sumatrana*), or densely stiff or woolly pubescent (*Q. elmeri, kerangasensis, kinabaluensis, lineata, steenisii,* and *treubiana*). In a combination with the other characters of the leaf the petiole morphology is very useful for identification.

In Malesia the leaf-blade is either elliptic- to lanceolate-oblong (*Q. argentata, elmeri, gaharuensis, gemelliflora, lineata, nivea, oidocarpa, pseudo-verticillata, sumatrana, valdinervosa,* and occasionally also in *subsericea*), or ovate-elliptic to ovate-lanceolate (*Q. chrysotricha, kerangasensis, kinabaluensis, lowii, merrillii, percoriacea, steenisii,* and occasionally also in *subsericea*), or rarely linear-lanceolate (*Q. treubiana*). The leaf varies from 2 to 24 cm in length and from 1 to 9 cm in width. On account of this character, three different species groups may be distinguished in Malesia, namely *Q. argentata, nivea, oidocarpa, percoriacea, pseudo-verticillata, sumatrana,* and occasionally also *subsericea,* which have

relatively large leaves, c. 10–17 by 3–5 cm; *Q. elmeri, gemelliflora, kerangasensis, kinabaluensis, lineata, lowii, steenisii,* and usually *subsericea,* which have medium sized leaves, c. 5–10 by 2–4 cm; and *Q. chrysotricha, merrillii* and *treubiana,* which have small leaves, c. 2–4 by 1.5–3 cm. There is however some overlapping, so that the size of the leaf should be used in conjunction with the other characters. The base of the leaf may be rounded, subcordate or auriculate (*Q. lowii, percoriacea, pseudo-verticillata* and *steenisii*), or attenuate-rounded or attenuate-acute in the other species. The margin is either entire as in *Q. argentata, chrysotricha, kerangasensis, kinabaluensis, nivea,* and *pseudo-verticillata,* or entire in the basal half and distantly serrulate in the apical half. The apex of the leaf is rounded, bluntly acute or rounded emarginate in *Q. chrysotricha, merrillii, pseudo-verticillata,* and *steenisii,* or more commonly shortly acute, acuminate to caudate. The texture of the leaf in *Q. kinabaluensis, nivea, percoriacea, pseudoverticillata, steenisii,* and *valdinervosa* is thickly coriaceous, whilst in *Q. argentata, chrysotricha, elmeri, gaharuensis, gemelliflora, kerangasensis, lineata, merrillii, oidocarpa,* and *subsericea* is thinly coriaceous. In *Q. sumatrana* and *treubiana,* the texture is thinly chartaceous.

Except for *Q. chrysotricha, kinabaluensis, lowii,* and *subsericea,* the midrib and lateral nerves are strongly prominent beneath. On the upper surface, these nerves are either slightly raised (*Q. elmeri, gaharuensis, gemelliflora, kinabaluensis, lineata, steenisii* and *treubiana*), or flattened to impressed in the other species. The number of lateral nerves varies considerably in the species, but fairly consistent numbers may be found in three species groups, viz. *Q. argentata, lineata, oidocarpa, pseudo-verticillata,* and *valdinervosa* which have c. 10–20 pairs; *Q. chrysotricha, kinabaluensis, lowii,* and *merrillii* which have c. 4–6 pairs, and the rest of the species which have c. 8–15 pairs. The angles between the lateral nerves and the midrib vary from 30° to 75°, with the majority of the species falling between 45° and 60°. In *Q. oidocarpa* and *pseudo-verticillata* the angle is about 30°–45°, whilst in *Q. argentata, chrysotricha, elmeri, gemelliflora, kerangasensis, nivea,* and *valdinervosa* is c. 60°–70°. The reticulation between the lateral nerves is generally parallel, very rarely more or less anastomosing (*Q. lowii*), and it is either distinct beneath (*Q. gaharuensis, lineata, oidocarpa, percoriacea, steenisii,* and *valdinervosa*) or more commonly obscure. In *Q. lineata, oidocarpa* and *steenisii* the reticulation is parallel and dense, whilst in the other species it is lax.

The type and density of the pubescence on the lower surface of the leaf is in some species rather consistent. This character however should be used with a great caution. In *Q. argentata, chrysotricha, gemelliflora, kerangasensis,* and *valdinervosa,* the mature

leaves are completely glabrous on both surfaces, whilst in *Q. gaharuensis, lowii, nivea, oidocarpa, percoriacea,* and *subsericea,* the lower surface of the adult leaf is densely or sparsely adpressed tomentose. In *Q. elmeri, kinabaluensis, lineata, merrillii, pseudoverticillata, steenisii, sumatrana,* and *treubiana,* the lower leaf surface is densely or sparsely stiff or woolly pubescent. On account of this character *Q. lineata* may be distinguished from the other species by its dense layer of straight, adpressed, simple hairs on the lower surface of the leaf, and *Q. steenisii* differs from the other species by its thick layer of yellowish-brown, woolly hairs which are caducous.

Inflorescene (Fig. 1, f. 1–3): Similar to that of the other anemophilous genera in *Fagaceae* (*Fagus, Nothofagus*), the inflorescence in the genus *Quercus* is either male or female. In *Quercus,* however, the inflorescence is catkin-like (condensed raceme of cymes), whilst in *Fagus* and *Nothofagus* it is simply a 1-many-flowered, somewhat modified dichasium. In the Malesian species the male inflorescence is as a rule compound, i.e. the flowers are in 3–4-flowered dichasial clusters, and very rarely simple, i.e. when the flowers are solitary along the catkin-axis; it is either solitary in the axil of a lower leaf (*Q. gaharuensis, gemelliflora, kinabaluensis, lineata, lowii, steenisii, subsericea, treubiana,* and *valdinervosa*) or in a paniculate clusters on the lateral or subterminal new shoot (*Q. argentata, kerangasensis, nivea,* and *oidocarpa*). The rachis may be very thin and slender (*Q. lowii*), or more commonly rather thick; in both cases it is either stellate tomentellous or sericeous. The female inflorescence is always simple, solitary in the axil of a higher leaf, unbranched and densely minutely tomentose.

Flowers (Fig. 1, f. 4–7): in each dichasial cluster, the flowers are always protected by ovate-acute, caducous bracts. *Male flower:* the perianth is densely minutely simple tomentose, 4–6-lobed, with the lobes connate at base; stamens 4–6, rarely up to 9 (*Q. valdinervosa*); filaments slender, filiform, glabrous or minutely puberulous at base; anthers c. 0.5–1 mm long, globular reniform, basifixed, longitudinally dehiscent, 2–locular, 4–lobed; ovary usually absent or abortive and represented by a cluster of stiff-simple hairs (*Q. gaharuensis, lineata, lowii, steenisii* and *treubiana*). *Female flowers:* the ovary is obtusely triangular, 3–locular, each locule contains 2 ovules; perianth (4)–6–(9)–lobed; staminodes absent in most species but 5–7 in *Q. gemelliflora, nivea, steenisii,* and *valdinervosa;* styles 3–(6), recurved and free or rarely connate (*Q. nivea*); stigmas always broadly capitate.

Pollen grains: from the study of no less than 100 species of *Fagaceae,* belonging to seven different genera, it appears that three different types of pollen grains exist,* namely *Quercus-type* (*Fagus, Quercus, Trigonobalanus*), *Castanea-type* (*Castanea, Castanopsis, Lithocarpus*) and *Nothofagus-type.*

* The characters used here are the size, general appearance of the pollen, the structure of the exine, and the number of apertures and pores.

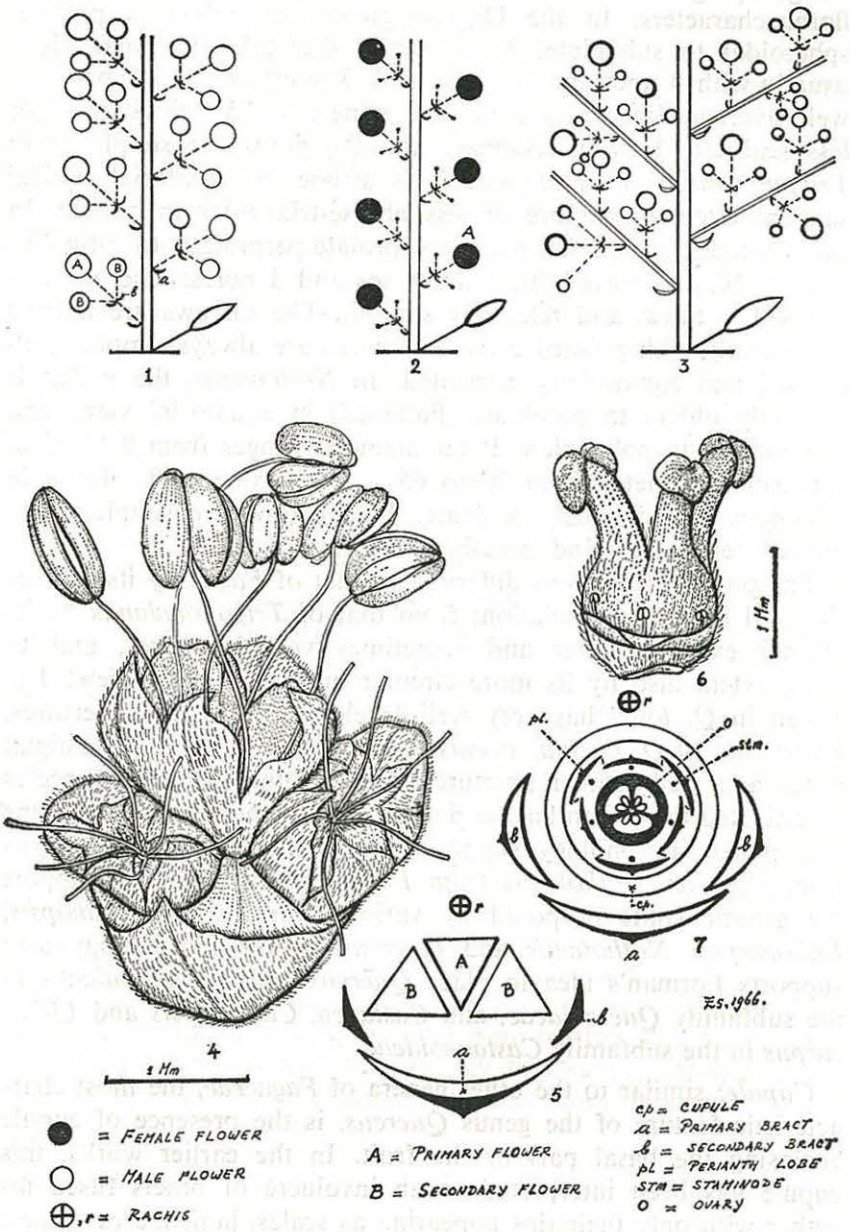

Fig. 1:

1 = diagram of a male inflorescence.
2 = diagram of a female inflorescence.
3 = diagram of a paniculate cluster of male inflorescences.
4 = 3-flowered male dichasium.
5 = diagram of figure 4.
6 = a pistillate flower with the perianth removed.
7 = diagram of a female flower.

Except for the pollen type in the genus *Fagus* therefore this generic grouping concurs with that based on the inflorescence and floral characters. In the Quercus-group the pollen is prolate-spheroidal to suboblate, 3– or rarely 4–angular in polar view; usually with 3 apertures only, or with 3 apertures and 3 pores as well; average size c. 30 × 20 μ. The exine c. 1–2.5 μ thick, more or less scabrate. Furrows elongate and the pores are simple or in *Trigonobalanus doichangensis* it is striate in equatorial optical section; circular or more or less obtuse-triangular in outline. In the Castanea-group the pollen is prolate-perprolate to ellipsoid, c. 18 × 10 μ; always with 3 apertures and 3 pores. The exine is c. 0.4–1 μ thick, and relatively smooth. The furrows are narrow and usually with pointed ends. The pores are always simple, well-defined and equatorially elongated. In *Nothofagus,* the pollen is distinctly oblate to peroblate (flattened) in equatorial view, and 4–9-angular in polar view. Polar diameter ranges from 9 to 16 μ, equatorial diameter from 20 to 65 μ. The exine c. 0.7–1.6 μ in thickness, and distinctly echinate. The furrows are simple, meridionally elongated, and usually with rounded ends.

The pollen of *Quercus* differs from that of *Fagus* by its smaller size and its finer reticulation; from that of *Trigonobalanus* by its thinner exine, simpler and sometimes vestigial pores, and to some extent also by its more circular outline in polar view. The pollen in *Q. lowii* has very well-developed pores and apertures, whilst that of *Q. lineata, steenisii,* and *valdinervosa* have vestigial pores and well-defined apertures. In the other Malesian species investigated the pollen has no pore. From this brief survey it seems that pollen morphology supports the separation of *Lithocarpus* from *Quercus, Nothofagus* from *Fagus,* but it does not support the generic splits proposed by various workers in *Castanopsis, Lithocarpus, Nothofagus* and *Quercus.* Pollen morphology also supports Forman's idea to place *Quercus* and *Trigonobalanus* in the subfamily *Quercoideae,* and *Castanea, Castanopsis* and *Lithocarpus* in the subfamily *Castaneoideae.*

Cupule: similar to the other genera of *Fagaceae,* the most characteristic feature of the genus *Quercus,* is the presence of cupule enclosing the basal part of the fruit. In the earlier works, this cupule has been interpreted as an involucre of bracts fused together with only their tips appearing as scales, lamellae or spines; or as an axial structure formed by an intercalary outgrowth of the meristematic tissue below the flower bearing modified leaves (scales or spines). In 1878 Eichler suggested a rather different interpretation, in which the cupule was regarded as a structure built up by the modification of the four bracteoles in the dichasium, and the scales or spines as simply external emergences. In the most recent works (Berridge, 1914, Langdon 1939, 1947, and Brett 1964) the cupule is considered as an axial structure formed by the modified axes of the next higher order flowers in the dichasium, and the scales, lamellae or spines as external appendages.

Development of the cupule: in the earlier stages of the pistillate flower development, the cupule primodium in *Quercus,* appears as a collar subtending the flower, and it is situated between the flower and the bracts. The growth of the cupule is at first faster than that of the flower, so that the partly developed fruit is completely enclosed by the cupule, except for the perianthodium and the styles. The faster growth of the cupule in the earlier stages gives rise to the ring-like marks on the perianthodium. Soon after fertilization, the elongation of the cupule slows down or stops before the fruit is fully developed. At maturity therefore the cupule usually covers not more than a quarter to two thirds of the fruit. As a rule the cupule in *Quercus* encloses one fruit only, but in *Q. lowii* it has been observed that in some specimens the cupule contains more than one fruit, usually two. There is, however, a clear evidence that this abnormality is caused by injury during the development of the fruit and cupule. A similar condition has been reported by Hjelmqvist in 1948 in *Q. acuta* from Japan, which induced him to conclude that the cupule in *Quercus* subgen. *Cyclobalanopsis* must have a different origin from that of subgenus *Quercus.* Another abnormality which should be mentioned here is that, while in most species the cupules are solitary along the rachis, in a few specimens of *Q. gemelliflora* from Java two or three cupules are grouped together in a dichasial cluster as normally occur in the genus *Lithocarpus.* It is not certain, however, whether this abnormality is a product of a teratological growth or that it is a genuine morphological feature.

Anatomy of the cupule: this investigation was performed mainly to find out whether the distribution of the vascular bundles in the cupule gives any clue towards a better understanding on the nature and probable evolutionary lines of the cupule in *Fagaceae.* The cupules were cut by razorblades in three different planes, viz. longitudinal sections following the axis of the catkin, longitudinal sections across the axis, and cross-sections through the cupules. The 0.5 to 2 mm thick sections then were treated with lactic acid and heated for about five minutes. By this simple method clear sections showing the distribution of the vascular supply were obtained.

In a series of longitudinal sections following the axis of the catkin (Fig. 2, f. 1), the vascular tissue at first appears as a central cylinder (M) originating from the vascular tissue supplying the rachis. Outside this main vascular cylinder, several smaller traces may be seen. These smaller traces supply the bracts and bracteoles, whilst the main vascular cylinder is leading to the flower and cupule. At the level above the insertion of the bract (*a*), i.e. from the lower part of the main vascular column, arise several ascendant lateral traces which are orientated and branched off towards the cupule. At the level of the insertion of the flower on the cupule, the main vascular cylinder is further subdivided into several separate bundles which supply the ovary, perianth, staminodes (if present) and the styles. In a series of longitudinal sections across the rachis (Fig. 2, f. 2) the organization of the vascular tissue is

exactly the same. In a cross-section through the basal part of the cupule (or peduncle), the vascular cylinder appears as a triangular ring of loose vascular traces (Fig. 2, f. 3). At the level of the insertion of the bracteoles (*b*) this vascular column becomes laterally elongated (Fig. 2, f. 4). Above this level, i.e. at the basal part of the cupule proper, the main vascular cylinder is subdivided into a central tract (M1) which directly supplies the flower, and numerous scattered traces which give rise to the vascularization of the cupule (Fig. 2, f. 5). At the region of the insertion of the fruits (Fig. 2, f. 6) the central vascular tract undergoes a further reorganization and is divided into at least 13 smaller groups of vascular traces. One of these vascular traces supplies the placental tissue, and the others are distributed in the periphery of the fruit wall and leading to the perianth, staminodes and styles. Further up from this level, where the fruit wall is completely free from the cupule, the separation of the central vascular tract is more prominent. In the fruit wall the vascular traces situated at the corners of the locules are clustered in threes, whilst those placed between the corners of the locules are solitary (Fig. 2, f. 7). At this level it may be noticed that the traces distributed in the cupule send off more smaller branches from which the vascular supply of the lamellae covering the cupule originates. It may be mentioned here that the pattern of vascular distribution in the cupule of *Quercus* just described is exactly the same as that of a solitary cupule in the genus *Lithocarpus*.

The nature of the cupule: The cup- or saucer-shaped, solitary cupule in *Quercus* is here regarded as an axial structure formed by the intercalary outgrowth of the meristematic tissue below the flower, bearing scales or lamellae as external emergences.

The evolutionary interpretation of the cupule: in 1878 Eichler assumed that the cupule in *Quercus* must have been derived from that of *Fagus-Castanea*-type, through a complete loss of the two lateral flowers in the originally 3-flowered dichasium, followed by a complete fusion of the four modified bracteoles. Prantl (1887), Celakovsky (1887, 1890, 1893), Palibin (1909), Lendner (1916), Troll (1926), Hjelmqvist (1948), on the other hand, regarded the cupule in *Quercus* as a type derived from a dichasial cluster of 3 cupules in the genus *Lithocarpus*, by means of complete reduction of the two lateral flowers and their cupules. Recently Brett (1964) suggested a different interpretation in which the cupule in *Quercus* subgen. *Cyclobalanopsis* (considered by him as a distinct genus) is regarded as derived from a cupule type occurring in *Castanopsis*, through a similar process of reduction to that of *Castanopsis fissa*-group, and that of the subgenus *Quercus* from a 3-flowered dichasial cluster of cupules in *Lithocarpus* through a similar way of reduction as has been proposed by Prantl and others. In his recent paper, Forman (1966, in press) considers the cupule in *Quercus* (incl. *Cyclobalanopsis*) as derived from a 3-lobed, 1-flowered cupule like that in *Trigonobalanus doichangensis*, by a complete fusion of the cupule lobes.

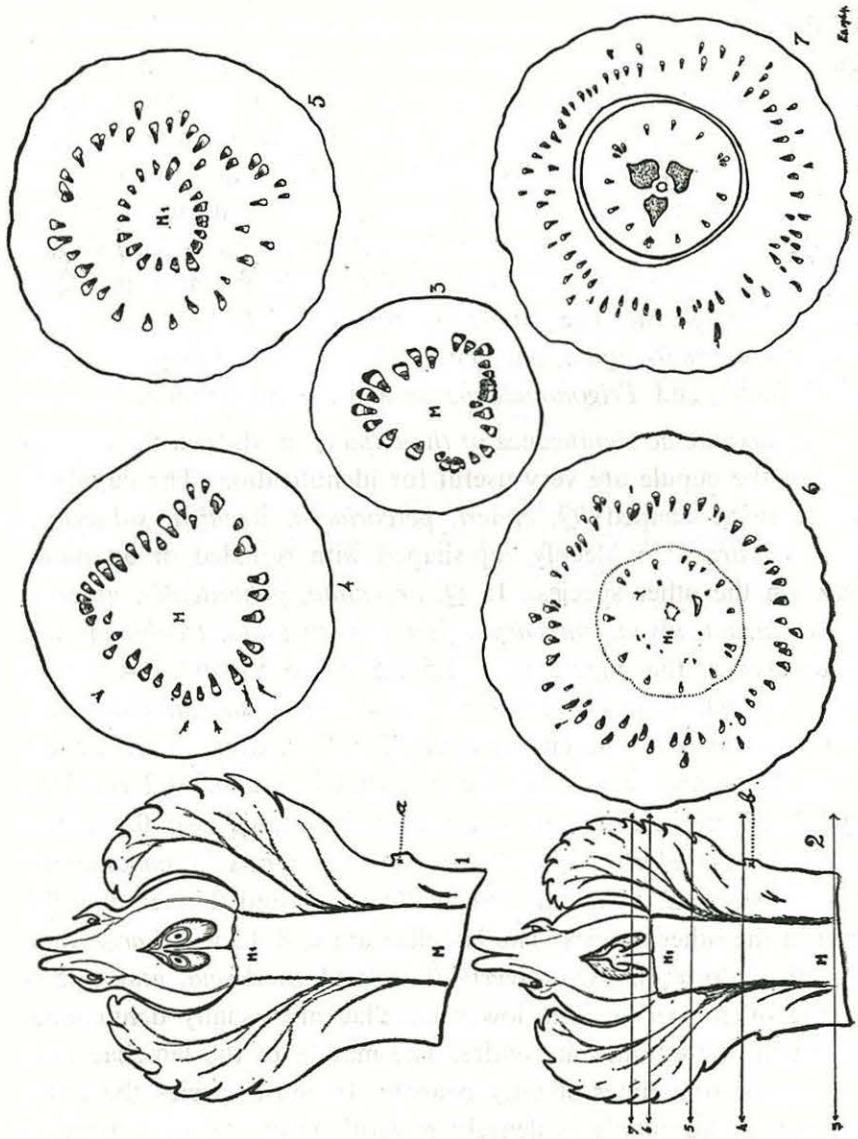

Fig. 2:

1 = a longitudinal section through the rachis of a young cupule.
2 = a longitudinal section across the rachis of a young cupule.
3–7 = cross-sections of a young cupule through the planes shown in figure 2.

I have pointed out elsewhere that from the earlier stages of development, there is no indication that the cupule in *Quercus* consists of separate lobes or that the cupule normally encloses more than one fruit. I also mentioned that the anatomical feature of the cupule in *Quercus* is exactly the same as that of a solitary cupule in *Lithocarpus*. Moreover, in *Lithocarpus* there is a gradual reduction from a dichasial cluster of cupules to a solitary condition by a complete abortion of the higher order flowers and their cupules. Therefore I conclude that the cupule in *Quercus* is closely allied to that of *Lithocarpus*, and it must have been derived from one of the types occurring in the latter. The cupule in these two genera represents a type distinct from that of the other genera in *Fagaceae*. The cupule in *Quercus* and *Lithocarpus* I consider as a flower-cupule, but that of *Castanea, Castanopsis, Fagus, Nothofagus*, and *Trigonobalanus* as a dichasium-cupule.*

The taxonomic significance of the cupule: in Malesia the characters of the cupule are very useful for identification. The cupule is either saucer-shaped (*Q. elmeri, percoriacea, steenisii, subsericea* and *sumatrana*) or deeply cup-shaped with rounded or attenuate base (in the other species). In *Q. argentata, gaharuensis, gemelliflora, lineata, nivea, oidocarpa, pseudo-verticillata, treubiana*, and *valdinervosa*, the cupule is c. 1.5–3.5 cm deep and 2–4 cm in diameter, whilst in *Q. chrysotricha, kerangasensis, kinabaluensis, lowii* and *merrillii* the cupule is c. 0.7–1.2 cm deep and 1–1.5 cm in diameter. In the other species the cupule is c. 0.5–1.2 cm deep and 2–2.5 cm in diameter. The rim of the cupule is c. 0.5–4 mm thick in *Q. elmeri, gemelliflora, kerangasensis, kinabaluensis, lineata, steenisii, treubiana* and *valdinervosa*, and thinner than 0.5 mm in the other species. The lamellae are c. 8–12 in *Q. argentata, lineata, oidocarpa, pseudo-verticillata*, and *treubiana*, and c. 5–8 in the other species. The lower lamellae are usually denticulate, whilst the upper ones are entire. The margin of the lamellae may be free or sometimes slightly connate. In most species the outer surface of the cupule is densely puberulous or stellate-tomentose and early glabrescent; the inner surface is densely covered with thick layer of silky to dark-brown, stiff simple hairs.

Fruit: according to Trelease (1924), Camus (1938), and Schwarz (1936 a, b) the maturity of the fruit in the genus *Quercus* may be annual (subgen. *Cyclobalanopsis* and subgen. *Quercus* sect. *Macrobalanus, Mesobalanus* and *Lepidobalanus*) or biennial (subgen. *Quercus* sect. *Erythrobalanus, Protobalanus*, and *Cerris*). In Malesia the data on this particular character are too scanty for a conclusion.

*(See Forman 1966, in press).

In the Malesian species the fruit is ovoid-globose, ovoid-conical or ovoid-cylindrical. The young fruit is usually densely sericeous, and gradually becomes glabrous towards maturity. In *Q. argentata, chrysotricha, gaharuensis, gemelliflora, lineata, merrillii, sumatrana* and *valdinervosa* the apex of the fruit is distinctly attenuate-acute, whilst in the other species it is either attenuate-rounded or depressed. The base of the fruit in most species is convex, in *Q. sumatrana* it is concave, and in *Q. elmeri, oidocarpa* and *pseudo-verticillata* it is either convex or flat. The fruit-wall is c. 1–2 mm thick, and usually woolly tomentose inside. The anatomical structure of the fruit-wall in *Quercus* is the same as that of *Castanea, Castanopsis* and *Lithocarpus*, i.e. composed of at least five different layers of cells. These layers are, from outside inwards: 1). the outer epidermal layer consisting of a single row of rectangular cells; 2). the pallisade layer which consists of several rows of radially elongated, thick-walled cells; 3). the outer parenchymatous layer which is usually very much thicker than the other layers and composed of more or less isodiametric, thin-walled cells, and containing the vascular tissue of the fruit-wall and the other floral parts; 4). the inner parenchymatous layer which has smaller cells than that of the former; 5). the inner epidermal layer consisting of a row of flattened, rectangular, thin-walled cells (Fig. 3 & 4). The anatomical structure of the fruit-wall just described differs from that of the other genera in *Fagaceae* by the position and type of the supporting layer, i.e. the layer which is composed of thick-walled cells. In *Nothofagus* (Fig. 5, f. 1–2) this supporting layer is situated near the centre of the fruit-wall, and consists of several rows of tranversely elongated thick-walled cells. In *Fagus* and *Trigonobalanus*, the supporting tissue is situated directly beneath the outer epidermal layer, and is composed of several rows of more or less isodiametric, polygonal, thick-walled cells (Fig 5, f. 3–4). In the examined specimens, the cotyledons are flat-convex, and fill the entire space of the surviving locule. The abortive ovules are apical, and the germination is hypogeal as in *Castanea, Castanopsis* and *Lithocarpus*.

Chromosomes number: chromosome counts in various species of *Quercus* subgen. *Quercus* have been made by several cytologists such as Ghimpu (1929), Sax (1930), Sugira (1931), Yamazaki (1936), and Duffield (1940). The diploid number reported is 24, similar to that of *Castanea* (Jaynes, 1962), and *Fagus* (Jaretzky, 1930). In the subgen. *Cyclobalanopsis* on the contrary no chromosome count has been made. The only information so far available is that given by Mr. Kwiton Jong (formerly Dept. of Botany, University of Malaya, Kuala Lumpur). He made some preliminary counts in several species of *Castanopsis, Lithocarpus, Quercus* (subgen. *Cyclobalanopsis*) and *Trigonobalanus*, and found that the diploid number in the first three genera is also 24, whilst that of *Trigonobalanus verticillata* is not yet fully understood. For comparison, it may be recalled here that in 1965, Armstrong & Wylie reported a diploid number of 26 in the four species of *Nothofagus* (*fusca, truncata, solandri,* and *menziesii*) from New Zealand.

