THE DEVELOPMENT OF THE NATURAL ORDER *MYRTACEÆ.*

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Introduction.—The present distribution of two Natural Orders of plants was considered with reference to their probable geographical environment in the past, and the environment, thus suggested, was compared with that succession of Cretaceous and Tertiary geographies, which had been deduced years before by the writer from physical data alone. The Orders Myrtaceæ and Leguminosæ were the two chosen in this connection, but the former alone is considered in the present paper.

Such a comparison was suggested by a knowledge of the peculiar assemblage of plants growing on the coarse, acid sandstone of the Sydney and Blue Mountain Districts. Although the sandy soil of this district appeared to be exceedingly sterile, nevertheless it supported a great number of species, as well as numerous genera. Moreover, although the individuals were dwarfed in appearance, yet were they clustered thickly together, and not scattered here and there as on an arid plain. This sandstone area was surrounded by formations of a clayey nature, and the soils from such formations, when protected from the desolating winds of the interior, and also when under the influence of a good rainfall, were observed to support luxuriant growths of plants belonging to types differing in many ways from those which flourished on the sandstones. It was noted, also, that the plant-types which were crowded together on the coarse sandstones were those which had been recognised by botanists as being practically confined to Australia, for example: *Bæckea, Banksia, Leptospermum, Melaleuca, Callistemon, Angophora, Kunzea, Calythrix, Darwinia, Pultenæa, Eutaxia, Bossiæa, Gompholobium, Styphelia, Monotoca, Epacris, Hakea, Grevillea, Xylomelum, Telopea, Persoonia, Boronia, Petrophila, Isopogon, Lambertia,* and others too numerous to mention. This, in itself, was remarkable, but when, in addition, it was noted that the rich, sheltered and well-watered pockets of soil, forming islands in this sandstone-setting, were avoided almost absolutely by the genera practically endemic in Australia, and were largely occupied by genera not peculiar to Australia, such as *Myrtus, Eugenia, Elæocarpus, Ficus, Livistona,* and others, the case became still more interesting, and suggested that the peculiar vegetation, for which Australia is noted, had been developed in an extremely sandy and porous soil. Especially was this idea strengthened by the knowledge that the extremely sandy granites of eastern New South Wales, and the sandstones of the Clarence River Basin supported a flora almost identical with that of the Sydney sandstones and the Blue Mountains. This conclusion received additional support, also, from the fact that this vegetation avoided the rich basaltic soil of the Northern rivers, yielding place there to dense growths belonging to genera not peculiar to Australia, such as *Dysoxylon, Echinocarpus, Panax, Sterculia, Cedrela, Gmelina,* and *Elæocarpus.* Moreover, although the individuals were closely-set together on the sandstone, nevertheless the sunlight had access to all their parts, whereas on the rich soil the genera, not peculiar to Australia, formed dense jungle-growths. This suggested that the vegetation peculiar to the continent had developed either in a rigorous climate or in one essentially sunny; whereas the other was of more recent origin, and depended on moist and sheltered conditions. But whereas the rich basalt-soils, of the sheltered portions of the Coast, supported dense jungle-growths, soils very similar on the plateaus and plains, when exposed to the desolating winds of the Central continent, whether hot in summer or cold in winter, were avoided alike, in great measure, by those types, whether peculiar or not peculiar to Australia. This suggested that:—

1. The basaltic soil plains were of later origin than the evolution of most of the genera peculiar to Australia, and such plants had not yet accommodated themselves to this soil.

2. The genera not peculiar to Australia were unaccustomed to desiccating and desolating influences, and had not yet accommodate themselves to such influences.

3. Or again, it suggested that, possibly, the basaltic soil, under dry and exposed climatic conditions, was peculiarly unfitted to support vegetation in abundance.

Several other interesting points also were suggested at this stage. The leaves of the sandstone-types were characteristically heath-like, or rigid or pungent; nevertheless, others again, such as the majority of the Leptospermums, Melaleucas, and Callistemons were observed to possess much larger leaves, and to frequent the moister situations on the sandstone-areas. The first suggested a general accommodation either to poor sandy soil, to xerophytic, or to cold and harsh conditions; while the second suggested evolution under more genial conditions than had genera, such as *Styphelia, Calythrix* and *Epacris.* The wealth of beautiful flowers, on the coarse acid sandstone-areas, also suggested evolution under strong sunlight.

Another point of interest noted was that in proportion to the mildness, the moisture, and the shelter attained in any locality, so, in that proportion, was there a tendency for those genera, which were not endemic in Australia, to oust those which were peculiar to Australia. This, again, suggested that the genera peculiar to Australasia had developed amid rigorous and harsh conditions, and had not yet accommodated themselves to a genial and extremely moist climate.

To most of these rules, however, the genera *Acacia* and *Eucalyptus* formed exceptions. Whether in harsh or genial surroundings, in heat or cold, in soil either good, poor, rich or sandy, these genera rarely failed to establish themselves firmly. Nevertheless, elastic of temperament as they were, *Acacia* and *Eucalyptus* both appeared to be ill-adapted to cope with the advance of those genera not peculiar to Australia, when in an environment of abundant shelter, good soil, and with heavy and continued precipitation. This suggested the failure of even *Acacia* and *Eucalyptus* to compete with the Indian and Antarctic floral elements, when the latter were in their true environment. The range of habitat of these genera, however, is highly instructive. Thus certain Eucalypts* with transverse leaf-venation, with a characteristic essential oil known as pinene, and with peculiar anthers, flourished on the poor sandy soils. Other Eucalypts, again, such as the Boxes, flourished in heavy clay soils, and possessed much cineol or eucalyptol, a characteristic leaf-venation, and, morever, they possessed peculiar anthers opening in pores. Still a third group, embracing such forms as the Peppermint and the Snow-Gums, possessed much phellandrene oil, a parallel venation, and kidney-shaped anthers; and they occupied the moister and cooler portions of the plateau-regions. The Acacias were found in all soils indifferently, but their morphology was found to be peculiar in proportion to their adaptation to certain climatic and soil-surroundings. In the case of the Eucalypt, this suggested an origin in open sandy country, but an ability later, by the production of special devices, to flourish on the heavy soils, and in cold, moist climates.

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* R. H. Cambage, Presidential Address. Journ. Proc. Roy. Soc. N. S. Wales, 1913.

In all these observations, the writer inferred that the predominant influence, in the plant-evolution, was geographical environment. Other factors in their evolution appeared to be Time, Heredity, Variation, and Selection. Time is a constantly flowing quantity, and, in the evolution of floras, such an evenly flowing quantity must be large, since the other factors produce only infinitesimal results when acting only during brief periods. The remaining factors are exceedingly variable in their action, and the sluggish or rapid response of the organism, along variable lines, is due mainly, either to the fixity of its climatic and soil-environment, or to a revolution in its geographical surroundings. A geographical revolution would tend to produce either plant-extinction in part or as a whole, or a relatively sudden deployment into new genera or even families, such as one sees among the Dicotyledons in later Mesozoic time.

The principle adopted, in the present note, is the application of the "Law of Probabilities" to the case of the development and distribution of the Myrtaceæ Thus the earlier types of the family have been sought by a consideration of those genera which possess the most points in common, consonant with certain facts known to be connected with the geographical setting of the earlier types. In this way, those types are considered as aberrant which, although excellently adapted to a definite set of local geographical conditions, nevertheless depart in essentials from the deduced primitive forms. Thus, for example, if it should be ascertained that the points common to all genera of the Myrtaceæ were much more characteristic of the genera not endemic to Australia, such as the Myrteæ; furthermore, if such Myrteæ were ascertained to be practically confined to the tropics; that they flourished in good soil and abundant rainfall; that their species far outnumbered those of types endemic to Australia; furthermore, if it were found that Australia had been isolated from the other parts of the tropics during the production of the endemic genera; that the Australian types flourished on porous, sandy soil, and in proportion as they tended to depauperate types, that they exhibited modifications of those organs typically developed in the Myrteæ, then these would be considered as the earlier type of Myrtaceæ, and the capsular-fruited genera would be considered as a type derived from Myrteæ, in harmony with local Australian conditions.

Bentham, in the concluding preface to his Flora Australiensis, made the accompanying statement, with regard to the Australian Flora: "The predominant portion appears to be strictly indigenous. Notwithstanding an evident though very remote ordinal tribual or generic connection with Africa, the great mass of purely Australian species and endemic genera, must have originated or been differentiated in Australia, and never have spread far out of it." The present report appears to bear out Bentham's contention

With the vast amount of information, concerning the Australian Flora, now assembled in the "Flora Australiensis" of George Bentham, "The Flora of Australia and of Tasmania" by Sir Joseph Hooker, "The Census of Australian Plants" and "The Eucalyptographia," by von Mueller, "The Index Kewensis" and its Supplements, "The Critical Revision of the Genus Eucalyptus," and "The Forest Flora of Australia" by J. H. Maiden, as well as the exceedingly numerous unpublished drawings of Eucalyptus anthers by J. H. Maiden, "The Research on the Eucalypts" and "The Research on the Pines of Australia" by Messrs. Baker and Smith, the Botanical Notes (16 papers in these Proceedings, 1900-1913), and other papers* by R. H. Cambage, various papers† on distribution by H. Deane, the papers‡ on Australian Vegetation by Professor R. Tate, the time appears now to be ripe for a statement as to the probable development, in Australia, of Orders such as those of the Myrtaceæ, the Compositæ, the Leguminosæ, the Proteaceæ, the Casuarineæ, or the Coniferæ.

