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

Juan J. MorroneA,* and Malte C. EbachB,C

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.
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 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 2015; 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 *Verbreitungszuzbirk 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 geographiczoologica 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).
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
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 Ėthiopian 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 endemicity 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
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 Arlert 1906 for further authors). The debate between Wallace and his adoptees

---

Fig. 3. Zoogeographic regions recognised by Wallace (1876a, 1876b) in The Geographical Distribution of Animals.
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 Palaearctic 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 Palaearctic 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 Palaearctic genera of birds which inhabit Alaska, and if I am not mistaken these are several Mammals also, making Alaska essentially Palaearctic [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 Palaearctic 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 Palaearctic [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

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

| Area or division | Region         | Subregion              | Remarks                        |
|------------------|----------------|------------------------|--------------------------------|
| Arctogae         | Palæarctic     | European               |                                |
|                  |                | Mediterranean          | Transition to Ethiopian        |
|                  |                | Siberian               | Transition to Nearctic         |
|                  |                | Manchurian             | Transition to Oriental         |
|                  |                | Californian            |                                 |
| Nearctic         |                | Rocky Mountain         | Transition to Neotropical      |
|                  |                | Alleghany              | Transition to Palaearctic      |
|                  | Ethiopian      | East African           | Transition to Palaearctic      |
|                  |                | West African           |                                 |
|                  |                | South African          |                                 |
|                  |                | Malagasy               |                                 |
| Oriental         |                | Indian                 | Transition to Ethiopian        |
|                  |                | Ceylonese              |                                 |
|                  |                | Indo-Chinese           | Transition to Palaearctic      |
|                  |                | Indo-Malayan           | Transition to Australian       |
| Notogae          | 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).

(j.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):
dialectician and well informed, has submitted a pretty argument in favour of the union of the North American or 'Nearctic' and Eurasian or 'Palaearctic' [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 Palaearctic represented two distinct faunas:

the Palaearctic 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 Palaearctic 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 Paleogeana are based on the notion that the regions of the New World, for instance, share a

---

Fig. 4. Zoogeographical areas illustrating the Distributions of Birds by R. Bowder Sharpe (1893). The classification is loyal to Wallace (1876a, 1876b) because it clearly distinguishes the Nearctic from the Palaearctic.
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 endemicity, 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 (1886), 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
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 Arctogæa 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:
Modern attempts to divide the world up into more or less equivalent floristic units mostly trace back to Engler’s scheme [Good 1963, p. 27].

Good (1947, 1963) simplified Engler’s classification system in his Geography of Flowering Plants, designating six floristic kingdoms, namely Boreal [sensu Holarctic], Paleotropical, Neotropical, South African, Australian and Antarctic (Table 2). Good continued:

This floristic classification may be epitomised by saying that it divides the land surfaces of the world into 37 regions [Good 1963, p. 31].

The other floristic classification scheme by Takhtajan (1978, 1986; Fig. 9) seemingly solidified phytoecography in the minds of 20th and 21st century biogeographers. Takhtajan reintroduced the Holarctic as a kingdom, converted Good’s Boreal kingdom into a subkingdom, and renamed Good’s South African and Antarctic kingdoms into the Cape and Holantarctic kingdoms respectively (Table 3). Takhtajan’s system may seem like Engler’s (1882, 1898); 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 regions (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; Rapport 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).

Fig. 9. Takhtajan’s floristic kingdoms and regions of the earth (Takhtajan 1978, separate map). Red solid and dashed lines indicate the boundaries of kingdoms; green solid and dashed lines indicate the boundaries of the regions.
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 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).
classifications had included the Holarctic, with the Palaearctic and Nearctic as subareas, including Nichols (1943), who divided the freshwater fish fauna into ‘II. Continental: 1. Northern: A. Holarctic, a. Palaearctic 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 Palaearctic 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 Arctogeian 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.
Further bioregionalisation analyses based on bat (Prochêş 2005) and gymnosperm distributions (Prochêş 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, Prochêş 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 Palaeotropical clusters [Prochêş 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
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
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); Newbiggin (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).

