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Notes

Chapter 3

Palaeozoic palaeogeographical and palaeobiogeographical nomenclature

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Abstract: Palaeogeographers, geographers and structural geologists use different well-defined terms to designate continental and tectonic units, whereas biogeographers, palaeobiogeographers and palaeontologists use a wide range of subjective terminologies to describe biogeographical and palaeobiogeographical units. The absence of clear definitions and of rules or guidelines for palaeobiogeographical nomenclature has resulted in frequent misunderstandings and general confusion, in particular when applied to ancient time periods, such as the Palaeozoic. Palaeogeographical and palaeobiogeographical terminology used in Palaeozoic geology and palaeontology is reviewed, and recent attempts to standardize palaeobiogeographical nomenclature summarized. We make a number of proposals for future use of terms to avoid confusion and misunderstandings.

Modern biogeographers study the geographical distribution of animal and plant taxa (neobiogeography), whereas palaeontologists attempt to understand the palaeogeographical distribution of their fossil groups (palaeobiogeography). While the palaeobiogeographers for the more recent geological (Mesozoic and Cenozoic) periods deal with post-Pangean palaeogeographies (after the break-up of the supercontinent Pangea at the beginning of the Mesozoic, which resulted in the continental arrangement that we know today), palaeontologists and palaeobiogeographers working in the Precambrian and Palaeozoic face a much more complex geodynamic history with ancient palaeocontinents that in most cases no longer exist and their exact boundaries are often unknown.

Palaeozoic palaeogeographical reconstructions are mainly based on results from research in various geological disciplines, including sedimentology, structural geology (tectonics), palaeomagnetism and palaeobiogeography (palaeontology). Historically, the different scientific communities (geologists, palaeontologists, geophysicists, etc.) use different terminologies. In recent years, there has been mounting confusion regarding the nomenclature of palaeogeographical (continents, plates, etc.) and palaeobiogeographical (provinces, etc.) units, which are intended as biotic, not physical entities. Most of the confusion is based on terminological misunderstandings between the different scientific disciplines. Palaeogeographical terms such as 'terrane', ('micro-') 'continent' and ('micro-') 'plate' are commonly used by tectonicists in geodynamic reconstructions, while palaeobiogeographical terms such as 'realm', 'territory' and 'province' have been used by palaeontologists in biogeographical studies aimed at describing the geographical distribution of fossil or living organisms.

In recent years, biogeographical 'provinces', defined on the basis of the spatial distribution of selected fossil groups, have sometimes been misinterpreted and confused with geographical ('continent', 'microcontinent') or tectonic ('terrane', 'plate', 'microplate', 'block', 'microblock') units without key evidence from sedimentary or structural geology that in any case do not correspond to biotic entities.

In addition, some palaeo(bio)geographers use several different geographical terms out of context. The term 'terrane', for example, has been used to describe major continents, contrary to its restricted and well-defined use in structural geology.

On the other hand, some palaeobiogeographers use a range of biogeographical units without a precise order or rank. Terms such as 'province', 'realm' or 'subprovince' are often used interchangeably without any consistency.

In the last decade, several attempts have been made to provide more stable palaeobiogeographical nomenclature, most commonly by Mesozoic and Cenozoic palaeobiogeographers and palaeontologists (e.g. Westermann 2000; Cecca & Westermann 2003). We believe that Palaeozoic palaeogeographers should also move towards use of a common language.

In this paper we review the terminology used in biogeography, palaeogeography and palaeobiogeography, in particular for the Palaeozoic Era. The use of palaeogeographical and palaeobiogeographical terms in Palaeozoic literature is summarized and proposals are made for future use of terms. The main objectives are to avoid confusion and misunderstandings, and to be in accordance with the guidelines proposed in recent publications, mainly for younger time periods.

The origins and outline of (palaeo-)biogeography

What is biogeography?

Biogeography is the study of the distribution of organisms, both past and present, and their variations over time. It is aimed at uncovering relationships between areas of endemism. Biogeography also attempts to explain processes that brought about the observed biotic distribution and document spatial patterns of biodiversity in both deep and present time.

Defined in this way, biogeography (and also palaeobiogeography) is a synthetic discipline, and it is clearly interdisciplinary

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between ecology (palaeoecology), systematic biology (systematic palaeontology), evolutionary biology (palaeobiology) and earth sciences. Biogeography is thus a branch of biology, and palaeobiogeography is therefore a branch of palaeobiology and palaeontology.

It should be noted that many palaeontologists are either palaeobiologists (with a biological training) or geologists (with a geological training), or both.

Logically, a biogeographer must have some knowledge of geography, that is, a biogeographer should display a comprehensive understanding of the location and topography of the continents, major islands and archipelagos (groups of islands), seas and oceans, but also of mountain ranges, deserts and lakes. A palaeogeographer must have a comprehensive knowledge of ancient geographies, that is, the position of ancient oceans and continents, their extents, depths and heights. In addition, a palaeobiogeographer working on marine faunas (most palaeontologists of the Lower Palaeozoic belong to this category), for example, must have a significant understanding of past climate regimes, ocean currents and tides, but also of water chemistry, salinity and other parameters.

First biogeographers and palaeobiogeographers

Biogeography is linked to evolutionary biology and ecology and it is not surprising that the pioneers of the field of evolutionary biology were also the first scientists to focus on biogeography and palaeobiogeography.

