

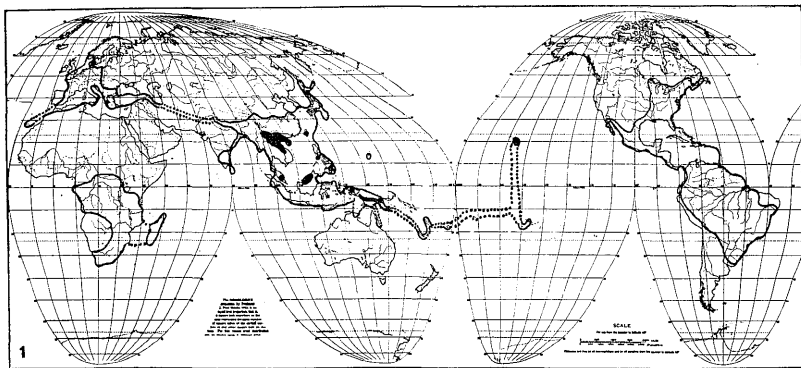
Shiu-ying Hu*: **The evolution and distribution of the species of Aquifoliaceae in the Pacific Area** (1)**

胡 秀英*: 太平洋地域におけるモチノキ科の種の進化と分布 (1)

Introduction

The importance of Aquifoliaceae in the study of the evolution and distribution of the biota of any region is significant and it is especially so for the Pacific area. This is because the species of this family provide excellent material for evolutionary and biogeographical studies. It favors us with two unique and long-lasting organs which are well preserved in many famous paleobotanical localities. These are the distinctively clavate-sculptured pollen grains and the smooth, striate-sulcate or rugose-pitted pyrenes. On account of these records our understanding of the evolutionary radiation of the species in the family is broadened in time and space. In addition to the fossil remains, the richly varied morphological diversities and the worldwide distribution of hundreds of contemporary species furnish us with an enormous amount of data which can be processed and used for deciphering the secret code of evolutionary radiation. Few families can top this in these respects.

The Aquifoliaceae has a special importance in the understanding of the evolution and distribution of biota in the Pacific area because all its primitive existing species occur here, in the islands and/or on the continent bordering the west coast of the



Map. 1. Worldwide distribution of Aquifoliaceae, the solid black spots indicating the areas where the primitive species occur. These areas are either in the islands of the Pacific or on the continental land mass bordering its west coast.

* The Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge 38, Mass., U. S. A.

** This research was aided by a grant from the Society of Sigma Xi and RESA Research Fund.

ocean. All the species in other continents and islands are derived forms (Map 1). For this reason, in our analysis of evolutionary evidences, only the Pacific species can lead us to the beginning of the development of the family. This is very important for the reconstruction of evolutionary trends and distributionary patterns of biota in the Pacific area.

On evolution of Aquifoliaceae in the Pacific

1. Number of species involved : The number of aquifoliaceous species involved in the entire course of evolutionary radiation in the Pacific area must be great. The investigation of the extinct species in this area is still a virgin field. As to the contemporary species, over 200 have been described. Some of them are simply no good. They were not described on characters of any specific importance. A conservative assessment made after careful examinations of the internal and external morphology allows about 170 species. These represent the adaptive peaks in the speciation and radiation of the family in the area. They can be arranged into 14 related but distinct groups. The number of species in each group is as listed below.

Major groups of Aquifoliaceae in the Pacific Area

Byronia	3	Aquifolium	55
Cymilex	20	Pseudehretia	5
Epiphytalex	20	Lioprinos	25
Pseudoaquifolium	10	Paltoria	12
Sideroxyloides	7	Prinos	5
Hexadica	6	Prinoides	3
Prinifoliae	3	Macroprinos	3

2. Organs of the plant affected : The selective pressure affects the organs of the species in many different ways. The morphological differences between members of the family brought about through evolutionary changes can be best visualized by examining the specific characters of two representatives, *Ilex hawaiiensis*,¹⁾ the most

- 1) ***Ilex hawaiiensis*** S. Y. Hu, sp. nov. Arbor glaberrima; foliis tenuiter coriaceis oblongis, 6-11.5 cm longis, 2.5-6 cm latis, basi obtusis vel cuneatis, apice obtusis vel rotundatis, petiolis 1.2-2 cm longis; inflorescentiis quater di- vel trichotomo-paniculatis; pedunculis 1.7-3 cm longis; axibus secundariis 8-12 mm longis, ceteris gradatim diminutis; pedicellis 5-8 mm longis; staminibus florum masculinarum quam petalis brevioribus, antheris subglobosis thecis minutis; ovario florum femineorum ovoideo, 20-24 carpellato.

Hawaiian Island: Maui, J. F. Rock no. 10078 (type in GH.)

primitive species of the family, and *I. aquifolium*, one of the most advanced and the type species of the genus *Ilex*. (Fig. 1 & 2).



Fig. 1. Habit sketches of *Ilex hawaiiensis* showing the morphological characters most primitive to the species of the family Aquifoliaceae.

