

Regionalización biogeográfica en Iberoamérica y tópicos afines

Primeras Jornadas Biogeográficas
de la Red Iberoamericana de Biogeografía
y Entomología Sistemática (RIBES XII.I-CYTED)





CONABIO

**Comisión Nacional para el Conocimiento
y Uso de la Biodiversidad**

Lic. Vicente Fox Quesada
Presidente

Ing. Alberto Cárdenas Jiménez
Secretario Técnico

Dr. José Sarukhán Kermez
Coordinador Nacional

Dr. Jorge Soberón Mainero
Secretario Ejecutivo

Fís. Ana Luisa Guzmán y López Figueroa
Directora de Evaluación de Proyectos



Universidad Nacional Autónoma de México

Dr. Juan Ramón de la Fuente
Rector

Dr. Ramón Peralta y Fabi
Director de la Facultad de Ciencias

Dra. Edna María Suárez Díaz
Coordinadora del Departamento de Biología Evolutiva

M. en C. Mercedes Perelló
Coordinadora de Servicios Editoriales

Regionalización biogeográfica en Iberoamérica y tópicos afines

**Primeras Jornadas Biogeográficas
de la Red Iberoamericana de Biogeografía
y Entomología Sistemática (RIBES XII.I-CYTED)**

Editores:

Jorge Llorente Bousquets

Juan J. Morrone

Facultad de Ciencias, UNAM

México, D.F., 2005



Diseño de portada e interiores: Adrián D. Fortino O.

Primera edición, 2005
Las Prensas de Ciencias, Facultad de Ciencias, UNAM

Regionalización biogeográfica en Iberoamérica y tópicos afines:

**Primeras Jornadas Biogeográficas
de la Red Iberoamericana de Biogeografía
y Entomología Sistemática (RIBES XII.I-CYTED)**

Editores:

Jorge Llorente Bousquets

Juan J. Morrone

ISBN-970-32-2509-8

**Impreso y hecho en México.
Queda prohibida la reproducción parcial o total de esta obra
por cualesquiera medios, sin el permiso escrito de los titulares de los derechos.**

The history and philosophy of panbiogeography

Michael Heads

*You start a question, and it's like starting a stone.
You sit quietly on the top of a hill; and away the
stone goes, starting others [...]*

Stevenson, 2002

*Our scientific ideas are of value to the degree in which
we have felt ourselves lost before a question; have
seen its problematic nature, and have realized that
we cannot find support in received notions, in pre-
scriptions, proverbs, mere words. The man who dis-
covers a new scientific truth has previously had to
smash to atoms almost everything he had learnt, and
arrives at the new truth with hands bloodstained from
the slaughter of a thousand platitudes.*

Ortega y Gasset, 1932

■ examine the history of panbiogeographic thought from its origins in the pre-Socratic philosophers of ancient Greece through to modern times. Parts of the same ground have been well covered by Llorente *et al.* (2000, 2001). Main themes include the following:

1. Teleological thinking and writing have no place in biology and have held up progress.
2. Earth and life evolve together.
3. The Scientific Revolution started with sixteenth century biology, not seventeenth century astronomy.
4. Cesalpino was the first true systematist and a major figure in the Scientific Revolution.
5. The Scientific Revolution and panbiogeography are branches of the North Italian Renaissance.
6. Evolution is not gradual or clock-like.
7. Orthogenetic development (phylogenetic constraint by molecular drive, etc.) is of primary importance in evolution.
8. Natural selection is of secondary importance, pruning but not creating evolutionary trends.
9. The vicariance/dispersal debate is less about ecology and means of dispersal than about modes of speciation: whether species evolve at a point (Darwin's

'chance dispersal', Mayr's 'founder dispersal' and Hennig's 'speciation by colonisation') or over a region (Mayr's dichopatric speciation, Croizat's vicariance).

10. Evolution by vicariance involves neither a center of origin nor migration over a barrier.

11. The basic concepts of Mayr, Hennig and modern phylogeographers (teleology, point center of origin, undifferentiated ancestor, progression rule) are derived from Aristotelian logocentrism and German idealism.

Evolution in the Greek and Roman classics

[...] from his [Aristotle's] frequent polemics against Empedocles, Heraclitus and Democritus we see how all these had a very much more correct insight into nature and had also paid more attention to experience than had the shallow prattler now before us.

Schopenhauer, 1974

Many, if not most, of the important principles of biogeography and evolution were elaborated, or at least initiated, in the Greek and Roman classics. For example, Huxley (quoted in Matthews, 1971) argued that Darwin's work was *revivified thought of ancient Greece*. Anaximander (610-546 B.C.) argued that organic life is the result of an historical process. From his observations on embryos, fossils (Burn, 1966), and habits of the smooth shark (*Galeus levis*), a fish that has some 'mammalian' characteristics (Kitto, 1951), he deduced that men are descended from fish. He suggested that: *Life comes from the sea, and by means of adaptation to the [terrestrial] environment the present forms of animals were evolved* (Copleston, 1962). He supported a concept of dispersal as physical movement and proposed *migration [of early forms] onto the drier land* (Toulmin and Goodfield, 1965). (In a vicariance view, the 'invasion' of the land is much more likely to have involved geological uplift of pre-adapted forms). Xenophanes (*fl.* 540) had de-

tected the phenomenon of raised beaches through the presence of shells and marine fossils inland and on mountains and the imprint of sea-weeds and fishes in the stone quarries of Syracuse (Farrington, 1949; Kitto, 1951). Heraclitus (*fl.* 504 B.C.) held the view that everything changes, all is flux. Empedocles (484–424 B.C.) proposed a version of natural selection, in which the genesis of mortal beings takes place in four stages (Cavendish, 1964): (1) the production of separate parts of plants and animals, not joined together; (2) the coming together of these parts to form a multitude of monsters; (3) the chance formation, among these monsters, of viable forms; and (4) the persistence of these viable forms by reproduction.

Thus, the pre-Socratic philosophers were well on the way to developing an evolutionary biology. Plato also supported a theory of the origin of species by evolution, but it was a theory of ‘degeneration’, with animals and plants descending from the highest form, man. Speusippus and certain Pythagoreans also accepted that organic evolution had occurred, but with the ‘best’ forms having developed last (Popper, 1984). The trend towards evolutionary thinking in biology was interrupted by the work of Aristotle, which denied evolution and set back the development of panbiogeography for two millennia.

Teleology

The theory of the four humors espoused by the school of Hippocrates was to exercise a thoroughly deleterious influence on medicine for 2,000 years; because under it one could account for anything, it blocked the way to further enquiry based on observation.

Burn, 1966

[...] every discipline as long as it has used the Aristotelian method of definition has remained arrested in a state of empty verbiage and barren scholasticism.

Popper, 1984

[...] overhead the branches met each other and interlaced their foliage; and though it had happened naturally this too gave the impression of having been done on purpose.

Longus, 1956

They were amazed to find that fish have fins, birds wings, seeds a husk – full of that philosophy which discovers virtuous intentions in nature and regards it as a kind of St Vincent de Paul always busy distributing benefits.

Flaubert, 1976

The teleological explanation of organic structure, accounting for a structure in terms of the ends and purposes it achieves (its ‘final cause’), has been a fundamental tenet of biology, especially popular biology, for over 2000 years. In the contemporary media, every night on television one can hear statements such as: *tiger sharks are beautifully adapted for eating large prey* (National Geographic Channel) or that a flower *has a beautiful scent in order to attract a pollinating insect*. Developing ‘a theory’ of any structure, such as the casque (‘helmet’) of the cassowary, means finding out what it is *for* (National Geographic Channel). Perhaps it is for pushing through the undergrowth –but juveniles do not have it and so perhaps it is for something else... Neo-Darwinians sometimes claim that this is only a ‘short-hand’ way of writing, and that what is really meant is that the effects of natural selection *look like* purposeful evolution; however, this claim is unlikely, at least for the vast majority of biologists, and teleological explanation is one of the few concepts that first-year university students in biology around the world are familiar and confident with.

Whether or not the idea of purpose is invoked, all teleological and selectionist accounts explain a structure in terms of how it functions *now*. If it is discovered, for example, that a particular structure previously seen as mysterious currently functions as a weapon in combat, or as a sexual attractant, this function will be seen as the cause of its evolution. On the other hand, panbiogeography argues that this is an end-point of evolution, and so cannot be a cause, at least outside of teleology. The (current) end-point of an evolving structure is thus of secondary importance to the explanation of the structure. A teleological theory of the cassowary casque involves its current function, while a non-teleological explanation could be, for example, that it is derived by reduction from a structure found in dinosaurs.

Plato taught a teleological conception of Nature and likewise in Aristotle’s metaphysics: *it is legitimate*

and necessary to ask always in the study of her [Nature's] works at what good she was aiming (Farrington, 1949). The teleology of Plato and subsequently that of the Christian writers invokes as a purpose the will of God, whereas Aristotle saw teleology as an activity immanent in nature itself: *nature never creates anything without a purpose, but always what is best in view of the possibilities allowed by the essence of each kind of animal* (Aristotle, 1968, *Progression of Animals*, II). 'The good', 'the advantageous' and 'the best' are not concepts that occur in the principles of the exact sciences and perhaps it was their teleological obsession—everything is for the best—that prevented Aristotelians from developing the ideas on evolution that had already been initiated by earlier Greek philosophers.

In his *Researches about Animals* (*Historia Animalium*), Aristotle recorded his observations on animals without referring to any reasons or causes of the phenomena; these are dealt with at length in his *Parts of Animals*, *Movement of Animals*, *Progression of Animals* and *Generation of Animals*. Aristotle cited four primary causes: formal (the eternal 'idea' or 'form' of a thing), material (what a thing is formed of), efficient (how it is formed), and final (what it is formed for). He recognized the importance of the efficient cause but assigned fuller significance to the final cause (see discussion in Arber, 1970). For Aristotle a biological species' *purpose* (the end towards which the living individuals strive) and its *form* (the immanent force by which their growth is directed) comprise its essence.

Modern science has rejected the use of formal and final cause in favor of efficient and material cause, and the critique of teleology in evolutionary biology is a major theme of panbiogeography. Croizat (1964: 495-499) discussed Aristotle's teleological views (*Physics* II, 8) and in particular his critique of the non-teleological approach of Empedocles (as cited by Aristotle). Aristotle (as translated in Zirkle, 1941) wrote: *Why not say, it is asked [by Empedocles], that Nature acts as Zeus drops the rain, not to make the corn grow, but of necessity (for the rising vapour must needs be condensed into water by the cold and must then descend, and incidentally, when this happens, the corn grows), just as, when a man loses his corn on the threshing floor, it did not rain on purpose to destroy the crop, but the result was*

merely incidental to the raining? So why should it not be the same with natural organs like the teeth? Why should it not be a coincidence that the front teeth come up with an edge, suited to dividing the food, and the back ones flat and good for grinding it, without there being any design in the matter? And so with all organs that seem to embody a purpose. In cases where a coincidence brought about such a combination as might have been arranged on purpose, the creatures, it is urged, having been suitably formed by the operation of chance, survived; otherwise they perished [...] (Darwin, 1971: 7 quoted this passage but thought that Aristotle was agreeing with it, whereas in fact he was criticizing it). Aristotle argued that these phenomena, such as the structure of teeth, were constant or normal, and so could not be the result of chance; however, he also argued, less convincingly, that *the only choice is to assign these occurrences to coincidence or to purpose, and if in these cases coincidence is out of the question [...] there is purpose then, in what is, and what happens in Nature.*

Croizat pointed out that Empedocles did not, as Aristotle felt he did, substitute chance—in the sense of blind hazard—to law. Empedocles emphasized instead that nature is bound by laws, for example, laws of condensation, and that rain does not fall in order to make wheat grow. Croizat concluded: *things are because they must be is the position of Empedocles; things are because there is a purpose in their being is the position of Aristotle.*

Aristotle insisted, as quoted above, that: *nature never creates anything without a purpose, but always what is best in view of the possibilities allowed by the essence of each kind of animal* (bold added). So as well as teleology, he also accepted a non-teleological necessity. As Windelband (1958a) commented, *Ancient philosophy did not overstep this dualism between the purposive activity of form and the resistance of matter; with the demand of the teleological view of the world it united the naïve honesty of experience, recognizing the necessity, purposeless and contrary to design, which asserts itself in the phenomena of the actual world.* Thus, Aristotle argued that: *There are more causes than one concerned in the formation of natural things: there is the cause for the sake of which the thing is formed*

['good purpose', final cause], and the cause to which **the beginning of the motion** [i.e. development] is due ['simple necessity'; material and efficient cause]. Therefore another point for us to decide is which of these two causes stands first and which comes second. Clearly the first is that which we call the 'Final Cause'—that for the sake of which the thing is formed—since that is the *logos* of the thing—its rational ground, and the *logos* is always the beginning for products of nature as well as those of Art. (Parts of Animals I, 1). Similarly, [...] whenever there is evidently an end towards which a motion goes forward unless something stands its way, then we always assert that the motion has the End for its purpose (Parts of Animals I, 1). In contrast with Aristotle, Empedocles and panbiogeography accept that only material and efficient cause ('necessity') are legitimate in biology; purposeful explanation is not.

Aristotle went on to cite both purpose and necessity in, for example, the very hairy head of man, the lips of man (which are soft and fleshy, to make speech possible), and animals' horns (the purpose is obvious, the necessity is that Nature has taken away from the teeth to add to the horns). Unlike kindred animals, snakes can turn their head backwards while the rest of the body remains still. The vertebrae are cartilaginous and flexible, and: *This then is the necessary cause why they have this ability; but it serves a good purpose too, for it enables them to guard against attacks from the rear [...]* (Parts of Animals IV, 11). Aristotle's teleological arguments often sound very modern, and also rather illogical: *The Carabi [Crustacea] find a tail useful because they are good swimmers* (Parts of Animals IV, 8)—but of course they are only good swimmers because they have a tail. *A tail would be useless to the Carcini, which spend their lives near the land and creep into holes and crannies—but if they had a tail they wouldn't spend their lives creeping.* Likewise, *It is for a good reason, too, that winged animals have feet, while fishes have none. The former live on dry land and cannot always remain up in the air, and so necessarily have feet; but fishes live in the water and not air. Their fins, then, are useful for swimming, whereas feet would be useless* (Progression of Animals XVIII).

At other times, Aristotle even denies some organs any purpose: *But the spleen, where present, is present*

of necessity in the sense of being an incidental concomitant, as are the residues in the stomach and in the bladder. So in some animals the spleen is deficient in size [...] (Parts of Animals III, 7). Likewise, *those who assert that the gallbladder is present for the sake of some sensation are wrong [e.g. there is no gallbladder in the seal or dolphin; it is large in sheep from Naxos but absent in sheep from Chalcis] [...]* No; it seems probable that just as the bile elsewhere in the body is a residue or colliquescence, so this bile around the liver is a residue and serves no **purpose** [...] *The truth is that some constituents are present for a definite purpose, and then many others are present of necessity in consequence of these* (Parts of Animals IV, 2). This interpretation of structures as 'epiphenomena' approaches the view of Empedocles and panbiogeography, but was not developed by Aristotle or his followers.

Immediately after Plato and Aristotle, teleology began to be criticized again. Farrington (1949) wrote that it is: *this whole conception [teleology] which Aristotle's student Theophrastus wishes to subject to fresh analysis [...]* *Having swept aside the whole effort to create a theology, in the manner of Plato and Aristotle, from what they thought they knew about the motions of the heavenly bodies, Theophrastus proceeds in his last chapter [of his Metaphysics] to lay hands on the Ark of the Covenant, the teleological principle itself [...]* *This protest against the glib assertion of the universality of purpose and the rashness with which some philosophers assign ends to things, he backs up with powerful arguments [...]* *His final opinion is that if science is to make progress this reckless teleology must be checked.*

The Roman author Lucretius (1973) also warned against teleology: *there is one illusion that you must do your level best to escape—an error to guard against with all your foresight. You must not imagine that the bright orbs of our eyes were created purposely, so that we might be able to look before us; that our need to stride ahead determined our equipment with the pliant props of thigh and ankle [...]* *To interpret these or any other phenomena on these lines is perversely to turn the truth upside down. In fact, nothing in our bodies was born in order that we might be able to use it, but the thing born creates the use* (Lucretius, 4, 823-835). Lucretius was a mechanist

and tended to minimize the personal activity of the gods, so his work was received with hostility both by the religion of his own day and Christianity which was soon to emerge. *The abuse and calumny which Lucretius received for over 1500 years is a matter of record* (Zirkle, 1941) and the overwhelming influence of Plato and Aristotle ensured that teleology remained a major tenet of scientific writing, at least in biology, for over 2000 years. For example, the early anatomists, notably Galen (129-216 A.D.), saw that most parts of the human body *were adapted with admirable Art to their several Functions* (Addison, in Steele and Addison, 1997). Likewise, Marcus Aurelius (121-180 A.D.) (1979) assumed that: *The purpose behind each thing's creation determines its development*. The teleology of the early Christian authors such as Lactantius (260-340 A.D.) have been well documented by Zirkle (1941). In Renaissance times, authors like Castiglione (1967) took it for granted that: *the feathers of birds and the leaves and branches of trees [...] are given by Nature to preserve their being*. Cesalpino (1583) retained the reliance on both efficient and final cause, and wrote, for example, that the 'purpose' of the corolla and stamens is the protection of the developing fruit (quoted in Arber, 1970).

The Scientific Revolution instigated a radical change of thinking. In the seventeenth century teleology was the second great cosmological movement (after 'naturalism') that modern science specially selected for critique (Collingwood, 1945). Bacon led the attack, writing memorably that teleology, *like a virgin consecrated to God, produces no offspring* (Bacon, 1970), in other words, teleological explanation tells us nothing. In the new theory of nature, observations are explained through efficient causes, that is, by the action of material things already existing. This critique successfully eliminated teleology from physics, chemistry, geology and the precursors of panbiogeography, although it remained of fundamental importance in mainstream biology.

Spinoza criticized the use of teleology in science in, writing, like Lucretius, that: [...] *this doctrine of final causes turns Nature completely upside-down, for it regards as an effect that which is in fact a cause, and vice versa* (Spinoza, 1982). Likewise, in the new approach heralded by Bacon, Hume (1977) wrote: *It is vain, therefore, to insist upon uses of the parts in*

animals or vegetables, and their curious adjustments to each other. I would fain know how an animal could subsist, unless its parts were so adjusted?

In contrast, the German philosophers accepted the use of teleology in practice, at least as an heuristic device, but they had qualms. The cosmology of Leibniz is like that of Spinoza but emphatically reaffirmed the doctrine of final causes. Half of Kant's (1790) *Critique of Judgment* (Kant 1978) is devoted to teleology. Kant agreed that the goal of science must always be to provide, as far as possible, a mechanical explanation (efficient cause), and that 'end' is not a category or a constitutive principle of objective knowledge; however, he felt that a mechanical explanation of the organism had not only not yet succeeded, but was impossible in principle. The whole of the organism is determined by the parts and the parts are determined by the whole; it is impossible to conceive how the mere 'mechanism of nature' should precisely and specifically lead to, for example, the growth of grass (Warnock, 1964), thus, the organism is the miracle in the world of experience. Therefore the teleological view of organisms is necessary and universally valid, although it must never profess to be anything else than a mode of consideration (Windelband 1958b). In other words, Kant regarded teleological language as unavoidable in accounting for natural phenomena, *but it must be understood as meaning only that organisms must be thought of 'as if' they were the product of design, and that is by no means the same as saying that they are deliberately produced*.

This rather confused stance, of writing but not thinking teleologically, was adopted by Mayr (1982c: 49-50), who inherited many ideas from the German idealists although he claimed to be criticizing them. Mayr accepted that ontogenetic and physiological processes can be 'goal-directed' and that: *It is the endpoints that produce the selection pressure which cause the historical construction of the genetic program*.

Kant's influence on Goethe is well-known, and the latter's biology is fundamentally and radically teleological in character, although, again, the teleology is not that of a designing creator (Lenoir, 1984). Herder, the philosopher and historian of culture, and Lamarck were both born in 1744 and wrote about history in the same manner. Herder's ideas were developed by Hegel, Comte and Marx, and in all these authors his-

tory is seen as teleological fulfillment of hidden purpose (Toulmin and Goodfield, 1965). The exact authorship of the important document 'The oldest systematic programme of German idealism' (1796/7) is unknown, but it is certain that Hölderlin, Schelling and Hegel took part in its writing and the concepts of teleology and organism determine its attitude towards state and society (Sturma, 2000).

Schopenhauer also accepted the perfect adaptation of organisms and their organs to their purpose; however, in his discussion of Schopenhauer's views, Taylor (1985) noted that since the seventeenth century men of science have looked with suspicion on all attempts to describe biological phenomena teleologically [...] Thus instead of saying after the manner of Schopenhauer that the ant eater has a glutinous tongue *in order to* pray on ants and termites, one can say, it is claimed, that **because** it has such a tongue, it does in fact prey upon ants and termites. Nevertheless, for Schopenhauer: concepts of purposes or ends seemed necessary for the manifest teleology of living things. Taylor concluded: *It is perhaps significant to note too, that Darwin, who is widely supposed to have banished teleology from nature altogether, was unable to dispense with it.*

In the nineteenth century 'adaptation' finally took over from God and unspecified immanent causes as the mechanism for teleology in biology. Discussing *that vast, and in many respects very magnificent, literature on design written by the natural theologians*, Mayr (1997) wrote that it was possible to take over almost all of this literature into Darwinism simply by replacing the explanatory causal factor: *it was not God who perfected the design but the action of natural selection [...]* **the essential structure of [the] theory was left untouched; only the basic causal factor was replaced** (Mayr, 1997; bold added). If the new 'basic causal factor' turns out to be wrong (see 'orthogenesis' below), we are simply left with a single body of theory, one of teleology. The structure has a function; the structure is there for the fulfillment of that function, and the function explains its structure.

O'Grady (1984) has summarized the role of teleology in Darwinism clearly. He wrote: *The order among and within living systems can be explained rationally by postulating a process of descent with modification, effected by factors which are extrinsic*

or intrinsic to the organisms. Because at the time Darwin proposed his theory of evolution there was no concept of intrinsic factors which could evolve, he postulated a process of extrinsic effects –natural selection. Biological order was thus seen as an imposed, rather than an emergent, property. Evolutionary change was seen as being determined by the functional efficiency (adaptedness) of the organism in its environment, rather than by spontaneous changes in intrinsically generated organizing factors. The initial incompleteness of Darwin's explanatory model, and the axiomatization of its postulates as neo-Darwinism, has resulted in a theory of functionalism, rather than structuralism. As such it introduces an unnecessary teleology which confounds evolutionary studies and reduces the usefulness of the theory. O'Grady cited Asa Gray (1874) who wrote: *Let us recognize Darwin's great service to Natural Science in bringing back to it Teleology: so that instead of having Morphology versus Teleology, we shall have Morphology wedded to Teleology.* In a letter to Gray, Darwin responded favorably: *What you say about Teleology pleases me especially* (F. Darwin, 1959). O'Grady also cited neo-Darwinist work suggesting that entire species are 'adaptive devices', and concluded that the theory not only fails to limit such hyperbole but actually encourages it.

As noted above, teleology is as ubiquitous in biology now, in both the popular media and the scientific press, as it has ever been. An example of a modern apologist for teleology is Vogel (1988), who wrote a book called 'Life's devices'. A dictionary definition of 'device' is 'plan, scheme, trick; contrivance, invention, thing adapted for a purpose or designed for a particular function'. Likewise, Vogel admitted that the use of the word 'design', which in his book he found 'hard to avoid', is: *seriously misleading –in common usage, design implies anticipation and purpose. The problem is not just terminological. Why do organisms appear to be well designed if they are not designed at all?* They obviously appear to be well designed to a teleologist; to a panbiogeographer they do not appear any better (or worse) designed than the sun or the moon. Vogel defended his position by arguing that *verbal simplicity is obtained by talking teleologically –teeth are for biting and ears are for hearing*, but actually it is verbally simpler to say 'teeth

bite and ears hear'. He supported the German idealist argument that: *the attribution of purpose isn't a bad guide to investigation*, but that is the whole point –it is a bad guide. In evolutionary studies, teleology leads to fanciful explanations of a structure, focused exclusively on its current function, rather than analysis of its evolutionary history. Vogel agreed that there are 'powerful constraints' to natural selection, but the only ones he referred to are: *the rules of the physical sciences and the basic properties of practical materials*; he did not cite biological or genetic constraints. At least Vogel admitted that his book is: *incorrigibly adaptationist in its outlook and teleological in its verbiage*. As a study of biomechanics, his book is useful, showing how, for example, a fish can swim faster than a duck can paddle. But as an explanation of evolution in fishes and ducks, and why they have the structure they do, it is practically worthless.

Rose and Lauder (1996) observed that in modern times: *A new adaptationism is creeping back into mainstream evolutionary biology*; however, this adaptationism is not really new, it is the same old teleology which has dominated biology since the time of Aristotle. The powerful influence of Aristotle in American scholarship is well-known (e.g. the neo-Aristotelian school of literary criticism at the University of Chicago) and it is easy to find examples in contemporary biology. In a publication from the Smithsonian Institution, Leigh (1999) wrote that: *This book presupposes the prevalence of adaptation among organisms [...] Aristotle recognized that organisms are like human artifacts that are built for a purpose, insofar as one understands neither artifact nor organism nor any part of an organism unless one understands the function for which it was designed (Parts of Animals 639b 14-20). Moreover an organism whose structure or behavior is abnormal for its species is usually dysfunctional (Physics 199a 33-b4), as if normal organisms are adapted to their ways of life [...] Aristotle recognized the purposiveness of organisms and emphasized that they cannot be understood without resorting to functional explanation, but he was unable to explain the source of this purposiveness*. As Leigh correctly observes, Darwin's theory does explain the purposiveness – it does not reject it. Throughout his book, Leigh's approach is to ask: *What problems must tree design solve? How can*

a tree be designed so as best to solve these problems? Leigh's answers to these questions all comprise arguments from design: *some trees are designed to avoid or shed lianes; the branches of Terminalia: are designed to intercept nearly all the light coming their way; the architecture of trees in cloud forest: seems designed not only to assure aerodynamic smoothness but to minimize the amount of shedding and rebuilding of branches; mangrove leaves are designed and arranged to avoid overheating; plant diameter varies with height so as to provide a margin of safety against a stem buckling under its crown weight* (in fact that is exactly what does happen in some plants –lianes by definition do buckle under their own weight, if there are no other plants present to support them).

Teleology and panselctionism vs. orthogenesis and morphogenesis

As far as the famous 'struggle for life' is concerned, it seems to me for the moment to be more asserted than proven. It occurs but it is the exception; life as a whole is not a state of crisis or hunger, but rather a richness, a luxuriance, even an absurd extravagance... Species do not grow in perfection [...].

Nietzsche, 1998

What are the practical implications of a non-teleological view? Denying that function determines structure, and accepting that structure determines function, places much more emphasis on structure, especially the series of homologous structures present in related taxa. In other words, the question becomes: What is the morphogenetic context of the variation? How did the variation come about in the first place? And if a structure *could* develop, would it not have come about anyway? In this view, the orthogenetic trend or trajectory formed by a whole series of different but related (homologous) structures –what Darwin called a 'Law of growth'– is the primary factor, not the individual points or morphologies (Grehan and Ainsworth, 1985). (Orthogenesis was later appropriated by North American authors and relabeled 'phylogenetic constraints'). Once the morphogenetic trajectory is established, the particular morphologies

and their different 'adaptations' are seen as merely secondary, as points along the trajectory. It is the discovery of the fundamental trajectories that should be the concern of the biologist, not overemphasis on particular morphologies as 'wonders of nature'. Everyone is impressed by the butterflies of the Malay Archipelago (*Doleschallia*: Nymphalidae) that closely resemble dead leaves, and no doubt neo-Darwinians have explained their structure in terms of this resemblance. But what about the related taxa that only look a little like leaves?

Neo-Darwinism played down Darwin's 'laws of growth' and instead stressed the effect of the external environment on the organism, almost supporting a kind of Lamarckism. For example, Matthew (1915) asserted that: *the whole of evolutionary progress may be interpreted as a response to external stimuli*. Panbiogeography takes a diametrically opposed view through supporting orthogenesis, which will lead to evolutionary development despite the environment, not because of it. Evolution will result in structure which, in a particular environment may be adaptive, non-adaptive (leading to extinction), or neutral, but it is never simply a function of the environment to start with.

