

Toward a terrestrial biogeographical regionalisation of the world: historical notes, characterisation and area nomenclature

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The publisher regrets to inform readers that the version of this paper published in issue 3 was missing its final page numbers 187–224, it was published with pages A–AL instead. The suggested citation for the LAS Johnson Review is as follows:

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There were also three other minor errors that should be corrected as follows.

The citation of ‘Wallaschek 2015’ on p. 188 (p. B) should have been ‘Wallaschek 2015a’.

In the Diagnosis section for ‘Arctic subregion LeConte (1859)’ (p. 204, p. Q), an additional closing parenthesis was included in the wrong place (after ‘Nunavut’). The text should be corrected as follows:

Alaska (including the St Lawrence, Diomedé and Aleutian Islands), northern Canada (Yukon, Northwest Territories and Nunavut, northern parts of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec, and Newfoundland and Labrador) and Greenland.

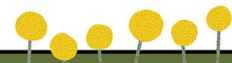
In the reference list, Wallaschek 2015 should have been deleted because it was a duplication of Wallaschek 2015a.

These errors have been corrected in the version that is available online. We apologise for the errors and any confusion this may have caused.

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Toward a terrestrial biogeographical regionalisation of the world: historical notes, characterisation and area nomenclature

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ABSTRACT

An interim hierarchical classification (i.e. biogeographical regionalisation or area taxonomy) of the world's terrestrial regions is provided, following the work of Morrone published in *Australian Systematic Botany* in 2015. Area names are listed according to the International Code of Area Nomenclature so as to synonymise redundant names. The interim global terrestrial regionalisation to the subregion level recognises 3 kingdoms, 2 subkingdoms, 8 regions, 21 subregions and 5 transition zones. No new names are proposed for the regions; however, Lydekker's Line is renamed Illiger's Line. We note that some regions still require area classification at the subregion level, particularly the Palearctic, Ethiopian and Oriental regions. Henceforth, the following interim global regionalisation may be used as a template for further revisions and additions of new areas in the future.

Keywords: area taxonomy, bioregionalisation, Ethiopian region, Holotropical kingdom, Nearctic region, Neotropical region, Neotropical subkingdom, Oriental region, Palearctic region, Paleotropical subkingdom, transition zones.

Introduction

North of the Equator also south we trace
Of either TROPIC the imagined place;
The space between, the TORRID ZONE we all;
Whose scorching belt surrounds this earthly ball;
Beyond the tropics, nearer to each pole,
More gentle skies the TEMPERATE ZONES control;
While at each pole is placed a FROZEN ZONE,
Where frost eternal rears his icy throne [Newton 1845, p. 2, The five zones of the Earth].

Our aim is to provide a detailed global biogeographical regionalisation (i.e. hierarchical classification) for the world's terrestrial biota to the subregion level. Our study will advance the scheme of Morrone (2015a) by using a thorough biogeographical classification or area taxonomy (see Ebach and Michaux 2017) to justify each area as well as using the International Code of Area Nomenclature (ICAN; Ebach *et al.* 2008) to stabilise the proliferation of names by providing a synonymy, diagnosis and discussion for each valid name. Names within the biogeographical hierarchy usually fall into five levels, namely kingdoms (also known as realms), regions, dominions, provinces and districts. In some cases subkingdoms, subregions or subprovinces are recognised. The resulting hierarchical area taxonomy may be used as the basis for future global, intercontinental or regional biogeographic studies, without the need to apply new names. This study does not propose how to discover or identify natural biogeographic areas (i.e. endemic areas), rather we use the biogeographical literature to build a database of available names with a list of synonymies within a biogeographical hierarchy called an area taxonomy. We hope our study builds towards a global standard and database for biogeographic areas and names.

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To understand the vast biogeographical literature and past discussions concerning the validity of certain areas, such as the Holarctic, a historical excerpt is presented below. For a full account, we recommend von Hofsten (1916) for early history of biogeography, Egerton (2012) for the history of ecological biogeography, Wallaschek (2009, 2010a, 2010b, 2011a, 2011b, 2012a, 2012b, 2012c, 2013a, 2013b, 2014, 2015a, 2015b) for the history of zoogeography, and Ebach (2015) for the history of 18th and 19th century regionalisation. The summary focuses on past controversies, including the description of natural regions and the acceptance of the Holarctic in the 19th, 20th and 21st centuries.

Summary of the history of biogeographical regionalisation

Global bioregionalisations were first proposed in the early 19th century, most notably by de Candolle (1805, 1820), Latreille (1815), Schouw (1823), Prichard (1826) and Swainson (1835). The first global hierarchical area classification was proposed by Wagner (1844, 1845, 1846a, 1846b) in a three-part monograph titled *Die Geographische Verbreitung*

der Säugethiere Dargestellt [The geographical distribution of mammals], which was based on the mammalian distributions proposed by Illiger (1815; see also von Hofsten 1916; Kendeigh 1954; Smith 2005; Egerton 2012; Wallaschek 2015a; Ebach 2021). Wagner's work contained the first global biogeographic map and area taxonomy (map republished in Hermogenes de Mendonça and Ebach 2020; area taxonomy republished in Ebach 2021; Fig. 1, Table 1). Unlike previous maps, such as Schouw's *Verbreitungsbezirk und Vertheilungsweise der Arten* [Distributional areas and distributions of species] (Schouw 1823), Wagner's map included all terrestrial areas rather than the distribution of economically important cereal crops (e.g. oats, wheat, maize, rice, rye). The map it most closely resembles is Zimmermann's *Tabula mundi geographico zoologica sistens quadrupedes: hucusque notos sedibus suis adscriptos* [Geographical map of the world's quadrupeds] (Zimmermann 1777, p. 1783; Fig. 2); however, Zimmermann's map simply shows the distributions of terrestrial quadrupeds over a map of the Old and New Worlds (i.e. North and South America, Africa, Europe, Asia and Australia). Wagner's map attempted to show the actual distributional areas of mammals as a whole. Wagner had created the first global biogeographic map that represented the first hierarchical classification (Table 1).

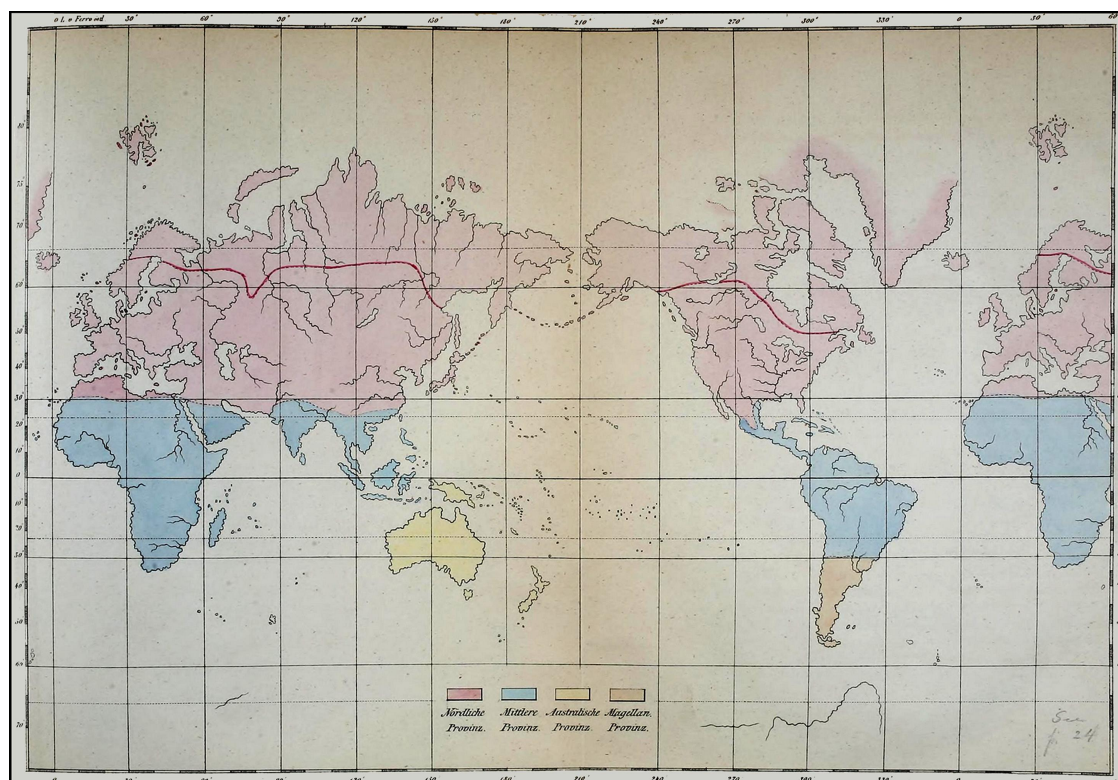


Fig. 1. Representation of the distribution of mammals according to their zones and provinces by Wagner (1844). The southern boundary of the northern polar province is indicated by a line of a different colour, drawn somewhat further south than the equatorial border of the Arctic fox (*Vulpes lagopus*), although not so far in some places as the reindeer may descend there on their summer migrations. The southern polar province is not included in this map, because it is only in the process of discovery and, according to all previous experience, it does not harbour land mammals (Wagner 1846b, p. 241; Table 1).

Table 1. The hierarchical classification of zones, provinces, subprovinces and regions listed by Wagner (1844, 1845, 1846a, 1846b).

Zone	Province	Subprovince	Region
Northern	Polar	Europe	
		Novaja Zemlja	
		Siberia	
		America	
		Greenland	
	Old World	Middle Europe	
		South Siberia	
		Inland Sea Steppes	
		Mediterranean Basin	
		High Asia	
		Japan	
		Temperate North America	
	North America		
Middle or Tropical	South Asia	–	
	Africa	South Africa	
		West Africa	
		Madagascar	
	Tropical America	Western Slopes	Coastal
			Western Sierra
			Cordilleran
		Eastern Slopes	Parana
			Eastern Sierra
			Forest
Southern	Australian	South-eastern Australia	
		South Australia	
		South-western Australia	
		North-western and northern Australia	
		Van Diemensland	
	Magellanian	Pamas	
		Patagonian	
		Chilean	
	Southern Polar	–	

Note that Wagner considered a Southern Polar province but omitted it partly because ‘we know too little about it and partly since it has no land-animals, and the marine mammals for the most part the same ones are found on the coasts of South America, South Africa, and Australia’ (Wagner 1844, p. 86).

Natural areas

Prior to Wagner, there was much discussion among zoogeographers over the ‘naturalness’ of areas. Early naturalists, such as Fabricius (1778) and Latreille (1815), had proposed areas that Swainson (1835) had considered to be artificial. In fact, Kirby and Spence (1826) stated:

...any division of the globe into climates, by means of equivalent parallels and meridians, wears the appearance of an artificial and arbitrary system, rather than to one according to nature [p. 487].

Yet, this is exactly what phytogeographers such as Schouw (1823), Meyen (1846) and Grisebach (1872) and later zoogeographers (e.g. Forbes 1846; Schmarda 1853; Merriam 1892) were practising during the 19th century, a method that continues to this day (see Olson *et al.* 2001).

This approach differs from the identification of natural areas, that is, the earth being divided into naturally occurring biogeographical units on the basis of their endemic taxa, in the same way the living world is divided into taxa (e.g. species, genera, families). A world naturally divided into units would also apply at the biotic level; Australia has a unique flora and fauna, that is, a biota, which is very different from the biota of other continents with similar climates. Yet, when we observe this biota, we discover that plant species interact with the landscape (i.e. topography, soil, climate) and, therefore, produce plant forms and vegetation types. For example, an arid area will not produce the same types of trees you find in say, a rainforest. The plant forms in an arid area are stunted, have small leaves, where rainforest plants would be taller, form canopies and have larger leaves. The whole vegetation in fact would be different. A rainforest would have dense foliage, high trees all competing for sunlight, where an arid area would have a vegetation type that suits the dry and hot environment that it grows in.

Both approaches, the taxonomic and vegetational, can be described as ‘natural’; the taxonomic is a result of biogeographical homology and the vegetational is a result of plant forms. Yet, only the taxonomic is in anyway evolutionary in the simplest sense of the word. If we say that the family Macropodidae, namely the kangaroos and their allies, is endemic to Australasia, then we mean that kangaroos and all their nearest relatives are more closely related to each other (a monophyletic or natural taxon) than they are to anything else; that is, they are endemic to one area. With vegetation, this becomes problematic. A rainforest may be defined in a particular way, on the basis of the types of unique plant forms, rainfall, soil type and so on. This means that there is a universal rainforest, but the taxa that inhabit one rainforest may share only a distant relationship with the taxa in another. In this sense the plant forms and vegetation appear to be natural, but from an evolutionary standpoint they are artificial groups. The difference between taxonomic and



Fig. 2. *Tabula mundi geographico zoologica sistens quadrupedes hucusque notos sedibus suis adscriptos*, second edition (Zimmermann 1783). The revised map in the 1783 German edition contains the newly discovered Sandwich Islands (Hawai'i) and the Seychelles, which were absent in the original 1777 edition (Ebach 2015, p. 31; source: National Library of Australia).

vegetational regionalisations jarred with early ecologists such as Cowles (1908), who chastised taxonomy for producing artificial species, believing that taxonomists should be concerned with populations and their physiological forms, given that it is the environment that controls these forms.

Hierarchical area taxonomy

For the practical purposes of area taxonomy (i.e. biogeographical regionalisation, bioregionalisation, area classification), how one determines an area is not critical. Rather, it is how these areas relate that determines naturalness, and that relationship is based on biogeographical homology (Morrone 2001a; Ebach and Michaux 2017). Sclater (1858) hinted at this relationship being vital:

...little or no attention is given to the fact that two or more of these geographical divisions may have much closer relations to each other than to any third, and due regard being paid to the general aspect of their Zoology and Botany, only form one natural province or kingdom (as it may perhaps be termed), equivalent in value to that third [p. 130].

A decade later, Huxley (1868) made a similar statement on relationship:

I think it becomes clear that the Nearctic province is really far more closely allied with the Palæarctic than with the Neotropical region, and that the inhabitants of the Indian and the Æthiopian regions are much more nearly connected with another and with this of the Palæarctic region than they are with those of Australia [p. 314].

Yet, few 19th century plant and animal geographers tried to uncover natural biotic relationships. The biogeographic map produced by de Candolle (1805) attempted to use soils, climate and drainage to justify a relationship or connection, but failed. The link between biotic relationships and biogeographic areas came much later in the 20th century (Platnick and Nelson 1978; Rosen 1979; Nelson and Platnick 1981; Nelson and Ladiges 1996).

Sclater (1858) did provide a method to determine potential 'natural' areas by measuring endemism and tallying the number of endemic bird taxa in each area. Essentially, Sclater's areas were hierarchical in nature and covered all territorial areas, with the exception of the newly explored Antarctica and Subantarctic Islands. Sclater's areas and his

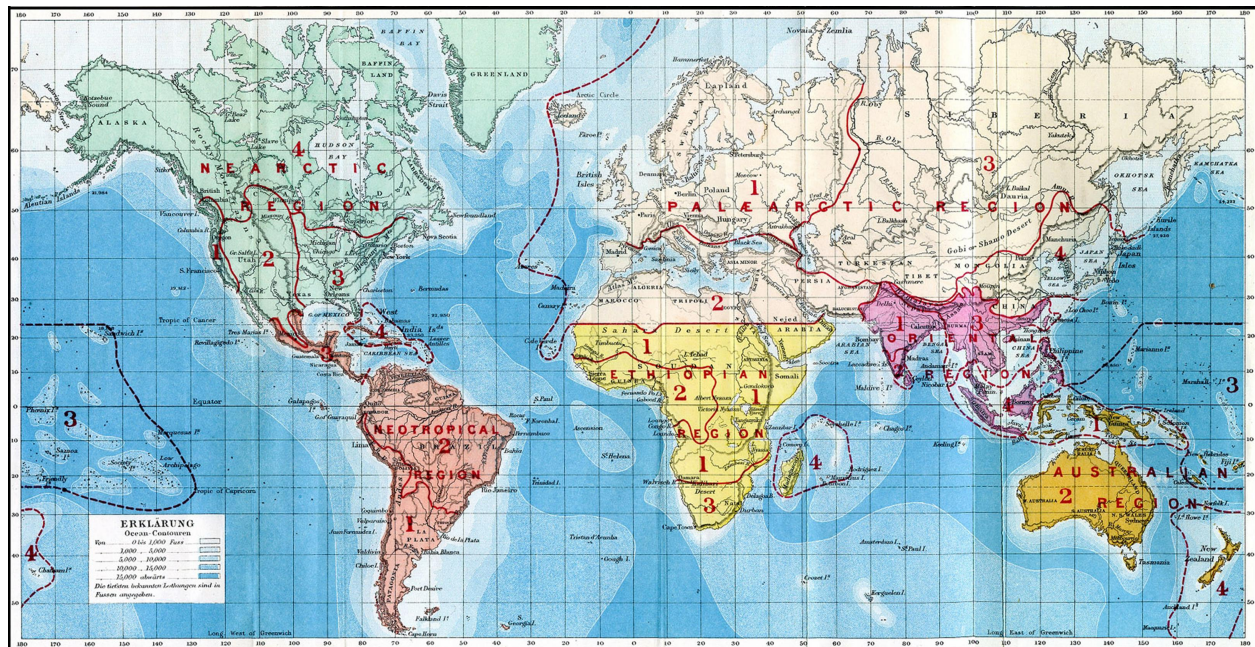


Fig. 3. Zoogeographic regions recognised by Wallace (1876a, 1876b) in *The Geographical Distribution of Animals*.

methodology of tallying up the numbers of taxa endemic to each area were adopted by Wallace (1876a, 1876b), who recognised Sclater's six avian zoogeographic regions based on vertebrate distributions (Fig. 3, Table 2). Wallace preferred Sclater's system because it initiated:

a more natural system, that of determining zoological regions, not by any arbitrary or a priori consideration but by studying the actual ranges of the more important groups of animals [Wallace 1876a, p. 53].

But not all of Sclater's areas were adopted:

Mr. Sclater had grouped his regions primarily into Palaeogæa and Neogæa, the Old and New Worlds of geographers; a division which strikingly accords with the distribution of the passerine birds, but not so well with that of mammalia or reptiles [Wallace 1876a, p. 59].

