

FORUM

**Into the storm: A personal retrospective on panbiogeography,
Part I**

John Grehan

PART I: NEW ZEALAND

Accidents happen. One just has to be in the right place and the right time and have the right (or wrong!) inclination. It was my fortune (or otherwise) to end up in just that kind of circumstance. As a result my life followed a very different path to that I had anticipated. Some of it was good, some of it not so much. The culprit, if the accident may be seen that way, was Croizat's panbiogeography. At a time when panbiogeography was almost completely marginalized in the literature of evolutionary biology, I happened to be exposed to the subject in a way that caught my attention and has since engaged my often passionate involvement.

But my advocacy for panbiogeography often brought me into conflict with many professional colleagues and exposed me to reactions for which I had no prior experience. The resulting interactions were sometimes intense and did not always reflect the best side of either myself or others. Of course, in hindsight and with some measure of wisdom gained over the years, the past mistakes on my part as well as those of various opponents may be self evident. But at the beginning I was unprepared to understand the depths of hostility that then existed towards panbiogeography, and I think many opponents also did not fully comprehend

their own antipathy towards this discipline.

At the time panbiogeography first came to my attention my exposure to evolutionary theory was principally limited to an isolated lecture on Darwin's argument for natural selection in the final year of high school and an undergraduate zoology lecture. From this I gained the impression that unless one was a geneticist or a paleontologist, evolution was not a subject one could directly investigate. My view of evolution was that of a background story that otherwise had little of significance for my interest in natural history.

My entry into biogeography was made even more unlikely by my failure to take an interest in the sciences of taxonomy or systematics. I had a lifelong interest in collecting, drawing, and identifying insects, but this somehow never translated into formal taxonomy or systematics. The obvious connection never occurred to me or to anyone else. Perhaps it did not help that my graduate classes on zoological systematics and plant geography were among the most uninspiring I ever experienced. I gained the impression that systematics was hopelessly confused, and plant geography almost sent me to sleep with stories of mysterious migrations from mysterious sources.

This state of affairs changed

precipitously in early 1982 when I found myself doing something unusual, and that was to find an obscure book by an obscure author. That book was Croizat's *Space, Time, Form: The Biological Synthesis*. This effort was because I was sufficiently annoyed by persistent questioning about science, biology, theory, philosophy, and all the various facets that affect one's personal approach to science. This was annoying because I was not used to thinking or even considering such esoteric matters. These questions did not come from department faculty, but from another PhD student - Robin Craw who had an office a few doors away from mine.

At that time I was only interested in observing and recording nature and I did not think of 'theory' as anything more than confused opinions that had no grounding in my personal experience. Robin's persistence on these matters was connected to his interest in Leon Croizat - a person who seemed to me to be a rather shadowy entity unconnected with what I had been taught in my undergraduate and graduate classes. Finally I became fed up with the intellectual disruption and I decided I needed to check for myself. I anticipated that this would be a dead end, another among the many theorists proclaiming this or that theory about the universe and everything. But I was surprised by the beginning of the book where Croizat advised: "To the buyer of this book, I would say as its sole manufacturer this much in the first place: I do admit that fully 99% of the pagination of my works

is wind, trifle, piffle, tripe, rot, stuff, in sum, entirely unworthy of the attention of a serious scientist." For most readers this was probably sufficient justification for them to immediately put the book back. Then I read the footnote about the "serious scientist" being someone who "...is by definition a man opposed to 'abstract thinking' and 'useless speculations', and devoted on the contrary body and soul to a single one "accepted specialty". Hmmm, I thought. No one had said that to me about science before. I immediately felt an affinity to his way of thinking and I resolved to read more. After all, it was only curiosity that killed the cat.

Space, Time, Form presented the appealing proposition that evolution could be made accessible to direct study by examining the results of that process - the geographic patterns of animal and plant differentiation. I was also intrigued by the way Croizat wrote a dialogue in which the reader was as much a participant as the author. I came to appreciate that evolution was geographic, and that the study of evolution required a foundation in biological geography. All of this was new and it was not an easy adjustment for me to make. But I found something important that was previously missing from my knowledge of evolution - a coherent and integrated framework connecting biology and geography.

