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MAJOR DISJUNCTIONS IN THE GEOGRAPHIC RANGES OF SEED PLANTS

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ABSTRACT

In attempting to review and classify the major intercontinental disjunctions in the geographic ranges of seed plants, six guiding principles are followed where possible. Sixteen categories and 34 subcategories of disjunct ranges of intercontinental magnitude (Table I) are classified according to continents and latitudinal bands involved. Widely distributed taxa are, by their very nature, disjunct; they are therefore classified along with the more traditionally discontinuous types. Thus, for the most part, only endemics and taxa with smaller intracontinental disjunctions are omitted from this review.

Generalized distribution maps are presented for selected taxa characteristic of each of the discontinuous types. Other taxa are listed for each of the categories and subcategories, and compendia of good distribution maps are cited for ready reference to additional examples. Possible explanations for the major discontinuities are discussed.

Finally, a statistical summary is given of the numbers of disjunct taxa and the largest disjunct categories. Among the Angiospermae (the flowering plants), approximately 78 per cent of the 324 families, 24 per cent of the genera, and 1 per cent of the species are widely disjunct. The largest number of disjunct genera are found among the African-Eurasian-(Pacific) (600), Asian-Pacific (460), Pacific (370), North American-South American (ca. 360), Pantropical (334), North Temperate (316), and Subcosmopolitan (125) categories; the largest number of disjunct families among the Subcosmopolitan (90), Pantropical (59), North Temperate (20), African-Eurasian-(Pacific) (17), and North American-South American (13) categories.

INTRODUCTION

AMONG the most fascinating aspects of plant geography are the very wide, intercontinental disjunctions in the natural geographic ranges of many seed-plant groups. Most intriguing to the geographer are the possible explanations for these wide gaps in range. In studying the floristic links between Africa and America, and their possible bearing upon the theory of continental displacement (Thorne, 1972), I became concerned also with other types of intercontinental discontinuities and the various hypotheses that have been suggested to explain them. It seemed desirable to review what is known about the major distributional disjunctions, to classify their patterns, to map or list examples of each major type, to cite useful compendia of range maps of seed plant taxa, and to discuss the possible explanations for the major discontinuities.

GUIDING PRINCIPLES

To achieve these goals I have been guided by several principles, or general considerations, which are herewith briefly stated. All should be self-evident but are all too often ignored. Some have recently been stated by Wood (1971) in his excellent paper on floristic relationships between the southern Appalachians and western North America, an intracontinental range disjunction not considered here.

1. *Only taxa that have been reliably revised should be seriously considered.* Incorrect or unreliable treatments can lead to misleading, sometimes very embarrassing, conclusions. For example, *Distylium* of the Hamamelidaceae is stated in Willis (1966) and van Balgooy (1966) to have a remarkable amphi-Pacific distribution. A recent thorough study of the Mexican and Central American species by Endress (1969) has shown, however, that they represent a new genus, *Molinadendron,* more closely related to the American *Fothergilla* and Himalayan *Parrotiopsis* than to the southeastern-Asiatic endemic *Distylium.* Willis and van Balgooy can hardly be held responsible for the error, for biogeographers are dependent upon the reliability of monographers in the treatment of their taxa.

2. *Only accurate distributional data should be used in constructing distribution maps.* Theoretically, only reliably determined herbarium specimens should be used to develop dot-maps. However, because only a relatively small number of herbarium specimens is available to the geographer at any given herbarium (the rest being distributed in herbaria throughout the world), he must rely also upon distribution maps published in monographs, statements of range in monographs and floras, and recent range extensions published in various journals. Even reports in floras can be misleading, as illustrated by the listing in the *Flora of West Tropical Africa* (Hutchinson and Dalziel, 1954–1968) of a species of the otherwise all-American genus *Miconia* of the Melastomataceae. Wurdack (1970) has identified *Miconia africana* Jacques-Felix as a Brazilian *Leandra* probably collected in Brazil. A mix-up in labels seems indicated.

The poorly botanized state of most of the world, combined with rapidly expanding collections and new range extensions, make almost any map prepared obsolescent before it is published. Most of the maps illustrating the present study must be considered highly generalized, although based upon the best information available to me.

3. *Almost all taxa have discontinuous ranges.* Rarely does any taxon have a completely continuous range in which all specimens are contiguous, for plants grow only within those climatic and edaphic conditions to which their individual ranges of tolerance adapt them. Only when the distributional gaps are greater than the normal dispersal capacity of a taxon, however, is that taxon said to have a disjunct range. In this study, I am treating only those taxa with gaps of intercontinental or equivalent size.

4. *The current distribution of a taxon may not indicate its past distribution.* Many taxa today have ranges that are only fragments of their past distribution, as known from the fossil record. Others may have migrated far from their original centers of distribution and evolution. Still, present distribution, combined with fossil evidence and thorough biosystematic and other monographic knowledge of the taxon, can tell us much about the past history and distribution of the taxon.

5. *Coincidence in range disjunction, although certainly suggestive, does not mean that two taxa have similar dispersal histories.* Each disjunction must be considered separately, for the coincident taxa may have attained their present discontinuous ranges either by restriction of a once wide range or by long-distance dispersal to a new area (Fryxell, 1967). If coincident taxa have attained their disjunct ranges by long-distance dispersal, they may have done so by different routes, by means of different vectors, from different dispersal centers, at different times. Each species has its own degree of vagility (dispersal capacity) and its own capacity to adapt to new or changing conditions.

6. *The smaller the rank of a taxon, the more instructive is its disjunct range.* The ranges of many large families and a good many large

genera are almost world-wide, or subcosmopolitan, but they tell us far less about the history of the taxon than does the widely discontinuous range of a species, a closely related species-pair, the section of a genus, or a small genus, all of which are more amenable to biosystematic analysis.

CLASSIFICATION OF INTERCONTINENTAL DISJUNCTIONS IN RANGE

In classifying the major types of intercontinental discontinuities in the ranges of seed plants (Table 1), I have had to make rather arbitrary decisions to limit the number of categories. Eurasia, Africa, and Australia are considered to be the Old World continents, although Australia is occasionally treated as a very large island. North and South America, the New World, are mostly treated as separate continents, but sometimes it is useful to treat the two as a unit. The Pacific-Indian Ocean basins and the Atlantic-Caribbean basins are both considered of continental rank with respect to marine seed plants. Australasia, as a phytogeographical area, here includes Australia and Tasmania, New Zealand, New Caledonia, and usually New Guinea, all with their satellite islands.

I. Eurasian-North American

Because Eurasia and North America lie across several major latitudinal belts, it seems best to subdivide this areal type into Arctic, Boreal, and Temperate.

1. *Arctic.*

Wide-ranging plants that display this far-northern distribution pattern, by geography, are necessarily disjunct between Eurasia and

TABLE I

Major disjunctions in the geographic ranges of seed plants

- I. Eurasian-North American
  - 1. Arctic
    - 1a. Circum-Arctic
    - 1b. Beringian-Arctic
    - 1c. Amphi-Atlantic-Arctic
  - 2. Boreal
    - 2a. Circum-Boreal
    - 2b. Beringian-Boreal
    - 2c. Amphi-Atlantic-Boreal
  - 3. Temperate
    - 3a. Circum-North Temperate
    - 3b. North and South Temperate
    - 3c. Fragmentary North Temperate
      - 3c-1. Amphi-Atlantic Temperate
      - 3c-2. Mediterranean-American
      - 3c-3. Eurasian-Eastern and Western American
      - 3c-4. Eurasian-Eastern American-Mexican
      - 3c-5. Asian-Eastern and Western American
      - 3c-6. Eurasian-Eastern American
      - 3c-7. Asian-Eastern American
      - 3c-8. Eurasian-Western American
      - 3c-9. Asian-Mexican Highland
    - 3d. Wide Intercontinental Disjuncts and Epibiotics
- II. Amphi-Pacific Tropical
- III. Pantropical
- IV. African-Eurasian (-Pacific)
  - 1. African-Mediterranean
  - 2. African-Eurasian
  - 3. African-Eurasian-Malesian
  - 4. African-Eurasian-Pacific
  - 5. African-Eurasian-Australasian
  - 6. Indian Ocean-Eurasian (-Pacific)
- V. Amphi-Indian Ocean
- VI. Asian-Pacific
  - 1. Asian-Papuan
  - 2. Asian-Papuan-Melanesian
  - 3. Asian-Papuan-Pacific Basin
  - 4. Asian-Papuan-Australasian
- VII. Pacific Ocean
- VIII. Pacific-Indian-Atlantic Oceans
- IX. American-African
- X. North American-South American
  - 1. Tropical
  - 2. Temperate
  - 3. Bipolar
- XI. South American-Australasian
  - 1. South American-Australasian
  - 2. South American-Australasian-Asian
  - 3. South American-Australasian-Madagascan
- XII. Temperate South American-Asian
- XIII. Circum-South Temperate
- XIV. Circum-Antarctic
- XV. Subcosmopolitan
- XVI. Anomalous

North America across the Arctic Sea, and often also across the North Atlantic between Europe-Iceland and Greenland-North America and across the Bering Sea between Alaska and Asia. These are plants which are believed by Hultén (1937) and Löve (1962) to have survived maximum Pleistocene glaciation in refugia mostly north of the ice sheets. With the melting back of the maximum ice, they have quickly spread into their present far northern ranges.

1a. *Circum-Arctic.* The circum-Arctic type of disjunction comprises the Arctic circumpolar and the circumpolar, Arctic-montane plants of Hultén (1937). The circum-Arctic species are found in northern Alaska and Canada, the Canadian archipelago, Greenland, Iceland, northern Scandinavia, Spitzbergen, Franz Josef Land, Novaya Zemlya, the Siberian Arctic, and often farther south at alpine levels in the Eurasian and North American mountains, although each is usually lacking from one or more of these areas. Few species are continuously circumpolar. Hultén (1963) counts 352 species as circumpolar or more or less circumpolar. He counts another 107 taxa as having a more or less circumpolar range but represented by different races or slightly different species on both sides of the Atlantic. He considers this flora an old one, and thinks it probable that it "may have been spread by wind blowing over the frozen Polar Sea or by floating on ice" (p. 72).

Only a relatively few small genera are largely restricted to circum-Arctic (and alpine) ranges, namely *Arctagrostis, Arctous, Braya, Diapensia, Dryas, Dupontia, Loiseleuria,* and *Oxyria. Honkenya, Koenigia,* and *Phippsia* are also essentially circum-Arctic, but they reappear in southern South America and will be discussed below. The species *Diapensia lapponica* L. (Fig. 1) illustrates this circum-Arctic type of distribution. A few other good examples, almost all actually circum-Arctic-alpine and all mapped by Hultén (1958, 1968) or by Meusel, Jager, and Winert (1965), are: *Arctagrostis latifolia* (R. Br.) Griseb., *Armeria maritima* (Mill.) Willd. (s.l.), *Carex rupestris* All., *Eriophorum scheuchzeri* Hoppe, *Oxyria digyna* (L.) Hill, *Polygonum viviparum* L., *Rubus chamaemorus* L., *Saxifraga caespitosa* L., *S. flagellaris* Willd., *S. oppositifolia* L., *Sparganium hyperboreum* Laest., and *Vaccinium vitis-idaea* L.

1b. *Beringian-Arctic.* This subgroup consists of those plants which are mainly distributed on the Arctic shores of North America and Eurasia on either side of the Bering Sea but which do not reach both sides of the North Atlantic. Included are the northern Beringia radiants and Arctic-Pacific plants of Hultén (1937). Hultén suggests that these plants probably survived the Pleistocene glaciations in refugia in Alaska-Yukon, the northern part of the present Bering Sea, and in northeastern Siberia. Some formerly may have had more complete circum-Arctic ranges that were much reduced by glaciation in eastern North America, Greenland, and the European Arctic.

One plant that shows the Beringian-Arctic type of disjunction is *Diapensia lapponica* L. subsp. *obovata* (Fr. Schm.) Hult. (Fig. 1), separated by considerable gaps in northern Canada and Siberia from the amphi-Atlantic *D. lapponica* L. subsp. *lapponica.* Some other examples, mapped by Hultén (1958, 1968) or Meusel, Jager, and Winert (1965) are *Aconitum delphinifolium* DC., *Arenaria macrocarpa* Pursh, *Arnica frigida* C. A. Mey., *Aster sibiricus* L., *Caltha natans* Pall., *Castilleja caudata* (Pennell) Rebr., *Lloydia serotina* (L.) Rchb., *Luzula tundricola* Gorodk., *Oxytropis arctica* R. Br., *Phlox sibirica* L., *Potentilla uniflora* Ledeb., *Primula borealis* Duby, *Rumex arcticus* Trautv., *Salix pulchra* Cham., *Sedum rosea* (L.) Scop. subsp. *integrifolium* (Raf.) Hult., and *Sium suave* Walt. Many others, including bryophytes and ferns, are listed by Schofield (1969) as amphi-Beringian.

1c. *Amphi-Atlantic-Arctic.* This group is the reverse of the Beringian group of Arctic disjuncts, for the species are mainly distributed on both sides of the North Atlantic. They have received much critical attention from Hultén (1958, 1963). Hultén (1958) maps 278 species, but these include Arctic, boreal, and temperate species, 129 of the Arctic and 148 of boreal or temperate distribution. Hultén (1963) explains many of these amphi-Atlantic plants as former circum-Arctic species whose ranges have been much reduced by changing climatic conditions. Some may have spread, however, from centers on one side or the other of the Atlantic. Certainly some of the maritime and aquatic species can be accounted for by long-distance dispersal by sea currents or by birds. There seems little need, if any at all, for a Late Tertiary or Quaternary land-bridge across the North Atlantic to account for plants having this type of disjunct range.

Diapensia lapponica L. subsp. *lapponica* (Fig. 1) and *Salix herbacea* L. (Fig. 2) illustrate this type of range discontinuity. Other examples, mapped by Hultén (1958) are *Bartsia alpina* L., *Cassiope hypnoides* (L.) Don, *Cerastium alpinum* L., *Juncus trifidus* L., *Pedicularis hirsuta* L., and *Saxifraga aizoides* L.

2. *Boreal.*

Plants considered to have a disrupted boreal range in North America and Eurasia are those whose northern limits generally lie south of the Arctic shores and whose upper altitudinal limits do not reach the alpine levels of the Arctic-alpine species. They are absent usually from Greenland and often from Iceland. Many have been mapped by Hultén (1958, 1968) and by Meusel, Jager, and Winert (1965). Unlike the Arctic disjuncts, these plants apparently survived maximum glaciation in refugia south of the ice (Hultén, 1937).

2a. *Circumboreal.* Plants having this wide distribution in the boreal belt of Eurasia and North America have been called boreal circumpolar plants by Hultén (1937), and they are very well known to temperate botanists. They are especially abundant in the coniferous forests, bogs, marshes, and oligotrophic lakes of this zone. One such bog plant, *Scheuchzeria palustris* L. (Fig. 3) of the Juncaginaceae is the only member of its genus. With the drainage of bogs and marshes or their rapid natural evolution into grassy meadows, this species is receding northward in America. It has apparently disappeared in Iowa, California, and other regions along its southern boundary within the last hundred years. The American representatives of this species are treated as a subspecies *americana* (Fern.) Hult., distinct from the Eurasian members.

Some of the more familiar species of this circumboreal disjunct group are *Adoxa moschatellina* L., *Calla palustris* L., *Caltha palustris* L. (s.l.), *Calypso bulbosa* (L.) Rchb. f., *Carex chordorrhiza* Ehrh., *C. disperma* Dew., *C. rostrata* Stokes, *Cypripedium calceolus* L., *Drosera rotundifolia* L., *Juniperus communis* L., *Menyanthes trifoliata* L., *Moneses uniflora* (L.) Fray, *Monotropa hypopitys* L., *Myrica gale* L., *Ranunculus reptans* L., *Rhynchospora alba* (L.) Vahl, *Rubus idaeus* L., *Sparganium angustifolium* Michx., *Subularia aquatica* L., *Veronica scutellata* L., and *Viburnum opulus* L. (s.l.).

Although many species possess the circumboreal type of disjunct range, only one family, the monotypic Adoxaceae, and about 50 genera are primarily circumboreal in distribution. Some of these better-known genera are *Abies, Andromeda, Calla, Cassandra, Cassiope, Comarum, Eriophorum, Larix, Ledum, Linnaea, Menyanthes, Phyllodoce, Picea, Scheuchzeria,* and *Sorbus.*

2b. *Beringian-Boreal.* Taxa of this subgroup have much less extensive ranges than the circumboreal species. They are primarily distributed on either side of the Bering Sea in eastern Eurasia and western North America, but they do not generally reach the Arctic shores of Beringia and they do extend farther south on either side of the Pacific Ocean. *Oplopanax* (Fig. 4), with two or three closely related species in North America, Japan, and Korea, is representative of this discontinuous type. In North America *O. horridus* (Sm.) Miq., the infamous Devil's Club of the wet coniferous forests of the Pacific Northwest, illustrates a well-known intracontinental disjunction by its jump from Montana to Isle Royale and adjacent islands on the north side of Lake Superior. At least eight additional genera, *Achlys, Chamaerhodos, Glehnia, Leptarrhena, Lysichitum, Nephrophyllidium, Smelowskia,* and *Thellungiella,* have a Beringian-boreal type of discontinuous distribution.

Some of the boreal species or species-pairs with ranges in eastern Asia and western America, a few reaching across boreal America to the Atlantic Coast, are *Achlys triphylla* (Smith) DC.–*A. japonica* Maxim., *Achillea sibirica* Ledeb., *Aruncus sylvester* Kostel., *Carex macrocephala* Willd., *Cassiope lycopodioides* (Pall.) D. Don, *Cornus canadensis* L., *Cypripedium guttatum* Sw., *Draba borealis* DC., *Fritillaria camschatcensis* (L.) Ker-Gawl, *Galium boreale* L. subsp. *septentrionale* (R. & S.) Hara, *Gentiana glauca* Pall., *Heracleum lanatum* L., *Iris setosa* Pall, *Juncus ensifolius* Wikstr., *Leptarrhena pyrolifolia* L., *Lysichitum americanum* Hult. & St. John–*L. camtschatense* (L.) Schott, *Maianthemum dilatatum* (How.) Nels. & Macbr., *Orchis aristata* Fisch., *Poa macrocalyx* Trautv. & Mey., *Ranunculus eschscholtzii* Schlecht., *Ribes lacustre* (Pers.) Poir., *Rubus spectabilis* Pursh, *Streptopus streptopoides* (Ledeb.) Frye & Rigg, *Thalictrum sparsiflorum* Turcz, and *Viola langsdorffii* Fisch. These and many more are mapped in Hultén's magnificent *Flora of Alaska and Neighboring Territories* (1968). Others, along with many bryophytes, are listed as North Pacific disjuncts by Schofield (1969).

2c. *Amphi-Atlantic-Boreal.* This subgroup, along with the more northerly amphi-Atlantic-Arctic group, has been thoroughly discussed by Hultén (1958, 1963). Because of their occurrence on both sides of the Atlantic Ocean, species having this type of disjunction are well known to European and American botanists. *Rhynchospora fusca* (L.) Ait. (Fig. 5) is just one of some 148 species, most of which belong to this group, that have been mapped by Hultén (1958). Other examples similarly mapped are *Eriocaulon septangulare* With., *Geum rivale* L., *Liparis loeselii* (L.) L. C. Rich., *Lobelia dortmanna* L., *Milium effusum* L., and *Spiranthes romanzoffiana* Cham. & Schlecht. Some may have extensive ranges across one continent, although limited to the Atlantic side of the opposing continent. Others are rather closely restricted to the Altantic areas of both continents.

3. *Temperate.*

This very large group of disjunct plants is certainly the best known and most frequently studied of all, as might be expected from the heavy concentration of the world's botanists in the North Temperate zone. To this group belong the many genera that dominate the temperate deciduous forests of Eurasia and North America. It is an ancient group, mostly originating no later than the widespread early Tertiary forests of the northern hemisphere. Many genera have retained their wide ranges of Tertiary times; others have become reduced to fragments of their former vast ranges. These latter have received much more attention because of their rather romantic, highly discontinuous ranges, but surely they are no more informative to the geographer than the genera that retain most of their former ranges. Both kinds of genera, however, together with the fairly extensive fossil record for the woody relicts, tell us much about the vicissitudes the Tertiary forests must have experienced to the present time.

The more fragmented North Temperate disjuncts are today preserved in the scattered deciduous forests of the North Temperate zone, primarily in eastern Asia (Japan, Korea, Taiwan, and China), the lower Himalayan slopes, the Near Eastern Caspian-Caucasus-Black Sea areas, Europe (including the Mediterranean region), eastern North America, the Mexican and Central American highlands, and western North America.

3a. *Circum-North Temperate.* By analyzing various regional temperate floras, Willis' *Dictionary* (1966), and Engler's *Syllabus* (1964), I have been able to list 118 wide-ranging, primarily temperate genera, 62 that are treated here as circum-North Temperate, and 56 that are equally widely distributed in the North Temperate zone but are also represented in the temperate areas of one or more of the southern continents. Most of the 118 possess relatively uninterrupted ranges across North America and across Eurasia. The 62 assigned to the circum-North Temperate group mostly do not cross the equator. The few that do, like *Acer, Alnus, Arabis, Campanula, Corydalis, Draba, Juniperus, Pinus* (Fig. 6), *Quercus, Rosa,* and *Sedum,* are confined in the southern hemisphere to the tropical mountains. Many of these genera are by no means restricted to the temperate zone but have one or more species represented in the Arctic or boreal zones (as *Arenaria, Armeria, Betula, Chimaphila, Draba, Juniperus, Mertensia, Orchis, Parnassia, Pedicularis,* and *Silene*) or in the tropics [as *Acer, Lonicera, Pinus* (Fig. 6), and *Quercus*]. Several of these genera with relatively continuous distribution in north temperate lands are mapped by Meusel, Jager, and Winert (1965) — *Betula, Cypripedium, Juniperus, Lilium, Orchis, Populus, Quercus,* and *Veratrum,* among others.

3b. *North and South Temperate.* Presumably most of the preceding circum-North-Temperate genera have achieved their far-reaching ranges through the normal dispersal capacities of their member species. Their species, at least in total, must have a wide amplitude of tolerance to often severe environmental conditions in the continental heartlands. Many of the 56 widely distributed North Temperate genera that have successfully migrated across the tropics into temperate areas of one or more of the three southern continents have likewise probably moved by normal short-range dispersal along relatively continuous mountain chains, as *Descurainia, Epilobium, Gentiana, Lotus, Ribes* (Fig. 7), *Salix, Saxifraga,* and *Trifolium,* many of which are mapped by Meusel, Jager, and Winert (1965). On the other hand, other genera show very large discontinuities across the tropics, as in *Anemone, Euphrasia* (Fig. 8), *Geum, Phalaris, Primula,* and *Sparganium,* also mostly mapped by Meusel, Jager, and Winert. These amphitropical genera may have achieved such large disjunctions by the extinction of montane species formerly spanning the gaps, or perhaps more likely, by having disseminules transported from one temperate zone to the other by migrating birds. More will be said about this below in connection with the North American-South American disjunct group.

There are several less continuously distributed genera of the North Temperate zone which by default probably should be treated in this disjunct group also. *Berberis* (s.s.), for example, has species in Europe, Asia, eastern North America, and down the Andes to Fuegia. *Hydrangea* has numerous species in eastern and southeastern Asia, a few in eastern North America, and a few more ranging along the mountains from Mexico to Chile.

