

**LÉON CROIZAT'S BIOGEOGRAPHY AND
MACROEVOLUTION, OR ...
"OUT OF NOTHING, NOTHING COMES"¹**

Carmine Colacino

Herbarium Lucanum [HLUC] &
Dipartimento di biologia, difesa e biotecnologie agro-forestali
Università degli Studi della Basilicata
I-85100 Potenza, Italy.

*"I wouldn't mean orthogenesis in a mystical sense at all.
I would simply mean by this: that adaptation works on structural possibilities.
If the structural possibility is not there you cannot have adaptation.
Simply because out of nothing, nothing comes."
from an Interview with Léon Croizat, Caracas 1974. (Baskin 1984)*

SUMMARY

In this paper Croizat's "Panbiogeographic Method" is briefly introduced. Some of the differences among the panbiogeographic method and Nelson's "Vicariance Biogeography" are then stressed. In particular because the latter has often been incorrectly considered an extension of the former (in an ambitious "synthesis" with Hennig's "Phylogenetic Systematics"), which is not the case. Eventually, Croizat's ideas on, and contributions to evolutionary theory, as well as the claim that phylogenetic considerations have no role in Croizat's biogeography are considered.

SUMMARIO

‘O “mètodo panbiogiugràfico” ‘e Léon Croizat è appresentato a ccurto. Se méttano a mmanése dapò certe differenze dinto ‘o mètodo ‘e Croizat e ‘a “bbiogiugràfia d’‘a vicarianza” ‘e Gareth Nelson, ca

Address for correspondence: COLACINO@UNIBAS.IT

¹From the title of an interview with Léon Croizat by Baskin (1984).

pe sbaglio fuje penzata pruvènere d' 'a panbiogiugrafia (pretennenno ufanamènte 'e nce fà na "sintese" cu 'a "sistemàtica filoggenètica" 'e Hennig). Cierte d' 'e ppenzate e assecurze 'e Croizat ncòppa â teoria evolutiva, accusí comme ll'erròneca pretennènzia ca 'a bbiogiugrafia 'e Croizat nun tene cunto d' 'a filoggenesi, songo asammenate a ll'úrdemo.

RESUMEN

Se presenta brevemente el "método panbiogeográfico" de Léon Croizat. Algunas diferencias entre el método panbiogeográfico y la "biogeografía de la vicariancia" de Gareth Nelson se indican además. Este última ha sido considerada incorrectamente una extensión de la panbiogeografía (en una ambiciosa "síntesis" con la "sistemática filogenética" de Hennig). Las ideas de Croizat y sus contribuciones a la teoría evolutiva, así como la pretensión que las consideraciones filogenéticas no tienen papel en la biogeografía de Croizat se consideran al fin.

Key words: Croizat, history of biology, hologenesis, orthogenesis, panbiogeography, phylogenetic systematics, vicariance biogeography

INTRODUCTION

Léon Croizat [krwä•zä'] (Torino, Italy: 16 July 1894 - Coro, Venezuela: 30 November 1982) is a controversial figure in the history of 20th century biological thought. He proposed in the 1950s a method of biogeographic analysis (Panbiogeography) whose results suggested the need for a profound revision of the prevailing ("orthodox") tenets upon which evolutionary theory was based (Croizat 1952, 1958, 1961, 1964). He was aware of his "unorthodoxy," even though he did not expect the "conjure of silence" that followed the publication of his more important works, in particular, *Panbiogeography* (1958) and *Space, Time, Form: The Biological Synthesis*, (1964). He [in his words] "happen to be by birth ... absolutely impervious to authority unable to demonstrate its tenets on grounds better than authority" (Croizat 1964: iii). This attitude caused him to produce one of the most fascinating critiques of Darwinism because he chose not to address directly the problem of form, but instead that of space. It is through time and space, in fact, that the forms of organisms change (see

Craw 1984a for a brief biography, as well as the short autobiographical notes at the end of Croizat 1982).