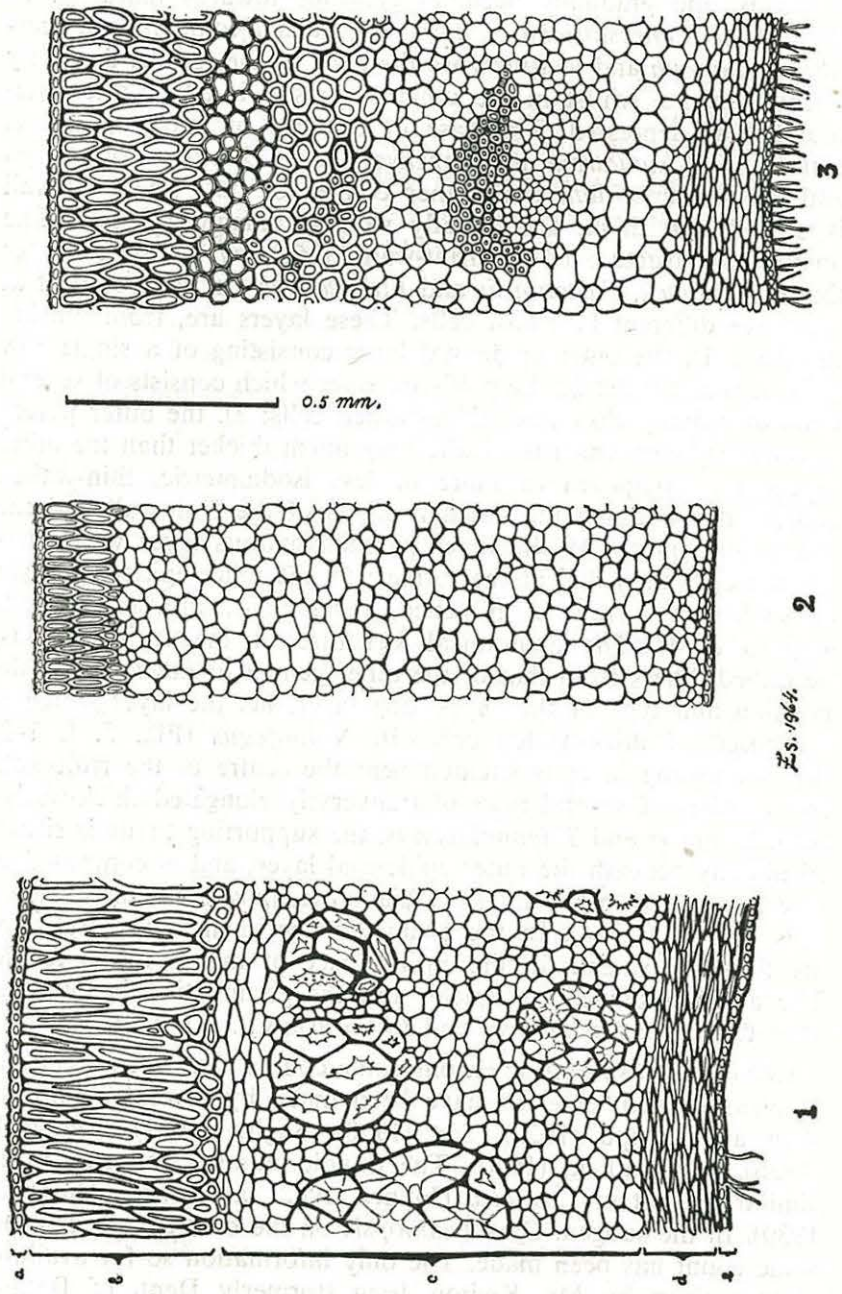

Fig. 3: cross-sections of the fruit-wall.

1 = *Q. oidocarpa;* 2 = *Q. suber;* 3 = *Castanopsis chrysophylla*; a = outer epidermal layer; b = pallisade layer; c = outer parenchymatous layer; d = inner parenchymatous layer; e = inner epidermal layer.

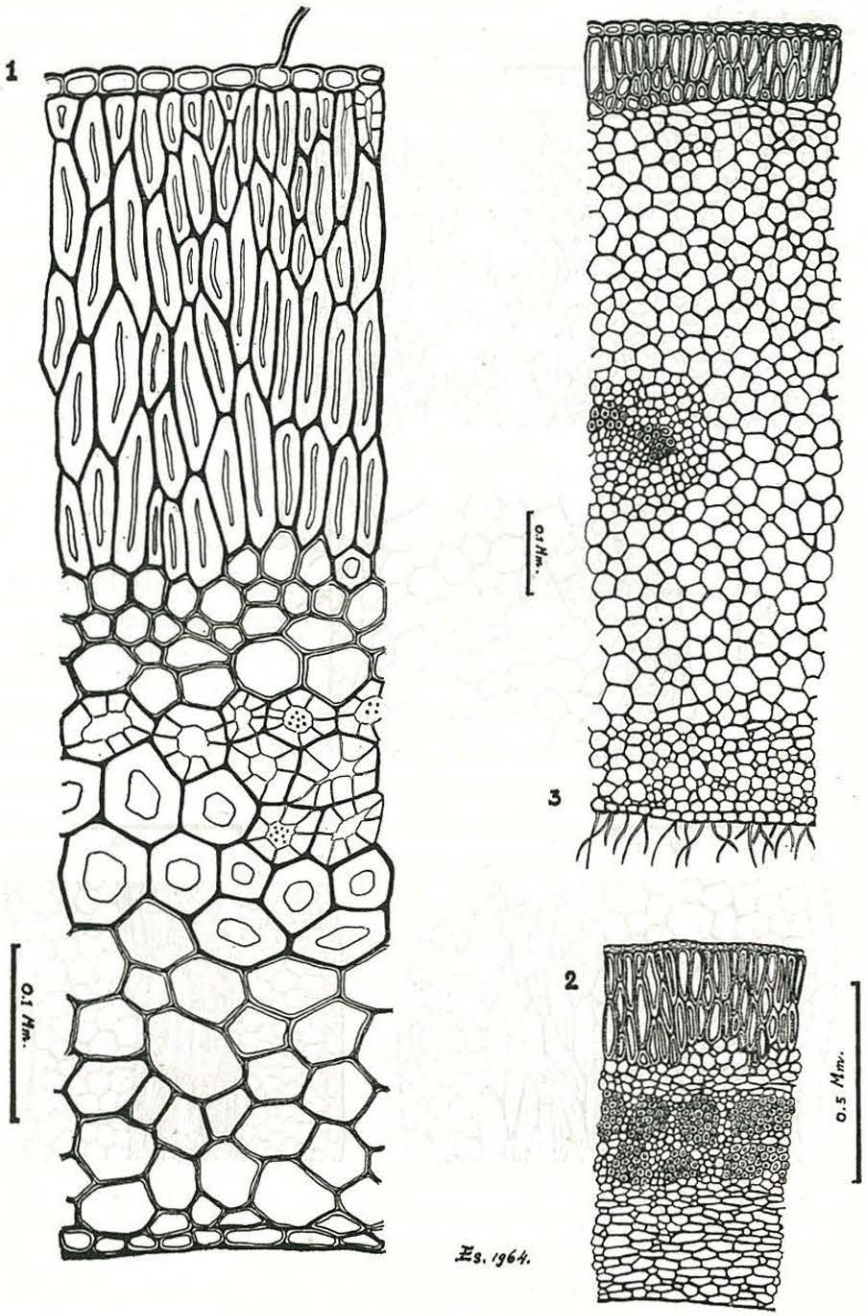

Fig. 4: cross-sections of the fruit-wall.
1 = *L. philippinensis;* 2 = *Castanopsis javanica;* 3 = *Castanea sativa.*

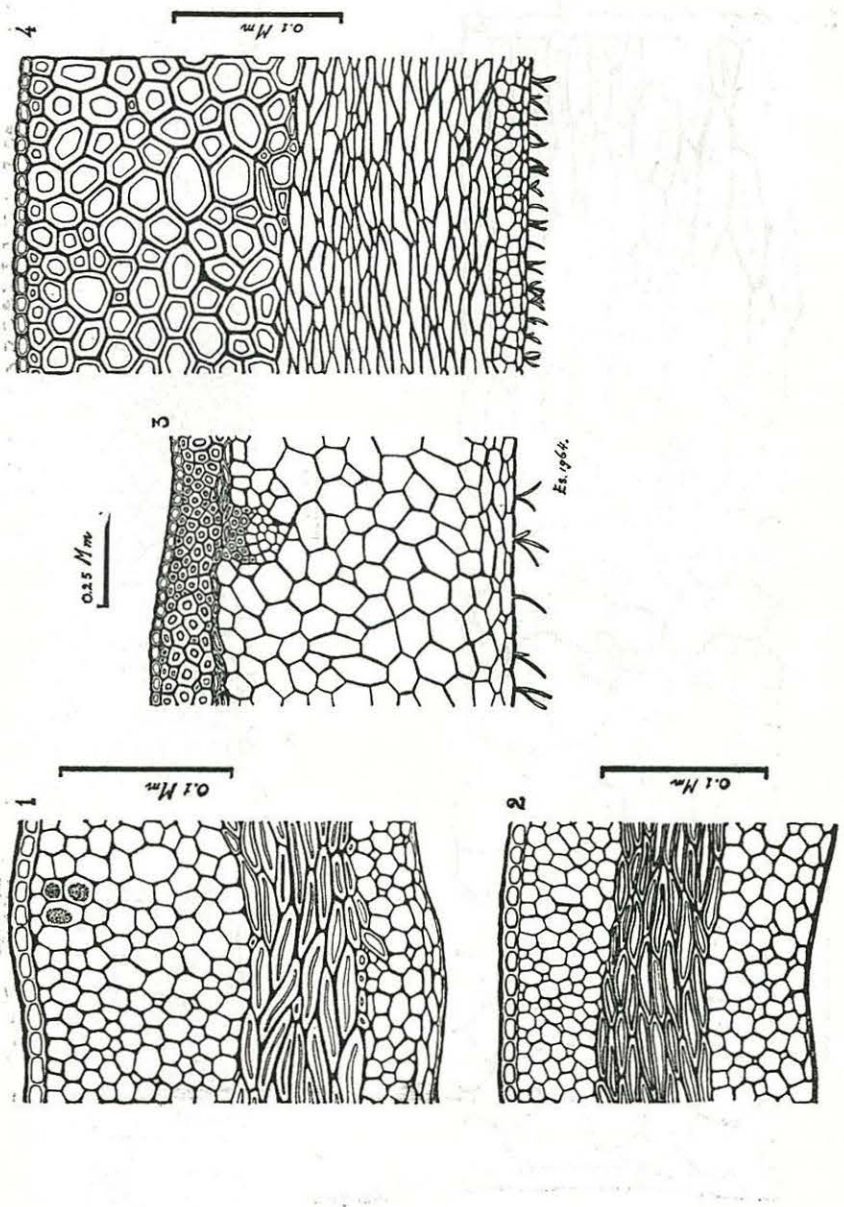

Fig. 5: cross-sections of the fruit-wall.

1 = *Nothofagus resinosa;* 2 = *Nothofagus antarctica;* 3 = *Trigonobalanus verticillata;* 4 = *Fagus sylvatica.*

TAXONOMY

The systematic position of the genus Quercus: on account of the inflorescence and stigma characters, Oersted (1867) subdivided the family *Fagaceae* into two subfamilies, viz. *Quercinae* and *Castaninae*. He included *Quercus, Cyclobalanopsis* and *Fagus* (incl. *Nothofagus*) in *Quercinae*, and *Castanea, Castanopsis, Pasania* and *Cyclobalanus* (incl. *Lithocarpus*) in the subfam. *Castaninae*. He distinguished the subfam. *Castaninae* from *Quercinae* by its rigid and erect male inflorescence and terminal punctiform stigmas.

In 1871, Oersted revised his classification and excluded *Fagus* and *Nothofagus* (in this paper *Nothofagus* was regarded as a separate genus) from the subfam. *Quercinae*, and placed them in a separate subfamily, *Fagineae*. In this new classification the subfam. *Quercinae* was maintained to include *Quercus* and *Cyclobalanopsis*. In the subfam. *Castaninae*, the genus *Castanopsis* was reduced to a subgeneric rank under *Castanea*, and *Pasania* was kept separate from *Cyclobalanus* (incl. *Lithocarpus*). Oersted distinguished the subfam. *Castaninae* from *Fagineae* and *Quercinae* by its terminal punctiform stigmas, and *Fagineae* from *Quercinae* by its plicate cotyledons and epigeal germination. Amongst later authors who basically accepted Oersted's subdivision of the family *Fagaceae* are Schwarz (1936 a, b), Melchior (1964), and Forman (1964). However, these later three workers added more characters which were not mentioned by Oersted or they used different combinations of characters to distinguish one subfamily from the others.

In 1894, Prantl introduced a rather different classification, in which he placed *Quercus* (incl. *Cyclobalanopsis*), *Castanea* (incl. *Castanopsis*) and *Pasania* (incl. *Cyclobalanus* and *Lithocarpus*) in the subfam. *Castaneae*, and included *Fagus* and *Nothofagus* in the subfam. *Fageae*. He distinguished these two subfamilies as follows:

Subfam. *Fageae:* flowers arranged in dichasial clusters, rarely solitary; fruit triangular; cotyledons plicate.

Subfam. *Castaneae:* flowers arranged in dichasial clusters or solitary along the catkin-axis; fruit rounded; cotyledons not plicate.

This classification was adopted by Dalla Torre & Harms (1907), Schottky (1912), and by Trelease (1924). A rather similar type of classification was proposed by Brett in 1964, though this author based his system mainly on the cupule characters.

In 1964, Forman suggested another type of classification which seems to represent a compromised scheme between Oersted's (1871) and Prantl's arrangements. Forman agreed with Oersted in subdividing the family *Fagaceae* into three different subfamilies,

but used the inflorescence and floral characters to distinguish subfam. *Fagoideae* from *Castaneoideae* and *Quercoideae* as was done by Prantl. Forman distinguished subfam. *Fagoideae* from the other subfamilies by the inflorescence which consists of a 1-many-flowered, axillary dichasial cluster, in contrast to that of subfam. *Castaneoideae* and *Quercoideae* which is catkin-like, and composed of dichasial clusters of flowers or solitary flowers. Subfamily *Castaneoideae* was distinguished from *Quercoideae* by the characters of the styles, stigmas, male inflorescence and flower, anthers, and the cupule. *Trigonobalanus* and *Quercus* were placed in the subfam. *Quercoideae.*

From the preceding discussion it is clear that the main difference between Oersted's (1871) and Prantl's classifications hingers on the question whether the genus *Quercus* (incl. *Cyclobalanopsis*) should be regarded as representing a distinct subfamily or should it be included in the same subfamily with *Castanea, Castanopsis,* and *Lithocarpus* (incl. *Pasania* and *Cyclobalanus*). It is also evident that though at the subfamily level Forman's classification is essentially similar to that of Oersted, at the generic level, except for the status of *Castanopsis,* it agrees better with Prantl's system.

Before deciding which of these three different classifications should be adopted here, it is necessary to discuss the generic affinity between *Quercus* and the other genera in *Fagaceae.* I have indicated elsewhere that *Quercus* possess many important consistent characters, viz. that of the inflorescence, flower, pollen grains, which distinguish this genus not only from *Lithocarpus* (s.l.) but also from *Castanea* and *Castanopsis.* The difference between *Quercus* and *Castanea-Castanopsis* are further strengthened by the characters of the cupule. In *Quercus* the cupule is always cup- or saucer-shaped, not lobed nor spiny; it encloses one fruit only, and is here regarded as flower cupule. In the genera *Castanea* and *Castanopsis* the cupule is a dichasium cupule, and in most species it is neither cup- nor saucer-shaped, but completely covering the fruits and eventually splits either into a definite number of lobes or irregularly; it encloses one to many fruits, and in the majority of the species it is either spiny or tubercled. In the earlier works, however, there has been some confusion with regard to the generic limit between *Quercus* and *Castanopsis.*

Species of *Quercus* are readily distinguished from those of *Fagus* and *Nothofagus* by their catkin-like inflorescence, cup- or saucer-shaped, not lobed cupule enclosing one fruit only, rounded ovary, flat-convex cotyledons, hypogeal germination, anatomical structure of the fruit-wall and the wood, and pollen characters. Taking all these characters into consideration, the genus *Quercus* should be placed in a different subfamily from *Fagus* and *Nothofagus.*

The affinity between *Quercus* and *Trigonobalanus* has been discussed in detail by Forman (1964). Amongst the characters mentioned by him which indicate the close relationship between these two genera are the presence of the catkin-like inflorescence, capitate stigmas, male flower with 6 stamens, anthers which are c. 0.5–1 mm long and more or less basifixed, and the absence of pistillode in the male flower. It is interesting to note here that the conclusion reached by Forman which was based on the characters just mentioned was subsequently supported by Cutler, who in 1964 investigated the wood anatomy of these two genera. Cutler, however, also stressed that the genera of *Fagaceae* are not always clearly defined from one another by the wood characters alone. In his classification, Forman regarded the lobed cupule and the triangular fruit in *Trigonobalanus,* and also the presence of androgynous and rigid and much branched male inflorescence in *T. verticillata* as ancient characters persisting in the subfam. *Quercoideae* rather than as evidence for a closed generic affinity between *Trigonobalanus* and the genera included in the subfam. *Fagoideae* or *Castaneoideae.* I have mentioned elsewhere that except for the detailed structure of the pores in the pollen of *T. doichangensis,* as for the pollen, *Trigonobalanus* agrees better with *Quercus* or *Fagus* than with the other genera of *Fagaceae.* As far as the characters of the flower are concerned therefore Forman's classification seems to be well-founded. As for the cupule and fruit characters, however, *Trigonobalanus* has nothing in common with *Quercus,* but it possess many characters in common with the subfam. *Fagoideae.* These characters are: the lobed cupule enclosing one to many fruits, trigonous and almost winged fruits, epigeal germination, and probably also the plicate cotyledons. Melchior (1964) included *Trigonobalanus* in subfam. *Fagoideae,* but his argument is not very convincing, as he indiscriminately mixed up the characters of the inflorescence, flower, cupule and fruit, which in combination are not always clearly defined in the subfamilies recognized by him. Great credit, however, should be given to Professor Melchior for suggesting the alternative systematic position of this enigmatic new genus.

Other characters which seem to contradict the disposition of *Trigonobalanus* in subfam. *Quercoideae* are the presence of androgynous and much-branched, erect, male inflorescences in *T. verticillata.* These characters which are usually associated with entomophily, persist in *Fagaceae* only in the *Castaneoideae.* Taking all the known characters into consideration, however, it is clear that placing *Trigonobalanus* in the subfam. *Castaneoideae* is out of question. It remains to be settled in the future, therefore, whether the genus *Trigonobalanus* should be placed in *Fagoideae* or *Quercoideae.*

Conclusion: on account of the inflorescence and floral characters, I agree with Forman (1964) to recognize in the family *Fagaceae* three subfamilies, viz. *Castaneoideae* (*Castanea, Castanopsis,* and *Lithocarpus* s.l.), *Fagoideae* (*Fagus* and *Nothofagus*), and *Quercoideae* (*Quercus* incl. *Cyclobalanopsis, Macrobalanus* and *Erythrobalanus*). A reservation should be made with regard to the position of *Trigonobalanus* until this genus is better understood.

NOTE ON THE IDENTITY OF SEVERAL MALESIAN SPECIES

Q. oidocarpa Korth., *Q. brevistyla* A. Camus, and *Q. gaharuensis* Soepadmo: the type of *Q. oidocarpa,* preserved in the Rijksherbarium, Leiden, was collected by Korthals in 1835 from the vicinity of Mt. Malintang in Central Sumatra. In 1888, Hooker f. cited several specimens from Malaya and Borneo under this species, which were accepted by most of the subsequent authors such as King (1889), Brandis (1906), Gamble (1915), Ridley (1924), Merrill (1921), and A. Camus (1938). In the present study, however, it was found that these specimens are quite different from Korthals' species, and they agree very well with *Q. gaharuensis* I described in April 1966. In 1933, A. Camus described a new species, viz. *Q. brevistyla,* based on specimens collected by Syed Ali (Kep. 22574) from Fraser's Hill, Malaya. She apparently did not see Korthals' specimens; I found that Syed Ali's specimens match very well those of Korthals. Therefore, I reduce *Q. brevistyla* to *Q. oidocarpa.*

Q. semiserrata Roxb.

In his account on the Indo-Malayan species of *Quercus* and *Castanopsis,* King (1889) erroneously reduced *Q. horsfieldii* Miquel (1856) from Bangka (Horsfield 11) and Sumatra (Diepenhorst 42) to *Q. semiserrata* Roxb. After comparing these two specimens with those of *Q. semiserrata,* I came to the conclusion that the Sumatran plants do not belong here, but should be included in *Q. gemelliflora* Bl. In 1904, Koorders & Valeton accepted King's reduction and credited several specimens from Java collected by Koorders to *Q. semiserrata.* I place Koorders' specimens in *Q. oidocarpa.*

Q. lowii King

King's original description of this species was based on the specimens collected by Low (*s.n.,* in Herbarium Calcutta) from Mt. Kinabalu in North Borneo. King (1889) indicated that this species may be distinguished by its coriaceous leaves which are narrowly ovate, bluntly acuminate, remotely serrate in the apical half, and with the base either rounded or slightly cordate. The lower surface of the leaf was described as minutely cinereous-tomentose, and the cupule as cup-shaped, c. 1.5 cm in diameter and 0.75 cm in height, minutely tomentose and covering c. ¼ part of the ovoid-cylindrical fruit. In King's illustrations (*l.c.,* Plate 21 B, f. 4–6) the leaf is figured as sharply and deeply serrate in the upper half. In the actual specimen, however, the leaf margin is not sharply and deeply serrate as in King's figures, but it is either shallowly, remotely serrate in the apical half or almost entire. King's exaggerated figures on the leaf margin have given rise to some doubt to most later botanists who tried to identify specimens of *Quercus* recently collected from Mt. Kinabalu. One of these even thought that *Q. lowii* must be a very rare species. From the specimens examined, however, I found that this species is not very rare as

has been assumed, but is very common in Mt. Kinabalu, especially at 1000–2000 m altitude. In the specimens studied, it appears that there are two forms, which differ from one another by their leaf pubescence. In one form the leaf is densely, minutely stellate-tomentose beneath, and almost completely glabrous in the other. The pubescent form is represented by several specimens (including the type), e.g. Clemens 10936, 32448, Meijer SAN. 24121, 28808, Chew & Corner RSNB. 4363, 4500, 4662, and Sow Kep. 71649. Except for Sow's specimen, all of these are from c. 1500–2500 m altitude. The majority of the examined specimens belong to the glabrous form, and most of them are from lower altitude. Clemens 30967, 32933, and 40231 are intermediates, with the leaf being neither glabrous nor densely, minutely stellate-tomentose, but sparsely stellate-tomentose. These three specimens were collected mainly between 1200 and 1500 m altitude. The cupules and fruits of the recently collected specimens (e.g. SAN. 28808 and RSNB. 4500) agree very well with King's description and illustration. Therefore, I consider the glabrous and pubescent forms as conspecific, representing King's *Q. lowii*. This species is closely allied to *Q. subsericea* A. Camus, which also occurs in Mt. Kinabalu, but *Q. lowii* differs from the latter by its thick-coriaceous leaves which have rounded to cordate base, sharply acuminate apex, more or less net-shaped reticulation, and by its cup-shaped, densely tomentose cupule.

Q. mespilifolia Wall. ex A.DC. var. **borneensis** Heine

Q. mespilifolia was first mentioned as a nomen nudum in Wallich's Catalogue (no. 2766, 1828). It extends from S.W. China (Yunnan) to the Northern parts of Burma, Laos and Vietnam (Tonkin). In 1935, A. Camus renamed this species *Q. mespilifolioides*, as she was of the opinion that Wallich's name was invalidly published. In 1864, however, A. DeCandolle validated Wallich's name, so that *Q. mespilifolioides* A. Camus is a superfluous name for Wallich's species. In 1953, Heine described *Q. mespilifolia* var. *borneensis*, based on Clemens 31238, 31317, and 31459, from Mt. Kinabalu. Heine distinguished the new variety by its densely ferrugineous-pubescent leaves which are serrate in the apical $\frac{1}{3}$–$\frac{1}{2}$ part. Recent collections from North Borneo and Sarawak added more information about this new variety, in which female inflorescences and fruits were gathered, unknown to Heine. After comparing the type specimens of *Q. mespilifolia* from the Upper Burma and some other specimens credited by King (1889) to this species with the Bornean materials, I have come to the conclusion that the Bornean plant represent a distinct species. It differs from *Q. mespilifolia* by the characters of the cupule, fruit, and leaf. The specific epithet *borneensis*, however, is preoccupied by *Q. borneensis* Merr. (1922), the basionym of *Lithocarpus borneensis* (Merr.) Rehder. I recognize this species as *Q. valdinervosa* to indicate the strong nervation of the leaf. Clemens 31317 is chosen as the lectotype, and Anderson S. 4547 as the paratype (fruits).

Q. gemelliflora Bl.

This species was first described and figured by Blume (1823) based on mixed specimens consisting of a leafy twig which belong to *Quercus* and fruits represent a species of *Lithocarpus* (cf. Blume's illustration in Verh. Bat. Genootsch. *9*, f. 6, 1823). In the type specimen at Leiden, I could not trace any fruit attached, and I discovered that the leaves are exactly the same as those of *Q. turbinata* Bl. (1825). Therefore, I reduce *Q. turbinata* to the synonymy of *Q. gemelliflora,* and choose the remaining sterile specimen (Blume s.n.) preserved at Leiden as the type.

In 1847, Endlicher erroneously renamed *Q. turbinata* Bl. as *Q. merkusii,* as he thought that the name *turbinata* had been used by Roxburgh (1832) for a different species from India, apparently not realizing that this was a later homonym. Therefore, *Q. merkusii* is a superfluous name for *Q. turbinata,* and accordingly it becomes another synonym of *Q. gemelliflora.* Roxburgh's *Q. turbinata* was eventually reduced by King (1889) to *Q. thomsonii* Miq. which in 1919 was transferred to the genus *Lithocarpus* by Rehder. In 1915, Gamble described under *Q. turbinata,* a new variety *crassilamellata,* based on Wray 1532 from Johore, Malaya. A Camus (1931) raised this variety to a specific rank. I reduce this variety to *Q. gemelliflora* Bl.

Q. hendersoniana A. Camus

This species was published by A. Camus in 1932, based on Henderson 18053 from Cameron Highlands, Pahang, Malaya. I reduce this species to *Q. lineata* Bl.

The other species of *Quercus* from Malesia which are not described in this paper are included in the genus *Lithocarpus* Bl.

GEOGRAPHICAL DISTRIBUTION

The distribution of *Quercus subgen. Quercus* extends from southern Scandinavia throughout Europe to northern Africa (Morocco, Algeria and Tunisia), Lebanon, Turkey, and spreads eastwards to the Caucasus ranges, northern Syria, Iraq, Persia, Afghanistan, Pakistan, India, Burma, Thailand, Laos and then northwards to Hainan, China, Formosa, eastern Manchuria, Korea, Japan and Sakhalin Isl. In America the distribution ranges from the south-eastern parts of Canada, southwards and westwards to the United States, Mexico, Cuba, Guatamala, Honduras, Nicaragua, Costa Rica, Panama and the Columbian Andes (Map I). Species of *Quercus* subgen. *Quercus* may be found up to c. 4300 m altitude, and the boundary of the distribution lies as far north as latitude 62° N. In Asia the centre of speciation of this subgenus is in China, from where not less than 40 species have been described. This subgenus is not represented in Malesia.