Carolus Linnæus, Carl von Linné (1707–1778), started the discipline of modern systematics and was a major contributor to the theory of hierarchical classification. He developed a scheme to classify all life in a binomial nomenclatural system that is still used today and that was the basis for the codes of biological nomenclature (such as the International Code of Zoological Nomenclature and the International Code of Botanical Nomenclature). Linnæus was also one of the earliest scientists to interpret the distribution of living organisms. However, he considered the earth and its living organisms as fixed and immutable. According to Linnæus, biogeographical distribution was a result of a spreading from a primordial island located in the tropics, from which new land emerged when the seas receded (from the slopes of Mount Ararat, where the ark was said to have landed). A fundamental idea of Linnæus was that all species originated and dispersed from a 'centre of origin' from which they developed, controlled by ecological conditions.

Georges-Louis Leclerc, Comte de Buffon (1707–1788), was one of the first to consider that the distribution of living organisms was the result of changing environmental conditions (especially changing climate) and changing species. Buffon established one of the first principles of biogeography: that distinct assemblages of mammals and birds occupy environmentally similar but isolated regions. He classified the world into the New World and Old World, whose biotas had a single origin in a centro creation. This is known as Buffon's law.

Karl Willdenow (1765–1812) published the first major synthesis of plant geography, but it was Alexander von Humboldt (1769–1859) who is generally viewed as the father of phytogeography. After conducting several surveys of the indigenous flora during his expeditions in South America, his important contributions were published and distributed in the wider context of biogeographical studies of plants in the late eighteenth and early nineteenth centuries.

Biogeography, as it is intended today, was initiated by Augustin-Pyramus de Candolle (1779–1841). He published (Candolle 1820) a classification of the Modern flora with the distinction of 20 botanical regions. In this work he introduced the concept of endemism, which is the basis of biogeography. An organism has an endemic distribution when it is limited to a specific area. Endemic refers to a taxon that occurs within a specific area. If endemism did not exist and distributions of organisms were cosmopolitan, biogeography simply would not exist.

Charles Lyell (1797–1875), considered the 'father of modern geology', influenced the development of biogeography in the nineteenth century through his major work, *Principles in Geology*, first published in 1830. Lyell rejected the ideas of evolution developed by the French scientists (such as Jean-Baptiste Lamarck, 1744–1829) and proposed the 'centres of creation' theory to explain the geographical distribution of species.

Charles Darwin (1809–1882) integrated this knowledge into his studies, becoming one of the major innovators of biogeography, as he incorporated the concepts of adaptation of organisms across time and space in *The Origin of Species*, published in 1859. Darwin's (1859, p. 353) idea 'that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted is the most probable' dramatically influenced the development of biogeography, opposing 'centre of origin' and 'vicariance' models in biogeography. However, Darwin could not believe in continent movements (1859, pp. 357–358) because convincing evidence of plate tectonics and ocean floor spreading were not yet available in his time (for a review see Cecca 2009).

Philip Lutley Sclater (1829–1913) published a significant paper on the general geographical distribution of birds in 1858, while Alfred Russel Wallace (1823–1913) published the fundamental concepts of the geographical distribution of animals in 1876. The first nomenclatural terms were introduced in these papers, and they are still widely used today: while Sclater divided the world in six biogeographical 'regions', Wallace called these faunal distributional areas 'realms'. Both Wallace and Sclater divided the world into six more-or-less similar units: the 'nearctic', 'neotropical' and 'ethiopian' units belonged to the 'new world', while the 'palaearctic', 'oriental' and 'australian' units were attributed to the 'old world' (Table 3.1). This first major subdivision, that attempted to divide landmasses into major classes reflecting affinities and differences among terrestrial biotas, is still widely accepted today. The major biogeographical units are separated by 'lines'. A prime example of such a sharp boundary between two different biogeographical units is 'Wallace's line', which is located between the Indonesian islands of Borneo and Sulawesi (Celebes) and Bali and Lombok. This boundary was and is largely accepted, but has subsequently been modified by other authors, representing the limit between the 'oriental' and the 'Australian' realms.

It was not before the second part of the twentieth century, however, that palaeobiogeographical models integrated the concept of plate tectonics. Although the German meteorologist Alfred Wegener (1880–1930) proposed the theory of continental drift in the 1910s (Wegener 1915), it was only in the 1960s, when geological evidence for plate tectonics was widely accepted, that geologists, followed by palaeobiogeographers, integrated the concept of moving continents into their explanation of the distributional patterns of fossil organisms.

However, the botanist Léon Croizat (1894–1982) advocated movements of the continental masses (1958, 1962–1964) before

Table 3.1. *The six biogeographical 'regions' established by Sclater and Wallace in the nineteenth century*

Nearctic (North America)	Palaearctic (Europe and Asia)
Neotropical (Mexico, Central and South America)	Indian or Oriental (SE Asia, Indonesia)
Ethiopian (Africa)	Australia (Australia and New Guinea)

The discontinuity between the Indian and the Australian regions is known as Wallace's line, a classical example of the boundary between biogeographical units.

geologists. He introduced the method called panbiogeography, which consists of drawing on a geographical map lines (called tracks) that join the known distributions of living, related organisms in the different areas. For example, the tracks for terrestrial organisms may cross the oceans and hence could not be explained by present-day geography. Croizat introduced the concept of vicariance, which is the separation of an ancestral biota in two or more biotas through the formation of a geographical barrier that stops the gene flow between populations. This concept explains the disjunct distributions as an alternative to the idea of dispersal from a centre of origin defended by Linnæus, Buffon and Darwin. Croizat's ideas were initially rejected by biogeographers, but after the acceptance of plate tectonics his work was considered in a different perspective.