ORGANS INVOLVED	<i>Ilex hawaiiensis</i>	<i>Ilex aquifolium</i>
Branch system	Generalization : current year's growth bearing both leaves and flowers	Specialization : vegetative shoot and floral shoot developed independently
Laevs	Evergreen, entire	Evergreen, spinose or entire

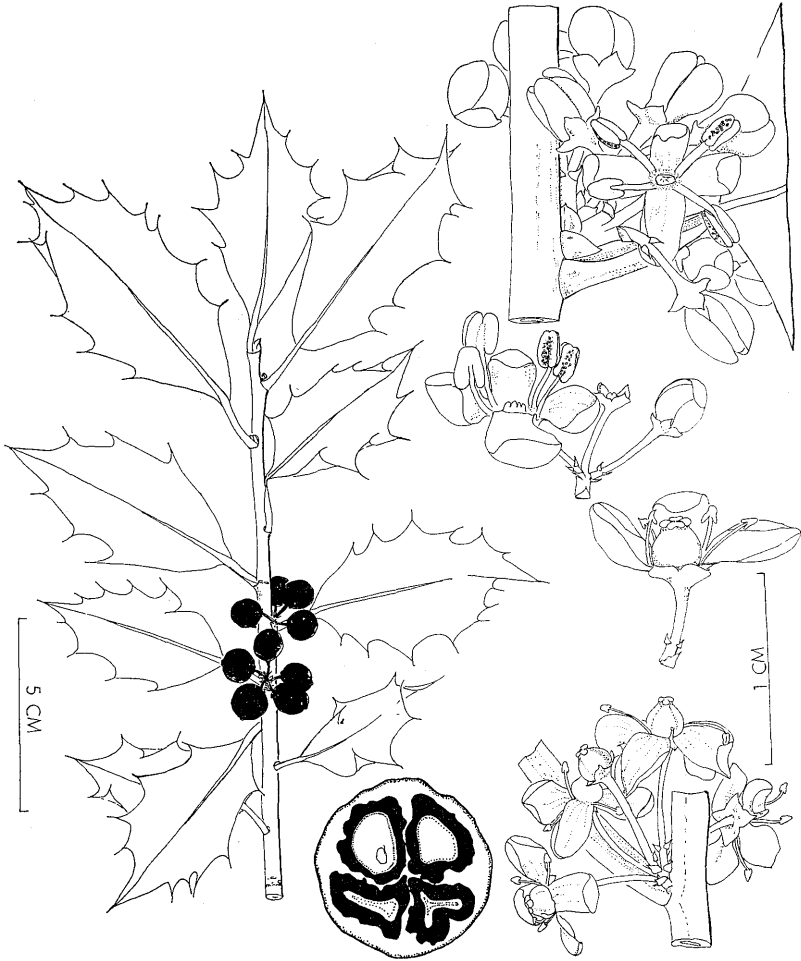


Fig. 2. Habit sketches of *I. aquifolium* showing the morphological characters of an advanced species in the family.

Inflorescences	Loose compound dichasia, solitary, axillary, to normal leaves; bracts numerous and large	Compact fascicles of reduced cymes, ♂ cyme 3-flowered and bracts small, basal; ♀ cyme 1-flowered with 2 prophylls indicating the lost flowers
Flowers	Heteromerous; filaments short, connectives broad	4-merous; filaments long, connectives narrow
Fruits	Purplish-black; pyrenes numerous, endocarp woody or fibrous	Red; pyrenes 4, endocarp stony
Pyrenes	Small, compressed, smooth and fibrous	Trigonous, rugose, wrinkled and pitted

3. Fundamental steps of evolution in the family: These represent major changes that occurred in the family. They indicate the outstanding landmarks of evolutionary changes that concern all the species throughout the world. They are found in the structure of secondary xylem, the reduction of floral parts accompanied by fusion of vascular supplies, the specialization of shoot system and the acquisition of deciduous habit.

The changes in the xylem: In the primitive species like *I. hawaiiensis* (Fig. 3 A-B), *I. cymosa*, etc., the secondary xylem has elongate vessel segments with thin lateral walls, angular in cross section, highly inclined end-walls, scalariform and reticulate intervascular pittings, numerous scalariform perforations, septate fibers, and the absence of tertiary spiral thickening and annual rings. In contrast to this, the wood of more advanced species such as *I. cornuta*, *I. serrata*, *I. opaca* (Fig. 4 A-B), etc., has shorter vessel elements, less inclined end-walls, fewer scalariform perforations, bordered intervascular pittings, spiral tertiary thickenings, distinct annual rings, and the absence of septate fibers.

Changes in the flowers: The fundamental changes in the flowers involve the reduction of floral parts accompanied by the fusion of vascular supplies. The condition is illustrated by the flowers of two primitive species, *I. hawaiiensis* and *I. vitiensis*.