Holarktis 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

---

**Area taxonomy**

**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); Newbiggin (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).

**Holarktis 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
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); Raptor (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); Hermogens 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).

Anglogean 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: Newtont (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, pp. 380–381, 1893, pp. 206, 1893, p. 122).

Canadian subregion: Wallace (1876b, p. 135); Sclater and Sclater (1899, p. 164); Escalante et al. (2013, p. 495).
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).
Hyperboric region: Schilder (1956, p. 76).
Arctic and Subarctic region: Good (1963, p. 30); Takhtajan (1986, p. 244).
Western subregion: Allen (1892, p. 219).
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, Diomede 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).
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 province: Cope (1873, p. 35, 1875, p. 68).
Alleghanian district: Cope (1875, p. 68).
Alleghany subregion: Wallace (1876a, p. 191).
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).

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).
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).

Mediterranean subarea: Clarke (1892, p. 377).

European 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 (1899, p. 187).

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).

Paleotropical kingdom: Schilder (1956, p. 76); Kreft and Jetz (2013, p. 343-c).

Paleotropical region: Poynton (1959, p. 26).

Palearotropical 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. 266); Kirby (1872, p. 434) (in part).

Western Palæotropical region: Sclater (1858, p. 138).

Africano-Indian region: Murray (1866, p. 308).

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

Western Palæotropical region: Kirby (1872, p. 434) (in part).

Afrogean kingdom: Gill (1885, p. 20).

Ethiopian kingdom: Heilprin (1887, p. 82).

Ethiopia area: Clarke (1892, p. 379).

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

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. 132).

Madagascan subkingdom: (in part) Takhtajan (1986, p. 202).

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

**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).

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).

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).
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 region: Diels (1908, p. 130).

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

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

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

Indian or Middle Palæotropical 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) Schilder (1956, p. 76).

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

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

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

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 Palæotropical region: Sclater (1858, p. 140).

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

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

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).](image-url)
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 Quy 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).

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

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

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

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

Neotropical subkingdom: Müller (1885, p. 20); Kreft and Jetz (2013, p. 343-c).

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); Sclater (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); Proché and Ramdhani (2012, p. 263); Rueda et al. (2013, p. 2217); Kreft and Jetz (2013a, p. 75).

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

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

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); Bányász and Bošcainu (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: Sclater (1858, p. 143).

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); Proché 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).
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)

Brazillian 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); Bañarescu and Boșcai (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: Scater and Scater (1899, p. 65) (in part); Morrone (1996, p. 6, 2001b, p. 67, 2005, p. 238); Vitoria (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).

Caribbean subregion: Morrone (1999, p. 2 (in part), 2001 b, 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: Sclater and Sclater (1899, p. 65) (in part).

Chacoan–Brazilian subregion: 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 subregion: Good (1963, p. 32).

Guianan–Brazilian subregion: Fittkau (1969, p. 636) (in part).

Brazilian subregion: Hershkovitz (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: Cabrera (1951)

Tropical American region: Engler (1882, p. 345) (in part).

Brasil Australis subarea: Clarke (1892, p. 381).

South Brazilian region: Good (1963, p. 32).

Guianan–Brazilian region: Fittkau (1969, p. 636) (in part).

Brazilian subregion: Hershkovitz (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, 2001 b, 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 (2015 a, p. 85, 2018, p. 29); Hermogenes de Mendoza 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).

Notogäa 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 2015 a, 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).

Anfígean 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: Ringuelet (1955, p. 84, 1961, p. 160).

Subantarctic–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).
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).
Valdivean-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).
Patagonian 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. 151); Cracraft (1985, p. 36).
Steppe zone: Cekalovic (1974, p. 308).
Patagonia province: Fittkau (1969, p. 462).
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 Dominguez (2001, p. 158).
Middle Chilean–Patagonian region: (in part) Rivad-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).