Orthogenesis is, of course, not a finalistic principle or teleological concept, as panselectionists such as Mayr (1982c: 517, 528-531) have confusingly claimed; in fact, it is the opposite. Mayr (1982c: 531) himself admitted that: *trends may be necessitated by the internal cohesion of the genotype which places severe constraints on the morphological changes that are possible*, and this is a good description of orthogenesis.

As well as teleology, other idealist modes of interpreting particular aspects of morphology were later adopted by the Darwinians and have persisted in biology, sometimes subconsciously, until now. They have had a tremendous influence on the way in which morphological series have been viewed. The idealist view inherited by Darwin is that the ancestor of a taxon is undifferentiated, not polymorphic, and that any complex organic structure is derived by elaboration from a simple one. This idea is seen repeatedly in modern accounts of morphology and was clearly expressed by Goethe (1962): *Here [in the Padua Botanical Garden], where I am confronted with a great variety of plants, my hypothesis that it might be pos-*

sible to derive all plant forms from one original plant becomes clearer to me and more exciting [...] I am on the way to discovering the manner in which Nature, with incomparable power, develops the greatest complexity from the simple [...] Among this multitude might I not discover the primal Plant? There must certainly be one [...] When walking in the Public Gardens of Palermo, it came to me in a flash that in the organ of the plant which we are accustomed to call the leaf lies the true Proteus who can hide or reveal himself in all vegetal forms. From first to last, the plant is nothing but leaf [...]. This idealized, primitive organ became the basis of Goethe's morphology. Croizat's (1961) *Principia Botanica* was in large part a critique of the idealist morphology of Goethe and his modern representative, Wilhelm Troll, that is still taught in all first year botany courses around the world. In this view, the plant is made up of three elements: stem, leaf, and root, and their modifications. Thus Léon Camille Marius Croizat defended botany against Teutonic idealism just as the Roman general Marius defended the republic from the Teutonic tribes that threatened it.

In contrast with Goethe and Troll, Croizat saw the leaf, the stem, and all the other plant (and animal) organs not as pure, irreducible elements, but as endpoints of long lines of reduction and fusion of complex precursors. Following the laws of symmetry that he deduced (Croizat 1961), Croizat proposed that structures with many smaller parts arranged in a high order of symmetry evolve into structures with few, larger parts in five-fold (2/5) and eventually three-fold (1/3) and bilateral (usually flat) (1/2) symmetry. (Arthur, 2002, argued that there is a: *fundamental gap between bilateral and pentaradial symmetry*, but did not seem to be aware of Croizat's, 1961, detailed explanation of how these two symmetries and triradial symmetry are closely linked). The sequence (1-7) given below is a typical morphogenetic trajectory ('morphogeny' in Croizat's terminology) of external organs involving suppression, reduction, and fusion of parts through evolutionary time:

1. Complex branched structure with sporangia.
2. Complex branched structure with fertile parts suppressed.
3. Simpler axial structure with parts fused (often reduced to 5-fold symmetry, e.g. vertebrate limbs,

leaves on a stem, flower).

4. Spine or bilateral organ.

5. Gland (*i.e.* an organ with 'hemmed-in' growth, producing a secretion such as sweat, scent, milk, poison, hormone, haploid reproductive cells, etc.).

6. Color spot.

7. 'Nothing' (at least on the surface).

All stages of this series are seen in many plants but the first two are very rare in most vertebrates, at least without dissection (stage 2 is seen in some fishes). Vertebrates and most animals are generally already much more reduced than plants and as a consequence are notably more glandular. Each morphological step in the series has quite a different function, but all steps are a function of a single morphogenetic trajectory—they are not each the result of separate adaptation, having evolved through selection for their function. Reduction/fusion may also lead to many other specific morphologies with important ecological implications, for example, the retention of a female spore in a sporangium, a crucial development leading to the seed habit in plants. These morphogenetic trends are often interpreted, following Goethe, in reverse order (especially for animals), with complex structures derived from simple ones and something developing essentially from nothing.

Cladistics (morphological or molecular) is not well suited to analyzing morphogenesis, as different morphological stages are seen in different groups and different morphogenies do not necessarily run together, or in congruence with phylogeny—thus many morphologies are simply dismissed as 'mere' homoplasy. In addition, cladistics aims to polarize characters into primitive or derivative, whereas two characters may be alternative states, neither derived from the other. For example, in birds, ground dwellers have flat, straight claws, perching birds have moderately curved claws, and trunk climbers have more highly curved claws (Feduccia, 1996). This is a good example of a trend in which structure determines function. Curved claws are not necessarily derived from straight ones or vice versa—the difference probably goes back to the origin of the tetrapod hand and foot by the same processes of reduction and fusion that are cited above.

Animal genitalia show enormous variation and are often conspicuously variable even in otherwise similar taxa. Rather than examining the origin of the

genitalia themselves (these are classic cases of organs derived by extreme reduction and fusion), panselectionists such as Hosken and Stockley (2004) assume that the genitalia of related forms were similar to begin with and have diverged. Thus, 'compelling evidence' shows that selection is 'clearly a potent force' and is 'the primary force driving genital diversity'. But this whole argument is based on assumption. For example, the authors feel that: *Complicated and divergent morphology is unlikely to have arisen purely for the relatively simple function of sperm transfer.* But in a panbiogeographic view, genitalian morphology has not evolved for sperm transfer (or anything else) at all.

Leigh (1999) argued that: *For Darwin, as for Aristotle, adaptation was the central feature of biological organization. No one who has spent a lifetime studying tropical nature could disagree with them.* This claim, however, represents either willful distortion or simple ignorance of the literature. Many, if not most, of the great tropical biologists, such as Darwin himself, Wallace, Croizat, Richards, Wild and van Steenis have disagreed fundamentally with panselectionism.

Although panselectionism has completely dominated biology since the hardening of the neo-Darwinian synthesis in the 1940s and 1950s, the original authors of the theory of natural selection were much less sanguine about its omnipotence. There is a common misconception that Darwin himself was a panselectionist and that he simply dismissed the 'biological laws' of the morphologist, assuming that natural selection does all the work of adapting populations (Lenoir 1984). Grehan and Ainsworth (1985) have emphasized the importance that Darwin placed not on selection but on prior, orthogenetic 'laws of growth' that exist independent of selection, and Craw (1984) compiled a list of quotations from Darwin's work supporting this. For example, Darwin (1860) wrote that: *We are far too ignorant in almost every case, to be enabled to assert that any part or organ is so unimportant for the welfare of a species, that modifications in its structure could not have been slowly accumulated by means of natural selection. But we may confidently believe that many modifications, wholly due to laws of growth, and at first in no way advantageous to a species, have been subsequently taken advantage of by the still further modified descendants of this species.* Thus, natural selec-

tion only operates on variation produced to begin with by an orthogenetic trend.

Wallace (1889) was also skeptical about the extent of the powers of adaptation; Wake's (2002) claim that he 'remained the ultimate panselctionist' is incorrect. For example, Wallace wrote: *In all works on Natural History, we constantly find details of the marvellous adaptation of animals to their food, their habits, and the localities in which they are found. But naturalists are now beginning to look beyond this, and to see that there must be some other principle regulating the infinitely varied forms of animal life. It must strike every one, that the numbers of birds and insects of different groups, having scarcely any resemblance to each other, which yet feed on the same food and inhabit the same localities, cannot have been so differently constructed and adorned for that purpose alone [...] What birds can have their bills more peculiarly formed than the ibis, the spoon-bill, and the heron? Yet they may be seen side by side, picking up the same food from the shallow water on the beach; and on opening their stomachs, we find the same little crustacea and shell-fish in them all. Then among the fruit-eating birds, there are pigeons, parrots, toucans and chatterers, –families as distinct and widely separated as possible, –which yet may be often seen feeding all together on the same tree; for in the forests of South America, certain fruits are favourites with almost every kind of fruit-eating bird. It has been assumed by some writers on Natural History, that every wild fruit is the food of some bird or animal, and that the varied forms and structures of their mouths may be necessitated by the peculiar character of the fruits they are to feed on; but there is more imagination than fact in this statement [...].*

One of the main themes in Richards' (1952, 1996) classic study of rain forest ecology is a critique of adaptation. Richards suggested that any usefulness in a plant structure is incidental, and not a cause. In other words, structure is the way it is primarily because of prior laws of growth, not because of any advantage. For example, it is often assumed that the red pigments in the young leaves of many tropical trees have an adaptive value; however, Richards (1996) cited recent work giving no support to the view that anthocyanins bestow a selective advantage to the tree, and suggested instead that they may be 'merely

byproducts' in the synthesis of flavonoid compounds in the young leaves. When it rains in tropical lowland rainforest, water on the leaves often runs off the 'drip-tips' of the aristate leaves found in many species there. The adaptationist view is that the drip-tips have evolved in order to facilitate this. Richards (1996), however, cited authors who give a number of reasons why drip-tips probably have little functional importance. For example, some leaves with drip-tips have unwettable leaf surfaces, some species have drip-tips on some leaves and not on others, and some plants with long drip-tips grow in dry environments. (The problem of the leaf and drip-tips is probably the same, structurally, as the problem of the grass lemma and its awn. Both involve interplay of a complex of parts; cf. Croizat, 1961: 994-1000). Richards (1996) concluded that: *The crude teleological 'explanations' [of leaf morphology in tropical rain forest] of the last century are no longer acceptable [this is correct] but there is as yet little to put in their place [this is incorrect].*

Hiram Wild, one of the most distinguished botanists of south-central Africa, also argued against anthropomorphism and teleology in biology and wrote that: *Teleological forms of expression should be avoided* (Wild, 1963). It is hardly surprising that the structuralist psychologist Piaget was manifestly against teleology in his botanical work, for example in his explanation of abscission zones at the base of the branches in *Sedum* (Piaget, 1966).

In one of his many critiques of panselctionism, van Steenis (1969) wrote that: *In this country [U.K.] it may appear blasphemy to say that the study of tropical plants has given my mind little satisfaction that adaptation has played an enormous rôle in the evolution of the plant kingdom, an opinion still strongly held by so many.* Fisher (1936) even declared: *'Evolution is progressive adaptation and nothing else'*. Like van Steenis, many other botanists have felt that: *The plant kingdom is rich in what appears to be non-adaptive evolution* (Juniper et al., 1989).

Gould and Lewontin (1979) provided an amusing critique of panselctionism, which they dubbed 'the Panglossian paradigm'. (Pangloss was the character in Voltaire's satire who felt that "everything was for the best"). Likewise, in a review of optimal foraging theory, Rapport (1991) concluded that optimality models in general are *far too simplistic [...]* [and] *lead to a*

dead end. The results of studies that have been carried out *provide much in the way of counter-examples*.

It has been suggested that: *the ingenious are always fanciful, and the truly imaginative never otherwise than analytic* (Poe, 1986), and there is never a shortage of ingenious teleological explanations to explain any and every biological structure. As Empedocles and Lucretius indicated, rather than function determining structure, structure may determine function. Rather than plants growing in order to reach the light, the ability of some plants to grow upwards and form a strong trunk means that they automatically reach the forest canopy as trees, whether this is beneficial or not. Rather than the giraffe having a long neck in order to reach taller trees, it has a long neck in the first place and does not have much choice as to its diet—it finds it much easier to eat from taller trees. Price (1980) considered thysanopteran males lack wings *so that* they will remain on the host plant for mating; however, Brooks (1981) suggested instead they might remain there *because* they lack wings. In the same way, as we grow older we may lose most or all of our teeth and be forced to change our diet to softer food. Kingdon (1982) noted, reasonably, that *The oryx's dislike for soft, wet ground may be related to the structure of the hoof*. In other words: structure determines function and ecology.

Despite many centuries of debate, there is still much confusion on this topic. Amazingly, in the course of a single review Sussman (1984) suggested both that: *morphological features related to feeding are quite conservative and place constraints on the diet of a species*—that is, structure determines function; and also that: *Tamarins have evolved claw-like nails in order to exploit [gums from trees]. –i.e. required function determines structure*. The argument followed here implies that there is no real adaptation, and that any adaptation is really the result of *pre-adaptation* inherent in parts of a morphogenetic trend. For example, plant families Proteaceae and Myrtaceae are pre-adapted for living in deserts (Raven, 1983). In birds, Charadrii have an aquatic origin as marine or freshwater birds and the arid zone taxa are more recent offshoots. These birds survive in the arid zones of the world through the successful use of adaptations previously evolved in a marine or brackish shoreline habitat, which are thus 'preadaptations' (Maclean, 1984).

In his study of primate evolution Groves (1989) supported *nomogenesis* (i.e. 'evolution by law'), and saw natural selection as 'fine-tuning', eliminating subviable forms, but not creating novelty. In other words: *The organism must make the most of what is 'given' in the best way it can* (Turk 1964, on Arachnida). The evolution of giant cavernicolous arachnids has been *dependent on certain ancient, pre-existent 'predispositions' in the ancestral stock*, and Turk supported *orthogenesis* in Croizat's sense.

Several authors have utilized the idea of 'genetic potential' to account for different degrees of evolution in different groups. For example, in the mountains of tropical East Africa, evolution has been relatively minor in plant families such as Juncaceae, Caryophyllaceae, Cruciferae, Crassulaceae, Labiatae and Rubiaceae, while much more extensive evolution has taken place in Lobeliaceae and Compositae. Mosquin (1971) concluded that differences of this kind could indicate inherent differences in 'evolutionary capacity' in the different groups. Many neo-Darwinians have argued that complete isolation of populations and enough time must eventually lead to speciation, but this is not necessarily true. This will only happen if the populations have enough 'genetic potential' for differentiation, and the levels of this will vary considerably in different groups. Traditionally, genetics assumes that any genetic similarity between populations is due either to similar selection pressure and random mutation, or gene flow, even when this is problematic (for example, the 'puzzling' conclusions of Lessios *et al.*, 2001, who also found: *some remarkable instances of high gene flow between very distant areas*). Parallelism or cladistic homoplasy in character distribution is very widespread in all groups and indicates that parallel evolution is one of the main modes of evolution. Parallel molecular evolution by orthogenetic mechanisms such as molecular drive means that DNA sequences of taxa will stay the same distance apart as they evolve.

The problem of 'parallelism'—how and why do unrelated and sometimes geographically distant plants or animals sometimes have one or more characters in common?—is only a problem if it assumed that taxa are monophyletic. If, because of orthogenesis, taxa develop not just once but many times at many different places from a diverse, widespread

ancestral complex, occasional striking 'parallelism' would be expected. As with the critique of the center of origin and of organs evolving 'de novo', out of nothing, the panbiogeographic view of phylogenesis involves always already diverse ancestral states, rather than a single, homogeneous ancestral state of full presence or absence.

In a similar view, Schwabe and Warr (1984) recognized that traditional theories of evolution are monophyletic in that they: *all start with the Urgene* [a single ancestral gene] *and the Urzelle* [the single ancestral cell] *which have given rise to all proteins and all species, respectively*. Schwabe and Warr took issue with this and argued instead for a polyphyletic view of evolution, in which the prior genetic potential of an entity, not random mutation/selection, is the primary determining factor.

In theory, cladistic analysis claims to stipulate no particular evolutionary process other than descent with modification and cladogenesis (Albert *et al.*, 1992). But in practice, there are underlying assumptions, as indicated. Crawford *et al.* (1992) pointed out that the annual habit may have evolved seven times in one genus, *Coreopsis*. (This is their cladistic interpretation of a pattern in which the annual habit occurs in seven clades). But why assume that the ancestor was either annual or perennial? Why not both? Could not it also have been biennial, etc.? If characters can evolve seven times, why not 7000 times? In other words, evolution probably generally takes place 'on a broad front' (cf. molecular drive – Dover *et al.*, 1993).

Arthur (2002) discussed the possibility that: *developmental reprogramming is, at least in some cases, systematically biased, in that mutation more readily produces changes in certain directions than others [...] Such a state of affairs has been referred to in general as mutation bias or developmental bias [...] Negative biases, both relative and absolute, constitute constraint, whereas positive biases have recently been termed developmental drive (quite distinct from meiotic drive, molecular drive, and dominance drive). Proposals that these biases can potentially lead to the direction of evolutionary change being determined by developmental dynamics as well as by population dynamics are in contrast with the historical thrust of Darwinism and neo-Darwinism, that the di-*

rection of change is determined exclusively by selection. The predominance of certain leaf-arrangement and floral-symmetry patterns in angiosperms have been proposed as examples of bias-led evolution. The fact that all 3,000 or so species of centipede have odd numbers of leg-bearing segments (from 15 to 191) also suggests developmental bias, and in this case an alternative selective explanation is highly implausible. Arthur concluded: Are such examples exceptions to a general rule that selection on its own determines evolutionary directionality, or are they an indication of a general but as yet largely undiscovered role for developmental bias? This is an entirely open and very important question.

The history of biogeography: Earth and life evolve together

As indicated, development of the evolutionary ideas of the early Greek philosophers was stymied by the rise of Aristotelian essentialism and teleology. This block was eventually by-passed, although it took many centuries. The history of the idea that earth and life evolve together is examined next. The history of biogeography is inextricably linked with global exploration, the Scientific Revolution, and the history of biological systematics in general, and these are also reviewed briefly here.

Middle Ages. Following the decline of the Roman Empire, little advance was made in Europe through the Middle Ages in the integrated study of earth and life; however, in Persia the famous Muslim scholar Avicenna (980-1037) described fossil remains of aquatic and other animals on many mountains and explained mountains as effects of upheavals of the crust of the earth (Toulmin and Goodfield, 1965). This was an important development in the history of panbiogeographic analysis, linking earth and life history in a dynamic way.

Fifteenth century. In his classic work on the origins of modern science, Butterfield (1957) suggested that fifteenth century Italian art was an early chapter of the Scientific Revolution; however, an art historian might suggest instead that modern science is a late

branch of fifteenth century art. (Singer, 1959 has a chapter 'Renaissance art versus modern science' pointing out, not very convincingly, all the differences). Bronowski and Maslish (1960) agreed with Butterfield (1957) that the most far-reaching change which grew out of the Renaissance was the evolution of the scientific method of enquiry, and they dated the Scientific Revolution from 1500-1700, rather than the more traditional 1600-1700.

What were the characteristic features of intellectual life in the North Italian Renaissance that led to the development of modern biology and eventually panbiogeography? The Renaissance is often seen mainly as a rediscovery of the Greek and Roman classics, for example, the architect Vitruvius, who lived at the time of Augustus, became an indispensable authority in the Renaissance. He had extolled *eurhythmia*, the repetition of parts, and *symmetria*, putting them in proportion (Huyghe, 1974). This deeply biological approach developed into the overtly anthropomorphic architectural theories of Michelangelo and Palladio. Many authors have played down the idea of the Renaissance as merely classical revival. Pater (1998) stressed instead: *the love of the things of the intellect and the imagination for their own sake* and emphasized the appeal of the novel: [...] *new experiences, new subjects of poetry, new forms of art*. Further, *One of the strongest characteristics of that outbreak of the reason and the imagination [...] which I have termed a mediaeval Renaissance, was its antinomianism, its spirit of rebellion and revolt ...* Renaissance 'artists' such as Alberti, Leonardo, and Masaccio explored maths, geometry, optics, and anatomy in considerable detail and were among the first to *cry out against authority* (Butterfield, 1957).

Nietzsche (1994) also stressed as characteristic of the Renaissance its *liberation of thought, disdain for authority, the triumph of education [...], [and] enthusiasm for science and men's scientific past [...]* Burckhardt (1990) cited: *The intellectual freedom and independence of Florence*. Of the Renaissance authors themselves, Petrarch vigorously attacked: *the pretensions of a philosophical and academic training, proudly professing and asserting his ignorance of such matters*. Leonardo *fought constantly against authority and tradition* and divided thinkers into two opposed groups: *the original discoverers and the*

imitators and commentators (Cassirer, 1963). Argan (1974) wrote that: *the outstanding characteristic of Leonardo's genius lies in his categorical rejection of all 'principles of authority'* (in contrast with, say, the Platonism of Michelangelo). In a similar way, Croizat (1964) would later write that he was: *absolutely impervious to authority unable to demonstrate its tenets on grounds better than authority: whether Aristotle or Darwin [...] a name means a round nothing to me*.

Burckhardt (1990) felt the essence of the Renaissance was not the revival of antiquity, but *the development of the individual and the discovery of the world and of man: Discovering the world and representing it in word and form [...] this investigation and this art were necessarily accompanied by a general spirit of doubt and inquiry [...] when once the dread of nature and the slavery to books and tradition were overcome, countless problems lay before them [the investigators and artists] for solution*. Burckhardt wrote that a comparison of the Italians' achievements in geography and oceanic travel with those of other nations: *shows an early and striking superiority on their part. Where, in the middle of the fifteenth century could be found, anywhere but in Italy, such a union of geographical, statistical and historical knowledge as was found in Aeneas Sylvius [the humanist writer Enea Silvio Piccolomini, later Pope Pius II] –the first who not only enjoyed the magnificence of the Italian landscape but described it down to its minutest details?* Burckhardt concluded that: *Italy, at the close of the fifteenth century, with Paolo Toscanelli, Luca Pacioli and Leonardo da Vinci, held incomparably the highest place among European nations in mathematics and the natural sciences [...]*. Burckhardt (1990) described the zeal: *at an early period for the collection and comparative study of plants and animals [...] King Emanuel the Great of Portugal knew well what he was about when [in 1515] he presented Pope Leo X with an elephant and a rhinoceros. It was under such circumstances that the foundations of a scientific zoology and botany were laid*. Emanuel also presented the Pope with the famous drawing of a rhinoceros by Dürer (Delaunay 1964). Burckhardt acknowledged the relationship of the new attitude to plants, animals and landscape with aesthetic, rather than immediately pragmatic

considerations: *Outside the sphere of scientific investigation, there is another way to draw near to nature. The Italians are the first among modern peoples by whom the outward world was seen and felt as something beautiful [...] Along with the careful cultivation of fruit, we find an interest in the plant for its own sake, on account of the pleasure it gives to the eye. We learn from the history of art at how late a period this passion for botanical collections was laid aside [but not by botanists] and gave place to what was considered the picturesque style of landscape gardening.*

Leonardo's perception that the presence of fossils is an indication of uplift is a good example of the integration of geology and biology in the Renaissance. In a fine essay, Gould (1998) pointed out that Leonardo also recognized the temporal and historical nature of horizontal strata; that rivers deposit large, angular rocks near their sources in high mountains and that transported blocks are progressively worn down in size until sluggish rivers deposit gravel and eventually fine clay near their mouths; that the presence of fossils in superposed layers proves their deposition at different and sequential times; that tracks and trails of organisms are often preserved on bedding planes of strata; that if both valves of a clam remain together in a fossil deposit the animal must have been buried where it lived, for any extensive transport by currents after death will disarticulate the valves; that no marine fossils have been found in regions or sediments not formerly covered by the seas; and that the elevation of strata with fossils must represent a general and repeatable feature of the earth's behavior, not an odd or anomalous event.

Sixteenth century. At the beginning of the sixteenth century both the Roman Church and the Holy Roman Empire were under attack and it is surprising that amid the political, social and military turmoil any real cultural advances were made. It was a dangerous time for writers. Bruno, Dolet, and Paleario were burnt at the stake. Berni was poisoned for refusing to take part in a plot to poison a cardinal. Ferreira died of the plague. Nevertheless, a tremendous revolution took place in art, science and literature, and the modern era is often dated from this time. Associated with the new attitude of disdain for mere authority already

referred to was the frequent use of satire by sixteenth century writers such as Quevedo, Régnier, and Marot. Aretino is well-known for his wit and impudence, and Rabelais' *Gargantua and Pantagruel* includes much mockery – it is the work of *the authentic scholar who ridicules scholarship* (Cohen in Introduction to Rabelais, 1974). There are obvious parallels with Croizat's style. (Delaunay, 1964 noted that it took a Rabelais to relegate unicorns, harpies, seleucid and stymphalid birds, and satyrs to the 'Land of Satin').

Along with the new attitudes, new practical developments facilitated the intellectual revolution. Gutenberg invented printing by moveable metal type in the middle of the fifteenth century and by the start of the sixteenth century practically every country in Europe had its own press: there were nearly 80 in Italy, 64 in Germany, and 45 in France (Hay, 1968). Once printing began, the total repression of books previously carried out by bishops or inquisitors became almost impossible. Another key practical development was oceanic navigation. In 1519 Cortés left Cuba to conquer Mexico, and in the same year Magellan left Spain to reach the east by sailing west. Magellan's men subsequently brought back the first bird of paradise seen in Europe. By the second half of the sixteenth century reasonably accurate maps of the explored regions of the globe appeared through the work of Ortelius and Mercator. As Hall (1968) wrote: *the men of the sixteenth century were confronted by a world extending from the northern tundra to the South African Cape, from the east to the West Indies.* They knew the Pacific as well: in 1516 the Dutch Schouten and Le Maire sighted the New Guinea islands Manus and New Ireland. In 1568 Mendaña discovered Santa Isabel in the Solomon Islands and later (1595) settled there, on Santa Cruz. Through the sixteenth century naturalists and explorers discovered the incredible biodiversity of the tropics. For example, in the New World Orellana made the first trip down the Amazon (in 1542), Oviedo y Valdez, based at Santo Domingo, produced the first account of natural history in America (in 1550), and Monardes, a trader in Seville, described the medicinal plants of the West Indies (from 1565-1574; Debus, 1978). Working at Goa and Bombay, the Portuguese physician Garcia de Orta produced a classic work (in 1563) on the medicinal plants of India.

In botany, the first revolution in plant description occurred in the sixteenth century: *when the tradition of scientific botany began* (Jacobs, 1980). Singer (1959) argued that Botticelli was the first painter of plants in modern times. Over thirty species can be detected in his famous 'Primavera' (1478), which is "largely a botanical study". Albrecht Dürer's (1503) 'Das grosse Rasenstück' is a painting of plants only, done with such 'scientific' accuracy that: *the species are easily recognizable* (Jacobs, 1980). Singer wrote that these two were the only serious rivals Leonardo had in plant illustration. He also pointed out that Leonardo's studies of human anatomy were at least a century in advance of their time. Leonardo also made observations on comparative anatomy, for example in his illustrations showing the homologies of the leg in horses and humans. One of Leonardo's discoveries can serve to illustrate the depth of his biological insight. Rather than simply assuming that the way in which the leaves are arranged on a stem (phyllotaxis) is adaptive and for the best, he was the first to actually describe the standard pattern of leaf arrangement, in the same way that he might have analyzed the structure of a crystal. He observed that in many species the leaves occur in cycles of fives, with the sixth leaf – the first in the next cycle – standing above the first leaf. This arrangement is referred to in botany as the phyllotactic mode of '2/5'. Croizat (1961: 634) seems to have been the only writer to have noticed Leonardo's discovery of this key pattern. (Gould, 1998 has pointed out the curious neglect of Leonardo's notebooks).

Bronowski and Maslish (1960) suggested that Leonardo: *found nothing that we should now call a scientific theory, because he lacked the gift to isolate those abstract concepts – gravitation, momentum, energy – in which science seeks the unity under the chaos of natural phenomena*. Leonardo's observation on phyllotaxis may or may not be a scientific 'theory', but it definitely does isolate unity under apparent chaos. The predominance of this phyllotactic pattern in vegetation throughout the world has still not been properly explained by mainstream botanists, but Croizat's (1961) massive analysis of it and comparison with five-fold symmetry in, for example, the flower and the hand, has hardly begun to be studied (Heads, 1984).

