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CHAPTER X

The classification and distribution of the Monimiaceae

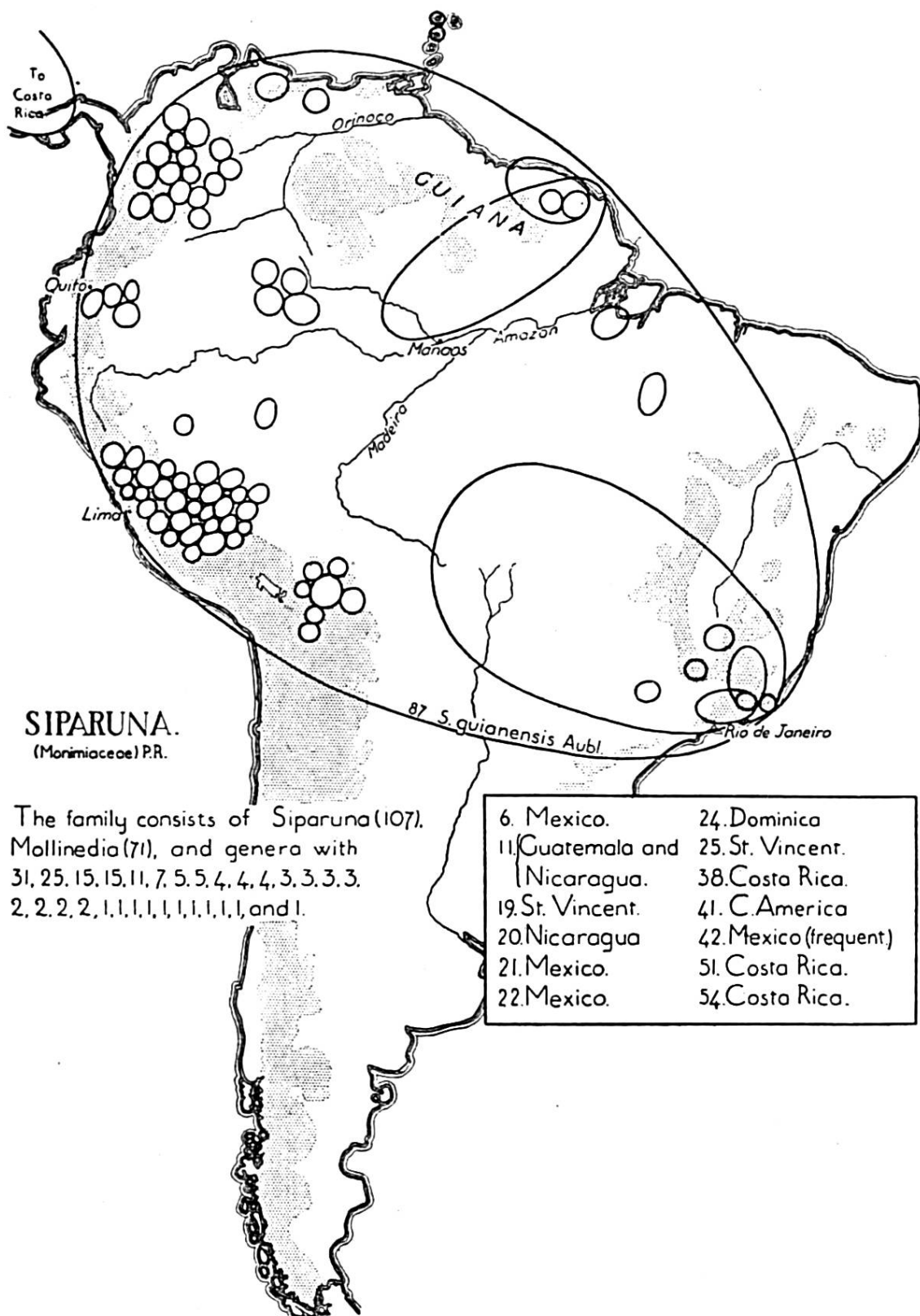
We have shown that small genera, being young and more or less confined to one continent, are less likely to have been interfered with in their obedience to the laws of ASA and of dichotomous division; and in this connection it will be worth while also to look at a small family, the *Monimiaceae*. It is classified, structurally and geographically, upon pp. 228 to 230, and when we compare these groupings, it is evident that each was drawn up without reference to the other. To begin with, there is no large genus like *Senecio* or *Justicia* that leads the family over most of its range. The nearest approach to such a thing is *Siparuna* (map at p. 224), which covers most of the American dispersal, but does not occur in the old world. It is followed in BRAZIL by the second genus *Mollinedia*, differing chiefly in the fact that its anthers open by slits, not by valves. These are the marks of the two sub-families, into which *Monimiaceae* are divided.

These characters, as so constantly occurs, not only separate the second genus (though sometimes only the third or fourth) from the first, but being handed down to a number of descendants, they give the characters to two separate sub-families, though themselves evidently those of father and son. This simple fact, abundantly demonstrated in Chap. VIII, that the leaders of the subgroups of a family are mainly to be found in the few, and obviously closely related, genera at the head of the family, is almost enough to prove our theory of "downward" evolution from family to species; and the dispersal area of *Mollinedia*, which only goes beyond that of *Siparuna* at its southernmost part, where

the conditions of life are rather different, fits in well with this theory, though taxonomically the two genera, as we shall see, are widely separated.

All the 36 genera which we now consider as belonging to *Monimiaceae* show one or the other of these divergent anther openings, together with sufficient general resemblance in other structural features to make it not improbable that they are all of one family. We therefore use this divergence, evidently very old in the family, and one which has persisted in the inheritance, as the main mark of the two sub-families, and it must be particularly noted that it occurs in the two oldest genera, whose regions of occurrence overlap. *Mollinedia* must have been born at some region south of the birthplace of *Siparuna*, at a time when that genus comprised only two to perhaps five species. The most widely dispersed, and therefore probably the oldest species, *S. guianensis*, covers the whole range of the genus in S. AMERICA, and one may expect the birthplace of *Mollinedia* to be somewhere within its range.

The dispersal of *Siparuna* is shown in a general way for South America, its most important centre, in the map at p. 224. It also reaches Mexico and the West Indian islands of Dominica and St Vincent (probably therefore by way of Trinidad). The striking feature in its dispersal map is the great crowd of localised endemic species at various points in the Andes, especially near the Isthmus of Panama, and in Peru. These are not shown in the map in their exact location, but are massed together in such a way as to give a good general idea of their dispersal. But it is fairly evident here that in so mountainous a country, the most recently formed species will not only be very slow in spreading on account of their small number of individuals, but will also be severely handicapped by the rapid and local changes of conditions, such as of soil with its composition and consistency, of slope with its direction and its degree of insolation, of water supply with its frequency and its differences at different times and places, and so on. To all these differences a new species will have to adapt itself as it spreads. Much time must therefore be allowed, and it may be a very long while before the species escapes from its beginnings, which are always a case of specialisation and localisation.