Many of the authors dealing in one way or another with Croizat's Panbiogeography have been misled by the improper association of Croizat's works with Vicariance Biogeography, a method that was initially considered as an extension and improvement of the panbiogeographic method (e.g., Patterson 1981), which actually is not (Craw 1984b, Croizat 1982, 1984). Previous workers may also have been put off by his unorthodox, and repetitive way of presenting his ideas, and misinterpretation and misrepresentation of Croizat's views has been the most common result (e.g., Ball 1976, Brundin 1981, Cracraft 1975, Croizat et al. 1974², Mayr 1982, Nelson and Platnick 1980, Nelson 1974, Rosen 1978). At the same time, some other authors preferred just to ignore Croizat's contributions *tout court*. In particular, Simpson was convinced that Croizat "is a member of the lunatic fringe," while Mayr considered Croizat as having a "totally unscientific style and methodology" and adding that "time is too short to argue with such authors", thus, dismissing unscrupulously Croizat's works as a whole (Nelson 1977 *fn* 3). Mayr finally mentioned Croizat in a book review (Mayr 1982, see also Croizat's 1984b reply). It is not surprising, therefore, that even one of the few (otherwise good) textbooks of biogeography citing Croizat misrepresent his ideas stating, for instance, that "Croizat categorically denounced Wagerism" (Brown and Gibson 1983: 267). But Croizat did not oppose continental drift because he thought it was false (as, for example, Simpson and Mayr maintained), but because the reconstruction of the continents into one supercontinent (Pangaea) conflicted with his results, especially in the Pacific area. Thus, he did not oppose, in principle, the idea of "floating continents"). Croizat (1952) did propose, however, a static geological model (see Craw and Weston 1984 for a discussion).

In this paper I will briefly introduce the fundamental notions of Croizat's Panbiogeographic Method, comparing it with Vicariance Biogeography. I will then consider its general contribution and relevance to

²The manuscript Croizat sent to Nelson was heavily revised by the other authors, without Croizat's consent (he only consented to the addition of the names of Nelson and Rosen as junior authors). Croizat does not consider this paper representing adequately his views (Croizat 1982)

evolutionary theory. Finally, I will focus on two of its more controversial aspects, "orthogeny", in the light of the current controversy on the importance of "constraints" in evolution (e.g., Gould and Lewontin 1979, Maynard Smith et al. 1985, Reif et al. 1985), and the claim that phylogenetic relationships have no role in Croizat's biogeography (e.g., Ball 1976, Cracraft 1975, McDowall 1978, Patterson 1981).

The Panbiogeographic Method

Panbiogeography is a method based on the analysis of distribution patterns of organisms over space through time.

The assumption underlying panbiogeography is that life and earth evolve together. Croizat states it clearly, and adds that

"1) Organic evolution is function of *space*, *time*, and *form*. 2) Of these three essential factors, *space* might be said to be the one with which biogeography (= panbiogeography, in my sense [Croizat's]) is primarily concerned. However, *space* necessarily interplays with *time* and *form*, therefore the three factors are as one of immediate biogeographic concern." (Croizat 1964: 707 [italics in the original]).

He continues stressing that vicariant differentiation is the process giving rise to geographic distribution:

"On account of its essentially consisting of the breaking down of an ancestral population into subordinate populations over space in time by modifications of form, the process of form-making essential to evolution yields geographic, taxonomic, and ecological vicariism as its main byproduct." (Croizat 1964: 711).

Here is evident the difference with vicariance biogeography, that only *assumes as possible* that life and earth may evolve together. This is an important point, as stressed by Craw (1982) and Craw and Weston (1984), because it implies a conceptual difference between the two methods. Vicariance biogeography establishes relationships from *form* (i.e., cladistics of structural, functional, behavioral aspects of organisms) without actually considering the *spatial* and *temporal* aspects of the organisms under study. The cladogram so obtained, therefore, does not contain any biogeographic information. The geographic distribution of the or-

ganisms (taxa) studied is then superimposed on the biological cladogram. Panbiogeography analyses biogeographic characters through the drawing of tracks, *and* derives information from *form* directly to orient those tracks. A track is a line connecting disjunct localities of a particular taxon. This track is interpreted as a graph of the geographic distribution of the taxon under consideration, and represents the “primary coordinates” in space of the taxon. Tracks are then oriented according to sea or ocean basins. This allows one to propose a hypothesis for the baseline (defining characteristic) for that track. The baseline represents a primary biogeographic homology (diagnostic character) for the taxon under study (Craw 1988). In the case of complex geographic distributions, information on the phylogenetic relationships of the group under study is needed to orient the track.

