

The Global Patterns of Life: A New Empiricism in Biogeography

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Evolutionary theory became respectable with Darwin, but the success of his work need not be taken as evidence of truth, or even maturity. Darwin's approach to species variability was simply the first one to be generally accepted, and although the 'Darwinian method' has been central to biology for over a century, signs of iconoclasm are beginning to emerge. The rise of 'vicariance biogeography' is one of these, and few comparisons show the nature and weakness of Darwin's approach more clearly than the juxtaposition of his biogeography with this more recent, and more mature version. Of course, a problem inherent in Darwin's method may well indicate one in large sectors of scientific theory, so ubiquitous is the form of thought. A critique of such broad habits of mind may intimate a paradigmatic shift rather than a simple correction, and the immediate future of Systematics promises to be quite interesting. In the following review I shall indicate, unhistorically, the weakness in Darwin's approach before I examine the more recent developments which made that weakness apparent.

Darwin

Biogeography is the study of distribution of the ranges of plants and animals. Because the patterns of distribution do not seem to be random, it is quite probable that such studies may contribute to evolutionary biology, if the import of the distribution patterns may be discovered. Darwin, in *The Origin of Species*, advanced a hypothesis to that end, suggesting that since each species must have emerged from a specific geographic location, which he termed a "centre of origin," and dispersed across the face of the globe from that point, distribution information should be examined for a record of that migration and its original centre. He wrote, in the recapitulation of the last chapter:

When we can feel assured that all the individuals of the same species, and all the closely allied species of most genera, have within a not very remote period descended from one parent and have migrated from some one birthplace, and when we better know the many means of migration, then, by the light which geology now throws, and will continue to throw, on former changes of climate and of the level of the land, we shall surely be enabled to trace in an admirable manner the former migrations of the inhabitants of the whole world. (pp. 486-7)

With this hopeful scenario in mind, he had studied the ranges of living animals in hopes that their point of origin might be traced. Later biologists continued the same search, with almost the same enthusiasm, but the centres of origin proved remarkably difficult to fix, and biologists differed on the nature of identifying criteria. While this did not discourage the majority, some worried voices were raised. S. A. Cain, a

botanist engaged in the search for “centres of origin,” wrote in 1943 that a review of the literature turned up 13 distinct criteria for the detection of centres of origin in use by varied authors, some of them conflicting. He wondered if biogeography had become confounded by its own theoretical framework:

The sciences of geobotany...carry a heavy burden of hypothesis and assumptions which has resulted from an overemployment of deductive reasoning....In many instances the assumptions arising from deductive reasoning have so thoroughly permeated the science of geography and have so long been part of its warp and woof that students of the field can only with difficulty distinguish fact from fiction.

To see what he meant by this remark we shall have to look more closely at the Darwinian project.

Darwin begins his discussion, in chapter eleven of *The Origin*, with the “great facts” of distribution. The most basic is that each area of the world has its own distinctive inhabitants (now called a distinctive *biota*). However closely an area in the new world may resemble another in the old, in terms of climate or other physical conditions, the majority of organisms that live in each will be peculiar to the region. Secondly, the regions showing very distinct biotas are distinguished from each other by natural barriers (i.e., oceans). Correlating barriers or great distance to difference and the lack of barriers and/or distance to similarity, Darwin argues that common origin can account for the similarities between groups, and time in isolation from one another for the degree of difference between them. He concludes, a few pages later:

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 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 on the agency of a miracle. (p. 352)

We see here the adversarial context within which Darwin constructs his discussion. He is making a case *against* a specific opponent — i.e., special creation — and is answering extra-textual criticisms. A theory of special creation would allow the same taxon to appear at several different places on the globe. The creationists argued that this was consistent with the discontinuous ranges of many taxa, while Darwin’s theory of single origin is not. Darwin admits, above, that discontinuous ranges provide a difficulty for the hypothesis. These were the “cases of extreme difficulty” above. (Fig. 1, a species of dandelion in the southern hemisphere) The rest of his chapter, and most of the following one, will deal with this possible falsifier.

Beginning, as we see above, from the strange argument that the simplicity of his thesis so captivates the mind that all alternatives to it must be supernatural, Darwin proceeds to argue that migration and subsequent extinction could produce a pattern of discontinuity.

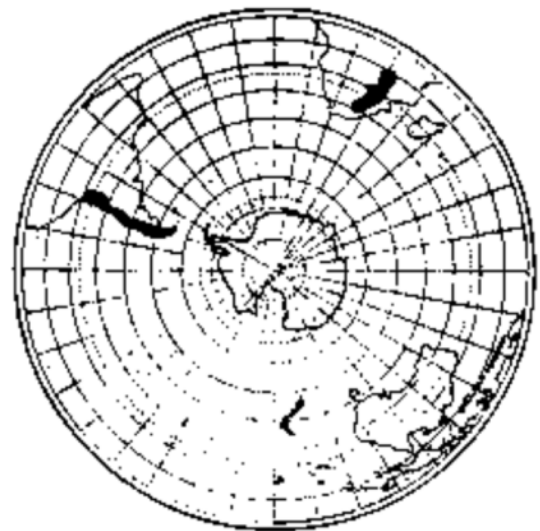


Figure 1. Distribution of *Taraxacum magellanicum* (Compositae). (After Croizat 1962,

Undoubtedly many cases occur, in which we cannot explain how the same species could have passed from one point to the other. But the geographic and climatal changes, which must certainly have occurred within recent geological times, must have interrupted and rendered discontinuous the formerly continuous range of many species. So that we are reduced to consider whether the exceptions to continuity of range are so numerous and of so grave a nature, that we ought to give up the belief, rendered probable by general considerations, that each species has been produced in one area, and has migrated as far as it could. (pp. 353-4)

The investigation proceeds with a case by case analysis arguing that in each case there exists a way in which migration from a common centre can be consistent with the discontinuous range of the organism. It is, for the most part, an easy task.