3c. *Fragmentary North Temperate.* Organized under this subheading is a variety of widely discontinuous groupings that have considerably less extensive ranges in Eurasia and North America than the groups discussed above. Their disjunctions in one or both continents probably represent severe restriction of ranges that were relatively continuous during more favorable Tertiary climates. Most of the taxa thus are Tertiary relicts. Long-distance dispersal, however, is more than likely for some of the maritime, marsh, and aquatic plants.

3c-1. *Amphi-Atlantic Temperate.* Since the warmer parts of Europe and North America lie widely separated by the Atlantic Ocean, with few islands of any consequence between the continents to serve as stepping-stones, it is not surprising that this type of discontinuity is very rare in comparison with the relatively frequent Arctic and boreal amphi-Atlantic disjuncts. It is best represented by *Corema* (Fig. 9), with *C. alba* (L.) D. Don along the western coast of the Iberian Peninsula and on the Azores and *C. conradii* Torr., the only other species, along the Atlantic coast of North America from Newfoundland to New Jersey The small, drupaceous fruits and the insular stations for both species suggest probable long-distance transport of the disseminules by birds. No other genus has quite this restricted range, although *Cneorum,* with species in the Mediterranean area, on the Canary Islands, and on Cuba, comes close; it is included in the next group. Because the several species of *Cakile* are restricted primarily to the sea coasts of western Eurasia, North Africa, eastern North America, and Caribbean South America (the western American plants are now thought to be adventive), *Cakile* is probably best treated here.

Of all the amphi-Atlantic species mapped by Hultén (1958), only 6 angiosperms are primarily temperate amphi-Atlantic disjuncts. They are *Drosera intermedia* Hayne, *Eriocaulon septangulare* With., *Juncus tenuis* Willd., *Limosella subulata* Ives, *Ranunculus hederaceus* L., and *Spartina patens* (Ait.) Muhl. It is surely no coincidence that these are all aquatic, maritime, or ruderal species. All the others mapped by Hultén are more wide-ranging or more boreal, at least in the American part of their ranges.

3c-2. *Mediterranean-American.* Approximately 35 genera have their maximum development in the xerothermic, Mediterranean climates of the Old World Mediterranean region and southwestern North America of the New World, some of them also ranging disjunctly to other areas of Mediterranean climate in South Africa, Australia, or Chile. This kind of discontinuity has been of special interest to Californians because the Mediterranean climate in North America is centered about Southern California. It has recently been discussed by Stebbins and Day (1967) and by Meusel (1969). Four families, the Cistaceae, Cneoraceae, Ephedraceae, and Resedaceae (Fig. 10); 18 groups of vicarious species or species-pairs, listed in Stebbins and Day; and one species, *Styrax officinalis* L., also possess this kind of major disjunction.

Oligomeris linifolia (Vahl) Macbr. (Fig. 10) is the only resedaceous species in the New World. It has a wide, apparently natural distribution through the Southwest and northern Mexico. A closely related species *O. subulata* Del., sometimes treated as conspecific with *O. linifolia,* has an enormous range, partly discontinuous, from the Canary Islands to North Africa and east to southern Iran and northern Pakistan. Other species of the 9 listed for the genus are found in South Africa and in India. Obviously, the members of this genus have enormous vagility, or capacity to be dispersed. If *Oligomeris* is indeed indigenous to the New World, one must almost assume that it reached North America by long-distance dispersal. I find it hard to accept Stebbins' contention that the American members of this disjunct category have reached the New World by stepping-stone dispersal through Beringia. It seems unlikely that pockets of warm, semiarid climate ever existed in Tertiary or more recent time in eastern Asia or northwestern North America. Furthermore, not all the members of this group are restricted to Califonia or even are present in the United States. The poaceous genera, *Brachypodium* and *Briza,* which have no indigenous species north of Mexico, range southward into South America; likewise, the asteraceous genus *Hypochoeris* has no indigenous species north of the southern half of South America, where it has speciated heavily. *Buxus* has 70 species mostly in temperate Eurasia, western Malesia (i.e., Malaya, Borneo, Philippines, and Lesser Sunda Islands), tropical and South Africa, and in the West Indies and Mexico south to Venezuela. The leguminous genus *Ornithopus* has 10 species in the Mediterranean area to West Asia and tropical Africa and in South America. *Cneorum,* the sole genus of the Cneoraceae, has one species in the central and western Mediterranean, one in the Canary Islands, and one in Cuba. Thus it has apparently not even reached the American mainland. The myrsinaceous *Heberdenia* has one species in the Canaries and Madeira and the other in Mexico. *Peganum* and *Pistachia* in the New World are distributed primarily from Texas to Mexico or Guatemala; they are absent from California. Also, *Centaurea* and *Corispermum,* as indigenes in the New World, are primarily in the central part of the United States.

Other genera belonging to this disjunct group do have heavy development in California and adjacent areas or are at least represented there. Those not already mentioned are *Antirrhinum, Arbutus, Arthrocnemum, Comandra, Cupressus, Damasonium, Datisca, Ephedra, Eurotia, Evax, Fagonia, Filago, Helianthemum* (s.l.), *Kochia, Lavatera, Laurentia, Loeflingia, Lupinus, Microcala, Micropus, Papaver, Prunus* sect. *Emplectocladus* (*Amygdalis*), *Stylocline,* and *Triodanis.*

Two genera listed by Stebbins and Day (1967), although well represented in the American Southwest, are actually not present in the Mediterranean region. The oleaceous *Menodora* has one or two species in South Africa (and another center in southern South America); and the rutaceous *Thamnosma* has one species in South Africa and one on Socotra Island. I have treated them elsewhere (Thorne, 1972) as members of the American-African disjunct group.

3c-3. *Eurasian-Eastern and Western American.* Of the North Temperate genera with fragmentary ranges this category of wide disjuncts has ranges most similar to the nearly continuous circum-North Temperate genera. At least 24 genera, although with rather large gaps on one or the other continent, and often on both, are found in Europe, one or more areas of Asia, and in both eastern and western North America. Among these relicts are such well-known temperate genera as *Aesculus, Amelanchier, Cercis, Corylus, Juglans, Ostrya, Platanus, Staphylea, Styrax,* and *Taxus.*

3c-4. *Eurasian-Eastern American-Mexican.* Hardly distinct from the above group, the genera in this subcategory are not found in the western United States and Canada but are found in the highlands of Mexico (and often in Guatemala or farther south). The 6 genera that have this special type of disjunct range are *Carpinus* (Fig. 11), *Clethra* (Fig. 12) (this genus is slightly aberrant since it is absent from Europe, but is found in Madeira), *Fagus, Halenia, Tilia,* and *Ulmus.* Some of the Eurasian-Eastern and Western American disjunct genera discussed above, like *Amelanchier, Juglans, Ostrya, Platanus, Styrax,* and *Taxus,* are also represented in the Mexican highlands and often farther south.

3c-5. *Asian-Eastern and Western American.* Another large category of Tertiary relicts are those genera, at least 38, that are represented in both eastern and western North America, but are now absent from Europe and mostly also from the Near East. They usually have their centers of development in eastern and southeastern Asia. Among these genera are *Aralia, Calycanthus, Chamaecyparis, Clintonia, Dicentra, Disporum, Leucothoë, Physocarpus, Smilacina, Thuja, Torreya, Toxicodendron, Trillium,* and *Tsuga.* Excellent maps showing the disjunct American ranges of some of these and some other genera have recently been published by Wood (1971).

3c-6. *Eurasian-Eastern North American.* There seem to be only four genera, *Castanea, Convallaria, Epigaea,* and *Polygonatum,* that occur both in Europe and Asia and only in the eastern part of North America. Presumably the east-west orientation of mountain chains and seas in Europe, which prevented the escape of temperate species southward before the Pleistocene glaciers, was almost as disastrous to the survival of Tertiary genera in Europe as was the severe deterioration of climate in western North America.

3c-7. *Asian-Eastern American.* This is the largest category of Tertiary relict temperate genera, the genera having found haven only in eastern North America and in Asia, most of them only in eastern and southeastern Asia. I have listed 74 genera in this much-studied group, early brought to our attention by Asa Gray (1846, 1859), and more recently discussed by Li (1952) and by Wood (1971). Among the more conspicuous or better known of these numerous genera are: *Arisaema, Carya, Catalpa, Caulophyllum, Cladrastis, Croomia, Gordonia, Hamamelis* (Fig. 13), *Illicium, Liquidambar, Liriodendron, Magnolia, Nelumbo* (Fig. 14), *Nyssa, Panax, Podophyllum, Sassafras, Saururus, Schisandra, Shortia, Stewartia, Symplocarpus, Wisteria,* and *Zizania.* Some of these are as correctly treated in the amphi-Pacific tropical disjunct category, for their ranges in either America or Asia or in both are as tropical as they are warm temperate. Among such genera are *Berchemia, Clethra* (Fig. 12), *Gordonia, Illicium, Magnolia, Nelumbo* (Fig. 14), *Sageretia,* and *Schisandra.* Two genera, *Arundinaria* and *Symplocos,* were placed in the amphi-Pacific tropical disjunct category because all but one of their American species are in the tropics, although often at montane elevations.

Because so many of the Asian-Eastern American disjuncts have preservable parts, they have left a rather rich fossil record in areas where they are now extinct. The distribution of fossils in such genera as *Liriodendron, Magnolia* (see Meusel, 1969), *Nelumbo* (Fig. 14), and *Nyssa* (Eyde and Barghoorn, 1963), indicates that these highly discontinuous temperate-to-tropical genera once had a nearly continuous distribution across Eurasia and North America in the Tertiary. Presumably the same is true for the herbaceous disjuncts, whose chances of being preserved as fossils are much less.

3c-8. *Eurasian-Western North American.* A small group of primarily temperate genera are the nine restricted to western North America and Eurasia, mostly eastern Asia. Because they are few and the disjunction is relatively less spectacular, this group has undeservedly received little attention. *Heterocodon, Paeonia* (Fig. 15), and several generic-pairs have been discussed by Stebbins (1940). According to Stebbins (1938) the two western American species of *Paeonia* are closer to *P. delavayi* Franch. of southwestern China than to the herbaceous species of Europe. The other genera with this type of disjunct range are *Adenocaulon, Boschniakia, Calocedrus, Mahonia, Photinia,* and *Pseudotsuga.* They are little different from the nine genera earlier listed as having a Beringian-boreal distribution. In fact, this Eurasian-western North American group could just as well be called Beringian-temperate or even amphi-Pacific North Temperate.

3c-9. *Asian-Mexican Highland.* Hardly distinct from the preceding group of genera are the six genera found only in eastern Asia and the Mexican highlands or farther south. Several of the preceding group, such as *Adenocaulon, Mahonia, Photinia,* and *Pseudotsuga,* occur also in the cool Mexican or Guatemalan highlands. The six that do not occur in North America north of Mexico are *Abelia, Deutzia, Engelhardtia, Leibnitzia, Mitrastemon* (Fig. 16), and *Sarcococca.* These could also be absorbed, perhaps as well, in the amphi-Pacific tropical group of discontinuous genera discussed next below.

In addition to the numerous genera, many listed above, that have a fragmentary North Temperate distribution, there are at least 18 families and three subfamilies so restricted: Calycanthaceae, Cistaceae, Cneoraceae, Datiscaceae, Ephedraceae, Hippocastanaceae, Hydrastoideae, Illiciaceae, Juglandaceae, Mitrastemonoideae, Nyssaceae, Paeoniaceae, Platanaceae, Podophylloideae, Resedaceae, Saururaceae, Schisandraceae, Stemonaceae, Styracaceae, Taxaceae, and Taxodiaceae.

3d. *Wide Intercontinental Disjuncts and Epibiotics.* Within the temperate zone of North America on the one hand and of Eurasia on the other there are taxa with spectacular disjunctions that are not considered here because they are intracontinental. In distances involved, however, they are often more widely discontinuous than those that we are attempting to classify here. Such North American endemic disjuncts as *Camassia, Dirca. Dulichium* (with fossil record in Europe), *Iliamna, Sullivantia,* and *Xerophyllum,* are mapped and many others are discussed by Wood (1971).

The temperate North American-Middle American highland disjuncts are rather conspicuous and often dominant in the moist, cool highlands of Mexico and Guatemala. Mostly these are conspecific with species in the southeastern United States. The relationships with temperate western American species are fewer and less close. These disjunctions have been discussed by a number of taxonomists (McVaugh, 1952; Sharp, 1946a, b; Miranda and Sharp, 1950; Steyermark, 1950; Hernández-X., Crum, Fox, and Sharp, 1951; and Dressler, 1954).

Meusel, Jager, and Winert (1965), Meusel (1969), and Meusel and Schubert (1971) have mapped such widely discontinuous Eurasian endemics as *Daphne* sect. *Daphnanthes, Callianthemum, Carpesium, Epimedium, Nerium,* and *Viscum album* L. Two other distinctive taxa with enormously disjunct ranges across North Africa and Eurasia from the Canary Islands to Japan are *Hedera* and *Theligonum,* the latter with its three species being the only genus of the Theligonaceae, a family which is enigmatic in its relationships.

Although also beyond the scope of this review of wide disjuncts, there are numerous primitive, ancient relict endemics (epibiotics) in eastern Asia and America, mostly with extremely small, relatively continuous ranges. Because they are woody and thus have parts that survive well as fossils, they mostly have left good fossil records throughout much of the northern hemisphere. Since, at one time, they surely had very discontinuous ranges, they can at least be mentioned here. In eastern Asia, where they are particularly numerous, some of the better known are *Amentotaxus, Cephalotaxus, Cercidiphyllum, Cryptomeria, Cunninghamia, Eucommia, Euptelea, Ginkgo, Glyptostrobus, Metasequoia, Pseudolarix, Pterocarya, Sciadopitys, Tetracentron* and *Trochodendron.* North America is much less rich in such woody relicts, but at least *Fothergilla, Sequoia, Sequoiadendron,* and *Taxodium* are known to have once possessed wide ranges in the northern hemisphere. Maps showing both the present and known fossil distribution of all the listed conifer genera were published by Florin (1963).

II. Amphi-Pacific Tropical

This discontinuous group includes all those taxa that are found both in tropical America and the tropical lands on the western borders of the Pacific Basin. A total of 89 genera, 4 tribes or subtribes, 3 or 4 subfamilies, and 8 to 11 families of flowering plants are amphi-Pacific tropical in their distribution. The number of taxa is inexact because of the overlap with categories discussed above. *Clethra* (Fig. 12), *Magnolia, Mitrastemon* (Fig. 16), and *Nelumbo* (Fig. 14), are particularly troublesome, and probably rightly should be included here. Van Steenis (1962) has presented a useful list of "amphi-transpacific genera and other affinities" organized in four latitudinal groups. Some of the most noteworthy amphi-Pacific tropical genera are: *Anaxagorea, Cleyera, Endiandra, Hedyosmum, Meliosma, Passiflora, Pentapanax, Perrottetia* (Fig. 17), *Persea, Phoebe, Picrasma, Rhynchoglossum, Saurauia, Sloanea, Spathiphyllum, Symplocos, Talauma, Turpinia,* and *Xylosma.* All of these and 27 more reach southeastern Asia, including the Malesian islands west of New Guinea. Sixteen additional genera range much farther to the Mascarene Islands, Madagascar, or even eastern tropical Africa. Among them are *Aphananthe, Calliandra, Callicarpa, Calophyllum, Clusia, Elaeocarpus, Glochidion, Protium,* and *Suriana.* Sixteen genera reach only to Australasia; these include *Batis, Bredemeyera, Epistephium, Iresine, Licania, Lindenia, Muehlenbeckia, Nicotiana,* and *Sicyos.* Four genera, *Allagoptera, Brachistus, Leucaena,* and *Pritchardia,* reach neither Australasia nor Asia but do reach Polynesia or as far west as the Fiji and Solomon Islands.

Of the larger categories, the families Actinidiaceae (including *Saurauia*), Clethraceae, Magnoliaceae, Nelumbonaceae, Sabiaceae (including *Meliosma*), Staphyleaceae, and Symplocaceae, although each has some warm temperate representatives, are essentially amphi-Pacific tropical in distribution. The Bataceae reach only Australasia, but the Trigoniaceae (Fig. 18), Elaeocarpaceae, and Chloranthaceae are represented not only in Asia but in Madagascar as well.

How and when these taxa achieved their present amphi-Pacific disjunct ranges have long been matters for speculation. Some, like van Steenis (1962), postulate complete or partial land-bridges across the widest and deepest parts of the Pacific Basin. Others would prefer rather recent continental splitting and displacement. Also suggested have been land-bridges across Beringia and Antarctica when periods of great warmth in the world permitted warm temperate or subtropical forests to flourish in those lands. Finally, long-distance disperal by birds and sea currents across the Pacific has been proposed for at least some of the disjuncts. The probable explanation must involve several of these possibilities. As explained elsewhere (Thorne, 1972), recent continental splitting is not a realistic explanation for most large discontinuities. Nor is a vast land-bridge across the Pacific Basin feasible in the light of our rapidly expanding knowledge of Pacific geology. The unquestioned existence of the Beringian land-bridge in the past and the discovery of fossil plant and animal genera, now restricted to the tropics, in Alaska and adjacent areas (see, for example, Wolfe, 1969) strongly support the Beringian passage for many of the disjuncts. A larger and warmer Antarctica in the past must have furnished a similar, though perhaps an incomplete, land-bridge for the passage of other tropical genera with austral relationships. Finally, long-distance dispersal is indicated for at least some of the genera with fleshy fruits or fruits able to float and remain viable for long periods in salt water. At least 25 of the 89 genera have migrated successfully over great distances of water to the Hawaiian (*Perrottetia*, Fig. 17) or other Polynesian islands in the Pacific Basin or to the Mascarene Islands in the Indian Ocean. There has been much time available for the accomplishment of successful migrations, and the varying taxonomic levels of divergence among the disjuncts indicate that their forebears rounded or crossed the Pacific at widely different times.

III. Pantropical

The same rather conservative approach to genera, as was used elsewhere in this survey with other taxa, has been used to draw up a list of 231 genera of seed plants that are truly pantropical, i.e., are represented by indigenous species in all the major tropical areas of the world. These major tropical areas are defined as including tropical America, tropical Africa, tropical Asia including Malesia, and tropical Australia. An additional 103 genera are not believed to have indigenous species in Australia (Burbidge, 1963) but occur elsewhere in all the major tropical areas. Thus, we can accept a total of 334 widely distributed tropical genera (many with some temperate species), a rather tiny total out of possibly 12,500 currently accepted genera of seed plants. Fifty-nine angiospermous families are also essentially pantropical.

In attempting to explain how and when these taxa attained their wide distribution about the world, the discussion for amphi-Pacific tropical taxa (above) can be applied here as well, for actually only mainland Africa is added to the problem. Disjunctions involving Africa will be discussed below. It is pertinent here to mention, though, that 194 of the 334 tropical wide-ranging genera have managed to reach oceanic islands in the Pacific Ocean, 56 genera being reported from the very isolated Hawaiian Islands in the center of the Pacific Basin (Fosberg, 1948; van Balgooy, 1971). Among the pantropical genera reaching the Hawaiian Islands are *Acacia, Caesalpinia, Cocculus, Cryptocarya, Diospyros* (Fig. 19), *Dodonaea, Erythrina, Eugenia, Gossypium, Gouania, Morinda, Myrsine, Peperomia, Pisonia, Psychotria, Rauvolfia, Trema,* and *Vitex*. Some of the pantropical genera apparently not established on oceanic islands are *Alchornea, Begonia, Beilschmiedia, Cleidion, Dacryodes, Dendrocnide, Dorstenia, Ehretia, Erythroxylum, Gleditsia, Hybanthus, Jatropha, Omphalea, Ouratea, Parkia, Quassia, Rinorea, Rourea, Strychnos, Ternstroemia, Tetracera, Xylopia,* and *Zizyphus*.

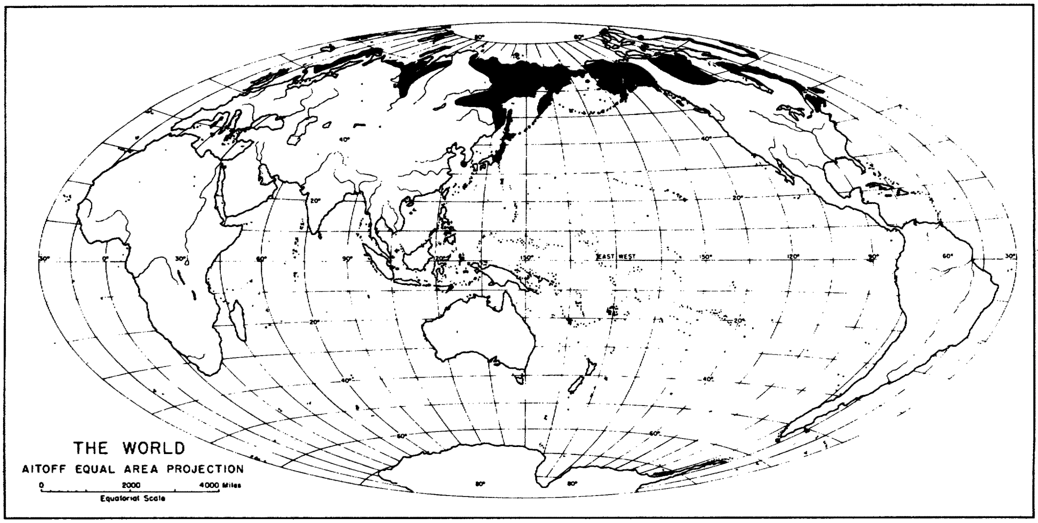

FIG. 1. THE KNOWN WORLD DISTRIBUTION OF THE CIRCUM-ARCTIC SPECIES *Diapensia lapponica*

The Beringian-Arctic portion of its range, between 120° W and 90° E is occupied by *D. lapponica* subsp. *obovata;* the Amphi-Atlantic-Arctic portion, between 90° E and 120° W, by *D. lapponica* subsp. *lapponica.* This map, drawn on an Aitoff Equal-Area Projection with the permission of John Belkin, Univ. of California, Los Angeles, is modified from Hultén (1958, 1968).

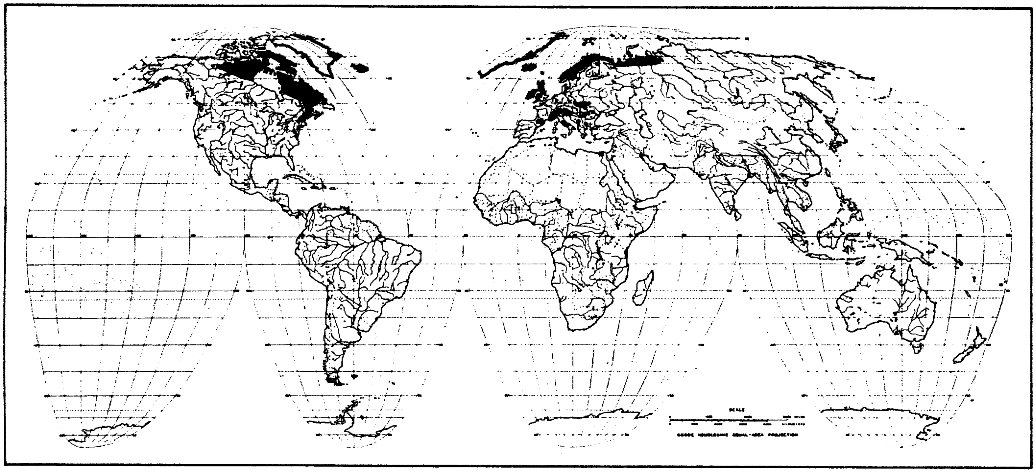

FIG. 2. GENERALIZED DISTRIBUTION OF THE AMPHI-ATLANTIC-ARCTIC SPECIES *Salix herbacea,* A DWARF ARCTIC-ALPINE WILLOW

This map, drawn on a Goode Homolosine Equal-Area Projection with the permission of the Department of Geography, Univ. of Chicago, is modified from Hultén (1958).

