Shiu-ying Hu*: The evolution and distribution of the species of Aquifoliaceae in the Pacific Area (2)

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 (2)

On Distribution of Aquifoliaceae in the Pacific

The distributional data and the units of classification of the species employed in this discussion are unpublished results of my investigations of the family Aquifoliaceae for a period of twenty-five years, first concentrating on the Chinese species and gradually enlarging the areas covered to Asia and then to the whole world. In 1963, through a grant from the American Sigma Xi Society, I was able to examine the type collections in many outstanding European herbaria. Then, my principal interest was to understand the species.

My most recent system is classifying the 177 Pacific species into 14 independent units which express a mosaic of the adaptive peaks in the family. The map for each group is constructed on the basis of detailed maps of individual species made when I examined specimens of the species. These were prepared merely to aid my memory and to obtain a clear record. Now, in using them to construct a general map of the group to which the species belong, I have been finding them both useful and meaningful. After the general maps of all the 14 groups were prepared, I compared them, and I see distinct patterns of distribution for the species in each group.

1. The distribution of groups limited to the Tropics: Three groups, the Byronia, Cymilex and Epiphytilex, are involved in this pattern of distribution. They contain a total of 43 species, approximately one-fourth of the entire Pacific aquifoliaceous species. Byronia (Map 2) is restricted to Polynesia. It contains the most primitive existing species of the family, and probably represents a very ancient migration and a long period of isolation.

The Cymilex and Epiphytilex are widespread in Indo-China, Malaysia, Indonesia, the Philippines, New Guinea, and/or eastward to Fiji. The Cymilex group (Map 2) has a wider range which begins at the Laos Highland, hence southward following the Mekong River down to Cambodia and Cochinchina, and then from the Malay Peninsula and Sumatra eastward to Java, Borneo, the Philippines via Palawan (but absent from Mindanao), the Celebes, New Guinea, Arnhemland and Queens-

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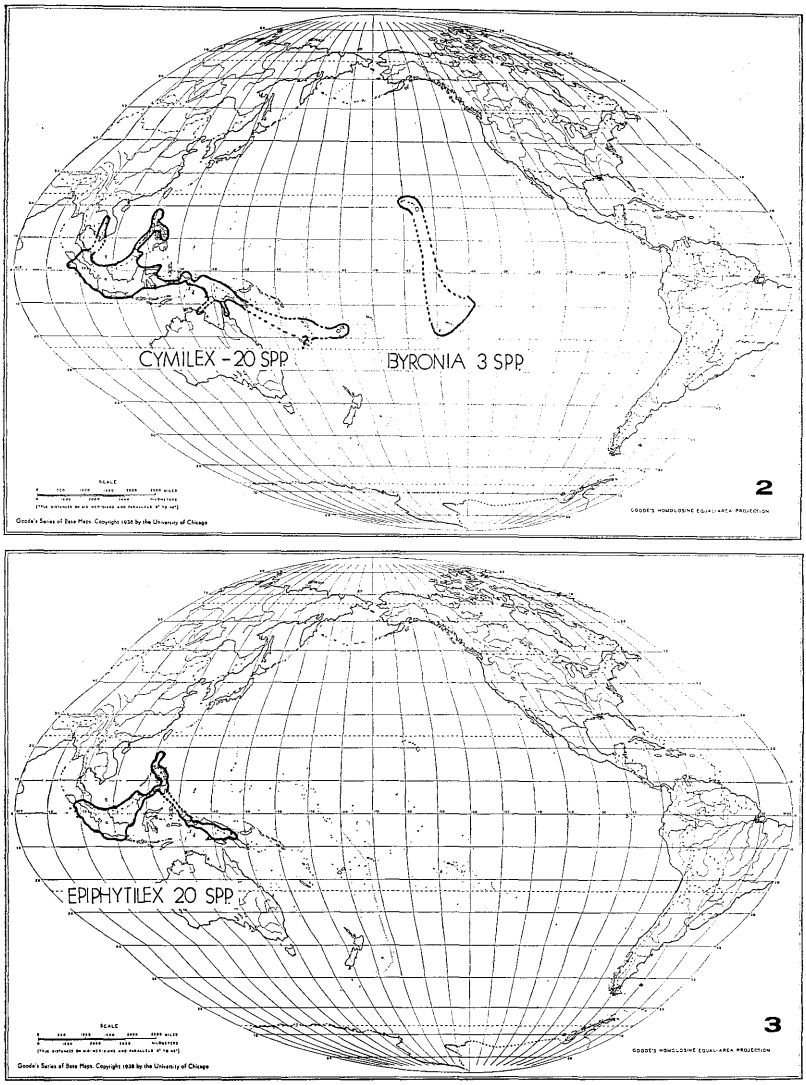
land in Australia, the New Hebrides and Fiji. The very unusual and rather advanced species in New Caledonia perhaps belongs here. It indicates a long separation from the group and in its adaptive radiation it attained further reduc-



