NATURE AND FORMULATION OF BIOGEOGRAPHICAL HYPOTHESES

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Abstract

Ball, I. R. (Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, Toronto, Ontario, M5S 2C6, Canada) 1976. Nature and formulation of biogeographical hypotheses. Syst. Zool. 24:407–430.—All biogeographical studies seem to pass through three main phases: an empirical or descriptive phase, a narrative phase, and an analytical phase, the last two being the true subject matter of explanatory historical biogeography. Narrative explanations are more or less inductively based and differ from the usual covering law models of explanation in that it is the particular circumstances in the form of an historical narrative that bear the explanatory load. Much biogeographical thinking is of this nature and the hypotheses so formulated suffer from their lack of predictive power and their basic untestability—usually they cannot be falsified and a preference between competing narrative hypotheses cannot be established on logical grounds. Examples of such hypotheses are given. The best biogeographical hypotheses are those that follow the hypothetico-deductive model and an example of how this may be done is provided. A phylogenetic systematic background is essential. Rigorously formulated hypotheses must have explanatory power, internal consistency, predictive power, and potential for falsification. Our aim should be to make our biogeographical hypotheses fit these requirements for only then will we begin to understand the history underlying modern distribution patterns. [Biogeography; Inductive and Deductive Methods; Dispersal.]

"The lyf so short—the craft so long to lerne" (Chaucer).

"I have an old belief that a good observer really means a good theorist" (Darwin, to Bates in 1860).

"A science of dispersal is at bottom a philosophy of evolution over space through time . . . . Biogeography, if correctly used, is, in sum, a primary science in its own right . . ." (Croizat, 1968:224–5).

"Anyone familiar with the history of science knows it is done in the most astonishing ways by the most improbable people and that its only real rules are honesty and validity of logic, and that even these are open to public scrutiny and correction" (MacArthur, 1972).

Biogeography means different things to different people depending, of course, upon their outlook and upon their biases. Most ecologists consider only the spatial aspects of the discipline with the result that they believe biogeography to be at best a part of ecology. Indeed, MacArthur and Wilson (1967) admitted to being unable to see any real distinction between these two subjects.[1] Certainly there are great parallels between the community structures of different continents of like climate and topography, but equally certainly there are great differences in the organisms that occupy the various levels in the structure. Consider, for example, longitudinal zonation in streams. In Europe a scheme of classification based very largely upon fishes has been established with four zones named after the trout, grayling, barbel and bream. These zones extend in that order from headwaters downstream. The principles of this classification can be applied easily to other biotic provinces, but certain of these fish may be absent for historical reasons, and hence are replaced by other species or genera (Hynes, 1970). These reasons are the target of the biogeographer. From my own area of speciality I can refer to the cold stenothermal freshwater planarians, characteristic of springs, wells, and montane waters, of Europe, North America, and Australasia. In each continent the niche is occupied by different species of widely disparate families, and whereas there are obvious ecological similarities in each case the differences have an historical element that is the responsibility of the biogeographer to attempt to explain.

There is, of course, an overlap between ecology and biogeography as is attested in several recent books (Udvardy, 1969; Watts, 1971; Cox et al., 1973; Illies, 1974). But ecology may be considered different in that it deals with distribution on a local scale, and with community structure and trophic relationships whereas biogeography is essentially the study of the distribution of living organisms in space and time, and of the principles, processes, and parameters influencing this distribution (Munro, 1963). Thus, biogeography is involved with both spatial and temporal factors, to which must be added the evolutionary background. The major synthesis of these aspects remains Croizat's "Space, Time, Form: The Biological Synthesis," a book of some 800 pages that he regards, modestly, as a summary of his views, and it is to him that belongs much of the credit for establishing biogeography as an independent discipline, valid in its own right. He has, I believe, laid a foundation, and the neglect that has been afforded him by many contemporary biogeographers is a sad reflection on our science.[2]

As with any other discipline biogeography must pass through different stages of maturity, and specialists dealing with different groups of organisms may be working at different levels because of the nature of their respective subdisciplines. While this seems obvious it is in fact the cause of much misunderstanding during dialogue. I find it convenient to recognize biogeography as passing through three phases: the descriptive or empirical phase, a narrative phase, and an analytical phase, the last two comprising historical biogeography. I propose to consider each of these in turn, the first very briefly indeed, from the point of view of methodology and heuristic value.

DESCRIPTIVE OR EMPIRICAL BIOGEOGRAPHY

Perhaps the first major impetus to biogeography as a science came from Sclater's review of the geographical distribution of birds (Sclater, 1858). He recognized six major groupings that were later refined and revised by Wallace (1876). That these regions are valid and static for a multitude of organisms is evidenced by the fact that regional floras and faunas are possible; they need not be revised annually. The boundaries of these divisions are commonly associated with climatic zones or with prominent topographic boundaries such as mountain ranges, sea coasts, rivers and the like. They may also be environmental, relating to altitude, rainfall, soil, etc. At this level biogeography is concerned merely with basic data, which is an important task, with establishing the complexity of the distributional patterns, and perhaps attempting to explain them primarily in ecological terms (e.g., de Beaufort, 1951; Schmidt, 1954; Briggs, 1974a). The heuristic value of these "descriptive hypotheses" rests purely on an inductive base of the sort that predicts that kangaroos will not be found in Europe because they have been seen, in the wild, only in Australia.

However, present distributions, even though complex, are but the surface of a pattern that extends millions of years into the past, and there is no justification for assuming a uniformitarian principle concerning it. Ekman's opinion that the final aim of zoogeography is not the graduated regional system in itself, but the history that this system reflects, that is, the history of the faunas (Ekman, 1953), is an opinion with which it is difficult to disagree. To elucidate this history, to see into the past, different methods are needed, and because of the limitations of the fossil record these methods are of necessity indirect. Thus, we leave the world of primary sense data and enter a world of ideas, of theoretical constructs.

HISTORICAL BIOGEOGRAPHY

Introductory Remarks

A traditional view of science is that we go through a sequence of observation or experiment, inductive generalization, hypothesis, attempted verification of the hypothesis, proof or disproof, and, finally, knowledge. According to this view scientists are looking for statements about the world that have the maximum degree of probability.

The inductive approach had great appeal for logicians and philosophers of the 19th and early 20th centuries, the period during which biogeography emerged as a science. It is not surprising, therefore, that biogeography developed with a strong inductive bias because just as no historian (and to some extent all systematists are historians) can write impartial history because he is a product of, and is greatly influenced by the requirements of, his own time (Carr, 1961) no scientist can be entirely divorced from the prevailing thought of his period.[3] It is true that Darwin, perhaps the first great biogeographer, to some extent untrammeled himself (Ghiselin, 1969; Hull, 1973), but by his own admission he remained influenced by the logical appeal of induction. Induction is a form of logic essential to the study of history says Carr (1961),[4] and some systematists and biogeographers continue to place great faith in it (Cain, 1944; Omodeo, 1963; Croizat, 1964; Crowson, 1970; Griffiths, 1972).[5] Indeed, Cain (1944:210) explicitly decries the overemployment of deductive reasoning in biogeography and calls for a complete return to an inductive basis, much as does Crowson (1970:133). Some other biogeographers are less explicit but seem to be more or less inductively biased (Simpson, 1953; Darlington, 1957; McDowall, 1973a).[6]

But inductive generalizations are valid for only a particular point in space and time, a point that there is no logical way of determining.[7] Furthermore, the criterion of maximum degree of probability is valueless because this can be achieved by reducing the information content of the proposition or hypothesis.[8] Inductive methods lead to explanations that are rational only in a retrospective manner, and one is reminded of Hegel's dictum to the effect that what is rational is real, and what is real is rational.

It has been said that biogeography is largely based on explanatory hypotheses that are supported by how well they cast light upon the known facts of distribution. From the time of Darwin it has been assumed that our methodology should consist of looking at the facts of distribution and then making up a story that is consistent with these facts (cf. Hegel: "what is rational is real"). The uncritical acceptance of this view leads to what one may call "narrative explanations," these being basically inductively derived and thus subject to the limitations discussed. It is my contention that much of today's historical biogeography is of this kind.[9]

Narrative Biogeography

The term "narrative explanation" in evolutionary biology seems first to have been introduced by Goudge (1961). Whether or not such explanations serve to distinguish the biological from the physical sciences need not concern us here because it has been discussed at length by others (Goudge, 1961; Ruse, 1973; Hull, 1974). Goudge (1961:71) gave as one example Romer's account of how Devonian vertebrates invaded the dry land and pointed out that although this explanation was part of a scientific discussion it was not aimed at the discovery or confirmation of a law, it did not establish any new empirical fact, and it makes no positive predictions about what may be found in future investigations. This is precisely the status of many biogeographical theories.