As Robert O’Hara has argued (1988), Darwin advances explanations for “how, possibly,” an event could have occurred. And there are certainly myriad possibilities by which migration could provide the phenomenon: discontinuity produced by widespread extinction of a formerly continuous range, discontinuity produced by migration across ocean basins (Darwin soaked seeds in salt water to make sure that this could be done without rendering the seeds unviable) — with a bit of thought one could probably find several narratives for each of his cases. As O’Hara points out:

How-possibly explanations...do not demonstrate why events or changes should necessarily have taken place. The success of a particular how-possibly explanation...depends on how well it answers or removes the objections a reader has thought of to the event’s having occurred....

Thus, aware of the argument that discontinuities of range make single centres of origin unlikely, Darwin reviews case after case to see whether they can falsify his account. Once satisfied that *all* ranges are consistent with the varied *possibilities* provided by his hypothesis, he concludes his investigation.

The attempted falsification was defeated, but Darwin was still unable to trace the “routes of migration” or locate “centres of origin.” After all, these tasks he gave to the future. “*When* we can feel assured...we shall surely be enabled to trace...former migrations...” And by assigning them to futurity, he admitted his inability to carry them out in the present.

Because the task has proven so difficult, it may be important that the argument by which Darwin assigned it contains a logical error. The argument proposes that if (1) each species had a single center of origin, and if (2) the “means of migration” are known, then (3) geographical and geological evidence (distribution, climate, land level, etc.) can be read to show “the former migrations.” That is, if (1) and (2) are true, (3) must follow. But the only conclusion that follows from (1) and (2) is that migrations *may* be traceable. After all, a knowledge of the *means* does not guarantee that any trace of the event now exists — perhaps dispersal does not leave an evidence of its passage. The mistake seems a rather small oversight, but it contains implications for methodology.

Table 1
Cain’s (1944) criteria for determining ‘centres of origin’

1. The location of the greatest variety of forms of the taxon.
2. The location of the area of greatest dominance and density of distribution.
3. The location of the most primitive form.

4. The location of the area exhibiting the maximum physical development of individuals.
 5. The location of the area of maximum ecological productivity of the taxon.
 6. Continuity and convergence in the lines of dispersal.
 7. The location of least dependence on a restricted habitat.
 8. The identification of continuity and directness of individual variations or modifications radiating from a 'centre of origin' along the highways of dispersal.
 9. The area of origin indicated by natural geographic affinities.
 10. The direction of origin indicated by the annual migration routes of animals, especially birds.
 11. The region of origin indicated by seasonal appearance or general *phenology*.
 12. An increase in the number of dominant genes towards the centre of origin.
 13. The concentricity of progressive equiformal areas.
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Consider the possibility that biologists, following Darwin's imagined future, would insist on tracing the routes of migration from geological evidence when traces of such routes were not there to be found. After all, by the forties three generations of biologists had attempted to find the centres of origin through patterns of distribution, with uncertain consequences. There was no clear way to identify the desired elements, although suggestions proliferated. As Cain indicated, biogeography suffered from an overabundance of advice but a poverty of results. He collected, in evidence of his claim, thirteen distinct and in part conflicting criteria (Table 1), which provide examples of the "heavy burden of hypothesis and assumptions" of geobotany. Leon Croizat noting, in 1962, that biologists were still projecting the success of the programme into the future, was less charitable than Cain:

So goes this "explanation" (the inception of which...may be credited to Darwin's own *Origin of Species*): it is true *today* that the "means of dispersal" of all too many plants and animals must be "mysterious" for we do not know how they operate to effect translation in space....All this is true and certain, BUT a day will come when we will at last understand how "means of dispersal" do operate which are today for us "mysterious." When that day dawns, we will explain everything of dispersal...that we do not understand today. Meantime, let us wait for the dawn of better times and — of course — continue jogging along the old rut. Were this not true it could hardly be believed by a young scientist. (Croizat, 1962)

Leon Croizat

Croizat could speak with authority, for it was his own work that demonstrated the weakness inherent in Darwin's programme. To understand his approach, however, we must go back over the ground we have just skimmed, this time in a more detailed manner.

One of the first things one may notice about distribution maps is the difference between a highly localized range (Fig. 1) and a cosmopolitan one occurring on all major continents. Localization in its most intense form will limit a taxon to a single range (the platypus in Australia), as cosmopolitanism extended to its limits will place the same taxon on all habitable ground. Darwin's first "great fact" was one of regional localization, or as it is known today, *endemism*. An *endemic* taxon is restricted to a single, localized range, and when an area possessing many such endemic taxa is identified, it is called an area of

endemism. An early attempt by Sclater (1858, Fig. 2) to identify the regions of endemism among birds was adopted by Wallace (1876) as a map of endemic realms which applied to animals in general. On the Sclater map one may see what Darwin meant. The animals found in Asian desert areas, for example, will be identifiably Asian, and those found in North American deserts, clearly North American, even though the local conditions are quite similar. The deserts of Australia will produce a third collection distinct from the other two.

