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Morphological and Molecular Diversity in *Lithocarpus* (Fagaceae) of Mount Kinabalu

Charles H. Cannon

Department of Botany,
Duke University,
Durham, NC 27708, U.S.A.

SUMMARY. Morphological and molecular diversity in *Lithocarpus* is discussed in the context of the 37 species of the genus occurring on Mount Kinabalu. *Lithocarpus* has been divided into 13 subgroups, five of which are represented on Kinabalu. Fruit-type evolution was explored in detail. An enclosed receptacle (ER) fruit occurs in at least two sections. Evolution of the ER fruit type appears to have been rapid, with little corresponding molecular change. In contrast, the genera *Lithocarpus* and *Quercus* have large amounts of genetic sequence change but little morphological differentiation of the acorn type of fruit. The ER fruit type is particularly common at higher elevations. It is suggested that this rapidly evolving characteristic may allow extended seed dormancy in the soil. Genetic diversity in the chloroplast genome was found to be high in landscape-level sequence variation, with two main lineages observed, one shared between mainland and island populations and the other confined to Borneo. The Kinabalu samples appear to be a mixture of the two lineages, and overall contained relatively low amounts of diversity. Macroevolutionary and biogeographic patterns in phenotype, nuclear genotype, and cytoplasmic genotype may differ greatly in different populations. Phenotypic evidence suggests convergent evolution in separate lineages toward the ER fruit type, significant decoupling of molecular and morphological change at important transitions, and considerable congruence between nuclear sequence data and morphology. Chloroplast genotypes shared between Kinabalu species and those in southern China, however, indicate ancient connections and support the hypothesis that northern Borneo has provided a refugium for mesic tropical rain forest since the Tertiary.

INTRODUCTION

The mixed communities of stone oak (*Lithocarpus)* found on Mount Kinabalu are an extraordinary natural laboratory and a readily accessible microcosm of the extensive highland areas found throughout northern Borneo. The Kinabalu flora with 37 species of *Lithocarpus* (Beaman *et al.* 2001) includes nearly two-thirds of the Bornean species (Soepadmo 1972, Soepadmo *et al.* 2000). Evolutionary and ecological processes affecting this large genus of trees are influenced by diverse soil types, sharp topographic features (Beaman & Beaman 1990), and a full range of habitats from lowland dipterocarp to high montane cloud forest (Meijer 1996). The common expression "oak-laurel forest" is perhaps a misnomer for the diverse montane communities in which *Lithocarpus* occurs, but the stone oaks do form a significant portion of the vegetation, both in structure and diversity (Aiba & Kitayama 1999).

This paper presents our current understanding of the morphological and molecular diversity of these trees on Mount Kinabalu. As an introduction, current taxonomic issues will be presented and discussed. The genus is relatively well known at the species level (Soepadmo 1972, Soepadmo *et al.* 2000, Cannon & Manos 2000), and keys for identification and field guides are available (Cockburn 1976, Soepadmo *et al.* 2000). Some of the noteworthy species are discussed below, including comments on field identification, allies, and taxonomic problems. Recent findings about fruit-type evolution and landscape-level genetic variation across Southeast Asia indicate that macroevolutionary patterns of phenotype and nuclear and cytoplasmic DNA data do not always agree. A brief outline of these findings sketches the background for a discussion of important life-history traits and possible dynamics of gene flow within the genus, particularly during possible refugial periods on Mount Kinabalu.

GENERAL DESCRIPTION OF THE GENUS

The stone oaks are the largest genus in the Castanoideae (Camus 1954), with more than 200 Asian species (Huang *et al.* 2000), including 61 in Borneo (Soepadmo 1972). All species are monoecious, although bisexual (functional?) flowers are occasionally found on androgynous spikes. Floral displays often consist of large numbers of spikes forming an "inflorescence," although most spikes are simple and arise from the axil of a much reduced leaf (Kaul 1986). Spikes bearing male flowers are always basal on the flowering branch in relation to the terminal androgynous and female spikes. Male flowers open first, releasing a heavy musky odor. Morphology of the male flower varies little in the genus, with a much reduced perianth, twelve dorsifixed exserted stamens, small anthers, and a tomentose pistillode present throughout the subfamily.

Pollinators include a diverse assemblage of insects, which apparently feed on pollen, most of which is trapped in the pistillode as the anthers extend at anthesis. The period of receptivity of the female flowers is unknown. Little morphological change occurs for up to six months after the flowers have opened. The successful pollination of the female flowers is a mystery as they provide little attraction to pollinators. During many hours of observation, I recorded a single visit by a potential pollinator to a female spike, which appeared to be accidental.

The fruit consists of a hard dry nut seated in a woody cupule, formed by a much reduced and compressed sterile branching structure (Forman 1966, Fey & Endress 1983, Nixon & Crepet 1989). Fruit morphology supports the majority of the infrageneric classification within the genus (Camus 1954). Two main fruit types are distinguished by differences in internal morphology: "acorns" are almost identical to temperate oak fruits, while "enclosed receptacle" (or "ER") nuts are almost completely fused to the cupule, forming a compound structure (Fig. 1). The cupule types are distinguished by the presence of scales, spines, or fused rings ("lamellae") on the outside of the cupule. Cupules can also enclose the acorn nut without being fused to it, a condition which occurs in most sections.