My receptivity to Croizat's geographic emphasis was not entirely without precedent. At the age of eight or nine years I was mapping

trails that I and other neighborhood boys made in the hillside adjacent to our neighborhood. And by the time I was 14 I mapped the contours and margins of a hillside stream I was examining for stream invertebrates (Fig. 1). But this geographic inclination subsequently remained dormant until

exemplified by the stature of geologist Sir Charles Fleming whose biogeographic reconstruction became the *de facto* 'official' story for New Zealand's evolution. It became the text book story and it was accepted in its entirety by everyone in established scientific circles. My first contact with

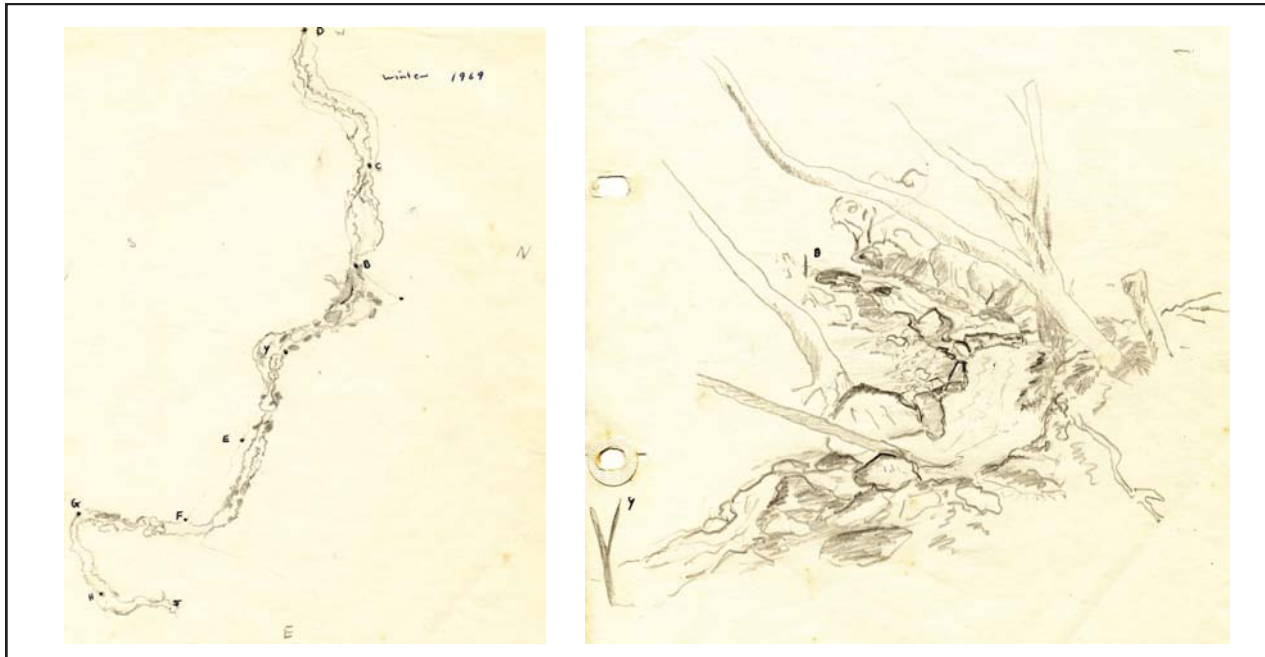


Fig. 1. Early biogeography. Left: Stream habitus, Wainuiomata, New Zealand drawn at about the age of 14 years. Right: Stream map showing reference markers for mapping stream boundaries.

rekindled by Croizat's thesis.

I then had no idea of the storm of controversy and emotion circulating around Croizat and his work and I was emotionally and academically unprepared to handle with grace the level of hostility or ridicule that I would come to encounter. The geographically isolated nature of New Zealand science generated a very homogenous social and academic structure that lent itself to a high degree of conformity. This was

Sir Charles occurred when I was about 15 years old. My father came across a newspaper announcement of a soiree to be hosted by Sir Charles at his home. At that time I had little awareness of the academic world and university was only a vague entity that lay far in the future. I had periodic contact with entomologists at the Wellington Museum, but no knowledge of this or any other science profession. Sir Charles was only known to me as someone working on cicadas and since I found these insects to be

interesting my father took me to hear his presentation. Sir Charles spoke to me encouragingly and suggested I join him on a future field expedition but I never heard from him. I wonder sometimes if he had contacted me whether I would have absorbed his evolutionary perspective like almost everyone else.

