DISTRIBUTION OF THE DIPTEROCARPACEAE

F. W. FOXWORTHY

There has been a good deal of study of this family during the past quarter century, and it is now possible to give a somewhat more detailed survey of its distribution than that made by Merrill in 1923 (6). Extensive studies of the family have been made in the regions where it is most highly developed. There have been changes in the notions of generic and specific limits, in records of distribution, and in the numbers of species recognized.

What was formerly recognized as the genus *Pachynocarpus* is now relegated to the status of a subgenus of *Vatica*. The genus *Balanocarpus* has been broken up and most of its species placed in *Hopea* or in *Shorea*. The only remaining species is *B. Heimii* King, which will need a new position. Two new genera, *Dioticarpus* and *Upuna*, have been described.

Brandis, in 1895 (2), listed some 325 species in this family, and about 220 of them are still regarded as good species. During the past half century, more than 200 additional species have been described, most of them from Western Malaysia. The principal publications in which the new species have been described are those of van Slooten (8–15), Symington (16–20), and Foxworthy (4, 5). These publications include the descriptions of more than 120 new species from Western Malaysia. Besides these there are scattered publications giving descriptions of new species from other parts of the range of the family, but these are relatively few in number.

I. GEOGRAPHIC DISTRIBUTION.

Six great regions of distribution are recognized, as follows: (1) Africa; (2) Ceylon; (3) India (Western Peninsula); (4) Eastern Peninsula or Further India; (5) Western Malaysia; and (6) Eastern Malaysia. Table I shows the distribution of the genera and species in the different regions. There are, as might be expected, transitional areas, where regions are adjacent or contiguous, and these will be noticed in discussing the different regions.

Region 1. AFRICA.

This great continent has been considered as outside the range of the typical representatives of the family. The genera *Marquesia*, with three species, and *Monotes*, with 31 species, are the only representatives known from Africa, and they are atypical and sometimes considered improperly placed in this family. However, the finding of fossil material of true

TABLE I.

GEOGRAPHIC DISTRIBUTION OF THE GENERA AND SPECIES OF DIPTEROCARPACEAE

Genus	Total spp.	Africa	Ceylon	India	Further India	Western Malaysia	Eastern Malaysia
Anisoptera	13				2	12	2
Balanocarpus	1					1	
Cotylelobium	5		1			4	
Dioticarpus	1			1			
Dipterocarpus	73		5	2	16	58	1
Doona	12		12				
Dryobalanops	9					9	
Hopea	73		4	8	13	49	4
Marquesia	3	3					
Monoporandra	2		2				
Monotes	31	31					
Parashorea	8				2	7	
Pentacme	3				1	3	
Shorea	131		5	3	20	107	3
Stemonoporus	14		14				
Upuna	1					1	
Vateria	51		2	2			
Vatica	65		3	1	11	52	3
Totals	450	34	48	17	65	303	13

¹ Includes *Vateria Seychellarum*, which does not fit exactly into any of the regions and is not included in the other columns.

dipterocarp wood at Mount Elgon (Kenya-Uganda) and in Italian Somaliland has indicated that the subfamily Dipterocarpoideae was well represented in Africa in *late* Tertiary times. Bancroft (1) and Burtt Davy (3) have recorded the finding of additional material. The following quotation is from Bancroft.

"It is, of course, well known to students of taxonomy and plant distribution that the typical living members of the *Dipterocarpaceae* are confined to Asia, their centre of distribution being most probably the 'Malaysian' area, from which distribution has taken place in a general north-westerly direction; and also that the family is represented in Africa only by an aberrant group, the *Monotoideae*, comprising some thirty species of *Monotes* and three of *Marquesia*. The members of this small group are not rain-forest trees, like the true Dipterocarps, but are scattered inhabitants of the savannah country at high altitudes and of acidic soil type it is evident that typical Dipterocarps were formerly more widely distributed than at the present day; and the inference is that, having reached Africa from Asia, they subsequently receded, leaving as representative of the family in Africa only the *Monotoideae*, which are well adapted to special conditions of habitat the former occurrence of true Dipterocarps in Somali-

land, and further to the southwest in British East Africa, when considered in relation to the present distribution of those living forms which they seem most closely to resemble, suggests that the extension of the family from Asia into Africa took place by way of a north-western

land-connexion between the two continents.

