The biogeographic regions reconsidered

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Abstract

Aim To evaluate the internal consistency and appropriateness of Takhtajan's system of world-wide floral Kingdoms in the light of modern knowledge, and similarly to re-examine the Wallacean system of mammal biogeographic regions.

Main conclusions It is suggested that Takhtajan's Cape and Antarctic floral Kingdoms should be deleted, and their constituent parts allocated to the neighbouring Kingdoms. The mammal biogeographic regions are to be restricted to the continents, as defined by the edges of the continental shelves, and the name 'Wallacea' is accepted for the area between the Southeast Asian and Australian continental shelves. Modifications are suggested for the names of some of the floral Kingdoms and mammal biogeographic regions.

Keywords
Plant biogeography, zoogeography, historical biogeography.

INTRODUCTION

The history of the concept of biogeographic regions has been well summarized by Nelson (1978). It was Buffon who first observed, in 1761, that the large mammals of the tropical regions of the Old World and the New World are quite different. von Humboldt (1816, 1820) noted that what Nelson has called 'Buffon's law' extended also to birds, reptiles, insects, spiders and flowering plants. However, the world-wide system of biogeographic regions was founded by Augustin de Candolle in 1820 on the basis of the distribution of plants. Like many of his successors, de Candolle was primarily interested in documenting the nature and floral composition of the plant 'formations' (what would now be called biomes) of the regions, and their relations to climate (i.e. their ecological biogeography). Nevertheless, he also defined 20 'areas of endemism', stating that each was characterized by numerous, sometimes endemic, plant species, whose distribution was bounded by natural barriers of ocean, desert or temperature change, or by the presence of competing plants. Of these 20 areas, 18 were continental masses or parts thereof, and two were island groups. Later (1838), de Candolle increased the number of areas of endemism to 40, of which 34 lay on continents.

However, de Candolle did not provide any maps to illustrate his views, and most vegetation maps of the early nineteenth century distinguish between floras that differ because of their different climates. It was only after acceptance of Darwin's theory of evolution that Engler

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(1879, 1882) emphasized that there was a historical aspect to the development of the floras of the different regions. His four 'Realms', which contained 32 regions, were based on de Candolle's climatic and physiological criteria, but Engler did attempt to trace the history of each of these floras back into the Tertiary. They were the Arcto-Tertiary Realm (the temperate and cold regions of the northern hemisphere), the Palaeotropical Realm (the old world tropics, extending from Africa to northern Australia), the Neotropical Realm (most of central and South America) and the 'ancient ocean' Realm (coastal Chile, Tierra del Fuego, the Cape region and south coast of South Africa, most of Australia, Tasmania, the South Island of New Zealand, and the islands in the southernmost Atlantic, Indian and Pacific Oceans). Presumably because of this scattered pattern of distribution, Engler stated that the floras of the 'ancient ocean' Realm were characterized by forms that had the ability to disperse across wide stretches of ocean and to diversify in island archipelagoes. This Realm was subdivided by Diels (1908) into an Antarctic Realm (southern South America and the islands lying at high southern latitudes in the Atlantic and Indian Oceans), a Cape Realm and an Australian Realm; he also placed New Zealand in the Palaeotropical Realm. The last important modification to this system was that of Good (1947, 1953, 1964, 1974), who named the major divisions 'Kingdoms' rather than 'Realms'. Good subdivided Diels' Palaeotropical unit into separate African, Indo-Malayan and Polynesian Subkingdoms, and returned New Zealand to the Antarctic Kingdom. Takhtajan's (1978, 1986) system is very similar to that of Good. However, none of these authors provided any systematic comparison and contrast of the composition of the different floras, even in the case of that

most surprising unit, the Antarctic Kingdom, spread over several areas that are widely separated geographically.

Zoogeography, too, had been developing from the early nineteenth century onwards, but in slightly different fashion. From the time of the earliest zoogeographers, such as Prichard (1826) and Swainson (1835), zoologists recognized no more than six continental regions. The formal recognition of these regions commenced with Sclater's work (1858) on the distribution of passerine birds, which divided the world into six Regions, later accepted by Wallace (1876) as applying also to the distribution of other animals, especially mammals. Wallace's maps showed the following Regions: Palaearctic (temperate Eurasia); Ethiopian (Africa south of the Tropic of Cancer); Oriental (tropical Asia, including the adjacent tropical Greater Sunda Islands); Australian (including New Guinea and adjacent islands); Nearctic (North America south to central Mexico) and Neotropical (South America and central America as far north as central Mexico). This scheme and names, applying mainly to the distribution of mammals and birds, have been largely accepted by zoogeographers ever since.

The zoogeographic system converged with that of the plant geographers when Wallace (1876) also defined 21 continental subregions, most of which, as Nelson & Platnick (1981) have noted, correspond fairly exactly to de Candolle's (1838) regions, while Engler (1879, 1882) and later plant geographers grouped these botanic regions into 4–6 Realms or Kingdoms. However, the two systems diverged again in the twentieth century, as zoogeographers such as Simpson (1953) and Darlington (1957) ignored the subdivisions, and concerned themselves only with the six faunal regions. This may have been because both birds and mammals have physical and physiological features that insulate their bodies from the surrounding environmental conditions. As a result, many of their families are found in a great variety of environments. It is, therefore, less easy to divide the zoogeographic regions into subregions that are characterized by different taxa of birds or mammals, than to make similar subdivisions of the plant regions. Because of this, zoogeographers have not had to concern themselves with itemizing the differences between subdivisions of these major units, in the way that has preoccupied plant geographers. They have also been more interested in historical biogeography, and less interested in ecological biogeography, than their botanical colleagues. Furthermore, as a result of the current pattern of barriers between the zoogeographic regions (see below), there is little overlap between the animals that characterize adjacent regions, the only exception being that between Southeast Asia and Australia. Wallace, who had himself collected for several years in the East Indies, was fascinated by the way in which the more western islands were overwhelmingly Oriental (Asian) in their fauna of birds and mammals, while those to the east were, equally, overwhelmingly Australian. Wallace, therefore, proposed his famous north/south 'Line' (Fig. 2), which marked the point at which there was a sudden change from a predominantly Oriental fauna to a predominantly Australian fauna.

This, then, was the situation in the mid-twentieth century, 100 years after the Darwinian revolution in the biological sciences had implicitly suggested that the contents of each of the biogeographic units might have changed and diversified through time, while palaeontological discoveries had in many cases documented these changes. But, as long as the earth's geography was thought to have been stable, problems remained in the explanation of at least some of the patterns of disjunct distribution. Some of these could be explained by patterns of extinction. For example, the presence of fossil camelids and tapirs in North America and Asia showed that the disjunct distribution of those groups today in South America and Southeast Asia did not have to be explained by some theory of the rafting of early camelids and tapirs across the Pacific. But, on the other hand, the presence today of the southern beech tree, *Nothofagus*, in Patagonia, Southeast Australia and New Zealand did provide a greater problem, as did the distribution of the Permo-Carboniferous *Glossopteris* flora in all the continents of what we now call Gondwana. If these areas had always been in their present positions, this disjunct pattern of distribution could only have been the result of dispersal across the intervening oceans. This led to such unlikely theories as Darlington's (1965) suggestion that the seeds of *Glossopteris* had been carried from the Southern Hemisphere to India by floating ice.