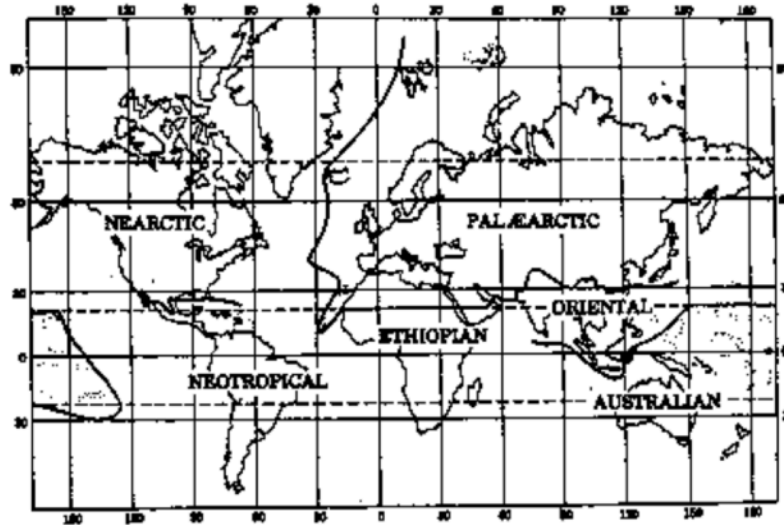


Figure 2. Faunal regions (or realms). (After Sclater and Wallace, as modified by Ross, 1950)

Of course, as we have seen, some species are cosmopolitan and are not part of this pattern, but the cosmopolitan distribution is rather uninformative due to the lack of distinctions. Things that show up everywhere tell us nothing about the relation between area and taxa. Things that are localized suggest a connection.

Looking therefore to the taxa that show localized patterns, we find Darwin's second fact. The salt water life on the two sides of the Isthmus of Panama seemed, to Darwin, to represent two distinct biotas (where a *biota* is the totality of animals found in a region), the ranges of which were determined by the barrier of the isthmus itself. Thus areas of endemism are delimited by barriers to migration, and very complete barriers, of course, will be ocean basins for land taxa, land masses for ocean taxa.

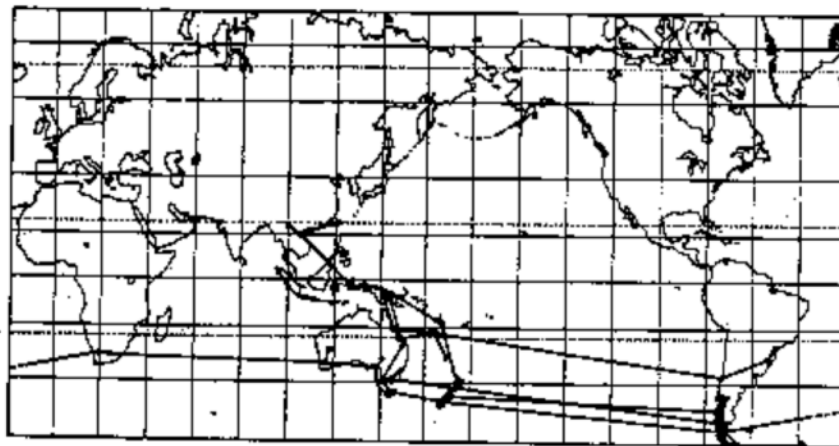


Figure 3. Some generalized tracks for the southern hemisphere and S. E. Asian tropics; Chironomid midges; *Nothofagus*; *Restionaceae*, *Araucaria*, *Libocedrus*. After Humphries and Parenti (1986, p. 19).

An examination of many distribution patterns will show that highly disjunctive distributions such as that shown in Fig. 1 are not uncommon. If Darwin's scenario is correct it has been played out many times, for discontinuous range is, along with endemic areas, a major localization pattern. It may in fact be conceived as a kind of endemism, since the species or genus so distributed is endemic to these few places.

(Sometimes the distribution is of a genus, and each area has its own endemic species.) Taking that suggestion, we may model the study of disjunction on that of endemism. In the former case we identify a localization of range common *to the whole biota*, the limits to the area being given not by the distribution of any single taxon, but by the congruent distribution of many. In like manner, when we find the pattern of disjunction we could ask "is the disjunctive distribution of this taxon *repeated by other taxa*?" Darwin did not ask this question because he was busy 'explaining' individual cases, but Croizat, who cared less for explanations, did ask it.

In his 'panbiogeographic' examination of distribution patterns Croizat compared the patterns globally rather than trying to explain each as a special case. He noticed that the same disjunctive distribution might be repeated by many organisms, even as the same area of endemism might be shared by many. According to the tale he discovered this while mapping the distribution of varied taxa using maps printed on sheets of cellophane, one sheet to a taxon. He would mark the distribution, and if it was discontinuous he would connect the ranges by a line which he called a 'track,' perhaps because it might indicate an earlier continuous range. Of course, the actual early range was not known so Croizat, attempting to gather a sense of the geographic relations, simply connected the disjunct ranges with a direct line.

