Evolutionary Stasis and Change in the Dominican Republic Neogene

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Evolutionary Stasis and Change in the Dominican Republic Neogene

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Preface

Science is supposedly ultimately constrained by the nature of the physical world, meaning that changes in scientific methods and practice are supposed to be away from those with less utility and toward those that are more revealing, useful, and productive of insights into the nature of that world. In practice, however, science is no less susceptible to fads, culture shifts, and pendulum swings than any other realm of human endeavor. This is an especially important feature of science to keep in mind in the present climate of shrinking government funding (at least in proportion to the demand) and the resulting susceptibility of individual scientists and entire disciplines to being influenced by the changing priorities of funding agencies (even if, as such agencies maintain, those priorities come ultimately “from the community”). The present volume is in several important respects a testimonial to both the threats and opportunities that such scientific culture swings pose, both for the individual researcher and a wider field.

When scientific research in the Dominican Republic Neogene began more than a century ago, paleontology was an essentially descriptive discipline, focused mainly on finding, describing, and documenting the taxa represented in the fossil record, and (especially in invertebrate paleontology) on using these taxa for biostratigraphic correlation. Despite the successful integration of paleontology into the Modern Evolutionary Synthesis in the middle of the twentieth century (Simpson, 1944, 1953; Jepsen et al., 1949; Gould, 1983), the vast majority of paleontological research continued in this tradition, and most paleontological papers – including the fundamental works on the Dominican Neogene – were some version of “a new X from the Y of Z-land” (Gould, 1989:114).

The structure of paleontology, at least in the U.S., began to change in the late 1960s and early 1970s in association with at least three significant developments, each of which was to have significant influence on paleontological research in the Dominican Republic Neogene. The first was an increased interest in the ecology of fossil taxa (in addition to simply using fossils for paleoenvironmental reconstruction). There was a burst of research activity around this new slant on “paleoecology” as a new generation of paleontologists sought to interpret fossil assemblages by close comparison with living communities. Although by the early 1980s this research program had lost much of its focus, it did produce some innovative and lasting contributions, including attempts at documenting long-term patterns of biological communities in the shallow ocean (Allmon and Bottjer, 2001).

The second major development was the Deep Sea Drilling Project (DSDP) (see, e.g., Hsu, 1992; Corfield, 2001). This enormous (and well-funded) project was influential to paleontology in two significant ways. Scientifically it provided both abundant new data and a new temporal and (in many ways) intellectual framework for applying fossils to answering questions of Earth history, including climate, sea-level, temperature, and ocean circulation and nutrient status. Although it was concerned almost exclusively with microfossils, the DSDP clearly demonstrated the unique value of paleontology to reconstructing the biotic and abiotic environment in a modern high-tech scientific context. Methodologically, it also demonstrated – not least to paleontologists themselves – how paleontology could be an integral part of large-scale, multidisciplinary "big science".

The third development was the percolation of aspirations among the younger generation of paleontologists to contribute in substantive and unique ways not just to geology but to evolutionary biology. These stirrings led to what became known broadly as "paleobiology", a major subfield of which became devoted to the compilation of taxonomic data from the literature, a research program that came to be known as "quantitative" or "analytical" paleobiology (Gilinsky and Signor, 1991; Sepkoski, 2005). This and related research programs emphasized theoretic over descriptive approaches and new methods of analysis of existing systematic data from the fossil record as much or more than the acquisition of new data. It brought paleontology to the "high table" of evolutionary theory (Maynard Smith, 1984; Eldredge, 1995), and – intentionally or not – it diminished the status of traditional descriptive systematics for its own sake.

The lessons and implications of the first two of these developments – the DSDP and paleoecology – were not lost on the founders of the Dominican Republic Project (DRP). In the late 1970s this group concluded that land-based, macropaleontology could benefit from a DSDP-style, large-scale, international, multi-investigator approach to creating and compiling taxonomic, stratigraphic, and paleoecological data (Saunders et al., 1986; Jung, 1993). At the core of the new project were two main ideas. First was an emphasis on a rigorous stratigraphic and sampling protocol that would be used by all project participants. This would, the organizers thought, avoid many of the biases inherent in different investigator's styles of sampling, and would allow data from many researchers to be readily compiled and compared. Second was the decision to distribute sorted samples to systematic specialists around the world. This would, thought the project leaders, bring to bear a much more powerful set of specialists than would be possible with only one or a very few systematists.

With the benefit of almost 30 years of hindsight, several aspects of the DRP experiment are noteworthy. Most conspicuously, the common stratigraphic and sampling regimes were enormously valuable and used by almost all participants, and provided an excellent model in these respects for the subsequent Panama Paleontology Project (PPP; see Jackson et al., 1996; Collins and Coates, 1999). By comparison, the DRP systematics results were both more and less successful than one might have anticipated or hoped. Although it received significant funding provided by the Swiss National Science Foundation, the DRP never had the financial resources to support the work of the individual systematic researchers who volunteered to take on various taxonomic groups. This inevitably contributed to sometimes lengthy delays in, and sometimes total abandonment of, production of the individual systematic monographs. Although DRP coordinators and collections staff at the Natural History Museum in Basel tried to keep close track of the collections that had been sent out, some were never seen or heard from again. (This experience was not lost on the coordinators of the PPP, who explicitly chose not to distribute material to numerous independent specialists.) Finally, although the DRP organizers certainly envisioned that the data resulting from the project would almost certainly be used for research into broader paleobiological topics, they did not specify in advance what those topics would or should be. Although the DRP was enormously innovative in its approach to centralizing stratigraphy and sampling while decentralizing its systematics, it was, *as a project*, not particularly innovative in the applications of the data that resulted. It was, rather, left to individual researchers to use their or others' data to investigate whatever topic was of interest to them.