As Robin was to later point out, Fleming's model represented an attempt within the natural sciences to demonstrate a natural identity for New Zealand's origin and evolution from an original birthplace whether the 'Gondwana' of the 1980's or the equally enigmatic 'Zealandia' of today. These origin myths (I call them that because they appeal to some sense of original national identity) left little room for approaching the subject in any other way. As the prominent New Zealand plant ecologist Peter Wardle (1988) noted, panbiogeography was unacceptable because it required a "rejection of compelling contrary evidence from geology, palaeobotany and evolutionary studies".

Soon after I declared my interest in panbiogeography, Robin happened to mention, almost as an aside, that there was a Michael Heads, then working on his botanical systematics doctorate at Otago University, who was also interested in panbiogeography. Mike had independently taken to panbiogeography and it was Croizat who informed Robin and Michael of their mutual interest. I found Mike to be another exceptional thinker who, like Robin, had a broad and comprehensive knowledge of biogeography,

systematics, and the history and philosophy of science. This tremendous intellectual gap notwithstanding, Robin and Michael accepted and encouraged my interest and desire to learn a new subject and tolerated by lapses in knowledge and understanding. Robin repeatedly emphasized that it was essential that I understood panbiogeography through my own efforts rather than being told what to think by him or anyone else.

Beginning with Robin and Michael, and later extending to other graduate students such as Ian Henderson, Tony Beauchamp, Wendy Baker, and Gordon MacArthur, my days were often filled with stimulating discussions that have since had no equal. The graduate program was based entirely on research so our time was not swamped with 'mindless' class work. And the research usually constituted independent projects where the content and perspectives were not linked to those of the thesis supervisor. This combination of circumstances provided the time to read, reflect, and think independently.

Panbiogeography gave me the opportunity to appreciate evolution through direct experience rather than pure theory. Distributions could be understood as traces of the past imbedded in the present. Michael pointed out that it was possible to be at any location and think of it as a matrix of geological and biological history through which the ancestral distributions were re-presented in the landscape of today. One could 'literally' experience walking within the weave of space

and time as when I visited Shag Point with Mike and Brian Patrick. This unassuming coastal bluff of pasture covered hillocks and gullies also supported plants and animals separated by thousands of kilometers of geographic space, and hundreds of meters of elevation, from their nearest relatives in mountains to the west. Beneath our feet was a major fault and tectonic boundary extending out to sea and back to those distant mountain locations. Standing on these Bluffs it felt like space and time was collapsing within the present.

Ultimately the best way to tackle a new subject is to try to write about it. There was no road map so I had to identify both the question and the answer while also learning about the subject in general. My initial efforts were, for the most part, naïve, superficial and unsuccessful. I think my first attempt was to write a rebuttal of Donn Rosen's (1982) paper on evolutionary explanation as my initial interest was the significance of panbiogeography as an evolutionary synthesis. My critique was well received by Croizat, but not by the reviewers. Looking back it was long on assertions and short on content (although that is what I thought of Rosen's paper as well). But the effort was not wasted as I was beginning to learn not only how I thought about such matters, but about how others (as reviewers) did also. I decided to peruse another line of investigation that was more directly related to my research project. While describing the biology of a wood boring ghost

moth (Lepidoptera: Hepialidae) I became aware of general theories about insect-plant relationships. The insect under study was relatively generalized in its host-plant range and mode of feeding, but many insects were involved in highly specialized interactions. One of these came to my attention through Croizat's evolutionary botany or *Principia Botanica*.

Effective reading of *Principia Botanica* requires a solid knowledge of botanical morphology without also being hidebound by traditional definitions. My undergraduate botanical courses covered plant anatomy, but not the scope of plant groups and morphology encompassed in the *Principia*. So it was an uphill struggle to grasp Croizat's alternative understanding, even for simple ideas such as the carpel being a compound rather than unitary structure (an option never presented in three years of botany classes). I was very fortunate that Mike's knowledge of plant anatomy enabled him to summarize many of the new concepts. My attention was drawn to Croizat's reference to the origin of ant 'adaptations' in *Cecropia* trees hosting *Azteca* ants that constructed nests within the hollow internode. To access the hollow, the ants chewed a hole through a small localized zone of soft tissue at the top of the internode just below the leaf bud at the base of the next internode. The ants also consumed glycogen rich bodies produced at the base of the leaves.