When he superimposed multiple maps upon each other by overlapping them on a backlight, 'generalized tracks,' shared by many different taxa, became visible. The contraction of a continuous range into fragments by extinction is a chance occurrence, and we do not expect to find it repeated — accidental events should produce random patterns. On the other hand an area of endemism is shared by many taxa, thus not accidental. If a generalized track, or disruption of range, is also shared by many taxa, it is not accidental either, yet many such shared tracks are now mapped. Humphries and Parenti (1986) write:

Of the better known examples of generalized tracks, we cite Hooker's example of the southern hemisphere areas of South America, Tasmania, Australia, and New Zealand. Different groups of organisms occur in these four southern areas that exhibit identical, or nearly identical, patterns of disjunction. Thus, the near identical distributions of freshwater fishes, earthworms, molluscs, birds, mammals, insects, mosses, and flowering plants pose a general problem concerning the original distribution and subsequent history of a pan-austral biota. (An *austral* range is the temperate region of the southern hemisphere, a *boreal* range would be northern temperate.)

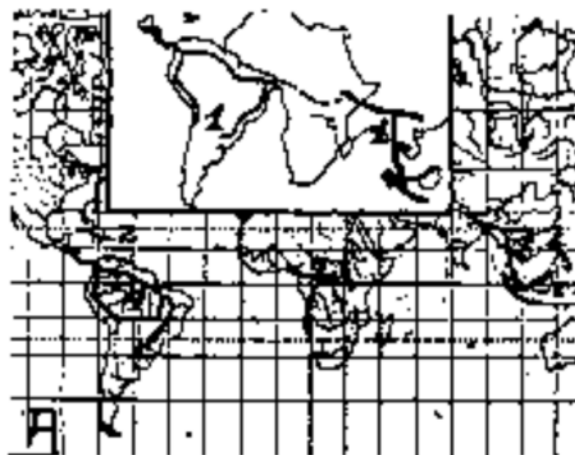


Figure 4. After Croizat (1962, p. 191).

We need to pause briefly for a methodological reflection. When I suggest that a pattern of disjunction common to many organisms is not accidental, I am assuming that the reappearance of the same indicates a common cause. ‘Accidental,’ in this context, would mean something like ‘deriving from multiple and unrelated causes.’ My assumption is commonplace, but in this case the prime candidate for common cause is the single element to which all others correlate — i.e., the barrier, which now looks to be the active element. In a temporal account one might abandon the usual supposition that the barrier pre-existed the distributions, and propose instead that the distributions pre-exist the barrier, which through its coming into being causes the common disjunctions. This interpretation, by which the immobile distributions preserve the disruptions of geography, was termed “vicariant” by Croizat.

As we can see from the map of the generalized tracks mentioned by Humphries and Parenti (Fig. 3), much of the disjunction, the track itself, is brought about by salt water. (None of the organisms mentioned can colonize deep salt water ranges.) At this point recent theories of earth history can suggest a causal framework. Croizat found salt water disjunction to be true of a great number of generalized tracks. It is often the case that the nearest living relative to an endemic coastal species (occurring at one point only) will be found on the other shore of the intervening ocean basin. He wondered why ocean basins were such popular centres for animals to orient themselves about, when it occurred to him that the multiplicity of common tracks across ocean basins might be the record of a one-time absence of the same basins. Perhaps the common ancestor of our two nearest relatives enjoyed their combined ranges, without the intervention of the present ocean.

Croizat had to wait until geology had reconstructed the tectonic history of the Earth’s crust as the progressive break-up of an original supercontinent (Pangea) and rearrangement of the resulting fragments before he could look for correlation from other evidence, but then he had the satisfaction of pointing to the apparent congruence between many generalized tracks and the reconstructed history. Even so he was distrustful of what he insisted on calling “wegnerism” (in deference to Alfred Wegner, the first man to propose the idea), since the reconstruction was not congruent with existent trans-Pacific tracks. (The Pacific was supposed the original ocean, surrounding Pangea, and therefore not produced by splitting a landmass.) But as we can see in the insert to his own map of common South American-African-Asian tracks (Fig. 4), the combined landmass now termed Pangea would connect the area of disjunction nicely, eliminating the salt water gaps.

Disjunctive distributions created a problem for Darwin, Croizat concluded, because such patterns are not records of migration — i.e., of changing range — but of a much simpler immobility. The observed pattern links the taxa to specific locales — it is essentially one of endemism. If we allow the linkage to stand — if the animals remain in place but the locales move apart, the generalized tracks for the Atlantic, or Indian Ocean, receive a *common* explanation. (Those across the Pacific await a solution. Some geologists have suggested that the west coast of North America is an amalgam of various terrains, some of which may be Asian in origin, and thus the connection represented by trans-Pacific tracks is repeated geologically, although without explanation as yet.)

Croizat’s whole development begins from Darwin’s first “great fact” — i.e., the observed correlation of particular biotas with particular areas. In Darwin’s treatment, however, the immobility seen in this connection is made epiphenomenal, either a terminal condition or a temporary appearance, and the real goal of investigation is the traces of movement which may lead back to centres of origin. There may well have been such movement at one time — a much earlier time — yet the present pattern, taken in itself, is one of distinctions of range, and the distinctions appear stable. (They are stable indeed if the congruence with tectonic patterns is correct.) To read such a pattern one must preserve its basic element, the tie between the organism and the land.

Modern Vicariance Biogeography

We are now in a position to perform such a ‘reading,’ and to develop a comparison between the dogmatic approach taken by Darwin and the empiricism inherent in the work of Croizat. Recent work in vicariance biogeography has developed the pattern of endemism to a greater degree than was possible by Croizat’s methods. As we have seen, endemism is a collective phenomenon, and areas of endemism are endemic for many species. Thus we may speak of ‘tracks’ or orientations across barriers common to many taxa. But we have not yet queried other relations possessed by these same groups. This question was posed by Sclater (1858), when he studied the early maps of endemism and remarked:

Little or no attention is given to the fact that two or more of these geographical divisions have much closer relations to each other than to any third.