“...the task of connecting the whole by ‘tracks’ proves exceedingly difficult unless the flow of the affinities in the group under study is perfectly known” (Croizat 1958[vol. 2]: 688; see also Craw 1983).

Several individual tracks from different taxonomic groups with the same baseline constitute a *generalized track*. A generalized track refers to the present day distribution of an ancestral biota of which the individual components are the relict fragments (Craw 1988). The generalized tracks for terrestrial life, as Croizat discovered in 1958 (see Fig. 1), have no apparent relationships to the distribution of continents today. Thus, *parts* of continents/islands, are related from one to another by tracks over sea and ocean basins, and not to the present day continental positions. They therefore do not constitute “biogeographic units equivalent to present day geographic areas” (Craw 1988). Several refinements of the technique are possible through the use of graph theory, for instance (Page 1987).

Only recently has Croizat's panbiogeographic method been seriously considered and used, with success, mainly by a group of young scientists in New Zealand (e.g., Craw 1982, 1983, 1988, Craw and Heads 1988, Craw and Weston 1984, Grehan and Ainsworth 1985, Heads 1985, 1993, Page 1987).

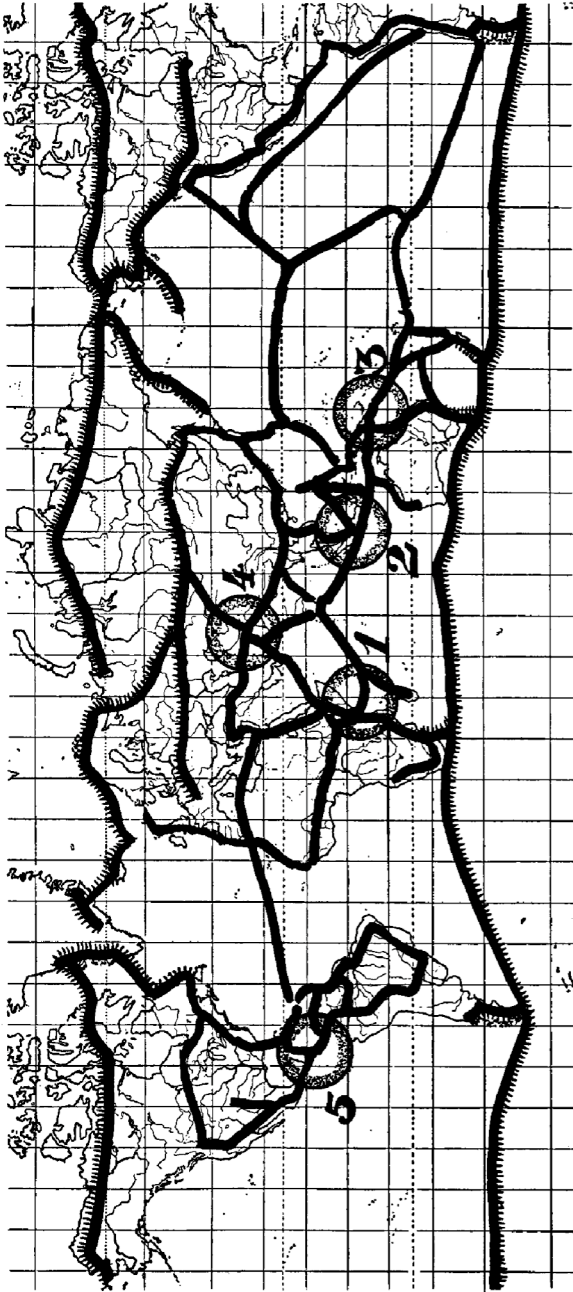


Fig. 259. The main channels of dispersal (plants and animals alike) of "modern" life, so called. Hatched in the high north and high south, respectively, are "tracks" that could with some propriety be identified as boreal ("Holarctic", "Palaeartic", "Nearctic" in conventional descriptive terminology), and as austral ("Antarctic", "Old Oceanic", etc., also of said terminology). Set out within stippled circles, 1, 2, 3, 4, 5 are the very main nodes controlling the course of important "tracks" on an intercontinental scale. The map of the New World to the left particularly stresses the "tracks" toward the Atlantic; that to the right those toward the Pacific. All these "tracks" and "nodes" are exhaustively discussed and figured in a strictly deductive pattern of inquiry throughout this book, and a preceding one (Croizat, L. "Manual of Phytogeography", 1952); three at least of the main nodes underscored in this Figure (namely, 1, 3, 4) having been pointedly identified as basic in regard of plantlife also in the pages of the above "Manual of Phytogeography".

Fig. 1. Generalized Tracks according to Croizat (1958, p.1018). Original caption.

Croizat's panbiogeography: Its general contribution and relevance to evolutionary theory

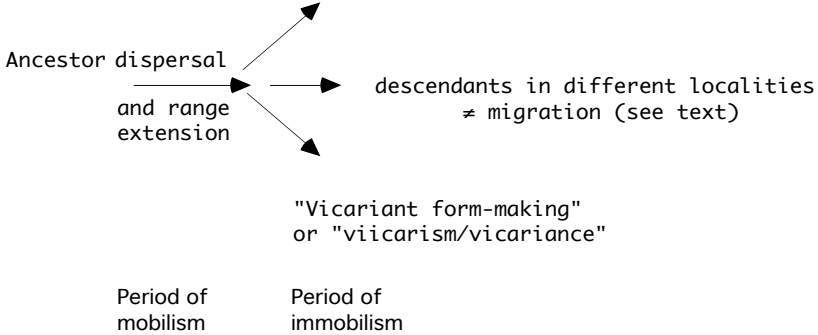