Which brings us to the third of those three critical 1970s-era developments in paleontology. As noted by Nehm and Budd in the present volume, many of the subsequent studies that used DRP data were of great significance for areas of paleobiology such as evolutionary tempo and mode and diversity, extinction and turnover. Yet these were not explicitly goals of the project at the outset. In other words, careful attention to making large, well-documented, and well-curated collections within a common, standardized, high-resolution stratigraphic framework made possible the fruitful application of the resulting data to larger theoretic questions. High-quality descriptive paleontology of the "traditional" sort permitted high-quality synthetic paleontology of the newer sort later.

Laudable though this outcome – and its copious illustration in the present volume – is, anyone who has written or reviewed an NSF proposal in the last 20 years knows that something is amiss here. It is almost impossible today to obtain funding for generation of basic systematic data without specifying beforehand to what larger (preferably pressing) theoretic use those data will be put. As an NSF program officer once put it to me, "there is an infinity of groups that need systematic revisions; we can only fund those that are interesting" because they can be used to address an "interesting" question. Thus the fundamental structure of the DRP, the success of which the present volume celebrates, would almost certainly not be fundable in this form by NSF or similar agencies today.

It has been frequently noted that paleontologists are a generally solitary lot, not especially well-suited to the large-scale collaboration and group-think often associated with "big science" projects. Historically, it is often observed, we have mostly pursued research that required relatively little infrastructure, aside from space to store our collections, a library, a microscope, and a means of travel. These attributes have been bemoaned as keeping paleontology out of the "big science" scene. We have, it is said, never "gotten our act together" and "gotten our share of the pie" the way the physicists, astronomers, or genomicists have. The difficulty of getting paleontologists to collaborate on one or a small number of larger topics or problems is highlighted by the multiplicity of national and international meetings and reports, most supported at least in part by NSF, that have attempted over the past couple of decades to chart a common, collaborative, "big-science" research agenda for paleontology (e.g., "Geobiology of Critical Intervals", Stanley et al., 1997; "Paleontology in the 21st Century", Lane et al., 2000; and most recently "Future Research Directions in Paleontology", FRDP, Bottjer, 2007).

It is noteworthy that the big collaborative projects in paleontology that *have* succeeded have been, in large part, not question-based, but (literally) data-based, such as the *Treatise on Invertebrate Paleontology* and the Paleobiology Database. In this context it is interesting that the recent FRDP report (Bottjer, 2007) includes as one of its five major objectives "Database and Museum Collection Development and Integration". The authors of the FRDP write: "Museum collections, databases and informatics are an integral part of the infrastructure of paleontology at present, and will continue to be so into the future. In order to be dynamic and useful resources, both require long-term support. Further, these two infrastructural resources are quite naturally complementary and interlinked. … Databases and museums undergird integrative multiuser research initiatives as well as individual projects. Being able to combine different datasets provides opportunities to ask new and more widely ranging questions in deep time studies. … Thus, both require long-term support and stability."

The present volume supports this objective and demonstrates the profound utility of well-coordinated data supported by carefully-collected and well-curated collections, and the editors have gone to considerable lengths to emphasize these themes. I suggest, however, that we might take this lesson even more seriously. As a discipline, paleontology might recognize, reiterate, and celebrate that "big paleontology" cannot be successfully modeled closely after "big physics" or "big astronomy" or "big molecular biology". Our major collaborations appear to be most fruitful in the coordination and assembling of large data sets, not necessarily in their interpretation around a narrow predetermined set of large or "important" questions. The actual generation of much of our data, especially systematics, and its application to questions about the history of the Earth and its life appear to require the dedicated attention of one or a very small number of individual researchers.

This does not make our science less than physics, astronomy, or genomics; it makes it different. It means that more projects like the DRP are needed – applied to both new field collections and existing museum collections (Jackson and Johnson, 2001; Allmon, 2005) – in order to generate and make available large quantities of new, high-quality systematic, stratigraphic, and paleoecologic data. It may be that the precise questions to which these data can be applied cannot now be specified. But that does not mean that the data are and will not be valuable. Indeed, many questions will not occur to us until the data are generated.

Finally, it should be noted that the DRP was and is a truly international, multi-institutional effort, involving museums, universities, and numerous individual researchers, including a number of Ph.D. students. The project was begun by Swiss paleontologists, and soon involved scientists from Tulane University, and eventually from dozens of other institutions around the world. In this context, I cannot help but note with pride (albeit more of the kind felt by the fan on the sidelines than of the player in the game) the prominent role that the Paleontological Research Institution (PRI) has played in this story since the early twentieth century. PRI's founder, Cornell professor Gilbert Harris, was the major advisor of Carlotta Maury, who conducted the first comprehensive overview of the macrofauna of the Cibao Valley, and published it in her landmark monograph (Maury, 1917a,b). Her collections remain today at PRI. When the DRP was started in the late 1970s, its architects chose PRI as the publisher of its systematic monographs in its journal, *Bulletins of American Paleontology*. To date, 22 such contributions have appeared, and more are in press and in preparation. With the retirement of Emily Vokes from Tulane in 1995 the large collections of Dominican fossils that she had assembled with her late husband Harold over more than three decades came to PRI. The involvement of a small museum in upstate New York in a project organized by a major European museum and a husband-and-wife academic team at a private university in Louisiana – now taken over by a new generation of researchers at an even more far-flung spectrum of institutions – is perhaps a fitting testament to how paleontology at its best (big, small, or otherwise) works.

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Chapter 1
Palaeobiological Research in the Cibao Valley of the Northern Dominican Republic

Ross H. Nehm[1] and Ann F. Budd[2]

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1.1 Introduction

The Cibao Valley of the northern Dominican Republic has been of great interest to geoscientists for more than a century because its rich fossil fauna, temporally long-ranging sections, and geographically widespread exposures collectively provide an excellent system for innovative palaeobiological research. In order to provide context for the research studies presented in this volume, we begin with a brief overview of the history of palaeobiological research in the Cibao Valley of the Dominican Republic from the 1800s to the present. Subsequently, we summarize new research on the DR Neogene in this volume as well as new educational efforts and infrastructure that have been developed to strengthen and support the evolution of this international research effort.