Subgenus *Cyclobalanopsis* is confined to the south-eastern and eastern parts of Asia, viz. from Japan (Kanto Prov., Honshu) to Korea, China, Formosa, Indo-China, Thailand, N. Burma, N.E. India, and southwards to western Malesia (Malaya, Singapore, Sumatra, Anambas Isl., Palawan Isl., Borneo and Java), with a centre of speciation in Indo-China. In Malesia (Map II) the centre of distribution is in Borneo from where 17 of the 19 known species have been recorded. Species of this subgenus may be found up to 3500 m altitude, more commonly at about 1000 to 1500 m. The northernmost boundary of the distribution lies at latitude c. 35° N. (Central Japan) and the southernmost limit is in Java at c. latitude 10° S.

Quercus L. subgen. **Cyclobalanopsis** (Oersted) Schneider

Quercus subgen. *Cyclobalanopsis* (Oersted) Schneider, Ill. Handb. Laubh. *1:* 210. 1906; Nakai in Bot. Mag. Tokyo *29:* 56. 1915; Koidzumi in Bot. Mag. Tokyo *30:* 199. 1916; A. Camus, Les Chênes *1:* 158. 1938; Rehder, Man. Cult. Trees & Shrubs, 2nd. ed.: 155. 1940. — *Quercus* sect. *Cyclobalanus* Endlicher, Gen. Pl., Suppl. *4,* 2: 28. 1847, p.p.; A.DC. in Ann. Sc. nat. Bot., Sér. IV, *18:* 55. 1862, p.p.; Prodr. *16,* 2: 91. 1864, p.p.; Oudemans, Annot. Cupul. Jav.: 22. 1865, p.p. — *Quercus* sect. *Gyrolecana* Blume, Mus. Bot. Lugd. Bat. *1:* 299. 1850, p.p.; Miquel, Fl. Ind. Bat. *1,* 1: 855. 1856. — *Cyclobalanopsis* Oersted in Vidensk. Medd. naturh. För. Kjöbn. *8:* 77. 1867; in Kong. Dansk. Vidensk. Selsk. Skr. *5,* 9: 69. 1871; Schottky in Bot. Jahrb. *47:* 645. 1912; Hayata, Icon. Pl. Form. *3:* 185. 1913; Markgraf in Bot. Jahrb. *59:* 59. 1924; Kudo & Masamune in J. Soc. Trop Agr. *2:* 148. 1930; in Trans. Nat. Hist. Soc. Form. *20:* 161. 1930; Schwarz in Notizbl. Bot. Gart. Berlin-Dahlem *13:* 5–8. 1936; in Fedde's Repert. Sonderbeiheft D.: 31–35. 1936; Nakai in J. Jap. Botany *15:* 201. 1939; Li in Bull. Torrey Bot. Club *80:* 323. 1953; Wood. Fl. Taiwan: 99. 1963. — *Quercus* sect. *Cyclobalanopsis* (Oersted) Benth. & Hook. f., Gen. Pl. *3:* 408. 1880; Hooker f., Fl. Brit. Ind. *5:* 603. 1888; King Ann. Roy. Bot. Gard. Calc. *2:* 27. 1889; Prantl in Engler & Prantl, Nat. Pfl. fam. *3,* 1: 55. 1894; Koorders & Valeton, Bijdr. Booms. Java *10:* 15. 1904; Brandis, Ind. Trees: 627. 1906; Gamble in J. As. Soc. Bengal *75:* 408. 1915; Barnett in Trans. & Proc. Bot. Soc. Edinburgh *34:* 164. 1994. — *Quercus* subgen. *Cyclotheca* Nakai, in Bot. Mag. Tokyo *29:* 57. 1915.

Type species: **Q. velutina** Lindl. ex Wall., non Lamarck.

Trees of medium to large size. *Buttresses* absent or up to 1–3 m in height, spreading. *Bark* smooth and lenticellate or finely fissured or scaly and peeling off profusely into rectangular pieces, pale grey to greenish-brown in colour; inner bark sometimes up to 2.5 cm in thickness, brittle, fibrous, ridged on the inner side, pale

yellow to reddish-brown. *Wood* pale yellow to pale brown, growth rings indistinct, heart-wood not well defined from the sapwood, hard but not durable, splitting very easily; vessel distribution denritic rarely solitary; rays uni- to multi-seriate, homogeneous; pitting of the vessel bordered; tannin content little to c. 20 per cent of dry weight. *Innovations* densely simple- or stellate-tomentose or densely brownish, stiff pubescent. *Branchlets* glabrous, smooth or shallowly fissured or markedly warty lenticellate. *Buds* ovoid-globose or ovoid-conical, rarely ovoid-ellipsoid; scales tomentose or densely brownish, woolly pubescent. *Stipules* extrapetiolar, linear-acute, densely tomentose or woolly pubescent, caducous. *Petiole* always thickened at its base, terete or flattened or sulcate on the adaxial side, densely tomentose or woolly pubescent or glabrous. *Leaves* spirally arranged or rarely pseudo-whorled, pen-ninerved; midrib and lateral nerves flattened or impressed or slightly raised above, more or less prominent beneath; margin entire or remotely minutely serrate in the apical half; glabrous or densely or sparsely simple or stellate-tomentose or densely or sparsely stiff or woolly pubescent at least on the lower surface. *Male inflorescence* solitary in the axil of a lower leaf or in paniculate clusters on the lateral or subterminal new shoots, flexuous, pendent, compound or simple, unbranched or much branched. *Male flower* in 3–4-flowered dichasial clusters or solitary along the rachis. Bracts ovate-linear, acute, densely tomentose, caducous. *Perianth* (4)–6-lobed, the lobes connate at base, densely tomentose; stamens (4)–6–(9), filaments slender, filiform, glabrous or tomentose at base; anthers c. 0.5–1 mm long, basifixed, 2-locular, 4-lobed, longitudinally dehiscent; pistillode normally absent, sometimes present but reduced to a cluster of stiff simple hairs. *Pollen grains* prolate, prolate-spheroidal or very rarely suboblate, 3-colpate, 3-colporate or 3-colporoidate; polar diameter c. 22–33 μ, equatorial diameter c. 15–30 μ; exine c. 1–1.5 μ thick, more or less scabrate; inner wall (endexine) thinner or thicker or as thick as the outer wall (ektexine); furrows elongate, tapering towards both ends; pores circular or elliptic. *Female inflorescence* solitary in the axil of a higher leaf, erect, densely woolly pubescent, few- to many-flowered. *Female flowers* always solitary along the rachis, sessile; bracts linear-acute, densely pubescent, caducous; perianth (4)–6–(9)-lobed; staminodes 0 or 5–7; styles 3–4–(6), cylindrical, glabrous or pubescent at base, free and recurved or connate at base; stigmas broadly capitate, glabrous; locules as many as styles; ovules 2 in each locule. *Cupule* cup- or saucer-shaped, obconical or obovoid-globose, lamellate, densely tomentose outside, densely silvery pubescent inside; lamellae c. 5–11, denticulate and free at the rim or more or less smooth and connate, thin or thick. *Fruit* ovoid-conical, ovoid-globose or ovoid-cylindrical; apex rounded, attenuate-acute or abruptly depressed, umbonate; perianthodium (umbo) ringed, well-developed; base rounded, truncate or concave; glabrous and shining or densely tomentose. *Cotyledons* flat-convex, filling the entire space of the surviving locule; germination hypogeal; abortive ovules apical; radicle vertical.

KEY TO THE SPECIES, BASED ON FLOWERING OR FRUITING SPECIMENS

1. Rim of the cupule thinner than 0.5 mm, lamellae with more or less free margin; female inflorescence usually many-flowered.
   2. Cupule deeply cup-shaped, covering c. ⅓–¾ part of the fruit, c. (1)–2–3–(3.5) cm deep and 2–4 cm in diameter.
      3. Cupule c. 2–3.5 cm deep and 2.5–4 cm in diameter. Fruit c. 3–5 cm long and 2–3 cm in diameter. Leaves pseudo-whorled, base cordate to auriculate; petiole c. 0.5–1 cm long ..... 1. *Q. pseudo-verticillata.*
      3. Cupule c. (1)–1.5–2–(2.5) cm deep and c. (1)–1.5–2–(2.5) cm in diameter. Fruit c. 2–3–(3.5) cm long and c. 1.5–2–(3) cm in diameter. Leaves not pseudo-whorled, base not cordate nor auriculate; petiole c. 1.5–5 cm long.
         4. Cupule tapering towards the base. Leaves densely stellate-tomentellous, glaucous or silvery beneath; margin entire.
            5. Fruit elongate conical or ovoid-globose. Styles free and recurved. Staminodes O. Leaves silvery beneath; petiole not deeply sulcate on the adaxial side ..... 2. *Q. argentata.*
            5. Fruit obovoid-globose. Styles connate, not recurved. Staminodes 5–7. Leaves glaucous beneath; petiole deeply sulcate on the adaxial side ..... 3. *Q. nivea.*
         4. Cupule rounded or truncate at base. Leaves glabrous or densely brownish stiff-pubescent or sparsely stellate-tomentose, neither glaucous nor silvery beneath; margin remotely minutely serrate in the apical half.
            6. Cupule c. 2–2.5 cm in depth and in diameter; lamellae 6–8. Fruit ovoid-conical, c. 2–3 cm in length and c. 2 cm in diameter; base convex ..... 4. *Q. gaharuensis.*
            6. Cupule c. 3–3.5 cm in depth and in diameter; lamellae c. 9–11. Fruit ovoid-globose or ovoid-cylindrical, c. 2.5–3.5 cm in length and c. 2–3 cm in diameter; base flat or convex ..... 5. *Q. oidocarpa.*
   2. Cupule shallowly cup-shaped or saucer-shaped, covering c. ⅙–½ part of the fruit, c. 0.5–1.2 cm in depth and c. (0.7)–1–1.8–(2.5) cm in diameter.
      7. Leaves elliptic-lanceolate or ovate-lanceolate, c. (3)–10–15–(24) by (1)–3–5–(9) cm; petiole c. 1–3 cm long.
         8. Leaves elliptic-lanceolate, chartaceous, base attenuate-acute.
            9. Cupule covering c. 1/6–1/5 part of the fruit, base of the fruit concave. Petiole terete or flattened on the adaxial side ..... 6. *Q. sumatrana.*
            9. Cupule covering c. ¼–½ part of the fruit; base of the fruit convex. Petiole sulcate on the adaxial side ..... 7. *Q. subsericea.*
         8. Leaves ovate-elliptic or ovate-lanceolate, thick-coriaceous; base rounded or cordate.
            10. Cupule covering c. ¼–⅓ part of the fruit; fruit ovoid-cylindrical. Leaves c. (3)–5–10–(14) by 2–5.5 cm, lower surface not glaucous; lateral nerves c. 5–8 pairs ..... 8. *Q. lowii.*
            10. Cupule covering c. 1/6–1/5 part of the ovoid-globose fruit. Leaves c. (10)–15–18–(20) by 5.9 cm, glaucous beneath; lateral nerves c. 8–10 pairs ..... 9. *Q. percoriacea.*
      7. Leaves obovate or elliptic-obovate, c. 1.5–5.5 by 0.7–3.5 cm; petiole c. 0.1–0.6 cm long.
            11. Leaves glabrous or with sparse pubescence beneath, upper surface shining, margin entire, apex rounded or truncate-emarginate; lateral nerves c. 4–5 pairs ..... 10. *Q. chrysotricha.*
            11. Leaves with dense pubescence on both surfaces, upper surface dull, margin remotely serrulate in the apical half, apex bluntly acute; lateral nerves c. 5–8 pairs ..... 11. *Q. merrillii.*

1. Rim of the cupule c. 0.5–4 mm in thickness, lamellae more or less connate at the rim; female inflorescence normally few-flowered.
   12. Cupule c. 0.7–1.2 cm deep, c. 1–2 cm in diameter; lamellae c. 5–8. Fruit c. 1–2–(3) by 1.2–1.5 cm. Leaves with entire margin.
      13. Leaves elliptic-lanceolate, glabrous, glaucous beneath, base attenuate-acute ..... 12. *Q. kerangasensis.*
      13. Leaves ovate-elliptic densely yellowish-brown pubescent, base rounded or acute ..... 13. *Q. kinabaluensis.*
   12. Cupule c. 1.5–2 cm deep and c. (1)–2–2.5 cm in diameter; lamellae c. (5)–8–10–(12). Fruit c. 2–5.5 by 1–2 cm. Leaves remotely serrulate in the apical half.
      14. Old leaves glabrous. Fruit c. 2–5.5 cm long.
         15. Leaves with strong and dense reticulation; lateral nerves c. 10–15 pairs. Stamens 5–9; styles connate at base; staminodes O ..... 14. *Q. valdinervosa.*
         15. Leaves with obscure and lax reticulation; lateral nerves c. 7–10 pairs. Stamens 3–6; styles free and recurved; staminodes 6–0 ..... 15. *Q. gemelliflora.*
      14. Old leaves with dense pubescence beneath. Fruit c. 1–3 cm long.
         16. Leaves with strong and dense reticulation.
            17. Cupule deeply cup-shaped, obconical, c. 1–1.2 cm in depth and c. 2–2.5 cm in diameter; lamellae 8–10. Fruit cylindrical-conical, c. 2–3 by 1–2 cm .... 16. *Q. lineata.*
            17. Cupule flattened cup-shaped or saucer-shaped, c. 0.7–1 cm in depth and c. 1.2–2.5 cm in diameter; lamellae 7–8. Fruit globose or ovoid, c. 1–2 cm in length and diameter ..... 17. *Q. steenisii.*
         16. Leaves with obscure and lax reticulation.
            18. Cupule cup-shaped, base rounded, c. 1.5–2 cm deep and c. 1.5–2 cm in diameter; lamellae 10–12. Fruit with convex base. Leaves linear-lanceolate .... 18. *Q. treubiana.*
            18. Cupule saucer-shaped, base flat, c. 0.5–0.7 cm deep and c. 2–2.5 cm in diameter; lamellae 5–7. Fruit with flat base. Leaves elliptic-oblong ..... 19. *Q. elmeri.*

KEY TO THE SPECIES, BASED ON STERILE SPECIMENS

1. Petiole c. (0.1)–0.3–0.5–(1) cm long. Leaves with rounded or bluntly acute apex.
   2. Leaves c. 6–17 by 3–6.5 cm, base rounded, subcordate or auriculate.
      3. Leaves elliptic-oblong or oblanceolate-oblong, c. 7–17 by 3–6.5 cm, margin entire; lower surface sparsely minutely pubescent; reticulation fine, dense, parallel ..... 1. *Q. pseudo-verticillata.*
      3. Leaves ovate-elliptic or ovate-orbicular, c. 3–8 by 2–5 cm, margin remotely serrulate in the apical half, lower surface with dense layer of brownish woolly pubescence; reticulation distinct, prominent on the lower surface ..... 17. *Q. steenisii.*
   2. Leaves c. 1.5–5 by 0.7–3.5 cm, base attenuate-acute or attenuate-rounded.
      4. Leaves glabrous on both surfaces, margin entire, apex rounded or truncate; lateral nerves c. 4–5 pairs ..... 10. *Q. chrysotricha.*
      4. Leaves with dense pubescence on both surfaces, at least on the midrib and lateral nerves, margin remotely serrulate in the apical half, apex bluntly acute, rarely rounded; lateral nerves c. 5–8 pairs ..... 11. *Q. merrillii.*

1. Petiole c. (1)–2–3–(4.5) cm long. Leaves with acute, acuminate or caudate apex.
5. Leaves elliptic-lanceolate, lanceolate-oblong or ovate-elliptic, c. (5)–10–17–(24) by (2)–3–5–(9) cm.
6. Leaf margin entire, recurved, reticulation obscure on both surfaces.
7. Lower surface of the leaf glaucous. Branchlets sparsely stellate-tomentose, shallowly fissured ..... 3. *Q. nivea.*
7. Lower surface of the leaf silvery. Branchlets glabrous densely and prominently lenticellate ..... 2. *Q. argentata.*
6. Leaves remotely serrulate in the apical half, reticulation distinct, at least on the lower surface.
8. Old leaf glabrous.
9. Leaves elliptic-oblong, lateral nerves c. 10–15 pairs; reticulation strong and dense ..... 14. *Q. valdinervosa.*
9. Leaves elliptic-lanceolate, lateral nerves c. 7–10 pairs; reticulation obscure, lax ..... 15. *Q. gemelliflora.*
8. Old leaves not glabrous.
10. Leaves ovate-elliptic, elliptic-oblong or oblong-lanceolate, c. (5)–10–20–(22) by (2.5)–5–7–(9) cm.
11. Leaves ovate-elliptic, lower surface glaucous .... 9. *Q. percoriacea.*
11. Leaves elliptic-oblong or oblong-lanceolate, lower surface not glaucous.
12. Leaves densely brownish, stiff-pubescent beneath; petiole and midrib not sulcate on the adaxial side ..... 4. *Q. gaharuensis.*
12. Leaves sparsely stellate-tomentose; petiole and midrib deeply sulcate on the adaxial side .... 5. *Q. oidocarpa.*
10. Leaves elliptic-lanceolate, c. (1.5)–5–13–(24) by 2.5–5 cm.
13. Leaves glaucous beneath, reticulation fine, obscure ... . 6. *Q. sumatrana.*
13. Leave not glaucous beneath; reticulation strong, distinct on the lower surface.
14. Leaves with dense, simple, adpressed pubescence beneath; lateral nerves c. 10–20 pairs, dense; reticulation distinct beneath ..... 16. *Q. lineata.*
14. Leaves with dense woolly, rufous-pubescence beneath; lateral nerves c. 5–12 pairs, lax; reticulation obscure and lax ..... 19. *Q. elmeri.*
5. Leaves linear-lanceolate or ovate-elliptic, c. 5–10 by 2–4 cm.
15. Leaves linear-lanceolate, with dense pubescence beneath. ..... 18. *Q. treubiana.*
15. Leaves ovate-elliptic, with dense or sparse stellate-tomentum or completely glabrous beneath.
16. Leaves with attenuate-acute or attenuate-rounded base, glabrous or sparsely stellate-tomentose beneath.
17. Leaves glabrous, glaucous beneath; petiole c. 0.8–1.2 cm long; branchlets with dense warty lenticels .... 12. *Q. kerangasensis.*
17. Leaves sparsely stellate-tomentose beneath, not glaucous; petiole c. 1–2.5 cm long; branchlets sparsely minute-lenticellate ..... 7. *Q. subsericea.*
16. Leaves with rounded or cordate base, lower surface with dense stellate-tomentum or simple-pubescence.
18. Leaf-margin remotely serrulate in the apical half; lower surface with dense stellate-tomentum or glabrous; reticulation more or less anastomosing .... 8. *Q. lowii.*
18. Leaf-margin entire; lower surface with dense yellowish simple-pubescence; reticulation parallel .... 13. *Q. kinabaluensis.*

1. **Quercus pseudo-verticillata** Soepadmo, Pl. 1, Map III.

Q. pseudo-verticillata Soepadmo in Gard. Bull. Singapore *21*, 3: 380, f. 1. 1966. — Type: *Chew & Corner RSNB. 4434*, Bembangan River, Mt. Kinabalu, Borneo, alt. c. 1650 m, Febr. fr. (Holotype: K; isotype L).

Tree c. 30 m tall, trunk c. 90 cm in diameter. *Buttresses* up to 2 m tall. *Bark* scaly, peeling off profusely into small, rectangular pieces. Branchlets glabrous, lenticellate. *Leaves* pseudo-whorled, thick-coriaceous, elliptic-lanceolate or oblanceolate-oblong, c. 7–17 by 3–6.5 cm; margin entire, base cordate to auriculate, apex rounded or bluntly acute; upper surface glabrous, lower surface with sparse minute simple-pubescence. *Midrib* and *lateral nerves* strongly prominent beneath, flattened to slightly impressed above, especially in the apical half. Lateral nerves c. 8–15 pairs, forming c. 30°–45° angle with the midrib, parallel, arcuating; reticulation obscure, parallel, dense. *Petiole* c. 0.5–1 cm long and 0.2 cm thick, tomentose, glabrescent, flattened on the adaxial side. Buds ovoid-globose, c. 0.2–0.3 cm in length and c. 0.2 cm in diameter. *Inflorescences* unknown. *Cupule* cup-shaped, obconical-globose, base pointed, covering c. $\frac{1}{3}$–$\frac{1}{2}$ part of the fruit; c. 2–3.5 cm deep and 2.5–4 cm in diameter; outside brownish-sericeous, glabrescent; inside with dense brownish, stiff-pubescence; lamellae c. 10–12, thin, free at the rims, dentate, especially the lower ones. *Fruit* cylindrical-globose, c. 3–5 cm in length and 2–3 cm in diameter, sericeous, apex rounded or depressed, umbo conical, ringed, base convex or flat.

Ecology: in montane rain forest at c. 1650 m alt. Fruiting in October-February.

Distribution: so far only known from Mt. Kinabalu, in North Borneo.

2. **Quercus argentata** Korth., Fig. 6, Map IV.

Q. argentata Korthals in Verh. Nat. Gesch. Bot.: 215, t. 47, f. 1–17, 1844; Blume, Mus. Bot. Lugd. Bat. *1:* 299. 1850; Miquel, Fl. Ind. Bat. *1*, 1: 858. 1856; in Ann. Mus. Bot. Lugd. Bat. *1:* 115. 1863; A. DeCandolle, Prodr. *16*, 2: 91. 1864; Scheffer in Nat. Tijdschr. Ned. Ind. *32:* 417. 1872; Wenzig in Jahrb. Kön. bot. Gart. & Mus. Berlin *4:* 230. 1886; King in Ann. Roy. Bot. Gard. Calc. *2:* 30, t. 24 A. 1889; von Seemen in Bull. Dép. Agr. Ind. Néerl. *1:* 3. 1906; Gamble in J. As. Soc. Bengal *75:* 408. 1915, p.p.; Merrill in J. Str. Br. Roy. As. Soc., Sp. No.: 211. 1921; Ridley, Fl. Mal. Pen. *3:* 373. 1924, p.p.; Moore in J. Bot. *63*, Suppl.: 114. 1925; A. Camus, Les Chênes *1:* 311. 1938; Atl. *1;* t. 23. f. 1–9. 1934. — *Cyclobalanopsis argentata* (Korth.) Oersted in Vidensk. Medd. naturh. För. Kjöbn. *8:* 79, t. I–II, f. 5–8. 1867; in Liebeman's Chênes Amér. Trop.: 20. 1889. — *Lithocarpus argentata* (Korth.) Merrill in Contr. Arn. Arb. *8:* 42. 1934. — Type: *Korthals s.n.*, in forest, Malintang, Sumatra, fruiting (Holotype: L).

Q. pinanga Blume, Mus. Bot. Lugd. Bat. *1:* 303. 1850. — Type: *Blume s.n.*, Java, st., (L); syn. nov.

Plate 1: *Quercus pseudo-verticillata.*

Natural habit, photographed by Prof. E. J. H. Corner in Mt. Kinabalu, North Borneo.

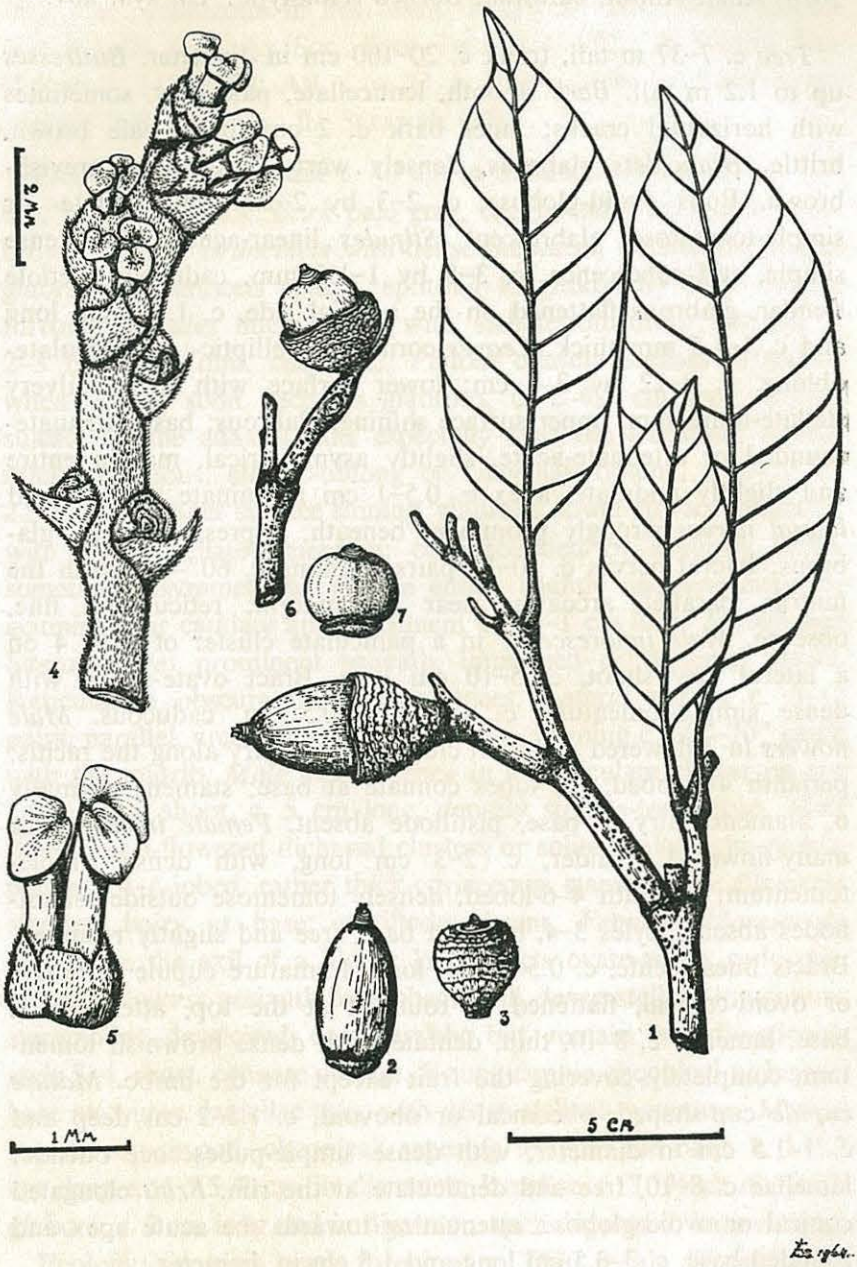

Fig. 6: *Quercus argentata:* 1, 2, 4, 5 after *Smythies S. 12165;* 3 after *Korthals s.n.* (Type); 6–7 after *Jacobs 5114.*

Q. wilhelminae von Seemen, l.c.: 9–10, p.p., excl. fructu; Merrill in J. Str. Br. Roy. As. Soc., Sp. No.: 216. 1921. — Type: *Hallier 2628*, Amai Ambit, Sarawak, Borneo (Holotype: L); syn. nov.

Tree c. 7–37 m tall, trunk c. 20–100 cm in diameter. *Buttresses* up to 1.2 m tall. *Bark* smooth, lenticellate, pale grey, sometimes with horizontal cracks; inner bark c. 2 cm thick, pale brown, brittle. *Branchlets* glabrous, densely warty lenticellate, greyish-brown. Buds ovoid-globose, c. 2–3 by 2–2.5 mm, stellate- or simple-tomentose, glabrescent. *Stipules* linear-acute, with dense simple, stiff-pubescence, c. 3–5 by 1–1.5 mm, caducous. Petiole slender, glabrous flattened on the adaxial side, c. 1.5–3 cm long and c. 1–1.5 mm thick. *Leaves* coriaceous, elliptic- or lanceolate-oblong, c. 8–22 by 3–7 cm; lower surface with dense silvery stellate-tomentum, upper surface shining, glabrous; base attenuate-rounded or attenuate-acute, slightly asymmetrical, margin entire and slightly undulate, apex c. 0.5–1 cm acuminate. *Midrib* and *lateral nerves* strongly prominent beneath, impressed above, glabrous; lateral nerves c. 10–17 pairs, forming c. 60°–75° with the midrib, parallel, arcuating near the margin; reticulation fine, obscure. *Male inflorescence* in a paniculate cluster of 3 or 4 on a lateral new shoot, c. 5–10 cm long. Bract ovate-acute, with dense simple-tomentum, c. 1–1.5 by 0.5 cm, caducous. *Male flowers* in 3-flowered dichasial clusters or solitary along the rachis; perianth 4–6-lobed, the lobes connate at base; stamens normally 6, filament hairy at base, pistillode absent. *Female inflorescence* many-flowered, slender, c. 2–3 cm long, with dense simple-tomentum; perianth 4–6-lobed, densely tomentose outside; staminodes absent; styles 3–4, hairy at base, free and slightly recurved. Bracts linear-acute, c. 0.5–1 mm long. Immature cupule turbinate or ovoid-conical, flattened or rounded at the top, attenuate at base; lamellae c. 8–10, thin, dentate, with dense brownish tomentum, completely covering the fruit except for the umbo. *Mature cupule* cup-shaped, obconical or obovoid, c. 1.5–2 cm deep and c. 1–1.5 cm in diameter, with dense simple-pubescence outside; lamellae c. 8–10, free and denticulate at the rim. *Fruit* elongated conical or ovoid-globose, attenuating towards the acute apex and rounded base, c. 3–3.5 cm long and 1.5 cm in diameter.