Consider, for example, the controversy between Omodeo (1963) and Gates (1929a, b, 1966, 1967, 1970) concerning the distribution of terrestrial oligochaetes in the Northern Hemisphere. Many lumbricid earthworms show typical amphi-atlantic distribution patterns such as are demonstrated by the broad lines in Figs. 1 and 2. Omodeo discounts the possibility of passive or accidental dispersal and assumes that the Lumbricidae evolved in Europe, the area of greatest diversity, and that they migrated to North America via a land-bridge.[10] His land-bridge occurred 'in a relatively ancient age, but not so ancient as to permit specific

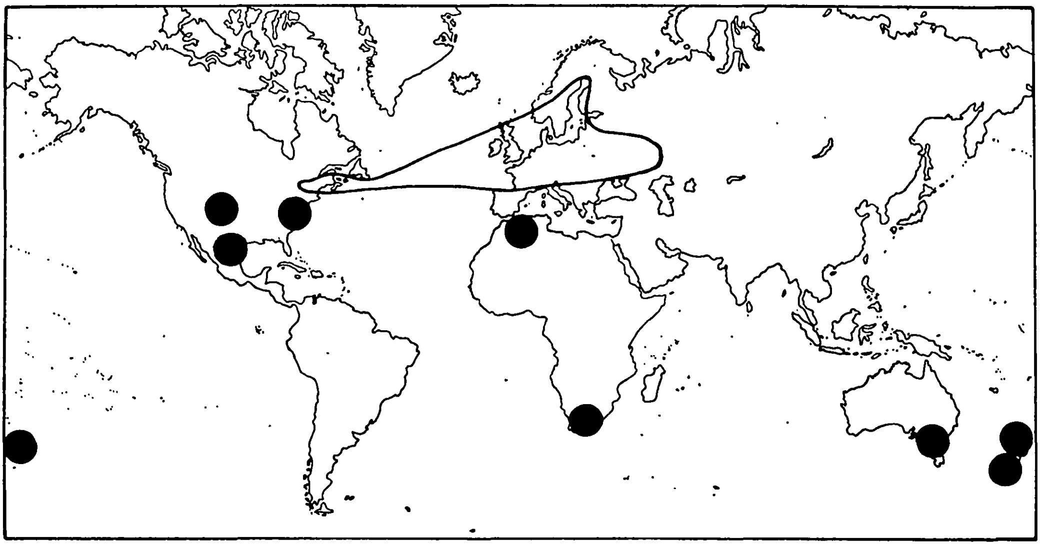

FIG. 1.—*Allolobophora longa.* Geographical distribution according to Omodeo (1963), solid line, with additions, black circles, from Gates (1972).

differentiation of most of the Lumbricidae' (Omodeo, 1963:150). Essentially Omodeo's entire argument is one of induction by elimination.[11]

Omodeo's explanation tells a rational historical story but it calls on no laws, nor even on hypotheses of relationships within the earthworms, and it enables no positive or negative predictions to be made. His explanation cannot be deduced from any premisses that he has put forward and, indeed, he indirectly refers to his own ideas as purely conjectural. Finally it may be noted that the only part of Omodeo's conjecture that can be falsified concerns the land-bridge itself, for direct proof that it could not possibly have existed would falsify his hypothesis; but is such direct proof obtainable?[12]

With Gates (op. cit.) we find a different story, but one no less rational. To the amphi-atlantic distributions shown in Figs. 1 and 2 I have added distributional data, as solid circles, derived from Gates (1972). This author (1966, 1967, 1970) appealing only to subjective estimates of what is rational, and invoking also Ockham's razor (Gates, 1966), claims that these data demonstrate clearly that the dispersal of, for example, *Lumbricus terrestris* to remote places is due entirely to man's activity in the last 400 years. By induction the amphi-atlantic distribution is similarly explained and this is reinforced by a further induction —that because some farmers in olden times remarked on the absence of earthworms in their soil, earthworms were absent from all of glaciated North America until introduced! Once more the explanation is both historical and rational but it offers no predictions, it cannot be falsified. We know that some earthworms have been transported by man, but we cannot from this logically infer that the entire distribution is a result of such transport. Gates is relying heavily on enumerative induction, a procedure that even Bacon and Mill viewed with considerable reserve when compared with other forms of induction such as by variation of circumstance (Cohen, 1970).

As formulated, the rival hypotheses of Gates and Omodeo are not mutually exclusive. Though rational, the explanations are immature, and neither possesses great information content; of the two Omodeo's is better in this respect because it is more

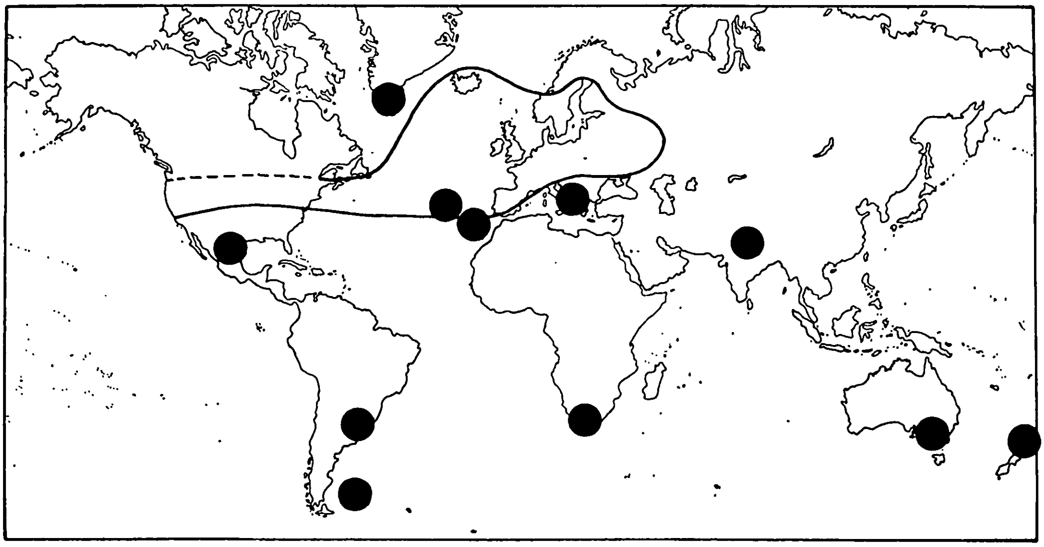

FIG. 2.—*Lumbricus terrestris.* Geographical distribution according to Omodeo (1963), solid line, with additions, black circles, from Gates (1972).

restrictive. In their present state it is not possible, on logical grounds, to state a preference for any one hypothesis over the other.[13] Nevertheless, had only one hypothesis been put forward it would have been accepted. Such was the case with Gates' anthropochore hypothesis prior to Omodeo's alternative narrative, for Lindroth (1957), seeking support for his own views of amphi-atlantic relationships, seized upon Gates' hypothesis for added strength. But we must not lose sight of the fact that any finite number of observations can be accommodated within an infinitely large number of different explanations. If we seek a preference for one or the other viewpoint then the hypotheses must be made more restrictive, and hence falsifiable. The fact is that earthworms at present have nothing to tell us concerning historical biogeography,[14] and the advocacy of one or another hypothesis concerning them on the basis of rhetoric or authority (another form of induction!) is no real service to the growth of objective knowledge.

In criticising narrative explanations, such as those discussed above, I do not wish to imply that all such explanations are worthless. These explanations differ from the usual covering law model in that it is the particular circumstances in the form of an historical narrative that seem to bear the brunt of the explanatory load (Hull, 1974). But frequently, they are all that is possible, in which case prolonged discourse about them is futile. I claim only that we should recognize their weaknesses and attempt to refine them sufficiently to make them true scientific hypotheses. Only then is a meaningful discussion of rival hypotheses possible, for otherwise we are reduced to a non-logical comparison of the type that attempts to demonstrate that cricket is a better game than baseball. One may state a preference, but one cannot justify it logically. Much has been made of a dictum by Hooker: "no speculation is idle or fruitless that is not opposed to truth or to probability, and which, while it co-ordinates a body of well-established facts, does so without violence to nature." But he concludes with: "and with a due regard to the possible results of future discoveries." This latter is the important point because narrative explanations are specially invented to match the particular requirements and have little validity without independent data.

Analytical Biogeography

The inductivist view of science, although defended eloquently by such spokesmen as Platt (1964), Crowson (1970), and Rosenblueth (1970), has been severly criticised by many recent philosophers of science, among the most vocal of whom has been Popper (e.g., 1959, 1968, 1972, 1975). According to Popper scientific enquiry proceeds from a problem, usually derived from an existing theory or expectation, to a proposed solution, or hypothesis, from which testable propositions are deduced. These deduced consequences are then tested by observation or experiment and a preference established between competing hypotheses.[15] All observations, according to Popper, are theory soaked, and knowledge progresses by the replacement of one hypothesis by another.[16] There is an asymmetry between verification and refutation for no theory can be proved true no matter how many observations support it, but a single observation may show it to be false. The most we can say of a favoured hypothesis is that it is supported by every observation so far, and yields more, and more precise, predictions than any known alternative. It is still replaceable by a better theory. The criterion of potential falsifiability is very important, for any hypothesis that cannot theoretically be refuted is at best pseudo-scientific.

There are many inherent difficulties in attempting to adopt such tenets for enquiries into historical biogeography. Nonetheless, by attacking these we may achieve a truly meaningful state of the science. I propose to demonstrate my approach to this third level of biogeography by referring to work on freshwater planarians, or triclads, not because I consider them to provide the best worked out example, but because I am most familiar with this group and its problems. Moreover, I wish to avoid the tendency, all too apparent in many recent contributions to debate on systematics, of arguing in a vacuum, using theoretical examples rather than real problems. The latter are never solved as neatly as the former, and it is illuminating in epistemological discussions to reveal everything, even the warts so beloved of Cromwell!

I am concerned with the phylogenetically most primitive family of the freshwater planarians, the Dugesiidae, the total distribution of which can be gleaned from Figs. 4–7. I shall not attempt to justify here my familial classification of the Tricladida Paludicola because this has been done in a previous publication (Ball, 1974a).[17] Prior to my revision the *Dugesia*-group (= Dugesiidae) comprised but two genera, *Cura* and *Dugesia*, but I divided the latter into several subgenera some of which have subsequently been erected to generic rank. Two new genera of Dugesiidae were described recently from Australia (Ball, 1974b, 1974c).

The first meaningful attempt to understand the biogeographical relationships of the freshwater planarians was made by Kawakatsu (1968). In discussing the genera *Cura* and *Dugesia* he states (in translation):

> "From its centre in the Balkans the genus *Dugesia* spread to the central and southern parts of Europe, and further on to the Near East, India, Australia and New Zealand. Its branches have even reached the Far East area, such as southern and central China and the Japanese islands . . . . One branch separated from the main group in Europe, invaded Africa, most probably reaching South America after crossing the Atlantic Ocean, and moving northwards to North America and up to the Hawaiian Islands. It is believed that when they reached South America a group with long auricles [*Girardia*] must have been differentiated. Furthermore, from the branch which separated from the main group in Africa, the genus *Cura* was differentiated, reached South America, and then dispersed northwards to North America. In view of the fact that the genus *Cura* is distributed in New Zealand and Australia I believe that there must have been a direct contact between South America, Australia and Africa . . ." (Kawakatsu, 1968:17).