In their outward appearances, these species are very similar. They both have entire leaves, cymose inflorescences solitary and axillary to leaves on the current year's growth, and nelumboid female flowers. However, in the structure of flowers, they are very different (Fig. 5). In *I. hawaiiensis* the ovary has 16-24 carpels arranged rather loosely in a parenchymatous mantle in a manner similar to that

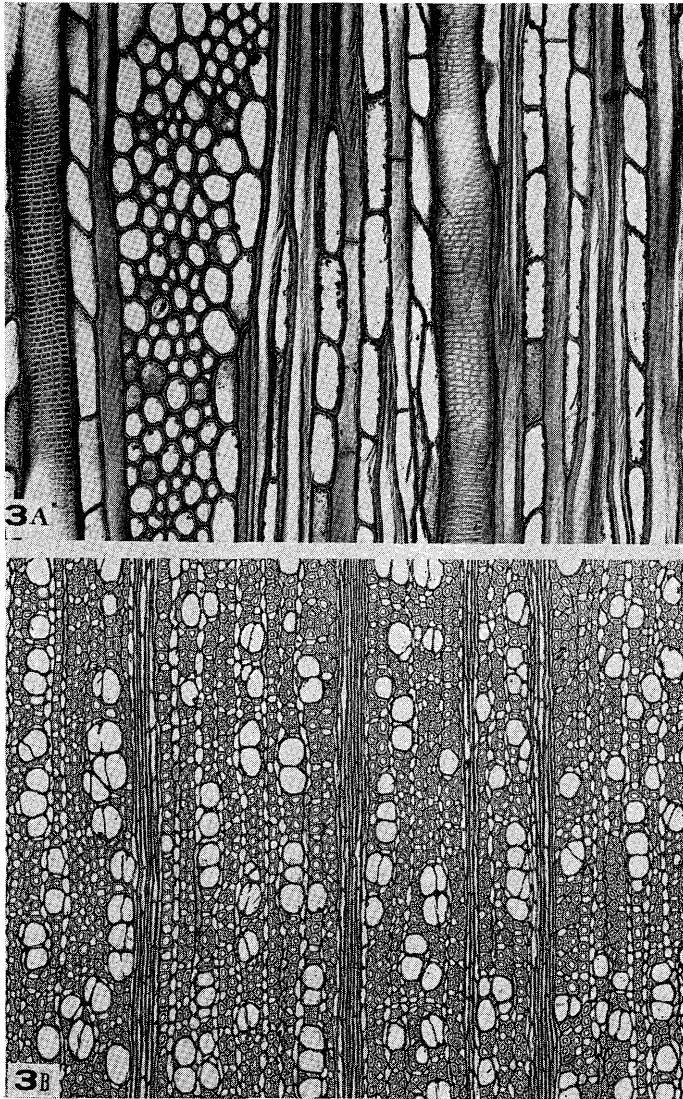


Fig. 3. Anatomical characters of the wood of *I. hawaiiensis*. 3A. Tangential section showing the nature of a magnoliaceous wood in the vessel elements, septate fibers, rays, rectangular and elongate pittings, etc. 3B. Transverse section showing the absence of annual rings and the grouping of the vessel elements.

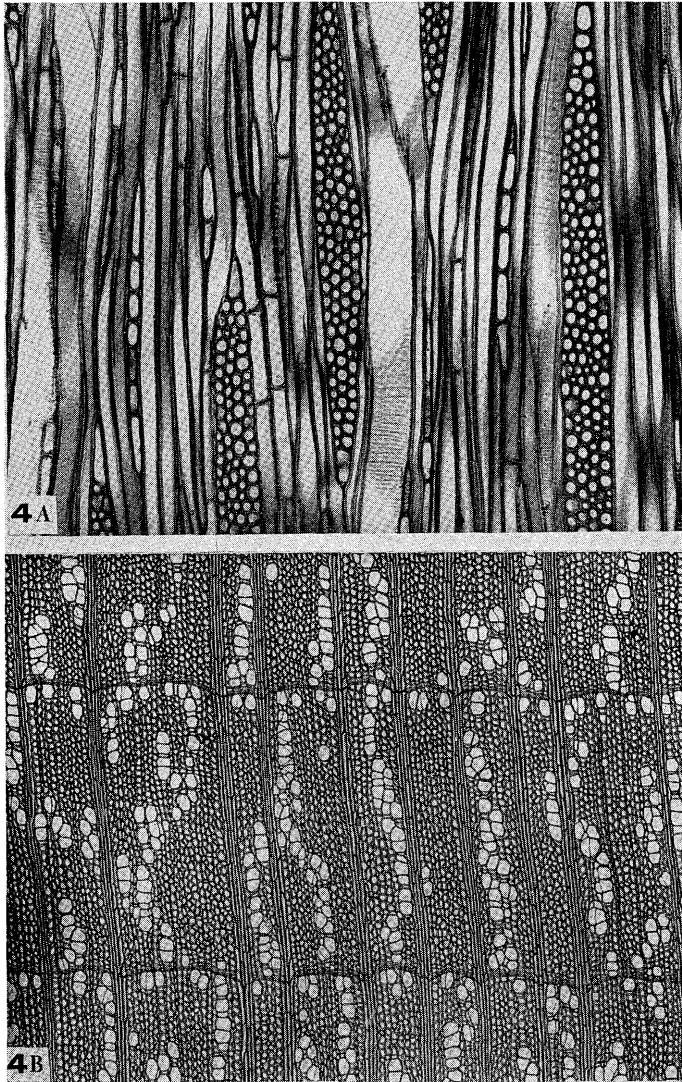


Fig. 4. Anatomical characters of the wood of *I. opaca*. 4A. Tangential section showing the more advanced characters in the vessel elements and fibers with their tertiary spiral thickening and the less heterogeneous ray cells. 4B. Transverse section showing the definite annual rings and the grouping of the vessel elements.