Ecology: in lowland to montane forests at c. 0–2700 m alt. Flowering between July and September; fruiting between October and May.

Distribution: Malaya, Singapore, Sumatra, Bangka, Anambas Isl., Borneo, and Java.

Notes: The majority of the examined specimens come from Borneo and Sumatra.

3. **Quercus nivea** King, Fig. 7, Map III.

Quercus nivea King in Ann. Roy. Bot. Gard. Calc. *2:* 31, Pl. 24B, 1889; Koidzumi in Bot. Mag. Tokyo *30:* 201. 1916; Merrill in J. Str. Br. Roy. As. Soc., Spec. No.: 214. 1921; A. Camus, Les Chênes *1:* 313. 1938; Atl. *1:* t. 23, f. 10–16. 1934. — Lecto-type: *Beccari P.B. 2551*, fr., fl., Sarawak (FI).

Tree c 25 m tall, trunk c. 40 cm in diameter. *Buttresses* c. 2 m tall, 10–15 cm thick. *Bark* pale grey, rough; inner bark chocolate-brown, fibrous. *Branchlets* with dense brownish, stellate-tomentum, glabrescent; lenticels sparse, splitting longitudinally into shallow furrows. *Stipules* linear-acute, with stellate-tomentum outside, c. 2–3 by 0.5–1 mm, caducous. *Petiole* densely stellate-tomentose when young, soon becomes glabrous, c. 2–4.5 cm long, deeply sulcate on the adaxial side, especially near the leaf-base. *Leaves* thick-coriaceous, elliptic-oblong or lanceolate-oblong, c. 6–15 by 2.5–5.5 cm; upper surface shining, glabrous, lower surface glaucous, with dense stellate-tomentum; base rounded or abruptly acute, sometimes asymmetrical, margin entire, slightly undulate near the acuminate or caudate apex, acument c. 0.5–1 cm long. *Midrib and lateral nerves* prominent beneath, impressed or flattened above. Reticulation obscure on both surfaces. Lateral nerves c. 6–12 pairs, parallel, arcuating near the margin, forming c. 60°–70° angle with the midrib. *Male inflorescence* in a paniculate cluster on the lateral new shoot, c. 5 cm long, densely stellate-tomentose. *Male flowers* in 3-flowered dichasial clusters or solitary along the rachis; perianth 4–6-lobed, rather thick-coriaceous; stamens 4–6; filaments slender, hairy at base; pistillode absent. *Female inflorescence* solitary in the axil of a higher leaf; bracts ovate-acute, caducous. *Female flowers:* perianth 5–6-lobed, with dense stellate tomentum; staminodes developed considerably but remain not functional; style 3–4, short, connate at base. Young cupule obconical-turbinate, base attenuate, lamellae thin, with dense stellate-tomentum. *Mature cupule* cup-shaped, obconical, tapering towards the base, c. 1–1.7 cm deep and 1.5–2 cm in diameter; lamellae c. 7. *Fruit* obovoid-globose, c. 2 cm long and in diameter, apex depressed, base convex.

Ecology: in high heath forest, at c. 1000 m alt. Flowering in January.

Distribution: endemic in Sarawak (Mts. Gaharu and Pueh).

Notes: This species is closely allied to *Q. argentata*, but differs from the latter by its thick-coriaceous leaves which are glaucous and densely stellate-tomentose beneath, fewer lateral nerves, deeply sulcate petiole, and by its shallowly furrowed, not warty lenticellate branchlets. The lamellae in *Q. nivea* are more or less connate, whilst in *Q. argentata*, they are free and denticulate.

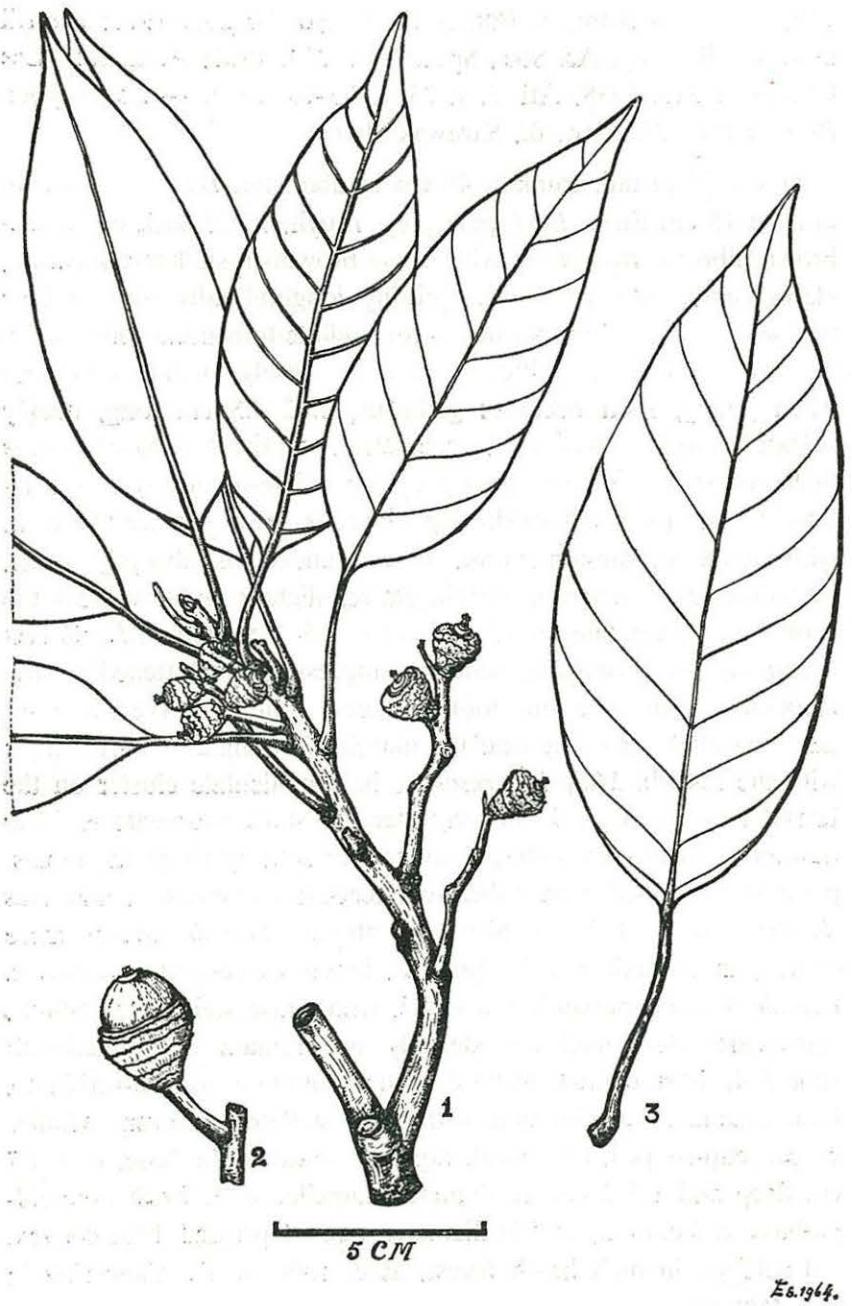

Fig. 7: *Quercus nivea*
1, 3 after *Beccari P.B. 2551* (Type); 2 after King, l.c. 1889.

4. **Quercus gaharuensis** Soepadmo, Map V.

Quercus gaharuensis Soepadmo in Gard. Bull. Singapore *21*, 3: 384, f. 3. 1966. — Type: *Anderson et alia S. 15534*, Serian, lower slope of Mt. Gaharu, Sarawak, alt. c. 100 m, October fr. (Holotype: K*; isotypes: BO, L, SAN, SAR).

Quercus oidocarpa (non Korth.) Hooker f., Fl. Brit. Ind. *5:* 603. 1888; King in Ann. Roy. Bot. Gard. Cal. *2:* 28, pl. 21A, 1889, p.p., quoad specim. ex Mal. Pen.; Brandis, Ind. Trees, 3rd. ed.: 629. 1906, p.p., quoad specim. ex Mal. Pen.; Gamble in J. As. Soc. Bengal *75:* 409. 1915, p.p., quoad specim. ex Mal. Pen.; Merrill in J. Str. Br. Roy. As. Soc., Spec. No.: 214. 1921, p.p., excl. *Beccari 2919;* in Contr. Arn. Arb. *8:* 42. 1934. p.p.; A. Camus, Les Chênes *1:* 213. 1938, p.p., excl. *Korthals s.n.*; Atl. 1, t. 7, f. 10–15. 1934.

Tree c. 10–30 m tall, trunk c. 30–100 cm in diameter. *Buttresses* short, spreading, up to 0.7 m tall. *Bark* smooth, mottled hooped, lenticels scattered in longitudinal rows. *Innovation* with dense stellate-tomentum. *Branchlets* glabrous, lenticellate. Buds ovoid-globose, c. 2 by 2 mm. *Stipules* linear-acute, c. 5 by 1 mm, caducous. *Petiole* slender, terete or flattened on the adaxial side, with dense stellate-tomentum, glabrescent, c. 1–3.5 cm long. *Leaves* elliptic-lanceolate or elliptic-oblong, c. 5–23 by 2–9 cm, thin coriaceous, base attenuate-acute or rounded, slightly asymmetrical, margin entire or remotely serrulate in the apical part, apex rounded or bluntly acute; upper surface glabrous, lower surface with dense stellate-pubescence, glabrescent. *Midrib* and *lateral nerves* prominent beneath, slightly so above; reticulation distinctly visible beneath; lateral nerves c. 8–15 pairs, parallel, arcuating towards the margin, forming c. 45°–60° angle with the midrib. *Male inflorescence* c. 1.5–3.5 cm long; bracts ovate-acute, c. 1–1.5 by 1 mm, caducous. *Male flowers* in 3-flowered dichasial clusters; perianth 4–6-lobed; stamens 4–6; filament hairy at base, c. 1–2 mm long; anthers c. 0.5 by 0.5 mm; pistillode reduced to a cluster of stiff hairs. *Female inflorescence* c. 1–1.5 cm long, carrying c. 2–5 solitary, sessile flowers; bracts ovate-linear, c. 1–2 by 0.5–1 mm. *Female flower:* perianth 5–6-lobed; staminodes absent; styles 3–4, slender, cylindrical, hairy at base, c. 1–2 mm long. Young cupule ovoid-globose, c. 1.5–2 cm in length and in diameter, covering the entire fruit; apex rounded or truncate, base attenuate-rounded, densely sericeous outside and densely brownish-stiff-pubescent inside. *Mature cupule* deeply cup-shaped, c. 2–2.5 cm in depth and in diameter; base rounded, enclosing c. $\frac{1}{2}$–$\frac{2}{3}$ part of the fruit; lamellae c. 6–8, rim thin, slightly recurved and denticulate. Young fruit ovoid or depressed conical, c. 1–1.5 cm in length and in diameter, densely sericeous, glabrescent; apex rounded or abruptly truncate. *Ripe fruit* ovoid-conical, c. 2–3 cm long and 2 cm in diameter, apex acute or rounded, base convex.

Ecology: in lowland mixed Dipterocarps to submontane forests, at c. 100–1400 m alt. Fruiting in September-February.

Distribution: Malaya (Penang, Perak), Borneo (Sarawak), Sumatra (Karolands, Painan, Asahan Forest Reserve).

Recently Mr. Forman informed me that the holotype of this species was redeposited at Kew.

5. **Quercus oidocarpa** Korth., Fig. 8, Map VI.

Quercus oidocarpa Korthals in Verh. Nat. Gesch. Bot.: 216, t. 47, f. 18, 1844; Blume, Mus. Bot. Lugd. Bat. *1:* 302. 1850; Miquel, Fl. Ind. Bat. *1*, 1: 856, 1856; in Ann. Mus. Bot. Lugd. Bat. *1:* 115. 1863; A. DeCandolle, Prodr. *16*, 2: 99. 1864; Wenzig in Jahrb. Kön. bot. Gart. & Mus. Berlin 4: 233. 1886; King in Ann. Roy. Bot. Gard. Calc. *2:* 28. 1889, p.p., quoad *Korthals* s.n.; A. Camus, Les Chênes *1:* 213. 1938, p.p., quoad *Korthals* s.n. — *Cyclobalanopsis oidocarpa* (Korth.) Oersted in Vidensk. Medd. naturh. För. Kjöbn. *8:* 78. 1867; Schottky in Bot. Jahrb. *47:* 151. 1912. — Type: *Korthals s.n.*, in forest, Malintang, Sumatra, fr. (Holotype: L).

Quercus brevistyla A. Camus in Bull. Soc. Bot. France *80:* 353. 1933; Les Chênes *1:* 276. 1938; Atl., t. 17. 1934. — Type: *Syed Alie Kep. 22574*, Fraser's Hill, Pahang, Malaya, Febr. fr. (Holotype: KEP; isotypes: P, SING); syn. nov.

Quercus semiserrata (non Roxb.) Koorders & Valeton, Bijdr. Booms. Java *10:* 25. 1904, p.p., quoad *Koorders 1488 & 1533;* Koorders, Exk. Fl. Java *2:* 16. 1912, p.p.

Tree c. 25–30 m tall, trunk c. 50 cm in diameter. *Bark* grey, scaly and peeling off profusely into-rectangular pieces. *Branchlets* with dense stiff-pubescence, glabrescent, lenticellate. Buds ovoid-globose, c. 3–5 by 2–3 mm. *Petiole* c. 1.5–3.5 cm long, shallowly furrowed on the adaxial side, especially near the leaf-base, glabrous. *Leaves* oblong-lanceolate or elliptic-oblong, c. 7–17 by 3–7 cm, base acute or rounded or subcordate, margin remotely serulate in the apical part, apex acute or 0.5–1.5 cm acuminate; upper surface glabrous, lower surface with spare stellate-tomentum. *Midrib* and *lateral nerves* prominent beneath, impressed above; lateral nerves c. 9–13 pairs, parallel, forming c. 45° angle with the midrib; reticulation distinct beneath, parallel, dense. *Male inflorescence* on a new shoot in the axil of a higher leaf, c. 5–7 cm long, with dense stiff-pubescence; bracts ovate-acute, c. 1.5–2 by 1–1.5 mm, glabrous, caducous. *Male flowers* in 3–4-flowered dichasial clusters or solitary along the rachis; perianth membranaceous, glabrous, 4–6-lobed; stamens 4–7; filaments slender, glabrous, c. 2 mm long; anthers c. 0.7 mm long; pistillode absent. *Female inflorescence* c. 3–7 cm long, subglabrous, in the axil of a higher leaf, carrying c. 3–7 flowers; bracts ovate-acute. *Female flowers:* perianth 4–6-lobed; staminodes absent; styles 3–4, free, recurved, c. 2 mm long, hairy at base. *Cupule* deeply cup-shaped, c. 3–3.5 cm in depth and c. 3–3.5 cm in diameter; base attenuate-rounded; lamellae thin, c. 9–11, the lower ones denticulate, the other entire, yellowish-brown tomentose. *Fruit* ovoid-globose or ovoid-cylindrical, c. 2.5–3.5 cm in length and c. 2–3 cm in diameter, apex rounded or abruptly depressed, base rounded or flat.

Ecology: in lowland to submontane forests, at c. 700–1500 m alt. Flowering between March and April; fruiting between April–February.

Distribution: Malaya, Sumatra, and Java.

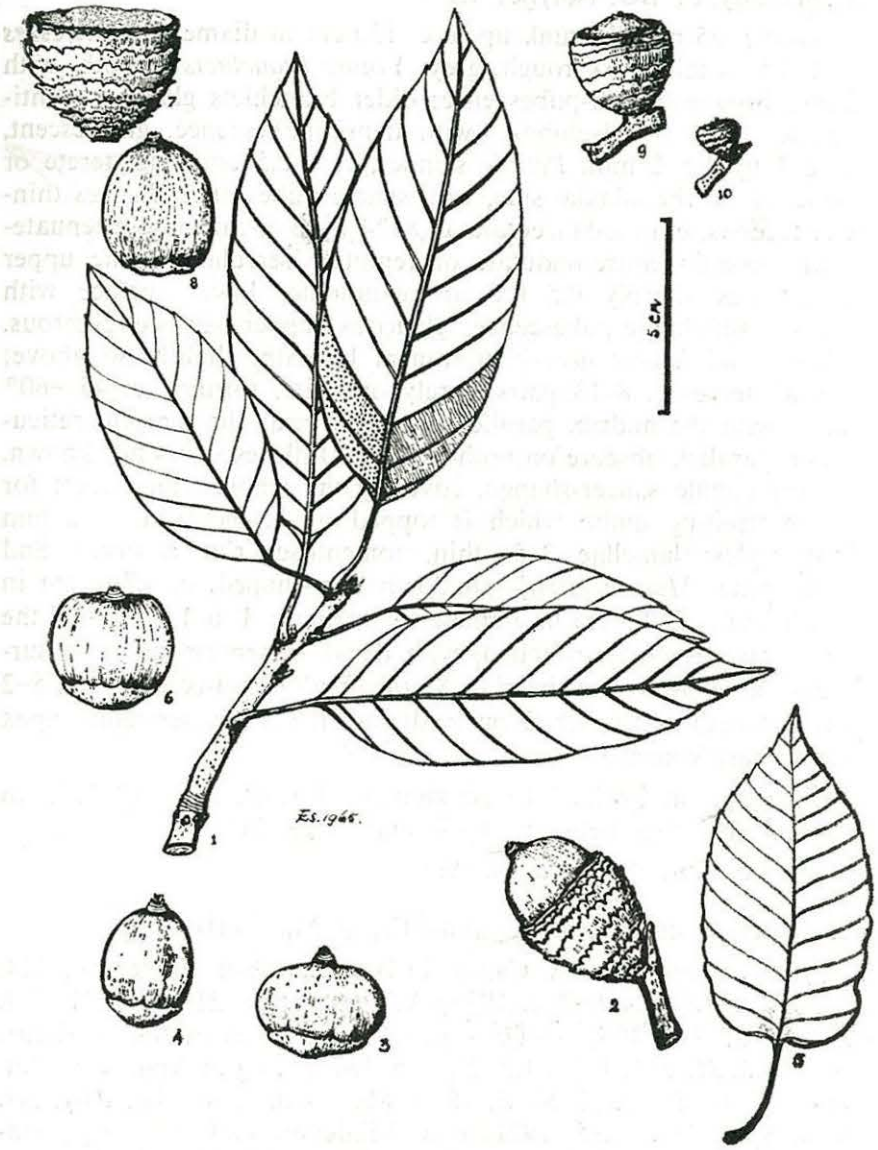

Fig. 8: *Quercus oidocarpa*

1–4 after *Symington Kep. 31071;* 5 after *Poore 1315*; 6 after *Syed Ali Kep. 22574*; 7–8 after *Md. Nur s.n.;* 9 after *Poore 1348;* 10 after *Poore 1315.*

6. **Quercus sumatrana** Soepadmo, Map VII.

Quercus sumatrana Soepadmo in Gard. Bull. Singapore *21*, 3: 387, f. 4, 1966. — Type: *Achmad 1501*, Tapah, N. Sumatra, Nov. fr. (Holotype: BO; isotype: L).

Tree c. 35 m tall, trunk up to c. 130 cm in diameter. *Buttresses* c. 1–2.5 m tall. *Bark* rough, grey. *Young branchlets* smooth, with dense brownish, stiff-pubescence; older branchlets glabrous, lenticellate. Buds ovoid-globose, with dense pubescence, glabrescent, c. 2–3 by 1.5–2 mm. *Petiole* slender, c. 1–2.5 cm long, terete or flattened on the adaxial side, with sparse pubescence. *Leaves* thin-chartaceous, elliptic-lanceolate, c. 8–24 by 2–8 cm, base attenuate-acute, margin entire-undulate or remotely serrulate in the upper part; apex sharply 0.5–1.5 cm acuminate; lower surface with sparse stiff-simple-pubescence, glaucous, upper surface glabrous. *Midrib* and *lateral nerves* prominent beneath, slightly so above; lateral nerves c. 8–13 pairs, rarely opposite, forming c. 45°–60° angle with the midrib, parallel, arcuating near the margin; reticulation parallel, obscure on both surfaces. Inflorescences not known. Young cupule saucer-shaped, covering the whole friut except for the protruding umbo which is topped by 3, recurved, c. 2 mm long styles; lamellae 3–5, thin, tomentose, rim recurved and denticulate. *Mature cupule* shallowly cup-shaped, c. 0.7–1 cm in depth and c. 2–2.5 cm in diameter, covering c. 1/6–1/5 part of the fruit, base attenuate-rounded, with dense tomentum on both surfaces; lamellae free at the rim. *Mature fruit* ovoid-conical, c. 1.8–2 cm in length and c. 1.5–2 cm in diameter, densely sericeous, apex acute, base concave.

Ecology: in lowland to submontane forests, at c. 10–1300 m alt. Fruiting between April and December.

Distribution: Sumatra, Borneo.

7. **Quercus subsericea** A. Camus Fig. 9, Map VIII.

Quercus subsericea A. Camus in Bull. Soc. Bot. France *80:* 354. 1933; Les Chênes *1:* 366. 1938; Atl. *1*, t. 33, f. 21–26. 1934; Atl. *3*, t. 347, f. 1–7. 1939. — *Quercus sericea* Scheffer in Nat. Tijdschr. Ned. Ind. *31:* 361. 1870; l.c. *32:* 416. 1873; King in Ann. Roy. Bot. Gard. Calc. *2:* 63, pl. 57 B. 1889; Merrill in J. Str. Br. Roy. As. Soc., Spec. No.: 215. 1921; non Willdenow (1805). — *Cyclobalanopsis sericea* (Scheff.) Schottky in Bot. Jahrb. *47:* 656. 1912. — *Synaedrys sericea* (Scheff.) Koidzumi in Bot. Mag. Tokyo *30:* 192. 1916. — Type: *Teijsmann HB. 21080*, Bangka, fr. (Holotype: BO; isotype: K).

Quercus lineata (non Bl.) S. Moore in J. Bot. *63*, Suppl.: 114. 1925, p.p., quoad specim. ex *Forbes 572*.

Quercus oidocarpa (non Korth.) Merrill, l.c.: 214. 1921, p.p., quoad specim. ex *Beccari 2919*.

Tree c. 6–15 cm tall, trunk c. 10–40 cm in diameter. *Bark* finely fissured or scaly, thin, greyish-brown; inner bark fibrous, brownish, c. 2.5 cm thick. *Innovations* with dense stiff-simple-pubescence or adpressed stellate-tomentum, glabrescent. *Older branchlets* sparsely

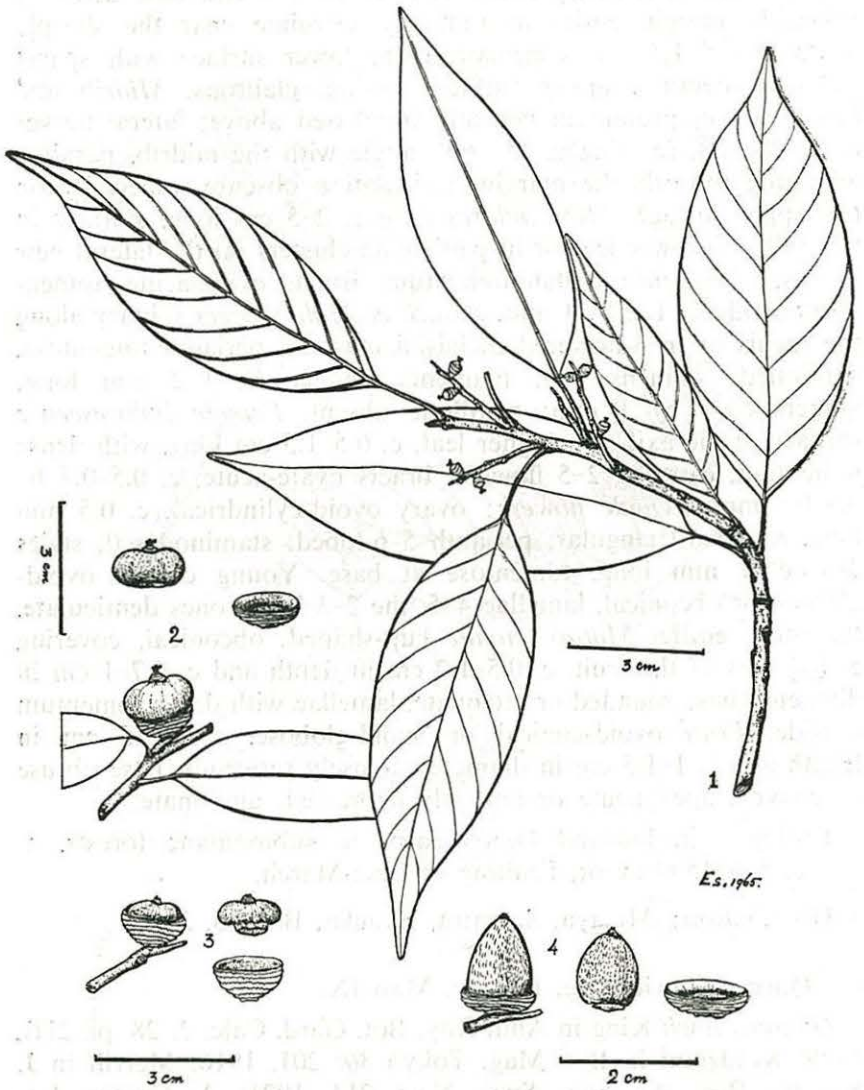

Fig 9: *Quercus subsericea*
1 after *Teijsmann H.B. 7638;* 2 after *Symington Kep. 37644;* 3 after *SAN. 25119;* 4 after *SAN. 28276.*

minute-lenticellate. *Stipules* linear-acute, with dense stiff-pubescence, c. 0.5–0.7 by 0.1–0.2 cm, caducous. *Petiole slender*, c. 1–2.5 cm long, furrowed on the adaxial side. *Leaves* thin-coriaceous, elliptic-lanceolate, rarely ovate, c. 5–16 by 1–5 cm, base acute or roundish, margin entire or remotely serrulate near the sharply acute or 0.5–1.5 cm acuminate apex; lower surface with sparse stellate-tomentum, upper surface shining, glabrous. *Midrib* and *lateral nerves* prominent beneath, impressed above; lateral nerves c. 6–12 pairs, forming c. 45°–60° angle with the midrib, parallel, arcuating towards the margin; reticulation obscure, especially on the upper surface. *Male inflorescence* c. 2–5 cm long, solitary in the axil of a lower leaf or in paniculate clusters on the lateral new shoots, with dense stellate-tomentum. Bracts ovate-acute, tomentose outside, c. 1–2 by 1 mm, caducous. *Male flowers* solitary along the rachis or in 3-flowered dichasial clusters; perianth tomentose, 4–6-lobed; stamens 4–6; filaments slender, c. 1–2 mm long; anthers c. 1 by 1 mm; pistillode absent. *Female inflorescence* solitary in the axil of a higher leaf, c. 0.5–1.5 cm long, with dense tomentum, carrying 2–5 flowers; bracts ovate-acute, c. 0.5–0.7 by 0.3–0.5 mm. *Female flowers*: ovary ovoid-cylindrical, c. 0.5 mm long, rounded-triangular; perianth 5–6-lobed; staminodes 0; styles 3–4, c. 1 mm long, tomentose at base. Young cupule ovoid-globose or obconical, lamellae 4–5, the 2–3 lower ones denticulate, the other entire. *Mature cupule* cup-shaped, obconical, covering c. $\frac{1}{4}$–$\frac{1}{2}$ part of the fruit, c. 0.5–1.2 cm in depth and c. 0.7–1 cm in diameter, base rounded or attenuate, lamellae with dense tomentum outside. *Fruit* ovoid-conical or ovoid-globose, c. 1–2.5 cm in length and c. 1–1.5 cm in diameter; densely sericeous, base obtuse or convex, apex acute or abruptly depressed, umbonate.