The geographical distribution of *Lithocarpus* extends from eastern India, southern China and into Japan to the north and through much of Southeast Asia, including New Guinea, to the south. One species, *Lithocarpus densiflorus*, is found in the northwestern U.S.A. Species diversity drops off sharply east of Wallace's line, although a morphologically diverse group of species is found in New Guinea. The trees are found on almost all soil types except limestone outcrops, where the absence of ectomycorrhizal symbionts may prevent establishment. Occupying all elevational zones and most habitats, except mangrove swamps, the genus attains its highest diversity and density in lower montane forests on relatively poor soils (1000–2000 m). Few species are found in secondary forests, although *L. havilandii*, *L. papillifer* and *L. conocarpus* occasionally form dense stands along forest margins and roadcuts at elevations above 1500 m.

Generally poorly formed, the stone oaks have never been considered "timber trees," because their boles often lean and their wood is not durable (Burgess 1966), and they often have little clear trunk before the first branch. Larger trees occasionally consist of several trunks which arise through continuous coppicing near the base, a behavior present to some extent in many species but never reaching the development seen in *Trigonobalanus verticillata* (Fagaceae) (Forman 1965, Corner 1996). The outer bark is generally smooth and light gray to silver in color, while a slash reveals the multiseriate rays in

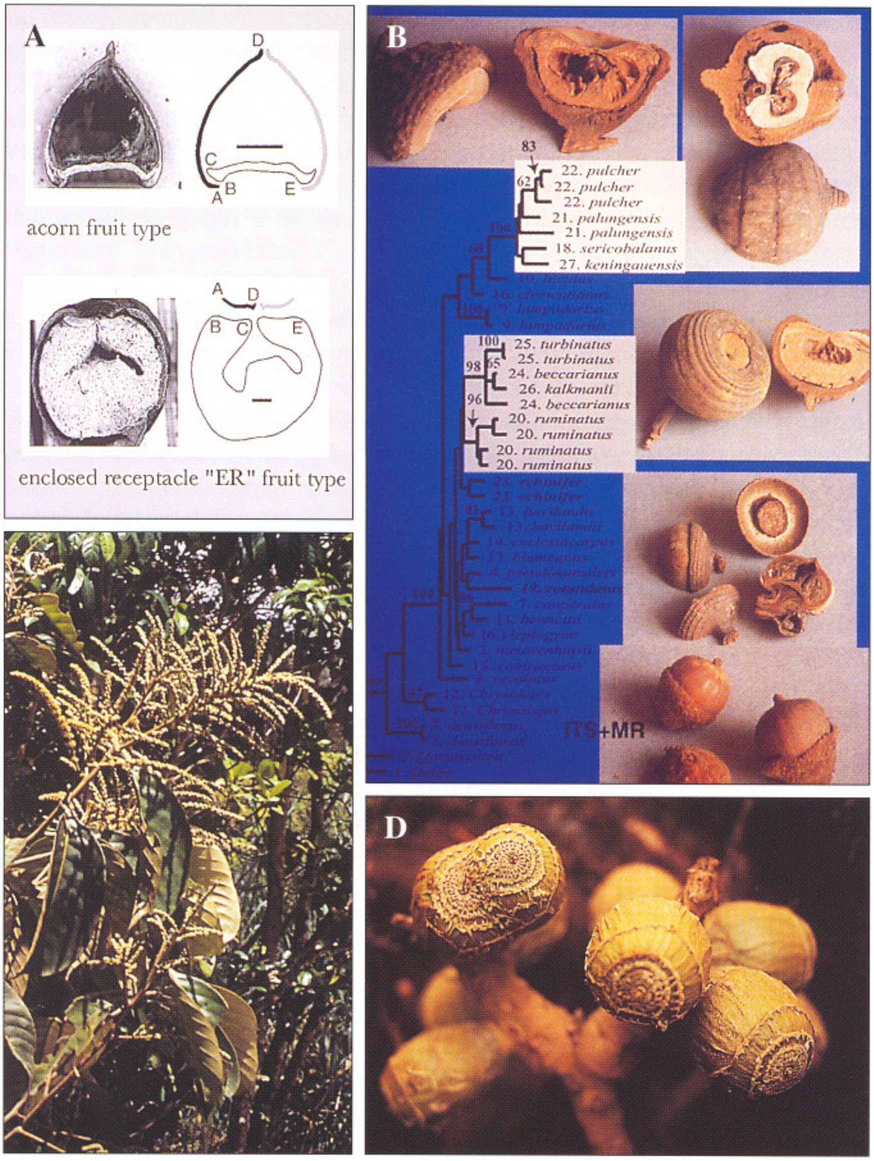

Fig. 1. (A) Homology of internal fruit morphology between the acorn and ER fruit types. Mature fruit of *L. conocarpus* (top) and *L. kalkmanii* (bottom) are shown. Labels A–E illustrate corresponding homologous points on the shape outline. Exocarp layers are shaded (black shapes were used in analyses) and the receptacle layer is clear. (B) Major fruit types and their phylogenetic relationships. From top to bottom; *L. pulcher*, *L. keningauensis*, *L. ruminatus*, *L. clementianus*, and *L. nieuwenhuisii*. (C) Typical floral display by *Lithocarpus hatusimae*. The majority of flowers are male with few terminal female flowers. (D) Young infructescence of *L. turbinatus*. Prominent lamellae ring the cupule, which completely encloses the fruit.

the sapwood (Aye *et al.* 1997). The outer bark strips away easily, without latex or strong odor, a slightly acrid scent arising sometimes. The inner bark or cambium has ridges that project into the sapwood. Small raised lenticels of various sizes and arrangements are usually obvious and the texture and shape of flaking is rather irregular. Buttresses, when present, are low and rounded. Stilt roots and flying buttresses can be found but are not well developed. Leaves have entire margins and short thick petioles which remain the same thickness to the blade base. The underside of the leaf is usually coated with closely appressed, thick walled trichomes, silver to rufous in color, normally too small to be distinguished with a 10× hand lens (Jones 1986).

