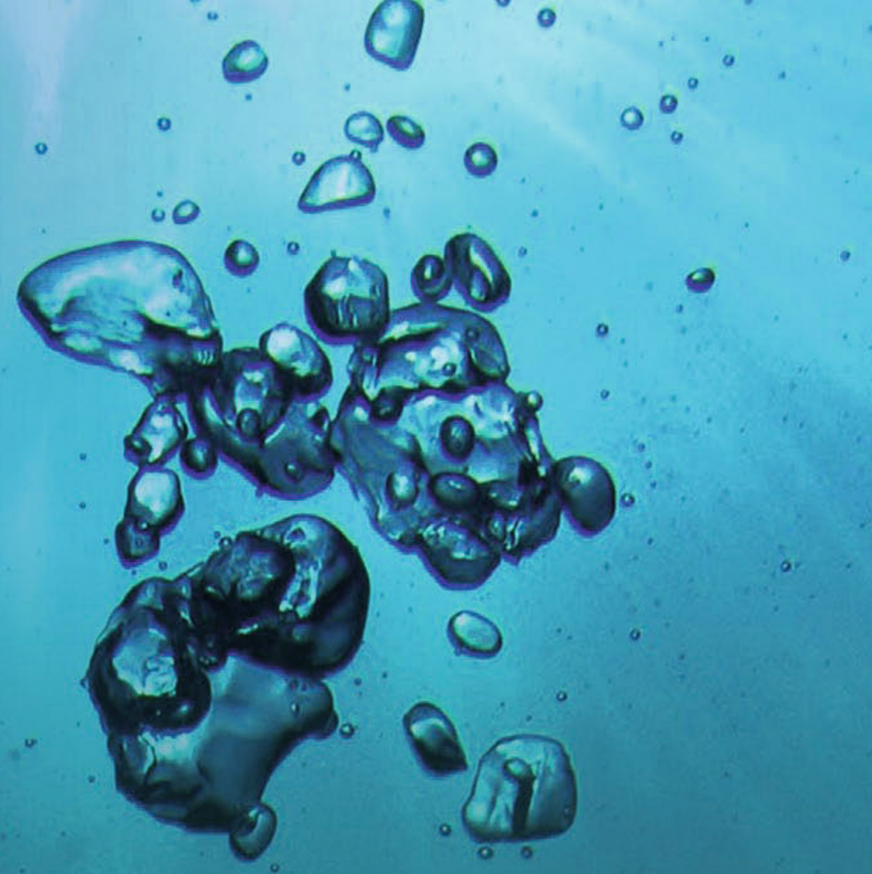
Humanity and the Sea



James Bowen

The Coral Reef Era: From Discovery to Decline

A history of scientific investigation from 1600 to the Anthropocene Epoch

Springer

Humanity and the Sea

Editor
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A&B Word Ltd, Halesworth, Suffolk, United Kingdom

The human race has always depended upon, and gravitated to the borders of the sea, and in times of economic pressure, the sea has perhaps received even enhanced focus. However, the sea's resources are not finite, and the sea, coastal and deep, simply cannot continue to absorb unwanted products of mankind in ever-increasing quantities. The need for better understanding of anthropogenic effects on and the results of uses of the sea has always been important, and is now crucial. This series seeks to address that need for more knowledge and understanding of the sea, and to place at the disposal of decision- and policy-makers, scientists and the educated public, potential and actual stakeholders the crucial information needed to take humanity into the future in a manner that enhances ability to make sound judgement on the use of the sea as a sustainable resource. The resources themselves are not the primary focus of this series, but the system within which they operate is. Consequently, the series will seek to publish regularly quality material related to the effects of marine renewable energy generation, marine spatial planning, including the optimal establishment of special areas of conservation, marine protected areas and no-take zones, climate impacts (including sea-level changes), the ecosystem approach to management (including resource management where appropriate), and the importance of sustainability and in some cases recovery activities back to sustainable levels.

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For those generations of dedicated scientists whose meticulous work in searching for truth and understanding has established the foundation blocks on which this history is based; and for all those who follow in their footsteps.

Preface

The genesis of this book lies in a research project that began 30 years ago. In 1982, I was one of an Australian university team beginning a study of the ecology of sea snakes in the Swain Reefs, the southernmost complex of the Great Barrier Reef some 220 km out to sea. Our days underwater took place in a wonderland of biological diversity with fish in a seemingly infinite variety of colour and species darting in and out of forests of branching, plate and clustering corals, and where Christmas-tree worms and small clams had burrowed into the *Porites* boulder corals. Squid passed overhead occasionally, the inevitable curious reef shark at times stationed itself nearby for a few minutes, later to disappear with a flick of its tail, while with some regularity came the startling experience of a metre-long venomous olive sea snake suddenly rising from below and peering intently into my facemask. Green algae waved in the current and anemone fish kept retreating into their protective refuges. The sandy coral cays, some hundreds of which comprise the Swains, were alive with nesting terns, shearwaters and boobies, and during the warm summers at the time of the full moon, green turtles clambered up the dunes to excavate depressions in which to lay their clutch of some 90 eggs.

Even after decades of diving, I remain fascinated by the beauty and complexity of the marine world, and particularly by the Great Barrier Reef. Throughout the 1970s, it became the scene of the greatest environmental protest movement ever witnessed in Australia after a corrupt Queensland Government had clandestinely leased its entire length in 1968 to six oil corporations for exploratory drilling. As my academic interests lie in the history of philosophical and scientific thought, it was with considerable enthusiasm that I joined the ecology project on the RV *Australiana* to begin research into the complex history of the Great Barrier Reef from its initial charting by James Cook in 1770 to the present day and the later revelations of the Royal Commission that swept the government from office.

As our ship navigated the complexity of islands, cays and shoals, cruise after cruise every semester vacation for several years, I became intrigued to discover that little in the literature dealt specifically with the exciting saga of the scientific quest to investigate and solve the centuries long coral reef enigma. How had dangerous reefs and atolls appeared across the great empty expanses of the Indian and Pacific oceans with their astonishingly diverse range of plants and animals?

By the time my study of the Great Barrier Reef was published in 2002, it had also become distressingly obvious wherever I travelled and dived, and from an increasing volume of disturbing reports appearing in the journals, that coral reefs had been silently but relentlessly degraded during the previous 20 years from rising water temperatures, disease, bleaching and often death. As a result, I believed it was imperative to record those alarming developments during the final decades of the 20th century, and to set them into the broader political context of today.

Essentially, the study is interpretive and begins with the discovery of coral reefs by Europeans, in the sense that "discovery" here means "revealed to knowledge" by early navigators, particularly their natural beauty. In "A Voyage to *Terra Australis*" of 1802, Matthew Flinders described reefs on its eastern coast "glowing under water with vivid tints of every shade betwixt green, purple, brown and white; equalling in beauty and excelling in grandeur the most favourite *parterre* [floral arrangement] of the curious florist". That sense of wonder led investigators over three centuries in Part I into a virtual scientific crusade to uncover every link in the chain of natural creation.

In Part II, the narrative moves to a phase marked by the suggestion of a Swedish chemist in 1896 that noticeable changes in surface temperature apparently affecting climate had been caused by increases in atmospheric carbon dioxide. With the rapid development and employment of carbon fuel technology in the 20th century, the entire world is now becoming overwhelmed by the inexorable processes of climate change. The concluding chapters therefore examine seminal evidence for our unprecedented global predicament, characterized by the progressive disturbance of the biosphere with coral reefs moving into a state of possibly terminal decline in what future generations will know as the Anthropocene Epoch. As civilization has only recently developed in the relatively warm interglacial Holocene Epoch beginning 10,000 years ago, and coral reefs entered our consciousness barely 400 years ago after a few western nations initiated the Age of Discovery, in less than 400 years we may be destroying an irreplaceable natural creation reaching back millions of years.

The Great Barrier Reef lost 50 % of its coral cover during the past 27 years, and although, like so many well-promoted holiday resorts, the atolls of the Tuomotu Archipelago and the volcanic eruptions of the Marquesas Islands of French Polynesia are enticingly beautiful in tourist brochures, beneath the waves are heartbreaking scenes of impoverished marine habitats. The seas of Indonesia, the Philippines, New Caledonia and the Caribbean are an even greater shock to the senses, human pressure in many places having created underwater wastelands. Present evidence indicates that if not by 2050, certainly by the 22nd century, coral reefs as we have known them, and the Great Barrier Reef in particular, may no longer exist, having possibly succumbed to an anthropogenic extinction.

Optimism, however, is still entertained by those scientists who believe that corals have an inherent capacity for survival and evolutionary adaptability, as demonstrated after the Permian Extinction that ended 225 million years ago when tabulate and rugose corals perished, and today's reef-building *Scleractinia* and other hermatypic genera succeeded them. Similar surprises may yet lie ahead, because the "coral reef enigma" was not simply an early impression of investigators, but a characteristic also of the unpredictable repertoire of coral polyp responses themselves.

As we ponder the evidence in the follow pages, it is necessary to remain aware that reefs have become indicators that in present decades signal the end of an environmental era. Consequently, the story of human impact on coral reefs over the past century becomes highly relevant to the need for informed decisive action on the entire range of global issues, because the time most assuredly will soon come when we can procrastinate no longer.

Acknowledgements

Research for this book came from original sources where possible, although those sources had to be selective. Within the extensive literature of the 19th and 20th centuries in particular, containing numerous valuable and exciting scientific reports, only the germane central studies could be examined to record the pattern of discovery. Quotations are almost always from actual texts or facsimiles, with the locus and a translation by the author where not otherwise acknowledged.

Library research was conducted in Canberra at the National Library of Australia and at the Menzies and Life Sciences Libraries of the Australian National University during my time as a Research Fellow at the Centre for Resource and Environment Studies; in the Australian Museum and Mitchell libraries in Sydney; and at the Oxley, Queensland Museum and University of Queensland libraries in Brisbane. In Townsville, the library of the Australian Institute of Marine Science (AIMS) and librarian Mary Anne Temby kindly provided access to the Yonge collection of rare books and the Low Isles Reports. For investigation overseas, valuable assistance came from Christiane Groeben, archivist and librarian of the *Stazione Zoologica di Napoli*, and Hugo Freudenthal in New York concerning his identification of *Symbiodinium microadriaticum*. Steve Coles in Hawaii and Drew Harvell at Cornell University kindly answered relevant questions regarding their research.

My friend Paul Full of Ace Photoshop Digital Imaging in nearby Ballina, New South Wales, prepared the illustrations. Throughout the past decade, essential support and at times enjoyment of the thrill of the chase for elusive sources came from the professional library staff at Southern Cross University, and particularly Sharon Wheeler of Document Supply.

Field research over 25 years began in 1982 on the Great Barrier Reef sea snake ecology project aboard the RV *Australiana* under the command of Max Allen and led by herpetologist Hal Heatwole, now at North Carolina State University. It then continued at AIMS and the Sir George Fisher Centre for Tropical Marine Studies of James Cook University in Townsville, which provided opportunity to study the Crown-of-Thorns outbreaks on the Great Barrier Reef and subsequent episodes of coral bleaching. Field studies were made on Ningaloo and other reefs in the Indian Ocean, but mainly along the Great Barrier Reef from research stations on Heron, One Tree and Orpheus islands. In the Pacific, investigation also extended to Lord Howe Island, New Guinea, New Britain, New Caledonia, Vanuatu and Moorea near Tahiti with CRIOBE (*Centre de Recherches et Observatoire de l'Environnement*) as well as at Fakarava and Rangiroa atolls and the Marquesas volcanic islands of French Polynesia. In the Caribbean, it continued from the Florida Keys to Aruba in the Netherlands Antilles and along the coast of Venezuela.

As every historian knows, the active support and encouragement of colleagues and librarians is essential to field research and writing and it is a huge pleasure to record the contributions of so many to the completion of this project. In particular, I am indebted to my close friends John "Charlie" Veron, former Chief Scientist at AIMS, Ove Hoegh-Guldberg, Head of the Global Change Institute at the University of Queensland and Director of the Heron

Island Research Station, and Clive Wilkinson, Coordinator of the Global Coral Reef Monitoring Network. Laboratory and field assistance was provided on request by many of the staff of AIMS, the Great Barrier Reef Marine Park Authority and the Queensland Parks and Wildlife Service in Cairns, Townsville and the Whitsunday Islands regions.

I also extend my appreciation to Cambridge University Press for their permission to include several abridged and revised passages from my book of 2002 on *The Great Barrier Reef: History, Science, Heritage*, edited by my late wife, scientist and field companion Margarita Bowen.

This work owes much to the support and assistance of my colleague and companion, Mavourna Collits. For several years she worked with me in an editorial role, acted as a sounding board and gave me the encouragement needed to complete the task when it appeared too daunting for me to continue. To her, I extend my sincere thanks.

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October 2012

Addendum James Bowen died suddenly in December 2012, with the manuscript neither edited nor for the most part formally reviewed. Fortunately he had made provision for this eventuality by entrusting to Mavourna Collits the responsibility of providing the balance of editorial effort necessary for its acceptance and publication.

The work was brought to its present state with scientific advice and critical assistance being provided by John "Charlie" Veron, with encouragement and administrative support from Springer Science and Business Media's Publishing Editor, Alexandrine Cheronet, and under the direction of the Humanity and the Sea Series Editor, Andrew I. L. Payne. Of the tasks required for publication, referencing was one of the most challenging; many crucial citations were of an historical nature, and errors and manifold queries had to be addressed without James Bowen's input. Reference checking, formal editing of text and compilation of the index were achieved through the collaborative efforts of the team above; their professionalism and commitment was critical to realizing publication.

The book is a testament to James Bowen's lifetime of scholarship and to his relentless search for truth and understanding that endured right up to his death.

By the Same Author

A History of Western Education (Methuen, London; St Martins, New York)

Volume One: The Ancient World: Orient and Mediterranean, 2000 B.C.—A.D. 1054 (1972)

Volume Two: Civilization of Europe: Sixth to Sixteenth Century (1975)

Volume Three: The Modern West: Europe and the New World (1983) Reprinted 2003 (Routledge, London)

The Great Barrier Reef: History, Science, Heritage (2003) Cambridge University Press, Melbourne and New York

Contents

Acronyms and Abbreviations

AAAS	American Association for the Advancement of Science
ABBs	Algae-based biofuels
ABH	Adaptive bleaching hypothesis
AIMS	Australian Institute of Marine Science
AVHRR	Advanced Very High Resolution Radiometer
BA	Short form of BAAS
BAAS	British Association for the Advancement of Science
BBD	Black band disease (of corals)
^{45}Ca	Radioactive calcium
$^{45}CaCl_2$	Radioactive calcium chloride
$CaCO_3$	Calcium carbonate
$^{14}CO_2$	Radioactive carbon dioxide
CBD	Convention on Biological Diversity
CDR	Carbon dioxide removal
CFC	Chlorofluorocarbons: common forms are CF_2Cl_2 and $CFCl_3$
CH_4	Methane
CH_2O	Carbohydrate
CLIVAR	Climate variation programme
CLO	Chlorine monoxide
CLO_3	Chlorate
CNES	Centre National d'Études Spatiales
CO	Carbon monoxide
CO_2	Carbon dioxide
COADS	Comprehensive Ocean and Atmosphere Data Set
COP	Conference of the Parties
COP 5	Fifth Conference of the Parties
CRTRP	Coral Reef Targeted Research Programme
CRW	Coral Reef Watch
CSIRO	Commonwealth Scientific and Industrial Research Organization
CZAR	Contribution of translocated carbon to animal maintenance respiration
DDT	Dichloro-diphenyl-trichloroethane
DHW	Degree heating weeks
DLR	Deutsches Zentrum für Luft-und-Raumfahrt (German Aerospace Centre)
DNA	Deoxyribonucleic acid
EDF	Environmental Defence Fund
EMBL	Enewetak Marine Biological Laboratory
ENCORE	The effect of nutrient enrichment on coral reefs
ENSO	*El Niño* Southern Oscillation
ERL	Environmental Research Laboratory

ETC	Environment, Technology and Communication Group
FAO	(United Nations) Food and Agriculture Organization
GBR	Great Barrier Reef
GBRMPA	Great Barrier Reef Marine Park Authority
GCRMN	Global Coral Reef Monitoring Network
GDP	Gross domestic product
GHG	Greenhouse gas
GISS	NASA's Goddard Institute for Space Studies
GMO	Genetically modified organism
GCOS	Global Climate Observing System
GOOS	Global Ocean Observing System
GOSIC	Global Observing Systems Information Centre
GRACE	Gravity Recovery and Climate Experiment
GRIP	Greenland Ice Core Project
Gt	Gigatonnes (billion tonnes)
H_2CO_3	Carbonic acid
H_2O	Water
HOME	"Hands off Mother Earth"
HMS	His (Her) Majesty's Ship
IBM	International Business Machines Corporation, now simply IBM
ICA	International Court of Arbitration
ICES	International Council for the Exploration of the Sea
ICLARM	International Centre for Living Aquatic Resources Management
ICOADS	International Comprehensive Ocean and Atmosphere Data Set
ICRS	International Coral Reef Society
ICRI	International Coral Reef Initiative
ICSU	International Council for Science
IGY	International Geophysical Year
IMD	India Meteorological Department
IOC	Intergovernmental Oceanographic Commission
IOD	Indian Ocean Dipole
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for the Conservation of Nature
JAMSTEC	Japanese Agency for Marine-Earth Science and Technology
KNMI	Royal Netherlands Meteorological Institute
LIA	Little Ice Age
LTMP	Long-Term Monitoring Programme of the GBRMPA
LMSL	Local mean sea level
L1	Lagrange Point
MIT	Massachusetts Institute of Technology
MPA	Marine Protected Area
MPML	Mid-Pacific Marine Laboratory
MOC	Meridional Overturning Circulation
Mya	Million years ago
$Na_2{}^{14}CO_3$	Radioactive sodium carbonate
NASA	National Aeronautics and Space Administration
NCAR	National Center for Atmospheric Research
NCDC	National Climate Data Center
NOAA	National Oceanic and Atmospheric Administration
NO_x	Collective term for various nitrogen compounds
N_2O	Nitrous oxide
NTC	Nutrient threshold concentrations
O_2	Oxygen

O_3	Ozone
OPEC	Organization of Petroleum Exporting Countries
OTI	One Tree Island
PCR	Polymerase chain reaction, for DNA analysis
PDO	Pacific Decadal Oscillation
PICES	North Pacific Marine Science Organization
PIRATA	Pilot Research Moored Array in the Tropical Atlantic
PMEL	Pacific Marine Environmental Laboratory
RAMA	Research Moored Array for African–Asian–Australian Monsoon Analysis
RFLP	Restriction fragment length polymorphism
RV	Research vessel
Scuba	Self-contained underwater breathing apparatus
SML	Surface mucopolysaccharide layer
SO_2	Sulphur dioxide
SOI	Southern Oscillation Index
SRM	Solar radiation management
SST	Sea surface temperature
TAO	Tropical Atmosphere Ocean study
THC	Thermohaline circulation
TOGA	Tropical Ocean Global Atmosphere Study
TOPEX	Topography Experiment over the ocean
TWAS	The World Academy of Sciences
UK	United Kingdom of Great Britain and Northern Ireland
UN	United Nations
UNEP	United Nations Environment Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
UNFCCC	United Nations Framework Convention on Climate Change
US(A)	United States (of America)
USCRTF	United States Coral Reef Task force
UV	Ultraviolet
WBD	White band disease (of corals)
WCRP	World Climate Research Programme
WGMS	World Glacier Monitoring Service
WHO	World Health Organization
WMO	World Meteorological Organization
WOCE	World Ocean Circulation Experiment
WRI	World Resources Institute
WWF	World Wildlife Fund

Part I

The Natural History Quest, 1600–1900

The Coral Reef Enigma

1

In the era of imperial expansion during the 16th and 17th centuries when European explorers rounded the Cape of Good Hope and sailed into the Indian and Pacific oceans in search of lands to occupy and exploit, coral reefs were one of their most feared hazards. In those early voyages by small, timber-hulled vessels, navigators were understandably apprehensive about striking unpredictable, almost invisible rock formations that seemingly appeared out of nowhere in the vast open expanses of both oceans to threaten the safety of craft and crew.

Alarming accounts of shipwrecks began to reach Europe in the 17th century that became published in increasing numbers of sensational popular stories of voyages to exotic, faraway lands. Their appeal to eager readers was heightened further by the complete lack of knowledge concerning those submerged formations, and their relationship to all other natural features. They were, quite literally, an enigma whose attempted solution began one of the most amazing quests in the history of science.

Early in the 16th century, the Portuguese had noted one such hazard in the Indian Ocean on their charts as an "abrolhos," a term of obscure origin but believed to have come from an imperative to mariners to keep a close lookout: *abro olhos*, "keep your eyes open!" The exact location of the abrolhos, however, is unknown because the map on which it first appeared no longer exists; it survives only on a copy of a French map made in the cartographic centre of Dieppe by Pierre Desceliers in 1550 and which is totally unreliable because they were then unable to measure longitude accurately. In the same period, the word reef, from Old Norse *rif*, a ridge, also came into use to describe such formations both on land and in the sea.[1]

In 1619, a Dutch merchant ship bound for the East Indies under command of Frederick Houtman came across such a dangerous shoal. Apparently using a version of that map, and believing it to be the reef marked by the Portuguese, he recorded it on his chart as Houtman Abrolhos, a name it retains to this day, designating a complex of islands, cays, and reefs off the West Australian coast, near the town of Geraldton, 28º46'S. The Houtman Abrolhos gained even greater notoriety a decade later in 1629 when the *Batavia*, pride of the Dutch East India Company fleet under command of Francisco Pelsaert, en route to the Spice Islands on its maiden voyage, struck and was totally wrecked on one of its submerged reefs. A bizarre episode ensued of treachery, rapine, murder, and even cannibalism among the survivors by the mutinous crew.

Probably the first person to create a sense of the mystique and dangers of coral reefs for European readers, who rarely left the familiarity of their towns and villages, was the French navigator François Pyrard de Laval, whose ship, crossing the Indian Ocean in the first decade of the 17th century, was wrecked on a reef in the Maldives. Laval lived there for five years. On his return, he wrote an account of his adventures that was translated into English and included in Samuel Purchas' famous set of dramatic travel tales (Purchas 1613–1626). Part II of Laval's account is an accurate description of that archipelago, a southern extension of the Indian subcontinent consisting of 26 atolls (Malay, *atolu*, "circular reef") and some 1192 islets dispersed over some 90,000 km^2, most of which are permanently submerged. With an uncanny flair for heightening reader interest, Laval described the Maldives as "twelve thousand Iles," noting in his original text that "*c'est une merville de voir chacun de ces atollons, enviaronné d'un grand banc de pierre tout autour, n'y ayant point d'artifice humain*." The translation by Purchas is briefer: "It is admirable to behold, how each of these Atollons are invironed around with a huge ledge of rocks," omitting Laval's significant final comment "with no human construction whatever."

Throughout, Purchas keeps the prose heightened and the region threatening: the outer edges of atolls are "a very fearfull thing even to the most couragious to approach this ledge, and so the waves come from afarre off and breake furiously

1 Cognates to the English "reef" appeared simultaneously in Portuguese as "recife," in Spanish as "arricefe," in Dutch as "rif" or "ref," and in German as "reff."