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* "Climatic and Geological Influence on the Flora of New South Wales." Rept. Aust. Assoc. Adv. Sci. 1907, Adelaide, p.476. Presidential Address, Journ. Proc., R. Soc. N. S. Wales, 1913.

† Presidential Addresses. These Proceedings, 1895 and 1896, also 1900.

‡ "On the Influence of Physiographic Changes in the Distribution of Life in Australia." Rept. Aust. Assoc. Adv. Science, 1889, Vol. i., p.512.

See also, "On the Myrtaceæ of Australia," by the Rev. W. Woolls. These Proceedings, 1884, pp.643-648.

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To Mr. Maiden, very cordial thanks are tendered for access at all times to the storehouse of literature and plants at the National Herbarium, attached to the Sydney Botanical Gardens; also for access to the very numerous unpublished drawings of Eucalypt anthers which he has prepared, and for his great personal kindness in answering any queries as to general botanical information bearing on the point under consideration. To Mr. E. Cheel and Mr. A. A. Hamilton also, the Writer desires to return sincere thanks for their kindness in facilitating research in the National Herbarium.

To Messrs. Baker and Smith, the Writer is deeply indebted for the new light which their "Research on the Eucalypts" has thrown upon the problem of Eucalypt-distribution and classification especially in connection with the relations existing between oil-contents and leaf-venation.

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Thesis.—The family Myrtaceæ originated in the fertile tropics, and had a much wider range in the late Mesozoic than at present, owing to the large epicontinental seas, the low-lying lands, and the mild and moist climate of the Cretaceous. With the great increase in size of the continents during Post-Cretaceous time, and the formation of high and broad mountain-borders to the continents, the genial climate of the Cretaceous became differentiated gradually into distinct zones, and the northern and southern range of Myrtaceæ became thereby much contracted. In certain countries, such as Australia and America, which, about that time, became partially or wholly isolated from other tropical regions, the Myrtaceæ underwent divergent transformations, the Eugenias, Myrtles, Campomanesias, Myrcias, Psidiums, Calyptranthes, and other types marking a deployment of genera in the fertile tropics, the capsular-fruited Myrtaceæ marking an adaptation to less genial conditions, while the Chamælaucieæ mark an organic response to severer conditions of climate, and to a greater poverty and porosity of soil, than the majority of the Leptospermeæ.

Geography.—The Cretaceous, in Australia, as in the greater part of the world, appears to have been a period at once of genial and moist climate, of reduction of the continental surface to low-lying plains by stream-action, and a period also of great sea-transgressions over the continent. The continent appears to have been connected with Asia, at least throughout the lower Cretaceous, and to have been separated therefrom at some period during the Upper Cretaceous.

New Zealand appears to have been connected with Australia or New Guinea by way of New Caledonia in the Cretaceous, and the first separation from the main Australo-Asiatic block appears to have been that of New Zealand*, then the Australian province appears to have been separated from Asia and its continuation south and east to Celebes and Borneo. New Caledonia and Fiji appear to have been separated later from the main mass, and Celebes became separated from both Asia and Australia. Timor and other Islands were separated from the continent at a later date.

In the Upper Cretaceous, the Australian Continent was occupied by a central sea. By analogy with a study of Northern American, Asiatic, and European conditions in the Upper Cretaceous, it would be reasonable to infer that the Cretaceous sea completely separated Western from Eastern Australia. There is no direct

* See also C. Hedley, "A Zoögeographic Scheme for the Mid-Pacific."

geological evidence, however, of a complete separation of West from East. This is all the more remarkable, because the period was one of great peneplanation, and a barrier to the junction of the Indian and Southern Oceans, across Australia, by the transgression of the Cretaceous Sea, is difficult to understand.

The characteristic soil of Australia, during the Cretaceous, is evidenced by the sandy and porous nature of the Cretaceous sediments.

A study of Western and Eastern Australian geology suggests that the surface of the continent was mostly sandy in nature, although the various slate- and shale-deposits formed local exceptions.

In the Lower Tertiary, the Cretaceous Sea was drained off the continent in great measure, and the climate of the centre began to change slowly, the old equable and genial conditions giving place to greater extremes of heat and cold, and increasing desiccation. The present stage of dryness over the whole central continent, however, appears to be a recent development.

In the Eocene, the Cretaceous Plain appears to have been warped somewhat on its eastern margins, and in both this and a later period of the Tertiary, deep leads were formed, and great floods of basalt covered many portions of the lowlying eastern continent. During the great "Deep Lead" Period, the warped eastern continent had been partly reduced again to a peneplain.

The Deep Leads contain infrequent traces of Eucalypts, but not of other Myrtaceæ, in fact the numerous plant-remains suggest the occupation of Eastern Australia, during that period, by Indian types,* although plants closely allied to Callitris and Banksia are frequently found in the leads. At the present day, the surface of the areas, in which these remnants of tropical types have been found in such abundance, is occupied mainly by cold-loving types of Australian plants, owing to the formation of plateaus in these areas.

* Baron von Mueller, New Vegetable Fossils. Decades i.-ii., 1874-1882.

During this period, the continent appears to have been co-extensive with New Guinea and Tasmania, and to have extended for a considerable distance southward of Tasmania.

In late Tertiary time, Eastern Australia was affected by a topographical revolution, during which, the low-lying land, near the sea, was disturbed and raised to form the plateaus of New Guinea, Queensland, New South Wales, Tasmania, and South Australia, as also that of Western Australia. The climate thereby became changed.

The central plains of Eastern Australia, which had been initially formed in the earlier and middle Tertiary, were much enlarged by the late Tertiary sedimentation, following upon the uplift.

In the Pleistocene came the general lowering of temperature over the whole world, and with it, the gradual desiccation of Central Australia, as is evidenced by the present process of the choking-up of the old stream-channels with waste. This may be seen well in such districts as that of Cobar.

The Geographical Distribution of Myrtaceæ.

The authorities consulted in this connection were Index Kewensis and the three Supplements thereto. For the Australian distribution of Myrtaceæ, von Mueller's Census for 1889 was used, as also Bentham's Flora Australiensis. With a very few exceptions, the terminology employed is that adopted in the Flora Australiensis (1866).

For the purposes of the accompanying lists of species, *Jambosa* and *Syzygium* are considered as included under *Eugenia,* as suggested by Bentham and Hooker. Lecythideæ is considered as a separate family, the reasons being assigned in a subsequent chapter.

Mr. Cambage has supplied the list of Eucalypts known in Eastern Australia, and Mr. Cheel the distribution in Australia of *Callistemon.*

All the other lists are only approximate.

DISTRIBUTION OF CHAMÆLAUCIEÆ.

	Eastern Australia.	Western Australia.	
Actinodium	......	......	......
**Darwinia* ... **Homoranthus* ... **Chamælaucium*	6 (approx.)	32 (approx.)	......
Verticordia	1	40	......
Pileanthus	......	3	......
**Calythrix*	12 (approx.)	29 (approx.)	*C. tetragona* found in all the States.
Llotzkya	1	10	*L. genetylloides* common in S. Australia and Victoria.
**Thryptomene*	......	33 species in Australia, mainly in W. Australia.	......
**Micromyrtus*	......	9 species in Australia, mainly in W. Australia.	......
Wehlia	......	3	......

* Lists not complete.

Distribution of Capsular-Fruited Myrtaceæ.