SIPARUNA.
(Morimiaceae) P.R.

The family consists of Siparuna (107),
Mollinedia (71), and genera with
31, 25, 15, 15, 11, 7, 5, 5, 4, 4, 4, 3, 3, 3, 3,
2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, and 1.

- | | |
|-------------------|-----------------------|
| 6. Mexico. | 24. Dominica |
| 11. Guatemala and | 25. St. Vincent. |
| Nicaragua. | 38. Costa Rica. |
| 19. St. Vincent. | 41. C. America |
| 20. Nicaragua | 42. Mexico (frequent) |
| 21. Mexico. | 51. Costa Rica. |
| 22. Mexico. | 54. Costa Rica. |

Upon my working hypothesis (p. 96), the birth was at some place where unusual conditions were encountered. As the present dispersal of *Mollinedia*, while largely included in that of *Siparuna*, goes beyond it mainly to the south, where it reaches MONTEVIDEO instead of RIO, one may imagine that perhaps colder winters formed part of the stimulus that gave birth to it. But taxonomically it belongs to *Monimioideae-Mollinedieae*, while *Siparuna* belongs to *Atherospermoideae-Siparuneae*, though evidently so closely related. They are thus not only in separate tribes, but in separate sub-families. Their chief difference, the way in which the anthers dehisce, is a perfectly simple mutation, which could hardly be anything else. *Siparuna* evidently carried the slit-opening as a recessive character, or potentiality, and gave it to *Mollinedia* full-blown. Had it been later in appearance in the family, it might only have been a separation mark of two tribes, or even of two genera, or only of two species. Its rank here as a sub-family mark is merely due to its age *in this family*, and gives no guarantee that it is of this, or of any other value, anywhere else.

This is the usual type of family formation, as the lists of the positions of leading genera, given on pp. 173, 174, clearly show. So far, there is no great difficulty about the grouping of the *Monimiaceae*, but as we begin to break it up upon structural grounds, the geographical and arithmetical difficulties continually increase.

But if *Siparuna* and *Mollinedia* thus stand in the relation of father and son, as seems practically certain, and if in our taxonomy we separate them so widely as we do, being in most cases compelled to put the first two genera of a family into different tribes, or even into what we consider as sub-families, it is clear that our classification, as at present accepted, is artificial. A divergence comes at every mutation, and sometimes we regard the resulting new genus as belonging to the same group as the parent, and sometimes as belonging to, or forming, another group. Yet in origin and in genetic relationship the two are apparently the same. But we consider the characters in one case as being more "important" than in the other, when the difference between the two cases is rather that in one the divergences happened to appear in characters that we were using as marks of a subgroup, and in the other case not so, but affecting something else, which

we are inclined to imagine as "less important", though we have no reason for making the assertion, other than their different degree of occurrence in the family, which as yet we do not properly understand, though it is evidently largely a function of age. It is primarily age that gives importance, and the nearer that we are to the largest or oldest genus, the head of the family, the more likely is the divergence to be of subfamily or tribal rank. In fact, one may in a general way say that the nearer to the top that a genus is, and therefore the more species that it comprises, the higher is its rank, for it will have correspondingly more descendant species and genera.

It is clear that each genus in turn is the head of the group that contains all its genetic descendants. Thus the first genus A gives rise all the time to species of A, but also, at intervals, to what we regard as new genera, and call successively B, C, D, &c. But we have little or nothing to go upon, *rightfully* to call these particular new species (as they *are*) of a different rank from those that we consider as simply new species of A. When there are many descendants showing these particular characters, and with other descendants showing well marked differences also, we have some reason for calling B a new genus, for from a practical, classificatory, point of view, the more we can break up the vast mass of species into genera and other divisions, the better. But we lack any really sound basis for definition of genus or species.

A natural or genetic classification should really be the expression of this continual dichotomy, and obviously would be impossible to make at the present time. It is clear that we have not arrived at that stage in our knowledge of past events, and of the laws that govern such things, that would enable us even to begin with any confidence a map of past evolution, and a great amount of work will yet have to be done. Geographical distribution, structural features, genetic relationships, and other things will have to be made out for most genera, and all will have to be fitted into one harmonious whole, showing everywhere the curves of compound interest, or something closely similar. One cannot but feel that there is some general law underlying the incidence of mutations. MENDEL's law, GALTON's law, the laws of ASA and of dichotomy all point so clearly to some general mathe-

mathematical law underlying the whole, that it is quite possible that when we gain some further knowledge, especially perhaps of the law of incidence of mutation, we may begin to perceive it.

But though such a system would be of great practical value to breeders and others, a natural system would be of little or no use for the actual identification of plants, and for that, which after all is one of the most important requirements, an artificial system must be used. Obviously, therefore, this should be the most convenient possible. But as yet, each new advance to the far away goal of a natural system has on the whole been a falling away from this object, and one that becomes continually worse rather than better. Even the admittedly artificial system of LINNAEUS brought together things like *Cruciferae*, or grasses, and more and more natural groupings show in each new system, but they become more and more difficult to use for practical purposes, because of the continually increasing numbers of exceptions, which are inevitable if characters are handed down from above, and in what as yet looks like a casual way. The average interested enquirer does not care about exact relationships; he wants to know the name of his plant, and something about it. We might even go so far as to suggest that a public herbarium, where at present the untrained enquirer is helpless, might have a public "enquirer's room", with a local, or a more general, herbarium, as local circumstances dictate. In this there might be a key to the flora, with pictures showing the divergences at every stage, leading gradually down to the individual plants, which should be mounted under glass or cellophane. In this room there might be a small library of books of reference, folklore, and other subjects, and pictures and descriptions of ecological associations to which the various plants belong, and so on.