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); Proches 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: 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).
Australasian subkingdom: Fleming (1987, p. 199).

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).

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

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

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)

Antarctic region: Blyth (1871)

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).

Remarks

Udvardy (1987) has recognised three provinces within this region, namely Insulantartica, 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,
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).

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

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).

Neotropical–Palearctic–Holarctic transition zone: Müller (1986, p. 21); Kret 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: Palestrini 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. Palestrini 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).

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

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

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

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

**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 ‘subtropical 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 endemicity 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); Scattered and Slater (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: Scattered and Slater (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).

Wallacea 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 endemcity, 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).

References

Acosta LE, Maury EA (1998a) Scorpiones. In ‘Biodiversidade de artrópodos argentinos: un enfoque biotaxonómico’. (Eds JJ Morrone, S Coscarón) pp. 545–559. (Ediciones Sur: La Plata, Argentina)

Acosta LE, Maury EA (1998b) Opiiones. In ‘Biodiversidade de artrópodos argentinos: un enfoque biotaxonómico’. (Eds JJ Morrone, S Coscarón) pp. 569–580. (Ediciones Sur: La Plata, Argentina)

Allen JA (1871) On the mammals and winter birds of east Florida, with an examination of certain assumed specific characters in birds, and a sketch of the bird-faunae of eastern North America. Bulletin of the Museum of Comparative Zoology at Harvard College 2, 161–450.

Allen JA (1892) The geographical distribution of North American mammals. Bulletin of the American Museum of Natural History 4, 199–243.

Allen JA (1893) The geographical origin and distribution of North American birds, considered in relation to faunal areas of North America. Auk 10, 97–150. doi:10.2307/4068104

Almirón A, Azpelucueda M, Casciotta J, López Cazorla A (1997) Ichthyogeographic boundary between the Brazilian and Austral sub-regions in South America. Argentina. Biogeographica 73, 23–30.

Amorim DS, Pires MRS (1996) Neotropical biogeography and a method for maximum biodiversity estimation. In ‘Biodiversidade de artrópodos argentinos: un enfoque biotaxonómico’. (Eds JJ Morrone, S Coscarón) pp. 183–219. (CNPq: São Paulo, Brazil)

Amorim DS, Tozoni SHS (1994) Phylogenetic and biogeographic analysis of the Anisopodoidea (Diptera, Bibionomorpha), with an area cladogram for intercontinental relationships. Revista Brasileira de Entomologia 38, 517–543.

Arana MD, Morrone JJ, Oggero AJ (2011) Lycophyta (Tracheophyta: Lycophodiophyta) de las Sierras Centrales de Argentina: un enfoque panbiogeográfico. Gayana. Botánica 68, 16–21. doi:10.4067/S0717-66432011000100002
Huber O, Riina R (2003) ‘Glosario ecológico de las Américas. Vol. 2. América del Sur: Países hispanoparlantes.’ (UNESCO: Caracas, Venezuela)

Hueck K (1957) Las regiones forestales de Sudamérica. Boletín del Instituto Forestal Latinoamericano de Investigación y Capacitación (Mérida) 2, 1–40.

Hueck K (1966) ‘Die Wälder Südamerikas.’ (Fischer: Stuttgart, Federal Republic of Germany)

Huxley TH (1868) On the classification and distribution of Alecctornorphae and Heterornorphae. Proceedings of the Zoological Society of London 1868, 294–319.

Illies J (1968) Buch Besprechung. Beitrag zur Neotropischen Fauna 5, 229–234.

Illiger JKW (1815) Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile. Abhandlungen der physikalische Klasse der Koeniglich-Preussischen Akademie der Wissenschaften 1804–1811, 39–159.

Kang B, Deng J, Wu Y, Chen L, Zhang J, Qiu H, Lu Y, He D (2014) Mapping China’s freshwater fishes: diversity and biogeography. Fish and Fisheries 15, 209–230. doi:10.1111/tafi.12011

Kendeigh SC (1954) History and evaluation of various concepts of plant and animal communities in North America. Ecology 35, 152–171. doi:10.2307/1931112

King AR, Ebach MC (2017) A novel approach to time-slicing areas and animal communities in North America. Proceedings of the Biological Society of Washington 7, 1–64.