The “relations” mentioned are taxonomic, and they are most descriptively studied today through display on a ‘cladogram,’ a branching diagram which displays a hierarchical summary (nested sets) of the character information (developed from the work of Willi Hennig 1966)). On a cladogram a single group (i.e., vertebrates) will be displayed as terminals of a single stem since they all possess the same defining character or characters (vertebral column), but that stem will branch for every difference found within the larger group. Thus the single stem displays what is common, while the division of the branching displays difference.

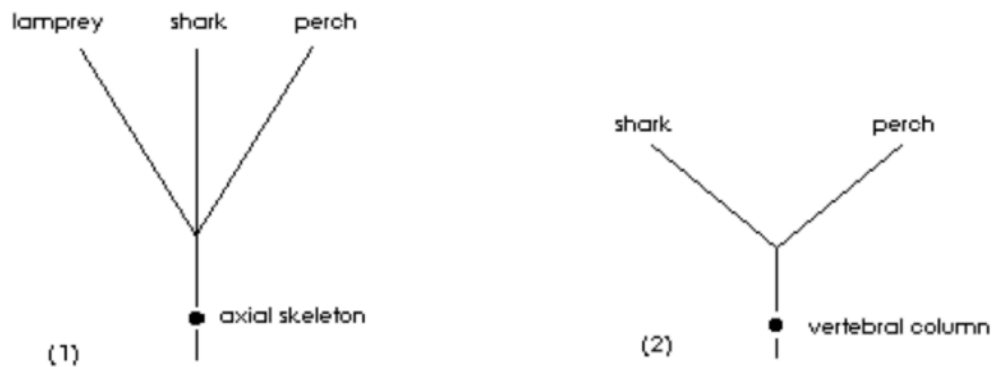


Figure 5.

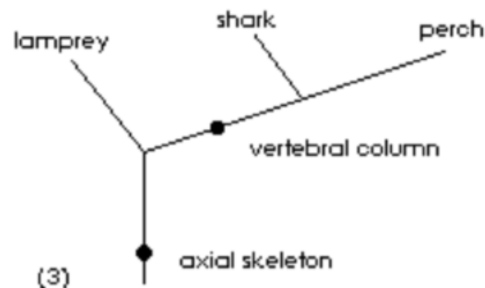


Figure 6.

In order to demonstrate the manner in which a cladogram summarizes character information I will borrow an instructive example from Nelson and Platnick (1981). Their cladogram states the morphological relation between the lamprey, the shark, and the perch. The fish are somewhat far apart, but they are still fish and will form a hierarchy if their character information is compared. The unifying character will be the *axial skeleton*, a feature which vertebrates share with other groups and therefore more general than a *vertebral column*, which becomes the second character under consideration. Thus each character defines a group (Fig. 5), all three forms possessing the axial skeleton but only the shark and the perch being vertebrates. When we combine the two group diagrams we get a hierarchical branching diagram of the character information, or a cladogram (Fig. 6).

Of course, each organism has more particular features as well. The lamprey has a notochord, while the shark and perch have vertebral columns, but the shark vertebrae are cartilage while the perch vertebrae are bony. But despite the fact that each organism is unique, the branching diagram does display hierarchical relation — i.e., all of these animals are more closely related to each other than either is to the lamprey because they both possess vertebral columns. The ‘relation’ displayed in a cladogram, therefore, is merely the logical summary of shared and unshared characters. (A thing is different from another to the degree that it possesses different characteristics, and the same to the degree that it possesses the same characteristics. ‘Relation’ is measured in terms of degree of departure from commonality — the smaller the departure the closer the relation. The shark and the perch have a spinal column in common and thus their departure from the lamprey, which does not possess the column, is greater than their departure from each other.)

Of course, one may make an evolutionary interpretation of this, proposing that all the groups on a single stem must spring from a common ancestor, and that the common ancestor of the shark and perch is more recent than the common ancestor of all three, making the lamprey the more ‘primitive’ form of the three and the other two forms more ‘derived.’ But such an interpretive programme should not eclipse our awareness that the programme adds the assumptions of common ancestry and differentiation by descent to *explain* the logical pattern — i.e., the logical relations are primary and must be discovered before the narrative can be advanced.

Humphries and Parenti (1986) demonstrate how a cladistic comparison of areas of endemism is made through an example which reproduces in a simple manner the type of pattern relation involved. In Fig. 7 they superimpose hypothetical cladograms of frogs (taxa F1, 2, 3, 4) and lizards (taxa L1, 2, 3, 4). Brackets above the taxa identify the areas of endemism in which the taxa are found (Australia, New Guinea, South America, and Africa). The obvious point is that the two cladograms have congruent patterns, which allows the ‘area component analysis’ of Fig. 8.

The cladograms in Fig. 7 would be read as expressing the judgement that the endemic species (frogs and lizards) of Australia and New Guinea are more closely related to each other than either is to the endemic species found in South America and Africa, and the South American taxa are more closely related to the western Pacific taxa than to the African. The area cladogram in Fig. 8 displays the area components common to both cladograms of Fig. 7, and suggests a system of biological affinities by which Australia and New Guinea are more closely related to each other than either is to Africa. If we now interpret this as geological history, we have a possible account of differentiation — i.e., area 1 was the combined continent; area 2 broke away, and after this the dividing process was repeated, area 3 breaking away from the combined area 2. Latest of all, Australia separated from New Guinea.