The prevailing theory for the evolution of specialized insect-plant relationships viewed the

Azteca-Cecropia relationship as mutually beneficial – the ants protecting the plant from herbivores, and the plant providing food and shelter. This mutual benefit was seen as the result of natural selection where the soft tissue region and the food bodies were attributed to random mutations that were somehow (and somehow they ‘knew’ the internode was hollow) selected by the ants. But Croizat pointed out that the location of the soft tissue zone conformed to its origin as the remaining trace of a former branch meristem, and that this process of reduction may go back to the beginnings of angiospermy. In this context the structure was not a random mutation, but the end point of a structural reduction that produced a feature that the ants were able to chew through and enter the internode hollow within.

In August of 1982 I wrote to Daniel Janzen who had published a variety of papers on the evolutionary ecology for this and other ant-plant relationships. There ensued a rather interesting exchange for the next three years. It was interesting (at least for me) to see how our contrasting orthogenetic and selection perspectives played out in our discussion. Not surprisingly we were as far apart at the end as in the beginning, but the exchange was helpful for me to better understand the selection argument for the origin of specialized plant features used by ants. I made two unsuccessful attempts to publish a paper on the contrasting models, but with the sole exception of the botanist Cornelis Berg,

reviewers objected to publication. Interestingly, Berg later collaborated on *Cecropia* with the panbiogeographer Pilar Franco-Rosselli (Franco-Rosselli & Berg 1997).

I was similarly unsuccessful with the journal *Oikos* where I tried to publish a paper critiquing the use of teleological explanations for the evolution of features that appeared to allow plants to survive grazing. I first learned about teleological reasoning and its pervasiveness in evolutionary biology when reading Croizat’s *Space, Time and Form*. I found that evolutionary biologists will insist on its use while at the same time arguing that there is no teleological intent. I realized just how entrenched teleological language was in biology when my *Oikos* paper was rejected because the reviewers did not see that there was any problem in the first place. Nevertheless, purposeful language that still cripples much of modern biology with explanations that Croizat showed to be both unnecessary and nonsensical.

About this time New Zealand panbiogeography was beginning to make its direct appearance in the scientific literature. Robin had already published a critique of vicariance biogeography and Michael was writing a review of Springer’s book on Pacific shore fishes, both appearing in *Systematic Zoology*. Robin then approached George Gibbs about publishing a special issue on Croizat’s panbiogeography and *Principia Botanica* in the journal *Tuatara* published and co-edited by the

Botany (Bruce Sampson) and Zoology departments (George Gibbs) at Victoria University of Wellington. George was agreeable but Bruce found Mike's article on the *Principia* and its critique of traditional botany to be so objectionable that he withdrew involvement. Fortunately George continued to support the project and the volume proceeded towards publication.

My small contribution to this volume emerged from my interest in Croizat's work as a study of evolution rather than as an evolutionary sub discipline. Needless to say, my familiarity with evolution was superficial. Robin pointed out that I had to develop something of substance and this led me to focus on orthogeny or orthogenesis - Croizat's alternative to the conventional theory of natural selection. I was interested in this concept because it addressed the origin of adaptation which was directly relevant to my interpretation and understanding of the insect-plant relationship I was studying.

It was necessary for me to not only grasp the natural selection argument, but also comprehend Croizat's support for the proposition that evolution could take place without differential survival through natural selection. I had never found the selection argument very satisfactory because it was presented in the form of an advantage conferred by a function that could not exist unless the structure itself already existed. The *Tuatara* project was published in 1984 and even though it was entirely the product of student

authors, and on a topic outside traditional evolutionary biology, the issue sold out. Reactions to the subject of panbiogeography from Zoology and Botany department faculty varied. Some were hostile, some were neutral, and some were positive. One geneticist was sympathetic to the orthogenesis concept, the other opposed. Among the other graduate students at Victoria, some were beginning to take an interest.