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1.2 Overview of Past Palaeobiological Research in the Cibao Valley

The Tainos, the indigenous inhabitants of Hispaniola, used the word "Cibao" to describe the rocky lands of the island's central mountain range. Today "Cibao" is used primarily to describe the fertile valley bordered on the north by the Cordillera Septentrional and on the south by the Cordillera Central. The Río Yaque del Norte bisects the valley along its east-west axis and drains westward towards Monte Cristi and into the Caribbean Sea. A series of north-south trending rivers (e.g., the Río Cana, Río Gurabo, and Río Mao) connect to the Río Yaque del Norte. It is these rivers that have collectively exposed the several thousand meters of fossil-rich sedimentary rock that have been the focus of palaeobiological inquiry for more than a century (Fig. 1.1).

Research in the Cibao Valley by European and North American scientists began in the mid-1800s. The first studies were very small in scope and involved single scientists

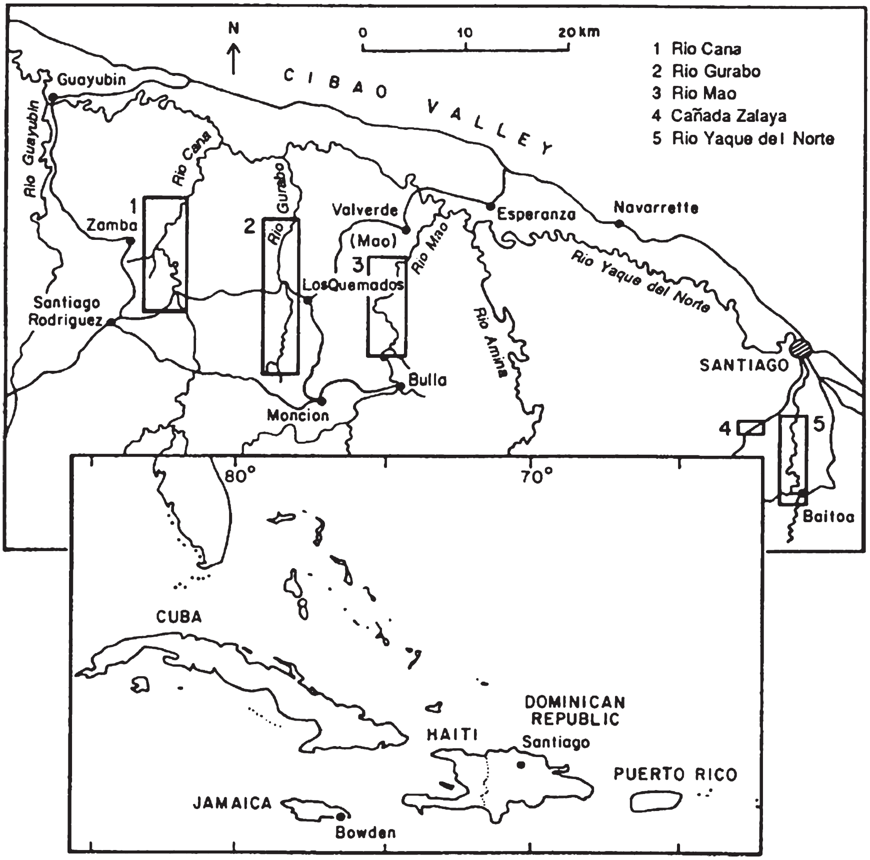

Fig. 1.1 Map of the Cibao Valley of the Northern Dominican Republic, with major river sections encompassed by boxes (Modified from Nehm and Geary, 1994)

rather than collaborative research teams. In the 1850s a series of papers by G.B. Sowerby II (1850), Lonsdale (1853), and Heneken (1853) described some of the first localities and fossil invertebrate species from the region. Duncan (1864) described 27 species of corals in the Heneken collections from the Dominican Republic, 20 of which were new. He also described two new genera: *Antillia* and *Teleiophyllia* (=*Manicina*). Type specimens were deposited in the Natural History Museum in London, UK. Eighteen of the new species are zooxanthellate corals, including three species of *Placocyathus*, two of *Stylophora*, one of *Dichocoenia*, three of *Antillia* (one of which is currently *Trachyphyllia bilobata*), two of *Teleiophyllia* (= *Manicina*), one of *Meandrina*, four of *Plesiastrea* (including two currently assigned to *Solenastrea*, one to *Stephanocoenia*, and one to *Montastraea*), one of *Siderastrea*, and one of *Pocillopora*. Three additional species were described in Duncan (1868). Vaughan (1919) later revised Duncan's names, finding a total of 28 species. Work on molluscs continued with Gabb (1873), Pilsbury and Johnson (1917), and Pilsbury (1922). But the most comprehensive work on the geology and fossils of the Cibao Valley in the early 20th century was conducted by Carlotta Joaquin Maury (Fig. 1.2).

Fig. 1.2 Major scientists instrumental in the development of the Dominican Republic Neogene as a palaeobiological research system. Top row, left to right: Carlotta Maury, T.W. Vaughan, and Peter Jung. Bottom row, left to right: John Saunders, Harold Vokes, and Emily Vokes

Maury was the first scientist to conduct a comprehensive overview of the fossils that occur in the layers of rock exposed by rivers in the Cibao Valley. Her tumultuous expedition of 1916 (during the Dominican revolution and American military invasion) involved collecting and identifying hundreds of new species of molluscs and many other invertebrates. Maury also revised estimates of the geological age of the sedimentary rocks and redefined geological formations. Dr. Maury is also noteworthy in being one of few women from the turn of the century to complete a doctorate in the sciences (at Cornell University) and be employed as a professional scientist. Her 1917 study is a classic reference that is still used today by mollusc researchers. Vaughan (1919) studied the corals in her collections and provided a chart listing the occurrences of coral species in each of Maury's zonal units.