Palaeobiogeographers were then able to understand and to develop completely new models for the distribution of fossil organisms in the Mesozoic and Cenozoic, that is, for the post-Pangean periods. However, pre-Pangean palaeobiogeographical distributions were used to test palaeogeogeographical reconstructions that are still challenging to reconstruct.

Significantly, the first accurate palaeogeographical reconstructions of the Early Palaeozoic were originally based on palaeontological studies from the early 1980s: the analyses of palaeobiogeographical distribution patterns of various fossil marine organisms allowed the distinction of several major marine provinces, related to the major palaeocontinents (e.g. Cocks & Fortey 1982).

Biogeographical entities: biomes and regions

Biogeographers and palaeobiogeographers attempt to analyse either the distribution of single species or that of communities of species. A first step is to determine the geographical range of a species or a community, for example, by producing maps. These maps can then provide evidence of physical barriers, delimiting the ranges of different organisms. Patterns of distribution used by biogeographers are either spatial (e.g. latitude, altitude) or temporal (e.g. seasonal, climate changes). Since the 1970s biologists have worked in collaboration with mathematicians to understand the distributional patterns, in particular using the development of sophisticated multivariate statistical techniques that allow quantification of the degree of similarities (or differences) of the distribution of different communities or species. With this objective, a great number of similarity indices have been proposed in the last few decades.

For continental environments, the term 'biome' has been introduced and is still largely used by botanists. Such 'biomes' include, for example, tropical rainforests, temperate grasslands or boreal forests or tundras. They represent the most easily recognizable terrestrial biogeographical regions that can easily be plotted on a 'climograph', that is a simple diagram that figures the mean annual precipitation on one hand and the mean annual temperature on the other. The term is also used by palaeobiogeographers of marine fossils (Cecca 2002, p. 89). However, the term 'community' was and is mainly used by neobiogeographers for marine biotas. Marine communities include, for example, coral reefs, estuaries, upwelling zones, continental shelves or the open ocean.

In addition, 'biogeographical regions' and 'climatic regions' are used to delimit biogeographical units in the oceans of the present day. The distinction of these is more complicated, as natural barriers limiting the distribution of species and communities are less evident, the ocean being essentially a large and continuous aquatic habitat.

Biogeographical regions of the marine realm are essentially delimited by water temperature, creating broad latitudinal zones that may be influenced and perturbed by oceanic currents, or interrupted by the presence of continents, islands or archipelagos.

Table 3.2. *'Biogeographical regions' and 'climatic regions' of the present-day oceans*

Biogeographical regions	Climatic regions
Arctic	
Subarctic	Arctic
Northern temperate	Northern boreal
Northern subtropical	Southern boreal
Tropical	Tropical
Southern subtropical	Equatorial
Southern temperate	Northern total
Subantarctic	Southern total
Antarctic	Antarctic

Today, the major 'biogeographical regions' of the world's oceans are the 'arctic', 'subarctic', 'northern temperate', 'northern subtropical', 'tropical', 'southern subtropical', 'southern temperate', 'subantarctic' and 'antarctic' regions. In addition, several major 'climatic regions' have been defined. These are the 'arctic', 'northern boreal', 'southern boreal', 'tropical', 'equatorial', 'northern total', 'southern total' and 'antarctic' climatic regions (Table 3.2).

It is particularly challenging for palaeontologists to trace these different units back in deep time: what were the communities, biogeographical regions and climate regions in the Early Palaeozoic, for example? This question is a major one because the barriers play a biogeographical role at a given time and may leave biogeographical signatures (difficult to detect) in more recent distributions. Former endemic areas still exist, for example, the disjunct distribution of Modern lungfishes indicates that they are endemic to Gondwana, which does not have a geographical reality in the Modern World.

Ecological entities: communities and ecosystems

A number of terms are used to designate ecological units that partly overlap with biogeographical units. Ecologists and biogeographers refer to 'life zones', 'ecoregions' or 'biomes', but also to 'communities' or 'ecosystems'. All of these terms are rather arbitrarily defined. A community, for example, can be considered a unit where different species live together in the same place. An ecosystem, on the other hand, includes not only all biotic relationships between species inhabiting a place, but also the features of the physical environment. For the palaeobiogeographer it is thus essential to understand not only the palaeogeographical or the palaeoecological distribution of a single fossil species or a fossil group, but also that of the entire 'palaeo-community' or of the entire 'palaeo-ecosystem'.

It is very important to emphasize that, within each of the marine regions, the ocean can also be divided vertically. Based on the penetration of sunlight, the oceans display a photic and an aphotic zone. In addition, the distance from shore also changes the distribution of species and communities. Marine organisms and communities are therefore also attributed to different zones corresponding to the bathymetry, that is, the depth and configuration of the ocean floor. Different zones have been defined, for example, the littoral, neritic or sublittoral, bathyal or abyssal zones.

Regarding the terminological complexity within (palaeo-) environmental and (palaeo-)geographical studies, for which no clear rules have been established but for which a common use of terms exists, the (palaeo-)ecological context must be added. The environments that occur in waters on the continental shelf are referred to as neritic, while those of the open ocean are considered pelagic, divided into epipelagic ($<$200 m water depth), mesopelagic ($<$1000 m), bathypelagic ($<$4000 m) and abyssopelagic ($<$11 000 m).

In addition, the life mode of marine organisms allows a classification into benthic or planktonic life styles, with some organisms occupying intermediate positions. Benthic organisms are bottom-living animals that may live on the sea-floor (epifauna) or below the sediment (infauna). Organisms in the open waters are usually divided into floating (plankton) and freely swimming (nekton) organisms.