For some people, the old theory of very gradual change has been replaced by a supposition of small, but distinct, changes of less than specific rank, due to small mutations. We have seen in our consideration of teratology (p. 100) that such mutations are common enough. It is therefore probable that they do occur in a more permanent form, as we have suggested for actual specific mutations, and that they give rise to varieties, of different degrees of importance in reference to species. But there seems no evidence that other small

mutations must follow in such a way that the variety must ultimately become a new species. A small variation does not usually make parent and child mutually sterile, and why should one variation only, in a series, be able to cross the sterility line? Probably it can, but if so, it will probably be one that would have made the specific difference by itself alone, without needing to be led up to by smaller, varietal, mutations. The method of evolution thus suggested has always appeared quite illogical to the writer, who since 1907 (131-2) has always stipulated for the whole change between one species or genus and another to be made at a single mutation, though there will probably be a few cumulative cases. This theory is now well supported by evidence, such as that of the formation of most endemics, or the formation of the early genera of a family such as we have seen in Chap. VIII. Under any theory of evolution, two characters, however divergent they may be, have got to unite somewhere in the past, and if, as so commonly happens, they are incompatible, then one must be recessive, the other dominant, in some ancestor, or, as under selection, we must call in destruction of transitions, often upon a truly colossal scale, for which we have no evidence available.

Upon pp. 228 and 229 we have given two groupings, one taxonomic, one geographical but also with genera in order of size, while upon p. 230 we have given the usual list of the few earliest genera in the family, to show the incongruity of all these groupings. The geographical facts are more absolute than the structural, so that it is the latter that will probably be those to give way most often.

Monimiaceae, taxonomically grouped

Sub-family I. MONIMIOIDEAE (anthers opening by slits)

Tribe I. *Hortoniace*

Spp.

- | | |
|-------------------------|-------------------------------------|
| 1. <i>Hortonia</i> | 3 Ceylon |
| 2. <i>Peumus</i> | 1 Chile |
| 3. <i>Amborella</i> | 1 New Caledonia |
| 4. <i>Hedycarya</i> | 20 Austr., N. Cal., N. Z., Polynes. |
| 5. <i>Levieria</i> | 6 N. Guin., Moluccas, Queensland |
| 6. <i>Decarydendron</i> | 1 Madagascar |
| 7. <i>Hedycariopsis</i> | 1 Madagascar |

Tribe II. *Trimenieae*

- | | |
|----------------------|---------------------|
| 8. <i>Trimenia</i> | 4 Fiji, &c |
| 9. <i>Piptocalyx</i> | 1 N. S. Wales |
| 10. <i>Xymalos</i> | 2 S. and trop. Afr. |

Tribe III. *Mollinedieae*

- | | |
|--------------------------|-----------------------------|
| 11. <i>Macropeplus</i> | 1 E. Brazil |
| 12. <i>Mollinedia</i> | 80 Trop. Am. |
| 13. <i>Macrotorus</i> | 1 Rio de Janeiro |
| 14. <i>Ephippiandra</i> | 1 Madagascar |
| 15. <i>Matthaea</i> | 15 Malaya, Phils. |
| 16. <i>Steganthera</i> | 15 New Guin., Celebes, &c |
| 17. <i>Anthobembix</i> | 4 New Guin. |
| 18. <i>Tetrasynandra</i> | 3 E. Australia |
| 19. <i>Wilkia</i> | 5 E. Australia |
| 20. <i>Kibara</i> | 30 Burma, Sumatra to Phils. |
| 21. <i>Lauterbachia</i> | 1 New Guin. |
| 22. <i>Carnegiea</i> | 1 New Caledonia |

Tribe IV. *Monimieae*

- | | |
|------------------------|---------------------------------|
| 23. <i>Palmeria</i> | 10 E. Austr., N. Guin., Celebes |
| 24. <i>Canaca</i> | 1 New Caled. |
| 25. <i>Monimia</i> | 4 Madagascar, Mascarenes |
| 26. <i>Tambourissa</i> | 25 Madagascar, Mascarenes |
| 27. <i>Schrameckia</i> | 1 Madagascar |
| 28. <i>Hennecartia</i> | 1 Paraguay, S. Brazil |

Sub-family II. ATHEROSPERMOIDEAE (anthers by valves)

Tribe V. *Laurelieae*

- | | |
|-------------------------|----------------------------|
| 29. <i>Nemuaron</i> | 2 New Caled. |
| 30. <i>Daphnandra</i> | 4 Queensland, N. S. Wales |
| 31. <i>Laurelia</i> | 3 Chile, Peru, New Zealand |
| 32. <i>Atherosperma</i> | 2 E. Austr., Tasmania |
| 33. <i>Doryphora</i> | 1 New S. Wales |

Tribe VI. *Siparuneae*

- | | |
|-------------------------|--------------------------|
| 34. <i>Siparuna</i> | 120 Trop. Am., W. Indies |
| 35. <i>Glossocalyx</i> | 3 W. Africa |
| 36. <i>Bracteanthus</i> | 1 Amazon region |

Monimiaceae, geographically grouped (in order of size)

America	Subgroup	Spp.
1. <i>Siparuna</i>	II. 6	120 Trop. Am., W. I.
2. <i>Mollinedia</i>	I. 3	80 Trop. Am.
3. <i>Laurelia</i>	II. 5	3 Chile, Peru, New Zealand
4. <i>Peumus</i>	I. 1	1 Chile
5. <i>Macropeplus</i>	I. 3	1 E. Brazil
6. <i>Macrotorus</i>	I. 3	1 Rio de Janeiro
7. <i>Hennecartia</i>	I. 4	1 Paraguay, S. Brazil
8. <i>Bracteanthus</i>	II. 6	1 Amazon region

<i>Africa</i>	Subgroup	Spp.
9. Glossocalyx	II. 6	3 W. Africa
10. Xymalos	I. 2	2 S. and trop. Afr.
<i>Madagascar</i>		
11. Tambourissa	I. 4	25 Madagascar, Mascarenes
12. Monimia	I. 4	4 Madagascar, Mascarenes
13. Decarydendron	I. 1	1 Madagascar
14. Hedycariopsis	I. 1	1 Madagascar
15. Ehippiandra	I. 3	1 Madagascar
16. Schrameckia	I. 4	1 Madagascar
<i>Ceylon</i>		
17. Hortonia	I. 1	3 Ceylon, SW and central
<i>Malaya, Polynesia, Australia</i>		
18. Kibara	I. 3	30 Burma, Sumatra to Phils.
19. Hedycarya	I. 1	20 Austr., N. Z., Polynes.
20. Matthea	I. 3	15 Malaya, Phils.
21. Steganthera	I. 3	15 New Guin., Celebes, &c
22. Palmeria	I. 4	10 E. Austr., New Guin., Celeb.
23. Levieria	I. 1	6 New Guin., Moluccas, Qnsld
24. Wilkiea	I. 3	5 E. Austr.
25. Trimenia	I. 2	4 Fiji
26. Anthobembix	I. 3	4 New Guin.
27. Daphnandra	II. 5	4 Queensland, N. S. Wales
28. Tetrasynandra	I. 3	3 E. Austr.
29. Laurelia	II. 5	3 Chile, Peru, New Zealand ¹
30. Nemuaron	II. 5	2 New Caledonia
31. Atherosperma	II. 5	2 E. Austr., Tasmania
32. Amborella	I. 1	1 New Caledonia
33. Piptocalyx	I. 2	1 New S. Wales
34. Lauterbachia	I. 3	1 New Guinea
35. Carnegiea	I. 3	1 New Caledonia
36. Canaca	I. 4	1 New Caledonia
37. Doryphora	II. 5	1 New S. Wales

