# The dispersal versus vicariance debate in biogeography

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#### **ABSTRACT**

Wild's 1964 study of the Chimanimani Mountain endemics is taken as an example of a vicariance model: endemics (1) are seen to have originated *in situ* from a residual fragment of an ancestral, once-continuous flora; (2) are held to present in themselves no history of major dispersal; and consequently a biogeographical intrepretation involving or presupposing their 'migrations' is not thought to be applicable. The preference Wild expressed for this model over a dispersalist model attributed to Levyns is investigated, making use of theoretical refinements developed in the dispersal vs vicariance debate within the past decade. The differences in intrepretations between Wild and Levyns appear to be unresolvable on account of their positions not being demarcated clearly enough, and the situation has not improved since then, underlining the need for attention to be given to the formulation of applicable, coherent and testable hypotheses in biogeography.

#### RESUME.

### LE DÉBAT BIOGÉOGRAPHIQUE ENTRE LA VICARIANCE ET LA DISPERSION

L'étude de Wild en 1964 sur les endémiques des monts Chimanimani est prise comme un example d'un modèle de vicariance: les endémiques (1) sont considérées comme étant originaires in situ d'un fragment résiduel d'une flore ancestrale, autrefois continue; (2) sont tenues comme ne présentant en elles-mêmes aucune histoire de dispersion majeure; et par conséquent une interprétation biogéographique impliquant au pré-supposant leurs 'migrations' n'est pas considérée comme applicable. La préférênce exprimée par Wild pour ce modèle contre le modèle de dispersion attribué à Levyns est investiguée, en faisant usage des perfectionnements des théories réalisés dans le débat 'dispersion ou vicariance' de la dernière décade. Les différences dans les interprétations entre Wild et Levyns apparaissent être insolubles parce que leurs positions ne sont pas assez clairement démarquées, et la situation ne s'est pas améliorée depuis lors. Ceci soulinge le besoin d'accorder une attention plus grande à la formulation d'hypothèses applicables, cohérentes et vérifiables en biogéographie.

This paper is concerned with a debate that took place mainly among North American biogeographers during the 1970's. The debate arose out of differing approaches and viewpoints that were in fact already causing disagreement among southern African phytogeographers in the 1960's, but there has been little attempt in this continent to clarify the issues involved, and we have much to learn from the argument that developed to the north in the past decade.

The debate among North American workers was largely sparked by members of the American Museum of Natural History, who gave support to the approach and methods of the South American botanist Leon Croizat. In several publications over the previous twenty years, Croizat had been contrasting his work with what he took to be orthodox biogeography. The latter was seen by him to have its origin in Darwin's work and to be grounded on the assumption that every taxon comes into being in a centre of origin, from which migration may occur by some means of dispersal. Yet the event of dispersal is only assumed, not demonstrated, and the means of dispersal are not specified — or are even not rigorously specifiable at all.

In a paper on African biogeography, Croizat (1968: 430) stated that 'In sharp opposition to conventional biogeography for which migration is the main problem, the (pan)biogeographic method I stand for emphasizes form-making as essentially

molded by vicariism'. Such 'vicariant form-making' is held to follow an 'original Permo-Jurassic "radiation" ' (p. 432 & 433), with the 'establishment of Triassic and Jurassic main centres of evolution and massings' (p. 433). Fragmentation of these 'centres and massings', such as through continental drift, results in related taxa occurring on different continents 'without the vicariant taxa ever having moved from their original centres of form-making' (p. 434). Thus (p. 434), 'An ancestral group, whether plants or animals, originally distributed by "radiation" to the lands become in our geographic maps, e.g., Brazil, Nigeria and Borneo, may by subsequent, strictly local form-making yield, e.g., three different genera in each one of these lands. To assume that the origin of these genera is due to the active "migration" of one of them from, e.g., Brazil to Borneo, Borneo to Nigeria, etc., is most certainly not what competently conducted analyses of dispersal show to be true and correct'.