In collaboration with Ruth Ainsworth, a graduate student in the Zoology Department, a more detailed historical and conceptual description of orthogenesis was submitted to *Systematic Zoology* which was at this time perhaps one of the few major journals in evolutionary biology where the editors encouraged debate between orthodox and unorthodox perspectives. The journal had a strong history of publishing controversial viewpoints, including those of Croizat. The first submission was rejected in early 1984. Of the three reviewers Soren Løvtrup felt that orthogenesis was falsified beyond rescue, while two anonymous reviewers (one we later learned was David Hull) made suggestions for improvements. We acted on those suggestions and submitted a revised paper which was accepted for publication conditional upon addressing points raised by the editor and reviewers. There were two reviewers, one was positive (Peter Bowler) and one neutral (Steven Jay Gould who still had objections but said he could not be bothered to make the effort to further

oppose publication). We made our final corrections and the paper came out in 1985. By coincidence (if there are such things) the same issue also had a paper by Michael Heads on the nature of ancestors that compared Croizat's model of a differentiated ancestor with the Darwinian concept of a homogenous ancestor.

From the late 1970's through the 1980's, publications on panbiogeography accumulated. Papers by Robin initially focused on New Zealand and included critiques of the works of Sir Charles Fleming and Robert McDowall. Later works were to expand to a global perspective, including two book chapters. Michael published a book review on a vicariance approach to Pacific Shore fishes where he pointed out the frequent use of panbiogeographic approaches in correlation fish distributions with tectonics.

In 1984 the Danish lepidopterist Niels Kristensen visited New Zealand to work on micropterygid moths with George Gibbs. As an editor for the journal *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, Niels saw Robin's panbiogeographic work as an opportunity to raise the journal's international profile and he encouraged Robin to submit his paper on the classic problems of southern hemisphere biogeography. But the paper was promptly rejected by the chief editor, S.L. Tuxen, who did not want work referring to Croizat's name to be published in the journal. I remember that Niels was rather stunned by the nature of this rejection, but when he returned to Europe he was able to

arrange for publication of Robin's paper the following year.

During the summers of the late 1980's I worked as a natural history guide for the Westland National Park at Franz Josef located on the tectonic boundary between the Pacific and Gondwanic (Australian) plates. Only 10 km east of the fault was the 3,500 m main divide of the Southern Alps. This region had long been a biogeographic puzzle with curious absences such as *Nothofagus* (the 'beech gap') that were attributed to Pleistocene glaciations wiping out all life so the absences were attributed to the slow pace of dispersal to reoccupy the region. But this explanation left its own puzzles such explaining how seemingly poor dispersers such as giant land snails were able to penetrate the entire region. While working at the park I was allowed to express panbiogeographic perspectives openly and without reprobation. I was even permitted to sell copies of the *Tuatara* special issue on panbiogeography and *Principia Botanica* at the visitor center (which certainly generated considerable surprise by some visiting overseas biologists). The Park administration also kindly afforded me the opportunity to meet the government's Minister of Conservation, the Honourable Helen Clark, during a tour of the region. I showed her biogeographic maps compiled by Michael Heads and she agreed that this approach represented a potentially useful approach to conservation science. But in the absence of subsequent support from her

Department scientists her initial interest was effectively neutralized.

A large carnivorous land snail genus called *Wainuia* that was present along the mountain range in the park caught my attention because it lacked any obvious ability to disperse into the region that would be required by the glacial gap theory. This led to my contacting the Museum of New Zealand (Te Papa) malacologist Frank Climo. I soon learned that he had recently become an enthusiastic panbiogeographic supporter after contact with Robin Craw. Upon my return to Wellington, Frank made the museum's land snail collections available for recording distribution information. There ensued many discussions at the museum on the potential and scope of panbiogeography.

By 1986-1987 there was an increasing number of people (mostly graduate students) interested in, or exploring, panbiogeography. And several published or pending articles were being generated. It was time for a symposium where proponents and critics could gather together and explore the case for or against panbiogeography. This opportunity was made possible because Frank was able to muster administrative support from the museum. The symposium was finally held in August 1987. The day was marked by violent storm which grounded flights from some parts of New Zealand and precluded some key people from attending. Despite this setback there was a full schedule that included critiques (although most opponents

declined to participate) as well as applications of panbiogeographic methods and concepts. The audience numbered about 75 which I view as very respectable given that the event was not under the umbrella of any of the New Zealand science societies.