The contributions of Croizat and his biogeographic methodology to evolutionary theory are insightful and profound. One point of importance is that his contribution derived from the application of his biogeographic method and not from *a priori* abstract speculation.

Croizat considers the evolutionary process to be composed of three factors: *space, time, form*. This approach is not particularly original *per se*. It can actually be considered a truism. Evolution in space and time results in the formation of distribution patterns that are the object of study of biogeography. Biogeography was very important in the early development and formulation of evolutionary theory (see Croizat 1984a, Grehan 1988). Darwin's "Natural Selection", however, had the effect of stressing the notion of evolution as a temporal change in *form* (intending the term *form* to include morphology, genes, development, behavior, etc.), while biogeography (*space*) became of limited importance, if not redundant (Grehan 1988). Darwin seemed to be aware of the importance of constraints, or "laws of growth", he referred to them, for instance, in the several edition of his opus magnum "*On the Origin of Species by Means of Natural Selection*" and in several of his published letters (see Craw 1984c for a compilation of relevant quotations). He admitted to have extended too far the action of natural selection. While recognizing that many morphological changes in plants could be "attributed to the laws of growth, independently of natural selection" (Darwin 1872: 175; see also Craw 1984b, Grehan 1984), the Modern Synthesis stressed exclusively natural selection as the factor directing the course of evolutionary change. This is reflected in one of the common definitions of evolution that equates evolution with "any change in gene frequency" (e.g., Wilson and Bossert 1971: 20). This unfortunate event, according to Croizat (1964), hindered the progress of evolutionary thinking, making it appear no more than a 20th century extension of a 19th century outlook. Moreover, this neo-Darwinian theory of evolution, explaining the natural pattern of classification as pattern of descent (phylogeny) without actually predicting or prohibiting any pattern, has, therefore not provided an explanation for macroevolutionary patterns.

Croizat's original approach to evolution was the use of the analysis of the present geographic distributions of organisms as the basis of an un-

Croizat's explanation of vicariant distributions (1958)

- 1) Translation in space: ancestor establishes its range during a period of mobilism. ordinary means of survival becomes means of dispersal.
Form-making: ancestor breaks apart as a consequence of different evolutionary trends taking place over its range.