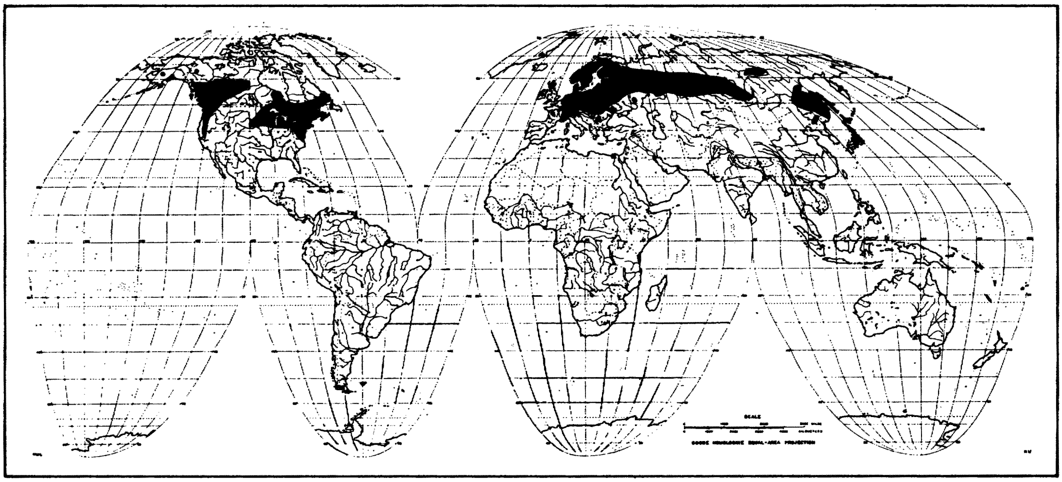

FIG. 3. GENERALIZED DISTRIBUTION OF THE CIRCUM-BOREAL BOG SPECIES, *Scheuchzeria palustris*

The typical subsp. *palustris* occurs in Eurasia and the subsp. *americana in* North America. Modified from Meusel, Jager, and Winert (1965) and Hultén (1968); base map as in Fig. 2.

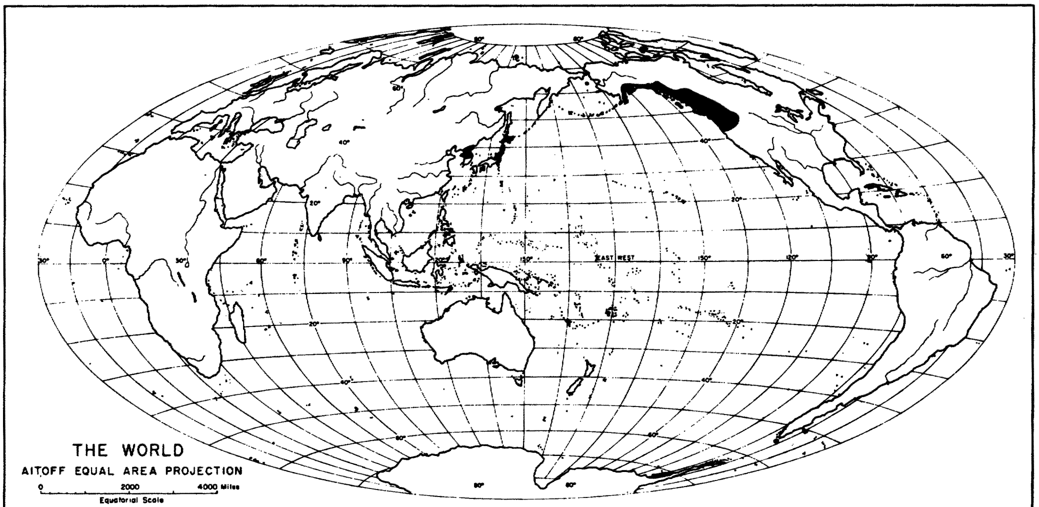

FIG. 4. GENERALIZED DISTRIBUTION OF THE BERINGIAN-BOREAL GENUS *Oplopanax,* THE DEVIL'S CLUB OF THE ARALIACEAE

Note the Isle Royal colony on the north side of Lake Superior. Modified from Fernald (1925) and Hultén (1968); base map as in Fig. 1.

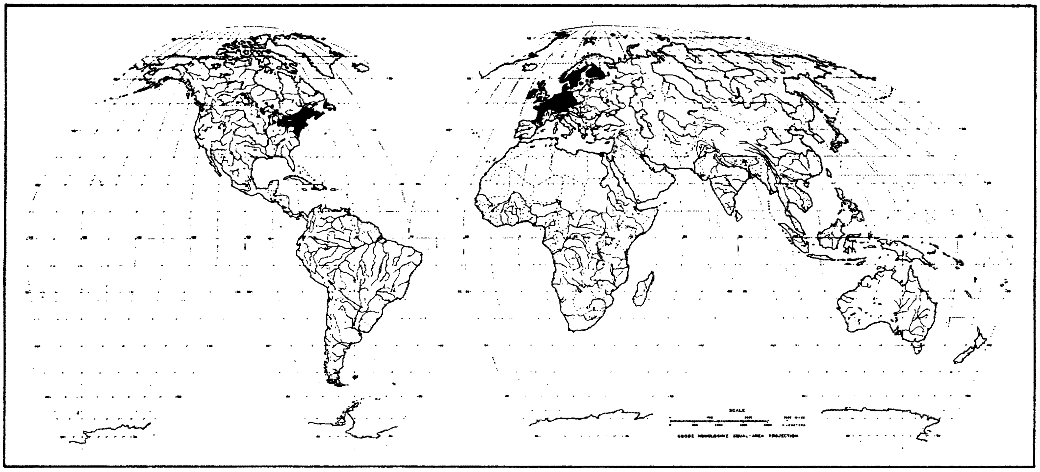

FIG. 5. GENERALIZED DISTRIBUTION OF THE AMPHI-ATLANTIC-BOREAL SPECIES *Rhynchospora fusca,* A BEAK-RUSH OF THE CYPERACEAE

Based largely upon Hultén (1958); base map as in Fig. 2.

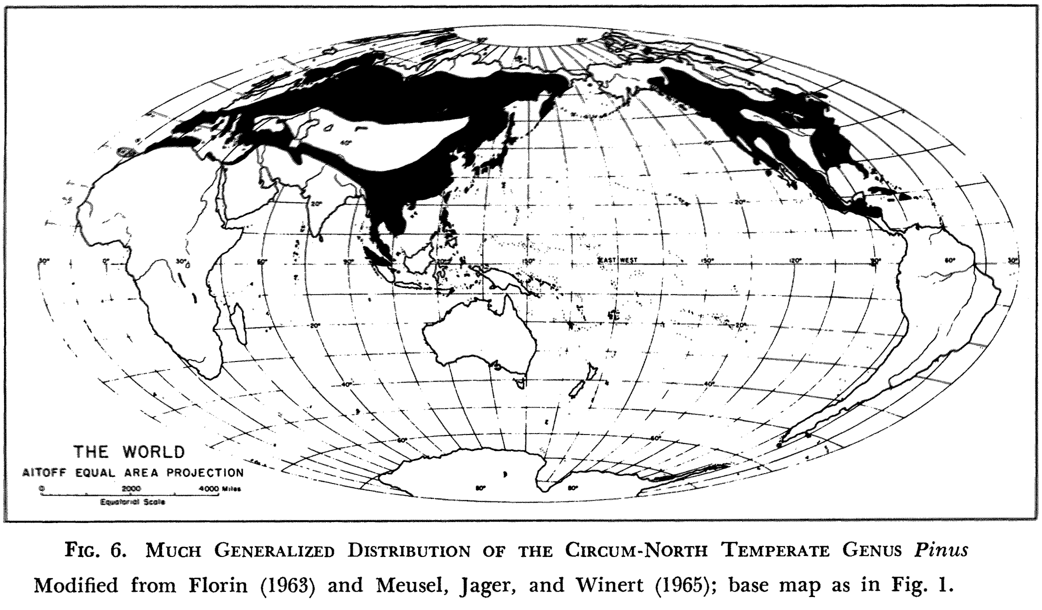

FIG. 6. MUCH GENERALIZED DISTRIBUTION OF THE CIRCUM-NORTH TEMPERATE GENUS *Pinus*

Modified from Florin (1963) and Meusel, Jager, and Winert (1965); base map as in Fig. 1.

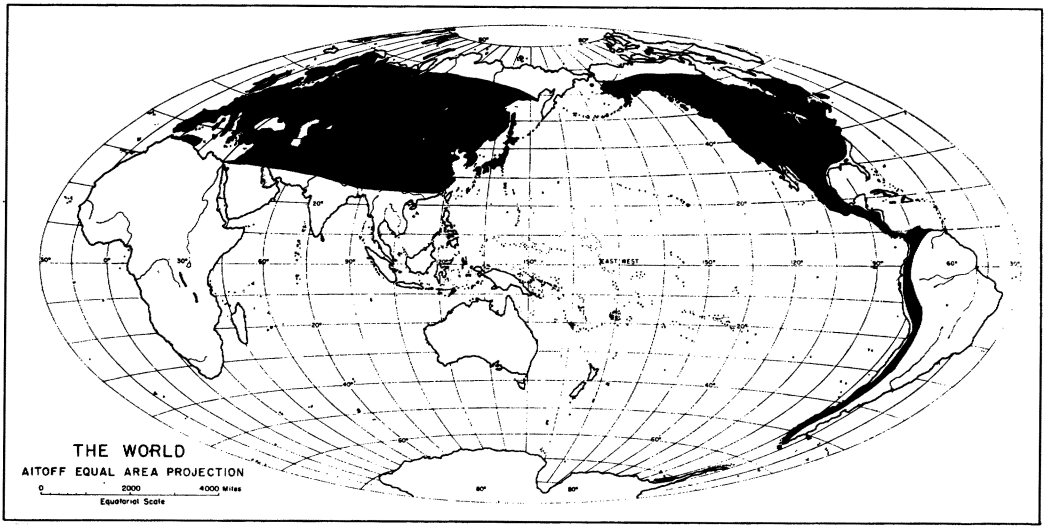

FIG. 7. GREATLY GENERALIZED DISTRIBUTION OF THE NORTH AND SOUTH TEMPERATE GENUS *Ribes,* THE CURRANTS AND GOOSEBERRIES OF THE SAXIFRAGACEAE

Modified from Hutchinson (1959); base map as in Fig. 1.

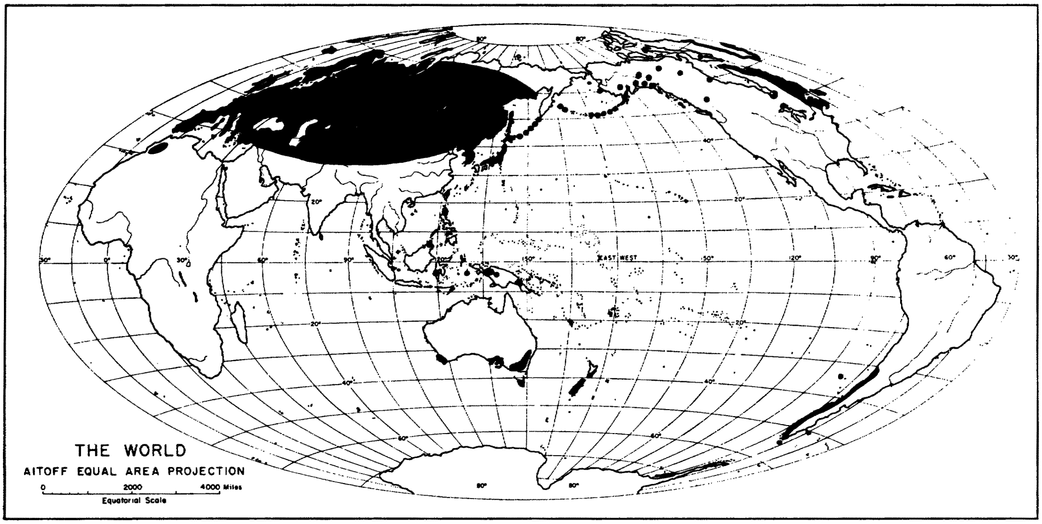

FIG. 8. GENERALIZED DISTRIBUTION OF THE NORTH AND SOUTH TEMPERATE, AND BIPOLAR, GENUS *Euphrasia* OF THE SCROPHULARIACEAE

Modified from Du Reitz (1960) and van Balgooy (1966); base map as in Fig. 1.

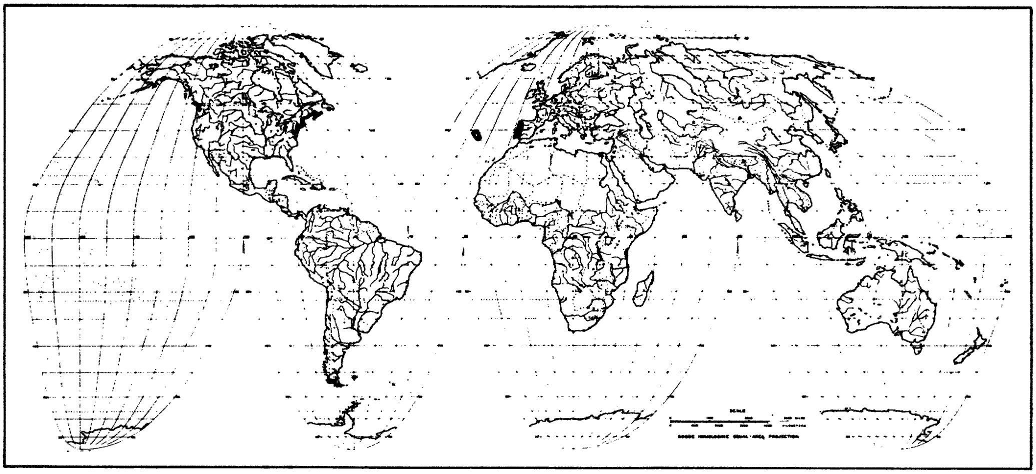

FIG. 9. KNOWN DISTRIBUTION OF THE AMPHI-ATLANTIC TEMPERATE GENUS *Corema*

C. alba occurs on the Azores and the western side of the Iberian Peninsula and *C. conradii* on the North American coast from Newfoundland to New Jersey. Largely after Hultén (1958); base map as in Fig. 2.

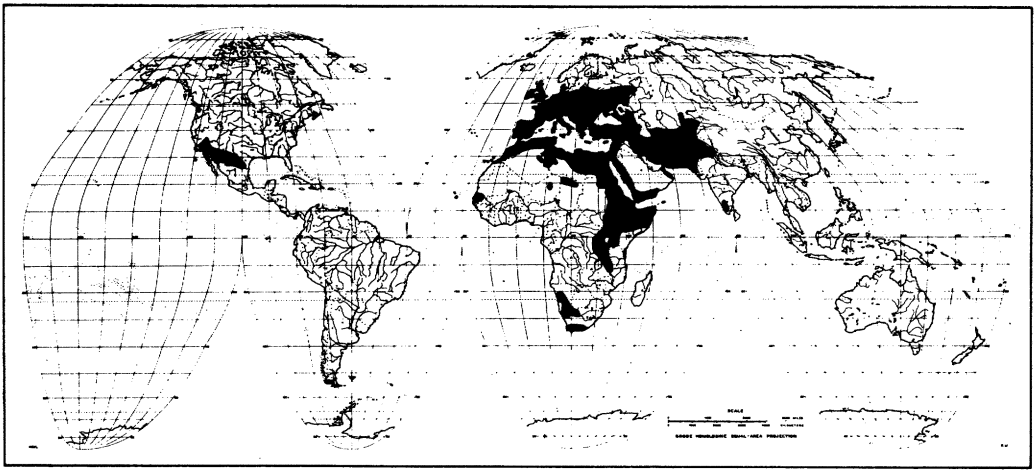

FIG. 10. GENERALIZED DISTRIBUTION OF THE MEDITERRANEAN-AMERICAN FAMILY RESEDACEAE, THE MIGNONETTES

Old World distribution modified from Meusel, Jager, and Winert (1965); base map as in Fig. 2.

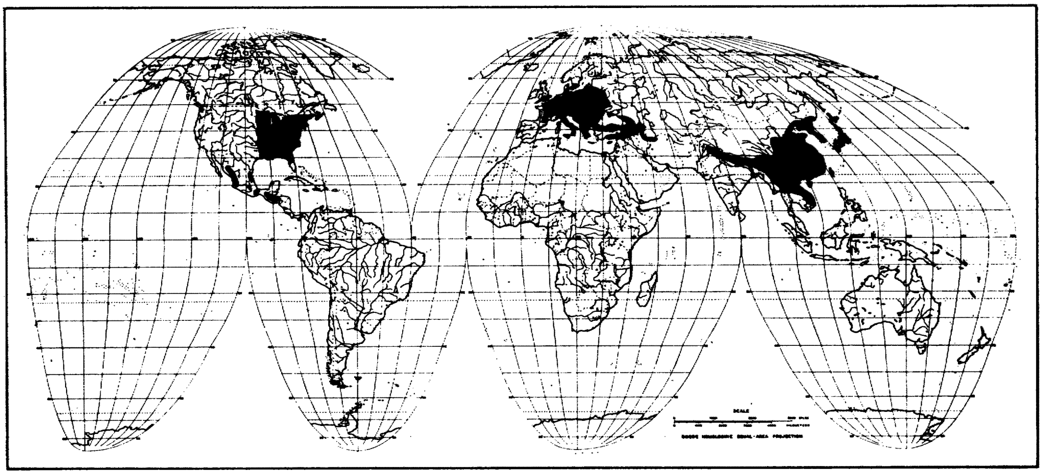

Fig. 11. Generalized Distribution of the Eurasian-Eastern American-Mexican Genus *Carpinus* of the Betulaceae

Old World distribution modified from Meusel, Jager, and Winert (1965); base map as in Fig. 2.

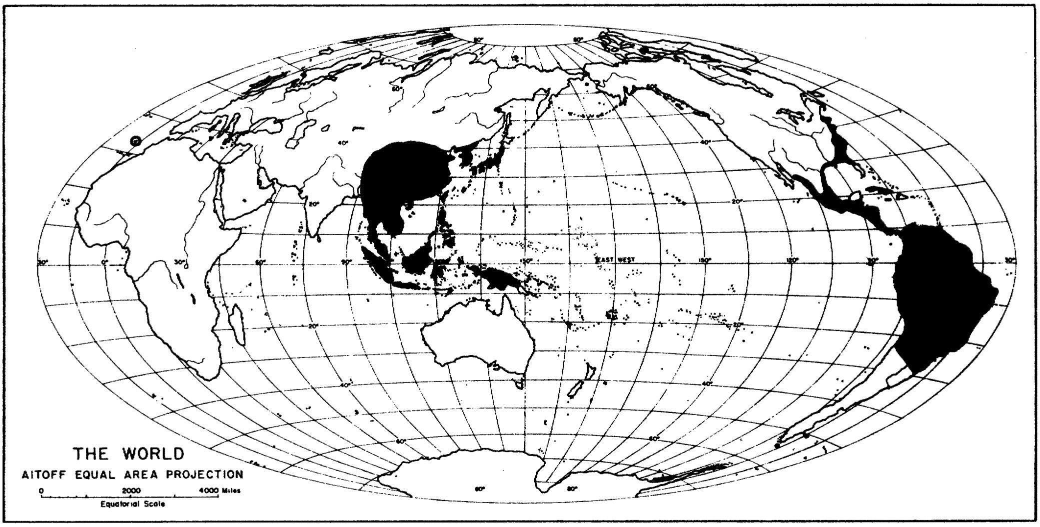

Fig. 12. Generalized Distribution of the Largely Amphi-Pacific Tropical, but in Part Eurasian-Eastern American-Mexican, Genus *Clethra*

Note especially the range of *C. arborea* L. of Madeira. Modified from Good (1964); base map as in Fig. 1.

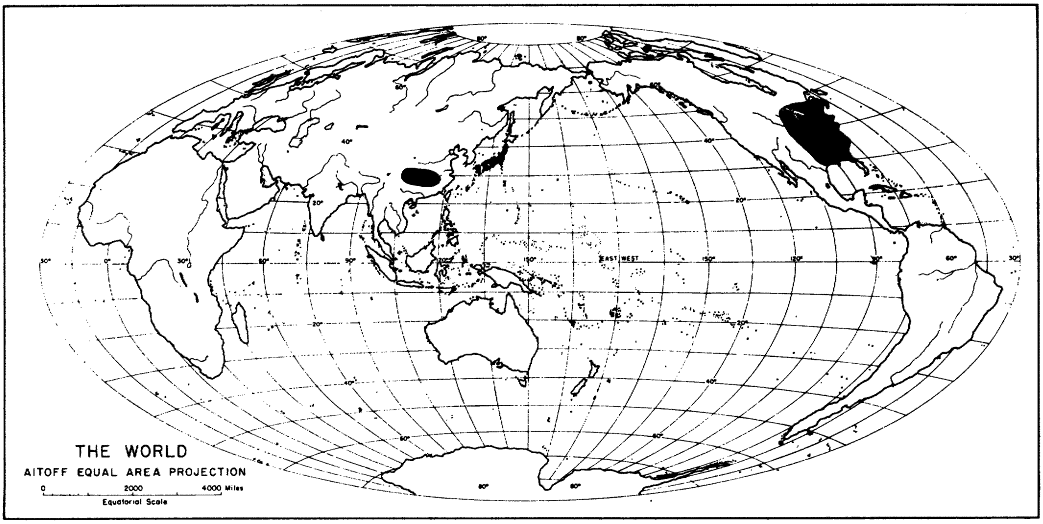

FIG. 13. GENERALIZED DISTRIBUTION OF THE ASIAN-EASTERN AMERICAN GENUS *Hamamelis,* THE WITCH-HAZELS

Based in part on Li (1952); base map as in Fig. 1.