The next obvious step was to publish the proceedings and, again Frank made this possible by offering his entire annual publications budget and obtaining support for this decision from the museum's director John C. Yaldwyn. The editor of the New Zealand Journal of Zoology, Craig Matthews, was approached about publishing a special issue. Craig understood the controversial nature of the subject but also recognized the potential interest for journal readership. It was agreed that Robin would facilitate peer review and processing of the articles. I contributed two articles, a historical review of panbiogeography in New Zealand, including reference to the early support by paleobotanist Lucy Cranwell in the 1960's, and a critique of the protected areas program of the Department of Conservation. In both instances I was assisted considerably by Robin with information content and analytical advice.

If I had not already dug my professional grave, my conservation paper probably did. The Department of Conservation had recently promoted the Protected Natural Areas Program (PNA) as a new strategy and breakthrough scientific method for the identification and protection of the best representative features of

the natural environment. At an estimated cost of \$30 million dollars (Anonymous 1987) this science program was strongly supported by the conservation and ecology community. In 1988 the New Zealand Ecological Society conference passed a resolution supporting the PNA program and the allocation of resources and permanent staffing (New Zealand Ecological Society Newsletter 52, February 1989).

Conservation was a natural fit as I had developed a strong interest in invertebrate conservation at a time when most of the attention was given to the much smaller diversity of vertebrates. By 1983 I was beginning to examine this subject and I first presented a brief panbiogeographic perspective at a symposium on ecological zones sponsored by the Systematics Association of New Zealand. A future career in conservation biology then seemed the most likely direction for me. Through Robin's exploration of panbiogeography I became aware that the New Zealand approach to conservation theory was highly problematic, particularly when it came to understanding the geographic landscape and the promotion of a New Zealand sense of identity.

With Robin's help I proceeded to present an extensive and detailed scientific argument to show that the units of analysis in PNA were neither natural nor scientifically defensible. I presented an alternative proposal for a panbiogeographic track atlas that would be scientifically valid and cost much less to produce. The problem with this endeavor is that I did not

realize that it would be a pointless exercise. Critiques like this, no matter how well founded, are not going to win friends or influence those who have already committed themselves to existing government projects. So naturally the alternative was ignored.

A second special panbiogeography issue was published in 1988 by the Italian journal *Rivista di Biologia Biology Forum*. In the late 1980's I visited the Honourable Simon Upton, Minister of Science in the National Government. Simon was aware of panbiogeography from Michael Heads and Brian Patrick and they had all participated in a research expedition to the sub Antarctic islands. Given his interest in the natural sciences as well as science in general, it seemed desirable to meet Simon to discuss the conundrum of developing panbiogeography in the face of rejection by most government scientists (pretty much all science in New Zealand was then directly or indirectly funded by the government). Simon informed me that the government was establishing a Foundation for Research, Science and Technology that would provide for competitive funding of all research and that anyone could apply. He thought this might provide an effective solution to our problem.

In July of 1988 I travelled to Venezuela to meet Catalina Croizat (Grehan 2007) and soon after I moved to Vermont to begin a post-doctoral project on the ecology of insect damage and forest decline. From Vermont I submitted three applications to the New Zealand Foundation for

Science and Technology to produce a panbiogeographic conservation atlas. After rejection of the first submission the next two were sequentially revised and improved in response to reviewer objections, but by the third submission it was apparent the project could never be funded. The problem did not lie with practical issues, but with the lack of widespread support among New Zealand ecologists and conservationists (overseas reviewers were always positive, but appeared to carry less authority than local reviewers). Without that support from within the New Zealand science and conservation establishment there was no way a 'competitive' panbiogeography grant application could ever be 'competitive'. A competitive program might be effective when all submissions share the same paradigm, but the system was ill prepared for competing paradigms.

I made one last effort with a new program called the Marsden Fund that was supposed to target innovative approaches but the outcome was the same. I finally gave up, although I am ever grateful to my colleagues for their support and involvement, particularly to Robin for help molding the content and to Ian Henderson for obtaining the support of the Biology Department at Massey University to house and administer the project. This failure ended my efforts to find a place for panbiogeography within New Zealand. I did express my frustration to Mr. Upton, but he said that once the government established a process it could no longer be involved or express any

influence. I guess I was a slow learner when it came to the realities of changing institutions. I now realize I had embarked on a futile exercise that was entirely counter-productive to having a science career in New Zealand. I now had to look to different horizons (see Part II in the next issue).

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John Grehan

Independent researcher

calabar.john@gmail.com