On a more local scale, Croizat (in litt., 1965) cited a passage from Wild's study of Chimanimani Mountain endemics as being 'precisely the leitmotif of the book [Space, time, form, Croizat, 1962], resuming all my work'. Wild's passage (1964: 129; see also Croizat, 1968: 87) reads: 'In discussing these vicariads, it will be noted that there is no tendency towards affinities in any particular geographical direction. In different genera the nearest affinity may be with the Cape, Tanganyika, Angola, or the next geological formation in the Chimanimanis. This would indicate evolution from a flora blanketing a large or even continental area and not from a flora moving along more or less narrow lines of migration'. Wild here finds 'migration' to have no

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explanatory value regarding the Chimanimani endemics: species in this flora may originate in situ, and need not present any history of dispersal. They are seen to be derived from a residual piece of a 'Cape Flora, or its direct evolutionary precursor,' which 'covered a large continuous area of the African Continent up to the early Tertiary,' but which subsequently became 'very much fragmented and remained in tropical Africa only in montane areas' (Wild, 1964: 132). According to this model, Capensis endemics would also be regarded as having originated in situ, in this case in the south-western and southern Cape as derivatives of another 'fragment' of the widespread 'Cape Flora [in a broad sense, or its direct evolutionary precursor'. Again, these endemics themselves would not be thought to present a history of migration or dispersal, having originated in situ.

In Wild's study, the Zambesi and Limpopo Basins are not treated as 'barriers' to northward or southward 'migration' of species: the basins are discussed as 'intervals', as factors in the 'fragmentation' of former more extensive ranges. This contrasts with a 'migrationist' viewpoint, which tends to see such basins as 'barriers' to the spread of alreadyformed species. Thus in a vicariance viewpoint, 'barriers' tend to be considered as factors prior to the event of speciation; in a dispersalist viewpoint, 'barriers' tend to be considered as factors affecting species mainly *after* their origin.

Like Croizat, Wild (1968: 210) saw an incompatibility between the vicariance and dispersalist viewpoints, preferring his 'explanation' that 'the Cape Flora became very much fragmented and remained in Tropical Africa only in montane areas' to the idea attributed to Levyns (1964) of a 'migration from Central Africa to the Cape' of several 'Cape' genera. He did not, however, totally reject every idea of 'migration' and 'barriers', especially in more 'recent time' (1968: 211), and the differing viewpoints did not develop into controversy: he did not take up Cain's (1944) or Croizat's criticisms of the idea of centres of origin and dispersal, even though he quoted both authors in other contexts.

It was in the mid-1970's that a major argument developed, initiated by two ichthyologists in the American Museum of Natural History, G. Nelson and D. E. Rosen. The events can be seen as something of a palace revolution in the American Museum, which for several decades had been the centre of an influential zoogeographical school, adhering to Darwinian views of an unchanging patterning of the continents and 'that species originate in a small area and thereafter expand in range according to the efficacy of their means of dispersal' (Nelson, 1973: 315). This viewpoint had been receiving Croizat's sustained criticism, and 'the recent and stunning breakthrough of the neowegenerians' (Nelson, 1973: 314) at this time gave Croizat's criticisms a fashionable touch.

The 'breakthrough' in plate tectonics also gave positive support to Croizat's idea of vicariism. Rosen (1975: 489) characterized Croizat's 'biogeography of

vicariance' as recognizing 'biotic patterns arising largely from biotic fragmentation in response to geographic change, rather than from dispersals from centres of origin'. Rosen pointed out that Cain and Croizat share several central concepts, yet he believed (1975: 490) 'it is evident that Cain failed . . . to achieve some general, synthetic approach which could give order and direction to biogeographic investigation'. Croizat, on the other hand, was held (Rosen, 1974: 289) to have developed 'a science of biogeography that depends on rigorous methods of analysis and the formation of testable hypotheses'.