The full potential of the new view of the biogeographic regions could not therefore be realized for over a century, until after the second revolution – that of acceptance of plate tectonics, in the 1960s. One implication of this theory was that some disjunct distributions might be the result of the intrusion of a new barrier, of sea, mountain or climate, within what had originally been a continuous pattern of distribution. This came to be known as vicariance, and there was a lengthy wrangle before it became commonly accepted that vicariance and dispersal must, *a priori*, be considered as equally possible as the cause of a disjunct pattern of distribution.

Acceptance of plate tectonics also made possible a new and simpler view of the problem of Wallace's Line in zoogeography. The fauna of the East Indies no longer had to be seen as the result of some strange process whereby marsupials, but not placentals, had succeeded in reaching Australia, only then to start to return westwards and meet their placental relatives, now tardily beginning to disperse eastwards. Instead, it was now clear that the most important agent has been the gradual coming-together of the two continents, each with its own endemic fauna of mammals, plus the separation of peripheral parts of those continents as rising sea-levels made them into islands, and the subsequent colonization of the intervening volcanic, smaller islands by both Asian placentals and Australian marsupials (Michaux, 1994).

There are three fundamental differences between the final faunal and floral systems described above (Fig. 1). The first is that the distribution of flowering plants shows no trace of this schism in the distribution of mammals and birds, for the lndo-Malayan plant region extends eastwards through the
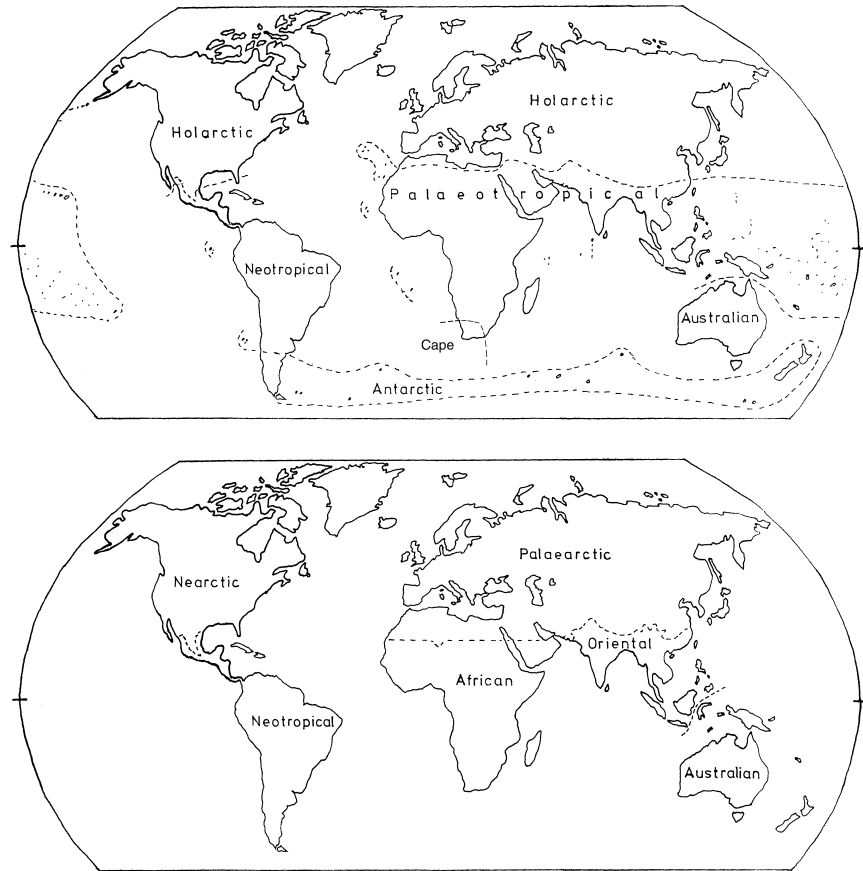
Figure 1 Floral Kingdoms (above) and zoogeographic Regions (below), as currently recognized.

whole of the East Indies, to embrace even New Guinea. Secondly, zoologists do not find any similarities between the faunas of the southernmost regions of the world similar to those that have led the botanists to establish the Antarctic floral region. Finally, zoologists also do not find any aspect of the fauna of the Cape region of South Africa that would demand recognition at the highest level, similar to that given to it by the botanists. These differences will now be considered in turn.

THE PROBLEM OF WALLACE'S LINE

The much greater dispersal power of plants has allowed those of Southeast Asia to spread, not only through the East Indies to New Guinea, but also across the vast reaches of the Pacific to even the most distant of the Pacific island groups. It is therefore reasonable, as Takhtajan (1986) has done, to include these areas as parts of the Old World tropical floral Kingdom, whereas the almost complete lack of mammals in these Pacific island groups makes it meaningless to attempt to follow a similar pattern in zoogeography. But, despite its historical importance as the suggestion of a man who was not only a great zoogeographer but was also the co-discoverer of the theory of evolution by natural selection, Wallace's Line has not had a beneficial effect on the modern study of zoogeography. This is because it has led many

workers (see Simpson, 1977) to try to find the 'best' place to draw a line between these two faunas – an essentially sterile enterprise, for there is no 'best' line, and the research does not lead to any more fundamental insight into biogeography, but merely becomes a comparative study of the dispersal and competitive abilities of the various groups of animals that have colonized the area.

The only alternative is to treat the island-studded area between the continental shelves as lying outside the zoogeographic regions. In fact, ever since MacArthur & Wilson's (1963, 1967) perceptive paper and book, the study of island biogeography has become a separate discipline within biogeography. Islands provide the opportunity for studying the detailed history of individual biotas and of the ways in which they may affect one another. The time-scale is limited, for most have existed for only a few million years at most. Similarly, the variety of taxa is limited, both by that comparatively small time-scale, and also by the fact that only a limited variety of organisms can cross the oceanic barrier that surrounds the islands. The shorelines of islands provide a natural frame and definition for the island biotas, so that one can study such problems as rates of colonization and extinction, and the effects of the size and distance of the sources of colonist organisms. Although similar phenomena must underlie the biogeographic processes that take place on the continental masses, their size, together with the much
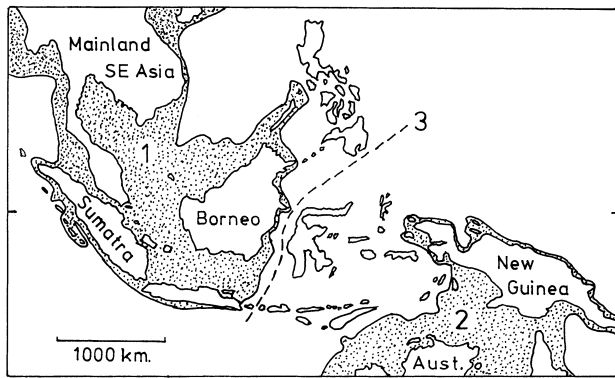
Figure 2 Map of Southeast Asia, the East Indies and northern Australasia. Aust, Australia. The areas of the continental shelves are stippled. (1) Sunda Continental Shelf; (2) Sahul (Australasian) Continental Shelf; (3) Wallaceís Line. After Moss & Wilson (1998).

greater variety of organisms and the far greater time-scale, make it impossible to identify these phenomena on the continents. Instead, continental biogeography is concerned with such topics as latitudinal variation in diversity, global climatic change, and the replacement of faunas and floras by evolutionary innovation and dispersal or vicariance.