In fact, Leonardo's is not the only Renaissance biology to have been overlooked – the whole field has been neglected. For example, Hall (1966) suggested that the biological and medicinal science of the sixteenth: *consisted of little more than herbalism and the endeavor to cure disease* and that: *the sixteenth century naturalists contributed little new* (Hall 1968). This view seems incorrect, but widely established; Ashworth (1990) observed that natural history in general: *occupies a shallow niche in most accounts of the Scientific Revolution [...] The implication [...] is that natural history played no formative role in those collective developments that we call the Scientific Revolution [...] the period between 1560 and 1660 is either ignored or belittled*. Likewise, Schmitt (1975) wrote that: *recent historiography of science has tended to see in the development of physical sciences the model by which other intellectual movements are to be judged. Nevertheless, there is an equally good reason to see medical and biological sciences as an important facet of the development of modern civilization and one which has its own internal logic [...] In botany we have, I think, one of the most important points of university scientific development of Renaissance Italy. This was the science **par excellence** which emerged from oblivion during the sixteenth century to become a growth point [...] The first separate chair of botany was established at Rome in 1513, but it seems to have been rather short-lived and did not exert any significant influence [...] A few years later we find other botanical chairs being founded with greater effect. These include Padua (1533), Bologna (1534), Ferrara (1543) and Pisa (1544)*.

In the magical year 1543 a translation of Archimedes appeared (Hall, 1968 suggested that the modern history of mathematics might be dated from this event), Copernicus published his famous book on astronomy, working at Padua Andreas Vesalius laid the foundations of anatomy in his *De Humani Corporis Fabrica* (the figures have been attributed to a member of Titian's school), and the first botanical garden was founded, in Pisa, by Luca Ghini (1490-1556) (it was paid for by the Medicis). Others, such as Wightman (1962), have suggested that the first botanic garden was the one at Padua, founded in 1542, but Whewell (1967) wrote that this was founded in 1545. In any case, it is interesting that

both the Padua and Pisa gardens were associated with universities, and Schmitt (1975) has pointed out that Renaissance biology and medicine (unlike the physical sciences) advanced nearly wholly within a university context. Botanical gardens were established at Florence and at Bologna (by Aldrovandi) in the 1550s (Schmitt, 1975 says 1568) and at the Vatican in the 1560s. Beyond the Alps, similar gardens were established at Leiden by Lécluse (1577), at Leipzig (1580), and at Montpellier by Henry IV (1597). Before the end of the century such gardens were relatively common.

Luca Ghini held one of the first chairs of botany, at Bologna, in 1534 and later moved to Pisa. None of Ghini's publications are known, but as well as establishing the botanic garden, he and his pupils pioneered the use of the herbarium. The earliest record is in 1551 when Ghini sent some specimens to Mattioli, but the oldest extant herbarium is that of Ghini's student, Gherardo Cibo, who started collecting in 1532 (Wightman, 1962). Among Ghini's students destined for future greatness were Cesalpino (1519-1603) and Aldrovandi (1522-1605). They made collections of dried plants, remains of which are still in existence (Singer, 1959) and some of Aldrovandi's natural history collections can be seen at the University of Bologna. Schmitt (1975) observed that: *already in the middle of the sixteenth century we find that specific field trips were being made, not only privately, but as extensions of university courses in botany* (Schmitt quoted an interesting itinerary for one such trip in 1557 from Aldrovandi's autobiography).

The Swiss Gesner (1516-1565) and Aldrovandi (*the most underappreciated naturalist of the early modern era*—Ashworth, 1990) were the most well-known of the new 'encyclopedist' biologists. Gesner wrote a huge work on animals including literally everything ever written about them, as well as much new information (e.g. an illustration of a bird of paradise). (The materials for his unpublished companion work on botany were only discovered in 1929 in Erlangen; in 1994 Isely wrote that they were being prepared for facsimile publication). The first systematic bibliography of any kind was Gesner's *Bibliotheca Universalis* (1545) (Hay, 1968). Whewell (1967) argued that: *Gesner saw the peculiar importance of flower and fruit, and that the botanical concept of genus is due mainly to his work*. In the sixteenth century: *The Alps*

came to be looked upon as the haunt not of unknown terrors but of unknown beauties, to be attained by human stamina and enterprise. Gesner was the pioneer of alpinism and the botany of high altitudes (Wightman, 1962). The exploration of pastoral themes in sixteenth century literature was a parallel development in the arts. Aldrovandi began to teach botany at Bologna in 1556 but about 1560 the name of the chair was changed to 'Lecturer in fossils, plants and animals'. He published a vast, 'improved' version of Gesner's *Historia Animalium* and paid more attention to anatomical features in arriving at a classification. Ley (1968) has reproduced one of his modern-looking pages of illustrations, showing many species of grasshoppers. Among the other zoologists were Guillaume Rondelet (1507-1566), who worked on marine animals, and Pierre Belon (1517-1564), who wrote a *History of Fishes* (1551) and a *History of Birds* (1553), and whose illustration comparing the skeleton of a bird with that of a man is still often reproduced.

Andrea Cesalpino ('Caesalpinus') took over the directorship of the Bologna botanical garden from Aldrovandi. Later he was professor at Pisa and finally became physician to Pope Clement VIII. (He is credited by Italian authors—but not the English—with having discovered the circulation of the blood). His 1583 work *De Plantis Libri XVI* is the first attempt to arrive in a truly scientific way at a classification of the known plants. It also marks the transition from herbals, accounts of useful plants, to floras, accounts of all known plants, whether useful or not (Isely 1994). This fundamental revolution in method and approach represents the beginning of systematic botany. Linnaeus (as quoted in Whewell, 1967) called him 'Primus verus systematicus', the first true systematist, but he is strangely overlooked by most biologists. Cesalpino summarized his work: *Since all science consists in the collection of similar, and the distinction of dissimilar things, and since the consequence of this is a distribution into genera and species, which are to be natural classes governed by real differences, I have attempted to execute this task for the whole range of plants* (quoted in Whewell, 1967). He classified the plants according to properties of their fruits and seeds and also considered ecology, citing, for example, ultramafic endemism in Italian plants

(Brooks, 1987). Bremekamp (1952) wrote that Cesalpino's writings towered above all that had been written on the subject before, and for the next hundred years no-one seems to have understood him.

Soon after Cesalpino and Aldrovandi had initiated systematic biology, the center of gravity of biological research moved north of the Alps. Clusius (Lécluse) (1526-1609) described as: *The greatest botanist at the beginning of the modern era* (Wolf, 1935), succeeded Dodoens in the chair of botany at Leiden, and at the time of his death Leiden had become the botanical center of Europe (Isely, 1994). Thus, by the end of the sixteenth century there were university professors of biology, biology courses with field trips on which plants were collected to be grown on in botanic gardens or preserved in herbaria, and surprisingly modern-looking illustrated accounts of faunas and floras.

Seventeenth century. After the sixteenth century it is no longer possible to talk about the arts in the traditional sense, as the world became dominated by one branch of northern Italian Renaissance art: science. The artist van Ruisdael (1628-1682) is famous for his paintings of landscapes and trees, but is also recognized as a precursor of the science of tree architecture (Ashton *et al.*, 1982). Since their architecture is rendered so accurately, many of the trees in his paintings are perfectly recognizable.

Harvey studied at Padua and his account of the circulation of the blood (1628) is often taken to mark the full arrival of the Scientific Revolution (although, as suggested here, this date is probably too late). According to Hall (1983): *Harvey's great merit was to re-order known but misunderstood facts and observations.* Harvey resembled Copernicus and Galileo in insisting upon a new view of what people thought they already understood – it looks as though the sun moves and the earth stands still, but Copernicus' system turned this on its head. This breakthrough was often used by Croizat as a metaphor for panbiogeography; it seems obvious that physical movement should be the means by which biotic distributions are formed, but paradoxically movement has little to do with the process, which depends more on evolution.

Cesalpino's *Flora* had treated all plant species, not just the useful ones. In *'The sceptical chymist'* (1661)

Robert Boyle argued in a similar way that chemistry should be studied for its own sake, to gain an insight into nature and not merely to make gold or medicines. Boyle criticized the current concepts behind the terms 'element' and 'principle', and instead supported atoms. Likewise, Croizat showed that the fundamental elements of twentieth century biology, such as the Goethian leaf or Wallace's biogeographic 'regions', were unsatisfactory and could be analyzed into distinct components. In this connection Croizat often cited Lavoisier's crucial demonstration in the eighteenth century that water, assumed for millennia to be an element, is actually a compound.

Like Avicenna and Leonardo, cited above, the seventeenth century writers Steno (= Steensen, Stenonis in latin, a Dane resident in Florence) and Hooke also realized the significance of fossils. Hooke wrote that fossils in inland mountains imply that: *a great part of the surface of the earth hath been since the creation transformed [...] parts which have been sea are now land; and diverse other parts are now a sea which were once a firm land; mountains have been turned into plains and plains into mountains and the like* (quoted in Toulmin and Goodfield, 1965). This is a truly dynamic theory of geological change, although Hooke had to try and compress geological history into a much reduced time scale.

Eighteenth century. Kant, in a 1753 dissertation, gave the first systematic, evolutionary account of cosmic history and was the first to talk of a past of millions of years (although after the death of Frederick the Great, Kant was forced to retract this). The possibility of intercontinental vicariance was also being discussed by this time. In 1769 Gilbert White answered a correspondent as follows: *The question that you put with regard to those genera of animals which are peculiar to America, viz. how they came there, and whence? Is too puzzling for me to answer; and yet so obvious as to often have struck me with wonder. If one looks into the writers on that subject little satisfaction is to be found. Ingenious men will readily advance plausible arguments to support whatever theory they shall choose to maintain; but then the misfortune is, everyone's hypothesis is each as good as another's, since they are all founded on conjecture. The late writers of this sort, in whom may be*

seen all the arguments of those that have gone before, as I remember, stock America from the western coast of Africa and the south of Europe; and then break down the isthmus that bridged over the Atlantic. But this is making use of a violent piece of machinery: it is a difficulty worthy of the interposition of a god! (White, 1977).

In the dispersalist tradition of African biogeography, everything originally migrated into Africa from the north, as inferior, primitive forms were forced out of Europe by new, competitively superior ones. Despite the widespread acceptance of this account, an alternative view has existed for over 200 years. Already in the eighteenth century there were suggestions of biogeographic affinities between the Cape region of South Africa and Australia (Willdenow, 1798, as cited by Weimarck, 1934). This affinity among southern lands is totally unexpected in the orthodox explanation. Weimarck (1934) wrote that: *As far as I am aware, Willdenow was the first scientist who assumed the occurrence of ancient land connections between south-hemispheric countries. In virtue of the relationship between the flora of the respective regions he (Willdenow, 1798, 430) says that New Holland [Australia] was once connected with the Cape and the Island of Norfolk with New Zealand.* Many texts on the history of systematic biology (e.g. Lomolino *et al.*, 2004) begin with Linnaeus' and Buffon's work in the eighteenth century, but this is a very late date to start with, and Linnaeus' work is usually only emphasized because of its importance for binomial nomenclature – a relatively minor aspect of systematics. (Linnaeus' attempts at a natural classification are usually overlooked). For Linnaeus, all species originated as a single pair (or a single hermaphrodite) and all genera originally consisted of one species (Larson, 1971). (This probably derives from the biblical account of the original parent pair, Adam and Eve in Eden). This idealist view was subsequently accepted, sometimes, it seems, almost unconsciously, by Darwin, the neo-Darwinians, and the cladists. It contrasts strongly with the panbiogeographic view of the origin of new taxa in which polymorphic ancestral complexes evolve over a broad front in 'phases of modernisation' (cf. Heads, 1985) and there is no point phylogenetic 'center of origin'. This is discussed further below.

In his '*Histoire Naturelle*' Buffon (1749-1788) described seven epochs of earth history. In epoch 3, the continents were covered with water, in 4, the oceans withdrew and there was volcanic activity, in 5, tropical animals spread across whole earth, and in 6, the continents separated. Note that the sequence of 5 and 6 suggests a vicariance model, and at one point Buffon wrote: *'To account for the origin of these animals [mammals] we must go back to the time when the two continents were not yet separated* (Buffon, 1766, *Histoire Naturelle* vol. 14, quoted in Hull, 1967 and Papavero *et al.*, 2003); however, Matthew's ideas on the 'Holarctic' center of origin for all the main groups can also be traced to Buffon's belief in the northern origin of the great mammals (Matthew, 1915: 178; Croizat, 1958, 1: 650). Croizat quoted Buffon (1779): *All the watery, oily and ductile components which must enter into the composition of organized beings have fallen with the waters on the northern parts of the globe, earlier and in much greater quantity than on the southern parts.* Croizat summarized Buffon: *When it got colder in Holarctis, the major animals migrated southwards, but were stopped on their way by the highlands of Panama. Therefore, South America is inhabited to this day by mammals that are puny by contrast with the boreal forms.*

Nineteenth century. The work of Hegel (1770-1831) on the philosophy of history is perhaps the most widely discussed of any in modern Europe and must have influenced Darwin's ideas on materialistic evolution, whether consciously and directly or not. For example, both Hegel and Darwin strongly supported the idea of *progress* in evolution. However, the Hegel/Darwin relationship is usually overlooked. In a typical example, Hegel is simply not mentioned in Desmond and Moore's (1992) otherwise excellent book, even though Desmond has written a book (1989) about the pre-Darwinian generation, and Moore has contributed a 1991 article 'Deconstructing darwinism: The politics of evolution in the 1860s'. Nevertheless, Desmond and Moore's book provides important background information on the question. From the beginning of his academic life, Darwin was around people who must have been aware of the developments in 'historical' thinking on the Continent. Darwin relied on Lyell who in turn acknowl-

edged the stimulus from the new school of critical historians, for example Niehbuhr, active in Berlin around 1810. The '*Origin of species*' was a late phase in this development of historical analysis. Darwin's early mentor in the 1820s, the sponge expert R. Grant, was known as a 'radical' and had visited universities in France, Germany, Italy and Switzerland, but in Desmond and Moore's (1992) book there is no mention of Hegel or indeed any European philosopher, apart from the biologists Lamarck and St. Hilaire who are always cited in books on Darwin. In 1836 Darwin met Owen, who was synthesizing German ideas on the forces regulating life and growth. Darwin's philologist relative Hensleigh studied the laws by which alphabets change and: *praised the Germans for understanding the organic development of language*. All Darwin's family: *were interested in German biblical criticism and language studies* and in 1837 *Politics, science and literature were all of a piece* in the conversation at Darwin's home. It would be strange if Hegel's ideas had not been discussed there.

So why has the Hegel-Darwin connection been overlooked? Everyone always cites the English influences, such as Spencer, Malthus, and Erasmus Darwin, but the only writer I know of to have linked Darwin directly to Hegel is Nietzsche (1910: sect. 357), who noted that with Hegel's work: *the thinkers in Europe were prepared for the last great scientific movement, for Darwinism –for without Hegel there would have been no Darwin [...]*.

What are the fundamental principles of Darwin's biogeography? Darwin wrote: *We are thus brought to the question which has been largely discussed by naturalists, namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the vera causa of ordinary generation with subsequent migration, and calls in the agency of a miracle.* (Darwin, 1971). Darwin gave no actual evidence to support the idea of a point center of origin, arguing merely that the simplicity of the idea 'captivates the

mind'. It probably derives from the earlier views of Linnaeus and others. Darwin's claim that: *He who rejects it [...] calls in the agency of a miracle* is obviously just propaganda –an aggressive feint designed to put off any closer examination of an argument that is very weak but fundamental in his synthesis. As Matthews (1971) noted in his introduction to the *Origin of Species*: *It is surprising how much of the book is given to arguments based on entirely suppositious premises [...]*.

A necessary corollary of a point center of origin is a process by which a biological form can spread out. Here Darwin invoked the physical movement and 'means of dispersal' so well-known in plants and animals, and 'chance dispersal' to account for difficult cases. Darwin's biogeography is thus based on a point center of origin and chance migration. On Chonos Archipelago in Chile, Darwin reported that a 'singular little mouse' was common on some islands but not on others. This led Darwin: *to wonder why colonization was such a serendipitous affair*. This is a classic example of Darwin as a good observer but an indifferent analyst. Why assume that the pattern was random? Why wonder about 'serendipity'? Why not actually work out the problem with reference to data on distribution, phylogeny, and ecology?

Desmond and Moore (1992) also provided useful information on Darwin's thinking on altitudinal distribution and the effects of uplift on biological communities. Darwin observed that the horizontal tree-line in Tierra del Fuego *looked like the 'high-water' mark on a beach*. At this time he was starting to realize the occurrence of geological uplift and soon he understood that the uplift of the Andes had been gradual and recent. But he remained obsessed with uplifted fossil beds and overlooked the living 'strata' that have also been raised. At 13 000' in the Andes, even though he felt himself in 'another world' biologically, fossils were still his over-riding interest. He never established any real integration of uplift and biological evolution. Even after the Concepción earthquake, when he observed freshly uplifted mussel beds with all the mussels having died, he overlooked the potential effect on terrestrial species that have been uplifted and survived.

Darwin held the idealist view that all taxa (and life itself) have originated only once, at a single morpho-

logical and biogeographic point, from which they spread. The importance of groups such as the species of Darwin's finches on the Galapagos was that they appeared to be derived from a single phylogenetic point (a single immigrant species) and a single geographic point, to produce an 'adaptive radiation'. But how could a species ever change if there was constant immigration? With this, Desmond and Moore (1992) wrote, Darwin was thrown back on the single, chance event – a 'few, stray colonists'. The botanist Joseph Hooker wondered, if this was a general principle, why some islands should have high endemism while others – he cited the Falklands and Iceland – should have none. In fact, Hooker disagreed strongly with Darwin on the significance of 'means of dispersal' and instead favored changing geography as an explanation for biogeographic affinities, for example, those linking Tasmania and Fuegia. Similarly, Edward Forbes supported a former continent: Ireland-Portugal-Azores to explain plant distribution in this region. Desmond and Moore agreed that Darwin's treatment of 'chance' was unsatisfactory. They wrote: *As chance crept into the picture [...] Darwin resorted to haphazard variations [...] But Darwin remained muzzy on the subject and never really let go of his harmonious law-based system. Sometimes he viewed 'chance' as the unintentional intersection of causal chains, an idea woolly enough to allow any number of accommodations. At others he spoke as deterministically as Martineau [...] It was the making of future confusion.* (Emphasis added).

Nietzsche (1955) named Darwin, John Stuart Mill and Herbert Spencer in his scathing reference to: *respectable but mediocre Englishmen [...] What is lacking is genuine power of intellect, genuine depth of intellectual perception.* One of Darwin's main achievements was to actually analyze much of what had previously been regarded as miraculous, for example, seeing instinct as unconscious memory, or the morphology of groups such as vines as the result of 'laws of growth'. But he created confusion by replacing the miraculous in evolution and biogeography with, respectively, teleology and chance.

Darwin did not write a great deal on biogeography (two chapters in the *Origin of Species*, parts of the *Voyage on the Beagle*), although what he did write was, of course, extremely influential. Wallace, on the

other hand, did write extensively on biogeography, but his views are quite varied and he changed his mind on many aspects. (In many ways modern dispersalism is a more direct reflection of the work of Matthew (1915), who simplified and codified certain aspects of Darwin's and Wallace's thought into a rigid dogma).

In his book on the Malay Archipelago, Wallace (1962) wrote: *There is nothing that geology teaches us that is more certain or more impressive than the extreme instability of the earth's surface. Everywhere beneath our feet we find proofs that what has land has been sea, and that where seas now spread out has once been land; and that this change, from sea to land, and from land to sea, has taken place not once or twice only, but again and again, during countless ages of past time. Now the study of the distribution of animal life upon the present surface of the earth causes us to look upon this constant interchange of land and sea – this making and unmaking of continents, this elevation and disappearance of islands – as a potent reality, which has always and everywhere been in progress, and has been the main agent in determining the manner in which living things are grouped and scattered over the earth's surface. And when we continually come upon such little anomalies of distribution as that just now described [the Sulawesi fauna], we find the only rational explanation of them in those repeated elevations and depressions which have left their record in mysterious, but still intelligible characters on the face of organic nature.* Thus, in 1869 Wallace explained the anomalies in the fauna of Sulawesi with reference to past connections with Africa and the Mascarenes ('Lemuria', a forerunner of 'Gondwana'); however, by the time he wrote his *Geographical distribution of animals* (1876) and *Island life* (1881) he had fallen under the spell of Darwin's views on dispersal, and decided that the continental outlines have remained essentially the same. (In the 10th edition of *The Malay Archipelago* (1890) he needed to add the footnote to the passage quoted above: *I have since come to the conclusion that no such connecting land as Lemuria is required to explain the facts*). This was the beginning of the long detour of 'continental stability' and Matthew's 'zoogeography'; however, before Matthew reaffirmed Wallace's views, these were subject to some searching criticism.

Von Ihering (1892) wrote on Pacific biogeography and followed the New Zealand zoologist Hutton (1872) in differing from Wallace in 'very essential points', notably the extent of former southern land connections. As for Wallace's core doctrine of the 'permanence of oceanic and continental areas', Von Ihering wrote: *I am as much convinced of the erroneousness of this doctrine [...] as I am that the ideas of Darwin and Wallace on 'natural selection' as the cause of the origin of species will have but a historical interest in the coming centuries. Mr Wallace's supposition that land and fresh-water mollusks, lizards, &c., were distributed over the whole Pacific Ocean by the waves of the sea I think to be more than bold [...] I agree with Professor Hutton in thinking that an ancient land-communication must have existed between South America and New Guinea, Australia, &c., to account for the close relations between the two territories in flora and fauna [...] Mr Wallace's explanation of the distribution of Lacertidae through Polynesia as far as the Sandwich Islands [Hawaii] by means of a migration across the ocean is just as bold a hypothesis as his attempt to explain the occurrence of identical fresh-water fishes in New Zealand and Patagonia by the transport of their fry on icebergs. To such theories may those adhere who wish to save Wallace's hypothesis of the stability of the continents and depths of the seas; but one cannot ask unprejudiced scientists to accept such incredible explanations.*

Von Ihering was strongly supported by the bryologist Müller (1893), who cited the baobab genus *Adansonia* in Africa and Australia: *the question, From which of these two points did the type originate? has lost its sense. Australia did not receive it from Africa, nor did Africa receive it from Australia – it is autochthonous in both places [...] the enigma cannot be explained by migration, for that necessarily includes the idea that the reproduction of the type was successful in one place only. This always makes on me the same impression as the idea of explaining the origin of organisms by deriving them from some other globe. What is gained by it? Nothing else but that the cause of origin is put further back; for, after all, one is obliged to ask, Where did the organisms of that strange globe come from? [...] With such explanations one wanders without knowing it in a circle, if one does not wish to arrive at the absurd conclu-*

sion that the creation of organisms was possible on one globe only. It is the same with migrations. I do not deny them when they are opportune, and I know very well that wind and weather, animals and men, are able to distribute species sometimes over large areas; but it is quite a different thing when we have to deal with whole floras, sufficient to impress one district with the stamp of another [...] so that one cannot be understood without the other. This cannot ever have been accomplished by a migration of a mechanical nature.

Twentieth century. The beginning of the twentieth century saw the critique of Wallace extended and the development of early panbiogeography. Croizat's (1958) main work is probably better known for rejecting the biogeography of Wallace, Matthew and their followers, but it also acknowledged the work of important, but largely unknown, workers in panbiogeography, such as the bat specialist K. Andersen, the ichthyologists C. Tate Regan and C. H. Eigenmann, the herpetologists T. Barbour, D. Cochran and H. W. Parker, the entomologists J. A. G. Rehn and G. Marcuzzi, and many others.

Ortmann (1902), for example, writing on Crustacea, concluded: *It is incorrect to regard the creation of a scheme [of regions] of animal distribution as an important feature or purpose of zoogeographical research. Thus we are justified in saying that zoogeographical study, as introduced by Wallace [and Sclater], is not directed in the proper channels [and results in] fruitless discussions on the limits of the different zoogeographical regions.* Ortmann considered it: *entirely a matter of indifference whether we accept any regions or not*, predicting later panbiogeographic treatments of 'biogeography without area' (Henderson, 1990). Instead: *the chief aim of zoogeographical study consists – as in any other branch of biology – in the demonstration of its geological development.* This is exactly the panbiogeographic approach. Likewise, White (1965) wrote that: *It seems to the author that recognition (and naming) of centers of endemism, which may occupy a small or large proportion of the total area of the Domain, and which may or may not overlap with other centers, provides a much truer picture of the chorological pattern than does the division of a Domain into wa-*

ter-tight units. As for the many distributions which do not conform with present topography and the usual biogeographic regions, Ortmann wrote that: instead of leaving them out of consideration we know that just these cases are the most interesting, since they demand closer investigation. In most cases we find that these instances of 'abnormal' distribution are to be traced back into the geological past in order to be properly understood [...] In many respects we have found a wonderful agreement between the distributional facts and what is known of the geology and tectonics of the respective parts.

Andersen (1912) concluded on Megachiroptera as follows: *The evidence afforded by the geographical distribution of Bats has generally been considered of doubtful value; hence they have either been entirely excluded from the material worked out by zoogeographers or at least treated with pronounced suspicion, as likely to be more or less unreliable documents of evidence. This unwillingness or hesitation to place Bats on an equal zoogeographic footing with non-flying Mammalia would seem to be due partly to the preconceived idea that owing to their power of flight Bats must evidently have been able easily to spread across barriers [...]. This may in theory appear plausible enough, but when tested on the actual distribution of the species and subspecies it proves to be of much less importance than commonly supposed; it rests, in reality, on a confusion of two different things: the power of flight would no doubt enable a Bat to spread over a much larger area than non-flying Mammalia, but, as a matter of fact, only in very few cases is there any reason to believe that it has caused it to do so [...]. Rather, local differentiation: tends to show that the present distribution of Megachiroptera has not been influenced to any great, and as a rule not even to any appreciable, extent by their power of flight; if it had, the Fruit-bat fauna of one group of islands could not, so commonly as is actually the case, differ from that of a neighboring group or continent, and the tendency to differentiation of insular species or forms would have been neutralised by the free intercourse between neighbouring faunas. Andersen, for example, recorded that of the 12 fruit bat genera in West Africa 9 are endemic there, and in modern times, Kingdon (1974) observed a: surprising degree of correspondence*

between some bat distributions and those of other mammals within the continent. In New Guinea, bats show a major distribution break at the craton margin (Heads, 2001a, 2002b) like that of many other groups.

Eigenmann (1921) argued that the freshwater fish fauna of Ecuador and its affinities with eastern South America antedate the Andes: *It is quite within reason, therefore, that the present fish-fauna of the Guayas [Ecuador] did not come from the east across a barrier but that at a time preceding the origin of the present species a section of a continuous fauna was segregated from the rest by the formation of the mountainous screen between them. Also writing on freshwater fishes, Tate Regan (1922) disagreed with both continental permanence and northern centers of origin, concluding that: in early Cretaceous times South America and Africa formed one continent, which must have extended to India [...] The alternative view, that the Ostariophysi originated in the north and spreads southwards, involves so many improbabilities as to be almost unbelievable.*

In stark opposition to these early panbiogeographers, Matthew's (1915) work (cf. Bowler, 1996 for a review) reaffirmed the core tenets of Wallace's biogeography, especially: *The permanence of the great features of the distribution of land and water on the earth's surface* (Wallace, 1998). In Wallace/Matthew biogeography, a Bering Land Bridge is accepted in the north, but land bridges in the south are either unacceptable, or if accepted, as they were after the 1960s, are deemed too old to be relevant.

The second axiom of Wallace and Matthew is that most forms of life have originated in northern centers of origin ('Holarctis'), Darwin's: *great evolutionary workshops of the north*. From here, new, superior life forms (Matthew's 'higher types') have driven out inferior forms southwards. Matthew wrote that the: *principal lines of migration [...] have been radial from Holarctic centers of dispersal* and reviewed all the orders of mammals, as well as many reptiles, birds and fishes to prove that all originated in Holarctis. (The base map he used, centered on the North Pole, is the same as that used in the United Nations symbol). Any resemblance between, in particular, African and South American forms cannot be direct, and must be due to extinction in the north or parallelism. The 'ape/man' skull from South Africa discovered by

Dart implied that Eurasia was not the center of origin of *Homo*, and so was greeted for many years with simple disbelief, eloquent testimony to the influence of Matthew's theories. Modern concepts such as massive groupings of African mammals (Afrotheria) and Australo-Papuan passerines are equally incompatible with the idea of the Holarctic origins of everything; these groups evidently do not, as was formerly thought, comprise many unrelated end-points of northern lineages.