Genus.	Eastern Australia.	Western Australia.	New Guinea.	New Caledonia.	New Zealand.	New Britain.	Timor.	Phil-ippines.	Borneo.	China.	India.	Java.	Sumatra.	Burmah.
Scholtzia	......	12	...	...	...	...	...	...	...	...	...	.	...	...
*†*Bæckea*	17(approx.)	48(approx.)	...	5	...	...	...	...	..	1	...	...	1	...
Astartea	......	3	...	...	...	...	...	...	...	...	...	...	...	...
Hypocalymna ..	......	12(approx.)	..	...	...	...	...	..	...	...	...	...	...	...
Balaustion	......	1	...	..	...	...	...	...	...	...	...	...	...	...
Agonis	1	12	...	...	...	...	...	...	...	...	...	...	...	...
§*Leptospermum*	16	7	...	..	3	...	...	1	1	..	...	1	...	1
**Kunzea*.	10	10	...	..	...	...	...	...	...	...	...	...	...	...
Callistemon .. .	16	2	...	2	...	...	...	...	...	...	...	...	...	...
***Melaleuca*	36	84‡	...	2	1	...	...	...	...	...	...	...	...	...
Conothamnus ..	.. ...	2	...	...	..	...	...	...	..	...	...	...	...	...
Beaufortia	......	18	...	...	...	...	...	...	...	...	...	...	...	...
Regelia ...	... ..	3	...	...	...	...	...	...	...	...	...	..	...	...
Phymatocarpus	... ..	2	...	...	...	...	...	...	..	...	...	...	...	...
Calothamnus.	... ...	23	...	...	...	...	.	..	..	...	...	...	...	...
Lamarchea ...	......	1	...	...	...	...	...	...	...	...	...	...	...	...
Eremæa	......	6	...	...	...	..	...	...	...		...	...	...	...
Angophora	5	......	...	...	...	..	...	...	...	...	...	...	...	...
Eucalyptus	200	70-100 (approx.)	4(?)	...	...	1‡‡	4‖	1‡‡	...	...	..	...	...	...

* Lists not complete. † *B. virgata* in New Caledonia and Australia; *B. frutescens* common in Eastern Archipelago and South China. § *L. flavescens* in Eastern Australia, Indian Archipelago, Malacca, etc.; *L. scoparium* in E. Australia and New Zealand. ** *M. leucadendron* abundant in E. Australia, Indian Archipelago, and Malayan Peninsula.

‡ 6 common to east and west. ‖ 3 species also in Moluccas. ‡‡ *E. Naudiniana*.

DISTRIBUTION OF METROSIDEREÆ.

Genus.	Eastern Australia.	Western Australia.	New Guinea.	New Caledonia.	New Zealand.	New Britain.	Timor.	Phil-ippines.	Borneo.	China.	India.	Java.	Sumatra.	Burmah.	Malaya.	Banca Is.
Tristania	14	...	1	7	...	...	...	1	...	...	...	...	...	3	3	1
**Metrosideros*	14	...	1	7	16	...	...	...	...	...	...	1	...	...	...	...
†*Syncarpia*	4	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Xanthostemon	2	...	...	1	...	...	...	1	...	...	...	...	...	...	...	...
Lysicarpus	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Nania	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...
Cloezia	...	...	...	6	...	...	...	...	...	...	...	...	...	...	...	...
Spermolepis	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...
Piliocalyx	...	...	...	6	...	...	...	...	...	...	...	...	...	...	...	...
Backhousia	5	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
‡*Osbornia*	1	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...

* *Metrosideros* also possesses one species in South Africa, two in the Moluccas, one in Madagascar, two in the Saudwich Islands, one in Lord Howe Island, one in Chili, and one in Tahiti. The African, American, Tahitian, and Hawaiian species appear to be anomalous and doubtful.

† *Syncarpia* possesses one species in the Amboin Is.

‡ The species in Australia and the Philippines is the same.

DISTRIBUTION OF MYRTEÆ.

Genus.	Tropical America (rarely extra-trop.).	Tropical Asia.	South Europe.	Pacific Islands.	Africa (mostly Trop.)	New Caledonia.	New Zealand.	Australia.	Islands between Asia & Australia.
	Species.	Species.	Species.	Species.	Species.	Species.	Species.	Species.	Species.
Eugenia	850 (approx.) ...	200(approx.)	......	55(approx.)	76(approx.)	20	......	40	96 (approx.)
Myrtus	135 (approx.), a few in extra-tropical America	8	1(*M. communis*; also in W. Asia)	......	2	8	4	16	6 (also in Japan)
**Myrcia*	320 (approx.) ..	......	......	......	......	......	......	......	......
**Campomanesia* ..	70	1 (doubtful)	......	......	......	......	......	......	......
**Calyptranthes* ...	100	......	......	3 (Fiji)	1 (1 also in Mauritius)	......	......	......	1 (Java)
**Calycolpus*	10 (approx.) ...	......	......	......	......	......	......	......	......
**Psidium*	130 (approx.) ...	7	......	A few	1 (2 also in Mauritius)	......	......	......	......
**Feijoa*	2	......	......	......	......	......	......	......	......
**Marlieria*	30	......	......	......	......	......	......	......	......
**Calycorectes*	10	......	......	......	......	......	......	......	......
**Decaspermum* ...	... ...	2	......	1	......	......	......	1	2
Rhodomyrtus ...	... ...	1	......	......	......	......	......	4	......
Rhodamnia	... ...	1	......	......	......	......	......	4	2
Nelitris	... ...	3	......	2	1	1	......	2 or 3	9
Fenzlia	...	......	......	......	......	......	......	2	......
Pimenta	4	1	......	......	......	......	......	......	......
Myrrhinum ...	4	......	......	......	......	......	......	......	......
Pleurocalyptus ..	... ...	......	......	......	......	1	......	......	......

***Aulacocarpus*, *Psidiopsis*, *Paivœa* and *Tepualia* 3, 1, 1 and 1 species, respectively, in South America.**

*** Lists not complete.**

Combining these approximate results we have:—

Eugenia with about 1,325 species.
Myrcia with about 320 species.
Eucalyptus with about 300 species.
Myrtus with about 180 species.
Psidium with about 140 species.
Melaleuca with about 135 species.
Calyptranthes with about 100 species.
Bæckea with about 80 species.
Campomanesia with about 70 species.

The other genera are much smaller as regards numbers of species.

In Myrtaceæ, there are approximately 3,100 species (Pflanzenfamilien, 1898, records about 2,750 species in Myrtaceæ) of which America (almost wholly tropical or subtropical) contains about 1,670, Australia about 800, Tropical Asia about 235, South Europe 1, Africa (mainly tropical) about 85, and the Pacific Islands, together with the Indian Archipelago, about 310 species. Of these 3,100 species, Tropical and Subtropical America contain about 54 per cent., while Australia and the surrounding Islands contain about 26 and 10 per cent. respectively. The fact that Europe contains only one species (common also in Western Asia) is most significant, as is also the fact that North America probably contains not more than 10 species. One genus alone, namely *Eugenia,* contains about 43 per cent. of the total species, but less than 3 per cent. of these occur in Australia.

The fleshy-fruited genera are widely spread over the tropics, the capsular genera are almost wholly Australian, while the Chamælaucieæ are almost wholly West Australian.

The Earlier Types of Myrtaceæ.

Several factors need consideration in this connection. Principal among these appear to be:—

(*a*) The present distribution of the family.

(*b*) The environment of present-day Myrtaceæ.

(*c*) The geography of the Cretaceous as compared with that of the Tertiary and the present.

(*d*) The practical isolation of Australia from the rest of the temperate and tropical world during the latest Cretaceous and a great portion of the Tertiary.

(*e*) The morphological characters common to the majority of the Myrtaceæ.

The present distribution of the family has already been considered, and may be stated very briefly in this connection.

The greatest number of species by far occur in tropical and subtropical America, while Australia is the area of greatest density after America. The family is practically absent in the cold temperate regions of both hemispheres. The fleshy-fruited genera are uncommon in Australia, but are extremely common in the tropics of both hemispheres. The capsular-fruited genera rarely get beyond the Australasian Region or the Indian Archipelago. The Chamælaucieæ are confined to Australia, especially to the Western half of the Continent.

The present environment of the Myrtaceæ is peculiar, one group, namely, the fleshy-fruited genera, characterised by abundant shelter, moisture and warmth; another group, namely, the Metrosidereæ, selecting situations of shelter, moisture and warmth, but not being so absolutely dependent on these factors acting in conjunction, as the Myrteæ; another group, namely, the Leptospermeæ, exclusive of Metrosidereæ, shows an ability to flourish in an excessively sandy and porous soil, and under moist or dry, hot or moderately cold conditions, while the Chamælaucieæ, and certain genera of the Leptospermeæ, such as the Bæckeæeæ, appear to flourish both in poor sandy soil and in dry situations.

The geography of the Cretaceous appears to have been one of lowlying plains, mild, genial and moist climate of almost cosmopolitan range. The soil of Australia, at that period, appears to have been very sandy and porous, taken as a whole.

High mountains, great deserts, glaciated polar regions and large continents characterise modern geographies, whereas, in the closing Mesozoic, the inland seas were large, the land-relief slight, and the climate genial and moist.

Australia appears to have been connected with Asia during the Jurassic and the Lower Cretaceous, but during some part of the Upper Cretaceous, it seems to have been cut off from Asia, and it is doubtful whether there has been any direct communication between the two continents since that date.

MORPHOLOGICAL CHARACTERS COMMON TO THE MYRTACEÆ.