TAXONOMY AND FIELD CHARACTERISTICS

Camus (1954) recognized 13 subgenera of *Lithocarpus*, which are here considered to be sections rather than subgenera. Five sections are represented on Mount Kinabalu. Most of the remaining groups are small in species number and are defined by qualitative morphological characters.

Section *Lithocarpus*

A small and primarily montane group, the species of section *Lithocarpus* are easily recognized by the large woody fruit with a smooth cupule with concentric or spiral rings (lamellae) completely enclosing the nut. Solitary fruits often have aborted flowers at their base and occasionally two mature fruits can be found fused together. The trees are often small in diameter (30–40 cm DBH) and most have smooth light-coloured bark with prominent and large lenticels. Floral spikes are short and stout and fruiting spikes seldom carry more than six fruit. Additional species are found in Java, Sumatra, and Peninsular Malaysia. Similar morphologies are found in Indochina as well (Camus 1954), although they may represent an independent lineage (Manos *et al.*, in review).

Lithocarpus turbinatus is common along the summit trail above 2000 m, particularly west of Pondok Lowi. This species is a high-elevation specialist, found only in Sabah, Central Kalimantan, and north-central Sarawak. *Lithocarpus beccarianus* is its low elevation counterpart, often found along the northwestern coast of Sabah and Sarawak (also found in West Kalimantan) but rare on Mount Kinabalu. *Lithocarpus kalkmanii* is gregarious on Kinabalu: the six individuals I have found are within 200 m of one another on the slope leading down to the Silau-silau River beyond the Bundu Tuhan lookout. I have seen scattered individuals in the Bario region of northeastern Sarawak. This species is one of the largest in the genus, both in trunk diameter and fruit size.

Lithocarpus ruminatus is a common and widespread species found throughout Borneo. These trees are generally small and rather cryptic and usually can be found by locating mature fruit or fallen leaves on the ground. The leaves are distinctive, being ovate-lanceolate with a short acuminate tip and having a short thickened black petiole. The first basal pair of secondary veins arise at a highly divergent angle from the rest of the veins. Numerous scattered individuals were found on the mountain, particularly along the Kiau View Trail.

Two other species in this section, *L. porcatus* and *L. hallieri*, also are found on Kinabalu but remain poorly known. Few collections are available, and I have encountered no reproductive individuals in the field. Some confusion with other species may exist, because during early stages of fruit maturation, related taxa may resemble these species.

Section *Synaedrys*

These are primarily coastal lowland trees. The section has been classically defined by spiny-cupped ER fruit, but molecular and morphometric evidence suggests that this definition should be expanded (Cannon 2000). The nut is distinctive when removed from the cupule and the "shoulder" ringing the perimeter of the fruit is visible. Floral spikes are usually short and thick and clusters are always reduced to a single female flower. As currently defined, this group includes two distinct leaf types: one stiff and rigid, having numerous strong parallel veins arising almost perpendicular to the midrib, prominently raised above the surface of the lamina on the underside, and the other flexible, with visible but not raised veins, arising at a low angle to the midrib. Additional species of this section are found in Indochina but molecular evidence suggests they may represent an independent lineage (Manos *et al.,* in review).

Lithocarpus rotundatus is the only species in this section found on Mount Kinabalu. Several individuals were observed in rocky stream beds near Kiau. The species becomes a large tree with dark bark. The fruits can be large, almost the size of a fist, with a dark brittle cupule with short, erect, simple spines. No rings or lines are apparent between the scales.

The remaining species are concentrated along the northwest coast with a sharp boundary in the distributions between *L. pulcher* and *L. echinifer*. *Lithocarpus palungensis* (Cannon & Manos 2000) has been collected in only two locations: the central Bornean highlands in northwest Sarawak and Gunung Palung, West Kalimantan. On the basis of molecular evidence, two species with smooth cupules, *L. sericobalanus* and *L. keningauensis*, belong in this group (see Fig. 2). *Lithocarpus sericobalanus* is a lowland counterpart of *L. pulcher*; *L. keningauensis* is a highland species which produces enormous fruits with a thick corky cupule completely fused around the nut, the internal structure of which is also highly modified.

Section *Gymnobalanus*

This is a small group with only two species occurring in Borneo, and is distinguished mainly by the presence of rufous-coloured glandular hairs on the underside of the leaves. The fruits are small and seated in a flattened cupule, which has reduced scales and obscure lamellae. Few fruits are present on the spikes. Thick cupules and fused scales are present in species found in mainland Asia and in New Guinea.