A more critical appraisal of biogeographical hypotheses was given by Ball in a symposium on perspectives in biogeography published in the 1975 volume of Systematic Zoology. Ball stated (1975: 419), 'I believe that Croizat has contributed more than any other single person to the science of biogeography'; nevertheless, he presented a zoogeography of planarians which made use of both vicariance and centre of origin/dispersal models — a practical rejection of Croizat's contention that one model 'rules out the other' (Croizat, 1968: 431). Ball stated (p. 415) that 'for austral distributions I am invoking a vicariance model for the older, more primitive taxa, whereas it seems proper to talk of centres of origin and dispersal' for genera reaching the northern hemisphere after the closure of the Tethys Sea, subsequent to the family becoming disjunct in the southern hemisphere through continental drift. Ball favoured the rejection of the concept of centres of origin by Croizat, Nelson and Rosen, either separately or jointly (Croizat, Nelson & Rosen, 1974), but only if the concept was rejected 'in a restricted sense, as a necessary initial premiss of all biogeographical enquiry'. (p. 420). Similarly, 'the rejection of casual or waif dispersal as a prior basis for biogeography is, to my mind, well founded. Nonetheless it does occur' (p. 420).

Ball's paper is particularly interesting because of its expression of freedom by a North American biogeographer who has broken out of the ruling 'center of origin/dispersal paradigm' (Nelson, 1975: 493). 'For me,' Ball wrote (1975: 422), 'Croizat's contribution is one of liberation'. He believed that Croizat's ideas 'have not destroyed the realities of "dispersal as translation in space" or "centres of origin," although they have released us from their tyranny' (p. 422). He stressed, however, that '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' (p. 422).

The justification that Ball gives for rejecting the centre of origin paradigm 'as a necessary initial premiss of all biogeographical enquiry' is as follows: some writers hold that 'it is the ancestral populations that remain at, or near, the point of origin, and the derived forms that migrate' (pp. 419–420). Other writers 'reject this reasoning and argue that it is the derived forms that force the ancestral forms to a peripheral situation' (p. 420). It is 'difficult to decide

a priori between these two possibilities', Ball believes. Indeed, several authors have argued that a decision of this kind cannot be made at all, because, even if the centre of origin paradigm be accepted, the centre of origin itself cannot be determined from the present range of a taxon (e.g. Udvardy, 1969: 240, 'Because of the temporal instability of the area, it is futile to search for centres of origin or dispersal within existing distribution areas.'). As will be noted later, it is important to bear this point in mind in any discussion of the 'origin' or 'migration' of the Cape Flora.

Regarding dispersal, Ball (1975: 420) observes that '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'. Examples of such hypotheses — if they can be called hypotheses — are common enough in African phytogeography: thus, 'Dietes probably achieved this distribution through long distance dispersal, although it is not possible to say when and how' (Goldblatt, 1978: 401-402). Of such hypotheses, Ball remarks, 'They are rational but they tell us little' (p. 422). He stresses the need for 'bold speculative hypotheses based on theories of descent ... 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' (p.

Did the vicariance viewpoint of Wild or the centre of origin/dispersal viewpoint of Levyns employ 'hypotheses' according to these specifications; or were the viewpoints based on mere 'narrative', as Ball termed it, telling 'a rational historical story but it calls on no laws, nor even hypotheses of relationships . . . and it enables no positive or negative predictions to be made' (Ball, 1975: 410)? If the latter is the case, then, as Ball (p. 411) observes, '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 biogeographical argument, as Ball points out, has in fact been of this kind.

Bearing all the foregoing in mind, we may now look critically at Wild's preference for his viewpoint over that attributed to Levyns. In the first place, did he have scientifically acceptable grounds for making a comparison at all, or was his preference similar to choosing between cricket and baseball?

Wild firstly satisfies Ball's requirement that the hypotheses should be 'based on theories of descent', since he considers the distribution of the 'nearest affinities' of Chimanimani endemics. The stated lack of 'any particular geographical direction in these affinities' is something that can be tested statistically. It leads by traceable logic to the inference that there is no evidence for 'more or less narrow lines of migration' (although no specifications are provided regarding the term 'narrow'). The other inference, of 'evolution from a flora blanketing a large or even continental area', is likewise logical, although

ambiguity is introduced in the statement (1964: 132) that it was 'the Cape Flora, or its direct evolutionary precursor' that did the blanketing. This phylogenetic ambiguity will be found to be troublesome later. At least the hypothesis of early Tertiary period for this 'blanketing' and its subsequent fragmentation is based on a review of the geological and palaeoclimatic evidence available at the time, so this hypothesis is readily testable.