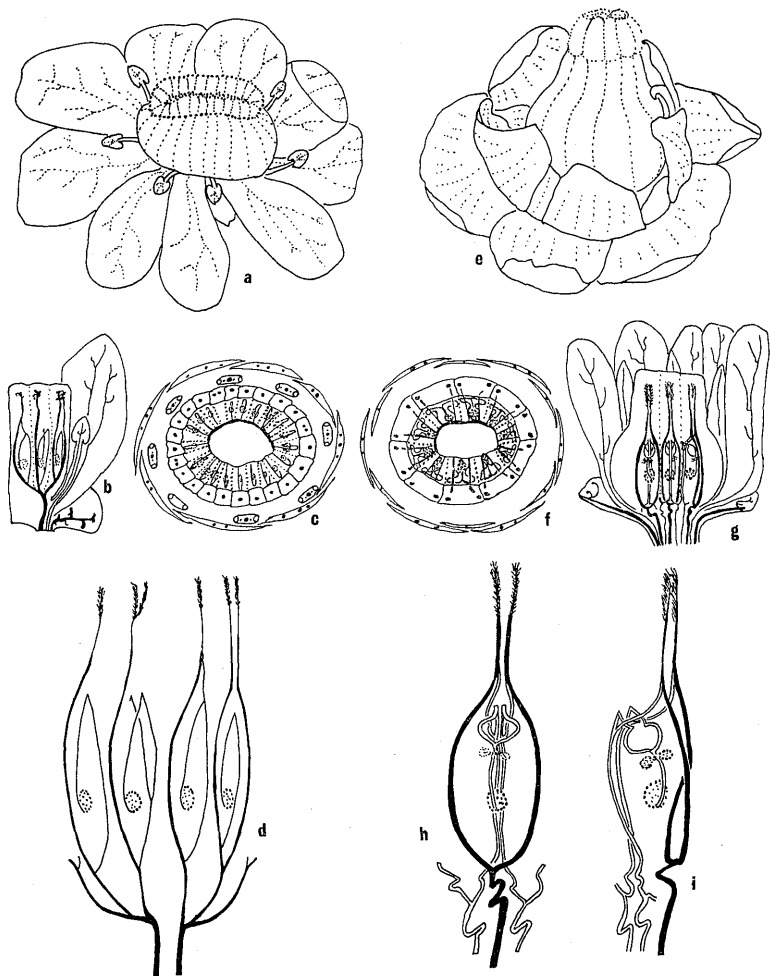


Fig. 5. Schematic diagrams of the flowers of *I. hawaiiensis* (a-d) and *I. vitiensis* (e-i) showing the fundamental changes in floral morphology and in vascularization in the evolution of Aquifoliaceae in the Pacific. a. The nelumboid female flower of *I. hawaiiensis* showing 1 sepal, 9 petals, 6 staminodes and a globose ovary with numerous carpels and sessile stigmas. b. The longitudinal section of the same showing the vascular supplies to a sepal, a petal, a staminode, and three carpels. c. The transverse section of the flower through the upper portion of the ovary showing vascular skeleton of the petals, anthers, and carpels. Only the ventral traces that supply the ovules are shown in full. d. The vascularization of four carpels, the dorsal traces in heavy lines and the ventral (Continued to the next page)

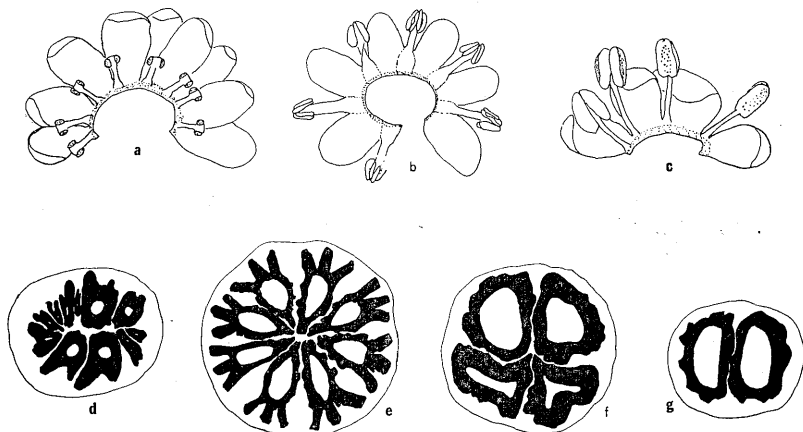


Fig. 6. Diagrammatic sketches of the corolla, androecium, and transverse section of fruit showing the reduction in the number of floral parts. a-c. The corollas and androecia of *I. hawaiiensis*, *I. vitiensis* and *I. aquifolium*, from left to right respectively. Note the progressive reduction in the number of petals and stamens, in the size of the connectives, and the simultaneous increases in the length of the filaments and in the sizes of the anthers. d-g. Transverse sections of the fruit of *I. hawaiiensis*, *I. macrocarpa*, *I. aquifolium* and *I. pernyi* var. *veitchii* showing 12, 8, 4, and 2 carpels.