Immediately one recognizes two important internal inconsistencies. First, it is evident that the principal criterion used for deciding on the centre of origin of a group is the old one of diversity (Kawakatsu, 1968:20). Yet in selecting the Balkans as the centre of origin of the *Dugesia*-group he has chosen an area where only two or three species occur, compared with the twenty or so in South America for example. Second, whereas Kawakatsu recognizes the distinctness of the Nearctic and Palaearctic Dugesiidae he gives no explanation of why they should have crossed the Atlantic in the southern hemisphere but not in the northern. His hint at a role for continental drift is puzzling because in accepting the possibility of a role for Gondwanaland, with its influence on austral disjunctions, he overlooks Laurasia, the supercontinent on which he claims *Dugesia* arose.

In addition the hypothesis presented by Kawakatsu is not so formulated that rigorous deductive inferences can be made, with the possible exception that *Cura* evolved later than *Dugesia*. But since Kawakatsu espouses no particular systematic or evolutionary principles one can deduce nothing concerning the comparative distributions of primitive and derived taxa. This becomes all the more apparent in recognizing that Kawakatsu seems prepared to work with paraphyletic or polyphyletic groups. Thus, in discussing the Australasian genus *Spathula* he states that it has some similarities with *Cura* (Kawakatsu, 1968:18), and in his Fig. IV-1 he indicates that these two genera are closer cladistically than either is to *Dugesia*. Yet elsewhere he claims that *Spathula* probably should be classified with *Dugesia* whilst retaining *Cura* as a distinct genus (Kawakatsu, 1968:12). Similarly, his phylogenetic tree is at odds with his familial classification. Consequently, from Kawakatsu's hypothesis we can predict nothing concerning possible future taxonomic or distributional findings. It is essentially a narrative hypothesis the explanatory power of which is weakened by the internal inconsistencies discussed.[18]

My own hypothesis (Ball, 1974a) was put forward to overcome these, and other, defects. The first task was to refine the data because in my view we must be sure in biogeography to make comparisons between real and similar units. Thus, we must know the phylogenetic status of the groups about which we are concerned, and the phylogeneticists insistence on working with rigidly monophyletic groups is one of their main contributions both to systematics and to biogeography. Nobody in their right mind would attempt to draw conclusions from the relative distributions of the "Gephyrea" and the "Vermes," for example, for neither is a real, or monophyletic, group. Yet analogous groups do form the basic units of much biogeographical work.

Following Løvtrup (1973) the simplest equation of set theory may be written as:

$$s + \bar{s} = U \qquad (1)$$

which is to say that since U represents the logical universe the definition of s automatically determines the complementary set $\bar{s}$, or not-s. We can apply this to systematics by making U equivalent to a higher taxon, and thus we can write:

$$s_1 + s_2 \ldots\ldots + s_n + \bar{s} = U \qquad (2)$$

where $s_1 - s_n$ represent subordinate taxa, or species groups. But in equation (1) it should be noted that $\bar{s}$ can only be defined by reference to s; it has no existence in its own right. Any theory of systematics and biogeography that deals primarily in units of $\bar{s}$ must be either trivial or meaningless.[19] Such groups, delimited only by primitive characters, have no real existence and represent the remnants of division of a larger group.

The first task, then, was a comparative anatomical study to determine the monophyletic subgroups of the Dugesiidae according to the systematic principles enunciated by Hennig (1966a) and Brundin (1966). The results (Ball, 1974a) indicated many more supra-specific categories than previously had been supposed. The hypothesized phylogenetic relationships of these taxa are summarized in Fig. 3, the evidence upon which they are based being given elsewhere (Ball, 1974a, 1974b). The systematic position of *Cura* remains uncertain; this genus occurs in eastern North America, Mexico, and throughout Australasia. Records from southern South America need

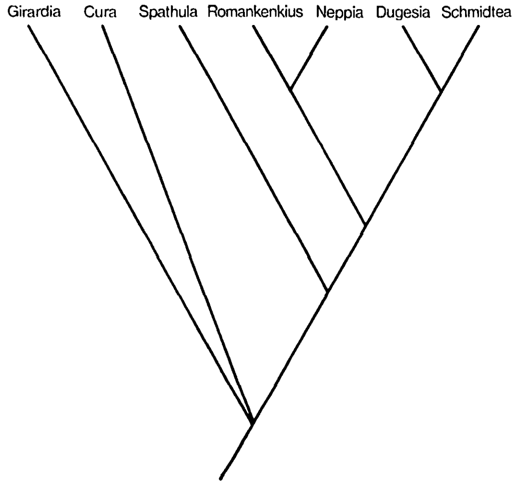

FIG. 3.—Hypothesized phylogenetic relationships of the principal genera and subgenera of the Dugesiidae. For discussion see text.

confirmation (Ball, 1974b:17), and the African species of the genus *sensu* Kawakatsu were transferred to the more derived genus *Neppia*. *Spathula* occurs in southeastern Australia and New Zealand (Ball, in preparation) and *Romankenkius* occurs only in Tasmania (Ball, 1974b). The distributions of the remaining taxa are shown in Figs. 4–7 beginning with the oldest and most primitive, *Girardia* (Fig. 4) and concluding with the most recent and derived, *Schmidtea* (Fig. 7).

Assuming the phylogeny to be true one hypothesis to explain the relative distributions of the monophyletic groups could be as follows (Ball, 1974a:389–390). Having suggested that the centre of dispersal, and probably of origin, of the Dugesiidae lies south of the present-day equator, where the primitive forms are found and where there is greatest taxonomic diversity, I further hypothesized that the group arose in Gondwanaland, probably in what is now Antarctica. By the commencement of the Mesozoic, some 220 mybp the early diversification of the Dugesiidae was complete, with a main massing of *Girardia* in the west, and of *Neppia* and *Spathula* in the east. The northwards dispersal of these elements coincided with the early stages of Gondwanaland break-up, leading to a concentration of *Girardia* in the Americas with outliers across the southern hemisphere to Australasia (Fig. 4), and of *Neppia* in Africa, and a few in Australasia with connections to South America (Fig. 5). After separation was well under way the *Dugesia gonocephala* group

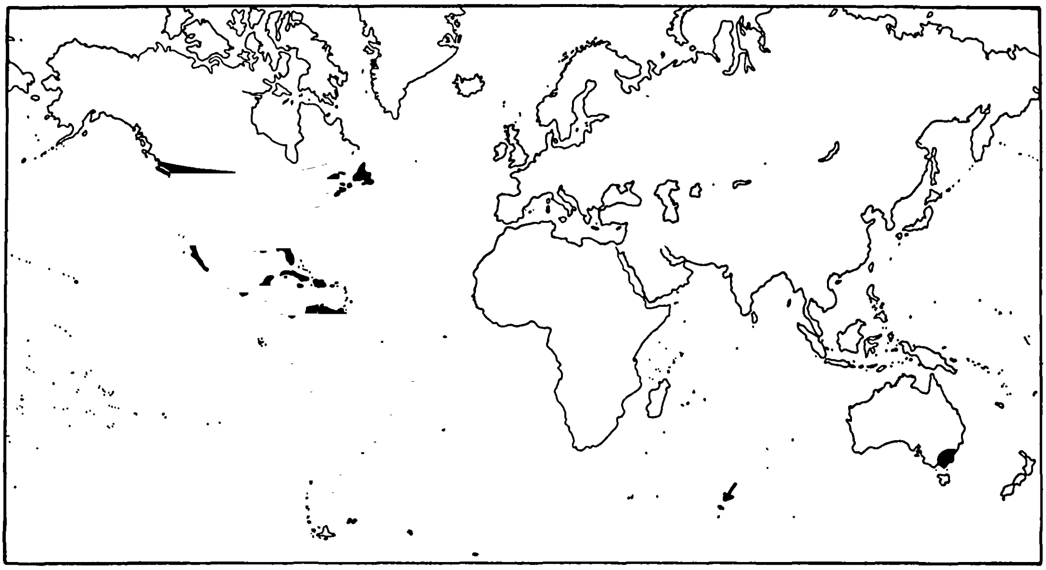

FIG. 4.—Geographical distribution of the subgenus *Girardia* of *Dugesia* (Dugesiidae).

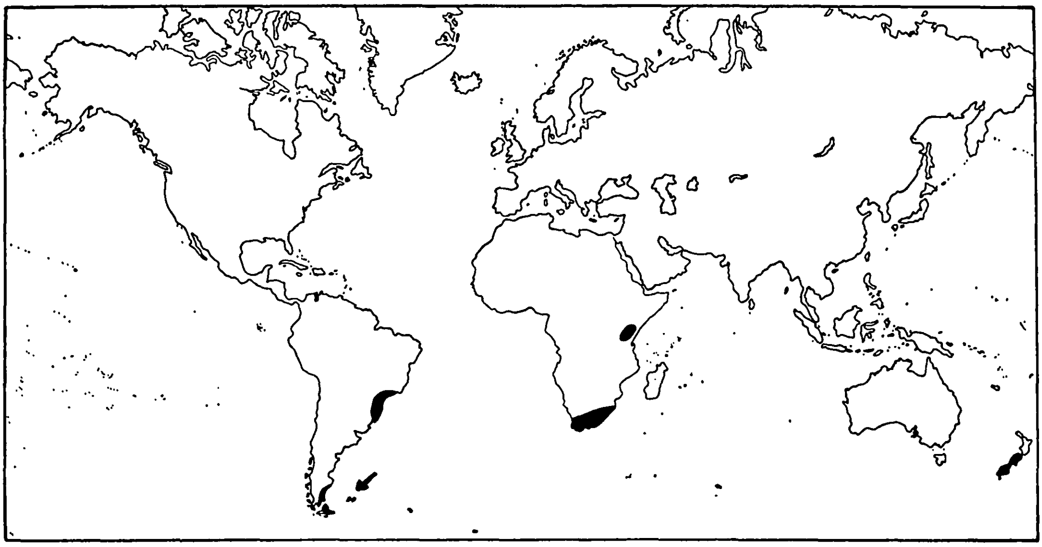

FIG. 5.—Geographical distribution of the genus *Neppia* (Dugesiidae).

arose in Africa, and after closure of the Tethys Sea dispersed northwards into Palaearctis, Africa, and eastwards to India, populated entirely from the north, and southeastern Asia (Fig. 6). *Schmidtea* arose later in Europe (Fig. 7). This scheme is summarized diagrammatically in Fig. 8. From the present taxonomic evidence it seems that no dispersal, or vicariance, of the Dugesiidae has occurred across Beringia, the North Atlantic Ocean, or Wallace's line.