Following the US invasion, T.W. Vaughan and his associates from the US Geological Survey conducted a major reconnaissance study of the general geology, stratigraphy, and economic geology of the Dominican Republic, including the regions of Cordillera Septentrional, Samaná Peninsula, Cibao Valley, Cordillera Central, as well as additional regions in the southern part of the country. Their work resulted in a 268 page memoir (Vaughan et al., 1921), two chapters of which have been particularly relevant to subsequent palaeontological studies of the Cibao Valley (chapter 4 by Wythe Cooke on geology and geologic history, and chapter 6 by T.W. Vaughan and W.P. Woodring on stratigraphic palaeontology). Chapter 6 of the memoir provides detailed descriptions of localities and faunal lists, including foraminifera, corals, bryozoans, molluscs, crustaceans, and echinoids, thereby setting the stage for the studies of systematics and palaeoecology in the present volume. Vaughan and Hoffmeister (1925) later described nine coral species based on the Gabb collections, all of which were new.

A series of other revisions of the ages and nomenclature of the Cibao sections were made by Maury (1929, 1931), Weyl (1940, 1966), Bermudez (1949), Butterlin (1954), Ramirez (1956), Van den Bold (1968, 1969), Bowin (1966), and Seiglie (1978) (see also McNeill et al., this volume). In 1961, Pflug illustrated and updated the scientific names of many of the species descriptions of Sowerby's Dominican fossil molluscs.

By the 1970s, Harold and Emily Vokes of Tulane University were working on the living and extinct molluscs of the Caribbean region (Vokes, 1979). Their field research efforts produced major new collections of mollusc material from the Cibao Valley (and elsewhere in the Caribbean) that remain of considerable importance (now housed at the Palaeontological Research Institution in Ithaca, New York). Unbeknownst to the Vokeses, a group of European scientists were planning a large-scale research project to resample, map, and study the fossil rich sedimentary rocks of the Cibao Valley. The two groups joined forces in the late 1970s and established the Dominican Republic Project (DRP), which moved our understanding of the system forward considerably.

To understand how and why the Dominican Republic Project progressed in the way it has, it is important to note how scientific research itself has changed over the past several decades. In some respects, the DRP was a harbinger of future geoscience research efforts. Today, large-scale, interdisciplinary, and international scientific research projects such as the Deep Sea Drilling Project in oceanography or the Human Genome Project in molecular biology are becoming increasingly common. By the 1970s, scientists in many fields were beginning to recognize that the amount of information, number of research methods, and range of specialties had increased to such a degree that it was difficult for a single scientist to possess the methodological tools and conceptual knowledge necessary for addressing many research questions. The recognition emerged that collaborative teams focused on the same research questions, but specializing in different subfields, could collectively test scientific hypotheses more accurately, efficiently, and economically. The DRP was one of the first multidisciplinary and international research projects in the field of palaeobiology.

In the mid-1970s, a group of European scientists (Peter Jung, macropalaeontologist, Switzerland; John Saunders, geologist and micropalaeontologist, England; and Bernard Biju-Duval, geologist, France) began planning a large-scale research project to resample the invertebrates of the Cibao Valley, re-map the region, and measure the stratigraphic sections with greater precision. The founders of the DRP embraced a collaborative approach to doing science. In order to understand the Cibao Valley system, many specialists were clearly necessary, including field geologists, geochronologists, stratigraphers, palaeobiologists, systematists, and evolutionary biologists. It is difficult, if not impossible, for any single researcher to have the breadth of knowledge to accomplish all of these goals.

The European team planned to precisely determine the ages of the sections, employ more appropriate sampling methods, and record locality information in greater detail by relying on different specialists. Each year from 1977 to 1980 Saunders, Jung, and Biju-Duval were joined in the field by several other scientists and Dominicans from nearby communities (see Saunders, Jung, and Biju-Duval, 1986, p. 9). A total of about 50 people were involved in the collection of fossil samples. Many of the river exposures that were studied are very remote and could only be reached on foot or on horseback. (Even today, burros are needed to help carry samples out of the river valleys).

The DRP field teams collected approximately 300 samples for macrofossil study and 500 samples for microfossil study. Overall, these samples contained millions of invertebrate specimens from several tons of material. These samples were sent to the Naturhistorishes Museum Basel (NMB) Switzerland for processing, sorting, identification, and curation. The results of many years of field research were published in the "Red Book" (Saunders, Jung, and Biju-Duval, 1986). It contains a series of detailed maps of collecting localities throughout the Cibao Valley, many of which are referenced throughout this volume.

Because the DRP field team collected considerably more material than Maury or any of the other scientists who had worked in the Cibao Valley previously, many new species of invertebrates (especially corals and molluscs) were discovered. In addition, larger sample sizes were now available to (1) explore morphological variability within and among species, (2) examine variation in relation to palaeoenvironmental and lithological variables, and (3) subsequently refine species definitions made by previous workers (e.g., Sowerby, Gabb, Pflug, etc.). The extensive sampling by the DRP team also produced specimens from previously unsampled times and locations, producing more accurate and precise spatial and temporal distributions of taxa.

The Swiss team recognized that in order to identify taxa accurately, and diagnose new species appropriately, it was necessary to send collections of sorted specimens to biologists or palaeobiologists who were specialists in particular invertebrate groups. When scientists and staff at the Naturhistorisches Museum

Basel finished processing the field samples, the specimens were sent to experts from around the world. Unfortunately, there are not enough trained systematists with knowledge about invertebrate biodiversity, so many groups remain unstudied and unknown to science. Nevertheless, those systematists who participated in the project spent many years working on the samples, comparing them to other living and fossil species, and visiting museums around the world to ensure that the scientific names assigned to the specimens were correct. Once the experts identified the specimens to the species level, and performed systematic revisions, these data could be used in geographic and temporal analyses of taxonomic distributions in the Cibao Valley and elsewhere. This information was then combined with data from other studies in order to determine where else Dominican species lived in the past and if these species are living in the Caribbean Sea today.

