

## LEON CROIZAT'S BIOGEOGRAPHIC WORK: A PERSONAL APPRECIATION

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### ABSTRACT

Leon Croizat's bold and novel attempts to empirically refute Charles Darwin's theory of geographical distribution of organisms by their "means of dispersal", A. R. Wallace's classification of zoogeographic regions, and Alfred Wegener's concept of Pangaea are discussed. Croizat's panbiogeographic methodology and synthesis, an alternative approach to these generally accepted views, is discussed in relation to vicariance cladistic biogeography with which it is often confused.

**Keywords:** biogeography, cladistics, Croizat, Darwin, dispersal, geology, pan-biogeography, vicariance, Wallace, Wegener.

"It may be said, indeed, that Charles Darwin's destiny in life was to watch physical movement—physical movement from the stir of an insect in the dust to the explosion of an earthquake all around." So wrote James Hutchinson Stirling, in his little known critique of Darwinism, published in 1894, and relegated to complete obscurity since (*Darwinianism, Workmen and Work*, Edinburgh, T. & T. Clark). Stirling's critique is philosophical, and heavily coloured by an abstruse Hegelianism, but it is nevertheless perceptive in that it strikes straight at the major weakness of Darwin's theory of evolution by natural selection: the notion that the differentiation of organisms in space and time is a consequence of their originating in specific centres of origin from whence they migrate by means of dispersal, thus to establish their geographic distribution. Darwin's world is a world where organisms are constantly moving, continually pouring forth from specific evolutionary centres that supply advanced and more competitive organisms to other areas of the globe.

There have been many critiques of Darwinism, both before, and after the publication of Stirling's work. Most, if not all, of these critiques focus upon the problem of form initially, and argue that natural selection, as conceived by Darwin cannot possibly account for the origin of new structural types of animals and plants. These critiques range from the superb to the indifferent. Some of these critiques like St. George Mivart's *On the Genesis of Species*, will never be surpassed. But only Leon Croizat's critique is unique.

Croizat's criticism of Darwinism is the most fascinating ever published, because he chose not to address himself primarily to the problem of form, but rather to the problem of space. For it is through space and in time that the forms of organisms change. Darwin too, of course, thought that biogeography was an interesting subject, for otherwise he would not have introduced "*On the Origin of Species*" to the world through the medium of this discipline:

"When on board H.M.S. *Beagle* as naturalist, I was much struck with certain facts in the distribution of the organic beings inhabiting South America..." (Introduction to "*On the Origin of Species*").

And this is Croizat's very point; Darwin knew the importance of the spatial aspect, but failed to capitalise on his initial insights into the problem as recorded in *The Voyage of the Beagle* when he came to write *The Origin* (see Croizat, 1964: *Space, Time, Form*, pp. 592-641).

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### Crawl: Croizat's Biogeographic Work

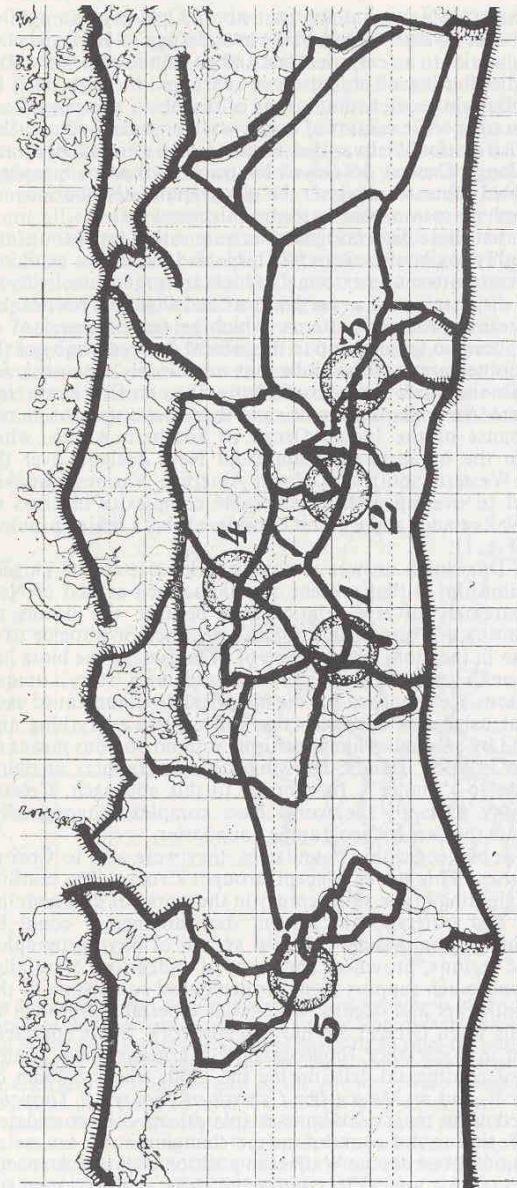


Fig 1. Croizat's 1958 (in *Panbiogeography*) summary of his biogeographic analyses. Note the complex overlap of tracks in present day landmasses, and the particular care taken to distinguish trans-Pacific tracks connecting North and South America with East Asia and Australasia, from the trans-Antarctic track (lower hatched line) linking the Southern Hemisphere landmasses and the trans-Atlantic track relating the Americas to Europe and Africa.