It should be noted that for austral distributions I am invoking a vicariance model (see below) for the older, more primitive taxa, whereas it seems proper to talk of centres of origin and dispersal for *Dugesia* (Africa) and *Schmidtea*, (Europe), for example. But by this model I explain the present disjunct distributions of the southern hemisphere and also the clear spatial and taxonomic separation of the North American and European dugesiids. For if the dugesiid planarians did not reach the northern hemisphere until after closure of the Tethys Sea then Laurasia, as a dispersal route between North America and Europe, was unavailable to them.

The hypothesis is more restrictive than Kawakatsu's, and therefore has greater informative content. Its explanatory power is increased because it encompasses more 'facts' and it lacks the internal inconsistencies present in the earlier hypothesis.[20] On these grounds alone the hypothesis is to be preferred. But what is its heuristic value? How can it be falsified?

The simplest predictions concern problematical taxa. For example, two species, "*Cura*" *jeanneli* from South Africa and "*C.*" *falklandica* from South America were difficult to place in the context of my original ideas (Ball, 1974a:378–379). Subsequently the type material was discovered and it was found that both had been described incorrectly by the original authors, and that they belonged, satisfactorily, in the genus *Neppia* (Ball, 1974b). Furthermore, because the distribution patterns are causally explained predictions concerning taxa to be found in respective regions are no longer inductive but have become deductive in nature.[7] Once we have a causal historical explanation of distribution patterns then the findings of taxa, or given character complexes, outside the normal range represent potential falsifiers.[21]

Of course the hypothesis could be falsified by refutation of the phylogeny upon which

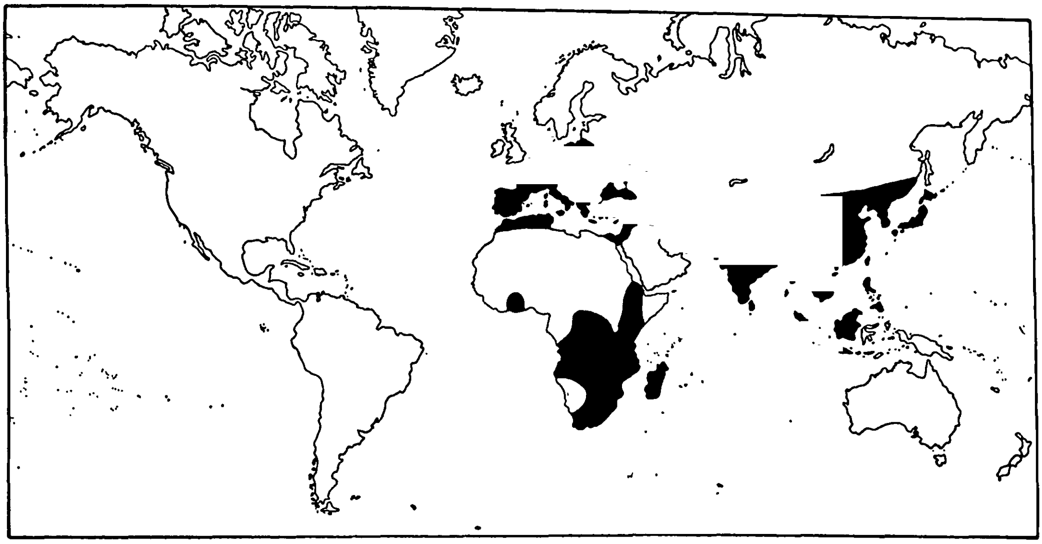

FIG. 6.—Geographical distribution of the nominate subgenus of *Dugesia* (Dugesiidae).

it is based. But perhaps the best area for refutation concerns regions across which dispersal, or vicariance, according to my hypothesis has not occurred. The North Atlantic Ocean is a case in point. If the Dugesiidae did not reach the northern hemisphere until after Tethys closure and Atlantic rifting then there should be no amphi-atlantic connections in the higher families (Planariidae and Dendrocoelidae, see Ball, 1974a:Fig. 1) either. The genus *Polycelis* (Planariidae) has been cited as a holarctic genus but in fact it occupies two main areas (Fig. 9). These are Europe and central Asia, and the Beringian Arc. The North American forms are unlike those of

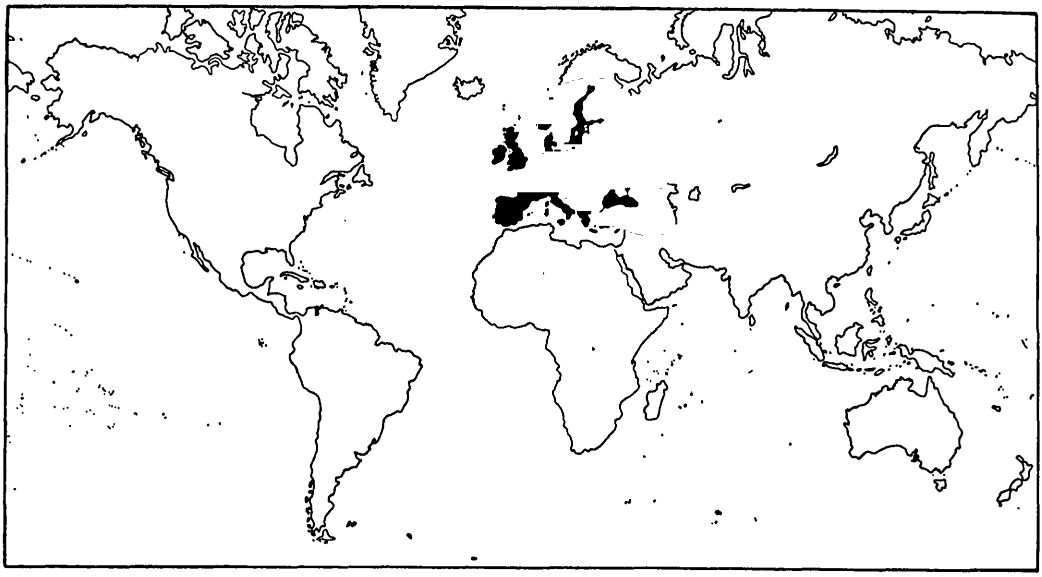

FIG. 7.—Geographical distribution of the subgenus *Schmidtea* of *Dugesia* (Dugesiidae).

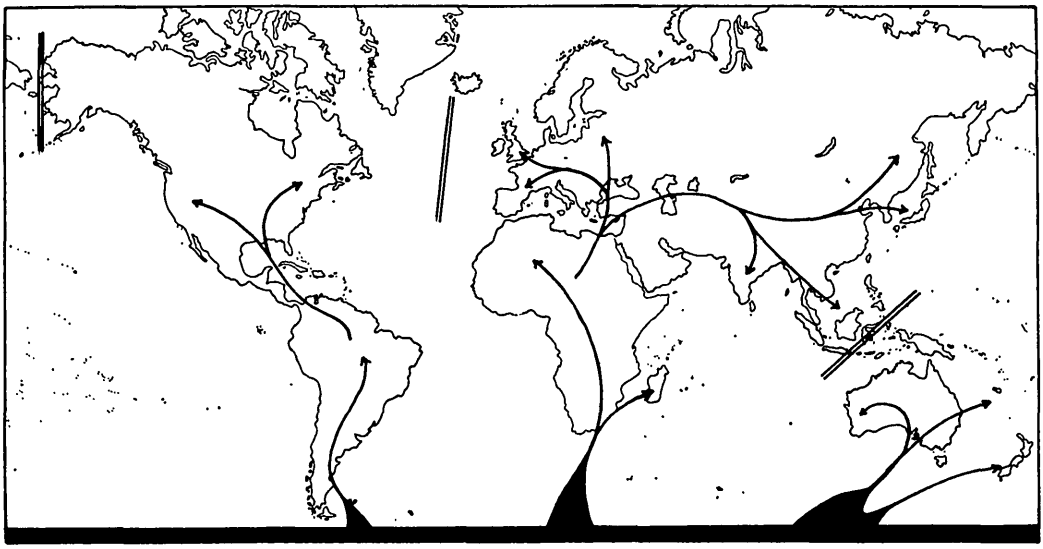

FIG. 8.—Hypothesized dispersal routes of the Dugesiidae from a vicarious austral ancestral fauna. The double lines indicate "barriers" across which dispersal, or vicariance, seems not to have occurred.

Europe and share features with the species of east and central Asia (Kenk, 1953:173; Ball and Fernando, 1968).

The genus *Phagocata* (Fig. 10) looks like a potential falsifier. It is a widespread holarctic genus with numerous species. If my hypothesis is correct then I must predict that when the phylogenetic relationships of the species are elucidated it will be found that all the American species are of Asian origin and it will not be necessary to invoke "trans-Atlantic" distribution. Already there

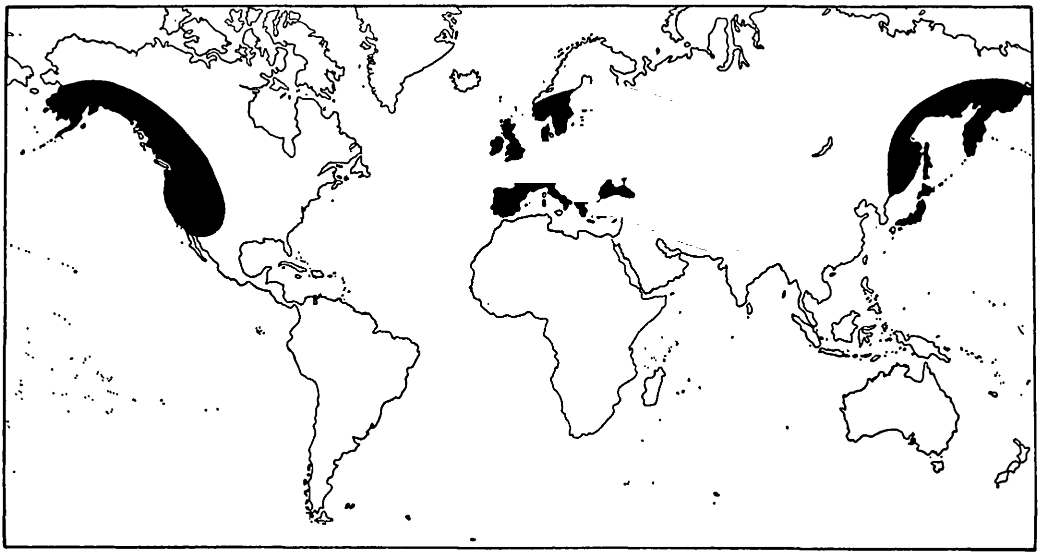

FIG. 9.—Geographical distribution of the genus *Polycelis* (Planariidae).