- 2) Disjunctions of descendants occur through extinctions in the formerly continuous range.

derstanding of the process causing variation of form through time and space. He tested Darwin's aprioristic and conjectural concepts of speciation in "centers of origins", and subsequent "migration" from those centers by the use of "means of dispersal", and found them in disagreement with his results. He found that the dispersal patterns were not only repetitive (following main general "channels" or "tracks") but also that they were independent of the various "means of dispersal" of taxa.

To explain vicariant distributions, he proposed the existence of a broadly distributed ancestor that established its range during a period of "mobilism" with its ordinary "means of survival" acting as means of dispersal. A period of "immobilism" follows in the course of which the ancestor will undergo active form-making around particular centers as a consequence of different evolutionary trends taking place over its range (Croizat 1958, 1964). "Form-making is an orderly process through time and over space. It takes place by the breaking down of an ancestral group (whatever its taxonomic rank) around essentially local centers of progressive differentiation." (Croizat 1958 [Vol. 2b]: 998). "[T]he descendants, therefore, evolve in different localities *as if* there had been actual migration between them" (Grehan and Ainsworth 1985). Disjunctions will oc-

cur through "extinctions" in the previously continuous range. Croizat, however, does not reject "dispersalism" as an impossible event: "...a biogeographer must be a vicarist in principle and a dispersalist in detail, case by case according to the merits of each case." (Croizat 1982).

The implication of this for evolutionary theory is that we must look for process(es) causing evolutionary change in the ancestor over a wide area and not in some particular "center of origin". Moreover, this approach causes predictions based only on the analysis of biogeographic evidence on the basis of biological relationships and distribution, and it is not based on any particular geological theory (it can, therefore, actually be used to test geological theories).

The process of evolution, according to Croizat (1958, 1964) is independent from environment, and directional (he does not exclude the possibility of local adaptations, but considers those of secondary importance for the evolutionary process); this leads to the following discussion of "orthogenesis".

Orthogenesis and its role in evolution

As I have already reported, Darwin seemed to be aware of the importance of "laws of growth", but he was not able to synthesize organically those laws in his theory. The so-called "Modern Synthesis" or "Neo-Darwinism" ignored completely factors other than Natural Selection, considering natural selection necessary and sufficient to explain all evolutionary change. More recently, some authors have begun to (re-)consider the possibility that other factors may play an important role in evolutionary change (e.g., Gould and Lewontin 1979, Maynard Smith et al. 1985, Reif et al. 1985).

That other factors may play a role in evolution is something well known in continental European literature on evolution from the last century and the beginning of the present one (e.g., Rosa, 1923, 1988; see Grehan and Ainsworth 1985, and Craw and Heads 1988 for a discussion on the history of orthogenesis).

Orthogenesis has often been incorrectly equated, especially by leading Anglo-American evolutionary theorists, with some kind of mystical belief, e.g., "...[orthogenesis] relies on some built-in tendency or drive toward perfection or progress. All these theories were finalistic: they postulated some form of cosmic teleology of purpose or program." (Mayr

1978); or has been referred to in terms of linear series or trends toward a non-adaptive state (e.g., Panchen 1992: 263).

Orthogenesis in the sense of Darwin, Croizat, Rosa (among others) has no teleological or mystical connotations. It simply refers to the fact that a variation in form is limited and constrained, by the initial state. "I use the term orthogeny in a purely mechanistic sense, not at all in a mystical one..." (Croizat 1964: 676). It does not imply any explanations in terms of *ends*, so common in adaptive "just-so" story-telling (and on this point, adaptive explanations appear to me to be far longer and teleological).

The main critique of orthogenesis is that, e.g.: "[It] must involve some form of unknown, and perhaps 'internal' mechanism... an appeal to mysticism." (Gould and Lewontin 1979). Orthogenesis is, therefore, rejected mainly because of lack of a known mechanism. I think that Gould and Lewontin's distinction between a "strong" and a "weak" form of orthogenesis (or any other name they may like to use, such as constraints, laws of growth, *élan vital*, effort), based on an idea that the weak form does not resort to an unknown process, is arbitrary. Indeed Gould and Lewontin do not give any "known" mechanism for "phyletic constraints" and "developmental constraints"; this does not seem to me very far from the "appeal to mysticism" they propose for the "strong" form. Therefore, I do not think the distinction between "strong" and "weak" is a real one, the argument resting only on semantic confusion (and not on a *pluralistic* view of evolution). Recently, molecular drive (Dover 1982) was indicated by Graham (1984) as one possible mechanism for orthogenesis even though Dover (1983) rejected this possibility (he, anyway, mistakenly assumed that Grehan was equating "orthogenesis" with "molecular drive", while he was only indicating it as *one of the possible* mechanisms for orthogenesis).