Early genera of the Monimiaceae, by size in the world

1. Siparuna	120 Trop. Am.	II. 6 Heading <i>Siparuneae</i>
2. Mollinedia	80 Trop. Am.	I. 3 Heading <i>Mollinedieae</i>
3. Kibara	30 Burm. Mal. Phils.	I. 3 2nd Mollin.
4. Tambourissa	25 Madagascar	I. 4 Heading <i>Monimieae</i>
5. Hedycarya	20 Austr. N. Z. Polyn.	I. 1 Heading <i>Hortonieae</i>
6. Matthaea	15 Malaya, Phils.	I. 3 3rd Mollin.
7. Steganthera	15 N. G., Cel., &c	1. 3 4th Mollin.

¹ A repetition of No. 3, making the total 37 against 36.

The other two tribes are headed by genera with four species each, *Trimenia* (I. 2) in FIJI, &c, *Daphnandra* (II. 5) in E. AUSTRALIA.

It is clear that among the leading genera, with few exceptions, the heads of subgroups must be found, and equally clear that each genus in general must have its parent in those above it; proper geographical relationships must also be evident. A very early and large parental genus might by direct divergences give rise to smaller heads of subgroups. But some geographical connection, even if now extinct, is required, if we are to work upon any theory of evolution, and what is most in favour at the present time is the destruction of the connecting links by lack of adaptation or other unfavourable attributes. In the colder temperate climates, where cold periods have alternated with warmer, and the plants have surged to and fro, such a thing is more possible, but the difficulties are just as marked in tropical families, where nothing of this kind seems to have occurred recently enough to have been within the lifetime of most of their members.

We have thus got various groupings of the *Monimiaceae*, which require to be harmonised in some way, and the same thing is equally true of many other families. All the work that we have done for many years upon endemism, upon distribution in general, upon curves of origin, and so on, which is described in many papers, and in *AA* and in *Evol.*, goes to show that we have no justification for the calling in of wholesale destruction of transitional or intermediate forms. This is especially the case with the great areas that are often concerned, and when the discontinuous plants are, as most commonly is the case, so small as genera that they must either be too young to have been alive at the time of separation, or must have suffered great destruction of species to bring them down to their present small size. Not only so, but the destruction would be required in very many directions, and vast geological and climatic changes would be necessary. We shall better understand our problems by discarding as much as possible of this speculation, which is so attractive that it has always been the bane of work upon origin and distribution. We must work by inductive methods, which we have now shown to be very applicable in such cases, and work by aid of the laws of ASA and of growth by

dichotomy, and with the knowledge that our present system of classification is often artificial.

Let us look at some of the many incongruities in these lists. Taking first the early genera, we find those at the top heading subgroups as usual. This of course is what one should expect, but up to the present the size of a genus as an important generic character has been entirely neglected. It is very noticeable that the large genera of a family tend to scatter themselves among any large structural groups that may be made, so that one cannot construct tribes without reference to the characters of these genera. This alone shows how much more important in classification is a large genus than a small one. Taking this list alone, it is clear that *Kibara* is too large to have sprung, at so great a distance away, from either *Siparuna* or *Mollinedia*, which are not so very much older than it is. The later genera, in fact, after the first two, have no geographical connection with them, *within the family*. They are separated by immense distances, and in two directions, from BRAZIL to MADAGASCAR, and to MALAYA and AUSTRALIA-NEW ZEALAND. But to make a natural grouping, upon genetic lines, there must either be some geographical continuity among the areas occupied, or there must have been some overriding genus of the group, or more probably of the family, *or even of some allied family like Lauraceae*, that might give rise to similar things in widely separated localities. With the vast numbers of permutations and combinations that are available, it is extremely unlikely that an overriding genus should belong to any family that was not, structurally, fairly close to *Monimiaceae*. It is fairly evident that any new form tends to inherit its characters (though a few are marked by distinct divergence) from its ancestors by something like GALTON's law of $\frac{1}{2}$ from parents, $\frac{1}{4}$ from grandparents, and so on, as indeed one might almost expect.

Failing one of these occurrences, we are forced to demand great selective destruction that will kill out all the intermediate geographical links, frequently whether transitional or not. There is very little evidence indeed for such happenings, and certainly not for their occurrence in the numbers and directions desired, whilst there is enormous difficulty—geographical, geological, and meteorological—in the way of its occurrence. There is also nothing in the structural

differences to show that there is any likelihood that it should happen.

The primary distinction into *Monimioideae* and *Atherospermoideae* has always been maintained, for the whole family, supposedly natural, shows one or the other type of anther dehiscence; but the members of *Monimioideae* have at times been shuffled. But one cannot make them up by structural characters so that these will agree with the geographical arrangement, to say nothing of the arithmetical.

Siparuna is the largest genus, yet has apparently only two other genera carrying its characters (*cf. Senecio*, p. 177), one in W. AFRICA, one in the AMAZON region, while the genus itself is purely American. *Mollinedia*, its most evident direct descendant, is widely separated taxonomically, and the rest of the American members of the family (*cf. p. 229*) are scattered over a number of tribes, two of which have only one representative each in AMERICA, in each case a monospecific genus.

Mollinedia (31 spp. RIO, 22 adjacent states, 55 altogether in BRAZIL and GUYANA, 16 PERU to MEXICO) covers less range than *Siparuna*, but mainly within the latter, only going beyond it to the south. If evolution went as we have hitherto supposed, species to family, there would be nothing specially surprising in its being placed so far from *Siparuna* taxonomically as it is, but now that it is enormously more probable that it went the other way, from family down to species, and that there must be some geographical links between genera that are related, even if only slight, the whole of the old position becomes untenable. In probable fact, the two genera are father and son, as closely related as is possible, and their ranking in different subfamilies is due to the great structural divergence that marks them. It is not possible to explain by selection, or by small mutations, why the chief divisions of a family have as their heads genera belonging to the first few (by size or age) in the family. Often the first two each head a sub-family.