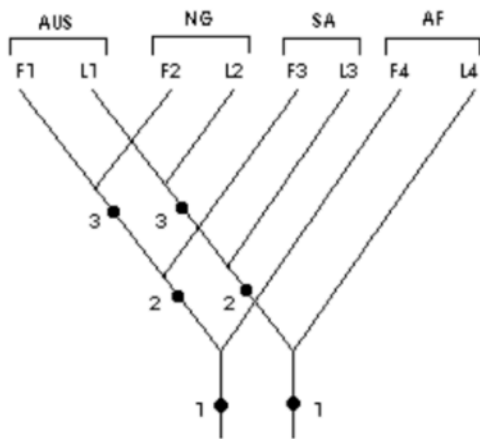


Fig. 7 Hypothetical cladograms for frogs (F) and lizards (L) occurring in Australia (AUS), New Guinea (NG), South America (SA) and Africa (AF). The identical area components are shown as dots labelled 1, 2, and 3. After Humphries and Parenti (1986, p. 40).

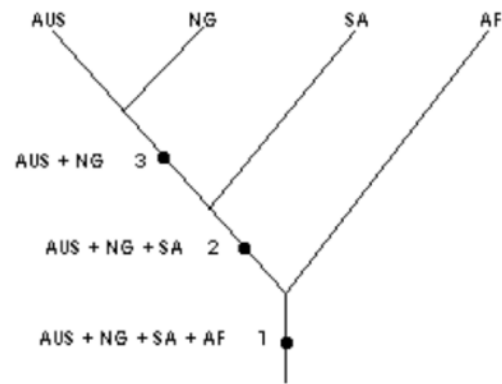


Fig. 8 Geological area cladogram with the area components for the four areas shown as dots and numbered 1, 2, and 3. After Humphries and Parenti (1986, p. 40).

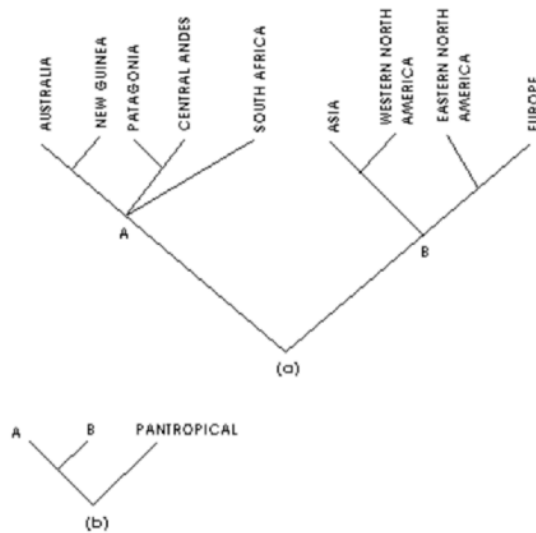


Figure 9. (a) Area cladogram for taxa on the southern continents (A) and their boreal relatives (B). (b) Small cladogram summarizing the relationship of A + B to taxa in the pantropical zone. After Humphries and Parenti (1986, p. 80).

Now that we have a way of reading area cladograms, we may turn to the suggestion by Humphries and Parenti (Fig. 9) of the relation of austral (southern temperate) and boreal (northern temperate) endemic distributions. They write:

This view of the world as presented in one area cladogram is derived from relationships among plants and animals. If we believe that the world and its biota have evolved together, this summary

of area cladograms should be able to tell us something about the historical relationships of land masses.

A glance over the cladogram will bring out what the relations mean. The basal branching separates components of Australia, New Guinea, South America and Africa, on the one side, and Asia, America (west and east) and Europe, on the other. These are taxonomic distinctions, but the former is a Gondwanaland pattern, the latter a Laurasian (the first two parts into which Pangea is thought to have broken). Within each branch we find information on the biological affinities of these ranges which can be read as geological history (the suggestion, for example, of trans-Pacific tracks and a compound North America), and in the single stem, an indication of a stem landmass (Pangea). The small cladogram shows the relation between austral, boreal and pan-tropical distributions, the latter being more general in the character information or, in historical terms, more primitive.

By now it is clear that a strong relation between taxonomic and distributional data is visible even *before* we make a historical interpretation. The general pattern is as follows. When we look at informative groups (groups which show restrictions of distribution as against those which show none), we find a good deal of endemism at the species level — i.e., animals restricted to a few areas or a single area. At the genus level of the kingdom, and most often before this level, everything is *globally* distributed (speaking now of living groups). Thus, geographic restriction grows with taxonomic differentiation, yielding a rough correlation between taxonomic and distributional differentiation. Common patterns evoke common cause explanations, and thus a historical interpretation would suggest that geographic differentiation (of the present landmasses) and the taxonomic differentiation (the branching of present taxonomic groups) are linked — the branching of cladograms represents the splitting of continents as well and, as Humphries and Parenti claim, “the world and its biota have evolved together.”

The Methodological Shift

While individual biologists may have their own explanatory speculations, as Croizat certainly did, I am tracing an empirical emphasis. Croizat called his ‘panbiogeography’ a ‘method’ rather than theory. Platnick and Nelson, who contributed the notion of the area cladogram (1978), concern themselves only with method. It is to the methodological shift from Darwin to vicariant approaches that I would draw the reader's attention.