Koeniglich-Preussischen Akademie der Wissenschaften (1957) Abhandlungen der physikalische Klasse der Koeniglich-Preussischen Akademie der Wissenschaften 1804–1811, 39–159.

Kreft H, Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. Journal of Biogeography 37, 2029–2053. doi:10.1111/j.1365-2699.2010.02375.x

Kreft H, Jetz W (2013) Comment on ‘An update of Wallace’s zoogeography: a compatibility analysis.’ Lichenologist 35, 33–53. doi:10.1006/litch.2002.0430

Ledykker BA (1896) ‘A geographical history of mammals.’ (Cambridge University Press)

Lopatin IK (1980) ‘Osnovy zoogeografii [Fundamentals of zoogeography].’ (Vishnyeshaya Shkola: Minsk, USSR) [In Russian]

Lorentz PG (1876) Cuadro de la vegetación de la República Argentina. In ‘La República Argentina’. (Ed. R Napp) pp. 77–136. (Sociedad Anónima de Tipografía, Litografía y Fundición de Tipos: Buenos Aires, Argentina)

Lücking R (2003) Takhtajan’s floristic regions and follicious lichen biogeography: a compatibility analysis. Lichenologist 35, 33–53. doi:10.1006/litch.2002.0430

Ludwig K (1966) ‘Die Wälder Südamerikas.’ (Fischer: Stuttgart, Federal Republic of Germany)

Martínez GA, Arana MD, Oggero AJ, Natate ES (2016) Biogeographic relationships and new regionalisation of high-altitude grasslands and woodlands of the central Pampean Ranges (Argentina), based on vascular plants and vertebrates. Australian Systematic Botany 29, 473–488. doi:10.1071/BS16046

McRae CH (1892) The geographic distribution of life in North America with special reference to the Mammalia. Proceedings of the Biological Society of Washington 7, 1–64.

Meyen FJF (1846) ‘Outlines of the geography of plants: with particular enquiries concerning the native country, the culture, and the uses of the principal cultivated plants on which the prosperity of nations is based.’ (Ray Society: London, UK)

Michaux B (2010) Biogeography of Wallacea: Geotectonic models, areas of endemism, and natural biogeographic units. Biological Journal of the Linnean Society. Linnean Society of London 101, 193–212. doi:10.1111/j.1095-8312.2010.01473.x

Michaux B (2019) ‘Biogeology: evolution in a changing landscape.’ (CRC Press: Boca Raton, FL, USA)

Mönö F (1958) Consideraciones sobre la fauna del sur de Chile y revisión de la tribus Stenomelini (Coleoptera, Chrysomelidae). Acta Zoológica Lilloana 15, 143–153.

Morrone JJ (2001) ‘Biogeography: a compatibility analysis.’ (Ray Society: London, UK)

Morrone JJ (1999) Presentación preliminar de un nuevo esquema biogeográfico de América del Sur. Biogeographica 75, 1–16. doi:10.11646/4058.4.4

Morrone JJ (2002) Biogeographic regions under track and cladistic scrutiny. Journal of Biogeography 29, 373–383. doi:10.1046/j.1365-2699.2002.00662.x

Morrone JJ (2004) Biogeographic areas and transition zones of Latin America. Journal of Biogeography 31, 523–534. doi:10.1111/j.0305-8791.2004.00712.x

Moreira-Muñoz A (2014) Central Chile ecoregion. In ‘Endemism in vascular plants’. (Ed. C Hobohm) pp. 221–233. (Springer Science: Dordrecht, Netherlands)

Morrell JJ (1996) The biogeographical Andean subregion: a proposal exemplified by Arthropod taxa (Arachnida, Crustacea, and Hexapoda). Neotropica 42, 103–114.