With the fragmentary knowledge available on fossil species and communities, it is often impossible to fully understand the life mode or the life habitat of marine organisms. It is therefore not always evident to palaeontologists how to apply these terminologies. A common problem for palaeontologists, for example, is to clearly distinguish between the influence of palaeogeographical (e.g. latitude) and of palaeoecological (e.g. water depth) parameters on the distribution of a fossil organism.

Nomenclatural rules and problems

While many scientific disciplines have nomenclatural rules, palaeogeographers and palaeobiogeographers commonly use a terminology based mostly on traditional use rather than being based on a clearly established nomenclatural code. This is partly due to conceptual confusion between biotic entities (endemic areas, biogeographical units) and physical entities (plates, terranes etc.), which exists in most palaeobiogeographical studies.

However, every scientific discipline requires a precise and simple terminology or nomenclature that should be used consistently by all scientists. Only such a code allows a standardized terminology that avoids misunderstandings and erroneous interpretations.

While the zoologists (and palaeontologists working with fossil organisms of the Animal Kingdom) use the International Code of Zoological Nomenclature, ICZN (Ride *et al.* 1999), for their taxonomical studies and classifications, botanists and palaeobotanists use the International Code of Botanical Nomenclature, ICBN (McNeill *et al.* 2012). Both codes are based on the classification system, established in the eighteenth century by Linnæus, and have a hierarchical structure and follow strict rules, providing a number of recommendations. Geological nomenclature also follows codes, for example for the description of minerals or of stratigraphical intervals. Stratigraphers, for example, follow the International Stratigraphic Guide (Hedberg 1976) to define and name different stratigraphical units.

However, a widely used and largely accepted nomenclature for palaeogeography does not exist to date. A code of nomenclature for geodynamic and palaeogeographical terminology has never been defined, for example. This is not surprising, because the discipline of palaeogeography incorporates scientists from various fields, who use different terminologies. In some cases they even use the same terms, but with a different meaning or definition, which inevitably leads to confusion and misunderstandings. In the following paragraphs, the nomenclatures of the palaeogeographers and that of the palaeobiogeographers are summarized, before some suggestions are provided for a future, more consistent use of terms applied to Palaeozoic palaeogeography and palaeobiogeography.

Basic terminology of (palaeo)geography in tectonics

The impact of the plate tectonic theory on (palaeo-)biogeography

The theory of continental drift dramatically changed the concept of biogeography, because this theory allowed for the first time explanation of the biogeographical distribution of both fossil and modern organisms that had remained (with the notable exception of Croizat, see above) so far, enigmatic. For instance, the same stratigraphical sequences can be found on both sides of an ocean, indicating that they were once deposited in the same sedimentary basin in close proximity. Another example is that of glacial sediments that have been deposited at high latitudes or near one of the Earth's poles, and that can now be found at low latitudes. However, many fossil organisms indicating tropical temperatures can now be found in localities at high latitudes. For all these geological problems the plate tectonic theory was finally able to provide simple, but testable answers.

For several decades, scientists from different disciplines have combined their studies to understand not only plate tectonics and continental drift, but also ancient palaeogeographies, with the main objective being to attempt to propose accurate reconstructions of the positions of former continents and oceans. As such, the results from the different disciplines of palaeontology, structural and sedimentary geology, together with those from palaeoclimate studies, allow us to retrace the drift of the various palaeocontinents and explain their tectonic history. In addition, palaeomagnetic studies provide a quantitative constraint on the positions and movements of palaeocontinents, because the magnetic minerals preserved within rocks retain a record of the magnetic field at the location where they were formed, turning these minerals into a fossil compass. Palaeogeography is thus clearly an interdisciplinary science, with specialists from different backgrounds, using different concepts.

A major discipline contributing to the science of palaeogeography is structural geology. Structural geologists analyse the origin and destruction of tectonic plates, and attempt to reconstruct their movement or drift. They search for structures such as subduction zones, spreading zones and ocean ridges, strike-slip faults, hot spots and triple junctions. Structural geologists use a specific terminology that is not necessarily shared with other geologists or palaeontologists. The palaeogeographical terms used by structural geologists include, among others, the terms 'plate', 'continent' and 'terrane'.

Plates and microplates

Plates, as understood by structural geologists, are the basic units of plate tectonic theory (Table 3.3). Plates are relatively rigid, about 100 km thick, and form the mechanically strong outer layer of the Earth: the lithosphere. These lithospheric plates

Table 3.3. *Terminology in tectonics (from the Oxford Dictionary of Earth Sciences, Allaby & Allaby 2003) except for the term terrane (from Collins Dictionary of Geology, Lapidus 2003)*

Plate	A segment of the lithosphere which has little volcanic or seismic activity but is bounded by almost continuous belts (known as plate margins) of earthquakes and, in most cases, by volcanic activity. . . . Most Earth scientists consider there are currently seven larger, major plates.
Microplate	Any small lithospheric plate.
Continental crust	That portion of the Earth's surface overlying the Mohorovicic discontinuity, and with an average density of 2700–3000 mg m^{-3}. The thickness is variable, mostly 30–40 km.
Microcontinents	Microplates with continental crust are also microcontinents.
Craton (cratonic shield)	Area of the Earth's crust, invariable part of a continent, which is no longer affected by orogenic activity.
Terrane (or terrain)	A fault-bounded portion of the Earth's crust that has a distinct geology differing sharply from the areas adjacent to it.