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on every side." Around them, he continued, swim "sharkes [that] devoure men and breake their legges and armes" while in the "depths of the Sea are generally very keene and sharpe Rockes" which include "a certain thing not unlike Corall,… branched and piercing,…all hollow and pierced with little holes and passages, yet abides hard and ponderous as a stone (Purchas 1613–1626, IX, pp. 508–509)." Titillating ethnography is featured: to heighten the sense of drama for eager readers, Purchas includes Laval's observations that "women of the poorer sort are naked without any shame (Purchas 1613–1626, IX, p. 515)." His descriptions of Maldives society are comprehensive and make fascinating reading.

The excitement presented in such dramatic travel accounts of shipwrecks stimulated wide interest in reef formation in the 17th century as naturalists began searching for answers to questions such as: What is the nature of the coral that forms such dangerous reefs? Is it a rock, or, as some contended, an underwater plant with peculiar characteristics that petrified in air due to a "stone-forming essence?" Do the New World atolls seen in the Caribbean and the Indian and Pacific oceans consist of the same coral that had been known since antiquity in the Mediterranean and the Red Sea? If so, what is the relationship? How had such vast circular assemblages—throughout the tropical seas with lagoons 20 sea miles or more across—been constructed in clear, deep blue water, far from land? What held them together in often-turbulent oceans? How can they rise from the unfathomable depths of the Pacific Ocean that stretches almost halfway across the globe to create clusters of great limestone atolls to water level: fearful hazards to navigation, "hard and ponderous as a stone" with waves coming "from afarre off and breake furiously on every side"? These questions became the chief aspect of coral reefs demanding understanding, which began in the era of European overseas exploration.

The Classical Tradition

Early investigators had to surmount an inherited tradition of mythology, superstition, and folklore. The earliest reasonably reliable account of coral appears in the work of Theophrastus (c. 372–c. 285 BC), who succeeded Aristotle as director of his school in Athens, the Lyceum. Its appearance, from specimens collected in the Mediterranean, suggested that it was some type of stone, which led him to mention them fleetingly in his study of minerals, *Peri lithon* (On Stones). This became known by its Latin title *De lapidus*, as indeed was most of Greek learning as it became transmitted through Latin in the succeeding Roman era and into scientific discourse ever since. In that treatise, Theophrastus introduced the word "coral" as *kouralion*, which was translated into Latin as *curalium* and later became *corallo* in Italian, *corail* in French, and cognates in all European languages. Only a fragment of the original Greek text of *Peri lithon* survives today, but we find there the first mention of the confusing nature of coral in a very short passage of just two lines: "coral is similar to a stone, is shaped like a root, and found in the sea."[2]

However, the root-like formation also suggested that it could equally be a plant, so he included corals briefly in his "Investigation into Plants," *Peri phyton historias* in Latin, *De historia plantarum*.[3] The dilemma he encountered had already puzzled his teacher Aristotle (384–322 BC). In composing his main work, *Historia animalium* (Inquiry into Animals),[4] Aristotle presented a classification of all nature, arranged in ascending order of complexity on what became known in later centuries as the "ladder of nature" (Lat. *scala naturae*), where he presented the first classification of life in the sea. Organizing them into groups with common features (Gk *genos*), and within those genera into individual forms (Gk *eide*), Aristotle provided the earliest account for the visible differences among groups of animals.

Where he encountered considerable difficulty, however, was with a number of marine forms that presented ambiguous characteristics and bedevilled marine science for centuries. Some he believed to be plants, e.g. the anemone and the sponge "which is very like a plant," but ascidians (sea squirts or cunjevoi) were more difficult: although they have something of an animal nature, exhibiting contractibility, he was still unclear how they should be classified.[5] Aristotle's astonishingly acute observations, moreover, were presented with a caveat that was to create a scientific puzzle for 2000 years. "The progressive changes of nature are so small and imperceptible," he wrote, "it is impossible to draw a boundary and determine their category," so we "are at a loss to know whether they are animals or plants."[6] Presumably, he regarded corals as rocks, though with a plant-like appearance, which led to their later designation as "lithophytes" (Gk *lithos*, "stone" + *phytos*, "plant").

There are only few references in the succeeding Latin literature, chiefly in the voluminous Roman author and encyclopaedist Gaius Plinius Secundus (23/24–79 AD). In his huge encyclopaedia *Naturalis historia* (literally, Natural History or Inquiry into Nature), Pliny had an entire entry on coral, which, he commented, "is found in numerous places

[2] *De lapidus* VII, p. 39. The original text reads: "*to gar kouralion, kai gar touth osper lithos, te chroa men erythron, periferes d'os an riza fyetai d'ente thalatte*."

[3] *Peri phyton historias* IV, p. 7.

[4] Aristotle's works, although written in Greek, are conventionally known by their Latin titles.

[5] *Historia animalium* VIII(I), p. 588b; *De partibus animalium* IV, p. 681a.

[6] *Historia animalium* VIII(4–10), p. 588b.

in the Mediterranean, [and] is also gathered in the Red Sea and the Persian Gulf, and is considered as valuable as pearls in India." In fact, once India had been incorporated into the Hellenistic Empire following the expeditions of Alexander the Great in the 4th century BC, trade in coral became a major item, being exchanged for pearls harvested along the Indian coasts. Pliny recorded that "coral berries are no less valued by Indian men than are large Indian pearls by Roman women" and that Indian soothsayers regard coral as "invested with both beauty and religious power." In addition, he made the sardonic comment that despite the dangers from ever-present sharks, it was men that faced the hazards of collecting corals and pearls, because "wealthy women must have them dangling from their ears, a disease for which there is no cure."[7]

Describing its characteristics, Pliny states that "it is like a shrub, colored green with white berries [*baccae*]" which, "once taken out of water immediately hardens and turns red" so that it must be cut quickly by a sharp knife. "That," he informed readers, "is why it is called coral," implying that the word coral came from the Greek verb *keiro* "to cut."[8] Like so many of Pliny's stories, however, that was a fanciful comment and modern philology has determined that the word coral, in the Greek form *kouralion*, is of obscure Semitic origin.[9]

From then to the late 16th century, corals were considered from their physical characteristics to be either mineral or plant formations: many are soft and pliant and respond gracefully to water currents and wave motion; others are hard and brittle, in their dried forms resembling honeycombed rocks. One species of coral in particular was of considerable commercial value. Regarded as a precious gem, second only to pearls, the relatively flexible species of red coral (*Corallium rubrum*) that grew in Mediterranean waters resembling a tree-like shrub with branches up to one inch (25 mm) in diameter formed the basis of an extensive jewelry trade. Indeed, for 2000 years, red coral was a staple of the jeweler's craft. Originally, it was retrieved by free swimming and diving, the stems being broken off, brought up, and allowed to dry out. As the easily accessible areas along the French and Italian coasts became depleted, however, *corailleurs* extended their operations to the North African Barbary coast and developed a technique of plumbing greater depths by means of a rimless iron cartwheel-like contrivance. With up to six radial arms and known by the French as the *croix des corailleurs*, it snapped off pieces which fell into a hempen net suspended below, and were then retrieved. These were sold to artisans who cut transverse slices across the stems and polished them into gem-like stones for setting into necklaces, rings, and other ornamental artifacts. Merchants carried them across the ancient world, as indicated by their wide distribution—specimens have been found in archaeological sites in Egypt, Persia, Great Britain, India, China, and Japan, and along many parts of the coast of Africa.

A Transitional Hybrid?

There remained an unanswered puzzle that occupied the minds of naturalists: What exactly was the process that caused the shrub to petrify once taken out of water? One of the most accepted explanations came from the 5th-century teachings of the great founding church father Saint Augustine of Hippo (354–430), that an innate plastic force (*vis plastica*) present in all things causes otherwise unaccountable changes. That, in turn, began the traditional belief that fossils, as they were increasingly unearthed and studied, had been created by "a petrifying agency." The same mysterious power of a "stone-forming essence," for example, was invoked to explain the hardening of red coral, and the same theory led to the belief that mushrooms that fell into the sea turned into stone. Consequently, the mushroom coral (*Fungia*) received its name.

By the 16th century, precious coral had become well integrated into the emerging literature on minerals and metals by numerous authors, predecessors of geology. It found its most acceptable expression in Book 4, *De natura fossilium* (On Fossils) in the famous 1545 treatise *De re metallica* (On metals), by Agricola (Georg Bauer). In a positive advance towards understanding the unknown process, he suggested that the inherent petrifying property of coral came not from *vis plastica* but, as he believed it was some kind of marine plant, from *succus lapidescens* (petrifying sap). He did not offer any personal comment but restricted himself to reporting "that some call it stonewood [*lithodendron*], partly because it turns into stone, and partly because it is a shrub [*arbuscula*]." In that Late Latin treatise, Agricola referred to Theophrastus, Pliny, Ovid, and Dioscorides, drawing all of their observations into his commentary. He then continued to discuss more recent uses, such as making rosary beads from red coral that had "religious value for warding off dangers, also allowing people to rejoice in its decorative and spiritual powers": *aruspices eorum vatesque imprimis religiosum id gestamen amoliendis periculus arbitrantur, & decore & religione gaudent* (Agricola 1556, p. 603). Again, the therapeutic properties are described, taken from Pliny 1500 years earlier: "when drunk with water it cures those who are spitting blood and suffering the gripes."

The popular acceptance by naturalists of coral and similar forms as marine plants, however, was to become seriously questioned. A defining development in the study of coral,

[7] *Naturalis historia* IX, p. 110.

[8] *Naturalis historia* XXXII(xi), p. 20–24.

[9] The Semitic origin is either the Hebrew *gōrál*, "pebble," or the related Arabic *garal*, "small stone."

which ramified throughout the ensuing centuries, had appeared in a phrase penned in 1535 by the French naturalist Giles d'Albi (Petrus Gyllius) in his study "On the French and Latin Names of the Fishes of the Marseilles Region." Commenting on the difficulty of determining the boundary between plants and animals, in the case of sea nettles and sponges, for example, he reached back to Pliny. Having previously drawn heavily on the surviving texts of Aristotle, Pliny had introduced a concept that was to cause considerable confusion, and to exercise a powerful influence on natural history until the 19th century. Where Aristotle had simply stated that the boundary between plants and animals was difficult to determine, Pliny—whose writings often display a cavalier disregard for fact—attempted to bridge the gap by asserting that creatures such as stinging sea nettles and sponges, "are neither animals nor plants, but are possessed of a third nature."[10] Gyllius followed that statement uncritically, but introduced a major change of term, writing that *Plinius urtiam et spongiam numerat inter ζωόφυτα* (cited in Milne-Edwards 1857, p. xiv). What, however, did the word ζωόφυτα signify that was to exercise such a continuing influence on coral science? Transliterated from Greek, it becomes "zoophyte," compounded of the Greek *zōon* (animal)[11] and *phyton* (plant), and in translation the phrase reads: "Pliny included nettles and sponges among the zoophytes." The term zoophyte has often been attributed to Aristotle, although it never appears in his writings or in any other classical Greek author. Pliny reveals no knowledge of the term and only used "third nature" *(tertius natura)*, and because it was not autochthonous Greek but a later neologism, its formative period remains unknown.

Neither the word zoophyte nor the taxonomic concept, however, is used in the sparse literature from Pliny until Gyllius introduced it in his 1535 study: it seems likely, as one eminent authority suggests, that he created it for that specific context.[12] As the boundary between plants and animals was still unresolved in the 16th century, the revived neologism by Gyllius took on a life of its own, and it was increasingly used by naturalists until the mid-19th century to describe a wide range of marine life forms that seemed to straddle the boundary. In many indeterminate cases, they were considered, in effect, hybrid plant–animals.

Yet a further development in coral studies came during the final decades of the 16th century when Ferrante Imperato (1550–1631) established an impressive museum of natural history in Naples, which held an extensive collection of dried corals, brought to him by seamen, mainly of the hard, porous varieties that were a menace to navigation. In 1599 he compiled, in Italian, *Dell' Historia naturale*, probably the first known natural history catalogue of that era. As he examined the external appearances of the limestone skeletons by unaided eye, Imperato suspected that corals may well be such transitional forms. From reports he received, their shape suggested to him that they had grown by "the accumulation of thick layers which included a fleshy pulp," and were possibly "a kind of vegetable, the substance of which resembles coral, but differs in being porous." Given their appearance, Imperato was inclined to believe that the structure was more likely a shell within which some other life forms lived, although he did not observe any living organisms. Using the analogy of the beehive, he speculated that the coral rock may well be "the mother within which marine animals are formed, just as bees live in a wax comb" and that "the small holes were nothing but the receptacles of animals." With the idea of "mother" in mind, he took the Italian *madre* and, on the analogy of mother-of-pearl, "*madreperla*," used "madrepora" for some of his stony specimens, a term readily adopted and remaining in use today.[13] Imperato then extended the suffix "pore" to name other taxa[14] with similar external porous characteristics in his collection, naming millepora, retepora, and frondipora.[15]

Unfortunately, because Imperato wrote in Italian and not the universal Latin of the period, his speculations seem to have had little distribution until 1672 when the Latin translation *Historia naturalis* was published and "madrepora" appeared as *porus matronalis* which became widely adopted for the hard, calcified species. However, the meaning of the word translated as "porus" is somewhat uncertain. Although *matronalis* certainly is Latin and means "motherly," *porus* is not: it was most likely a latinate neologism taken from the Italian *poro* for "pore." The etymological problem is that in Greek from which Imperato probably derived the concept of "pore," there are two words with slightly different spellings and pronunciation: *πορος* (pore) and *πώρος* (stone), both transliterated into Roman script as *poros*. The most likely intention seems to have been to describe a "porous mother,"

[10] Pliny, *Naturalis historia* IX(lxviii), p. 146.

[11] Greek has two forms of the letter "o": long (o-mega, ω) and short (o-micron, ο). To pronounce words correctly in biology based on *zōon (ζωον)*, such as zoology, zooxanthellae and epizootic, the two letters are separated as in cooperation. The pronunciation as zoo-ology is a vulgar abomination.

[12] Milne-Edwards inferred that it most likely originated with Gyllius, making the editorial comment that "*C'est, croyons-nous, la première fois qu'on ait employé ce mot, au moins sous cette forme.*": "that, I believe, is the first time that word has been used, at least in that form." Milne-Edwards 1857, p. xiv.

[13] This explanation follows British Museum taxonomist George Brook (1893).

[14] The word "Taxa," (sing. "taxon"; Gk *taxis*, "order," "regularity") is used to designate a similar group of plants or animals at any level. The term "taxonomy," consequently, is compounded of "taxon" and *nomos*, "law": hence, the rules of classification.

[15] Millepora: Italian *mille*, "thousand"; rete, "net"; *fronda*, "bush, leafy." These three terms have Latin cognates—*mille, rete, frondeus*—which Imperato may have used.

although it could possibly have been "a stony mother."[16] Regardless, both derivations are plausible.

The 17th century was an age when economic power depended on command of the high seas, and prosperity at home grew out of the control of areas once dominated by the Portuguese and Spanish, and through expansion of trade with the New World and the East Indies. As a consequence, more seafaring explorers, especially the Dutch, the English and the French, crossed the oceans in search of new lands and trade routes. It became fashionable for travellers to record and subsequently to publish much of what they saw, so a growing body of widely available travel literature appeared, often with titles beginning with "Voyages of …" or "Travels to …" and translated into other European languages. Between 1660 and 1800, more than 100 such collections appeared in print, providing both travel adventure stories and interesting observations of marine life, and importantly charting many previously unexplored waters. These accounts regularly described corals and coral reefs and atolls, often after close and dangerous encounters, and aroused much interest among marine and coral students, giving rise to such questions as those outlined at the end of the introduction to this chapter (see p. 4) regarding the nature of corals and how coral reefs were formed. Such questions demanded explanation and understanding. At the same time and through into the early 18th century, the French and the English in particular were leading the charge to discover and, if deemed feasible, to occupy and colonize the still unknown, unmapped part of the globe known as *Terra Australis* in the hope that it would offer economic advantages.

The result of this interest in exploration, of course, was that many vessels started to carry naturalists and other explorers. For instance, the voyages of Louis Antoine de Bougainville in command of *Boudeuse*, 1766–1768, and James Cook on the *Endeavour*, 1769–1771, carried naturalists: Philibert Commerson on the *Boudeuse*, Joseph Banks and Daniel Solander on the *Endeavour*. From those voyages on, all naval ships carried naturalists and they, like their commanders, were instructed to collect any evidence that would contribute to a better understanding of global geology, and most particularly of coral reefs.

The task at the time was daunting. In the early voyages of exploration, the naturalists had almost no body of organized geological knowledge to guide them: on the contrary, information about the earth and its processes was largely compounded of folk superstition embedded within the restrictive framework of religious belief. Even the word "geology" with its present connotation did not exist. It had occasional medieval Latin usage as *geologia* for the study of "earthly things," but it only began to take on a more modern cast when used by Dethlevus Cluverus in 1700 in the title of his Hamburg publication, *Geologica, sive Philosophemata de genesi ac structura globi terreni* (Geological or Scientific Study of the Origin and Structure of the Terrestrial Globe). Not until 1798, however, did it assume its now-familiar meaning as the study of the physical composition and processes of the earth, initiated in the late 18th-century theory of James Hutton.

To achieve any meaningful knowledge of reef structure, the pioneering geologists—known at the time as mineralogists until the neologism of "geologist" appeared in 1795—first had to surmount a formidable coalition of Biblical authority, mythology, and faulty assumptions. Their task, moreover, was extremely dangerous because they were challenged all the way by the theocratic teachings of the Catholic Church—and after the 16th century by the Protestant Evangelical Church as well—which threatened their safety and their liberty.

Faith and Reason: The Theocratic Context

Geology as a science grew out of the medieval activities of alchemy on the one hand and mining on the other. During the 17th century, however, new directions of inquiry began to emerge, and in the search for an understanding of the origin and structure of the earth, visible evidence of coral and other marine deposits in elevated strata had begun to attract considerable attention, particularly when they began to be displayed in museums from specimens collected by mariners. Constraining all inquiry, however, was the authoritative dogma of the creation of the earth given in *Genesis*, the first of the five foundational books of the Bible (Gk *Pentateuch*, "five books"), believed to have been written by Moses himself, until the late 19th century when discovered by the new sciences of palaeography and philology to be unsupportable legend.

The central issue at the time was the unquestioned power exercised by the Catholic Church. As Europe became more settled following barbarian migrations, which succeeded the sack of Rome by the Goths in 410 and the subsequent collapse of the Roman Empire, the Roman Catholic Church (Gk *katholikos*, "universal") was the only unifying power, with a presence in every former Roman diocese (Gk *diokesis*, "administrative province"). Following formation of the Holy Roman Empire in the 9th century from the central European states, along with the Kingdoms of France, Portugal, and Spain, as supreme leader, the Pope (Lat. *papa*, from *pater patrum*, "father of fathers") came to exercise absolute power, and it was from him whom the Emperor himself, and each king, prince, elector, duke, and count derived legitimacy. So far-reaching was papal power that every document regulating society came from the quill of a Benedictine monk in a cathedral scriptorium.

[16] First suggested by Brook (1893).

Consequently, to preserve the authority of the church, any critical speculation concerning the narration of Moses would be ruthlessly suppressed: publications were closely monitored for adherence to scriptural truth, particularly those that attempted to explain the physical formation of the Earth and the origin of marine sediments. The account of creation in *Genesis* 1 that in the beginning the earth was entirely covered by water and that the land only appeared later at God's command, and of the great Noachian flood in *Genesis* 6–8 in which the heavenly deluge was said to have covered even the highest mountains for 40 days, could not be questioned. Strictly enforced for more than a millennium, such doctrines only began to be doubted cautiously as scientific curiosity gathered pace during the 16th-century Renaissance.

The Rise of Geological Speculation

The first great mind to question the heavenly deluge closely was Leonardo da Vinci (1452–1519), who committed his thoughts on the matter to his private notebooks in a secret script, sometime in the late 15th or early 16th century. Deciphered in the 19th century and later edited by Jean Paul Richter, we are now able to experience the temper of one of the greatest and most inventive minds of the Renaissance, indeed of all time.

One of the earliest relevant records on which Leonardo relied came as early as the 5th century BC from the *Histories* of Herodotus where he related that he had seen shells on the hillside plateaus above the Nile, and that they must have been deposited there, in some way, by the sea.[17] Two millennia later, Leonardo wondered how great assemblages of corals along with shells of oysters, sea snails, and other testacea, many intact, could be transported hundreds of metres up into the valleys of the Alps in a vortex of turbulent waters. How could there be sufficient rainwater to submerge every landform with even the highest peak covered by seven cubits? He ridiculed an alternative explanation that molluscs had somehow made their way up during the deluge, and then remained around the lakes in Como, Fiesole, and Perugia, among others, after the waters subsided. Molluscs, he observed, could travel but three or four handspans (*braccia*) a day through burrows: How could they cover 250 miles in 40 days? And what happened to all the water when the flood subsided? "We must," he speculated, "call in a miracle to help us [*chiamare il miracolo per aiuto*] and declare that all the excess water was evaporated by the sun [*o dire che tale acqua fu vaporata dal calore del sole*]."[18] The problem lay in explaining how so many shells and other marine creatures such as ammonites (extinct cuttlefish and octopods) had appeared where they were found lying on the surface or dug up in fields and mines and whether they actually were of marine origin because they were often discovered far from the sea. If they were identifiably genuine, and not merely deceptive games—"sports of nature" (*lusus naturae*)—played by a capricious Nature to resemble real objects as was also believed, or to test mankind's steadfast belief in Church doctrine, then surely for the faithful they were evidence of the great Biblical flood.

Although Leonardo's thoughts were never published at the time, they do indicate a style of thinking that was occurring to others in that period. The most notable was Bernard Palissy (1510–1590), a French naturalist and potter by trade who lectured publicly on his avocation of palaeontology and committed his thoughts to a lengthy book setting out his *Discours admirables* (Admirable Discourses) (Palissy 1580). Palissy was one of a growing number of naturalists who had begun the foundation of museums to hold their collections of fossils, among which those of Ferrante Imperato in Naples, Ulisse Aldrovandi in Florence, Francesco Calzolari in Venice, and Ole Worm in Lyons, were to become widely known and visited. The museum of Palissy contained a large number of marine specimens he had collected in the Ardennes, northeast of Paris near Reims, which included "petrified shells of oysters, cockles, hard-shell clams, scallops, crayfish, snails, and all kinds of other snails that live in [the] Ocean sea" (Palissy 1580, p. 164). For him, extensive investigation of the region around the Ardennes, and the large number of marine remains he found, were evidence that "the sea did not bring in these shells at the time of the Flood"; rather, they had been "born on the very spot, petrified together with these fishes" (Palissy 1580, pp. 159, 161). This was a brave statement to be published at the time and, along with his public lecturing on that sensitive theme, it aroused the ire of the Faculty of Theology at the Sorbonne, who had Palissy tried for heresy. He was found guilty and imprisoned in the Bastille, where he was held until his death.