Croizat considered orthogenesis as the principal factor in evolutionary change, i.e.:

"Natural selection is powerless to 'select' anything which does not exist. Variability in a definitely 'oriented' sense must be in act before natural selection can intervene. In sum, structural 'adaptation' rests in a prior time and place in the laps of laws of growth. These laws (= oriented evolution) must themselves furnish the complex set-up of parts, which made the fangs of the adder and the ovopositor of the ichneumon

possible and eventually actual as a whole organ, before natural selection could go to work on this organ, perhaps to refine it in certain aspects of function. Indeed, it may not be certain that these refinements are due to natural selection, for they may be sheer byproduct of correlations of which as little is known today as is Darwin's own times." (Croizat 1964: 650-651).

He considers evolution as consisting of two processes in interplay, i.e., orthogenesis (type of organization, *Bauplan*) and adaptation (to different environments), with the first being the most important to explain [macro]evolutionary change. He even assigns the relative importance of these two processes with orthogenesis being in play for at least the 75% of the times (Croizat 1964: 655 *fn* 2).

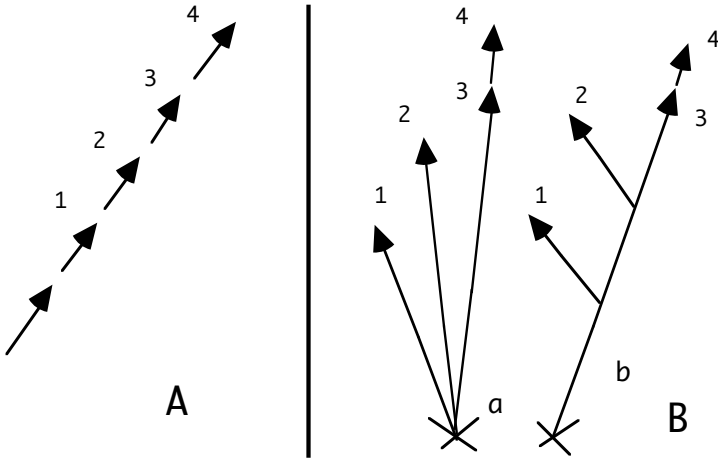
Aside from this last point (because of the objective difficulty of quantification), I believe Croizat's method and ideas are worthy of consideration; thus its uncritical dismissal is unjustifiable.

Phylogenetic relationships in Croizat's biogeography

The last point I will consider here very briefly is the alleged tenet that phylogenetic considerations have no role in Croizat's biogeography (e.g., Ball 1986, Cracraft 1975, McDowall 1978, Patterson 1981). This is false as Croizat was aware; he included in his analyses concepts of ancestor-descendent and common ancestry (see Croizat 1958[1]: 726, see also Craw 1979).

In particular, this can be evinced from the figure (redrawn) and the original notes partially reproduced on the next page (Croizat 1964, fig. 89: 783).

It is true, however, that Croizat was very critical of Hennig's "Phylogenetic Systematics". He, first of all (and he was right on this point, in my opinion), did not consider Hennig's approach to be original, but conceptually a compilation of the previous work of Rosa (1923, 1988), and, in particular on the Theory of Hologenesis. As Croizat (1979) reports, citing Rosa, "the dichotomous ramification of taxa stands indeed as the third and last fundamental thesis of Ologenesis". Croizat did not believe a dichotomous ramification of taxa as representing a natural phenomenon. He thought that was possible to perform parsimony analyses without the need of the "theoretical notion" of dichotomous cladograms. Finally,