Upon an examination of the family, it will be at once apparent that certain morphological characters run throughout the various genera. In proportion to the xerophytic nature, or harsh environment, of the genus or species, so are the characters common to the family obscured in that genus or species, and the morphological clue is not readily seen, but, on the other hand, in proportion as the fertile tropics are approached, especially those of America, so, in the Myrtaceæ of these regions, is the morphological clue most easily retained. In those genera which are partly depauperate in type, such as Bæckea, it may be noted that the species which are not depauperate, have more points in common with the family, as a whole, than those species of the genus, which live amid harsher conditions. *Eucalyptus* possesses a cap to its young flower, and, with this protection to its reproductive organs in their earlier stages, it has accommodated itself to various climates and soils, and it departs markedly from the generality of the family in many particulars. The extremes are probably exhibited by Chamælaucieæ and Myrteæ respectively, the one being confined practically to the fertile tropics, the other, in great measure, to the relatively sterile tracts of Western Australia. The capsular genera occupy a middle position, and exhibit, on the one hand, a great resemblance to Myrteæ, and, on the other hand, to the Chamælaucieæ.

The question then arises, what were the characters of the earlier types? Are we to conclude that some form, such as *Eucalyptus,* was the early type, that it had a cosmopolitan range, and that, later, it became extinct in the world generally, nevertheless flourishing in Australia, and giving rise, in the meantime, to the fleshy-fruited genera, all of which show a marvellous likeness to each other, but very little resemblance to the Eucalyptus? Or are we to consider that the more or less xerophytic types, such as *Eucalyp-*

tus, originated in Australia, and then, in some way, crossed the oceans to Asia, Africa, and America, giving rise there to types very similar to each other; nevertheless differing widely from the capsular types? Or are we to consider that the localised form is the more or less depauperate descendant of a type belonging to the moist and fertile tropics?

An application of the Law of Probabilities suggests that either the localised and isolated xerophytic, or the more or less depauperate forms, which all exhibit great morphological differences among themselves, are the descendants of types, possessing at once a range world-wide as regards the fertile tropics, a close similarity of morphological characters, and a great wealth of species. This idea is strengthened by the fact, that the Cretaceous Period was one of genial and moist climate, and that Australia has been isolated from the tropical world since the close of the Cretaceous.

A consideration of these points suggests an appearance as outlined hereunder for the earlier forms of the family:—A tree or shrub, generally large. Leaves simple, entire, opposite, penniveined, dotted and possessing intramarginal veins. Calyx-lobes and petals imbricate. Petals 4 or 5 (probably five). Flowers regular, solitary or in cymes. Stamens indefinite, numerous, free, often crimson or brightly coloured, and generally exceeding the petals Anthers two-celled, versatile, the cells parallel and opening in longitudinal slits. Ovary inferior with two or more cells. Style simple. Ovules two or more to each placenta. Fruit inferior and crowned by the persistent limb, indehiscent, succulent or fleshy, rarely dry. Albumen none. Cotyledons thick and fleshy, with a short radicle.

This plant appears to have possessed a graceful and umbrageous habit, with dense, glossy and beautiful foliage. Wherever possible, exposed situations were avoided, as also sandy porous soils.

Home of the Earlier Types.

This difficult question is best approached from three view-points, namely, the areas of greatest density, as regards species, at the present time; the location of modern types most closely allied to the deduced original Myrtacean type; and the typical geographical conditions of the Cretaceous Period.

The areas of greatest density, to-day, are Tropical America, and warm, temperate Australia.

The families most closely related in morphological characters to the Myrtaceæ, are the Combretaceæ, the Melastomaceæ, the Rhizophoreæ, and the tribe known as Lecythideæ, included by Bentham and Hooker under Myrtaceæ. Combretaceæ is a tropical family, Rhizophoreæ is also mainly a tropical family, while Melastomaceæ forms a large family, and is found mostly in the tropics, chiefly American.

Upon a careful comparison of various members of the Lecythideæ, and a knowledge of their distribution, the Writer has considered it advisable to treat it as a family distinct from Myrtaceæ. For, if one considers its confinement to the fertile tropics, and its development in freedom from those harsh conditions which have left their traces so indelibly upon the majority of Australian Myrtaceæ, one would expect it to exhibit morphological characters more in harmony with those of the Myrtaceæ of the fertile tropics, and to retain the morphological clue, which is so easily traced in *Eugenia, Myrtus,* and allied genera in Myrteæ. Nevertheless, the clue is not at all easily retained in Lecythideæ. The characteristic opposite and dotted leaves are missing, the general appearance of the leaves otherwise is not like those of Myrteæ, the flower-spikes are unfamiliar in connection with Myrtaceæ, and the fruit-forms are not at all suggestive of Myrtaceæ. Nevertheless, Lecythideæ must be considered as a closely allied family.

The consideration of the home of the family, from this double point of view alone, strongly suggests that the Myrtaceæ originated in the tropics, but the questions then arise:—

(*a*) Did the Myrtaceæ originate in the Old World tropics, then extend to America and Australia, and become strongly differentiated in these localities, while evolution lagged in the intermediate area, owing to severe competition? or:—

(*b*) Did Myrtaceæ originate in Tropical America, and spread thence to Asia and Australia?

The answer to these, is practically insoluble without a knowledge of the geographical factor. The study of the geological record undoubtedly suggests that the earth has passed through various periods of genial and almost cosmopolitan climates, and that these have alternated with periods of marked differential climate. The cosmopolitan and genial climates have tended to produce cosmopolitan, or at least widely-spread, floras whenever sea-barriers have not been opposed to distribution. On the other hand, the variation of climates has tended to floral differentiations.

The Cretaceous was a period of such marked tendency to genial climate, and the fertile tropical flora appears to have possessed a wide range in that time. On the other hand, xerophytic and depauperate types are almost wholly wanting in the collections obtained from the Cretaceous and earlier Tertiary deposits.

The Pliocene and later periods have presented marked differentiations of climate, culminating in the Pleistocene glaciation. This would tend to produce marked local variations in the floras (and faunas), and thus an erstwhile, widely-spread type would, upon a gradual differentiation of climate, tend to contract its range altogether as regards the primitive type, and to bring it nearer the equator; while local floras would arise as the result of adaptation to new environments under conditions of isolation.

One would, therefore, expect the primitive types of Myrtaceæ to have had a great tropical range in the Cretaceous, probably extending into the regions now temperate in both Hemispheres, and later, upon the great Post-Cretaceous changes of climate, to have been confined to the tropics, and to have become locally differentiated in such places as America and Australia, where they were not opposed by such severe competition as in the Northern Hemisphere.

Differentiation of Myrtaceæ.

The Eugenias and and the Myrtles appear to be the genera nearest in morphological characters to the earlier types of the family. In the wide belt of the fertile tropics during Cretaceous time, where large deserts and high land-barriers were very rare, there was a tendency for the Myrtaceæ to become cosmopolitan in range, and for that family to preserve, therein, the purity of the types already firmly established..

A slight difficulty arises in attempting to establish the order of the appearance of the Eugenias and the Myrtles. Both contain single flowers in certain species; the Eugenias are plants typically with embryos possessing large cotyledons and small radicles, with flowers of four petals, and with inflorescences racemose or clustered; while the Myrtles are plants in which there is a typical development of large radicles and small cotyledons, of flowers with five petals, and of rather simple inflorescences.

The evidence suggests that *Eugenia* was more nearly related to the earlier type, by reason of its embryo, and the extratropical range of Myrtus. On the other hand, the 4-petalled-flower of *Eugenia* is a departure from type, and it would appear that there were still earlier types, from which both these important genera deployed. Moreover, in *Rhodamnia* and *Rhodomyrtus* among the Myrteæ, and in *Leptospermum*, *Melaleuca* and *Callistemon* among the Leptospermeæ, the leaves are generally strongly nerved, and this interesting survival likewise suggests that nerved leaves existed among some of the earlier, but now extinct, forms of the family.

Apparently a land-bridge existed in the Cretaceous between some portions of tropical America and tropical Africa. The land-bridge between Asia and Australia appears to have been destroyed in the Upper Cretaceous.

This led to two important modifications of the Myrtaceæ. In Asia, fertile tropical conditions still continued, but there arose a severe floral competition during later and Post-Cretaceous times in Asia, owing to the deployment there of other vigorous and aggressive families. In America, fertile tropical conditions continued; while, in Australia, the vigorous outside competition was not experienced, but the soil there was neither so fertile, nor was the climate so genial, as in the other regions. These conditions were most noticeable in the south-west of Australia, where great sandy expanses of land existed*; while the northern portion of Australia probably was very similar to the other portions of the tropics.

* See also A. R. Wallace, "Island Life," (1892), pp. 487-508.