Many systematists have published these results in the journal *Bulletins of American Palaeontology*. Currently, 22 systematic monographs on Dominican taxa have been completed (Table 1.1). After publication, the fossil material used in the

Table 1.1 Monographs in the *Bulletins of American Palaeontology* series "Neogene Palaeontology in the northern Dominican Republic"

Series #	Year	Topic	Authors
1	1986	Field surveys, lithology, environment, and age	Saunders, J., Jung P. and Biju-Duval B.
2	1986	Genus *Strombina*	Jung, P.
3	1986	Family Poritidae	Foster, A.B.
4	1987	Genus *Stephanocoenia*	Foster, A.B.
5	1987	Suborders Caryophylliina and Dendrophylliina	Caims, S.D. and Wells J.W.
6	1987	Phylum Brachipoda	Logan, A.
7	1988	Subclass Ostracoda	van den Bold, W.A.
8	1989	Family Muricidae	Vokes, E.H.
9	1989	Family Cardiidae	Vokes, H.E.
10	1990	Family Cancellaridae	Jung, P. and Petit R.E.
11	1991	Family Faviidae (Part I)	Budd, A.F.
12	1992	Genus *Spondylus*	Vokes, H.E. and Vokes E.H.
13	1992	Class Echinoidea	Kier, P.M.
14	1992	Otoliths of teleostean fishes	Nolf, D. and Stringer G.L.
15	1994	Genera *Columbella, Eurypyrene, Parametaria, Conella, Nitidella* and *Metulella*.	Jung, P
16	1996	Family Corbulidae	Anderson, L.C.
17	1996	Families Cuspidariidae and Verticordiidae	Jung, P.
18	1998	Superfamily Volutacea	Vokes, E.H.
19	1999	Family Faviidae (Part II)	Budd, A.F. and Johnson K.G.
20	2000	The Family Agariciidae	Stemann, T.A.
21	2001a	Genus *Prunum*	Nehm, R.H.
22	2001	Family Neritidae	Costa, F.H.A., Nehm R.H. and Hickman C.S.

studies was returned to the Naturhistorisches Museum Basel in Switzerland. To date, more than 300 Dominican invertebrate species have been studied in great detail (taxonomically, stratigraphically, and ecologically) by systematists who are experts on their respective biological groups. We know of no other geological research system that offers *species-level* data of this quality. These data form the raw material for many other scientific research questions, as discussed below and in other chapters of this volume.

In addition to basic research on the age, lithology, and environment of the Cibao Valley sections and particular taxonomic groups, additional effort has focused on evolutionary questions (e.g., Cheetham, 1987; Cheetham et al., 2001; Nehm, 2001a, b, c, d, 2005; Budd et al., 1996; Budd, 2000; Costa et al., 2001). For example, Dominican invertebrate groups have been used in several detailed quantitative analyses of evolutionary change (e.g., Cheetham, 1986, 1987; Nehm and Geary, 1994; Anderson, 1994; Nehm, 2001a, b, c, d; Cheetham and Jackson, 1996; Marshall, 1995). Some of these studies (e.g., Cheetham, 1986, 1987) figure prominently in evolutionary biology textbooks as benchmark cases of punctuated equilibrium (for example, see Futuyma, 1998). Additionally, speciation research in the Dominican Republic is important because the DRP is one of only a few research systems in the world where several unambiguous cases of morphological stasis and punctuated speciation in multiple lineages of invertebrate animals are known to occur (Cheetham, 1986, 1987; Nehm and Geary, 1994). Finally, the Dominican Republic Neogene provides an important window into the biodiversity of the Caribbean region prior to the Plio-Pleistocene mass extinction (Allmon et al., 1993) (see Table 1.2 for a list of major studies).

The first major attempt at synthesizing DRP research was a symposium organized by Nehm and Budd and held at the 2001 North American Palaeontological Convention (NAPC) in Berkeley, California. This symposium (Species-level and Community-level Stability: Case Studies from the Dominican Republic Neogene) brought together researchers from around the world, reviewed what we had learned in the past 20 years, and included examples of how the DRP research system could be used to address new questions in ecology and evolution. The present edited volume is an outgrowth of that symposium, and summarizes ongoing collaborative research that is currently being conducted as part of a new phase of the DRP.

1.3 Review of Chapters in this Volume

1.3.1 Geology, Paleoenvironment and Taphonomy

The first set of chapters, by McNeill et al., Dennison et al., and Nehm and Hickman, explore geological, palaeoenvironmental, and taphonomic issues relating to the Cibao Valley sections. Of particular importance is McNeill et al.'s revised temporal framework for the Río Cana and Río Gurabo sections, which has been incorporated

Table 1.2 A summary of published palaeobiological research studies employing the Dominican Republic Neogene

