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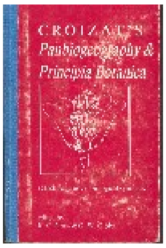

Title: Evolution By Law: Croizat's 'Orthogeny' and Darwin's 'Laws of Growth'

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Abstract

A concept of internally directed evolution is recognised in Croizat's pan-biogeographic synthesis as being fundamental to an understanding of the evolutionary process. The meaning and application of Croizat's concept (orthogeny) is briefly discussed. Reference is made to similar concepts by other biologists, in particular the "laws of growth" by Charles Darwin. Contrast is made between the primary role of orthogenesis attributed by Croizat, and the viewpoints of contemporary evolutionary thought.

Keywords: adaptation, Croizat, Darwin, natural selection, orthogeny.

An exciting aspect of Croizat's "panbiogeography" is that the formerly disparate disciplines of biogeography and evolution become integrated within the framework of a single general synthesis. This synthesis recognises evolution as the interaction of "space, time and form" and Croizat summarises the concept of evolution by the formula: Evolution equals space + time + form. In contrast, orthodox evolutionary studies concentrate on form (over time) and this is reflected in the definitions given by Eldredge (1979) of "descent with modification" and "change in gene frequencies".

Croizat's unique approach to evolution is to use biogeographic analysis as the basis for understanding the process responsible for change in form through time and over space. This analysis has furbished concepts that lead not only to a re-evaluation of Darwin's understanding of dispersal but also the role of natural selection as the primary mechanism of change. Although not the first to question the power of natural selection, Croizat discusses extensively the concept and role of another evolutionary process called "orthogeny" and investigates its relationship to adaptation and other aspects of organic evolution.

The orthodox evolutionary framework recognises directionality (or trend) in evolution but attributes this to natural selection (Stebbins 1967,139; Dobzhansky 1970,391; Dobzhansky et al. 1977,120; Mayr 1978,47; Gould 1982,381; Campbell 1982,192). However there exist in nature, "types of organisation" (recognisable "structural" groups) to which the member organisms are seen to conform, regardless of their environment or manner of adaptation. This shows that despite variation in environment acting on an organisim through natural selection, the form of the organism is already determined according to the type of organisation inherited. This process of non-environmental determination is therefore a set of inherent tendencies which "orient" evolution regardless of environment. This is the process Croizat (1964,678) refers to as "orthogeny". By way of example, a scorpion "adapted" to the desert is a "scorpion" rather than the type of organisation of similarly "adapted" organisms such as a "tortoise" or a "camel".

Apart form "orthogeny" a variety of terms have been used in reference to internally directed evolution or inherent tendencies, including "orthogenesis" (first used by William Haake in 1893 and later adopted by Eimer 1898,19); "nomogenesis" (Berg 1926); "germinal stream" (Metcalf 1928); and "internal factors" (Whyte 1963, Grasse 1977). Less explicit reference has been made by other biologists using terms such as "oriented evolution" (Simpson 1960); "nature of the organism" (Dobzansky 1960,407); and "historical burden" (Wiley & Brooks 1982). Athough page 15 differing perhaps in detail, all of these terms encompass a fundamental concept of inherent directionality and in the following discussion of this concept Croizat's term will be used.

Although well known for the evolutionary synthesis "Origin of Species by Natural Selection" Darwin also attributed evolution to directional factors independent of the environment which he repeatedly referred to as "laws of growth". Some of these statements are reproduced elsewhere in this issue. Darwin's reference to laws of growth is important because it shows that just as Darwin knew of vicariant form making (Croizat 1964;621) he was also aware of orthogeny, Vicariant form making is a fundamental aspect of dispersal (and therefore evolution in general). During evolution different forms evolve in different localities so they replace each other over space to form a mosaic pattern (Croizat 1961,1454). Examples and the implications of vicariism are discussed extensively throughout Croizat's work. However vicariism was subsumed by Darwin under "centres of origin" and "means of dispersal" while orthogeny was neglected in favour of "natural selection" in his general synthesis.

The essence of what Darwin (1860,205) had to say was that although we may be ignorant of the nature of many features, evolution by orthogeny could be regarded as the origin of many structures and this did not require *immediate* usefulness or advantage. Even though

Darwin's evolutionary synthesis favoured the role of natural selection, he expressed some doubt (Darwin and Seaward 1903) over this decision and believed that there was much yet to be learned about “laws of growth”. Darwin (1888,61) clearly indicated that natural selection came to work on what laws of growth (orthogeny) provided. Because of this Croizat (1964,657) notes that while some might rank Darwin as an “orthogenist” others would deny this, and suggested that Darwin himself may not have been able to resolve the question. Darwin was certainly aware of more than one agent of change, this apparently being the basis of Gould and Lewontin's (1979) description of “pluralistic” to Darwin's approach of identifying the agents of evolutionary change. However “pluralistic” falls far short of “synthesis” and while Darwin was pluralistic in recognising the existence of vicariism and orthogeny, he failed to underscore their relative importance in evolution. This failure set the pattern for much of biogeography and evolution to this date.