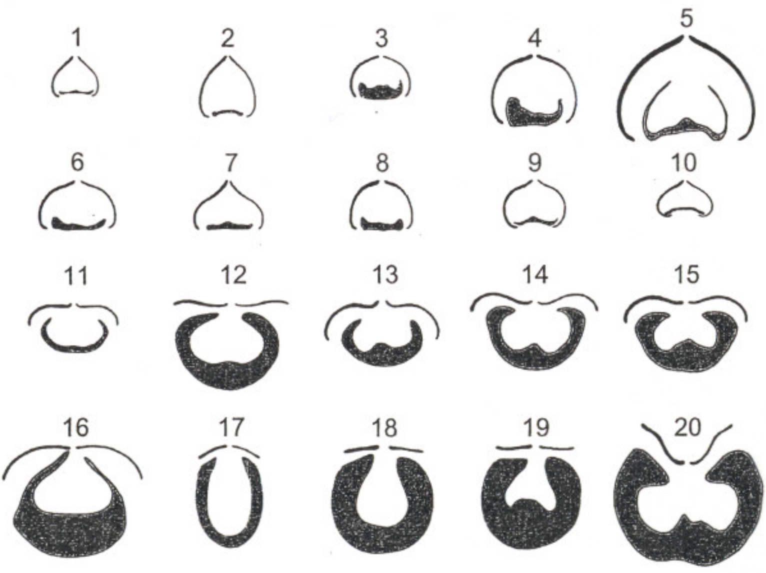

Fig. 2. Mean shape of mature fruit for twenty species of *Lithocarpus* (Fagaceae). (1) *L. bennettii*, (2) *L. conocarpus*, (3) *L. luteus*, (4) *L. lampadarius*, (5) *L. revolutus*, (6) *L. clementianus*, (7) *L. blumeanus*, (8) *L. lucidus*, (9) *L. enclesiacarpus*, (10) *L. havilandii*, (11) *L. echinifer*, (12) *L. rotundatus*, (13) *L. sericobalanus*, (14) *L. pulcher*, (15) *L. palungensis*, (16) *L. ruminatus*, (17) *L. beccarianus*, (18) *L. turbinatus*, (19) *L. kalkmanii*, (20) *L. keningauensis*. Outlines of radial sections, centered on the style, of the exocarp (black) and receptacle (gray) are shown. Pericarp and seed not shown.

Lithocarpus havilandii is the most common stone oak along Park Headquarters roads and on the road to the Power Station. The leaves are densely covered on the underside with large rufous multiradiate hairs while the upper side is dark glossy green. These trees may be the closest thing in the genus to a secondary species, because they regenerate readily along roadcuts and in open areas. Populations appear to flower and fruit somewhat continuously, with individuals flushing asynchronously. This species is also one of the few found on both sides of Wallace's Line, suggesting that the small fruits may be dispersed by birds.

Lithocarpus papillifer also inhabits roadcuts and exposed areas, and is easily confused with the preceding species. Although the *L. havilandii* hair type can be found occasionally on the petioles and developing leaves of this species, it is marked by dark, scattered papillae. Intermediate forms occur, suggesting hybridization between the two species.

Section *Pasania*

This most widespread section is found throughout the range of the genus. The section is common and diverse at mid-elevations, often forming mixed communities of ten or more sympatric species, all having rather low population densities. They are mostly medium-sized trees, and all produce acorn fruits, with the fusion between cupule and nut being restricted to a small basal area. The amount of cupule enclosure ranges from minimal to complete. The cupules are densely covered with whorled scales, varying from reduced bracts to erect simple spines. Fruiting spikes are often large, with numerous clusters of mature and aborted fruits. Frequently, more than one fruit per cluster will mature.

Few characteristics other than the cupule scales unite the group. Several species described by Soepadmo (1972) have greatly thickened cupules with fused scales and are only tentatively placed in this section. Although a few intermediate morphologies are found, the lack of structural novelty would make circumscription of a new section of dubious utility.

Lithocarpus elegans is the most widespread species in the section, occurring from southern China to Sulawesi. It is the most "oak-like" of all stone oaks, having thin, glabrous leaves that are clustered at the twig tips. The fruits are often in clusters of three or more and the nuts can become so crowded on the spike that they are misshapen at maturity. The species usually is not found above 1500 m elevation. *Lithocarpus pseudokunstleri* is similar but less frequent and found mostly above 1500 m. *Lithocarpus nieuwenhuisii*, *L. ferrugineus*, and *L. jacobsii* are occasional trees, mostly in the lowlands, with dense rufous tomentum on thin cupules which have well spaced scales. The leaves are largely glabrous with scattered erect bifid trichomes visible with the naked eye. Individuals of *L. nieuwenhuisii* are often small in diameter and stature and are found in rocky areas along rivers and on exposed ridges up to 1000 m. The cupules loosely hold the nut and their edges can become reflexed or revolute. *Lithocarpus ferrugineus* has thick oblong leaves and is found in a range of habitats, always at low densities. *Lithocarpus jacobsii* is rare, normally found above 1000 m, and the leaf blades have distinct auricles at their base.

Lithocarpus lampadarius and *L. revolutus* appear closely related. They are always poorly formed, leaning heavily, often with multiple trunks, and the bark is dark and crumbly-flaky. The leaves are large, thick, and tumescent. The latter species is distinguished primarily by the revolute leaf margins. Both species produce large nuts, often in clusters of three, with the cupules fused and pressed together (see Meijer 1996, p. 177, Fig. 13). The scales are thick and fused. *Lithocarpus lampadarius* is frequent around Park Headquarters and along Silau-silau Trail.

Lithocarpus luteus and *L. confragosus* are easily confused and are only tentatively placed in this section. The former species is frequent on the Kiau View Trail and several large individuals can be found near the Park staff quarters. The cupule is very thick and the scales are almost completely fused. The nuts, covered with silvery hair, are deeply seated in this structure and have a flat abscission scar. *Lithocarpus confragosus* is distinguished by the brittle, woody nature of the cupule, its complete enclosure of the nut, and a somewhat regular dehiscence at maturity along "valves."

Lithocarpus conocarpus is a small tree, widespread throughout the lowlands, and widely distributed on Kinabalu. It is often found near forest margins or in disturbed areas. Thin spikes bear numerous small fruit, often tightly clustered together, frequently with three fruits maturing equally. The cupules have short pedicels and are small, saucer-shaped with minute scales, and the nuts are usually glabrous, rounded, with the abscission scar small and deeply concave. The leaves often have a rather golden colour, and the secondary veins loop and fuse at the margin. The leaf base is often slightly asymmetrical. *Lithocarpus leptogyne*, a closely related species, is distinguished by the sharply acuminate apex of ripening nuts, which are solitary along the fruiting spike.