To find parentage for the other American genera, except *Bracteanthus* in *Siparuneae*, within the limits of dispersal of *Siparuna* itself, is not easy, unless we disregard the taxonomic classification altogether, for, though only seven in number, they belong to the groups *Hortoniaceae*, *Mollinediaceae*, *Monimieae*, and *Laurelieae*, and are all small (young). Those in

Mollinedieae can of course be fathered upon *Mollinedia*, but there is nothing in *Hortonieae* for *Peumus*, nor in *Monimieae* for *Hennecartia*, and they must look for parents to one of the other groups. Going by size, it is clear that the *Atherospermoideae* make no serious approach to a hollow curve, dropping from 120 to 4 in the second place, while *Monimioideae*, with a leader of only 80, show 30, 25, 20, 15, 15, 10, 6, 5, 4, 4, 4, $2/3$, $1/2$, $13/1$, an almost equally improbable curve, especially when broken into its four tribes.

Not only should there be geographical continuity in the family as a whole, but it should also be shown by the members of any sub-family or tribe, if they are in reality descended, directly or indirectly, from their own leading genus. Thus here all the tribes with the possible exception of *Laurelieae*, which itself has no likely leader, are greatly confused when taken from a geographical point of view, as the list on p. 229 shows. The most probable explanation is that all the characters shown in all the genera were handed down by ancestors which carried them in a dominant or recessive condition, and that their appearances were often polyphyletic, the same character sometimes appearing more than once in widely separated genera (like *Hibbertia* in AUSTRALIA and *Schumacheria* in CEYLON, described on pp. 145, 146), so that a character might easily be shown without having anything of the same kind in its immediate ancestry. It is possible, too, that it might have an immediate ancestor showing the character, in some nearly related family like the *Lauraceae*.

Or let us take the *Monimiaceae* of MADAGASCAR in the two lists and compare them. *Tambourissa* (25 spp.), *Monimia* (4), and *Schrameckia* (1) are all in the tribe *Monimieae*, but *Decarydendron* and *Hedycariopsis* are in *Hortonieae*, and *Ephippiandra* in *Mollinedieae*. How did so many of the tribes, not always very large ones, come to be represented upon MADAGASCAR? And the question is not made easier by looking at the genera of continental AFRICA, which are only two, with independent areas, *Glossocalyx* in W. AFRICA with 3 spp. and belonging to yet another tribe, the *Siparuneae*, and *Xymalos* with 2 in S. and tropical AFRICA, in the *Trimeenieae*. All the groups but the *Laurelieae* occur in this handful of genera, quite separated geographically from the rest of the family!

Another stage eastwards brings us to CEYLON, which has

one isolated genus, *Hortonia*, endemic there, with three species, one with an area about 60 miles in diameter, the other two less, as one would expect if one was born from another. Finally, there is a considerable group in MALAYA, AUSTRALIA, NEW CALEDONIA, NEW ZEALAND, and POLYNESIA broken as to area, especially by stretches of sea, but at least forming a possible curve (*Kibara* 30, 20, 15, 15, 10, 6, 5, $3/4$, $2/3$, $2/2$, $6/1$). But they belong to the tribes *Hortonieae*, *Trimenieae*, *Mollinedieae*, *Monimieae*, and *Laurelieae*, all the tribes in fact but the one that contains the leader of the family. In any case *Laurelieae* with genera of only 4, 3, 2, 2, 1 is not a group that one would expect to find in CHILE and PERU as well as NEW ZEALAND, when the rest are only in eastern AUSTRALIA and NEW CALEDONIA. NEW CALEDONIA, which is much smaller than MADAGASCAR, shows more tribes than the whole of ASIA.

If we take the individual taxonomic groups, we get the same kind of complications in other ways. *Hortonieae* alone contains genera of 3 CEYLON, 1 CHILE, 1 NEW CALEDONIA, all much too small (young) to have been alive at the formation of the vast oceanic separations. The chief genus is confined to eastern AUSTRALIA and POLYNESIA and NEW ZEALAND, centring with most of its species in NEW CALEDONIA, so that it does not reach, nor even suggest that it ever reached, CEYLON or CHILE. In fact the CEYLON genus is not near any of the real *Monimiaceae*, however wide a view we may take of them. Nor, though not quite so definitely, is *Peumus* in CHILE, though *Laurelia* in *Atherospermoideae-Laureliae* occurs in CHILE, PERU, and NEW ZEALAND. Any of the six taxonomic groups, in fact, will provide almost hopeless problems for the man who works only upon structural resemblance, while the principles that we are advocating here do at least provide some hope of future understanding.

This general occurrence everywhere of so many subgroups, often only represented by one or two very small genera, which may be widely separated geographically from others of the same subgroup, makes it extremely probable that the subgroups are not natural, but artificial. Even genera or families seem somewhat artificial at times. In fact, it is quite possible, though it may be thought improbable, that new members of sub-groups may be formed at any period in the life of a family in the same way as the first members

were formed in the early days of the family, by divergent mutation. On the other hand, such divergences as may give rise to what we consider to be new subgroups seem to become rarer as the family grows older. There are various explanations of this fact that are possible, and we must briefly consider them. It may be, for example, that in a certain family, certain combinations of characters only are possible, and may have already been used, or that as one comes downwards from the head of a family, the mutations become less marked. But before we can express an opinion upon these matters that will have any real value, we must have a much better knowledge of characters and their incidence. We know, for example, that the character that appears to be the principal one dividing *Acanthaceae* into A and B, or the character that divides the *Monimiaceae* into two sub-families, may appear elsewhere, where it is younger in the family concerned, and is therefore shown by a smaller proportion of the family, its descendants.

At the present time, this fact is translated into the current botanical language of the day by saying that the character is "less important" there, though no attempt was made to show why it was less important, until the writer showed that importance was an accompaniment of age. But this one particular divergence of character in the *Acanthaceae* or in the *Monimiaceae* has remained so persistent in the heredity that either one side or the other of the divergence marks one or the other of the two great divisions into which the family is split. Other characters or divergences accompany this one, however, and to say what really happens at any single mutation becomes a complicated problem, upon which it is at present very rash to give any decided opinion. Let us leave it, therefore, with a leaning towards the idea that mutations become less complex as one comes downward, as this helps to explain the great differences that mark the great groups into which plants are divided, though it is largely true that they owe much of their importance to their age, which has produced many descendants with the same general character as themselves and has given these forms a great dispersal over the earth.