Ecology: in lowland Dipterocarps to submontane forests, at c. 500–1500 m alt. Fruiting in June-March.

Distribution: Malaya, Sumatra, Bangka, Borneo, Java.

8. **Quercus lowii** King, Fig. 10, Map IX.

Quercus lowii King in Ann. Roy. Bot. Gard. Calc. *2:* 28, pl. 21B, 1889; Koidzumi in Bot. Mag. Tokyo *30:* 201. 1916; Merrill in J. Str. Br. Roy. As. Soc., Spec. No.: 214. 1921; A. Camus, Les Chênes *1:* 366. 1938; Atl. *1*, t. 33, f. 27-19. 1934. — *Cyclobalanopsis lowii* (King) Schottky in Bot. Jahrb. *47:* 653. 1912. — Type: *Low s.n.*, fr., Mt. Kinabalu, Borneo (CALC).

Tree c. 10–20 m tall, trunk c. 30–40 cm in diameter. *Branchlets* dark-grey, shallowly fissured, with dense brownish, stellate-tomentum; older branchlets lenticellate, glabrous. Buds ovoid- globose, densely tomentose. *Stipules* linear-acute, c. 2–4 by 0.3–0.5 cm, with dense tomentum, caducous. *Petiole* c. 1–2.5 cm long, sulcate on the adaxial side, with dense simple- or stellate-tomentum. *Leaves* thick-coriaceous, ovate-elliptic or ovate-lanceolate, c. (3)–5–10–(14) by 2–5.5 cm, base rounded or cordate, slightly asymmetrical, margin entire or remotely serrulate in the apical half, apex sharply acute or 0.5–2 cm acuminate; lower surface with dense, brownish stellate-tomentum or almost glabrous, upper surface glabrous and shining

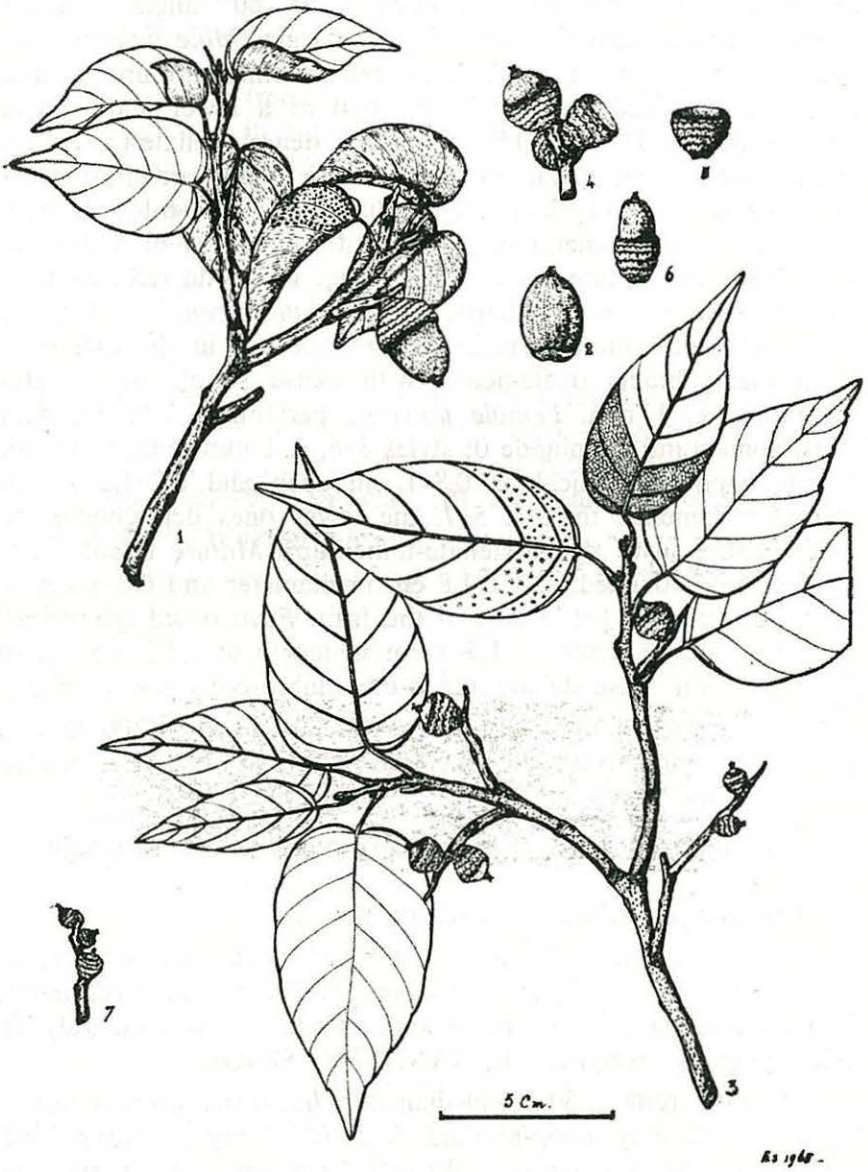

Fig. 10: *Quercus lowii*
1–2 after *SAN. 28808*; 3 after *Clemens 40533;* 4–7 after *Chew & Corner RSNB. 4500.*

or with sparse stellate-tomentum, especially on the midrib. *Midrib* and *lateral nerves* impressed above, prominent or flattened beneath; reticulation fine, more or less anastomosing, distinct beneath. *Lateral nerves* c. 5–8 pairs, forming c. 50°–60° angle with the midrib, parallel, arcuating towards the margin. *Male inflorescence* slender, c. 5–10 cm long, with dense stellate-tomentum, unbranched or rarely branched, solitary in the axil of a lower leaf; bracts ovate-acute, c. 1–2 by 0.5 mm, with dense stellate-tomentum outside, glabrescent, caducous. *Male flowers* solitary or in 3-flowered dichasial clusters along the rachis; perianth 4–6-lobed, with simple or stellate-tomentum, glabrescent; stamens 4–6; anthers c. 1 by 0.5–1 mm; filaments c. 1 mm long; pistillode reduced to a cluster of woolly simple hairs. *Female inflorescence* c. 1–2 cm long, with 2–5 solitary female flowers; solitary in the axil of a higher leaf; bracts ovate-acute, with dense simple or stellate-tomentum, c. 1 mm. *Female flowers*: perianth 4–7-lobed, with dense tomentum; staminode 0; styles 3–6, c. 1 mm long, recurved. Young cupule obconical, c. 0.8–1 cm deep and 0.7–1.2 cm in diameter; lamellae thin, c. 5–7, the lower ones denticulate, the others entire, with dense stellate-tomentum. *Mature cupule* cup-shaped, base rounded, c. 1.3–1.8 cm in diameter and 0.8–1 cm in depth, covering c. $\frac{1}{4}$–1/3 part of the fruit. *Fruit* ovoid-cylindrical, apex rounded or acute, c. 1.5–2 cm in length and 1.3–1.5 cm in diameter, with dense stellate-tomentum, glabrescent; base convex.

Ecology: in lowland to montane forests, at c. 0–2500 m alt., more commonly between c. 1000–1500 m alt. Fruiting between July and March.

Distribution: endemic in Borneo; common in Mt. Kinabalu.

9. **Quercus percoriacea** Soepadmo, Map VI.

Quercus percoriacea Soepadmo in Gard. Bull. Singapore *21*, 3: 382, f. 2. 1966. — Type: *Anderson S. 20226*, Sarawak, Bario, Ulu Baram, on path to Pa' Ukad, at alt. c. 1100 m, July fr. (Holotype: K; isotypes: L, SAN, SAR, SING).

Tree with trunk c. 50 cm in diameter. *Buttresses* up to 1 m tall. *Bark* smooth, grey, hoop-marked. *Branchlets* grey, glabrous, lenticellate. Buds ovoid-globose, c. 0.3 by 0.2 cm, with dense tomentum. *Petiole* c. 2–3.5 cm long, glabrous, terete or slightly grooved on the adaxial side. *Leaves* thick-coriaceous, ovate-elliptic, c. (10)–15–18–(20) by 5–9 cm, base rounded, margin incurved, remotely serrulate in the apical half; apex acute or 1–1.5 cm acuminate, lower surface with sparse stellate-tomentum, glaucous, upper surface shining, glabrous. *Midrib* and *lateral nerves* prominent beneath, impressed and obscure above. *Lateral nerves* c. 8–10 pairs, forming c. 45°–60° angle with the midrib, parallel, arcuating towards the margin; reticulation parallel, prominent beneath. *Male and female inflorescence* not known. Young infructescence c. 2–3 cm long, sericeous, glabrescent, lenticellate, with 1–4 solitary young fruits. Young cupule obovoid, sericeous, c. 0–7–1 cm deep,

0.8–1 cm in diameter; base attenuate; lamellae c. 4–8, the lower ones denticulate, the others entire. Young fruits ovoid-globose, attenuate towards the conical, ringed umbo, sericeous; styles 3, recurved, sericeous. *Mature cupule* flattened cup-shaped, c. 0.7–1 cm in depth and c. 2 cm in diameter, covering c. $\frac{1}{6}-\frac{1}{5}$ part of the fruit, with dense tomentum, base rounded; lamellae c. 6–8, thin, more or less free at the rim. *Mature fruit* ovoid-globose, c. 2 cm in length and in diameter, with dense tomentum, apex rounded, umbonate, base convex.

Ecology: in primary heath forest on terrace sands, at alt. c. 1200 m. Fruiting in June-July.

Distribution: so far only known from Sarawak.

10. **Quercus chrysotricha** A. Camus, Fig. 11 — 1a-c, Map X.

Quercus chrysotricha A. Camus, Les Chênes *3*, Expl. Pl.: 50; Atl. t. 347, f. 8–14. 1948; Text: 1212. 1954. — *Quercus arbutifolia* (non Hickel & A. Camus) Warburg in Kew Bull.: 19. 1936. — Type: *Richards 1885*, Sarawak, Mt. Dulit, alt. c. 1300 m, Sept. fr. (Holotype: K; isotype: L).

Tree c. 19 m tall, trunk c. 30 cm in diameter. *Bark* smooth or finely fissured. Young branchlets with dense, brownish, simple-pubescence; older branchlets glabrous, lenticellate. *Petiole* c. 1.0–0.5 cm long, flattened on the adaxial side, with dense pubescence, glabrescent. *Leaves* thin-coriaceous, obovate-elliptic, base attenuate-rounded or attenuate-acute, slightly asymmetrical, margin entire, apex rounded or truncate-emarginate; c. 1–5.5 by 1.5–3.5 cm; upper surface shining, glabrous, lower surface glabrous or with sparse pubescence. *Midrib* and *lateral nerves* slightly prominent beneath, flattened or slightly impressed above; reticulation obscure on both surfaces. *Lateral nerves* c. 4–5 pairs, forming c. 60°–70° angle with the midrib, parallel, arcuating towards the margin. *Cupule* cup-shaped, obconical, c. 1–1.5 cm in depth and in diameter, base attenuate-acute, covering c. $\frac{1}{4}-\frac{1}{3}$ part of the fruit; lamellae thin, c. 6–7, with dense tomentum outside, denticulate. *Fruit* ovoid-conical, c. 1.5–2 cm in length and c. 1–1.5 cm in diameter, with dense tomentum, glabrescent; apex attenuate-acute, base convex.

Ecology: in submontane forests, at c. 1200–1300 m alt. Fruiting in September.

Distribution: endemic in Borneo (Mt. Dulit, Sarawak).

11. **Quercus merrillii** von Seemen, Fig. 11 — 2a-c, Map X.

Quercus merrillii von Seemen in Fedde's Rep. *5:* 21. 1908; Merrill in Philip. J. Sc. Bot. *3:* 329. 1908; Enum. Philip. Fl. Pl. *2:* 28. 1923; Koidzumi in Bot. Mag. Tokyo *30;* 201. 1916; A. Camus, Les Chênes *1:* 210. 1938; Atl. *1*, t. 7, f. 6–9. 1934. — *Cyclobalanopsis merrillii* (v. Seemen) Schottky in Bot. Jahrb. *47:* 649. 1912. — Type: *Foxworthy 566*, Palawan Isl., fr. April 1906 (Holotype: K).

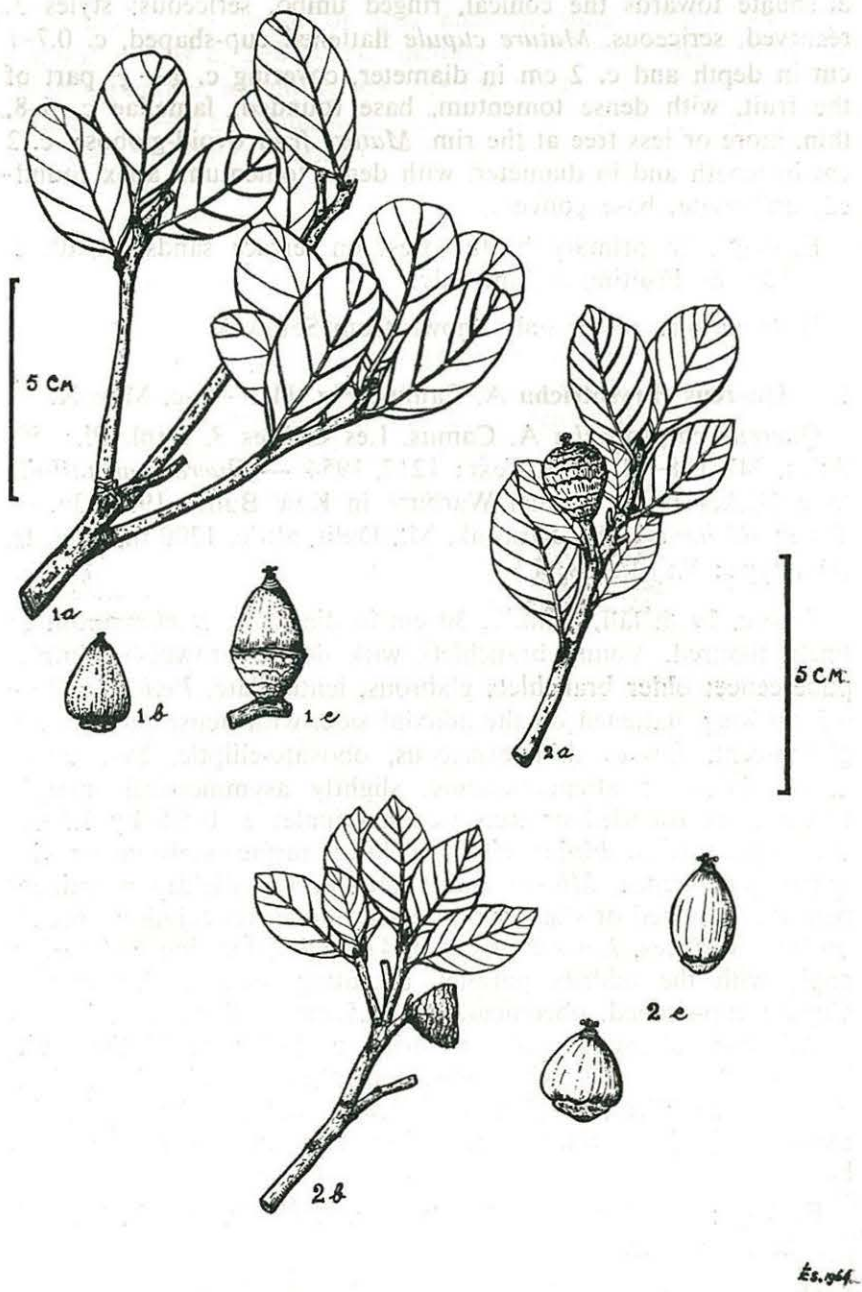

Fig. 11. 1a-c = *Quercus chrysotricha*, after *Richards 1885* (Type).
2a-c = *Quercus merrilli*, after *Curran 3858*.

Small tree. *Young branchlets* with dense brownish, stiff-pubescence; older branchlets glabrous, lenticellate. *Stipules* linear-acute, with dense pubescence outside, c. 0.5–1 by 0.1 cm. caducous. *Petiole* c. 0.3–0.6 cm long, flattened on the adaxial side, with dense pubescence, glabrescent. Leaves thin-coriaceous, obovate or elliptic-ovate, c. 1.5–5 by 0.7–2.5 cm, base attenuate-acute, margin remotely serrulate in the apical half, apex bluntly acute; with dense pubescence on both surfaces, glabrescent. *Midrib* and *lateral nerves* prominent beneath, flattened or impressed above; reticulation obscure on both surfaces. *Lateral nerves* c. 5–8 pairs, parallel, forming c. 50°-60° angle with the midrib, arcuating towards the margin. *Inflorescences* unknown. Young infructescence c. 1–2 cm long, with dense tomentum, glabrescent, lenticellate, with 1–2 solitary young fruits. Young cupule obovoid or obconical, c. 0.5 cm in depth and in diameter, with dense tomentum; styles 3, c. 1–2 mm long, with sparse tomentum at base. *Mature cupule* cup-shaped, obconical, covering c. $\frac{1}{4}$–$\frac{1}{3}$ part of the fruit, c. 1 cm deep and 1–1.5 cm in diameter; lamellae c. 7–8, thin, denticulate, with dense tomentum outside. *Fruit* ovoid or ovoid-cylindrical, c. 2–2.5 cm long and 1–1.5 cm in diameter, shining, glabrous; apex acute, base convex.

Ecology: in lowland forest, at c. 100–500 m alt. Fruiting between April and August.

Distribution: Borneo and Palawan Isl.

12. **Quercus kerangasensis** Soepadmo, spec. nov., Fig. 12, Map XI.

Arbor c. 20–30 m alta, trunco c. 25–50 cm lata; cortice laevi vel scabro, grisei-lenticellato. *Ramuli* laeves vel dense lenticellati annulati, grisseo-brunnei, dense et rigide pubescentes, glabrecentes. Alabastra c. 2–4 × 3–4 mm, ovoideo-globosa, dense pubescens. *Stipulae* lineares acutae, c. 2–3 × 0.5–1 mm, dense pubescentes, glabrescentes. *Petiolus* gracilis, c. 8–12 × 0.5–1 mm, ad basim incrassatus, supra applanatus vel subsulcatus. *Lamina* c. 4–11 × 2–4 cm, elliptico-lanceolata, coriacea, subtus glabra, glaucescens, supra nitida glabra; costa nervisque lateralibus subtus prominentibus, supra vix elevatis; nervis lateralibus c. 7–10, angulo 60°–70° exorientibus, ascendentibus, marginem versus arcuatis; nervis reticulatis invisibilibus.

Inflorescentia mascula c. 1–2 cm longa, axillaris semiterminalis, dense pallide brunneo-pubescens. Bracteae c. 1 × 1 mm, ovatae acutae, dense et rigide brunneo-pubescentes; cymulis trifloris. Perianthium 5–6-lobatum, extus pubescens; stamina 5–6; filamentis c. 1–2 cm longis, glabris filiformibus; antheris c. 0.5 × 0.5 mm. *Inflorescentia feminea* ignota.

Cupula matura obconica cupuliformis, c. 0.8–1.2 cm alta, 1.5–2 cm lata, dense brunneo-sericea; lamellae c. 5–7, crasse, marginem crenato vel integro. *Nux* matura c. 2–3 cm longa, 1.2–1.5 cm lata, ovoideo-conica vel obovoideo-cylindrica, dense sericea, glabrescens; apice rotundato vel acuto, ad basim rotundato; hilum convexum.

Type: *Brunig S. 1065*, Badas Forest Reserve, Sarawak, alt. c. 10 m, September fr. (Holotype: K; isotypes: L, SAR).

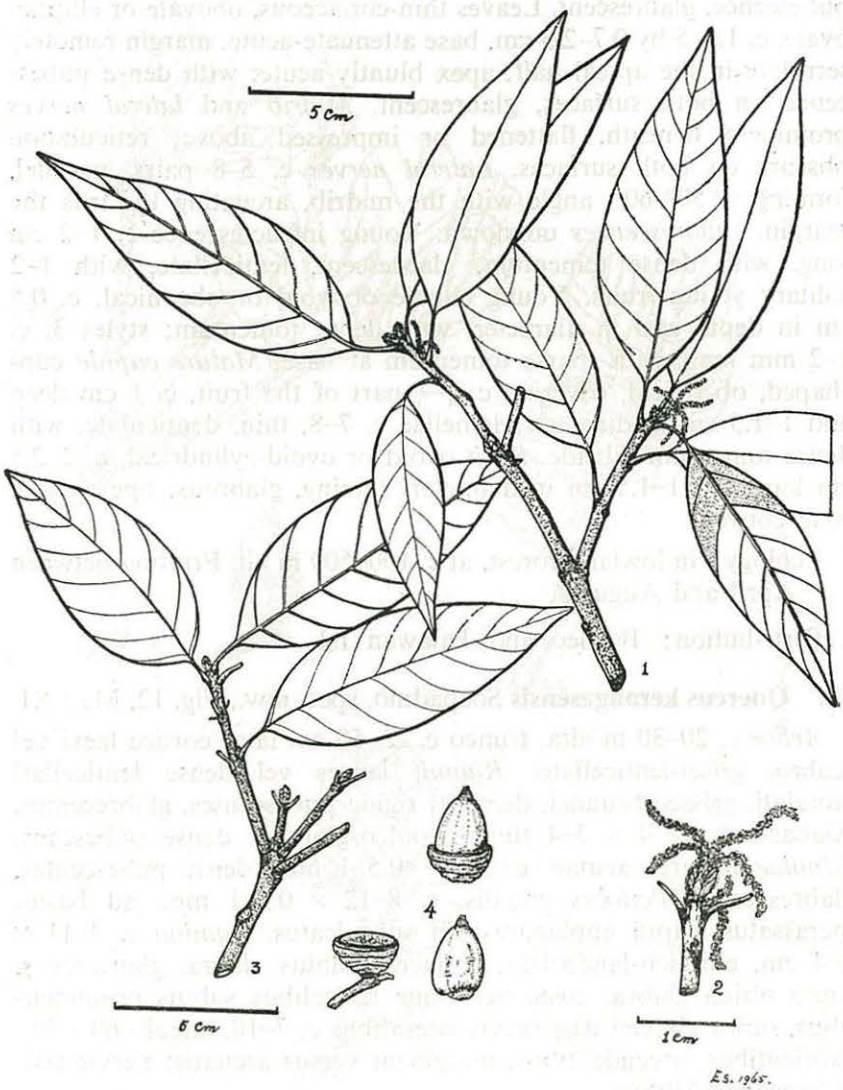

Fig. 12: *Quercus kerangasensis*
1–2 after *Brunig 4661* (2 = male inflorescences); 3–4 after *Brunig 1065* (Type).

Tree c. 20–30 m tall, trunk c. 25–50 cm in diameter. *Buttresses* small, fluted. *Bark* smooth or rough, lenticellate, grey. *Young branchlets* with dense stiff-pubescence, smooth or horizontally crasked; older branchlets glabrous, greyish-brown, with dense warty lenticels. Buds ovoid-globose, with dense yellowish-brown pubescence, c. 3–6 by 3–4 mm. *Stipules* linear-acute, c. 2–3 by 0.5–1 mm, caducous. *Petioles* slender, c. 0.8–1.2 cm long and 0.5–1 mm thick, with dense pubescence, glabrescent, thickened at base, flattened or shallowly furrowed on the adaxial side. *Leaves* elliptic-lanceolate, coriaceous, c. 4–11 by 2–4 cm, upper surface shining, glabrous, lower surface pale glaucous, glabrous except the midrib; margin entire, base attenuate-acute, apex acute or 0.5–1 cm acuminate. *Midrib* and *lateral nerves* prominent beneath, slightly so above. *Lateral nerves* c. 7–10 pairs, ascendant, subparallel, arcuating towards the margin, forming c. 60°–70° angle with the midrib; reticulation obscure on both surfaces. *Male inflorescence* in paniculate clusters on the lateral or subterminal new shoots, with dense yellowish-brown pubescence. c. 1–2 cm long. Bracts membranous, ovate-acute, with dense stiff-pubescence outside, c. 1 by 1 mm. *Male flowers* in 3-flowered dichasial clusters; perianth membranous, 5–6-lobed; stamens 5–6; filaments glabrous, filiform, c. 1–2 mm long; pistillode absent. *Female inflorescence* not known. *Mature cupule* cup-shaped, obconical, c. 0.8–1.2 cm in depth and 1.5–2 cm in diameter, base attenuate, rim c. 1–1.5 mm thick, with dense brownish tomentum on both surfaces; lamellae c. 5–7, margin entire or denticulate. *Mature fruit* ovoid-conical or ovoid-cylindrical, c. 2–3 cm long and 1.2–1.5 cm in diameter, densely sericeous, glabrescent, shining; apex rounded or acute, base convex.

Ecology: in primary heath forests, at c. 10–100 m alt. Flowering in June, fruiting in September.

Distribution: endemic in Borneo (Brunei, Sarawak).

Notes: This species is named after the local name of heath forest, viz. "kerangas" forest, from where the specimens were mainly collected. It may be recognized by its elliptic-lanceolate leaves with entire margin and pale glaucous lower surface, and by its small fruit and cupule.

13. **Quercus kinabaluensis** Soepadmo, spec. nov., Fig. 13, Map XI.

Arbor c. 10–40 m alta, trunco c. 20–30 cm lato; cortice laevi. *Ramuli* sparsim lenticellati, dense et ridgide brunneolo-pubescentes, glabrescentes. Alabastra, c. 4–10 × 3–4 mm, ovoideo-globosa vel ovoideo-conica. *Stipulae* c. 5–10 × 0.5–1 mm, lineares acutae, dense et rigide pubescentes, caducae. *Petiolus* c. 1–1.5 cm longus, 1–1.5 mm crassus, dense brunneolo-pubescens, glabrescens, ad basim incrassatus, supra applanatus. *Lamina* c. 5–10 × 2–5 cm, ovato-elliptica, crasse coriacea, dense flavo-brunneolo-pubescens, glabrescens; margine integro, basi asymmetrico rotundato vel acuto; apice acuto acuminato, 0.5–1.5 cm longo; costa nervisque lateralibus subtus vix elevatis, supra applanatis vel subsulcatis; nervis lateralibus c. 6–8, ascendentibus, marginem versus arcuatis, angulo 45°–60° exorientibus; nervulis reticulatis invisibilibus.