Against this background, it seems quite clear that we should no longer view the islands between the continental shelves of Southeast Asia and Australia as belonging to either the Oriental or the Australian zoogeographic regions. It is, nevertheless, convenient to have a name to describe this area which, over the last 50 Myr, has been continually altered by the processes of plate tectonics, as the Australian plate and some surrounding islands steadily approached the Asian plate (Hall & Holloway, 1998). Fortunately, an entirely appropriate name has already been coined by Dickerson (1928), who referred to the area lying between the continental shelves as 'Wallacea' (Fig. 2). This course is also the one finally approved by Simpson, who wrote 'If we like (on the whole I do), let us keep the Oriental Region bounded by the Sunda Shelf and Huxley's Line and the Australian Region, bounded by the Sahul Shelf and Lydekker's Line, but let us not assign the intervening islands to any region, subregion, transitional or intermediate zone, or the like. That will not inhibit, in fact it should promote, study of the faunas of these islands, their compositions, affinities, histories, and ecologies.' (Simpson, 1977, p. 118). More recently, the term Wallacea has also become used by many biogeographers of the region (e.g. see several papers in Hall & Holloway, 1998), but in their usage it only refers to the islands east of Wallace's Line (so excluding the Philippines group), rather than to all of the oceanic islands between the two Shelves. It would seem to be more consistent and useful to include all of these oceanic islands in Wallacea, for the reasons outlined above.

Before considering the problems posed by the Cape and Antarctic floral Kingdoms, it is necessary first to examine in more detail Takhtajan's system of plant geography, of which

they form a part. As will be seen, this also reveals a number of other anomalies, and leads to a general review of the other floral Kingdoms, which in turn leads to a re-evaluation of the whole concept of floral Kingdoms.

TAKHTAJAN'S FLORISTIC SYSTEM

Takhtajan was the first plant geographer to introduce a comprehensive, detailed system of floral units, or 'phytochoria', at four different levels, and to provide criteria for recognizing each of these levels. In the Introduction to the (1986) English-language edition of his book, Takhtajan states that a floristic system is a hierarchical classification of coordinated natural floristic areas. He defines six Kingdoms or 'Realms', and states that these are characterized by containing endemic families, subfamilies and tribes, with very high generic and species endemism. They are divided into 35 Regions, said to be characterized by high generic and species endemism, sometimes even by endemism at the level of families and orders. (Takhtajan also quotes Tolmatchev (1974) as stating that each Region contains a definite set of dominant families, in a relatively stable quantitative relationship, but he does not document this characteristic.) These 35 Regions are divided into 153 Provinces, in which endemism is characteristically at the species level; if endemic genera exist, they usually contain only a single species or a few species. The Provinces can be divided into Districts, which are characterized mainly by endemism at the subspecies level, but Takhtajan does not list or describe these. Although Takhtajan mentions orders, subfamilies and tribes in these definitions, he hardly mentions them in the descriptive part of his book. Effectively, therefore, Takhtajan's analysis is at the level of families, genera and species.

The principle underlying Takhtajan's system is presumably that the distinctiveness of each floral unit is the result of isolation, which has permitted independent evolution within the area in question. This would lead to the gradual appearance of novelty at a level that would at first be recognized by a taxonomist as a new species. Later, with additional evolutionary change, and an increase in the number of species, recognition at the generic level would seem appropriate. A continuing increase in diversity might eventually lead to the appearance of so many taxa and so much diversity, that a taxonomist would wish to place all of these in a separate family, and so on. The geographical range of a genus would inevitably be equal to or greater than that of any one of the individual species of which it is composed, and would similarly be equal to or less than that of the family to which it belonged. This, together with the sequential nature of the antiquity of the taxa involved (species, genus, family, etc.), is the process underlying the hierarchical nature of Takhtajan's system, at least in the case of stable continental areas, for which it was designed.

In this context, it is interesting to note the work of McLaughlin (1992), who took 101 local floras in the western United States and analysed them in two different ways. In one of these, the choria were defined using a species matrix (the original data base of presence–absence values for

all species), a genus matrix constructed from the species presence-absence data base with elements equal to the number of species in each genus in each local flora, and a family matrix with elements equal to the number of species in each family in each local flora. McLaughlin comments that the two family-level choria that result from his analysis are best recognized as 'Regions', that the five genus-level choria correspond closely to the 'Provinces' of the western USA as mapped by Takhtajan (1986), and that the species-level choria are best ranked as 'Subprovinces'. As McLaughlin notes, these results document a natural hierarchy of successively larger natural choria, that are presumably the result of a series of historical events of vicariance and dispersal. He has thus provided clear and direct evidence for the reality underlying Takhtajan's system.

[There is, of course, no such hierarchy in the relationship between the environments that are occupied by the choria. For example, the African Subkingdom is divided into Regions that are made up of desert (the Saharan and Karoo–Namib Regions), tropical forest (the Guinea–Congo Region), coastal areas (the Uzambaru–Zululand Region) and woodland-savanna-grassland (the Sudano–Zambesi Region). There is no hierarchical relationship between these different Regions, which are each dominated by a different biome.]

The data contained in Takhtajan's book are summarized in the first and second columns of Table 1; where he does not give totals, his lists of continental angiosperm taxa have been counted. Two points arise from these figures.

Firstly, Takhtajan writes of 'levels' of endemicity, and he presumably intended this to refer to percentage endemicity – there would be little significance in the simple totals of endemic taxa, as these would depend on area and ecological richness. However, he nowhere gives figures for the total number of families or genera in the different Kingdoms. It is nevertheless possible to make some estimates of percentage endemicity at family level by using the data provided in Heywood's (1978) set of maps, and these are shown in Table 1, columns 3–5. (Heywood documents only 306 families, compared with Takhtajan's 500 families, but there is no reason to believe that this has led to any systematic distortion of the biogeographic nature of the data.) Figures are not available for the Antarctic Kingdom, as no-one has as yet added together the families that are found in each of these scattered areas. (I have followed most plant geogra-

phers in using Drude's (1890) term here, rather than Takhtajan's 'Holantarctic').

Secondly, Takhtajan (1986, p. 3) introduced an additional rule "that floristic differences between choria of any category (e.g. provinces) are inversely proportional to their size. In other words, the smaller the territory constituting our provinces (or choria of any other category), the stronger must be the expression of its floristic distinctiveness, and vice versa. Thus such provinces as the Eastern European, Northern European and Western Siberian are not separated by any appreciative (*sic* – he presumably means 'appreciable') floristic peculiarities, and endemism in those provinces is poorly expressed (especially in the last two). But as these provinces occupy a vast territory, their separation is considered justified". This rule would lead one to expect a low level of endemicity in the Holarctic Kingdom, which covers more than half of the world's land area, whereas in fact it shows a high level of endemicity. Conversely, one would expect a high level of endemicity in the Cape Kingdom, which has the smallest area, but in fact shows a lower level (see Table 1, columns 3–5).