"Other African fossil woods are now under consideration, and these, again taken into consideration with the present distribution of related forms, point to a similar conclusion of north-westward migration of Asiatic types. If such migration did in fact take place in Tertiary (or perhaps earlier) times, the climate of the then-existing land-connexion must have been much more humid than that of the corresponding area at the present day.

"Within the past few months, herbarium material has come to hand, from areas as far removed as Nigeria, Gabon, and the Belgian Congo, which indicates that true Dipterocarps (the sub-family Dipterocar-

poideae) are still living in the primitive forests of Africa."

So far as known, the identifications of these recent collections have not

yet been published.

The only possible transitional form that has been recorded between this region and the next is *Vateria Seychellarum* Dyer, from the Seychelles. This species seems to be closely related to its congeners in Ceylon and India.

The very distinct character of the hitherto recorded forms from Africa would seem to indicate that the African forms have long been separated from those of the regions to the east.

Region 2. CEYLON.

This island seems to constitute a very compact province of distribution. There are 48 species recorded, in nine genera, and only a single species, *Vatica chinensis* L., is known to have a range extending to India. Three genera, *Doona*, *Monoporandra*, and *Stemonoporus*, are known only from Ceylon. There is a higher proportion of endemism than is found in any of the eastern range of the family.

A few of the species of the larger genera (Dipterocarpus, Hopea, Shorea, and Vatica) show close relationship to other species of the same genera

in India and Malaya.

All but one of the Ceylon species are found in the moister parts of the island. A single species, *Vatica obscura* Trimen, is recorded as characteristic of the drier part of the island.

Region 3. India (Western Peninsula).

This region, as indicated by Brandis, is bounded on the east by Assam, which is transitional to the next region.

The Indian region, as thus limited, contains but 17 species, 15 of them endemic. The small number of species may be due to the large areas of dry country and to unfavorable soil conditions. There are fairly extensive areas of tropical rain-forest, and all the species but *Shorea robusta* and *S. Tumbuggaia* are restricted to the moist regions.

The monotypic genus *Dioticarpus* is peculiar to a limited area in South India. *Vatica chinensis* L. is found also in Ceylon and *Shorea robusta* Gaertn. f. extends into Assam. *Dipterocarpus indicus* Bedd. is very closely related to *D. turbinatus* Gaertn. f., of the next region, and has sometimes been considered to belong to that species. *Shorea talura* Roxb. is very close to *S. floribunda* Kurz, of Burma, and possibly not distinct.

The transitional area of Assam is separated from India proper by mountainous country. Six species are represented in Assam, two of them endemic; one is Indian, and the others are found in the next region.

Region 4. EASTERN PENINSULA (Further India).

This includes Burma, Siam down to 10° N. lat., Indo-China, and the tropical portion of China. There is a great deal of mountainous country and the distribution of dipterocarps is limited by elevation and climate.

To the south there is land connection with the Malay Peninsula, which begins at the Isthmus of Kra, at about 10° N. lat. The Malay Peninsula is a part of Western Malaysia. There is a climatic change at about 7° N. lat., and few species cross this line. The area between 7° and 10° N. lat. is transitional between regions 4 and 5. South of 7° the flora is distinctly Malayan and north of 10° it definitely belongs to region 4. In recent geologic time, the Malay Peninsula south of 7° was an island.

Within region 4 are found most of the species that show distinct adaptation to a prolonged and severe dry season. There are also considerable areas of rain-forest, where the conditions approach those of the next region and are most favorable for the development of dipterocarps. Of the 65 species recorded from region 4, 31 are endemic. Most of the species are in the moister parts.

The most striking feature of the distribution of dipterocarps in this region is what has been called the *dry deciduous dipterocarp forests* of Burma, Siam, and Indo-China. These forests are extensive and are most often found on laterite, though sometimes on sandy or gravelly soil. The dominant and strikingly gregarious species are *Dipterocarpus tuberculatus* Roxb., *D. obtusifolius* T. & B., and *Pentacme suavis* A. DC. The last named species occurs in the driest situations and often on other soils than laterite. It has been found on calcareous soil and as far south as 7° N. lat.