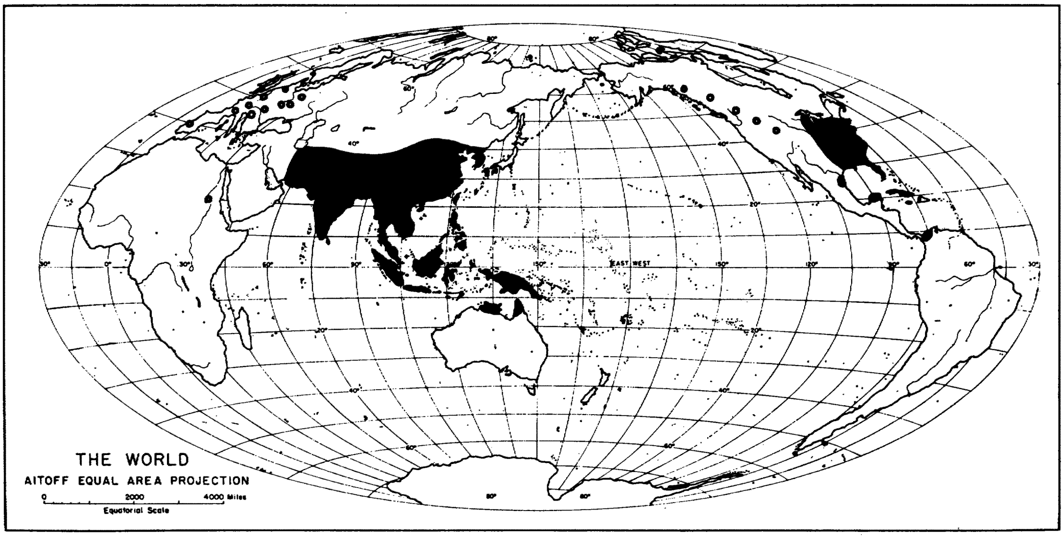

FIG. 14. PAST AND PRESENT KNOWN DISTRIBUTION OF THE ASIAN-EASTERN AMERICAN, OR PERHAPS BETTER AMPHI-PACIFIC TROPICAL, GENUS *Nelumbo,* WATER-LOTUS

Modified from Good (1964); base map as in Fig. 1. The black circles represent fossil records.

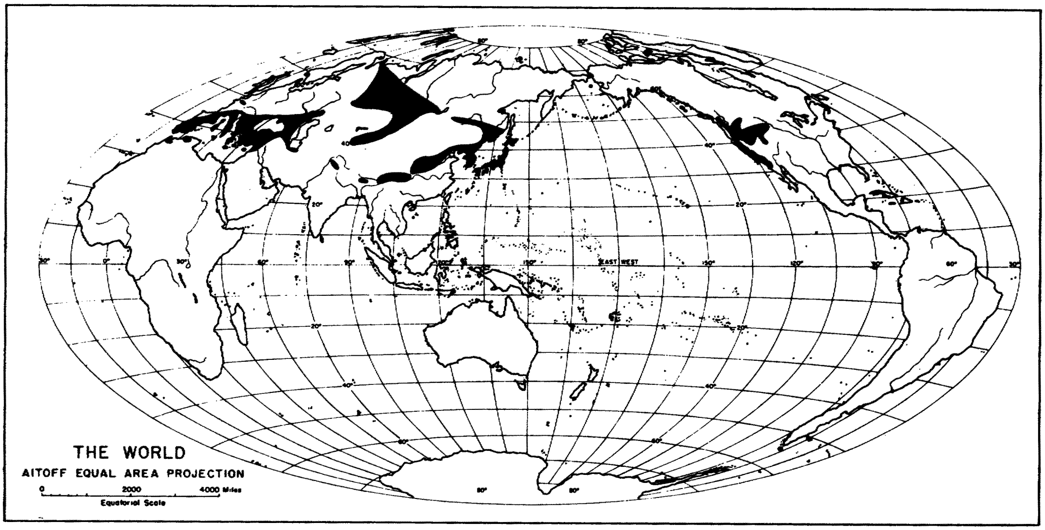

Fig. 15. Generalized Distribution of the Eurasian-Western North American Genus *Paeonia,* the Peonies
Modified from Stern (1946); base map as in Fig. 1.

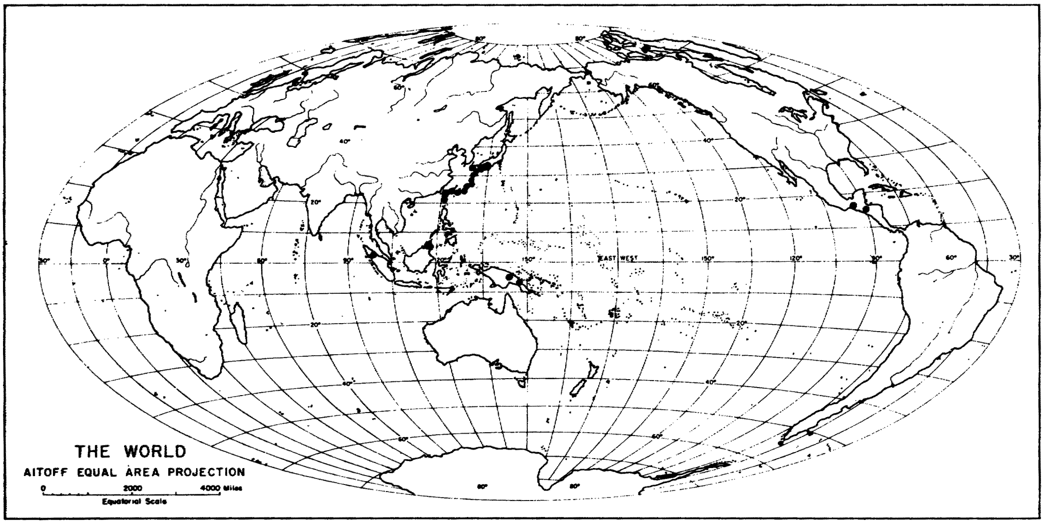

Fig. 16. Distribution of the Asian-Mexican Highland Parasitic Genus *Mitrastemon* of the Rafflesiaceae
Modified from van Balgooy (1966); base map as in Fig. 1.

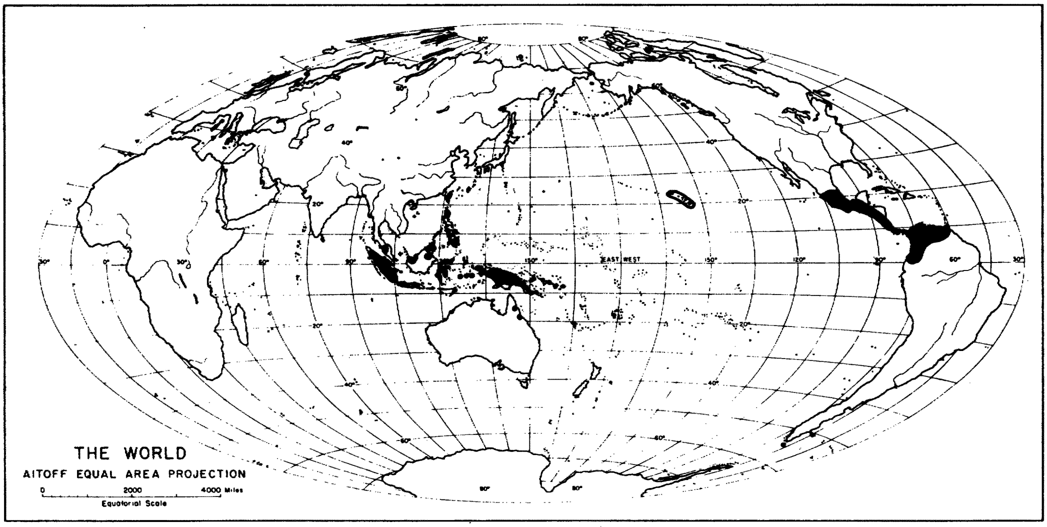

FIG. 17. GENERALIZED DISTRIBUTION OF THE AMPHI-PACIFIC-HAWAIIAN GENUS *Perrottetia* OF THE CELASTRACEAE

Modified from van Balgooy and Hou (1966); base map as in Fig. 1.

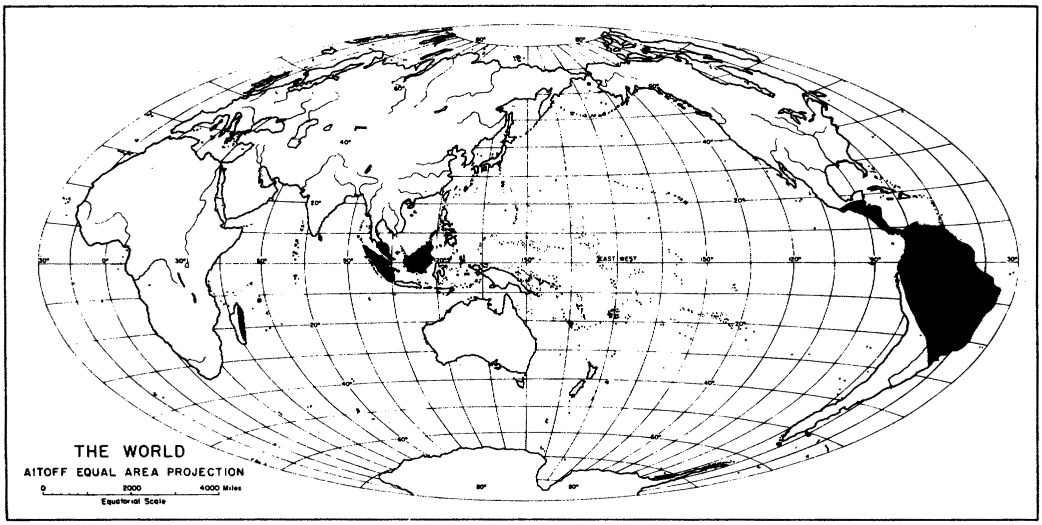

FIG. 18. GENERALIZED DISTRIBUTION OF THE TROPICAL AMPHI-PACIFIC-MADAGASCAN FAMILY TRIGONIACEAE

South American distribution modified from Vester (1940); base map as in Fig. 1.

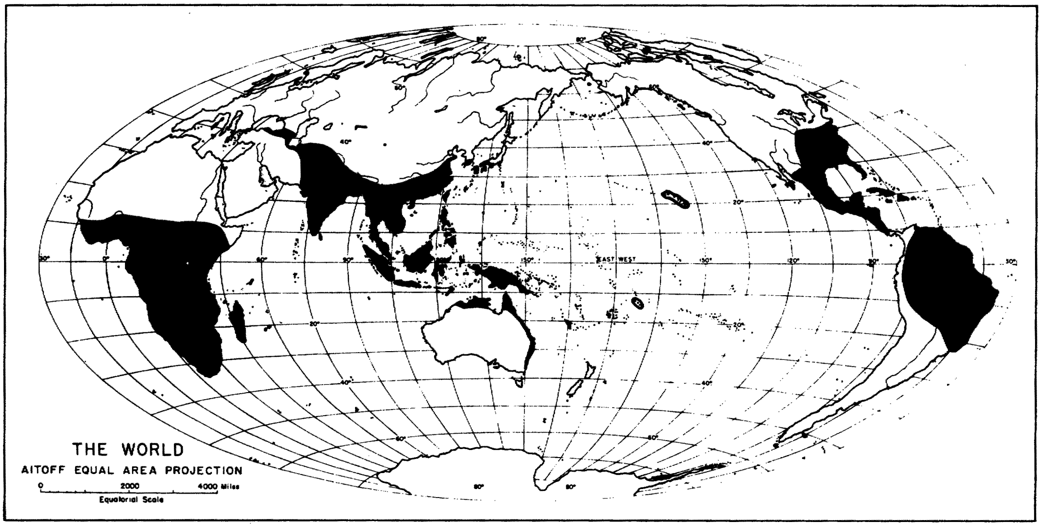

FIG. 19. GENERALIZED DISTRIBUTION OF THE PANTROPICAL GENUS *Diospyros* (S. L.) OF THE EBENACEAE
Much modified from Fernald (1931); base map as in Fig. 1.

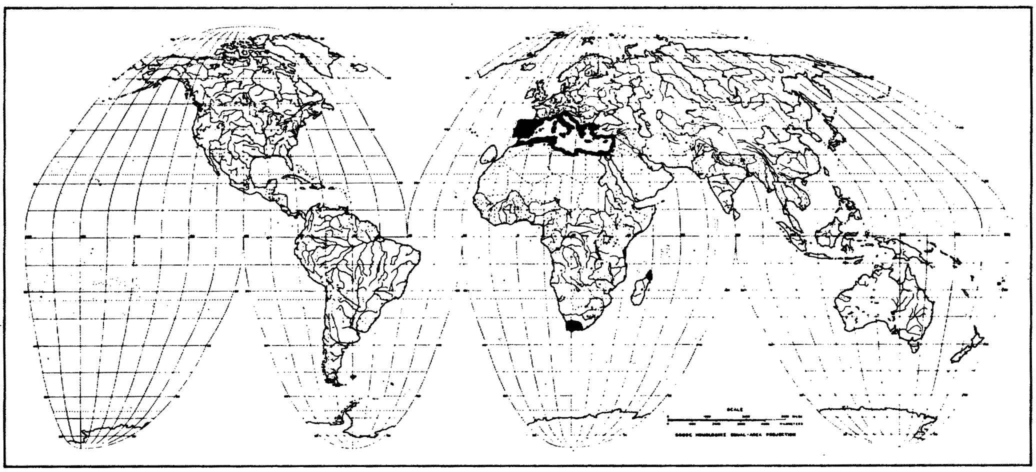

FIG. 20. GENERALIZED DISTRIBUTION OF THE AFRICAN-MEDITERRANEAN GENUS *Cytinus* OF THE PARASITIC RAFFLESIACEAE

Modified from Vester (1940); base map as in Fig. 2.

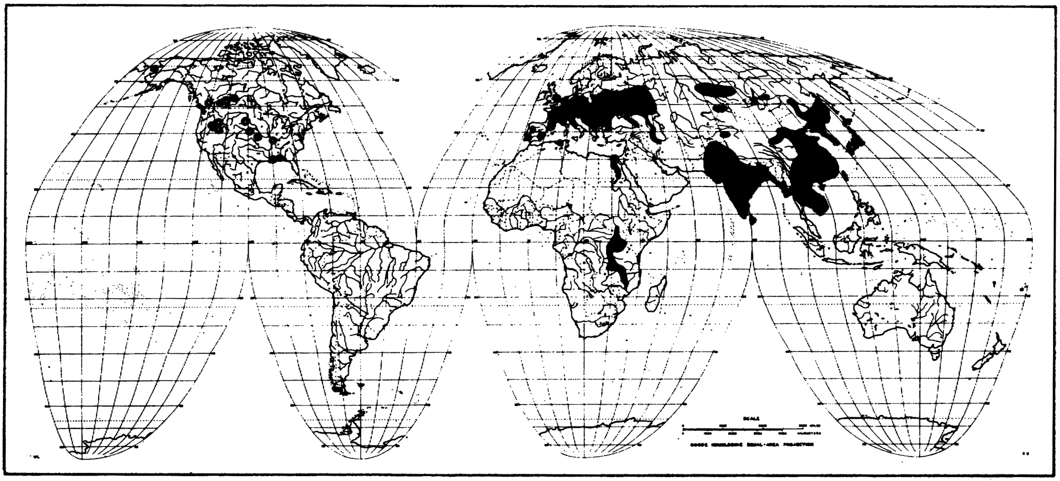

FIG. 21. FOSSIL AND EXTANT NATURAL DISTRIBUTION OF THE PRESENTLY AFRICAN-EURASIAN GENUS *Trapa*, WATER-CHESTNUT

Modified from Gams (1927). The black circles represent fossil records, indicating that the genus was once much more widespread, especially in Europe and North America; base map as in Fig. 2.

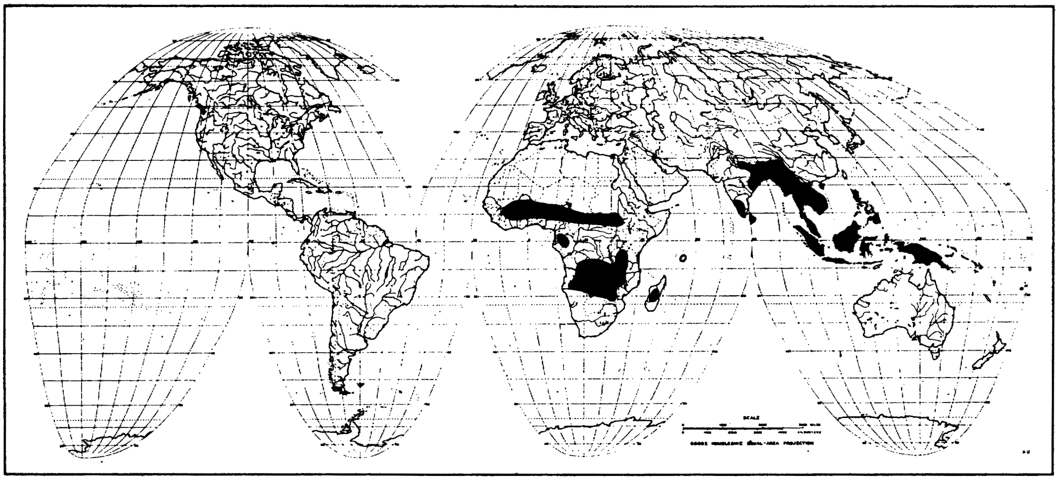

FIG. 22. ORIGINAL GENERALIZED MAP OF THE TROPICAL AFRICAN-ASIAN-MALESIAN FAMILY DIPTEROCARPACEAE

Drawn by Chris Davidson; base map as in Fig. 2.

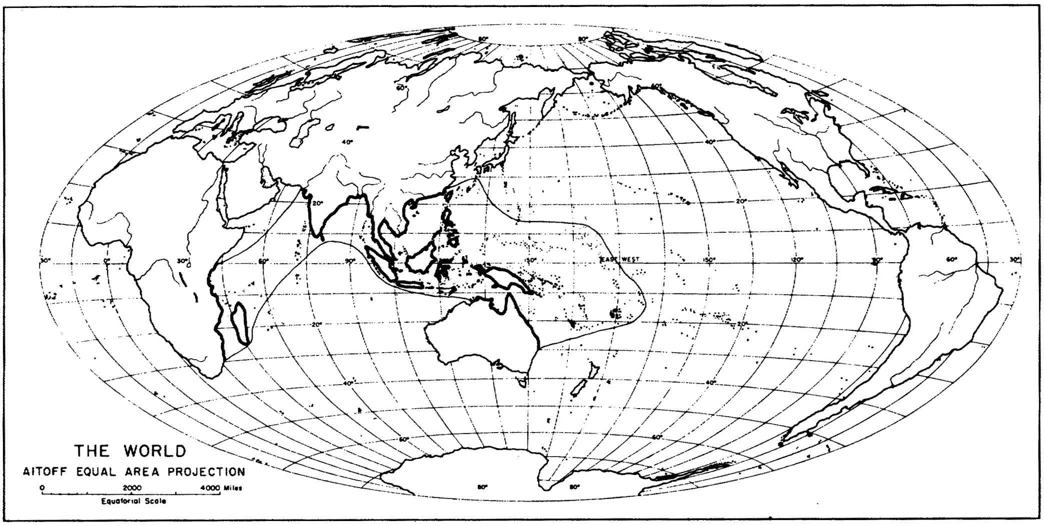

Fig. 23. Generalized Map of the Tropical Coastal African-Asian-Pacific Mangrove Genus *Bruguiera* of the Rhizophoraceae

Modified from Hou and van Steenis (1963); base map as in Fig. 1.

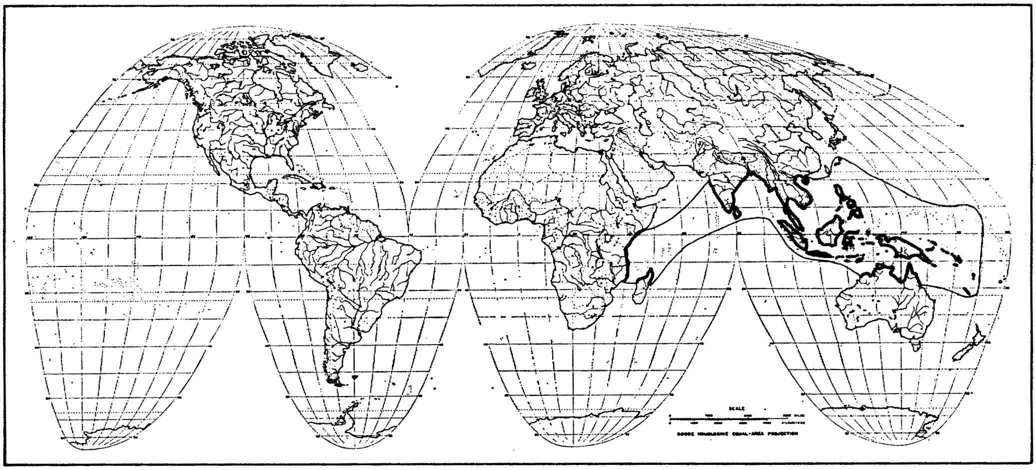

Fig. 24. Generalized Map of the Tropical Coastal African-Asian-Australasian Mangrove Genus *Sonneratia* of the Lythraceae

Modified from van Balgooy (1966); base map as in Fig. 2.

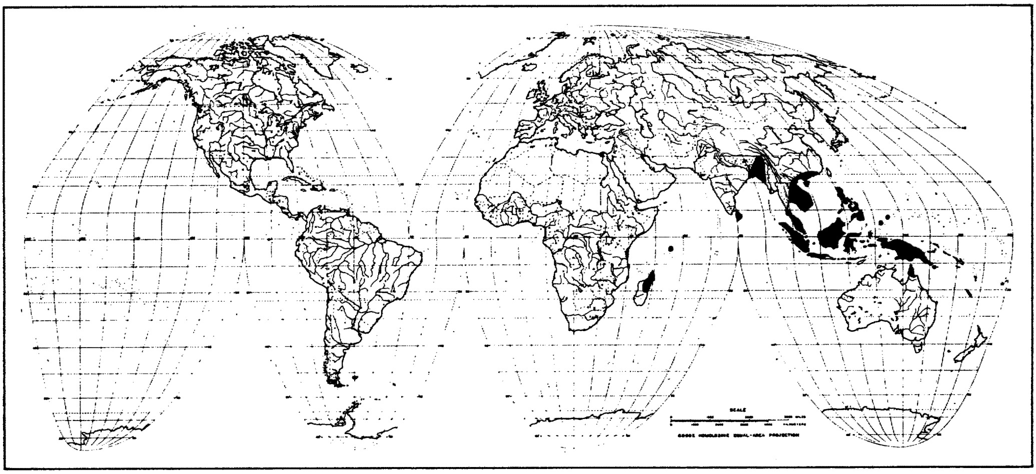

FIG. 25. GENERALIZED DISTRIBUTION OF THE INDIAN OCEAN-ASIAN-AUSTRALASIAN GENUS *Nepenthes,* TROPICAL PITCHER PLANTS

Modified from Good (1964) and van Balgooy (1966); base map as in Fig. 2.