There still remains the question of how, by what movements, the early Tertiary 'blanketing' was accomplished. The blanketing could be seen as the product of Croizat's postulated 'Triassic and Jurassic main centres of evolution and massings', established after the upheavals of the Permo-Carboniferous Ice Age. The vicariance model necessarily holds that the 'radiation' which led to the establishment of these 'massings' was performed by taxa mostly ancestral to the ones now present. Theories regarding the spread of these ancestral forms at such remote times, over a geography markedly different from the present, obviously must belong to a set different from the set of theories concerned with later in situ diversification. Croizat (1962: 184; 1981) indeed takes this into account in recognizing alternating phases of 'mobilism' and 'immobilism'; major phases of mobilism are seen to be initiated by environmental 'revolutions' such as the Permo-Carboniferous and Plio-Pleistocene Ice Ages, separated by periods of more stable environment with consequent immobilism and vicariation or 'local form-making' (Croizat, 1968: 434). Wild does not attempt to describe events during the phase of largely pre-Tertiary mobilism no firm suggestions are made as to how, and by what movements, the early Tertiary 'blanketing' came about; and little is put forward as testable hypothesis by Croizat regarding mobilism or radiation in southern Africa. This lack of firm hypothesis is important to bear in mind when considering the views of Levyns, with which Wild states disagreement.

It may be noted that Levyns (1964) starts from a position very similar to that of Wild. Writing on primitive species found in upland outliers of the Cape Flora in central Africa, she states (p. 91), 'It is difficult to avoid the conclusion that they represent relics of a once widespread flora, forced by changes of climate to take refuge on mountains which alone provide conditions necessary for survival.' From the Cape genera she reviews, however, she finds (p. 94) the repeated 'picture of a genus arising in the north, leaving behind scattered records of its journey southwards, and finally undergoing intensive speciation in the south-west'. Thus, in the Persoonioideae (Proteaceae), 'The paths are marked by relics of the two oldest genera, Faurea and Protea' (p. 93). This 'picture', not of a 'once widespread flora' but of genera 'arising in the north' and then proceeding on a 'journey southwards', was seen by Wild to be incompatible with his picture of in situ evolution by isolated fragments of a formerly continuous flora.

If Levyns's 'picture' allows for the occurrence of evolutionary change during the course of migration southwards, then the differences between her interpretation and that of Wild finds a parallel in the differences between the 'phylogenetic biogeography' of Hennig and Brundin (Brundin, 1981) and the 'vicariance biogeography' of Croizat, Nelson and Rosen. The differences between these two schools have recently been discussed in some detail at a symposium (Nelson & Rosen, 1981), and the arguments cast some potentially clarifying light on the 'origin of the Cape Flora' debate.

Brundin, the author of classic work on austral vicariance patterns in chironomid midges, states (1981: 95) that phylogenetic biogeography is the 'biogeographical implication' of Hennig's phylogenetic systematics (Hennig, 1966), providing an 'alternative model' to the Croizat-Nelson-Rosen vicariance model. In complete contrast to Croizat, Nelson and Rosen, dispersal is taken to be of fundamental importance, 'dispersal' in this context being defined as 'the stepwise progression in space by marginal portions (border populations) of the gross population of a species' (Brundin, 1981: 107). This peripheral spread is taken to be the result of environmental change, the 'disappearance of a former barrier' (p. 107). Such geographical progression can be accompanied by phylogenetic progression: 'Dispersal by an incipient ancestral species followed by isolation and speciation will give rise to peripheral apomorphy [phylogenetic advancement], not to peripheral plesiomorphy [conservatism]' (p. 108). If such dispersal occurs, 'then the comparatively plesiomorphic species or group will be closer to the initial range of the common ancestral species than the apomorphic sister species or sister group' (p. 109). Therefore, in contrast to Croizat's idea that 'form-making' occurs not at a time of 'mobilism' but of 'immobilism', the Hennig-Brundin 'progression rule' directly couples 'form-making' and 'mobilism'; and further, makes a prediction that more primitive forms will be found in the 'initial range'.

In the context of southern African phytogeography, the Hennig-Brundin model would see Capensis as the endpoint in a geographical and phylogenetic 'progression' from an ancestral range in central Africa, and not the result of *in situ* evolution in an already-dispersed and now immobile and fragmenting 'blanketing'. Yet there is, of course, no logical inconsistency in applying *both* models to Capensis: the 'journey southwards' envisaged by Levyns could involve some phylogenetic progression, which would then be taken further by *in situ* evolution once populations were established in the south-western Cape.