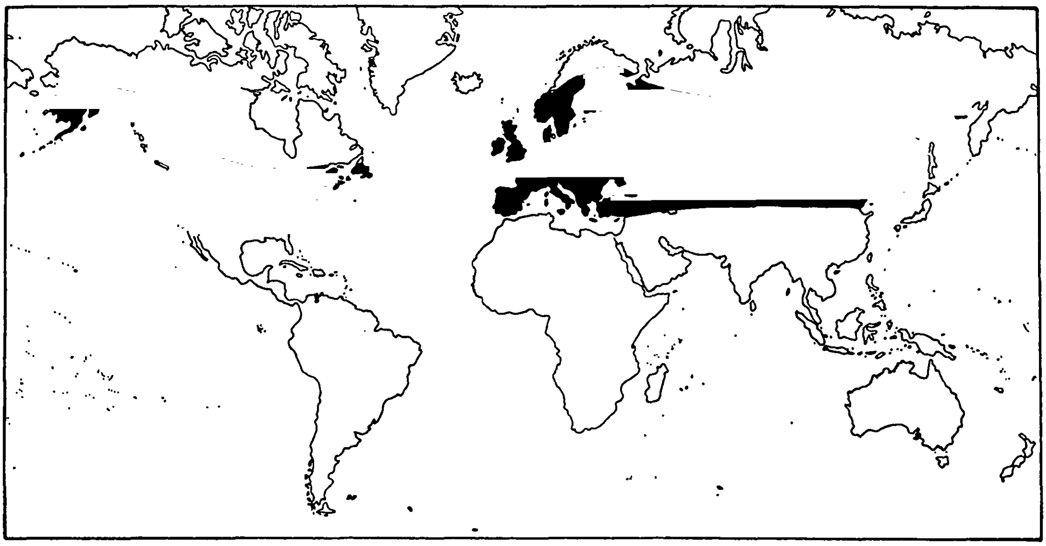

FIG. 10.—Geographical distribution of the genus *Phagocata* (Planariidae).

is some evidence for this prediction and there is no doubt that the genus is probably paraphyletic in that it is defined only by primitive characters (Ball and Gourbault, 1975). In the terminology used earlier it is an s̄-group in that it comprises all Planariidae that cannot be assigned to other genera on the basis of derived character states (Ball and Gourbault, 1975:12).[19]

The distribution of the genus *Planaria* (Fig. 11) is, however, totally incompatible with my hypothesis. I predict, therefore, that careful study will show that this genus is not monophyletic and that the American species have evolved independently of the single European one. The one character that distinguishes the "genus" from *Phagocata* is the presence of a certain type of accessory muscular-gland organ, or adenodactyl, in the copulatory apparatus. It will be necessary for me to demonstrate convincingly that the adenodactyls of the two disjunct groups are not homologous. Already, Kenk (1969:556) has indicated that the adenodactyl of *Planaria occulta* (North America) differs from that of *P. torva* (Europe), and in all the American forms the adenodactyl seems to be but a diverticulum of the atrium rather than a dactylose organ projecting into the atrium as in *P. torva* (Ball et al., 1969:Fig. 3b). But further morphological and histological work is necessary. Furthermore this prediction can be investigated cytologically because already we know that the karyotype of *P. torva* is quite different than the karyotype of all European and North American *Phagocata* species that have been examined. If the karyotypes of the North American species of *Planaria* are more similar to those of the nearctic *Phagocata* species than to those of *P. torva*, then my prediction is corroborated.[22]

There are other predictions that could be made, but these examples suffice. What I have attempted to do is to demonstrate that it is possible, even with "difficult" and "poorly known" groups, to produce biogeographical hypotheses that meet Popper's criteria of true science: explanatory power, internal consistency, predictive power, and potential for falsification. The methodological approach used here (Ball, 1974a) follows that developed by Hennig (1960, 1966a, 1966b) and Brundin (1966), and elegant examples of its application are to be found in Besch (1964), Illies (1965), Edmunds (1972), Cracraft (1974b), and

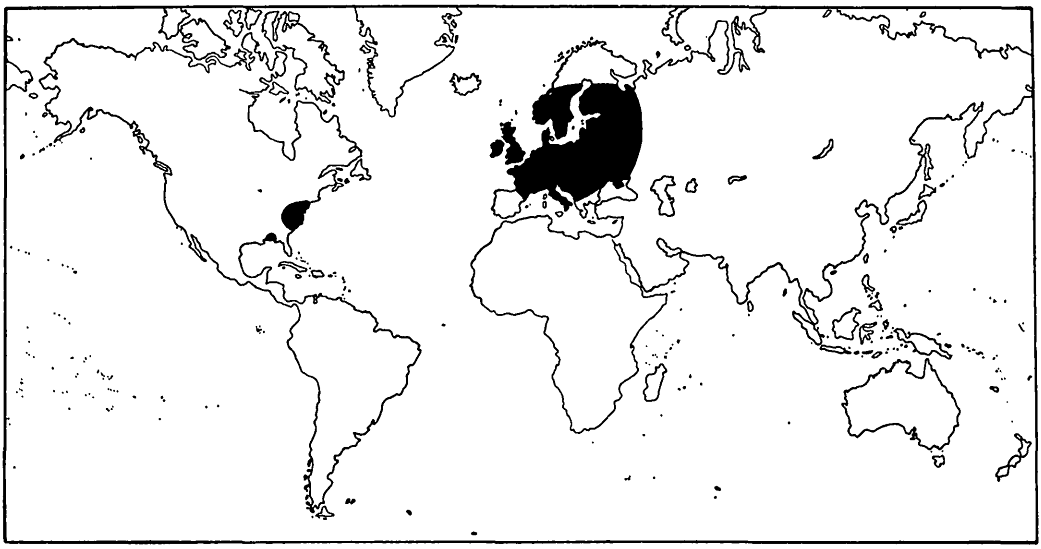

FIG. 11.—Geographical distribution of the genus *Planaria* (Planariidae).

Schminke (1974) among others, with general reviews by Nelson (1969), Ross (1974), and Ashlock (1974). But in none of these works are the ideas set explicitly in the epistemological and philosophical framework here adopted, although for the most part they do in fact conform with it. In doing so they have advanced knowledge and they form a basis from which to proceed further.

COMMENTS ON DISPERSAL AND VICARIANCE MODELS

Recently, there has been a revival of interest in the views of biogeography put forward so persistently over a period of years by Leon Croizat. It so happens that I believe that Croizat has contributed more than any other single person to the science of biogeography; he has, as Corner (1959) put it, shown us whereon to stand. Nevertheless, I believe that to some extent two of the most persuasive of Croizat's supporters, Nelson (1973, 1974) and Rosen (1974a, 1974b, 1975, see also Croizat et al., 1974) have claimed too much for some of his contributions, real though most of them are, with the consequent danger of their being rejected once more by the large majority of biogeographers that have hitherto all but ignored Croizat's major works (e.g. Croizat, 1958b, 1964, 1968a,b; see also Nelson, 1973).

> "Croizat's method has been to plot with herculean industry the detailed distributions of an immense number of organisms . . . . On his maps patterns [generalized tracks] continually reappear, regardless of biological category, and these patterns he identifies with landmarks of Cretaceous geography. Birds, mammals, reptiles, fish, crabs, beetles, ferns and flowering plants pin-point forelands, synclines, horsts, and other features established by geologists for this period of the earth . . . . Particularly is he incensed against the fruitless idea of random distribution, and a great part of [his work] is spent in disproving hypotheses of transmarine colonization. He hammers this home *ad nauseam* because, as he says, modern life shows this *ad nauseam* if the time is taken to work out the thousands of distributions" (Corner 1959:237).

Two of the cornerstones of Croizat's work are here touched upon, generalized tracks and waif dispersal.

Traditionally biogeographers have worked from the principle of centres of origin with subsequent dispersal or migration of the evolving organisms. According to Hennig's (1966b) progression rule it is the ancestral populations that remain at, or near, the point of origin, and the derived forms that migrate. Consequently, by plotting a phylogenetic tree on a map an estimate of the distributional history of the taxa can be made (e.g., Nelson, 1969). Thus a prior phylogenetic analysis is essential to the biogeographer. In contrast Darlington (1957, 1970) and Briggs (1974b) reject this reasoning and argue that it is the derived forms that force the ancestral forms to a peripheral situation. Since it is difficult to decide *a priori* between these two possibilities, Croizat et al. (1974) are justified in rejecting the concept of centre of origin, in a restricted sense, as a necessary initial premiss of all biogeographical enquiry.[23] Croizat (1968a:167fn), however, does not hesitate to use such expressions as "node of form-making" and "distribution within more or less 'concentric rings'." Furthermore, his various "Gates of Angiospermy" (Croizat, 1952) come very close to representing centres of origin in some sense. Thus, "the concept of an African Gate of Angiospermy, meaning, centre of primary importance for ancient and modern angiospermy, in which Africa not only is directly interested as a major *centre of form-making and origins* but as the *hub* of fundamental tracks running to America, Europe, Asia, Malaysia, Australasia etc." (Croizat, 1964:49 fn, my italics). Clearly, then, the concept is not quite dead even if its aprioristic use is suspect.