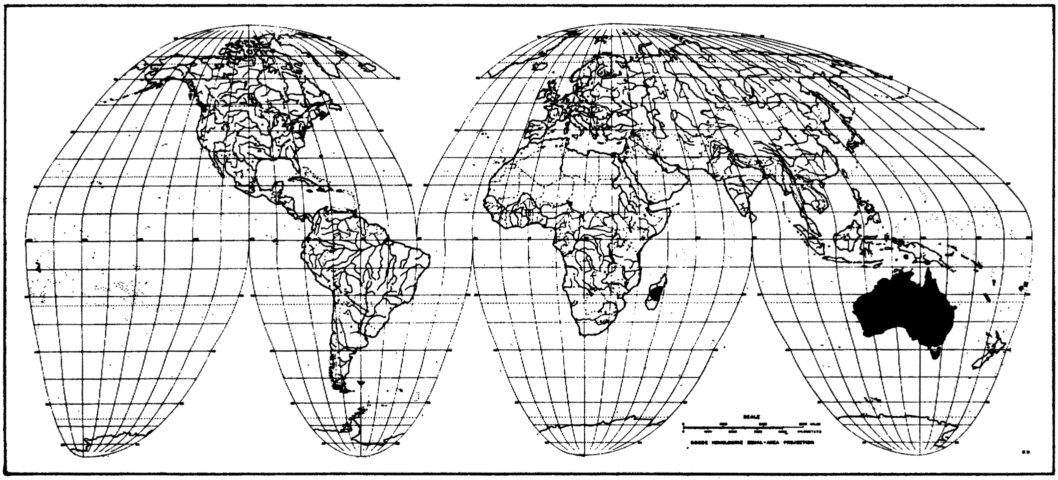

FIG. 26. GENERALIZED DISTRIBUTION OF THE AMPHI-INDIAN OCEAN GENUS *Hibbertia* OF THE DILLENIACEAE

Modified from Good (1964) and van Balgooy (1966); base map as in Fig. 2.

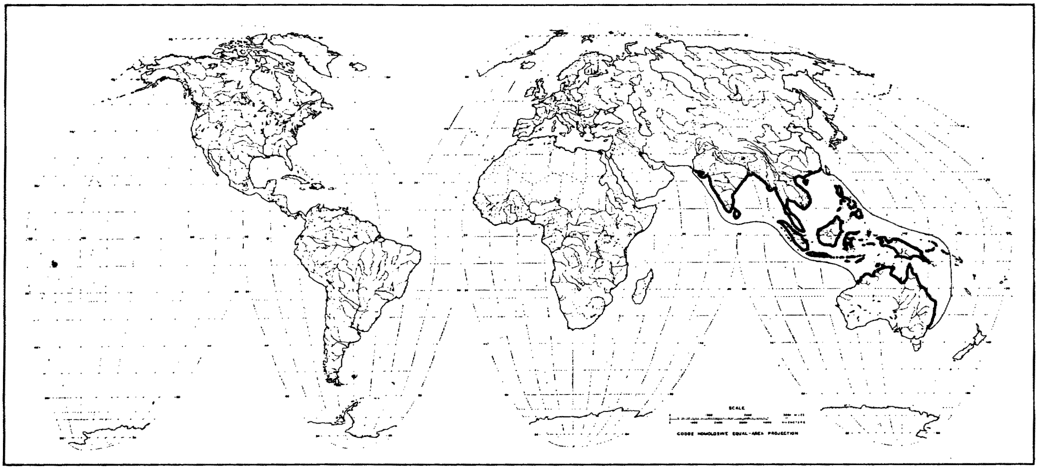

FIG. 27. GENERALIZED DISTRIBUTION OF THE TROPICAL COASTAL ASIAN-PAPUAN-MELANESIAN MANGROVE GENUS *Aegiceras* OF THE MYRSINACEAE

Modified from van Balgooy (1966); base map as in Fig. 2.

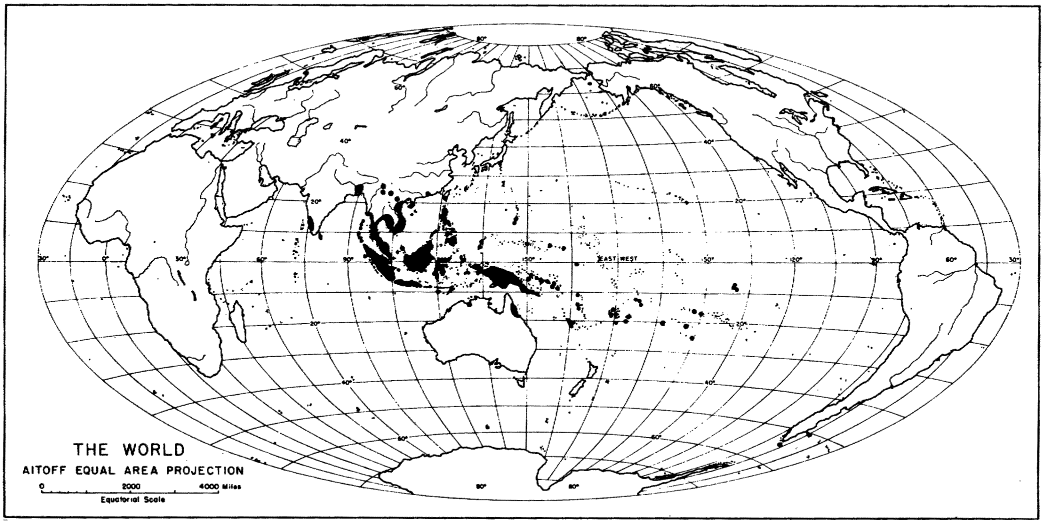

FIG. 28. DISTRIBUTION OF THE TROPICAL ASIAN-PAPUAN-PACIFIC BASIN GENUS *Fagraea* OF THE LOGANIACEAE

Modified from van Balgooy and Leenhouts (1966); base map as in Fig. 1.

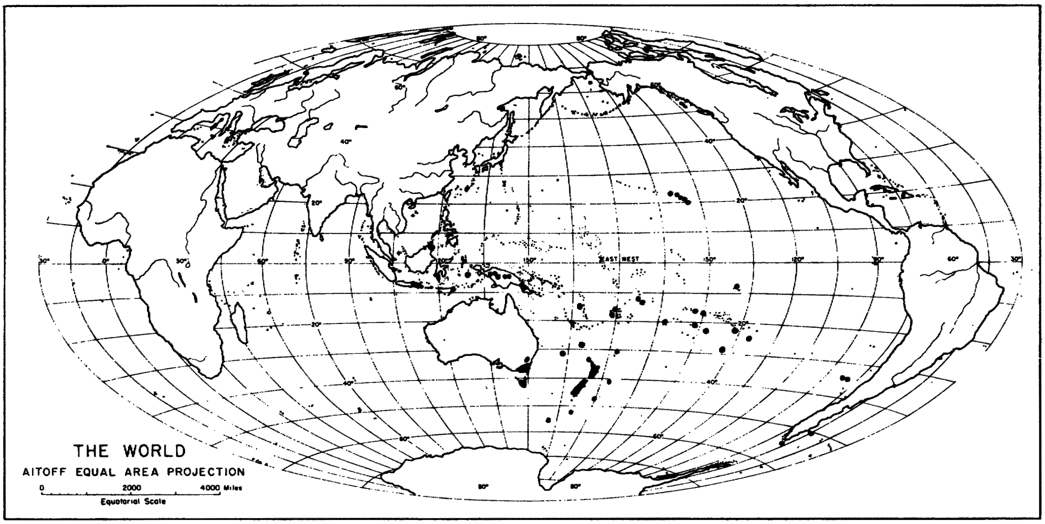

FIG. 29. DISTRIBUTION OF THE TROPICAL PACIFIC OCEAN GENUS *Coprosma* OF THE RUBIACEAE
Modified from van Balgooy (1966); base map as in Fig. 1.

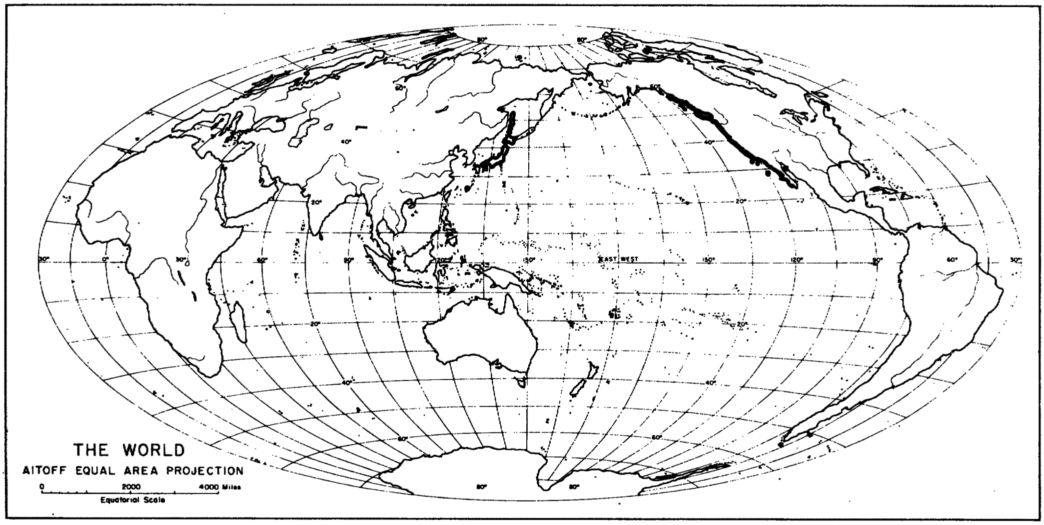

FIG. 30. DISTRIBUTION OF THE NORTH PACIFIC OCEAN GENUS *Phyllospadix*, THE MARITIME SURFWEEDS OF THE ZOSTERACEAE

Much modified from Ostenfeld (1927b) and Hultén (1968); base map as in Fig. 1.

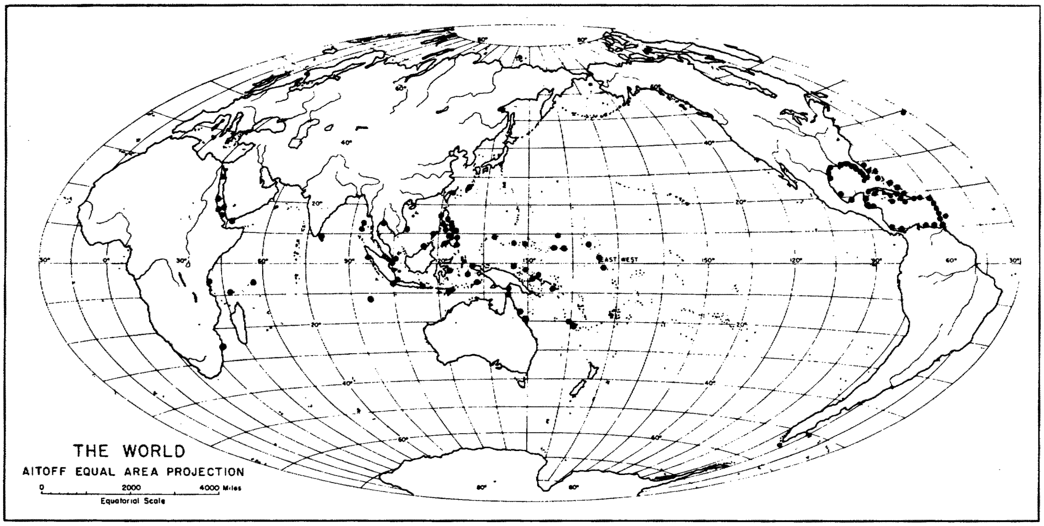

FIG. 31. INTEROCEANIC DISTRIBUTION OF THE SEA-GRASS GENUS *Thalassia,* TURTLE-GRASS OF THE HYDROCHARITACEAE, IN THE INDIAN-PACIFIC-ATLANTIC OCEANS

Based in part on Ostenfeld (1927a) and den Hartog (1966); base map as in Fig. 1.

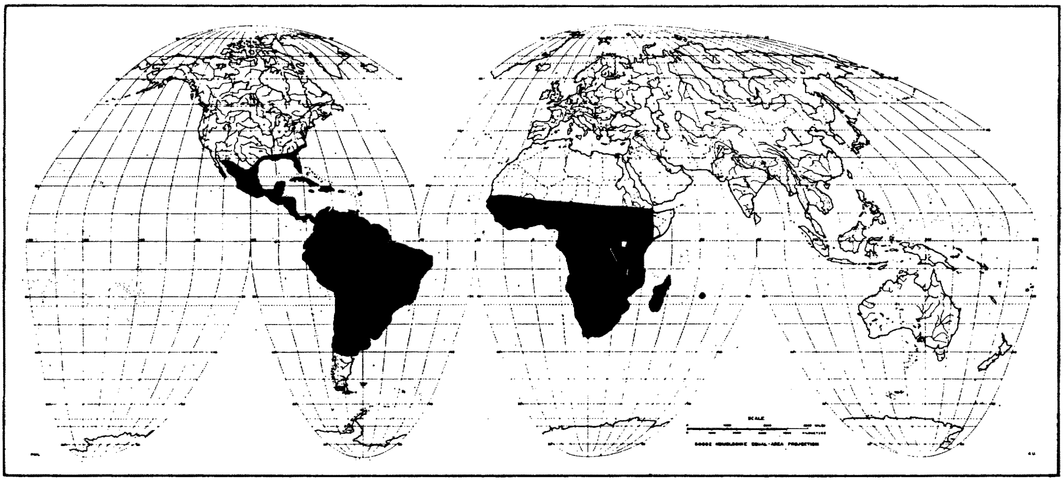

FIG. 32. HIGHLY GENERALIZED DISTRIBUTION OF THE AMERICAN-AFRICAN FAMILY TURNERACEAE

Modified from Vester (1940); base map as in Fig. 2.

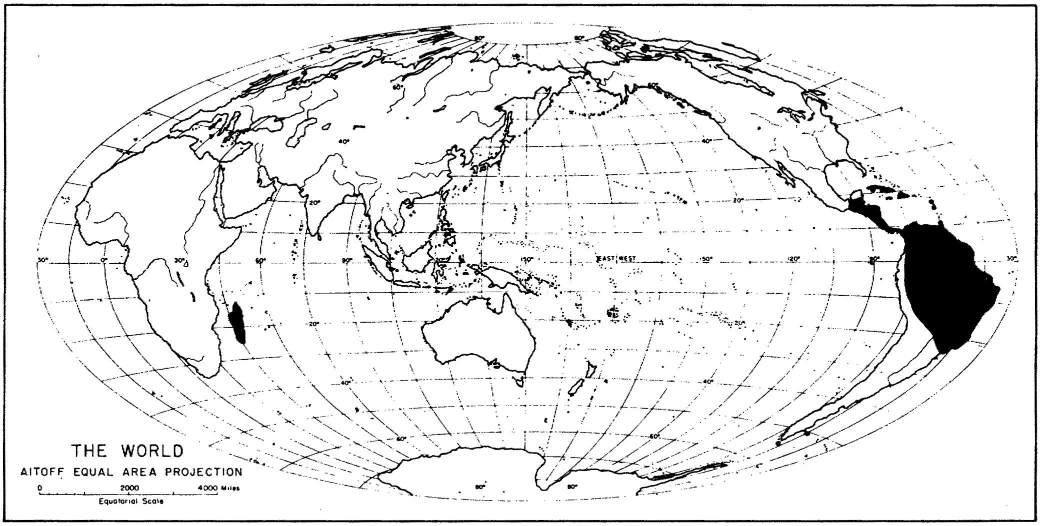

FIG. 33. GENERALIZED DISTRIBUTION OF THE AMERICAN-MADAGASCAN GENUS *Rheedia* OF THE HYPERICACEAE

Base map as in Fig. 1.

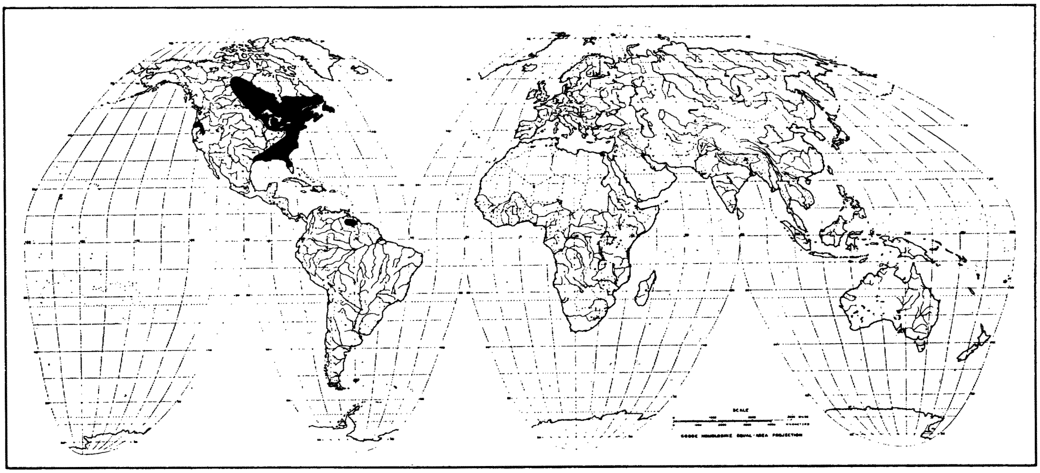

FIG. 34. GENERALIZED DISTRIBUTION OF THE NORTH AMERICAN-SOUTH AMERICAN FAMILY SARRACENIACEAE, PITCHER PLANTS

Sarracenia occurs in eastern North America, *Heliamphora* in the Guyana Highlands, and *Darlingtonia* in California-Oregon; base map as in Fig. 2.

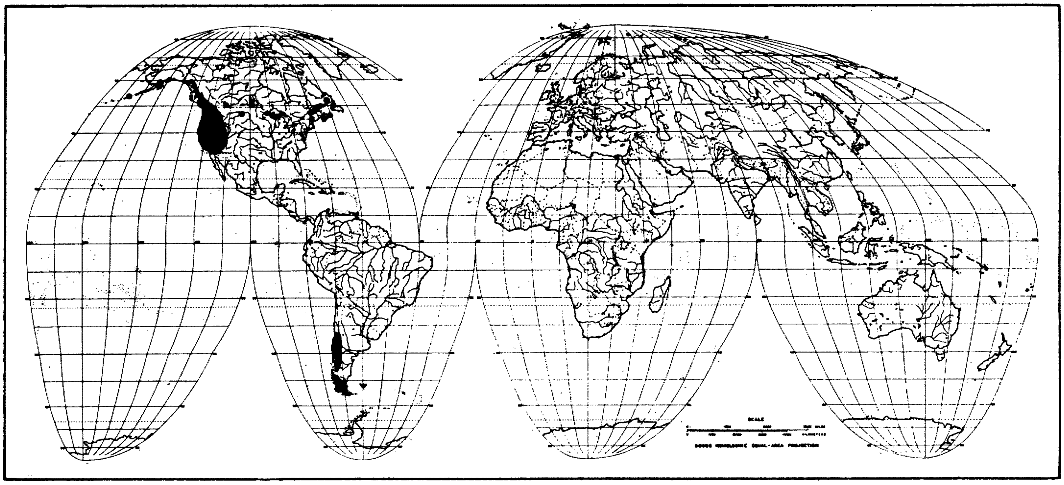

FIG. 35. DISTRIBUTION OF THE TEMPERATE NORTH AMERICAN-SOUTH AMERICAN APIOID SPECIES *Osmorhiza chilensis* OF THE ARALIACEAE

Modified from Constance (1963) and Hultén (1968); base map as in Fig. 2.

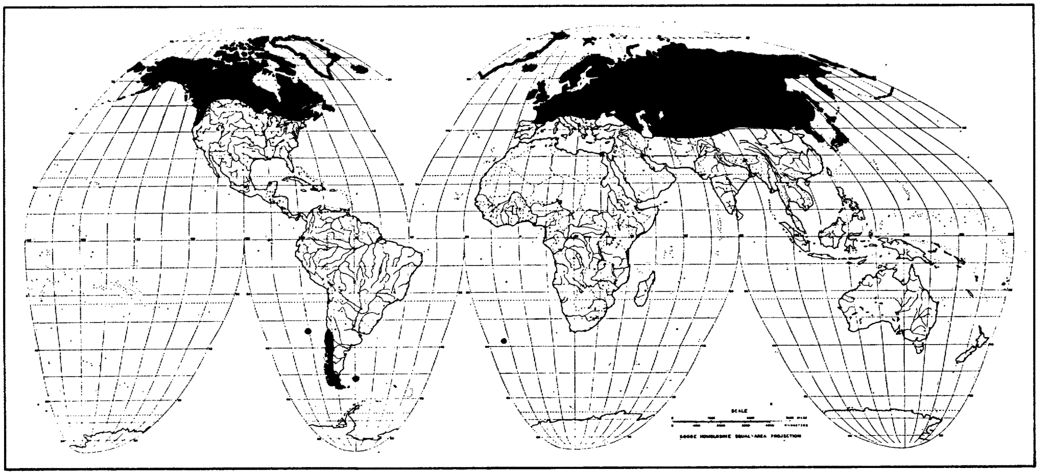

FIG. 36. MUCH GENERALIZED DISTRIBUTION OF THE CIRCUM-ARCTIC, CIRCUM-BOREAL, AND BIPOLAR GENUS *Empetrum,* THE CROWBERRIES

Based largely upon Good (1964); base map as in Fig. 2.

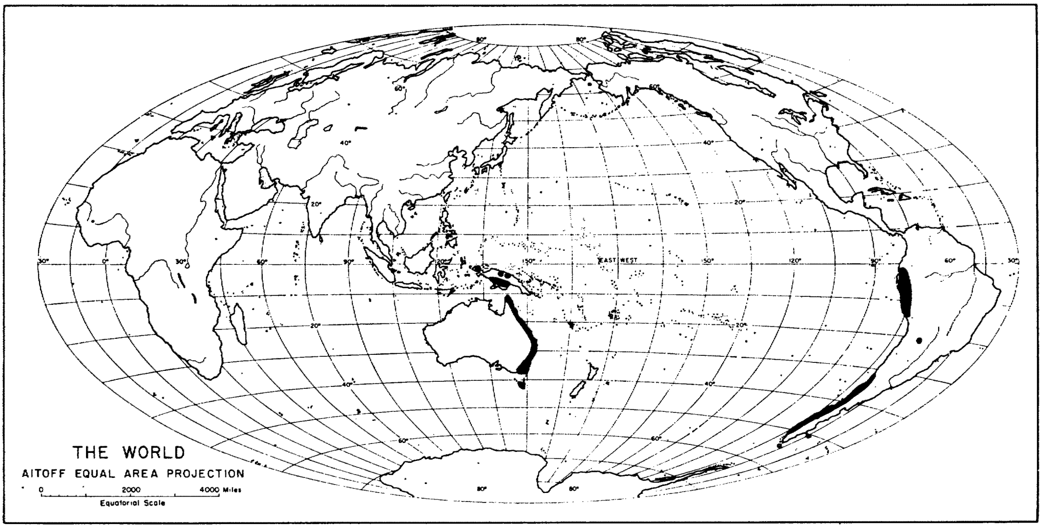

FIG. 37. GENERALIZED MAP OF THE COMBINED RANGES OF THE FOUR SOUTH AMERICAN-AUSTRALASIAN GREVILLEOID GENERA *Gevuina, Lomatia, Oreocallis,* AND *Orites* OF THE PROTEACEAE

Modified from Sleumer (1955), Burbidge (1960), and van Balgooy (1966); base map as in Fig. 1.