The species of the dry deciduous forests usually have a thick bark, which enables them to resist ground fires.

Region 5. Western Malaysia.

This includes the Malay Peninsula, the part of the Malay Archipelago west of Wallace's Line, and the Philippine Islands. The land is generally covered with tropical rain-forest, soil and climate being most favorable to the development of high forest. The most representative species of these forests are members of the family Dipterocarpaceae, which usually provide the largest volume of timber. Fully two-thirds of the species of

the family are found in this region. Twenty-four of the species extend into region 4 and only two species into Eastern Malaysia.

The genera *Dryobalanops*, *Balanocarpus*, and *Upuna* are known only from this region; and all of the larger genera of the family also have their greatest development in this region. What was formerly regarded as the genus *Isoptera* is now considered to be a section of the genus *Shorea*.

Table II shows the distribution of species and genera in the different parts of Western Malaysia.

TABLE II.

Genus	Malay Peninsula	Sumatra	Java	Borneo	Philippines	Total spp. W. Malaysia
Anisoptera	7	4		3	4	12
Balanocarpus	1					1
Cotylelobium	2	2		3		4
Dipterocarpus	24	22	5	34	11	58
Dryobalanops	2	2		9		9
Hopea	25	8	1	20	9	49
Parashorea	4	3		2	2	7
Pentacme	1				2	3
Shorea	54	22	1	60	15	107
Upuna				1		1
Vatica	21	10	3	21	8	52
Totals	141	73	10	153	51	303

This region is generally considered to be the centre of distribution of the family. The great island of Borneo has the largest number of species and the Malay Peninsula only slightly less. Considerable parts of Borneo are very imperfectly known botanically, and it is probable that the number of species from the island will be considerably increased. Of the 153 species found in Borneo, 52 are known from the Malay Peninsula, 33 from Sumatra, 15 from the Philippines, three from Java, and two from Eastern Malaysia.

It seems that Sumatra, the Malay Peninsula, and the Philippine Islands have had former land connections with Borneo and that this land was the region where the family originated and from which it spread out.

The most widely distributed species are: Dipterocarpus grandiflorus Blanco, from Burma, Siam, the Malay Peninsula, Sumatra, Borneo, and the Philippines; D. gracilis Bl., from Assam, the Malay Peninsula, Sumatra, Java, Borneo, and the Philippines; and Shorea guiso (Blanco) Bl., from Indo-China, Siam, the Malay Peninsula, Borneo, and the Philippines.

Region 6. EASTERN MALAYSIA.

This includes that part of the Malay Archipelago east of Wallace's

Line, — extending as far to the east and south as the great island of New Guinea. It is an extensive area, but contains very few representatives of this family, — a total of 13 species, as follows:—

Anisoptera — two species. One of these, A. costata Korth., is widely distributed in Western Malaysia. The other is restricted to New Guinea.

Hopea — four species in New Guinea, one of them also in Celebes.

Shorea — three species — one in New Guinea, one in the Moluccas, and one in Celebes and the Moluccas.

Vatica — three species — one of wide distribution and two restricted to Celebes.
The species of wide distribution, V. papuana Dyer, seems to be adapted to distribution by sea-currents. It is found along the coasts of the southern Philippines,
East Borneo, the Moluccas (Ternate, Obi, Batjan, Aru Islands), and New Guinea.
Dipterocarpus — a single species, D. retusus Bl., as far to the east as Sumbawa.

It would seem that the barrier indicated by Wallace's Line (or its modification by Merrill) has been sufficient to prevent the spread of many

species to this region.

Van Slooten (14, p. 434), impressed by the finding of two species of *Dipterocarpus* in Bali and one species in Sumbawa, stated, "... it is certain that the distribution of the genus *Dipterocarpus* has nothing to do neither with a line of demarcation through Central Java, nor with the so-called line of Wallace."

Nevertheless, it seems to me that this line is important and marks the limit beyond which few species of dipterocarps have gone.