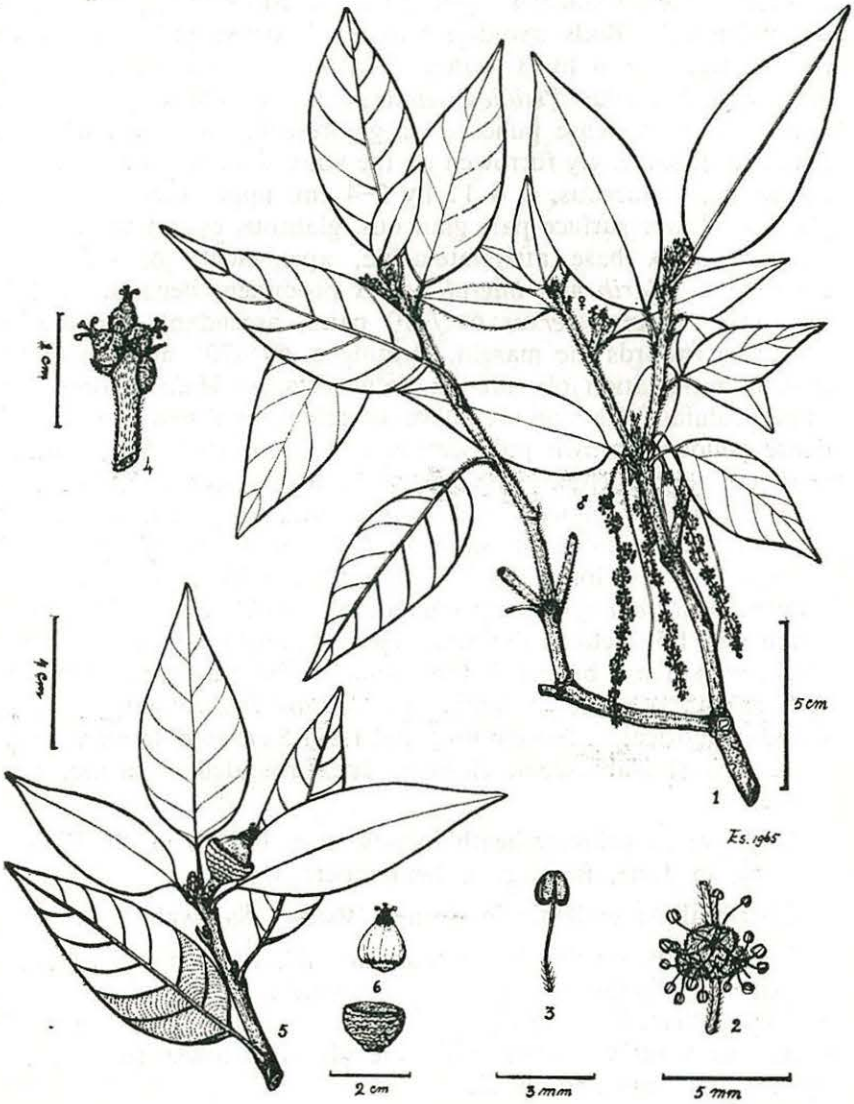

Fig. 13: *Quercus kinabaluensis*
1–4 after *Chew & Corner RSNB. 4451;* 5–6 after *Chew & Corner RSNB. 7148* (2 = a 3-flowered male dichasium; 4 = female inflorescence).

Inflorescentia mascula gracilis flexuosa, c. 50–110 × 1 mm, dense brunneo-pubescens; cymulis tri vel uni-floris. Bracteae c. 2–3 × 1–2 mm, ovatae acutae, tenue, extus dense pubescentes. Perianthium 4–7-lobatum, extus dense brunneo-pubescens, glabrescens; stamina 4–7; filamentia c. 2 mm, glabris; antheris c. 1 × 1 mm.

Inflorescentia feminea c. 10–30 × 2–3 mm, dense et rigide brunneo-pubescens, 1–3-flores gerens. *Flores femini* solitarii. Bracteae c. 1–2 × 0.5–1 mm, dense pubescentes, glabrescentes. Perianthium 5–6-lobatum, crasse coriaceum, extus dense brunneo-pubescens; staminodia nil; stili 3–5, recurvi, ad basim versus hirti, c. 2–3 × 0.5–1 mm.

Cupula immatura obconica cupuliformis, c. 0.7–1 cm alta, 1–1.5 cm lata, margine crassa, basi attenuati; lamellae 6–8, dense pubescentes, denticulo vel integro. *Nux* c. 1–1.2 cm alta, 0.8–1 cm lata, ovoideo-conica, dense brunneo-sericea, glabrescens; apice rotundato vel attenuato, basi convexo.

Type: *Chew & Corner RSNB. 7148,* Mt. Kinabalu, Mentaki ridges, alt. c. 2600 m, March fr. (Holoytpe: K; isotypes: L).

Tree c. 10–40 m tall, trunk c. 20–30 cm in diameter. *Bark* smooth, brownish with white patches. *Innovations* with dense brownish, stiff-pubescence, glabrescent. *Branchlets* glabrous, with sparse lenticels. Buds ovoid-globose or ovoid-conical, c. 0.4–1 by 0.3–0.4 cm. *Stipules* linear-acute, c. 5–10 by 0.5–1 mm, caducous, *Petiole* c. 1–1.5 cm long and 1–1.5 mm thick, with dense brownish, stiff-pubescence, glabrescent, slightly thicken at base, flattened on the adaxial side. *Leaves* c. 5–10 by 2–5 cm, ovate-elliptic, thick-coriaceous, with dense yellowish-brown pubescence on both surfaces, glabrescent; margin entire, base asymmetrical, rounded or acute, apex acute or 0.5–1.5 cm acuminate. *Midrib* and *lateral nerves* slightly prominent beneath, flattened or impressed above. Lateral nerves c. 6–8 pairs, ascendant, arcuating towards the margin, forming a c. 45°–60° angle with the midrib; reticulation obscure on both surfaces. *Male inflorescence* in paniculate clusters on a lateral new shoots, with dense yellowish-brown, stiff-pubescence c. 5–11 cm long and 1 mm thick; bracts ovate-acute, membranous, with dense pubescence outside, c. 2–3 by 1–2 mm. *Male flowers* in 3-flowered dichasial clusters or solitary along the rachis perianth 4–7-lobed, with brownish-pubescence outside, glabrescent; stamens 4–7; filaments c. 2 mm long, glabrous; anthers c. 1 × 1 mm. *Female inflorescence* c. 1–3 cm long, 2–3 mm thick, with dense stiff-pubescence, carrying 1–3 flowers. *Female flower*: perianth thick-coriaceous, with dense brownish-pubescence outside, 5–6-lobed; staminodes 0; styles 3–5, hairy at base, recurved, c. 2–3 by 0.5–1 mm. *Immature cupule* cup-shaped, obconical, c. 0.7–1 cm deep and 1–1.5 cm in diameter, rim thick, base attenuate; lamellae c. 6–8, denticulate or entire, with brownish-pubescence on both surfaces. *Fruit* ovoid-conical, with dense brownish tomentum, glabrescent, c. 1–1.2 cm long and 0.8–1 cm in diameter; apex rounded or attenuate; base convex.

Ecology: in ridge or montane forests, at c. 500–2600 m alt. Fruiting between March and May.

Distribution: endemic in Mt. Kinabalu, Borneo.

Notes: In vegetative characters *Q. kinabaluensis* is closely allied to *lowii,* but differs from the latter by its thick-rimed cupule and different type of pubescence.

14. **Quercus valdinervosa** Soepadmo, spec. et stat. nov., Fig. 14, Map XII.

Quercus mespilifolia Wall. ex A.DC. var. *borneensis* Heine in Fedde's Rep. *54:* 225. 1951. — Lectotype: *Clemens 31317,* Mt. Kinabalu, North Borneo, June fl. (Holotype: K; isotypes: A, B, K, L, SING, UC); paratype: *Anderson S. 4547,* Baram, path to the summit of Mt. Mulu, Sarawak, alt. c. 1900–2100 m, fr. 2-VII-1961 (A, K, L, SAR, SING).

Tree c. 20–35 m tall, trunk c. 30–60 cm in diameter. *Bark* smooth, grey. *Innovations* with dense brownish, stiff, simple- or stellate-pubescence. *Branchlets* glabrous, lenticellate. Buds ovoid-conical; scales arranged in four vertical rows. *Stipules* linear-acute, tomentose outside, c. 1–1.5 cm long, 1–2 mm wide, caducous. *Petiole* c. 1–2.5 cm long, glabrous, flattened on the adaxial side. *Leaves* elliptic or obovate-oblong, c. 8–15 by 3–6 cm, thick-coriaceous; upper surface glabrous, lower surface with dense simple pubescence, soon becomes completely glabrous; base acute or attenuate-rounded, margin remotely serrulate in the apical half, apex 0.5–1 cm acuminate. *Midrib* and *lateral nerves* prominent beneath, flattened or impressed above; reticulation dense, parallel, prominent beneath. *Lateral nerves* c. 10–15 pairs, dense, parallel and straight, arcuating near the margin, forming c. 60° angle with the midrib. *Male inflorescence* c. 5–10 cm; bracts lanceolate or linear-acute, membranous, c. 3–5 by 2–3 mm. *Male flowers* in 3-flowered dichasial clusters along the rachis; perianth 4–6-lobed, with dense tomentum outside; stamens 5–9; filaments c. 3–4 mm long, glabrous; anthers c. 1 × 1 mm; pistillode 0. *Female inflorescence* c. 1–1.5 cm long, with dense tomentum, carrying 4–6 female flowers; bracts ovate or linear, c. 2–3 by 1 mm. *Female flowers*: perianth 6-lobed, with dense tomentum outside; staminodes 0; styles 3–6, c. 1–2 mm long, tomentose at base. *Mature cupule* cup-shaped, obconical, base attenuate, c. 1.5–1.7 cm in depth and 1–2.5 cm in diameter, covering c. 1/3–1/6 part of the fruit; lamellae 7–8, rim crenate and thick, with dense tomentum outside. *Fruit* cylindrical-conical or ellipsoid, apex acute, base convex, c. 3–3.7 cm in length, 1.3–1.7 cm in diameter, tomentose.

Ecology: in submontane to montane forests, at c. 1300–2300 m alt. Fruiting between February and August.

Distribution: Borneo (Mt. Kinabalu, Brunei, Sarawak, W. Kutei).

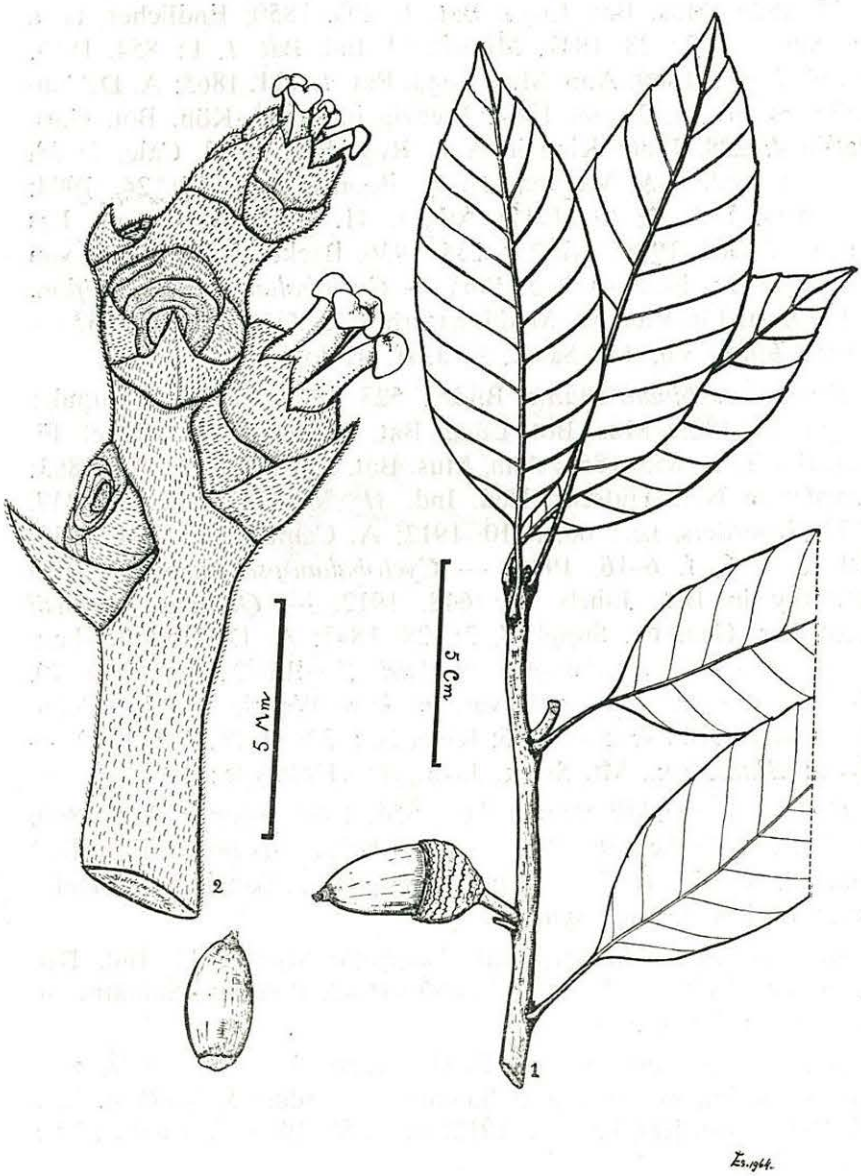

Fig. 14: *Quercus valdinervosa*
1 after *Ashton Brun. 2378;* after *Meijer SAN. 29134.*

15. **Quercus gemelliflora** Bl., Fig. 15, Map XIII.

Quercus gemelliflora Blume in Verh. Bat. Genootsch. *9:* 223, t. 6. 1823, p.p., excl. fructu; Bijdr.: 523. 1825; Fl. Javae Cupul.: 30, t. 17. 1829; Mus. Bot. Lugd. Bat. *1:* 295. 1850; Endlicher, Gen. Pl., Suppl. *4,* 2: 28. 1847; Miquel, Fl. Ind. Bat. *1,* 1: 854. 1856; Suppl. *1:* 854. 1860; Ann. Mus. Lugd. Bat. *1:* 111. 1863; A. DeCandolle, Prodr. *16,* 2: 88. 1864; Wenzig in Jahrb. Kön. Bot. Gart. Berlin *4:* 228. 1886; King in Ann. Roy. Bot. Gard. Calc. *2:* 88. 1889; Koorders & Valeton, Bijdr. Booms. Java *10:* 24. 1904; Koorders, Exk. *2:* 61. 1912; Atl., t. 41. 1913; A. Camus, Les Chênes *1;* 363. 1938; Atl. *2,* t. 234. 1936; Backer & Bakhuizen van den Brink Jr., Fl. Java *2:* 5. 1965. — *Cyclobalanopsis gemelliflora* (Bl.) Oersted in Vidensk. Medd. naturh. För. Kjöbn. *8:* 77. 1867. — Type: *Blume s.n.,* Mt. Salak, Java, st. (Holotype: L).

Quercus turbinata Blume, Bijdr.: 523. 1825; Fl. Javae Cupul.: 31, pl. 18. 1829; Mus. Bot. Lugd. Bat. *1:* 302. 1850; Miquel, Fl. Ind. Bat. *1,* 1: 855. 1856; Ann. Mus. Bot. Lugd. Bat. *1:* 114. 1863; Scheffer in Nat. Tijdschr. Ned. Ind. *31:* 361. 1870; l.c. *32:* 417. 1872; Koorders, l.c.: 60, f. 10. 1912; A. Camus, l.c.: 204. 1938; Atl. *1,* t. 6, f. 6–16. 1934. — *Cyclobalanopsis turbinata* (Bl.) Schottky in Bot. Jahrb. *47;* 648. 1912. — *Quercus merkusii* Endlicher, Gen. Pl., Suppl. *4,* 2: 28. 1847; A. DeCandolle, l.c.: 98. 1864; — *Cyclobalanopsis merkusii* (Endl.) Oersted, l.c.: 79. 1867. — *Quercus lineata* Bl. var. *merkusii* Wenzig in Jahrb. Kön. Bot. Gart. Berlin *4:* 232. 1886; King, l.c.: 32, pl. 26, f. 2. 1889. — Type: *Blume s.n.,* Mt. Salak, Java, yfr. (Holotype: L).

Quercus horsfieldii Miquel, l.c.: 856. 1856; Suppl.: 869. 1860; A. DeCandolle, l.c.: 99. 1864. — *Cyclobalanopsis horsfieldii* (Miq.) Oersted, l.c.: 78. 1867. — Type: *Horsfield 11,* Bangka, yfr. (Holotype: U; isotype: K); syn. nov.

Quercus horsfieldii Miq. var. *longifolia* Miquel, Fl. Ind. Bat. *1,* 1: 869. 1856. — Type: *Diepenhorst* 42, Priaman, Sumatra, st. (Holotype: U); syn. nov.

Quercus semiserrata (non Roxb.) King, l.c.: 28. 1889, p.p., quoad specim. ex Bangka et Sumatra; Koorders & Valeton, l.c.: 25. 1904; Koorders, l.c.: 61. 1912; l.c. t. 55. 1913; A. Camus, l.c.: 186. 1938.

Quercus turbinata Bl. var. *crassilamellata* Gamble in J. As. Soc. Bengal *75:* 410. 1915; Ridley, Fl. Mal. Pen. *3:* 373. 1924. — *Quercus crassilamellata* (Gamble) A. Camus in Bull. Mus. Paris, Ser. II, *3:* 689. 1931; Les Chênes *1;* 226. 1938; Atl. *1,* pl. 10, f. 1–7. 1934. — Type: *Wray 1532,* Kampong Ulu Batang Padang, Perak, Malaya, at c. 1600 m alt., fr. (Holotype: K; isotype: SING); syn. nov.

Tree c. 20–30 m tall, trunk c. 20–60 cm in diameter. *Buttresses* up to 1 m tall. *Bark* smooth or finely fissured, greyish-brown. *Young branchlets* and buds with dense tomentum; older branchlets glabrous, lenticellate. *Stipules* linear-acute, c. 0.5–1 by 0.1–0.2 cm, with dense tomentum outside, caducous. *Petiole* c. 1–3 cm long

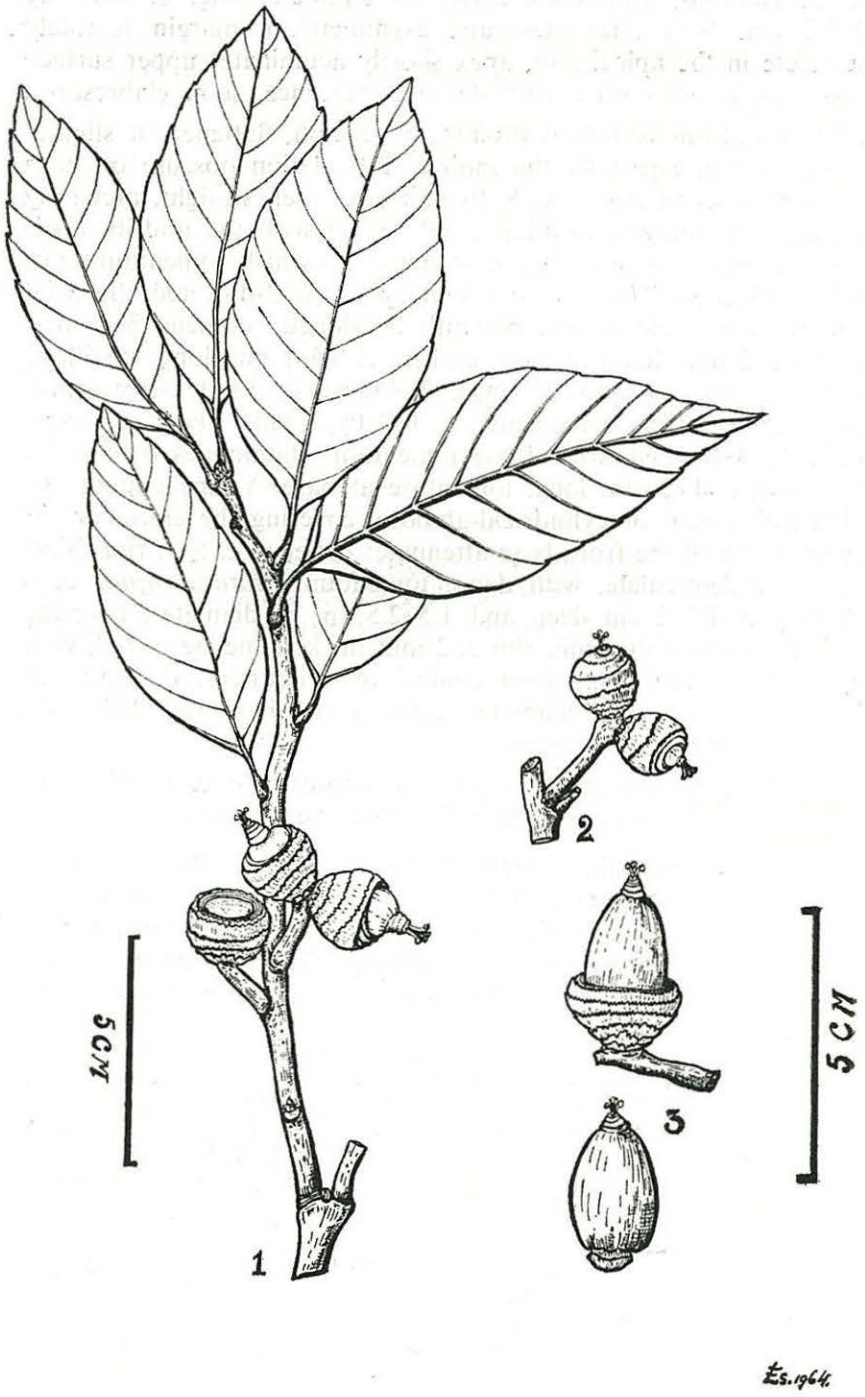

Fig. 15: *Quercus gemelliflora*
1 after *Rastini s.n.;* 2 after *Bünnermeijer 1880;* 3 after *Teijsmann s.n.*

and 0.1–0.2 cm thick, with dense tomentum, glabrescent. *Leaves* thin-coriaceous, elliptic-lanceolate or elliptic-oblong, c. 5–15 by 2–5.5 cm; base attenuate-acute, asymmetrical, margin remotely serrulate in the apical half, apex shortly acuminate; upper surface glabrous, lower surface with dense pubescence, soon glabrescent. *Midrib* and *lateral nerves* prominent beneath, flattened or slightly raised above, especially the midrib; reticulation obscure on both surfaces. *Lateral nerves* c. 8–10 pairs, parallel, straight, arcuating towards the margin, forming c. 60° angle with the midrib. *Male inflorescence* c. 6 cm long, with dense brownish tomentum; outside, caducous. *Male flowers* solitary or in 3-flowered dichasial clusters along the rachis; perianth 3–6-lobed; stamens 3–6; filaments c. 2 mm, hairy at base; anthers c. 0.5–1 mm long; pistillode 0. *Female inflorescence* carrying c. 2–7 flowers, with dense brownish pubescence; bracts ovate-acute, c. 1–2 by 1 mm. *Female flowers:* perianth 4–6-lobed, with dense tomentum; staminodes 0–6; styles recurved, c. 1–2 mm long, tomentose at base. Young cupule turbinate-obconical or cylindrical-globose, covering the entire or the greater part of the fruit, base attenuate; lamellae c. 5–7, rim thick, entire or denticulate, with dense tomentum. *Mature cupule* cup-shaped, c. 1.5–2 cm deep and 1.5–2.5 cm in diameter, covering c. ½–1/3 part of the fruit, rim c. 2 mm thick; lamellae c. 7–8, with dense tomentum. *Ripe fruit* conical or cylindrical, c. 2–5.5 cm long and 1–2 cm in diameter, apex acute, base rounded, with dense tomentum, glabrescent.

Ecology: in lowland to submontane forests, at c. 100–1600 m alt. Flowering and fruiting the whole year round.

Distribution: Malaya (Kedah, Penang, Perak Pahang, Negri Sembilan, Malacca, Johore), Sumatra (Atjeh, Sibolangit, Tapanuli, Padang, Pajakumbuh, Mt. Sago, Indragiri, Pematang Siantar, Banjuasin-Palembang), Bangka, Borneo (Sandakan, Mt. Kinabalu, Sarawak, W. Kutei, Martapura and vicinity), Java.

16. **Quercus lineata** Bl., Fig. 16, Map XIV.

Quercus lineata Blume, Bijdr.: 523. 1825; Fl. Javae Cupul.: 32, pl. 19. 1829; Mus. Bot. Lugd. Bat. *1:* 302. 1850; Miquel, Fl. Ind. Bat. *1*, 1: 855. 1856; in Ann. Mus. Bot. Lugd. Bat. *1:* 114. 1863; A. DeCandolle, Prodr. *16*, 2: 98. 1864; Wenzig in Jahrb. Kön. Bot. Gart. Berlin *4:* 232. 1886; Koorders & Valeton, Bijdr. Booms. Java *10:* 20. 1904; Koorders, Exk. *2:* 60. 1912; Atl. Baumart. Java *1:* pl. 58. 1913; A. Camus, Les Chênes *1:* 207. 1938; Atl. *1:* t. 6, f. 1–5. 1934; Backer & Bakhuizen van den Brink Jr., Fl. Java *2:* 5. 1965. — *Cyclobalanopsis lineata* (Bl.) Oersted in Vidensk. Medd. naturh. För. Kjöbn. *8:* 78. 1867; in Libmann. Chênes Am. Trop. *1:* 20. 1869. — *Quercus lineata* Bl. var. *typica* King in Ann. Roy. Bot. Gard. Calc. *2:* 33, pl. 26, f. 1. 1889. — Type: *Blume s.n.*, Java, fl. (Holotype: L; isotypes: A, BO).

Quercus polyneura Miquel, Pl. Jungh. *1:* 11. 1851. — *Quercus lineata* Bl. var. *heterochroa* Miquel, l.c.: 855. 1856. — Type: *Junghuhn 9*, Priangan, Java, yfr. (Holotype: U).

Quercus oxyrhyncha Miquel, Fl. Ind. Bat., Suppl. *1:* 347. 1860 —*Quercus lineata* Bl. var. *oxyrhyncha* (Miq.) von Seemen in Bull. Dép. Agr. Ind. Néerl. *1:* 4. 1906. — Type: *Teijsmann H.B. 676*, Alahan Pandjang, Sumatra, st. (Holotype: U).

Quercus hendersoniana A. Camus in Bull. Mus. Paris, Sér. I., *4:* 123. 1932; Les Chênes *1:* 210. 1938; Atl. *1:* t. 6, f. 6–8. 1934. — Type: *Henderson SFN. 18053*, Batu Brinchang, Pahang, Malaya, alt. c. 1600 m, Nov. fr. (Holotype: SING).

Tree c. 20–30 m tall, trunk c. 20–60 cm in diameter. *Bark* smooth grey; inner bark fibrous, reddish-brown. *Young branchlets* dark-grey with sparse lenticels, with dense stiff-pubescence, glabrescent; older branchlets glabrous, lenticellate. Buds globose or ovoid-conical, densely puberulous, glabrescent. *Stipules* linear-acute, c. 1–1.5 by 0.1–0.2 mm, with dense pubescence outside, caducous. *Petiole* c. 1–2 cm long, shallowly furrowed on the adaxial side, with dense pubescence, glabrescent. *Leaves* thin-coriaceous, ovate-elliptic or ovate-lanceolate, c. 5–16 by 2–6 cm, base attenuate-acute, sometimes asymmetrical, margin remotely serrulate in the apical half, apex acute, acuminate or c. 0.5–1.5 cm caudate; upper surface with sparse pubescence, especially on the midrib and lateral nerves, lower surface with dense, adpressed, simple-pubescence. *Midrib* and *lateral nerves* prominent beneath, slightly so above; reticulation prominent below, obscure above, dense, parallel. *Lateral nerves* c. 10–20 pairs, straight, parallel, dense, arcuating near the margin but not anastomosing; forming c. 45°–60° angle with the midrib. *Male inflorescence* c. 5–10 cm long, with dense pubescence; bracts ovate-acute, c. 2–3 by 2 mm, membranous, densely sericeous outside, glabrescent. *Male flowers* solitary or in 3-flowered dichasial clusters along the rachis; perianth 5–6-lobed, with dense tomentum outside; stamens normally 6; filaments c. 0.5–1 mm long, glabrous; anthers c. 0.5 by 0.5 mm; pistillode reduced to a cluster of stiff, simple-hairs. *Female inflorescence* c. 1.5–2 cm long, with dense pubescence, carrying c. 5–6 flowers. Bracts ovate-acute, c. 1–2 mm, with dense tomentum. *Female flowers*: perianth 5–6-lobed; staminodes 0; styles 3 recurved, c. 1–3 mm long. Young cupule ovoid-globose, densely sericeous, lamellae c. 3–4, thick, the 2 lower ones denticulate, the rest entire. *Mature cupule* cup-shaped, obconical, c. 1–1.2 cm deep, 2–2.5 cm in diameter, attenuating towards the base, with dense tomentum outside, rim thick; lamellae c. 8–10, free. *Mature fruit* conical-cylindrical, c. 2–3 cm in length, 1–2 cm in diameter, with dense tomentum; apex attenuate-rounded, base convex.

Ecology: in submontane to montane forests, at c. 1000–2000 alt. Fruiting between August and April.