Wallace's biggest problem was the push back from other vertebrate zoologists, such as Heilprin (1882) and Allen (1871), who regarded the circumpolar zones as valid climatic areas based on a law of the distribution of life in circumpolar zones, which was addressed in some detail by Wallace (1876a):

But this supposed 'law' [of Allen 1871] only applies to the smallest details of distribution – to the range and increasing and decreasing numbers of *species* as well pass from north to south, or the reverse; while it has little bearing on the great features of zoological geography – the

limitation of groups of *genera* and *families* to certain areas. It is analogous to the 'law of adaptation' in the organisation of animals, by which members of various groups are suited for an aerial, an aquatic, a desert, or an arboreal life; are herbivorous, carnivorous, or insectivorous; are fitted to live underground, or in fresh waters, or on polar ice [Wallace 1876a, p. 67, original emphasis].

Wallace here conjures up the stations and habitations of de Candolle (1820):

By the term *station* I mean the special nature of the locality in which each species customarily grows; and by the term *habitation*, a general indication of the country wherein the plant is native. The term *station* relates essentially to climate, to the terrain of a given place; the term *habitation* relates to geographical, and even geological, circumstances [de Candolle translated in Nelson 1978, p. 280, original emphasis].

Allen states:

The recognition of a 'Nearctic' as contradistinguished from a 'Palæarctic region' is almost equally arbitrary and at variance with the law of the distribution of life in circumpolar zones [Allen 1871, p. 382].

Other zoogeographers adopted the Holarctic including Blanford (1890), who used the term Aquilonian as an equivalent, and Lydekker (1896; see Arldt 1906 for further authors). The debate between Wallace and his adoptees

Table 2. The Sclater–Wallacean areas based on vertebrate distributions.

Area or division	Region	Subregion	Remarks
Arctogæa	Palæarctic	European	
		Mediterranean	Transition to Ethiopian
		Siberian	Transition to Nearctic
	Nearctic	Manchurian	Transition to Oriental
		Californian	
		Rocky Mountain	Transition to Neotropical
		Alleghany	
		Canadian	Transition to Palæarctic
	Ethiopian	East African	Transition to Palæarctic
		West African	
		South African	
	Oriental	Malagasy	
		Indian	Transition to Ethiopian
		Ceylonese	
		Indo-Chinese	Transition to Palæarctic
		Indo-Malayan	Transition to Australian
Notogæa	Australian	Austro-Malayan	Transition to Oriental
		Australian	
		Polynesian	
		New Zealand	Transition to Neotropical
	Neotropical	Brazilian	
		Chilean	
		Mexican	Transition to Nearctic
		Antillean	

The table is a reproduction of the 'Table of Regions and Sub-regions' (Wallace 1876a, p. 81) and includes names that are consistent with Wallace's maps (Wallace 1876a, pp. 181, 251, 315, 387, 1876b, pp. 3, 115) and his discussion on the regions and subregions (Wallace 1876a, pp. 71–81). The Nearctic has been placed after the tropical to better fit Wallace's areas or divisions (Wallace 1876a, p. 66).

(i.e. Sharpe 1893; Sclater and Sclater 1899; Fig. 4, 5) and North American zoologists such as Allen, Heilprin, Gill, Günther and Cope (neither of whom published a map) continued in society journals (see Ebach 2015). English ornithologist Alfred Newton, friend to both sides, tried to convince Wallace of the reality of a Holarctic by private correspondence shortly before the publication of the *The Geographical Distribution of Animals* (Wallace 1876a, 1876b):

Now taking the distribution of these genera from Baird and Sclater I find there are 13 genera wholly confined to the Nearctic region; 20 more of which all the species are

Nearctic, but some of them extend to Mexico[,] a few more to Guatemala... [Wallace to Newton, 8 May 1875, *Wallace Letters Online*, see <https://www.nhm.ac.uk/research-curation/scientific-resources/collections/library-collections/wallace-letters-online/4048/3992/B/details.html>].

I am sorry you are so disturbed about distinctness of Nearctic and Neotrop[ic] regions. Your statistics do not in the slightest degree affect my conviction that they sh[oul]d be kept absolutely distinct [Wallace to Newton, 26 May 1875, *Wallace Letters Online*, see <https://www.nhm.ac.uk/research-curation/scientific-resources/collections/library-collections/wallace-letters-online/4049/3993/B/details.html>].

I will only remark now that you proceed on your supposition that my 'Holarctic' region = your Palæarctic and Nearctic – whereas the southern boundaries of this last are, in my opinion and that of several American zoologists, very uncertain... Thus a very considerable number of the genera, which you assign to your Nearctic and Palæarctic regions, belong really to more southern areas, and by their elimination your lists would present a very different aspect. Again too, you have omitted from your Nearctic list all the Palæarctic genera of birds which inhabit Alaska, and if I am not mistaken these are several Mammals also, making Alaska essentially Palæarctic [Newton to Wallace, 17 June 1894, *Wallace Letters Online*, see <https://www.nhm.ac.uk/research-curation/scientific-resources/collections/library-collections/wallace-letters-online/4300/4425/T/details.html>].

Wallace was not persuaded by Newton's argument and, by 1882, the argument has spilled over into the pages of *Nature* (see Ebach 2015):

[Heilprin] seeks to show that the Neoarctic [*sic*] and Palæarctic should form one region, for which he proposes the somewhat awkward name 'Triarctic region', or the region of three northern continents [Wallace 1883, p. 482].

Briefly stated, it is maintained that ... the Neoarctic [*sic*] and the Palæoarctic [*sic*] faunas taken individually exhibit, in comparison with the other regional faunas (at least the Neotropical, Ethiopian, and Australian), a marked absence of positive distinguishing characters, a deficiency which in the mammal extends to families, genera, and species, and one which, in the case of the Neoarctic [*sic*] region, also equally (or nearly so) distinguishes the reptilian and amphibian faunas [Heilprin 1883, p. 605].

The facts of zoogeography are so involved, and often apparently contradictory, that a skilful dialectician with the requisite knowledge can make plausible argument for antithetical postulates. Prof. Heilprin, being a skilful



Fig. 4. Zoogeographical areas illustrating the *Distributions of Birds* by R. Bowdler Sharpe (1893). The classification is loyal to Wallace (1876a, 1876b) because it clearly distinguishes the Nearctic from the Palearctic.

dialectician and well informed, has submitted a pretty argument in favour of the union of the North American or 'Nearctic' and Eurasiatic or 'Palearctic' [Gill 1885, p. 124].

We reject the term 'Nearctic' proposed by Mr. P. L. Sclater, and adopted by Mr. A. R. Wallace, for America north of Central America, for the reason that it seems to us an unnatural and artificial term... It is to be hoped that the term will not be adopted by American writers, as it is not by German and French writers, and we heartily endorse Mr. J. A. Allen's protest against the use of the term by American writers on this subject [Packard 1883, p. 363; also in Allen 1892, p. 212, footnote 1; also see Ebach 2015, footnote 26].

Others retained Wallace's usage for purely nomenclatural reasons:

I cannot understand why the word 'Nearctic' should be discarded. It was given by Dr. Sclater not in the sense of 'arctic' but 'northern' region of the New World, and is, in my opinion, apart from the priority which commands respect for its retention, a most simple and expressive term. My American colleagues will understand that if I have not

carried their system of nomenclature unto the zoogeographical regions of the Old World, it is not from any want of respect to their work, for I heartily agree with their conclusions as regards North America [Sharpe 1893, p. 101].

Sclater (1897) and later in their *Geography of Mammals* father and son Sclater and Sclater (1899) sided with Wallace for the simple reason that the Nearctic and Palearctic represented two distinct faunas:

the Palearctic and Nearctic regions have now, and have had in the past, quite sufficiently distinct faunas to warrant their division into two primary regions [Sclater 1897, p. 67].

[Allen's] figures show that there is, as has indeed never been disputed, a great amount of similarity between the Nearctic and Palearctic faunas, but not enough to justify the junction of these two great land-masses into one 'region' or 'realm'. [Sclater and Sclater 1899, p. 14].

Given this heated debate, are both sides talking past each other? If we look back to Sclater (1858), we find that his creations Neogeana and Palæogeana are based on the notion that the regions of the New World, for instance, share a

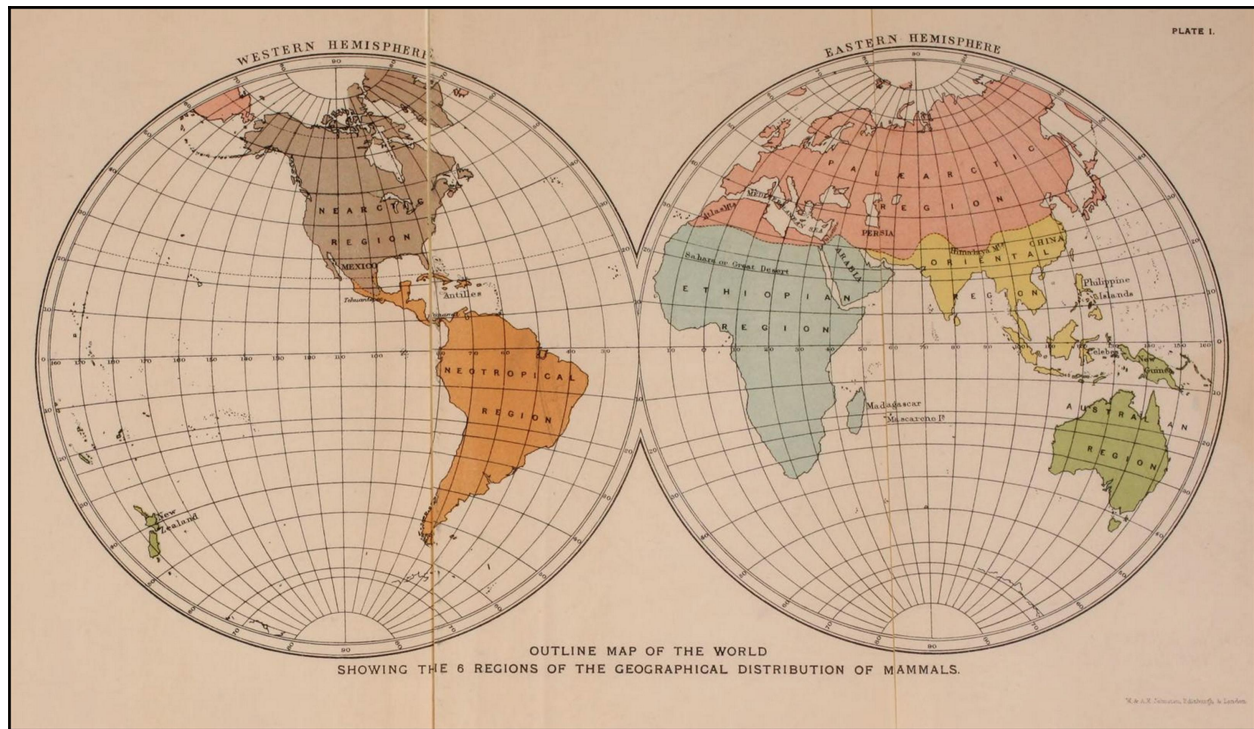


Fig. 5. Outline map of the world, showing the six regions of the geographical distribution of mammals (Sclater and Sclater 1899, map opposite p. 16).

closer relationship to each other than they do to the regions of the Old World and *vice versa*:

There are very many natural families which are quite peculiar to one or the other of these great divisions of the earth's surface, more subfamilies, few genera really common to the two, and very few, if any, species [Sclater 1858, p. 133].

It is through classification, rather than through any distributional 'laws' that Sclater viewed zoogeography; after all, he firmly believed that each World was created by God (hence 'creatio'). The notion that any distributional laws were in effect was never entertained. Wallace carried on this notion of relationship by tabling the world's areas on the basis of vertebrates (Table 2). By placing the Australian and Neotropical regions into Notogea, he assumed relationship and not distributional laws. The idea that distributional laws shape area classification was introduced by the American zoogeographers who were more influenced by the proto-ecological ideas of the Humboldtians, who decided that the environment had a greater part to play in determining distribution. Again, here we see the division between those who see taxonomic distributions as natural versus those who feel that naturalness is something environmental. Nelson (1978) attempted to separate out these two practitioners into historical and ecological biogeographers, on the basis of the stations and habitations divide of de Candolle (1820).

One may wonder whether the Holarctic is the first major ecological zoogeographical region ever proposed. If so, it runs contrary to the Sclater–Wallacean or historical theme of natural areas based on endemism, rather than on distributional 'laws'.

The final word on 19th century zoogeographical regionalisation is that of Bartholomew *et al.* (1911). In their colourfully illustrated *Physical Atlas*, they redrew the published maps of Sclater (1858, 1897), Wallace (1876a, 1876b), Heilprin (1887), Lydekker (1896), Ortmann (1896) and Sclater and Sclater (1899). Bartholomew *et al.* (1911) admitted that:

...in a work of this kind it is impossible to attain absolute accuracy. Zoological literature has assumed such enormous proportions that a complete survey is quite impracticable... In the Text, a short historical account is given of the various systems propounded for the sub-division of the World Zoogeographic Regions, wherein the views of the leading authorities are considered... Most of these are based upon the study of particular groups of animals – such as Mammals – but that of Dr Alfred Russel Wallace has a wider bearing, and hence has been accepted as a basis for the text of the present volume [Bartholomew *et al.* 1911, preface].

The short account of Bartholomew *et al.* (1911) starts with Sclater (1858) and ends with Sclater and Sclater (1899). Bartholomew *et al.* (1911) adopted the area classification of Wallace (1876a, 1876b), which is reiterated in Beddard (1895), a work that they describe as presenting 'the subject in a different

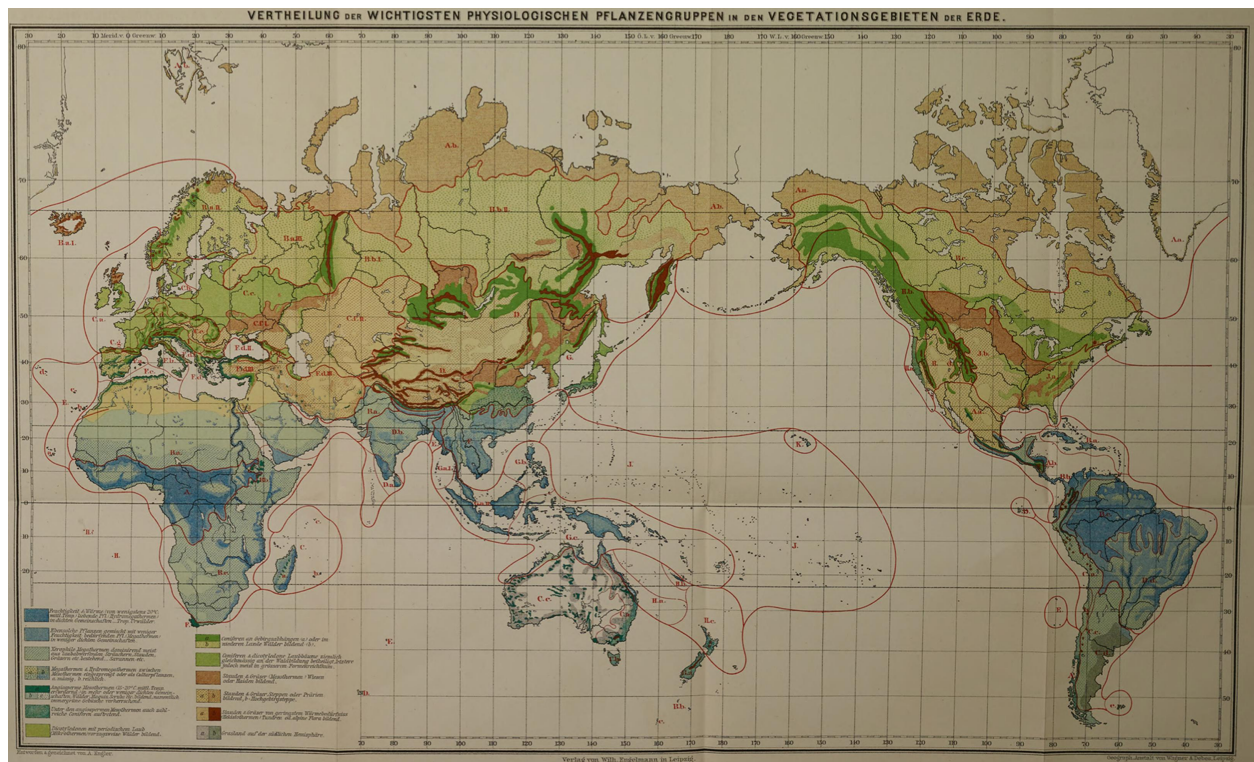


Fig. 6. Verteilung der wichtigsten physiologischen Pflanzengruppen in den Vegetationsgebieten der Erde [Division of the important physiological plant groups in the vegetation of the earth] (Engler 1882, p. 387).

light from any of its predecessors'. Why Bartholomew *et al.* (1911) thought Beddard (1895) was any different to say Sclater and Sclater (1899) is unclear, as Beddard has adopted Wallace's areas without any reference to the Holarctic. The wholesale disregard of the Holarctic is unusual, given that Wallace's own Arctogaea incorporates the Nearctic and Palearctic.

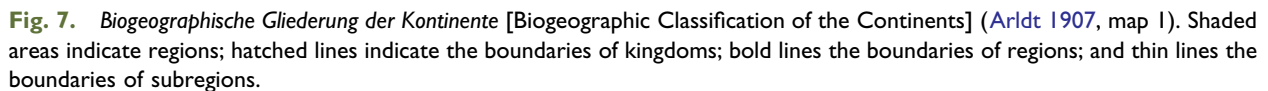
In the spirit of Sclater and Wallace, we view the Holarctic as nothing more than a higher level area (a division of a larger area perhaps) that groups two regions on the basis of the notion of relatedness; that is, the Nearctic and the Palearctic share a greater relationship on the basis of the taxa they share, than to any other region. Yet, the adoption of the Holarctic, especially by zoologists, had taken much longer, with similar debates about its validity appearing in the early part of the 21st century (e.g. Escalante 2017), whereas others simply ignored it as a possible relationship among larger areas (e.g. Holt *et al.* 2013a, 2013b).