II. LATITUDINAL RANGE.

The family is, as is well known, a tropical one and has its best development in the equatorial region. A few species extend to the northern limits of the tropics and have an extreme range to a short distance outside the tropics. The known species with such distribution are:—

In India — Shorea robusta Gaertn. f. — to 32° N. lat.
In Burma — Dipterocarpus tuberculatus Roxb. — to 25° N. lat.
D. obtusifolius T. & B. — to 24° N. lat.
Shorea obtusa Wall. — to 24° N. lat.
Pentacme suavis A. DC. — to 25° N. lat.

III. ALTITUDINAL RANGE AND SOIL CONDITIONS.

Most species are found in lowland forest, usually below 2,000 ft. The highest elevation recorded is a little over 5,000 ft. This has been recorded for *Shorea robusta* and for two species of *Dipterocarpus*.

Certain species are usually found on low ridges, and certain others are usually found at the higher elevations. However, characteristically high hill forms are sometimes found at lower elevations, and the lowland forms may be found up to 2,500 feet or more, apparently depending upon conditions of exposure and drainage.

Soil conditions influencing distribution.

The relatively small numbers of species found in dry or deciduous forests

are greatly influenced by the nature or condition of the soil. The most characteristic case is that of *Dipterocarpus tuberculatus* Roxb., which is most often found on lateritic soil. Other species characteristic of the dry deciduous forests have been mentioned. *Shorea robusta* Gaertn. f. thrives on moist deep sandy loam with good subsoil drainage. It may occur on several types of soil, but it needs moist soil and good drainage.

Most species of dipterocarps occur in tropical rain-forest, where there is a good deal of soil moisture and high humidity. Under these conditions, the nature of the soil is of less importance. Drainage is, however, important. Most species, while requiring a good deal of moisture, do not thrive in a water-logged or swampy soil. Nevertheless, there are a number of species which thrive in fresh water swamps. Some of the species found in fresh water swamps, or at the edge of the swamp, and their distribution, are:—

Anisoptera marginata Korth. — Malay Peninsula, Sumatra, Bangka, Borneo.

Dipterocarpus costulatus v. Sl. - Malay Peninsula, Sumatra, Borneo.

Dipterocarpus Dyeri Pierre — Burma, Indo-China, Malay Peninsula.

Dryobalanops Rappa Becc. — Borneo.

Shorea albida Sym. — Borneo.

S. Pinanga Scheff. - Borneo.

- S. Teysmanniana Dyer Malay Peninsula, Sumatra, Borneo.
- S. platycarpa Heim Malay Peninsula, Borneo.
- S. rugosa Heim Borneo.
- S. uliginosa Foxw. Malay Peninsula, Sumatra.
- S. inaequilateralis Sym. Borneo.

Vatica imbricata v. Sl. — Borneo.

V. Wallichii Dyer — Malay Peninsula, Sumatra.

IV. METHODS OF DISTRIBUTION.

1. By water.

A few species seem to be adapted to distribution by water. The single species believed to be distributed by sea-currents, *Vatica papuana* Dyer, has already been mentioned.

Several species of river valleys are believed to be distributed by fresh water. Examples are *Shorea seminis* (De Vr.) v. Sl. and *S. sumatrana* (Thor.) Sym.

2. By wind.

Most species have fruits that are equipped with wings several times longer than the seed. These wings aid in the dispersal of the fruits by wind action.

The rain-forest, where most of the species grow, is so dense that there is comparatively little action by strong winds within the forest and there is consequently little opportunity for distribution to long distances. Ridley (7, pp. 104–109) has stated that dipterocarp fruits are usually not carried by wind to a distance of more than 30 or 40 yards from the parent tree, and, exceptionally, to only about 100 yards.

This statement may be rather too conservative, in that it does not give sufficient importance to the occasional wind storm. Webber (21) has given an account of a small wind storm, in the Malay Peninsula, that carried large numbers of dipterocarp fruits to a height of several hundred feet and a distance of at least half a mile. Forms represented among the fruits thus carried were: — Shorea leprosula, S. parvifolia, S. macroptera, S. bracteolata, Anisoptera spp., Dipterocarpus spp., and Hopea spp.

Similar observations have been made in the Philippine Islands, where fruits of *Parashorea plicata* Brandis were carried to distances in excess

of a half-mile by typhoon winds.

Such wind storms as those mentioned are, doubtless, infrequent, but may occur a number of times during the life of a tree. It is evident that wind is an important agency in the distribution of members of this family.

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