Unfortunately, there seems little indication that Levyns took a clear position in this respect. In concluding her 1964 paper she stated (p. 103) that 'much of the Cape Flora had its origin north of its present station and that it migrated southwards'; but she did not specify whether the migrating 'it' was intended to refer to the present assemblage or to some 'evolutionary precursor', to use Wild's phrase—although, as already noted, Wild himself was ambiguous on this phylogenetic point. Levyns observed (p. 97) that 'it is not impossible that in the course of evolution some species may have been

transferred from one community to another . . . It is not difficult to visualise a descendant of this adaptable species ultimately becoming a member of a flora quite different from that in which it originated'. This suggests some idea of evolutionary change occurring during the course of migration, conforming to some extent with Hennig's progression rule. Yet another migratory mechanism is considered later (p. 105), namely that 'The northward movement of Africa as a result of continental drift would result in changes of climate of the very type needed to explain the southward movement of floras'. This suggestion, notably modern for its time, does not shed light on exactly what the 'stream of migration' to the Cape was considered to consist of phylogenetically. But it does suggest some point in time for the event, and in another paper (Levyns, 1962: 8) a corresponding point in time is suggested: since 'certain elements of the montane flora of Madagascar clearly belong to the Cape Flora and have their nearest relatives on the mountains of East Africa . . . the Cape Flora must have been in existence before the separation took place'. This time would be mid-Cretaceous to early Tertiary, as reviewed in Axelrod & Raven (1978). Another piece of evidence that Levyns (1964: 92) brings forward regarding time is the absence of pollen grains of Ericaceae from the Knysna lignites, pointing to the conclusion that by the probable time of early Tertiary, 'the Ericaceae had not at that time arrived in southern Africa'.

It may be noted that the time suggested by her for the 'stream of migration' is not markedly different from the time suggested by Wild for the 'blanketing' of the Cape or pre-Cape flora. One wonders whether Wild and Levyns were in fact talking at least partly about the same thing from their different viewpoints; yet because their positions were not demarcated sufficiently clearly — Levyns's in particular has a strong admixture of 'narrative' in Ball's sense — the matter remains unresolvable. This highlights the need that Ball (1975: 422) stressed regarding biogeographical hypotheses: 'What matters is their formulation, consistency, predictive power, and testability, in short, the total heuristic value'.

The aim of this paper is not to argue for the correctness of either a vicariance or a dispersalist viewpoint in the context of African biogeography. In this complex field of study, both are applicable, both can yield testable hypotheses, as Ball showed in the case of planarians. Further, vicariance and dispersal can be seen as 'each other's corollaries' (Brundin, 1981: 130) in the viewpoint of phylogenetic biogeography. It is much to the credit of Levyns and Wild that they both recognized the importance of continental drift and its vicariance implications for southern floras at a time when the weight of biogeographical opinion outside Africa was against the idea. Thus Levyns was free of some of the major constraints of the centre of origin/dispersal paradigm, even if she evidently took other aspects, including a search for 'paths of migration', to be as Ball (1975: 420) put it — 'a necessary initial premiss of all biogeographical enquiry.' A conseJ. C. POYNTON

quence of this programming is the tendency to overlook or underestimate the signs of extensive in situ evolution of endemics, to which interpretations involving 'paths of migration' are simply inapplicable.