Morrell JJ (1999) Presentación preliminar de un nuevo esquema biogeográfico de América del Sur. Biogeographica 75, 1–16. doi:10.11646/4058.4.4

Morrell JJ (2001) ‘Biogeography and areas of endemism.’ Diversity & Distributions 7, 297–300. doi:10.1046/j.1366-9516.2001.00116.x

Morrell JJ (2001b) ‘Biogeografía de América Latina y el Caribe. Vol. 3.’ (M&T-Manuales and Tesis SEA, Sociedad Entomológica Aragonesa: Zaragoza, Spain)

Morrell JJ (2002) Biogeographic regions under track and cladistic scrutiny. Journal of Biogeography 29, 149–152. doi:10.1046/j.1365-2699.2002.00662.x

Morrell JJ (2004a) Panbiogeography, componentes bióticos y zonas de transición. Revista Brasileira de Entomologia 40, 149–162. doi:10.1590/S0085-56262004000200001

Morrell JJ (2004b) La zona de transición Sudamericana: caracterización y relevancia evolutiva. Acta Entomológica Chilena 28, 41–50.

Morrell JJ (2005) Hacia una síntesis biogeográfica de México. Revista Mexicana de Biodiversidad 76, 207–252. doi:10.22201/ib.20078706.e.2005.002.303

Morrell JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Annual Review of Entomology 51, 467–494. doi:10.1146/annurev.ento.50.071803.130447

Morrell JJ (2011) Island evolutionary biogeography: analysis of the weevils (Coleoptera: Curculionidae) of the Falkland Islands (Islas Malvinas). Journal of Biogeography 38, 2078–2090. doi:10.1111/j.1365-2699.2011.02553.x
Rivas-Martínez S, Navarro G, Penas Á, Costa M (2011) Biogeographic map of South America. A preliminary survey. *International Journal of Geobotanical Research*, 1, 20–41. doi:10.5616/ijgr110002

Roig-Juñent S, Domínguez MC (2001) Diversidad de la familia Carabidae (Coléoptera) en Chile. *Revista Chilena de Historia Natural* 74, 549–571. doi:10.4067/S0716-076X-2001000300006

Roig-Juñent S, Domínguez MC, Flores GE, Mattoni C (2006) Biogeographic history of South American arid lands: a view from its arthropods using TASS analysis. *Journal of Arid Environments* 66, 404–420. doi:10.1016/j.jaridenv.2006.01.005

Roig-Juñent SA, Griotti M, Domínguez MC, Agrain FA, Campos-Soldini Santos D, Ribeiro GC (2022) Areas of endemism in the Afrotropical region. *Australian Systematic Botany* 46, 276–293.

Rosen DE (1979) Fishes of the uplands and intermontane basins: revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History* 162, 1–176.

Rueda M, Rodríguez MA, Hawkins B (2013) Identifying global zoogeographical regions: lessons from Wallace. *Journal of Biogeography* 40, 2215–2225. doi:10.1111/jbi.12214

Rzedowski J (1978) ‘La vegetación de México.’ (Editorial Limusa: Mexico City, Mexico)

Samek V, del Risco E, Vandana R (1988) Fitorregionalización del área de origen de Los Llanos de Venezuela. *Sierrita* 3, 241–244. doi:10.1111/j.1600-0787.1988.tb00712.x

Schmarda KL (1853) ‘Die geographische Verbreitung der thiere.’ (Carl Gerold and Son: Vienna, Austria)

Schneider FA (1956) ‘Lehrbuch der Allgemeinen Zoogeographie.’ (Gustav Fischer Verlag: Jena, German Democratic Republic)

Schneider WR (1963) Biotic distributions in the tropical Pacific. In ‘Pacific basin biogeography: a symposium: Tenth Pacific Science Congress’, 21 August–6 September 1961, Honolulu, HI, USA. (Eds JL Gressitt, CH Lindroth, FR Frobsing, CA Fleming, EG Turbott) pp. 23–28. (Bishop Museum Press: Honolulu, HI, USA)

Sclater PL (1858) On the general geographic distribution of the animals. (Longman, Brown, Green, and Longman: London, UK)

Sclater WL (1897) The geography of mammals. No. VI. The Nearctic Region (continued). *The Geographical Journal* 2, 130–145.