Such speculation, however, could not be contained, and was pursued by Girolamo Fracastoro (1483–1533), although, given the sensitivity of the times, his ideas were not published until 1662, when they were edited by Benedetto Ceruti and Andrea Chiocco and appeared in the catalogue of the *Musaeum calceolarium*. Discussing excavations near Venice, Fracastoro recorded that workers uncovered "sea-urchins of stone, crabs, sea-snails, cockles, oysters, star-fish, bird's beaks, and many other things of that sort." In the conjectures of his scientific colleagues, he recorded, the Noachian flood was dismissed as a cause because it was not waters from the seas that rose, "but torrents from the heavens" that supposedly fell. Moreover, the remains were found not just on the mountain tops as might be expected, but all through the hillside as the men dug through. "Sports of nature" were also dismissed, because the remains were obviously genuine: the only reasonable inference was that they had originated in the sea that was once where the mountains

[17] *Histories* II, pp. 12–15.

[18] Leonardo, edited by Richter 1939: II.vi.986, p. 168; II.vi.992, p. 175.

Fakarava Atoll, Îsles Tuomotu, French Polynesia, at sunset, illustrating the dangers of collision at night when the freeboard at high tide can be as low as 2 m. (Photographed by the author in 2005)

now were, such as "near Ravenna where the sea has receded a hundred paces."[19]

Before further progress was possible, however, the dominance of mythical religious dogma had to be challenged successfully. The first repudiation of ecclesiastical authority began in the 16th century when the monolithic unity of the Catholic Church was fractured by the Lutheran revolt of 1519 against its corrupt activities—epitomized in the selling of "indulgences" to relatives to reduce the time spent by souls of their deceased family members in purgatory—which had spread throughout northern Europe.

By 1560, two-thirds of the political entities constituting the Holy Roman Empire repudiated papal authority, strengthened by the rise of the evangelicals Jean Cauvin (John Calvin) in Geneva and John Knox in Scotland, accompanied by demands for greater freedom of both religious conscience and political freedom in the Spanish Netherlands. In 1572, the Dutch finally revolted against Spanish rule and Catholic domination: after 40 years of struggle, the independent, Protestant, Dutch Republic was separated in 1609. Although the reforming Vatican response in the Council of Trent, 1546–1563, and the energy of the new Jesuit order brought much of lower Germany back into the Catholic fold, nonetheless the Evangelische Kirche had come to stay throughout the north.

Peace, however, was not to prevail, and the ensuing 17th century saw religious and political conflict become even more exacerbated between Catholic and Protestant forces, marked primarily by the Thirty Years War, 1618–1648, which raged across much of central Europe. In England, it appeared as a Civil War between 1642 and 1651 between a Catholic king and a Protestant parliament led by Oliver Cromwell, the conflict finally terminating with the beheading of Charles I in January 1649 and the establishment of a Commonwealth. The Peace of Westphalia the previous year had marked the beginning of a period of relative quiet, but the forces for change generating throughout those years continued to grow, and become ever stronger.

As the narrative that follows illustrates, however, conflict between faith and reason never entirely disappeared. The history of science, and particularly the investigation of coral reefs, shows that the conflict continued well into the 19th century, and it still lingers in various obscure variations.

[19] Text in Edwards (1967), pp. 19–21.

2 The Scientific Revolution of the 17th Century

With the formation of a new Protestant court in England under James I, it was there that a great revolution in science took hold and began to flourish. Led by Francis Bacon (1561–1626), an administrator in the court of Elizabeth and then James I, his vigorous denunciation of the dead hand of the medieval past which had fostered such beliefs that a purposive nature had created material changes in corals and marine fossils through an innate mystical force of "stone-forming essences" began the complete revision of knowledge.

The main problem natural historians faced was that throughout the medieval millennium, many of the classical Greek manuscripts had either disappeared or been destroyed by zealous Christians intent on obliterating pagan culture. Fortunately, Aristotle's surviving writings, like so much of the *corpus classicum*, had become transmitted in Latin translations, many in Arabic versions in the era of Muslim high civilization, 8th to 13th centuries, and then retranslated into Latin and finally back to Greek, although often in faulty versions by barely literate scribes in the monastic scriptoria. Probably the most extreme example was the fate of *De plantis* which went from Greek to Latin to Arabic, then back to Latin by an incompetent translator, and finally again to Greek. To this day, we have only a limited idea of exactly what Aristotle wrote or actually intended in his study "On Plants".

Bacon was intolerant of the continued acceptance of debased Aristotelian teachings that had been transmitted uncritically for nearly two thousand years. "The entire fabric of human reason", he began in the *Prooemium* to his outline sketch in the "Great Instauration", a manifesto for reform, "is badly put together and built up, like some magnificent structure without any foundation". It was essential, he wrote, "to try the whole thing anew on a better plan, and to commence a total reconstruction of sciences, arts, and all human knowledge, raised upon the proper foundations". In 1605, he published the first part of that project under the title "The Advancement of Learning".

All knowledge, he argued, comes primarily from experience of the sensible external world, echoing a fundamental Aristotelian doctrine. To that time, Christianity had been mainly influenced by the Neoplatonic view propounded by St Augustine in the 5th century that all human knowledge begins with divine illumination of ideas implanted by God. By the 12th century, however, in the furious debates that raged in the early foundation years of medieval universities, the Dominican monk Thomas Aquinas created an ecclesiastical frenzy with his assertion, following Aristotle, that despite the creation of the world by an omnipotent God, nothing exists in the mind that had not come first through the senses: *nihil est in intellectu quod non prius fuerit in sensu*.[1] So incensed was the Catholic Church that on his death, Aquinas was buried in unconsecrated ground, although 50 years later in 1323 after the debates of the Scholastic Controversy had been resolved and his views became acceptable, he was rehabilitated. Miracles were attributed to him; he was canonized as St Thomas and named one of the great foundation fathers of the Church.

Following that Thomist precedent, Bacon continued his pressure for reform in 1620 with the publication of further stringent criticisms of existing natural history in *De augmentatis scientiarum* (The Enrichment of Knowledge). His revolutionary proposal was to replace the corrupted tradition that relied heavily on dialectical reasoning rather than field study, with his new instrument for achieving certainty, *Novum Organum*, which he set out clearly in the subtitle as "True Directions concerning the Interpretation of Nature". A fresh start was urgent, a renovation of all existing knowledge, and he advocated new methods of intensive observation, experiment, and the careful, wide-scale collection of data. In his various works, the doctrine of inductive scientific method, later called empiricism (Gk *empeiria*, "experience"), was introduced which codified a methodology of investigation that began to challenge a 2000-year tradition of reliance on authority.

After Bacon's dramatic declaration in 1605 to discard the "false idols" of the past and to begin a complete renovation of knowledge, two complementary themes of reef investigation

[1] Aquinas: *Quaestiones disputatae, De veritate*, q. 2, argument 19.

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
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emerged as the revolution gathered pace. Initially, how were the necessary geological structures formed that allow corals to become established? Then, following closely, what exactly are the biological processes underlying the development of what is essentially a veneer of living organisms—plant and animal—that collectively build the ecosystems known as coral reefs? The biological quest soon became as equally absorbing a scientific pursuit as the geological problem. The history of coral science, in fact, has proceeded in a fascinating counterpoint as the two issues interacted, each discovery casting light on the other.

At that time too, a new concept also began to appear when science (from the present participle stem of the Latin *scire*, "to know") began to replace natural history, with a totally different emphasis. Bacon continued to use the term "natural history", although he regarded it as the preliminary stage of collecting facts and recording the events themselves: he reserved the term "science" for the more probing, experimental investigation of nature. Bacon's call for a renovation of knowledge, despite church condemnation, continued to spread, and it began to be pursued with the increasing foundation of learned societies. The lead had already been taken in 1601 when, under the patronage of Prince Federigo Cesi in Rome with the support of the humanist scholar Nicolas-Claude Fabri de Peiresc and scientist Galileo Galilei, a group formed Europe's first scientific society which met under the name Accademia dei Lincei, literally "Academy of the Lynx-Eyed". With the name suggesting a penetrating observation of nature, it made some of the first uses of the microscope, possibly devised by Galileo based on his invention of the telescope, and in 1625, the Academy published a study of the honeybee, the world's first microscopic report, in its Proceedings, *Gesta Lynceorum*.[2]

New vistas of the universe that had been initiated in the Renaissance from the astronomical work of Copernicus and Galileo, and the incredibly dynamic impact of Bacon's uncompromising manifesto began to stimulate scientific enquiry continent-wide that was extended rapidly by the new medium of the printing press. Scholars across Europe came together to form radically different investigation societies, and their reports of experiments and investigations multiplied and were disseminated ever more rapidly. Reef science in particular was swept up in those new developments.

Two particular centres in Paris became major distribution outlets for publications, founded sometime around 1610 when two brothers, Pierre and Jacques Dupuy, formed a small group to meet in their home, which evolved into the Cabinet des Frères Dupuy, significantly, with a portrait of Francis Bacon the centrepiece. The other was in the cell of the Minimist friar Marin Mersenne in the Couvent de l'Annonciade in Paris, and it was to those early editors that papers were sent and disseminated throughout Western Europe in the early decades of the scientific revolution (Bowen (1981, III: p. 46 f.).

In 1630, a similar society was founded in Florence under the patronage of the Medici which called itself the Accademia del Cimento (Academy of Experimentation), with the motto *Provando et riprovando* (Test and test again), their proceedings being published in the *Saggi di naturali Esperienze* (Reports of Experiments in Natural History). Then, in 1633, came the papal condemnation and house arrest of Galileo for his heretical claim that the earth revolved around the sun. The repressive hand of the Inquisition, which monitored all scientific investigation closely, forced the closure of the scientific societies in Italy, confirming the popular jest of the time that Italy could lead the world in science whenever the Inquisition would let it.

Of the large number of scientific societies that appeared in the mid- to late 17th century, three became pre-eminent, all in operation to the present day. The first was the Collegium Naturae Curiosorum (Society for the Investigation of Nature), founded in 1652 by a group of physicians in the German city of Schweinfurt, some 115 km east of Frankfurt, followed by the Royal Society of London, founded in 1660 and chartered by Charles II in 1662, quite explicitly, on Baconian principles. The third, a French equivalent, arose slightly later, founded by Chief Minister Colbert in 1666 as the Acadèmie des Sciences, which built upon the work of earlier French societies. Through those organizations, and others that followed in Denmark, Holland and Italy in particular, the new spirit of Baconian-inductive empiricism became dominant, and it was the consequent burst of activity on so many fronts that gathered momentum and created an ever-growing ferment of ideas in natural history.

Following the foundation of those societies, a number of journals soon appeared, originally independently financed, expressly designed to disseminate the increasing volume of scientific findings. The first came in January 1665 when Denis de Sallo of the French parliament founded the *Journal des Sçavans*, followed in March the same year in London by the *Philosophical Transactions;* Italian, Danish, Dutch and German journals then appeared between 1668 and 1682. In the late 18th century, the *Philosophical Transactions* became formally linked to the Royal Society of London, and in 1903 the *Journal des Sçavans* received official government sponsorship under the Institut de France.

New Directions: Earth Processes and Natural Causes

Meantime, throughout the 16th and 17th centuries, as mining progressed and men dug more deeply into the surface of the earth, marine remains, now termed fossils (Lat. *fossilis*, from

[2] Italian, *gesta:* deeds, achievements (of the lynx-eyed).

fodere, to dig) continued to be found in increasing numbers, as Fracastoro had observed, scattered throughout the layers of unconsolidated earth being excavated. That raised two related issues: How had the visible layers of the earth been formed within which marine fossils were being found, and how had the landscape been shaped?

That is when we find the beginnings of a theory of stratification of the earth's surface set out by Niels Stensen (1638–1687) of Denmark in his 1669 study with the opaque title *De solido intra solidum naturaliter contento dissertatio prodromus* (perhaps best translated as "A theory of the interaction of natural pressures within the solid earth") in which he attributed the energizing force to volcanic activity. Volcanoes, clearly related to the natural pressures operating within the earth, were particularly threatening phenomena, carrying a mass of superstition. The first major historical account is in the *Timaeus* by Plato, c. 340 BC. In a battle between Athenians and Atlanteans, the conflict ended abruptly during a period of violent earthquakes and floods when, in a single horrendous day and night, all the warriors were swallowed up by the earth, and the island of Atlantis similarly disappeared beneath the sea: *e te Atlantis nesos osautos kata tes thalattes dusa efanisthe*.[3] That legend, believed to have been based on the destruction of the Minoan civilization on Crete as a result of the volcanic explosion of the nearby island of Santorini, perhaps around 1500 BC, became a central feature of all volcanic knowledge thereafter.

Accounts recorded subsequently were historically accurate. Several have become folklore: the explosion of Vesuvius in 79 AD, in which Pliny died from asphyxiation aboard his yacht in the Bay of Naples in a foolhardy endeavour to observe its activity at close range; and the subsequent eruption of Etna on the eastern coast of Sicily in 353. The eruption of Hekla in Iceland in 1104 received powerful religious sanction when it was authoritatively declared by the resident Benedictine monks that its fiery crater was the portal to Hell itself. As the New World became progressively explored, so accounts came in from the Caribbean Antilles, the Dutch East Indies and the Pacific Ocean. By 1650, Varenius, considered to be the founder of modern geography, published a list of the then 27 known volcanoes in his great treatise, *Geographia generalis*.

To explain the entrapped marine remains, Nicolas Steno, as Niels Stensen was known in the latinized form of his Danish name, argued that, in the course of time, the earth had been covered by water-borne sediments that formed layers of sedimentary beds, although, when the first layer was formed, "none of the upper Beds was extant". Owing to continued subterranean water erosion and disturbance from volcanoes and "underground fire", he continued, the superimposed strata eventually gave way and became "either perpendicular to the Horizon, or inclined to it", and "such changed situation of the beds is the chief cause of mountains". Steno had made a significant linkage between fossils and rock strata, and the natural forces of erosion that shape surface topography. One of his most tantalizing comments, which hinted at continuing surface movements, was the statement that "All mountains at this day have not existed from the beginning of things" (Stensen 1669, p. 28). Unfortunately for Steno, those views clearly contradicted Biblical dogma, and so great was the pressure from the Evangelical Lutheran bishops of Copenhagen that he was forced to abandon further geological speculation.

The deposition of sediments containing fossils and the stratification of the earth was a puzzle also examined critically in Protestant England by Robert Hooke, Curator of Experiments for the Royal Society in 1662 and thereafter Gresham Professor of Geometry. A controversial scientist of equal stature and achievements as his adversary Isaac Newton, he published *Micrographia*, a pioneering work describing his investigations into minute life, in 1665. Presented in English instead of the customary Latin, it is a compendium of 60 separate Observations on a wide range of subjects, from ants to writing. Each observation, most of several pages, with the majority on living organisms, generally covered a number of related issues, into which Hooke inserted his conviction that most of the daily operations of the world proceed according to natural laws. Following the same line of reasoning as Steno, after a short vacation to his childhood region on the Isle of Wight, Hooke recorded his exploration of the sedimentary strata of the cliffs. On one occasion, he recollected, from a "Layer, as I may call it, or a Vein of Shells…I digg'd out, and examin'd many hundreds and found them to be perfect Shells of Cockles, Periwinkles, Muscles, and divers sorts of small Shell-Fishes…some perfectly intire". What also captured his imagination was the composition of the rock face itself which, he reasoned, had originally been composed of suspended earthy particles and "in tract of time had settled and congealed into…hard, fixt, solid and permanent forms" (Hooke 1665, p. 176).

From his investigation of elevated strata and temperamentally driven by his inner demon—often to the irritation of his colleagues and senior fellows of the Royal Society—Hooke dismissed the sports of nature as absurd myths. In particular, in one of his most extensive and critically analytical descriptions in Observation XVII of *Micrographia*, "Of Petrify'd wood, and other Petrify'd bodies", dealing specifically with frequently found fossilized sports of nature, he totally rejected Augustine's belief in stone-forming essences (Hooke 1665, pp. 107–112). On the contrary, he argued, they were the empty shells of once living animals—"*Nautili* or Porcelane shells;…shells of *Cockles, Muscles, Periwinkles, Scolops*, &c. of various sorts"—which "came to be thrown to that place… by some Deluge, Inundation, Earthquake…

[3] *Timaeus* 25 D.

there to be fill'd with some kind of Mudd or Clay, or *petrifying* Water" and not by means of "some extraordinary *Plastick virtue latent* in the Earth itself" (Hooke 1665, p. 110). Petrified marine objects, he argued, were comparable with the remains found in classical civilizations, declaring that "shells are the medals, urns, or monuments of nature…discoverable to any unbiased person" that would afford more information about the past than "all the pyramids, obelisks, mummies, hieroglyphs and coins provide to archaeologists". The only limitation, he added, was that in the present state of knowledge "it is very difficult to read them, and to raise a *Chronology* out of them, and to state the intervals of the times wherein such catastrophies and mutations have happened".[4]

Hooke's investigations with the microscope led him to speculate at the same time on the broad geological features of the earth, particularly the action of volcanoes, earthquakes and other surface movements of the crust. Over a 30-year period, he developed those ideas into a series of lectures and discourses for the Royal Society, mainly in the two years 1668 and 1669, and which, following his death in 1703, were collected and edited by Richard Waller and published in 1705 by the Royal Society under the title *Lectures and Discourses of Earthquakes and Subterranean Eruptions*.

Hooke's "Discourses" were equally controversial. Earthquakes and volcanic action, he argued, were not events expressing some mysterious divine wrath, with the lava foreboding the fury of Hell, but a major natural phenomenon resulting from the spontaneous combustion of sulphur, pyrite (iron sulphide, FeS_2), air and salt water—because most volcanoes then known were either in the sea or along coastlines—which subsequently created uplift and modelled the landscape. His approach consequently marks one of the most significant changes in our understanding of the formation of coral reefs, when the speculations of earlier naturalists were consolidated into a firm theory that paved the way for systematic, rational scientific investigation. Just as he had explained the petrification process in fossils, so Hooke proposed the manner by which sedimentary strata became consolidated, and that "every part hath, at some time or other, been shaken, overturned, or some way subject to earthquakes, and been transformed by them. It seems to me", he argued, "very absurd to conclude, that from the beginning things have continued in the same state that we now find them" (Hooke 1705, p. 450). Those conclusions were a remarkable advance in geological thinking.

Perhaps even greater evidence of Hooke's inductive genius was the observation that many of the fossils being unearthed in England were also coming from tropical regions: perhaps other scientists, he suggested, would consider that "this very land of England…did at a certain time for some ages past, lie within the torrid zone".[5] Equally indicative was his anticipation of some kind of evolutionary mechanism directing animal life. From available evidence, he argued that because there were "many other species of creatures in former ages, of which we can find none at present…'tis not unlikely also that there may be divers new kinds now, which have not been from the beginning". Moreover, it cannot "be doubted but that alterations of this nature may cause a great change in the shape, and other accidents of an animated body" (Hooke 1705, pp. 342–343, 435). With the thoughts of Steno and Hooke, which brought together the concepts of sedimentation, fossil entrapment and the activity of surface water and volcanoes, the groundwork for the emerging science of geology was created.

Even more evidence came in 1707, just two years after the publication of Hooke's discourses on earthquakes, when Europe was astonished by the incredible news of the eruption of the Mediterranean island of Nea Kameni from the legendary volcanic caldera of Santorini, in many minds confirming the legend in *Timaeus*. Reasoning from that event, and from his investigations in the Italian mountains, in 1740 the Carmelite priest Anton-Lazzaro Moro published *De Crostacei degli altri marini corpi che si truovano su' monti* (Crustacea and other marine bodies found in mountains). Despite his vocation, he supported the views of Steno and Hooke that volcanoes were the active agents in shaping the landscape, and that eruptions trigger uplift of the surrounding terrain, thereby accounting for elevated marine strata.

A Flowering of the Intellect: The European Enlightenment

The intellectual temper of northern Europe was rapidly moving into a new phase. The manifesto of Francis Bacon in 1620—*De augmentatis scientiarum*—for a repudiation of the heavy hand of medieval tradition and in its place a complete renovation of knowledge, along with the formation of scientific societies, despite their closure in Italy by the Inquisition, marked the beginning of a new spirit of scientific enquiry. Although the authority of the various religious confessions was still intimidating, demanding belief in a universe constantly under the direct guidance of a transcendent God—a doctrine known as Theism—thereby encouraging supplication during volcanic eruptions and other catastrophes for miraculous intervention, scientific thought was beginning, nonetheless, to take firm hold. Initiated in large part by the quest to solve the coral reef enigma, it had begun to exercise a pervasive influence, particularly evident in the growing acceptance of earthly processes as resulting from natural causes.

[4] Hooke (1705, pp. 335, 431). Published posthumously two years after his death in 1703.

[5] Current geological knowledge places England at 35°N in the Triassic period, c. 251–206 million years ago (Mya).

A defiant stand was taken in 1687 when Isaac Newton (1642–1727) presented his wide range of investigations in one of the most influential books yet published, *Philosophiae naturalis principia mathematica* (Mathematical principles underlying nature). Although it drew from the ancient philosophies of Pythagoras and Plato by asserting that the universe originated from a divine mathematical design, once created, he argued, its daily operations follow fundamental physical and mechanical laws. With the powerful stimulus of Newton's *Principia* asserting the primacy of natural processes, and an increasingly frequent denial by philosophers of the direct activity of God in daily events, scientific thought came to reflect an alternative, rational approach known as Deism. A neologism created in 1678 by Ralph Cudworth, Deism was developed extensively by John Toland (1670–1722), an Irish convert to Protestantism, who attempted to relate the evidence of natural history and scientific discovery to issues of faith. Strongly influenced by the "Ethics" of Benedict Spinoza of 1670 in which God and nature were presented as an entity, expressed in the intriguing double entendre *Deus sive natura* (God is Nature, and Nature is God)[6] to describe that new conception, Toland introduced a new term into the religious lexicon to define that indissoluble unity: Pantheism. Toland's numerous writings initiated a great wave of radical thought that swept throughout northern Europe, Britain and the American colonies for the following century and began the movement known as Natural Theology, which became especially popular in England.

The Deist position was argued even more forcefully by John Locke (1622–1704) in his challenging *Essay Concerning Human Understanding*, c. 1690, where he rejected the conventional theological view of St Augustine, derived originally from Plato and steadfastly maintained down through the centuries, that our ability to reason and reach valid knowledge depends on ideas implanted by God at birth (*a priori*). Adopting a more radical position than Aquinas and presenting it in a school-room metaphor, Locke asserted that at birth the mind is a blank tablet (*tabula rasa*) and that all human knowledge is written on it throughout life by experience (*a posteriori*). Then, going further, in his 1695 treatise *Reasonableness of Christianity*, he also argued that earthly operations occur solely according to natural laws. Science, for Locke, had to be based entirely on human observation and reasoning inductively from data obtained empirically. Even more radically, he wrote, from that viewpoint it becomes impossible even to speak of divine processes because they are, by definition, beyond empirical confirmation. Committed believers, in significant contrast, were compelled to remain subject to the coercive power of ecclesiastical institutions, especially in Catholic countries where the Congregation for the Doctrine of Faith, the dreaded "Hammer of Heretics" (*Malleus malefactorum*) founded around 1230 and known generally as the Inquisition, continued to be repressive.