Adoption of Wallace's areas by phytogeographers

Until the late 19th century, zoo- and phytogeography adopted separate classifications. For example, Engler (1882) divided the world's flora into five main areas, namely the Northern and Southern Extratropical kingdoms, the Palaeotropical kingdom of the Old World, and the South American and Old Oceanic

kingdoms (Fig. 6). Engler (1882) placed the Arctic region within the Northern Extratropical kingdom, an area resembling the Holotropical kingdom. Engler (1899) slightly altered the names and placed them all into the following five kingdoms: Northern Extratropical or Boreal, Palaeotropical, Central and South American, Austral (Old Oceanic) and Oceanic. The last kingdom was missing in the scheme of Engler (1882). Arldt (1907, map 1) used the same term 'Arctic region' to describe his circumpolar area in his *Biogeographic Classification of the Continents* (Fig. 7), which he classified as the Känogäisches kingdom, which includes the Holarctic region and three subregions, the Palearctic, Boreal and Nearctic. Arldt's classification is unique, because it is based on terrestrial, freshwater, marine plant and animal distributions as well as the work of both zoo- and phytogeographers. His classification maybe seen as a review and an amalgam of 19th century plant and animal geography. Unfortunately, Arldt's work is often overlooked in the history of biogeography (see Dowding and Ebach 2018), even though his own biogeographic classification looks incredibly modern by comparison to other early 20th century plant and animal geographers. In any case, Arldt (1907) preserved all of the Sclater–Wallacean regions as well as incorporating those of Heilprin (i.e. Holarctic) and Engler (i.e. Arctic) and served as a great revisionary work for 19th century biogeography.

Another work on global phytogeography is Good (1947, 1963; Fig. 8), who noted that:



system may seem like Engler's (1882, 1908); however, it does incorporate Heilprin's Holarctic and several of the Sclater–Wallacean regions (Table 3), which were absent in previous floristic schemes (Engler 1882, 1899).

Later 20th and 21st century global biogeographic regionalisations

Global regionalisation after 1946 follows a similar theme of that of later 19th century area classification, including how to reconcile the Holarctic with the Nearctic and Palearctic regions. Late 20th and 21st century biogeographical regionalisation may be divided into the following three groups: those who, knowingly or unknowingly, rejected the Holarctic in favour of the Nearctic and Palearctic (Udvardy 1975; Smith 1983; Kreft and Jetz 2010; Procheş and Ramdhani 2012; Holt *et al.* 2013a, 2013b; Rueda *et al.* 2013); those who accepted only a unified Holarctic (e.g. Schmidt 1954; de Lattin 1967; Rapoport 1968; Müller 1986; Cox 2001); and those who attempted to incorporate each under a larger

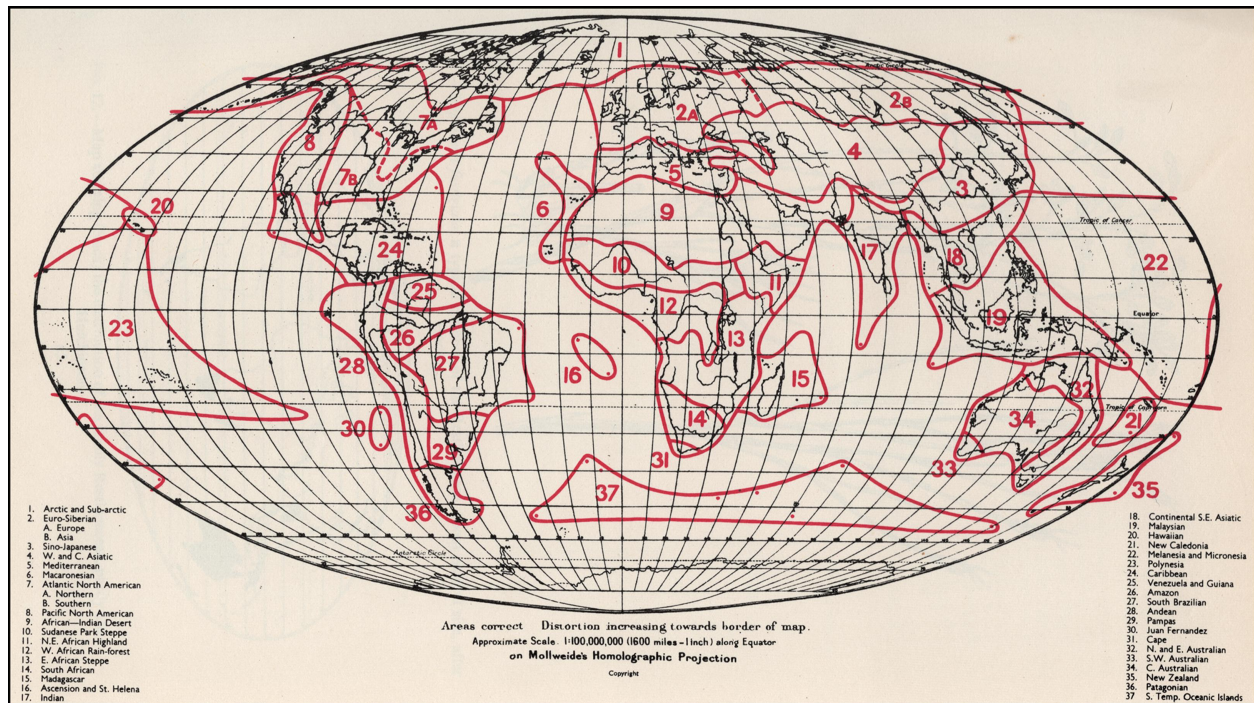


Fig. 8. Map of the world showing Good's floristic regions (Good 1963, plate 4).

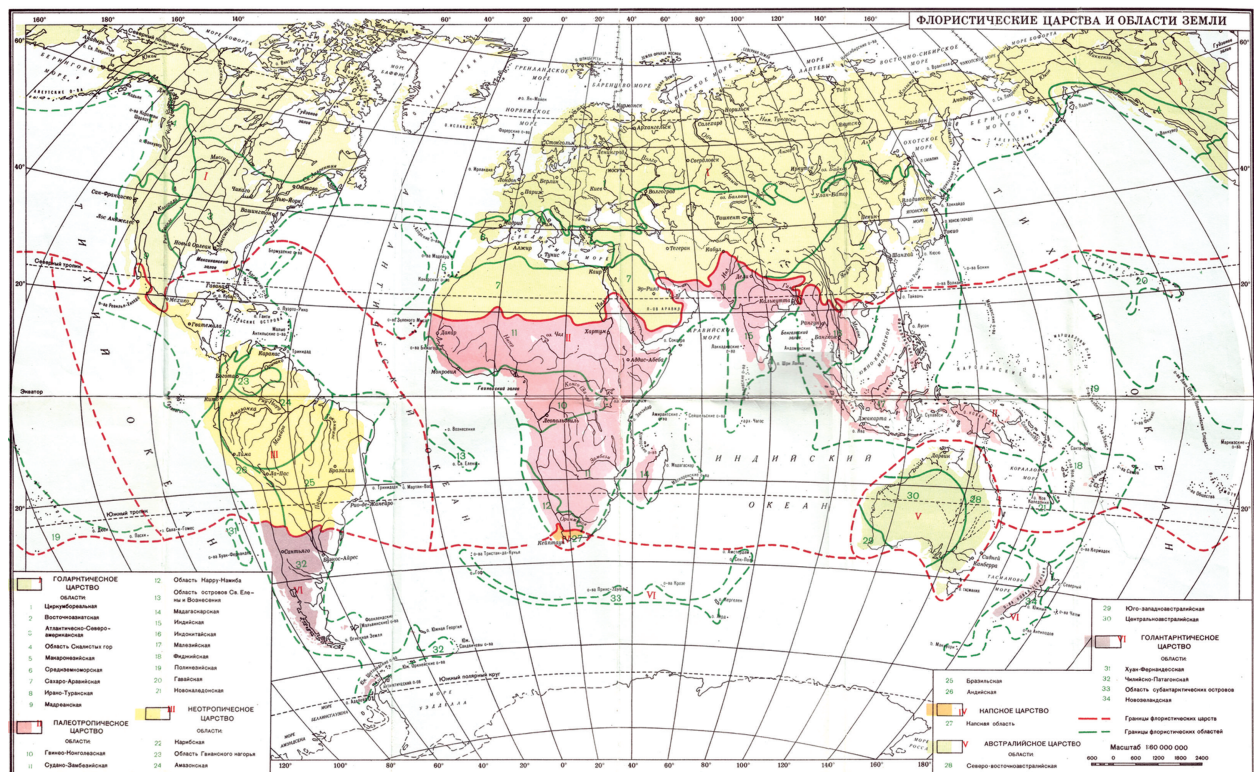


Table 3. Classifications of Wallace (1876a, 1876b), Engler (1882), Good (1947) and Takhtajan (1978, 1986) compared.

Wallace (1876a, 1876b)	Engler (1882)	Good (1947)	Takhtajan (1978, 1986)
Arctogæa			
	Northern extratropical kingdom	Boreal kingdom	Holarctic kingdom
Palearctic + Nearctic regions			Boreal subkingdom
		Arctic and Subarctic region	Circumboreal region
		Euro-Siberian region	
Nearctic region		North Atlantic American region	Atlantic–North American region
		Pacific–North American region	Rocky Mountain region
Palearctic region		Sino-Japanese region	Eastern Asiatic region
		Asiatic region	
			Tethyan subkingdom
		W. and Central Asiatic region	Irano-Turanian region
		Mediterranean region	Mediterranean region
		Macaronesian region	Macaronesian region
		Pacific–North American region	Madrean subkingdom
	Palaeotropical kingdom	Palaeotropical kingdom	Palaeotropical kingdom
Ethiopian region		African subkingdom	African subkingdom
			Madagascan subkingdom
		Indo-Malaysian subkingdom	Indo-Malesian subkingdom
		Polynesian subkingdom	Polynesian subkingdom
			Neocaledonian subkingdom
Ethiopian region		South African kingdom	Cape kingdom
Notogæa			
Neotropical region	South American kingdom	Neotropical kingdom	Neotropical kingdom
Australian region	Old Oceanic kingdom	Australian kingdom	Australian kingdom
		Antarctic kingdom	Holantarctic kingdom

The kingdoms of Engler, Good and Takhtajan fall neatly into Arctogæa and Notogæa, justifying Wallace's relationship among the regions of these divisions. Parts of Good's Pacific N. American region occur in Takhtajan's Boreal and Madrean subkingdoms. In contrary to good nomenclatural practise, Takhtajan gave each kingdom a secondary name, herein considered synonymous with the primary name: Holarctic kingdom (=Holarctis); Palaeotropical kingdom (=Palaeotropis); Neotropical kingdom (=Australis); and Holantarctic kingdom (=Holantarctis).

division (Darlington 1957; Poynton 1959; Lopatin 1980; Morrone 2002, 2015a). Other problems raised in generating classification were the inclusion of New Zealand into the Antarctic or Holantarctic kingdom (i.e. Udvardy 1975), and whether to include or not transition zones (see Hermogenes de Mendonça and Ebach 2020 for a recent review).

Establishment of the Holarctic as a unified biogeographic area

The arguments for retaining the Holarctic are numerous. Darlington (1957) recognised six regions grouped into the following three kingdoms: Megagea (Ethiopian, Indomalayan, Palearctic and Nearctic regions), Neogea

(Neotropical region) and Notogea (Australian region). Rather than choosing one classification over another, Darlington diplomatically noted:

Heilprin (1887) combined the two northern regions, the Palearctic and the Nearctic, into a Holarctic region. They are not combined here, but they may be called the Holarctic regions, and the animals which occur in both are often called Holarctic [Darlington 1957, p. 425].

If animals are Holarctic because they occur in both northern temperate zones, why not create a higher area 'Holarctic' in which the Nearctic and Palearctic are classified as subregions, as proposed earlier by Schmidt (1954) and Hershkovitz (1958)? Earlier 20th century zoogeographical

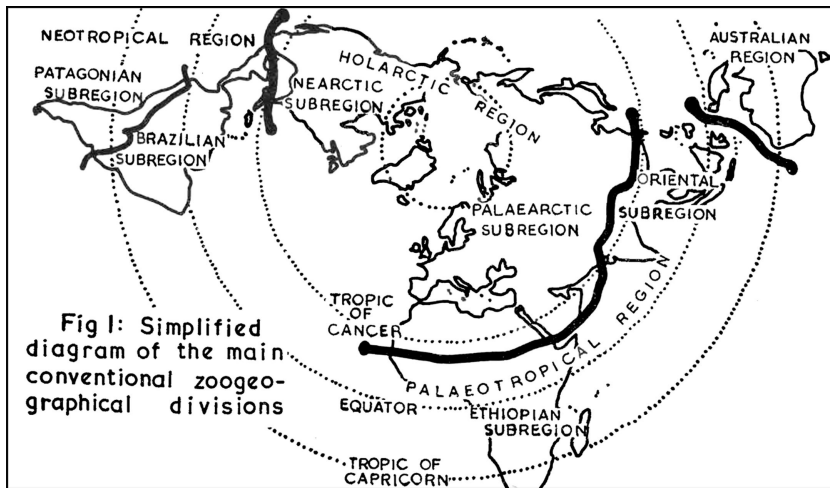


Fig. 10. Simplified diagram of the main conventional zoogeographical subdivisions (Poynton 1959, fig. 1). The Palearctic and Nearctic are treated as subregions within a larger Holarctic region.

classifications had included the Holarctic, with the Palearctic and Nearctic as subareas, including Nichols (1943), who divided the freshwater fish fauna into 'II. Continental: 1. Northern: A. Holarctic, a. Palearctic and, b. Nearctic' (Nichols 1943, p. 3); and Bobrinskiy *et al.* (1946), who placed the Holarctic region within Arctogea (see Beron 2018, p. 906). Herschkovitz noted that:

Darlington's *Zoogeography: the geographical distribution of animals* [Darlington 1957] was received while the present paper was in press [Herschkovitz 1958, p. 594, footnote 1, original emphasis].

Poynton (1959), referring to Herschkovitz (1958), classified the Nearctic and Palearctic as subregions within a larger Holarctic region (Fig. 10), although without referring to Schmidt (1954).

Whereas the Holarctic was accepted by mammalogists (e.g. Herschkovitz) and herpetologists (e.g. Schmidt), entomologists were less convinced. German entomologist Gustav de Lattin in his *Grundriß der Zoogeographie* (de Lattin 1967) was one of the few to recognise the challenge, and formalised the Holarctic as a zoogeographic area, with the Palearctic and Nearctic as subregions (see Beron 2018), in what Illies called:

ein echter Fortschritt gegenüber der Darstellung durch DARLINGTON 1957 zu verzeichnen ist. Die wohlinformierte und ausgewogene Darstellung des holarktischen Raumes macht das Buch zu einem wichtigen Ereignis in der tiergeographischen Literatur [a real step forward when compared to the example by DARLINGTON in 1957. The well-informed and balanced representation of the Holarctic region makes the book (de Lattin 1967) an important event in the zoogeographic literature] [Illies 1968, p. 230].

Illies' (1968) reference to Darlington is remarkable, given the number of already existing studies that accepted the Holarctic.

The acceptance of the Holarctic as a major area, which represents the Nearctic and Palearctic in their entirety or as subregions, was common in the second half of the 20th century. Rapoport (1968) proposed a biogeographic division of the earth into three regions or 'biogeographic belts', named Holarctic, Holotropical and Holantarctic (Fig. 11). Müller (1986) recognised nine divisions grouped into the following five kingdoms: Holarctic (Nearctic and Palearctic regions), Paleotropical (Ethiopian, Madagascan and Oriental regions), Australian (Australian, Oceanic, New Zealand and Hawaiian regions), Neotropical (Neotropical region) and Archinotic (Archinotic region). Bănărescu (1975) also recognised the Holarctic as a freshwater region, but not the Nearctic or Palearctic regions. Lopatin (1980) recognised the Arctogean kingdom containing the Palearctic and Nearctic regions, possibly because of the seniority of the name (Wallace 1876a, 1876b) to the later Holarctic (Heilprin 1882). The acceptance of the Holarctic continued into the late 20th and early 21st centuries. For example, Morrone (2002, 2015a) recognised the Holarctic as a kingdom and the Nearctic and Palearctic as its regions. Yet, the rejection of the Holarctic as a relational region began with the quantification of bioregionalisation.

Quantification of areas and the fate of the Holarctic

With the development of faster computer algorithms and the emergence of distributional databases, bioregionalisation entered a quantitative phase by the early 2000s. Early studies on global bioregionalisation included analyses using the distributional data of conifers (Sneath 1967), mammals (Smith 1983), Liliiforae (Conran 1995) and bumble-bees (Williams 1996). Both Sneath (1967) and Smith (1983) recovered the Holarctic, whereas the analyses by Conran (1995) and Williams (1996) did not.



Fig. 11. Biogeographic regionalisation of Rapoport (1968) recognising the Holarctic, Holotropical and Holantarctic belts.

Further bioregionalisation analyses based on bat (Procheş 2005) and gymnosperm distributions (Procheş 2006) found the Palearctic and Nearctic, but little similarity between them (i.e. they are more similar to other areas than to each other). The trend between recovering and not recovering the Holarctic continued with studies in the 2010s. In an analysis using vertebrate distributional data, Procheş and Ramdhani (2012) recovered both the Nearctic and Palearctic but failed to recover the Holarctic. They did admit, however, that using:

Wildfinder data, both of these approaches tended to yield clusters of very uneven geographic coverage, often small clusters in tropical America and large Holarctic or Palaetropical clusters [Procheş and Ramdhani 2012, p. 261].

Rueda *et al.* (2013) recovered regions similar to those of Wallace (1876a, 1876b), using amphibian, bird and mammal data, and Escalante (2017) recovered Wallace's Australian, Ethiopian, Neotropical, and Oriental regions by using mammal data. Neither study found evidence for the Holarctic.

Two studies that recovered the Holarctic were those of Kreft and Jetz (2010; Fig. 12), which used mammal distributional data, and Holt *et al.* (2013a, 2013b; Fig. 13), which used vertebrate data. The analysis of Kreft and Jetz (2010) found the Nearctic and Palearctic to have a greater similarity to each other, thereby justifying a Holarctic at the level of species, genus and family of volant and non-volant taxa (Kreft and Jetz 2010; Fig. 6). The analysis of Holt *et al.* (2013a) failed to mention the significance of their findings. Tucked away in the appendices is a dendrogram 'of cross-taxon zoogeographic realms based on phyla-distributional data for amphibian, bird and non-marine mammal species of the world' (Holt *et al.* 2013a, fig. S1), which shows the

phylogenetic β diversity values between the Nearctic and Palearctic to justify a Holarctic kingdom; yet, the term was not used in the paper or in the appendices.

The usage of the Holarctic is justified both historically and quantitatively. Most quantitative studies have recovered the Holarctic, and, in doing so, the Holotropical. Given this long tradition that extends back to Heilprin (1882), we feel confident that future studies will recover the Holarctic, and by definition the Holotropical. A recent quantitative study using plant data did, indeed, recover three clusters that correspond strongly to the Holarctic, Austral and Holotropical.