Apart from Croizat, substantial discussion of orthogeny includes Eimer (1898) (Eimer's ideas are discussed in some detail by Bowler 1979), Berg (1926), Metcalf (1928), Trueman (1940), and Whyte (1965). (Whyte's background is primarily with physics and the philosophy of science and apparently he was not aware of Croizat's work). Orthogeny also formed the basis for Rosa's theory of holpgenesis (Rosa 1923, IB). Much smaller contributions are given by other biologists such as Grasse (1977) and Riedl (1978). The major irony of post-Darwinian orthodoxy is that while orthogeny was explicitly ignored or condemned, the very same biologists when faced with the facts, resorted to descriptions that were of an orthogenetic content. Examples are Simpson (Croizat 1964, 622-644), Huxley and Mayr (Brundin 1968, 487-493).

The mainstream of orthodoxy, exemplified by Darwinism and neo-Darwinism, placed orthogeny as unscientific. Mayr (1978,42) claimed that those who reject natural selection and put forward the alternative of orthogeny, “relied on some inbuilt tendency, drive toward perfection or page 16 progress” and were therefore “finalistic” postulating some form of “cosmic teleology, of purpose or programme”. Similar sentiments were again expressed by Mayr (1980,4). Gould (1980,129) claimed orthogeny to be mysterious but at the same time accepted “internal factors” which channel and constrain “Darwinian” forces, and earlier (Gould 1972, 93) had noted that Trueman (1940) “carefully” disavowed any mystical connotations. To Dawkins and Krebs (1979,507) the idea that orthogeny could direct evolution was “obviously” absurd. Rosen (1982,271) invoked the authority of the philosopher of science Karl Popper to declare the subject (of orthogeny) a “nineteenth century mistake” although Rosen (1974,290) was aware of Croizat's (1964) arguments and reasoning.

Orthogeny in the sense of Darwin, Berg, Croizat, Whyte, etc (and see Rosa 1923,124) is not at all mysterious or teleological. Change in form is merely a consequence of the initial state, followed by evolution according to laws and potential. It is of interest to note in reference to Mayr's (1978) denouncement of orthogeny because of teleology, that orthodox evolutionary views of adaptation involve explaining the origin of a structure in terms of *ends* and can therefore be described as teleological (e.g. Dobzhansky 1970, 4; Ruse 1982).

Some biologists have referred to orthogeny in terms of a pattern of linear series or trends, often in reference to the fossil record (Shull 1936, Simpson 1960, Eaton 1970, Avers 1974, Dobzhansky et al. 1977, Mayr 1978, Stanley 1979, Minkoff 1983). In this context, “examples” of orthogeny are criticised for failing to conform to an arbitrary requirement for some sort of linearity or undeviating constancy. Such an approach has obscured the *primary* concept of orthogeny as a process involving inherent tendencies, and determinant change (cf Trueman 1940,87). Also ignored is the role of dispersal (evolution through space and time) whereby characters displayed in the ancestor become differentially represented in the descendants (Croizat 1961,1566). The recombination may sometimes produce varied and novel forms, but they remain within the possibilities determined by the particular orthogeny.

Orthogeny is an important concept in biology because the implications of such a process for understanding the relationship of plants and animals with the environment, are radically different to that provided by the orthodox evolutionary framework. Lewontin (1982) claims that internal and external processes are equal and there is a “coevolution” between the two. However, Croizat (1964,683) points out that with orthogeny dertermining the type and range of variation natural selection can at best have only a secondary role because it cannot act beyond the variation provided. Berg (1926) believed that natural selection could have no evolutionary role at all.

Natural selection as the main creative mechanism of evolution is considered by Toumi (1981) and Gould (1982,380) to be a central part of Darwinism. According to Mayr (1982,165) long term evolution is inconceivable without natural selection. Eldredge and Gould (1974) went so far as to exclaim, “surely we ‘believe’ in regimes of natural selection which affect a transformation of the gene frequency of populations, in a regular and progressive manner. How else can we explain adaptation?” Lewontin (1978) believed “adaptation” to be sometimes hard to define and described the “modern” view of adaptation as “problems set by the environment which organisms need to solve”. Gould (1982,383) admitted that the page 17 present utility of a structure (its adaptation) permitted no assumption that selection shaped it and he considered the possibility that:

> “the constraints of inherited form and developmental pathways may so channel any change, even though selection induces motion down permitted paths, the channel itself represents the primary determinant of evolutionary direction.”