Deism developed ever more strongly as the 18th century progressed, and it rapidly spread to France where demands for freedom from ecclesiastical authority and for independence of thought were stimulated by the writings of Voltaire, Rousseau and the *Encyclopédistes*, in particular those by Denis Diderot and the political philosopher Montesquieu. Believing themselves to be particularly enlightened, their writings began the intellectual movement of the Enlightenment, known in France as *l'Éclairissement*, and in Germany as *die Aufklärung*, where Christian Wolff and Immanuel Kant were the major influences.

In Britain, some of the greatest British radical thinkers achieved equal prominence, including economists Adam Smith and Jeremy Bentham, historian Edward Gibbon and scientist Joseph Priestly. It was in Edinburgh, in particular, then Europe's leading intellectual centre, and known as "Athens of the North", where it burgeoned into a brilliant flowering of the intellect. During the aptly named "Scottish Enlightenment", its greatest luminary, David Hume (1711–1776), achieved fame for a number of highly provocative, challenging philosophical works, continuing the pattern created by Locke.

Considered by many the finest philosopher ever to write in English, the leading thrust of Hume's thought was to reject all metaphysical constructions, and to assert the principle of skepticism as the fundamental framework within which scientific inquiry must proceed, based on reasoning solely from observable, natural causes (Hume 1748). Direct knowledge of God, the *via negativa* or apophatic approach of mystics, Hume asserted, is "altogether incomprehensible and unknown to us": our idea of God can only come from observation of "effects that resemble each other" created by the "Author of Nature". Only "by this argument *a posteriori*, and by this argument alone", he asserted, "do we prove the existence of a Deity" (Hume 1779, pp. 700–701). Even causes as such were rejected by Hume who pointed out that causes can never be observed: they are inferences drawn from analysis of a sequence of events. Although he accepted an original Author of Nature, in his view science was the patient investigation of phenomena, gained solely from a multitude of observations through our senses, and the inferences drawn by the association of ideas and valid logical reasoning. Such inferences, he asserted, constitute the totality of all human knowledge. Even more significant was Hume's assertion that nothing is ever completely predictable because so-called scientific truths are constantly overturned as new discoveries, based on observations, continue to be made.

The philosophical position of Hume marked a turning point where Theism and the belief that all creation came according to a Divine Design were becoming forced into apologetic and defensive responses. Henceforth, neither

[6] Literally, God or Nature.

the Inquisition nor the bishops of Copenhagen could direct scientific inquiry along theological channels: geology was to become uncompromisingly Newtonian in approach and many scientists began to use only physical and material concepts to report their discoveries, which became apparent in the continuing geological quest to understand the origin and formation of coral reefs. The impact on subsequent scientific endeavour was to be enormous, e.g. the puzzle of explaining the origin of the extensive relict coral reefs in the French Jura Mountains.

Rational Science and Earthly Operations: Neptunists and Plutonists

Throughout those years of the scientific revolution, the geological issues raised by Steno and Hooke continued unabated, and they reached a climactic phase with the conflict between conservative professors of mining practices and scientists attempting to understand earth processes as natural phenomena. The quest of the empirical scientists was to establish a valid body of evidence to challenge the traditional belief that the rocky earth had developed from precipitation of chemicals within the primeval waters of Divine Creation and in some mysterious way had assumed its modern appearance.

Mining professors were naturally resistant to emerging ideas: their craft had a venerable history reaching back to the Bronze Age 5000 years earlier when ores were first mined, smelted and fashioned into an increasing range of artefacts. As the earth is composed mainly of inorganic crystalline chemical elements and compounds, collectively termed minerals, within which reside a smaller range of elements and compounds with workable qualities of malleability and ductility, known as metals, the mining quest was to discover those places with sufficient concentrations of metallic ores to justify economic extraction. By the time of Agricola in the 16th century, when he presented a remarkable scheme of classification of metals in his 1545 treatise *De re metallica*, along, as mentioned previously, with a short section on corals, mining had become a highly developed occupation with a considerable body of practical knowledge. By the 18th century, schools of mines in Europe, particularly in Germany and Hungary, had become well established, and their approach was to enable students to identify various strata based on qualitative criteria of mineral and metal content, now even more important for the increasing needs of industry as the new machine-based technological era was beginning.

Strong leadership for the conventional miners began in 1775 when, at the age of 26, Abraham Gottlob Werner (1749–1817) was appointed Director of the Freiberg School of Mines. Holding that position for 40 years, he developed a theory of earth formation that eclipsed all others and drew a succession of students from all over Europe, so coming to influence an entire generation. Werner was controversial from the start with his firm belief in the Biblical theory of the original formation of the earth from water, and the ensuing 40-day deluge. In his day, there was no technology for investigating the physical processes within the interior of the earth or for estimating its age; chemistry was still in its early formative stages, crystallography was not to become a science until after the 1850s. How the hard rocks had been formed remained a mystery, but Werner, himself a Deist, was dogmatic in his assertion they had been precipitated from dissolved minerals within the primeval fluid at Creation and subsequently shaped by catastrophes and inundations, from which softer strata had then been weathered.

Unfortunately for the historical record, Werner wrote just two short books, and most of his theory, which he named Geognosy (Gk *geo*, "earth" + *gnosis*, "knowledge"), was generated around Freiberg in the central European regions of Saxony, Hesse, Bohemia and the Erzgebirge (literally, ore-bearing ranges), then the greatest mining region in Europe. Apart from his brief and highly regarded *Von den ässerlichen Kennzeichen der Fossilien* (On the exterior characteristics of fossils), his only work on mineralogy was the *Kurze Klassification und Beschreibung der verschiedenen gebirgsarten* (Short classification and description of various types of mountains) of 1787, in which he classified strata according to their mineral content. In those works, Werner taught that the interior of the earth is cold and that volcanoes are caused by the underground combustion of coal; they are, in effect, mere epiphenomena on the earth's crust that make no significant contribution to its structure and had not existed at the time of original creation.

Beginnings of Dissent: The Influence of Volcanoes

Werner's teachings, however, became increasingly challenged as a considerable body of evidence became coordinated into an alternative theory of earth formation, centring on the role of volcanoes, and expressing doubt that basalt, granite and similar hard rocks had been consolidated from underwater precipitation. Werner, though, had generalized from his limited field experience in Saxony and adjacent Hesse, where all of the accessible basalt lay in elevated strata on the top of hills. Beyond, in the valleys of the appropriately named Massif Central in the French Auvergne, lay the great basaltic formations of the Chaîne des Puys (Chain of Peaks) west of Clermont-Ferrand, of which he had no knowledge. Several decades earlier in 1752, in a *Mémoire* to the Académie Royale des Sciences, entitled *Sur quelques Montagnes de France qui ont été volcani*, Jean Etienne Guettard reported that his study of a number of former volcanoes in France revealed they had been formed by subterranean activity.

Basaltic rocks were central to the entire issue of geology then. One of the most abundant minerals on earth, the growing controversy and heated conflict with Werner arose from the latter's insistence that basalt, the hardest rock on the planet—first named "basalts" by Pliny from the Greek *basanos*, the touchstone against which gold and silver could be tested for purity by their streak, and known popularly as "whinstone"—came from precipitation in the primeval waters of Creation. Yet its chemical composition, dominated by iron, manganese and calcium, from the tests available at the time and confirmed by numerous observations, gave clear indication that it had been formed by fusion at great heat. In search of evidence, for nearly 30 years, between 1766 and 1794, the British ambassador to the Court of Naples, Sir William Hamilton, an enthusiastic student of volcanoes, had made more than 60 expeditions up Vesuvius to observe it erupting and to collect specimens. In the same period, in 1771 Nicolaus Desmaret continued investigations into the Chaîne des Puys and from his observations, and the collections of lava made by Hamilton at Vesuvius, established that basalt and lava are the same mineral: he reported it as so in his *Mémoire sur l'Origine et la nature du basalte à grandes colonnes polygones* (Memoir on the nature and origin of the great basalt columns).

Providing further confirmation were the findings of Peter Pallas (1741–1811), a German in the service of Catherine the Great in the Academy of St Petersburg whose research, in both Europe and Russia, came to advance coral reef studies considerably. In his major work published in Paris in 1782, *Observations sur la formation des montagnes, et les changemens arrivés à notre globe* (Observations on the formation of mountains and the changes effected in the world), he invoked both fire and water as the forces of change, writing that "The operations of volcanoes have continued in different places, especially in the vicinity and at the bottom of the seas up to our own day. It is by their agency that new islands have been seen to rise from the depths of the ocean; it is probably they which raised all those enormous calcareous Alps, formerly coral rocks and beds of shells, such as are still found today in the seas which foster these productions" (Pallas 1782, p. 76). Of great significance in that statement of Pallas is the comment "up to our own day", a theme that rests implicitly in all investigations into the formation of strata. Despite the attempted forcing of science into a restrictive theological mould, it had become clear to all investigators that formative influences were continuing to operate. What remained to be determined were the relative contributions of catastrophes, chiefly volcanic activity and devastating atmospheric events such as cyclones and tsunamis (Japanese, "harbour waves"), and the unseen, mostly subliminal operation of forces deep within the earth.

By the final decade of the 18th century, the debate over earth formation had become seriously polarized. Werner's followers, from their adherence to Biblical doctrine and steadfast belief in post-diluvial rock formation from precipitation, were dismissed by their critics as Neptunists (after Neptunus, the Roman god of water), whereas those who were convinced that the earth's formative processes came mainly from volcanic action were in turn labelled Vulcanists (after Vulcanus, the Roman fire god). Later, with a deliberate sneer, they were derided by their arch opponent, the chemist and fundamentalist Anglican, Richard Kirwan, President of the Royal Irish Academy, as Plutonists (Pluton, the Greek god of Hades). Actually, the latter was a more accurate description, and became the accepted term. For nearly 50 years, from the final decades of the 18th century through the first three of the 19th, the debate continued, often with great intensity, with one crucial element yet to be discovered: the time required to create the earth's rocks and then to model the landscape.

A Radical Theory: Inner Pressure and Geological Processes

Throughout those decades, it was commonly believed that the earth was but 6000 years old. That figure had been calculated by Anglican Archbishop James Ussher of Armagh in Northern Ireland, who, from evidence within the scriptures, determined that Creation had taken place during Saturday afternoon on 10 October 4004 BC. Over four years, 1650–1654, he published his findings in the *Annales veteris et novi testamenti* (Historical records of the Old and New Testaments) and from 1701 the dates he assigned for each biblical event were inserted in the left margin of printed Bibles that were becoming ever more widely distributed as literacy spread. Yet clearly, at least for Plutonists, the figure was far too small. On 7 March 1785 came the greatest challenge to Biblical authority so far: on that day, the first half of a four-part *Dissertation on the System of the Earth, its Duration and Stability* by James Hutton was read to a meeting of the Royal Society of Edinburgh, followed by the second half a month later. That lengthy paper, more than 35,000 words, changed geological thinking forever.

A Scottish gentleman farmer, James Hutton (1726–1797) was an active member of the intellectual circles in Edinburgh that founded the Philosophical Society in 1738 which subsequently evolved into the Royal Society of Edinburgh in 1783. Hutton was on close terms with some of the leading Enlightenment thinkers of the city, especially philosopher David Hume, economist and professor of moral philosophy Adam Smith, engineer James Watt, professor of chemistry Joseph Black and his younger assistant James Hall. That particular group formed a small coterie—the Oyster Club—

which met periodically over a convivial supper to discuss the great issues of the day, of which geology was a major element, especially the debate developing between Neptunists and Plutonists.

On 7 March 1785, Joseph Black read the first part of a dissertation by Hutton to a meeting of the Royal Society of Edinburgh entitled a *Theory of the Earth; or an Investigation of the Laws Observable in the Composition, Dissolution, and Restoration of Land upon the Globe*. In that paper, Hutton set out to show, by a steady, methodical presentation of empirical evidence, that the Neptunian theory was untenable, and that earth processes could only be explained in terms of subterranean heat and fusion. Modelling of the landscape consequently came from catastrophic subterranean activity in which volcanoes were not mere epiphenomena as Werner taught, but general to the globe, and they acted as "spiracles to the subterranean furnace in order to prevent the unnecessary elevation of the land, and the fatal effects of earthquakes", thereby contributing to the formation of convoluted and twisted strata (Hutton 1788, pp. 238–239). In fine Humean fashion, Hutton inferred, from the visible evidence of ongoing processes of surface activity such as natural decay, soil formation, erosion, sedimentation, etc., there had necessarily been "an immense time required for this destruction of the land".

Warming to his central theme, and the evidence of "the relics of sea-animals of every kind in the solid body of our earth" and their orderly deposition, it was essential to put aside the Mosaic theory with its bare 6000-year time frame, which allowed the "beginning of man at no great distance", and clearly lacked congruence with visible evidence. Hutton's sustained argument was based on the abundance of "immense masses, which…appear to have been formed by the calcareous *exuviae* of marine animals". At the top of the Alps, as well as the Andes, shells and corals have been found that must have "been originally formed at the bottom of the sea". The vast calcareous deposits and limestone strata, he argued, were absolute evidence of "some consolidating power by which the loose materials that had subsided from water should be formed into masses of the most perfect solidity" (Hutton 1788, p. 209).

A month later, on 4 April, Hutton personally read the second part in which he examined the various processes that led to "congelation", and drew on the extensive experimental activity of James Watt and Joseph Black, who had already conducted experiments that resulted in crystalline fusion of pyrites, galena (lead sulphate) and quartz, among other ores, at extremely high temperatures. He proposed that there are only two ways by which rocks can become consolidated into hard masses: either by water or by fire, the latter acting by heat and fusion. He conceded that water certainly produced some effects whereby dissolved particles can be precipitated, but, he observed, not all chemical elements and compounds can be so dissolved, citing fluor (fluorine, CaF_2) and sulphurous, bituminous and siliceous compounds. His assertion that "no siliceous body having the hardness of flint…has ever been formed, except by fusion" was a direct attack on Neptunism (Hutton 1788, p. 214). Proceeding to list a large number of other minerals, which had also been fused by experimental heat, Hutton claimed to have proved that "those strata have been consolidated by simple fusion, and second, that this operation is universal in relation to the strata of the earth" (Hutton 1788, p. 225).

Hutton continued to deal with the fundamental issue of earth formation: the Mosaic theory—held by Neptunists as an article of faith—which he dismissed out of hand because there was, as many others before had observed, no place "to provide for the retirement of the waters of the globe". His argument asserted that the "operation by means of which masses of loose materials, collected at the bottom of the sea, were raised above its surface, and transformed into solid land" was simply due to "extreme heat [which] expanded with amazing force" and which continues "at present with undiminished activity…in the fulness of their power" (Hutton 1788, pp. 231–234).

Finally, Hutton covered the cyclic processes observable in the earth, as he termed them, decay and renovation. Those processes, consonant with the thought of the time, were evidence of "order and design, of provident wisdom and benevolence", of the earth, its plants and animals, for the benefit of mankind, ordained by the "Author of Nature" (Hutton 1788, p. 245). The antiquity of the earth was clearly evident: the fossils in the strata of "the former world must have been sustained during the indefinite succession of ages…a system by which they are intended to continue those revolutions". It is in vain, he concluded in his final paragraph, "to look for anything higher in the origin of the earth. The result, therefore, of our present enquiry is that we find no vestige of a beginning, no prospect of an end" (Hutton 1788, p. 255). Deluges and divine catastrophes were rejected as significant agents of change and the Biblical assertion that the earth and all of nature came into existence only 6000 years ago was now challenged by the revolutionary conception of time reaching back through uncountable eons.

Hutton's *Theory of the Earth* was published in 1788, which he elaborated in 1795 in a two-volume *Theory of the Earth* (a third volume was published posthumously a century later). In that subsequent work, the character of his deductive approach is well illustrated in his statement that it was not based on extensive fieldwork but rather generated out of an hypothesis, drawn from the observations of others, and a giant speculative leap: "I just saw it, and no more, at Petershead and Aberdeen, but that was all the granite I had ever seen when I wrote my *Theory of the Earth*. I have, since that time, seen it in different places; because I went on purpose to examine it" (Hutton 1795, I: p. 214). Hutton's two dense volumes were redrafted after his death in more popular, readable form by the mathematician John Playfair in 1802 as "Illustrations of the Huttonian Theory of the Earth" generating considerable support.

Hutton's theory, however, continued to be criticized for the next 20 years, chiefly by Kirwan from a theological standpoint, who attacked it for being atheistic. Some Neptunists, however, following Hutton, were beginning to waver as further proof of fusion from heat became advanced, chiefly by James Hall with the assistance of Watt and Black. In a series of some 500 experiments beginning as early as 1790 and continuing into the 1820s, Hall demonstrated that crushed granite and basalt could be melted in a high-temperature furnace and then allowed to cool slowly. His first significant report appeared in a *Memoir* to the Royal Society of Edinburgh in 1805 (Hall 1805, pp. 43–48), in which he concluded that "the stony character of lava is fully accounted for by slow cooling after the most perfect fusion". The way was now being prepared for the development of a theory of reef formation from volcanism and basaltic earth movements, and the complementary reef processes exhibited in the coral specimens collected by naturalists during their voyages of exploration.

3 Discovery of the Polyp

Before a theory of reef formation based on the work of Hutton and Hall could be developed further, more precise knowledge of corals was required beyond the study of calcified coral skeletons, and that began with microscopes in the early 17th century allowing close inspection of living forms. The precise date of the invention of the microscope, sometime in the period 1590–1610, and the identity of its inventor—whether Galileo, Hans and Zacharias Janssen or Hans Lippershey, or any of their contemporaries—has always been debatable, although the first mention of the word microscope appears in a letter to Prince Federigo Cesi by Johannes Faber dated 13 April 1625 (Fournier 1996, p. 11). By the 1650s, the microscope was being employed more as a curiosity than for explicit scientific purpose because initially it was a very simple device, with little more than a single lens mounted in a short brass tube and having several legs that could be placed over the specimen. The first lenses were probably ground rock crystal given that glass was very poor and full of impurities and had casting defects. Compound achromatic lenses, specimen stages, light sources and other refinements came later.

Despite strenuous opposition by religious fundamentalists as contrary to Divine Will, because they believed it enabled men to peer more closely into nature than God had ordained, and closely monitored by both Catholic and Protestant theocrats, no technology ever invented has been put aside. What remains incontrovertible was the steady application of the new technology to natural history as all western nations embraced the technocratic imperative. The microscope, like the printing press, was no exception.

Early Microscopy: Hooke, Leeuwenhoek and Marsilius

By the mid-17th century, a number of scientists began adopting the simple microscope to pursue their investigations, some of the most prominent in Europe being Marcello Malphigi, Professor of Medicine at Bologna, and Jan Swammerdam, Professor of Medicine at Leiden. In England, it was central to much of the work of Robert Hooke reported in *Micrographia*. In Observation XVII, "Of Petrify'd wood, and other Petrify'd bodies", Hooke reported his fascination with the ordered regularity of nature once magnified: "the Pearl-colour'd substance of the inside of a Shell…seem'd to divide into a multitude of very proportionate and regular *cells* and *caverns*…very perfect and compleat" (Hooke 1665, pp. 110–111). In the following Observation XVIII, "Of the Schematisme or Texture of Cork", he discussed the "cell" metaphor (Lat. *Cellula*, a little chamber) in one of his most enduring contributions to early microscopy, in a lengthy passage in which he described formerly living matter as composed of "pores or cells…[which] consisted of a great many little Boxes" (Hooke 1665, p. 113).

One of Hooke's most innovative achievements came from further discrediting Aristotle's theory of spontaneous generation, already dismissed by Leonardo da Vinci the previous century. Recording his observations of organisms found in infusions of decaying matter in Observation LV, "Of Mites", he stated that he had observed "the least of the Reptiles I have met with" to be laying "seeds" or "eggs" for "the hatching and nourishing their young" and from such locations "the most sorts of Animals, generally accounted *spontaneous*, have their *origination*" (Hooke 1665, pp. 214–215). By the end of the century, that judgement had become accepted by numerous authorities, including Francesco Redi, Antony van Leeuwenhoek, Jan Swammerdam and Marcello Malphigi.

At the same time, however, in Observation XXIII, "Of the curious texture of Sea-weeds", Hooke revealed the scientific ambiguity in that early period of enquiry into nature. Turning to current opinions on "many *Zoophytes*, and sensitive Plants, divers of which I have seen, which are of a middle nature, and seem to be Nature's transition from one degree to another…some Authors", he wrote, provide "Instances of Plants turning into Animals, and Animals into Plants, and the like" (Hooke 1665, p. 124). He had, however, no alternative explanation: simply, he added, "the Omnipotent and

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All-wise Creator might as directly design the structure of such a Vegetable, or such an Animal to be produc'd".

In that era, as the microscope revealed the complexity of nature's architecture, it was confirmed in most minds that discovering the biological relationships of all life, their so-called affinities, would reveal the Divine Design, arranged in a completely interconnected unity. That attitude was clearly evident in Hooke, who, despite his avowed intention in the dedication of *Micrographia* to the Royal Society to follow the Baconian method by "avoiding Dogmatizing, and the espousal of any Hypothesis not sufficiently grounded and confirm'd by Experiments", also praised the microscope as providing evidence to confirm God's will. In one of the most remarkable of his Observations, XXXIX, "Of the Eyes and Head of a Grey Drone-Fly and of several other creatures", he described the eyes of several crustaceans, and was able to present his findings of compound eyes as evidence of "the products of the Highest Wisdom and Providence" of the "All-wise Creator" (Hooke 1665, pp. 177–179). For Hooke's generation, clearly, along with the revealed theology given in *Genesis*, the microscope provided a confirmatory Natural Theology that could be read in the Book of Nature which rapidly took hold in England, unlike France which remained dominated by Catholic doctrine as transmitted through the Regulations of Authority, the *Magisterium ordinarium.*

Following the lead established by Hooke, microscopic investigations into minute organic life forms were pursued with considerable zeal by the Dutch citizen of Delft and court official Antony van Leeuwenhoek (1632–1723). His studies of organisms growing on duckweed in a pond led to a fundamental redirection in the understanding of organic life, and the first significant understanding of the true nature of corals. To make his observations, Leeuwenhoek used some of the 26 microscopes he had constructed with tiny lenses scarcely larger than a grain of rice held firmly between two metal plates attached to a board, employing a simple metal pin to hold the specimen and an adjustable screw to move it into focus. Leeuwenhoek was always reticent about providing details of his microscopes, although surviving models reveal remarkable magnification powers ranging from ×40 to nearly ×133 (Dobell 1932, p. 319), with one lens having the extraordinary resolution of 1.35 μm, i.e. the ability to discriminate two points no more than 0.00135 mm apart (Ruestow 1996, p. 14). Fellow citizen Reinier de Graaf urged him to send his investigations to the Royal Society of London, whereupon Leeuwenhoek commenced a sustained correspondence in 1673 with its secretary, Henry Oldenburg, and then with Nehemia Grew. Consequently, nearly all of his more than 400 surviving letters, most written in Dutch because Leeuwenhoek had little Latin, remain in the archives of the Royal Society, from which a selection was translated and then edited and published (Dobell 1932).