THE PROBLEM OF THE CAPE KINGDOM

'The Cape Kingdom is the smallest of the world's floristic kingdoms, but because of its exceptionally distinctive flora and its independent historical development, phytogeographers unanimously separate it from the rest of Africa.' (Takhtajan, 1978, p. 263). The number of endemic families and genera that he lists in this Kingdom (seven or eight endemic families, 200 endemic genera) is not very different from that of the Northeast Australian *Region* (eight endemic families, 150+ endemic genera), and is less than that of the East Asiatic *Region* (20 endemic families, *c.* 300 endemic genera). In fact, the endemicity of the Cape area is primarily shown at the species level, for it contains 8550 species, of which 73% are endemic, while most of the endemic genera contain only one species or a few species. This is a pattern that, according to Takhtajan's own criteria quoted above, is characteristic of a Province, rather than of a Region or Kingdom. However, here Takhtajan may be basing his judgement on the very high *density* of endemic taxa, which are found in a very small area of the Cape. It may be reasonable to recognize this ecological diversity by some

Table 1 Levels of endemicity in Takhtajan's Kingdoms

	Numbers of endemic taxa, from Takhtajan		Families, from Heywood		
	Fams.	Genera	Total no.	Endemics	Endemics (%)
Holarctic Kingdom	52	1280+	202	13	6.4
Palaeotropical Kingdom	25	(no estimate)	342	13	3.4
Neotropical Kingdom	25	3000–3660	223	17	7.6
Cape Kingdom	8	200	150	7	4.7*
Australian Kingdom	17	550	177	10	5.6
Antarctic Kingdom	11	34	?	?	?

*From Bond & Goldblatt (1984).

degree of up-grading of the level of phytogeographic recognition. However, to raise the Cape area to a Kingdom raises it to the same level as the whole of the Palaeotropical Kingdom, which stretches from southern Africa to beyond Southeast Asia and to the most distant Pacific island. Such a decision suggests that the Cape flora is as different from that of the rest of Africa as is that of the Neotropical Kingdom, whereas in fact it is merely a flora that contains over 140 families that are also found in adjacent parts of southern Africa, plus a few unusual, endemic families.

Recent research has shown that the Cape area is merely one of five areas that have a mediterranean-type climate (warm, dry summers and cool, wet winters) and therefore is not particularly abnormal. The other areas are California, central Chile, south-western Australia and the Mediterranean Basin itself, and the research has recently been reviewed by Cowling *et al.* (1996). 'The five mediterranean-climate regions of the world occupy less than 5% of the earth's surface yet harbour about 48,250 known vascular plant species, almost 20% of the world total. These regions also have exceptionally high numbers of rare and locally endemic plants and include two recognized species flocks, one in south-western Australia and the other in the south-western Cape, South Africa.' (*loc. cit.* 362). 'Regional diversity (at a scale of $10–10^6$ km^2) in mediterranean-climate regions ranks among the highest in the world. The south-western zone of the Cape has the highest diversity at this scale: for a given area, this region has, on average, 1.7 times the diversity of south-western Australia, about 2.2 times the diversity of the south-eastern Cape, California and the Mediterranean Basin, and 3.3 times the diversity of Chile. ….Diversity in small areas (> 30 km^2) of south-western Australia is not significantly different from similar areas of the south-western Cape.' (*loc. cit.* 363).

These are two comments from a body of research which shows that the Cape flora is not a unique phenomenon, demanding unique recognition at the highest level of the biogeographic system. Instead, it is merely one of several floras that have resulted from similar ecological/evolutionary histories. Before the beginning of global cooling and drying in the Pliocene, all five regions were covered by subtropical forests, but now have a mixture of floras that include some relics of the former forest, plus sclerophyllous shrublands and woodlands, with drought- and fire-adapted lineages predominating (Cowling *et al.*, 1996). It follows that all five floras should be treated similarly in the biogeographic system. Takhtajan (1986) recognizes both the Mediterranean flora and the Southwest Australian flora as plant-geographical Regions, but recognizes the central Chilean and Californian floras only as Provinces. In view of the long tradition of regarding the Cape flora as a Kingdom, it might be best to 'demote' it only to the rank of a Region rather than viewing it merely as a Province.

Takhtajan's principle of recognizing the density of endemic taxa also led him to an up-grading of the Pacific island of New Caledonia, recognizing it as the Neocaledonian Subkingdom of the Palaeotropical Kingdom. Its unusual ecology (its soils are dominated by serpentine rocks) and long isolation have led to the evolution of many endemic taxa. Its flora has most recently been described by Morat (1993), who states that its flowering plant flora contains five endemic families and 108 endemic genera, while 80% of its 3061 species are endemic. As in the case of the Cape flora, this high level of endemicity nevertheless does not suggest that the flora should be given so high a ranking in the system of plant biogeography, and it would be more consistent to give it the rank of a Region.

It is confusing that the principle used by Takhtajan in the cases of the floras of the Cape and of New Caledonia is quite the opposite of the principle introduced in the case of the Provinces of the Circumboreal Region, where large *area* was recognized despite the extremely low density of their endemicity. There may be a case for some modifications of the overall scheme where local ecology has provided an unusual opportunity for adaptive radiation. However, it is unnecessary and confusing to allow the results to reach to the topmost level of the biogeographic hierarchy, which should be using a single, consistent criterion to display the patterns found at the most general level of analysis. Identification of the plant biogeographic Kingdoms is the concern of historical biogeography. This can document the events that led to the area in question becoming isolated from other areas or joined to them, and the resulting patterns of palaeogeography. This, may in turn, allow the identification of the sources and times of immigration of new groups that diversified in the area, perhaps leading also to the extinction of groups that were already there. In contrast, the identification of the relative rank of the lower levels of the biogeographic system is the concern of ecological biogeography. This can explain the patterns of exploitation of the area by the different elements of the biota, and may also explain why some regions contain levels of endemicity that are very different from those of other regions. Confusion between these two approaches and disciplines has lain at the heart of many of the problems addressed in this paper.

THE PROBLEM OF THE HOLARCTIC KINGDOM

As can be seen from Table 1, there is a further anomaly in the fact that the Holarctic Kingdom contains a far greater number of endemic angiosperm families than any other Kingdom. There are two possible explanations of that. First, it might be suggested that it was the result of the evolution of new families in response to the progressive cooling of the Holarctic environment that began in the early Tertiary, continued through the late Tertiary, and culminated in the Ice Ages. However, of the fifty-two families that are endemic to the Holarctic Kingdom, Takhtajan lists twenty-eight as being endemic to only one of its nine constituent regions, i.e. nearly half of these genera are comparatively widespread. Analysis of the number of genera in each of the fifty-two endemic families, as listed in the Appendix to his book, shows that forty of them contain only a single genus, eleven contain two to six genera and one contains ten genera. Such a pattern is more plausibly explained as the result of

impoverishment of already widespread genera because of repeated north–south changes in range during the series of Quaternary glacials and interglacials, rather than as the result of the extension of range of newly evolved genera.