Towards a terrestrial biogeographical regionalisation of the world

The biogeographical regionalisation presented below divides the world into three kingdoms, following Newbigin (1950), Kuschel (1963), Rapoport (1968), Morrone (2002, 2015a), Moreira-Muñoz (2007) and Carta *et al.* (2022). Within these kingdoms, we recognise 2 subkingdoms, 8 regions, 21 subregions and 5 transition zones (Fig. 14, Table 4). This interim global biogeographic classification to the subregion level takes into account all previous classifications and names within a formal nomenclatural synonymy that follows the ICAN (Ebach *et al.* 2008; and see below). Each list of synonymies is followed by a diagnosis and a list of regions. The name of each region is followed by a list of synonymies, a diagnosis and remarks. Within each region, the proposed subregions are provided, although we note that some of them, particularly in the Palearctic, Ethiopian and Oriental regions, still need analysis. In the areas of overlap between regions belonging to different kingdoms, five transition zones are delimited, as formerly recognised by several

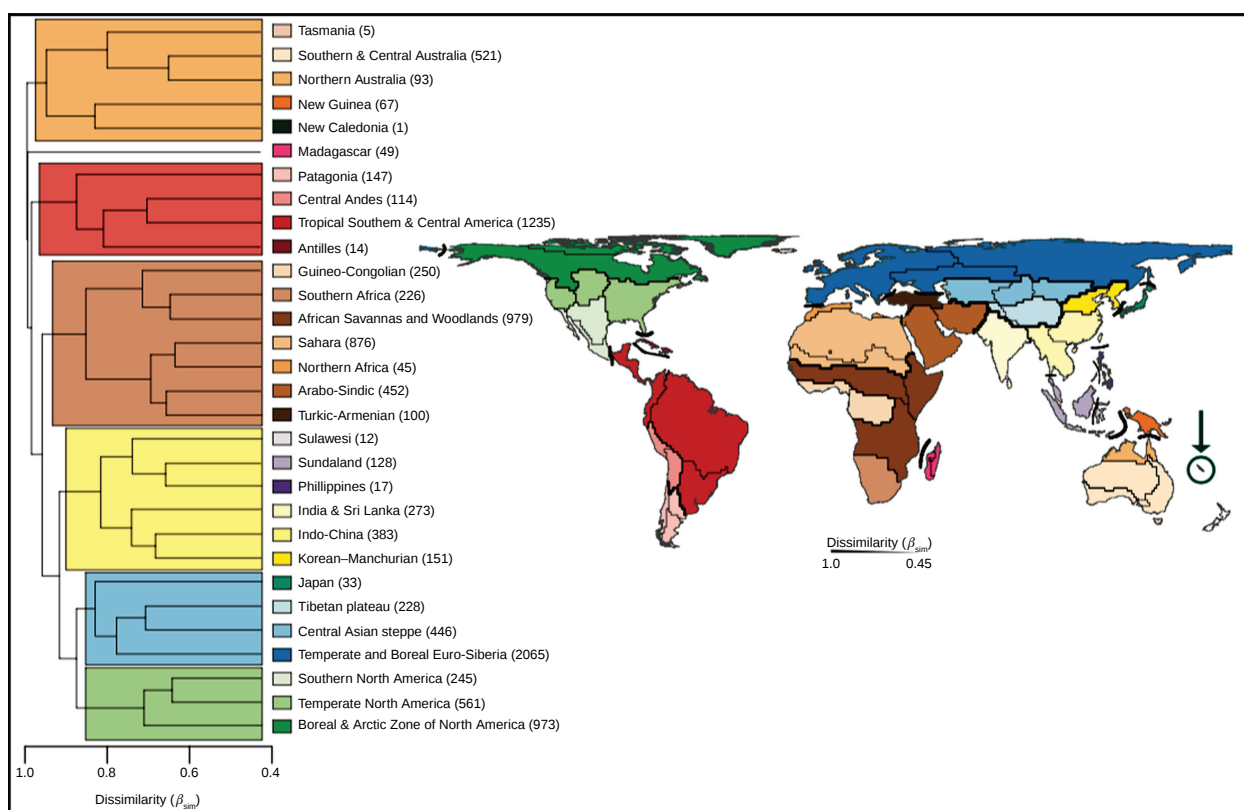


Fig. 12. The six major biogeographical divisions of [Kreft and Jetz \(2010\)](#) are highlighted in the dendrogram with large coloured rectangles: Australian (orange); Neotropical (red); African (brown); Oriental (yellow); Palearctic (blue); Nearctic (green). The first 30 groups in the dendrogram (small rectangles) and in the map are displayed in different colours. Additionally, the first 60 groups are indicated with black boundaries in the map ([Kreft and Jetz 2010](#), fig 9).

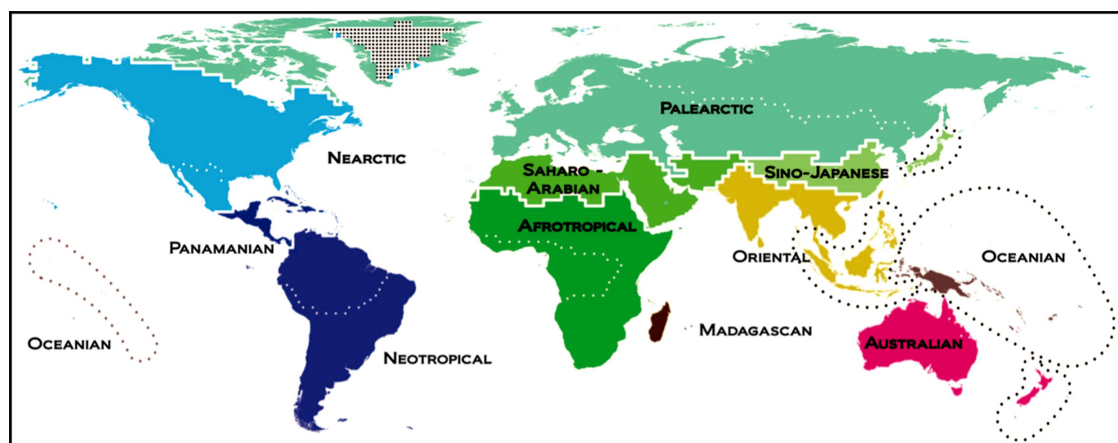


Fig. 13. Map of the terrestrial zoogeographic realms and regions of the world ([Holt et al. 2013a](#), fig. 1).

authors (e.g. [Müller 1986](#); [Halffter 1987](#); [Morrone 2006, 2014, 2015a, 2015b](#); [Kreft and Jetz 2013](#)). No new names are proposed in this study.

The naming system within this and other biogeographic classifications follows the ICAN ([Ebach et al. 2008](#)). The ICAN was proposed so as to stem the flow of area names and to

formalise a practise, so that one diagnosed area is assigned a single name. A biogeographical nomenclature as proposed by [Wallace \(1894\)](#) did not question:

who is right and who is wrong in the naming and grouping of these regions, or of determining what are the true

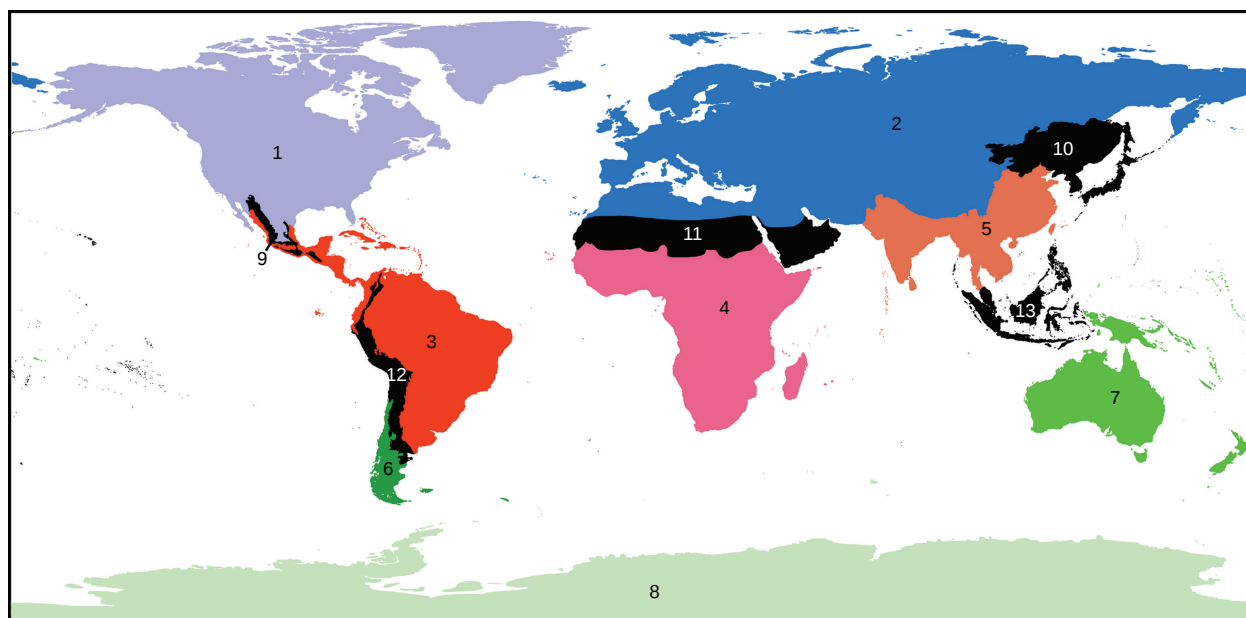


Fig. 14. World biogeographical regionalisation, with indication of the regions and transition zones. (1) Nearctic region; (2) Palearctic region; (3) Neotropical region; (4) Ethiopian region; (5) Oriental region; (6) Andean region; (7) Australian region; (8) Antarctic region; (9) Mexican transition zone; (10) Chinese transition zone; (11) Saharo-Arabian transition zone; (12) South American transition zone; (13) Indo-Malayan transition zone.

primary regions. All proposed regions are, from some points of view, natural, but the whole question of their grouping and nomenclature is one of convenience and of utility in relation to the object aimed at [p. 613].

In other words, nomenclature, that is how biogeographers name areas, is not part of the discovery process of biogeography, but rather a convenient way to organise names without confusion. We may draw an analogy to the Botanical and Zoological Codes of Nomenclature that ensure one taxon is assigned a single name for the purposes of unambiguous communication of names. How biogeographers discover natural areas is another topic entirely and should not be confused with area nomenclature.

The biogeographic names proposed by de Candolle (1820), Prichard (1826), Schouw (1823), Wagner (1844, 1845, 1846a, 1846b) and Schmarda (1853) are not included in the synonyms, because they were published before Sclater's (1858) regionalisation. We apply a criterion analogous to the *nomen conservandum* convention of taxonomical nomenclature to provide a greater stability (Morrone 2014). Changing well known area names from the Sclaterian–Wallacean system to the names used by these authors will only confuse the area nomenclature further. Given that areas such as the Nearctic and Palearctic are already widely used in the biogeographic literature, keeping them seems to be prudent and in keeping with a stable area nomenclature.

Area taxonomy

Holarctic kingdom: Heilprin (1882)

Extratropical Northern kingdom: Engler (1882, p. 334).

Triarctic region: Heilprin (1882, p. 266); Wallace (1883, p. 482).

Holarctic region: Heilprin (1882, p. 270); Newton (1893, p. 328); Lydekker (1896, p. 308); Newbigin (1913, p. 216); de Mello-Leitão (1937, p. 169); Diels (1908, p. 137); Schmidt (1954, p. 328); Poynton (1959, p. 26); Thorne (1963, p. 333); de Lattin (1967, p. 283); Rapoport (1968, p. 85); Cabrera and Willink (1973, p. 25); Smith (1983, p. 462); Stoddart (1992, p. 278); Morrone (1996, p. 104).

Holarctis kingdom: Schilder (1956, p. 76).

North Temperate realm: Allen (1892, p. 207).

Holarctic kingdom: Diels (1908, p. 137); Müller (1986, p. 20); Takhtajan (1986, p. 242); Cox (2001, p. 519); Morrone (2002, p. 149); Kreft and Jetz (2013, p. 343-c); Morrone (2015a, p. 84); Hermogenes de Mendonça and Ebach (2020, p. 721); Carta *et al.* (2022, table 1).

Boreal kingdom: Good (1963, p. 30); Glasby (2005, p. 242).

Boreal subkingdom: Takhtajan (1986, p. 243).

Diagnosis

North America, Greenland, Europe, Africa north of the Atlas mountains and Asia north of the Himalayan mountains.

Remarks

In contrast to some authors that have considered the Holarctic to represent a region, we treat it as a kingdom and

Table 4. The terrestrial kingdoms, subkingdoms, regions, subregions and transition zones of the world recognised herein.

Kingdom	Subkingdom	Region	Subregion or transition zone	
Holarctic		Nearctic	Arctic	
			Western	
			Alleghany	
		Palearctic	European	
			Mediterranean	
			Siberian	
Holotropical	Paleotropical	Ethiopian	East African	
			West African	
			Cape	
			Malagasy	
		Oriental	Indian	
			Indo-Chinese	
	Neotropical	Neotropical	Antillean	
			Brazilian	
			Chacoan	
		Austral	Andean	Subantarctic
				Central Chilean
				Patagonian
Australian	Australian			
	Polynesian			
	New Zealand			
Antarctic	—			
	—			
			Mexican	
			South American	
		Saharo-Arabian		
		Chinese		
		Indo-Malayan		

subordinate the Nearctic and Palearctic to it (Morrone 2002, 2015a; Carta *et al.* 2022). From a palaeogeographic viewpoint, it corresponds to the palaeocontinent of Laurasia (Amorim and Tozoni 1994).

Regions

The Holarctic kingdom comprises two regions, Nearctic and Palearctic.

Nearctic region: Sclater (1858)

Nearctic region: Sclater (1858, p. 142); Kirby (1872, p. 437); Wallace (1876b, p. 114); Sharpe (1884, p. 102); Heilprin (1887,

p. 62); Sclater (1894, p. 98); Sclater and Sclater (1899, p. 153); Bartholomew *et al.* (1911, p. 10); Darlington (1957, p. 442); Rapoport (1968, p. 94); Morrone (2002, p. 150, 2006, p. 469); Procheş and Ramdhani (2012, p. 263); Kreft and Jetz (2013, p. 343-c); Rueda *et al.* (2013, p. 2217); Ribeiro *et al.* (2014, p. 249); Morrone (2015a, p. 84); Escalante (2017, p. 357); Hermogenes de Mendonça and Ebach (2020, p. 721); Escalante *et al.* (2021, p. 354).

North American region: Sclater (1858, p. 142).

American region: Murray (1866, p. 311) (in part).

Nearctic province: Huxley (1868, p. 315).

Neoseptentrional subregion: Blyth (1871, p. 427).

North American region: Kirby (1872, p. 437); Diels (1908, p. 148); Cox (2001, p. 519).

North Temperate realm: (in part) Allen (1892, p. 207).

Angloean kingdom: Gill (1885, p. 17).

Arctamerican kingdom: Gill (1885, p. 17).

Nearctica area: Clarke (1892, p. 380).

Boreal region: Merriam (1892, p. 22).

Nearctic subregion: Newton (1893, p. 333); Schmidt (1954, p. 328); Poynton (1959, p. 26); Thorne (1963, p. 333); Smith (1983, p. 462); Stoddart (1992, p. 278); Morrone (1996, p. 104).

Sonoran region: Lydekker (1896, p. 363).

Sonoran kingdom: Schilder (1956, p. 76).

Nearctic kingdom: Udvardy (1975, p. 14); Morain (1984, p. 151); Udvardy (1987, p. 187); Kreft and Jetz (2010, p. 2044); Holt *et al.* (2013a, p. 75).

Madrean (Sonoran) subkingdom: Takhtajan (1986, p. 246).

North American–Atlantic region: Carta *et al.* (2022, table 2).

Diagnosis

Canada, mainland USA, central and northern Mexico and Greenland.

Remarks

So as to accommodate both the Nearctic and Holarctic in a single classification, without revising or synonymising these areas, we place the Nearctic and Palearctic as regions within the Holarctic kingdom.

Subregions

The Nearctic region comprises the Arctic, Western and Alleghany subregions (Escalante *et al.* 2021; Fig. 15).

Arctic subregion: LeConte (1859)

Atlantic district: (in part) LeConte (1859, pp. iii–iv).

Arctic realm: Allen (1871, p. 380–381, 1893, p. 206, 1893, p. 122).

Canadian subregion: Wallace (1876b, p. 135); Sclater and Sclater (1899, p. 164); Escalante *et al.* (2013, p. 495).



Fig. 15. The subregions and transition zone of the Nearctic region (after [Escalante et al. 2021](#)).

Arctic region: [Engler \(1882, p. 334\)](#); [Good \(1963, p. 30\)](#).

Arctic division: [Merriam \(1892, p. 8\)](#).

Boreal division: [Merriam \(1892, p. 8\)](#).

American Arctic region: [Allen \(1892, p. 219\)](#).

Cold Temperate subregion: [Allen \(1892, p. 210, 1893, pl. III\)](#).

Arctic subregion: [Schmidt \(1954, p. 328\)](#); [Escalante et al. \(2021, p. 355\)](#).

Hyperborean region: [Schilder \(1956, p. 76\)](#).

Arctic and Subarctic region: [Good \(1963, p. 30\)](#); [Takhtajan \(1986, p. 244\)](#).

Pacific North American region: [Good \(1963, p. 30\)](#)

Coniferan subregion: [Hagmeier and Stults \(1964, p. 140\)](#); [Hagmeier \(1966, p. 293\)](#).

Tundran subregion: [Hagmeier and Stults \(1964, p. 140\)](#); [Hagmeier \(1966, p. 293\)](#).

Circumboreal region: [Carta et al. \(2022, table 2\)](#).

Diagnosis

Alaska (including the St Lawrence, Diomedes and Aleutian Islands), northern Canada (Yukon, Northwest Territories and Nunavut, northern parts of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario and Quebec, and Newfoundland and Labrador) and Greenland.

Western subregion: Allen (1871)

Western province: [Allen \(1871, p. 381\)](#).

Western or Californian subregion: [Wallace \(1876b, p. 127\)](#).

The central or Rock Mountain subregion: [Wallace \(1876b, p. 129\)](#).

Pacific North America area: [Engler \(1882, p. 341\)](#).