Let us remember that Darwin never detected the patterns I have been tracing since the beginning of the section on Croizat. This was not due to a lack of the relevant data. Croizat himself remarked that Darwin had the relevant data before him, but remained oblivious to the pattern of common disjunctions. And, of course, he failed to ask Sclater's question of the relation between areas of endemism. This was not a random failure, but a systematic one.

Darwin began his examination from a narrative which, as he admitted “so captivates the mind” that he could imagine no scientific alternative. Holding to such an explanatory narrative, he was willing to interpret actual observation by its light, but here a problem entered. He examined the data only for possible falsifiers to this narrative, and found none. But then biogeographic pattern seems to be almost neutral with regard to centres of origin — it neither tells against nor for. Silence is not approval — the lack of evidence is not evidence — but Darwin acted as if it were. Let us take a modern example.

A search for a centre of origin would usually study distributions for some sense of a radiation from a central point. There are many different ways of looking, as we can see from Cain's list (Table 1). Two

rather obvious possibilities would be (f) continuity and convergence of the lines of dispersal, and (c) the location of the most primitive forms.



Figure 10. Distribution and phylogeny of *Wormaldia*. The circle in Japan is *W. kisoensis*, that in eastern N. America *W. mohri* (from Ross, 1974, p. 217).

The idea appears again in Hennig's 'progression rule' (1966), which places the most primitive members of a cladogram closest to the centre of origin. This has been applied by Ross (1974) to a group of caddis flies (*Wormaldia*), which appear in the Pacific from Sarawak to Japan, and in North America in the Smoky Mountains (Fig. 10). The American form was the least primitive or most derived, so Ross assumed a centre of origin in Asia and a dispersal across the Bering straits to North America. It appears that the evidence establishes the *possibility* of a radial dispersion from a point of Asian origin, since it is consistent with that hypothesis.

Upon reflection, however, this cannot be a determination of the evidence at all. Geometry demands that, given any point on the surface of a sphere, all other points on the surface *must* lie on some radius extending from the first point. Thus the possibility of a radial pattern of dispersal is given *a priori* — before any reference to actual observation — and the impression that this conclusion is derived from observation is misleading. The second criterion — the 'progression rule' — is an *a priori* prescription following from our narrative. The correlation between degree of derivation and distance from origin that it dictates is *added to* rather than *derived from* the observed data, which data contain no such relation. By comparison, the reader will remember the story of Croizat's discovery of common tracks (when he superimposed several cellophane maps). The pattern of orientation around a common barrier was determined by observation, a discovered regularity in nature rather than a theorized possibility. Similar judgments hold for the cladistic comparison of areas of endemism. Again we trace regularities, this time in the repetition of the taxonomic relations among the many different organisms that share the endemic areas. Our summaries are the result of empirical examination, but they are not yet allied to an explanation and remain a pattern *to be explained*.

The detection and description of repeated phenomenal relations — i.e., 'pattern' — independent of explanation, is a capacity exercised many times in the history of science. Of course, such discovery requires a conceptual guide, for observational data are always *selected* in some sense, and thus it contains

a theoretical level. It is just here — at the discovery of a theoretical requirement — that many are thrown back to a dependence on explanatory scenarios for such guidance. The mistake is worth its own discussion.

Pattern Detection

If we suggest that since Darwin did not see the vicariant patterns due to his wrong-headed theory, Croizat must have seen them due to a better theory, we set up the wrong dichotomy. Such a thesis is broadly contradicted by the history of the standing patterns of biology discussed above. The other logical possibility — that Croizat saw them *in spite* of his theoretical preference, or even due to an *absence* of explanatory theory — is far more consistent with the evidence. Croizat was obviously ‘pattern-hunting’ when he set up his panbiogeographic method — i.e., when he decided to compare patterns *globally*. He had no explanation guiding this decision, and of course, he needed none to be startled by the generalized tracks. Upon reflection, such tracks are an anomaly for dispersalist programmes, but this reflection is neither necessary for the surprise that Croizat must have felt nor anywhere near as powerful a stimulus for wonder as the simple discovery of a strong but previously unknown regularity in nature. After all, regularity of relation, which is the defining feature of pattern, was exactly what Croizat was looking for — this was the guide. The conceptual contribution underlying this type of ‘selection’ is ‘theoretical’ in a very different sense from that of the usual meaning of ‘explanatory theory.’

Pattern is recurrent relation, but no relation is itself sensible but a matter for ‘the eye of the mind.’ It must be thought, or ‘intended,’ to be perceived, and until we think it we cannot ‘see’ it, no matter how clearly it lies before the physical eye. As Croizat remarked, Darwin was looking right at the evidence without seeing the patterns. In like vein, Goethe once remarked that a forerunner had provided an example of “looking and yet overlooking.” But Goethe was particularly acute on this subject. He argued, in fact, that his notion of ‘morphology’ (he coined the term) was that of a science which “nur Darstellung und nicht erklären will” — i.e., would only portray and not explain (1963). A *Darstellung*, in his usage, was something like an ‘interpretive portrayal’ — observations which have been conceptualized and set forth in that form. Thus the relations implicit within phenomena have been made explicit by the mind — in the above discussion, spatial and logical relations. ‘Theory’ in this case is the conceptual contribution by which we perceive these relations. ‘Explanation,’ as *distinct* from description, has not yet made any contribution.

This distinction is well brought out by comparison with the Darwinian narrative. Narratives contain ‘pseudo-phenomena’ — objects or events that we do not observe but assume to have existed, like ocean-circumventing migrations. When investigation consists in the articulation of relations between observed phenomena, the latter can provide a determining factor in fixing relations out of the flux of possibilities that the mind offers. But when phenomena are also supplied by the mind, the possibility of determination of relation by evidence drops away. Observations can only comment on relations between observed elements. Assumed objects and events carry their own relations with them.