found in a flower of *Nelumbium*. Each carpel is very small and the distinction between the ovary and style is obscure. The stigmatic surface lies on the subterminal slightly recurved adaxial surface in a manner similar to that found in the carpel of *Amborella trichopoda*, a vesselless dicotyledonous species. The vascular skeleton of the carpel is very simple, consisting of a single strand which bifurcates before entering the carpel. The stronger dorsal trace travels up straight to the stigmatic region and becomes brush-like in appearance, and the weaker ventral trace bends 180° and travels down to supply the ovule. This trace may or may not bifurcate.

The staminodes of the female flower of *I. vitiensis* become petaloid. This is a common phenomenon in the Cymilex group. The ovary has 8 carpels, also arranged in one whorl in a parenchymatous mantle, as in *I. hawaiiensis*. It has an evident stylar region. The vascular skeleton of the carpel constitutes the fusion of strands from three different origins. These strands enter the carpel at the base of the

traces in thin lines. e. A female flower of *I. vitiensis* showing the petals, petaloid staminodes and the ovoid ovary with 8 carpels. f. The transverse section of the flower through the upper portion of the ovary showing the branching of two parallel ventral traces, the independent entry to the locule and their union before supplying the ovule in each carpel. g. The longitudinal section of a flower showing the vascular supply to the sepals, petals, staminodes and to three carpels, in dorsal, ventral and lateral views from left to right respectively. h-i. The vascular system of the carpel in dorsal and lateral views, the dorsal traces in heavy lines and the ventral traces in double thin lines. Note the three origins of the dorsal and the ventral traces.

ovary, the dorsal strand from an outer whorl of bundles in the torus and two ventral strands each from a branch of two bifurcate neighboring bundles of an inner whorl of bundles in the torus. The dorsal strand bifurcates soon after entering the carpel and gives rise to two parallel dorsal traces which run upward, enter the stigmatic region and become brush-like. The ventral strands travel close together upward and bifurcate below the region of the future germination pore. Each strand sends a branch to the styler region. The other daughter traces both bend 90° , unite at the opposite side of the carpel and travel downward to supply the ovule at the middle of the carpel. This is the beginning of a very complex system of reduction of carpels and fusion of vascular bundles in the ovaries of Aquifoliaceae. In the advanced groups where the ovaries have only four carpels, there are various forms of reticulation in the torus before the bundles enter the carpels.

The microscopic changes in the vascular system in the flowers are accompanied by the outward reduction in the number of floral parts, especially in the number of petals, stamens and carpels. There is also a simultaneous increase in the sizes of the anthers and the fruit (Fig. 6).

Specialization of branch system: This phenomenon occurs in several lines of evolutions in Aquifoliaceae. Here six species, three with punctate leaves (*I. macydenii*, *I. coriacea*, *I. amara*) and three with epunctate leaves (*I. chinensis*, *I. opaca*, *I. cornuta*), are selected to illustrate the general, intermediate and specialized types of branch system (Fig. 7). In the general type, a bud unfolds into a shoot which bears normal leaves with axillary flower clusters. In the intermediate types a bud unfolds into a shoot which bears solitary flowers or flower clusters in the axils of small scales at the basal portion and leaves at the apical portion. In the specialized types, the floral shoots and the vegetative shoots originate from specialized buds. The mid-lateral buds of last year's growth unfold into fascicles or panicles of flowers and the subterminal and terminal buds unfold into vegetative shoots. The kind of shoot system of a species is a generic character of that species. It is not affected by the altitudes or latitudes of the habitat of the species.