Western North America: [Hemsley \(1887, p. 223\)](#).

Canada subarea: [Clarke \(1892, p. 380\)](#) (in part).

United States Occidentalis subarea: [Clarke \(1892, p. 380\)](#).

Central or Middle division: [Merriam \(1892, p. 12\)](#).

Pacific or California division: [Merriam \(1892, p. 13\)](#).

Western or Arid subregion: [Sclater and Sclater \(1899, p. 167\)](#).

Rocky-Mountains subregion: [Smith \(1941, p. 97\)](#).

Pacific North American region: [Good \(1947, p. 30\)](#).

Coniferan subregion: [Hagmeier and Stults \(1964, p. 140\)](#); [Hagmeier \(1966, p. 293\)](#).

Sonoran subregion: [Hagmeier and Stults \(1964, p. 140\)](#); [Hagmeier \(1966, p. 293\)](#).

Rocky Mountain region: [Takhtajan \(1986, p. 244\)](#). Paleotropical subkingdom

North American Pacific subregion: [Morrone et al. \(1999, p. 510\)](#).

Californian-Rocky Mountain subregion: [Escalante et al. \(2013, p. 495\)](#).

Madrean region: [Carta et al. \(2022, table 2\)](#).

Western subregion: [Escalante et al. \(2021, p. 357\)](#).

Diagnosis

The area west of, and including, the Rocky Mountains and its eastern foothills, Graham Island (British Columbia) in the north-west, following the lowlands south of Peace River (British Columbia) to Winnipeg (Manitoba). The eastern boundary follows the whole Eastern System of the Western Cordillera of North America, starting from Regina (Saskatchewan). The southern boundary extends to the Sierras Madre and the Baja California Peninsula to the south-west in Mexico.

Alleghany subregion: [Cooper \(1859\)](#)

Alleghany region: [Cooper \(1859, p. 268\)](#).

Atlantic Ocean district: [LeConte \(1859, p. iii\)](#).

Eastern province: [Allen \(1871, p. 381\)](#).

Austro-Riparian region: [Cope \(1873, map\)](#).

Eastern region: [Cope \(1873, p. 35, 1875, p. 68\)](#).

Alleghanian district: [Cope \(1875, p. 68\)](#).

Alleghany subregion: [Wallace \(1876b, p. 131\)](#); [Escalante et al. \(2021, p. 364\)](#).

Atlantic North America area: [Engler \(1882, p. 342\)](#).

Appalachian province: [Engler \(1882, p. 342\)](#).

Prairie province: [Engler \(1882, p. 342\)](#).

Alleghanian subregion: [Heilprin \(1887, p. 72\)](#); [Escalante et al. \(2013, p. 495\)](#).

Eastern North America: [Hemsley \(1887, p. 223\)](#).

Warm Temperate subregion: [Allen \(1892, p. 210\)](#).

Humid or Eastern province: [Allen \(1892, p. 219\)](#).

Canada subarea: [Clarke \(1892, p. 380\)](#) (in part).

United States Orientalis subarea: [Clarke \(1892, p. 380\)](#).

Atlantic or Eastern Forest region: [Merriam \(1892, p. 11\)](#).

Warm Temperate subregion: [Allen \(1893, pl. III\)](#).

Humid province: [Allen \(1893, pl. III\)](#).

Eastern or Humid subregion: [Sclater and Sclater \(1899, p. 169\)](#).

Atlantic North American region: [Good \(1963, p. 30\)](#); [Takhtajan \(1986, p. 244\)](#).

Deciduan subregion: [Hagmeier and Stults \(1964, p. 140\)](#); [Hagmeier \(1966, p. 293\)](#).

Alleghenian province: [Hagmeier \(1966, p. 293\)](#).

Canadian-Appalachian subregion: [Takhtajan \(1986, p. 244\)](#).

North American Atlantic region: [Carta et al. \(2022, table 2\)](#).

Diagnosis

The area east of the Eastern System of the Western Cordillera of North America, south of the Arctic subregion

(including Nova Scotia) and east of the Mid Atlantic Ridge (not including Iceland).

Palearctic region: [Sclater \(1858\)](#)

Palearctic region: [Sclater \(1858, p. 137\)](#); [Kirby \(1872, p. 432\)](#); [Wallace \(1876a, p. 180\)](#); [Sharpe \(1884, p. 104\)](#); [Sclater \(1894, p. 99\)](#); [Sclater and Sclater \(1899, p. 177\)](#); [Bartholomew et al. \(1911, p. 5\)](#); [Schilder \(1956, p. 76\)](#); [Darlington \(1957, p. 438\)](#); [Poynton \(2000, p. 39\)](#); [Morrone \(2002, p. 150\)](#); [Procheş and Ramdhani \(2012, p. 263\)](#); [Kreft and Jetz \(2013, p. 343-c\)](#); [Rueda et al. \(2013, p. 2217\)](#); [Ribeiro et al. \(2014, p. 249\)](#); [Escalante \(2017, p. 358\)](#); [Morrone \(2015a, p. 85\)](#); [Escalante \(2017, p. 358\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#).

Europeo-Asiatic region: [Murray \(1866, p. 304\)](#).

Paleomeridional subregion: [Blyth \(1871, p. 427\)](#).

Paleoseptentrional subregion: [Blyth \(1871, p. 427\)](#).

North Temperate realm: (in part) [Allen \(1892, p. 207\)](#).

Eurasiatic kingdom: [Gill \(1885, p. 19\)](#).

Eurygean kingdom: [Gill \(1885, p. 19\)](#).

Eurasiatic region: [Heilprin \(1887, p. 58\)](#); [Carta et al. \(2022, table 2\)](#).

Palearctica area: [Clarke \(1892, p. 377\)](#).

Palearctic subregion: [Newton \(1893, p. 333\)](#); [Schmidt \(1954, p. 328\)](#); [Poynton \(1959, p. 26\)](#); [Thorne \(1963, p. 333\)](#); [Smith \(1983, p. 462\)](#); [Morrone \(1996, p. 104\)](#).

Eurasiatic region: [Diels \(1908, p. 145\)](#).

Palearctic kingdom: [Udvardy \(1975, p. 22\)](#); [Morain \(1984, p. 201\)](#); [Udvardy \(1987, p. 187\)](#); [Kreft and Jetz \(2010, p. 2044\)](#); [Holt et al. \(2013a, p. 75\)](#).

Tethyan (Ancient Mediterranean) subkingdom: [Takhtajan \(1986, p. 245\)](#).

Eurasian region: [Cox \(2001, p. 519\)](#).

Tethyan region: [Lücking \(2003, p. 43\)](#).

Diagnosis

Eurasia, northern China, Japan and Africa north of the Sahara.

Remarks

The Palearctic is included as a region within the Holarctic kingdom so as to accommodate to conflicting classifications (see discussion above).

Subregions

The Palearctic region has been classically divided into three subregions, namely European, Mediterranean and Siberian ([Fig. 16](#)). Further studies are still needed to corroborate them.

European subregion: [Wallace \(1876a\)](#)

European subregion: [Wallace \(1876a, p. 191\)](#).

Europa Frigida subarea: [Clarke \(1892, p. 377\)](#).



Fig. 16. The subregions and transition (t.) zones of the Palearctic region (after Wallace 1876a).

Europasian subregion: (in part) [Sclater and Sclater \(1899, p. 187\)](#).

European subprovince: [Schilder \(1956, p. 76\)](#).

Euro-Siberian region: [Good \(1963, p. 30\)](#); [Takhtajan \(1986, p. 243\)](#).

Irano-Turanian region: [Takhtajan \(1986, p. 245\)](#).

Diagnosis

European continent south of the geographical North Pole (including Svalbard, Novaya Zemlya and Franz Joseph Land); north of the Pyrenees, Alps, Carpathian, Caucasus and Balkan mountains and Black Sea (including the Sea of Azov); west of the Mid Atlantic Ridge (including Iceland and Jan Mayen island); and west of the Ural Mountains, Volga and Don rivers.

Mediterranean subregion: [Wallace \(1876a, 1876b\)](#)

Mediterranean subregion: [Wallace \(1876a, p. 199\)](#).

Mediterranea subarea: [Clarke \(1892, p. 377\)](#).

Europasian subregion: (in part) [Sclater and Sclater \(1899, p. 187\)](#).

Eremian (in part) subregion: [Sclater and Sclater \(1899, p. 189\)](#).

Mediterranean region: [Good \(1963, p. 30\)](#); [Takhtajan \(1986, p. 245\)](#).

Mediterranean province: [Schilder \(1956, p. 76\)](#).

Mediterranean–Iranian region: [Carta et al. \(2022, table 2\)](#).

Diagnosis

Area south of the Pyrenees, Alps, Carpathian, Caucasus and Balkan mountains, the Sea of Azov, the Volga and Don Rivers, the Caspian Sea, and the Tibetan Plateau; west of the Indus River valley; north of the Persian Gulf (from Bahrain) and the Gulf of Oman. The southern boundary runs from Bahrain to the north of the Red Sea (Suez, Egypt) to the southern border of Western Sahara (including Macaronesia).

Siberian subregion: [Wallace \(1876a, 1876b\)](#)

Siberian or Northern Asian subregion: [Wallace \(1876a, p. 216\)](#).

Mongolia subarea: [Clarke \(1892, p. 377\)](#).

Europasian subregion: (in part) [Sclater and Sclater \(1899, p. 187\)](#).

Eremian (in part) subregion: [Sclater and Sclater \(1899, p. 189\)](#).

Turkestanian subprovince: [Schilder \(1956, p. 76\)](#).

Siberian subprovince: [Schilder \(1956, p. 76\)](#).

Euro-Siberian region: (in part) [Good \(1963, p. 30\)](#).

Diagnosis

Area east of the Ural Mountains, including Siberia, Caspian Sea ending at Kamchatka and the Bering Strait. Includes the Tibetan Plateau and Mongolia and Gobi deserts.

Holotropical kingdom: [Rapoport \(1968\)](#)

Holotropical region: [Rapoport \(1968, p. 85\)](#); [Morrone \(1996, p. 104\)](#).

Holotropical kingdom: [Morrone \(2002, p. 150, 2015a, p. 85\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#); [Carta et al. \(2022, table 1\)](#).

Pantropical kingdom: [Glasby \(2005, p. 242\)](#).

Diagnosis

Tropical areas of the world, between 30° south latitude and 30° north latitude.

Remarks

It corresponds to Tropical Gondwanaland ([Amorim and Tozoni 1994](#)).

Subkingdoms

We follow the recent analysis of [Carta et al. \(2022\)](#), who postulated the existence of two subkingdoms, namely Paleotropical and Neotropical.

Paleotropical subkingdom: [Engler \(1882\)](#)

Paleotropical kingdom: [Engler \(1882, p. 343\)](#); [Diels \(1908, p. 126\)](#); [Good \(1963, p. 31\)](#); [Takhtajan \(1986, p. 246\)](#).

Paleotropic kingdom: [Schilder \(1956, p. 76\)](#); [Kreft and Jetz \(2013, p. 343-c\)](#).

Paleotropical region: [Poynton \(1959, p. 26\)](#).

Palaeotropical subkingdom: [Carta et al. \(2022, table 1\)](#).

Diagnosis

Tropical areas within the continents of Africa and Asia ([Carta *et al.* 2022](#)).

Regions

The Paleotropical subkingdom comprises two regions, namely Ethiopian and Oriental.

Ethiopian region: [Sclater \(1858\)](#)

Ethiopian region: [Sclater \(1858, p. 138\)](#); [Blyth \(1871, p. 428\)](#); [Kirby \(1872, p. 434\)](#); [Wallace \(1876a, p. 251\)](#); [Sharpe \(1884, p. 105\)](#); [Newton \(1893, p. 345\)](#); [Sclater \(1894, p. 98\)](#); [Lydekker \(1896, p. 227\)](#); [Sclater and Sclater \(1899, p. 84\)](#); [Bartholomew *et al.* \(1911, p. 6\)](#); [Newbigin \(1913, p. 215\)](#); [de Mello-Leitão \(1937, p. 183\)](#); [Darlington \(1957, p. 428\)](#); [de Lattin \(1967, p. 280\)](#); [Cabrera and Willink \(1973, p. 27\)](#); [Smith \(1983, p. 462\)](#); [Morrone \(1996, p. 104\)](#); [Kreft and Jetz \(2013, p. 343-c\)](#); [Rueda *et al.* \(2013, p. 2217\)](#); [Ribeiro *et al.* \(2014, p. 249\)](#); [Morrone \(2015a, p. 85\)](#); [Escalante \(2017, p. 359\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#).

Western Palæotropical region: [Sclater \(1858, p. 138\)](#).

Africano-Indian region: [Murray \(1866, p. 308\)](#).

Ethiopian province: [Huxley \(1868, p. 315\)](#).

Western Paleotropical region: [Kirby \(1872, p. 434\)](#) (in part).

Afrogean kingdom: [Gill \(1885, p. 20\)](#).

Ethiopian kingdom: [Heilprin \(1887, p. 82\)](#).

Indo-African realm: (in part) [Allen \(1892, p. 207\)](#).

Ethiopia area: [Clarke \(1892, p. 379\)](#).

Indo-African region: [Diels \(1908, p. 130\)](#).

Ethiopian subregion: [Schmidt \(1954, p. 328\)](#); [Poynton \(1959, p. 26\)](#); [Smith \(1983, p. 462\)](#).

African region: [Schilder \(1956, p. 76\)](#); [Cox \(2001, p. 519\)](#); [Carta *et al.* \(2022, table 2\)](#).

African subkingdom: [Good \(1963, p. 31\)](#); [Takhtajan \(1986, p. 247\)](#).

Afrotropical kingdom: [Udvardy \(1975, p. 25\)](#); [Morain \(1984, p. 219\)](#); [Fleming \(1987, p. 199\)](#).

Afrotropical kingdom: [Udvardy \(1987, p. 187\)](#); [Holt *et al.* \(2013a, p. 75, 2013b, p. 343-d\)](#).

Afrotropical subregion: [Morrone \(1996, p. 104\)](#).

Afrotropical region: [Poynton \(2000, p. 39\)](#); [Morrone \(2002, p. 150\)](#); [Procheş and Ramdhani \(2012, p. 263\)](#).

African kingdom: [Cox \(2001, p. 519\)](#); [Kreft and Jetz \(2010, p. 2044\)](#).

African Paleotropics region: [Lücking \(2003, p. 43\)](#).

Southern African region: (in part) [Carta *et al.* \(2022, table 2\)](#).

Diagnosis

Central and southern Africa, the northern part of the Arabian peninsula, Madagascar and the West Indian Ocean islands.

Remarks

The Cape region of previous regionalisations is demoted to a subregion of the Ethiopian region following [Carta *et al.* \(2022\)](#) and [Santos and Ribeiro \(2022\)](#). Further studies using phylogenetic data within a comparative biogeographic analysis are needed to confirm this classification.

Subregions

The Ethiopian region comprises the following four subregions: East African, West African, Cape and Malagasy ([Fig. 17](#)).

East African subregion: [Wallace \(1876a\)](#)

East African subregion: or Central and East Africa [Wallace \(1876a, p. 258\)](#).

South African subregion: [Wallace \(1876a, p. 266\)](#).

Africa Tropica Borealis subarea: [Clarke \(1892, p. 379\)](#) (in part).

Saharan subregion: (in part) [Sclater and Sclater \(1899, p. 117\)](#).

Cape subregion: (in part) [Sclater and Sclater \(1899, p. 113\)](#).

East African province: [Schilder \(1956, p. 76\)](#).

East African Steppe region: [Good \(1963, p. 31\)](#).

Saharo-Arabian region: (in part) [Takhtajan \(1986, p. 132\)](#).

Sudano-Zambezian subregion: (in part) [Takhtajan \(1986, p. 202\)](#).

Madagascan subkingdom: (in part) [Takhtajan \(1986, p. 249\)](#).

Pandora subregion: (in part) [Parenti and Ebach \(2010, p. 312, 2013, p. 815\)](#).

Central Africa subregion: (in part) [Santos and Ribeiro \(2022, p. 13\)](#).

Diagnosis

Highland areas along the eastern and south-western part of the African continent (including Angola and northern part of Namibia); including a portion of the south-western and southern Sahara (southern parts of Mauritania, Mali, Niger, Chad, Sudan), the Rift Valley (including the Horn of Africa), and the southern part of the Arabian Peninsula (from Bahrain to Suez, Egypt), going as far south, but not including, the Cape subregion.

West African subregion: [Wallace \(1876a\)](#)

West-African subregion: [Wallace \(1876a, p. 262\)](#).

Africa Tropica Australis subarea: [Clarke \(1892, p. 379\)](#).

Africa Tropica Borealis subarea: [Clarke \(1892, p. 379\)](#) (in part).

West African subregion: [Sclater and Sclater \(1899, p. 110\)](#).

Ethiopic subregion: [Schilder \(1956, p. 76\)](#).

Ascension and St Helena region: [Good \(1963, p. 31\)](#); [Takhtajan \(1986, p. 248\)](#).

Macaronesian region: [Good \(1963, p. 30\)](#); [Takhtajan \(1986, p. 245\)](#).

West African Rainforest region: [Good \(1963, p. 31\)](#).

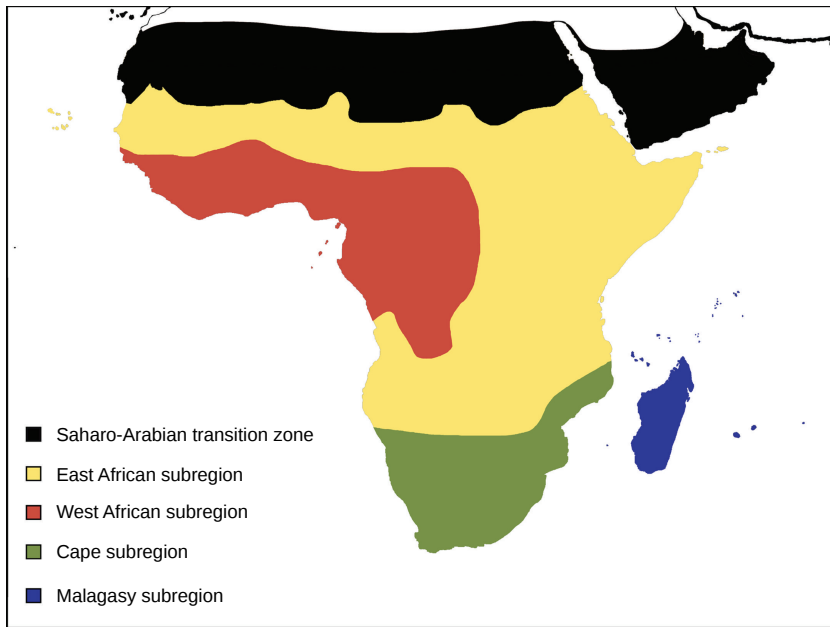


Fig. 17. The subregions and transition zone of the Ethiopian region (after [Wallace 1876a](#)).