Topic	Taxon	Year	Authors
Evolutionary stasis and change	Bryozoa	1986	Cheetham, A.H.
	Coral	1986	Foster, A.B.
	Coral	1987	Foster, A.B.
	Bryozoa	1987	Cheetham, A.H.
	Coral	1988	Budd, A.F.
	Bryozoa	1999	Jackson, J.B.C. and Cheetham, A.H.
	Coral	1990	Budd, A.F.
	Coral	1991	Budd, A.F.
	Bryozoa	1994	Jackson, J.B.C. and Cheetham, A.H.
	Gastropoda	1994	Nehm, R.H. and Geary, D.H.
	Bryozoa	1995	Cheetham, A.H. and Jackson, J.B.C.
	Gastropoda	2001a	Nehm, R.H.
	Gastropoda	2005	Nehm, R.H.
	Bryozoa	2007	Cheetham, A.H. et al.
Environment and evolution	Coral	1990	Budd, A.F.
	Gastropoda	1991	Budd, A.F. and Johnson, K.G.
	Coral	1993	Budd, A.F.
	Bivalvia	1994	Anderson, L.C.
Diversity, extinction, and turnover	Coral	1995	Johnson, K.G. et al.
	Coral	1996	Budd, A.F., Johnson, K.G. and Stemann, T.A.
	Coral	1996	Budd, A.F. et al.
	Bryozoa	1996	Cheetham, A.H. and Jackson, J.B.C.
	Coral	1997	Budd, A.F. and Johnson, K.G.
	Bryozoa	1998	Cheetham, A.H. and Jackson, J.B.C.
	Coral	1999	Budd, A.F. and Johnson, K.G.
	Bryozoa	1999	Cheetham, A.H. et al.
	Coral	2000	Jackson, J.B.C. and Johnson, K.G.
	Coral	2000	Budd, A.F.
	Coral	2001	Budd, A.F. and Johnson, K.G.
	Coral	2003	Klaus, J.S., and Budd, A.F.
Development and evolution	Coral	1983	Foster, A.B.
	Coral	1988	Foster, A.B. et al.
	Bryozoa	2001	Cheetham, A.H. et al.
	Gastropoda	2001b	Nehm, R.H.
	Gastropoda	2001c	Nehm, R.H.
Community evolution	Coral	2003	Klaus, J. and Budd, A.F.
	Coral	1996	Jackson, J.B.C. et al.
Biogeography	Coral	1989	Budd, A.F.
	Coral	1994	Budd, A.F. and Guzman, H.
Phylogeny reconstruction	Coral	1993	Potts, D.C. et al.
	Bryozoa	1994	Jackson, J.B.C. and Cheetham, A.H.
	Coral	2001	Budd, A.F. and Klaus, J.

in all subsequent chapters. The newly reported age dates are not only more tightly constrained but they also suggest that the lower portions of the Río Gurabo and Río Cana sections are considerably younger than previously interpreted (see also Johnson et al., this volume). McNeill et al. review basic background information about the geologic setting and regional stratigraphy of the Cibao Valley and provide a historical overview of past stratigraphic research. They describe how the observed patterns are related to changes in climate and sea level as well as closure of the Central American isthmus. Their interpretations of water depth in the Mao Formation differ significantly from previous work in that a shallowing upward trend is detected which corresponds with the onset of Northern Hemisphere glaciation.

As a first step toward better understanding the link between changing environmental conditions and shallow marine species diversity, Denniston et al. construct carbon and oxygen isotope and Sr/Ca profiles from an exceptionally well-preserved coral collected along Rio Gurabo in the Gurabo Formation. Stable isotope ratios reveal well-behaved sinusoids, indicating primary isotopic signals, but their attempts to deconvolve subannual salinity and sea surface temperature ranges were hampered by the poor fit of modern Sr/Ca-SST relationships to their Miocene coral. The oxygen isotope ratios, if assumed to represent water temperature alone, suggest a seasonal range of approximately 2°C.

Despite growing interest in the effects of taphonomic processes on palaeobiological patterns (Kidwell, 2001), little work has investigated these relationships in the DR Neogene. Nehm and Hickman use the unique morphological attributes of turbinid gastropod species—each animal possesses two skeletal hardparts (shell and operculum) with different preservation potentials—to investigate and compare palaeobiological signals using the two structures in the Río Cana and Gurabo sections. They reject the hypothesis that shells and opercula from the same species produce similar measures of diversity, abundance, and stratigraphic range. If turbinid shells alone had been studied, abundance would have been underestimated by 75% and species richness would have been underestimated by 60%. Although they found that significantly fewer shells were preserved and/or sampled than opercula, studies of size patterns in shells and opercula were similar. Their broadest finding is that "taphonomic extrapolation" between morphologically similar objects may be problematic: they find that unique biological and ecological factors likely influence palaeobiological signals to an equal or greater extent than physical biostratinomic processes. Clearly, much greater consideration of taphonomic processes is necessary in the DR and perhaps other regions.

1.3.2 Species-Level Patterns of Evolutionary Stasis and Change

Four chapters in this volume focus on patterns of evolutionary stasis and change in coral and mollusc species: Budd and Klaus, Schultz and Budd, Beck and Budd, and Nehm.

Budd and Klaus examine evolutionary patterns within an ecologically dominant species complex of reef corals, the *Montastaea "annularis"* complex, which is widely distributed across the Caribbean today. Using both a geometric morphometric dataset and a dataset consisting of traditional linear measurements, they perform a series of canonical discriminant analyses to recognize species, trace their stratigraphic distributions, and examine morphologic change within the complex as a whole and within individual species. The results show that a total of eight species existed in the northern Dominican Republic during the Mio-Pliocene, and that diversity remained roughly constant (3–5 species per formation) through the three Yaque Group formations (Cercado, Gurabo, Mao), covering a time span of approximately 3 million years. This diversity is comparable to that previously observed in the complex both during the Plio-Pleistocene and today. Speciation and extinction rates were approximately 1–2 species per million years through the DR sequence, and the complex as a whole exhibited morphologic stasis. However, morphologic disparity (differences among species) was higher in the Mio-Pliocene than it is today. In contrast, careful examination of one relatively long-ranging species within the complex revealed directional change in some, but not all, species diagnostic morphologic features.