Explanation and/or Description

The opposition between explanation and description that I have recognized here is not a necessary one. It arises through our propensity to consider ‘explanation’ to be a narrative of objects and events (which are taken as ‘causes’) beyond our descriptive abilities. In this form ‘explanation’ interferes with description, for the latter does nothing but articulate relations between observations, while the former introduces a set

of pseudo-phenomena. The statement “the world and its biota have evolved together” evokes both a sense of history and of explanation, but the statement itself seems to result from mere description — i.e., discovery and correlation — of convergent patterns. Let us see to what extent the statement may be reconstructed as descriptive.

To arrive at the statement above we began with patterns of distribution which show certain regularities of disjunction (generalized tracks). We added taxonomic pattern by asking the taxonomic relation of the areas of endemism, and found that we get a generalized pattern of many taxa following producing the same or closely related cladograms. This allows the combination of spatial and logical information into an area cladogram, showing the taxonomic relations of the endemic distributions. The patterns described thus far require only the articulation and comparison of spatial and logical relations, but there is a conceptual framework to all scientific activity that manifest its heuristic potential.

As things are brought from indifference into relation they are also brought from unintelligibility to intelligibility. As the unity of relations becomes more intense, so does intelligibility, and thus the demand for *causal* relation, for scientific investigation cannot stop with existent patterns. The observed world does not merely exist, but also *becomes*, and the patterns under examination presuppose development. There were two patterns (logical and spatial), each requires a becoming, and these developments must also be brought into relation.

Development cannot be examined unless we have it at hand, and since the existent pattern is our only evidence, that development becomes visible in one of two ways — we can fill in an imagined narrative, or we can produce another type of narrative through a temporal redescription of the pattern itself. Temporal relations are those of simultaneity and *succession*. In order to reorder the information successively the different logical levels of the cladogram must be taken as stages of becoming and the cladogram read as *successive* differentiation, from stem to terminals. We can do the same with the differentiation of ranges, since on a large enough cladogram this differentiation will be absent at the stem level (global distribution) but will increase (endemic distributions) as one moves toward the terminals. Thus, the two patterns may be recast as patterns of succession, but when this is done they are still convergent, the recasting has the same effect on either. (Notice that this redescription does not yield a history — i.e., events — but only the *form* of a development — that is, the structural relations such a history will possess.)

Turning now to geological pattern we have a geological affinity between certain continents (proposed by Wegener) and the magnetic patterns of the ocean floors between these continents. The magnetic pattern consists of a progression of bands of differing magnetic signature — corresponding to changes in the Earth’s magnetism — on either side of a central zone (fault line). The progression of bands on one side of the central zone corresponds, of course, with the progression on the other. When this progression in space is projected into time — when the progressive change of magnetic signature is seen as a *successive* becoming — it yields a *history* of events — of seafloor spreading and thus the disjunction of once unified land masses. The pattern of area cladograms above is convergent with the structure of this history, for in each, a whole is progressively differentiated and the differentiations seem to be the same (save for the problem of the Pacific Basin). The picture, as Croizat once described it, is of a unified surface that progressively differentiates — like a sheet of glass that breaks into several large fragments, after which each fragment breaks further, and each resultant fragment breaks again — and so on. The differentiation of many groups of animals follows the same succession, the stem of the cladogram correlating with the unbroken sheet, the basal branches with the first fragments, and the further differentiation of each branch with the further break-up of each fragment. This is what is meant by the statement: “The world and its biota have evolved [read: differentiated] together.”

Taken in the sense reconstructed by this exercise, the statement indicates a common becoming between biological and tectonic differentiation, a more detailed account to follow. The crucial point is that when each pattern is ordered by succession, *all converge*. This is the beginning of a common cause account, for causality is the concept by which we relate the earlier to the later according to a *determinate* rather than indifferent sequence. Thus the three convergent sequences indicate a common cause by sharing the same relation between earlier and later, but without the addition of purely hypothetical mechanisms or events. I do not mean to claim that this account must be true because it is descriptive — it too is only hypothetical — but simply that because its explanatory powers proceed only from the conceptual articulation of observation it is determinable by evidence in a manner that Darwinian scenarios are not.

Further illumination is needed, to be sure, but if it is to be empirically determined it must await further description — i.e., further analysis of biogeographic and tectonic patterns about the Pacific Basin, or further examination of the form-making potentials possessed by organisms that allow them to differentiate when isolated (see the Sermonti paper for Croizat's reflections on this problem). But in such an investigation it is advantageous to let pattern detection and the articulation of relations guide our effort, and form our explanation. Certainly Darwin's assumption that the data of observation would contain determining evidence for or against *any* theory has proven too dangerous. We do not need another century of searching the data of observation for what it does not contain, while overlooking the relations that it does.

Since pattern detection has proven so important to evolutionary study, future progress may depend on how well we can perceive and articulate relations between phenomena on a global scale. As this essay has argued, the global level is the only one that could test the convergence of differentiation patterns (by integrating the Pacific Basin), and thus Croizat's move away from Darwinian localization to a 'panbiogeographic' consideration was one of two key factors in the new methodology. The discipline to resist the lure of invented narratives was the other factor. The difference between descriptive and narrative approaches, if largely unnoticed, is still central to the project of science.

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