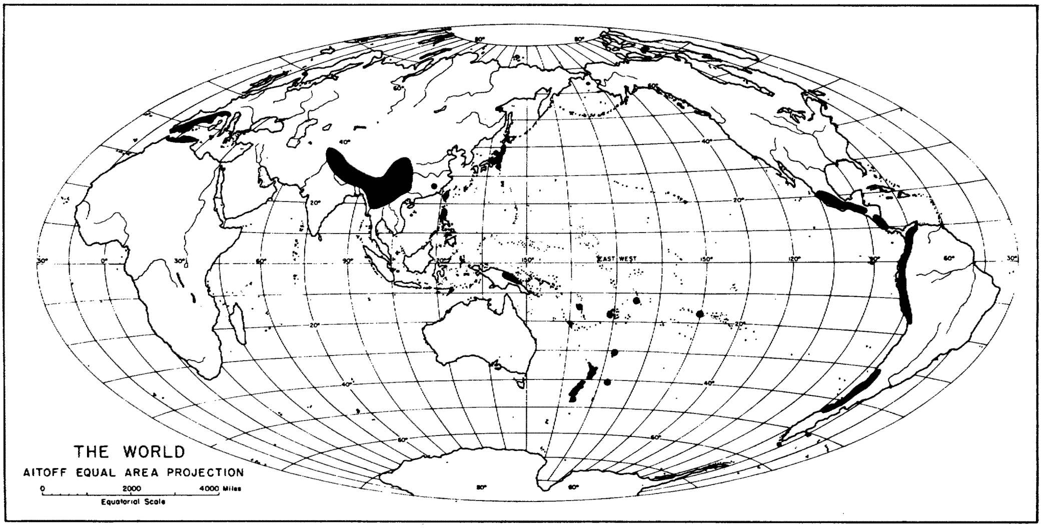

FIG. 38. GENERALIZED DISTRIBUTION OF THE SOUTH AMERICAN-AUSTRALASIAN-EURASIAN GENUS *Coriaria*

Modified from Good (1964) and van Balgooy (1966); base map as in Fig. 1.

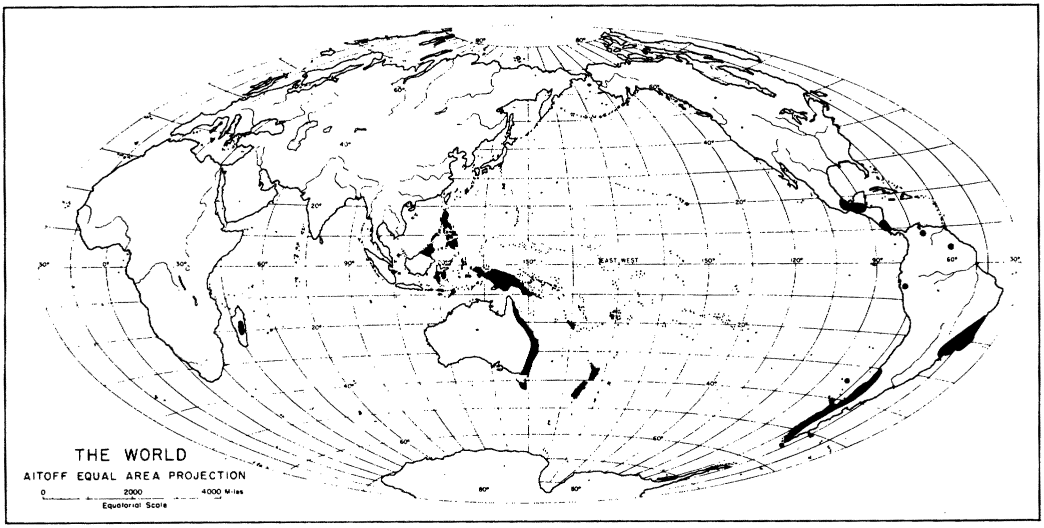

FIG. 39. DISTRIBUTION OF THE AMERICAN-AUSTRALASIAN-MADAGASCAN FAMILY WINTERACEAE

Modified from Smith (1943a, b); base map as in Fig. 1.

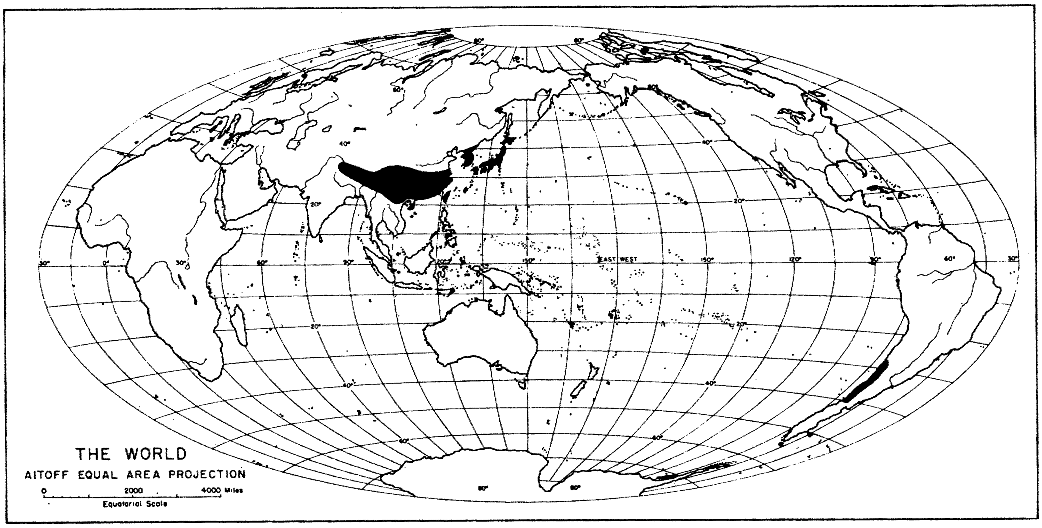

FIG. 40. GENERALIZED DISTRIBUTION OF THE SOUTH AMERICAN-ASIAN FAMILY LARDIZABALACEAE

The two genera *Boquila* and *Lardizabala* occur in central Chile and five others in eastern Asia. Modified from Hutchinson (1959); base map as in Fig. 1.

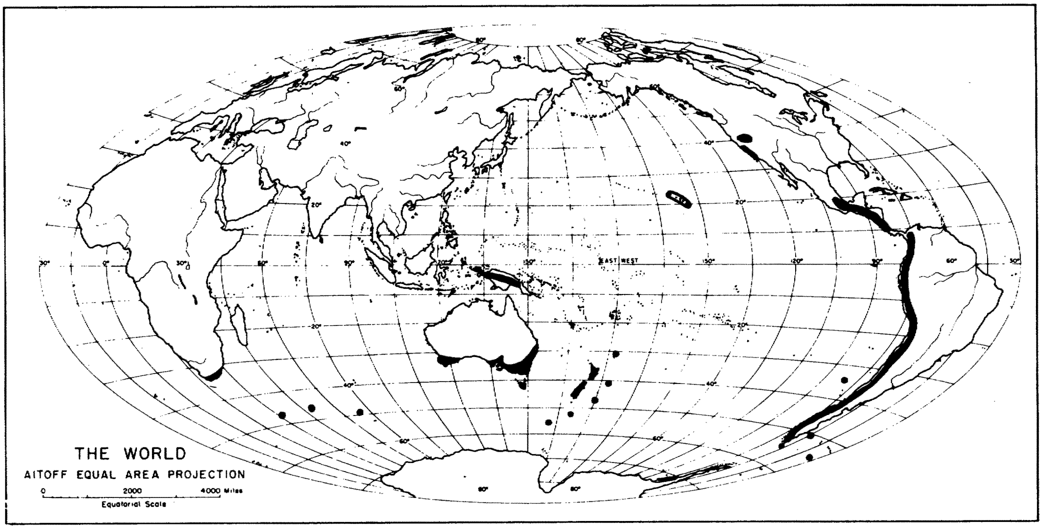

FIG. 41. GENERALIZED DISTRIBUTION OF THE LARGELY CIRCUM-SOUTH TEMPERATE (BUT ALSO HAWAIIAN, CALIFORNIAN, AND CIRCUM-ANTARCTIC) GENUS *Acaena* OF THE ROSACEAE

Base map as in Fig. 1.

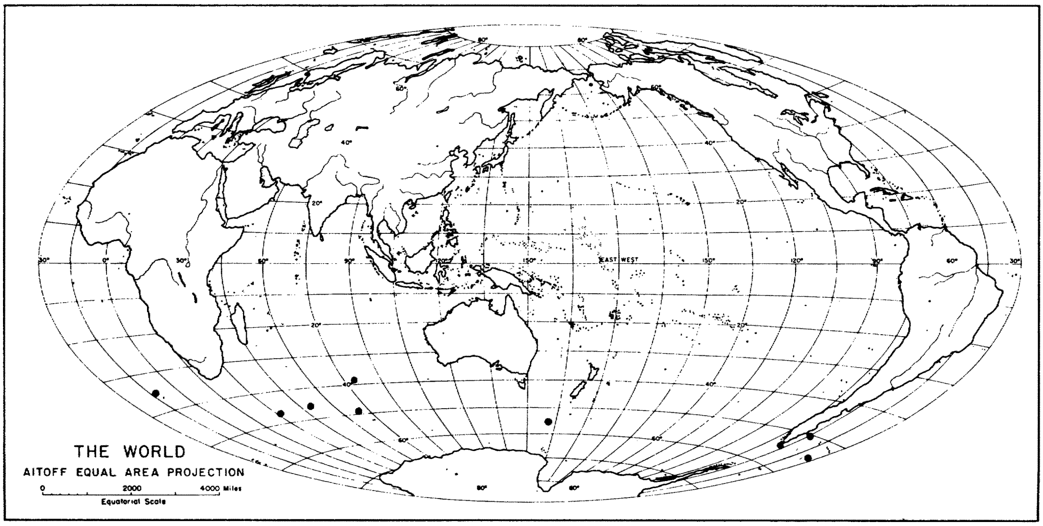

FIG. 42. DISTRIBUTION OF THE CIRCUM-ANTARCTIC SPECIES *Ranunculus biternatus*

Base map as in Fig. 1.

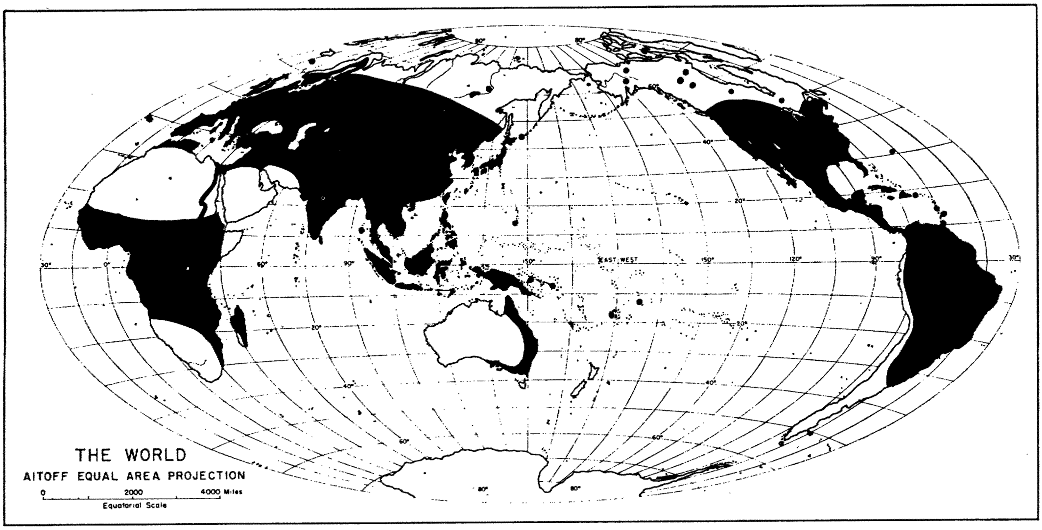

FIG. 43. MUCH GENERALIZED DISTRIBUTION OF THE SUBCOSMOPOLITAN AQUATIC SPECIES *Ceratophyllum demersum*

Modified in part from Hultén (1968); base map as in Fig. 1.

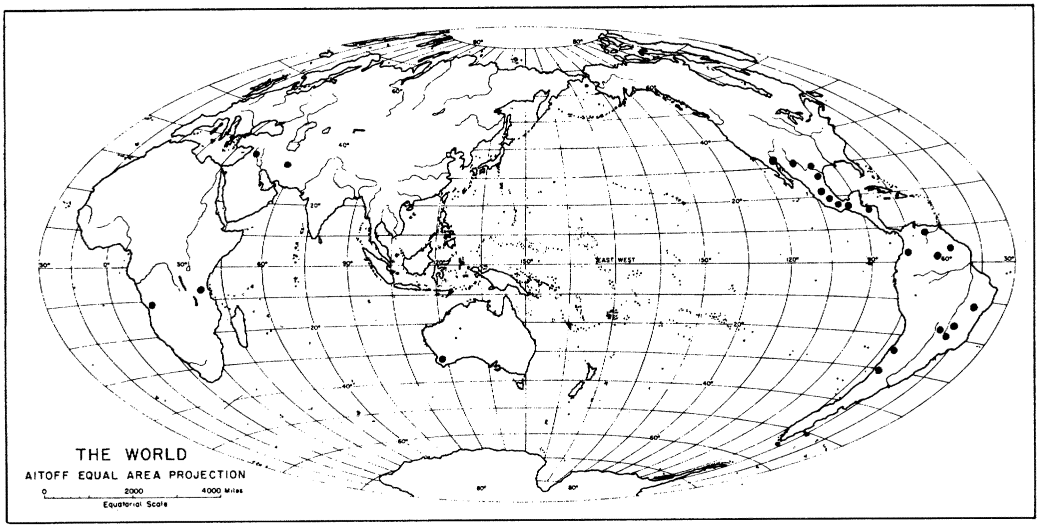

FIG. 44. ANOMALOUS DISTRIBUTION OF THE INTERNAL STEM PARASITE *Pilostyles* OF THE RAFFLESIACEAE

Based in part upon a map supplied by R. Rutherford, Kent State University, Ohio.

IV. *African-Eurasian (-Pacific)*

An analysis of Willis' *Dictionary* (1966) produced 555 currently accepted genera that range from mainland Africa to Eurasia or beyond. They are readily divisible into six subcategories.

1. *African-Mediterranean.*

Only about 9 genera are restricted essentially to Africa south of the Sahara and to the Mediterranean region, a few extending north into Europe or east into the Orient. These are *Althenia, Capnophyllum, Coris, Cytinus* (Fig. 20), *Desmazeria, Erica, Hyacinthus, Romulea,* and *Tolpis.*

2. *African-Eurasian.*

Thirty-eight genera, including such well-known plants as *Adenium, Aeonium, Aloë, Catha, Cotyledon, Huernia, Hyphaene, Fissenia,* and *Sanseverinia,* and the family Barbeyaceae, extend from Africa only to Arabia. At least 200 genera and 3 families, Trapaceae (Fig. 21), Tamaricaceae, and Moringaceae, reach farther into Asia, usually at least to India, but do not extend into Malesia. These include *Balanites, Borassus, Boswellia, Cicer, Commiphora, Gladiolus, Moringa, Ochna, Pedalium, Phoenix, Salvadora, Scilla, Sesamum, Tamarindus,* and *Trapa* (Fig. 21).

3. *African-Eurasian-Malesian.*

Another 106 genera have representatives in Malesia, which here is defined to include all the island groups from Malaya to the New Hebrides. A few of these are *Angraecum, Asparagus, Azima, Cnestis, Combretodendron, Ellepanthus, Ensete, Irvingia, Phrynium, Pothos, Quisqualis, Sauromatium, Stromboisia,* and *Wrightia.* Six families have a similar disrupted range: Ancistrocladaceae, Ctenolophonaceae, Dipsacaceae, Dipterocarpaceae (Fig. 22), Pandaceae, and Salvadoraceae.

4. *African-Eurasian-Pacific.*

Another 100 discontinuous genera have representatives also in Fiji, Tonga, Samoa, or more distant islands in the Pacific Basin, as *Alangium, Barringtonia, Bruguiera* (Fig. 23), *Canarium, Cerbera, Claoxylon, Elatostema, Flagellaria, Gardenia, Grewia, Jasminum, Korthalsella, Leea, Lumnitzera, Myristica, Olea, Pandanus, Pittosporum, Premna, Syzygium, Taeniophyllum, Xylocarpus,* and *Zeuxine.* Six families extend disjunctly from Africa to Fiji or the Pacific Basin: Alangiaceae, Casuarinaceae, Cycadaceae, Flagellariaceae, Pandanaceae, and Pittosporaceae.

5. *African-Eurasian-Australasian.*

Ninety-six additional genera extend south into Australasia, some with representatives on New Caledonia (*Acanthus, Acridocarpus, Aponogeton, Ceriops, Olax, Sonneratia* (Fig. 24), and *Tristellateia*) or New Zealand (*Gastrodia, Glossostigma, Iphigenia, Pelargonium,* and *Sebaea*). Actually 205 of the 555 African-Eurasian-Pacific disjunct genera have representatives on the continent of Australia, although many were included in other totals above because they extend farther east into the Pacific.

6. *Indian Ocean-Eurasian (-Pacific).*

Forty-seven genera that do not reach mainland Africa do have discontinuous ranges from Madagascar, the Mascarene, Comoro, or Seychelle Islands to Eurasia, mostly to southeastern and eastern Asia and to Malesia, and often to Australia or the oceanic islands of the Pacific Basin. Some of the better known of these genera are *Allantospermum, Alyxia, Balanophora, Carallia, Deeringia, Dillenia, Elaeocarpus, Erythrospermum, Foetidia, Geniostoma, Haloragis, Hedychium, Hiptage, Myoporum, Nepenthes* (Fig. 25), *Ochrosia, Pipturus, Sandoricum, Timonius,* and *Vateria.* When added to the mainland African-Eurasian (-Pacific) disjunct genera, slightly more than 600 genera share this common pattern of disjunction.

In view of the relatively large number of discontinuous families and genera reaching Eurasia and beyond from Africa and adjoining islands, one must seek an explanation other than long-range dispersal to account for this very common type of disjunction. Some of the maritime, aquatic, and fleshy-fruited taxa on islands most likely are dispersed over large distances by sea currents and birds. However, many of the wide-ranging taxa have probably migrated over land or over small water gaps by normal methods of short-distance dispersal at a time when much of northern Africa, Arabia, and southern Asia were much moister than they are at present. In addition, there may have been much more land between the continental Seychelle Islands and Ceylon and India in the past, over which some of the taxa might have migrated. The usual Gondwanaland, continental-drift, tectonic-plate movement, and similar explanations have little if any bearing here because such geological phenomena must have taken place, if ever, long before even these relict distributions were initiated.

V. Amphi-Indian Ocean

Very few taxa are restricted just to Africa and Australasia, thus disjunct across the Indian Ocean. Only 18 genera apparently are so discontinuous between mainland Africa and Australasia, mostly Australia, with another 11 having representation in Australasia and only Madagascar, the Mascarene, or the Seychelle Islands. This total is likely to be reduced as species are found to be naturalized in one area or the other or as careful revisions show the representation on either side of the Indian Ocean to be generically distinct or to belong to larger, wider-ranging genera. This rather rare type of major discontinuity directly contradicts the rather loose speculation of some authors that there is a close relationship between the floras of Australia and Africa. Inasmuch as 15 of the 29 genera have Madagascan, Mascarene, or Seychelle representatives and 13 have insular populations east of the Indian Ocean other than those in Australia-Tasmania, long-distance dispersal would seem to be the logical explanation for these disjuncts. *Adansonia, Anacampseros, Chrysithrix, Dietes,* and *Triraphis* are primarily African or Madagascan; whereas *Arthropodium, Bubbia, Caesia, Cassinia, Cunonia, Helipterum, Hibbertia* (Fig. 26), *Humea, Keraudrenia, Macadamia, Rulingia, Soulamea,* and *Villarsia* are primarily Australian, Papuan, or New Caledonian. Other genera are more evenly divided (*Australina, Brachyachne, Bulbinella, Costularia, Entolasia, Grammatotheca, Potamophila, and Wurmbea*), or are primarily oceanic (*Astelia, Cohnia, and Cossinia*).

VI. Asian-Pacific

Another large discontinuous category, but one somewhat less wide-ranging usually than the African-Asian (-Pacific) type of distribution, is represented by about 460 genera and five families. These taxa have species in mainland Asia and others in eastern Malesia to the Bismarcks, in the Solomons, in the New Hebrides, in Fiji-Tonga-Samoa, or on more distant islands in the Pacific Basin. These disjuncts are best treated in four subcategories.

1. *Asian-Papuan.*

Nearly 200 genera range from Asia to New Guinea or the Bismarck Archipelago: *Anisoptera, Hopea, Ixonanthes, Kadsura, Lithocarpus, Pentaphragma, Ploiarum, Pometia, Sarcandra, Shorea, Sycopsis, Tetrameles, Walsura,* and *Zanonia* among other genera, and the two families Crypteroniaceae and Pentaphragmataceae.

2. *Asian-Papuan-Melanesian.*

Another 130 genera reach beyond the Bismarcks to the Solomon Islands (46), the Santa Cruz and New Hebrides Islands (15), Fiji (29), Tonga (19), or Samoa (21), including *Aegiceras* (Fig. 27), *Ailanthus, Alpinia, Amoora, Artocarpus, Caryota, Dischidia, Dysoxylum, Hanguana, Hoya, Hydnophytum, Koelreuteria, Livistona, Madhuca, Mangifera, Melicope, Metroxylon, Nypa, Palaquium, Semecarpus, Tristania,* and *Xanthophyllum* and the family Daphniphyllaceae.

3. *Asian-Papuan-Pacific Basin.*

Well beyond the Andesite Line in the Pacific Basin, about 40 genera have representation on the islands of Polynesia (many on the distant islands of the Hawaiian chain): e.g., *Alectryon, Alstonia, Berrya, Cyrtandra, Dendrobium, Fagraea* (Fig. 28), *Freycinetia, Gahnia, Melastoma, Planchonella,* and *Wikstroemia.*

4. *Asian-Papuan-Australasian.*

To the south 91 additional genera have ranges terminating in Australia (62), New Caledonia (23), or New Zealand (6), including *Aegialitis, Apostasia, Bassia, Cardiopteris, Curcuma, Helicia, Melaleuca, Neolitsea, Philydrum, Polyosma, Siphonodon, Stemona, Stylidium, Vanda,* and *Zingiber,* and the two families Cardiopteridaceae and Philydraceae. Actually, if one counts those genera (as in Figs. 27 and 28) credited to the Solomons and islands farther east in the Pacific, 194 of the Asian-Pacific disjunct category are believed to have indigenous species in Australia.

For many of these taxa, reaching only to eastern Malesia, Australia, or the other continental islands, normal methods of short-distance dispersal are probably adequate to explain the currently disjunct ranges. It is assumed that in the past, particularly during periods of great tectonic activity and during the glacial lowering of sea-levels, much more land at times connected Malesia to mainland Asia, and Australia to Malesia. For various good biogeographical considerations, short over-water hops may have been necessary for disseminules to reach such presently isolated continental islands as New Caledonia, New Zealand, the Solomons, New Hebrides, Fiji, and Tonga (Thorne, 1965, 1969). Beyond the Andesite Line lie only islands of oceanic, volcanic origin. These must have been reached by disseminules carried over long distances by birds, sea or air currents, or by man, although numerous atolls and guyots, flat-topped sea-mounts, in the western Pacific Basin do indicate that once there were more high islands available there for stepping-stones (Thorne, 1963).