A third component of the Matthewian synthesis is the belief that climate change is crucial for biogeography. As his title '*Climate and evolution*' indicates, Matthew (1915) argued that climate change has been an important factor in the evolution of the vertebrates and is the *principal known cause* of the distribution of the land vertebrates. Later authors have followed his lead in attributing many aspects of biogeography to the effect of the Pleistocene Ice Ages and this was, for example, the basis of the 'refugium theory' of biogeography. Croizat was opposed to this chronology and argued at length that the Pleistocene was much too late to have played an important role in shaping major aspects of distribution, although it has locally modified ranges and caused much extinction. This view has been repeatedly vindicated over the last decade or so and it is now widely accepted that the evolution of modern groups is the result of earlier events. For example, in a study of rainforest faunas, Moritz *et al.* (2000) found that: *in most cases, the divergence of extant sister taxa predates the Pleistocene*, and Voelker (1999) concluded that: *the Pleistocene may have had little effect in generating modern species*. Other references are cited in Heads (2001a: 918-919).

Perhaps the greatest early exponent of panbiogeography, Knud Andersen, died in World War I early in his career and amid the upheavals of this time Matthew's (1915) work criticizing Andersen (1912), Ortman (1902) and others, found little opposition. Matthew's book capitalized on the fascination of the American public with vertebrate paleontology which had existed since the time of Thomas Jefferson's exploits and became the most influential text in the history of biogeography. Its ideas were promulgated by Simpson, Mayr, Darlington and others, forming what Croizat (1958) labelled the 'New York school of zoo-

geography' (cf. Croizat, 1984; Nelson and Ladiges, 2001; for some reason Nelson and Ladiges did not include Mayr in the school). Simpson (*in litt.* 3 April 1959 to Croizat) denied that such a school existed, and claimed that Darlington: *is known as the strongest opponent of Matthew's views* (emphasis in original). This is inaccurate; for example, Darlington (1959: 488) wrote that: *after the two chapters on geographical distribution and parts of other chapters in Darwin's Origin of Species the next really important treatment of the subject was by Matthew (1915)*.

The New York school was adopted as the 'official' biogeography by the architects of the 'Modern Synthesis' of evolution, Mayr, Simpson and Jepsen. These three formed the core of the Committee on Common Problems of Genetics, Paleontology and Systematics, established in 1943. As a result of their strong partisan support of certain ideas, Schwartz (1999) wrote that: *alternative theories, which had kept the possibility of intellectual novelty alive through the debates they provoked, were submerged. The synthesis that emerged [e.g. Jepsen, Mayr and Simpson, 1949] was, by stark contrast, largely intolerant of criticism and resistant to change*. The dogma of this group on evolution in space and time was Matthewian, and on evolution of form it was strictly panselectionist. Gould (2002) has accurately described the 'hardening' of the adaptationist perspective in the 'Modern Synthesis'; this can be seen in the difference between Simpson (1944) and Simpson (1953), and between Mayr (1942) and Mayr 1963), and Gould showed clearly that evolutionary teaching under the hegemony of this school became *almost blindly channelled*.

Through the 1960s and 1970s the core beliefs of the New York school –continental permanency and northern centers of origin– came under growing attack, with earlier members of the school, such as the ichthyologist Myers, *deserting the gospel according to St. Matthew* (Myers, *in litt.* to Darlington, Jan. 21, 1964, quoted in Nelson and Ladiges, 2001). In fact, Wallacean biogeography and its main mouthpiece, the New York school, led to an unproductive detour that has lasted for well over a century. Even following the acceptance of continental drift, Wallacean dispersal has been kept alive by many authors who have simply applied the old migration routes (e.g. Europe-Asia-South Pacific) to new paleogeography,

and/or argued that drift took place too long ago to be relevant.

The huge influence of Wallace and Matthew's biogeography was a disaster for the science as it smothered the growth of an analytical methodology which was beginning, with Andersen and the others, to produce excellent results. Up until modern times it has been normal to follow the New York school in ridiculing many of these authors as 'land-bridge builders', but this is an inaccurate caricature of their work; discussion of prior land formed only a small part of their analyses. In any case, predictions about paleogeography framed on the basis of biogeographic distributions led to Wegener's (1924) work on continental drift which will probably outlast Wallace, Matthew and Simpson's notions on continental stability. A century later the texts of the early panbiogeographers are still largely ignored because of Matthew's enduring legacy, but the work of Ortmann, Andersen, Regan, Eigenmann and others, quoted above, comes across as surprisingly modern.

Croizat's work and the contemporary reception of panbiogeography

At last I salute a science that gives results.

Horace, *Epodes*, as translated in Montaigne, 1958

His observations on life are equally just, pertinent, and uncommon.

Smollett, 1967

An independent and cautious scientific attitude is almost thought to be a kind of madness: the free spirit is brought into disrepute, particularly by scholars who miss their own thoroughness and antlike industry in his talent for observation, and would gladly confine him to a single corner of science [...]

Nietzsche, 1994

If this work seems so threatening to them, this is because it isn't simply eccentric or strange, incomprehensible or exotic (which would allow them to dispose of it easily), but as I myself hope, and as they believe more than they admit, competent, rigorously argued, and carrying conviction in its re-examination

of the fundamental norms and premises of a number of dominant discourses, the principles underlying many of their evaluations, the structures of academic institutions, and the research that goes on within them.

Derrida, 1995

Before his grandfather moved to Turin, Croizat's family had lived for centuries in the triangle Lyon-Geneva-Chambéry. The family had included in its branches St. Francis of Sales (1567-1622), the patron saint of writers; Mme. de Roland (1754-1793), a well-known figure in the French Revolution and famous for her memoirs written in prison; and Alphonse de Lamartine (1790-1869), whose poetry began the Romantic movement in French literature. Croizat was born (1894) in Turin and in his younger days botanized on the slopes of Mt. Viso in the nearby Alps. Here he began to wonder about questions of distribution, for example, why certain *Euphorbia* species from the Alps and eastern Mongolia very nearly duplicate one another, without there being any known records between these two localities. (Ekman, 1953 wrote: *To older zoogeographers the great similarities between the Mediterranean and Japanese fauna were a source of surprise. The discovery of the former extent of the Tethys Sea has solved this riddle*). Croizat later returned to a study of the Mt. Viso region in his book on Hannibal's route across the Alps (Croizat, 1975b). The natural environment, the cultural environment, and the long history of biological enquiry in the area together provided the stimulus for Croizat's earliest investigations and it can hardly be a coincidence that panbiogeography originated in northern Italy.

The key texts in the history of panbiogeography are Croizat's two massive global analyses (1958 and 1968a-c, 1975a), which still appear to have been read by very few biogeographers. Croizat's (1958) work is a true synthesis of tropical biology, accounting for evolution of earth and life in northern South America, Africa and tropical Asia/Pacific, and is 2749 pages long. Among his other major publications are studies on Euphorbiaceae (Croizat, 1965, 1967, 1972, 1973) (see Heads and Craw, 1984 for a bibliography).

Although the scientific aspects of Croizat's work have been discussed by many authors, his general philosophy has seldom been examined. Croizat ar-

gued that neither Darwinian center of origin/dispersal biogeography nor vicariance cladistics was capable of effective biogeographic analysis and he observed that in both these schools of thought, and thus most biogeographic literature, there is a great discrepancy between the nature of the phenomena and the means used to explain them. Croizat concluded that a critical underlying factor missing from biogeography was a sense of proportion or of humor –what the French call a sense of the ridiculous. The relationship between these has been expressed by other authors, for example, during the war in Egypt, Douglas wrote that: *my senses of proportion and humor, like two court jesters, chased away the tragic poet* [...] (Douglas, 1966).

Croizat often wrote that what was most needed to produce a valid, creative biogeography was the use of ‘disciplined imagination’. For example, after having been brought up with the very mechanical Darwinian view of dispersal as physical movement from a point center of origin, some creative thinking is required to shift to a concept of dispersal as differentiation, a process resembling the way in which the vein in a leaf develops out of its ground tissue. This sort of thinking is currently rare in comparative biology; most is unimaginative, unoriginal, and consequently, as noted below, often very boring. At best, the arguments in this kind of work follow logically from the premises, but the premises themselves are hardly ever examined critically. Rouse (1941) suggested that: *In Greece alone do we find a people strong both in imagination and in the reason that regulates imagination* [...]; however, other authors are more optimistic. Pater (1998) felt that: *Art addresses [...] the imaginative reason*. Philips (in Introduction to Pater, 1998) noted that the phrase ‘imaginative reason’ is taken from Matthew Arnold’s essay ‘Pagan and mediaeval religious sentiment’ (1864), which he quotes: *The main element of the modern spirit’s life is neither the senses and understanding, not the heart and imagination, it is the imaginative reason*. Likewise, in ‘*The dagger with wings*’, Chesterton (1981) wrote that: *All things are from God; and above all, reason and imagination and the great gifts of the mind*. Leopardi (1905) wrote that: *subtlety of talent and power of reasoning do not suffice to form a great philosopher; he must also have a considerable share of imagination* (Leopardi felt that the former is much

more widespread among men than the latter). In the same way, Popper (1984) argued that: *rationalism must encourage the use of imagination because it needs it*.

Through the 1960s Croizat’s work found sympathetic readers around the world, including supportive editors in Paris (Aubréville), Coimbra (Fernandes), Florence (Moggi) and Pavia (Tomaselli) who published his lengthy monographs. Hostility towards his work was naturally greatest in the United States, the home of Matthew and the New York school. However, through the 1970s there was a major change in attitude at the American Museum of Natural History towards his ideas. Nelson, Rosen and Platnick wrote extensively and positively on panbiogeography, and enabled Croizat to publish in *Systematic Zoology* (Croizat *et al.*, 1974; Croizat, 1977a, 1978, 1979, 1981). Subsequent publications (especially Nelson and Platnick, 1981) indicated that this group was more intent on developing the cladistic research program than panbiogeography, and Croizat lost interest in the collaboration.

In New Zealand, Craw, then a Ph.D. student, published a vigorous defence of Croizat (Craw, 1978), and in the early 1980s he was joined by other Ph.D. students (myself, then Grehan, then Henderson) to form the New Zealand school of panbiogeography). Croizat took a close and active interest in this group until his death in 1982, when, on Catalina Croizat’s invitation, I visited Coro and acted as Croizat’s literary executor. The New Zealand group continued to attract other New Zealand workers through the 1980s, and publications include Craw and Gibbs (1984), and Craw and Sermonti (1988). A panbiogeography conference was held at the New Zealand National Museum in 1989 (papers in Matthews, 1989), but at this point there was an overt response by the New Zealand establishment. The local panbiogeographers all either lost their jobs (Climo and Craw), kept their jobs but stopped writing and talking about panbiogeography (Gray and Henderson), or after completing Ph.D.s had to find employment overseas (Grehan, Page, and Heads).

In 1988 Crisci had met with Craw and myself in Auckland for intensive discussions, and at the same time as the New Zealand school was being suppressed and dispersed through the 1990s, the formidable new

Latin school of panbiogeography was emerging in Argentina, Brazil, Mexico, Venezuela, Colombia, Italy, and France. A few examples of the many publications of this school are Morrone and Crisci (1990), Llorente (1991), Zunino (1992), Crisci and Morrone (1992), Fortino and Morrone (1997), Colacino (1997), Cortés and Franco (1997), Lourenço (1998), Hajdu (1998), Morrone (2000a, b), Llorente *et al.* (2000), de Marmels (2000, 2002), a new journal, *Croizatia*, published in Venezuela, and two books dedicated to Croizat (Llorente Bousquets and Morrone, 2001; Zunino and Zullini, 1995, 2003).

Critique of contemporary biogeography: Vicariance versus dispersal

Do you want to start off our squabbles again? Did we not agree not to explain this word proximate, and both to utter it without saying what it signifies?

Pascal, 1967

Much of the debate in current biogeography concerns the concept of 'dispersal'. Croizat followed authors such as Clements and Shelford (1939) who suggested that 'dispersal' or 'migration' should include: *any and all changes in position*. Anyone who has ever actually read Croizat knows it is simply untrue that he ever denied that dispersal occurs, although many authors have claimed that he did. One of his major works (1968b) is even titled '*The biogeography of the tropical lands and islands east of Suez-Madagascar, with particular reference to the dispersal and form-making of Ficus L.*'. Like Clements and Shelford, Croizat used the term 'dispersal' to mean the processes that have led to distribution – any and all changes in position. It is the particular nature of these processes that is controversial. Croizat argued that an efficient concept of dispersal must involve evolution, as well as physical movement; an organism can change its position to include a locality not just by moving there, but by evolving there.

As recently as 15 years ago the term 'vicariance', introduced by Croizat, was rarely seen in print but now it features in many papers on biogeography and evolution, even in journals, such as *Evolution*, long dominated by the New York school. Biogeographic

debate following the work of Croizat has often taken the form of an argument 'vicariance vs. dispersal'. Many authors have argued that both processes occur and are important. This recalls Popper's (1984) comment on Aristotle's work, where: *Instead of Plato's flashes of penetrating insight, we find dry systematization and the love, shared by so many mediocre writers of later times, for settling any question whatever by issuing a 'sound and balanced judgment' that does justice to everybody; which means, at times, by elaborately and solemnly missing the point.*

The debate between vicariance and dispersal often focuses on whether the physical movement required by 'dispersal' is possible, and on the means of dispersal involved in a particular case. These topics, however, are really irrelevant, as panbiogeography accepts both that individual plants and animals move, and that taxa may expand their range. The latter occurs during periods of mobilism, for example around the coasts of the late Mesozoic epicontinental seas. Vicariant form-making cannot take place during periods of mobilism, but occurs during phases of immobilism when large blocks of fauna and flora are relatively sessile (e.g. the passerine avifauna of today's world).

It is often felt that organisms such as birds 'must' disperse, but the records of distribution, with massive endemism and vicariance at all levels, show that this is not true. Thus Wiens (1991) noted that: *Because birds are mobile creatures, one might expect the distributional boundaries that define biogeographic patterns to be blurred within continents or biogeographic realms. In fact, many species have quite limited distributions.* Albatrosses roam the oceans, but return to breeding sites that are often very localized and vicariant with those of their relatives. Many passerines, such as birds of paradise, are highly sessile and individuals may spend much of their lives in a single tree.

Rather than focusing on 'means of dispersal', the vicariance vs. dispersal difference can perhaps be better appreciated by considering the two as different modes of speciation. Mayr and Croizat have both emphasized that the prevailing mode of speciation is geographical, as in Mayr's 'allopatric speciation' and Croizat's 'vicariance'. Mayr (1997), however, argued that this occurs in two forms, and: *actually, the two allopatric models are worlds apart* (Mayr, 1982a). In the first model, Mayr's 'dichopatric speciation', a pre-

viously continuous set of populations is disrupted by a newly arisen barrier, such as a mountain range or a new arm of the sea, and populations of each sector evolve into a new species over a wide area: there is no center of origin. In the second model, Mayr's 'peripatric speciation', a founder population is established through dispersal: *by a single inseminated female or by a few individuals* (a clear reference to a Darwinian 'ancestor'). At some point, and somehow (Mayr does not explain how, exactly –chance plays a major role) migration stops and the founder becomes isolated from its parent population. Dichopatric and peripatric modes of speciation are usually known as 'vicariance' and 'dispersal', respectively. (These are not the only synonyms for the same two processes; for example, in anthropology, there is the 'out-of-Africa' model (dispersal) and the 'multi-regional hypothesis' (vicariance) for the evolution of Man). Hennig's (1966) German idealist views closely resemble those of Mayr on most important topics. For example, both accept that all taxa derive from single species and both accept (in contrast with Darwin and Matthew) that the 'primitive species' stay at the center of origin while advanced forms move out. Hennig also accepted 'peripatric speciation', referring to it as 'speciation by colonization'.

In some of his writings Mayr seems to accept only peripatric speciation as common and dismisses the importance of dichopatric speciation: *Quite obviously, except for a few extreme [local?] endemics, every species is a colonizer because it would not have the range it has, if it had not spread there by range expansion, by 'colonization', from some original place of origin* (Mayr, 1965). Here Mayr ignores the possibility of 'dichopatric speciation' involving two or more widespread species, for example, a split between a Laurasian form and a Gondwanan form, or even between north New Guinea and south New Guinea forms. Most widespread groups show a mosaic pattern, with many genera, species and practically all subspecies showing vicariant ranges. Under Mayr's view, this standard pattern would require a huge number of founding events, point centers of origin, and range expansions, rather than the simple breakup of a widespread common ancestor.

Mayr proposed his 'peripatric model' ('*an entirely new theory of allopatric speciation*', Mayr, 1982a) in

a 1954 paper on New Guinea birds. (He introduced the term 'peripatric speciation' in 1982a; in 1954 he referred to the idea as the 'founder population' model). The model was based largely on the occurrence of highly 'aberrant' populations of bird species on islands off New Guinea, peripheral to the main distribution, and the 'amazingly great differences' among populations of adjacent islands in New Guinea. Mayr (1954) admitted that 'much' of his paper is 'frankly speculative' but he did not refer to any geology in his study, even speculatively. The distributions he dealt with have been analysed in a very different way in panbiogeographic work (Croizat, 1958; Heads, 2001a, 2002a), in which models of New Guinea as a geological and biological composite have been discussed fully. These studies concluded that there is no need to invoke 'founder populations' and that massive movements of geological terranes, not 'chance dispersal', account for facts of bird distribution in the region, such as the aberrant populations studied by Mayr and the total absence of birds of paradise from Biak and the Bismarck Archipelago. The other example that Mayr and many others have based their theories on is the bird *Zosterops* in New Zealand. Mayr (1954) stated that: *a small flock found its way in 1856 from Australia to New Zealand*, but this apparently classic example of a founding population is not supported by a closer reading of the literature. Buller ([1888] 1967) and Mees (1969) have both indicated an earlier presence of this bird in New Zealand and as ornithology in New Zealand only started at about this time, *Zosterops* may well have been in the country from ancient times, becoming more abundant with the advent of European settlement and agriculture.

The whole field of founder effects is problematic. Futuyma (1998) has noted that "founder effect speciation" is "very controversial" and that: *a great deal of controversy surrounds the genetic changes postulated for the founder populations in peripatric speciation*. Ayala *et al.* (1995) observed that the prevalence of founder events in speciation is a matter of 'acrimonious debate', with some authors rejecting the purported genetic consequences on theoretical grounds. Whittaker (1998) noted that: *It is particularly problematic that founding events (i.e. colonization) have been theorized to produce a variety of rather different founder effects* [...emphasis in original],

and that some authors have queried the significance of founder effects. Tokeshi (1999) argued that: [...] despite the conceptual appeal and Mayr's emphasis in his monograph, data which can unequivocally be related to such peripatric speciation are not easy to identify [...] Rather than hard empirical evidence of contemporary and historical distribution patterns in faunas and floras, the interest in the peripatric perspective has mainly revolved around its theoretical implications from population genetics. In an attempt to explain the divergence of peripheral populations, Mayr (1954, 1963) advocated the concept of the founder effect [...] theoretically, however, the founder effect based on random genetic drift does not seem to be an effective means of speciation [...]. Nei (2002) wrote that while the theory of speciation by the founder principle has been popular for the past 40 years, it is: speculation, and there has been no empirical study of this hypothesis. Recent studies of MHC loci in Galapagos finches and cichlid fishes in African lakes, both model cases of speciation by the founder principle: led to one of the most important findings in evolutionary biology in recent years: that speciation by the founder principle may not be very common after all.

Thus, of the two modes of speciation that Mayr himself agreed were 'worlds apart', dichopatric speciation or vicariance is accepted by most authors, whereas peripatric speciation (founder effect, speciation by colonization, 'dispersal') is highly controversial; biogeographers such as Croizat and geneticists such as Nei have simply rejected it.

Centers of origin and dispersal

As noted: *the ingenious are always fanciful, and the truly imaginative never otherwise than analytic*. Darwinism is nothing if not ingenious and fanciful; for example in biogeography, 'the simplicity' of the view that dispersal starts from a single point center of origin and spreads out by physical movement was a fancy of Darwin's (1971) which "captivates the mind". The obsession with a center of origin is not restricted to biology. For example, in literary studies: *many Finnish scholars shared Lang's unhappiness with the tendency of Benfey and others to trace every story back*

to some hypothetical origin in India. However, the Finnish folklorists shared the diffusionists' preoccupation with discovering the starting places of stories (Irwin, 1994). In another field, Fernández-Amesto (2000) has written that: *All history, I have come to believe, is the history of colonization because all of us got to where we are from somewhere else*. This may be true, or may be not. One school of thought believes that groups of *Homo sapiens* have evolved into modern humans there, where they are. One thing does seem clear: over a century of argument –about means of dispersal, dispersal vs. vicariance, and much else– has shown that the Darwinian concepts of 'center' and 'dispersal' lead only to endless controversy, not to an efficient biogeography. This requires instead long, detailed and imaginative analysis to identify the nodes and tracks of distribution, and to integrate these with tectonics.

As George (1987) pointed out, it was discrepancies between theories of centers of origin, in particular how one located the center of origin, that led to Croizat's development of the generalized tracks/vicariance approach. For example, authors like Darwin (1971), Matthew (1915), Darlington (1966), Frey (1993), and Briggs (2003) have assumed that the most advanced species occur at the center of origin and out-compete the primitive ones which migrate away. In contrast, other dispersalist authors, such as Mayr (1942), Hennig (1966) and modern phylogeographers (Avice, 2000), assume that the most primitive taxa occur at the center of origin and it is the advanced ones which have migrated away ('Progression Rule'). (Nelson, in press, noted that 'Hennig's rule is now reborn –as if it were for the first time– within phylogeography'). This is a fundamental split within the dispersalist school, but neither assumption is used in vicariance cladistics (e.g. Platnick, 1981; Nelson, in press) or in panbiogeography.

In the twentieth century, Darwin and Wallace's concepts of biogeographic processes have been less dominant outside the Anglophone world. For example, leading tropical botanists in France have simply dismissed long-distance dispersal: *Schnell* [1970] *doesn't believe in it, neither do I* (Aubréville, 1971). Nevertheless, Darwin and Matthew's ideas live on. In particular, the point center of origin idea currently shows no signs of abating. For example, Wilkinson

(2003) argued that plate tectonics may have been important in the evolution of the order Carnivora, but: *if I am interested in the biogeography of the tiger **Panthera tigris**, and if we assume that this species had a point of origin in space-time in the recent geological past, then dispersal will be one of the key relevant mechanisms in understanding its current distribution* (emphasis added). But why assume a point center of origin? Did the tiger really evolve at a single spot, perhaps under a particularly auspicious banyan tree? Might not the evolution of the tiger have involved dichopatric vicariance?

McDowall (2004) has argued that centers of origin do exist and are of interest and relevant because: *the overall [distribution] patterns we observe are the accumulation of the individual patterns*. This does not follow logically: no reason is given why an individual pattern requires a center of origin. McDowall may be trying to say that there are no standard patterns, only individual patterns. But even if this were true, which it obviously isn't, it would not in itself be a justification for centers of origin.

The miracle and mystery of chance dispersal

These marvels (like all marvels) are mere repetitions of the ages.

Melville, 1998

As discussed above, critique of teleology developed during the seventeenth century and at the same time an important attack was launched on the so-called 'naturalism' of the Renaissance –the belief in panpsychism and animism which gives everything a soul and sees miracles everywhere in nature. Thus, whereas people had previously sought to demonstrate God through miracles and divine caprice, Kepler sought to demonstrate God through divine order and self-consistency. Likewise, for panbiogeography, the real miracle is the incredible repetition in the biogeographic patterns of all kinds of organisms –plants and animals, lowland and alpine, terrestrial and marine. However, it is not a mystery and it can be analyzed.

On the other hand, the basis of all dispersal biogeography is a mystery and a miracle: the un-analyzable chance event, that, given enough time,

becomes a certainty. For example, Mayr and Phelps (1967) accepted that the eastern Pacific islands were populated by animals through long-distance, over-water dispersal, and they wrote that: *the distances involved in some of these colonizations are truly miraculous*. Croizat pointed out that the almost unanimous acceptance of this 'process' in biogeography reflects a psychological phenomenon: people find mysteries and miracles attractive, even though in science they are the antithesis of an acceptable explanation.

In classical times Tacitus noted that man's character is such that: *he will always prefer to believe in mysteries* (Tacitus, 1972), and in Renaissance Italy Burckhardt (1990) referred to the: popular craving for the miraculous which was satisfied by the many miraculous pictures of the Virgin. In 1498 Fra Girolamo was already arguing that miracles: *should not be used except in dire necessity when reasoning and experience proved insufficient [...]*. (Guicciardini, 1966) and another Renaissance author, Ficino, wrote: *In our time we are no longer satisfied with the miracle; we must have a rational, philosophic explanation* (quoted in Battisti, 1974).

In many ways the belief in chance dispersal is the belief in the miraculous, one-off event that defies all explanation. Why, without any geographical change, should an organism that is arriving more or less regularly on, say, an offshore island, change its ecology and stop dispersing there, thus enabling the island population to change into a new species? How and why should an organism disperse hundreds or even thousands of kilometers to establish a massively disjunct population, without leaving any populations in the gap? And above all, why should these patterns be repeated in countless groups with totally different ecology and means of dispersal? There is no rational explanation for the mysterious 'chance dispersal' which is invoked to explain these common patterns, and as Avise (1994) admitted, in an understated way: *Dispersalist explanations sometimes become quite strained*.

In fact, using Darwin, Wallace and the New York school's concepts of dispersal and center of origin does not solve biogeographic problems efficiently but simply leads to confusion, mystery and paradox, as leading dispersalists often find themselves forced to

admit. Birds are the best-known group of animals, and the influential dispersalist biogeographer Darlington (1966) had 'unusual opportunities' in studying their biogeography, including discussions with, and assistance from leading North American ornithologists. 'Nevertheless', he concluded: *I still find the distribution of birds very hard to understand. The present pattern is clear enough, though complex. But the processes that have produced the pattern –the evolution and dispersal of birds– are very difficult to trace and understand.*

Describing the birds of Melanesia, Mayr and Diamond (2001: 249) posed the question: *Why is the San Cristobal avifauna so distinctive in its endemism, absentees, eastern specialties and differentiation?* They concluded [...] *some mystery remains and we do not claim to have a complete answer.* Discussing another island, they wrote (2001: 254): *We are uncertain whether these three factors [colonizing ability, wind direction, and ecology] suffice to resolve the paradox of Rennell's avifauna [...] This paradox deserves more attention.* In a further example, they referred (2001: 229) to the absence of the New Guinea species *Monarcha chrysomela* from New Britain as: *the most surprising distributional gap in the whole Bismarck avifauna* and wrote that the reason for its *presumed disappearance on New Britain remains mysterious.* They also failed to account for the even more striking absence of birds of paradise from the Bismarck Archipelago. In fact the whole fauna and flora is quite different from that of the mainland. Do San Cristobal, Rennell and New Britain really represent zones of 'mystery' and 'paradox'? As noted, the public always loves a mystery and the 'chance dispersal' favored by neo-Darwinians such as Mayr and Diamond is inherently mysterious, but outside dispersal theory there appears to be no real reason for accepting biogeographic nodes as centers of mystery or paradox. Mayr and Diamond did not mention any geological development earlier than the Pleistocene, but this earlier history is probably crucial to a resolution of their mysteries. For example, Hall's (1998, 2001) reconstruction of the region for 30 Ma shows the east Philippines, northern Moluccas and north New Guinea terranes (including New Britain) forming a relatively continuous arc, running parallel with and 1-2000 km north of proto-New Guinea,

before moving south and west and docking. This would explain the close connections among these regions and also the great difference between the northern and southern Moluccas, and the Bismarck Archipelago and mainland New Guinea.

Matthew ridiculed the early panbiogeographers for discussing 'landbridges', in fact these authors were simply discussing prior land which may have comprised biogeographic centers in their own right. The idea of prior areas of land merely being land-bridges –means of getting from point a to b of current topography– is a speciality of dispersalist biogeography. For example, Mayr and Diamond (2001) invoked Pleistocene landbridges in their only reference to changing topography.

The writing of many biogeographers and evolutionists resembles: *the English of administrators, politicians, and important people who write letters to The Times. Imprecision would seem to be the chief quality of this language, but for its weary pomposity and its childish delight in foolish metaphors* (Kitto, 1951). With the usual North American penchant for crude, mechanical metaphor, Mayr and Diamond concluded that the: *whole movie of speciation begins with the arrival of colonists overseas, however, in a notable omission from a 22 page bibliography, an absence that is in fact a characteristic mark of these authors' work, Croizat's (1958, 1968b) detailed analyses of the northern Melanesian avifauna are not even mentioned.*

Chance and dispersal

Some think that all things are subject to the chances of Fortune; these believe that the world has no governor to move it.