'float' on the underlying viscous asthenosphere. Lithospheric plates can contain both oceanic and continental crust. The Pacific Plate, for example, is mostly built of oceanic crust; the Eurasian Plate is largely composed of continental crust, while the Indo-Australian Plate has significant proportions of both oceanic and continental crust.

In order to understand the position of former continents and oceans and with the objective of reconstructing ancient palaeogeographies, it is essential to locate plate boundaries; these take three basic forms: divergent plate boundaries correspond to spreading zones (ocean ridges); convergent plate boundaries are associated with collision or subduction (trenches or mountains chains, subduction and collision zones); and conservative plate boundaries correspond to transform zones. When three plate boundaries are located together, the resulting structure is a triple junction.

The globe is composed of a great number of lithospheric plates that all are in continuous movement, relatively rapidly. Some of the plates are very large (e.g. the Pacific Plate with an estimated area of over 100 million km^2, the North American Plate, or the African Plate), while others are much smaller (e.g. the Arabian Plate, the Indian Plate or the Philippine Plate). Some very much smaller plates are also named 'microplates'. They are smaller than 10^5 km^2 (Howell 1995) and usually occur in complex plate tectonic settings in between major plates in regions of continental convergence. The West Coast of North America hosts some such smaller plates (Cocos Plate, Rivera Plate, Juan de Fuca Plate and the Corda Plate, which is only roughly 750 km^2) squeezed between the Pacific and the North American Plate. Another example of an amalgamation of microplates is the SE Asian region, where over 60 microplates are defined between the Indian–Australian, Pacific and Eurasian plates (Hall 1997).

Most modern plates and microplates are well defined. It is also possible to trace back their history for most of the last 200 million years. However, the recognition of the older Palaeozoic plates is more difficult. The recognition of these 'palaeoplates' is not straightforward, because they have been largely or even completely consumed by subduction. Generally only some remnants of the continental parts of the palaeoplates are preserved. Because most of the palaeoplates have been consumed, many palaeoplate-tectonic reconstructions in the past are highly speculative. For the Lower Palaeozoic, it is therefore extremely difficult to define former tectonic plates, and the use of terms such as 'microplates' (as defined by some palaeontologists) should be regarded with caution (e.g. Havlíček *et al.* 1994).

It is also important to consider plate motions as a long-term phenomenon: lithospheric plates normally drift in a given direction for a considerable period of time (Euler theorem), and normally change direction only as a result of a major change in the plate boundary configuration. They do not usually change their direction abruptly and neither do they reverse their direction of travel. Several of the palaeogeographical reconstructions published in the literature by palaeobiogeographers do not take into account these basic principles of plate tectonics.

The velocity of movement is also an important factor. Several published palaeogeographical reconstructions (in particular those that explain the movements of 'microplates') would necessitate very rapid movements that are significantly greater than those we observe at the present day. Among the most rapidly drifting plates known today are some parts of the Pacific Plate, that reach a speed of about 7 cm per year in an 'absolute' framework (DeMets *et al.* 2010). While some reconstructions integrate these basic geological principles (e.g. Stampfli & Borel 2002; Linnemann *et al.* 2004), several Lower Palaeozoic palaeobiogeographical studies unfortunately ignore the basic principles of geodynamics, and the palaeogeographical reconstructions based on these analyses must be considered as flawed, because the necessary kinematic continuity between successive maps is not addressed.

Any attempt to propose Early Palaeozoic plate reconstructions is very challenging. How many plates, for example, were present between Gondwana and Laurentia? Such plate reconstructions would, however, mostly be based on pure speculation, because only limited evidence for the presence of Lower Palaeozoic palaeoplates is present, as the oceanic plates have been almost completely subducted.

In conclusion, it appears evident that tectonic plates and microplates can only be defined by structural geologists who are able to detect and to describe the plate boundaries. Palaeobiogeographical differences (in faunas or floras) are not sufficient to define ancient palaeoplates.

Continent – microcontinent – craton

By definition, a continent is a major land mass. On the modern globe these continents usually include the following: Africa, Antarctica, Asia, Australia, Europe, North American and South America. In terms of structural geology, a continent is, however, a large, discrete landmass, including the continental shelves (that sometimes are larger than the landmass itself), founded on a continental crust (Table 3.3). Most continents consist of a cratonic core surrounded by a 'mobile belt' composed of an orogenic mosaic of 'terranes'.

A stable craton commonly consists of an old (Precambrian) core of continental crust that is characterized by the lack of a geologically recent orogenic modification. A typically stable craton is the African continent, for example. Orogenic activity is concentrated along the margins of these cratons, within a 'mobile belt'. Such ancient cratons could be considered as 'supercontinents'. However, in palaeogeographical terms, a 'supercontinent' is generally considered to be a very large continent where most landmasses are united. Pangea is the best-known supercontinent; its assembly occurred during the Late Palaeozoic. Other supercontinents are Rodinia at the end of the Mesoproterozoic and Gondwana at the end of the Neoproterozoic and during most of the Palaeozoic.

The term 'microcontinent' is not clearly defined, although it is commonly used in Palaeozoic palaeogeographical reconstructions (Table 3.3). Typical present-day examples of microcontinents could be Madagascar, Greenland, New Zealand and Borneo.

The island of Madagascar is a typical example of the complexity of terminology: it is clearly an island (surrounded by water masses) and it could be considered a microcontinent. However, Madagascar is part of the African Plate, and it is linked to the African continent by the continental shelf. Africa and Madagascar are thus two continental masses on the same African Plate with clearly different biogeographical provinces, established by their contrasting faunas and floras.