The true Eugenias appear to have been developed in Central and tropical South America, and these underwent parallel transformations with the Myrtles, into the Myrcias, Psidiums, Campomanesias, Calyptranthes, Myrrhinums, Blephærocalices, Myrierias and other types. In all these forms, one may note the similarity of the types evolved, a similarity suggestive of the continuity of fertile and tropical conditions. In Asia, *Jambosa* and *Syzygium* are the representatives of *Eugenia*, but in their geographical distribution, in their inflorescence of trichotomous cymes or panicles, and in their petals more or less cohering in calyptra, it would appear advisable to include *Jambosa* and *Syzygium* under genera separate from *Eugenia.*

In studying the various types of *Eugenia, Jambosa,* and *Syzygium,* one notes, at times, the peculiar sessile, opposite and somewhat cordate leaves, which suggest the peculiar juvenile leaves of certain seedling Eucalypts. *Syzygium propinquum,* in addition, has a venation suggestive of the corymbose Eucalypts. In one species, at least, of Eugenia, again, the buds are strikingly suggestive of certain Eucalyptus-types, while strong intramarginal veins are not uncommon in some Eugenias. The absence of *Myrtus* and *Eugenia* in Europe and extra-tropical Asia, with the exception of *Myrtus communis* in Southern Europe and Western Asia, and the almost complete absence of these genera in Patagonia, Southern Chili, the Argentine, and the United States of America, as also their absence in Southern Australia, except for *Eugenia* (*Syzygium*) *Smithii* in Victoria, indicates unmistakably that the Myrteæ have not been enabled to adapt themselves to cool, temperate conditions, especially in a direction northwards, in the face of the aggressiveness of the Scandinavian flora. It is a rather remarkable fact that *Eugenia* (*Syzygium*) *Smithii* is the one species, at least in the Eastern Hemisphere, which possesses kidney-shaped anthers.

The presence of 40 species of the genera *Jambosa* and *Syzygium* in Australia, suggests that these genera entered Australia, or at least the southern portion of what is now the Malay Archipelago, in Cretaceous time, and that they are ill-adapted to compete with the endemic flora under existing geographical conditions.

The interesting problem of the development of Myrteæ in extra-Australian areas, is one which can be settled at all definitely only by long and continued study of the habit of each tree, the soil in which it grows, and the climatic aspect which it favours, in tropical America, Asia and Africa.

The origin of the capsular-fruited Myrtaceæ may now be considered.

In Upper Cretaceous time, Australia doubtless extended much farther northward and southward than it does at present, and a long and wide inland sea practically separated the continent into two portions, with a possible connection to the south between east and western points, but such possible connection could not have affected the distribution of the Myrtaceæ for a long period of time. The south-western portion of the continent was very large, and doubtless had a considerable extension beyond its present limits.*

Tasmania and Antarctica appear to have been joined to Australia, and the Eastern portion of the continent probably had a moderate extension seawards.†

New Zealand also probably had a connection indirectly with Australia by way of New Caledonia, the North-eastern corner of the continent, on the one hand, and by way of Antarctica, on the other hand.

In this northern portion of Australia, before separation from Asia, the fleshy-fruited Myrtaceæ found themselves in an area of warm and moist climate, but of relatively poor soil. The land to the south awaited occupation by hardy types, and the Leptospermeæ, with the exception of the Eucalypteæ and the Metrosidereæ, appear to have been developed in response to the existence of this poor soil. There appear to have been two divergent developments from the earlier forms of the capsular types. The one was represented by the broader-leaved forms of the Euleptosper-

* See also A. R. Wallace, "Island Life," p.487-508.

† See also C. Hedley, "Zoögeographic Scheme for the Mid-Pacific." These Proceedings, 1899; and Benham, Rept. Austr. Assoc. Adv. Sci., 1902, pp.319-343.

meæ, and the other by the Metrosidereæ. For the Metrosidereæ, the transition from the Myrteæ is suggested by *Backhousia* and *Osbornia*, which have capsular but indehiscent fruits. The transition to Euleptospermeæ is not at all well defined, and the earlier forms appear to be extinct. The Leptospermeæ are possessed of long and often richly-coloured stamens, but some of the genera possess well-marked nerves, whereas the Metrosidereæ contain no nerved leaves. The Euleptospermeæ, moreover, are not often possessed of opposite leaves.

After the evolution of *Bœckea*, *Leptospermum*, *Melaleuca*, *Callistemon*, *Metrosideros*, *Tristania*, *Syncarpia*, *Xanthostemon*, and others, there was a tendency to disperse from the Australian centre. The Leptospermeæ, with the exception of Metrosidereæ, suggest an adaptation to the poor soil, and more temperate and dry climate of the main continent; while the Metrosidereæ are closely allied to the Myrteæ, and were unable to push their way southwards. In the same way, the Leptospermeæ, with the exception of the Metrosidereæ, were not well adapted to compete with the Asiatic vegetation in the fertile tropics. The Metrosidereæ thus had a better chance of being distributed throughout the long, narrow, fertile land-connections with Fiji, New Caledonia, New Zealand and Asia. On the other hand, the only chance which presented itself for the distribution of the remainder of the Leptospermeæ in these directions, was the infrequent existence of poorer soils existing to the north and east.

From these considerations, it is evident that the chances of distribution for the Metrosidereæ throughout what is now the Malay Archipelago, New Caledonia, and New Zealand, were much greater than for the remainder of the Leptospermeæ; and when one finds *Bœckea* in the Malay Islands, Southern China, Sumatra, Malaya and New Caledonia (5 species); *Leptospermum* in the Malay Islands, Burmah, Malaya, and New Zealand (3 species); *Melaleuca* in New Caledonia, the Malay Islands, New Zealand, and Tahiti; *Callistemon* in New Caledonia; while *Metrosideros* occurs in New Zealand, New Caledonia, the Moluccas, South Africa(?), Java, Tahiti(?), Chili(?), Lord Howe Island, Madagascar(?), and the

Sandwich Islands (?); *Tristania* in Burmah, New Caledonia, Malaya, Borneo, Banca Islands, and the Philippines; *Syncarpia* in the Amboyne Islands; *Cloezia* in New Caledonia; *Spermolepis* in New Caledonia; and *Piliocalyx* in New Caledonia, one is rather at a loss to which subtribe to ascribe the greater age From the distribution alone it would seem, at first glance, that the Metrosidereæ had the greater age, but when the Australian range of the Euleptospermeæ and of Bæckeæ, is also taken into consideration, it seems advisable to assign a Cretaceous age for each, the one working towards the tropics, the other acclimatising itself to more southern and exposed conditions.

Bœckea appears to be somewhat younger than *Leptospermum* and *Melaleuca,* partly because of its more restricted range, and partly by reason of its specialised structures. The distribution also indicates the separation of New Zealand from Australia long before that of New Caledonia, and the separation of Asia from Australia at a later date than that of New Zealand.

The separation of New Caledonia, from Australia, appears to have taken place at a considerably later date, and New Caledonia itself appears to be a mere residual of a much larger land-mass, from a consideration of the number of genera endemic to it, such as *Cloezia, Piliocalyx, Spermolepis,* and *Nania.*

A consideration of Bæckeæ and Euleptospermeæ strongly suggests that the earlier types developed in a very poor soil, but in a moist and mild climate, and that the more xerophytic types are of decidedly younger age. In other words, the distribution suggests that the subarid types are much later modifications of the younger and less pauperate types. Nevertheless, the Euleptospermeæ are, on the whole, decidedly depauperate types as compared with Metrosidereæ.

Eucalypteæ.—This subtribe, which comprises the Eucalypts and the Angophoras, appears to have descended through the earlier types of the Metrosidereæ, at a date later than the separation of Australia from Asia, and of New Caledonia from Australia. No undoubted Eucalypt has been recorded from New Zealand, Fiji, New Caledonia, Borneo, Sumatra, or Asia. Several important points impress the student, at the very outset, in the study of Eucalyptus.

(1) It did not spring from a depauperate type.

(2) It is intimately related to *Angophora, Tristania, Metrosideros* and *Syncarpia.*

(3) Its earliest leaves were opposite, cordate, sessile and peculiarly veined.

(4) Its stamens are frequently very brightly coloured in some Northern and Western Australian species.

(5) It is separated into several groups, quite distinct from each other, and with little or no trace of connecting links.

(6) It is a type adapted either to resist hot, subarid, or cold, moist conditions, in the main, by reason of its operculum, its oil-contents, its wax-like bloom, its twisted leafstalks, its thick leaves, its enlarged root-stocks, as well as other adaptations.

(7) It has little or no striking morphological resemblance to the Euleptospermeæ and the Beaufortieæ, except for the long and brightly coloured stamens.

It would appear that both the Eucalypteæ and the Euleptospermeæ were, in the first instance, an organic response to a poor soil, and only secondly, after a long lapse of time, to a drying climate.

With regard to the question of its evident adaptation, in the first place, to a poor soil, and next to a subarid climate, it seems impossible for such a type to have existed in America, Europe, and Asia during the Cretaceous, when the types of plants found, are such as do not at all suggest arid or subarid conditions. Deane has advanced cogent reasons* in support of the growing belief that the older determinations of *Eucalyptus* in the Cretaceous and Tertiary of the Northern Hemisphere, by Ettingshausen, cannot be accepted. Hooker (quoted by A. R. Wallace, in "Island Life," p. 486) also appears to have considered the determinations of fossil Eucalypt-remains, in the Tertiary and Cretaceous of the Northern Hemisphere, as valueless. Bentham also appears to have disbelieved

* See "Observations on the Tertiary Flora of Australia." These Proceedings, xxv., 1900. See also R. H. Cambage, "Development and Distribution of the Genus Eucalyptus," Presidential Address, Journ. Proc. Roy. Soc. N. S. Wales, 1913.