The acquisition of deciduous habit: Deciduousness in Aquifoliaceae is more of a generic trait than a physiological function. The primitive deciduous species in this family (*I. micrococca*) occurs in subtropical forest in association with evergreen species of Lauraceae, Theaceae, Rubiaceae, etc. The acquisition of deciduousness took place early in the development of the family. It probably came through mutation or hybridization which introduced a fundamental quality of certain deci-

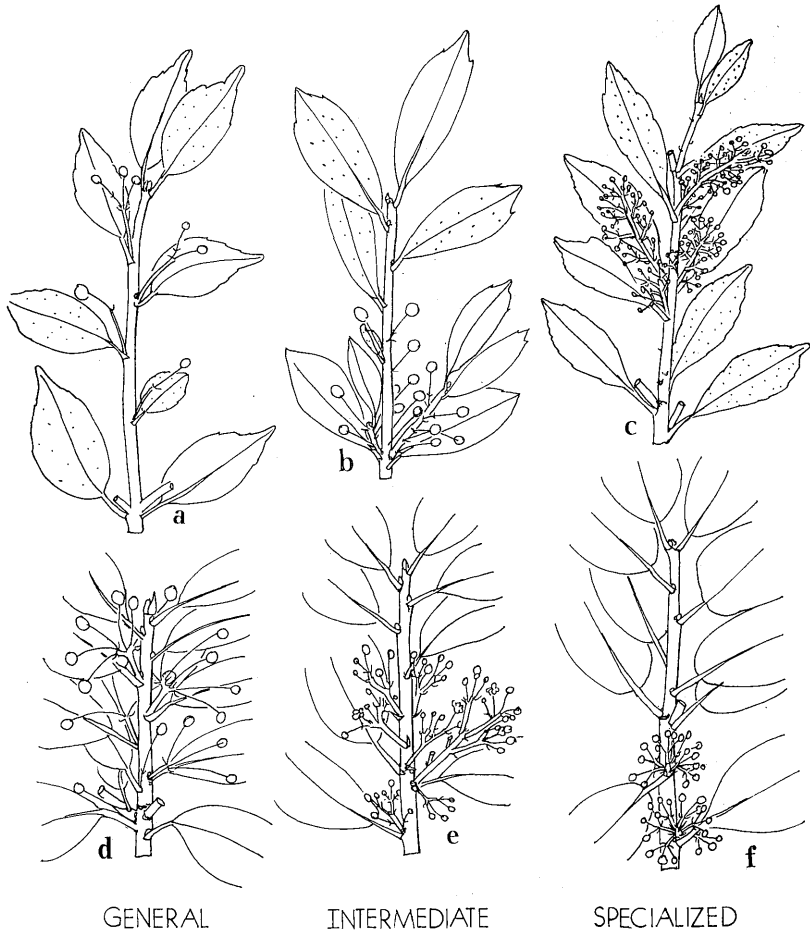


Fig. 7. Habit sketches of the flowering branches of six species of *Ilex* showing the steps of evolutionary changes in the branch system of Aquifoliaceae. a. *I. macfadynii*, b. *I. coriacea*, c. *I. amara*, d. *I. chinensis*, e. *I. opaca*, f. *I. cornuta* (see text for explanations).

duous woody Ranales into the ancestral stock of the Prinos line of evolution. A very primitive deciduous species of Aquifoliaceae, *I. fragilis*, has many vegetative characters in common with *Euptelea franchetii*, a woody ranalian species. However, deciduousness is associated with the power of tolerance for cold and periodical drought, and it favors the development of temperate species such as *I. serrata*, *I. geniculata* in Japan, and *I. verticillata* and *I. laevigata* in eastern North America.

4. Secondary evolutionary steps: The secondary evolutionary steps indicate the potentials of the major groups to adjust to less favorable conditions in their respective floristic regions. The selective pressures of lowered temperature, decreased water supply, increased aridity in the air or acidity in the soil operate most effectively on the leaves, inflorescences, indumentum and other superficial processes. Consequently the evolution trends become obvious in the reduced size accompanied with changed shape and texture in leaves, reduction in number of flowers and simplification of inflorescences, and production of hairs and other excrescent growth on the stems. Convergent evolution between members of unrelated stocks is expressed