In the Lower Palaeozoic, the principal major landmasses, and thus continents, are the three classical palaeocontinents of Baltica, Gondwana and Laurentia. Based on its large size, Siberia can also be considered as a Palaeozoic palaeocontinent.

Terrane – terrane assemblage

The term 'terrane' is one of the most frequently used jargons in tectonics and other fields of geology including palaeogeography. The current use of the term originated in the studies of W. P. Irwin into the geology of California in the1950s (Irwin 1960), where he identified several 'belts' within the Klamath Mountains characterized by different lithologies and ages. The belts were labelled 'terranes' by modifying the ordinary English word 'terrain', when Irwin needed to describe several Palaeozoic–Mesozoic geological units in the western USA that were characterized by complicated rock assemblages and multiple episodes of deformations

(Irwin 1972). In modern geological terms, most of these units are precisely described as ancient accretionary complexes and their high-pressure metamorphosed equivalents formed in ancient subduction-related orogenic belts, such as modern circum-Pacific domains.

Unfortunately in the late 1970s, however, the use of 'terrane' was partly modified by false connotation of the fault-bounded nature that was automatically connected to long-distance displacement under the strong influence of plate tectonics. According to the 'terrane geologists' in California during the 1980s, a terrane is defined as 'a fault-bounded package of rocks with a distinctive stratigraphy that characterizes a particular geological/palaeogeographical setting' (Howell 1995). Terranes were thus (re-)defined by two criteria: that they are fault-bounded, and they show a distinctive tectono-stratigraphical history (see also Table 3.3).

A 'tectonostratigraphic terrane' is characterized by a geological history that is different from the histories of contiguous terranes' (Jones *et al.* 1983) or continents. A 'suspect terrane' is one where the palaeogeographical linkage with adjoining terranes and/or continents is not obvious. Some authors used the term 'composite terrane' to refer to the result of the amalgamation of several terranes.

However, the term 'terrane' was subsequently used in many different ways. Similar to taxonomical splitters, which define a great number of new species and genera, the terrane concept allowed many palaeogeographers to create new terms by naming new unnecessary terranes, and there has been a literal explosion of such terms in the last decades (e.g. Servais & Sintubin 2009). Most interestingly, in some of the most recent Lower Palaeozoic reconstructions (e.g. Cocks & Torsvik 2005, 2007), some major palaeocontinents (e.g. Siberia) are named terranes, which neither correspond to the basic definition of the term, nor to the terrane concept, adding more confusion.

It is not the objective of the present paper to provide a comprehensive summary of the evolution of the term 'terrane'. However, it should be noted that not all 'terranes' should be considered as palaeocontinents (microcontinents), nor are all these 'terranes' palaeoplates (microplates; see also discussion in Harper *et al.* 1996; Benedetto 1998; Erdtmann 2000; Finney *et al.* 2003; von Raumer *et al.* 2003).

However, most importantly, palaeobiogeographers (palaeontologists), but also palaeogeographers (e.g. specialists of palaeomagnetism), who do not take into account the principles of tectonics and structural geology should avoid the use of the terms 'terranes', 'continents' and 'plates'.

Basic terminology in palaeo(bio)geography

What is palaeobiogeography?

Rosen (1992, 1994) suggested that the terms neobiogeography and palaeobiogeography can be used to describe 'special cases' of biogeography because they define the endpoints of a continuum. Cecca (2002) has noted that philosophical and conceptual differences between neo- and palaeobiogeography are not profound but there are fundamental methodological contrasts that derive from the practical problems encountered in working with fossil data. Palaeobiogeographers are forced to work with assumptions about ancient geographical and environmental conditions. Taxonomic methods are obviously different. Palaeobiogeography, however, has the advantage of direct access to the temporal dimension, thus focusing on changes in distributional patterns through time.

Whereas palaeogeography is the study of ancient geographies, and thus documenting continental movements during Earth history, biogeography is the study of the geographical distribution of faunas and floras in the modern world. The combination of both disciplines, palaeobiogeography, is the study of the geographical distribution of ancient faunas and floras and its implication for biology and geology. Palaeobiogeography is thus at the interface between earth and life sciences. It is neither a pure geological, nor a pure palaeobiological discipline. With a position at the interface between geology and biology, palaeobiogeography uses a mixture of terminology drawn from different scientific communities.

Traditionally palaeobiogeography has two aims: (1) the use of palaeobiogeographical distributions may serve as a guide to Earth history; and (2) the application of theories of Earth history and evolution may explain palaeobiogeographical distributions (e.g. Cecca 2002). Rosen (1988) distinguished a 'pure' biogeography (analysing biogeographical distributions) from 'applied' biogeography (applying biogeographical distributions to understand ecology, evolutionary biology and geology). Additionally, Cecca (2002) subdivided the 'pure' biogeography into two parts: the descriptive and the causal biogeographies. The first involves the recognition and description of biogeographical distributions with qualitative and quantitative approaches. Causal biogeography integrates the investigation of the causes of distributions, and it was divided into ecological biogeography and historical biogeography (Cecca 2002).

Terminology in palaeobiogeography

A number of terms have been used in descriptive biogeography and palaeobiogeography. These terms have not been used with any consistency, because their authors are from different scientific disciplines, or have been working with different types of living or fossil organisms.

Descriptive biogeography starts with the documentation of biogeographical distributions, using maps and delimitating areas of geographical distributions of the selected organisms, with the definition of biogeographical units such as 'provinces', 'realms' or 'regions', based on qualitative or quantitative definitions.