Juvenal, in Juvenal and Persius, 1969

Fortune reigns in gifts of the world, not in the lineaments of nature.

Shakespeare, *As You Like It*

[...] *those more numerous Copyings, which are found among the Vessels of the same Body, are evident Demonstrations that they could not be the Work of Chance.*

Addison, 1712, in Steele and Addison, 1997

Aristotle implied that some aspects of things are accidental; caused by matter, things only imitate transcendent forms and the imitation is imperfect. The imperfections are not of scientific interest and: *It wasn't until the Aristotelian cosmology was swept clean away that scientists could begin to take nature seriously and [...] treat her lightest word as deserving of attention and respect. This new attitude was firmly established by the time of Leonardo da Vinci* (Collingwood, 1945). Croizat's deconstructive analyses often focused on Nature's 'lightest words' –apparently minor, anomalous aspects of biogeography and morphology which would usually be treated as insignificant and accidental, but which he showed are crucial and revealing parts of larger patterns, for example, in demonstrating that commonly accepted units such as 'North America' or 'leaf' are in fact hybrid composites and not natural entities.

While 'accident' plays no role in panbiogeography, chance dispersal and random mutation are the core concepts used in the Darwinian and neo-Darwinian programs to account for differentiation in space and form, respectively. In contrast, panbiogeography sees the far from random laws of growth (*i.e.* orthogenesis/phylogenetic constraint) generated by processes such as molecular drive (Dover *et al.*, 1993; Dover, 2000; Craw *et al.*, 1999) as providing the variation on which selection can work, and thus of primary importance. Evolution proceeds whether or not the direction is especially adaptive; if the new mutation is subviable the lineage goes extinct. Extinction has always been a rather problematic topic for neo-Darwinism. Why do some taxa but not others fail to adapt? Extinction is usually interpreted as a function of the environment; for example, Keast (1996) asked: *Why has there been extinction in seemingly benign New Caledonia?* The panbiogeographic interpretation is that taxa will eventually go extinct because of intrinsic tendencies in their morphological evolution, not necessarily because of unfavorable climatic or habitat change. However, environmental change may cause extinction before orthogenesis does.

The uncritical use of 'chance' and 'accident' in biology, whether as 'chance dispersal' to explain biogeographic patterns or 'random mutation' and natural selection to explain phylogeny and morphology, was one of Croizat's main targets. He pointed out

that 'chance' has been used in two quite distinct ways in biology. First, it can mean a mathematically calculable probability; for example, a seed has a chance of 1/n of being blown 1 km. Alternatively, 'due to chance' can simply mean 'due to unknown factors', for example many authors regard the biogeographic connection between Hawaii and the Marquesas Islands as due to 'chance' events in dispersal. One of Matthew's (1915) main arguments ran as follows: if there is the slightest possibility of an 'exceedingly improbable accident' of long-distance colonization, given the vast amount of geological time available, an 'almost infinitesimal chance' becomes a 'quite probable chance'. Likewise, over geological time, even a slow rate of dispersal can eventually take a worm around the world. However, if the probability of an event occurring is zero, it will never happen.

Dispersal in groups with 'massive capacity for spread': Ferns, sharks, and albatrosses

Ebach and Humphries (2003) contributed a useful, concise critique of dispersalism. In a negative response, McDowall (2004) commented that: *Interestingly, Ebach and Humphries [2003] do not seem to invest much effort in vicariance theories for the biogeography of albatrosses or oceanic sharks. And what of ferns, which seem to have massive capacity for spread [...]?* In fact, Ebach and Humphries did not refer to albatrosses, sharks or ferns at all. But this omission is hardly 'interesting', as their article was only three pages long. McDowall himself has not supplied a dispersal account of these groups, which all show distribution patterns that are quite standard and strikingly precise. Other authors have questioned the importance of dispersal in these groups and McDowall's snide implication that vicariance analysis of them is not possible is incorrect.

Discussing ferns, Cockayne (1928) wrote that: *The case of **Hymenophyllum ferrugineum** of Juan Fernández, Chile and New Zealand is hard to explain on the supposition of wind-carriage and equally difficult is that of **H. malingii**, a pseudo-epiphyte, of quite local occurrence [...] in New Zealand and Tasmania [...] Were spores as readily carried by the wind as is supposed there should be no special fern floras,*

which is not the case; nor should the endemic *Polypodium novae-zelandiae* be confined to one portion of North Island. Lovis (1959) argued similarly: *It is sometimes somewhat facetiously supposed that on account of their copious production of spores [...] pteridophytes must be more widely diffused and distributed than are flowering plants [...] Study of actual plant distributions shows this generalization to be manifestly unjustifiable [...] pteridophytes, and bryophytes and orchids as well, have distributions which by and large show the same characteristics [...] as do flowering plants which possess relatively heavy disseminules.* The striking distributions of many ferns in New Zealand (Heads, 1990a), New Guinea (Heads, 2001a, b, 2002a) and the Malay Archipelago (Heads, 2003a) have been interpreted in a vicariance context and shown to be components of general patterns correlated with tectonic events. I am not aware of any dispersalist interpretations for any of these patterns.

As another example, consider *Acrostichum aureum*. This distinctive fern is widespread in the tropics, where it typically grows in mangrove forests and reedbeds and is able to tolerate very saline conditions. In southern Africa it is recorded along the coasts of Natal and Mozambique by Burrows (1990) who added, significantly, that: *There is an extraordinary record of Acrostichum growing next to some hot-springs in south-eastern Zimbabwe, at an altitude of 550 metres and 400 kilometres away from the coast. Although it is easy to understand its ability to withstand the highly saline or mineralized soils around the hot springs, it is interesting to speculate how it arrived there. Apart from the possibility of normal spore dispersal by wind, it is widely accepted that the entire south-eastern portion of Zimbabwe was, during earlier times, submerged below the sea – indeed the original dunes are still discernible in places. It may be that Acrostichum once grew along this ‘inland’ coastline and, as the sea receded eastwards, a relic population was able to remain intact alongside a mineral spring.* This is pure panbiogeography. Note that there is no dogmatic assertion of any theory, simply a juxtaposition of facts and an opening up of new and interesting possibilities.

Albatross distribution has been analyzed elsewhere (Heads, in press a). Despite their legendary powers of flight, after roaming the oceans at will, all albatross

species return to very precise and often very localized sites to breed. Vicariance occurs at all ranks. As a generic example, *Diomedea* of the Southern Hemisphere is sister to *Phoebastria* in the north Pacific. At species level, *D. exulans* (Indian Ocean islands, Tristan and South Georgia in the Atlantic Ocean, southern islands in New Zealand: Macquarie, Auckland, Campbell, Antipodes Islands) is related to *D. epomophora* of New Zealand: Auckland and Campbell Islands, Otago Peninsula, Chatham Island. The distributions are largely vicariant, with overlap only on Auckland and Campbell Islands. The third species in the genus, *D. amsterdamensis* of Amsterdam Island is vicariant with the other two species. Most or all subspecies of albatross are vicariant with the related subspecies.

I am not aware of any vicariance studies of sharks, although the distribution of the east Australian endemic *Brachaelurus colcloughi*, disjunct between the McPherson-MacLeay Overlap and Cape York (Last and Stevens, 1994) is identical to that of many terrestrial plants. The disjunction in the latter is usually attributed to extinction caused by increasing aridity, but the affects of terrane accretion have been overlooked and a dispassionate study of comparative biogeography in these sharks and trees would be of great interest. Although vicariance in sharks appears to be a neglected field, this is not true for the highly diverse and endemic Australasian skates (Last and Yearsley, 2002). These authors found ‘striking’ compositional differences between the faunas of New Zealand/New Caledonia and of Australia. The subfamily Arhynchobatinae is particularly speciose in the region and the New Zealand/New Caledonian fauna is dominated by species and supraspecific taxa of this group. The Australian fauna, on the other hand, although including many arhynchobatins is dominated instead by members of subfamily Rajinae and shows little overlap in species composition with the fauna of New Zealand and New Caledonia. The extant Australasian fauna: *appears to be derived from elements of Gondwanan origin, dispersal from the eastern and western Tethys Sea, and intraregional vicariance speciation [...] The Tasman Sea, which is thought to have divided Australia and New Zealand since the Late Cretaceous, has formed an effective barrier to the dispersal of obligate benthic fishes typified by most rays [...] the main ancient mechanism*

of derivation is almost certainly vicariance. Note that Last and Yearsley did not invoke any dispersal at all across current geography.

'Unknown means' of dispersal and galaxiid fishes

Conjecture, expectation, and surmise

Of aids uncertain should not be admitted

Shakespeare, *Second Part of King Henry the Fourth*

Darwin (1971) cited freshwater fishes found in New Zealand and other countries as examples of groups that have dispersed across open ocean by 'unknown means'. The classic examples are the galaxiid fishes, several of which have a marine phase in their life cycle. They have been the topic of much debate between dispersalists (McDowall, 1964, 2002) who have argued for an Australian center of origin followed by dispersal to New Zealand and South America (Matthew, 1915 considered the case for transoceanic dispersal in *Galaxias* 'proven'), and panbiogeographers (Croizat *et al.*, 1974; Rosen, 1978) who favor vicariance of a widespread southern ancestor. Fortunately, this debate may be approaching a resolution.

A study of *Galaxias maculatus*, one of the world's most widespread freshwater fishes, found: *extremely strong intercontinental geographical structure*, i.e. vicariance, with well-supported clades for Tasmanian, New Zealand, and Chilean haplotypes (Waters *et al.*, 2000). Waters *et al.* wrote: *This leads us to question the assertion that trans-Pacific dispersal is going on in this species [...] our data indicate that the dispersal powers of G. maculatus may be more limited than previously suggested and a vicariant role in the divergence of eastern and western Pacific G. maculatus cannot be rejected.* Genetic divergences (implying maximum divergence dates of 36 Ma) *may be consistent with a vicariance model.* For forty years McDowall has argued strongly for a dispersal model of *Galaxias* biogeography, and so this study, in which he played 'a major role', represents a significant reversal in the dispersal/vicariance debate. The dispersalists, however, have not yet become fully-fledged panbiogeographers. Waters *et al.* (2000) also argued that the topology of the *G. maculatus* cladogram, ((Tasmania, New Zealand) Chile), conflicts with 'the pattern

of continental fragmentation' and that this means the Tasmania/New Zealand relationship is due to dispersal. Writing in a more popular publication less likely to be exposed to critical examination, Wallis and Waters (2003) even wrote that: *At first sight, this [Tasmania, New Zealand, Chile differentiation] might appear to support a Gondwanan explanation for their origin but this is not the case*, contradicting Waters *et al.*'s more cautious and realistic statement that "vicariance cannot be rejected". Waters *et al.*'s and Wallis and Waters' absolute faith in geology is naive: they cite no geological publications, presumably because they think that 'the pattern' is all worked out and agreed on. In fact the current geographic/political entities (Tasmania, New Zealand, Chile) are not geological entities but geological composites, and the simple split sequence between them may not be relevant. The sequence and timing of accretion of the component terranes and their distinct biogeographic affinities are topics of current investigation (Heads, 1999) and the ad hoc invocation of dispersal to explain apparent biological/geological incongruence in this region is unjustified. In fact, while vicariance-cladistic biogeography has predicted congruence between phylogeny and 'split sequences' of early (pre-terranic) plate tectonics, panbiogeography has criticized this as simplistic and misleading (Craw, 1982; Heads, 1999). Congruence between split sequence and phylogeny would only be predicted if the areas were biogeographically homogeneous before the split and this seems very unlikely.

As indicated by Heads and Craw (2004), the dispersalist biogeography of Wallis resembles that of Wallace in most aspects, for example in basing biogeographic conclusions on theories from another field, geology, not on biological data. Privileging certain currently accepted theories from a field in which they have little expertise means that biogeographers can never make new predictions about either geology, as did, for example, workers such as Wegener or Croizat, or biology. The way in which Waters *et al.* (2000) presented their data reflects their underlying commitment to dispersal. For example, in their abstract they point out that: *a lack of genetic structure among New Zealand samples suggests that marine dispersal [occurs within New Zealand], and that: marine dispersal is an important biogeographical*

mechanism for this species. However, in the abstract they conspicuously avoid even mentioning the main overall pattern, the *extremely strong intercontinental geographic structure* among Tasmania, New Zealand and South America, which contradicts dispersal. In their paper lack of genetic structure is taken to imply dispersal, but extremely strong genetic structure is not taken to imply vicariance. This biased approach does scant justice to the very interesting data.

Likewise, in an earlier study of *Galaxias maculatus* Berra *et al.* (1996) wrote that: *Significant genetic heterogeneity between populations would be consistent with a vicariant model, whereas its absence would support a dispersal model* (italics added). This also reveals the prejudiced stance of the authors: why would genetic heterogeneity not support vicariance and its absence be consistent with dispersal? In any case, dispersalists can always change the rules: when strong vicariant genetic heterogeneity was subsequently discovered, Waters *et al.* (2000) and Wallis and Waters (2003) backtracked on Berra *et al.*'s prediction.

Dating evolutionary events and distinguishing between dispersal and vicariance

Dating evolutionary events has been done by correlating the age of taxa with the age of the oldest fossil, with the age of strata bearing endemic taxa, and with the age of paleogeographic events. (This topic is treated in more detail elsewhere; Heads, in press b). By dating phylogenetic events with a molecular clock and comparing these dates with the age of tectonic events, phylogeography claims to be able to test dispersal and vicariance hypotheses. How reliable are these claims?

In Matthewian studies of phylogeny, biogeography and evolution, fossils are given extraordinary significance, although Darwin himself emphasized the fragmentary nature of the fossil record. Matthew (1915) favored a literal reading of the fossil record, in which the taxon is taken to be the same age as its oldest known fossil and the absence of earlier fossils is taken as significant. But when even a paleontologist (Gould, 1989) can cite: *the most treacherous kind of argument that a scientist can ever use –negative evidence*, it is clear that the direct method for dating the origin

of taxa has unstable foundations. Occasionally, doubts about the method and its results are expressed. For example, based on the stunningly preserved fossils in Messel, Germany, G. Storch (quoted in Hoffmann, 2000) proposed that: *Bats were already advanced 49 million years ago. I'm convinced they originated much earlier than you read in textbooks*. However, the major problems with the Matthewian approach are usually ignored and there is even a recent book titled '*The adequacy of the fossil record*' (Donovan and Paul, 1998a). The title is probably a reference to Darwin's (1971) chapter 'On the imperfection of the geological record'. In the introduction to their book, Donovan and Paul (1998b) refer to Darwin's 'bias' in his well-known argument that the fossil record must be very incomplete but I would suggest that it is Donovan and Paul, not Darwin, who are biased. A member of the New York school (Darlington, 1966: 320) has proposed that the fossil record: *allows an almost magical view into the past*, and Briggs (1974: 249) used exactly the same words. In this approach, termed by Croizat (1952) *the cult of the petrifact*, the age of the earliest known fossil of a group is the age of the group, the location of that fossil is the group's center of origin, and the fossil itself, a material trace from the prehistory of nature, is the group's ancestor. In contrast, Croizat insisted on the distinction between *age of being* and *age of fossilization*, and the idea that fossils are ancestors was severely criticized by the cladists (Gee, 1999; Williams and Ebach, 2004).

What the fossil record can do is give broad averages of level of organization through time. The names of the geological eras reflect the fact that Cenozoic members of a group (*kainos* = new) have a modern stamp and usually look rather different from Mesozoic and Paleozoic members. But a literal reading of the details of the fossil record is bound to be misleading and new discoveries of fossils much older than the previously known oldest members of a group are made regularly.

In a second method of dating evolution, taxa are assumed to be the same age as the strata they occur on, for example on recent volcanic islands. This ignores the possibility of prior islands in the region on which taxa can survive.

In a third method of dating, the age of taxa has been correlated with paleogeographic events, but

these correlations have often been very simplistic. The three methods have been taken over by phylogeography, and are discussed further below.

Dating evolutionary events in phylogeography

The results of molecular systematics produced over the last 15 years represent great scientific advance. Croizat (1977b) regarded evolutionary development as: *a function of (a) panbiogeography and (b) molecular biology*. Molecular cladograms are often extremely valuable and of great interest for biogeography and general evolutionary studies. In contrast, the associated molecular clock studies generally seem almost worthless. Clock calibrations have been made using the three techniques cited above that have been used to date evolutionary events in general.

Calibrations based on fossils. In most phylogeographic studies the fossil record is taken at face value and the age of a taxon is equated with the age of the oldest known fossil. Clock calibrations and the chronology of the phylogenetic tree are based on this age. As indicated above, this is simplistic and misleading. Although more and more credence is apparently being given to the idea that age of fossilization is less or much less than the age of being and Croizat's dictum that age of fossils only gives a minimum age for a taxon is cited frequently, in practice it is usually assumed that the age of the fossil equals the age of the taxon, and other ages of clades within a group based on this are given as absolute, not minimum ages. In panbiogeography the age of the oldest fossil is never assumed to represent the age of the taxon and so a calibration based on the oldest known fossil cannot be accepted either.

Calibration using age of strata that endemic taxa occur on. A common logical mistake that biologists make in reading geology is to take geologists' suggestion that: *there is no evidence for land* in a region for a particular period, to mean *there is evidence for no land*. Wallacean biogeographers believe that the age of an island (*i.e.* of the currently exposed strata) *indirectly places a maximum age limit on any endemic plants that have evolved in situ*, but as noted, this ig-

nores the possibility of other former islands in the area, or older strata buried beneath present topography.

Calibrations using paleogeographic events. Most of the standard correlations between distribution and paleogeographic events used to calibrate clocks are highly simplistic. A classic example is the rise of the Isthmus of Panama at about 3 Ma, which is widely assumed to have brought about vicariance between Atlantic and Pacific marine taxa. The rise of the Isthmus is also one of the most important dates in dispersal biogeography of terrestrial taxa as it is supposed to mark the beginning of the 'Great American Interchange' of terrestrial faunas, one of the central pillars of Wallace/Matthew orthodoxy. The 3 Ma age for the isthmus is very often used as the basis for clock calibrations, however, many authors have pointed out Atlantic/Pacific pairs of taxa that must have diverged well before the final rise of the isthmus (Heads, in press a). Croizat (1975a) questioned the significance of the Isthmus of Panama and emphasized instead the complex earlier geology of the Colombia-Central America region. Other geologists and biologists have also suggested much earlier isthmian links between North and South America in the late Mesozoic or early Cenozoic that may have led to Pacific/Atlantic isolation and differentiation of marine taxa.

In conclusion, phylogeography resembles ordinary biogeography in most ways, studying distributions of characters in space. The results are notable for the very high levels of vicariance they have revealed. The one way in which phylogeography really differs from previous biogeography lies in its claims about evolutionary clocks and its ability to date evolutionary events. Because of this, it also claims to be able to test whether an event is due to vicariance or dispersal. However, there are notable difficulties with this whole line of reasoning which are seldom acknowledged, let alone discussed. Perhaps the most obvious and common fallacy involves assuming a clock and calibrating it with the oldest known fossil of a group. The divergence points on a cladogram are then given as absolute or maximum dates, whereas in fact this is a simple, logical mistake: all these will be minimum dates.

In sum, as Ebach and Humphries (2002) noted: *Phylogeography has re-invented dispersal biogeography [...] Phylogeography is limited in its perspec-*

tive, as it has not overcome the logical hurdles already addressed in cladistic biogeographical methodology over the last two decades. Prior knowledge, it seems, is neither assumed nor necessary in phylogeography. Humphries (2000) observed that: *despite four decades of analytical criticism, narrative biogeography [progression rule and its opposite] still seems to persist and is indeed growing with renewed vigor amongst contemporary evolutionists. Fossils and ancestors still assume cardinal importance and centers of origin are alive and kicking.* Nelson (2004) agreed, writing that the paleontology of earlier authors, especially Matthew and Simpson, *is revived in molecular systematics of the present, in the search for ancestors and centers of origin.*

Some current trends in systematics: hypocladistics vs. cladocentrism

Ignorance at the top fraternizing with impudence, cliquishness in place of merit, utter chaos of all fundamental concepts [...].

Schopenhauer, 1974,
describing philosophy in German universities

Cladocentrism. In modern systematics the taxon or a clade, a phylogenetic branch, is central to all studies. Current systematics is derived from German idealism through the work of authors such as Hegel, Hennig, and Mayr, and is concerned with pure, authentic, monophyletic branches or races derived from a parent pair or homogeneous 'stem species', not from a polymorphic ancestral complex. The use of botanical metaphor here is not accidental, and in studies of genealogy and phylogeny this use goes back at least to the biblical branch of David; however, I believe that modern systematics seems to have misread, 'overconcretized' or 'misconcretized' the metaphor, and become, as a result, 'cladocentric'.

The evolution of taxa (phylogenesis or taxogenesis) is only one aspect of form-making, which also includes the evolution of characters. Form-making may or may not result in well-defined groups. In weakly delimited 'complexes', often interpreted as hybrid swarms, it is the kaleidoscopic recombination of characters which is striking, rather than any distinct groups. Thus, the

monophyletic group cannot really be a fundamental unit for general, comparative biology and systematics. Nor can the species be fundamental, as even species are constituted by characters, the most 'essential' of which may 'drop out' unexpectedly.

In panbiogeography there is nothing special about species (or clades of any rank). The species level is simply another point on the trajectory of differentiation, lying between subspecies and genus. The process of form-making is the important thing. The emphasis on species as a privileged category is a classic feature of neo-Darwinism (as usual, Darwin himself, despite the title of his famous book, was much less rigid in his views than the neo-Darwinians and did not regard species as very special). The modern view is well exemplified by Cracraft (2002) who included the following in his "seven great questions of systematic biology": "What is a species?", "How many species are there?", "Where are the Earth's species distributed?", and "How have species' distributions changed over time?" In equally myopic species-centrism, Hubbell (2001) even regarded biodiversity as: *synonymous with species richness and relative species abundance and ecology as the scientific study of the distribution and abundance of species.*

Character analysis. Comparative morphology nowadays is often subsumed in cladistics, for example in tables showing 'primitive' vs. 'derived' states of characters. The 'outgroup method' used by many authors is a more or less hopeful attempt at morphogenetic analysis. Nevertheless, character analysis cannot be simply 'probabilistic', as is so-called 'parsimony' analysis. For example, consider the character of epiphyllly in plants, in which flowers grow from the surface of a leaf. This is a very rare condition, found only in a handful of unrelated taxa. So it is usually assumed (by 'outgroup analysis') to be secondarily 'derived', and a 'parallelism' in the different groups. This apparently obvious conclusion is probably wrong, as emerges from a deconstruction of the concept 'leaf'. In the idealist morphology that is taught in all first-year university botany courses, leaf, stem and root are the only three elements in a plant's structure; for example, the parts of the flower are interpreted as 'modified leaves'. Naturally, this begs the question, just what is a 'leaf'? Rather than having always been

there, or simply developing out of nothing, the modern leaf, as indicated above, is more likely to be the end result of a long process of reduction and simplification from a much more complex structure that was branched and probably fertile (sporogenous) (Croizat, 1961; Heads, 1984). One of the main results of the reduction of the protolife has been sterilization, now virtually complete in all taxa except the epiphyllous ones, although traces of the 'leaf's' former self (or selves) are seen everywhere in reduced form, as glands, teeth, venation, domatia, hairs, torsions, coloured areas, and occasionally epiphyllous flowers. The wings of some insects provide a parallel case of the evolution of planar structure in animals, and occasionally bear 'eye-spots' and 'osmophore glands' suggestive of relic structures. Androconial organs which release scents or pheromones occur on the wings and other parts of Lepidoptera and are perhaps morphogenetically homologous to the axillary glands and domatia of angiosperm leaves; however, most studies of androconia (e.g. Hall and Harvey, 2002) overlook their evolutionary morphogenesis, seeing them merely as later 'add-ons' resulting from 'sexual selection', and instead emphasize their function and systematic significance.

The status of an organ's morphology cannot be assessed simply by using taxonomy, by seeing how it is distributed in groups. It is necessary to look at the comparative organogeny of each particular case in detail. In practice, taxonomic monographs seldom concern themselves with morphological controversies. The (idealist) morphologists of the nineteenth century and early twentieth century were in many cases the only workers to have carried out detailed analyses of particular morphological trends, and attempted to find a structural explanation or a general view. Where idealism fails in morphology is in its tendency to invoke purely theoretical 'constructions' (and in a tendency to follow heroes, such as Goethe, and their concepts uncritically). In biology, the modern descendants of the idealists, the cladists, use traditional ('classic') concepts of leaf, flower, carpel etc. without question, but apart from purposes of description and cataloguing, it is difficult to see the use of knowing whether the leaf of a given species is 'large' or 'small', if it is not at all clear what a 'leaf' is. What is the point of comparing the small 'leaves' of ericoid

shrubs such as *Leonohebe* (Scrophulariaceae) or *Erica* (Ericaceae), with the large 'leaves' of *Hebe* and *Rhododendron* which have a different origin and structure (Heads, 1994, 2003a)? A full morphogenetic analysis is always needed, not just a cladistic analysis of preconceived categories. In any case, what exactly is the outgroup? This is a notorious problem, obvious at once to any student beginning a cladistic analysis. In any truly comparative morphology or biogeography, the outgroup can only be all other known biological taxa.

Hypocladistics. Instead of a cladocentric view which accepts taxa (especially the species) as the fundamental units of biological existence, a direct study of characters and, especially, recombination of characters can help solve many problems. This approach aims to get 'behind' the taxonomic classification –which is a summary– to the characters themselves, which are the basis of the taxonomy. For example, consider the 'hypocladistics' of the following examples:

1. Piculet woodpeckers (Picidae: Picumninae) are a classic case of what Croizat called 'wing dispersal'. The group (Winkler *et al.*, 1995) comprises three genera: *Picumnus* in tropical America from Honduras to NW Argentina (mainly in Brazil), *Nesoctites* in Hispaniola, *Sasia* with one species (formerly *Verreauxia*) in central Africa (Nigeria to Congo), and two species from the Himalayas to Borneo, and finally *Picumnus* again, with one species, *P. innominatus*, from the Himalayas to Borneo. (Short, 1973 confirmed that the last species does belong in *Picumnus*). Thus, *Picumnus* occurs in two regions, in the far west and the far east, but is strikingly absent from Africa. A virtually identical pattern is seen in the dispersal of Thymelaeaceae tribe Dicranolepideae (Domke, 1934; Nevling, 1961a, b) which comprises three related genera (*Dicranolepis*, *Synaptolepis* and *Craterosiphon*) in tropical Africa, and *Lophostoma* of Brazil closely related to *Enkleia* and *Linostoma* of NE India to W New Guinea. In both the Picumninae and the Dicranolepideae the characters have recombined in a similar way 'in the wings' of the range, with an enormous disjunction between localities in South America and SE Asia. This does not mean that there has been any migration between the two areas, or extinction in the center, simply that the characters of the groups have recombined in the same way at widely separated localities.

2. 'Divaricating' shrubs show a distinctive shoot architectural syndrome with brachyblasts (short or spur shoots) and determinate long shoots which abort apically. (Although I have pointed out repeatedly that these are the two key characters (Heads, 1990b, 1996, 1998a, c, 2003a), McGlone *et al.* (2004) asserted, quite erroneously, that the long shoots are 'indeterminate' in classic divaricates such as *Pseudopanax anomalum*). Divaricate architecture occurs in a few species in each of many different families and the group is obviously not monophyletic. It appears to be most diverse in parts of the SW Indian Ocean (East Africa, South Africa, and Madagascar) and SW Pacific (Australia/New Zealand), but is notably very rare in New Guinea and the central Pacific islands. The distribution is a standard one for monophyletic taxa, indicating that the biogeography of symplesiomorphy is the same as that of synapomorphy (Heads, 1990b).