In rejecting, as an initial premiss, the concept of centre or origin, Croizat, Nelson, and Rosen also similarly reject dispersal or migration. The rejection of casual or waif dispersal as a prior basis for biogeography is, to my mind, well founded. Nonetheless it does occur (e.g., Gislen, 1948; Maguire, 1963; Udvardy, 1969). Groups which are known to be distributed by passive dispersal make poor subjects for biogeographical enquiry (e.g., Besch, 1969; Schminke, 1974; Corliss, 1974); and should not form part of general hypotheses. In his paper in this Symposium Rosen (1975) has pointed out the difficulties of testing for chance dispersal for complex biotas. In fact clues may be obtained by studying the biotas of the opposing shores of narrow sea straits that were totally glaciated (Ball, 1974a:385). It is also noteworthy that those biogeographers who rely on passive dispersal as a "causal" explanation invariably are working inductively. There is little doubt, for example, that at least three species of freshwater planarian have been transported by man. Yet the inductive leap to the assumption that their entire distribution is so caused, is totally unwarranted (cf. Gates' hypothesis for earthworms), for the evidence is to the contrary (Ball, 1974a). Similarly, McDowall (1973a) in discussing my views on the distribution of austral planarians points to the occurrence of a species of *Dugesia* on the Crozet Islands. Since he will not accept the possibility of the Crozets being a fragment of Gondwanaland (cf. Ball, 1974b:31), his only alternative (induction by elimination) is passive dispersal, and if this can occur in one planarian it can occur in all (induction by enumeration and/or analogy). Such an *ad hoc* narrative is unacceptable. One reason for rejecting chance dispersal *a priori* as a causal factor in biogeography is that it leads to poorly formulated and usually untestable hypotheses. Schopf (1970:658) made the point most cogently: "the stochastic hypothesis is expressly designed to take advantage of the impossibility of proving a negative and in nullifying systematic methods of explanation by emphasizing the improbable." In those groups for which passive dispersal cannot be demonstrated it simply does not make sense to assume, *a priori,* that it does (because it might) occur—to do so is to end all meaningful enquiry.

The principal element of the procedures of Croizat et al. is the concept of the generalized track. "If a given type of geographical distribution (individual track) recurs in group after group of organisms, the region delineated by the coincidental distributions (generalized track) becomes statistically and, therefore, geographically significant, and invites explanation on a general level" (Croizat et al., 1974:266). And Rosen (1974b:321) claims that the concept of "tracks" forms the only existing scientific basis for biogeographic analysis. Interestingly enough, both Rosen and Nelson introduce the ideas of phylogenetic systematics into the concept, even though these play no part in the original expositions by Croizat and even though the generalized tracks recognized by Croizat are not explicitly based on studies of rigidly monophyletic groups. Rosen's (1975) claim that recognized distribution patterns, as general statements about biotic distribution, are the end-products of an inductive process is simply false. Description is not logic. As pointed out by Croizat himself (1967:121fn) "a track is a line connecting within a whole *factual records* of consanguineous distribution. It cannot be, accordingly, more 'hypothetical' than these records themselves." We are forced to ask how Nelson (1974: 314) can then refer to testing Croizat's proposition that generalized tracks reflect bona-fide parameters of biotic distribution by repeated sampling on a random basis? In the first place I do not know what "bona-fide parameters of biotic distribution" are. In the second place if generalized tracks are empirical facts I don't see how they can be tested—all we can do is add to the information by further observation.[24]

The questions may then be raised as to what do generalized tracks mean? How can they can be explained? As statistical measures of the overall similarity of disjunct biotas they mean about the same as measures of overall similarity in systematics; the latter being a taxonomic concept not acceptable to Rosen and Nelson. It would be most interesting, to take all groups that are known to be good dispersers and to plot the generalized tracks for them—to my knowledge this has not been done. If they conformed to the generalized tracks of Croizat then by the inductive logic of Rosen two explanations are obvious, and they are of equal probability. Generalized tracks become meaningful only when strict phylogenetic principles have been applied, which Croizat never did, and then we find that the method is little different from the multiple sister-group rule of Hennig (1966b; also Ashlock, 1974). Brundin's (1966) 20 transantarctic sister-group relationships in chironomid midges do in fact represent a highly meaningful generalized track, one from which the "noise" has been removed, and these conclusions are corroborated, for example, by Edmunds' (1972) work on mayflies. The significance of a track, as an indicator of former geographical relations, is a product not of the number of instances that conform to it, but of their quality; a prior phylogenetic analysis is essential. It is true, however, that most biogeographers have tended to be restricted to their respective groups and the point of Croizat et al. that our biogeographical hypotheses must be congruent for a wide range of organisms, is one that is well taken.

Croizat's other contributions lie in his concepts of vicariance (the embodiment of geographical isolation and allopatric speciation acting as the explanation of tracks) and migration. He has repeatedly pointed out that "migration," or "dispersal," does not necessarily mean translation in space. Croizat (1968a:325) has indicated, for example, that vicariant form-making will simulate migration, and that as well as active migration, and seed dispersal there may be migration due to "epochs of violent, continuous geographic alterations." Moreover, when we study the distributions of monophyletic groups we are dealing with character complexes as representatives of units of evolution. A given complex may be vicariated by some event in earth history, disperse through an existing widespread group by interbreeding, or disperse as a result of dispersal (translation in space) of the carrying organism.[25] In only one of these cases would it be correct to talk of dispersal, meaning movement away from a centre, in the traditional sense. Thus we are moving towards a biogeography embracing the principle of primitive cosmopolitanism (Croizat et al., 1974:314).

For me, Croizat's contribution is one of liberation. Once we have escaped from the *necessity* of seeking restricted centres of origin, and from the *necessity* of plotting routes of dispersal from these centres, and once we have seen the possibilities unfolded by concepts of vicariance and differential form-making then a new world of ideas opens up for us. But this freedom does not relieve us of the responsibility of formulating our hypotheses properly, so that they can be refuted. Croizat failed to do this and I can detect no greater success in the writings of Rosen or Nelson. However, Croizat et al. (1974:266) devote some space to a criticism of McDowall's (1973a, 1973b) dispersal hypothesis of the austral distribution of galaxiid fishes. His hypothesis, a narrative one bolstered by much *ad hoc* reasoning, is indeed weakly formulated by my criteria, but their proposed alternative is no better because it is based solely on induction by analogy in that it is based merely on the assumption, untestable without the phylogenetic background, that all co-incident elements of a generalized track are subject to the same causal explanation.[26] Equally facile is the statement that the only conclusive evidence for chance dispersal may be the demonstration that a given distribution is unique, unparalleled by that of any other living organisms. This simply is erroneous (see for example Lindroth, 1957; Udvardy, 1969) and it is undeniable that much waif dispersal is orderly. The concepts of "tracks," vicariance," and "differential form-making," valuable though they are, have not destroyed the realities of "dispersal as translation in space" or "centres of origin," although they have released us from their tyranny. Croizat et al., in their concern with criticising the "apriorism" of their opponents seem to have forgotten that our arguments should centre on the deduced consequences of our hypotheses and not on our methods of constructing, or inventing, them. All hypotheses are "aprioristic" in that they are based on initial premisses.

EPILOGUE

I wish it to be understood that I am not suggesting that the different viewpoints of biogeography outlined throughout this paper are necessarily on trial. What I am saying is that in advocating a hypothesis to account for observed distributional data we must be clear into what category our explanation falls and proceed accordingly. The controversy between Omodeo and Gates is sterile not because the rival hypotheses are bad; they are all that is possible from the available data. But with this limitation they are necessarily formulated in such a way that they cannot be tested. They are rational but they tell us little. If present day distributions are indeed a reflection of the past history of the faunas then we have need of bold speculative hypotheses based on theories of descent. I use the word "speculative" with deliberation. There is no golden rule for erecting hypotheses; the creation of an hypothesis is outside the realm of logic. If the Popperian conception of science is accepted then it is largely irrelevant as to how hypotheses are derived. What matters is their formulation, consistency, predictive power, and testability, in short, the total heuristic value. We are indeed concerned not with the logic of discovery, but with the logic of justification. We would do well to remember this, for by doing so we may avoid much discussion that is sterile because it revolves around methodology and not around the hypotheses themselves. Furthermore, I would stress, with Croizat, the independence of historical biogeography. Most biogeographers try to check their conclusions against the background of geological concepts to the best of their ability, but in their turn geologists should spend some time on attempts to understand and evaluate the biological data (Lindroth, 1972). I disagree very strongly with the viewpoint that biogeographers should rationalize their data so as to conform with the current geological opinion (McDowall, 1973a:91–92). As knowledge progresses we can expect our hypotheses to become consistent for a wide range or organisms and we may hope for a synthesis between biogeography and the earth sciences.[27] But this will be achieved only if we have a biogeography in which hypotheses are made to conform with the hypothetico-deductive model. Where this is not possible, either because of the nature of the data or the state of maturity of the science, we must accept the limitations and not waste our efforts on futile or sterile discussions of opposing hypotheses that are not rigorously formulated. In erecting a biogeographical hypothesis we have a responsibility to do more than simply explain the facts at our immediate disposal.

ACKNOWLEDGMENTS

I thank the American Society of Zoologists for providing the travel funds that enabled me to attend the Symposium at Tucson, Arizona where this lecture was first presented in December 1974. A modified version of this paper was read at the 1st International Conference on the Meiofauna Species in Space and Time, held in Bermuda in September 1975. At both Tucson and Bermuda, as well as here in Toronto, I have benefited greatly from discussions with many colleagues although frequently we have had to agree to disagree. I had the benefit of seeing Donn Rosen's paper in full, prior to publication in this issue. I did not return the courtesy because of my tardiness in preparing my own lecture for the press, and for this I seek his forgiveness.

NOTES

[1] That ecologists should take this view is perhaps not unexpected. What is surprising is that so frequently palaeontologists are of the same viewpoint even though they, more than anybody, should be aware of the historical aspects. For an extreme case see Ager (1971).