Section *Cyclobalanus*

This section has its main centre of distribution in Borneo, although it occurs throughout the Malay Archipelago west of Wallace's Line. The fruits of all species are of the acorn type and have smooth lamellate cups. Most cupules enclose only a small portion of the nut, although some taxa have the cupule completely enclosing the nut. In these cases, the nut is largely free of the cupule. Floral displays can be large, involving numerous slender male spikes topped by a few androgynous or female spikes. The leaves are usually rather nondescript but always with tightly appressed silvery or whitish tomentum.

Lithocarpus clementianus is perhaps the largest tree in the genus, frequently becoming >60 cm in diameter and well over 30 m tall. It is found throughout Borneo. The leaves are stiff and brittle, with close-set, prominently raised secondary veins, the lamina often drying with a peculiar powdery whitish texture. The fruiting spikes are often found with numerous aborted fruits, many of them in clusters of three. The cupule encloses the nut for much of its development and has a whitish aspect similar to the leaves. At maturity the cupule encloses half of the nut.

Lithocarpus hatusimae, *L. bullatus*, and *L. meijeri* are all similar species, being medium sized trees at 1500–2000 m in the lower montane zone. *Lithocarpus bullatus* is the most distinctive of these species, having clearly bullate lamina and smallish rounded leaves. It is often found on exposed ridges, such as the top of Bukit Ular. The primary lowland species in this section is *L. lucidus*, a large tree with unique, completely glabrous, narrowly oblong leaves.

RESULTS

Fruit-type evolution

Although many stone oaks produce fruits analogous to the typical *Quercus* acorn, innovations in internal structure have generated an enclosed receptacle or ER fruit (Cannon & Manos 2000) in at least two sections (Cannon 2000). These fruits are unusual because the seed develops within the thickened and woody receptacle, which provides mechanical protection against seed predation (Figs. 1 & 2). A phylogenetic analysis of almost half the Bornean species, encompassing all of the morphological variation in fruit type, indicates a number of interesting macroevolutionary patterns in both combined and comparative analyses of molecular and morphometric data (Cannon & Manos in press). The majority of species having ER fruit were found in two well-supported clades of a maximum parsimony reconstruction of nuclear rDNA internally transcribed spacer sequence data, suggesting evolutionary convergence on this unusual fruit type in at least two separate lineages.

In a combined analysis of nuclear rDNA data and continuous morphometric shape descriptors, two acorn-bearing taxa (*L. lucidus* and *L. clementianus*, both in section *Cyclobalanus*) were supported as being basal to the members of section *Synaedrys*, while section *Lithocarpus* may have been derived from something similar to *L. echinifer* or *L. rotundatus* (Fig. 3). Given the best combined reconstruction of the historical relationships among species, a comparative analysis of molecular and morphometric data demonstrated sharp incongruities in the amount of molecular and morphological change at important transitional nodes. A large amount of morphometric change is observed, with little corresponding change in molecular sequences inferred between acorn and ER lineages at both nodes leading to major ER clades. This situation suggests rapid morphological evolution of the highly specialized fruit type. In contrast, the acorn fruits found in *Quercus* are almost identical in structure to many acorn fruits produced by stone oaks, despite large amounts of sequence change between ingroup and outgroup. This pattern suggests relative evolutionary stasis of fruit morphology and perhaps strong stabilizing selection. Significant differences in branch-length estimates for all well-supported nodes were determined by comparing the distribution of estimates for 100 bootstrapped data sets, given the combined topology. While further exploration of the validity of these tests is necessary, the large differences in inferred change for each data set at well-supported transitional nodes clearly demonstrate these incongruities in rate.

The highest concentration of sympatric species with the ER fruit type (at least four) occurs in the 1500–2000 m elevational zone of the mountain, with *L. turbinatus* particularly prevalent above 2000 m. If this novel fruit type were an adaptation against seed predation, it is odd that it is not more successful in the lowlands, where a more diverse and extensive group of large-bodied vertebrates occur (Payne *et al.* 1985). Few ER species are found in the lowlands, and only *L. pulcher*, largely confined to the northwestern and southwestern coasts, reaches any appreciable density. Perhaps this fruit type allows instead an extended dormancy in the soil (Ng 1991), which would be unusual among primary tropical rain forest trees. Several additional ecological characteristics should be examined, including tannic acid concentration in the seed, timing and frequency of fruiting behavior, germination and regeneration patterns, and vertebrate dispersal patterns. Further study into the development of internal fruit morphology should be pursued as well, as heterochrony and retention of the immature condition may be responsible for the derivation of the ER fruit type in sections *Lithocarpus* and *Synaedrys*.