Maps 2-3. Distribution of groups containing species occurring in the tropics only (see text for explanations).

tion of the numbers of carpels and many secondary changes.

The Epiphytilex group (Map 3) is more restricted in distribution than the Cymilex. It is absent from Indochina, the Celebes and the Palawan Island of the Philippines. The centers of species concentration are in Borneo and the Philippines. The eastern limit of its range is New Guinea, where two-thirds of the species are very primitive. Borneo has eight species and the Philippines have nine, including both primitive and advanced species. The absence of Epiphytilex in Palawan seems to indicate that the exchange of species of this group between the Philippines and Borneo took place by a southern route through the Sulu archipelago and Mindanao.

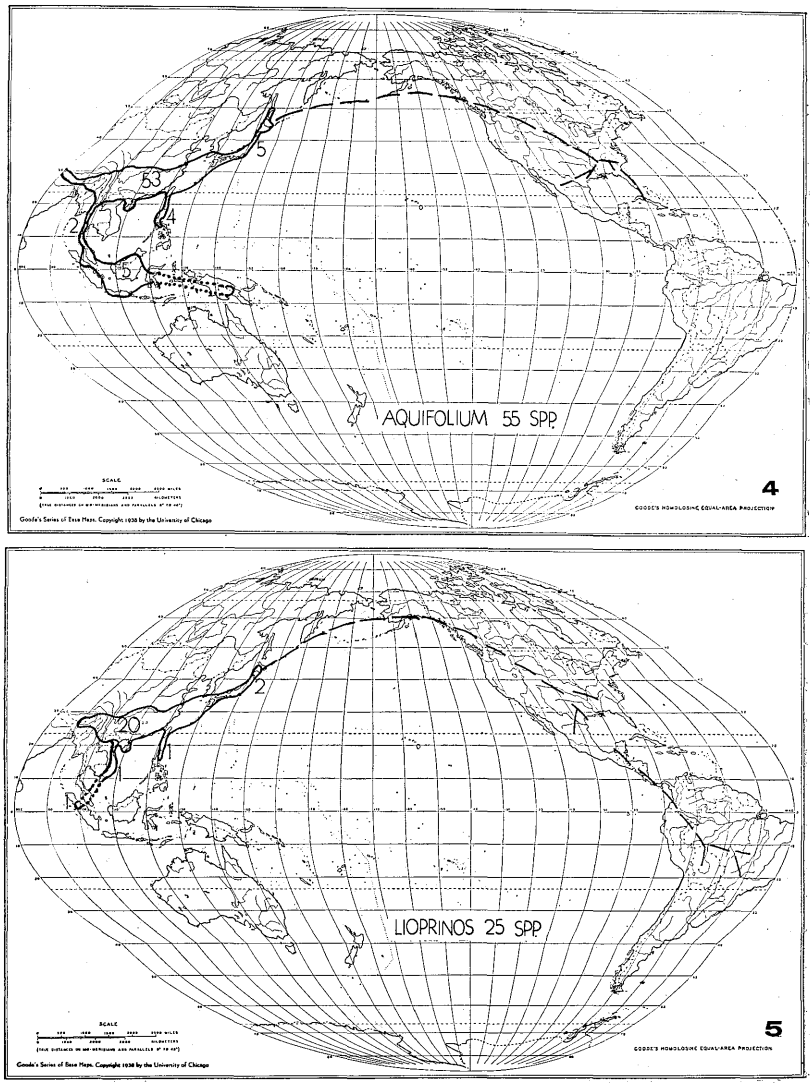
Cymilex and Epiphytilex have about the same number of species. The species of Cymilex cover a wider range, while those of Epiphytilex occur in a more diversified topography of smaller area. The latter group may represent a group with more recent evolutionary history and with higher adaptive potentialities.