A more plausible possibility is that the taxonomic diversity of the Holarctic Kingdom has been artificially inflated. This is supported by the comments of Good (1974, p. 27): 'many similar classifications made by botanists of the northern temperate regions are marred by the exaggerated importance given to this part of the world'. (It is worth noting in this context that 64% of that part of Takhtajan's (1986) book that deals with the system of floral units is devoted to the Holarctic Kingdom, and only 36% to the whole of the rest of the world.) Although comparative figures for angiosperms are not available, there can be little doubt that their diversity follows the usual pattern of relationship to latitude, i.e. that diversity is low in high latitudes, and high in low latitudes. The low diversity of the angiosperm flora of the Holarctic Kingdom might well also have tempted the many northern hemisphere botanists to raise the taxonomic rank of the taxa they studied, while the greater diversity of the taxa in the tropics might well have discouraged such a tendency. The suggestion that there may have been taxonomic inflation in Takhtajan's data base for the Holarctic Kingdom is supported by comparison of his figures for endemic families with those derived from Heywood's (1978) atlas (compare columns 1 and 3 in Table 1). Although in most of the Kingdoms Heywood's figures are half those of Takhtajan, in the Holarctic Kingdom they are only one quarter those of Takhtajan. All of these observations support the view that the high figure for endemic genera (and therefore also for percentage endemicity) in the Holarctic Kingdom is a taxonomic artefact.

It is worth noting here, in passing, that both zoologists and botanists have been uncertain as to where to draw the line between the Holarctic fauna or flora and that of Africa. As detailed by Takhtajan, some botanists have drawn this line along the northern edge of the Sahara Desert, and others along its southern edge; the most recent analysis is that of Quèzel (1978). Similarly, for the zoologists, while Sclater (1858) placed the boundary in the more northern location, Wallace (1876) instead placed it across the middle of the Sahara.

Consideration of the history of the European/North African area provides a useful perspective to the problem. As late as the Miocene, there was a gradual climatic/biotic transition between the tropical flora of central Africa and the cool-temperate flora of northern Europe. Southern Europe was then covered by subtropical forest. As climates cooled in the Pliocene, that of southern Europe first became warm-temperate and then transformed into the present Mediterranean climate, while the Saharan Desert extended to include the continent-wide stretch of Africa immediately to the south. So, from the point of view of historical biogeography, the Mediterranean region is a modification of the old southern European flora, while the Saharan flora is a modification of the old flora of northern Africa.

So both the Mediterranean flora and the Sahara Desert are interpolations within the former, mid-Cenozoic, floral transition between Africa and Europe. The Sahara is therefore an area in which the former tropical flora of northern Africa has become impoverished, and it is logical to view it as a part of the African floral Kingdom. In general terms, as the mammal and bird fauna of the Sahara will have followed the fate of its flora, it is reasonable to allocate its fauna, too, to the African rather than to the Palaearctic zoogeographic region, and to view the presence of macaque monkeys in North Africa as merely an example of a relict fauna. All this suggests that the southern border of the Holarctic Kingdom should be drawn along the southern edge of the Mediterranean Region, i.e. within Africa but close to the Mediterranean coast and along the northern edge of the Sahara Desert.

THE PROBLEM OF THE ANTARCTIC FLORAL KINGDOM

Compared with the other floral Kingdoms, the Antarctic floral Kingdom presents two unusual features: it encompasses territories that are separated by wide stretches of ocean, and it is difficult to define. All of this is the result of its tectonic and climatic history.

In the late Cretaceous, after Africa and South America had separated from one another, northern South America developed a tropical North Gondwanan flora, while a more humid South Gondwanan flora developed in southern South America, Antarctica and Australia (all still linked together, and still lacking any polar icecap) (Crane, 1987). This latter flora was the fore-runner of what we today call the Antarctic flora, characterized by *Nothofagus*, podocarp and araucarian conifers and many ferns. Later, after these continents had separated from one another, Australia moved northwards into latitudes with low rainfall, and most of it developed the sclerophyll vegetation that now characterizes the Australian floral Kingdom. The old Antarctic flora is, therefore, now found in southernmost Chile, and in the areas peripheral to the aridity-adapted Australian flora, i.e. in parts of Tasmania, and in the cooler high ground of the mountains of the eastern border of Australia and of New Guinea, as well as in New Caledonia and New Zealand. So today's Neotropical, Antarctic and Australian floral Kingdoms have evolved from one another in response to climatic differences, rather than having evolved in isolation from one another, like the various tropical floras.

The fact that New Guinea, as the leading edge of the northward-moving Australian tectonic plate, eventually came into relationship with Southeast Asia, had added a final layer of complexity to all this. Although the Southeast Asian and Australian continental masses have never been close to one another, the intervening islands have long provided a complex pattern across which some flowering plants have been able to disperse without difficulty. Those of Southeast Asia (the Indo-Malesian flora) have, therefore, successfully colonized not only New Guinea, but also the scattered island groups of the Pacific, and have therefore

provided the overwhelming majority of their flowering plants. As a result, plant geographers view New Guinea as part of the Indo-Malesian floral Kingdom, although its higher altitudes bear a flora that includes elements of the Antarctic flora, such as *Nothofagus*.

The distribution of the Antarctic flora provides problems of definition, at more than one level. For example, Good (1974) includes only the south-western, coastal, parts of Chile, the Falkland Islands, and New Zealand and its associated islands. Takhtajan, on the other hand, also includes more northern parts of South America, up to the latitude of southern Brazil. This is presumably because *Nothofagus*, *Araucaria* and *Podocarpus* form a strong Antarctic element in the forests of the southern Paranà Plateau in Brazil (Hueck, 1966; quoted in de Laubenfels, 1975). But these more northern areas also include desert and pampas, which totally lack the Antarctic flora. Neither Good nor Takhtajan include eastern Tasmania, the mountainous parts of eastern Australia and New Guinea, or New Caledonia, in the Antarctic floral kingdom, despite the presence of Antarctic floral elements in these areas.

This situation provides a biogeographic dilemma, which has so far been confronted only in superficial and inconsistent fashion – by including some of these areas in the Antarctic floral Kingdom, but not others. With our modern knowledge of historical plant biogeography, we can see that Engler's Antarctic floral Kingdom merely contains some (but not all) of the remains of a once-continuous southern Gondwana cool-temperate flora, now scattered into a relict distribution by the processes of plate tectonics, and present only where the persistence of cool, moist climates has allowed it to survive. Each of these areas should, then, be allocated to whatever Kingdom it is now adjacent to, its definition or description in each case containing a mention of its history. The Chile-Patagonian Region would accordingly become a region of the Neotropical Kingdom. It would then follow that the Fernandezian Region and the Region of the South Subantarctic islands (including the Tristan-Goughian Province and the Kerguelenian Province) which according to Takhtajan, have floras closest to that of southern South America, should also be transferred to the Neotropical Kingdom. In contrast, the flora of New Zealand is, according to Pole (1994), basically of an Australian character, the present evergreen forests having only become established since the late Tertiary or early Pleistocene, most or all of it by long-distance dispersal. Accordingly, New Zealand and its surrounding islands should be transferred to the Australian floral Kingdom.

THE PROBLEMS OF THE TROPICAL KINGDOMS

As already noted, Takhtajan (1978) recognizes the flora of South and Central America as the Neotropical Kingdom, but he joins that of Africa with that of the tropical floras to the east as merely Subkingdoms of a single Palaeotropical Kingdom that extends as far as the eastern Pacific islands. His lists show the following: twenty-five endemic Neotrop-

ical families (excluding one found only in the West Indies), twenty endemic families on the African mainland (including the Cape), while three others are shared with the Oriental area; twelve endemic families in Madagascar, while one other is shared with the Oriental area; eleven in the Oriental area, while three others are shared with mainland Africa and one other is shared with Madagascar.