Guineo-Congolian region: [Takhtajan \(1986, p. 198\)](#).

Central Africa subregion: (in part) [Santos and Ribeiro \(2022, p. 13\)](#).

Diagnosis

Lowland sub-Saharan areas to the west and north of the East African subregion.

Cape subregion: [Grisebach \(1872\)](#)

Cape region: [Grisebach \(1872, p. 179\)](#); [Engler \(1882, p. 347\)](#); [Good \(1963, p. 32\)](#); [Cabrera and Willink \(1973, p. 26\)](#); [Takhtajan \(1986, p. 252\)](#); [Morrone \(2002, p. 150\)](#); [Galley and Linder \(2006, p. 237\)](#); [Morrone \(2015a, p. 86\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#).

South African subregion: [Wallace \(1876a, p. 266\)](#); [Sharpe \(1884, p. 106\)](#); [Bartholomew *et al.* \(1911, p. 6\)](#); [Kuschel \(1963, p. 447\)](#).

Caput subarea: [Clarke \(1892, p. 379\)](#).

South African region: [Good \(1963, p. 31\)](#).

Caffrarian province: [Newton \(1893, p. 347\)](#).

Cape subregion: [Sclater and Sclater \(1899, p. 113\)](#); [Morrone \(1996, p. 104\)](#).

Cape kingdom: [Diels \(1908, p. 135\)](#); [Takhtajan \(1986, p. 252\)](#); [van Rooy and van Wyck \(2012, p. 111\)](#).

Südafrikanish Provinz (in part) [Schilder \(1956, p. 76\)](#).

South African kingdom: [Good \(1963, p. 32\)](#).

Western Cape province: [Takhtajan \(1986, p. 213\)](#).

Afrotemperate region: [Linder \(1994, p. 913\)](#); [Poynton \(2000, p. 39\)](#); [Morrone \(2002, p. 150\)](#); [Galley *et al.* \(2007, p. 535\)](#).

Greater Cape region: [Born *et al.* \(2007, p. 147\)](#).

Southern African region: (in part) [Carta *et al.* \(2022, table 2\)](#).

Southern Africa subregion: [Santos and Ribeiro \(2022, p. 10\)](#).

Diagnosis

The area south-east of Lake Malawi in the Rift Valley (Mozambique), south of the Zambezi River (Zimbabwe) and along the northern borders of Botswana and Namibia.

Malagasy subregion: [Wallace \(1876a\)](#)

Malagasy subregion: [Wallace \(1876a, p. 272\)](#); [Sclater and Sclater \(1899, p. 101\)](#); [Schmidt \(1954, p. 328\)](#).

Mascarenia subarea: [Clarke \(1892, p. 379\)](#).

Lemurian subregion: [Schilder \(1956, p. 76\)](#).

Madagascar region: [Good \(1963, p. 31\)](#).

Madagascan subkingdom: (in part) [Takhtajan \(1986, p. 249\)](#).

Pandora subregion: (in part) [Parenti and Ebach \(2010, p. 312, 2013, p. 815\)](#).

Madagascan region: [Carta *et al.* \(2022, table 2\)](#).

Indian subregion: [Santos and Ribeiro \(2022, p. 7\)](#) (*non* [Wallace 1876a, 1876b](#)).

Diagnosis

Madagascar and surrounding islands (Seychelles, Comoros, Mayotte and Mascarene islands).

Oriental region: [Wallace \(1876a\)](#)

Indian region: [Sclater \(1858, p. 140\)](#); [Kirby \(1872, p. 435\)](#); [Sharpe \(1884, p. 107\)](#); [Newton \(1893, p. 355\)](#).

Australasian region: [Blyth \(1871, p. 428\)](#).

Middle Paleotropical region: [Kirby \(1872, p. 435\)](#).

Oriental region: [Wallace \(1876a, p. 314\)](#); [Heilprin \(1887, p. 91\)](#); [Sclater \(1894, p. 98\)](#); [Lydekker \(1896, p. 264\)](#); [Sclater and Sclater \(1899, p. 123\)](#).

Bartholomew *et al.* (1911, p. 7); Newbigin (1913, p. 217); de Mello-Leitão (1937, p. 196); Schilder (1956, p. 76); Darlington (1957, p. 433); Kuschel (1963, p. 447); Thorne (1963, p. 332); de Lattin (1967, p. 282); Cabrera and Willink (1973, p. 27); Stoddart (1992, p. 278); Morrone (2002, p. 150); Kreft and Jetz (2013, p. 343-c); Rueda *et al.* (2013, p. 2217); Ribeiro *et al.* (2014, p. 249); Morrone (2015a, p. 85); Escalante (2017, p. 359); Hermogenes de Mendonça and Ebach (2020, p. 721).

Indogean kingdom: Gill (1885, p. 19).

Oriental kingdom: Heilprin (1887, p. 90); Morain (1984, p. 239); Kreft and Jetz (2010, p. 2044); Holt *et al.* (2013a, p. 75).

Indo-African realm: (in part) Allen (1892, p. 207).

Indo-China area: Clarke (1892, p. 379).

Indo-African region: Diels (1908, p. 130).

Oriental subregion: Schmidt (1954, p. 328); Poynton (1959, p. 26); Smith (1983, p. 462); Morrone (1996, p. 104).

Palaearctic region: (in part) Schilder (1956, p. 76).

Indo-Malaysian subkingdom: Good (1963, p. 31).

Malaysian region: Good (1963, p. 31).

Indomalayan kingdom: Udvardy (1975, p. 30) (in part).

Indo-Malesian subkingdom: Takhtajan (1986, p. 249).

Indomalayan kingdom: Udvardy (1987, p. 187).

Eastern Palearctic region: Lücking (2003, p. 43).

Indo-Malaysian region: Procheş and Ramdhani (2012, p. 263).

Diagnosis

All areas south of the Tibetan Plateau and the Yellow River and west of Weber's Line.

Remarks

A comparative biogeographic analysis by King and Ebach (2017) has shown that Palaeogene genera from Australia, southern New Guinea and eastern Sulawesi share a greater relationship to another than they do to Neogene genera (ages based on molecular dating). The results support Wallace's Line as the border between the Oriental and Australian region, rather than Weber's or Lydekker's lines.

Subregions

The Oriental region comprises two subregions, Indian and Indo-Chinese (Fig. 18).

Indian subregion: Sclater (1858)

Indian or Middle Palaeotropical region: Sclater (1858, p. 140).

Hindustan or Indian subregion: Wallace (1876a, p. 321).

Ceylon and South India Wallace (1876a, p. 326).

Indo-African realm: (in part) Allen (1892, p. 207).

Eastern Indian province: Schilder (1956, p. 76).

Indian region: Good (1963, p. 31); Takhtajan (1986, p. 249).

Diagnosis

Indian subcontinent, including the island of Sri Lanka, south of the Himalayas bordered by the Indus to the west and the Chittagongs to the east.

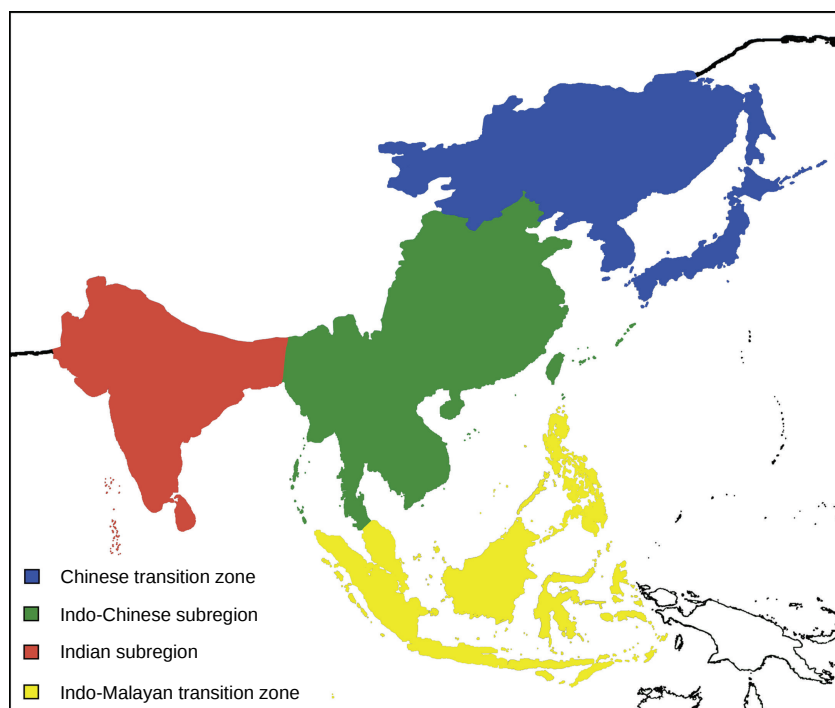


Fig. 18. The subregions and transition zones of the Oriental region (after Wallace 1876a).

Indo-Chinese subregion: Wallace (1876a)

Himalayan or Indo-Chinese subregion: Wallace (1876a, p. 329); Thorne (1963, p. 332).

Burmo-Chinese subregion: Sclater and Sclater (1899, p. 137).

South Chinese province: Schilder (1956, p. 76).

Indo-Chinese region: Takhtajan (1986, p. 249).

Indian-Indochinese region: Carta *et al.* (2022, table 2).

Diagnosis

Areas east of the Chittagongs, including the Andaman and Nicobar Islands, north of the Ta Pi River including the Phuket Range, bordered by the South China Sea in the west, by the islands of Taiwan and Hainan as well as the Ryukyu islands south of and including the Amami Islands (Japan) marked in the north-east by the Watase Line. Area bordered in the south by the Balintang Channel north of the Philippines, the Parcel Islands south of China, and Phú Quý and Côn Đảo islands to the south-east of Vietnam.

Neotropical subkingdom: Sclater (1858)

Neotropical region: Sclater (1858, p. 143).

South American kingdom: Engler (1882, p. 345); Cox (2001, p. 519).

Dendrogean kingdom: Gill (1885, p. 21).

Neotropical kingdom: Heilprin (1887, p. 73); Diels (1908, p. 150); Good (1963, p. 32); Udvardy (1975, p. 43); Morain (1984, p. 177); Takhtajan (1986, p. 250); Fleming (1987, p. 199); Udvardy (1987, p. 187); Kreft and Jetz (2010, p. 2044); Holt *et al.* (2013a, p. 75).

American Tropical kingdom: Allen (1892, p. 207).

Neogeic kingdom: Lydekker (1896, p. 64).

Neogean kingdom: Schmidt (1954, p. 328).

Neogea kingdom: Schilder (1956, p. 76).

Neotropic kingdom: Müller (1986, p. 20); Kreft and Jetz (2013, p. 343-c).

Neotropical subkingdom: Rivas-Martínez and Navarro (1994, map); Carta *et al.* (2022, table 1).

Diagnosis

Tropical South America, Central America, south-central Mexico and the Caribbean.

Regions

The Neotropical subkingdom comprises the Neotropical region.

Neotropical region: Sclater (1858)

Neotropical region: Sclater (1858, p. 143); Kirby (1872, p. 437); Wallace (1876b, p. 3); Sharpe (1884, p. 102); Newton (1893, p. 321);

Sclater (1894, p. 98); Lydekker (1896, p. 64); Sclater and Sclater (1899, p. 52); Bartholomew *et al.* (1911, p. 9); Newbigin (1913, p. 221); de Mello-Leitão (1937, p. 221); Schmidt (1954, p. 328); Schilder (1956, p. 76); Darlington (1957, p. 446); Poynton (1959, p. 26); Thorne (1963, p. 333); de Lattin (1967, p. 271); Rapoport 1968, p. 61); Cabrera and Willink (1973, p. 26); Stoddart (1992, p. 278); Morrone (2002, p. 150); Morrone (2006, p. 477); Procheş and Ramdhani (2012, p. 263); Rueda *et al.* (2013, p. 2217); Morrone (2014, p. 26); Ribeiro *et al.* (2014, p. 249); Morrone (2015a, p. 85); Escalante (2017, p. 358); Morrone (2017, p. 41); Hermogenes de Mendonça and Ebach (2020, p. 721).

American region: Murray (1866, p. 311) (in part).

Austro-Columbia province: Huxley (1868, p. 315).

Columbian region: Blyth (1871, p. 428).

South American region: Kirby (1872, p. 437); Cox (2001, p. 519).

Tropical America region: Engler (1882, p. 345).

Neotropica area: Clarke (1892, p. 381).

Tropical region: Merriam (1892, p. 33).

Neotropical subregion: Smith (1983, p. 462); Morrone (1996, p. 104).

Neotropics region: Lücking (2003, p. 43).

Diagnosis

The same as the subkingdom.

Subregions

The Neotropical region comprises three subregions, namely Antillean, Brazilian and Chacoan (Morrone 2014, 2017; Fig. 19).

Antillean subregion: Wallace (1876a)

Antillean subregion: Wallace (1876b, p. 79); Heilprin (1887, p. 80); Lydekker (1896, p. 136); Sclater and Sclater (1899, p. 65); Bartholomew *et al.* (1911, p. 9); de Mello-Leitão (1937, p. 229); Rapoport (1968, p. 71); Bănărescu and Boşcaiu (1978, p. 259); Samek *et al.* (1988, p. 29); Del Risco and Vandama (1989, p. X.2.4); Huber and Riina (2003, p. 23); Echeverry and Morrone (2013, p. 1628); Morrone (2014, p. 35); Klassa and Santos (2015, p. 520).

West Indian province: Engler (1882, p. 345).

America Centralis subarea: Clarke (1892, p. 381).

Antillean division: Merriam (1892, p. 18).

Caribbean province: de Mello-Leitão (1937, p. 246); Cabrera and Willink (1973, p. 38); Brown *et al.* (1998, p. 32).

Caribbean region: Good (1963, p. 32); Rzedowski (1978, p. 107); Takhtajan (1986, p. 251); Samek *et al.* (1988, p. 26); Huber and Riina (1997, p. 119); Procheş and Ramdhani (2012, p. 263).

West Indian subregion: Hershkovitz (1969, p. 9); Smith (1983, p. 462); Sánchez Osés and Pérez-Hernández (2005, p. 168).

Caribbean dominion: Cabrera and Willink (1973, p. 32) (in part); Zuloaga *et al.* (1999, p. 18).

Caribbean subregion: Schmidt (1954, p. 328); Rivas-Martínez and Navarro (1994, map) (in part); Morrone (1999, p. 2); Morrone *et al.* (1999, p. 510); Morrone (2001b, p. 30, 2005, p. 238); Lamas *et al.* (2014, p. 955).



Fig. 19. The subregions and transition zones of the Neotropical region (after Morrone 2017).

Antillean province: [Rivas-Martínez and Navarro \(1994, map\)](#).

Caribbean area: [Coscarón and Coscarón-Arias \(1995, p. 726\)](#).

Caribbean bioregion: [Dinerstein *et al.* \(1995, map\)](#).

Antillean region: [Huber and Riina \(2003, p. 23\)](#).

Antillean dominion: [Morrone \(2004a, p. 157\)](#); [Corona and Morrone \(2005, p. 38\)](#); [Morrone \(2006, p. 479\)](#).

Caribbean component: [Nihei and de Carvalho \(2004, p. 271\)](#).

Greater Antilles area: [Porzecanski and Cracraft \(2005, p. 266\)](#).

Central-Eastern Antilles superprovince: [Cano *et al.* \(2009, p. 543\)](#).

Western Antilles superprovince: [Cano *et al.* \(2009, p. 543\)](#).

Caribbean–Mesoamerican region: [Rivas-Martínez *et al.* \(2011, p. 26\)](#) (in part).

Panamanian region: [Holt *et al.* \(2013a, p. 77\)](#) (in part).

Diagnosis

The Antillean subregion comprises the Antilles or West Indies (Greater and Lesser Antilles) and the Bahamas. The Greater Antilles include Cuba, Jamaica, Hispaniola and Puerto Rico, and the Lesser Antilles include Grenada, The Grenadines, St Vincent, Barbados, St Lucia, Martinique, Dominica, Marie Galante, Guadeloupe, La Desirade, Montserrat, Antigua, Nevis, St Kitts, Barbuda, St Eustatius, Saba, St Barthélemy, St Martin and Anguilla ([Morrone 2017](#)).

Brazilian subregion: Blyth (1871)

Brazilian subregion: [Blyth \(1871, p. 428\)](#); [Wallace, \(1876b, p. 78\)](#); [Heilprin \(1887, p. 80\)](#); [Lydekker \(1896, p. 135\)](#); [Bartholomew *et al.* \(1911, p. 9\)](#); [de Mello-Leitão \(1937, p. 244\)](#); [Hershkovitz \(1969, p. 3\)](#); [Kuschel \(1969, p. 710\)](#); [Bănărescu and Boşcaiu \(1978, p. 258\)](#); [Almirón *et al.* \(1997, p. 23\)](#); [Ojeda *et al.* \(2002, p. 23\)](#); [Morrone \(2014, p. 45\)](#); [Klassa and Santos \(2015, p. 520\)](#).

Tropical American region: [Engler \(1882, p. 345\)](#) (in part).

Brasil Borealis subarea: [Clarke \(1892, p. 381\)](#).

Amazonian subregion: [Sclater and Sclater \(1899, p. 65\)](#) (in part); [Morrone \(1996, p. 6, 2001b, p. 67, 2005, p. 238\)](#); [Viloria \(2005, p. 449\)](#); [Morrone \(2006, p. 480\)](#); [Pires and Marinoni \(2011, p. 8\)](#).

Amazonian district: [Cabrera and Yepes \(1940, p. 14\)](#) (in part).

Amazonian dominion: [Orfila \(1941, p. 86\)](#); [Huber and Riina \(1997, p. 150\)](#); [Ojeda *et al.* \(2002, p. 24\)](#); [Huber and Riina \(2003, p. 124\)](#).

Guianan–Brazilian subregion: [de Mello-Leitão \(1943, p. 128\)](#) (in part); [Ringuelet \(1961, p. 156\)](#); [Rapoport \(1968, p. 72\)](#); [Ringuelet \(1978, p. 255\)](#); [de Paggi \(1990, p. 303\)](#); [Sánchez Osés and Pérez-Hernández \(2005, p. 168\)](#).