2. The distribution of widespread and discontinuous groups: Five groups share this pattern of distribution. They are Aquifolium, Lioprinos, Paltoria, Prinos and Prinoides (Maps 4–8). The first three groups contain all evergreen species and the last two have deciduous species only. A total of 100 species (a little over 56% of the Pacific aquifoliaceous species) are included in these five groups. The centers of species concentration of all five groups are in subtropical and warm temperate continental eastern Asia, thence the ranges extend northward and southward and the number of species reduces progressively.

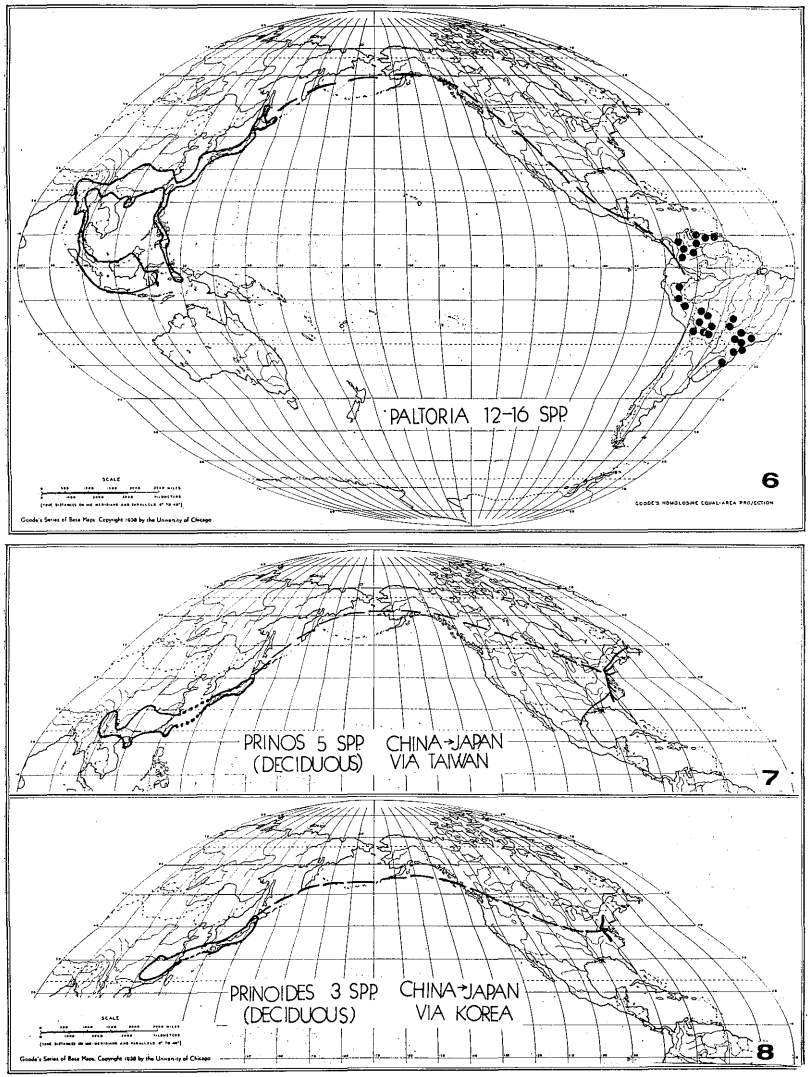
The Aquifolium (Map 4) is the most inclusive group of the Pacific Aquifoliaceae. Fifty-three out of its 55 species occur in southern China. The distributions of the common species shared between China and its neighboring countries correspond with the westward, eastward and southward extensions of its range from the center of species concentration to the periphery. In the west, *I. dipyrena* extends from southwestern China to Sikkim, Nepal and Kashmir. In the south, *I. hookeri* extends from Yunnan to Sikkim, Malay and Sumatra, and *I. glomerata* is found from Kwangtung to Indochina, Malaya, Sumatra, Java, Borneo, and New Guinea (?). In the east, *I. cornuta* extends from eastern China to Korea, *I. buergeri* from southeastern China to Japan via Taiwan, and a closely related species, *I. warburgii*, from southeastern China to the Philippines via Taiwan. Actually, out of the four species of this group recorded from the Philippines, three also occur in Taiwan and Japan.