At the risk of misconstruing Gould's arguments it would seem that they come as close to orthogeny as possible without admitting it and Gould (1977,85; 1982,383) only avoids this by claiming that the channels may be set by past adaptations so selection remains pre-eminent. However, with orthogeny this “pre-eminence” is not possible. Because Gould and Lewontin (1979,593) believe orthogeny must be rejected as a “close appeal to mysticism”, they claim (p594) that change in structural organisation “may” be mediated by natural selection and yet they believe that constraints become “much the most interesting” aspect of evolution! The “pluralism” of Gould and Lewontin appears to provide no more synthesis than Darwin over 150 years ago. The only biologist to attack this crippling confusion at its roots is Croizat.

In contrast to Gould's contradictive manoeuvering between “constraints” and “natural selection”, the process of adaptation by orthogeny is much more straightforward. Natural selection can only be secondary to orthogeny and so interpretation of adaptation must look first to structure, not the resulting function. Adaptation is seen as the result of 2 distinct components, “structural adaptation” which is primary and orthogenetic, and "environmental adaptation" which is secondary and mediated by natural selection (Croizat 1964, 709). This understanding of adaptation does not rely on guessing the original relationship to be "advantageous", "selective", "non-adapative", "neutral", "preadaptive", etc. Gould and Vrba (1982) argue for a missing concept in evolution which they call "exaptation" so to encompass the evolution of features not due to present utility. However the missing concept is not exaptation but orthogeny which eliminates the "problems" experienced by Gould and Vrba (1982).

The underlying mechanism of orthogeny is identified by Croizat (1964,680) as a prime goal of evolutionary research. The main concern of evolutionary genetics has been with natural selection and the relationship of environment to gene frequency and expression (Dobzhansky 1970, Berry 1982). A concept of orthogeny calls for re-evaluation of genetic interpretation, including the nature and role of mutation. In its genetic aspect, biological study has not yet generated a comprehensive understanding of orthogenetic processes. Although Dobzhansky et al. (1977,77) claimed "the birth of molecular genetics has finally disposed of any the oretical basis for internally directed orthogenetic evolutionary trends", the mechanism of "molecular drive" proposed by Dover (1982) gives explicit recognition to a possible directional quality in evolution. (See also Campbell 1982, Hunkapiller et al. 1982).

It has been stated in the analysis of Darwinian evolutionary study by Hull (1974,120) that:

> "Future biologists may produce new biological theories, perhaps new versions of evolutionary theory, that make no reference to organisms, or the reproductive relationship between them…the conceptual revolution necessary for such a change would be enormous".

The concepts of dispersal and orthogeny introduced by Croizat, in a comprehensive evolutionary synthesis involving space, time, and form, clearly indicate that such a revolution in biology has already begun.

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individuals that carry those traits. Those who have bad traits don't survive or create very few off spring due to then dying from the same bad traits. Descent with modification. The publication of Darwin's On the Origin of Species in 1859 brought scientific credibility to evolution, and made it a respectable field of study.[27]. Despite the intense interest in the religious implications of Darwin's book, theological controversy over higher criticism set out in Essays and Reviews (1860) largely diverted the Church of England's attention. Creationists had lobbied aggressively for the law, arguing that the act was about academic freedom for teachers, an argument adopted by the state in support of the act. Lower courts ruled that the State's actual purpose was to promote the religious doctrine of creation science, but the State appealed to the Supreme Court. Darwin tried to distinguish his theories from these by arguing that evolutionary changes were based only on naturally occurring processes – processes that are still occurring around us now. 2 / 30. The Theory of Evolution by Natural Selection. The theory of evolution by natural selection is a theory about the mechanism by which evolution occurred in the past, and is still occurring now. § Beginning in the end of the 18th century, the rising industrialism in Britain created a massive growth of urban poor. This lead to the rise of poverty as a social problem and to various attempts to address it. § In 1798, Thomas Malthus (1766–1834) published his Essay on the Principle of Population. You see, Darwin’s theories were incomplete, and not accepted by themselves today. Mostly correct, but incomplete. Our understanding of evolution has been expanded and improved by a multitude of great minds since then. Our understanding of genetics, something that Darwin lacked, filled in many of the gaps and corrected the errors Darwin made in his assumptions. To this day, we are still making new discoveries in this field.