Amazon region: [Good \(1963, p. 32\)](#).

Venezuela and Guiana region: [Good \(1963, p. 32\)](#).

Guianan–Brazilian region: [Fittkau \(1969, p. 636\)](#).

Amazonian Basin area: [Sick \(1969, p. 451\)](#).

Non-Andean East area: [Sick \(1969, p. 451\)](#) (in part).

Caribbean dominion: [Cabrera and Willink \(1973, p. 32\)](#) (in part); [Huber and Riina \(1997, p. 151\)](#); [Zuloaga *et al.* \(1999, p. 18\)](#); [Huber and Riina \(2003, p. 124\)](#).

Caribbean Amazonian subkingdom: [Rivas-Martínez and Tovar \(1983, p. 521\)](#) (in part).

Caribbean region: [Takhtajan \(1986, p. 251\)](#) (in part); [Samek *et al.* \(1988, p. 26\)](#); [Huber and Riina \(1997, p. 119\)](#); [Huber and Riina \(2003, p. 97\)](#).

Amazonian region: [Rivas-Martínez and Navarro \(1994, map\)](#).

Amazonian area: [Coscarón and Coscarón-Arias \(1995, p. 726\)](#).

Caribbean subregion: [Morrone \(1999, p. 2\)](#) (in part), [2001b, p. 30](#); [Corona and Morrone \(2005, p. 38\)](#); [Morrone \(2005, p. 238\)](#); [Viloria \(2005, p. 449\)](#); [Morrone \(2006, p. 478\)](#); [Lamas *et al.* \(2014, p. 955\)](#).

North-western component: [Nihei and de Carvalho \(2004, p. 271\)](#).

Amazonic dominion: [Donato \(2006, p. 422\)](#).

Amazon dominion: [Fiaschi and Pirani \(2009, p. 480\)](#).

Amazonian component: [Sigrist and de Carvalho \(2009, p. 81\)](#).

Amazon subregion: [Lamas *et al.* \(2014, p. 955\)](#) (in part).

Diagnosis

The Brazilian subregion comprises central and southern Mexico, Central America, and north-western South America ([Morrone 2017](#)).

Chacoan subregion: Cabrera (1951)

Tropical American region: [Engler \(1882, p. 345\)](#) (in part).

Brasil Australis subarea: [Clarke \(1892, p. 381\)](#).

South Brazilian subregion: [Sclater and Sclater \(1899, p. 65\)](#) (in part).

Chacoan dominion: [Cabrera \(1951, p. 32, 1971, p. 15\)](#); [Cabrera and Willink \(1973, p. 69\)](#); [Huber and Riina \(1997, p. 151\)](#); [Ojeda *et al.* \(2002, p. 24\)](#).

Guianan–Brazilian subregion: [Ringuelet \(1961, p. 156\)](#) (in part); [Rapoport \(1968, p. 72\)](#); [Ringuelet \(1978, p. 255\)](#); [de Paggi \(1990, p. 303\)](#).

South Brazilian region: [Good \(1963, p. 32\)](#).

Guianan–Brazilian region: [Fittkau \(1969, p. 636\)](#) (in part).

Brazilian subregion: [Herskovitz \(1969, p. 3\)](#) (in part); [Kuschel \(1969, p. 710\)](#).

Non-Andean East area: [Sick \(1969, p. 451\)](#) (in part).

Caribbean Amazonian subkingdom: [Rivas-Martínez and Tovar \(1983, p. 521\)](#) (in part).

Central Brazilian region: [Takhtajan \(1986, p. 251\)](#) (in part).

Brazilian Paraná subregion: [Rivas-Martínez and Navarro \(1994, map\)](#) (in part).

Eastern South America bioregion: [Dinerstein *et al.* \(1995, map\)](#) (in part); [Huber and Riina \(1997, p. 37\)](#).

Chacoan subregion: [Morrone \(1999, p. 9, 2001b, p. 83, 2005, p. 238, 2006, p. 481\)](#); [Ramos and Melo \(2010, p. 449\)](#); [Arana *et al.* \(2011, p. 17\)](#); [Moreira *et al.* \(2011, p. 29\)](#); [Pires and Marinoni \(2011, p. 8\)](#); [Lamas *et al.* \(2014, p. 955\)](#); [Morrone \(2014, p. 72\)](#); [Klassa and Santos \(2015, p. 520\)](#).

South-eastern component: [Nihei and de Carvalho \(2004, p. 271\)](#).

Atlantic Forest region: [Pellegrino *et al.* \(2005, p. 14\)](#).

Atlantic Forest component: [Sigrist and de Carvalho \(2009, p. 81\)](#).

Chacoan–Brazilian superegion: [Rivas-Martínez *et al.* \(2011, p. 27\)](#).

Diagnosis

The Chacoan subregion comprises south-eastern South America ([Morrone 2017](#)).

Austral kingdom: Engler (1899)

Old Oceanic region: [Engler \(1882, p. 346\)](#).

Antarctic kingdom: [Drude \(1890, p. 158\)](#); [Udvardy \(1975, p. 37\)](#); [Takhtajan \(1986, p. 252\)](#).

Austral kingdom: [Engler \(1899, p. 149\)](#); [Morrone \(2002, p. 150\)](#); [Glasby \(2005, p. 243\)](#); [Moreira-Muñoz \(2007, p. 1652\)](#); [Ebach *et al.* \(2015, p. 265\)](#); [Morrone \(2015a, p. 85, 2018, p. 29\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#); [Carta *et al.* \(2022, table 1\)](#).

Austral region: [Newbigin \(1950, p. 145\)](#); [Kuschel \(1963, p. 447\)](#); [Morrone \(1996, p. 104\)](#).

Notogaa kingdom: [Schilder \(1956, p. 72\)](#).

Neantarctic region: [Monrós \(1958, p. 145\)](#).

Notogean kingdom: [de Lattin \(1967, p. 276\)](#).

Holantarctic region: [Rapoport \(1968, p. 88\)](#).

Antarctic region: [Cabrera and Willink \(1973, p. 26\)](#) (*non* [Grisebach 1872](#)).

Archinotic kingdom: [Müller \(1986, p. 20\)](#); [Kreft and Jetz \(2013, p. 343-c\)](#).

Holantarctic kingdom: [Takhtajan \(1986, p. 276\)](#).

Antarctic subkingdom: [Carta *et al.* \(2022, table 1\)](#).

Diagnosis

Southern temperate areas in South America, South Africa, Australasia and Antarctica.

Remarks

It corresponds to Temperate Gondwanaland ([Amorim and Tozoni 1994](#); [Ebach *et al.* 2015](#); [Morrone 2015a, 2018](#)). The Cape region, previously assigned to this kingdom, is here transferred to the Ethiopian region.

Regions

The Austral kingdom comprises three regions, namely Andean, Australian and Antarctic.

Andean region: Engler (1882)

American region: [Murray \(1866, p. 311\)](#) (in part).

Andisian subregion: [Blyth \(1871, p. 427\)](#).

Peruvian subregion: Blyth (1871, p. 428); Thorne (1963, p. 333).

Chilean subregion: Wallace (1876b, p. 36) (in part); Bartholomew *et al.* (1911, p. 9); Thorne (1963, p. 333); Stoddart (1992, p. 278).

Andean region: Engler (1882, p. 346); Good (1963, p. 32); Morain (1984, p. 178); Takhtajan (1986, p. 251); Morrone (2002, p. 150, 2006, p. 483); Procheş and Ramdhani (2012, p. 263); Morrone (2015a, p. 86); Escalante (2017, p. 358); Morrone (2018, p. 43); Hermogenes de Mendonça and Ebach (2020, p. 721).

Anfigean kingdom: Gill (1885, p. 22).

South American Temperate kingdom: Allen (1892, p. 207) (in part).

Argentina subarea: Clarke (1892, p. 381) (in part).

Patagonian subregion: Sclater and Sclater (1899, p. 77); Sharpe (1884, p. 103); Newton (1893, p. 324); Poynton (1959, p. 26); Kuschel (1963, p. 447).

Andean dominion: Hauman (1931, p. 62).

Temperate South America dominion: Hauman (1931, p. 62).

Andean–Patagonian subregion: de Mello-Leitão (1937, p. 232); Rapoport (1968, p. 75).

Andean province: Schilder (1956, p. 76).

Patagonian region: Good (1963, p. 32); Takhtajan (1986, p. 253).

Andean–Patagonian dominion: Cabrera (1971, p. 29).

Austral subregion: Ringelet (1975, p. 107).

Andean subkingdom: Rivas-Martínez and Tovar (1983, p. 516).

Argentine subregion: Smith (1983, p. 462).

Austroamerican subkingdom: Rivas-Martínez and Navarro (1994, map).

Neotemperate region: Amorim and Pires (1996, p. 187).

Andean subregion: Morrone (1996, p. 105).

Patagonian–Andean region: Daniels and Veblen (2000, p. 225).

Andean–Argentinian region: Carta *et al.* (2022, table 2).

Neozelandic–Patagonian region: (in part) Carta *et al.* (2022, table 2).

Diagnosis

Southern South America below 30° south latitude.

Remarks

Roig-Juñent *et al.* (2018) considered that the Patagonian biogeographic province should be considered as belonging to the South American transition zone, but we keep it in the Andean region.

Subregions

The Andean regions comprises three subregions, namely Subantarctic, Central Chilean and Patagonian (Morrone 2015b, 2018; Fig. 20).

Subantarctic subregion: Skottsberg (1905)

Subantarctic dominion: Skottsberg (1905, p. 415); Cabrera (1951, p. 57, 1971, p. 36); Cabrera and Willink (1973, p. 96).

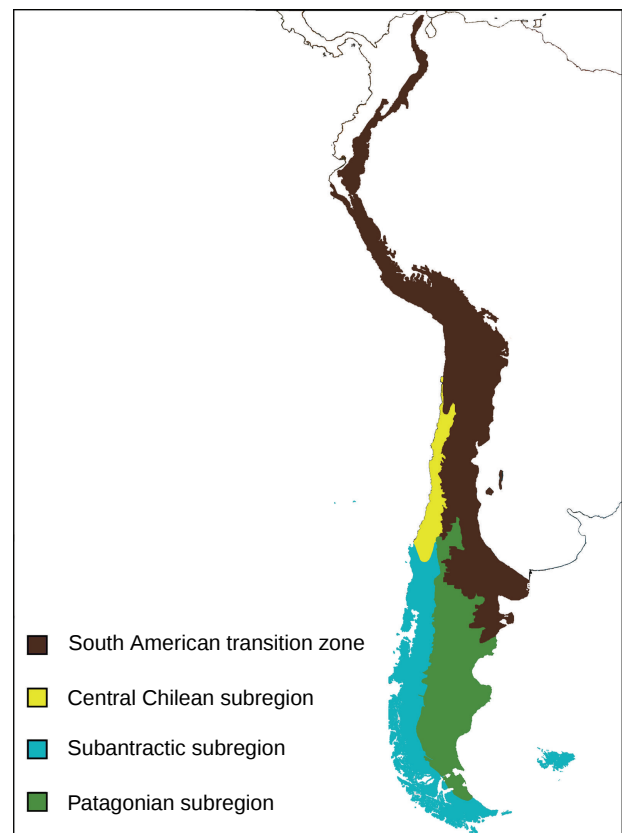


Fig. 20. The subregions and transition zone of the Andean region (after Morrone 2018).

Subantarctic Forests area: Hauman (1920, p. 52); Parodi (1934, p. 171).

Moist Andean zone: Shannon (1927, p. 3).

Forests region: Goetsch (1931, p. 2).

Subantarctic Andes province: Hauman (1931, p. 62).

Subantarctic Forests province: Hauman (1931, p. 62).

Subantarctic province: Cabrera (1951, p. 58, 1971, p. 37); Cabrera and Willink (1973, p. 97); Morrone (1996, p. 106); Posadas *et al.* (1997, p. 2); Sérsic *et al.* (2011, p. 477); Apodaca *et al.* (2015a, p. 97).

Austral–Cordilleran dominion: Ringelet (1955, p. 84, 1961, p. 160).

Subantarctic forests region: Hueck (1957, p. 40).

Araucanian subregion: Monrós (1958, p. 145); Ringelet (1961, p. 156); Rapoport (1968, p. 75).

Subantarctic subregion: Thorne (1963, p. 333); Morrone (1999, p. 13, 2001b, p. 118, 2004a, p. 158, 2006, p. 484, 2011, p. 2085, 2015b, p. 213); Arana *et al.* (2017, p. 421).

Chile province: (in part) Fittkau (1969, p. 642).

Southern Andes area: (in part) Sick (1969, p. 465).

Nothofagus centre: Müller (1973, p. 155); Cracraft (1985, p. 36).

Andean Subantarctic region: Rivas-Martínez and Tovar (1983, p. 521).

Neotropic–Archinotic transition zone: Müller (1986, p. 24).

Insular Antarctica province: Udvardy (1987, p. 188) (in part).

Chilean subregion: (in part) Flint (1989, p. 1).

Valdivian–Magellanic region: [Rivas-Martínez and Navarro \(1994, map\)](#).
 Subantarctic area: [Coscarón and Coscarón-Arias \(1995, p. 726\)](#); [Apodaca et al. \(2015b, p. 5\)](#).
 Patagonian Forests ecoregion: [Burkart et al. \(1999, p. 35\)](#).
 Valdivian–Magellanian province: [Rivas-Martínez et al. \(2011, p. 27\)](#).
 Valdivian region: [Lücking \(2003, p. 43\)](#).

Diagnosis

This subregion represents the core of the Andean region, and corresponds to Austral Chile from 37° south latitude to Cabo de Hornos, the archipelago of southern Chile and Argentina, and the Falklands (Malvinas), South Georgia and Juan Fernández islands ([Morrone 2018](#)).

Central Chilean subregion: [Hauman \(1931\)](#)

Central Chilean province: [Hauman \(1931, p. 62\)](#); [Cabrera and Willink \(1973, p. 92\)](#); [Morrone \(1996, p. 107\)](#); [Posadas et al. \(1997, p. 2\)](#).
 Chilean district: [Cabrera and Yepes \(1940, p. 16\)](#).
 Chilean province: [de Mello-Leitão \(1943, p. 130\)](#); [Ringuelet \(1975, p. 107\)](#).
 Peruvian subprovince: [Schilder \(1956, p. 76\)](#).
 Chilean subregion: [Thorne \(1963, p. 333\)](#); [Paulson \(1979, p. 170\)](#); [Flint \(1989, p. 1\)](#); [Rivas-Martínez and Navarro \(1994, map\)](#).
 Chile province: (in part) [Fittkau \(1969, p. 642\)](#).
 Southern Andes area: (in part) [Sick \(1969, p. 465\)](#).
 Chilean subcentre: (in part) [Müller \(1973, p. 101\)](#).
 Central Andean zone: (in part) [Artigas \(1975, map\)](#).
 Central Chilean region: [Rivas-Martínez and Tovar \(1983, p. 516\)](#).
 Central Chile area: [Coscarón and Coscarón-Arias \(1995, p. 726\)](#); [Roig-Juñent et al. \(2006, p. 408\)](#).
 Chilean Matorral ecoregion: [Dinerstein et al. \(1995, p. 103\)](#); [Locklin \(2017, p. 1\)](#).
 Central Chilean subregion: [Morrone \(1999, p. 13\)](#); [Morrone \(2001b, p. 114, 2004a, p. 158, 2006, p. 484, 2015b, p. 209\)](#).
 Central region: [Roig-Juñent and Domínguez \(2001, p. 557\)](#).
 Middle Chilean–Patagonian region: (in part) [Rivas-Martínez et al. \(2011, p. 27\)](#).
 Central Chile ecoregion: [Moreira-Muñoz \(2014, p. 221\)](#).

Diagnosis

Area that corresponds to Central Chile between 26 and 37° south latitude ([Morrone 2018](#)).

Patagonian subregion: [Lorentz \(1876\)](#)

Patagonian formation: [Lorentz \(1876, p. 92\)](#).
 Argentinean Patagonian province: [Engler \(1882, p. 346\)](#).

Patagonian region: [Delachaux \(1920, p. 127\)](#); [Rivas-Martínez and Tovar \(1983, p. 516\)](#).
 Patagonian Steppes area: [Hauman \(1920, p. 47\)](#); [Holdgate \(1961, p. 560\)](#); [Hueck \(1966, p. 3\)](#).
 Patagonian Steppes province: [Hauman \(1931, p. 62\)](#).
 Patagonian Desert area: [Parodi \(1934, p. 171\)](#).
 Patagonian district: [Cabrera and Yepes \(1940, p. 15\)](#).
 Patagonian subprovince: [Schilder \(1956, p. 76\)](#).
 Patagonian Savannas and Deserts area: [Hueck \(1957, p. 40\)](#).
 Patagonian Steppes zone: [Kuschel \(1960, p. 546\)](#).
 Patagonian dominion: [Ringuelet \(1961, p. 160\)](#).
 Patagonian Steppe region: [Peña \(1966, p. 15\)](#); [Roig-Juñent and Domínguez \(2001, p. 558\)](#).
 Patagonia province: [Fittkau \(1969, p. 642\)](#); [Baranzelli et al. \(2014, p. 752\)](#).
 East Patagonia area: [Sick \(1969, p. 452\)](#).
 Patagonian centre: [Müller \(1973, p. 151\)](#); [Cracraft \(1985, p. 36\)](#).
 Steppe zone: [Cekalovic \(1974, p. 308\)](#).
 Patagonia area: [Coscarón and Coscarón-Arias \(1995, p. 726\)](#); [Apodaca et al. \(2015b, p. 5\)](#).
 Patagonian area: [Acosta and Maury \(1998a, p. 554, 1998b, p. 573\)](#).
 Patagonian subregion: [Morrone \(1999, p. 15, 2001b, p. 129, 2004a, p. 158, 2006, p. 486, 2015b, p. 222\)](#); [Arana et al. \(2017, p. 421\)](#).
 Patagonian Steppe subregion: [Spinelli et al. \(2006, p. 302\)](#).
 Middle Chilean–Patagonian region: (in part) [Rivas-Martínez et al. \(2011, p. 27\)](#).

Diagnosis

Southern Argentina, from central Mendoza, widening through Neuquén, Río Negro, Chubut and Santa Cruz, to northern Tierra del Fuego; and reaching Chile in Malleco, Aisén and Magallanes provinces ([Morrone 2018](#)).