[2] The rehabilitation of Croizat, begun by Brundin (1966), has been continued by Udvardy (1969), Ball (1971, 1974 a, b), Nelson (1973) and Rosen (1974) among others. A recent brief exposition of his views is contained in Croizat *et al.* (1974) and an interesting review of his work that has been overlooked by most commentators has been given by the botanist Corner (1959). That a distinguished evolutionist and palaeontologist could write as recently as 1971 that

> "The factors that control the distribution through time of animals and plants are far more complicated than those which can be comprehended by the theory of organic evolution. We are dealing not only with the changes which have occurred in the organisms themselves, but also with the evolution of the whole of their environment, with the evolution of continents and oceans; with changes in climate and coastline; with the rise and decay of mountains; with the spreading and shrinking of ice sheets and deserts, and of forests and swamps" (Sylvester-Bradley, 1971:2),

without in any way acknowledging the herculean labours of Croizat for the previous 20 years on precisely these topics is nothing short of astonishing.

[3] The impossibility of writing truly impartial history is ably discussed by Carr (1961) in his stimulating book. As an example one may cite the Baconian view of history espoused by Collingwood (1956) whose major works appeared when the modern British empiricist tradition was at its height. The influence of political and social considerations on science are covered in a recent essay by Ravetz (1975). Many will be offended by his categorizations of 'pointless publication' and 'shoddy science' but his argument that the progress of science is assessed and perceived within frameworks of ideas that are historically and culturally conditioned is a cogent one. The social dimensions of science are further discussed at length by Ziman (1968). Whilst on this subject I cannot resist adding that the inductive method, with its stress on the accumulation of facts and instances, achieved perhaps its greatest advocacy at the hands of Francis Bacon during the Reformation —an age of realism as witnessed also in art and music. Even the bizarre and futuristic notions of Hieronymus Bosch are effected with a realistic technique like that of his contemporaries and successors. And in music we find the human voice, a natural instrument, supreme and all instrumentalists were urged to imitate it. The favoured instruments were the winds, particularly recorders and cornetti whose timbres approach most closely that of the voice. In contrast the 20th century has witnessed a rise in abstract and surrealistic art, in serialism and music concrete, and a revolution in modes of thought brought about largely by the revolution in theoretical physics, and in which bold conjectures, rather than the accumulation of facts, play an important role. It is hard to say which way the influence flowed; nevertheless objectivity, true independence of thought, is difficult to achieve for we are all men of our time.

[4] Two misapprehensions concerning induction and deduction are frequently encountered and need to be dispensed with here. First, deduction often is said to involve inferences from the general to the particular whereas induction is inference from the particular to the general. This is an oversimplification. The real difference resides in the fact that in induction the inferential content exceeds that of the initial premisses whereas in deduction it

is contained wholly within them. Thus, a valid deductive argument must, if the premisses are true, lead to a true conclusion. In contrast, a valid inductive argument, if the premisses are true, leads to a conclusion that may be either true or false; the truth of the conclusion is a matter of probability, not certainty. Second, it is a common mistake to believe that we deduce hypotheses; hypotheses are what we deduce things from (Medawar, 1969). This is the error into which Croizat seems to have fallen[5], as, surprisingly, does Hennig (1966a:201). And if Bock (1973: 382) really does believe that biological classifications are scientific theories then he is in error in writing of deducing classifications by phenetic methods (1973:375). Finally, it needs to be said that induction is of several sorts and may be by enumeration, elimination, analogy, and variation of circumstance, although Bunge (1963) does not agree with this. A valuable discussion of induction within an evolutionary context has been given by Hull (1973).

[5] Croizat's use of the terms induction and deduction can be misleading. In his essay on the biogeographic thinking of Willis he criticised the inductivism of Darwin and Willis yet made no recommendations for methods that are outside the inductive framework (Croizat, 1958a). In his major work (Croizat, 1958b:1179) he referred to deduction as leading to generalities and claimed that his book serves as an introduction to the establishment of biogeographical principles and methods by deductive approaches—a claim that is manifestly false. When finally he recognized his misuse of these terms it was to imply disapproval of deduction in the conventional sense because it was used for "arguments rigged up to bolster aprioristic, theoretical assumptions" (Croizat, 1964:595fn)—a statement that indicates he has no concept of what the deductive method really is. And now (Croizat et al., 1974), he has returned to the inductive fold.

[6] The disagreement between Phylogenetic Systematists over the role of induction is worthy of note. Griffiths (1972:28) clearly believes in the overriding importance of inductive hypotheses and Crowson (1970:1–17) has given a most eloquent defence of the use of inductive generalizations and implied that strict deductive methods are inapplicable to natural history. In contrast, Wiley (1975) has made a rewarding attempt to apply the logico-deductive method to Phylogenetic Systematics and has pointed out the inherent errors in the inductive approach to that subject. Nevertheless, he still seems to believe that hypotheses are inductively derived from sensory data (Wiley, 1975:236). Cracraft (1974a:87), too, has recognized the importance of axiomatization of phylogenetic hypotheses within a deductive framework.

[7] The problem of induction has been discussed at great length by Karl Popper (e.g., 1959, 1968, 1972). Taking the three classical examples of inductive inference, that the sun will rise and set once every 24 hours, that all men are mortal, and that bread nourishes, he demonstrated that all are refuted in their original sense (Popper, 1972:10). "Induction, i.e. inference based on many observations, is a myth. It is neither a psychological fact, nor a fact of ordinary life, nor one of scientific procedure" (Popper, 1968:53). It can be argued, for example, that our previous belief that the sun would rise tomorrow was irrational, but it is now a deduced consequence from our theories concerning celestial mechanics. Another interesting discussion of induction is that of Bunge (1963) who agreed with Popper that the theory of probability does not solve the riddles of induction and does not provide a warrant for inductive leaps. Bunge retained a role for induction but argued that it "is certainly powerless without the invention of audacious transcendent hypotheses which could not possibly be suggested by the mere examination of experiential data" (Bunge, 1963:151). T. H. Huxley's aphorism, to the effect that those who refuse to go beyond the facts rarely get as far, is particularly apt here. Medawar (1969), too, has argued eloquently against the validity of induction. Rosenblueth, on the contrary, believed that if inductions were barred from science we could not have any premisses from which to deduce (Rosenblueth, 1970:78). His support of inductivism is matched by some recent philosophical writings (Cohen, 1970; Swinburne, 1974).

[8] If growth of knowledge means that we operate with theories of increasing content, it must also mean that we operate with theories of decreasing probability (in the sense of calculus probability). Thus if our aim is the advancement or growth of knowledge, then a high probability (in the sense of calculus of probability) cannot possibly be our aim as well" (Popper, 1968:218). "In short, we prefer an interesting, daring, and highly informative theory to a trivial one" (ibid., p. 217). Thus, rather than seek highly probable theories we should seek theories with a high degree of corroboration (Popper, 1959; see also, Bunge, 1963; Bock, 1973).

[9] A colleague once wrote to me to the effect that "what we need is more facts; gather the facts and they will speak for themselves." This widespread view is surely erroneous for repeated observation is not the generative act in scientific discovery, and one must speak on behalf of the facts; unbiased observation is a myth (Medawar, 1969). Inductivists are never able to tell us when enough facts are in to enable a valid hypothesis to be constructed.

[10] Omodeo explained boreal distributions with a land-bridge and austral distributions by invoking continental drift. His sole reason for this catholicity seems to be based on eclecticism (Omodeo, 1963: 142)!

[11] Induction by elimination usually takes the form of: either A, B, or C can cause E. A and B

are absent. Hence C must cause E. For the inference to be valid A, B, and C must represent *all* of the alternative causes of E, and this cannot be known. Such arguments can often simulate deduction, but only when the suppressed premisses are added does the argument become deductive (see Hull, 1973). For both Herschel and Mill induction by elimination was the key tool in the logic of discovery and verification, and Darwin used it frequently although his faith in it was shattered when his theory of the Parallel Roads of Glen Roy was shown to be wrong (Hull, 1973:25). Bunge (1963:138) defined induction restrictively as "the type of nondemonstrative reasoning consisting in obtaining or validating general propositions on the basis of the examination of cases," and thus he excludes induction by elimination.[13] The procedure has been defended forcefully by Platt (1964).

[12] In the same symposium as Omodeo's paper Lindroth (1963) argued for an Atlantic land-bridge, but one extending only westwards as far as the Davis Strait. He makes the interesting point that had Greenland belonged to North America politically and not only geographically, everybody would have noticed the strange composition of its flora and fauna.

[13] In his most recent work Popper (1975:82) has once more stressed that new theories should conflict with their predecessors. A new theory must also yield results as good or better than the successes of its predecessor, and also something new. Only then can a choice between competing theories be made. It is for the want of these factors that we are unable to make a valid choice between the rival hypotheses of Omodeo and Gates. Either, or both, could be true, or false. I should also remark here that I suspect that this desired competition between hypotheses has been confused with eliminative induction by Bunge (1963:139).

[14] This is further evidenced in a recent paper dealing principally with austral forms (Jamieson, 1974).

[15] Apart from the works of Medawar and Popper already cited an illuminating account of the hypothetico-deductive approach has been given by Northrop (1962) in his Introduction to Heisenberg's "Physics and Philosophy." Ghiselin (1974: Ch. 1) is also worth reading on this topic. A readable popular account of Popper's view of science, sociology and philosophy has been written by Magee (1973).

[16] That our perceptions are but hypotheses is an argument well presented by Gregory (1973). It should also be noted that according to the views presented here there is no "method" of deriving an hypothesis. The establishment of an hypothesis is a creative leap, and one may land on firm or soft ground. If the latter one changes course as quickly as possible. It follows that Popper's most celebrated book is mistitled, for he is not concerned with the logic of discovery, but only with the logic of justification (Popper, 1959). And if science does progress by the elimination of error then our hypotheses must be so formulated that they are testable.