Of preliminary relevance to the coral issue was Leeuwenhoek's investigation in 1674 of what he took to be aquatic plants attached to the stems of duckweed. His curiosity aroused, in Letter 6, he described how on some of them he "saw two little legs near the head and two little fins at the hindmost end of the body". Numerous similar observations followed and in his famous Letter 18 of 9 October 1676, in which he described at length the large number of aquatic creatures and other "animalcules" (from the commonly used Latin diminutive *animalculus*, little animal) he had found in rainwater, river water and seawater during an extended period of investigation.[1] One of his most significant findings, reported in Letter 149 of 25 December 1702, was the plant-like budding by one particular green organism, barely 10–20 mm long and the thickness of a hair, which he believed could be evidence of animal nature. In his report, he described it as growing "two little horns" that continued to increase on either side into four, of which two were "much bigger; and at last the little animals stuck out at full length…another three hours later [one of them had] gone off from his mother". Although plant budding and grafting was well understood in horticultural practice, Leuwenhoek's astonishing account, the first recorded observation of animal reproduction by budding, which in effect was a description of one form of parthenogenesis, failed to elicit any significant response among the scientific community, despite having been reported in the 1703 issue of the *Philosophical Transactions*.[2]

For several decades, Leeuwenhoek continued to produce a remarkable range of reports dealing, *inter alia*, with his observations on a considerable diversity of materials including blood, milk, fat, the optic nerve, seeds, duckweed and red coral. One of his discoveries, which would have profound ramifications throughout the following 18th century, was identification of the human spermatozoon, later believed by some to be a miniature adult which grew simply by increasing in size and not by differentiation of tissues, leading to the theory of preformation. Named by Nicolaas Hartsoecker as "homunculus" (Latin diminutive of *homo*, tiny man), it led to a bizarre era of speculation on forms of human generation until it was finally discredited in 1759 from the pioneer embryological research of Caspar Friedrich Wolff.

The next significant development in the microscopic study of marine life came from an Italian nobleman and military commander in the service of the Emperor Leopold of Austria, Luigi Fernando Marsigli di Bologna (1638–1730)—known in Latin as Marsilius—who wrote in French under the name Louis Ferdinand, Comte de Marsilli. Following his military campaigns in the Danube, in retirement and as a

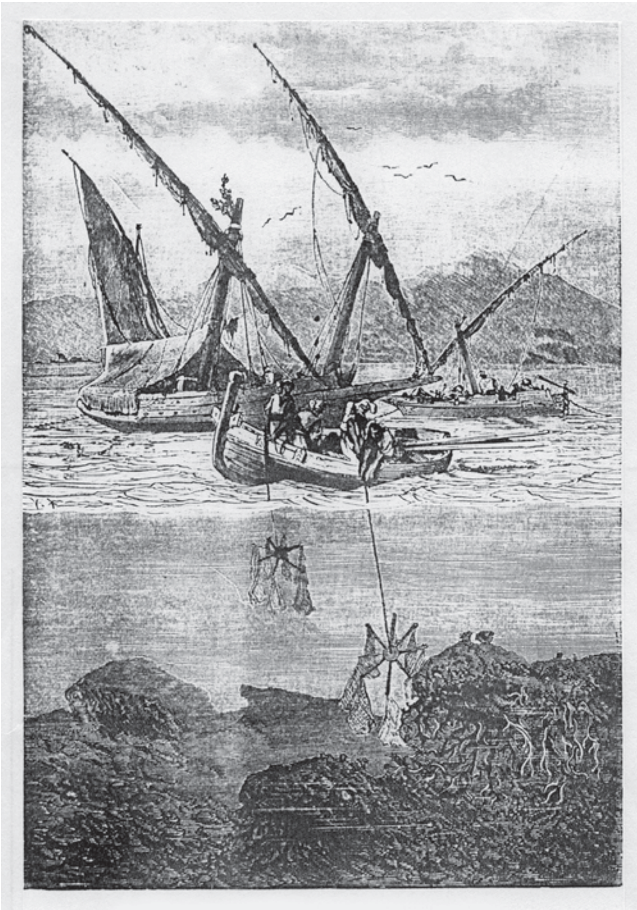
[1] *Philosophical Transactions of the Royal Society* 1677, XII, p. 133, 821–831; letter reproduced in Dobell 1932, p. 117f.

[2] *Philosophical Transactions of the Royal Society* 1703, XXIII, p. 283, 1304–1311.

Collecting red coral in the Mediterranean, early 17th century. Note the use of goggles

lifelong student of the sea, he devoted his energies to natural history, founding the Accademia delle Scienze dell' Instituto di Bologna in 1712. His crowning work came in 1725 when he published the world's first treatise on oceanography, *Histoire Physique de la Mer* (Natural History of the Sea) which dealt with tides, currents and properties of water, and the first detailed description of corals appears in a section of Part 4 (Natural History of Stony Plants) under the heading *Du Corail*. It was a very detailed, 68-page study of corals, with botanical descriptions of the species examined within the appended catalogue of *Des Madrepores*, illustrated with a large number of high-quality steel engravings. As the title of Part 4 indicates, Marsilius, familiar mainly with soft corals which are widely distributed even in cool temperate waters, was convinced that corals were plants and not simply mineral formations resembling plants that had been shaped by mysterious "petrifying agencies". Corals, Marsilius asserted, had a true vegetative character, citing himself as one of the "most modern of observers…which he would prove in the following pages". Enlisting the aid of *corailleurs* to retrieve specimens from the depths, all of which were the soft, flexible varieties, and following Imperato in calling corals "madrepores", he searched for characteristics that he believed met all the criteria of plants. Their external form obviously resembled plants, and he identified what he believed to be calices, branches, leaves, bark and roots, all of which he studied closely with the aid of the microscope (Marsilius 1725, p. 106). By squeezing the stems, he could force out a liquid similar to that in milk thistles, confirming his belief that the outer covering was bark.

Marsilius' major achievement, however, was the first-ever identification and description of the flowers produced by coral stems. Placing living specimens in vases of seawater, he began to observe their behaviour. After several hours, a white flower emerged from each opening, revealing a stem with eight petals, the formation having the beauty and outward appearance of a spice clove: *au bout de quelques heures on voit de châque Tubule sortir une fleure blanche, ayant son pedicule, & huit feuilles, le tout ensemble étant de la grandeur, & figure d'un clou de girofle* (Marsilius 1725, p. 115). He then observed that touching the extended "flowers" caused them to retract instantly (*toutes les fleurs se retirent dans les Tubules*) and how, after a time, they came back out. With most probably a hand lens (*si alors on les regarde promptement avec une verre*), he believed that he had verified their floral character from the radial pattern of the eight extended equal-length "petals" (using the term *feuilles*, leaves, rather than the more precise *pétales*). The flowers lasted in their vases, he recorded, for around 5 or 6 days, some up to 12. To test his theories further, he extracted the contents of the coral stems, and by chemical analysis found that they produced an odour similar to cabbages and other plants of the family Brassicaceae. He concluded his study of corals with a final assertion that he had proven, incontrovertibly, that corals were genuine plants growing according to the laws of nature: *si étoient de veritables Plantes, qui vegetassent dans un ordre reglé*. The conclusive evidence came from their possession of flowers, and his own investigations as *le plus moderne des Observateurs* (Marsilius 1725, p. 106).



Red coral harvesting in the Mediterranean with the *Croix des corailleurs*, showing the hempen nets suspended beneath the boats

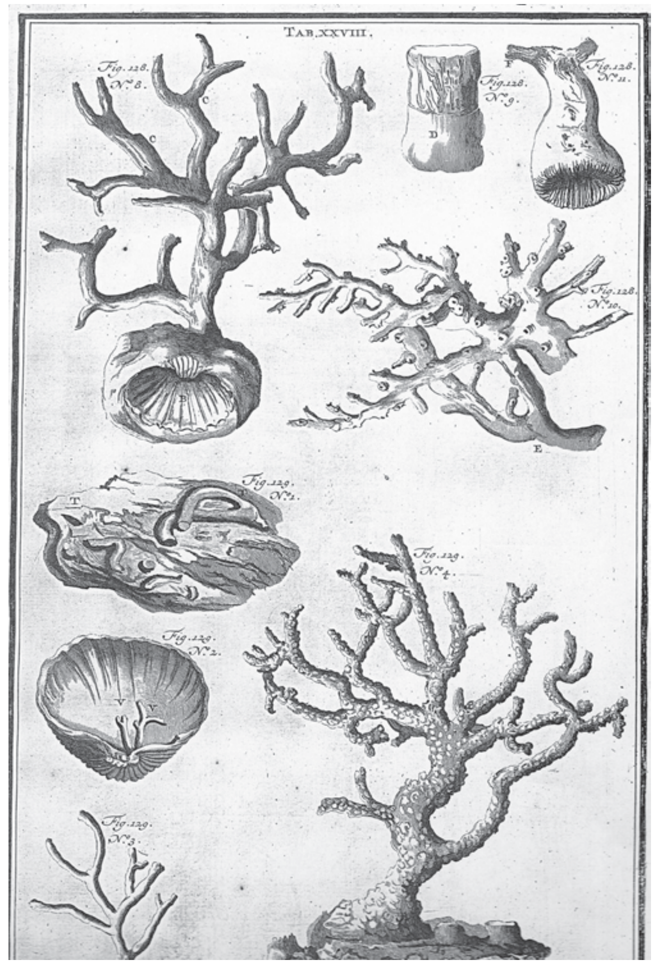


Plate from Marsilius' *Du Corail* of 1725, to emphasize the floral character of coral

At the time, Marsilius' treatise was very persuasive and met with wide acceptance. He was invited to London to receive a fellowship of the Royal Society, and Sir Isaac Newton himself insisted on making the award. His work was definitely an advance: he had disposed of the belief that corals are simply mineral constructions and established that they were living organisms.

Turning Point: Peyssonnel, Trembley and Direct Experiment

Contemporaneous with Marsilius was Jean-André Peyssonnel (1694–1759), who set enquiry in an opposing direction, which engendered considerable controversy, in fact, hostile opposition. A physician in Marseilles, Peyssonnel spent his free time pursuing his great love of marine studies. After a plague in 1720 killed many of the city's inhabitants, his considerable efforts to help the victims were rewarded with a royal pension. Now of independent means, Peyssonnel was free to continue marine studies in his chosen location of North Africa—the Mediterranean region then known as the Barbary Coast—where, as he recorded, he was required by the king to report on its marine natural history.

Having read the work of Marsilius concerning coral "flowers" with reservation, he decided in 1723 to check the conclusions personally and went with *corailleurs* to collect samples for direct experiment. Going beyond the simple observational methods of Marsilius, he manipulated specimens in various ways and conducted a number of tests, beginning by heating the water and noting that, like shellfish, they expanded and stayed out as temperature rose. He then dissected them to determine their structure and the arrangement of the eight radial "petals". After letting them die out of water, he recorded that their putrefaction gave a repulsive odour like burning animal horn (*une odeur très désagréable, approchant de celle de la corne brûlée*). Finally, he tested them chemically with various acids to observe responses, which he found were exactly the same as those made by other marine animals.[3]

[3] Peyssonnel (1744, I, pp. 44–47); partly reproduced in Milne-Edwards (1857, p. XVII).

In 1726, Peyssonnel sent a résumé of his research and conclusions to Abbé Jean-Paul Bignon, president of the Académie des Sciences in Paris, claiming a totally new discovery. Expansion and contraction, he asserted, were evidence of animal behaviour: the sap of the bark was really the blood or natural fluid of insects arranged along the stem (*le lait ducorail est le sang ou le suc naturel de tous les insectes placés le long du corail*). Most importantly, as Imperato had hypothesized, the cavities were the abode of stinging corals (*Ces cavités sont les niches ou le séjour des orties corallines*); and the petals were in fact "claws… which they occasionally protrude from their cells, and seize their prey, as it passes by them; and thus they are nourished, and increase, according to their particular mechanism and construction" (Peyssonnel 1744, II, p. 97; Milne-Edwards 1857, p. XVII).

From his dissections, Peyssonnel discovered that all the minute animals, unlike plants, had exactly the same biological structure and differed only in size and shape. He was also the first to record qualitative differences between the stem structure and function of two major groups, the flexible so-called soft corals with eight "petals"—*Antipathes* (red and black corals) and *Lithophitons* (Gorgonians)—and the stony, hard, inflexible, reef-building corals with six "petals". "*Le corps de l'Antipathes*", he recorded, "*est souple et pliant, qualités differentes du corail qui est pierreux, dur, inflexible*". Bignon, in turn, sent the paper to René-Antoine Ferchault de Réaumur for an opinion; he was the most influential member of the Academy and regarded as France's greatest living scientist and an authority on insects. Réaumur was sceptical, in fact totally disbelieving, because like all others he believed that Marsilius had settled the question in his *Histoire Physique des Plantes pierreuses* and that no one would accept the insect theory. At the time too, Réaumur was investigating animal life in a study that had been published in 1727 in the *Mémoirs* of the Paris Academy under the title *Observations sur le formation du corail et des autres productions appelées plants pierreuses* (on corals and other plants called lithophytes) (Réaumur 1727). Even so, with great reservation, he agreed that Peyssonnel's paper could be read, but acting from the best of motives to save him from humiliation following the expected rejection, Réaumur suggested that it be presented from an anonymous correspondent. Peyssonnel agreed, and as Réaumur predicted, it was greeted in 1727 with howls of derision. Coral reefs the production of insects? Nothing more ridiculous could be proposed.

Peyssonnel, however, whatever his personal feelings, was not crushed, and persisted with his enquiries, but not on the Barbary Coast. The same year, he accepted appointment as *Médecin botaniste* (Royal Botanist) to Guadaloupe in the French Caribbean Lesser Antilles islands, where he married, raised a family and lived for the rest of his life. While there, in an ideal location for coral studies with a wider range of species, he pursued for 25 years his belief that he had correctly determined the animal nature of the coral-forming organism and that reefs were limestone structures created by "insects" living in large colonies.

While Peyssonnel was conducting further investigations in the Caribbean, a totally different development, with profound implications for the study of coral "insects", was taking place in the country estate of Count William Bentinck at Sorgvliet, a few kilometres outside The Hague in what is now the Netherlands. By that time, with the notion of spontaneous generation having been discarded, developments in microscopy stimulated a great interest in the animal nature of minute organisms found in pond and river water, now named Infusoria from their provenance in infusions of decaying matter by Hooke in 1665 (Hooke 1665, p. 214). The resident gentleman naturalist Abraham Trembley of Geneva (1710–1784), essentially tutor to the count's two sons, had begun observations on pond life in 1740. Like Leeuwenhoek, of whose earlier findings he was unaware, he had come across some small bright green organisms attached to stalks in nearby ditches which he collected, placed in large jars of water on the windowsill of his study and began observing. Exhibiting behaviour he had not observed previously, Trembley's curiosity was aroused, and with the aid of a hand lens, he noticed them moving in the water, clustered on the sunny side of the jar. Reversing the jar, he found they returned to the sunny side. Projecting outwards were the same small hair-like processes described by Leewenhoek that Trembley called "arms" (Fr. *bras*), varying in number from 4 to 12, and which waved around, even when the body remained stationary. On being touched, just like the horns on snails with which he was familiar, they instantly retracted. "This contraction", he wrote, "and all the movements that I saw them make when they extended themselves again, awakened sharply in my mind the idea of an animal".[4]

So began a series of experimental observations to discover whether they were some kind of aquatic plants, or possibly, as he speculated, little insects. The first test was to cut them up and see what happened. The results astonished him: the cut pieces regenerated into complete wholes and attached themselves to the stems, identical with the original organism. "I no longer found any difference between the second part and one that had never been cut. When I observed them with a magnifying glass…each of the two appeared perceptibly to be complete, and they performed all the functions that were known to me: they extended, contracted, and walked".[5] Even when sections of the tube-like animal were turned inside out, they continued to regenerate.

[4] Text from Baker (1952, p. 29).

[5] Text from Baker (1952, p. 32).

Because each animal, as he was now certain they were, grew new parts even after being cut many times, even longitudinally and thereby growing two separate heads, he reached back into classical mythology to the legend of Hercules who had the task of cutting off the head of the dreaded snake, the Hydra. No matter how many times Hercules cut it off, other heads grew. Therefore, Trembley found a name for Leewenhoek's "animalcules": hydra.

Pursuing his investigations and finding increasing supportive evidence, Trembley sent his observations to Réaumur who was most intrigued and replied in early 1741 giving the animal another name: *polipe*, later *polype* and finally polyp, borrowed from the classical Greek word *polypous* (many feet) of an octopus, to describe the fine, hair-like mobile appendages around the head.[6] That was the first use of the word polyp, applied generically at the time to many zoophytes. Réaumur urged Trembley to publish and included Trembley's preliminary investigations of 13 December 1740 in the preface to his own *Mémoires pour servir d'histoire des insectes* in 1742. Unlike the lack of response to Leuwenhoek's description of the budding of hydra in the *Philosophical Transactions* of 1702, Trembley's discovery created widespread interest: the Royal Society wrote for further information and discussed it at two meetings in January 1743. Trembley presented his pioneering work in a monograph of 1744, *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce, à bras en forme de cornes* (Observations on freshwater polyps, with hornlike arms). Four months later, he was elected a Fellow of the Royal Society and awarded its highest tribute, the Copley Medal, with his discoveries printed in the *Philosophical Transactions*.[7]

That *Mémoire* created a major change of direction. Trembley had not only finally determined the animal nature of hydra, but, as he made clear in the preface on hydra or *polypes d'eau douce* (freshwater polyps), he had distinguished them from *polypes de mer*. Trembley's findings had confirmed the animal nature of marine corals determined by Peyssonnel, previously rejected by the Académie des Sciences. Réaumur was convinced that Peyssonnel had been right all along, and readily admitted his error, writing in the *Introduction* to Volume 6 of his *Histoire des insectes* that "the care taken by Monsieur Peyssonnel in making his observations should have convinced me sooner that the flowers, attributed by Count de Marsigli to the various productions…were really little animals". The Paris Academy accepted the accuracy of Peyssonnel's work and elected him a Corresponding Member. As Peyssonnel was to write later, confirming the efficacy of the Baconian empirical approach, "experiments are the only way of assuring ourselves of the truth…what Marsigli took for flowers were truly insects".[8]

Meanwhile, by 1744, Peyssonnel had completed his exhaustive research in a huge treatise of more than 400 pp. under the title *Traité du Corail*. Clearly hurt from his rejection by the Paris Academy of Sciences in 1727, and having received significant support from the Royal Society of London, he sent his treatise from Guadeloupe to one of its fellows, Dr William Watson, who translated and read a 25-page précis to their meeting on 7 May 1752. With masterly understatement, Watson commented in his presentation that "M. de Peyssonnel's discoveries…[reported to] the Royal Academy of Science in Paris…were not much attended to". The Royal Society published a short abridgement,[9] but the full text was never printed, the autograph consigned to the archives of the Bibliothéque du Muséum d'Histoire naturelle. Fortunately, a century later, as coral research intensified, some of the essential passages were rescued by French marine scientist Henri Milne-Edwards and included in his magisterial *Histoire naturelle des Coralliaires* of 1857.

Even so, there was still great resistance to the notion that coral reefs were constructed by animals. Voltaire satirized the findings of Trembley as similar to attempting to prove that twigs cut from trees which took root were therefore animals, and more serious opposition came from naturalists who continued to believe that coral polyps, along with other marine organisms, were genuine intermediate forms, zoophytes. That word, in the absence of any demonstrative proof, was a useful hybrid because its Greek provenance from *zōon* (animal) and *phytos* (plant), introduced by Gyllius back in 1535, dealt conveniently with the ambiguity that was unresolvable then. Once revived in that period of controversy, it continued to be employed as a wide-ranging taxon, even though it was becoming more generally understood that many zoophytes were animals. The problem now was to determine exactly the type of animal that zoophytes were. What was their relationship to all other animals within the Divine Design so carefully and comprehensively constructed by the Author of Nature?

A Platonic Legacy: The Great Chain of Being

In their foundation years, the interests of the scientific societies had been focused on attaining a more exact understanding of the relationships linking the natural world, which, by the 17th century, had become conceived as a

[6] Trembley and Guyénot (1943), *Correspondance inédite* 63; Dawson (1987, p. 105).

[7] Philosophical Transactions of the Royal Society 1744, 42, pp. 281–282.

[8] *Philosophical Transactions of the Royal Society* 1751–1752, 47, pp. 449, 452.

[9] *Philosophical Transactions of the Royal Society* 1751–1752, 47, pp. 445–469.

Great Chain of Being: a single integrated structure of life exemplifying God's Creation. That was the intellectual and political context within which natural history proceeded: in the words of Thomas Sprat, first historian of the Royal Society of London, in referring to its motto, *Nullius in verba* (trust nothing in words), it became a quest by means of empirical observation and experiment "to follow all links of this chain, till all their secrets are open to our minds" (Sprat 1667, p. 110). The concept of the Great Chain of Being, though, was no sudden discovery: its earliest expression appeared in Plato's dialogue *Timaeus*, named after the central character, in which he developed his theory of the formation of the existent, visible world. To explain, Plato employed a creation myth to set the scene. In the beginning, he related, the physical earth was in a "discordant and disorderly" condition (*plemmelos kai ataktos*). Desiring that all should be in harmony, the creative "architect" (*tektainomenos*) without any suggestion of a Biblical anthropomorphic god such as we find described in *Genesis* 1.27,[10] arranged all life in perfect, complete, natural succession. Consequently, the cosmos appeared as a living being, endowed with soul and intelligence, whereas every idea in the mind of the architect became manifested in physical form as plants, animals and humans, with no empty spaces.[11]

In the 3rd century AD, the "ideas in the mind of the architect" were hypostatized by the philosopher Plotinus as "the thoughts of God". Underlying the form of every visible object, he wrote in his *Enneads*, an idea (Gk *eidos*) or archetype, which emanated from the "will of the Divine Creator."[12] At that time, Christian church fathers, particularly St Augustine in the late 4th century, felt a pressing need to secure strong philosophical support among the educated classes for the new creed of Christianity. Consequently, the Neoplatonism of Plotinus (c. 205–270), with further glosses by Augustine, became a significant foundation doctrine of Christian belief.

As described in Latin medieval terms, the Creator had furnished the universe with a complete range of forms: a *plenum formarum*, organized into a Great Chain of Being (see Lovejoy 1936). That belief system, as investigation into natural history accelerated in the 17th century and continued throughout the 18th and 19th centuries, and became an endeavour to uncover every detail of divine creation: to repeat the words of Thomas Sprat, "to follow all links of this chain, till all their secrets are open to our minds".

[10] *Genesis* 1.27: "So God created man in his own image, in the image of God he created him."

[11] Timaeus Section 30 paragraphs b and c: *"ton kosmon zoon empsychon ennoun te ti aletheia dia ten theou genesthai pronoian"*.

[12] Plotinus, *Ennead* V, 1.4.