The northern limit of the range of Aquifolium in the Pacific area is about 48°

latitude, in northern Japan, southern Sakhalin and the Kuriles where it is represented by *I. rugosa*. Species of this alliance appear again in southeastern United States and Mexico, represented by *I. vomitoria* and related species.



Maps 4-5. The widespread and disjunct distribution of groups containing evergreen species only (see text for explanations).



Map 6. Asian—South American discontinuous distribution of groups containing species with punctate leaves only.

Maps 7-8. Asian—North American discontinuous distribution of groups containing deciduous species only.

The Lioprinos (Map 5) is comparatively a smaller group. The center of the concentration of its 20 species is eastern Asia. The western limit of its range is Yunnan and Upper Burma, where it is represented by *I. yunnanensis*. The northern extension of its range is Hokkaido, Japan, as represented by *I. sugeroki*. Two very interesting species, one from the Mountain Region of northern Luzon, *I. permicrophylla*, and the other from the mountains of Sumatra, *I. apiculata*, both belong to the Lioprinos. Species of the Lioprinos group appear in North and South Americas, represented by *I. cassine*, *I. loranthoides*, etc.

The Paltoria (Map 6) is the most pazzling group to me as yet. In the Pacific area, it contains a relatively small number (12–16) of species, with faintly definable specific characters. All the species are derived forms. No primitive species is discovered yet. The center of species concentration is subtropical continental eastern Asia, thence its range extends northward and southward in similar manner as described in Aquifolium. In the north, *I. crenata* var. *radicans* penetrates southern Sakhalin. In the south the species take two different migration routes. The Sino-Himalayan elements extend from southwestern China to Malaya, Sumatra, Borneo, Java and Celebes via Tennaserim of Burma, and the Sino-Japanese elements extend from southeastern China to the Philippines and Ceram of the Molucca Islands via Taiwan. The fact that the Philippine species, *I. luzonica*, has been named *I. crenata* var. *typica* f. *luzonica* shows how close is the relationship between the Japanese and the Philippine species.

The Prinos and Prinoides express the classical pattern of eastern Asian and eastern North American disjunct distribution of elements of temperate forests. Both groups have a small number of species. In Prinos (Map 7) there is a primitive species, *I. micrococca*, which occurs in subtropical and warm temperate forests, extending from Yunnan eastward through North Vietnam, South China, Hainan Island, Taiwan to Japan. The temperate species are best developed in Japan as represented by *I. geniculata*, *I. serrata* and related species. A species of this group reappears in northeastern United States as *I. verticillata*.

The Prinoides group (Map 8) has smaller numbers of species and more restricted range in the Pacific area. The southern limit of its range is along the Tropic of Cancer in eastern Kwangtung. From southeastern and central China, the range extends eastward to Japan via Quelpaert (Chejü) Island of Korea. Species of the Prinoides group reappear in eastern North America. The similarity between some Asian and American species is astounding, as illustrated by *I. tsoii* of Ho-yuen