Heer's and Unger's determinations of genera upon the evidence of leaves alone.*

Another strong reason for not accepting the statement that *Eucalyptus* flourished in the Northern Hemisphere during the Cretaceous and Tertiary, is to be found by observations of the juvenile leaves of the genus. The obstinate persistence of juvenile opposite, cordate, sessile, and horizontal leaves in the genus, indicates that such leaf-types had been thoroughly well established for a very long period, in the family, before the evolution of the genus *Eucalyptus;* and that the later, typical Eucalyptus-leaf, with twisted stalk, is a more unstable adaptation to a harsher climate, and one which would tend to become extinct, in favour of the old persistent type, under certain favourable climatic conditions. But it is exactly the later, more or less xerophytic and unstable form, which has been always reported as existing in the Cretaceous and Tertiary beds of the Northern Hemisphere, beds strongly suggestive of moist genial climates; and, moreover, even so, as Deane† has pointed out, such leaves recorded as Eucalypts, might equally be made to fit the plants of other families. Furthermore, such recorded leaves would not be regarded, by a student of Australian Eucalypts, as being suggestive of even the adult Eucalyptus-leaf of later xerophytic origin.

The existence of several distinct groups of Eucalypts, in regions partly overlapping, is very instructive in any discussion as to the origin of the Eucalypts. Indeed, a careful examination of this genus would serve well as a guide to the methods employed by the Myrtaceæ in the development of the endemic types of Australasia. The group which presents the most striking morphological similarities to the generalised type of the Myrtaceæ, includes

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* Island Life. p.486.

† "Observations on Tertiary Flora of Australia." These Proceedings, 1900, pp.463-475. Deane, however, suggests that the capsular-fruited Myrtaceæ originated in Northern or North-eastern Australia, then attained their maximum development in Western Australia, and gave rise to the fleshy-fruited Myrtaceæ, which later spread to Asia and Europe, as differentiations of the primitive capsular type (*ibid.*, p.474).

the Bloodwoods. The members of the group possess widely divergent, almost transverse, secondary venation; the leaves are of luxuriant type; the principal oil is probably pinene; the anthers possess parallel cells opening in longitudinal slits; the flowers are corymbose; the fruits are urceolate, the valves deeply enclosed; and the soil in which they grow, is of the poorest sandy nature. Another point in which they conform to the generalised type of Myrtaceæ is, that they are confined to the warmer and peripheral portions of the continent, avoiding the deserts and the colder portions of Australia. Of these forms, two only, *E. calophylla* and *E. ficifolia*, grow in South-Western Australia. [*E. sepulchralis* is an aberrant member of the group, in which the anthers and the leaf-venation have been much modified.] Fifteen belong to the northern portion of Australia, namely, *E. Abergiana*, *E. clavigera*, *E. corymbosa*, *E. dichromophloia*, *E. ferruginea*, *E. Foelscheana*, *E. miniata*, *E. peltata*, *E. perfoliata*, *E. phœnicea*, *E. pyrophora*, *E. ptychocarpa, E. setosa, E. terminalis,* and *E. Watsoniana;* while six belong to the eastern side of Australia, namely, *E. corymbosa, E. eximia, E. intermedia* (R. T. Baker), *E. terminalis, E. trachyphloia,* and *E. Watsoniana.* Of these, *E. pyrophora* and *E. intermedia* are very close to *E. corymbosa. E. maculata, E. botryoides, E. resinifera, E. robusta, E. saligna,* and *E. tesselaris* are generally considered as belonging to the Bloodwoods, but they are all aberrant types in which either the bark and fruits, or the soils in which they grow, differ from the generalised type, and the soil in which the Bloodwood-type flourishes.

These points, as also the fact that *E. setosa, E. peltata, E. perfoliata,* and *E. ferruginea,* in the North, possess the peculiar leaves similar to the generalised type of the Order, strongly suggest that the cradle of the Eucalypts was in the north of Australia. This group, moreover, frequently possesses brightly coloured stamens, and exhibits strong affinities with the Angophoras.

A smaller section, namely, the Eudesmieæ, with opposite leaves, peculiar fruits, stamens, and notched calyces, is found in Northern and Western Australia. These also appear to preserve traces of the early Eucalypt-leaves. So peculiar is this group, that Robert

Brown proposed to raise it to generic rank, under the name of *Eudesmia*.

A third group comprises the Ironbarks and the Boxes, characterised by the possession of small anthers opening in pores, of peculiar barks and timbers, and a predominance of cineol.* The members of the group are numerous. They are confined to the Eastern half of the continent, and they grow, as a rule, in the heavier clay-soils, in contradistinction to the barren, sandy soils chosen by the Bloodwoods.

It is instructive, in this connection, to remember that the alluvial plains of Australia were formed during a period subsequent to the origin of the early Eucalypts. The Box-Ironbark group represents a main, but double, limb springing from the generalised type, at a period later than the secretion of cineol and phellandrene. The extreme twigs of this great, double limb, represent types such as *E. melliodora*, *E. sideroxylon*, *E. Cayleyi*, *E. leucoxylon*, *E. gracilis*, and *E. uncinata*, and are the farthest removed from the direct line of succession, in the genealogical tree of the Eucalypts, besides being far removed, also, from the generalised type of the Myrtaceæ.

A fourth group comprises the Stringybarks, the Peppermints and allied types, which possess kidney-shaped anthers of two types, each opening in divergent and confluent slits; peculiar leaves, fruits, and bark; as also a preponderance, in the main, of phellandrene oil and piperitone.† These grow in moist, and cool to cold climates, and are confined to the Southeastern portion of the continent, particularly in the plateau and mountainous regions of recent origin. *E. acmenioides*, *E. Naudiniana*, and *E. microcorys*‡ are aberrant types of the group.

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* For analyses of these oils, see "Research on the Eucalypts." Baker and Smith (1902).

† This subject of the oils is dealt with by Messrs. Baker and Smith, in their "Research on the Eucalypts" (1902), forming a very valuable contribution to the hypothesis of the origin of the Eucalypts.

‡ Mr. J. H. Maiden appears to have been the first to consider *E. microcorys* and *E. Naudiniana* as anomalous forms, from a consideration of their anthers. [Critical Revision of the Genus Eucalyptus].

This group forms another great, bifurcating limb springing from a point higher up the stem of the genealogical tree of the Eucalypts, than that which gave rise to the Boxes and the Ironbarks; and their extreme types, such as *E. microcorys, E. stellulata*, *E. coriacea*, *E. coccifera*, and *E. hæmastoma* are as far removed from the general succession as are the extreme types of the Boxes and Ironbarks.

In the more arid portions of the continent, lying between these various groups, the desert-types were developed in the fulness of time. Types, *E. oleosa, E. dumosa, E. incrassata, E. uncinata, E gracilis, and E. pachyphylla.*

In brief, the history of *Eucalyptus* appears to have been as follows : A prototype of the Metrosidereæ, in the late Cretaceous, secreted a pinene oil, in Northern Australia or the neighbouring regions, and succeeded in forming an operculum by the coherence of its petals, for the protection of its reproductive organs. The earlier types appear to have possessed parallel anthers opening in longitudinal slits, stamens often brightly coloured, large glossy leaves, with transverse venation, a thick bark, pinene oil; and they appear to have grown in a porous sandy soil, and in a warm to hot climate. Moreover, the earlier leaves were opposite, sessile, and cordate, with horizontal surfaces. Protected by the operculum and the essential oil, the new plant began to push its way into the cooler country to the south. In proportion to such progress, and to its adaptation to a porous soil, it lost its juvenile opposite leaves.

With the retreat of the Cretaceous Sea, the Eastern side of Australia underwent a geological and geographical transformation, and, in their attempts to respond to their peculiar environment, the Eucalypts secreted a non-volatile wax-bloom, and two fresh oils, cineol and phellandrene. The function of the oils appears to be, in the main, to form a thin spray to withstand desiccation, but also, in the case of phellandrene and certain other constituents, their function appears to have been in part, at least, to resist cold, because the Metrosidereæ, with the Myrteæ, are unable to resist cold equally with aridity. The twisting of the leaf-stalk, and the development of the wax-bloom on the tender parts of the plant, appear also to be provisions against aridity.*

A group of the new genus appears to have detached itself gradually from the Corymbosæ members, and to have pressed its way far to the south. This was made possible by the protection of the tender reproductive organs, partly by the operculum during the earlier stages, and partly by reason of the thick capsule generally, for the typical Myrteæ have never been enabled to move far from the tropics, owing to the tender nature of their structures. This southward-moving group acclimatised itself to temperate, moist, and sheltered conditions, and there, it tended to revive the old, opposite, cordate, sessile, and horizontal leaves of the tribe, whereas the early, or corymbose, Eucalypts had practically discarded such leaf-types. The thinness and delicacy of the juvenile leaves belonging to some of these southern forms, suggest a development in the absence of strong light. The abundant development of cineol, among these types, also suggests protection from severe climatic conditions. Survivals of these types include *E. globulus, E. goniocalyx,* and *E. Maideni.* More modified types are *E. Cambagei* and *E. rubida.* In this group, the generalised type of anther for the Order is unaltered.