It will probably be found, now, to be more difficult than before to make a genetic group. If any character of a family, or even a character as yet only known in some other family,

like the superior ovary in *Gaertnera* of the *Rubiaceae*, may thus suddenly appear in that family, we have no longer any assurance that two things that show it are necessarily any more closely related than are any two others, while any mutation may produce something that breaks away from its existing structural relationship to place itself in another one. While age seems to be the most important feature of a character, we must not forget that though, for example *Ruellia* in arising from *Justicia* changed its aestivation, it also changed other characters, so that the divergences shown in them are just as old as those in the aestivation. But they seem to be less steadfast in their subsequent appearances, showing occasional new divergences to something different, while in the aestivation there have been few *new* divergences, though there may have been cross-mutations, for anything that we can tell. It is this lack of permanence in the inheritance that has caused other characters to be regarded as of less importance *in the family concerned*, while in other families they may have the greatest importance possible. With our present complete ignorance of why a divergence appears, why it is what it is, and so many other problems here concerned one cannot yet go beyond the stage of vague suggestion.

If a character is found to be common to a considerable number of species in a large genus, it is probably old, and certainly so if a number of those species prove to be of the widest possible distribution in that genus. In that case it is quite probably of the same age as the genus itself, whose number of species shows its age as compared with others in its own family. A character is simply a character, liable to divergent change by rules that we do not understand, and whose importance is given to it, in each case, (1) by its age there, and (2) by its persistence in heredity there.

To feel more sure about relationship we shall have to take into account more characters than hitherto, including geographical and genetic. How little progress, other than continual shuffling of families and genera, is likely to be made under our present system of using structural resemblances only, or, be it at once admitted, under any system based upon geographical continuity only, may easily be gathered from any comparison that is made upon the lines that we have adopted for the *Acanthaceae* and the *Monimiaceae*. Some congruity must be brought into the results

given by structure and by geography, not forgetting the possible overriding genus or family, which may cause great resemblances to appear at great distances apart. The geographical facts are less easily made to support any particular theory, so that we shall have to be very careful in our handling of the whole subject. The appreciation of the possibilities of divergence at a single stroke that have now been shown to be the rule rather than the exception, alters our outlook upon such problems very materially.

A diminishing number of us can remember the flourish of trumpets with which the supposed supersession of BENTHAM and HOOKER's *Incompletae* was greeted, and it is of interest to look at the result after many years, for they are now largely to be found in the first 15 orders of *Archichlamydeae*, which, with the exception of 5 and 10, composed only of *Garryaceae*, and *Julianaceae*, contain nothing else, and might quite well be labelled *Incompletae*. In the orders after 15 there are also families of *Incompletae*.

One cannot but suspect that the *Monimiaceae* are not a simple genetic family, and the same is true of many others. *Siparuna* and *Mollinedia* start off in proper order and position, the older spreading over a greater area, and reaching the WEST INDIES, which the latter, apparently born further south, fails to do, though as old as many genera that have arrived there. One rather expects to find more *Siparuneae* in AMERICA, and must suppose that the genera intermediate between the one very small one that is found, and the large top genus have mutated out of that group, and are to be found in other places, even in other families, like *Lauraceae*, which probably belongs also to the *Monimiaceae*-complex. This passage of species or genera into some other group was first suggested by BOWER in connection with the genera of the ferns (16).

In ENGLER-DIELS, 11th. ed., *Monimiaceae* is placed in *Ranales*, §4 *Magnoliinae*, and in the present connection, as showing the shuffling that goes on when the only criterion is a structural one, it is of interest to find that HUTCHINSON (68) places the same group in four different orders — *Magnoliales*, *Annonales*, *Laurales*, and *Rosales*, and puts the first three groups of ENGLER-DIELS into his own *Ranales* and *Berberidales*. The tendency in recent groupings is to postpone the difficulties that we have been pointing out, and that

have arisen partly on account of the use of too few criteria, by increasing the number of groups, whether genera, families, or orders. Thus, where BENTHAM-HOOKER have 120 families in 23 orders of *Archichlamydeae*, ENGLER-DIELS have 201 in 33, HUTCHINSON 213 in 59.

Probably a mutation of long ago gave rise to the *Monimiaceae* proper, a S. American family, which lost some of its members by cross-mutation into other families like *Lauraceae*, while perhaps other mutations came in from this or other allied families like *Lauraceae*, giving rise to the present *Monimiaceae* of MADAGASCAR, MALAYA, AUSTRALIA, NEW ZEALAND, &c, which are not geographically connected by other members of the family. But if it be recognised that the family is artificial, they may quite well remain in it. But we are here entering the very attractive, but deceptive, realm of speculation, and must return to the paths of induction.

Less marked structural features. A feature of the present family is the structural variety of the receptacle and perianth, showing suggestions of features that one may see in other families of this complex. Now that we have seen what mutation can do, it is clearly not impossible, even perhaps not improbable, that a feature supposed to mark one family only may at any time appear in another family, usually, one may suppose, related to the first. In fact, everything goes to show that characters are handed down by inheritance from above. Those of the immediate parent are those that are most likely to appear in the offspring (*cf.* GALTON's law, p. 232). Most characters, when they once appear, seem to be more or less adhered to for a number of generations, but in how many of these this may be the case, we have no idea at present. One cotyledon, for example, seems a very permanent character, but we cannot guarantee that it may not disappear at the very next mutation of some Monocot.

It may be worth while to look at one or two of the characters that are less widespread in the family, or in general younger, than the form of anther-dehiscence, and to compare their geographical and taxonomical incidence. There is an orthotropous ovule in *Amborella* (*Monimioideae-Hortoniaceae*, 1 NEW CALED.) and in *Daphnandra* (*Atherospermoideae-Laurelieae*, 4 QUEENSLAND, N. S. WALES), geographically near enough, but taxonomically in separate sub-families. Though the character does not lend itself to selection, and

thus has an added "importance", it is a simple change for mutation, and must probably be of polyphyletic origin here. One of the rather impossible so-called natural families made of recent years, the *Phrymaceae*, with two genera, *Phryma* (1 E. AS., ATL. N. AM.) and *Denisia* (1 S. AFR.), depends upon its possession of an orthotropous ovule for its extrusion from *Verbenaceae* (of BENTHAM and HOOKER). The writer, before he had fully grasped the possibilities of mutation, split off *Tristichaceae* from *Podostemaceae* (138), as more natural by reason of their completely different morphological structure, a change which could not be passed over by gradual stages. He now realises that this was easily possible to mutation in such plastic material as submerged water plants, so that it is perhaps not impossible that other solitary water plants, separated by wide divergences from other plants, whether land or water, may really be closely allied genetically. The same may be the case with some of the parasites and saprophytes.