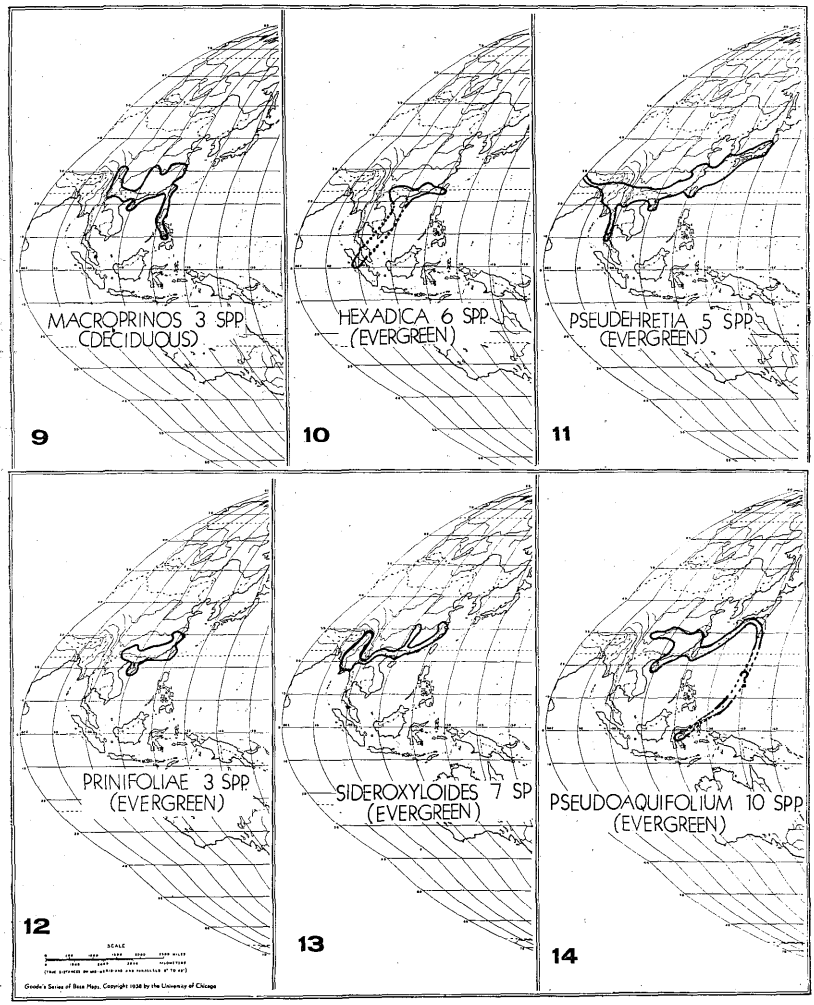
District (Lat. 23°30′ N) in Kwangtung and *I. montana* from Fayette County (Lat. 40° N) in Pennsylvania. It is very likely that both species are relict species from the once widespread Tertiary flora. The latitudinal differences between the very similar contemporary species of Asia and N. America is sixteen and a half degrees. The fossil pyrenes in Brandon lignite establishes the fact that during the Oligocene period, representatives of this group occurred another four degrees farther north.

The data presented here on the distributional patterns of widespread Pacific aquifoliaceous groups with disjunct distributions in the Old World and the New World answer an important question asked by many biogeographers. The question is, "Is it possible for tropical elements to cross the corridors of temperate nature in the exchanges of biota of the two hemispheres during the ancient geological time?" Our answer is "Yes". In the three groups with evergreen species (Aquifolium, Lioprinos, and Paltoria) there are species in every one that penetrate to the tropics as well as the cold temperate zone. However, the great bulk of their species are in the subtropical and the warm temperate zones. Both of the groups with deciduous species extend their ranges from the tropics to the temperate zones. This phenomenon indicates that the ancestral stocks of these groups which now have discontinuous Asian-American distributions had produced species with potential adaptability, species that can survive climatic differences of 15–20 degrees, as illustrated by *I. tsoii* and *I. montana*, species with very little morphological differences.

3. Continental distribution with or without extension to some adjacent islands: Six groups, the Hexadica, Pseudehretia, Prinifoliae, Sideroxyloides, Pseudoaquifolium and Macroprinos have this pattern of distribution. They contain a total of 34 species (about 19% of the total Pacific Aquifoliaceae). Each group represents certain major changes in the evolution of the family. Together they demonstrate the fact that subtropical eastern Asia is a generator of species. It is in this region alone that many unusual species occur. From the widespread groups with discontinuous distribution in the east and west hemisphere we know that subtropical and warm temperate eastern Asia has produced many forms that have spread to many areas of the world through adaptive radiation and speciation. From this six continental groups we know that many other forms were produced through evolutionary changes but they are left in their motherland (Maps 9–14).