Another section with opposite juvenile leaves, is represented by types such as *E. viminalis, E. amygdalina,* and *E. radiata.* These opposite, sessile leaves, however, in order to adapt themselves to varied conditions, have adopted a thicker leaf-type, the breadth of the leaf is much reduced, and the leaf is held almost vertically.

At a much later period, namely, after the formation of the great plateaus of Eastern Australia, these Eucalypts gradually worked their way northwards as far as Queensland, and, to-day, along the plateaus, one may see the effect of this wonderful reinvasion by southern Eucalypt-types.

But prior to this stage, the eastern side of Australia became flooded with basalts; and heavy, rich clay-soils were formed in the area which had been vacated by the Cretaceous Sea. The Boxes

* Robert Brown, quoted by Schimper, in Plant-Geography.

and Ironbarks established themselves, in part, upon this, and became so modified in the process, that the links connecting this group and the earlier Bloodwoods, have practically vanished.

Similarly, as the eastern periphery of Australia became roughened, two other, but allied, groups of Eucalypts gradually developed in the more southern portions, and as the climate became colder, they slowly extended their way northwards. These groups include the Stringybarks, Peppermints, Mountain-Ashes, Messmates and the majority of the Mountain-Gums. They possess peculiar, kidney-shaped anthers, which again fall naturally into two types; they also possess a peculiar leaf-venation, and their oils are likewise characteristic.*

With the formation of the great plateaus of Eastern Australia during the Kosciusko-Period, the Eastern Eucalypts became differentiated into fresh species and varieties, while the Boxes, Ironbarks, and Bloodwoods remained but slightly modified.

Thus, at present, along the highlands of Victoria, New South Wales, and Southern Queensland, may be seen the effect of reinvasion by forms of Eucalypts, which had been developed in regions further to the south.

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* In attempting to work out a scheme for the evolution of the Eucalypts, special attention should be directed to anthers, leaves, oils, soil, and climate. With regard to anthers, the work of Bentham, von Mueller, and Maiden is invaluable. So important a factor did the anthers appear to the great Bentham, that he actually established a sound classification of the Eucalypts upon such basis, its imperfections being due merely to his lack of knowledge of the growing plants and their environment. This difficult task, commenced by Bentham, is being carried on by Mr. J. H. Maiden, whose views have been, and are being, expressed in the "Critical Revision of the Eucalypts" and "The Forest Flora." The work also of Baker and Smith is highly important in Eucalypt-studies. The great resemblance between *Angophora* and the Corymbosæ Eucalypts is clearly pointed out by them. Especially clearly have they shown the intimate relations existing between the development of the leaves and the oils of the genus, as also the relations existing between the Peppermint and Stringybark groups. Recently, the influence of the soils, and the climate has been perceived by Mr. Cambage; and he has accomplished the difficult and highly important task of co-ordinating the different lines of evidence yielded by a study of soil and climate.

An examination of the several distinct groups of Eucalypts living in different soils, in different climates, and possessing leaves, barks, inflorescences, and anthers strikingly dissimilar in character, suggests that here, probably, several genera have been grouped together, groups apparently quite as distinct from each other as *Beaufortia*, *Regelia*, *Melaleuca* and *Callistemon*, or as *Leptospermum* and *Kunzea*, or as *Kunzea* and *Bæckea*. Thus *E. tetrodonta*, *E. erythrocorys*, *E. eudesmioides*, *E. tetragona*, and *E. odontocarpa*, with their 4-toothed calyces, their stamens more or less united into four clusters, their 3-flowered peduncles, their leaves opposite, and their very limited geographical range, might well be restored to generic rank as *Eudesmia*. In the writer's opinion, this appears to be but just to Robert Brown.

The work of Bentham, followed up by that of von Mueller and Maiden, the edaphic studies of Cambage, and the oil-studies by Baker and Smith have shown conclusively that the Section Corymbosæ is the oldest, and the Peppermint-section* the youngest, nevertheless the intermediate forms have vanished, and it may be shown, on morphological and geographical grounds, that the types which, at first sight, apparently show connection between the groups, are really only aberrant or specialised forms of *much later* origin.

The name Eucalyptus was proposed by l'Heritier for a genus, of which the present *E. obliqua* is the type. This type is included by Bentham in his Section Renantheræ under Eucalyptus. The group appears to be easily divisible into the Stringybarks, Peppermints, Mountain-Ashes, and their specialised forms, the Sallies, the Tallow-wood, etc. Of these, the Stringybarks, in part at least, appear to be the older members. The name Eucalyptus might be reserved for these plants. As already mentioned, they possess reniform anthers, a tendency to arrange the secondary leaf-veins parallel to the midrib, they possess varying quantities of phellandrene and piperitone oils, and they are confined to South-eastern Australia, a region of rugged and well watered topography. The types include forms such as *E. Delegetensis*, *E.*

* Certain desert-types also appear to be fairly youthful.

obliqua, *E. dives*, *E. amygdalina*, *E. piperita*, *E. Risdoni*, *E. pilularis*, *E. capitellata*, *E. lævopinea*, *E. eugenioides*, *E. macrorhyncha*, *E. Muelleriana*, etc.

Specialised or aberrant forms include *E. coriacea*, *E. stellulata*, *E. coccifera*, *E. vitrea*, *E. Smithii*, *E. acmenioides*, and *E. microcorys*, the last two varying in the opposite direction to that taken by the first-named four types. A careful examination of *E. buprestium*, *E. marginata*, and *E. santalifolia* from W. Australia indicates that they are specialised forms only of Bentham's Normales, and are only analogous forms to what are here called the true Eucalypts (Renantheræ of Bentham). Moreover, the study of the geographical conditions shows that the Eucalypts, of which *E. obliqua* is the type, have originated in the mountainous topography of South-eastern Australia, at a time during which the climate and topography of the region separating Western from South-eastern Australia, have been such as to forbid the migration of the *E. obliqua*-type to the west. In Western Australia, one finds only the Normales-type, with its peculiar aberrant or specialised forms. Even the great Section of the Porantheræ is there unrepresented. Moreover, *E. buprestium*, *E. marginata*, and *E. santalifolia* have neither phellandrene nor piperitone contents. Thus they may be removed from the true Eucalypts.

Types, such as *E. corymbosa*, *E. setosa*, *E. miniata*, *E. ficifolia*, *E. calophylla*, *E. terminalis*, *E. trachyphloia*, *E. eximia*, *E. peltata*, *E. perfoliata*, *E. Abergiana* and *E. ferruginea*, might be called Corymbosa. In this, as in some other groups, the bark is not to be relied upon always for purposes of natural classification. In the earlier types of the genus, it appears to have been thick, and more or less charged with kinos and other material for the purpose of resisting the excessive transpiration to which the ancestral form of the primitive type had been a stranger; but with types such as *E. maculata* and *E. tesselaris*, this property could be dispensed with, owing to the ability of such later forms to reach a water-supply easily. Nevertheless, vestigial traces of the primitive, thick bark remain still on these types. *E. coriacea*, *E. stellulata*, *E. hæmastoma*, *E. vitrea*, and *E. coccifera* are still more striking instances of this feature (namely, rejection of the primitive thick, and more or less corky bark) in the case of the true Eucalypts.

Another Eastern Australian group may be raised to generic rank, under the name of Poranthera. This includes the Boxes and Ironbarks, whose special features have been considered elsewhere. These, among others, include *E. albens*, *E. hemiphloia*, *E. odorata*, *E. Woollsiana*, *E. microtheca*, *E. polyanthemos*, *E. populifolia*, *E. conica*, *E. crebra*, *E. Cayleyi*, and *E. siderophloia*. Aberrant or specialised forms (widely separated from the primitive Corymbosa, on the one hand, and the younger Eucalypt, on the other hand) include *E. melliodora*, *E. Bosistoana*, *E. paniculata*, *E. leucoxylon*, *E. Behriana*, *E. uncinata*, and *E. gracilis*. This genus is divisible, again, into Boxes, Ironbarks, and certain Mallees. The bark here becomes a powerful aid in classification. Connecting links with the earlier forms possibly are to be found in *E. pruinosa* and *E. melanoxylon*.