Sneath PHA (1967) Conifer distributions and continental drift. *Nature* 215, 467–470. doi:10.1038/215467a0

Spinelli GR, Marino PI, Posadas P (2006) The Patagonian species of the genus Arichthopogon Kieffer, with a biogeographic analysis based on Forcipomyiinae (Diptera: Ceratopogonidae). *Insect Systematics & Evolution* 37, 301–324. doi:10.1163/187631206778835851

Stoddart DR (1992) Biogeography of the tropical Pacific. *Pacific Science* 46, 276–293.

Swainson W (1835) ‘A treatise on the geography and classification of animals.’ (Longman, Brown, Green, and Longman: London, UK)

Takhtajan A (1978) ‘The floristic regions of the world.’ (‘Nauka’ Publishing: Leningrad, USSR) [In Russian]

Takhtajan A (1986) ‘Floristic regions of the world.’ (University of California Press: Berkeley, CA, USA)

Tatewaki M (1963) Phytogeography of the oceanic area of the North Pacific Ocean. In ‘Pacific Ocean biogeography: a symposium: Tenth Pacific Science Congress’, 21 August–6 September 1961, Honolulu, HI, USA. (Eds JL Gressitt, CH Lindroth, FR Frobsing, CA Fleming, EG Turbott) pp. 215–228. (Bishop Museum Press: Honolulu, HI, USA)

Thorne RF (1963) Biotic distributions in the tropical Pacific. In ‘Pacific basin biogeography: a symposium: Tenth Pacific Science Congress’, 21 August–6 September 1961, Honolulu, HI, USA. (Eds JL Gressitt, CH Lindroth, FR Frobsing, CA Fleming, EG Turbott) pp. 311–350. (Bishop Museum Press: Honolulu, HI, USA)

Udvardy MDF (1975) A biogeographic classification of the biogeographical provinces of the world. Occasional Paper 18. (International Union for Conservation of Nature and Natural Resources: Morges, Switzerland) Available at https://portals.iucn.org/library/sites/library/files/documents/OP-018.pdf.

Udvardy MDF (1987) The biogeographical realm Antarctica: a proposal. *Journal of the Royal Society of New Zealand* 17, 187–194. doi:10.1080/03036758.1987.10423347

Urbuey E, Stuessy TF, Trenetsberger K, Morrone JJ (2010) The South American biogeographic transition zone: An analysis from Asteraceae. *Taxon* 59, 505–509. doi:10.1080/tax.592015

Vallejo B (2011) The Philippines in Wallacea. In ‘Biodiversity, biogeography and nature conservation in Wallacea and New Guinea’ (Ed. D Telnov) Vol. I, pp. 27–42. (The Entomological Society of Latvia: Riga, Latvia)

von Hofsten NGE (1916) Zur älteren Geschichte des Diskontinuitätsproblems in der Biogeographie. *Zeologische Annalen Zeitschrift für die Geschichte der Zoologie* 77, 197–353.

van Rooy J, van Wyk AE (2012) Phytogeographical and ecological affinities of the bryofloristic regions of southern Africa. *Polish Botanical Journal* 37, 109–118.

Viloria AL (2005). Las mariposas (Lepidoptera: Papilionoidea) y la regionalización biogeográfica de Venezuela. In ‘Regionalización biogeográfica en Iberoamérica y tópicos afines– Primera Jornadas Biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistématica (RIBES XII. I–CYTED). Las Prensas de Ciencias’. (Eds J Llorente Bouquest, JJ Morrone) pp. 495–508. (UNAM: Mexico City, Mexico)

Wagner JA (1844) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b

Wagner JA (1846) Die Geographische Verbreitung der Säugethiere b
Wallace AR (1876a) ‘The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the earth’s surface. Vol. I.’ (Harper and Brothers: New York, NY, USA)

Wallace AR (1876b) ‘The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the earth’s surface. Vol. II.’ (Harper and Brothers: New York, NY, USA)

Wallace AR (1883) On the value of the ‘Neoarctic’ [sic] as one of the primary zoological regions. Nature 27, 482–483.