However, using the data in Heywood (1978), and excluding world-wide families from the analysis, one finds the following pattern. The Neotropical flora contains 137 families, 89 of which it shares with the flora of Africa, the latter containing 117 families. Of these 117 African families, 83 are shared with the flora of the India/Southeast Asia area, which contains 108 families.

These figures do not suggest that the flora of Africa is more similar, in numerical terms, to that of India/Southeast Asia than to that of South America. Of course, the similarity between the two Old World floras may be of a different kind, both of them being dominated by the same families, while that of South America is dominated by different families. However, several articles in Goldblatt's (1993) edited volume, which compares the biogeography of Africa with that of South America, make one hesitate to accept unquestioningly the prevailing assumptions on such floral comparisons. For example, Gentry (1993) finds that much of the supposed differences between the lowland tropical forests of the two continents is biogeographic artefact based on provincial taxonomy. He believes that many of the genera on opposite sides of the South Atlantic are closer to one another than either is to other genera on the same continent, and would probably have been placed in a single genus but for the fact that the wide ocean that separates the plants themselves also separates the botanists who have studied them. This similarity persists even at the community level, for comparison of 0.1 ha samples shows that the African sites average 31.3% of genera shared with South America, while Madagascar sites average 40% – the difference between these two figures probably being the result of the floral changes in Africa produced by the increasing aridity of that continent that took place during the Cenozoic. At family level, the composition of the lowland tropical forests is virtually identical in the two continents, and Gentry concludes that the similarities result much more from common origin than from chance immigration. This conclusion is strongly supported by McNaughton *et al.* (1993), who similarly conclude that the arid to subhumid floras (grassland, bushland, savanna, etc.) of the two continents 'had identical origins in vast tracts of West Gondwana before the two continents were separated by continental drift'. Although it may well be that many of the similarities are the result of parallel evolution in two continental floras that started with a similar floral heritage in the mid-Cretaceous, none of these comments suggest that there is a much greater divide between the floras of Africa and South America than between those of Africa and Southeast Asia.

The preceding analysis suggests that each of the three areas that contain a tropical flora (South America, Africa and India/Southeast Asia) should be recognized as a separate

floral Kingdom. This requires at least some new names for the Kingdoms, and in turn provides an opportunity to modernize the nomenclature in both plant biogeography and zoogeography. The term Neotropical has never been truly appropriate for the flora of South America, for the geographical limits of its flora extend far beyond the tropics, and cover the whole of the continent, to its southern extremity. It would be far simpler to refer to the flora as simply 'South American'. Its extension into central America is not a serious obstacle to this course of action, and does not merit the complication of referring instead to a flora of 'South and Central America'. The flora of Africa could simply be called the 'African Kingdom' (the continent itself being recognized as the Ethiopian Subkingdom, of which the Cape flora would become a Region, as discussed above, and that of Madagascar being a second Subkingdom). The remaining area, from India to the Pacific islands, could be called the Indo-Pacific Kingdom. As discussed earlier, the flora of New Caledonia should be recognized as a Region rather than a Subkingdom. Morat's (1993) figures on the affinities of the New Caledonian flora show that, although its largest single affinity is with that of Australia (28.6%), the sum of its floral affinities with areas within the Indo-Pacific kingdom (Malesia, New Guinea, the Solomon Islands, New Hebrides, Fiji, Tonga, Samoa, and the islands of Polynesia and the North Pacific) are nearly 50% of all its

affinities. It would, therefore, be appropriate if the New Caledonian floral Region were assigned to the Indo-Pacific floral Kingdom rather than to the Australian Kingdom.

The changes proposed above are shown in Fig. 3, and would have the following effects on Takhtajan's system.

The Holarctic Kingdom remains unchanged.

The new African Kingdom contains an Ethiopian Subkingdom (containing the Cape Region in addition to the other regions listed by Takhtajan) and the Madagascan Subkingdom.

The new Indo-Pacific Kingdom contains the Indomalesian Subkingdom and the Polynesian Subkingdom.

The South American Kingdom contains, in addition to the regions on the continent itself, the Chile-Patagonian, Fernandezian and South Subantarctic islands Regions.

The Australian Kingdom now contains the New Zealand Region in addition to its former Regions.

In view of the wide-ranging nature of these proposed changes, it is appropriate to pay tribute to Takhtajan's scheme, for he was the first to undertake and publish a hierarchical scheme of the phytochoria down to the level of Province, with an immense documentation of the geographical limits and contents of each. It is always far easier to criticize and amend such a scheme (especially after the passage of many years of increasing knowledge) than to construct it in the first place.
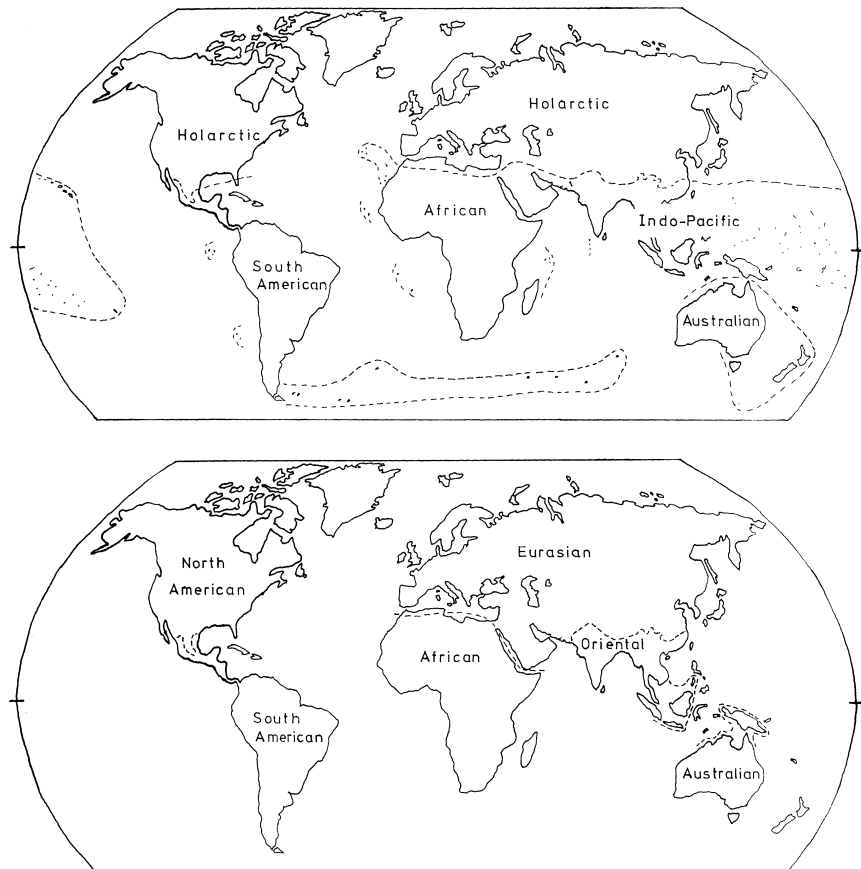

Figure 3 Floral Kingdoms (above) and mammal zoogeographic Regions (below), as now suggested.

THE ROLE OF FLORAL KINGDOMS, AND THEIR DEFINITION

In the preceding pages, I have attempted to suggest a system of floral Kingdoms that is internally consistent. As we have seen, this reconsideration has identified a number of difficulties. These provoke two questions.