The Pattern of Nature: Linnaeus and Systematic Classification

Although new insights into the nature of corals continued to be reported, with an increasing number of scientific societies and journals providing a forum for their dissemination, taxonomic issues remained: How could the still uncoordinated discoveries of numerous types of marine plant and zoophyte become organized into meaningful relationships in order to form a unified body of scientific knowledge? What was the fundamental structure of all natural phenomena? How did the world of everyday reality reflect the Divine Design of the Author of Nature? Where did zoophytes fit within the Great Chain of Being?

In the same years that Trembley and Peyssonnel were reporting their findings, a new descriptive approach to classification was being proposed by Carl von Linné (1707–1778) of Sweden. As a medical student at the University of Upsala, in conjunction with fellow student Peter Artedi, Linné conceived the grand idea of a comprehensive encyclopaedia of all living beings arranged and described in natural order according to the principles of Divine Creation. Tragically, Artedi died soon after in a drowning accident, leaving Linné to continue the quest, a task to which he devoted his remaining four decades of life.

Linné, who Latinized his name to Linnaeus to accord with the universal language of science, was essentially a botanist, a passion he held all his life, and from which he drew his inspiration, turning particularly to his predecessors Andrea Cesalpino (1519–1603), Director of the botanical gardens in Pisa, and John Ray (1627–1705), Fellow of the Royal Society. In *De plantis libri* XVI (On Plants, in 16 books) of 1583, Cesalpino, following Theophrastus two millennia later, had attempted to move beyond the pharmacological listing of particular qualities (*accidentiae*) for possible therapeutic value to discover the essential qualities and natural affinities (*differentia characteristicae*) exhibited in the structural patterns of trees, shrubs and herbs. From the examination of such definitive characteristics as seeds, leaves and flowers, Cesalpino attempted to determine related groupings of genera and species and thereby discover each ultimate unit of creation, the *infima* species.

Ray, author of a number of influential works, *Methodus nova* (1682), *Historia plantarum* (1686) and *Methodus emendata* (1703), continued that task and identified flowers, and therefore the reproductive seeds, as the determining criterion of plant organization, thus establishing the botanical research pattern for the future. From their efforts, subsequently, the first detailed mapping of all botanical creation was attempted by Linnaeus under the term "system", later named "taxonomy" by the Swiss naturalist Augustin de Candolle in 1813, who continued Ray's quest to discard the fanciful and anthropocentric categories of previous eras and put natural history into some kind of methodical order.

In all his scientific activity, Linnaeus worked within the unquestioned 2000-year-old Aristotelian assumption of a *scala naturae*, now comfortably accommodated within Christian belief of a divinely designed universe, with all species in place at the moment of Creation. His approach, as developed in his *Philosophia botanica*, the first modern exposition of a philosophy of nature, was, in many ways, close to Spinozan pantheism, which viewed nature as the immanent Deity—and had achieved realization in the *plenum formarum*—in complete and perfect series. His task, Linnaeus believed, was to discover and reveal to humans the natural system: the order in which all species had been created, and were fixed for all time.

Following Ray, Linnaeus identified the visible generative organs of plants, stamens and pistils as the basis of his botanical classification, and in the first edition of his *Systema naturae* published in 1736 (Linnaeus 1736), his "Key to the Sexual System" introduced the unfortunate metaphor of "marriages" of plants as the organizing criterion for sexual union. Flowers can have 1–20 or more stamens, which he identified as male organs, and usually one pistil to hold the seeds that he called a *gynoecium*, Greek for women's quarters (*gyne*, "woman" + *oikos*, "abode"). His schema therefore listed such relationships as females in bed with one or more males, even many males (Gk *polyandria*, "many men") and clandestine marriages, whereas plants with scarcely visible flowers were called hidden husbands: *cryptogamia* (Gk *kryptos*, "hidden" + *gamos*, "marriage partner"). Barely published, his system aroused violent moral condemnation from conservative bourgeois readers because the relationships he identified within nature "would never have been allowed by the Creator", the *Systema naturae* was condemned by botanist Johann Siegsbeck as licentious and "loathsome harlotry", and it was banned from the sight of carefully bred young women.

Learning from that *faux pas*, in his more diplomatically expressed *Species plantarum* of 1753, Linnaeus expanded his taxonomy to 25 discrete classes to include algae and lichens, whose sexual characteristics could not be readily identified. As some algae, the Melobesiae, are calcareous and therefore superficially indistinguishable from corals, considerable confusion existed in arriving at a definitive scheme. Always thinking as a botanist, Linnaeus also attempted to determine the natural classification of the entire animal kingdom. To effect this, he created a vast network of more than 600 informants throughout the world of natural science, scouring every journal article possible and corresponding with his contemporaries, including all the leading coral researchers: Peyssonnel, Trembley, Pallas, Ellis, Lamarck, Lamouroux, Marsilius and Réaumur. From 1735 on, his taxonomy was continually enlarged through successive editions as ever more discoveries were reported from around the globe.

The taxonomic problem with which both Ray and Linnaeus were grappled, however, was one of the most intractable problems confronting all naturalists: What exactly is the nature of reality? In effect, is taxonomy a classification of phenomena (appearances) or noumena (ideas)? Whether species have an independent existence, or are merely mental artefacts, however, remains an area of considerable debate.[13] The task for Linnaeus was unattainable, and by 1750, he was forced to realize that nature could not be arranged in serial order and that he was unable to devise a natural system based on precisely identified affinities (genetic relationships). His recourse was to an alternative, but very effective, artificial system of information classification and retrieval from an identification key of sexual parts. His original slim volume of 1735 passed through continuing revisions as increasing numbers of species were described, reaching definitive form for plants in the fifth edition of the *Genera plantarum* in 1754, and for animals in the 1758 tenth edition of *Systema naturae* (Linnaeus 1758), which changed natural history forever. These became the foundation works of a new taxonomy in which he created the binomial system of species classification, which was progressively refined in a sequence of revisions throughout the 19th and 20th centuries to the current fourth edition of the International Code of Zoological Nomenclature of the year 2000, and the 2005 International Code of Botanical Nomenclature.

Today, it is for his pioneering work in taxonomy, and chiefly the binomial system, that Linnaeus holds his place in the history of science. Of primary significance was the introduction of Latin, and an extensive range of Greek borrowings for which there were no Latin terms, for all description. Linnaeus thus created a common language through which scientists could now communicate, replacing the multitude of vernaculars across Europe, many of which were inadequate for scientific purposes. And the Latin was neither classical Ciceronian, nor medieval Chancery nor Renaissance revival, but a spare version designed for recording and not for discourse, dominated by descriptive nouns and adjectives with numerous neologisms, simplifying the task of investigators. As a guide, each succeeding edition of his *Systema naturae* after 1758 contained an Appendix entitled *Caroli Linnaei, Sveci, Methodus* (The Method of Carolus Linnaeus, of Sweden), organized into seven sections with details on the correct form of describing and the pertinent features to be included.

"Describing" in itself is a complex procedure that has strict protocols to be observed. Although no precise order has to be followed, the description must identify the family and genus of the new specimen and previous reports and be sufficiently detailed to separate it from all others with which

[13] The incredible complexity of species taxonomy at the present day is covered by one of the world's leading coral taxonomists in Veron, 1995, *Corals in Space and Time*, Chapter 4, Species Concepts and Species Diversity.

it shares affinities. Turning, for example, to *Fungites*, the mushroom coral or *fungia* species, Linnaeus described it as *Madrepora simplex acaulis convexa, lamellis simplex, habitat in M. Mediterraneo* (a single convex Madrepore with one opening and simple plates, found in the Mediterranean) (Linnaeus 1758, p. 793). As the decades progressed, discoveries multiplied, and finer degrees of species identification were achieved, so descriptions became more complex and detailed.

The Foundation of Animal Taxonomy: The *Systema Naturae*

In 1758, the *Systema naturae* became the fundamental reference work for all zoological reporting. A lengthy Latin publication of 824 pages, the title page, in full, reads: *SYSTEMA NATURAE, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (A systematic organization of all three kingdoms of nature, arranged into classes, orders, genera and species, with their characteristics, differences, synonyms and habitats). In six sequential sections, the first four covered all known vertebrates: mammals, birds, amphibians (including reptiles) and fish, and the other two dealt with invertebrates, designated simply Insecta (Lat. *inseco*, cut-up, notched) and Vermes (Lat. worms). The section on insects approximated modern categories, but in Vermes, he collected everything else, virtually unknown at the time, that could not be placed in distinctive categories, and which he characterized as "imperfect" and "slow moving". In that section, he placed worms, molluscs, lithophytes, zoophytes and, in the 12th edition of 1767, four genera of the newly discovered "mysterious living molecules" of single-celled protists: *Volvox*, *Vorticella, Chaos* and *Furia*.[14]

Of significant interest here is a seemingly innocuous passage at the bottom of an introductory page, which had implications for coral taxonomy for decades to come. The three kingdoms referred to on the title page are *Lapides* (Rocks), *Vegetabilia* (Plants) and *Animalia*, but mention of the three is preceded by the phrase *Regna Naturae in tria divisa, quorum limites concurrent in lithophyta.* In translation, that reads that "The Kingdom of Nature has three divisions, although all three co-exist in the lithophytes" (Linnaeus 1758, p. 6), a reference to the calcified character, floral appearance and presumed vegetative stems of many "imperfect" taxa. Linnaeus was at the time in the early stages of pioneering plant and animal taxonomy and a vast range of organisms remained to be described, the corallines being particularly difficult because their generative organs are hidden (*cryptogamia*) so are not amenable to sexual identification. The taxonomic problem, however, remained, and despite the incontrovertible evidence by Trembley and Peyssonnel, both of whom acknowledged that zoophytes are animals, Linnaeus could not shake his conviction that at least some species, the "corallines", were not entirely animal in nature (Linnaeus 1758, p. 642).

On 16 September 1761, Linnaeus wrote to correspondent John Ellis, who was also pioneering coral taxonomy, expressing his conviction that zoophytes have but "a mere vegetable life, and are increased every year under their bark, like trees, as it appears from the annual rings in a section of the trunk of a Gorgonia. They are therefore vegetables, with flowers like small animals. As zoophytes are, many of them, covered with a stony coat, the Creator has been pleased that they should receive nourishment by their naked flowers. He has therefore furnished each with a pore, which we call a mouth."[15] Soon thereafter, following Ellis in devising the analogous term *Actinia sociata* (clustering star-like flower) from the radial pattern of the tentacles for one species of soft coral, Linnaeus classified them collectively, in subsequent editions, as they remain to this day, as anthozoans (Gk *anthos*, "flower'' + *zōon*, "animal''). This category included the highly prized red coral of antiquity, which he named *Corallium rubrum*.

In an attempt to resolve the vexing problem of determining animal nature while retaining the concept of coexistence, Linnaeus began by separating Class VI, *Vermes*, into two Orders: Lithophyta and Zoophyta. Accepting Lithophyta as a historically established term for the hard, reef-building species,[16] they were defined as *Animalia Mollusca composita, pullulantia e Corallio Lapideo subjecto, cui inserta, quodque aedificant*, which, translated, means "composite animal molluscs, with flowers on a stony stem, which it builds itself". These he separated into three genera of Animalia: Tubipora, Millepora and Madrepora, citing as authorities Marsilius, Peyssonnel, Trembley and Ellis (Linnaeus 1758, p. 642). All other organisms were placed in the composite Order Zoophyta, justified by the famous quote from Pliny that they are neither animals nor plants but are possessed of "a third nature" and so were described as *ZOOPHYTA composita Animalcula, in bivio Animalium Vegetabiliumque constituta*: ZOOPHYTES, a composite small organism, with both animal and plant characteristics (Linnaeus 1758, p. 643). Here, under the section heading *Animalia composita, efflorescentia, Stirps vegetans* (composite flowering animals with a plant stem) were placed the so-called soft corals: *Isis, Gorgonia, Tubularia, Eschara, Corallina, Sertularia, Hydra, Pennulata, Taenia* and *Volvox*, most of which were relocated in later revisions.

[14] Linnaeus was mistaken: *Volvox* is a spherical multicellular alga, a fact corrected in a later edition.

[15] Linnaeus, Letter 2955; Smith (1821, I, p. 151).

[16] Linguistic usage readily accommodates oxymoronic hybrids: Modern English, for example, finds no difficulty with the term "cotton wool".

Corals as Animals: John Ellis and a New Taxonomy

Throughout the late 17th century and the early decades of the 18th century, the work of Leeuwenhoek, Trembley and Peyssonnel, in contradicting the received tradition of stony formations and lithophytes, had created an era of sustained instability in natural history. It was becoming essential among naturalists to determine finally the status of zoophytes, particularly given the ambiguous definitions in the *Systema naturae*, and that came in the work of John Ellis.

All naturalists and their patrons in the formative period of coral studies had to be wealthy and self-employed, some coming from the nobility, such as the Dowager Princess of Wales, the Duke of Richmond (who entertained Trembley in England) and Count Marsigli, and some who were classed as "gentlemen", a term designating those with private incomes and an avocation for extended leisure pursuits. Irish-born John Ellis (1710–1776) was an accepted gentleman of the inner circle: Fellow of the Royal Society, botanist for Kew Gardens and a wealthy London merchant who devoted virtually all his time to coral research. Concentrating chiefly on the cool temperate waters around the British Isles, Ellis employed collectors, illustrators and engravers, and had the means to print his monographs privately.

Working contemporaneously, but independently of Peyssonnel, whose work he was following closely, Ellis set himself the task of attempting to bring order and clarity into the masses of findings that were accumulating. At the time, the zoophyte of Linnaeus was a term still being used to describe a much wider range of related organisms including hydroids, anemones, sea-mats, sponges and sea-pens, many of which have a strengthening concentration of lime in their bodies. It was that calcified characteristic, discovered in his primary inspections of the specimens collected off Dublin and the nearby island of Anglesea off the northwest coast of Wales, which convinced him "the Subjects themselves…which had hitherto been considered by Naturalists, as Marine Vegetable, were in Reality of Animal Production" (Ellis 1755, p. vii).

In 1755, Ellis presented to the Royal Society his first synthesis of marine organism research under the title "An Essay towards a Natural History of the Corallines and other Marine Productions of the like Kind", which he dedicated to his patron, Augusta of Saxe-Gotha, the Dowager Princess of Wales and widow of Prince Frederick. Consisting of an Introduction followed by the Essay, the bulk of the volume is a taxonomy of corallines describing his investigative approach, basically that of collecting some specimens alive in seawater to study their behaviour, whereas others were plunged immediately into brandy as a spirit preservative for dissection. The specimens, he commented, were classified morphologically by microscopic description of shape, texture, colour, secretions and chemical analysis of the tissues, and were illustrated by his field companion, "Mr. Brooking, a celebrated Painter of Sea-pieces".

The Essay of 1755, however, was actually a trial run and was followed by a continuing stream of observations, carefully recorded and sent to the Royal Society where they were published in the *Philosophical Transactions*. His crowning achievement came in two later papers: on the animal nature of Zoophytes, called *Corallina*, read to the Royal Society on 9 July 1767, followed by *Actinia sociata* or Clustered Animal Flower on 12 November 1767. His fame spread, and on 30 November 1768, President Sir John Pringle, with a flattering encomium referring to those two papers, stated that he had "opened such a wonderful view of some of the most extraordinary productions of nature" that the Society wished to recognize his contributions by presenting him, as they had for Trembley, with the Copley Medal.

Ellis then set himself to collate the huge accumulation of specimens, which continued to arrive, especially from the West Indies, for which he had been appointed King's Agent for West Florida in 1764 and Dominica in 1770. By the early 1770s, he had enlarged his original Essay into a huge catalogue of every coral species then known, hard and soft, having collected and begun to describe 16 genera, containing 279 species. Even though Ellis was uncertain "what or where the link is that unites the animal and vegetable kingdoms of Nature", he was certain that "the calcareous covering, though it be ever so thin, shews us that they can not be vegetables" (Ellis 1786, pp. 108–109). Accordingly, he continued to exert pressure on Linnaeus, with whom he had regular and warm correspondence, and who described him in his acknowledgements as a "lynx-eyed discoverer of zoophytes" (*zoophytorum lynceus Ellisius*) (Linnaeus 1758, p. 643), to abandon the entire notion of zoophytes and to reclassify many as animals. Despite his promptings, and the growing body of incontrovertible evidence, Linnaeus, a devout believer in Divine Design, remained unconvinced.

Ellis was also instrumental in furthering knowledge of the link between the polyp and the reefs they constructed. The dominant belief at the time followed Imperato's theory in *Dell' Historia naturale* of 1599 which became widely promoted in the Latin version of 1672 where the calcified structure was translated as *porus matronalis* from the original Italian "madrepora", literally, a porous mother. When Vitaliano Donati translated Imperato into French in 1753, he described the external coral structure as "a marine vegetable, which in shape nearly resembles a shrub stripped of its leaves", and in which, from borings made by "a sort of *teredo* or worm", a home for "the *polypi* of the coral" is created. In those "cellules", the polypi lay their eggs, which develop into a "somewhat transparent *polypus*, which, in shape, resembles a star with eight equal rays" (Donati 1750, pp. 95, 97, 101). From its dried honeycomb appearance, he continued the analogy of "bees in a hive made of wax, with the corallum merely a receptacle for the animals": *on croit que c'est une mère où se forment des animaux marins comme les abeilles dans les gâteaux de cire…La tabulaire n'est qu'un réservoir d'animaux*.[17]

The analogy of the beehive theory, expressed in the French term "*polipydom*", from the Latin *domus* (a house), to designate the limestone reef structure, however, was becoming increasingly questioned. The discoveries of Trembley indicated a more complex process than the visual observation that the limestone corallae were simply habitations analogous to beehives and birds' nests as expressed in the ideas of Donati, Réaumur and Peyssonnel. Trembley, in fact, had already established that the calcified exterior was integral with the living body of the polyp, as did Ellis, who believed it to be a much more complex process, supported by Linnaeus' definition of Lithophytes in the *Systema naturae*, actively building their structure (*quodque aedificant*) as an essential part of their body. "The animals of the Lithophyta, or Corals", Ellis wrote, "construct their own cells by depositing under them a coralline matter". Eventually, it was confirmed that the limestone structure of reefs is secreted from the tissues of the polyps: the structure is, in effect, an integral organic matrix or exoskeleton.

In those years, however, Ellis' health had begun to fail, although he continued his painstaking investigations right to the final days. The end came on 15 October 1776, his *magnum opus* still unfinished. The task of preparing it for publication was undertaken by the distinguished botanist Daniel Solander, who had gained direct knowledge of coral reefs during the voyage of His Majesty's Barque *Endeavour* in 1769–1771, when James Cook carried a party of scientists to Tahiti to observe the Transit of Venus in an effort to improve the prevailing astronomical navigation tables. While the scientists were busy with their observations in the Society Islands, and during the subsequent course of the voyage, he was able to examine coral reefs of the Pacific and the east coast of New Holland. Solander barely completed his work before his own untimely death in 1782, aged 49: Ellis' life work, "The Natural History of many curious and Uncommon Zoophytes", appeared four years later.

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[17] Donati, *Transactions of the Royal Society* 1753, cited in Brook 1893, p. 1.

4 Origin and Structure of Coral Reefs

By the end of the 18th century, investigation into the major problems of reef formation and the nature of coral "insects" had advanced considerably: the geological issues of earth movements from volcanism and hitherto unknown inner pressures had been brought to near universal scientific consensus in the work of James Hutton. Equally significant were the definitive investigations of Peysonnell and John Ellis which resulted in general agreement that reefs were created in some mysterious way by animals. What, however, were the inexplicable processes by which minuscule zoophytes barely 3 or 4 mm wide were able to construct such vast reefs and atolls across all of the tropic oceans?

With the Portuguese, Spanish and Dutch dominance of the New World successfully challenged by the emerging maritime nations of France and England, a new contest developed as those latecomers sought to discover and, if feasible, occupy and colonize that still unknown, unmapped part of the globe. In a renewed effort to discover *Terra Australis*, with the hope that it would offer economic advantages, the voyages of Louis-Antoine de Bougainville, in command of *Boudeuse* from 1766 to 1768, and James Cook, on the *Endeavour* from 1769 to 1771, carried naturalists: Philibert Commerson on the *Boudeuse* and Joseph Banks and Daniel Solander on the *Endeavour*. From those voyages on, all naval ships carried naturalists, and they, like their commanders, were instructed to collect any evidence that would contribute to a better understanding of global geology, and particularly coral reefs.

Intensified speculation began to mount when the awesome destructive power of coral reefs received sensational publicity in James Cook's account of his successful discovery in 1770 of an uncharted coast of the mysterious and elusive Great South Land, following the scientific expedition to Tahiti in 1769. Released by the Admiralty in 1773 in an impressive, dramatically edited publication by John Hawkesworth entitled *An Account of the Voyages Undertaken by Order of His Present Majesty for Making Discoveries in the Southern Hemisphere* (Hawkesworth 1773), nothing in the literature equalled his description of those dangerous waters. The book was an instant success and was reprinted within months; the following year, it was published in the USA, then in French and German translations and later in other European languages. In 1789, it appeared in pocket-sized versions, and became serialized in popular journals in 60 weekly sections.

While exploring that unknown eastern coast of New Holland, which he named New South Wales, Cook became aware as the ship sailed north that it had begun to enter enclosed waters with an increasing frequency of submerged reefs. His anxiety to escape into the open sea comes through in his Log, which describes how, for more than two weeks, the ship had "…been intangled among them more or less ever sence the 26th of May, in which time we have sailed 360 leagues [1800 km] without ever having a man out of the cheans heaving the lead when the ship was under way, a circumstance that I dare say never happen'd to any ship before and yet here was absolutely necessary" (Cook 1770/1771, p. 375). Then the inevitable happened. Continuing heading north, one moonlit night the *Endeavour* crashed into one of the myriads of almost invisible reefs. Cook's description of the impact on 11 June 1770, the desperate efforts to beach the vessel for repairs, and the eventual discovery of a way out of the bewildering complexity of submerged reefs created a sensation, especially when it appeared in the heightened prose of Hawkesworth.