Croizat thought of doing something that no one had ever thought of doing before, and that no one will probably ever do again. He decided to subject Darwin's theories to an empirical test and posed the question: "Did the geographical distribution of organisms in space and through time, by form support the Darwinian view that means of dispersal, and migrations by these means out of specific centres of origin was the process responsible for geographic distribution?" In order to undertake this massive and challenging experiment Croizat developed his track method of investigation, which enabled him to analyse the geographic distributions of organisms and graph them into what he termed dispersal patterns.

Croizat found that these dispersal patterns were rather repetitious, and that apparently highly vagile organisms like birds and butterflies exhibited very similar dispersal patterns to extremely sedentary organisms, with no obvious means of dispersal, such as earthworms and flightless beetles. He discovered that these repetitious patterns, which he termed standard or generalised tracks, bore no relationship to the present day geography of the world, but rather joined areas of the globe that were widely separated; for instance one of his standard tracks crossed the Tasman Sea from New Zealand to Southern Australia/Tasmania, and then drove straight on out over the vast expanse of the Indian Ocean to Southern Africa, while another headed in the opposite direction from New Zealand over the Pacific Ocean to Western South and North America. Various standard tracks were found to overlap with considerable complexity in areas of endemism like New Zealand, and Croizat considered this a major problem of biogeography (Fig. 1).

Of course, the Darwinian answer to this complex pattern of biogeographic area relationships is that present day biota, such as that of New Zealand, have extremely diverse relationships because the means of dispersal of organisms are responsible for the presence or absence of a particular organism in the biota. Each group of organisms in the biota has had a history unique to itself. Biogeography is just telling a 'story': unique narrative explanations are proposed for the historical development of each group studied. But using this approach one can explain everything and anything, and faced by anomalies like organisms with no obvious means of dispersal living on isolated islands, Darwinian biogeographers attribute their presence there to "chance". In contrast to this approach, Croizat suggested that many parts of the world have complex biogeographic relationships because they are biogeographic boundaries.

Because they are biogeographic boundaries, they were also to Croizat geological boundaries. This novel concept brought Croizat into conflict with the view, (originating in the 19th century in the works of de Candolle, Sclater, Wallace, and others), that present day landmasses could be classified and divided up into some coherent system of phytogeographic and zoogeographic regions, provinces and areas of endemism. Naturally, this latter view found much support from the geological conception of the permanence of continents and oceans, which was especially prevalent in the 1940s and 1950s when Croizat did most of his work. Some commentators (e.g. Nelson in *Vicariance Biogeography: a critique*) have argued that "the revival of continental drift during the 1960s was the doom of Wallace's synthesis". But as Mayr (*The Growth of Biological Thought*) has recently argued "the major landmasses (plates) are still considered permanent, their positions and connections are changing in the course of time". Mayr ingeniously rescues the Wallacean position of the permanence of continents, through his appeal to continental drift, and its attendant

notions of a single Permian supercontinent Pangaea, which fragments successively into Laurasia and Gondwana components, and then into the continents as we know them today.

To Croizat though, the concept of Pangaea was wrong because it conflicted with evidence he had obtained from his purely biogeographic studies. The continents are not permanent, he repeatedly stated: one cannot pull them all back into a single supercontinent as Wegener did, and modern plate tectonic proponents do. Very recently geologists have begun to unearth evidence (review in *Jl. Geophys. Res.* 87: 3644-3661) that most, if not all, of the world's continental landmasses are not permanent and stable, but rather composite formations that have been formed by the accretion of crustal blocks since the Permian. The geological and geophysical findings of the 1980s promise to corroborate Croizat's biogeographic work, in novel and exciting ways.

The regions, subregions, areas of endemism, etc., of de Candollean phytogeography and Wallacean zoogeography, based on the idea of the permanence of continents and other landmasses, are thus not parts of the real, natural world to Croizat (Fig. 2). But what is needed to demonstrate that the "unproblematical" areas of endemism of Nelson and Platnick