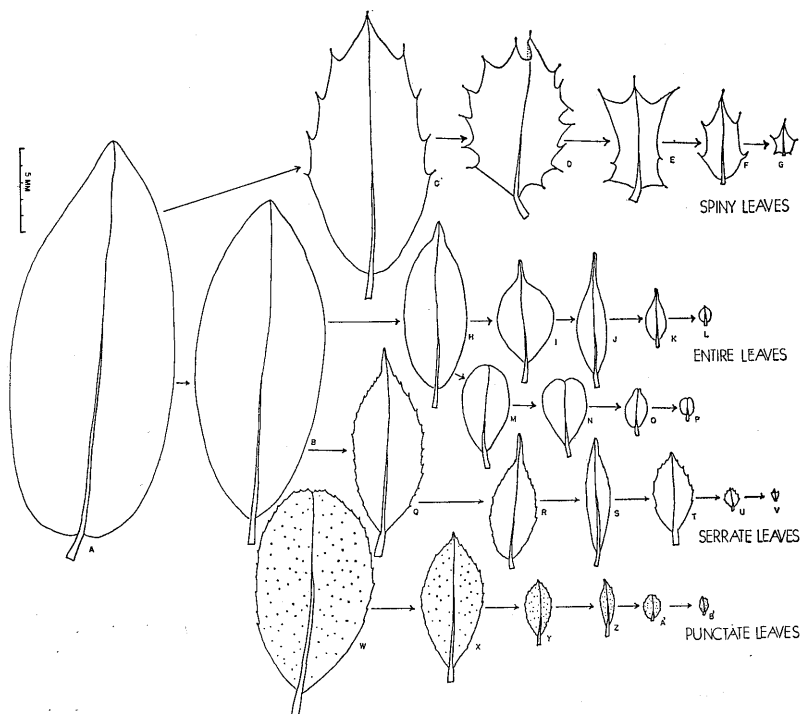


Fig. 8. Habit sketches of the outline of leaves of 28 species and varieties of *Ilex* showing the evolutionary changes in the size, shape, margin, apex and base. a. *I. grandifolia*, b. *I. maclurei*, c. *I. aquifolium* var. *camelliaefolia*, d. *I. aquifolium* var. *aurea regina*, e. *I. cornuta*, f. *I. pernyi* var. *veitchii*, g. *I. pernyi*, h. *I. cymosa*, i. *I. foxworthyi*, j. *I. longicaudata*, k. *I. racemifera*, l. *I. permicophylla*, m. *I. sideroxyloides*, n. *I. tutcheri*, o. *I. lohfausensis*, p. *I. obcordata*, q. *I. chieniana*, r. *I. cyrtoura*, s. *I. peiradenia*, t. *I. microdentata*, u. *I. nothofagifolia*, v. *I. colombiana*, w. *I. amplifolia*, x. *I. triflora*, y. *I. crenata*, z. *I. crenata* var. *longifolia*, a'. *I. ovalis*, b'. *I. crenata* var. *microphylla*.

repeatedly in these changes.

Changes in leaf-size, -shape and -texture : The primitive species in Aquifoliaceae have large entire leathery leaves. *Ilex grandifolia* of Sumatra has the largest leaves known to me (Fig. 8). These measure up to 29 cm. long and 10 cm. wide. In areas such as Borneo, where varied topography supports aquifoliaceous species from sea-level to 3,600 meters altitude, or such as Japan, where the species of Aquifoliaceae grow as far north as 48° latitude, there is a prevailing phenomenon of progressively reduced leaves accompanied with thickened texture and changed shape. In these areas the species with smaller leaves in Aquifoliaceae have higher adaptive power, especially for tolerance for cold, drought, higher soil acidity, stronger wind or other adverse growing conditions.

The selective pressure of the tropical forests seems to favor the production of species with long-caudate leaf-apices in Aquifoliaceae, while that of the mossy forest favors the production of species of small obcordate leaves in the family. Leaves of similar size, shape and texture may be produced under similar environmental conditions in different parts of the world between members of unrelated stocks. For the species with long-caudate apices, we have examples in *Ilex longicaudata* from China, *I. cyrtoura* from Burma, *I. spicata* from Indonesia and *I. loranthoides* from Brazil. For the species with small obcordate leaves, we have examples in *I. havi-landii* of Mt. Kinabalu in Borneo, *I. archboldiana* of Mt. Tafa in New Guinea and *I. obcordata* of Blue Mountain in Jamaica.

Simplification of the inflorescences : The reduction of the number of flowers in the inflorescences and the consequent simplification of the inflorescences is a common trend of evolution in Aquifoliaceae. It is expressed in many unrelated groups (Fig. 9). In the *Byronia* line of evolution, *I. hawaiiensis* has the largest inflorescence. It is a loosely arranged, 3- to 5-times trichotomously branched dichasium with rather large bracts. In *I. anomala* the dichasium has less flowers and it becomes more compact. In *I. marquesensis* the inflorescence becomes a simple 3-flowered cyme. In the *Paltoria* group, *I. teratopsis* has the largest inflorescence. It is a 3- or 4-times trichotomously branched dichasium. In *I. ampli-fo- lia*, *I. boliviensis* and *I. paltoria* the flowers are progressively reduced from many to few and to one. This condition is found in the *Prinos* group, with *I. micrococca* having the most complex inflorescences. Reduction is evident in *I. serrata*, *I. verticillata* and *I. laevigata*. The same phenomenon is found in the *Lioprinos* group.