To return to our theme, let us consider the presence of glands at the base of the stamen, found in various places, e.g. in *Hortoniaceae* (*Hortonia* in CEYLON, *Peumus* in CHILE, &c), in *Monimiaceae* (*Monimia* in MADAGASCAR), and in *Laurelieae* (E. AUSTR. NEW CALED., N. ZEAL., CHILE, PERU). Both this character and the last, with their wide discontinuity in what are almost certainly very young genera, far too young to have been present at the formation of the PACIFIC, for example, come under the head of what in Chap. IV we called character-discontinuity, which cannot be explained by the destruction of transitional or intermediate forms. As there is no overriding genus in *Monimiaceae*, the character must be polyphyletic so far as they are concerned. As the same thing is shown by several *Lauraceae*, it has probably come down at least from the common ancestor of both, turning up independently here and there. There are a number of such scattered characters of interest in the *Monimiaceae*, but space will not allow of their discussion. For instance there are the very different male and female flowers in some species of *Siparuna*. Here we may note, with reference to complexes, that we find the *leader* of the family showing a character which is otherwise only shown by the distantly related *Laurelia sempervirens* and *Atherosperma moschata*, both, it is perhaps worth noting, in the sub-family

in which *Siparuna* itself is found. Such behaviour as we have outlined in these two examples of character-discontinuity is not uncommon, and goes to prove our contention that the potentialities of all characters in a family are already existent in the head of the family, though only appearing under certain circumstances—perhaps, for example, only being able to appear after something else has happened in the mutations that go on in the family. Other examples of interesting characters are to be noted in the different types of receptacle in *Hortonia*, *Levieria*, *Trimenia*, *Xymalos*, *Siparuna*, *Mollinedia*, *Macrotorus*, *Wilkia*, &c; the velum, shown in great variety in *Siparuna*, where some species have none, *Lauterbachia*, *Glossocalyx*, &c; the stamens, usually ∞ , but only four in *Matthaea*, *Steganthera*, *Anthobembix*, united to a tube in *Tetrasynandra*, and so on. The incidence of characters in this and other (allied) families is well worth detailed study, and character-discontinuity should be studied in connection with the characters of the head of the family, as with *Senecio*, where one finds many species, or groups of species, that show characters that especially mark certain of the smaller genera of the family. While such facts as these are not unfamiliar, it is perhaps not fully realised how important is their bearing when we reverse the order of evolution to the direction family-species, when at once they fall into their proper place.

It is also interesting to study the contrasts provided by the two methods of grouping. The *Hortonieae* are headed by *Hedycarya* (20 AUSTR., NEW CALED., N. Z., POLYNESIA); half the genus is confined to NEW CALEDONIA, from which it evidently spread (terrestrially) to the rest, which lie in a circle round it at not greatly differing distances away. This is a normal dispersal, and *Hedycarya* could not have been the parent of such things as *Hortonia* in CEYLON, or probably of *Peumus* in CHILE. The hermaphrodite flowers of *Hortonia* are unique in the group and it shares opposite leaves with *Peumus*, while the alternate leafed *Amborella* (1 NEW CALED.) is probably a direct mutation from *Hedycarya*, so recent that it is endemic. *Levieria* is a doubtful mutation from *Hedycarya*, all but one of its species being confined to NEW GUINEA, which is therefore probably its birthplace, and is outside the range of *Hedycarya*. If, therefore, *Hortonieae* are to be retained as a natural group, we are left to explain the far

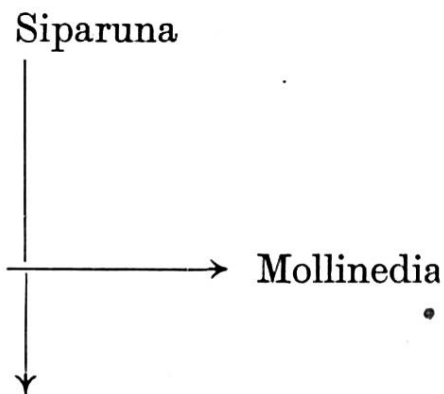
outlying *Hortonia*, *Levieria*, and *Peumus*. None of these are individually discontinuous, but if they are genetically closely related, their mutual discontinuity, without any overriding genus in *Hortonieae*, is very great, while the genera are too young to explain it without vast destruction, for which there is no evidence, especially when we see how well *Hedycarya* has followed the usual laws.

It is therefore almost certain that these outlying genera must owe their origin to descent from one or more genera that did not belong to *Hortonieae*, and the question at once arises whether it or they belonged to *Monimiaceae* at all. This, it must not be forgotten, is a small family, allied to *Annonaceae*, *Myristicaceae*, and *Lauraceae*, and perhaps other *Ranales*. Its small size is often put down to destruction, especially by the breaking up of the land of the southern hemisphere, but more than half its species are in the two normal S. American genera *Siparuna* and *Mollinedia*. To suggest that the rest of the family are relics does not in the least agree with what has been set out above as to their dispersal and taxonomy. Similar criticism may be applied to other subgroups of *Monimiaceae*.

The distribution of species or genera. For many years we have tried to prove that the evolution of species is *downward* from the original parent of the genus, that differed so markedly from the grandparent that taxonomists finally agreed that it should be considered as a new genus. This view of course reverses the Darwinian conception, going back to the pre-Darwinian. Our book upon *Evolution*, seven years ago, was largely devoted to this theme, and gave many convincing crucial test-cases. We have tried also to show that the most probable mechanism of the process is that one new species is formed at each birth, and that this fact did not affect the parent, which survived the birth, and went on as before to the next birth, survived that, and so on. If the offspring, as one would expect, inherited the adaptation of its parent to the conditions of the locality, it would survive; if there were any inferiority in adaptation, it would probably be killed out at once by selection, which of course is in continual operation. If, on the other hand, there were any appreciable superiority, the offspring would be likely to get a better start than usual, so that it might ultimately achieve a somewhat greater distribution than

that to which its actual age would entitle it. It is to allow for slight differences of this kind that we drew up the rule that calculations for age and area should be based on ten allies compared with ten others allied to the first. It must not be forgotten that the already established parent starts with a great advantage over its offspring. In the majority of cases, probably, the offspring of a genus will be a new species of that genus, but at times, perhaps when the stimulus of changed conditions is unusually great, it may be what we regard as a new genus, or even a new family.

The first genus of a family probably always behaves in much the same way. *Siparuna*, for example, beginning as a single species, perhaps as *S. guianensis* (see map) probably started somewhere not far from the ANDES, in western BRAZIL. The great mass of mountain species seems to point to the likelihood that it soon reached the mountains, in which, though the broken nature of the country encourages the formation of many species, travel, especially upwards, will on the other hand be slower than upon the more level lower country. All the time, the genus is increasing by the production of more species, especially in the hills. At certain times, and perhaps more in the direct line from *Siparuna* than in the side lines of other genera (though as these grow older and more numerous they will probably, on the total, surpass *Siparuna*), new genera will appear instead of simply new *Siparunas*.