The remaining types fall into groups to which the name Parallelanthera may be applied. Members of this Section are to be found in all parts of Australia; representatives are to be found in the deserts, others in the moisture-laden coastal ravines, others in the hot north, others on the exposed subalpine plateaus.

They represent, with the exception of Eudesmia, Eucalyptus, Poranthera, and Corymbosa, all the forms possessing caps to the unexpanded flower. With the knowledge of this wide geographical range, the variety of climates, the oft-changing topography, and the long time-factor involved, to which the earlier forms of this Section were subjected, it is not strange that members of the same should have proved a veritable puzzle to systematists. It is as if representatives of the earlier types had penetrated into remote corners of the continent, and then being cut off later from intercommunication, they had become more and more specialised, yet not so markedly as to have given rise to new genera. A few examples will suffice to establish this point. *E. globulus*, *E. goniocalyx*, *E. Cambagei*, *E. Maideni*, *E. Nova-Anglica*, *E. viminalis*, *E. cinerea*, *E. pulvigera*, *E. cordata* and similar types, have developed in abundance of moisture and shade, with moderate shelter, in the recently formed plateau-province of South-eastern Australia. *E. Perriniana*, *E. urnigera*, *E. alpina*, *E. Gunnii*, and *E. vernicosa* have evolved on the wind-swept and snow-laden plateaus to the south; while *E. viridis*, *E. Morrisii*, *E. platyphylla*, *E. oleosa*, and *E. dumosa* are a response to the hot and subarid to arid portions of the continent. *E. rostrata* has spread across Australia by creeping along watercourses, and thus defying the surrounding desert-conditions; while *E. cornuta*, *E. gomphocephala*, *E. cosmophylla*, *E. macrocarpa*, *E. pyriformis*, *E. cæsia*, *E. megacarpa*, *E. fœcunda*, *E. loxophleba*, *E. diversicolor*, *E. redunca* and others, occur in Western Australia, and are found neither in Northern nor Eastern Australia. In most cases, the peculiarities of these various assemblages are suggestive of a response to xerophytic conditions. This is, however, not applicable to the famous *globulus*-group, whose youthful stages indicate an immediate ancestor which flourished in cool, temperate, moist, shady and moderately sheltered situations. In a word, so effectively has the general development progressed, and so universally have the intermediate or connecting forms been stamped out, that no systematist can state from which group either the Eucalypts or the Porantheras have sprung. Neither can the origin of the *globulus*-group be traced back more than one step. All that is known is, that the *globulus*-group is relatively young, so also the Eucalypts, while the Corymbosæ are old.

Angophora presents a peculiar problem to the student of distribution. Indistinguishable from the Corymbosæ Eucalypts, except for the coherence of the petals to form an operculum to the unopened flower, it occurs only in the milder extratropical portions of Eastern Australia; its anthers are parallel, and they open in longitudinal slits; its stamens are not brightly coloured; its bark, with one exception, is rough; its leaves are mostly opposite and sessile; with one exception, the soils it seeks, are extremely sandy, porous, and lacking in fertility; and the distribution of the species is exceedingly limited, being confined, with one exception, to small patches of barren sandstone. Such are *A. cordifolia*, a stunted type, confined to the

Sydney sandstone ; *A. lanceolata*, confined to sandstone patches along the coastal regions as far north as Rockhampton ; *A. melanoxylon*, limited to small patches of gravel and sand in north-western New South Wales; while *A. intermedia* has a considerable range in the warmer portions of extratropical Eastern Australia; but this type has succeeded in establishing itself upon the light clay-soils, and is, apparently, a much more recent type than *A. cordifolia* and *A. melanoxylon.*

Angophora, indeed, appears to be a type which deployed, with *Eucalyptus*, from the ancestors of the Metrosidereæ, but which did not succeed in developing protective characters to such an extent as *Eucalyptus* did. It failed, therefore, to populate Australia, and as *Eucalyptus* extended its borders, with the development of each new protective character, so, to that extent, the less elastic type, namely, *Angophora,* was crowded out until, at the present day, it appears to be a genus rapidly undergoing extinction, and existing only in outposts, as regards its former distribution. *A. cordifolia* and *A. melanoxylon* are splendid examples of this contraction of habitat, while *A. intermedia* is a striking example of the success of a species which has become modified with respect to the type.* It is highly probable that, in Tertiary time, *Angophora* had both many species, and a wide distribution in warmer Eastern Australia. The failure to supersede the obstinately persistent, opposite and sessile leaves, except in rare instances, appears to have been one reason for its extremely limited development.

Chamœlaucieœ, etc.—In dealing with Chamælaucieæ, Beaufortieæ, and certain other groups of Myrtaceæ, it may be advisable to consider them from a general point of view.

It will be found that, in proportion as the climatic and soil-conditions, in which a Myrtacean genus occurs, vary from those of the fertile tropics, so do the morphological characters of such genera undergo a distinct change. This suggests a corresponding youthfulness for the genera considered.

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* Mr. Maiden has drawn attention to the great similarity between *A. intermedia* and *A. subvelutina.*

In this connection, it may be advisable to consider leaves, stamens, anthers, and the habits of individuals.

The leaves of Myrtaceæ are typically opposite, glossy, broad, penniveined, and dotted. In many Bæckeas, Darwinias, Kunzeas, Verticordias, Chamælauciums, Melaleucas, Thryptomenes, Micromyrtus, and other types, the leaves are rigid, terete, and generally depauperate in form. Such suggest development under harsh climatic, or impoverished soil-conditions; and such species are mainly the younger forms of the genera which have accommodated themselves to the Post-Cretaceous and later Tertiary, or even Post-Tertiary, conditions.

The stamens of Myrtaceæ are characteristically numerous, free, long, and often brightly coloured. In Chamælaucieæ and some Leptospermeæ, the stamens are frequently much reduced in size and number, and such condition is accompanied, as a rule, by severe climatic and soil-environment. Those species of the genera, thus affected, are apparently of more recent development than the typical types of the genera.

The typical anthers of the family are versatile, the cells parallel and opening longitudinally. Thus the Angophoras and Corymbosas have the typical anthers of Myrtaceæ, but the Boxes and Ironbarks possess peculiar porose or truncate anthers, and the Stringybarks, Peppermints, Messmates, Mountain-Ashes, and some Mountain-Gums, possess kidney-shaped anthers. The Melaleucas, Callistemons, Leptospermums, and Kunzeas possess typical anthers, but *Beaufortia, Regelia, Pileanthus,* and *Verticordia* possess peculiar varieties of porose and grooved anthers, and such peculiar types, moreover, are endemic in Western Australia. Again, the Bæckeas of Eastern Australia are mostly possessed of typical anthers, whereas the majority of the species, endemic in Western Australia, possess anthers very divergent from the type.

These interesting facts, coupled with a knowledge of the geographical environments, indicate that those Eucalypts, Bæckeas, Chamælauciums, and Beaufortieæ, with peculiar leaves and anthers, are recent in proportion as they depart, in morphological characters, from the generalised type of the fertile tropics, and that they have been evolved in response to some particular, physical revolution, such as a change to a sandy, a clay, a dry, or a cold environment.

Similarly, the fruits of the earlier types of Myrtaceæ were fleshy, and the capsular-types, in this instance, appear to be a response to less fertile and less sheltered habitats. The depauperate fruit of the Chamælaucieæ here suggests a much more recent response again to conditions more generally severe.

The habit of the individual is again instructive. The typical Myrteæ either may be the largest of forest-trees or they may be elegant shrubs, with full habit and glossy foliage. The typical Chamælaucieæ, and many of the Leptospermeæ, are very depauperate in form, and not at all suggestive of the stately and handsome Myrteæ and Metrosidereæ. Such depauperate forms, moreover, abound in the subarid and barren, sandy areas of Australia. From this consideration, also, such forms appear to be much more recent developments. Furthermore, almost without exception, such depauperate and apparently aberrant types have a limited range, being endemic to Australia, frequently Western Australia. This restricted geographical range, moreover, suggests a much more recent origin than that of the widely-spread Myrteæ.

The distinctive characters, however, of the majority of Western Australian from Eastern Australian species of Myrtaceæ, in view of the fact that the areas considered are mainly sandy in nature, and the centre of Australia arid, strongly suggest that the Central Australian desert was a hindrance rather than an impetus to Myrtaceous differentiation; and that the peculiar sandy soil of Eastern and Western Australia, formed one of the most potent influences in the production of new species, and that, whereas, probably in earlier Tertiary time, the Eastern and Western species commingled, they have more recently developed along divergent lines, since the interposition of an arid barrier of less sandy soil, in Central Australia.

From these considerations, it would appear that the Myrteæ are much the oldest branch of the family, that Euleptospermeæ and

Metrosidereæ are of great age, the Angophoras and Eucalypts being much younger than these, while the Chamælaucieæ and Beaufortieæ are still more recent modifications of types, probably such as *Leptospermum*, *Kunzea* and *Bæckea*, on the one hand, and of *Melaleuca*, on the other.

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