Australian region: [Sclater \(1858\)](#)

Australian region: [Sclater \(1858, p. 141\)](#); [Murray \(1866, p. 310\)](#); [Grisebach \(1872, p. 203\)](#); [Kirby \(1872, p. 436\)](#); [Wallace \(1876a, p. 387\)](#); [Engler \(1882, p. 347\)](#); [Sharpe \(1884, p. 108\)](#); [Heilprin \(1887, p. 97\)](#); [Newton \(1893, p. 317\)](#); [Sclater \(1894, p. 97\)](#); [Lydekker \(1896, p. 30\)](#); [Sclater and Sclater \(1899, p. 18\)](#); [Bartholomew et al. \(1911, p. 8\)](#); [Newbigin \(1913, p. 223\)](#); [de Mello-Leitão \(1937, p. 209\)](#); [Schmidt \(1954, p. 328\)](#); [Darlington \(1957, p. 449\)](#); [Poynton \(1959, p. 26\)](#); [Thorne \(1963, p. 333\)](#); [Cabrera and Willink \(1973, p. 26\)](#); [Stoddart \(1992, p. 278\)](#); [Cox \(2001, p. 519\)](#); [Procheş and Ramdhani \(2012, p. 263\)](#); [Rueda et al. \(2013, p. 2217\)](#); [Ribeiro et al. \(2014, p. 249\)](#); [Ebach et al. \(2015, p. 266\)](#); [Morrone \(2015a, p. 86\)](#); [Escalante \(2017, p. 359\)](#); [Hermogenes de Mendonça and Ebach \(2020, p. 721\)](#).
 Western Paleotropical region: [Sclater \(1858, p. 141\)](#); [Kirby \(1872, p. 436\)](#) (in part).
 Australian province: [Huxley \(1868, p. 315\)](#).

Australian subregion: Blyth (1871, p. 428); Schmidt (1954, p. 328); Kuschel (1963, p. 447); Thorne (1963, p. 333); Smith (1983, p. 462); Stoddart (1992, p. 278).

Austrogean kingdom: Gill (1885, p. 22).

Australian kingdom: Heilprin (1887, p. 97); Allen (1892, p. 207); Diels (1908, p. 156); Good (1963, p. 32); Udvardy (1975, p. 34); Morain (1984, p. 265); Müller (1986, p. 20); Takhtajan (1986, p. 252); Udvardy (1987, p. 187); Cox (2001, p. 519); Kreft and Jetz (2010, p. 2044); Holt *et al.* (2013a, p. 75); Kreft and Jetz (2013, p. 343-c); Ebach *et al.* (2015, p. 266).

Oceania area: Clarke (1892, p. 380).

Austral Oceanic subregion: Schilder (1956, p. 76).

Notogaeic kingdom: Lydekker (1896, p. 28).

Notogaeic kingdom: Schmidt (1954, p. 328).

Island region: Smith (1983, p. 462).

Australasian kingdom: Fleming (1987, p. 199).

Australian subkingdom: Fleming (1987, p. 199); Carta *et al.* (2022, table 1).

New Guinean region: Procheş and Ramdhani (2012, p. 263).

Eremaean region: Carta *et al.* (2022, table 2).

Northern Australian region: Carta *et al.* (2022, table 2).

Diagnosis

Australian continent, New Guinea and western islands, eastern Sulawesi, southern Philippines, New Caledonia, and New Zealand.

Remarks

Wallace's original classification is used herein, which includes the southern Philippines.

Subregions

The Australian region comprises three subregions, namely Australian, Polynesian and New Zealand (Fig. 21).

Australian subregion: Wallace (1876a)

Australia and Tasmania or Australian subregion: Wallace (1876a, p. 438).

Australia subarea: Clarke (1892, p. 380).

Austral subregion: Sclater and Sclater (1899, p. 22).

Australian province: Schilder (1956, p. 76).

Papuan province: (in part) Schilder (1956, p. 76).

Central Australian region: Good (1963, p. 32).

North and East Australian region: Good (1963, p. 32).

South-West Australian region: Good (1963, p. 32).

Australian kingdom: Doing (1970, pp. 84–85); Takhtajan (1986, p. 268).

Australasia subkingdom: Fleming (1987, p. 199).

Pandora subregion: (in part) Parenti and Ebach (2010, p. 312, 2013, p. 815).

Diagnosis

The Australian continent, including southern New Guinea (south of the Central Range) and Aru Islands Regency.

Polynesian subregion: Wallace (1876a)

Pacific Islands or Polynesian subregion: Wallace (1876a, p. 442); Thorne (1963, p. 332).

Polynesia subarea: Clarke (1892, p. 380).

Sandwich subarea: Clarke (1892, p. 380).

Polynesian subregion: Sclater and Sclater (1899, p. 48); Schilder (1956, p. 76).

Hawaiian subregion: Sclater and Sclater (1899, p. 49).

Oceanic subregion: Schmidt (1954, p. 328).

Polynesian subkingdom: Good (1963, p. 31); Takhtajan (1986, p. 249).

Hawaiian region: Good (1963, p. 31); Takhtajan (1986, p. 249).

Melanesia and Micronesia region: Good (1963, p. 31).

Oceanian kingdom: Udvardy (1975, p. 31).

Fijian region: Takhtajan (1986, p. 249).

Polynesian region: Takhtajan (1986, p. 249).

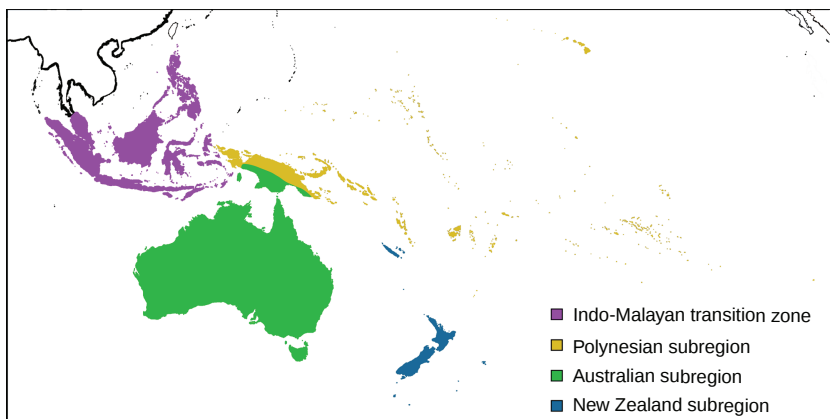


Fig. 21. The subregions and transition zone of the Australian region.

Diagnosis

The islands of the tropical Pacific Ocean, from the Pitcairn Islands in the east to the Hawaiian Islands in the north-east, to Palau and Mariana Islands in the north-west, to Illiger's Line in the west, including Northern Papua, the Central Ranges and the Solomons, to Vanuatu and Austral islands to the south.

Remarks

New Caledonia (Grande Terre and the Loyalty Islands) is not included in the Polynesian subregion because it shares Australian taxa and taxa that are sister to New Zealand. Although there are connections to both the Oriental and the Neotropical regions, the relationship with the Australian biota is significant (Heads 2014). Given that the boundary known as Lydekker's Line (Lydekker 1896) was proposed by Illiger (1815) 81 years earlier in his *Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile* [A Review of Mammals based on their Global Distribution], the boundary is renamed herein Illiger's Line, after the German zoologist Johann Karl Wilhelm Illiger (1775–1813).

New Zealand subregion: Wallace (1876a)

New Zealand subregion: Wallace (1876a, p. 449), Procheş and Ramdhani (2012, p. 263).

Neo-Zeelandia subarea: Clarke (1892, p. 380).

Maorian subregion: Sclater and Sclater (1899, p. 43).

New Zealandian subregion: Schmidt (1954, p. 328).

Neozeylandic subregion: Schilder (1956, p. 76); Thorne (1963, p. 333).

New Caledonian region: Good (1963, p. 31).

New Zealand region: Good (1963, p. 32); Takhtajan (1986, p. 252).

Neocaledonian subregion: Thorne (1963, p. 332).

Neocaledonian subkingdom: Takhtajan (1986, p. 250).

Neozeylandic region: Takhtajan (1986, p. 250).

Neozelandia subkingdom: Fleming (1987, p. 199).

Neozelandia province: Udvardy (1987, p. 188).

Neozelandic-Patagonian region: (in part) Carta *et al.* (2022, table 2).

Diagnosis

The area encompassing New Zealand and surrounding islands (Stewart, Lord Howe, Norfolk, Chathams, Campbell) and New Caledonia (see remarks above).

Antarctic region: Blyth (1871)

Antarctic subregion: Blyth (1871, p. 428); Schmidt (1954, p. 328); Morrone (1996, p. 104).

Antarctic region: Grisebach (1872, p. 481); Engler (1882, p. 347); Schilder (1956, p. 76); Thorne (1963, p. 333); Morrone (2002, p. 150); Procheş and Ramdhani (2012, p. 263); Morrone (2015a, p. 86); Hermogenes de Mendonça and Ebach (2020, p. 721).

Antarctic kingdom: Allen (1892, p. 207); Diels (1908, p. 154); Good (1963, p. 32); Udvardy (1975, p. 38); Takhtajan (1986, p. 253); Fleming (1987, p. 199); Udvardy (1987, p. 187).

Diagnosis

Antarctica and surrounding islands.

Remarks

Udvardy (1987) has recognised three provinces within this region, namely Insulantarctica, Marielandia and Maudlandia.

Transition zones

Areas that are defined through the overlap of two different kingdoms are called transition zones (*sensu lato* Morrone 2015a; *sensu stricto* Hermogenes de Mendonça and Ebach (2020; Table 5). Transition zones, by their composite nature,

Table 5. The regions, divided into kingdoms, which overlap within transition zones (TZ).

Kingdom	Region	Transition zone				
Kingdom	Region	Mexican	Saharo-Arabian	Chinese	Indo-Malayan	South American
Holarctic	Nearctic	×				
	Palearctic		×	×		
Holotropical	Ethiopian		×			
	Oriental			×	×	
	Neotropical	×				×
Austral	Andean					×
	Australian				×	
	Antarctic					

The Mexican, Saharo-African, Chinese TZ are Holotropical + Holarctic; Indo-Malayan TZ is Holotropical + Austral; South American TZ is Holotropical + Austral. There are no known Holarctic + Austral transition zones, although Hawaiian Islands may be a potential candidate.

have no place in a hierarchal classification; rather they form a separate non-hierarchal classification detailed below.

Mexican transition zone: Grisebach (1872)

Mexican region: Grisebach (1872, p. 314).

Mexican subregion: Wallace (1876b, p. 78) (in part); Heilprin (1887, p. 81); Lydekker (1896, p. 136); Bartholomew *et al.* (1911, p. 10); de Mello-Leitão (1937, p. 222).

Mexican Highlands region: Engler (1882, p. 345).

Aztec province: Engler (1882, p. 345).

Mexican province: Sharpe (1884, p. 102).

Neoarctic–Neotropical transition zone: Forsyth Major (1884, p. 113).

Sonoran transition zone: Heilprin (1887, p. 106).

Sonoran region: Merriam (1892, p. 26) (in part); Lydekker (1896, p. 363).

Central American subregion: Sclater and Sclater (1899, p. 72).

Central American–Mexican transition zone: Darlington (1957, p. 456).

Extratropical Highlands kingdom: West (1964, p. 365).

Mountain Mesoamerican province: Cabrera and Willink (1973, p. 32).

Mountain Mesoamerican region: Rzedowski (1978, p. 101).

Neotropic–Paleotropic–Holarctic transition zone: Müller (1986, p. 21); Kreft and Jetz (2013, p. 343-c).

Mexican Highlands province: Takhtajan (1986, p. 183).

Mexican transition zone: Halffter (1987, p. 95); Morrone (2006, p. 475, 2014, p. 27, 2015a, p. 86); Halffter and Morrone (2017, p. 2); Hermogenes de Mendonça and Ebach (2020, p. 721); Morrone (2020, p. 107).

Mexican Mountains kingdom: Huber and Riina (2003, p. 167).

Mexican Mountain transition zone: Espinosa Organista *et al.* (2008, p. 54).

Central American subregion: Procheş and Ramdhani (2012, p. 263).

Panamanian kingdom: Holt *et al.* (2013a, p. 75, 2013b, p. 343-d).

Madrean region: Carta *et al.* (2022, table 2).

Diagnosis

Mountainous areas of Mexico, Guatemala, Honduras, El Salvador and Nicaragua north of lake Nicaragua (Morrone 2014, 2015a; Halffter and Morrone 2017). It corresponds with the boundary between the Nearctic and Neotropical regions, and comprises the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, Transmexican Volcanic Belt and Chiapas highlands (Morrone 2014, 2015a).

Remarks

Halffter (1987) considered that the Mexican transition zone extends to southern United States as well as the Mexican lowlands.

Chinese transition zone: Sclater and Sclater (1899)

Manchurian subregion: Wallace (1876a, p. 220).

Mantchurian subregion: Sharpe (1884, p. 105).

Himalo-Chinese subregion: Newton (1893, p. 356).

Chinese subregion: Sclater and Sclater (1899, p. 191).

Intermediate region: Tatewaki (1963, p. 26).

Chinese transition zone: Palestini *et al.* (1985, p. 195); Morrone (2015a, p. 86); Hermogenes de Mendonça and Ebach (2020, p. 721).

Sino-Himalayan subregion: Procheş and Ramdhani (2012, p. 263).

Sino-Japanese kingdom: Holt *et al.* (2013a, p. 75, 2013b, p. 343-d).

Diagnosis

It corresponds to the boundary between the Palearctic and Oriental regions (Palestrini *et al.* 1985; Müller 1986; Kreft and Jetz 2013).

Remarks

Müller (1979) suggested that this zone extends from the Yang Tsê–Kiang River to the 21st parallel, including also Taiwan. Palestini *et al.* (1985) analysed the geographical distribution of some groups of Scarabaeoidea (Coleoptera) of this area and detected the overlap of Palearctic, Oriental and Sino-Japanese cenocrons.

Saharo-Arabian transition zone: Holt *et al.* (2013a)

Sahara region: Grisebach (1872, p. 74).

Mediterranean transition zone: Forsyth Major (1884, p. 113).

Tyrrhenian transition zone: Heilprin (1887, p. 105).

Saharan subregion: Sclater and Sclater (1899, p. 117); Sharpe (1884, p. 105).

North African–Indian Desert region: Good (1963, p. 31).

Paleotropic–Holarctic transition zone: Müller (1986, p. 22).

Saharo-Sindian region: Takhtajan (1986, p. 247).

Sahero-Arabian subregion: Procheş and Ramdhani (2012, p. 263).

Saharo-Arabian kingdom: Holt *et al.* (2013a, p. 75, 2013b, p. 343-d).

Saharo-Arabian transition zone: Kreft and Jetz (2013, p. 343-c); Morrone (2015a, p. 86); Hermogenes de Mendonça and Ebach (2020, p. 721).

Arabian region: Carta *et al.* (2022, table 2).

Arabian subregion: Santos and Ribeiro (2022, p. 5).

Diagnosis

It comprises the Sahara Desert and the Arabian Peninsula (Müller 1986; Kreft and Jetz 2013). It corresponds to the boundary between the Palearctic and Ethiopian regions.

South American transition zone: Morrone (2004)

Chilean transition zone: Grisebach (1872, p. 627).

South American transition zone: Morrone (2004b, p. 41, 2006, p. 482); Urtubey *et al.* (2010, p. 505); Morrone (2014, p. 83, 2015a, p. 86); Martínez *et al.* (2016, p. 479); Escalante (2017, p. 352); Hermogenes de Mendonça and Ebach (2020, p. 721).

Diagnosis

It comprises the Andean highlands between western Venezuela and northern Chile and central western Argentina (Morrone 2006, 2014; Martínez *et al.* 2016). It corresponds to the boundary between the Neotropical and Andean regions, which was analysed by Rapoport (1968), who discussed the alternative placements given by different authors to the 'sub-tropical line' that separates these regions.

Remarks

Urtubey *et al.* (2010) analysed the distribution of some Asteraceae within this transition zone. Escalante (2017) recovered this transition zone in an endemism analysis of the terrestrial mammals of the world and noted its close relationship with the Andean region. More recently, Roig-Juñent *et al.* (2018) considered that the Patagonian biogeographic province should be considered as belonging to the South American Transition Zone instead of the Andean region in the strict sense.

Indo-Malayan transition zone: Wallace (1876a)

Austro-Oriental transition zone: Forsyth Major (1884, p. 113).

Malayan subregion: Blyth (1871, p. 428); Lydekker (1896, p. 294); Sclater and Sclater (1899, p. 141).

Indo-Malayan or Malayan subregion: Wallace (1876a, p. 334); Newton (1893, p. 360); Bartholomew *et al.* (1911, p. 7); Thorne (1963, p. 332); Parenti and Ebach (2010, p. 312, 2013, p. 815).

Austro-Malaysian transition zone: Heilprin (1887, p. 107).

Austro-Malayan region: Lydekker (1896, p. 45).

Malayan subregion: Sclater and Sclater (1899, p. 141).

Indo-Australian region: Raven (1935, p. 284).

Intermediate area: Rensch (1936, p. 265).

Malayan province: Schilder (1956, p. 76).

Wallacea: Dickerson *et al.* (1928, p. 302); Darlington (1957, p. 462); Escalante (2017, p. 359).

Indo-Malayan subkingdom: Good (1963, p. 31).

Indomalayan kingdom: Udvardy (1975, p. 30) (in part).

Australian-Oriental transition zone: Müller (1986, p. 20); Kreft and Jetz (2013, p. 343-c).

Malesian region: Takhtajan (1986, p. 249); Carta *et al.* (2022, table 2).

Indo-Pacific kingdom: Cox (2001, p. 519).

Wallacean region: Procheş and Ramdhani (2012, p. 263).

Indo-Malayan transition zone: Morrone (2015a, p. 86); Hermogenes de Mendonça and Ebach (2020, p. 721).

Diagnosis

It corresponds to the boundary between the Oriental and Australian regions (Illiger's Line in the east).

Remarks

Müller (1986) discussed its boundaries and gave examples of Oriental and Australian taxa overlapping in this transition zone. Michaux (2010) analysed the geological development of this area, identified areas of endemism and concluded that the latter are linked to geological processes resulting from the interaction between the Eurasian and Australian continents, and the Philippine Sea Plate. King and Ebach (2017) showed that it is a temporally composite area. Michaux (2019) undertook a parsimony analysis of endemism, finding that the areas assigned to this transition zone may constitute a natural area if the Philippines are included, as proposed previously by Dickerson *et al.* (1928).

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