Schultz and Budd expand previous work on the less common *Montastraea "cavernosa"* complex by using larger sample sizes and employing geometric morphometrics in concert with traditional distance measurements. Their study reveals significantly more variation within the complex, three new species, and several very short-lived species. Thus, some of the species delineated by Budd (1991) are likely more than one species. Schultz and Budd's work underscores how systematic work dramatically affects interpretations of stasis and change, and corroborates Jackson and Cheetham's (1999) findings that rigorous taxonomy and splitting morphospecies as finely as possible are essential for testing the theory of punctuated equilibrium.

Beck and Budd's chapter explores evolutionary patterns in the reef coral *Siderastrea* using geometric morphometric and traditional techniques. Unlike the previous two chapters, the four species that are distinguished are discrete and do not overlap, and have relatively long stratigraphic ranges. They find that several species display evolutionary stasis over a period of approximately >5 million years. Methodologically they demonstrate that traditional measures, if used exclusively, may cause the misidentification of colonies and that 2D geometric morphometrics are the most accurate method for species diagnosis.

Nehm focuses on evolutionary stasis and change within species of the abundant and widely distributed *Prunum maoense* group. Because *Prunum* species possess clear morphological markers of adulthood, it was possible to compare equivalent ontogenetic stages through time and space. Morphometric analyses using traditional distance measurements and geometric landmarks produced generally similar evolutionary patterns, with no net morphological change characterizing adults through time. Perhaps the most interesting problem raised by the chapter is the meaning and significance of rare "*P. latissimum*" phenotypes throughout the spatial and temporal range of *P. maoense*. Are these individuals iteratively produced parallelisms arising from the *P. maoense* lineage, or persisting holdouts of the ancestral *P. latissimum* lineage? Nehm discusses the significance of each interpretation for models of species-level change in the fossil record and goes on to argue that such outliers may be crucial for understanding evolutionary stasis.

Previous studies of species-level change in DR invertebrates have indicated that, in general, no long-term directional evolutionary trends occur (Foster, 1986; Cheetham, 1986, 1987; Anderson, 1994; Nehm and Geary, 1994; Nehm, 2001a; Nehm 2005; Cheetham et al., 2007). Overall, the four new studies of species-level stasis and change in this volume generally corroborate these previous findings. More detailed comparisons are problematic, however, due to the different methodological approaches used in these studies. Additionally, reef corals tend to be restricted to a narrow range of environmental conditions and their species are widely distributed across the Caribbean region. They therefore have low numbers of stratigraphic occurrences relative to other taxonomic groups. The question remains as to whether similar processes are responsible for patterns of stasis in corals, mollusks, and bryozoans. One important factor that has received increasing attention in recent years is community-level processes, which are addressed in the next section.

1.3.3 Stability and Change in Coral and Mollusc Assemblages

Coordinated stasis is an observed pattern in which faunal assemblages and their constituent species appear to stay stable for millions of years prior to experiencing rapid faunal turnover. This pattern has generated considerable interest in the palaeontological community, and has been used to hypothesize that community stability and species-level morphological stability may be associated over long time spans (Brett and Baird, 1995; Ivany and Schopf, 1996, and references therein). Considering that species-level stasis characterizes many of the species studied from the DR Neogene (see above), do their associated communities also display stability in time and space?

Reef corals represent one of the best studied faunal groups in the Dominican Republic Neogene. Klaus et al. examine changes in coral communities through the sequence using three different approaches: (1) Persistence of individual species from one formation to the next, (2) quantitative analysis of presence/absence data within 21 lithostratigraphic units, and (3) quantitative analysis of relative abundance data obtained from line transects. The results indicate that 61% of species persist from the oldest to youngest formation in the sequence, and that presence/absences of species do not change through the sequence, suggesting community stasis. However, statistical analyses show that the relative abundances of species and the ecological dominance structures of reef communities (grouped into massive and branching subsets) do in fact change. The abundances of two *Goniopora* species, *Gardineroseris*, and *Montastraea endothecata* decrease through geologic time; whereas the abundances of massive *Porites* and *Montastraea cavernosa* increase. *Pocillopora* decreases in branching coral communities. The observed changes appear to be related to a combination of environmental (both local and regional) and evolutionary factors, leading up to the closure of the Central American Isthmus.

Although the Río Gurabo has figured prominently in studies of evolutionary stasis and change within coral, bryozoan, and mollusc species, little work has explored the associated mollusc assemblages. Rivera et al., like Klaus et al., investigate faunal-level patterns in the Cibao valley sections. Rivera et al. specifically investigate faunal change in mollusc-rich assemblages from the Río Gurabo section and find that the assemblages display considerable variability in composition, relative abundance, species richness, and trophic distributions through time. As the authors note, their study of >16,000 individuals from more than 300 species encompasses only a small portion of the exposed section, and consequently it will be necessary to study other portions of the section before a complete understanding of faunal change within Río Gurabo is attained. Nevertheless, Rivera et al. do demonstrate that significant faunal differences characterize the lower and upper regions of the section. Expansion of their work should be able to provide a more precise analysis of the relationships between species-level and community-level change throughout this important section.

Johnson et al.'s study is of the broadest scale in this volume, and tests: (1) the effects of revised age dates (based on McNeill et al., this volume) on the timing and magnitude of origination and extinction events in the Caribbean reef coral fauna as a whole, and its patterns of diversity through time, and (2) the importance of the DR fossil reef coral occurrences in general in understanding origination and extinction events in Neogene Caribbean reef corals, as well as their patterns of diversity through time. Comparisons of first occurrences in the DR based on old and new age dates reveal a shift in regional first occurrences from 7–9 Ma to 5–7 Ma using new age dates, and an unrecognized sampling gap across the Caribbean during the late Miocene. These patterns are further accentuated when the DR reef coral occurrences are excluded altogether from the database. In contrast, excluding occurrences from the Plio-Pleistocene Limon Basin of Costa Rica resulted in only minor change in the timing of origination and extinction events, although they do affect estimates of the magnitude of Plio-Pleistocene extinction. The study attests to the importance of incorporating multiple taxonomic and stratigraphic interpretations into palaeontological databases, and comparing analyses using data based on different interpretations.