Distribution: Malaya (Pahang), Sumatra (Lake Toba vicinity, Tapanuli, Alahan Pandjang), Borneo (Mt. Kinabalu), Java (Mt. Karang, Mt. Malabar, Mt. Salak, Mt. Tangkuban Prahu, Mt. Papandajan, Tjidatar, Tjigenteng, Mt. Telomojo, Madiun).

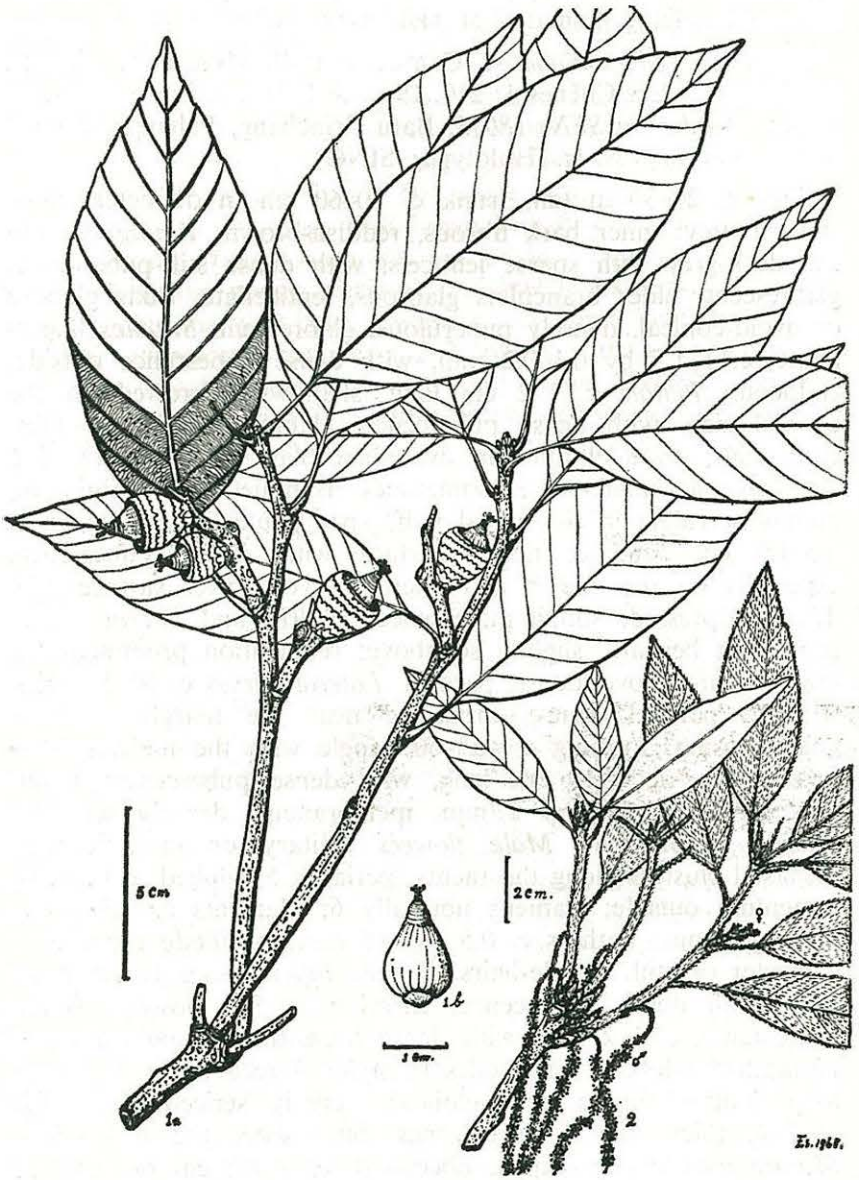

Fig. 16: *Quercus lineata*
1a-b after *Chew & Corner RSNB. 4561;* after *Chew & Corner RSNB. 4927.*

17. **Quercus steenisii** Soepadmo, Map III.

Quercus steenisii Soepadmo in Gard. Bull. Singapore *21*, 3: 389, f. 5. 1966. — Type: *van Steenis 8607*, Mt. Losir, Atjeh, N. Sumatra, alt. c. 3300–3460 m. Febr. fr. (Holotype: BO; insotypes: K, L, SING); paratype: *van Steenis 8379*, Putjuk Angasan, Atjeh, N. Sumatra, alt. c. 2000 m, Jan. fl. (BO, K, L, PNH, SING).

Tree c. 15 m tall, trunk c. 60 cm in diameter. *Young branchlets* with dense brownish-stiff-pubescence; older branchlets glabrous, lenticellate. Buds ovoid-ellipsoid, c. 1–1.5 by 0.5 cm. *Stipules* linear with blunt tip, c. 0.5–1 by 0.1–0.2 cm, with dense pubescence, caducous. *Petiole* c. 0.2–0.5 cm long, thickened at base, flattened on the adaxial side, with dense pubescence, glabrescent. *Leaves* thick-coriaceous, ovate-elliptic or ovate-orbicular, c. 3–8 by 2–5 cm, base rounded, obtuse, or cordate, margin entire or remotely serrulate in the apical half, apex rounded emarginate or bluntly acute; upper surface of the young leaf with dense brownish, stiff-simple-pubescence, glabrescent, lower surface with thick layer of brownish, woolly pubescence, glabrescent. *Midrib* and *lateral nerves* prominent beneath, keeled or flattened above; reticulation prominent beneath, parallel, dense. *Lateral nerves* c. 6–10 pairs, straight, parallel, arcuating towards the margin, forming c. 45°–60° angle with the midrib. *Male inflorescence* c. 5 cm long, with dense pubescence; bracts ovate-obtuse, c. 0.2 by 0.1 cm, densely pubescent. *Male flowers* in 3-flowered dichasial clusters; perianth 4–6-lobed; stamens 4–6; filaments glabrous, c. 1–1.3 mm long; anthers c. 1 by 0.5–1 mm; pistillode reduced to a cluster of stiff, simple-hairs. *Female inflorescence* not known. Young infructescence c. 1.5–3 cm long, with spares lenticels, with brownish, simple-pubescence; carrying 2–7 young fruits; bracts ovate-acute, caducous. Perianth of the female flowers (seen in the young fruit) thick-coriaceous, 5–6-lobed, with dense pubescence outside; staminodes 0–6, rudimentary; styles 3–4, recurved, c. 1–2 mm long. Young cupule ovoid-globose, with dense pubescence ouside; lamellae thick, c. 3–4, the 2 lower ones denticulate, the others entire. *Mature cupule* cup-shaped, obconical, or patelliform, c. 0.7–1 cm in depth, 1.2–2.5 cm in diameter, enclosing c. $\frac{1}{3}$–$\frac{1}{4}$ part of the fruit; lamellae c. 7–8, more or less recurved, with dense brownish pubescence. *Fruit* globose or ovoid, with dense brownish-tomentum, glabrescent, c. 1–2 cm in length and in diameter, apex rounded- or depressed-umbonate, base convex or flat.

Ecology: in montane forest, at c. 2500–3500 m alt. Flowering in January 28, 1937; fruiting in February 2, 1937.

Distribution: so far only known from Mt. Losir, Atjeh, N. Sumatra.

18. **Quercus treubiana** von Seemen, Fig. 17, Map XV.

Quercus treubiana von Seemen in Bull. Dép. Agr. Ind. Néerl. *1*: 3. 1906; in Fedde's Rep. *3*: 173. 1907; Merrill in J. Str. Br. Roy. As. Soc., Spec. No.: 216. 1921; A, Camus, Les Chênes *1*: 368. 1938; Alt. *1*: t. 33, f. 15–17. 1934. — *Cyclobalanopsis treubiana* (v. Seem.) Schottky in Bot. Jahrb. *47*: 648. 1912. — Type: *Hallier 2915*, Mt. Liang Gagang, Borneo, fr. (Holotype: L; isotypes: K, SAR).

Tree c. 30 m tall, trunk c. 60 cm in diameter, bole irregular. *Buttresses* up to 1 m tall. *Bark* rough,, peeling off profusely into rectangular pieces, rusty; inner bark c. 1.5 cm thick, ridged. *Innovations* with dense brownish-simple-pubescence. *Older branchlets* glabrous, lenticellate. Buds ovoid-ellipsoid; scales linear-acute. *Stipules* linear-acute, c. 5–10 mm long, caducous, densely pubescent outside. *Petiole* c. 0.5–1.5 cm long, flattened on the adaxial side, with dense pubescence, glabrescent. *Leaves* thin-chartaceous, linear-lanceolate or elliptic-lanceolate, c. 3–10 by 1–3 cm; base attenuate-acute, sometimes asymmetrical, margin remotely serrulate in the apical half, apex sharply acute or 0.5–1 cm acuminate; lower surface with dense simple-pubescence, glabrescent, upper surface glabrous, except for the midrib and lateral nerves. *Midrib* and *lateral nerves* more or less prominent on both surfaces; reticulation obscure on both surfaces. *Lateral nerves* c. 5–10 pairs, straight, parallel, arcuating towards the margin, forming c. 45°–60° angle with the midrib. *Male inflorescence* c. 3 cm long, rachis c. 0.1 cm thick, with dense pubescence; bracts and bracteoles linear-acute, densely sericeous outside, glabrescent. *Male flowers* solitary or in 3-flowered dichasial clusters along the rachis; perianth 5–6-lobed, the lobes densely sericeous outside; stamens 5–6; filament c. 2 mm long, puberulous at base; anthers c. 0.5–1 mm in length; pistillode reduced to a cluster of stiff-simple hairs. *Female inflorescence* not known. Young infructescence c. 1–2 cm long, rachis c. 1–2 mm thick, with dense woolly pubescence, glabrescent, carrying 2–5 young fruits; bracts ovate-acute, c. 1–1.5 by 0.5–1 mm, with dense tomentum outside. Perianth of the female flowers (seen on the young fruit) 5–6-lobed; styles 3, recurved, c. 2 mm long, with dense tomentum at base. Young cupule ovoid-globose or obconical, lamellae c. 6, with dense tomentum outside. *Mature cupule* cup-shaped, subglobose, base attenuate-rounded, c. 1.5–2 cm deep, 1–2 cm in diameter, covering c. $\frac{1}{3}$–$\frac{1}{2}$ part of the fruit; lamellae 10–12, thick, densely sericeous outside. *Mature fruit* cylindrical-globose, c. 2–3 cm long and 1.5–2 cm in diameter; apex depressed-umbonate; base convex.

Ecology: in low ridges to montane forests at c. 600–2000 m alt. Fruiting in July-August.

Distribution: Sumatra (Palembang), Borneo (Mt. Kinabalu, Mt. Liang Gagang, Mt. Beratus, Mt. Palimasan).

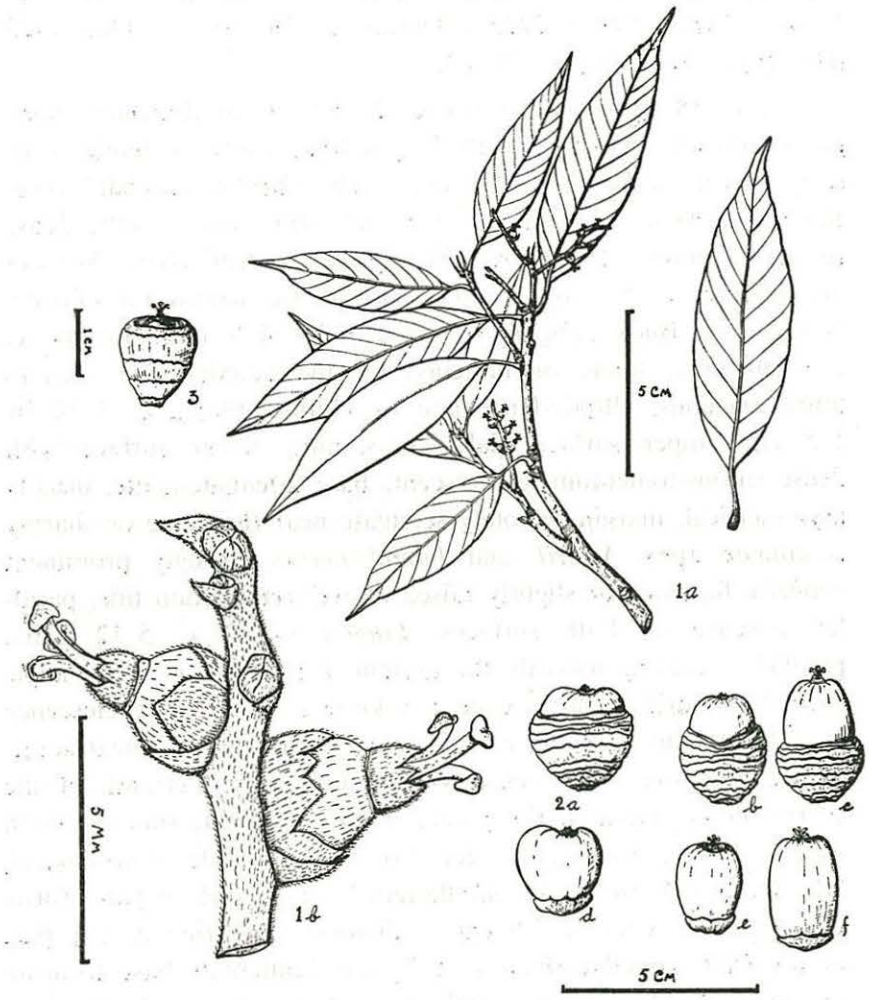

Fig. 17: *Quercus treubiana*
1a-b after *Tikau SAN. 34643;* 2a-f after *Kostermans 7442*; 3 after *Clemens 30465.*

19. **Quercus elmeri** Merr., Fig. 18, Map XVI.

Quercus elmeri Merrill in Univ. Calif. Publ. Bot. *15:* 43. 1925; A. Camus, Les Chênes, *1*: 194. 1938; Atl. *1*: t. 4, f. 9–12. 1934. — Type: *Elmer 21213*, Tawao, N. Borneo, fr. Oct. 1923 (Holotype: K; isotypes: A, L).

Tree c. 18–40 m tall, trunk c. 25–60 cm in diameter. *Bark* greyish-brown, cankered with longitudinal rows of lenticels or scaly; inner bark c. 0.5–1.5 cm thick, fibrous, reddish-brown. *Buttresses* narrow, up to 1.3–3 m tall. *Innovations* with dense rufous-tomentum. *Older branchlets* glabrous, lenticellate. *Stipules* linear-acute, c. 5–7 by 1 mm, with dense tomentum outside, glabrescent. Buds subglobose, c. 3–5 by 4–5 mm. *Petiole* c. 1–3 cm long, terete or flattened on the adaxial side. *Leaves* thin-coriaceous, elliptic-lanceolate or elliptic-oblong, c. 5–14 by 1–5 cm; upper surface glabrous, shining, lower surface with dense rufous-tomentum, glabrescent; base attenuate-acute, usually asymmetrical, margin remotely serrulate near the acute or sharply acuminate apex. *Midrib* and *lateral nerves* strongly prominent beneath, flattened or slightly raised above; reticulation fine, parallel, obscure on both surfaces. *Lateral nerves* c. 5–12 pairs, parallel, arcuating towards the margin, forming c. 60°–70° angle with the midrib. Inflorescence not known. Young infructescence c. 1–2 cm long, carrying c. 1–5 young fruits; bracts linear-acute, c. 1–2 mm long, with dense tomentum outside. Perianth of the female flower (seen in the young fruit) 6–9-lobed; staminodes 0; styles 3–5, c. 2–3 mm long, recurved. Young cupule ovoid-conical, lamellae c. 3–4. *Mature cupule* flattened cup-shaped, or patelliform, c. 0.5–0.7 cm deep, 2–2.5 cm in diameter, covering c. $\frac{1}{3}$–$\frac{1}{4}$ part of the fruit; lamellae thick, c. 5–7; rim denticulate base truncate or rounded. *Mature fruit* ovoid-conical or conical-cylindrical, c. 2–3 cm in length and 1.5–2 cm in diameter, densely sericeous, glabrescent; base truncate or convex, apex rounded — or depressed-umbonate.

Ecology: in lowland to submontane forests, at c. 30–1300 m alt. Fruiting in September-April.

Distribution: Malaya (Pahang, Selangor), Sumatra (Agam, Pajakumbuh, Indragiri), Borneo (Bukit Kalong, Ranau; Mt. Kinabalu, Tawao, Sarawak, Samarinda vicinity).

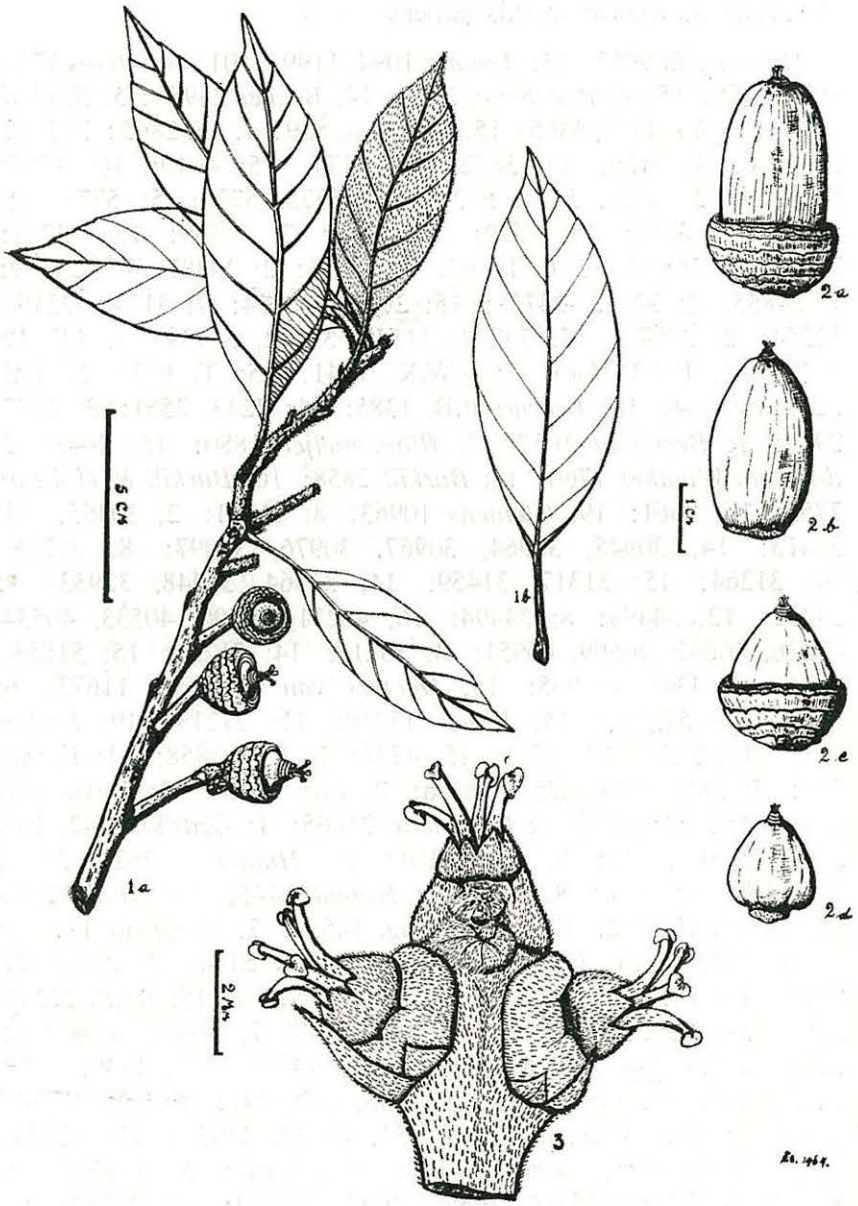

Fig. 18: *Quercus elmeri*
1a-b after *Singh SAN. 28310*; 2a-d after *Elmer 21213;* 3 after *Anderson et alia S. 15374.*

List of identifications

(The number following the colon corresponds to the number of species as treated in this paper).

Abbe et alia 9957: 13; *Achmat* 1094, 1199, 1501: 6; *Alvins* 1723, HS. 14675: 15; *Ashton Brun.* 2378: 14; *Backer* 25956: 5; *Bakhuizen v.d. Brink* 4451, 6465: 15; *Bangham* 859: 4; *bb.* 2865: 2; 3102: 5; 3106: 4; 3126: 15; 3832: 16; 4177: 15; 4640: 16; 4784: 5; 5219: 2; 5326, 5471, 5624: 15; 5775, 5776: 5; 5778: 15; 5882: 19; 6521: 15; 6572: 19; 6739: 2; 10389: 15; 12708: 7; 14468: 16; 15952; 6; 16103: 7; 18994: 2; 20387: 15; 20389: 7; 20855: 2; 22382, 24758: 15; 29598, 30134: 7; 31703, 32190, 32254: 2; 33943: 15; 34224, 34346, 34392, 34439: 7; *bb.* Ja. 3029: 15; P.T.P. 740: 7; S.W.K. 1–41: 15; T. 937: 2; T.B. 211: 15; 604: 18; *Beccari* P.B. 1385: 11; 2243, 2551: 3; 2757, 2919: 7; *Berkhout* 1057: 7; *Bünnemeijer* 1880: 15; 2048: 2; *Borssum Waalkes* 1760: 15; *Burkill* 2858: 16; *Burkill & Holttum* 7753: 16; 8661: 19; *Clemens* 10963: 8; 11211: 2; 30465: 15; 30813: 14; 30948, 30964, 30967, 30976, 31097: 8; 31238: 14; 31264: 15; 31317, 31459: 14; 32364, 32448, 32933: 8; 34492: 12; 34493: 8; 34494: 16; 40231, 40390, 40533, 40534, 40536, 40637, 40699, 40951: 8; 50215: 14; 51254: 15; 51658: 2; *Curtis* 434: 4; 905: 15; *Docters van Leeuwen* 11673: 6; *Elbert* 56, 57, 58: 15; *Elmer* 13219: 11; 21213: 19; *Endert* 3215: 15; 3624: 14; 4511: 15; 4731: 2; *F.B.* 3858: 11; *Forbes* 572: 7; 585, 2719, 2753, 3834a: 2; *Fox* 14536: 2; *Foxworthy* B.S. 566: : 11; *Fuchs & Collenette* 21665: 1; *Grashoff* 142, 160, 230: 2; 800, 842: 7; 907, 1101: 15; *Hallier f.* 2628, 2864: 2; 2915: 18; 2950: 8; 3349: 2; *Hamid* 5445: 15; *Haniff* 231: 15; *Haviland* 1772: 12; *Herb. Sing.* 14534: 7; *Horsfield* 11: 15; *Hotta* 14732: 14; *Ichlas* 102: 15; *Jacobs* 5114: 2; *Junghuhn* 9, 63: 16; 70: 15; *Kadir* 63: 7; *Kalshoven* 10: 15; *KEP.* 22574, 29828, 31071: 5; 34029, 34031: 15; 38048: 7; 71649: 8; 99590: 2; *Koorders* 1407, 1408, 1410, 1418, 1435, 1439, 1440, 1468, 1472, 1475: 15; 1487, 1488: 5; 1503, 1526: 15; 1533: 5; 10940, 10941, 10946, 11729, 11928, 11931, 11932, 11933: 15; 12453: 16; 13859, 13955, 14051, 14118: 15; 14184: 5; 14930: 15; 15342: 5; 23863, 25716, 26562, 26670, 26784: 15; 27713: 16; 29204, 29247, 32762: 15; 33299: 5; 33415, 33737: 15; 33745: 16; 33762: 15; 37141, 37146: 16; 38144, 38145, 38151: 15; 38484: 5; 38624, 38689, 38695, 38698: 15; 38784: 5; 38801: 15; 39430: 5; 39608: 15; 40101: 16; *Korthals* HB. 7949: 2; *Kostermans* S. 92: 2; 4078, 4180; 7; 4433: 6; 4474, 6368: 7; 6530: 6; 7442: 18; 8963: 11; 10235, 12795: 7; 13030: 18; *Kostermans & Anta* 99: 15; 152: 7; 419, 463, 514, 801: 15; 1240, 1324, 1326: 7; *Krukoff* 4016: 15; *Kunstler* (King's collector) 3723, 8258: 4; *Labohm* 1130: 2; *Lands* 27204: 16; *Lörzing* 11449: 15; 15661: 16; *Meijer* 3253: 16; 5879: 15; 8687: 5; *Meijer &Amiruddin* 23: 19; *Monterie* 51: 16; *Nur*

7378: 15; *Poore* HS. 14900: 16; *Poore* 855: 15; 1315: 5; 1321: 16; 1334: 15; 1348, 1378: 5; *Purseglove* 4263: 19; *Rajab* 482, 483: 5; 607: 16; *Richards* 1885: 10; *Ridley* 6443: 2; *RSNB.* 490: 2; 4248: 19; 4363: 8; 4427: 2; 4434: 1; 4451: 13; 4500: 8; 4533: 2; 4534, 4564: 16; 4792: 14; 4893, 4927: 16; 4976: 19; 7002: 14; 7096: 16; 7148: 13; 8411: 2; *SAN.* 3621a: 15; 16188, 16565: 6; 16683, 16811: 4; 19129: 15; 19868: 7; 20219: 2; 20731: 15; 20732: 2; 20973: 13; 21088: 8; 21342: 19; 24051: 18; 24106, 24121: 8; 24353: 15; 25119: 7; 25336: 13; 28276: 7; 28307: 15; 28310: 19; 28808: 8; 28919: 7; 28991: 16; 29060: 8; 29131: 14; 29134: 14; 30869: 16; 31936: 15; 32253: 11; 33131: 16; 33714: 2; 33949: 14; 34504: 8; 34643: 18; 34742: 7; 38069: 16; 38608, 39135: 8; 41832: 16; 42096, 44309, 44478: 8; 48115: 13; 49459, 49749: 15; 51434, 51438: 8; 53861: 15; *SAR.* 154: 4; 1065, 1070: 12; 2999: 10; 3919, 3946: 3; 4504, 4543, 4547: 14; 4580: 19; 4661: 12; 7553: 3; 12615: 2; 12622: 19; 12624, 13182, 13315: 2; 13562, 13565: 7; 15095: 14; 15374: 15534: 4; 16315: 2; 20011, 20021: 14; 20107: 2; 20115: 3; 20121: 9; 20135: 2; 20226: 9; 20801, 20802: 11; 22462: 6; 22650: 2; *Sauveur* 14, 70: 7; *SFN.* 10252: 3; 11798: 15; 18053: 16; 20191: 2; 23545, 23547: 16; 36268, 27668: 8; 27794: 15; 31253: 16; 31798: 5; 31973: 15; 35936: 19; 36275: 15; 36398: 2; *Soekaria* 107: 2; *Strugnell* 20308: 15; *Symington* 37664: 7; *Teijsmann* HB. 676: 16; 7595: 15; 7638, 7642, 7643: 7; 7649: 2; 3882, 21080: 7; *Toha* 2057: 2; *van Steenis* 904: 2; 8264: 16; 8379, 8607: 17; *Verhoef* 104: 2; *van de Vreeden* 93: 7; *Watson* 5817: 15; *Winckel* 970: 5; *Wind* 43: 16; *Wray* 1532: 15.