Once safely back on the dark blue depths of the Pacific, Cook charted those nightmare waters with the sinister name of the Labyrinth, an allusion to the classical Greek legend of the deliberately contrived complexity of passages guarding the underground lair of the dreaded bull-headed Minotaur in Crete. In the legend, the hero Perseus descended to slay the monster and was able to return only because, as he entered, his lover Ariadne had given him a ball of twine to unwind to retrace his way through the maze. With great relief, Cook, a modern Perseus, sailed through the pass he aptly named Providential Passage into the Pacific. As he gazed on the foaming wave front from a safe distance, he wrote one of the world's most powerful coral reef images which beggared belief at the

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
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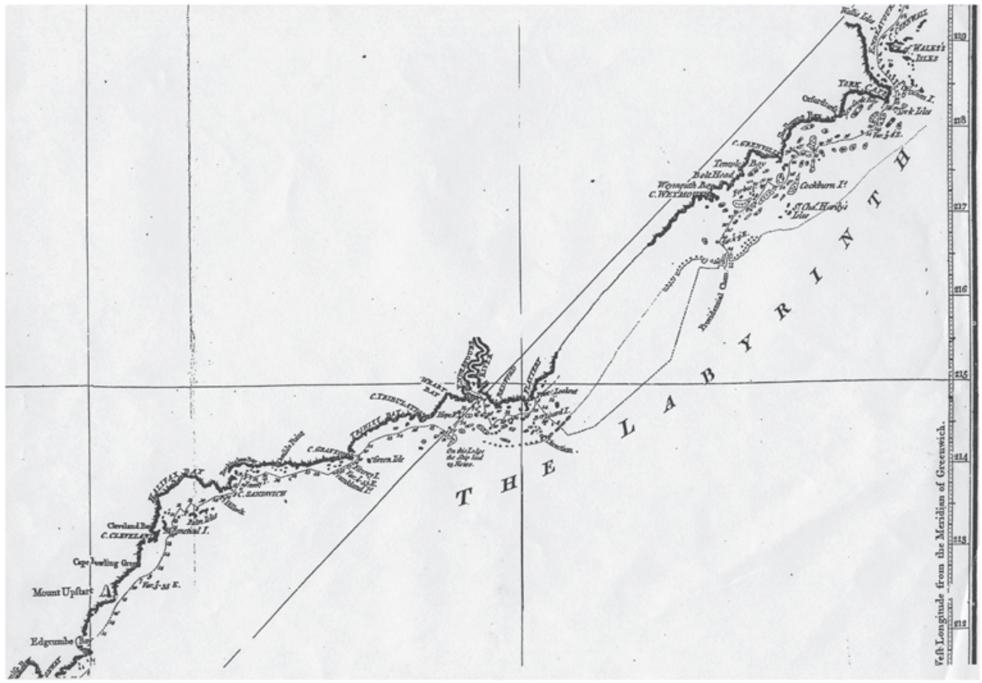

Cook's chart of the Labyrinth reaching from Cape Cleveland at the left (*southern end*) to Cape York at the right (*northern end*) from the Hawkesworth edition of 1773

time: "A Reef such as is here spoke of is scarcely known in Europe, it is a wall of Coral Rock rising all most perpendicular out of the unfathomable Ocean…the large waves of the vast Ocean meeting with so sudden a resistance make a most terrible surf breaking mountains high" (Cook 1770/1771, p. 378).

Following his encounter with the Labyrinth—which Matthew Flinders renamed the Great Barrier Reef in 1802—Cook had become aware of the increasingly feasible supposition among European and British naturalists that in some mysterious way coral reefs were the production of microscopically small "insects". Barely 4 years later, during his second voyage in the Pacific in command of the *Resolution*, accompanied by the *Adventure*, this time in an effort to discover Antarctica and then to revisit Tahiti and the central Pacific, he navigated past continental islands with elevated relict fringing reefs and recorded in his *Journal* for June 1774 his puzzlement that "If these Coral rockes were first formed in the Sea by animals, how came they thrown up, to such a height? Has this Island been raised by an earth quake or has the sea receded from it? Some philosophers [scientists] have attempted to account for the formation of low isles such as are in this Sea, but I do not know of any thing has been said of high Islands or such as I have been speaking of" (Cook 1774, p. 438).

Hypotheses on Reef Formation

Throughout the history of science, as Hume observed, problems are never solved: their solution simply raises yet another difficulty, which in coral reef science first entered the historical record during Cook's second cruise. Accompanying Cook was the German naturalist Johann Reinhold Forster (1729–1798), who recorded his own explanation in considerable detail and proposed one of the first hypotheses regarding reef formation. When describing the atolls of the Tuamotu Archipelago near Tahiti, for example, Forster suggested that "if the question be put, how it comes that the Madrepores form such circular or oval ridges of rocks; it seems to me that they do it by instinct, to shelter themselves the better against the impetuosity and constance of the SW winds; so that within the ridge there is always a fine calm Bason, where they feel nothing of the effects of the most blowing weather".[1]

After his return to London, those notes in his shipboard journal were expanded into an official record for the Admiralty, and published in 1778 as *Observations Made during a Voyage around the World*. In Sect. 4, "*Theory of the Formation of Isles*", Forster further developed his concept of polyp instinct whereby they "endeavour to stretch only a ledge, within which is a lagoon, which is certainly entirely screened against the power [of the ocean and winds]". This, he continued, "seems to me the most probable cause of THE ORIGIN of all THE TROPICAL LOW ISLES, over the whole South-sea".[2] Despite the apparent simplicity of his explanation, Forster had distinguished a fundamental feature of atolls, namely that the formation of a circular structure enables the coral colonies to resist the "rage and power of the ocean".

[1] Forster 15 August 1773, cited in Hoare (1982, p. 324, cf. 494).

[2] Forster (1778, pp. 150–151) (Forster's capital letters).

Many other questions, however, remained unanswered. Given the enormous depth of surrounding waters, unable to be sounded by the technology of the times, how had polyps established themselves in the first place? Upon what foundations had they erected their limestone structures? What was the nature of that instinct by which "the animalcules forming these reefs…shelter their habitation from the impetuosity of the winds"? (Forster 1778, p. 151) Most importantly, why were the atolls—many miles in diameter—circular or oval in shape, readily confirmed from the crow's nest of the exploring ships?

Further investigation of coral reefs was checked for a time when the French Revolution of 1789 and the subsequent Napoleonic Wars pressed all fighting ships into military service. Even so, the French and British were able to dispatch a few exploration vessels in the first years of the 19th century, chiefly the corvette *Le Géographe* accompanied by the storeship *Naturaliste* commanded by Nicolas Baudin in the years 1800–1804, and the *Investigator*, 1801–1803, under Matthew Flinders. Both expeditions, in fact, were competing because the French were looking for regions of *Terra Australis* not already claimed by Cook as a Pacific base.

Whereas the marginally seaworthy *Investigator* sailed unaccompanied with only Robert Brown and the artist Ferdinand Bauer to record the natural history—both of whom were to create a major expansion of botanical knowledge with their amazingly skilled discovery and description of the exciting, completely novel exotic flora of New Holland; the Baudin expedition was lavishly funded and equipped. In all, 22 civilian scientists were selected by Napoleon himself, comprising "astronomers, geographers, mineralogists, botanists, zoologists, draughtsmen and horticulturalists".[3] Among those, Philibert Commerson made extensive botanical collections for the *Jardin des Plantes* in Paris, and the zoologist François-Auguste Péron collected for the Muséum d'histoire naturelle more than "one hundred thousand specimens of animals, large and small, …among which are several important genera…[with] many more to be described, [while] the number of new species…[were] upwards of 2500".[4] In contrast, the *Investigator* carried neither a mineralogist nor a zoologist: Flinders was to report on whatever mineral deposits he considered exploitable, and any interesting animal life was to be reported by the ship's surgeon.

Unfortunately for France, the Baudin expedition of 1800–1804 became a fiasco, marred by conflict between Baudin and Péron, by the scurvy that ravaged the efficiency of his crew and finally Baudin's death on Île-de-France (present-day Mauritius). The scientific results provided by Péron and the graphic artist Charles-Alexandre Lesueur, however, salvaged the expedition's reputation, including their significant observations relevant to the coral animal issue on the medusae (jellyfish) they were able to collect by netting. In addition to the specimens collected, an enduring achievement was the extensive descriptive record written by Péron in his *Voyage of Discovery to the Southern Hemisphere* published in French in Paris in 1806 and translated into English just three years later, barely a year before he died of tuberculosis in 1810.

Following the British victory at Waterloo and the subsequent Treaty of Vienna in 1815, a new era of intensified exploration began, accompanied by the necessary charting of the myriad reefs of the Pacific and Indian oceans, which surrounded the island clusters and were subject to European hegemony and exploitation. The naturalists aboard both vessels, however, continued to be primarily botanists because the economic emphasis of the period was directed towards establishing plantations in the new colonies and cultivating whatever natural products could be found, of which rubber, coffee, tea, grains, spices, sugar, opium and cinchona were particularly sought. As well as that express concern, because coral reefs were also beginning to attract increasing scientific interest, many ships began to carry zoologists in addition to botanists and mineralogists.

In the same period, the Russians also became active once they gained control of the North Pacific with their warm water port of Vladivostok. Of early significance were the findings of Adelbert von Chamisso, the naturalist who sailed on the first voyage of the Russian ship *Rurik* from 1815 to 1818 under command of Otto von Kotzebue around the Pacific from Kamchatka to Alaska, California, and then to the Hawaiian, Marshall and Mariana groups situated between the north tropic and the equator. In an account entitled *On the Coral Islands*, included as an appendix to Kotzebue's narrative of the voyage, Chamisso made two important observations. First, in contradistinction to Forster, he pointed out that corals thrived best in turbulent reef fronts, stating that "the larger species of corals, which form blocks measuring several fathoms in thickness seem to prefer the more violent surf on the external edge of the reef", a point amplified further on, that the windward "side of the reef, exposed to the unremitting fury of the ocean, should first rise above the element that created it". His second observation attempted to explain why atolls appear in wide expanses of the oceans, almost out of nowhere. That, he reasoned, was because "the corals have founded their buildings on shoals in the sea or, to speak more correctly, on the top of mountains lying under the water". Further, the variation in magnitude and distribution of atoll clusters "probably depends on the size of the submarine mountain tops, on which their basis is founded" (Chamisso 1821, III, pp. 331, 334).

Another essential element was contributed at much the same time by Jean René Quoy and Joseph Paul Gaimard, naturalists aboard the French corvette *l'Uranie* on its Pacific

[3] Péron (1809, p. 10) (English translation of the French 1806 edition).

[4] Cuvier, Introduction to Péron (1809, pp. iii–iv).

voyage of 1817–1820, chiefly to the Mariana, Hawaiian and Dutch East Indies island groups. Presenting their findings in a joint paper of 1823 entitled "*Mémoire sur l'Accroissement des polypes lithophytes considéré géologiquement*" (Geological aspects of coral formation), they argued from their extensive examination of reefs in Pacific tropical waters that it would be a mistake to ascribe all atoll formation to polyps alone growing up from the ocean floor. Rather, they believed that coral reefs are surface features that "have as a base the same element, the same minerals which concur to form all the known islands and continents…that [in effect] they build their dwellings on the submarine rocks, enveloping them entirely, or in part, but properly speaking they do not form them". Therefore, "all these reefs", they conclude, "are, in our opinion, platforms arising from the conformation of the primitive surface" (Quoy and Gaimard 1823, pp. 273, 290).

Neither the *Rurik* nor the *l'Uranie* visited the completely different formation of the Great Barrier Reef of Australia, which only British ships had surveyed up to then. From Flinders' apt description, it was not an atoll formation but, quite literally, a great barrier that paralleled the coast for a thousand miles, at varying distances from the mainland. What, it was also being asked, are the processes that form barrier reefs such as those in eastern Australia, New Caledonia and British Honduras (present-day Belize), given that the polyps are of the same species as those found on atolls? Answers to such questions were being sought in the new geological and similar societies being established on the model of the Geological Society of London, founded in 1807. At their meetings, papers were being presented attempting to draw together the increasing volume of findings from the survey voyages of various nations, particularly French, English and Russian, including the important geological section written by William Fitton in the 1827 *Narrative of the Great Barrier Reef Survey* by Phillip Parker King in command of *Mermaid*. Although the findings of coastal geology seemed unrelated to atoll formation, they were part of the growing accumulation of evidence on both the coral reef question and the broader issues involved in establishing a general theory of geology.

One of the most penetrating commentaries on those issues came from the Prussian naturalist Alexander von Humboldt (1769–1859). Accompanied by the French botanist Aimé Bonpland (1773–1858), the two explorers travelled throughout the Caribbean and adjacent regions of central and South America from 1799 to 1804, making the first geological survey of those lands. Paying particular attention to the limestone strata, Humboldt observed their similarity with both the Jura Mountains of Europe, which he had previously described in 1795—rich in fossilized ammonites—and the similar rock of the Cayman Islands, and considered this relevant to the question of coral reef origins. Building on his concept of the earth crust as an integrated complex, subject to immense structural change over the millennia, Humboldt sought an understanding of coral reef formation in terms of global processes, setting down his conclusions in a *Personal Narrative of Travels* published in Paris between 1814 and 1825. Earlier, he had been a staunch neptunist, but by that time the evidence for plutonism was irrefutable, and aware of current hypotheses on reef formation, he doubted that atolls rising from great depths could have been built up entirely by coral polyps. In fact, he was unsure whether "rocks formed by polypi still living are found at great depth below this fragmentary rock of coral". He did suspect, however, that "those huge masses which are said to rise from the abyss of the Pacific to the surface of the water…had some primitive or volcanic rock for a basis, to which they adhere at small depths".[5]

By that time, with the Great Barrier Reef of eastern Australia having become one of the most important global locales for reef analysis, the British Admiralty issued specific instructions to its captains to continue observations on the structure of coral reefs. John Stokes, captain of HMS *Beagle* during its survey of the Great Barrier Reef, 1837–1844, recorded those *Instructions* verbatim in his narrative *Discoveries in Australia:* "It has been suggested by some geologists that the coral insect, instead of raising its superstructure directly from the bottom of the sea, works only on the summits of submarine mountains, which have been projected upwards by volcanic action. They account, therefore, for the basin-like form so generally observed in coral islands, by supposing that they insist on the circular lip of extinct volcanic craters; and as much of your work will lie among islands and cays of coral formation, you should collect every fact which can throw any light on the subject" (Stokes 1846, I, p. 21). In fact, during his two brief traverses of reef waters in the course of the survey, Stokes made some important observations. At Cape Upstart (near modern Townsville), he recorded that he "found a flat nearly a quarter of a mile broad, in a quiet sheltered cove, within the cape, thickly strewed with dead coral and shells, forming, in fact, a perfect bed of them—a raised beach of twelve feet above high water mark" (Stokes 1846, I, p. 332).

Geological discoveries continued to be made of ever more numerous examples of marine strata inland from the coast and at elevations well above sea level that defied ready understanding. What possible explanations could be advanced? In his report to the Admiralty, Stokes commented on one particular formation that "had it been on the seaward side, I might have been readier to imagine that it could have

[5] Humboldt (1850, III: p. 186) (English translation by Ross of his 1814–1825 edn).

been thrown up by the sea in its ordinary action, or when suddenly disturbed by an earthquake wave; but as the contrary is the case, it seemed impossible to come to any other conclusion, than that an upheaval had taken place" (Stokes 1846, I, pp. 332–333). That observation was amplified further in his significant comment that "the remarkable breaks in this singularly great extent of coral reefs, known as the Barrier of Australia, being in direction varying from W. to W.N.W., generally speaking N.W., leads me to believe that the upheaval by which the base of this huge coral building was formed, partakes of the general north-westerly direction, in which a large portion of the eastern world apparently emerged from the water" (Stokes 1846, I, p. 375)

Lyell's Solution of 1832

What, then, was the origin of the platforms of Quoy and Gaimard? What could have caused a "heaving up of the land"? How, asked Péron, during the voyage of *Le Géographe*, could "marine shells…in cemented masses, at heights above the sea, to which no ordinary natural operations could have conveyed them", be accounted for "in the mountains in the interior of Timor, in the very heart of the deep valleys and torrents, [where we] everywhere find the remains of these astonishing animals, although it is utterly impossible for the mind to conceive how or by what means nature has raised these large madreporic plots to such great heights above the present level of the seas".[6] How, in effect, were the curious atolls and barrier reefs related to the structure of the earth? In 1832, a solution was proposed by Charles Lyell based on what he argued was "an attempt to explain the former changes of the earth's surface by reference to causes now in operation", following the ideas in Hutton's *Theory of the Earth*.

Born in the year of Hutton's death, Charles Lyell (1797–1875), also a Scot from Edinburgh, was his uncompromising follower. Indeed, Hutton's theories were developed in Lyell's great three-volume *Principles of Geology*, published successively in 1830, 1832 and 1833, which came to dominate geological thought throughout much of that century, although not without considerable dissent. In 1881, Lyell's sister-in-law Katherine collected, edited and published his papers posthumously, and there we find the most succinct summary of Lyell's work. In his own words, he attempted to demonstrate that a proper understanding of geological processes comes from the fundamental premise that "neither more nor less than that *no causes whatever* have from earliest times to the present, ever acted, but those *now acting*; and that they never acted with different degrees of energy from which they now exert".[7] The accumulating evidence of marine deposits—shells, ancient coral reefs, fossilized animals—discovered in strata sometimes hundreds, even thousands, of metres above current sea levels, along with massive unconformities of convoluted strata, often with intrusions of other very different rocks, as revealed by engineering excavations in mountainous regions, especially as the industrial revolution accelerated the pace of canal and railway construction, led him to argue that the crust of the earth had been, over aeons, imperceptibly but relentlessly subjected to alternating periods of inner forces of elevation and subsidence. That was the doctrine defined in William Whewell's 1837 *History of the Inductive Sciences* as "uniformitarianism", to distinguish it from the prevailing belief in "catastrophism", which held that earth processes are driven by violent, unpredictable volcanic eruptions and earthquakes.

Departing from Bacon's assertion that scientific theory must be based only on direct observation, Lyell, who never saw a coral reef, gathered evidence from those who had voyaged in tropical waters and brought them together in his second volume into a sweeping synthesis. Coral atolls, he concluded, are built by an infinitely slow process on the summits of submerged volcanoes on the ocean floor by "branched madrepores…which may form the first foundation". Continuing, "the volcanic isles of the Pacific", he wrote, "shoot up ten or fifteen thousand feet above the level of the ocean. These islands bear evident marks of having been produced by successive volcanic eruptions; and coral reefs are sometimes found on the volcanic soil, reaching for some distance from the sea-shore into the interior". Pressing home his uniformitarian argument, Lyell dismissed any objection to the time required for such structures to be created, "on the ground of the slowness of the operations of lithogenous polyps" (Lyell 1830–1833, II, p. 288). Two pages on, he concluded: "The circular or oval forms of the numerous coral isles of the Pacific, with the lagoons in their centre, naturally suggest the idea that they are nothing more than the crests of submarine volcanos, having the rims and bottoms of their craters overgrown by corals" (Lyell 1830–1833, II, p. 290). Lyell attributed the formation of archipelagos, fringing and barrier reefs to the ejection of volcanic ashes and sand that served as foundations for yet further reefs, to the extent that, in the Pacific, "they present the appearance of troops marching upon the surface of the ocean" (Lyell 1830–1833, II, p. 295).

One significant feature still needed explanation. Why, Lyell continued, is it that "there should be so immense an area in eastern Oceania, studded with minute islands, without one single spot where there is a wider extent of land than belongs to such islands as Otaheite [Tahiti], Owhyhee [Hawaii], and a few others, which either have been, or are still the seats of active volcanoes"? The answer he provided was that "the amount of subsidence by earthquakes exceeds in that quarter of the globe at present the elevation due to the same cause" (Lyell 1830–1833, II, p. 296). The uniformitarian, or,

[6] Péron (1809, p. 117) (English translation of the French 1806 edition).

[7] Lyell (1881, I: p. 234) (Charles Lyell's own emphasis).

more accurately, the actualist argument, that only the physical laws remain constant, and present changes do not exactly parallel the past, which accommodates catastrophism to a limited extent, was advanced as demonstrative proof. Active volcanoes, he stated, certainly are brief catastrophic events, indicative of the release of subterranean energy, but they remain, nonetheless, mere transitory epiphenomena on the continuing elevation and subsidence of the earth's crust. The Pacific, he reasoned, had simply sunk as the underlying forces were released, and in corresponding movement, the nearby Andes had slowly arisen from the sea, carrying their marine depositions with them.

In effect, Lyell had confirmed the earlier observations of Forster, Chamisso, Quoy and Gaimard. His further development was to argue that atolls were formed on the summits of subterranean volcanoes that had emerged from the ocean floor, and then "*gradually* elevated by earthquakes".[8] Periods of continuing elevation and subsidence would follow, and when the water was shallow enough to allow polyp growth, coral colonies would build upon the detritus of previous formations. As examples of that alternating process, Lyell cited the Maldive and Laccadive archipelagos in the Indian Ocean, the Great Barrier Reef and the Rowley Shoals in northwestern Australia surveyed by King and some 32 of the reefs examined by Captain Frederick Beechey, commander of HMS *Blossom* during his Pacific survey in the years 1825–1828. The issue of the slightly horseshoe shape of most atolls Lyell attributed, as did earlier explorers, to the formation of inner rainwater lagoons which, on flowing out to the surrounding sea, thereby killed the polyps in their path, and to periods of "alternate elevation and depression…[which] might produce still greater inequality in the two sides…while the action of the breakers contributes to raise the windward barrier" (Lyell 1830–1833, II, p. 294).

Lyell had made an ingenious attempt to fit field observations of numerous naturalists into his theory in order to solve the atoll creation puzzle, including an explanation for their near-circular shape. Five years later, in 1837, that explanation was challenged by a new one, developed by the 28-year-old Charles Darwin, gentleman naturalist and neophyte geologist, recently returned from a five-year voyage around the world on board HMS *Beagle*. Darwin had prepared a paper for the Geological Society of London "On certain areas of elevation and subsidence in the Pacific and Indian Oceans, as deduced from the study of coral formations" that contradicted Lyell's theory of the formation of atolls. What, then, was the theory presented by Darwin, and what effects did it have on coral reef science and geology generally?

[8] Lyell (1830–1833, II: p. 292) (his own emphasis).

Charles Darwin and the Voyage of the *Beagle*, 1831–1836

Born 12 February 1809, son of Robert Darwin, a wealthy medical practitioner and astute investor, Charles was educated in the exclusive Shrewsbury school of Dr Butler where, inducted into the mandatory classical education of the privileged classes, he claimed later to have forgotten all of it: natural history was everything that occupied his mind and activities. After a short period in the famous Edinburgh medical school from 1825 to 1827, where he avoided the nauseating, unhygienic hospitals, he spent much of his time in the company of Robert Grant, a medical doctor who had moved into marine biology, with a particular interest in sponges and barnacles, at the time two of the most enigmatic of marine organisms.

Long irritated by Charles' passions for the active outdoor life of nature, along with shooting, fox-hunting and riding pursued by the English upper classes, his father attempted to attach at least a patina of cultural attainment by withdrawing him from Edinburgh and consigning him to Cambridge to study for the Anglican ministry. There, Charles was advised by John Stevens Henslow, professor of botany, and formerly of mineralogy, to attend the lectures in geology of Professor Adam Sedgwick. Charles needed no encouragement and proved a keen student of geology, at the time a growing interest of more curious clerics as the biblical account of Genesis became increasingly questioned. Indeed, the famous Royal Commission of 1864 into the elite private grammar schools expressed alarm at the teaching of science being introduced to complement the curriculum dominated by Greek and Latin. In particular, it warned, "few boys could study geology without a violent disturbance to their religious beliefs" (Royal Commission 1864, III, xxi, p. 4750).