A comparison of the groups having distributions restricted to the continent and those with distributions limited to the tropical islands reveals a fundamental difference between them. The number of species of six continental groups amounts

to a little over 19% of the total Pacific aquifoliaceous species. The number of species of three insular groups amounts to over 24% of the total species. These figures indicate that in the evolution of continental groups more fundamental changes were accomplished while in the evolution of insular groups more secondary



Maps 9-14. Distribution of groups containing species restricted primarily to the continent on the west coast of the Pacific (see text for explanations).

changes were involved. The latter phenomenon can be explained by explosive speciation in isolation.

Organs for distribution: The distribution of the species of Aquifoliaceae is effected by the passive movement of pyrenes by birds, wind, water or other agents. A pyrene is a seed covered by a hard woody, leathery or stony endocarp. In an aquifoliaceous pyrene, nature has expressed its perfect design in compactness, lightweight and safety for transporting a small package of life. In this pyrene the embryo is minute and incipient. It is microscopic in size, thickly and completely wrapped in the best insulating material, the oily endosperm, and a membranaceous seed coat. This inner package is protected by a thick and reinforced case, the endocarp, which leaves a pin-point-sized opening, the germination pore. This passageway is plugged up by a hydrodynamically selective spongy material of funicular tissue. A structure like this can almost protect embryo indefinitely. For example, a pyrene of Clemens 40954 collected from Borneo in 1933 was transversally cut open. The endosperm inside was full, fresh, oily and light brown in color. Twelve hours later, the same endosperm exposed only by the cutting surface has shrunk to one-third of its original size and the color has changed to blackish chestnut.

To determine the weight of some aquifoliaceous seed, I have investigated five fruits of *I. hawaiensis* (R. A. Howard 15300). Thirty-seven out of 82 pyrenes contain full seeds. These were air-dried in room temperature for a month. These seeds weigh 0.1432 grams. The average weight of a seed of *I. hawaiensis* is 38 milligrams. The seed of *I. racemifera* is smaller and about three times lighter than the seed of *I. hawaiensis*, while the seed of *I. aquifolium* is larger and about 8-10 times heavier than that of *I. hawaiensis*. There is no weight problem for the dissemination of the seed of any species of Aquifoliaceae.

Summary

One hundred and seventy odd species are recognized for the Aquifoliaceae of the Pacific area. They form a mosaic showing adaptive peaks in the family. They are subdivided into 14 groups. These are used as units in the discussion on distribution.

All the contemporary primitive species of the family occur in the Pacific area. The age of the evolution of the Pacific Aquifoliaceae is estimated with the inference of the fossil species of Aquifoliaceae preserved in the Brandon lignite discovered

at Vermont, U. S. A. The evolutionary lines that involve the widespread advanced groups of the family were well established in the Oligocene. The more primitive groups of the Pacific area must have much older evolutionary history.

Perhaps in the beginning of modern forest species in the Cretaceous period, from the ancestral stock of Ranales, a tree species was evolved. It was related to the ancestral species of Magnoliaceae, Lauraceae, Menispermaceae, etc. but different from all of them. It had the secondary xylem of the Magnoliaceae, the small unisexual flower of Lauraceae, the nelumboid structure of the carpel of Nymphaeaceae, and the potentials of becoming lianoid like the Menispermaceae, and becoming deciduous like the Eupteleaceae. Such an ancestral stock is extinct but its numerous descendants have inherited one or more of its unusual characters and exist as contemporary species of Aquifoliaceae.

The problem of the place of origin of the family is unsolvable. However, there are numerous evidences to indicate that the subtropical continental eastern Asia is the primary generator of species that constitute the major groups of the family. Perhaps the large Pacific islands like Borneo and New Guinea are secondary cradles for some groups. The primitive groups of the Pacific islands are restricted in their distribution to the tropics. There is no evidence for a migration across the tropics to form an amphi-Pacific relationship. All the groups that have Old—New World disjunct distributions have subtropical, temperate as well as tropical species.