3. *Jagera* and *Trigonachras* (Sapindaceae) are related genera of trees which range from the Moluccas to northern New South Wales, and the Malay Peninsula to New Guinea, respectively (Adema and van der Ham, 1993). The more perforate form of pollen found in these two genera occurs in the northwestern part of the range (several *Trigonachras* species and *J. javanica*), while the more reticulate form occurs in the southeastern part (several *Jagera* species and *T. papuensis*). The traditional explanation of this sort of pattern is that some casual, chance parallelism has been at work, giving a pattern of incongruent differentiation which runs counter to the other characters on which the genera are differentiated. The geographical vicariance of the pollen characters is, again, supposedly the result of chance dispersal. The occurrence of overlap only in New Guinea is supposedly the result of migration of the two pollen types into New Guinea from somewhere else. Other traditional explanations of this sort of parallelism are that the taxonomy is wrong, or that there must be some mysterious 'ecological' correlation. Nevertheless, there is no real need for any of these speculations. Characters have their own geographic and phylogenetic distribution and 'the group' can only be congruent with a limited number of the characters. The other, 'incongruent' characters, comprising parallelism or homoplasy, are routinely ignored, but in fact furnish an equal or greater amount of biogeographic data.

Jagera and *Trigonachras* may be sympatric over a large area, but underlying this is a fundamental split in the pollen types which show a clear geographic vicariance running counter to the taxonomy. The different characters have 'crystallized out' in different ways. There are no true synapomorphies or symplesiomorphies, and the rigorous distinction usually made between these two types of characters, with the former always privileged, has acted as a conceptual road-block which preventing biogeographic analysis.

The problem of 'parallelism' –How and why do unrelated and sometimes geographically distant plants or animals so often have one or more ecologically insignificant characters in common?– is only a problem if it assumed that taxa are monophyletic. In center of origin/dispersal biogeography, characters and taxa are assumed to develop just once, at a single point and to radiate out from there. In panbiogeography, however, a widespread ancestral complex in, say, northern South America, could differentiate out into, say, three components, one in each of Ecuador, Colombia, and Venezuela, with each developing their individual identity over the broad region of an entire country. Thus phylogenesis occurs on a broad front. In the latter view, but not the former, occasional striking 'parallelism' would be expected. As with the center of origin, and the morphogenetic equivalent concept of organs evolving 'de novo', out of 'nothing' (or rather a homogeneous prior structure), it is a question of an ancestral state/s or organ which are always already diverse no matter how far back in time they are traced, rather than a homogeneous center/organ or source of full presence or absence.

There are obvious parallels between these arguments and those of structuralism. What would a structuralist biology be like? Perhaps it would hold that there are no taxa, only differences between 'taxa'. Perhaps there are also no characters, only differences between characters. Such a view contrasts with the base concepts of cladistics: the 'full presence' of characters, localities and taxa (including species) as entities, either as types, kinds, classes or individuals; the semaphoront; the concept of center in dispersalist and vicariance cladistics, and the node as center of simple presence. Modern, decadent phylogeography (analyzed well by Nelson, 2004) has reverted to an early 1960s, pre-Brundin outlook, exemplified by the

idea that small sister taxa –‘basal’ groups– are primitive and ancestral, and located near the group’s original center of origin. In fact, a ‘basal’ group is just the smaller of two sister groups. Both will have the same age and neither one is derived from the other.

Instead of these concepts, emphasis is laid here on the processes of differentiation, vicariance and morphogenesis. For example, a node may be a center of both presence and absence. The biogeography of synapomorphy or presence (the Madagascar-Australasia sector as a zone of endemism for many monophyletic groups) is the same as the biogeography of symplesiomorphy (the same distribution shown in many polyphyletic groups (characters) such as the divaricating plants), and also the biogeography of absence (groups such as woodpeckers are strikingly absent there). Form-making is probably better seen as a ‘metamorphic overprint’ or a ‘remelting’ and recrystallisation’ than as a ‘radiation’ out from a point ‘center of origin’, a purely theoretical locus of original, full, homogeneous presence. This regional metamorphism often results in relatively widespread forms meeting at a node or a series of nodes. The boundary zone is often itself the site of highly localized endemism. In addition, these local endemics may have highly disjunct affinities or be disjunct themselves. Disjunction, local endemism and widespread taxa can all be the end result of form-making which is basically vicariant around a small number of nodes.

Much of this topic depends on the particular concept of ‘ancestor’ used. The common ancestor of one or more groups is usually assumed to be a single uniform species. For example, in cladistics, Wiley *et al.* (1991) asserted that: *Each monophyletic group begins as a single species, and only species can be ancestral taxa [...] there are no known processes [in neocladistic theory] that allow for a genus or a family to give rise to other taxa that contain two or more species.* Outside the conceptual straitjacket of idealist theory, however, such processes are acknowledged (for example, molecular drive or concerted evolution) and are closely akin to the well-known phenomenon of parallel evolution. Even Hennig (1966) accepted orthogenesis and the real reason for the cladists’ acceptance of the homogeneous ancestor would seem to be a subconscious adherence to the logocentric metaphysics of presence and idealist notions of Plato

and Aristotle, not any lack of mechanism for orthogenesis. If the idealist position was correct, and the ancestor was monomorphic, all the unique characters found in the descendant groups would be advanced or ‘derived’. However, it seems safer to assume that ancestors in general are not necessarily single species but may be polymorphic complexes, with many different states already present for each character (Hedges, 1985).

The ontology of systematics

Any literature, including that of biogeography, biodiversity and conservation, has its own ontology or view on the nature of entities as beings, and on existence itself. The broader ontology of a science has far-reaching effects on the theory and practice of that science. What is the ontology of ‘biology’ at the beginning of the third millennium?

Within the conceptual framework of ‘semaphoront’, ‘monophyletic group’ and ‘progression rule’, cladistics aims to ‘polarize’ alternative character states in terms of which state was derived from which. The argument again is one of ‘center of origin’, represented by the prehistorical, the primordial, or primitive, vs. the advanced or derived. The opposition of the primordial to the derivative is a standard metaphysical approach (cf. Derrida, 1982: 63) and in general, Derrida has questioned the approach of modern Platonic/Hegelian thinking with its basis of dichotomous, polarized oppositions (e.g. presence/absence, identity/difference, nature/culture, animate/inanimate) rather than specific analysis. Morphogenetic analysis often shows instead that two alternative morphologies are inherited, not one from the other, but both from a third.

The cladocentric system of systematics outlined above, derived from Plato and Hegel’s philosophy of history, accepts that being is determined by presence (rather than, say, difference) and at the origin of any entity there is an ancestral homogeneity, an absence of differentiation. In metaphysical idealism and its derivatives, differentiation, as history and materiality, lies a step outside identity, property and presence and is of secondary interest. The logocentric and cladocentric bases of Hennig’s (1950, 1966) work is

evident in his concepts of 'stem species' (possessing fully present synapomorphies of the group), and the typical idealist *Konstruktion*, the 'semaphoront'. The stem species resembles Husserl's: *punctual present moment or point of presence – a unique and original point of plenitude from which repetition as re-presentation and difference, the displacement of presence, supposedly derive* (Ryan 1982). The semaphoront is supposedly the character bearer, the biological individual during a minimal time period, and the ultimate element of systematics. In contrast with these approaches, in panbiogeography and hypocladistics there is a movement away from a rigid emphasis on the clade. Indeed, Croizat's life and work can be read as a critique of the cladocentric approach, with a notable focus on German idealism and Italian fascism.

Nothing important in biology is ever unique, as biological phenomena occur and recur in series and averages by reiteration, replication and reproduction. This is shown particularly clearly in biogeography. A critique of the 'center of origin' as an ideal, theoretical source is the same as a critique of the origin of complexity from simplicity, the stem species, the semaphoront, the monophyletic group, and the synapomorphy. Croizat aimed to dissolve the myth of the 'center of origin', and likewise, Nietzsche's *suspicion with respect to origins is matched by a conviction that origins are not single points of departure but complex and ramified intersections of multiple forces* (Smith, in the Introduction to Nietzsche, 2000). This theme was also taken up and elaborated by Derrida, for example in a discussion of 'representation': *In this play of representation, the point of origin becomes ungraspable. There are things like reflecting pools and images, an infinite reference from one to the other, but no longer a source, a spring. There is no longer a simple origin* (Derrida, 1976).

Earlier (Craw and Heads, 1988) I explored the affinities between the work of Croizat and Derrida, comparing, for example, the 'track' and 'form-making' of Croizat, with the 'trace' and 'differance' of Derrida. Clark (2001) recently discussed and extended this work, and concluded that although: *Scarcely tapped by the humanities, the leads 'panbiogeographers' have offered seem to have considerable potential for disenthraling conservation of its metaphysics of presence, in New Zealand and beyond.*

A specific onto-theology of biology is revealed, for example, in concepts of 'nature sanctuary' or 'reserve', set apart in the name of conservation. While a sanctuary was earlier a place that is 'holy', set apart for God (cf. the taxon as 'set apart' by the synapomorphy), the 'nature reserve' is now a place which is supposed to typify, save, and, above all, represent, an ideal, earlier landscape, or a romantic or political vision. Historic, scientific conferences have often been held at nature sanctuaries, for example that of Hermann Goering, with systematists such as Hennig in attendance.

A naïve view of 'the wonders of nature' is often revealed in the boast that the nature reserve of concern to an author includes "one of the biggest/ smallest/ heaviest/ loudest/ rarest/ most beautiful (trees, snails, birds etc.) in the world". This is related to the absolutist view of the 'virgin climax' rain-forest, and ignores the relatedness of biogeographic phenomena, including taxa and localities. As argued elsewhere (Craw *et al.*, 1999), nature conservation should instead aim to preserve biogeographic structure, *i.e.* networks of nodes.

In many ways conservationists are the missionaries of modern biology. Many remote villages in the tropics have a missionary and a conservationist, both out to 'save the world'. (Landes, 1999 writes of a *new world of peripatetically eager experts and technicians – eager to spend money, to do good, to wield power*). This relates to the triumphalist interpretation of natural history as seen on television, with breathless, sentimental accounts of conservationists' struggles and the miracles of nature accompanied by harps, trumpets, lyrical flutes, soaring violins, and angelic choirs. The ambience is similar to that at the end of a cowboy or war movie, with the victory of the 'good guys'.

Why biogeography is so boring

One must get rid of the bad taste of wishing to agree with many others.

Nietzsche, 1955

I know of no country in which there is so little independence of mind and real freedom of discussion as

in America. The majority raises formidable barriers around the liberty of opinion; within these barriers an author may write what he pleases, but woe to him if he goes beyond them.

de Tocqueville, 1835, *Democracy in America*,
as quoted in Barzun, 2000

[...] *the transformations of American universities, formerly citadels of thought, into organizations where, nowadays, no one has a moment in which to stop and think.*

Leigh, 1999

I feel they [contemporary 'novelties'] hold nothing essentially new and are really no more than timid variations [...].

Borges, 1978

Current biogeography is undertaken mainly by authors who seem afraid to think (or at least write) outside the strict orthodoxy. The only variations in the literature are few and very minor, and the subject has become boring to read. Croizat (1964) wrote that the panbiogeographic method is Socratic, *asking questions in lieu of taking axioms for granted*, but in contemporary work basic assumptions, including ideas now well over a century old, remain unquestioned. Cato attributed the Romans' success to their bringing 'untrammelled minds' (*animus in consulundo liber*) to the council chamber (Sallust, 1964), and this is exactly what is needed in biogeography in order to escape from the conceptual net our subject has inherited from Wallace and Matthew.

The philosophy of biology is in a similar situation. A typical treatment, such as Sterelny and Griffiths (1999), illustrates a parochialism and poverty of thinking marked in particular by a total neglect of anything outside mainstream North American orthodoxy. For example, the most-cited authors are Gould, Eldredge, Hull, Sober, Lewontin, and Dawkins, while on the other hand neither Hegel, Derrida nor Croizat are even mentioned.

In his satires Juvenal derided: *The derivative, artificial, cliché-ridden nature of contemporary literature* (P. Green, in the Introduction to Juvenal, 1967). Juvenal's observation, that: *All gabble off the same stale old couplets and catchphrases* applies equally

to contemporary literature on evolution and biogeography. There are also indications (for example, the overuse of words such as 'clearly' and 'appropriate') that the language of the bureaucrats is infiltrating biology. A list of the worst clichés in the field would need to include 'Explosive speciation', 'laboratory of speciation', 'drivers of evolution', 'species pumps' and especially the horrible 'pattern and process'. Following the appearance of the Hollywood film 'Out of Africa', the phrase has been wheeled out in every study dealing with Africa, apart from those written by Africans or people working in Africa, who know better. Most authors seem unaware that the phrase does not mean things have moved out of Africa (the quote is *out of Africa, always something new*). Recent publications feature 'out-of-India' (Conti *et al.*, 2002) and even 'out-of-Madagascar' (Raxworthy *et al.*, 2002) models. Orthodox taxonomic accounts are usually better written; when Klass *et al.* (2002) did discover something really new 'out of Africa' they managed to get through the whole article without using the phrase.

Dogmatism, deliberate falsehood, suppression and plagiarism: a natural progression

[...] *there is nothing more difficult or dangerous, or more doubtful of success, than an attempt to introduce a new order of things in any state. For the innovator has for enemies all those who derived advantages from the old order of things.*

Macchiavelli, 1997

The opponents of panbiogeography, mainly dispersalists of the Matthew/New York school, have dominated all phases of biogeography for the last century and held a virtual monopoly on academic posts, research grants, access to students, and even publishing outlets. They have protected their position and privileges in a variety of ways, notably by dogmatic repetition of the infallibility of their views and by spreading deliberate falsehoods about panbiogeography, suppressing publication of panbiogeography, and plagiarizing panbiogeography.

Dogmatism. The biogeographic literature is full of dogmatic statements that a particular pattern can *only*

be explained by dispersal, it *must* have been dispersal, no other mechanism is possible or even conceivable. No arguments are presented to support these declarations; the views are simply asserted. For example, Renner *et al.* (2000) wrote that numerous disjunctions between South American and Australasian sister species of Compositae: *must have resulted from long-distance dispersal*, as the family is *not old enough* for the pattern to be caused by vicariance. Fukuda *et al.* (2001) wrote that: *It is obvious [...] that Lycium sandwicense of the Pacific Islands originated in the New World*, simply because it and a group of New World species are sister taxa (which instead suggests vicariance). Meve and Liede (2002) stated that: *The African-Malagasy distributions [in Apocynaceae] can only be explained by long-distance dispersal events [...]*. Eibl *et al.* (2001) asserted that *Polyscias joskei* in Fiji, sister to a New Caledonian group, *can be explained only by dispersal*. All this is simply propaganda. As Pascal said, *It cannot be as certain as all that [...] because where there is dispute, there is uncertainty*. (Pascal, 1988). Of course, it is simply foolish to assume that anyone knows for sure what happened tens of millions of years ago.

Deliberate falsehoods. Raxworthy *et al.* (2002) wrote that: *Historical biogeography is dominated by vicariance methods*. This extravagant claim was introduced simply to make the authors' conclusions appear new, interesting, and opposed to current orthodoxy. In fact, they are none of these; they simply restate the dispersalist dogma that has been dominant since the time of Matthew. Rieppel (2002) also argued that: *dispersalist explanations in biogeography had [when?] fallen from favor*, but again, this has never been the case. It is true that Croizat's reputation has risen steadily since the 1960s and that in the last few years the word vicariance has actually been allowed in respectable journals, but this hardly makes it dominant. It would be easy to show that dispersalism is so ingrained in the subject that the vast majority of biogeographers simply assume it. For example, the tree frog family Rhacophoridae, with over 300 species in ten genera, is known from Africa, Madagascar and southern India to SE Asia. Wilkinson *et al.* (2002) found 'unexpectedly', that *Chirixalus doriae* from SE Asia forms a clade with African spe-

cies of *Chiromantis* suggesting that *Chiromantis* dispersed to Africa from Asia even though it is geographically well separated; however, it will only suggest this to authors already committed to a dispersalist world-view to start with. Likewise, Bossuyt and Milinkovitch (2001) argued that *Chiromantis* is nested well within an Asian clade so it *must have reached Africa overland*. Waters and Roy (2004) have claimed that: *It is unfortunate, then, that some biogeographers actively discourage the examination of biogeographic mechanisms. For instance, Croizat (1964) recommended that biogeographic processes should be ignored [...]*. This statement is, of course, a deliberate falsehood and would never stand up in a court of law. The standards of the journal in which Waters and Roy (2004) made their claim have sunk dramatically in recent times, as the next example shows.

Suppression

What freedom was there, they asked, when there was no freedom of speech?

Livy, 1976

I do not see how Plato's method of impressing upon his readers the belief that all important theories have been examined can be reconciled with the standards of intellectual honesty.

Popper, 1984

The process by which panbiogeography was suppressed in New Zealand after the 1989 National Museum conference on the subject is described elsewhere (Colacino and Grehan, 2003; Heads, 2003b, c). It is not surprising that biologists have subsequently failed to carry out panbiogeographic work in New Zealand; after 1989 no funding proposal for panbiogeographic research has succeeded, no panbiogeographers have been employed there, and no panbiogeographic work has been accepted for publication either in the government or the Royal Society journals.

Suppression of panbiogeography also has a long history in other countries, as a recent example shows. In 2000 Wallis and Trewick submitted a manuscript to *Systematic Biology* criticizing my analysis of Al-

pine fault disjunction in New Zealand plants and animals (Heads, 1998b). The editor, R. Olmstead, sent me the manuscript for review and I found it so bad that I recommended it be published as it was, as long as I could have the right of reply. Olmstead promised me I would have the opportunity to respond. The article was published (as Wallis and Trewick, 2001) and the reply I wrote with Robin Craw was submitted to *Systematic Biology*. Unfortunately, the new editor, C. Simon, had herself coauthored a recent paper on the same subject heavily critical of my views (Buckley *et al.*, 2001; cf. especially the first and last sentences in this paper) and despite Olmstead's promise our reply was rejected. It has since been published elsewhere (Heads and Craw, 2004). As the Roman historian wrote: *to use one's official position for the furtherance of private animosities was to set a bad enough example [...] it degraded the authority of that college* (Livy, 1976).

Donoghue (2001) argued that the key to attracting the most interesting work to *Systematic Biology* is publishing papers that are controversial because they push the envelope in one way or another. In this connection I'm concerned about the 'Points of View' and 'Book Review' sections. In the 1970's and 1980's these generated a lot of excitement and were must reading for everyone in the field. My impression is that they have lost their edge [...].

Plagiarism

If Owen could steal the credit for someone else's achievements, he would always do so; if he could not, he would strive to discredit the achievement.

Barber, 1980

The two 'original' platforms on which Gould built his synthesis, namely 'punctuated equilibria' (Eldredge and Gould, 1972) and anti-panselectionism (Gould and Lewontin, 1979), both formed an important part of Croizat's (1958, 1964) synthesis. Gould presented himself as an omnivorous reader and remarkably learned, and it is striking that he did not even mention Croizat in any of his many books (including one on evolutionary theory 1433 pages long) or any other writing. This is in spite the fact that Gould had been

familiar with, and interested in, Croizat's work since his student days (Gould *in litt.*, to Croizat, 22 June 1978). In fact, Gould made many unjustified claims of originality, for example, in writing (Gould, 2002) that prior to his book *Historians of science had not previously discussed orthogenetic theories in this fairest light*, again 'overlooking' all of Croizat's work and the panbiogeographic analysis of the topic by Grehan and Ainsworth (1985). Recent commentators have noted that Gould's work is "annoyingly self-congratulatory" (Wake, 2002) and *approaches traditional neo-Darwinism far more closely than he explicitly admits* (Futuyma, 2002).

Thus, while one Harvard professor, Mayr, 'overlooked' Croizat's work (Mayr mentioned Croizat only once – Mayr, 1982b; cf. Croizat, 1984), because he totally disagreed with it and wanted to suppress it, another Harvard professor, Gould, subsequently 'overlooked' Croizat's work for a rather different reason. The link between suppression and plagiarism is generally overlooked by historians of science, but has certainly been important in the development of panbiogeography.

The conjoint plagiarism and suppression of panbiogeographic work in New Zealand is documented elsewhere (Heads, 2003b). In a related case, in 2000 I submitted a manuscript to the American journal *The Auk* presenting a new analysis of evolution in New Guinea birds. The article was rejected but soon afterwards, and before I had resubmitted it, I had a query about certain aspects of it from a graduate student at a well-known North American university. The systematics group there had been discussing the paper at their weekly meeting.

Conclusions

Teleology and natural selection vs. orthogenesis. While Croizat's critique of Darwin's natural selection and centers of origin theory is more well-known, at a deeper level panbiogeography is largely a critique of teleological explanation and the metaphysics of presence in biology. Teleological reasoning was strongly supported by Plato and Aristotle (authors whose work was brilliantly presented by Popper (1984) as the original totalitarian fascism), by the German idealists, and

by modern writers such as Mayr and Vogel. Panbiogeography instead follows Empedocles, writers of the Scientific Revolution such as Bacon, Spinoza, and Hume, and many modern tropical biologists in being unabashedly anti-teleological. Rejecting teleology means that structure can be seen as determining function, not the other way around, and refocuses attention on broad morphological trends rather than the current ecology of particular cases. Morphological trends are the result of orthogenetic development – non-random genetic changes caused by processes such as molecular drive. Natural selection only works on variation supplied in the first place by orthogenetic development. Orthogenesis was misleadingly portrayed by Mayr (1982c) as mystical and teleological, whereas in panbiogeography it is a purely material, non-goal-directed process. The morphogenetic trends themselves are not necessarily adaptive; subviable ones lead to extinction.

Most neo-Darwinian ecological discourse reflects an acceptance of the ‘empty niche syndrome’, in which authors imagine natural selection forcing structure into a particular part of the environment. With purely random mutation and ‘selection pressure’ towards an ‘empty niche’ anything is possible. Whatever the mechanism, the results of totipotent natural selection and totipotent teleology are the same. Everything is for the best, for the good/advantage of the species. Orthogenesis or a neutral model, however, will not give this result, and a concept of evolution by ‘adaptation’ in response to selection pressure can be replaced with one of morphogenetic series, structured eterring function, and pre-adaptation.

Adaptive radiation vs. non-adaptive juxtaposition.

Mayr is the most well-known member of the New York school of zoogeography and was probably the most influential comparative biologist of the twentieth century. He formulated his key concept of founder dispersal based on his interpretations of New Guinea bird biogeography. This work and subsequent studies in the region (Mayr and Diamond, 2001) completely overlooked the complex geological history of New Guinea and its relevance for evolution. The importance of terrane tectonics for the biogeography of New Zealand, New Guinea and Indonesia has been explored elsewhere (Heads, 1990, 2001a, 2002a,

2003a) and this work indicates that founder dispersal is simply unnecessary. Its existence has also been repeatedly questioned by geneticists. Using founder dispersal leads merely to conclusions of biogeographic ‘miracles’, ‘mysteries’ and ‘paradoxes’, as its own authors have admitted (Mayr and Phelps, 1967; Mayr and Diamond, 2001, as discussed above).

Distributions elsewhere have also been accounted for using tectonics, rather than founder dispersal. For example, La Greca (1998) attributed evolution in Mediterranean Orthoptera to Paleogene terrane tectonics: a western terrane (Alborana) broke off from the African plate and crossing the Tethys docked with the Iberian-Sarfian-Corsican plate, while one or more eastern terranes accreted with the Afghanian-Iranian edge of the Eurasian plate.

The highest diversity of Neotropical Ericaceae occurs in Antioquia, NW Colombia (23 genera, over 100 species). This has been attributed to ‘adaptive radiation’ in the very wet climate there, but a similar pattern occurs in pantropical marine groups, such as fiddler crabs (*Uca*), which have maximum diversity around the coasts of NW Colombia. This pattern and its occurrence in both marine and alpine groups can easily be explained as the result of terrane accretion from the Pacific side (Heads, 2003a). In North America, the very high plant diversity in California can likewise be accounted for by terrane accretion.

The synthetic concept of ‘adaptive radiation’ relies on two of the older concepts, teleological adaptation and center of origin/dispersal. (A radiation must, by definition, be from a central point). Recognition of the importance of non-teleological evolution by orthogenesis and the significance of terrane accretion for biogeography in areas such as the SW Pacific, the Mediterranean, Colombia, and California indicates that diverse groups there may be better seen as the result of non-adaptive juxtaposition rather than adaptive radiation.

Panbiogeography and metapopulations. Hubbell (2001) termed MacArthur and Wilson’s (1967) ‘equilibrium theory’ of island biogeography a ‘radical theory’, but this is not an accurate description. Equilibrium theory is simply an extrapolation of Darwin-Wallace dispersal biogeography, with founder dispersal from a mainland center of origin playing the

dominant role. In contrast, panbiogeography theory does not rely on a totally hypothetical mainland source or on equally hypothetical founder effect dispersal; instead it stresses normal migration by ordinary means of survival among unstable local populations, any of which may go extinct, and regional persistence. This 'metapopulation' approach is eminently panbiogeographic and, like panbiogeography, suggests that taxa may survive environmental change by persisting more or less *in situ*, not in a few, large 'refugia', but in many, small ones. These latter hardly warrant the name 'refugia' as they are individually ephemeral and so small that they are ecological rather than geographic entities. Thus in northern Sweden, contrary to the conventional view that isolated mountains were completely covered with forest some thousands of years ago, Bruun and Moen (2003) concluded that many alpine plants survived the forest period on the isolated mountains, probably on cliffs and slopes too steep for closed forest. Conversely, taxa can survive glaciations on nunataks, rocky areas projecting above ice and snow. For example, disjunct NE American populations of otherwise Cordilleran species may be relictual and have survived the ice ages in this way, and thus do not require theories of long-distance dispersal (Weber, 2003).

Biogeography and geology. As indicated above, geologists have no real expertise or even interest in deciding whether or not there were small areas of emergent land in a region. In this and many other cases biologists have vastly more potentially valuable information. Usually this is ignored because chance distribution is assumed and geological evidence or even theory is treated as 'harder' than biological data. Thus, biologists usually defer to geologists' opinions on paleogeography. History shows that biological information can be used as effectively as geological information in making predictions about paleogeography. For example, land connections between South America and Africa, Africa and Australia, and Australia and South America were postulated by biologists centuries before their acceptance by geologists, and Wegener (1924) used these as key evidence in his argument for continental drift. Likewise, Croizat (1961) predicted the hybrid nature of North America based on biogeographic analysis decades before the

development of modern geological ideas on accreted terranes in the west.

Phylogeography, paleontology and Matthewian dispersalism. Genes and fossils are specially privileged entities in neo-Darwinism, and geneticists and paleontologists have historically been the most unquestioning followers of this orthodoxy. Ecologists and, above all, systematists have been more reticent about the claims of the Modern Synthesis. Paleontology has been the subject of much critique by the cladists as well as by panbiogeography, while genetics has had a new lease of life with the development of molecular techniques. However, the basic assumptions of the science have not changed for decades. For example, genetic similarity of populations is still seen as the result of either similar selection pressure (and random mutation) or gene flow. Phylogeography generally presents a technically advanced form of founder dispersalism, based on the same key concepts of 'center of origin' and 'means of dispersal'. The modern phylogeographers are the *pale, emaciated epigones* (Nietzsche, 2000) of the nineteenth century dispersalists, held in thrall to the idea of a center of origin, the simplicity of which 'captivates the mind'.

Many phylogeographers are genetics technicians working within a very narrow speciality. Unlike traditional systematists they do not develop a familiarity with a wide range of disciplines, each with its own history and concepts. If a biogeographer wishes to investigate a group of, say, 20 species, obviously it is ideal to have both molecular and traditional studies available. However, it is generally more useful to have a thorough traditional taxonomic revision with all described taxa and a significant number of specimens accounted for, morphological descriptions, detailed maps, notes on ecology, discussion of puzzling specimens, anomalous altitude records, etc., than a molecular cladogram, which usually will not even include all the described taxa.

Geneticists and paleontologists have traditionally shown little real interest in biogeography. For example, one paleontologist's book on evolutionary theory (Gould, 2002) comprises 1433 pages of which only three (pp. 113-115), *i.e.* 0.2%, deal with biogeography. Very few paleontological papers include dis-

tribution maps of fossil taxa or (as would be most desirable) maps of fossil and extant members of a group (Matthew, 1915 is an impressive exception). In paleontology and genetics, biogeography is regarded as a minor, 'add-on' to a phylogeny (Williams and Ebach, 2004) and the spatial context of evolution is basically ignored. In most phylogeographic studies the geographic distribution is not shown on the cladograms and any maps show only sampling sites.