For numerous accurate dot maps of taxa with disjunct ranges in the Pacific area the biogeographer is fortunate to have available the two volumes of *Pacific Plant Areas* edited by van Steenis (1963) and by van Steenis and van Balgooy (1966). Included are 173 maps by various authorities. No less important in the two volumes is the bibliography of distribution maps for seed plant taxa of the Malesian and Pacific areas, the first supplement being prepared by van Steenis-Kruseman (1966). Many additional maps of Malesian taxa are published in the continuing *Flora Malesiana*. The latest, and very useful, work on Pacific plants is a volume by van Balgooy, *Plant-Geography of the Pacific* (1971). Our knowledge of 1666 Pacific genera is here brought up to date, with an appendix of charts listing all the genera and indicating their distribution in the various Pacific island groups and the continents surrounding the Indo-Pacific basins. Distribution types found in the Pacific are discussed, and maps with delineated areas are given as examples of the various types of ranges.

VII. *Pacific Ocean*

Approximately 370 genera and 7 families that reach neither the Asiatic nor the American mainland have discontinuous distributions between at least two Pacific island groups (Australia here being treated as a very large Pacific island). These are truly Pacific taxa. Some have relatively restricted ranges that hardly merit comparison with taxa showing intercontinental disjunctions. Such are the 44 genera disjunct between western Malesia (east to the Moluccas) and eastern Malesia (New Guinea and the Bismarcks); 19 genera between Australia and New Caledonia; 48 between Australia and New Zealand; 5 between Australia and the New Hebrides or Fijis; 16 between New Guinea and New Caledonia (mostly also on intermediate Melanesian islands or in Queensland); one, *Carpodetus*, between New Guinea and New Zealand; 43 between western Malesia or New Guinea and the Fiji, Tonga, or Samoan Islands. Similar western Pacific disjuncts are the Stackhousiaceae and the 5 genera that each represent monogeneric families: *Balanops*, *Byblis*, *Corynocarpus*, *Eupomatia*, and *Galbulimima*. Somewhat wider gaps in range are shown by the 39 genera distributed from western Malesia to Australia (18), to New Caledonia (11), and to New Zealand (10).

More wide-ranging in the Pacific are at least 38 genera that have representation from western Malesia or New Guinea to the Hawaiian or other Polynesian islands (22), including *Ascarina, Astronia, Coprosma* (Fig. 29), *Cyathodes, Faradaya, Lepinia, Neubergia, Olearia, Pseudomorus, Santalum, Tetraplasandra,* and *Trimenia* (Trimeniaceae); from Australia to the Hawaiian or other Polynesian islands (*Nestegis* and *Corokia*); or are disjunct within the Pacific Basin (14): *Apetahia, Charpentiera, Cheirodendron, Crossostylis, Earina, Fitchia, Meryta, Nesoluma, Oparanthus, Pelea, Pelagodoxa, Phyllostegia, Reynoldsia,* and *Sclerotheca.*

Some of the widely distributed genera of the Pacific-Indian Ocean areas discussed under categories IV and V could as well be treated here as a subcategory, Pacific-Indian Ocean disjuncts. At least 14 genera range from the Indian Ocean islands, including Madagascar, to Australia or islands beyond: *Arthropodium, Astelia, Bleekeria, Bubbia, Cohnia, Cossinia, Geniostoma, Hibbertia* (Fig. 26), *Humea, Keraudrenia, Macadamia, Pipturus, Rulingia,* and *Soulamea.*

Because its species are entirely restricted to to the cool, shallow coastal waters of the Pacific Ocean and its tributary seas and gulfs along both the North American and Asiatic continents, *Phyllospadix* (Fig. 30) of the Zosteraceae must be considered a Pacific genus. It could, however, with some justification have been included under Category I as a Eurasian-Western North American (Beringian-Temperate or Amphi-Pacific North Temperate) disjunct. Similarly, the more tropical sea-grasses, *Enhalus* and *Thalassodendron,* of shallow waters of the Indian and western Pacific Oceans belong here in the Pacific-Indian Oceans subcategory of wide disjuncts.

VIII. Pacific-Indian-Atlantic Oceans

Instead of being intercontinental disjuncts separated by the oceans, the taxa of this category are interoceanic disjuncts separated by the continents. By definition, relatively few taxa belong to this group. Most notable are the widely distributed genera of marine phanerogams. *Zostera* (s.l.) forms marine meadows in shallow, cool waters off the coasts of all the continents on either side of the equator to the subarctic or subantarctic. The more tropical *Halodule, Halophila, Syringodium,* and *Thalassia* (Fig. 31) have extraordinarily large and discontinuous ranges in the shallow waters of the Indian Ocean-Red Sea-western Pacific Ocean and the Caribbean Sea and Gulf of Mexico, all extending via the Gulf Stream to Bermuda in the Atlantic. One species of *Halophila* extends south to Brazilian coasts and another has entered the eastern Mediterranean Sea from the Red Sea via the Suez Canal. The eastern Atlantic Ocean seems to be strangely lacking in these genera except for records of *Halodule* from Mauritania, Senegal, and Angola (den Hartog, 1970). *Cymodocea* (s.s.) and *Posidonia,* the sole genus of the Posidoniaceae, have rather different disjunct patterns. Neither is found in tropical American waters, but each has a species that ranges from the Atlantic coasts of North Africa or of the Iberian Peninsula through the Mediterranean Sea and one or more species in Australian waters. *Posidonia* is extratropical, but the more tropical *Cymodocea* ranges widely in the Indian Ocean-Red Sea areas and into the western Pacific as far as the Ryukyu Islands and New Caledonia.

Perhaps the only terrestrial angiosperm possessing a somewhat similar pattern of disjunction is the palm genus *Pritchardia,* assuming that the Cuban genus *Colpothrinax* is indeed congeneric with it. The combined range is Fiji, Tonga, Tuamotus, Hawaii, and Cuba (van Balgooy, 1971), a truly remarkable, if not anomalous, range. Most of the circumtropical strand plants reach continental as well as island shores, hence are technically and just barely excluded from this category.

How the marine phanerogams have achieved their present distribution has long fascinated plant geographers (Ostenfeld, 1915; Setchell, 1920, 1935). The presence of several Caribbean species on the Pacific side of Central America and of the several largely Indo-Pacific genera in the Mediterranean or even along the Atlantic coasts of Africa indicate a relict pattern that must date back to the Tethys Sea of early Tertiary time or at least to pre-Miocene or pre-Pliocene time when the Mediterranean was closed off from the Red Sea (Miocene) and the Central American isthmus was elevated (Pliocene). The fossil record certifies at least Eocene or Upper Cretaceous age for some of the sea-grasses. Den Hartog's suggestion (1970) that the sea-grasses crossed the Atlantic rather than the eastern Pacific has much merit in view of the present distribution of *Halodule, Conocarpus,* other Caribbean-African mangroves and strand plants, and various marine invertebrates. Probably most of the marine phanerogamic genera once had much more extensive and less discontinuous ranges than they have today.

IX. American-African

Since I have in press (Thorne, 1972) a lengthy discussion of this disjunct category, I shall give just a brief summary here. Twelve angiospermous families, most of them largely American, are limited essentially to America and Africa (including Madagascar): Bromeliaceae, Cactaceae, Canellaceae. Caricaceae. Humiriaceae, Hydnoraceae, Loasaceae, Mayacaceae, Rapateaceae, Turneraceae (Fig. 32), Velloziaceae, and Vochysiaceae. Seven subfamilies, including Napoleonoideae of the Lecythidaceae, Siparunoideae of the Monimiaceae, and Strelitzioideae of the Musaceae; 10 tribes and subtribes, including the rafflesiaceous Cytineae and the leguminous Swartzieae; and 111 genera, as *Annona, Barbacenia, Chrysobalanus, Elaeis, Guarea, Hyptis, Menodora, Ocotea, Pitcairnia, Raphia, Sacoglottis, Symphonia,* and *Vismia,* are restricted to America and Africa. In analyzing the "Flora of West Tropical Africa" (Hutchinson and Dalziel, 1927–1936, 1954–1968), I listed 108 species believed to be indigenous just in America and Africa. These, probably recent immigrants from one continent to the other, are almost all aquatic, semi-aquatic, maritime, riparian, or ruderal plants.

The floristic relationships of Africa to Eurasia-Australasia and of America to Eurasia-Australasia are much stronger than those linking Africa and America. The vast number of taxa on the two continents that have been unable to span the Atlantic far outweighs the relatively few amphi-Atlantic taxa. The greatly varying degree of divergence characterizing the American-African disjuncts reflects roughly the varying lengths of time the various taxa have been separated on the two continents. Consequently, only long-distance dispersal is adequate to explain the widely spaced events of immigration across the Atlantic that must have continued throughout the history of the dispersal of seed plants in the southern hemisphere. In view of all these facts, neither continental displacement via the currently popular tectonic-plate movements nor trans-Atlantic land-bridges are realistic explanations for this category of major discontinuities.

Some value might be found in subdividing this category into three subcategories reflecting the distribution of the taxa in America, Africa, and the major island of Madagascar. I have discussed above a good many taxa that are shared with other areas by either the African mainland or by Madagascar, but not by both. Of the 12 families just mentioned, only the Cactaceae, Canellaceae, Hydnoraceae, Turneraceae (Fig. 32), and Velloziaceae have representatives in both Africa and Madagascar as well as in America. None is restricted just to Madagascar and America. However, among the 111 genera three, *Echinolaena, Phenax,* and *Rheedia* (Fig. 33), are apparently restricted to America and Madagascar. *Rheedia,* with perhaps 45 species, has 13 in Madagascar and none reported from Africa. Seventy-one genera are American-African and 37 American-African-Madagascan. Of the latter 37, 24 have more species in Africa than in Madagascar, 7 have a single species in both, 1 has two in each, and only 5 (*Desmanthus, Ocotea, Piriqueta, Savia,* and *Symphonia*) have more species in Madagascar than in Africa; and only *Symphonia,* with 16 species in Madagascar and 1 wide-ranging species in tropical Africa and America, is manifestly a Madagascan genus. One can only speculate on how the American-Madagascan taxa achieved their disjunction. Possibly they migrated across the Pacific and Indian Oceans without involvement of Africa, or perhaps they crossed the Atlantic with subsequent extinction in Africa.

X. *North American-South American*

The taxa discontinuous between North and South America are best considered under several subcategories, depending upon whether their areas are primarily tropical, temperate (amphitropical), or bipolar.

1. *Tropical.*

Possibly 3,000 seed-plant genera are endemic in tropical America (Good, 1964). Surely, a very large percentage of these, not analyzed for this study, are common to North and South America. This is not surprising considering the massively effective land-bridge furnished since Pliocene time by Central America and the diagramatically placed West Indian islands linking Florida to northern South America. In subtropical Florida (Long and Lakela, 1971) alone there are 150 neotropical genera that are disjunct between the southern tip of the peninsula and the Antilles, Mexico, or South America. Of 228 seed-plant families indigenous in South America, all but 27 are represented also in Mexico, and 7 more have reached at least Panama in Central America. Thirteen largely tropical families are restricted to the two continents: Bixaceae, Brunelliaceae, Cabombaceae, Cannaceae, Cyclanthaceae, Cyrillaceae, Krameriaceae, Lennoaceae, Marcgraviaceae, Martyniaceae, Theophrastaceae, Tropaeolaceae (primarily Andean), and Zamiaceae. The North American Garryaceae and South American Quiinaceae both reach the Greater Antilles and Middle America; and 8 of the 12 American-African tropical families reach Mexico, at least, and most of them reach Florida or farther north in North America. The Sarraceniaceae (Fig. 34), partly tropical but largely temperate, are classical in their disjunction between the Guyana Highlands (*Heliamphora*), California-Oregon (*Darlingtonia*), and eastern North America (*Sarracenia*).

2. *Temperate.*

The amphitropical American disjuncts have recently received considerable attention (Constance, Heckard, Chambers, Ornduff, and Raven, 1963; Thorne and Lathrop, 1970). At least 65 primarily temperate American genera are widely discontinuous across the American tropics, including *Agoseris, Amsinckia, Bahia, Blennosperma, Camissonia, Chorizanthe, Clarkia, Cryptantha, Downingia, Gaillardia, Galvezia, Gaura, Gilia, Haplopappus, Lasthenia, Lepuropetalon, Lesquerella, Madia, Monanthochloe, Orthocarpus, Oxytheca, Phacelia, Plectritis,* and *Schedonnardus.* At least 90 more widely ranging temperate genera show similar disjunctions within the New World, as *Adenocaulon, Androsace, Antennaria, Calandrinia, Deschampsia, Ephedra, Elatine, Fagonia, Fragaria, Frankenia, Gleditsia, Lepichinia, Lilaeopsis, Lotus, Lupinus, Menodora, Mimulus, Myosotis, Myosurus, Orobanche, Plagiobothrys, Sanicula, Taraxacum,* and *Thlaspi.* Raven (1963) lists 128 species, species-pairs, or species-groups of seed plants that have disjunct ranges in temperate North and South America. He treats in another group the temperate disjuncts, many of them woody, that occur in the deserts of the two continents. Some of these taxa are especially prominent in the American Southwest: *Atamisquea emarginata* Miers, *Errazurizia, Fagonia, Gutierrezia, Helietta, Hoffmanseggia, Koeberlinia spinosa* Zucc., *Larrea, Menodora, Prosopidastrum,* and *Prosopis.* Raven lists also 22 species or species-pairs of grasses and forbs that are likewise desert disjuncts.

Raven (1963) concluded that the amphitropical disjuncts probably migrated by long-distance dispersal in late Pliocene or Pleistocene time or even more recently. The largely herbaceous temperate and bipolar disjuncts mostly have dispersed from North to South America; whereas, the more woody desert disjuncts mostly evolved in South America or perhaps in part diverged from a common tropical ancestor. The considerations upon which he bases his logical conclusions are that the unbalanced assemblage of disjuncts, mostly self-compatible and autogamous, are quite unrepresentative of the distinctive floras of the two extratropical areas, which have been distinct since the middle Cretaceous. Further, the disjuncts on either side of the tropics are closely related, often conspecific, and they occupy mostly open plant communities, as grasslands and vernal marshes (Thorne and Lathrop, 1970), easily penetrated by migrants. Few insects and no terrestrial vertebrates correspond to these seed plant disjuncts. *Osmorhiza chilensis* H. & A. (Fig. 35) is somewhat unusual for the temperate nondesert disjuncts because it is a plant of wooded habitats and is also discontinuous across North America to the Great Lakes area and thence to the Maritime Provinces. The great majority of the amphitropical American taxa are found in the areas of Mediterranean climate in California and Chile.

An alternative explanation with some merit is that the discontinuous taxa may have migrated by normal short-distance dispersal or by stepping-stone movements along the more or less continuous western American mountain system. Certainly this explanation is valid for the dozens of genera like *Ribes* (Fig. 7) that are nearly continuous in the American highlands from Alaska to Fuegia. Some of the other genera with relatively continuous montane distribution across the American tropics are *Alchemilla, Alnus, Berberis, Caltha, Carex, Castilleja, Epilobium, Gentianella, Geum, Hydrangea, Montia, Thalictum, Valeriana,* and *Viburnum.* Unlike these, however, most of the temperate taxa discussed above are unrepresented on the Andean cordillera across the American tropics. Most are not montane at all, and many are adapted to the Mediterranean climate of the Pacific coastal areas. Thus, long-distance dispersal rather than continuous migration is strongly indicated for them.

3. *Bipolar.*

Also discussed by Raven (1963) were the bipolar disjuncts. He listed 26 species or species-pairs of seed plants with bipolar distribution, all but two of them circum-Arctic or circumboreal as well. Nearly a dozen genera conform to this pattern: *Armeria, Catabrosa, Empetrum* (Fig. 36), *Euphrasia* (Fig. 8), *Hippuris, Honkenya, Koenigia, Littorella, Monolepis, Phippsia,* and *Primula.* Long-distance dispersal from northern North America in Pleistocene or later times seems to be indicated here, as with the temperate disjuncts. However, at least *Euphrasia* (Fig. 8) is an exception to this probable route. The South American species of this genus, according to Du Rietz (1960), are more closely related to the southern and western Pacific species than they are to the North American species.

XI. South American-Australasian

At least 48 genera and 7 families of seed plants are essentially restricted to temperate South America (some passing into the tropics along the Andes) and Australasia, with a few following tropical highlands to southeastern Asia or rarely reaching Madagascar. An additional 28 more widely distributed genera and 2 families are linked to Australasia by common species or closely related species represented in the two regions. The largely Pacific genera, *Coprosma* (Fig. 29), *Haloragis,* and *Santalum,* reach the Juan Fernandez Islands but not the South American mainland. These taxa are perhaps better analyzed by treating them in three minor subcategories.

1. *South American-Australasian.*

This is the largest subcategory, containing those taxa with representatives only in temperate South America (a few passing along the western American cordillera to Mexico) and the Australasian area, including New Zealand and its subantarctic islands, Tasmania, Australia, New Caledonia, and New Guinea (a few reaching the mountains of Borneo or Taiwan or even, in the other direction, the Polynesian and Hawaiian mountains). Groups that possess this spectacular type of discontinuity are the Araucariaceae and Eucryphiaceae and at least 36 genera: *Gevuina, Lomatia, Oreocallis,* and *Orites* (combined ranges in Fig. 37), *Amphibromus, Araucaria, Aristotelia, Azorella, Celmisia, Colobanthus, Discaria, Donatia, Eucryphia, Fuchsia, Gaimardia, Griselinia, Hebe, Hypsela, Jovellana, Laurelia, Libertia, Marsippospermum, Muehlenbeckia, Nothofagus, Oreomyrrhis, Ourisia, Pernettya, Phyllachne, Pseudopanax, Rostkovia, Schizellema, Selliera, Tetrachondra, Trichocline, Uncinia,* and *Vittadinia.* Three American amphitropical disjuncts, *Calandrinia, Lilaeopsis,* and *Plagiobothrys,* are also disjunct from temperate South America to Australasia. Most of the other 25 widely ranging genera mentioned above reach only Australasia, and hence also belong in this subcategory.

2. *South American-Australasian-Asian.*

This subcategory is quite artificial, since it includes wide disjuncts almost identical to the preceding except that they have species successfully established on the mainland of southeastern Asia. Four primarily Australasian families have thus reached at least mainland Asia to the west and temperate South America to the east. They are the Centrolepidaceae, Coriariaceae (Fig. 38), Epacridaceae, and Stylidiaceae. Seven genera that likewise fit in this subcategory are *Coriaria* (Fig. 38), *Dacrydium, Euphrasia* (Fig. 8, with also extensive holarctic distribution), *Gaultheria, Lagenifera, Leptocarpus,* and *Oreobolus. Coriaria* is somewhat anomalous here, for in addition to one species reaching Tahiti and north along the Andes and Middle American mountains to Mexico, it has another in the Mediterranean region.

3. *South American-Australasian-Madagascan.*

Likewise little different from the two preceding subcategories are those taxa that extend their wide discontinuities from South America to Australasia and on to the Mascarene Islands or Madagascar, also in some cases involving Malesia and southeastern Asia. The one family, Winteraceae (Fig. 39), with this type of disjunct range has not been found on the Asiatic mainland but members have reached north to Mexico in America, north to Borneo and the Philippines in Malesia, and south to the highlands of Madagascar. It is worthy of note here that this vesselless family in most of its features is the most primitive living family of the Angiospermae. Five genera also with these enormous gaps across the Pacific and Indian Oceans are *Abrotanella* and *Astelia* (to the Mascarenes), *Nertera* and *Weinmannia* (to Madagascar), and *Dianella* (on Madagascar and also in mainland East Africa).

For some of the plants of this temperate South American-Australasian disjunct category, especially those with fleshy, bird-dispersed fruit that have far-flung distributions on oceanic islands of the Pacific and Indian Oceans, long-distance dispersal by birds is the rather obvious explanation for the discontinuities. Genera with fruit that must be especially attractive to birds are *Aristotelia, Astelia, Coprosma, Coriaria, Dacrydium, Dianella, Fuchsia, Gaultheria, Griselinia, Nertera, Pernettya,* and *Pseudopanax.* Other genera that appear to require and be capable of long-distance dispersal are *Abrotanella, Azorella, Colobanthus, Gaimardia, Haloragis, Lagenifera, Leptocarpus, Oreobolus, Oreomyrrhis, Ourisia, Rostkovia, Schizellema, Selliera, Tetrachondra, Vittadinia, Uncinia,* and *Weinmannia.* There are several taxa, however, which because of large, dry or heavy cones, fruits, or seeds are not logically explained by bird-carriage or other forms of long-distance dispersal. Among these are *Araucaria, Eucryphia, Laurelia, Nothofagus,* and the four genera of Proteaceae (Fig. 37).

Many authors (listed in Thorne, 1963) have suggested that Antarctica, much warmer, forested, and probably a more extensive archipelago in Cretaceous and Tertiary times, must have served formerly as a "sweepstakes" migration route for many seed plants and animals. Distances between Antarctica and Tasmania-Australia, Antarctica and New Zealand, and Antarctica and South America may have been much less in the past. Biological evidence that Antarctica ever furnished a continuous land-bridge like Beringia, however, is unconvincing. Plate tectonics, now currently accepted by many geologists, has most recently been suggested (Raven and Axelrod, 1972) as the ultimate answer to many of the problems of Australasian-temperate South American paleobiogeography. According to this hypothesis, about 100 million years before the present (B. P.), Antarctica linked South America with New Zealand and with Australia, furnishing an effective pathway for migration of temperate forest plants and associated animals. Later the various tectonic plates moved apart to their present positions, causing considerable tectonic disturbance in the southwestern Pacific. This is a rather attractive hypothesis which one hopes the geologists and paleontologists can in time substantiate.

XII. Temperate South American-Asian

This type of disjunction in which the representatives of a taxon are separated by the entire width of the Pacific Ocean is expectedly quite rare. The outstanding example of this huge discontinuity is the family Lardizabalaceae (Fig. 40), with 2 genera, *Boquila* and *Lardizabala,* in central Chile and 5 in eastern Asia from Japan and Korea to the Himalayas. A few other examples of this South American-Asian disjunction were discussed by Stebbins (1940). He suggested that the largely Andean mutisioid genera *Hyaloseris* and *Proustia* are possibly closely related to *Catamixis* of the northwestern Himalaya and *Nouelia* of Yunnan, to *Hesperomannia* of Hawaii, and perhaps to *Stifftia* of Brazil. He considers to be even more closely related to the mutisioid *Leucomeris* of southeastern Asia the genus *Gochnatia* of the Andes and Brazil north to Mexico and Texas. *Hypochoeris* of the Lactuceae has speciated heavily in southern South America and has a secondary center in the Mediterranean Sea area and a few species across Europe to northeastern Asia. There are no native species of either *Hypochoeris* or of the Lardizabalaceae in North America. Stebbins also suggested that the bignoniaceous perennial herb *Argylia* of Andean Peru to temperate South America has its closest relatives in the equally herbaceous *Incarvillea* of the Sino-Himalayan region.