Phylogeography

Among- and between-population sequence variation was sampled from numerous individuals of stone oaks from Indochina to central Borneo. The taxonomic breadth of the sample included six sections and 49 species. The

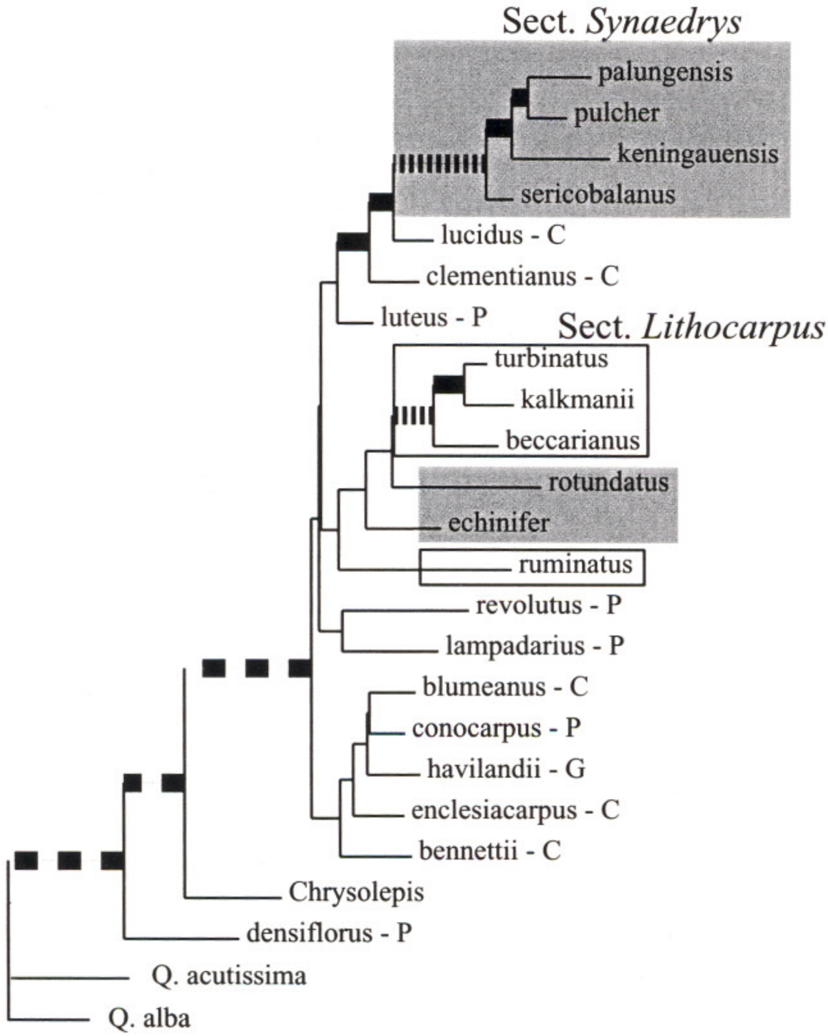

Fig. 3. Combined phylogenetic reconstruction of nuclear rDNA sequence and continuous morphometric data. Single most parsimonious tree (216.1 steps, CI=0.80, RCI=0.64) of 732 characters is shown. Members of the two sections with 'enclosed receptacle' fruit are labeled according to traditional circumscription; *Lithocarpus* (clear box) and *Synaedrys* (gray box). Members of other sections are marked by "C"-Cyclobalanus, "P"-Pasania, and "G"-Gymnobalanus. Well-supported branches (>65% bootstrap values) are shown in bold. Comparative analysis between molecular and morphometric data was only performed on well-supported branches and branch lengths were assessed for 100 bootstrapped data sets. Significantly greater molecular over morphometric change was inferred along branches with broad dashing. Significantly greater morphometric over molecular change was inferred along branches with narrow dashing.

overall genetic diversity in a single intergenic spacer region on the chloroplast genome, *rbcL-atpB* (Hodges & Arnold 1994) was high, with 66 unique genotypes observed in 167 individuals in eight locations (Cannon 2000). Two main lineages were present (Fig. 4), one shared between mainland and island populations ("continental") and the other confined to Borneo ("Bornean") (Cannon & Manos 2001). The ancestral type in the shared lineage was frequent on Mount Kinabalu and was found in a number of different species. This persistence of an ancient neutral polymorphism between two widely separated populations, for which other molecular data exhibit a deep phylogenetic split (Manos *et al.*, in review), suggests incomplete lineage sorting and generally slow overall genetic drift in the group. Almost all locations contained endemic phylogenetic structure, suggesting little gene flow between populations over extended periods of time.

The samples collected on Mount Kinabalu appear to be a mixture of the two lineages. Types belonging to the Bornean lineage found on the mountain were highly derived and distantly related to those in the continental lineage, suggesting great evolutionary separation. Overall, the Kinabalu populations contained relatively low amounts of diversity, particularly in comparison to those collected in southwestern Sarawak. If Kinabalu acted as a refugium during the climatic fluctuations of the late Tertiary and Quaternary periods (Morley 2000), this would explain the high frequency of ancestral continental types. Subsequent vicariance, possibly through climatic fluctuations, and then reinvasion of the western edge of the island from the mainland and diffusion into northern Borneo and Mount Kinabalu could then explain the mixture of divergent types found in this one location. Samples are necessary from central Borneo, the other Sunda Shelf islands and Peninsular Malaysia to fully investigate the connections between these land masses and to understand patterns of migration and diversification across the Malay Archipelago.

LIFE HISTORY AND EVOLUTIONARY PROCESS

Generalized patterns of gene flow

Male and female flower morphology of the stone oaks falls within a narrow and nondescript spectrum, a situation familiar to many SE Asian woody plant taxonomists (Ashton 1984, Schot 1998). A wide assortment of insects, including flies, wasps, bees, beetles, butterflies and moths, visit the male flowers to obtain pollen (Momose *et al.* 1998). There is little indication of pollinator specialization. Generalized insect pollination systems are ecologically dominant in the paleotropics (Momose *et al.* 1998) and are understudied (Waser *et al.* 1996). Given the predominance of wind-pollination systems in the Fagales, the stone oaks are probably predisposed for such a pollination system. The clouds of diverse insects visiting an inflorescence probably act as a generalized wind-like vector in the closed forest canopy, where little air movement occurs.