The reconstruction of palaeobiogeographical 'provinces' was particularly important in pre-Pangean palaeogeography. Many Palaeozoic palaeogeographical reconstructions were originally based on the analyses of palaeobiogeographical distributions of various fossil organisms (e.g. Cocks & Fortey 1982). For many geoscientists, palaeobiogeography is limited to the 'applied' part, that is, the essential part of palaeobiogeography (by using the geographical distribution of fossil organisms) is to infer past palaeogeographical reconstructions and plate tectonic movements.

Endemic, pandemic and cosmopolitan distribution

The distributional range of a given organism depends on physical parameters (e.g. geographical, climatic and oceanographic discontinuities) and biotic factors (e.g. biological tolerance to physicochemical parameters and interaction with other species). These distributional patterns are described and interpreted in various terms. No species is present everywhere; all taxa, even the majority of orders and families, are restricted to certain regions or environments.

Augustin de Candolle not only introduced the concept of endemism (1820). He also distinguished floral distributions controlled by factors like soil characteristics and climate, from distributions controlled by other, different, factors. He called the first distributions '*stations*', which today would be called habitats, and the second ones '*habitations*'. These concepts correspond to the current distinction between ecological biogeography and historical biogeography.

Organisms can be endemic to a location because they originated at that place and never dispersed or they survived in a small part of their former distributional area. Palaeontologists must be

Table 3.4. *Endemism – pandemism – cosmopolitism*

Endemism*	Situation in which a species or other taxonomic group is restricted to a particular geographic region . . . Such a taxon is said to be endemic to that region.
Pandemism	Situation in which a species or other taxonomic group is present at several geographic regions . . . Such a taxon is said to be pandemic to these regions.
Cosmopolitism*	Distribution of an organism that is world-wide . . . There are relatively few organisms that occur on all six of the widely inhabited continents.

*After the *Oxford Dictionary of Earth Sciences*, Allaby & Allaby 2003.

particularly careful in defining endemic species, taxa or communities, because the fossil record is mostly incomplete and the absence of a fossil species does not necessarily imply that the species was not present in that locality.

However, if an organism is not limited to a specific area, but has a wider geographical distribution, it is considered to display a pandemic distribution (e.g. across several continents). If an organism can be found in every part of the world, it is considered to have a cosmopolitan distribution (Table 3.4). Although the global oceans are a continuous space where organisms could be potentially present everywhere, there are currently relatively few species or genera that are actually found in all the oceans. Even phytoplankton, considered as not very useful for palaeogeographical reconstructions, clearly follow latitudinal belts and continental margins to show endemic or at least pandemic distribution patterns. True cosmopolitan species, that occur everywhere in the world, do not exist.

The disjunct distribution (or disjunct endemism) is an endemic distribution that shows the presence of representatives of the same taxon in localities that are separated by barriers. The absence in the intervening areas can be due to extinction or can be the result of different factors. Most palaeobiogeographical distributions are disjunct, because the dataset and the fossil record are usually incomplete.

The recognition of endemism from the distributional data of fossils forms the basis for all palaeobiogeographical analyses (Smith 1988). It is evident that only organisms with a limited (endemic) geographical distribution may be useful for palaeogeographical applications in palaeogeography or palaeoecology.

Provincialism – biogeographical units

Biogeographical units may be defined on the basis of single taxa, which may be species, genera or higher ranks (e.g. families and orders), or assemblages of taxa (several species or taxa of the same organisms), or communities of different organisms. The first step in distinguishing biogeographical units is qualitative: the absence or presence of an organism defines its geographical distribution. Biogeographical units are thus basically recognized on the endemicity of taxa.

Most commonly, the endemic distribution of plants or animals has driven the definition of 'provinces', that is, restricted geographical areas. If a variety of plants or animals tend to show a similar pattern of endemism, they show a provincialism, that is, they are distributed in a common province. The coincident distribution of different endemics forming a province does not necessarily correspond to specific boundaries of continents and oceans, and it is often difficult to precisely delimit it.

The first biogeographers in the nineteenth century quickly noted the presence of provinces, because the different continents display different biotas. A classic example of a biogeographical region is Australia, with a clearly endemic terrestrial fauna typified by marsupials (e.g. kangaroos and koalas). Biogeographers are, nevertheless, able to easily distinguish two major subregions and four different subregions (Brown & Lomolino 1998). Similarly, rather obvious definitions of biogeographical units have been proposed since the nineteenth century for many plants and animals (in particular birds and mammals) for most continents, leading to the distinction of the six major faunal 'regions' of Sclater or 'realms' of Wallace (see above).

Valentine (1973) observed that there is no special reason to employ any particular arbitrary level of endemism because a province could possess no endemic species at all and yet have distinctive communities. This is a very important point because only the establishment of relationships between endemic biotas can help in testing palaeogeographical reconstructions.

Proposal for a consistent use of palaeobiogeographical nomenclature

Ranks of palaeobiogeographical nomenclature

The concept of biogeographical units dates back to the studies of Sclater, Wallace and de Candolle. The most common term in biogeography and palaeobiogeography is the term 'province', a term that Neumayr (1883) proposed to define a large area characterized by a common particular fauna, caused by geographical position (e.g. barriers and latitude) but independent of facies. Uhlig (1911) introduced the more inclusive rank 'realm'.