First, is the concept of floral Kingdoms still useful and necessary? Perhaps they have outlived whatever usefulness they may once have had, and we should now revert to a purely geographical concept, referring only to floras within South America, North America, Africa, etc. One might also reflect that it is only the fact that plate tectonics have led to the appearance of a number of almost completely separate continents that has made it possible to frame the concept of floral Kingdoms at all. In a Pangaea world, a biogeographer would only be concerned with the analysis of the all-pervading examples of gradients of diversity associated with latitude, altitude, etc. But, in fact, plate tectonics has given us the opportunity to identify major units that are, almost without exception, easy to define because they are mainly surrounded by seas. Furthermore, to jettison the concept of floral Kingdoms would be to leave the remainder of Takhtajan's system of phytochoria headless. It would provide no system that would enable the plant biogeographer to show in simple fashion that, for example, the floras of North America and Eurasia are more similar to one another than either is to the floras that border them to the south, or to indicate that the flora of Madagascar is allied to that of Africa, or that the floras of Oceania are derivatives of that of Southeast Asia and not of those of the Americas.

If, then, the concept of a floral Kingdom is still useful, the second question arises: how *should* a Kingdom be defined? On examination, this single question in fact turns into two inter-related problems – that of defining the contents of a Kingdom, and that of defining its boundaries. Obviously enough, any phytochorion can only be recognized if it is separated from its neighbour(s) by an area of ecological difference or change, for that will both encourage floral differences between the neighbouring phytochoria and limit the extent and rate of dispersal between them. As a result, the contents of the neighbouring phytochoria will come to differ from one another. At the most major and dramatic level, these regions of ecological change are ones that are completely, or almost completely, inimical to the presence of flowering plants; these are exemplified by the seas, oceans, mountain chains or deserts that separate the floral Kingdoms. At lower levels of phytochoria, the clarity of the boundary will depend on the rate of change of factors such as temperature and solar radiation (both of which are affected by latitude and altitude), water availability and the nature of the soil (the latter in turn being affected by local geology). The more rapid the rate of change of these factors spatially, the clearer will be the boundary between the neighbouring phytochoria, so that the clearest examples are where hills or mountains rise steeply from the plains.

As already noted, Takhtajan was the first to provide a detailed system of floral units and of criteria for recognizing them, using levels of endemicity. But he accepted the concepts and maps of Engler (1879, 1882) and Diels (1908), and did not discuss where the lines between the floral Kingdoms should be drawn. Furthermore, apart from criteria of endemicity, Takhtajan did not suggest other requirements for recognizing a floral Kingdom. Although Good, like Takhtajan, accepted the pre-existing concepts and maps, he did go on to discuss these issues and stated (1974, p. 27) 'The object has been to divide the land surfaces of the world into a convenient but not too large number of regions, each of which may be regarded as supporting a flora of its own, that is to say a flora which is characteristic of the region, which, allowing for possible global floral migrations, has largely developed within the region.' In similar vein, Wallace (1876, p. 54) commented that faunal regions: 'should evidently be of a moderate number, corresponding as far as possible with the great natural divisions of the globe marked out by nature, and which have always been recognized by geographers. There should be some approximation to equality of size.' He also noted that the regions which he suggested were similar in area, compact and easily defined. Similarity of area is perhaps the most important of these, for it is a major parameter in the control of diversity. The larger the area, the more likely it is to contain a diversity of environments, within each of which an adaptive radiation of the biota may have taken place, leading to a corresponding increase in biotic diversity.

Following Wallace, we might stipulate that floral Kingdoms, like zoogeographic regions, must be areas of similar size, compact and easily defined. The only difficulty that then arises is that, in some cases, adjacent floras blend into one another, so that no single, clear line can be drawn between them. These cases arise from two quite different historical processes, one geological and the other biological. The geological process has been that of plate tectonics that, as noted above, brought together the floras of Southeast Asia and of Australia/New Guinea. Until then, these floras had never coexisted, having been separated by wide stretches of the Pacific Ocean. The biological process has been that of simple evolution that, as noted earlier, led to the differentiation of the old Gondwana flora, in two stages. First, it differentiated into broadly latitudinal North Gondwanan and South Gondwanan floras, and then the latter differentiated into an 'Antarctic' flora adapted to the cold climates of the far South, and an Australian flora adapted to the aridity and poor soils of that continent. All of these floral provinces or floras, then, differentiated from one another, and they could never have been separated by the clear lines delimiting them into floral Kingdoms similar to those that we recognize in the world today. This pattern has been further complicated by the climatic changes of the Ice Ages, which have left patches of 'Antarctic' flora isolated in areas north of its main area of distribution (for example, in southern Brazil), in a manner analogous to the scattered 'glacial relicts' of the northern hemisphere. There are similar problems where the tropical flora of Southeast Asia gradually intergrades northwards around the eastern edge of the Himalayan mountain chain and into the cooler floras of eastern China, and where

the tropical flora of South America intergrades with that of North America in northern Mexico.

Quite obviously, the clarity of the boundaries between the floral Kingdoms (and between the phytochoria at lower levels of Takhtajan's system) is variable, depending on the nature of the barrier between them and on the history of their floras. But biologists are accustomed to variation of this kind in their systems – in similar fashion, the precise nature of taxa such as a family or species inevitably differs from phylum to phylum in the plant or animal world. Biology is not physics, and it need not seek to establish rigid and unvarying laws. Biogeographical texts can, and should, consider and explain the varying clarity of the boundaries between the different floral Kingdoms, and such an explanation will have the additional advantage of ensuring that the reader is aware of the historical dimension of the subject. (This last observation reminds us that the historical dimension is a fundamental difference between floral Kingdoms and the lower levels in Takhtajan's hierarchical system. As noted earlier, Takhtajan's Regions differ from one another in their ecology, rather than their history, and the same is true of the lower levels in his system.)

THE HISTORICAL BIOGEOGRAPHY OF FLOWERING PLANTS

The patterns of distribution of the mammals is comparatively easy to understand, because there are only approximately 100 families of living terrestrial mammals. Further- more, because they find it difficult to cross ocean barriers, most of these families are restricted to a limited number of continents. Finally, it is not difficult to identify their fossil remains and to reconstruct the complete animal, and it is therefore comparatively easy to work out the history and patterns of diversification of their lineages in the different continents. By contrast, there are over 300 living families of flowering plants, they are much better at dispersing over ocean barriers, and it is often difficult to progress from individual fossil plant specimens (pollen, leaves, stems, only rarely flowers) to a restoration of the complete plant. It has, therefore, been difficult to reconstruct the history and relationships of the angiosperm families, and to subdivide them into groups showing a comprehensible biogeographic history. For example, of the families whose distribution is documented by Heywood (1978), most are widespread in their distribution; only fifty-six (18%) are endemic to a single biogeographic region, and most of these are relatively unimportant families, restricted to only a few genera.