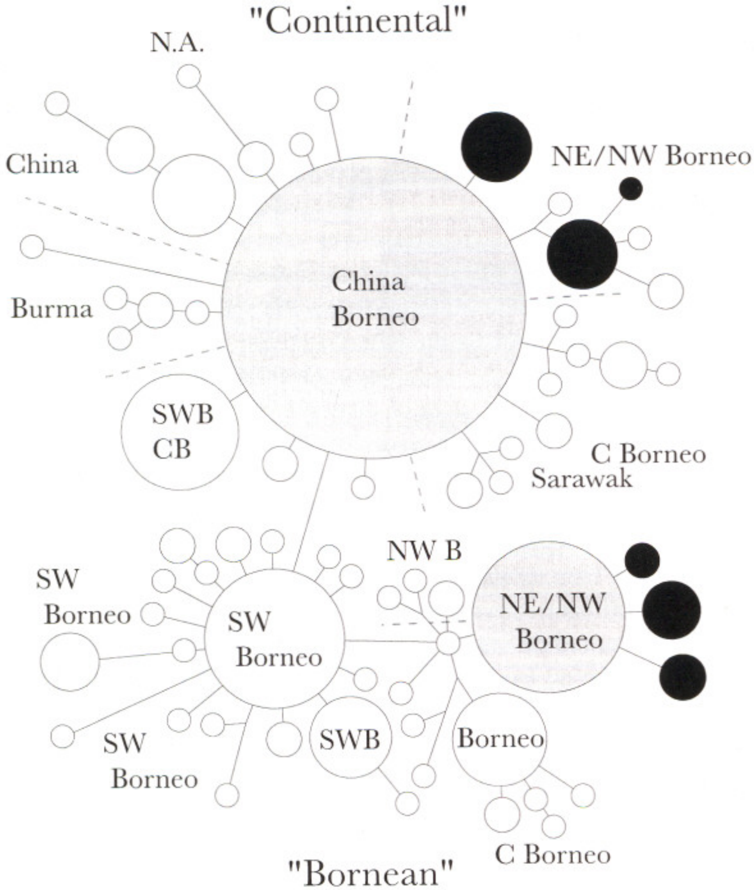

Fig. 4. Genetic network of landscape-level variation in chloroplast sequence among 167 individuals in eight locations; 66 genotypes were identified and the network was constructed from the strict consensus tree of numerous equally parsimonious trees. Unique genotypes are represented by circles and number of individuals possessing that genotype are represent by the diameter of the circle, *i.e.*, large circles were frequent genotypes; small circles, infrequent. Length of stems connecting circles are proportional to the amount of molecular change inferred. Geographic location of genotypes is indicated by labels and dashed lines. Genotypes observed only on Mount Kinabalu are solid black and those shared with other locations are gray.

While temperate oaks are noted for mast fruiting (Sork 1993, Koenig *et al.* 1994), little is known about the seasonality of reproduction among stone oaks (Kaul 1989). Some species (*e.g., L. havilandii*) appear to continuously flower and fruit (N. Nomura, pers. comm.), while other species appear to fruit suprannually outside of the general community-wide mast (Cannon, pers. obs.). The large woody ER fruit, in particular, must have an extended period of development (>>1 year?), which would prevent species with this fruit type from participating in the synchronized seed maturation which typifies community-wide mast events (Appanah 1993, Curran *et al.* 1999).

Seed dispersal mechanisms remain obscure. The vast majority of fruits tumble to the ground directly beneath the mother tree, as they do in *Quercus* (Dow & Ashley 1996). The Dipterocarpaceae and Fagaceae share a number of similar ecological traits with respect to seed dispersal, including the production of a fat-rich, phenolic laden, single-seeded nut with apparently limited dispersal ability (Ashton 1988), and the two families have similar biogeographical patterns (Ashton 1982). Long-distance dispersal is probably a rare event and may be more likely to occur among species which produce small acorn-type fruits.

Evidence for gene flow from nuclear and cytoplasmic molecular markers conflict (Cannon 2000). Preliminary evidence for nuclear markers, which are biparentally inherited and transferred by both pollen and seed, largely agrees with traditional species concepts and does not contain strong geographical structure, other than the split between Indochina and Borneo (Manos *et al.*, in review). Cytoplasmic markers, inherited maternally and transferred only through seed (Mogensen 1996), show strong geographic structure and have little congruence with traditional species concepts. An appreciation of the interaction and difference of life-history traits, such as generation time and reproductive biology, and macroevolutionary processes, such as lineage sorting and hybridization, is necessary to properly interpret these disparate patterns.

Long generation time

The majority of *Lithocarpus* species are found in primary forests and form part of the main canopy, seldom appearing in early successional stages. The trees probably live for hundreds of years, although no documentation exists. Robert May observed that body size in animals changes in response to spatial environmental heterogeneity (Tilman & Pacala 1996). In a similar fashion, organisms with different generation times will respond in different ways to temporal environmental heterogeneity, having a strong influence on overall genetic structure (Hamrick *et al.* 1993, Hamrick & Godt 1996) and macroevolutionary pattern. In particular, the ability to adapt to environmental conditions relies on the intensity and frequency of selection pressure in relation to the time between recombination events (Lande 1980).