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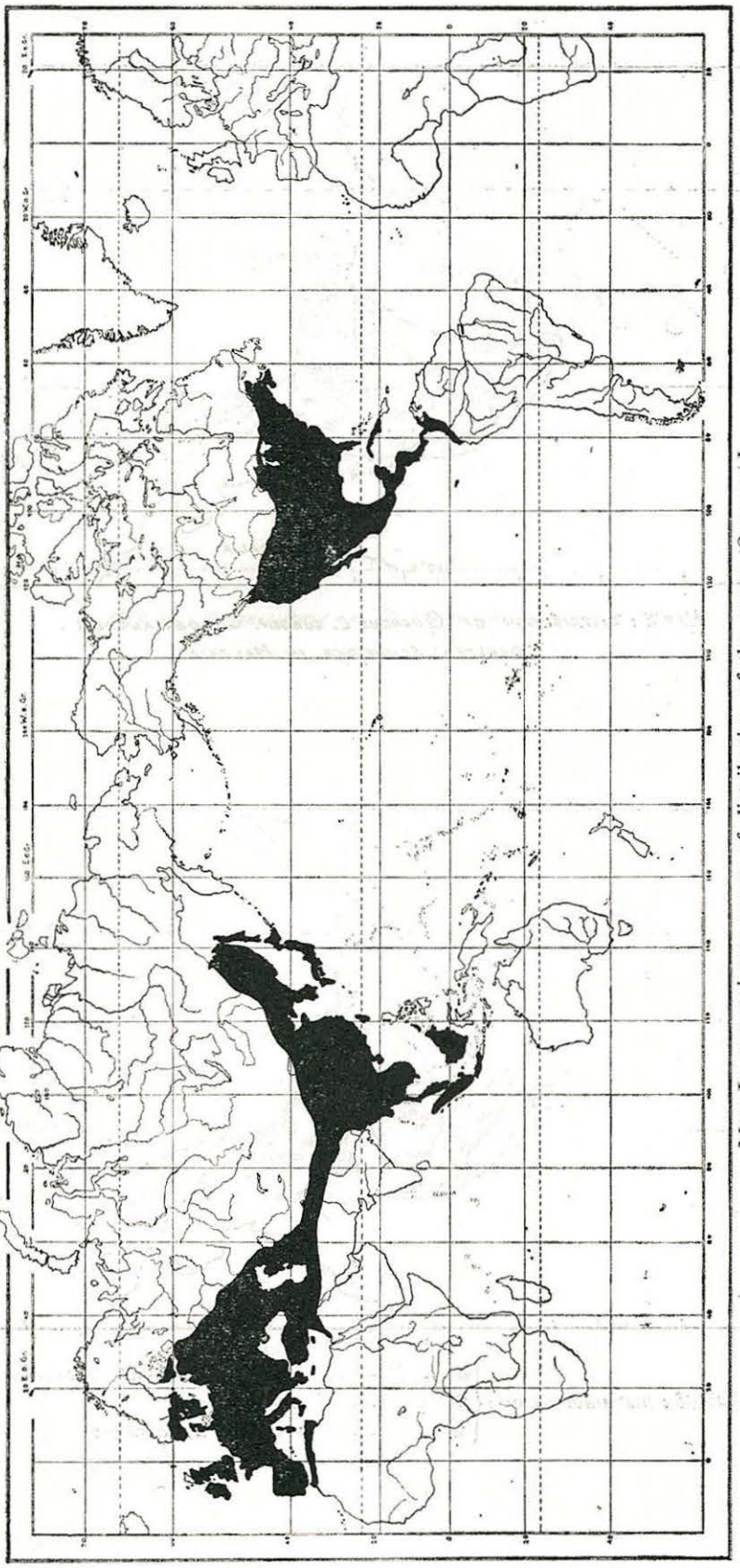
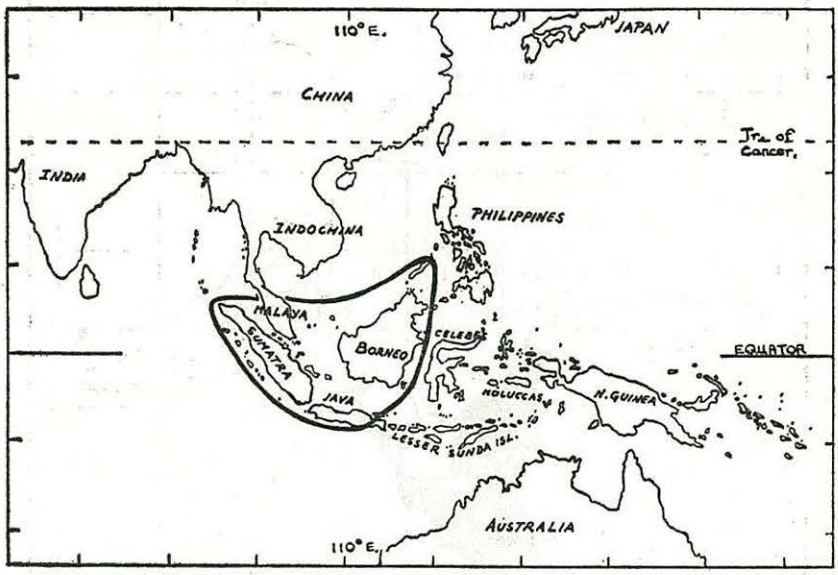
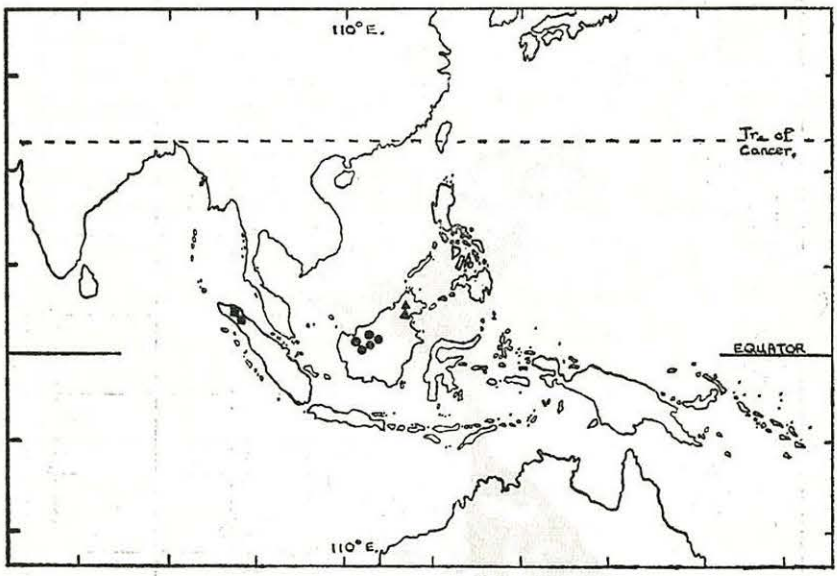


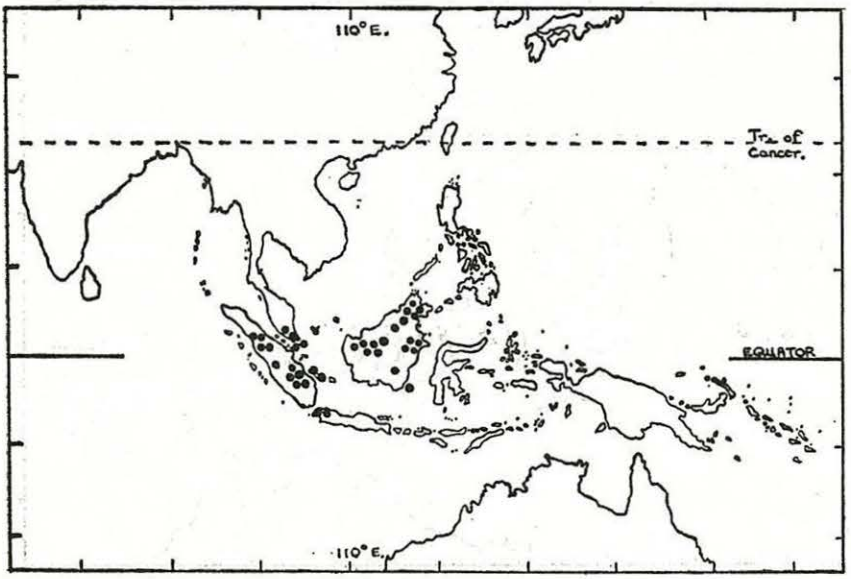
Map 1: approximate range of distribution of the genus *Quercus* L.



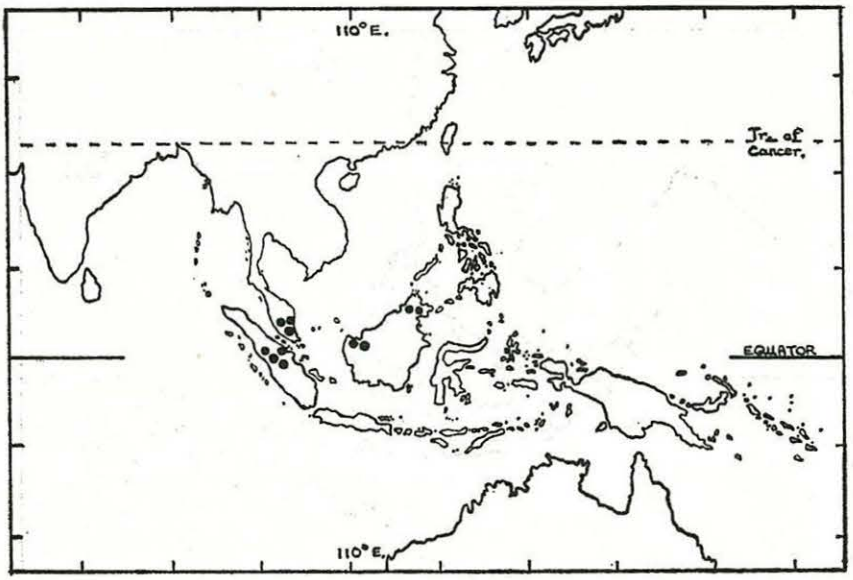
MAP II : DISTRIBUTION OF *QUERCUS* L. SUBGEN. CYCLOBALANOPSIS (OERSTED) SCHNEIDER IN MALESIA.



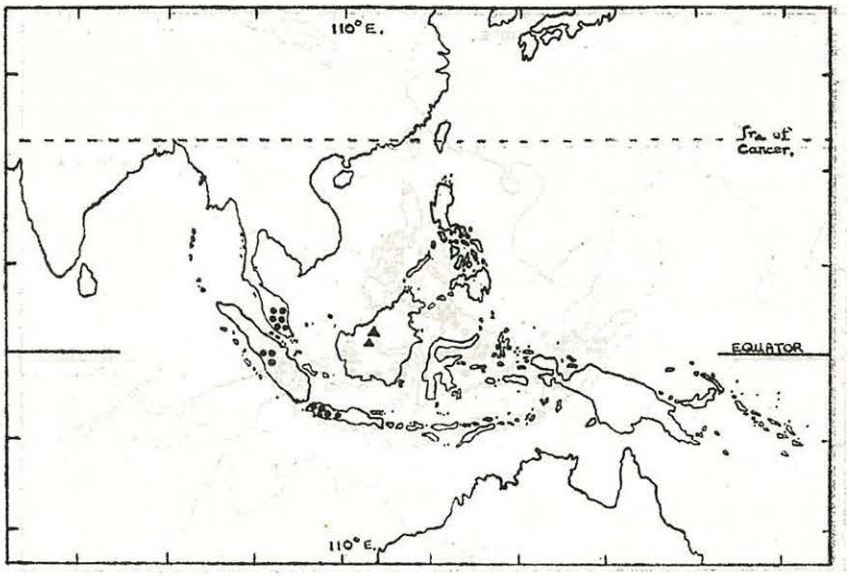
MAP III : DISTRIBUTION OF :
- ▲ = *QUERCUS PSEUDO-VERTICILLATA* E. SOEPADMO
- ● = -"- *NIVEA* KING
- ■ = -"- *STEENISII* E. SOEPADMO



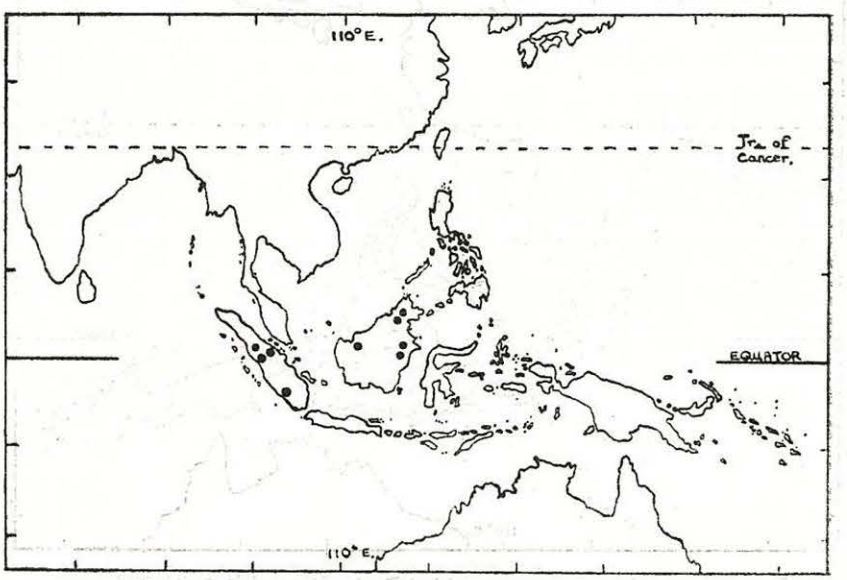
MAP IV : DISTRIBUTION OF *Q.* ARGENTATA KORTH.



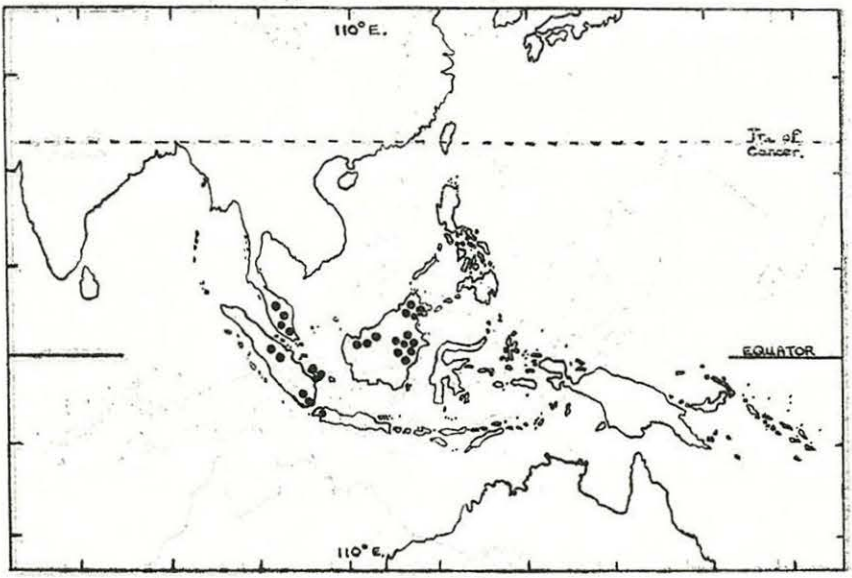
MAP V : DISTRIBUTION OF *Q.* GAHARUENSIS E. SOEPADMO



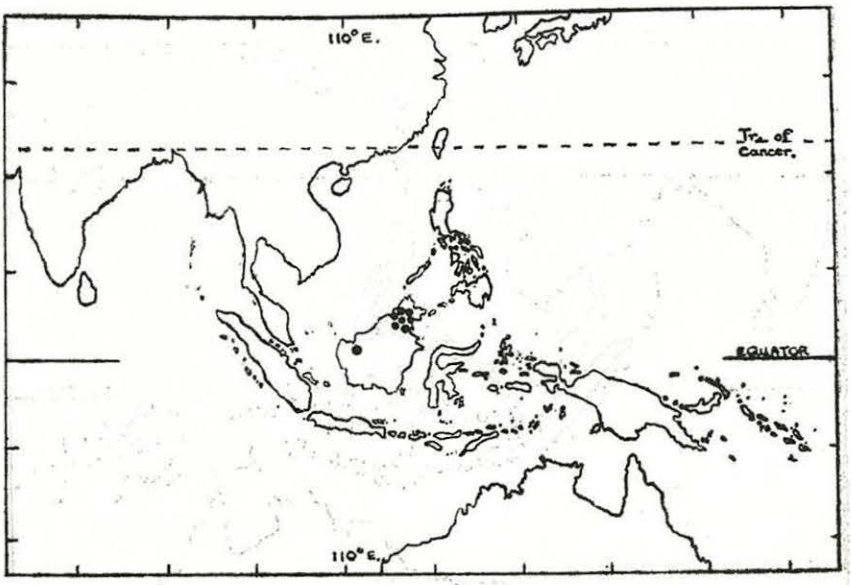
MAP VI : DISTRIBUTION OF ● = *Q. OIDOCARPA* KORTH. ▲ = *Q. PERCORIACEA* E. SOEPADMO



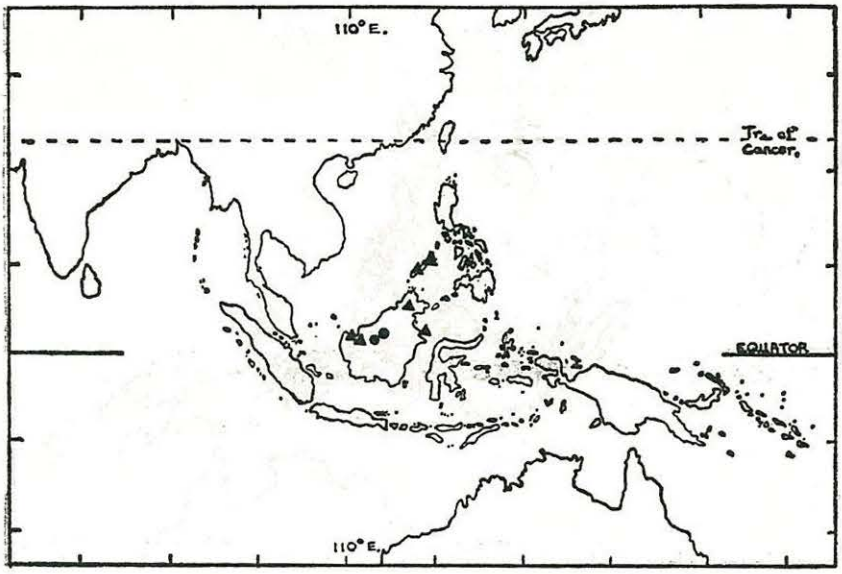
MAP VII : DISTRIBUTION OF *Q. SUMATRANA* E. SOEPADMO



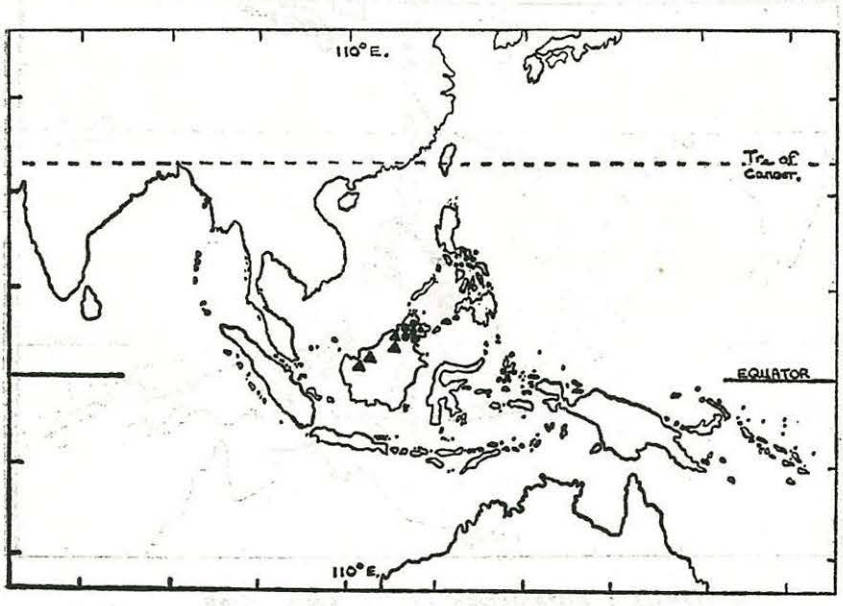
MAP VIII : DISTRIBUTION OF *Q. SUBSERICEA* A. CAMUS



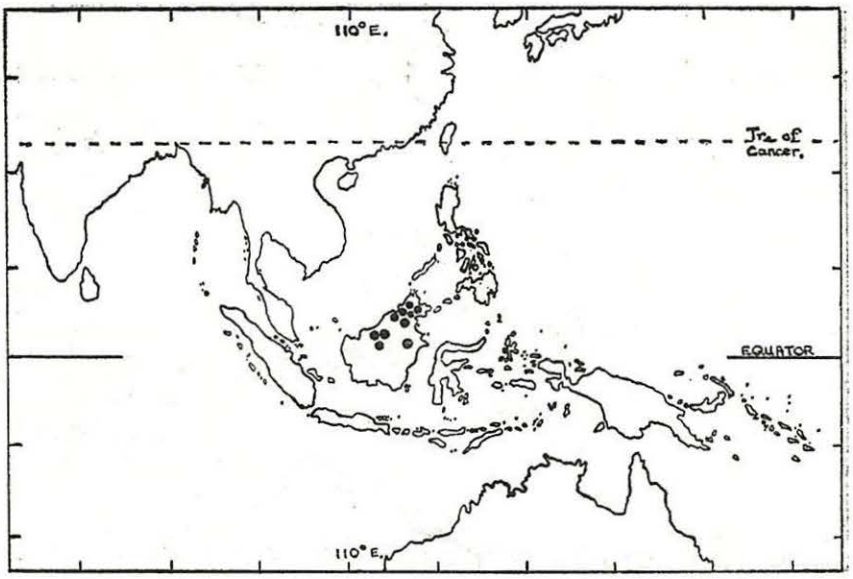
MAP IX : DISTRIBUTION OF *Q. LOWII* KING



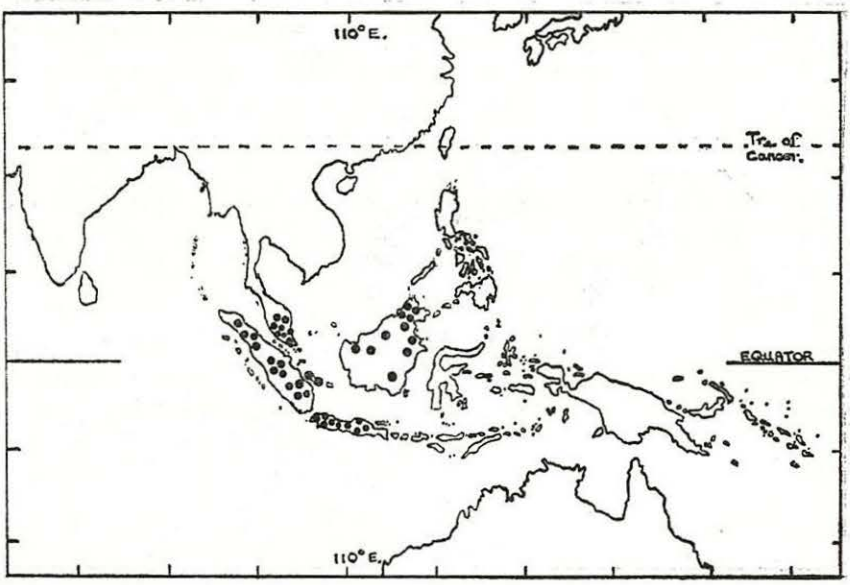
MAP X: DISTRIBUTION OF ● = *Q. CHRYSOTRICHA* A. CAMUS; ▲ = *Q. MERRILLII* v. SEEMEN



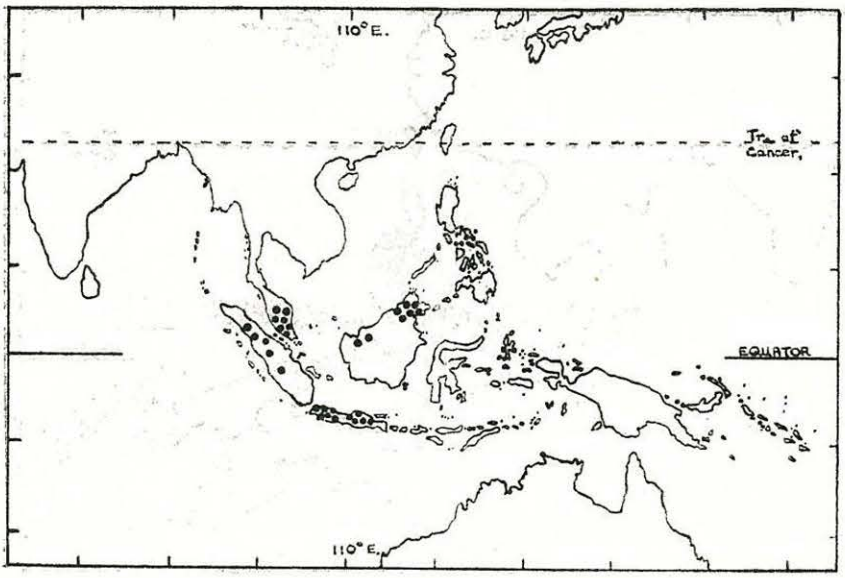
MAP XI: DISTRIBUTION OF ▲ = *Q. KERANGASENSIS* E. SOEPADMO; ● = *Q. KINABALUENSIS* E. SOEPADMO



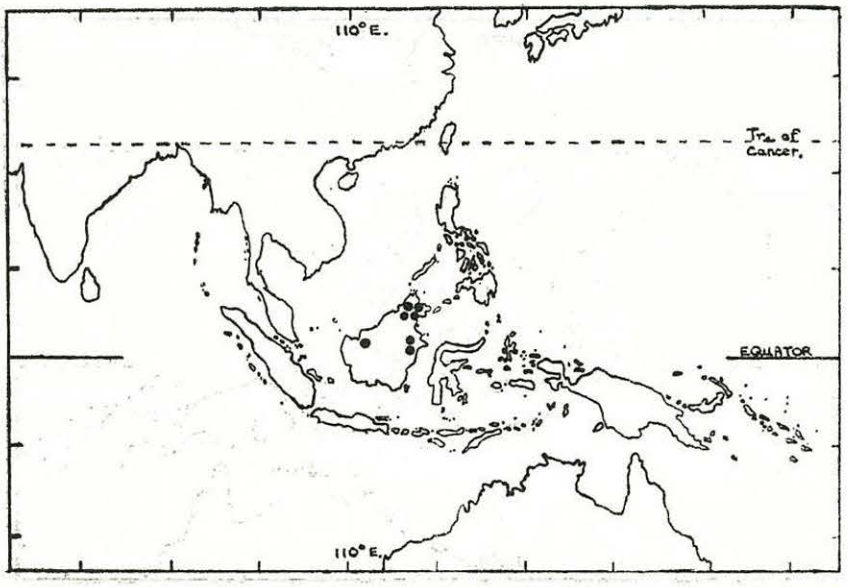
MAP XII : DISTRIBUTION OF *Q. VALDINERVOSA* A. SOEPADMO



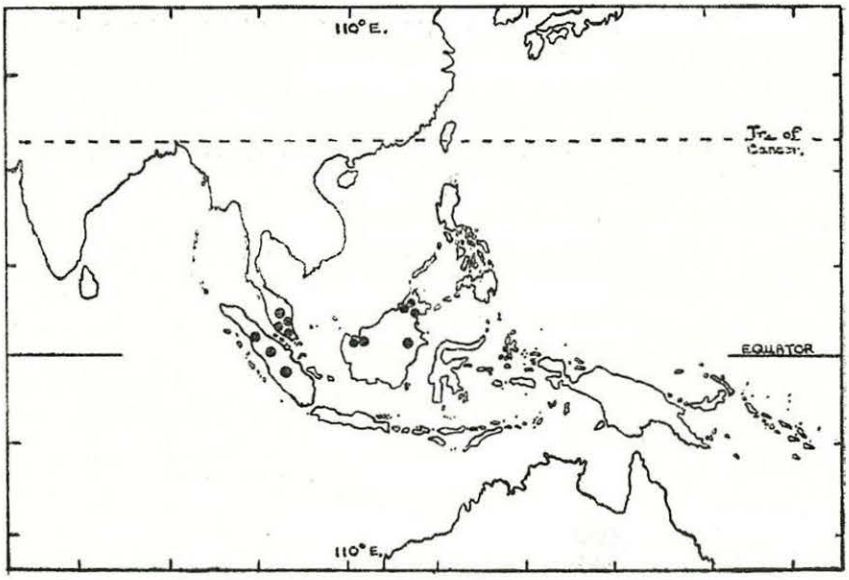
MAP XIII : DISTRIBUTION OF *Q. GEMELLIFLORA* BL.



MAP XIV : DISTRIBUTION OF *Q. LINEATA* BL.



MAP XV : DISTRIBUTION OF *Q. TREUBIANA* v. SEEMEN



MAP XVI : DISTRIBUTION OF *Q. ELMERI* MERR.