Of all the disjunct categories discussed, this is the most difficult to explain. The species of Lardizabalaceae have baccate fruit, but to explain this discontinuity by direct bird-carriage between Chile and eastern Asia rather strains credulity. The distribution of *Coriaria* (Fig. 38) may be instructive here. *Coriaria,* with fruit a pseudo-drupe of cocci surrounded by persistent fleshy petals at maturity, is greatly favored by many birds and is almost certainly dispersed by them. If the northern South and

Central American, Pacific, and Mediterranean species were deleted from the map, it would show a distribution pattern similar to that of the Lardizabalaceae. However, if the latter family dispersed like *Coriaria* across the southern Pacific, it should have left some traces along the way. One can as well adduce the bipolar distribution of *Empetrum* (Fig. 36). If the circumpolar, European, and North American parts of its range are eliminated, a similar pattern again emerges. Surely, however, as in *Coriaria, Empetrum*'s disjunct distribution has recently been achieved by long-distance dispersal with birds as vectors. The temperate South American-Asian disjunction appears to be, at least in part, a relict pattern. I would expect that fossils of the Lardizabalaceae will ultimately be identified from North American Cretaceous or Tertiary deposits.

XIII. Circum-South Temperate

Considering the paucity of land in relation to water in the south temperate zone, it is understandable that relatively few taxa are present in, and largely restricted to, the temperate portions of the three southern continents. Five families, the Cunoniaceae, Gunneraceae, Podocarpaceae, Proteaceae, and Restionaceae, and two subfamilies, Escallonioideae of the Saxifragaceae and Luzuriagoideae of the Liliaceae, are largely circum-south temperate in their distribution. Yet all of these have representatives in the tropics, at least in the tropical highlands, and all reach north of the equator. The 9 genera which likewise have a primarily circum-south temperate type of discontinuous distribution are *Acaena* (Fig. 41), *Carpha, Cotula, Carpobrotus, Gunnera, Podocarpus, Pratia, Wahlenbergia,* and *Tetragonia.*

Some of these taxa are well equipped for bird or sea-current dispersal over large distances, as *Acaena, Carpobrotus, Gunnera, Podocarpus, Tetragonia,* and the luzuriagoids. Many members, however, of the Cunoniaceae, Proteaceae, and Escallonioideae are much less well adapted for long-distance dispersal and would seem to require more nearly complete land connections for normal short-range or stepping-stone dispersal. Their present wide ranges may have resulted from migration over a once warmer and more extensive Antarctic archipelago between South America and Australia. Their South African presence is more likely due to migration from Australia through the Indonesian-Asian and East African highlands. The often called-upon breakup of a possible Gondwanaland, if it ever existed, must have taken place far too long ago to have had any impact upon the present distribution of seed plants.

XIV. Circum-Antarctic

The land areas defined here as circum-Antarctic are the Grahamland peninsula of Antarctica, the southern tip of South America (especially Tierra del Fuego), and the high latitude islands surrounding the Antarctic, such as the Falklands, South Georgia, Tristan da Cunha, Gough, Marion, Crozet, Heard, Kerguelen, St. Paul, New Amsterdam, and Macquarie Islands, mostly within or near the northern limit of drift ice. The subantarctic lands have a very small flora, as might be expected from the strong cold winds, small and remote land areas, and great amounts of permanent ice. Yet their meager flora of perhaps 100 species (Good, 1964) is a rather characteristic, constant one, with perhaps 30 species with wide distributions in the circum-Antarctic region (Dawson, 1958). Among these species are *Acaena adscendens* Vahl (included in Fig. 41), *Azorella selago* Hook.f., *Callitriche antarctica* Engelm. ex Hegel, *Montia fontana* L., *Myriophyllum elatinoides* Gaud., and *Ranunculus biternatus* Sm. in Rees (Fig. 42). During the Pleistocene ice age most of these circum-Antarctic lands were covered with ice, as were Macquarie, Kerguelen, Heard, and South Georgia Islands and Grahamland. Consequently, the circumpolar flora must be post-Pleistocene and must have reached these remote islands by long-distance dispersal, presumably via oceanic birds (Falla, 1960; Holdgate, 1960) mostly from southern South America and New Zealand.

XV. Subcosmopolitan

Plant taxa that are not primarily temperate nor tropical and that have indigenous representatives on all the continents (including Australia) can be described as subcosmopolitan. Truly cosmopolitan taxa that have representatives on all parts of the earth's surface do not, of course, exist. The most nearly cosmopolitan family of seed plants is the Poaceae, which has species native in all habitable parts of all the continents and even in Grahamland of Antarctica. Ninety families (among those listed by Thorne, 1968) and about 125 genera of seed plants are subcosmopolitan in their distribution and in their disjunction. It is certainly no coincidence that at least 72 of the subcosmopolitan genera are largely aquatic or at least have species that inhabit shallow water, wet, open places, maritime situations, or riparian habitats. A few of these are *Callitriche, Carex, Crassula, Drosera, Elatine, Eleocharis, Juncus, Lemna, Montia, Myriophyllum, Najas, Nymphaea, Potamogeton, Ranunculus, Ruppia, Triglochin, Typha, Utricularia, Vallisneria,* and *Wolffia.* An additional 26 genera have species with weedy tendencies, as *Amaranthus, Cenchrus, Centaurea, Cuscuta, Euphorbia, Gnaphalium, Lepidium, Oxalis, Senecio, Setaria,* and *Urtica.* Thus, about four-fifths of the genera have members that by habitat are readily dispersible. The remaining genera are small-seeded herbs or woody plants with mostly succulent, bird-dispersed fruit.

Very few species can be described as subcosmopolitan, and these are almost all of necessity aquatics, like *Ceratophyllum demersum* L. (Fig. 43). Some other aquatics that also have vast if somewhat sporadic distributions on all or nearly all the continents are *Anagallis minimus* (L.) Krause, *Brasenia schreberi* J. F. Gmel., *Callitriche verna* L., *Chenopodium glaucum* L., *Cladium mariscus* L. (s.l.), *Cyperus flavescens* L., *Juncus bufonius* L., *J. effusus* L., *Lemna gibba* L., *L. minor* L., *L. trisulca* L., *Ludwigia palustris* (L.) Ell., *Montia fontana* L., *Myriophyllum spicatum* L., *Najas marina* L., *Phragmites australis* (Cav.) Trin., *Potamogeton pectinatus* L., *Ranunculus trichophyllus* Chaix., *Ruppia cirrhosa* (Petag.) Grande, *Scirpus maritimus* L., *Spirodela polyrhiza* (L.) Schleid., *Triglochin palustris* L., and *Zanichellia palustris* L. Several of these are mapped by Meusel, Jager, and Winert (1965). There can be little doubt of the efficacy of water and shore birds in the dispersal of these species about the world.

XVI. Anomalous

The final category of major types of discontinuous taxa is a wastebasket for those few genera that I am unable to fit comfortably into the preceding categories. In some instances, further exploration and discovery of the taxon, as is surely to be expected with the rafflesiaceous parasite *Pilostyles* (Fig. 44), may clarify its position, which, in this case, is already approaching circumtropical. *Myrica* also falls a little short of being subcosmopolitan because of its absence from Australasia. If the circumboreal disjunct *Gale belgica* Dum. (*Myrica gale* L.) is removed from *Myrica,* the genus is also unrepresented in Europe and boreal North America. The present disjunct range of *Myrica* is certainly a relic of a once worldwide distribution. The santalaceous *Thesium* falls somewhat short of being circumtropical because of its extremely weak presence in southeastern Asia-Australasia and in southern Brazil (map in Meusel, Jager, and Winert, 1965). It might better be considered an African-Eurasian-Australasian disjunct with a small outlier in southern Brazil, as in the family Pedaliaceae, in which only *Rogeria* reaches the New World with a species in Brazil (so also with the crassulaceous *Kalanchoë*). Likewise, the American-African-Madagascan *Urera* of the Urticaceae transgresses its pattern by having a species in the Hawaiian Islands. Perhaps the most anomalous disjunction of all is found in the chiefly Indomalesian-American genus *Thismia* of the Burmanniaceae. Among these fleshy saprophytes the small section *Rodwaya* has one species, *T. rodwayi* F. v. Muell., in Victoria, Tasmania, and New Zealand; and another, *T. americana* N. E. Pfeiff., found a couple of times many years ago in a moist prairie in Chicago, Illinois.

STATISTICAL SUMMARY

Some authors, vide Good (1964), divide taxa geographically into three major categories, depending upon whether they are widely distributed about the world, are discontinuous, or are endemic in a limited area. This division is artificial, since widely distributed taxa, because of the juxtaposition of continents and seas, are almost always discontinuous in their areas. Thus, we are left practically with only disjunct vs. endemic taxa. The latter present no great phytogeographic problems other than the formerly much greater and often discontinuous ranges of many of the relict endemics, or epibiotics. Therefore, our interest here is centered on the discontinuous taxa.

The larger the category of the taxon, the greater the likelihood that its distribution will bė more or less wide-ranging and hence disjunct. Of 324 families that I currently recognize [a total somewhat larger than in my *Synopsis* (Thorne, 1968)] 254, or 78.4 per cent, have intercontinental or equivalent discontinuities. If the 273 recognized additional subfamilies are added to the family total, 462 of 597 families and subfamilies, about the same percentage, 77.4 per cent, have major discontinuities in their ranges. Of the perhaps 12,500 angiosperm genera usually recognized (Good, 1964), a total of nearly 3,000 are counted in this study as having major range disjunctions. Thus only 24 per cent of flowering plant genera are intercontinentally disjunct. Species have not been thoroughly analyzed for major disjunctions, but a rough estimation from this study would be about 2,000 with wide natural range disjunctions. If 225,000 is accepted as a reasonable estimate of the named valid species of flowering plants (Good, 1964), fewer than 1 per cent of angiospermous species are widely disjunct.

Of the many categories of major disjunctions, those encompassing the largest number of genera are: African-Eurasian-(Pacific), 600; Asian-Pacific, 460; Pacific, 370; North American-South American, ca. 360 (surely a serious underestimate since Middle America is disregarded here); Pantropical, 334; North Temperate, 316; Subcosmopolitan, 125; African-American, 111; and Amphi-Pacific Tropical, 85. Those with the largest number of seed-plant families are: Subcosmopolitan, 90; Pantropical, 59; North Temperate, 20; African-Eurasian-(Pacific), 17; North American-South American, 13; African-American, 12; Tropical Amphi-Pacific, 11; South American-Australasian, 7; and Pacific, 7.

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LIST OF LITERATURE

BALGOOY, M. M. J. VAN. 1966. Distribution maps of Pacific plants. In C. G. G. J. van Steenis and M. M. J. van Balgooy (eds.), *Pacific Plant Areas,* Vol. 2, p. 76–77, 96–97, 114–115, 122–123, 150–151, 170–171, 240–241, 248–249, 268–269. *Blumea,* Suppl., 5: 1–312.

——. 1971. Plant-geography of the Pacific. *Blumea,* Suppl., 6: 1–222.

BALGOOY, M. M. J. VAN, and DING HOU. 1966. *Perrottetia* H. B. K. In C. G. G. J. van Steenis and M. M. J. van Balgooy (eds.), *Pacific Plant Areas,* Vol. 2, p. 94–95. *Blumea,* Suppl., 5: 1–312.

BALGOOY, M. M. J. VAN, and P. W. LEENHOUTS. 1966. *Fagraea* Thunb. In C. G. G. J. van Steenis and M. M. J. van Balgooy (eds.), *Pacific Plant Areas,* Vol. 2, p. 168–169. *Blumea,* Suppl., 5: 1–312.

BURBIDGE, N. T. 1960. The phytogeography of the Australian region. *Austral. J. Bot.,* 8: 75–212.

——. 1963. *Dictionary of Australian Plant Genera.* Angus and Robertson, Sydney.

CONSTANCE, L. 1963. Introduction and historical review. In *Amphitropical Relationships in the Herbaceous Flora of the Pacific Coast of North and South America: A Symposium,* p. 109–116. *Quart. Rev. Biol.,* 38: 109–177.

CONSTANCE, L., L. R. HECKARD, K. L. CHAMBERS, R. ORNDUFF, and P. H. RAVEN. 1963. Amphitropical relationships in the herbaceous flora of the Pacific Coast of North and South America: a symposium. *Quart. Rev. Biol.,* 38: 109–177.

DAWSON, J. W. 1958. Interrelationships of the Australasian and South American floras. *Tuatara,* 7: 1–6.

DRESSLER, R. L. 1954. Some floristic relationships between Mexico and the United States. *Rhodora,* 56: 81–96.

DU RIETZ, G. E. 1960. Remarks on the botany of the southern cold temperate zone. In C. F. A. Pantin (ed.), *A Discussion on the Biology of the Southern Cold Temperate Zone,* p. 500–507. *Proc. Roy. Soc. (London),* Ser. B, Biol. Sci., 152: 429–682.

ENDRESS, P. K. 1969. *Molinadendron,* eine neue Hamamelidaceen-Gattung aus Zentralamerika. *Bot. Jb.,* 89: 353–358.

ENGLER, A. 1964. *Syllabus der Pflanzenfamilien.* 12th ed., H. Melchior (ed.), Vol. 2. Gebruder Borntraeger, Berlin.

EYDE, R. H., and E. S. BARGHOORN. 1963. Morphological and paleobotanical studies of the Nyssaceae, II. The fossil record. *J. Arnold Arbor.,* 44: 328–376.

FALLA, R. A. 1960. Oceanic birds as dispersal agents. In C. F. A. Pantin (ed.), *A Discussion on the Biology of the Southern Cold Temperate Zone,* p. 655–659. *Proc. Roy. Soc. (London),* Ser. B, Biol. Sci., 152: 429–682.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. *Mem. Am. Acad. Arts & Sci.,* 15: 239–342.

——. 1931. Specific segregations and identities in some floras of eastern North America and the Old World. *Rhodora,* 33: 25–63.

FLORIN, R. 1963. The distribution of conifer and taxad genera in time and space. *Acta Hort. Berg.,* 20: 121–312.

FOSBERG, F. R. 1948. Derivation of the flora of the Hawaiian Islands. In E. C. Zimmerman (ed.), *Insects of Hawaii.* Vol. 1, Introduction, p. 107–119. Univ. Hawaii Press, Honolulu.

FRYXELL, P. A. 1967. The interpretation of disjunct distributions. *Taxon,* 16: 316–324.

GAMS, H. 1927. Die Gattung *Trapa* L. In E. Hannig and H. Winkler (eds.), *Die Pflanzenareale,* Vol. 1(3), p. 39–41, maps 25–27. Gustav Fischer, Jena.

GOOD, R. 1964. *The Geography of the Flowering Plants.* 3rd ed. Wiley & Sons, New York.

GRAY, A. 1846. Analogy between the flora of Japan and that of the United States. *Am. J. Sci. & Arts,* II, 2: 135–136.

——. 1859. Diagnostic characters of new species of phaenogamous plants, collected in Japan by Charles Wright, Botanist of the U. S. North Pacific Exploring Expedition. (Published by request of Captain John Rodgers, Commander of the Expedition.) With observations upon the relations of the Japanese flora to that of North America, and of other parts of the Northern Temperate Zone. *Mem. Am. Acad. Arts & Sci.,* II, 6: 377–452.

HARTOG, C. DEN. 1966. *Thalassia hemprichii* (Ehrenb.) Aschers. In C. G. G. J. van Steenis and M. M. J. van Balgooy (eds.), *Pacific Plant Areas,* Vol. 2, p. 210–211. *Blumea,* Suppl., 5: 1–312.

——. 1970. The sea-grasses of the world. *Verh. Koninklijke Nederl. Akad. Wetenschappen, Afd. Natuurkunde,* 59 (I): 1–275.

HERNANDEZ-X., E., E. H. CRUM, W. B. FOX, and A. J. SHARP. 1951. A unique vegetational area in Tamaulipas. *Bull. Torrey Bot. Club,* 78: 458–463.

HOLDGATE, M. W. 1960. Final discussion. In C. F. A. Pantin (ed.), *A Discussion on the Biology of the Southern Cold Temperate Zone,* p. 674–675. *Proc. Roy. Soc. (London),* Ser. B, Biol. Sci., 152: 429–682.

HOU, D., and C. G. G. J. VAN STEENIS. 1963. *Bruguiera gymnorrhiza* (L.) Lamk. In C. G. G. J. van Steenis (ed.), *Pacific Plant Areas.* Vol. 1, p. 260–261. National Institute of Science and Technology, Manila.

HULTÉN, E. 1937. *Outline of the History of Arctic and Boreal Biota during the Quarternary Period.* Bokforlags Akteibolaget Thyle, Stockholm.

——. 1958. The amphi-Atlantic plants and their phytogeographical connections. *Kung. Svenska Vetenskapsakad. Handl.,* Fjarde Ser. 7 (I): 1–340, 279 maps.

——. 1963. Phytogeographical connections of the North Atlantic. In A. Löve and D. Löve (eds.), *North Atlantic Biota and Their History,* p. 45–72. Pergamon Press, Oxford.

——. 1968. *Flora of Alaska and Neighboring Territories.* Stanford Univ. Press, Stanford.

HUTCHINSON, J. 1959. *The Families of Flowering Plants. Vol. 1, Dicotyledons.* 2nd ed. Oxford Univ. Press, London.

HUTCHINSON, J., and J. M. DALZIEL. 1927-1936. *Flora of West Tropical Africa.* 2 vols. Crown Agents, London.

——, and ——. 1954-1968. *Flora of West Tropical Africa.* 2nd ed. Edited by R. W. J. Keay and F. N. Hepper. 3 vols. Crown Agents, London.

LI, H.-L. 1952. Floristic relationships between eastern Asia and eastern North America. *Trans. Am. Phil. Soc.,* New Ser., 42: 371-429.

LONG, R. W., and O. LAKELA. 1971. *A Flora of Tropical Florida.* Univ. Miami Press, Coral Gables.

LÖVE, D. 1962. Plants and Pleistocene — problems of the Pleistocene and Arctic. McGill Univ. Museums Publ., 2: 17-39.

MCVAUGH, R. 1952. Suggested phylogeny of *Prunus serotina* and other wide-ranging phylads in North America. *Brittonia,* 7: 317-346.

MEUSEL, H. 1969. Beziehungen in der Florendifferenzierung von Eurasien und Nordamerika. *Flora,* Abt. B, 158: 537-564.

MEUSEL, H., E. JAGER, and E. WINERT. 1965. Vergleichende Chorologie der Zentral-europaischen Flora. Karten. Gustav Fischer, Jena.

MEUSEL, H., and R. SCHUBERT. 1971. Beitrage zur Pflanzengeographie des Westhimaljas. I. Teil: Die Arealtypen. *Flora,* 160: 137-194.

MIRANDA, F., and A. J. SHARP. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology,* 31: 313-333.

OSTENFELD, C. H. 1915. On the distribution of the sea-grasses. A preliminary communication. *Proc. Roy. Soc. Victoria,* 27: 179-191.

——. 1927a. Meeresgräser 1. Marine Hydrocharitaceae. In E. Hannig and H. Winkler (eds.), *Die Pflanzenareale,* Vol. 1 (3), p. 35-38, maps 21-24.

——. 1927b. Meeresgräser 2. Marine Potamogetonaceae. In E. Hannig and H. Winkler (eds.), *Die Pflanzenareale,* Vol. 1(4), p. 46-50, maps 34-39.

RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.,* 38: 151-177.

RAVEN, P. H., and D. I. AXELROD. 1972. Plate tectonics and Australasian paleobiogeography. The complex biogeographic relations of the region reflect its geologic history. *Science,* 176: 1379-1386.

SCHOFIELD, W. B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. *Madroño,* 20: 155-207.

SETCHELL, W. A. 1920. Geographical distribution of the marine spermatophytes. *Bull. Torrey Bot. Club,* 47: 563-579.

——. 1935. Geographic elements of the marine flora of the North Pacific Ocean. *Am. Natur.,* 69: 560-577.

SHARP, A. J. 1946a. Informe preliminar sobre algunos estudios fitogeograficos efectuados in Mexico y Guatemala. *Rev. Soc. Mex. Hist. Nat.,* 7: 35-39, 5 maps.

——. 1946b. *Pinus strobus* south of the United States. *J. Elisha Mitchell Sci. Soc.,* 62: 229-230.

SLEUMER, H. 1955. Proteaceae. *Flora Malesiana,* 5: 147-206.

SMITH, A. C. 1943a. The American species of *Drimys. J. Arnold Arbor.,* 24: 1-33.

——. 1943b. Taxonomic notes on the Old World species of Winteraceae. *J. Arnold Arbor.,* 24: 119-164.

STEBBINS, G. L., JR. 1938. The western American species of *Paeonia. Madroño,* 4: 252-260.

——. 1940. Additional evidence for a holarctic dispersal of flowering plants in the Mesozoic era. *Proc. Sixth Pacific Sci. Congr.,* 4: 649-660.

STEBBINS, G. L. JR., and A. DAY. 1967. Cytogenetic evidence for long continued stability in the genus *Plantago. Evolution,* 21: 409-428.

STEENIS, C. G. G. J. VAN. 1962. The land-bridge theory in botany. *Blumea,* 11: 235-372.

—— (ed.) 1963. *Pacific Plant Areas. Vol. 1.* National Institute of Science and Technology, Manila.

STEENIS, C. G. G. J., VAN, and M. M. J. VAN BALGOOY (eds.). 1966. *Pacific Plant Areas. Vol. 2. Blumea,* Suppl., 5: 1-312, 147 maps.

STEENIS-KRUSEMAN, M. J. VAN. 1966. Bibliography of Pacific and Malesian plant maps of phanerogams, first supplement. In C. G. G. J. van Steenis and M. M. J. van Balgooy (eds.), *Pacific Plant Areas,* Vol. 2, p. 7-52. *Blumea,* Suppl., 5: 1-312.

STERN, F. C. 1946. *A Study of the Genus* Paeonia. Roy. Hort. Soc., London.

STEYERMARK, J. A. 1950. Flora of Guatemala. *Ecology,* 31: 368-372.

THORNE, R. F. 1963. Biotic distribution patterns in the tropical Pacific. In J. L. Gressitt (ed.), *Pacific Basin Biogeography,* p. 311-354. Bishop Museum, Honolulu.

——. 1965. Floristic relationships of New Caledonia. *Univ. Iowa Studies Natur. Hist.,* 20 (7): 1-14.

——. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso,* 6 (4): 57-66.

——. 1969. Floristic relationships between New Caledonia and the Solomon Islands. *Phil. Trans. Roy. Soc. (London),* B, 255: 595-602.

———. 1972. Floristic relationships between tropical Africa and tropical America. In B. J. Meggers, E. S. Ayensu, and W. D. Duckworth (eds.), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review* (in press). Smithsonian Inst. Press, Washington, D. C.

THORNE, R. F., and E. W. LATHROP. 1970. *Pilularia americana* on the Santa Rosa Plateau, Riverside County, California. *Aliso,* 7 (2): 149–155.

VESTER, H. 1940. Die Areale und Arealtypen der Angiospermen-Familien. *Bot. Arch.,* 41: 203–275, 295–356, 520–577.

WILLIS, J. C. 1966. *A Dictionary of the Flowering Plants and Ferns.* 7th ed. Revised by H. K. Airy Shaw. Cambridge Univ. Press, Cambridge.

WOLFE, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. *Madroño,* 20: 83–110.

WOOD, C. E., JR. 1971. Some floristic relationships between the southern Appalachians and western North America. In P. C. Holdt (ed.), *The Distributional History of the Biota of the Southern Appalachians,* Part II., *Flora,* p. 331–404. Res. Div. Monogr. 2, Virginia Polyt. Inst. and State Univ., Blacksburg.

WURDACK, J. J. 1970. Certamen Melastomataceis. XV. *Phytologia,* 20: 369–389.