Environmental heterogeneity

The SE Asian archipelago has been a tectonically active region throughout the Cenozoic (Hall 1998). Connections among current landmasses, through exposed continental shelf or volcanic islands, have been established and broken numerous times with tectonic activity and changing sea levels (Moss & Wilson 1998, Voris 2000). The island of Borneo has remained relatively stable in latitude and has undergone only a small counterclockwise rotation since the early Eocene (Lumadyo *et al.* 1993). Recent reconstructions suggest that the western and central parts of the island have been exposed since the early Eocene while the western and central mountain ranges appeared in the early Miocene (Moss & Wilson 1998). The northern part of the island has undergone the most recent and rapid changes during the last 10 my, including the spectacular uplift of Mount Kinabalu (Hall 1998). Fluctuations of sea level, warping of the crust and changing alluvial patterns have created heterogeneous patterns of soil type and sharp topography throughout Sarawak and Sabah, both spatially and historically (Tongkul 1991, Ashton 1995).

Glacial and interglacial periods have recurred in the temperate zones throughout the Quaternary period, apparently causing prolonged episodes of drier and cooler conditions in the SE Asian archipelago (Morley & Flenley 1987, Flenley 1997, Morley 1998). Interglacial periods, like the present, have actually been rather infrequent through the last two million years (Webb & Bartlein 1992). The most recent glacial maximum was only 20,000 years ago (Hewitt 1999) and dramatic temperature shifts appear to have occurred during the warming trend (Dansgaard *et al.* 1993). During these periods, sea level, global atmospheric conditions, rainfall patterns, and seasonality were significantly altered (Urushibara-Yoshino & Yoshino 1997, Verstappen 1997). High elevations may have experienced more extreme temperature fluctuations than the lowlands (Flenley 1996).

These processes, both geological and climatic, should have profound effects on tropical tree evolutionary dynamics in the archipelago. Given generation times of hundreds of years, the number of recombination events since the last glacial maximum (<20,000 years) cannot be greater than one hundred. This amount of evolutionary time could allow significant phenotypic change through the forces of strong directional selection (Lande 1979) but not through random drift (Lande 1980). Because environmental conditions may have reversed themselves several times, on an unpredictable and evolutionarily frequent schedule, perhaps the only way to avoid extinction in this situation is to track the movements of a particular set of environmental conditions (Pease *et al.* 1989) or simply persist in pockets of refugial habitat. Given the limited dispersal ability of *Lithocarpus* and the complexity of Borneo's topography and climatic history, refugial areas, such as Mount Kinabalu, have been crucial in the maintenance of viable populations of diverse, mixed communities.

Refugial population dynamics

The fragmentation and contraction of populations into refugia during generally unfavorable climatic conditions leaves a strong imprint on the current landscape-level genetic structure of plants, both in the temperate (Ferris *et al.* 1998, Taberlet *et al.* 1998) and tropical zones (Newton *et al.* 1999, Lowe *et al.* 2000). This evidence suggests that populations are significantly reduced in size and isolated from one another, causing fixation and endemic diversification. As discussed above, the pace of climatic fluctuations in relation to dispersal biology and generation time should have profound implications for the dynamics of gene flow within these refugial populations. Given the predominance of glacial conditions through much of the Quaternary, refugial population dynamics may have played a more important role in the macroevolutionary history of woody tropical plants, such as *Lithocarpus*, than have current interglacial conditions.

For *Lithocarpus* populations within the Kinabalu refugium, population sizes for any one species could be expected to be effectively smaller than at present. These conditions would expose species to strong forces of genetic drift, potential inbreeding (Utelli *et al.* 1999), and potentially explosive speciation (Kato 1992). For *Lithocarpus* species with long generation times and limited dispersal ability, a facultative ability to hybridize and subsequently backcross could be an advantageous macroevolutionary strategy, as has been suggested for other plant groups under different circumstances. Introgression of molecular and morphological markers has been widely documented in temperate oaks (Hardin 1975, Whittemore & Schaal 1991). Conspecific pollen precedence (Howard *et al.* 1998, Howard 1999) could be the primary ecological determinant of this quantitative behavior. As the quantity and quality of conspecific pollen rain decrease, the potential for interspecific hybridization increases because of great interspecific pollen competition (Williams *et al.* 1999, Winsor *et al.* 2000). From the perspective of a tropical tree such as *Lithocarpus* in SE Asia, the evolutionary persistence of a particular habitat may fluctuate greatly in geographic distribution and connection. Facultative introgressive hybridization could buffer the impact of these fluctuations, allow populations to persist for long periods of time in refugial pockets, and to adapt locally to changing environmental conditions.

CONCLUSIONS

Our current knowledge about the biogeography of the Bornean stone oaks suggests that macroevolutionary and biogeographic patterns in phenotype, nuclear genotype and cytoplasmic genotype may differ radically in different populations. The strong geographic structure and numerous transspecific polymorphisms seen in the chloroplast data is perhaps due to a combination of limited migration, incomplete lineage sorting, and introgressive hybridization. Monophyletic morphospecies and absence of strong geographic structure in the nuclear data indicate widespread pollen dispersal and rapid concerted evolution of rDNA. Phenotypic evidence suggests convergent evolution in separate lineages toward the ER fruit type, significant decoupling of molecular and morphometric change at important transitions, and a relatively high level of congruence with nuclear sequence data in overall structure.

The populations found on Mount Kinabalu provide an excellent opportunity for further exploration into these challenging questions. The presence of chloroplast genotypes shared with numerous individuals found in southern China indicate ancient connections between Indochina and Sundaland and support the hypothesis that northern Borneo has provided a refugium since the Tertiary for mesic tropical rain forest. The rich and diverse communities, including several distinct sections of *Lithocarpus*, will allow detailed study of gene flow at different taxonomic levels and among different hereditary pathways. Finally, the prominence of Kinabalu as one of the premier natural systems and tourist destinations in Southeast Asia should help assure its long-term protection and management.

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