... i) Clearly “polytopic” over space, through time by form is the process by which 1, 2, and 3-4 do emerge from a distally common ancestral group (diagonal crosses in the figure); ii) There is no difference otherwise than as postulated time between the processes displayed in a and b; iii) The assumed historical derivation of 4 from 3 might at the most be entertained as a very special case ..., observing at any rate that what it postulates is quite typical of the “old scheme” (A) ...; iv) It is evident that the process displayed in A and B, respectively, remains substantially unaltered whether 1, 2, 3, and 4 refer to ... races or varieties of one or the other zoological or botanical species, finally to families, subfamilies, genera, etc., bound within a common ultimate consanguinity; v) The concept of vicariism ... is incompatible with the “old scheme” in A, and hardly compatible, if indeed at all, with the derivation of 4 from 3 in B; vi) Biogeography agrees with the remaining sciences that the process of form-making displayed in B (except, in principle, as to 3-4) is the correct one. (Croizat 1964). Redrawn.

Croizat concludes that the essence of all form of classification is character weighting, *i.e.*, any classification is fundamentally based on a correct appreciation of the characters of the organisms under study. (This can be included in phylogenetic systematics, of course.) To reach this appreciation he considers it necessary for one to be free of theoretical biases (referring here to the need of dichotomous bifurcations).

CONCLUSIONS

In conclusion, Croizat's ideas are the development of a long line of evolutionary thought that has its bases in continental Europe. His panbiogeographic method (not to be confused with vicariance biogeography) is

an original and fruitful method of investigation worthy of consideration, as proven by its recent use and by the improvements and extensions made to it by New Zealand scientists. Its uncritical dismissal is, from a scientific point of view, unjustifiable. Many authors have confused Croizat's many negative comments on Hennigian systematics (cladistics) as a lack of understanding of phylogenetic relationships on his part but of which he was certainly aware and had even included in his analyses. It is apparent that the acknowledgment of Croizat's contributions in the 1950s and 1960s (and later) was eschewed because of sociological reasons (and not lack of scientific value), when the "modern synthesis" became established as the scientific orthodoxy.

LITERATURE CITED

- Ball, IR. 1976. Nature and formulation of biogeographical hypotheses. *Syst Zool* 24: 407-430.
- Baskin J. 1984. Interview with Léon Croizat. *Rivista di Biologia - Biology Forum* 81: 589-611.
- Brown JS, Gibson AC. 1983. *Biogeography*. Mosby, St. Louis.
- Brundin L. 1972. Phylogenetics and Biogeography. *Syst Zool* 21: 69-79.
- Cracraft J. 1975. Historical biogeography and earth history: Perspectives for a future synthesis. *Annals Missouri Bot Gard* 62:227-250.
- Craw RC. 1978. Generalized tracks and dispersal in biogeography: A response to R. M. McDowell. *Syst Zool* 28:99-107.
- Craw RC. 1982. Phylogenetics, areas, geology and the biogeography of Croizat: A radical view. *Syst Zool* 31:304-316.
- Craw RC. 1983. Panbiogeography and vicariance cladistics: Are they truly different? *Syst Zool* 32:431-438.
- Craw RC. 1984a. Never a serious scientist: The life of Léon Croizat. *Tuatara* 27:5-7.

- Craw RC. 1984b. Léon Croizat's biogeographic work: A personal appreciation. *Tuatara* 27:8-13.
- Craw RC. (compiler), 1984c. Charles Darwin on "Laws of Growth". *Tuatara* 27:19-20.
- Craw RC. 1988. Panbiogeography: method and synthesis in biogeography. In Myers AA, Giller PS eds. *Analytical biogeography*. Chapman and Hall: London, 405-435.
- Craw RC. Heads M. 1988. Reading Croizat. On the edge of biology. *Rivista di Biologia - Biology Forum* 81:499-532.
- Craw RC, Weston P. 1984. Panbiogeography: A progressive research program? *Syst Zool* 33:1-13.
- Croizat, L. 1952. *Manual of phytogeography*. Junk: 's Gravenhage, Nederland.
- Croizat L. 1958. Panbiogeography or an introductory synthesis of zoogeography, phytogeography, and zoology. With notes on evolution, systematics, ecology, anthropology, etc. Vol. 1 - The New World. Vol. 2 - The Old World. Published by the author, Caracas, Venezuela.
- Croizat L. 1961. *Principia botanica or beginnings of botany* (with sketches by the author). Published by the author, Caracas, Venezuela. ("1960" on title page)
- Croizat L. 1964. *Space, time, form: The biological synthesis*. Published by the author, Caracas, Venezuela.
- Croizat L. 1982. Vicariance/vicariism, panbiogeography, "vicariance biogeography," etc.: A clarification. *Syst Zool* 31:291-304.
- Croizat L. 1984a. Charles Darwin and his theories. *Tuatara* 27: 21-25.
- Croizat L. 1984b. Mayr vs. Croizat: Croizat vs. Mayr - An enquiry. *Tuatara* 27:49-66.
- Croizat L, Nelson G, Rosen DE. 1974. Centers of origins and related concepts. *Syst Zool* 23:265-287.