Going on from this point it is not difficult to make further predictions which, if as successful as several hundreds have now been, will give further evidence greatly in favour of our general contentions. In the first place, it is clear, and indeed it is a not unfamiliar fact, that the central part of the

area occupied by a genus should in general carry the largest proportion of its species. The evolution of a genus will of course begin somewhere about the centre of its ultimate area, and it will spread in all directions, though probably conditions will soon ensure that it goes more rapidly in some directions than in others. The earliest dichotomies will probably not be very far from this centre, and the results of these dichotomies will on the whole get the start of dichotomies further away from the centre. The tendency will thus be to get the greatest proportion of the species occurring in the most central region. Going outwards from it, the numbers will automatically tend to decrease, and will cease altogether at a greater or less distance away. But one must not forget that there are two ways in which this limit may come. If it is simply the limit imposed by time in a fairly uniform country, one will expect to find it occupied only, or almost only, by the oldest species of all, provided that the edge is still under conditions not very far removed from those at the centre. But if conditions have seriously changed on the way, one will expect a new species to have formed somewhere, which is better suited to the outlying conditions, and which has probably been able to outrun the original first species. In BRITAIN, for example, families like *Malvaceae*, mainly tropical, with *Hibiscus* (not British) as the leading genus, are not led in BRITAIN by a species of *Hibiscus*, but by one of *Malva*, which is a much smaller and younger genus, but centred on more temperate-zone conditions.

The other type of termination of area in any direction is where it is due to the formation of a definite barrier to further passage, by sea, or by a range of mountains, or a desert &c. For example, in CEYLON further expansion southwards has for an immensely long time been prevented by the INDIAN OCEAN, and the result has been to allow later genera and species to overtake the first arrivals, and to allow endemic species to appear much nearer to the boundary, and in greater numbers, by reason of the time available during which the first comers have been held in position and not allowed to go any further.

All these facts give strong support to our contention that the dispersal of a species is a more or less mechanical phenomenon, once the species is formed. There is no evidence of any serious competition between one species and

another, and much less between one genus and another, though the structural differences on the whole are larger.

We may make a second prediction upon somewhat different lines. Assuming, as we have now every right to do, that evolution goes by divergent mutation, then in the central region where the earliest part of the evolution of a genus went on, and the greatest number of species occur, there should be also the greatest structural variety in every way, while at the edge of the dispersal of the genus, there should only be one or two of the very oldest species, but these should show very clearly marked divergences, as we have seen above with the earliest species.

The keys that are given in monographs of course place most nearly together the species that are nearest in structural relationship, no other characters being employed, except that sometimes a block of species is marked as being for example all African or all American. It may be worth while, however, to point out that this is a comparatively rare event, the blocks of species made up by structure only being most often geographically mixed, as we are trying to make clear. In a key, the *attempt* always is first to divide into A and B, then to divide A into a and b, a into 1 and 2, and so on, till at last one comes down to the individual species. Thus if of two species, one shows the character A, one B, they will be divided by the most widespread divergence in the genus, which is also as a rule a well marked one. Two species, on the other hand, that only separate after having agreed in showing A, a, 1, &c &c, are species that agree in many characters. But on the whole it is evident that wide separation in the key means structural separation by many characters, while close proximity means separation only by a few; and a scattering of species from one geographical region over most of the key means that most of the characters have come into use in that set of species.

It is fairly evident, from the map at p. 224, that *Siparuna guianensis* is the parent, direct or indirect, of all the species in S. AMERICA, and probably at any rate the immediate parent of *S. cujabana*, which occupies the second largest area, beginning at RIO. But, as seems to be the all but universal rule, these two are well separated in the classification, by a well marked divergence, the former being in Bc—, the later in Aa—.

Suppose we look at the great crowd of species of *Siparuna* in PERU, where they are all local, except for *S. guianensis*, we find their numbers in the key to be as follows, the key numbers running from 1 to 89 (*PR*), to which new species were added in (*PR* suppl.) by a or b at proper places. The 36 species are Nos. 7, 7a, 11a, 12a, 15, 17, 18a, 18b, 26, 26a, 27, 33, 33a, 36, 37, 39, 39b, 41b, 44a, 45, 45a, 47, 49, 52, 56, 61, 66, 66a, 72, 73, 79, 81, 84, 85, 87 (*S. guianensis*), 88. *S. guianensis* is separated from its next neighbour, 88, by connate as against free styles. It will be seen that the numbers of the Peruvian species run through the whole gamut of possible characters for a species of *Siparuna*, and the phenomena here described will be found to make a very general rule for incidence of characters. It will be seen that they agree with the way in which the incidence of the characters happened in the *Compositae* (Chap. VIII).

If we look at *Mollinedia* in the same way, we find it to centre in the (mountainous) state of RIO DE JANEIRO, and to show 71 species in its key, with a few of a or b. Thirty-one are confined to the state, or endemic there, and they show the following numbers: 3, 4, 5, 7, 8, 10, 11, 12, 13 (so far evidently closely structurally related), 17, 18, 19, 20, 23, 33, 34, 37, 39, 44, 45, 46, 49, 56, 57, 58, 59, 60, 64, 66, 68, 68a. The numbers cover so much of the list that it is clear that the RIO species cover most of the structural variation, including many in both of the sub-genera *Exappendiculata*, without appendages to the lower tepals, and *Appendiculata*, with appendages, a simple mutation, but well marked, probably shown at the very first mutation in the genus.

If the structural characters went with the geographical separation of the species, all would be well, and structure and geography would agree, but this is just what does *not* happen, probably in the majority of the cases. For example, in *Mollinedia*, species 9 in PERU comes in the middle of a whole lot of RIO species, yet they are separated by a vast distance, mainly covered with heavy forest. Cases like this may be found in great numbers, and it is clear that structural characters do not go with the geographical distribution of forms. When there is no overriding genus from which the same character in the same family can have come in two widely separated places, it is necessary to suppose that it came from separate genera in different families, presumably of the

same complex of families. Failing that, enormous destruction according to the older views is often needful, and often (across oceans, for example) at a date too far back in time.

It thus seems fairly evident that the dispersal of the *Monimiaceae* cannot be explained upon the supposition that a character is necessarily handed down in such a way that in the parent one may see an earlier stage of what occurs in the child, or that it may be, except perhaps in very rare cases, acquired by selection. Divergence at mutation, which probably has some electrical rule behind it, seems to be general everywhere, and the characters are handed down as some kind of potentiality from above. The family is probably largely artificial, with a polyphyletic origin. We shall consider this matter further in the next chapter.