It will not escape the discerning reader that the empty, arrogant claims typical of both the New York school and its modern derivative, phylogeography, are simply inflated self-publicity. Genetics has been the 'star' of biology for decades, and perhaps it is natural that its practitioners have become so narcissistic. They assume they can wander into a field like biogeography and make original, valid contributions without knowing even the basics of the subject. Cladistics was an attempt to get away from using absolute degree of difference in systematics. But in modern phylogeography degree of difference is again taken to be meaningful and even of fundamental importance, especially with respect to time. Degree of divergence, whether molecular or morphological, may have very little to do with either the age of a group or the time involved in its evolution, and may be determined rather by the evolutionary potential of the group. Under this view, in any given phase of evolution, for example, during a period of rifting, some groups will diverge to species level, others to generic level, while yet others may diverge only cryptically or not at all. This explains why the same biogeographic track is always held by taxa of obviously different rank. The different groups sharing a distribution pattern always involve differing degrees of differentiation, due to differing original genetic potential and thus different responses in a single phase of evolution. Phylogeography, however, assumes that the pattern, and the differing degrees of difference, are due to different phases of evolution and thus sees the groups as having different histories. The biogeographic pattern is assumed to be a pseudo-pattern caused by chance congruence. This is just chance dispersal all over again.

German idealism in modern biology: Mayr, Hennig and phylogeography. Modern dispersalism, cladis-

tics and phylogeography are all based on precepts of German idealism, and this is especially clear in the work of Mayr and Hennig which is idealist by root and implication. For example, the work of these authors always assumes an ancestor which is homogeneous, either a single parent pair or a monomorphic species, whereas panbiogeography utilizes a concept of polymorphous ancestral complex. A second important concept linking Mayr and Hennig's work concerns 'dispersal' and speciation: Darwin's 'chance dispersal', Mayr's 'founder dispersal' and Hennig's 'speciation by colonization' all refer to the same process. A further fundamental concept linking Hennig and Mayr's work, as well as modern phylogeography, is the 'progression rule', in which primitive taxa are assumed to remain near the center of origin and advanced taxa migrate away.

Criticism of panbiogeography. The neo-Darwinian 'Modern Synthesis', having incorporated the New York school of zoogeography, hardened through the late 1940s and 1950s into the sclerotic institution that still dominates biology today. Schwartz (1999) described its intolerance of any criticism and active suppression of any alternative ideas. It has successfully immunized itself from attack by misrepresenting any criticism of it as unscientific denial of evolution itself, and the authors of critique as dangerous and anti-social. For example, G. G. Simpson (quoted in Nelson, 1977, and Hull, 1988) described Croizat as a member of the 'lunatic fringe'.

Contemporary biogeography, especially phylogeography, is simply boring to read because the 'mindless slaves' that produce it ignore Horace's dictum *sapere aude* (*Epistle* 1, 2) – "dare to be wise" – and are not bold enough to produce anything new. Their only novelties are timid variations, and the trite stories they tell involve the same old ideas that have been worked and reworked for over 2000 years. Ancient teleology is replayed every night on television, and 'mysterious means of dispersal' and 'perfect adaptations' are extolled as 'wonders of nature'.

Most critics of panbiogeography are taxonomic specialists in particular groups and have little if any expertise in general biogeography. Few seem to have made any positive contribution to comparative biogeography, such as describing a previously unknown

biogeographic pattern— not just a species distribution, but a general pattern, shared by different taxa. Of course, the critics, such as McDowall (2004), feel comparative studies are not a valid approach anyway, and Briggs (2004) even advised the biogeographer against comparing the distributions of many taxa, as this involves *combing through an enormous literature*. Instead he suggested that a student should concentrate on a *particular group* and by learning *as much as possible about its anatomy, physiology, behavior, systematics, biochemistry, paleontology and evolution [...] let that particular group speak to you [...]*. But why should we all have to play his game? Obviously, learning all about the biochemistry, paleontology, etc. of a group would take a life-time and leave no time for comparative analysis. A mystic or a taxonomic specialist may feel it is possible to understand everything about the nature of the ‘leaf’, of a species, or of a country by spending a life-time studying a single leaf, species or country, but a comparative or structuralist biologist forsakes this detailed knowledge for the perspective of a broader approach.

Acknowledgments

I thank Mauro Cavalcanti, Frank Climo, Karin Mahlfeld and Andrés Moreira-Muñoz for commenting on an early draft and supplying literature; to Peter Ashton, Jorge Crisci, Malte Ebach, Niles Eldredge, David Hull, Juerg de Marmels, Juan J. Morrone, Gary Nelson, Richard O’Grady, Brian Patrick, Susanne Renner, Tim Waters, J.A. Wilkinson, Bastow Wilson, and Mario Zunino for data and literature; and to Juan J. Morrone and Jorge Llorente for inviting me to contribute to this volume.

References

Adema, F. and R.W.J.M. van der Ham. 1993. *Cnesmocarpon* (gen. nov.), *Jagera*, and *Trigonachras* (Sapindaceae-Cupanieae): phylogeny and systematics. *Blumea*, 38: 173-215.

Albert, V.A., B.D. Mishler and M.W. Chase. 1992. Character-state weighting for restriction site data in phylogenetic reconstruction, with an example from chloroplast DNA, pp. 369-403. In: P.S. Soltis, D.E. Soltis

and J.J. Doyle (eds.). *Molecular systematics of plants*. Chapman and Hall, New York.

Andersen, K. 1912. *A catalogue of the Megachiroptera in the British Museum*. British Museum (Natural History), London.

Andrewes, A. 1967. *The greeks*. Hutchinson, London.

Arber, A. [1950] 1970. *The natural philosophy of plant form*. Hafner, Darien, Connecticut.

Argan, C.G. 1974. The Italian Cinquecento and idealism, pp. 118-133. In: Huyghe, R. (ed.). *Larousse encyclopedia of Renaissance and Baroque art*. Hamlyn, London.

Aristotle. [c. 340 B.C.] 1968. *Parts of animals. Movement of animals. Progression of animals*. Transl. A.L. Peck and E.S. Forster. Heinemann, London.

Arthur, W. 2002. The emerging conceptual framework of evolutionary developmental biology. *Nature*, 415: 757-764.

Ashton, P.S., S. Slive and A. Davies. 1982. Jacob van Ruisdael’s trees. *Arnoldia*, 42: 2-31.

Ashworth, W.B. Jr. 1990. Natural history and the emblematic world view, pp. 303-332. In: D.C. Lindberg and R. S. Westman (eds). *Reappraisals of the Scientific Revolution*. Cambridge University Press, Cambridge.

Aubréville, A. 1971. À propos de l’ ‘Introduction à la phytogéographie des pays tropicaux’ de R. Schnell. *Adansonia sér. 2*, 11: 691-698.

Aurelius Antoninus, M. 1979. *Meditations*. Transl. M. Staniforth. Penguin, Harmondsworth.

Avise, J.C. 1994. *Molecular markers, natural history and evolution*. Chapman and Hall, New York.

Avise, J.C. 2000. *Phylogeography: The history and formation of species*. Harvard University Press, Cambridge, Massachusetts.

Ayala, F. J, A. Escalante, C. O’Huigin and J. Klein. 1995. Molecular genetics of speciation and human origins, pp. 187-207. In: W.M. Fitch and F.J. Ayala (eds.). *Tempo and mode in evolution: Genetics and paleontology 50 years after Simpson*. National Academy Press, Washington D.C.

Bacon, F. [1623] 1970. *De augmentis scientiarum* (in *The philosophical works of Francis Bacon*), transl. Ellis & Speding. Books for Libraries Press Freeport, New York.

Barber, L. 1980. *The hey-day of natural history 1820-1870*. Jonathan Cape, London.

Barzun, J. 2000. *From dawn to decadence: 500 years of Western cultural life*. HarperCollins, New York.

Battisti, E. 1974. The Italian Renaissance and the ideal of beauty: the Quattrocento, pp. 98-112. In: R.

- Huyghe (ed.). *Larousse encyclopedia of Renaissance and Baroque art*. Hamlyn, London.
- Berra T.M., L.E.L.M. Crowley, W. Ivantsoff and P.A. Fuerst.** 1996. *Galaxias maculatus*: An explanation of its biogeography. *Mar. Freshwater Res.*, 47: 845-849.
- Borges, J.L.** 1978. *The book of sand*. Dutton, New York.
- Bossuyt, F. and M.C. Milinkovitch.** 2001. Amphibians as indicators of early Tertiary 'out-of-India' dispersal of vertebrates. *Science*, 292: 93-95.
- Bowler, P.J.** 1996. *Life's splendid drama: Evolutionary biology and the reconstruction of life's ancestry, 1860-1940*. University of Chicago Press, Chicago.
- Bremekamp, C.E.B.** 1952. A re-examination of Caesalpino's system. *Acta Bot. Neerlandica*, 1: 580-593.
- Briggs, J.C.** 1974. Operation of marine zoogeographic barriers. *Syst. Zool.*, 23: 248-256.
- Briggs, J.C.** 2003. Marine centers of origin as evolutionary engines. *J. Biogeogr.*, 30: 1-18.
- Briggs, J.C.** 2004. The ultimate expanding earth hypothesis. *J. Biogeogr.*, 31: 855-857.
- Bronowski, J. and B. Maslish.** 1960. *The Western intellectual tradition: From Leonardo to Hegel*. Penguin, Harmondsworth.
- Brooks, D.R.** 1981. Review of P.W. Price, 1980, 'Evolutionary biology of parasites'. *Syst. Zool.*, 30: 104-107.
- Brooks, R.R.** 1987. *Serpentine and its vegetation: A multidisciplinary approach*. Dioscorides Press, Portland.
- Bruun, H.H. and J. Moen.** 2003. Nested communities of alpine plants on isolated mountains: Relative importance of colonization and extinction. *J. Biogeogr.*, 30: 297-303.
- Buckley, T.R., C. Simon and G.K. Chambers.** 2001. Phylogeography of the New Zealand cicada *Maoricicada campbelli* based on mitochondrial DNA sequences: ancient clades associated with Cenozoic environmental change. *Evolution*, 55: 1395-1407.
- Buffon, G.L.L. de.** 1749-1789. *Histoire naturelle*. 36 vols. Paris.
- Buller, W.L.** [1888]. 1967. *Birds of New Zealand*. 2nd ed. Whitcoulls, Christchurch.
- Burckhardt, J.** [1860] 1990. *The civilization of the Renaissance in Italy*. Penguin, Harmondsworth.
- Burn, A.R.** 1966. *The Pelican history of Greece*. Penguin, Harmondsworth.
- Burrows, J.E.** 1990. *Southern African ferns and fern allies*. Frandsen, Sandton.
- Butterfield, H.** 1957. *The origins of modern science 1300-1800* (revised ed.). Free Press, New York.
- Cary, M. and T.J. Haarhoff.** 1940. *Life and thought in the Greek and Roman world*. Methuen, London.
- Cassirer, E.** [1927] 1963. *The individual and the cosmos in Renaissance philosophy*. Transl. M. Domandi. Blackwell, Oxford.
- Castiglione, B.** [1528] 1967. *The book of the courtier*. Transl. G. Bull. Penguin, Harmondsworth.
- Cavendish, A.P.** 1964. Early Greek philosophers, pp. 1-13. In: D.J. O'Connor (ed). *A critical history of Western philosophy*. Free Press, New York.
- Caesalpino, A.** 1583. *De plantis libri XVI*. Florence.
- Chesterton, G.K.** 1981. *The Penguin complete Father Brown*. Penguin, Harmondsworth.
- Clark, N.** 2001. De/feral: Introduced species and the metaphysics of conservation, pp. 86-106. In: L. Simons and H. Worth (eds.). *Derrida downunder*. Dunmore, Palmerston North.
- Clements, F.E. and V.E. Shelford.** 1939. *Bioecology*. Wiley, New York.
- Cockayne, L.** 1928. *The vegetation of New Zealand*. 2nd ed. Leipzig.
- Colacino, C.** 1997. Léon Croizat's biogeography and macroevolution, or... 'out of nothing, nothing comes'. *Philipp. Scient.*, 34: 73-88.
- Colacino, C. and J. Grehan.** 2003. Ostracismo alle frontiera della biologia evoluzionistica: Il caso Léon Croizat, pp. 195-220. In: M.M. Capria (ed.), *Scienza e democrazia*. Liguori, Naples.
- Collingwood, R.G.** 1945. *The idea of nature*. Clarendon Press, Oxford.
- Conti, E., T. Eriksson, J. Schönenberger, K.J. Sytsma and D.A. Baum.** 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: Evidence from phylogeny and molecular dating. *Evolution*, 56: 1931-1942.
- Copleston, F.** 1962. *A history of philosophy. Vol. 1. Greece and Rome. Pt. 1*. Doubleday, New York.
- Cortés B., R. and P. Franco R.** 1997. Análisis panbiogeográfico de la flora de Chiribiquete, Colombia. *Caldasia*, 19: 465-478.
- Cracraft, J.** 2002. The seven great questions of systematic biology: an essential foundation for conservation and the sustainable use of biodiversity. *Ann. Missouri Bot. Gard.*, 89: 127-144.
- Craw, R.C.** 1978. Two biogeographical frameworks: implications for the biogeography of New Zealand. A review. *Tuatara*, 23: 81-114.

- Craw, R.C.** 1984. Charles Darwin on 'laws of growth', pp. 19-20. In: R.C. Craw and G.W. Gibbs (eds.). *Croizat's panbiogeography and Principia botanica: Search for a novel biological synthesis*. Victoria University Press, Wellington.
- Craw, R.C. and G.W. Gibbs (eds.)**. 1984. *Croizat's Panbiogeography and Principia botanica: Search for a novel biological synthesis*. Victoria University Press, Wellington.
- Craw, R.C., J.R. Grehan and M.J. Heads**. 1999. *Panbiogeography: Tracking the history of life*. Oxford University Press, New York.
- Craw, R. and M. Heads**. 1988. Reading Croizat. *Rivista di Biologia – Biology Forum* [Perugia], 81: 499-532.
- Craw, R.C. and G. Sermonti (eds.)**. 1988. Special issue on panbiogeography. *Rivista di Biologia – Biology Forum* [Perugia], 81(4): 457-615.
- Crawford, D.J., J.D. Palmer and M. Kobayashi**. 1992. Chloroplast DNA restriction site variation and the evolution of the annual habit in North American *Coreopsis* (Asteraceae), pp. 280-294. In: P.S. Soltis, D.E. Soltis and J.J. Doyle (eds.). *Molecular systematics of plants*. Chapman and Hall, New York.
- Crisci J.V. and J.J. Morrone**. 1992. Panbiogeografía y biogeografía cladística: paradigmas actuales de la biogeografía histórica. *Ciencias* No. special 6 (Noviembre): 87-97.
- Croizat, L.** 1952. *Manual of phytogeography*. Junk, The Hague.
- Croizat, L.** 1958. *Panbiogeography*. Published by the Author, Caracas.
- Croizat, L.** 1961. *Principia botanica*. Published by the Author, Caracas.
- Croizat, L.** 1964. *Space, time form: The biological synthesis*. Published by the Author, Caracas.
- Croizat, L.** 1965. An introduction to the subgeneric classification of *Euphorbia* L. with stress on the South African and Malagasy species. I. *Webbia*, 20: 573-706.
- Croizat, L.** 1967. An introduction to the subgeneric classification of *Euphorbia* L. with stress on the South African and Malagasy species. II. *Webbia*, 22: 83-202.
- Croizat, L.** 1968a. Introduction raisonnée à la biogéographie de l'Afrique. *Mems. Bot. Soc. Broteriana* [Coimbra], 20: 1-400.
- Croizat, L.** 1968b. The biogeography of the tropical lands and islands east of Suez –Madagascar: with particular reference to the dispersal and form-making of *Ficus* L., and different other vegetal and animal groups. *Atti Ist. Bot. Lab. Crittogam. Università di Pavia* ser. 6, 4: 1-400.
- Croizat, L.** 1968c. Riflessioni sulla biogeografia in generale, e su quella della Malesia in particolare. *Atti Ist. Bot. Lab. Crittogam. Università di Pavia* ser. 6, 5: 19-190.
- Croizat, L.** 1972. An introduction to the subgeneric classification of *Euphorbia* L. with stress on the South African and Malagasy species. III. *Webbia*, 27: 1-221.
- Croizat, L.** 1973. Les Euphorbiacées vues en elles-mêmes, et dans leurs rapports envers l'angiospermie en général. *Mem. Soc. Broteriana*, 23: 5-207.
- Croizat, L.** 1975a. Biogeografía analítica y sintética ("Panbiogeografía") de las Américas. *Bol. Acad. Cienc. Fís., Mat. Nat.* [Caracas], 35: (103-106). 890 p. [Also published as *Bibl. Acad. Cienc. Fís., Mat. Nat.* [Caracas] 15 and 16. 1976.]
- Croizat, L.** 1975b. *Relación de las guerras entre Aníbal y Roma, 218-202 a.d.C.* Ministry of Defence, Caracas.
- Croizat, L.** 1977a. Review of 'Areografía: Estrategia geográfica de las especies' by E.H. Rapoport. *Syst. Zool.*, 26: 230-233.
- Croizat, L.** 1977b. Carlos Darwin y sus teorías. *Bol. Acad. Ciencias Fís., Mat. Nat.* [Caracas] 37 (no. 113): 15-90. ['Conclusions' also published in English translation as 'Charles Darwin and his theories', pp. 21-25. In: R. C. Craw and G. W. Gibbs (eds.). *Croizat's panbiogeography and principia botanica: Search for a novel biological synthesis*. Victoria University Press, Wellington. 1984].
- Croizat, L.** 1978. Deduction, induction, and biogeography. *Syst. Zool.*, 27: 209-213.
- Croizat, L.** 1979. Review of 'Biogeographie: Fauna und Flora der Erde und ihre geschichtliche Entwicklung' by P. Bănărescu and N. Bocaiu. *Syst. Zool.*, 28: 250-252.
- Croizat, L.** 1981. Vicariance/vicariism, panbiogeography, 'vicariance biogeography', etc.: a clarification. *Syst. Zool.*, 31: 291-304.
- Croizat, L.** 1984. Mayr vs. Croizat: Croizat vs. Mayr –an enquiry, pp. 49-66. In: R.C. Craw and G.W. Gibbs (eds.). *Croizat's panbiogeography and principia botanica: Search for a novel biological synthesis*. Victoria University Press, Wellington.
- Croizat, L., G.J. Nelson and D.E. Rosen**. 1974. Centers of origin and related concepts. *Syst. Zool.*, 23: 265-287.

- Darlington, P.D.** [1957] 1966. *Zoogeography: The geographical distribution of animals*. Wiley, New York.
- Darlington, P.D.** 1959. Area, climate and evolution. *Evolution*, 13: 488-510.
- Darwin, C.** 1860. *On the origin of species*. 1st ed., 5th thousand. John Murray, London.
- Darwin, C.** [1882] 1971. *On the origin of species*. 6th ed. Dent, London.
- Darwin, F.** 1959. *The life and letters of Charles Darwin*. Vol. 2. Basic Books, New York.
- Debus, A.G.** 1978. *Man and nature in the Renaissance*. Cambridge University Press, Cambridge.
- Delaunay, P.** 1964. The Renaissance: the descriptive sciences. Zoology, pp. 149-156. In: R. Taton (ed.). *The beginnings of modern science*. Thames and Hudson, London.
- Derrida, J.** 1976. *Of grammatology*. Transl. G. Spivak. Johns Hopkins University Press, Baltimore.
- Derrida, J.** 1982. *Margins of philosophy*. Transl. A. Bass. Harvester Press, University of Chicago, Chicago.
- Derrida, J.** 1995. *Points... interviews, 1974-1994*. Stanford University Press, Stanford.
- Desmond, A.** 1989. *Politics of evolution: Morphology, medicine, and reform in radical London*. University of Chicago Press, Chicago.
- Desmond, A. and J. Moore.** 1992. *Darwin*. Penguin, London.
- Domke, W.** 1934. Untersuchungen über die systematische und geographische Gliederung der Thymelaeaceen. *Bibliot. Bot.*, 27: 1-151.
- Donovan, S.K. and C.R.C. Paul. (eds.)** 1998a. *The adequacy of the fossil record*. Wiley, Chichester.
- Donovan, S.K. and C.R.C. Paul.** 1998b. Introduction: adequacy vs. incompleteness, pp. ix-x. In: **Donovan, S.K. and C.R.C. Paul. (eds.)**. *The adequacy of the fossil record*. Wiley, Chichester.
- Donoghue M.J.** 2001. A wish list for Systematic Biology. *Syst. Biol.*, 50: 755-757.
- Douglas, K.** 1966. *Alamein to Zem Zem*. Faber and Faber, London.
- Dover, G.A.** 2000. *Dear Mr Darwin: Letters on the evolution of life and human nature*. Weidenfeld and Nicolson, London.
- Dover, G.A., A.R. Linares, T. Bowen and J.M. Hancock.** 1993. Detection and quantification of concerted evolution and molecular drive. *Methods in Enzymology*, 224: 631-646.
- Ebach, M. and C.J. Humphries.** 2002. Cladistic biogeography and the art of discovery. *J. Biogeogr.* 29: 427-444.
- Ebach, M. and C.J. Humphries.** 2003. Ontology of biogeography. *J. Biogeogr.*, 30: 959-962.
- Eibl, J.M., G.M. Plunkett and P.P. Lowry II.** 2001. Evolution of *Polyscias* sect. *Tieghemopanax* (Araliaceae) based on nuclear and chloroplast DNA sequence data. *Adansonia*, sér. 3, 23: 23-48.
- Eigenmann, C.H.** 1921. The nature and origin of the fishes of the pacific slope of Ecuador, Peru and Chili. *Proc. Amer. Phil. Soc.*, 60: 503-523.
- Ekman, S.** 1953. *Zoogeography of the sea*. Sidgwick and Jackson, London.
- Eldredge, N. and S.J. Gould.** 1972. Punctuated equilibria: an alternative to phyletic gradualism, pp. 82-115. In: T.J.M. Schopf (ed.). *Models in paleobiology*. Freeman, San Francisco.
- Farrington, B.** 1961. *Greek science. 1. Thales to Aristotle*. Penguin, Harmondsworth.
- Farrington, B.** 1949. *Greek science. 2. Theophrastus to Galen*. Penguin, Harmondsworth.
- Feduccia, A.** 1996. *The origin and evolution of birds*. Yale Univ. Press, New Haven.
- Fernández-Amesto, F.** 2000. *Civilisations*. Macmillan, London.
- Fisher, R.A.** 1936. The measurement of selective intensity. *Proc. Roy. Soc. London B*, 121: 58-62.
- Flaubert, G.** [1881] 1976. *Bouvard and Pécuchet*. Transl. A.J. Krailsheimer. Penguin, Harmondsworth.
- Fortino, A.D. and J.J. Morrone.** 1997. Signos gráficos para la representación de análisis panbiogeográficos. *Biogeographica* [Paris], 73: 49-56.
- Frey, J.K.** 1993. Modes of peripheral isolate formation and speciation. *Syst. Zool.*, 42: 373-381.
- Fukuda, T., J. Yokoyama and H. Ohashi.** 2001. Phylogeny and biogeography of *Lycium* (Solanaceae): inferences from chloroplast DNA sequences. *Mol. Phylog. Evol.*, 19: 246-258.
- Futuyma, D.J.** 1998. *Evolutionary biology*. 3rd ed. Sinauer, Sunderland, Massachusetts.
- Futuyma, D.J.** 2002. Stephen Jay Gould à la recherche du temps perdu. *Science*, 296: 661-663.
- Gee, H.** 1999. *In search of deep time: Beyond the fossil record to a new history of life*. Free Press, New York.
- George, W.** 1987. Complex origins, pp. 19-131. In: T.C. Whitmore (ed.). *Biogeographical evolution of the Malay Archipelago*. Clarendon Press, Oxford.

- Goethe, J. von.** [1786-1788] 1962. *Italian journey*. Transl. W.H. Auden and E. Mayer. Collins, London.
- Gould, S.J.** 1989. *The Burgess Shale and the nature of history*. Penguin, London.
- Gould, S.J.** 1998. *Leonardo's mountain of clams and the diet of Worms: Essays on natural history*. Three Rivers Press, New York.
- Gould, S.J.** 2002. *The structure of evolutionary theory*. Belknap Press, Harvard University, Cambridge.
- Gould, S.J. and R.C. Lewontin.** 1979. The span-drels of San Marco and the Panglossian paradigm. A critique of the adaptationist program. *Proc. Roy. Soc. London B*, 205: 581-598.
- Gray, A.** 1874. Letter. *Nature*, 10: 79.
- Grehan, J.R. and R. Ainsworth.** 1985. Orthogenesis and evolution. *Syst. Zool.*, 34: 174-192.
- Groves, C.P.** 1989. *A theory of primate and human evolution*. Oxford University Press, New York.
- Guicciardini, F.** [1532] 1966. *The history of Florence*. Transl. C. Grayson. New English Library, London.
- Hajdu, E.** 1998. Toward a panbiogeography of the seas: sponge phylogenies and general tracks, pp. 95-108. In: Y. Watanabe and N. Fusetani (eds). *Sponge sciences: Multidisciplinary perspectives*. Springer, Tokyo.
- Hall, A.R.** 1966. *The Scientific Revolution 1500-1800: The formation of the modern scientific attitude*. Beacon Press, Boston.
- Hall, A.R.** 1968. Intellectual tendencies. *Science*, pp. 386-413. In: G.R. Elton (ed.). *The new Cambridge modern history. Vol. II. The Reformation 1520-1559*. Cambridge University Press, Cambridge.
- Hall, A.R.** 1983. *The revolution in science 1500-1750*. Longman, London.
- Hall, J.P. and D.J. Harvey.** 2002. A survey of androconial organs in Riodinidae (Lepidoptera). *Zool. J. Linn. Soc.* 136: 171-197.
- Hall, R.** 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea, pp. 99-131. In: R. Hall and J.D. Holloway (eds.). *Biogeography and geological evolution of SE Asia*. Backhuys, Leiden.
- Hall, R.** 2001. Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea, pp. 35-56. In: I. Metcalfe, J.M.B. Smith, M. Morwood and I.D. Davidson (eds.), *Faunal and floral migrations and evolution of SE Asia and Australia*. Balkema, Rotterdam.
- Hay, D.** 1968. Intellectual tendencies. Literature: the printed book, pp. 359-386. In: G.R. Elton (ed.). *The new Cambridge modern history. Vol. II. The Reformation 1520-1559*. Cambridge University Press, Cambridge.
- Heads, M.** 1984. Principia botanica: Croizat's contribution to botany, pp. 26-48. In: R.C. Craw and G.W. Gibbs (eds.). *Croizat's panbiogeography and principia botanica: Search for a novel biological synthesis*. Victoria University Press, Wellington.
- Heads, M.** 1985. On the nature of ancestors. *Syst. Zool.*, 34: 205-215.
- Heads, M.** 1990a. Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand J. Zool.*, 16: 549-586.
- Heads, M.** 1990b. Mesozoic tectonics and the deconstruction of biogeography: a new model of Australasian biology. *J. Biogeogr.*, 17: 223-225.
- Heads, M.** 1994. Morphology, architecture and taxonomy in the *Hebe* complex (Scrophulariaceae). *Bull. Mus. nat. d'Histoire nat. Paris 4e sér.*, 16, sect. B, *Adansonia*, 163-191.
- Heads, M.** 1996. Biogeography, evolution and taxonomy in the Pacific genus *Coprosma* (Rubiaceae). *Candollea*, 51: 381-405.
- Heads, M.** 1998a. *Coprosma decurva* (Rubiaceae), a new species from New Zealand. *New Zealand J. Bot.*, 36: 65-69.
- Heads, M.** 1998b. Biogeographic disjunction along the Alpine fault, New Zealand. *Biol. J. Linn. Soc.*, 63: 161-176.
- Heads, M.** 1998c. Biodiversity in the New Zealand divaricating tree daisies: *Olearia* sect. nov. (Compositae: Astereae). *Bot. J. Linn. Soc.*, 127: 239-285.
- Heads, M.** 2001a. Birds of paradise, biogeography and ecology in New Guinea: a review. *J. Biogeogr.*, 28: 893-927.
- Heads, M.** 2001b. Regional patterns of biodiversity in New Guinea plants. *Bot. J. Linn. Soc.*, 136: 67-73.
- Heads, M.** 2002a. Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. *J. Biogeogr.*, 29: 261-284.
- Heads, M.** 2002b. Regional patterns of biodiversity in New Guinea animals. *J. Biogeogr.*, 29: 285-294.
- Heads, M.** 2003a. Ericaceae in Malesia: vicariance biogeography, terrane tectonics and ecology. *Telopea*, 10: 311-449.
- Heads, M.** 2003b. A note on some attitudes in New Zealand botany. *New Zealand Bot. Soc. Newsl.*, 72: 12-14.
- Heads, M.** 2003c. The current status of biogeography in New Zealand. *J. Auckland Bot. Soc.*, 58: 83-84.