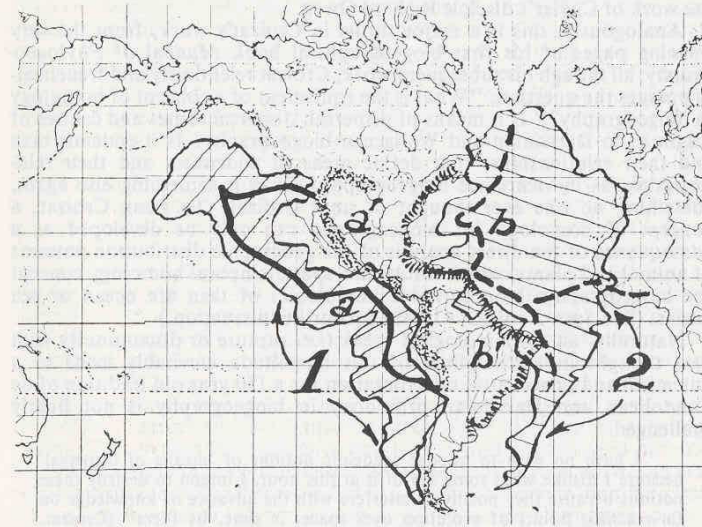


Fig 2. Croizat's 1961 (in *Principia Botanica*) hypothesis of the composite geological nature of the Americas based on his strictly biogeographic analyses. Western North and South America are postulated to have drifted from the west as a consequence of the opening or widening of the Pacific Ocean, while Eastern North and South America drifted from the east as the Atlantic Ocean opened. These continental fragments then fused to form one modern geography: North and South America. Wallace's Nearctic (North America) and Neotropical (Central and South America) regions are thus not natural biogeographic or geologic taxa. In the last five years some geologists and other scientists have begun to accept this novel concept which originates in Croizat's panbiogeographic synthesis.



(*Systematics and Biogeography: Cladistics and Vicariance*) are not natural biogeographic taxa is the equivalent of a concept of homology in biogeography.

In his study of epistemological ruptures in Western thought, Michael Foucault (*The Order of Things*), argues that scientific animal and plant systematics did not exist in the 18th century. Foucault locates the essential discontinuity in the history of biological systematics between Linnaeus and Cuvier:

"...Cuvier....introduced a radical discontinuity into the Classical scale of beings; and by that very fact he gave rise to such notions...that make possible...the idea of evolution....With spatial discontinuity, the breaking up of the great table, and the fragmentation of the surface upon which all natural beings had taken their ordered places, it became possible, to replace natural history with a 'history' of nature. It is true that the Classical space...did not exclude the possibility of development, but that development did no more than provide a means of traversing the discreetly preordained table of possible variations. The breaking up of that space made it possible to reveal a historicity proper to life itself..." (p. 275)

That historicity, the breaking up of the organism, that analysis; the becoming of animal and plant systematics as a science is a direct consequence of the development of a concept of homology, particularly in the work of Cuvier's disciple Richard Owen.

Analogously, this is a major thrust in Croizat's work, from the very opening pages of his first biogeographical book *Manual of Phytogeography*, all though his subsequent work, Croizat relentlessly and frenetically pursues the question: "What is the equivalent of a concept of homology in biogeography?" Is it means of dispersal, dispersal routes and centres of origin as in Darwinian and Wallacean biogeography? Is it endemic taxa and their relationships, that define areas of endemism and their relationships, as in vicariance biogeography? Or is it something else again, something no one ever thought of until Croizat? To Leon Croizat, a concept of homology for biogeography can only be developed as a consequence of the direct analysis of the geographic distribution patterns of animal and plants, which results in a spatiotemporal homology concept for biogeography: biogeographic homologies of taxa are ocean or sea basins. (See *Syst. Zool.* 32: 431-438 for further discussion.)

Naturally, an epistemological break (i.e. rupture or discontinuity with past thought in a discipline) of this magnitude inevitably leads to a polemical and provocative confrontation for a 150 year old tradition of de Candolle and Darwinian orthodoxy in biogeography is not lightly challenged:

"I have no wish to oppose academic notions of 'means of dispersal' because I dislike what some say of it at this hour. I intend to destroy these notions because they positively interfere with the advance of knowledge on far-reaching points of evolution over space, in time, by form" (Croizat, *Space, Time, Form*, p. vi)

while:

"It is of course well known that the time-honoured pastime of rigging up ever better 'zoogeographic' provinces or the like has no end because...life perversely tends to interdigitate all over, thus voiding man's clever schemes" (Croizat, *Panbiogeography*, Vol. 2a: 131).

Croizat's work is popularly, but erroneously, associated with the New York school of vicariance cladistic biogeography, developed by workers such as Nelson's, Rosen and Platnick. In fact, shortly before his death

#### Craw: Croizat's Biogeographic Work

Croizat, in an as yet unpublished manuscript reviewing Nelson and Platnick's well known work *Systematics and Biogeography* was uncompromising in his opposition to vicariance biogeography:

"Croizat has...worked hard and long to rid biogeography of the 'definitive authority' of Simpson, Mayr, Darlington, etc., and is now working, because of the very same reasons, against the 'authority' of Nelson and his acolytes. Croizat offers no 'authority', just a method of positive investigation—the panbiogeography."

True Croizat's style is lively and vigorous, and ruthlessly uncompromising in criticism of those with whom he disagreed. For these very human errors he has been much criticized by those for whom science is an occupation rather than a passion. It is because his books are intense and ardent conversations on the development of methods for investigating biogeographic and systematic problems that they will live. Panbiogeographic methodology and synthesis is here to stay.