[17] Originally the family Dugesiidae was defined symplesiomorphically (Ball, 1974a:346) but later a synapomorphy uniting all the species of the family was discovered (Ball, 1974c:154). The search for this synapomorphy took 2 years (my earlier paper although published in 1974 was actually completed in 1971) and thus when it was found it formed a test (corroboration) of the proposed phylogeny. Had the search been unsuccessful the monophyly of the Dugesiidae would have been in doubt. The question of using synapomorphies to refute alternate hypotheses rather than as evidence for one specific phylogenetic scheme has been discussed by Miles (1973) and his reviewer Bonde (1974). I do not agree entirely with their views even though they have embraced the Popperian concepts favoured here. It seems to me that synapomorphies serve primarily to delimit monophyletic groups, the basic units of systematic thinking, which is a procedure justifiable on both evolutionary (Hennig, 1966a; Brundin, 1966) and logical grounds (Note 19 and associated text). Then we hypothesize a phylogenetic system relating these groups and accepting certain criteria that will lead to the most parsimonious tree. In this sense the synapomorphies must be used as part of the evidence for one specific phylogenetic hypothesis. The search for other synapomorphies will, if successful, tend to corroborate the scheme, and each new taxon discovered is a potential falsifier. Phylogenetic hypotheses may further be falsified by successfully demonstrating that one or more of the synapomorphies used is in fact based on comparisons of non-homologous character states. Conversely, the demonstration that rejected non-congruent apomorph character states are in fact homologous to the same logical degree as one or more of the congruent apomorph states used in the phylogenetic reconstruction would falsify the hypothesis (Wiley, 1975).

[18] One could overcome one of Kawakatsu's inconsistencies by claiming that the Dugesiidae originated in South America and that here arose both *Dugesia* and *Cura*. From here they emigrated northwards and also transoceanically to Africa, and thence Palaearctis, and also to Australasia. The question as to why *Cura* stopped in Africa is countered by saying that under Kawakatsu's hypothesis one would also expect *Cura* to migrate northwards. This is another "acceptable" narrative explanation, just as likely as Kawakatsu's, and a little more consistent. But even so there is no logical basis for preferring one over the other. That is why new hypotheses must be formulated rigorously and restrictively if they are intended to *compete* with the old.

[19] Throughout this paper I am using "monophyly" in the sense of Hennig (1966a). Thus, a monophyletic group includes only and all the descendents of the most recent common ancestor of the group. Monophyletic groups are products of the evolutionary process and they have a real existence—they are not conveniences of man's making—and our task is to discover them. In doing so we define them by the unique attributes that they possess and not in terms of comparisons with other taxa (I am making a distinction here between definition and diagnosis). Thus in equation (1) in the main text it is clear that $\bar{s}$ is an almost meaningless set. If, for example, s means flatworm then an equivalent group 'not-flatworm' ($\bar{s}$) has very little value, especially as it needs total awareness of s for its specification. To the question 'what is this?' the answer 'not a flatworm' is indeed a trivial reply for it conveys no information about what *this* is. Each set must have its own specification of unique characters. In systematics, of course, the unique characters are the products of evolution, the "synapomorphies" of the phylogenetic systematists. To define two related phyletic lines an apomorph character is required for each and thus we need at least two characters, that is four character states, for their definition. It is most surprising how frequently, especially at lower taxonomic levels, this simple maxim is overlooked, and hence the prevalence of "$\bar{s}$ groups" in present systematic work. Nobody, I think, would suggest a class Invertebrata ($\bar{s}$) co-equal to the Vertebrata (s). But there are many less obvious examples of such absurdities that do prevail. In the triclads, for example, the genus *Phagocata* is defined currently by listing the positive attributes of the family Planariidae together with the negative (lack) attributes of all the other genera, which all specialists agree are derived with respect to *Phagocata*. Thus *Phagocata* is equivalent to $\bar{s}$ in equation (2) and the remaining genera, *Planaria, Crenobia, Polycelis* etc. are equivalent to S_{1-n}, and *Phagocata* is in effect defined as any planariid which cannot be assigned to any other genus (Ball and Gourbault, 1975). The biological inadequacies, whatever the convenience, of such an approach are surely clear. Those systematists who explicitly permit paraphyletic groupings in their classifications are indeed accepting '$\bar{s}$-groups' and they will find it necessary to use broad polythetic definitions.

[20] I stress here that it is not my purpose to claim that my hypothesis is "right" (Ball, 1974a:391)—indeed I know now that it is capable of much refinement. In the present paper I am concerned only with modes of thought, with demonstrating that biogeographical hypotheses can and must be formulated so as to compete with their predecessors. And although the examples given here are presented for their pedagogical value it should be pointed out that Kawakatsu (1973:921fn) has begun to modify his views since our discussions in Chicago in 1970, although he is not explicit concerning his reasons for doing so. And his statements are formulated no more rigorously than before.

[21] Such potential falsifiers of my hypothesis are *Dugesia* (*Girardia*) *tigrina*, a common North American species that occurs sporadically in Europe and Japan, and *Dugesia* (*Schmidtea*) *polychroa*, a widespread European form occurring also in Lake Ontario, the St. Lawrence River, and Lake Champlain in eastern North America. If these are natural distributions then my hypothesis is in trouble, but, in fact, everything we know about these species indicates that their occurrence in the unexpected continents is a result of recent transport by man (Ball, 1969, 1974a; Mettrick et al., 1970). Consequently the potential falsification disappears.

[22] The systematic relationships of the Nearctic species of *Planaria* are now under investigation by Dr. Nicole Gourbault (Paris) and me.

[23] Concerning the controversy surrounding the problem of whether or not primitive forms remain at or near their place of origin Howden (1972:130) expressed his suspicion that some do and some do not. This seems to me to be a reasonable stance irrespective of the use of the term primitive in a phenetic or genealogical sense. Nelson (1972:341), in his reply to Howden, in effect defends the progression rule though now (Nelson, 1974:557) he regards it as a rejectable apriorism (also Croizat, et al., 1974). Yet in his paper summarizing the views of Croizat we find: "Thus, a track does not necessarily reflect an actual channel of past migration or dispersal (but it may do so if it happens to estimate not a single ancestral distribution . . . but a series of ancestral-descendant distributions changing through time . . . ," Nelson, 1973:313), and later: "Tracks are, in effect, phylogenetic trees mapped according to the criterion of minimal geographical spread" (Nelson, 1973: 314). And Rosen (1974b:321) is still able to write: "Within such a framework of "tracks," cladistic phylogenies provide the input for interpreting points of origin and direction of dispersal in an individual group." Nelson's confusion may be considered a product of what I believe is a mistaken view of how knowledge advances. To Howden's (1972:130) statement: "I think it unreasonable to expect all cases to fit one type of developmental pattern. It seems even less reasonable to argue against theories that are as well documented as the ones discussed here. It would seem more logical to spend time objectively accumulating and analysing the data on various groups to see how well they fit a particular pattern." Nelson (1972:341) replies; "Different approaches . . . are apt to give different results and forever continue to do so; how, then, without investigation, discussion and, hopefully, eventual understanding of the approaches (and all of their implications if need be) are their relative merits ever to be appreciated?" The answer is easy. The relative merits will be

appreciated according to what the hypotheses tell us. If the initial assumptions are clearly stated, which is all that matters, they become a part of the biogeographical hypothesis and stand or fall according to the corroboration or falsity of the consequences of that hypothesis. Howden implies a search for falsifiers, Nelson seems to be seeking a reliable guide to the invention of hypotheses, and in this he is likely to be disappointed. The "progression rule," Darlington's "rule of thumb" and Croizat's "vicariance" all can be used as starting points for the erection of biogeographical hypotheses, providing that the latter are rigorously formulated, and hence testable.

Cracraft (1974b:215) believes that the biogeographical history of a group is deduced from the phylogenetic history. "Reconstruction of biogeographic patterns is thus a deductive inference from a prior phyletic analysis, and as a result of this inference statements about centers of origin and pathways of dispersal can be made" (Cracraft, 1974b:221). But this, too, I believe to be mistaken. We erect biogeographical hypotheses (but not according to aprioristic methodological rules) to explain the distribution patterns exhibited by a given set of phylogenetic data; they cannot be deduced from the data.

[24] Of course it is not really the track, but the disjunction it connects, that is the empirical observation. Even so, one can no more test a generalized track, or distribution by average, than one can test a statistico-phenetic measure of overall similarity. One simply adds more data. And the claims made by Rosen (1964b:289) that the "generalized track method and the concept of vicariism may lead to inferences about the physical history of the world that may be tested by modern geophysical methods, [and] conversely, geophysical conclusions can be tested by application of the panbiogeographical method." are, of course, true. They are also trivial in the sense that they are also true of Hennig's progression rule, Darlington's rule of thumb, and pure intuition. Generalized tracks have no preeminence here; it is the conclusion, however derived, that counts.

[25] The continual reference throughout Croizat's major works to "differential form making," "recombination of characters," etc., and the way in which they may simulate migration, indicates his awareness of the problems of reticulate evolution. If this is a more wide-spread phenomenon than is generally believed (also Nelson, 1973 on hologenesis) then the vicariance model will be essential to a full understanding of the evolution of the taxa, because under these conditions the procedures of phylogenetic systematists are likely to fail (Sneath, 1975).

[26] Generalized tracks contain as much "noise" as do classifications based on concepts of overall similarity (cf. "distribution by averages" with "similarity by averages"). Passive dispersal is an established phenomenon and many of the "tracks" in Lindroth's (1957) book, for example, have nothing to do with the vicariance of ancestral biotas even though they co-incide with a generalised track. The statement that "According to Croizat, it is only with reference to a generalized track that individual tracks become worthy of interpretation" (Nelson, 1973:313) seems to me to be a case of putting the cart before the horse. Individual tracks, in the sense of disjunct sister-group relations (Hennig, 1960; Brundin, 1966) are the refined data of historical biogeography, as so often acknowledged by both Nelson and Rosen. *After* we have these for particular groups we may then join Cracraft (1974b:215) and ask: "Are there general patterns of distribution that are common to many different kinds of organisms? If so, what are these patterns, how have the patterns themselves changed through time, and are they correlated with the past spatial relationships of the continents and ocean basins, and with past climates."

[27] Corner (1959) in his review of Croizat's major work, subtitled as an Introductory Synthesis of Zoogeography, Phytogeography and Geology, stated that the effect of the book would be long in the making, as indeed it has. The breadth of vision and unity that Croizat has brought to evolutionary biogeography are worthy achievements. Those who have found his work difficult and tiresome to read may note that he has been anticipated, this time in exquisite English, in the poetry of Walt Whitman: "A vast similitude interlocks all,/ . . . . All distances of space however wide,/ All distances of time, all things inanimate,/ All souls, all living bodies though they be ever so different . . . ."

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