- Croizat-Chaley L. 1979. Hennig (1966) entre Rosa (1918) y Løvtrup (1977): medio siglo de "sistemática filogenética." Boletín de la Academia de Ciencias Físicas, Matemáticas y Naturales (Caracas) 38:59-147.
- Darwin C. 1872. On the origin of species by means of natural selection, 6th Edn. Murray, London, UK.
- Dover GA. 1982. Molecular drive: A cohesive mode of species evolution. Nature 299:111-117.
- Dover GA 1983. Molecular drive. New Scient. 98:808.
- Gould SJ, Lewontin RC. 1979. The Spandrels of San Marco and the Panglossian Paradigm: A critique to the adaptionist programme. Proc R Soc London 205:851-998.
- Graham JR. Ainsworth R. 1985. Orthogenesis and evolution. Syst Zool 34:174-192.
- Grehan JR. 1984. Evolution by law: Croizat's "Orthogeny" and Darwin's "Laws of Growth". Tuatara 27:14-18.
- Grehan JR. 1988. Panbiogeography: Evolution in space and time. Rivista di Biologia - Biology Forum 81:469-498.
- Heads M. 1985. Biogeographic analysis of *Nothofagus* (Fagaceae). Taxon 34: 474-492.
- Heads M. 1985. Biogeographic and biodiversity in *Hebe*, a South Pacific genus of Scrophulariaceae. Candollea 48:19-60.
- McDowall RM. 1978. Generalized tracks and dispersal in biogeography. Syst Zool 27:88-104.
- Maynard Smith, J, Buriam R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L. 1985. Developmental constraints and evolution. Q Rev Biol 60:265-287.
- Mayr E. 1978. Evolution. Scient Am 239:39-47.
- Mayr E. 1982. Vicariance biogeography [Review]. Auk 99:618-620.

- Nelson G. 1977. Biogeografía analítica y sintética ("Panbiogeografía") de las Americas. [Review] *Syst Zool* 26:449-452. Reprinted (1979 with a Spanish translation) in *Buletín de la Academia de Ciencias Físicas, Matemáticas y Naturales (Caracas)* 37:65-71 (Spanish, 57-63).
- Nelson G. Platnick NI, 1980. A vicariance approach to historical biogeography. *Bioscience* 30:339-343;
- Page RD.,1987. Graphs and generalized tracks: quantifying Croizat's panbiogeography. *Syst Zool* 36:1-17.
- Panchen AL. 1992. Classification, evolution, and the nature of biology. Cambridge University Press, New York.
- Patterson C 1981. Methods of paleobiogeography. In Nelson G, Rosen DE eds. *Vicariance biogeography: A critique*. Columbia University Press: New York, 446-497.
- Reif W-E, Thomas RDK, Fischer MS. 1985. Constructional morphology: the analysis of constraints in evolution. *Acta Biotheoretica* 34:233-248.
- Rosa D. 1923. Qu'est-ce que l'Hologenèse? *Scientia* 33:113-124.
- Rosa D. 1988. Theory of hologenesis. *Rivista di Biologia - Biology Forum* 81:613-615.
- Wilson EO, Bossert WH. 1971. *A primer of population biology*. Sinauer, Sunderland MA.