However, it is evident that neobiogeographers (studying the biogeography of modern living organisms) and palaeobiogeographers (studying the biogeography of fossil organisms, including extinct and living representatives) do not always use the same terminology. A range of biogeographical units has been defined, ranging from the term 'realm' to 'region', or 'biome', but also including the terms 'province' and 'subprovince'. The hierarchy of these units was not always clearly defined, and biogeographers working on different groups of organisms commonly use different terminologies. Palaeobiogeographers studying different geological eras or working on different fossil groups do not use the same terminology. As a result, it is possible to have completely different ranks for biogeographical units for the same stratigraphical interval and the same palaeocontinents but for different fossil groups. In addition, different units are used for the same fossil group but through different stratigraphical intervals.

Kauffmann (1973), for example, noted that neobiogeographers mainly use the following units in a decreasing rank: planetary biota (cosmopolitan), realm, region, province or subregion, subprovince, endemic centre and community (Table 3.5). Kauffmann (1973) also noted that some authors abandoned 'realm' or replaced it with 'region'. In addition, he observed that most Late Cenozoic workers use this same terminology.

Kauffmann (1973) also noted that some specialists proposed percentages of endemism to define biogeographical provinces. For Cretaceous bivalves, for example, endemic centres display 5–10% endemism, subprovinces 10–25%, provinces 25–50%, regions 50–75% and realms >75%.

Palaeobiogeographers have used some of these terms, but not necessarily in the same sense. McKerrow & Cocks (1986) in

Table 3.5. *Ranks of biogeographical units used by neobiogeographers (Kauffmann 1973)*

Planetary biota (cosmopolitan)
Realm
Region
Province or subregion
Subprovince
Endemic centre
Community

their survey of faunal distributions that recognized more precisely the Iapetus Ocean in the Early Palaeozoic proposed the use of the term 'province' for biogeographical units separated by physical barriers to migration and the term 'realm' for climatically controlled faunas and floras. As pointed out by Cecca (2002), this proposal has not been followed.

As already noted above, the key issue is the establishment of relationships between areas of endemism and not arbitrarily selected levels of endemism.

Towards the standardization of palaeobiogeographical nomenclature

Similar to the ICZN or the ICBN, but also to the International Guide of Stratigraphical Terminology, a standardized nomenclature would help provide greater uniformity and clarity in palaeobiogeographical nomenclature. Palaeobiogeographers from all countries and all different fossil groups could use the same terminology and apply it in the same sense, following a consistent, stable method and avoiding unnecessary additional names.

A first version of an 'International Code of Area Nomenclature' (ICAN) was proposed by Ebach *et al.* (2008). This proposal aimed to standardize area names used in biogeography and was a step towards a more influential discipline of biogeography. However, Zaragüeta-Bagils *et al.* (2009) noted not only that ICAN's foundations lacked precision, but also that ICAN could actually complicate the naming of areas. Although based on clear objectives and key concepts, the 'International Code of Area Nomenclature' has not yet gained a significant following.

However, Westermann (2000), Cecca (2002) and Cecca & Westermann (2003) proposed a series of more informal rules to rationalize the use of palaeobiogeographical nomenclature to provide a terminology that will be used consistently by all Phanerozoic palaeobiogeographers. The 'attempt at order' (Westermann 2000) or 'guide to palaeobiogeographical classification' (Cecca & Westermann 2003) was based on a larger consensus of the 'Friends of palaeobiogeography' and was intended to complement the principles of neobiogeography, aimed at enhancing palaeobiogeography in general by a simplified and standardized terminology. The basic guidelines of the proposal are as follows:

(1) Definition of biogeographical units (biochores) – a biochore is defined by the overall endemism of its biota (not particular taxa) within a geographical envelope around a core area, whereas biochore boundaries are defined by the temporary range limits of their constituent endemic taxa.
(2) The ranks for biogeographical units should be in descending order – realm, subrealm (optional), province and subprovince (optional). The term 'region' should only be used informally. These ranks scale with the degree of endemism as well as duration and biota distribution (range).
(3) A typical region or 'chorotype' and a typical stage (age) or chronotype are designated for each biochore.
(4) Biochore nomenclature – names are geographical and related terms, not taxa-based.

Although not yet accepted as a standard, several palaeobiogeographers have expressed a consensus by using the terminology proposed by Westermann (2000) and Cecca & Westermann (2003).

The use of these basic principles was suggested to all authors of the different chapters of the present volume on Early Palaeozoic palaeo(bio)geographies.

Conclusion

Palaeontological studies have contributed a great deal to Palaeozoic palaeogeographical reconstructions in recent decades, together with investigations from other geological disciplines, including sedimentology, structural geology (tectonics) and palaeomagnetism. However, there has been increasing confusion regarding the nomenclature of palaeogeographical (continents, plates, etc.) and palaeobiogeographical (provinces, etc.) units in recent years. For example, distinct fossil assemblages attributed to 'provinces', defined on the basis of the spatial distribution of selected fossil groups, have sometimes been interpreted as geographical or tectonic units without key evidence from sedimentary or structural geology. In addition, palaeogeographical reconstructions by palaeobiologists did not necessarily take into account some of the basic principles of structural geology or did not respect the necessary kinematic continuity between successive maps. Palaeobiogeographers also used a wide range of biogeographical units without a precise order or rank.

Following previous attempts that have been made to provide more stable palaeobiogeographical nomenclature (Westermann 2000; Cecca & Westermann 2003), we propose a consistent use of palaeobiogeographical units or 'biochores', that should have a clear rank, but also clearly defined typical areas ('chorotypes') and time intervals ('chronotypes'), whereas the names should be geographical terms and not taxa-based.

Most importantly, palaeontologists and palaeobiologists should avoid the use of terminologies of structural geology and tectonics.

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