The inflorescences of the *Aquifolium* group are of a different nature. Ontolo-

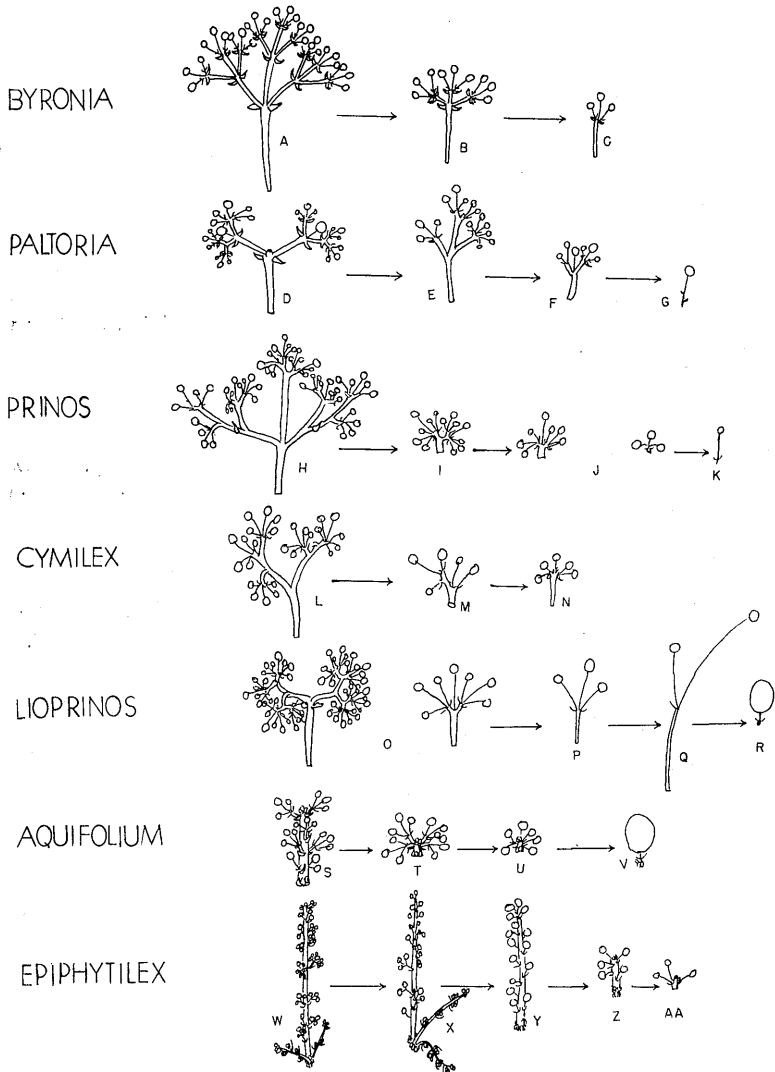


Fig. 9. Schematic diagrams of the inflorescences of 27 species of *Ilex* showing the reduction of the number of flowers in the evolutionary changes of seven groups. a-c. Byronia : a. *I. hawaiiensis*, b. *I. anomala*, and c. *I. marquesensis*. d-g. Paltoria : d. *I. teratopsis*, e. *I. amplifolia*, f. *I. boliviensis*, and g. *I. paltoria*. h-k. Prinos : h. *I. micrococca*, i. *I. serrata*, j. *I. verticillata* (male and female), and k. *I. laevigata* (male). l-n. Cymilex :
(Continued to the next page)

gically each inflorescence is developed from specialized bud and morphologically it is a complex containing a central axis which bears from many to two or even one 1—3-flowered cymes. In the simplification of the inflorescences of this group, it is the shortening of the central axis that is significant. In *I. latifolia*, the axis is long and it bears many 1—3-flowered cymes. In *I. aquifolium* (type species of the genus *Ilex*), the shorter axis bears fewer 1—3-flowered cymes. In *I. pernyi* and *I. chingiana*, there is more reduction until the whole inflorescence contains a few flowers or sometimes only 1 flower. The phenomenon is expressed repeatedly in many sections of this group.

The inflorescences of the Epiphytalex group are of still another nature. Ontologically each inflorescence is developed from a row of superposed buds with the anterior one unfolds first (Fig. 9 w-x). In the evolutionary changes of the inflorescences of this group reduction occurs both in the number of the superposed buds and in the complexity of the inflorescences. In *I. asahanensis* and *I. cissooides* usually three buds in a row develop and bear flowers. These produce a panicle-like structure. In *I. spicata* one bud develops while a dormant posterior one is evident. The inflorescence appears like a raceme. In *I. orestes* and *I. havilandii* the positions of the posterior buds are merely indicated by a space between the inflorescence and the insertion of the leaf.

Indumentum and other excrescent growth: The indumentum and excrescent growth on the stems seem to have very little role in the evolution of the aquifoliaceous species in the Pacific area, except with some species on the high mountains of New Guinea. Most species have glabrous or very minutely puberulous stems. In the Lake Habbema region of New Guinea (2,900 meters altitude), certain selective pressure favors the development of scabrousness on the stem of *I. scabridula*. A young shoot of this species is villose with white multicellular hairs swollen at the base. As the stem grows and attains maturity, the hairs persist with the bases increased in length and thickness. Consequently the stem looks scabrous. *Ilex intricata* and *I. nothofagifolia* of similar altitudes (2,300–3,200 meters) in Yunnan and Sikkim have corky warts on the stems. This condition is not found among the Pacific species.

l. *I. cymosa*, m. *I. vitiensis*, and n. *I. zygophylla*. o-r. Lioprinis: o. *I. chinensis* (male and female), p. *I. dasyphylla*, q. *I. pedunculosa*, and r. *I. lancilimba*. s-v. Aquifolium: s. *I. latifolia* (male), t. *I. aquifolium*, u. *I. pernyi*, and v. *I. chingiana*. w-aa. Epiphytalex: w. *I. asahanensis*, x. *I. cissooides*, y. *I. spicata*, z. *I. orestes*, and aa. *I. havilandii*.