1.3.4 Education and Infrastructure

The final two chapters of this volume focus on the importance of education and infrastructure in international multidisciplinary research and development. In a departure from the science research focus of other chapters, Nehm, Luna, and Budd discuss two science education projects closely tied to the Dominican Republic Project: (1) Science education in US schools with predominantly

Dominican American students, and (2) international outreach and development work with Dominican undergraduates. Both projects were spurred by the recognition that the persistent lack of Dominican and Dominican American involvement in the DR project over the past 30 years would require new approaches and greater attention to outreach. The chapter begins with a review of four interrelated DRP science education efforts with Dominican American students: (1) 'Funds of knowledge' research relating to 'sense of place' in immigrant secondary students; (2) development of curricula and resources relating to the DRP; (3) science teacher professional development; and (4) involvement of Dominican American middle school, high school, and college students and teachers in DRP research projects. The chapter continues with an overview of two workshops for Dominican undergraduates. The goal of the first workshop (based in Santo Domingo) was to demonstrate how studies of fossil reef systems, thousands to millions of years old, are relevant to addressing modern-day issues in reef conservation. The second workshop (based in Mao) trained students and researchers in collection care and management, including preventive conservation, collection organization, and data preservation and management. Overall, the chapter highlights the importance of science education in the development and maintenance of successful international science research efforts.

A final goal of this edited volume is to demonstrate the importance of specimen-based research in palaeontology to the study of evolution. As described in McNeill et al. (this volume), one of the chief goals of a new phase of the DR project is to expand collections so that patterns of evolutionary stasis and change can be analyzed within individual lineages, as well as in benthic marine communities. Two important infrastructural components are essential to specimen-based research: (1) museum collections, and (2) databases.

Government agencies and administrators of natural history museums must be made aware of the central importance that care and maintenance of collections play in quality studies of species and communities through geological time. Collections are made during fieldwork and are costly to collect or recollect. They therefore should be maintained and developed for future research. Many collecting sites become inaccessible over time because of building development, access and collecting restrictions, or are collected out (e.g., the NMB localities in the Baitoa Formation along Río Yaque del Norte south of Santiago). As collections develop and grow they contain more material and information than could be collected in a single fieldwork project. This mass of information provides a valuable contribution to, and forms the basis of, many large scale database initiatives and literature-based research, as well as primary research. Collections often contain material that is later recognized or rediscovered as being scientifically important according to research developments. As new research techniques are discovered, collections continue to be important sources of information. In the case of modern endangered species (e.g., corals), use of museum collections reduces the necessity to collect threatened populations and lessens the negative impacts of scientific collecting.

The collections on which the research in this book is based are deposited primarily at the Natural History Museum in Basel, Switzerland (NMB;

http://www.nmb.bs.ch), the Paleontology Repository of the University of Iowa (SUI; http://www.uiow.edu/~geology/paleo), and the Paleontological Research Institution in Ithaca, New York (PRI; http://ww.pri.org). Lists of studied specimens are provided in the appendices to chapters by Budd and Klaus, Schultz and Budd, and Beck and Budd.

Another, equally important infrastructural component of specimen-based research involves databases containing specimen, locality, and taxonomic information and facilitating taxonomic standardization (described by Budd et al., this volume, in the chapter on the NMITA database). Today, databases not only contain the information traditionally held in museum specimen catalogues and locality registers, but they also allow this information to be searchable in many different ways, and make it readily available online to the scientific community. In addition, databases contain the information traditionally assembled by systematists to make specimen identifications, recognize new species, evaluate the status of existing species, and revise higher level classification. They provide a mechanism for standardizing taxonomy so that palaeontological occurrence data can be used to perform spatial and temporal analyses of biodiversity. Moreover, as described in Budd et al. (this volume), taxonomic databases facilitate gathering, organizing, and sorting information that is routinely assembled when preparing a taxonomic monograph. Finally, as demonstrated in Johnson et al. (this volume), modern databases can be designed to allow for multiple interpretations (e.g., multiple alternative identifications for any given specimen, age interpretations for any given stratigraphic unit, and classification systems for higher level taxa). Databases for reef corals (described in Budd et al., this volume) have been developed for: (1) specimen and locality data, and stratigraphic interpretations (Cenozoic Coral Database, 'CCD', in Microsoft Access and available to project members), (2) taxonomic data (Neogene Marine Biota of Tropical America, 'NMITA', in Oracle and available online), and (3) palaeontological occurrence data (Statistical Analysis of Palaeontological Occurrence Data, 'STATPOD', originally in R and available to project members). Queries of the first database provide the foundation for the second and third databases. Information in the second database are shared with other community databases in palaeontology.

1.4 Goals of this Book

The past decade has witnessed the gradual departure of the scientists most instrumental to the development of the Dominican Republic Neogene into a modern palaeobiological research system. The chief architects of the Dominican Republic Project (Peter Jung and John Saunders) have retired, Harold Vokes has passed away, and Emily Vokes has retired. Additionally, the Naturhistorisches Museum Basel, which served as a locus for DR research for the past 30 years, has directed its scientific focus to other topics. In light of these changes, we view this edited volume as a transitional effort that attempts to build an empirical, conceptual, and historical bridge between the accomplishments of past DR project workers and future students, scientists, and research questions.

While past work on the Dominican Republic Neogene has explored a diverse array of palaeobiological questions, this volume demonstrates that many revisions need to be made to our understanding of the geological and palaeoenvironmental framework, and many significant macroevolutionary questions remain to be answered. The expansion of geoscience research to include educational outreach has also fostered the development of two science education projects. We hope that this volume serves as a vehicle for moving research on the Dominican Republic Neogene forward, and provides a useful starting point for the next generation of students and researchers.

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