There is an obvious poverty of species on the American land masses bordering the east coast of the Pacific. There is a complete absence of species in the temperate zones of western North and South Americas. The few tropical species that have Pacific relations seem to have migrated to the Americas via the North Pacific.

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モチノキ科植物は太平洋地域で 177 種が認められ，著者はこれを 14 群に分類した。本科の最も原始的な種は太平洋地域にあり，他地域のものはこれからでたものとみられるので，本科の発達の歴史を分析するには太平洋地域の種を考慮すれば足りる。進化による形態的の変化は，最も原始的な *Ilex hawaiensis* と最も進化した形の一つである *I. aquifolium* の両種を比較検討することによってよく示され (Figs. 1 & 2)，花枝の着き方，花序の形，花・果・核の形態に差異がみられる。進化の基本的段階を示す変化は，材の 2 次木部の構造，維管束の癒合にともなう花部の退化，分枝の仕方 (Fig. 7)，落葉などの形質に現われる。それに各地域内で，それぞれの環境的条件に応じた二次的な進化の段階が加わる。例えば葉の大きさ・形・質の変化 (Fig. 8)，花序の単純化 (Fig.

9), 毛などがあげられる。

次に 14 群について分布を図示した。Byronia など3群 (Maps 1—3) は計 43 種をふくみ，熱帯に限って分布し，Byronia は本科の中で最も原始的な種をふくみ，非常に古い長い間隔離されたものである。他の5群 (Maps 4—8) には約 100 種が属し，広く太平洋の両側に隔離分布を示すが，その分布の中心は東亜の亜熱帯と暖帯で古型の種をふくみ，それから南北にひろがっている。残りの6群 (Maps 9—14) は計 34 種で主に東南アジア大陸に分布している。

モチノキ科の進化の歴史は化石から推察され，漸新世にはすでに広分布のかなり進んだ群があったことから，その原始形はもっと古いものと考えられる。多分白亜紀に Ranales の祖先形から起源を発し，その原始形は絶滅したが，それからでた多くの子孫が色々な形質をつたえて現在のモチノキ科植物ができたのであろう。東亜大陸の亜熱帯が本科の主な群を構成する種の第一次の発生地であり，ある群ではボルネオやニューギニアが第二次の中心である。太平洋の東側のアメリカ大陸には種類は全く貧弱である。

□П. Г. ГОРОВОЙ: **зонтичные приморья и приамурья** (沿海州及び黒竜州のセリ科植物) pp. 293, figs. 152. HAYKA, 1966. ウラジオストックの Institute of Biologically Active Substances, Far-eastern Branch of the Siberian Department, Academy of Sciences of USSR の candidate である P. G. Gorovoi 氏の著作であり，極東地方のセリ科植物を約9年間に亘って調査研究した結果報告である。内容は 1) 資料の調査，2) 研究沿革，3) 分類学的見解，4) 生態，5) 地理的分布，6) 化学的成分，7) 経済的意義の7項目に分けられ，詳細に意見が盛られている。分類の項では殆んど各種の全形図，果実の断面図，分布図等が挿入してあり，特に果実の写生図は細かく描かれているので，属や種の鑑別に非常に役に立つ。この書は日本のセリ科植物を調べる上にも大いに参考になるものである。同氏は昨年開催された太平洋学術会議に出席していた為，二度会談する機会を得，色々意見の交換をする事が出来た。その結果，オオバミツバ (*Ostericum melanotilingia* (De Boissieu) Kitagawa=*O. crassum* (Nakai) Kitagawa) と *Ligusticum purpureopetalum* Komarov とが同一種である事が確認され，又 *Angelica polymorpha* Maximowicz 即ちシラネセンキュウと見なされている原標本はヤマゼリ (*Ostericum Sieboldi* (Miquel) Nakai) である事が判り，更にアジア東北部のハナウド属で，オオハナウド，ウラゲハナウドと呼ばれている種は北米の *Heracleum lanatum* Michaux では決してなく，私が最初採用した事のある *H. dulce* Fischer が正当な学名であると強調されていたので，ここに一応報告して置く。

(北 川 政 夫)