It seems fair to say that neither the dispersalist nor vicariance model has gained further status as a scientific hypothesis at the hands of subsequent writers on the major features of African phytogeography. Leach (1976) has pointed out errors in Croizat's (1965, 1967, 1972) treatment of African Euphorbia, and the historical phytogeography of this 'frighteningly large genus' (Leach, 1976: 17) still awaits a fresh review. The different viewpoints of Wild and Levyns received coverage but no elaboration in Werger's Biogeography and ecology of southern Africa (Killick, 1978: 520-521). An attempt at rigorousness within the centre of origin/dispersal paradigm was recently made by Holland (1978) in his study of the genus Aloe. An 'index of dispersal' based on values reflecting 'the greatest variety of forms and a concentration of the more primitive of them' (p. 222) is used to identify the 'centre of origin of a taxon'. Zimbabwe is shown to have the greatest diversity and highest concentration of primitive species of aloe as judged by vegetative characters, and it is held (p. 224) that 'the ancestral aloes first appeared in southeast Africa some time before land connections with Malagasy were severed in the late Mesozoic — early Tertiary. From there they dispersed along the rising highlands of eastern and southern Africa . . .'. Holland perceptively states (p. 224) that 'Everything depends on the ordering of the aloes in an evolutionary sequence, and it is by no means certain that the proposed system is the most efficient'. His analysis and resulting biogeographical thesis to some extent resemble the techniques and the results of the phylogenetic biogeography of Hennig and Brundin, and their rigorous procedures could well be tried by African phytogeographers.

At present the tendency is more for dispersalist models to be presupposed or adopted unthinkingly, or else be used as a 'waste-basket category': if no definite hypothesis to account for a feature of distribution emerges, then the 'explanation' must be some kind of dispersal. This is unfair to the concept of long-distance dispersal, which certainly can stand as a testable and heuristically useful hypothesis in many particular cases (e.g. Udvardy, 1969 & 1981; Pielou, 1979), and which has been recognized by many biogeographers as being one of two basically different processes by which the geographical isolation of populations occurs; range subdivision and barrier-crossing dispersal. As summarized by Haffer (1981: 390), the two processes are: '(1) fragmentation (sub-division, "vicariance") of a pre-xisting continuous species range, or (2) crossing of a pre-existing barrier by some dispersing individuals that establish a founder population'.

Dispersal must also stand as a general background presumption in areas such as North Africa with its 'constant climatic disturbances . . . since the

end of the Tertiary' (Quezel, 1978: 531); indeed, it is applicable to all areas of Africa during this present Quaternary phase of 'mobilism', to use Croizat's term. It can in fact be held (contrary to the views of Croizat's school) that the upheavals during Quaternary times show vicariance and dispersal events to be the two sides of the same coin (cf. Udvardy, 1981; Brundin, 1981). Vicariance and dispersal can be seen to accompany the contraction and expansion of ranges as they follow the cyclic changes in Quaternary climate. Expanding ranges at any one time show a radial pattern, a pattern of dispersal; while contemporaneously contracting ranges show relict patterns, characterized by fragmentation with incipient or actual vicariance. In the present post-glacial epoch, for example, groupings of ranges into radiating 'tropical' and contracting 'nontropical' faunas and floras are discernible in southern Africa (e.g. Poynton & Broadley, 1978): radiating patterns of a diversity of plants and animals seem centred on the warm eastern lowlands (Poynton, 1961), and they interdigitate with patterns showing fragmentation and sometimes taxonomic differentiation on isolated cool uplands (e.g. White, 1978; Poynton & Broadley, 1978; cf. Haffer, 1981, for South American birds).

There is a tendency in the vicariance vs dispersal debate, as presently conducted, to divert attention from the vicariant and dispersal events occurring all around us at the present time. At a symposium centred on vicariance held at the American Museum of Natural History in 1979 (Nelson & Rosen, 1981), Tattersall (1981: 410) remarked of Haffer's contribution on Neotropical bird speciation: 'Haffer's contribution seems likely to appeal more to those who view biogeography as a set of real-world problems seeking solution than to those who regard it as a science in search of a paradigm'. Yet, bearing in mind Popper's argument (Popper & Eccles, 1977: 39) that it is indeed 'real-world problems' that science starts from, it is hardly surprising if the current debate makes only limited sense to many of us studying patterns of current vicariance and dispersal in Africa. Does a vigorous science spend time 'in search of a paradigm'? The vicariance vs dispersal debate, as I have tried to show, has stressed the need for scientists to be philosophers also, and scrutinize the presuppositions and programmes within which they carry out their work. On that score we should avoid being faulted; yet beyond that, let us associate ourselves with the breadth and freedom of those like Wild and Levyns who, unconstrained by paradigms such as the anti-Wegenerism which gripped their overseas contemporaries in the 1960's, were ready to explore whatever Africa had to show them.

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