Wallace AR (1894) What are zoological regions? Nature 49, 610–613.

Wallace M (2015) Johann Andreas Wagner (1797–1861) und “Die geographische Verbreitung der Säugthiere”. Beiträge zur Geschichte der Zoogeographie 1, 3–24.

Wallace M (2009) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: Die Begriffe Zoogeographie, Arealsystem und Areal.’ (Published by the author: Halle, Germany)

Wallace M (2010a) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: II. Die Begriffe Fauna und Faunistik.’ (Published by the author: Halle, Germany)

Wallace M (2011a) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: IV. Die chorologische Zoogeographie und ihre Anfänge.’ (Published by the author: Halle, Germany)

Wallace M (2011b) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: V. Die chorologische Zoogeographie und ihr Fortgang.’ (Published by the author: Halle, Germany)

Wallace M (2012a) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: VI. Vergleichende Zoogeographie.’ (Published by the author: Halle, Germany)

Wallace M (2012b) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: VI. Vergleichende Zoogeographie.’ (Published by the author: Halle, Germany)

Wallaschek M (2012c) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: VII. Die ökologische Zoogeographie.’ (Published by the author: Halle, Germany)

Wallaschek M (2013a) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: VIII. Die historische Zoogeographie.’ (Published by the author: Halle, Germany)

Wallaschek M (2013b) ‘Fragmente zur Geschichte und Theorie der Zoogeographie: IX. Fazit, Literatur, Glossar, Zoogeographienverzeichnis.’ (Published by the author: Halle, Germany)

Wallaschek M (2014) ‘Ludwig Karl Schmarda (1819–1908): Leben und Werk.’ (Published by the author: Halle, Germany)

Wallaschek M (2015a) Johann Andreas Wagner (1797–1861) and “Die geographische Verbreitung der Säugthiere”. Beiträge zur Geschichte der Zoogeographie 1, 3–24.

Wallaschek M (2015b) Johann Friedrich Blumenbach (1752–1840) and the Zoogeography in the “Handbuch der Naturgeschichte”. Philippa 16, 237–262.

West RC (1964) The natural regions of Middle America. In ‘Handbook of Middle American Indians, vol 1’. (Ed. RC West) pp. 363–383. (University of Texas Press: Austin, TX, USA)

Williams PH (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. Proceedings of the Royal Society of London – B. Biological Sciences 263, 579–588. doi:10.1098/rspb.1996.0087

Zhang CL (1954) The distribution of the freshwater fishes of China. Journal of Geographical Sciences 3, 279–284. [In Chinese]

Zimmermann EAW (1777) ‘Specimen zoologiae geographicae, Quadrupedum domicilia et migrationes sistens.’ (Theodorum Haak: Leiden, Netherlands)

Zimmermann EAW (1783) ‘Geographische Geschichte des Menschen, und der allgemein verbreiteten vierfussigen Thiere.’ (Weygandschen Buchhandlung: Leiden, Netherlands)

Zuloaga FO, Morrone O, Rodriguez D (1999) Análisis de la biodiversidad en plantas vasculares de la Argentina. Kurtziana 27, 17–167.

Data availability. Data sharing is not applicable as no new data were generated or analysed during this study.

Conflicts of interest. Malte Ebach is an Associate Editor of Australian Systematic Botany but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. Australian Systematic Botany encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. We acknowledge the valuable comments by three anonymous reviewers.

Author affiliations
Museo de Zoología ‘Alfonso L. Herrera’, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), 04510 Mexico City, Mexico.
Earth and Sustainability Science Research, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.
Palaeontology Department, Australian Museum Research Institute, Sydney, NSW 2010, Australia.