However, it does seem as if we are now on the verge of a break-through in this. For example, the superorder Liliiflorae is currently divided into 48–56 families. Although many of these show interesting biogeographic patterns, these have hitherto been seen as isolated, uncoordinated phenomena, rather than as being parts of an overall pattern. However, Conran (1995), has subdivided the superorder into ninety-one smaller taxa that are more likely to be monophyletic, and, therefore, more likely to show clear biogeographic patterns resulting from their evolution and dispersal. He has analysed the distribution of these taxa among Takhtajan's thiryt-seven floral regions, and shown that these provide a pattern of relationship that closely mirrors the current pattern of continents and climates (Fig. 4). This is, at first sight, slightly surprising, for one might have supposed that the early appearance and good dispersal abilities of flowering plants might have resulted in the appearance of floral links reflecting the early Cenozoic patterns of geography. However, of course, the taxonomic groups that Conran is

Figure 4 Relationships between the Liliiflorae floras of Takhtajan's (1986) floral regions, after Conran (1995). (1) Circumboreal; (2) Mediterranean; (3) Middle East and central Asian; (4) Saharo–Arabian; (5) Karoo–Namib; (6) Cape; (7) Sudano–Angolan; (8) West African; (9) Madagascan; (10) Indian; (11) East Asian; (12) Indochinese; (13) Malesian; (14) Papuan; (15) northern and eastern Australian; (16) South-western Australian; (17) central Australian; (18) New Zealand; (19) Rocky Mountains; (20) Atlantic North American; (21) Madrean; (22) Caribbean; (23) Eastern Brazilian; (24) Pampas; (25) Amazonian; (26) Venezuela–Surinam; (27) Andean; (28) Patagonian. The frame and its numbers are from Conran's multidimensional scaling analysis.
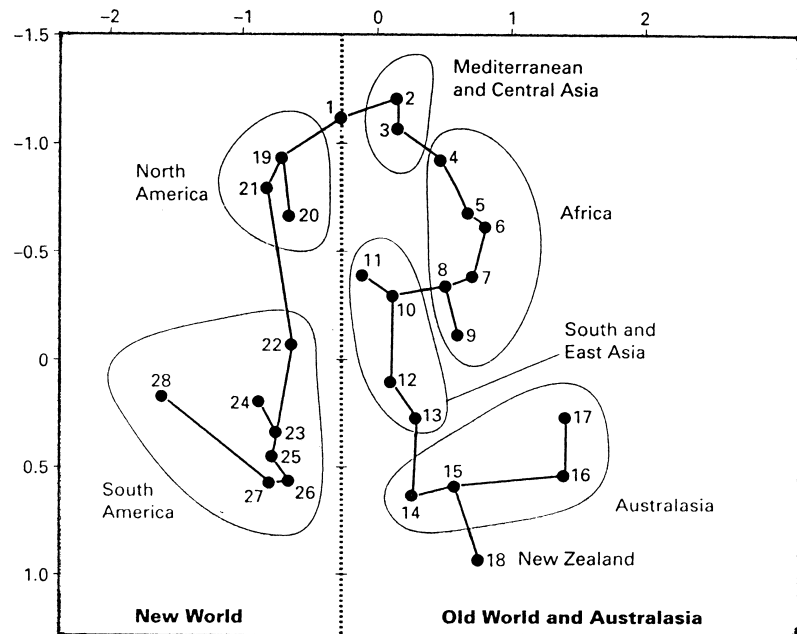
analysing are not the families, which do seem to have appeared much earlier than the mammalian families, but groups of lower taxonomic status, which are likely to have differentiated much later, when the world's geography was similar to, or identical with, that of today. By combining the newer molecular methods to evaluate relationships and to suggest the times of divergence of lineages, it should be possible to put a time-scale into analyses such as that of Conran, and therefore to build up a picture of how and when the lineages of angiosperm spread and diversified, in the same way that fossils are used to document this in the case of mammals. However, the number of monophyletic lineages in Conran's analysis was approximately double the number of families in the conventional classification of the Liliiflorae. If that proves to be the norm, plant scientists will have to identify and interpret the biogeographic relationships of over 600 lineages of angiosperm – a considerable enterprise!

(The reason why there are so many more living lineages of flowering plant than of mammal may be that, because plants are sedentary, they have both the opportunity and the need to become genetically adapted to a much more precise set of environmental conditions than animals, many of which daily traverse a wide range of environments.)

NAMES AND GROUPS IN ZOOGEOGRAPHY

As we have seen, the zoogeographic regions that Wallace suggested were based mainly on the patterns of distribution of terrestrial mammals, which are confined to the continental areas (apart from a few types of rat, which have spread from Southeast Asia to Australasia). However, mammals are unusual in their inability to cross even comparatively narrow stretches of ocean barrier, and this is doubtlessly correlated with their homoiothermal physiology, as a result of which they cannot survive for very long without food, and need a fairly frequent supply of fresh water. Most other groups of terrestrial animals show biogeographic patterns more similar to those of the flowering plants, in which at least some members of the group have developed methods of overcoming the ocean barriers, either by having special dispersal mechanisms to do so actively, or by adaptations for passive dispersal on or in the bodies of birds or bats.

Under these circumstances, it seems to be inappropriate to call Wallace's Regions 'zoogeographic Regions', with the implication that these are the patterns of distribution of animals in general. It would, therefore, be better to refer to them more specifically as 'mammal zoogeographic Regions', with the implication that other groups of animals may have different patterns (as they do).

Furthermore, just as the opportunity was taken earlier in this paper to suggest the modernization and simplification of the names of the floral Kingdoms, so one could do the same with the names of the mammal biogeographic Regions. Although generations of students have had to learn the names Neotropical, Nearctic and Palaearctic, these could simply be renamed as South American, North American and

Eurasian mammal biogeographic Regions. The effects of this change, and of the recognition of Wallacea for the area between the Oriental and the Australian Regions, are shown in Fig. 3.

CONCLUSIONS

The histories of the concepts of floral Kingdoms from de Candolle and Engler, and of zoogeographic Regions from Sclater and Wallace, to the concepts in use today are briefly reviewed, and the differences between them are analysed.

It is concluded that the concept of Wallace's Line as a division between the faunas of the Oriental and Australian Regions is not helpful or heuristic. It would be more scientifically productive to restrict the two Regions to the continents, as defined by the edges of the continental shelves, and to accept the name 'Wallacea' for the intervening area, within which the focus of research is on the phenomena of island biogeography, rather than on those of continental biogeography.

The methodology of Takhtajan's system of phytochoria, using levels of endemism, is reviewed and shown to be inconsistent. The Cape phytochorion is merely one of five with mediterranean-type climates, all of which show high levels of diversity, and it should be recognized only as a Region, not as a Kingdom.

The Antarctic floral Kingdom is composed of some, but not all, of the disjunct fragments of the Late Cretaceous South Gondwana flora. Unlike the other Kingdoms, it is small, scattered and difficult to define. The consistency of the plant geographical system is better served by transferring some of the Regions of the Antarctic Kingdom to the South American Kingdom and the rest to the Australian Kingdom, in each case noting their individual historical and ecological characteristics.

Comparison of modern accounts of the floras of South America, Africa and India/Southeast Asia suggest that they are of equal distinctiveness, and should be viewed as three separate floral Kingdoms.

The biogeographical names Neotropical, Nearctic and Palaearctic for floral Kingdoms and zoogeographic Regions, coined in the nineteenth century, are cumbersome and unnecessary, and should be replaced by the simple terms South American, North American and Eurasian. Wallace's 'zoogeographic Regions' are based on the distribution of mammals, which have very little ability to cross ocean gaps. Because many other animal groups are better at this dispersal, and have been able to colonize oceanic islands, these show quite different patterns of distribution. It would therefore be better to refer to Wallace's regions as 'mammal zoogeographic Regions'.

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BIOSKETCH

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