- Heads, M.** In press a. Towards a panbiogeography of the seas. *Biol. J. Linn. Soc.*
- Heads, M.** In press b. Dating evolutionary events: A critique of the molecular clock approach. *Cladistics*.
- Heads, M. and R. Craw.** 1984. Bibliography of the scientific work of Leon Croizat, 1930-1984. *Tuatara*, 27: 67-75.
- Heads, M., and Craw, R.** 2004. The Alpine fault biogeographic hypothesis revisited. *Cladistics*, 20: 184-190.
- Henderson, I.** 1990. Biogeography without area?, pp. 59-72. In: P.Y. Ladiges, C.J. Humphries and L.W. Martinielli (eds.). *Austral biogeography*. CSIRO, Melbourne.
- Hennig, W.** 1950. *Grundzüge einer theorie der phylogenetischen systematik*. Deutscher Zentralverlag, Berlin.
- Hennig, W.** 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Hoffmann, H.** 2000. The rise of life on earth: Messel –window on an ancient world. *Nat. Geog. Mag.*, 2000 (2): 34-51.
- Hosken, D.J. and P. Stockley.** 2004. Sexual selection and genital evolution. *Trends Ecol. Evol.*, 19: 87-93.
- Hubbell, S.P.** 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.
- Hull, D.** 1967. The metaphysics of evolution. *Brit. J. Hist. Sci.*, 3: 309-337.
- Hull, D.** 1988. *Science as a process: An evolutionary account of the social and conceptual development of science*. University of Chicago Press, Chicago.
- Hume, D.** [1779] 1977. *Dialogues concerning natural religion*. Bobbs-Merrill, Indianapolis.
- Humphries, C.J.** 2000. Form, space, time: which comes first? *J. Biogeogr.*, 27: 11-15.
- Hutton, F.J.** 1872. On the geographic relations of the New Zealand fauna. *Trans. New Zealand Inst.*, 5: 227-256.
- Huxley, J. (ed.).** 1940. *The new systematics*. Clarendon Press, Oxford.
- Huyghe, R.** 1974. The Italian Renaissance and the ideal of beauty: art forms and society, pp. 88-97. In: R. Huyghe (ed.). *Larousse encyclopedia of Renaissance and Baroque art*. Hamlyn, London.
- Ihering, H. von.** 1892. On the ancient relations between New Zealand and South America. *Trans. New Zealand Inst.*, 24: 431-445.
- Irwin, R.** 1994. *The Arabian nights: A companion*. Penguin, London.
- Isely, D.** 1994. *One hundred and one botanists*. Iowa State University Press, Ames.
- Jacobs, M.** 1980. Revolutions in plant description. *Misc. Papers Landbouwhogeschool Wageningen*, 19: 155-181.
- Jepsen, G.L., E. Mayr and G.G. Simpson (eds.).** 1949. *Genetics, paleontology and evolution*. (Edited for the Committee for Common Problems of Genetics, Paleontology and Systematics of the National Research Council). Princeton University Press, Princeton.
- Juniper, B.E., R.J. Robins and D.M. Joel.** 1989. *The carnivorous plants*. Academic Press, London.
- Juvenal. [c. 100 A. D.] 1967. *The sixteen satires*. Transl. P. Green. Penguin, Harmondsworth.
- Juvenal and Persius.** 1969. *Satires*. Transl. G.G. Ramsay. Heinemann, London.
- Kant, I.** [1790] 1978. *The critique of judgment*. Transl. J.C. Meredith. Clarendon Press, Oxford.
- Keast, A.** 1996. Pacific biogeography: patterns and processes, pp. 477-512. In: A. Keast and S.E. Miller (eds.). *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: Patterns and processes*. SPB Academic Publishing, Amsterdam.
- Kingdon, J.** 1974. *East African mammals*. Vol. 2A. Academic Press, New York.
- Kingdon, J.** 1982. *East African mammals*. Vol. 3D. Academic Press, New York.
- Kirkpatrick, R.** 2001. *The European Renaissance 1400-1600*. Longman, London.
- Kitto, H.D.F.** 1951. *The Greeks*. Penguin, Harmondsworth.
- Klass K.D., O. Zompro, N.P. Kristensen and J. Adis.** 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Science*, 296: 1456-1459.
- La Greca, M.** 1998. Biogeography of the palearctic Pamphagidae (Orthoptera). *Mem. Soc. Entomol. Ital.*, 77: 123-159.
- Landes, D.S.** 1999. *The wealth and poverty of nations: Why some are so rich and some are so poor*. Norton, New York.
- Larson, J.L.** 1971. *Reason and experience: The representation of natural order in the work of Carl von Linné*. University of California Press, Berkeley.
- Last, P.R. and J.D. Stevens.** 1994. *Sharks and rays of Australia*. CSIRO, Melbourne.
- Last, P.R. and G.K. Yearsley.** 2002. Zoogeography and relationships of Australasian skates (Chondrichthyes: Rajidae). *J. Biogeogr.*, 29: 1627-1641.

- Leigh, E.G. Jr.** 1999. *Tropical forest ecology: A view from Barro Colorado Island*. Oxford University Press, New York.
- Lenoir, T.** 1984. The eternal laws of form: morphotypes and the conditions of existence in Goethe's biological thought. *J. Social Biol. Structures*, 7: 1-8.
- Leopardi, G.** [1827] 1905. *Essays, dialogues and thoughts (Operette morali and Pensieri)*. Transl. J. Thomson. Routledge, London.
- Lessios, H.A., B.D. Kessing and J.S. Pearse.** 2001. Population structure and speciation in the tropical seas: global phylogeography of the sea urchin *Diodema*. *Evolution*, 55: 955-975.
- Ley, W.** 1968. *Dawn of zoology*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Livy** [c. 10 B.C.] 1976. *Rome and the Mediterranean*. Transl. H. Bettenson. Penguin, Harmondsworth.
- Llorente B., J. (ed.)**. 1991. *Historia de la biogeografía: Centros de origen y vicarianza*. Universidad Nacional Autónoma de México, Mexico City.
- Llorente Bousquets, J. and J. J. Morrone (eds.)**. 2001. *Introducción a la biogeografía en Latinoamérica: Teorías, conceptos, métodos y aplicaciones*. Universidad Nacional Autónoma de México, Mexico City.
- Llorente, J., J.J. Morrone, A. Bueno, R. Pérez-Hernández, A. Vilorio and D. Espinosa.** 2000. Historia del desarrollo y la recepción de las ideas panbiogeográficas de León Croizat. *Rev. Acad. Colomb. Cienc.*, 24: 549-557.
- Lockhart, P. J., P. A. McLenachan, D. Havell, D. Glenny, D. Huson and U. Jensen.** 2001. Phylogeny, radiation, and transoceanic dispersal of New Zealand alpine buttercups: molecular evidence under split decomposition. *Ann. Missouri Bot. Gard.* 88: 462-477.
- Lomolino, M.V., D.F. Sax and J.H. Brown (eds)**. 2004. *Foundations of biogeography: Classic papers with commentaries*. University of Chicago Press, Chicago.
- Longus.** [3rd century A.D.] 1956. *Daphnis and Chloe*. Transl. P. Turner. Penguin, Harmondsworth.
- Lourenço, W.R.** 1998. Panbiogéographie, les distributions disjointes et le concepte de famille relictuelle chez les scorpions. *Biogeographica* [Paris], 74: 133-144.
- Lovis, J.D.** 1959. The geographical affinities of the New Zealand pteridophyte flora. *Brit. Fern Gaz.*, 9: 16-23.
- Lucretius** [c. 50 B.C.] 1973. *On the nature of the universe*. Transl. R. Latham. Penguin, Harmondsworth.
- MacArthur, R.H. and E.O. Wilson.** 1967. *The theory of island biogeography*. Princeton University Press, New Jersey.
- McDowall, R.M.** 1964. The affinities and derivation of the New Zealand fresh-water fish fauna. *Tuatara*, 12: 59-67.
- McDowall, R.M.** 2002. Accumulating evidence for a dispersal biogeography of southern cool temperate freshwater fishes. *J. Biogeogr.*, 29: 207-219.
- McDowall, R.M.** 2004. What biogeography is: a place for process. *J. Biogeogr.*, 31: 345-351.
- McGlone, M.S., R.J. Dungan, G.M.J. Hall and R.B. Allen.** 2004. Winter leaf loss in the New Zealand woody flora. *New Zealand J. Bot.*, 42: 1-19.
- Machiavelli, N.** [1513] 1997]. *The prince*. Transl. C. E. Detmold. Wordsworth editions, Ware, Hertfordshire.
- Maclean, G.L.** 1984. Arid-zone adaptations of waders (Aves: Charadrii). *S. Afr. J. Zool.*, 19: 78-81.
- McPeck, M.A. and T.E. Miller.** 1996. Evolutionary biology and community ecology. *Ecology*, 77: 1319-1320.
- Marmels, J. de.** 2000. The larva of *Allopetalia pustulosa* Selys, 1873 (Anisoptera: Aeshnidae), with notes on Aeshnoid evolution and biogeography. *Odonatologica*, 29: 113-128.
- Marmels, J. de.** 2002. A study of *Chromagrion* Needham, 1903, *Hesperagrion* Calvert, 1902, and *Zoniagrion* Kennedy, 1917: three monotypic North American damselfly genera with uncertain generic relationships (Zygoptera: Coenagruidae). *Odonatologica*, 31: 139-150.
- Matthew, W.D.** 1915. Climate and evolution. *Anns. New York Acad. Sci.*, 24: 171-318.
- Matthews, C. (ed.)**. 1989. Panbiogeography special issue. *New Zealand J. Zool.*, 16(4): 471-815.
- Matthews, L.H.** 1971. Introduction to C. Darwin, *Origin of Species*. Dent, London.
- Mayr, E.** 1942. *Systematics and the origin of species*. Columbia University Press, New York.
- Mayr, E.** 1954. Change of genetic environment and evolution, pp. 157-180. In: J. Huxley, A.C. Hardy and E.B. Ford (eds.). *Evolution as a process*. Allen and Unwin, London.
- Mayr, E.** 1963. *Animal species and evolution*. Harvard University Press, Cambridge, Massachusetts.
- Mayr, E.** 1965. Summary, pp. 553-562. In: H.G. Baker and G.L. Stebbins (eds). *The genetics of colonizing species*. Academic Press, New York.

- Mayr, E.** 1982a. Processes of speciation in animals, pp. 1-19. In: C. Barigozzi (ed.). *Mechanisms of speciation*. Liss, New York.
- Mayr, E.** 1982b. Review of G. Nelson and D.E. Rosen 'Vicariance Biogeography'. *Auk*, 99: 618-622.
- Mayr, E.** 1982c. *The growth of biological thought: Diversity, evolution and inheritance*. Harvard University Press, Cambridge.
- Mayr, E.** 1997. *This is biology: The science of the living world*. Harvard University Press, Cambridge.
- Mayr, E. and J. Diamond.** 2001. *The birds of northern Melanesia: Speciation, ecology and biogeography*. Oxford University Press, New York.
- Mayr, E. and W. H. Phelps Jr.** 1967. The origin of the bird fauna of the south Venezuelan highlands. *Bull. Amer. Mus. Nat. Hist.*, 136: 269-328.
- Mees, G.F.** 1969. A systematic review of the Indo-Australian Zosteropidae (part III). *Zoolog. Verhand.*, 102:1-390.
- Melville, H.** [1851] 1998. *Moby Dick, or The Whale*. Oxford University Press, Oxford.
- Meve, U. and S. Liede.** 2002. Floristic exchange between mainland Africa and Madagascar: case studies in Apocynaceae - Asclepiadoideae. *J. Biogeogr.*, 29: 865-873.
- Meyer, C.P.** 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biol. J. Linn. Soc.*, 79: 401-459.
- Montaigne M. de.** [1595] 1958. *Essays*. Transl. J. M. Cohen. Penguin, Harmondsworth.
- Moore, J.** 1991. Deconstructing darwinism: the politics of evolution in the 1860s. *J. Hist. Biol.*, 24: 353-408.
- Moritz, C., J. Patten, C. Schneider and T.B. Smith.** 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annu. Rev. Ecol. Syst.*, 31: 533-563.
- Morrone, J.J.** 2000a. El tiempo de Darwin y el espacio de Croizat: rupturas epistémicas en los estudios evolutivos. *Ciencia*, 51: 39-46.
- Morrone, J.J.** 2000b. Entre el escarnio y el encomio: León Croizat y la panbiogeografía. *Interciencia*, 25: 41-47.
- Morrone, J.J. and J.V. Crisci.** 1990. Panbiogeografía: Fundamentos y métodos. *Evol. Biol.* [Bogotá], 4: 119-140.
- Mosquin, T.** 1971. Evolutionary aspects of endemism. *Natur. Can.*, 98: 121-130.
- Müller, K.** 1893. Remarks on Dr H. von Jhering's paper 'On the ancient relations between New Zealand and South America'. *Trans. New Zealand Inst.*, 25: 428-434.
- Nei, M.** 2002. Review of 'Where do we come from? Molecular evidence for human descent', by J. Lein and N. Takahata. *Nature*, 417: 899-900.
- Nelson, G.** 1977. Review of 'Biogeografía analítica y sintética ("Panbiogeografía") de las Américas' by L. Croizat, 1976. *Syst. Zool.*, 26: 449-452.
- Nelson, G.** In press. Cladistics: its arrested development. In: D.M. Williams and P.L. Forey (eds.). *Milestones in systematics: The development of comparative biology*. Taylor and Francis, London.
- Nelson, G. and P.Y. Ladiges.** 2001. Gondwana, vicariance biogeography, and the New York school revisited. *Austral. J. Bot.*, 49, 389-409.
- Nelson, G. and N. Platnick.** 1981. *Systematics and biogeography: Cladistics and vicariance*. Columbia University Press, New York.
- Nevling, L.I. Jr.** 1961a. A revision of the Asiatic genus *Linostoma* (Thymelaeaceae). *J. Arnold Arbor.*, 42: 295-320.
- Nevling, L.I. Jr.** 1961b. A revision of the Asiatic genus *Enkleia* (Thymelaeaceae). *J. Arnold. Arbor.*, 42: 373-396.
- Nietzsche, F.** [1872] 2000. *The birth of tragedy*. Transl. D. Smith. Oxford University Press, New York.
- Nietzsche, F.** [1878] 1994. *Human, all too human*. Transl. M. Faber and S. Lehmann. Penguin, Harmondsworth.
- Nietzsche, F.** [1882] 1910. *The joyful wisdom ('La gaya scienza')*. Transl. T. Common. Foulis, London.
- Nietzsche, F.** [1886] 1955. *Beyond good and evil*. Transl. M. Cowan. Regnery, Chicago.
- Nietzsche, F.** [1888]. 1998. *Twilight of the idols, or How to philosophize with a hammer*. Transl. D. Large. Oxford University Press, Oxford.
- O'Grady, R.T.** 1984. Evolutionary theory and teleology. *J. Theor. Biol.*, 107: 563-578.
- Ortega y Gasset, J.** 1932. *The revolt of the masses*. Norton, New York.
- Ortmann, A.E.** 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proc. Amer. Philosoph. Soc.*, 41: 267-397.
- Papavero, N, M. Souto Couri, W.L. Overal and D. Martins Teixeira.** 2003. The 'Physical dissertation on the former union and separation of the Old and New Worlds, and the peopling of the West Indies' (1764):

- the first proposal of a 'Pangaea supercontinent, pp. 9-18. In: J.J. Morrone and J. Llorente Bousquets (eds). *Una perspectiva Latinoamericana de la biogeografía*. Universidad Nacional Autónoma de México, Mexico City.
- Pascal, B.** [1657] 1967. *The provincial letters*. Transl. A.J. Krailsheimer. Penguin, Harmondsworth.
- Pascal, B.** [1657-1662] 1988. *Pensées*. Transl. A.J. Krailsheimer. Penguin, Harmondsworth.
- Pater, W.** [1873] 1998. *The Renaissance*. Edited with notes by A. Philips. Oxford University Press, Oxford.
- Piaget, J.** 1966. Observations sur le mode d'insertion et la chute des rameaux secondaires chez les *Sedum*. *Candollea*, 21: 137-239.
- Platnick, N.** 1981. Progression rule or progress beyond rules in biogeography. In: G. Nelson and D.E. Rosen (eds.). *Vicariance biogeography: A critique*. Columbia University Press, New York.
- Poe, E.A.** 1986. *The fall of the house of Usher and other writings*. Penguin, Harmondsworth.
- Popper, K.** [1945] 1984. *The open society and its enemies*. 2 vols. Routledge and Kegan Paul, London.
- Price, P.W.** 1980. *Evolutionary biology of parasites*. Princeton University Press, Princeton, New Jersey.
- Rabelais, F.** [1532-1534] 1974. *The histories of Gargantua and Pantagruel*. Transl. J.M. Cohen. Penguin, Harmondsworth.
- Rapport, D.J.** 1991. Myths in the foundations of economics and ecology. *Biol. J. Linn. Soc.*, 44: 185-202.
- Raven, P.H.** 1983. The migration and evolution of floras in the southern hemisphere. *Bothalia*, 14: 325-328.
- Raxworthy, C.J., M.R.J. Forstner and R.A. Nussbaum.** 2002. Chameleon radiation by oceanic dispersal. *Nature*, 415: 784-787.
- Renner, S.S., D.B. Foreman and D. Murray.** 2000. Timing transantarctic disjunctions in the Atherospermataceae (Laurales): evidence from coding and non-coding chloroplast sequences. *Syst.Bot.*, 49: 579-591.
- Richards, P.W.** 1952. *The tropical rain forest: An ecological study*. Cambridge Univ. Press, Cambridge.
- Richards, P.W., with contributions by R.P.D. Walsh, I.C. Baillie and P. Grieg-Smith.** 1996. *The tropical rain forest: An ecological study*. 2nd ed. Cambridge Univ. Press, Cambridge.
- Rieppel, O.** 2002. A case of dispersing chameleons. *Nature*, 415: 744-745.
- Robertson, C.J.R. and G.B. Nunn.** 1998. Towards a new taxonomy for albatrosses, pp. 13-19. In: G. Robertson and R. Gales (eds.), *Proc. First Internatl. Conference on the Biology and Conservation of Albatrosses*. Surrey Beatty and Sons, Chipping Norton, New South Wales.
- Rose, M.R. and G.V. Lauder.** 1996. Post-spandrel adaptationism, pp. 1-8. In: M.R. Rose and G.V. Lauder (eds.). *Adaptation*. Academic Press, San Diego.
- Rosen, D.E.** 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.*, 27: 159-188.
- Rouse, W.H.D.** 1941. Introduction to *The poetical works of John Milton*. Dent, London.
- Ryan, M.** 1982. *Marxism and deconstruction: A critical articulation*. Johns Hopkins University Press, Baltimore.
- Sallust, G.** [c. 50 B.C.] 1964. *The Jugurthine war and The conspiracy of Catiline*, transl. S.A. Handford. Penguin, Harmondsworth.
- Schmitt, C.B.** 1975. Science in the Italian universities in the sixteenth and early seventeenth centuries, pp. 35-56. In: M. Crosland (ed.) *The emergence of science in Western Europe*. Macmillan, London.
- Schnell, R.** 1970. *Introduction à la phytogéographie des pays tropicaux*. Vol. 1. Gauthier-Villars, Paris.
- Schopenhauer, A.** [1851] 1974. *Parerga and paralipomena: Short philosophical essays*. Transl. E.F.J. Payne. Clarendon Press, Oxford.
- Schwabe, C. and G. W. Warr.** 1984. A polyphyletic view of evolution: the genetic potential hypothesis. *Perspectives in Biology and Medicine*, 27: 465-485.
- Schwartz, J.** 1999. *Sudden origins: Fossils, genes, and the emergence of species*. Wiley, New York.
- Short, L.** 1973. Habits of some Asian woodpeckers (Aves, Picidae). *Bull. Amer. Mus. Nat. Hist.*, 152: 253-364.
- Simpson, G.G.** 1944. *Tempo and mode in evolution*. Hafner, New York.
- Simpson, G.G.** 1953. *The major features of evolution*. Columbia University Press, New York.
- Singer, C.** 1959. *A history of biology*. Abelard and Schuman, London.
- Smollett, T.** [1771]. 1967. *The expedition of Humphry Clinker*. Penguin, Harmondsworth.
- Spinoza, B.** [1677] 1982. *The ethics, and Selected letters*. Transl. S. Shirley. Hackett, Indianapolis.
- Steele, R. and J. Addison.** [1709-1713] 1997. *Selections from The Tatler and The Spectator*. Penguin, Harmondsworth.
- Steenis, C.G.G.J. van.** 1969. Plant speciation in Malasia, with special reference to the theory of non-adaptive saltatory evolution. *Biol. J. Linn. Soc.*, 1: 97-133.

- Sterelny, K. and P.E. Griffiths.** 1999. *Sex and death: An introduction to philosophy of biology*. University of Chicago Press, Chicago.
- Stevenson, R.L.** [1886] 2002. *The strange case of Dr Jekyll and Mr Hyde*. Penguin, Harmondsworth.
- Sturma, D.** 2000. Politics and the new mythology: the return to late Romanticism, pp. 219-238. In: K. Ameriks (ed.). *The Cambridge companion to German idealism*. Cambridge University Press, Cambridge.
- Sussman, R. W.** 1984. Anatomy and behaviour (review). *Science*, 226: 1187-1188.
- Tacitus, C.** 1972. *The histories*. Transl. K. Wellesley. Penguin, Harmondsworth.
- Tate Regan, C.** 1922. The distribution of the fishes of the order Ostariophysi. *Bijdrage tot de Dierkunde*, 22: 203-207.
- Taylor, R.** 1985. Schopenhauer, pp. 365-371. In: D.J. O'Connor (ed.) *A critical history of Western philosophy*. Free Press, New York.
- Tokeshi, M.** 1999. *Species coexistence: Ecological and evolutionary perspectives*. Blackwell, Oxford.
- Toulmin, S. and J. Goodfield.** 1965. *The discovery of time*. Hutchinson, London.
- Turk, F.A.** 1964. Form, size, macromutation and orthogenesis in the Arachnida: an essay. *Ann. Natal Mus.*, 16: 236-255.
- Vogel, S.** 1988. *Life's devices: The physical world of animals and plants*. Princeton University Press, Princeton.
- Wake, D.B.** 2002. A few words about evolution. *Nature*, 416: 787-788.
- Wallace, A.R.** [1869] 1962. *The Malay Archipelago: The land of the orang-utan and the bird of paradise*. Dover, New York.
- Wallace, A.R.** 1876. *The geographical distribution of animals*. Macmillan, London.
- Wallace, A.R.** [1881] 1998. *Island life*. Prometheus, New York.
- Wallace, A.R.** 1889. *A narrative of travels on the Amazon and Rio Negro*. 2nd ed. Ward Lock, London.
- Wallace, A.R.** [1890]. *The Malay Archipelago: The land of the orang-utan and the bird of paradise*. 10th ed. Periplus, Singapore.
- Wallis, G.P. and S.A. Trewick.** 2001. Finding fault with vicariance: a critique of Heads (1998). *Syst. Biol.*, 50: 602-609.
- Wallis, G.P. and J.M. Waters.** 2003. The phylogeography of southern galaxiid fishes, pp. 101-104. In: J. Darby, R.E. Fordyce, A. Mark, K. Probert and C. Townsend (eds.). *The natural history of southern New Zealand*. University of Otago Press, Dunedin.
- Warnock, G.J.** 1964. Kant, pp. 296-318. In: D.J. O'Connor (ed.) *A critical history of Western philosophy*. Free Press, New York.
- Waters, J.M., L.H. Dijkstra and G.P. Wallis.** 2000. Biogeography of a southern hemisphere freshwater fish: how important is marine dispersal? *Mol. Ecol.*, 9: 1815-1821.
- Waters, J.M. and M.S. Roy.** 2004. Out of Africa: the slow train to Australasia. *Syst. Biol.*, 53: 18-24.
- Weber W.A.** 2003. The Middle Asian Element in the Southern Rocky Mountain Flora of the western United States: a critical biogeographic review. *J. Biogeogr.*, 30: 649-685.
- Wegener, A.** 1924. *The origin of continents and oceans*. Methuen, London.
- Weimarck, H.** 1934. *Monograph of the genus Cliffortia*. Lund.
- Whewell, W.** [1847] 1967. *History of the inductive sciences, from the earliest to the present time*. Part 3. Frank Cass, London.
- White, F.** 1965. The savanna woodlands of the Zambesian and Sudanian domains: an ecological and phytogeographical comparison. *Webbia*, 19: 651-681.
- White, G.** [1769] 1977. *The natural history of Selbourne*. Penguin, Harmondsworth.
- Whittaker, R.J.** 1998. *Island biogeography: Ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Wiens, J.A.** 1991. Evolutionary biogeography, pp. 157-161. In: M. Brooke and T. Birkhead (eds.). *The Cambridge encyclopedia of ornithology*. Cambridge University Press, Cambridge.
- Wightman, W.P.D.** 1962. *Science and the Renaissance: An introduction to the study of the emergence of the sciences in the sixteenth century*. Oliver and Boyd, Edinburgh.
- Wild, H.** 1963. Review of B.J.D. Meeuse 'The Story of Pollination'. *Kirkia*, 3: 216-217.
- Wiley, E.O., D. Siegel-Causey, D.R. Brooks and V.A. Funk.** 1991. *The complete cladist: A primer of phylogenetic procedures*. University of Kansas Museum of Natural History, Lawrence.
- Wilkinson, D.** 2003. Dispersal, cladistics and the nature of biogeography. *J. Biogeogr.*, 30: 1779-1780.

- Wilkinson, J.A., R.C. Drewes, O.L. Tatum.** 2002. A molecular phylogenetic analysis of the family Rha-cophoridae with an emphasis on the Asian and Afri-can genera. *Mol. Phylogen. Evol.*, 24: 265-273.
- Willdenow, K.L.** 1798. *Grundriss der Kräuterkunde zu Vorlesungen entworfen*. Berlin.
- Williams, D.M. and M.C. Ebach.** 2004. The reform of palaeontology and the rise of biogeography –25 years after ‘ontogeny, phylogeny, paleontology and the biogenetic law’ (Nelson, 1978). *J. Biogeogr.*, 31: 685-712.
- Windelband, W.** 1958a. *A history of philosophy. Vol. I. Greek, Roman and Medieval*. Harper and Brothers, New York.
- Windelband, W.** 1958b. *A history of philosophy. Vol II. Renaissance, Enlightenment, and Modern*. Harper and Brothers, New York.
- Winkler, H, D.A. Christie and D. Nurney.** 1995. *Woodpeckers: A guide to the woodpeckers of the world*. Houghton Mifflin, Boston.
- Wolf, A.** 1935. *A history of science, technology, and philosophy in the 16th and 17th centuries*. Allen and Unwin, London.
- Zirkle, C.** 1941. Natural selection before the ‘Origin of Species.’ *Proc. Amer. Philosoph. Soc.*, 84: 71-123.
- Zunino, M.** 1992. Per rileggere Croizat. *Biogeogra-phia* [Bologna], 16: 11-23.
- Zunino, M. and A. Zullini.** 1995. *Biogeografia: La dimensione spaziale dell’evoluzione*. Casa Editrice Ambrosiana, Milan.
- Zunino, M. and A. Zullini.** 2003. *Biogeografía: La dimensión espacial de la evolución*. Fondo de Cultura Económica, México D.F.