In 1831, under command of Robert FitzRoy, the *Beagle* was sent to continue the survey of the eastern Atlantic coast from Bahia (present-day Salvador on the mid-Brazilian coastline, 15°S) to Cape Horn, designated as the Royal Navy's "South American Station". On its previous voyage, while surveying Patagonian waters, Lieutenant FitzRoy had been one of the officers aboard when the intensely depressed captain, Pringle Stokes, committed suicide. Aware of the length and difficulty of the proposed two-year voyage, and certainly mindful of the obligation for a captain to eat alone in his cabin apart from the other officers, which may have driven Pringle Stokes to end his life, the aristocratic FitzRoy, son of an army general, grandson of a duke and a marquess, great-grandson of Charles II, sought a congenial companion. After much searching, his request was finally relayed to Prof. Henslow in Cambridge, who knew that Darwin would be ideal. As Henslow phrased it emphatically in a letter to Darwin of 24 August 1831, urging acceptance, "Capt. F. wants a man…more as a companion than a mere collector &

would not take any one however good a Naturalist *who was not recommended to him likewise as a gentleman*" (Darwin 1985–1998, I, pp. 128–129); a good class distinction.

When the *Beagle* left Plymouth on 27 December 1831, Darwin was barely two months short of his 22nd birthday: even so, by that time he had already demonstrated prodigious talent in a number of branches of natural science. He prepared carefully for the planned two-year voyage, taking a microscope with the magnification power of × 160, and a collection of books, including his personal copy of Volume I of Lyell's *Principles of Geology*, published in 1830. Volume II, published in 1832, he found waiting for him in Montevideo, and Volume III of 1833 in Valparaiso. Between them, Fitz-Roy and Darwin packed their books into the tiny 10 × 11 ft (3 × 3.3 m) poop cabin where Darwin also had his hammock, and a worktable he shared with mate and assistant surveyor John Lort Stokes and midshipman Philip Gidley King.

Less than a month out of Plymouth and 6 weeks before first setting foot on South American soil at Bahia, Darwin determined on making geology his main pursuit. Carrying his copy of Lyell's first volume, which he studied attentively while the ship was travelling south, he wrote to Henslow from Rio on 18 May 1832 that "Geology & the invertebrate animals will be my chief object of pursuit through the whole voyage" (Darwin 1985–1998, I, p. 237). In his autobiography produced 45 years later, Darwin recollected that at that time it "first dawned on me that I might perhaps write a book on the geology of the countries visited, and this made me thrill with delight" (Darwin 1876, pp. 77, 81).

Formation of Barrier Reefs and Atolls: "So Deductive a Theory"

While the *Beagle* surveyed both east and west coasts of South America and then the wider expanses of the Pacific, Darwin travelled as a supernumerary, i.e. a civilian, with his servant Syms Covington, funded by his wealthy and indulgent father. For 18 months aboard and 39 ashore, mostly in South America, Darwin was free to make his numerous geological and biological expeditions that provided data for his two great and contentious publications. Not subject to ship's discipline, the two spent most of their time ashore in field excursions covering a wide spectrum: plants, insects, fossil bones, marine depositions and geological specimens. The expeditions often went inland and lasted for months, and with the first two volumes of Lyell's *Principles of Geology* in his rucksack, Darwin explored the coastline and hinterland of South America, for which he hired guides, supplies and pack animals.

Writing to his cousin William Darwin Fox from Lima in August 1835, he enthused that "I am becoming a zealous disciple of Mr Lyell's views as known in his admirable book". Then, with a tyro's pretension, reinforced by his "Geologizing in S. America", confided that "I am tempted to carry parts to a greater extent, even than he does". The next line points to his naiveté at the time: "Geology is a capital science to begin, as it requires nothing but a little reading, thinking & hammering" (Darwin 1876, I, p. 460). In the process of following Lyell, he became ever more committed to the concepts of uniformitarianism and continental subsidence and elevation.

Wherever Darwin went, he saw raised sedimentary strata and collected the embedded organic remains, chiefly marine shells, to support the uplift theory. He found the most dramatic evidence in marine deposits inland from Valparaiso in the Peuquene range where "at the height of 13,210 feet, and above it, the black-clay slate contained numerous marine remains…which formerly were crawling about the bottom of the sea, now being elevated nearly 14,000 ft [4200 m] above its level" (Darwin 1839b, p. 245). Equally interesting is his report on the examination of the "step-formed terraces of shingle running up a valley at Guasco [Huasco] for some 37 miles (60 km) which "Mr Lyell concluded…must have been formed by the sea during the gradual rising of the land" and which contained not only marine shells but also "the teeth of a gigantic shark, closely allied to, or identical with the *Carcharias Megalodon* of ancient Europe", ancestor of today's great white shark, *Carcharodon carcharias* (Darwin 1839b, p. 261).

The *Beagle* left South America in September 1835, sailing to the Galapagos Islands where Darwin made extensive observations that were to provide significant material for his controversial theory of evolution by natural selection in *Origin of Species*. Leaving the Galapagos for Tahiti on 20 October, the *Beagle* first had to negotiate the extensive Low Isles Archipelago (present-day Îles Tuamotu of French Polynesia) and charted at the time as the Dangerous Isles from its 76 atolls and submerged reefs, stretching some 1700 km in a northwesterly direction, where he saw his first coral atoll.

From his description of "those most curious rings of coral land, just rising above the water's edge…[revealing] a long and brilliantly-white beach capped by a margin of green vegetation; and the strip, looking either way, [which] rapidly narrows away in the distance, and sinks beneath the horizon [and where] from the mast-head a wide expanse of smooth water can be seen within the ring", his readers would have gained no idea of the immense size of the larger atolls. The oval lagoon of Rangiroa, one of the largest in the world, is 80 km long and 35 km wide (50 × 22 miles); the next two, Makemo and Fakarava are of similar size, 70 and 60 km long, respectively, and most of the smaller atolls are between 20 and 30 km long. Moreover, the land surface of all atolls is quite small, consisting of intermittent patches of vegetated soil a few kilometres long and in no case even reaching 1 km wide and barely a few metres above high tide.

On the evening of 26 November 1835, "with a gentle land-breeze a course was steered for New Zealand" (Darwin 1839a, p. 304), passing that land on 19 December, and 3 weeks later, on 12 January 1836, the *Beagle* anchored in Sydney Harbour. A little more than 2 weeks later, the ship sailed south for Hobart, and, although the voyage had taken much longer than planned, FitzRoy decided to head north to the Keeling (present-day Cocos) group of atolls in the Indian Ocean, as suggested in his *Instructions*, arriving there on 1 April. Over the 12-day sojourn, Darwin was able to make his first extensive examination of Keeling Island, an atoll with a lagoon 16 km long, 10 km wide (8 × 5 miles) and with three small landmasses around the perimeter where he recorded his findings in detail. Leaving Keeling on 12 April, the *Beagle* set course for England, stopping on the way in Mauritius, Cape Town and St Helena, where Darwin made yet more field excursions.

After the *Beagle* docked at Falmouth on 2 October 1836—the planned two years having stretched to five—Darwin went to Shrewsbury, and then to meet Henslow in Cambridge, where he renewed his contacts. A few weeks later in London, he met Charles Lyell, with whom he formed a lifelong friendship.

In March 1837, Darwin took up residence in London, where he began to prepare his official report, working from an autograph diary of 751 pages composed aboard the ship, and 18 small pocket notebooks in which he had pencilled observations from his field trips throughout the voyage, as well as one notebook of recollections made from 1837 to 1839 while he was writing. In 1839, it appeared under his name as *Journal of Researches… 1832–1836*, part of Volume III of the *Narrative of the Surveying Voyages of His Majesty's Ships Adventure and Beagle*.

In the Journal, the only source available to the public at the time, Darwin rearranged his observations and discoveries into topics of common interest, often drawing together separate excursions into a single chapter, although it was presented as a diary with a sequence of dates. That practice now presents a major difficulty in seeking to understand the development of his theory of the formation of atolls and coral reefs: it is virtually impossible to determine exactly how he reached it. The only clue comes from his retrospective *Autobiography*, in which he made the oft-quoted statement that opens by neatly undermining Bacon's dogmatic prescription for inductive science that direct observation must come before theory. "No other work of mine was begun in so deductive a spirit as this; for the whole theory was thought out on the west coast of South America before I had seen a true coral reef." He then continued that "I had only therefore to verify and extend my views by a careful examination of living reefs". In the same passage, he continued to explain that his observations in South America "necessarily led me to reflect much on the effects of subsidence, and it was easy to replace in imagination the continued deposition of sediment by the upward growth of coral. To do this was to form my theory of the formation of barrier-reefs and atolls" (Darwin 1839b, pp. 98–99).

Darwin's Subsidence Theory, 1839–1842

It was then that Lyell urged Darwin to present his new theory of coral reefs to meetings of the Geological Society. In response, Darwin sent a short paper "Proofs of recent elevation on the coast of Chile" that was read on 4 January 1837. A second paper, dealing specifically with his theory of reef formation, was sent a few months later on 31 May. Drawn from his *Journal* entry for 12 April 1836 and written on Keeling, it was entitled "On certain areas of elevation and subsidence in the Pacific and Indian Oceans, as deduced from the study of coral formations" and published the following year in the Geological Society's *Proceedings*.

After surveying all previous theories, he presented his own conclusions under an entry for 12 April 1836, which stands as his original extended explanation of the structure and formation of coral reefs: "The theory which I offer, is, simply, that as land with the attached reefs subsides very gradually from subterranean causes, the coral-building polypi soon raise again their solid masses to the level of the water: but not so with the land; each inch lost is irreclaimably gone; as the whole gradually sinks, the water gains foot by foot on the shore, till the last and highest peak is finally submerged" (Darwin 1839b, p. 345). Having made that assertion, Darwin then extrapolated it to apply to what he termed fringing and barrier reefs. They were created by the same process of subsidence, he argued, with the enclosed waters becoming turbid and "injurious to all zoophytes", and because—evidently following Chamisso—they only "flourish on the outer edge amidst the breakers of the open sea" (Darwin 1839b, p. 345).

In that second paper, Darwin reiterated his *Journal* comment that presented his famous classification, still used today, of the three kinds of reefs he termed lagoon (or atoll), fringing and barrier, making the point, although he never saw it, that the "Barrier reef, running for nearly 1000 miles parallel to the North-east coast of Australia, and including a wide and deep arm of the sea…is the grandest and most extraordinary coral formation in the world" (Darwin 1838, p. 552). Departing from Lyell's volcanic crater theory, which asserted that volcanoes came from underwater quakes and that, when extinct, polyps subsequently built upon them, he argued that, on the contrary, elevated regions of volcanic activity, having become extinct, had later subsided from tectonic activity and took former volcanoes down with them. As a compensatory mechanism, subsidence of much of the Pacific had pushed the earth's crust up to form the Andes, raising oceanic sediments with them, thus explaining the numerous marine findings high in the mountains of Peru and Chile.

All along, like Lyell, Darwin had been anticipating the concept of isostasy developed in the 1850s,[9] writing in his diary in April 1836 that he was "inclined to believe that the level of the ground was constantly oscillating up and down, [and that]…the amount of subsidence had been equal to that of elevation" (Darwin 1839b, p. 354). In 1842, *The Structure and Distribution of Coral Reefs* was published, and that work developed in greater detail his theories that immediately initiated a century of controversy from the basic uniformitarian assumption that the crust of earth has always been in continuous, mostly imperceptible, oscillation. The monograph itself is an impressive achievement. For the first time in the history of natural science, Darwin brought together all available data from explorers on coral reefs and in six chapters elaborated the subsidence theory comprehensively. In a deliberate manner, he also examined and refuted all objections raised so far.

In Chapter 5 of *The Structure and Distribution of Coral Reefs*, Darwin worked meticulously through his subsidence explanation yet again, pursuing the questiofn "On what foundations, then, have these reefs and islets of coral been constructed?" Granted that the "many widely-scattered atolls must…rest on rocky bases…we are compelled to believe that the bases of many atolls…were brought into the requisite position or level…through movements in the earth's crust" and because this "could not have been effected by elevation…they must, of necessity have subsided into it, and this at once solves every difficulty" (Darwin 1839b, pp. 92–94). Therefore, "if the shore of a continent fringed by a reef had subsided, a great barrier-reef, like that on the N.E. coast of Australia, would have necessarily resulted…[and] continued subsidence of a great barrier-reef of this kind" would most likely have developed "into a chain of separate atolls" (Darwin 1839b, p. 102). Darwin then moved to deal with "a formidable objection to my theory", namely the "vast amount of subsidence necessary to have submerged every mountain". His answer was simple: given the immense seabed elevation found in the Andes, "no reason can be assigned why subsidences should not have occurred in some parts of the earth's crust on as great a scale both in extent and amount as those of elevation" (Darwin 1839b, p. 114).

His final Chapter 6 of *The Structure and Distribution of Coral Reefs*, which contained a coloured map of the Indian and Pacific oceans, discussed in detail the geomorphology of that enormous expanse of water on which he plotted all three kinds of reefs as then known, colour-coding them in bright blue (lagoon and atoll), pale blue (barrier) and red (fringing). From the data available, he was able to demonstrate that fringing reefs (those attached to the land) were in active volcanic areas which were either geologically stationary or else in process of elevation, while the barrier and atoll reefs, free of volcanic eruptions, were in deeper waters and areas of subsidence. To support the theory of elevation in volcanic areas, he pointed out that "on fringed coasts…the presence of upraised marine bodies of a recent epoch plainly show, that these coasts…have generally been elevated" (Darwin 1839b, p. 147). His concluding paragraph to the main body of text contains a final summary "derived from a study of coral formations": "We there see vast areas rising, with volcanic matter every now and then bursting forth through the vents or fissures with which they are traversed. We see other wide spaces slowly sinking without any volcanic outbursts", which present "a magnificent and harmonious picture of the movements, which the crust of the earth has within a late period undergone" (Darwin 1839b, p. 148).

Once Darwin's theories were published, Humboldt, now a converted plutonist, gave strong support. In his earlier observations on coral reef theories in the *Personal Narrative of Travels* (first published in French between 1814 and 1825), he remained sceptical of the theory "that atolls…owe their origins to submarine volcanic craters" because some have diameters up to 60 miles (100 km). Two decades later in the 1849 edition of his celebrated essays on natural history, "Views of Nature" (the English translation was published in 1850), Humboldt gave a more detailed review of recent research where he surveyed the history of reef theories from Forster, Chamisso, Péron, Quoy, Gaimard, Flinders, Lütke, Beechey, Darwin and D'Urville to Moresby and Powell. There he concluded that the explanations of Quoy and Gaimard, which guided Darwin, were heading in the right direction and that coral reefs, as Cook and Forster believed, did not grow from great depths, but from submerged platforms closer to the surface. Darwin's theory of gradual subsidence was a convincing solution: as an island mountain slowly sinks, the coral polyps of its fringing reef continue to grow upwards, "forming first a reef encircling the island at a distance", and then, when the enclosed island subsides below the surface, an atoll.

Humboldt paid gracious tribute to that achievement, commenting that "Charles Darwin has with great ingenuity developed the genetic connection between shore-reefs, island-encircling reefs, and lagoon islands [atolls]": all mark the prominent points of submerged lands, indicating the former topography of the area (Humboldt 1850, p. 261). No greater imprimatur could have come at the time.

[9] Tendency of earth's crust to remain in equilibrium by compensating for changes in loading, such as by ice sheets or emergence of mountain chains (Gk *isos*, "same"; *stasis*, "standing or level"). The word "tectonic" did not appear in geological discussion until the 1960s, when plate movements were finally confirmed.

5 The Era of Intensive Investigation, 1788–1857

As the age of European exploration gathered pace and corals from exploring ships continued to arrive in Europe in ever-increasing numbers, following the example set by Linnaeus, the task confronting scientists had become one of imposing some kind of order on the growing accumulation of specimens in museums and laboratories everywhere. The two chief institutions for the reception of coral species were in London and Paris, which rapidly emerged as the most vigorous centres.

In Britain, there were two institutions: the British Museum of Natural History, founded by Hans Sloane in 1753, and the Linnean Society, established in 1788 in the London home of James Edward Smith, taking its seemingly anomalous name from Linné and not the latinized Linnaeus. In that year, immediately following the death of Linnaeus, Smith purchased his entire library of 3000 books, along with specimens, manuscripts and an enormous correspondence with some 600 scientists, from his son and heir Carl, for the then-immense sum of £1000. Collaborating with those two institutions was the Royal Society of London, the main forum for the dissemination of research, and their *Philosophical Transactions* was the premier publication.

France, however, had taken the lead, which it maintained for several decades. Throughout the 18th century, a network of regional academies had sustained a rich intellectual culture, of which the scientific epicentre was the *Jardin royal des Plantes médicinales*. Conceived by Gui de la Brosse, personal physician to Louis XIII, in 1626 and inaugurated in 1635, it had been known from 1718 to 1793 as the *Jardin royal des Plantes*, although it was much more than a pharmaceutical and horticultural establishment. Under the stimulating leadership of Georges-Louis Leclerc, le Comte de Buffon (1707–1788), who became Director in 1739 and remained in post until his death, it developed into a flourishing organization in all branches of natural history. Following the Revolution of 1789, and the only scientific institution to survive its Reign of Terror, it was renamed the *Jardin des Plantes* by the National Assembly, and on 10 June 1793, its successor, the National Convention, established the Muséum nationale d'Histoire naturelle within its grounds, with an endowment of 13 professorships.

New Directions in Reef Biology: Lamarck and the Invertebrates

Unlike Britain, Germany and the rest of Europe, where scientists worked either independently or within universities, the state-financed Muséum centralized much of French science in Paris, and thereby came to exercise a high degree of control over research and publishing. Of the 13 initial professors, all with lifetime tenure, two were to achieve lasting fame: Jean-Baptiste Antoine de Monet de Lamarck, appointed in 1793, and Georges Léopole Chrétien Cuvier, appointed in 1802.

Originally a botanist—virtually the entry occupation for all naturalists in that era—Lamarck (1744–1829) began his scientific career after graduating as a medical doctor, with an initial position in the Academy of Sciences on recommendation from Buffon. He soon began to distinguish himself with publications in botany, mainly the highly regarded three-volume *Flore Française* of 1779 (further editions in 1795 and 1805) and the *Dictionnaire de Botanique* (four volumes completed between 1783 and 1795, of a projected eight volumes). Engaged on those and numerous other publications with the continuing patronage of Buffon, Lamarck in 1788 became an assistant botanist in the Jardin des Plantes. Then, in 1793, the year when Marie Antoinette went to the guillotine, Lamarck was appointed professor in the Muséum where he remained for the ensuing 26 years, in that period coming to exercise an immense—if fiercely debated—influence on natural history. Lamarck's position was for the study of the most numerous and least understood group of all animals: those placed at the end of the *Systema naturae* as Insecta and Vermes. The task had defied all who went before: although the four classes of vertebrates—Mammals, Birds, Reptiles, Fish—had been reasonably well organized by Linnaeus, Lamarck complained that "the class of Insects and that of

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worms described in the *Systema naturae* are extremely badly determined" (Lamarck 1801, p. 231).

Whereas the vertebrates had received their designation from the Latin *vertere* (to turn), the Insecta and Vermes had no such collective name. An ingenious deviser of neologisms, such as the term "biology" in 1802, and having identified their major distinguishing characteristic as the lack of a flexible, bony framework, Lamarck defined them negatively as *animaux sans vertèbres*, later revised by Cuvier to *invertèbres*. In 1800, after just 7 years, Lamarck gave a lecture in the Muséum entitled *Systême des Animaux sans vertèbres*, which he published the following year as his first work on the taxonomy of invertebrates.

There he set out a new *scala naturae* of seven classes and 20 orders, arranged in descending degrees of "perfection" from molluscs, down through crustaceans, arachnids, insects, worms, Radiata (his term for echinoderms) and finally, polyps. Coral polyps, he observed, were the most imperfect because they alone had no alimentary canal, but instead "a sac of greater or lesser length, [which] has only one opening—at once both mouth and anus" (Lamarck 1801, p. 248). Simple as it may seem, that recognition was to constitute a major step forward in the morphology of coral polyps by identifying them as biologically unique among all animal life, and in future decades helped identify them as a distinctive taxon within the still-confusing range of zoophytes. Moreover, his concept of perfection in animal form at the time was a gross heresy because he believed that coral polyps were "perhaps, the ones with which nature began, while it formed all others with the help of much time and of favourable circumstances" (Lamarck 1801, p 237).

Lamarck had been profoundly influenced by advances in palaeontology, having become unrelenting in his conviction of the immensity of time that existed before the present and his total rejection of traditional belief that the arrangement of all animal life represented any divine plan. It was, he argued, an evolutionary pattern, brought out quite explicitly in his major work of 1809, the *Zoological Philosophy* (*Philosophie Zoologique*). In that grand exposition which prepared the way for his great and influential study of 1815–1822, the *Histoire naturelle des Animaux sans Vertèbres*, Lamarck revised his taxonomy of 1801 by adding three more classes. He separated the Cirripedes (barnacles) from molluscs and crustaceans, the segmented annelids from flatworms, and devised a third class of "infusorians", Hooke's neologism having become a general term for all microscopically small animals. In his new system, polyps moved one rung up *l'échelle de la nature:* below them, he placed the infusorians, which in 1801 he had described as nothing more than "animated particles". Lamarck had finally made significant progress in reducing the intractable chaos of Vermes to significant order, promoting his own conception of *série* (sequence).

The infusorians stimulated him to speculate on the most profound of issues. If nature is indeed an hierarchical organization from the least to the most perfect, what is the mechanism of ascent to perfection? As life is the defining characteristic of all animals, what, then, is life? Writing with the freedom provided by the Revolution's rejection of all religious dogma, Lamarck invoked the classic logical process of regression of causes to what Aristotle termed the "first cause" (*to proton kinoun*), the initial creative act of the author of Nature. If the infusorians were the first forms of life, then how did they appear? Larmarck's answer was by spontaneous generation (*genération spontané*). Although that belief had been discredited by his time, he was reaching for the absolute origin of life on earth, to the beginnings of geological time: How, in effect, did the very first life forms originate? The most profound of all questions, that question remains unanswered to this day, except by recourse to divine creation, or else, arguably, to experimental demonstration.[1]

Moving on from that speculative issue, Lamarck erected on the foundation of Infusoria and polyps his theory of *transformisme*, the progressive development of animal evolution by the transmission of acquired characteristics. Foreshadowing his revolutionary and controversial theory of transformism, he asserted that nature formed neither classes, orders, families, genera nor invariable species, but only individuals that follow one another and resemble those from which they have been generated: "*la nature n'a réellement formé ni classes ni ordres, ni familles, ni genres, ni espèces constants, mais seulement des individus qui se succèdent les uns aux autres et qui resemblement à ceux qui les ont produits*" (Lamarck 1809a, p. 21). After an infinite series of generations, he argued, "the organization of these bodies has advanced in complexity and has extended ever more widely the animal faculties of the numerous resulting races…[and] by this procedure, maintained for many centuries, nature has succeeded in forming successively all the living bodies that exist" (Lamarck 1809a, p. 187).

Continuing his radical approach to taxonomy, Lamarck also dealt with the vexed issue of the definition of species, especially because the increasing number of discoveries in the New World, particularly the strange fauna found in Australia—the kangaroo, the echidna and the platypus—were, to say the least, perplexing. Arguing that even if scientists become able to determine an order of nature (*ordre naturel*), "the classes which we are obliged to establish in it will always be fundamentally artificial divisions". The ex-

[1] In 1953, Stanley Miller and Harold Urey at the University of Chicago conducted an experiment in which they combined what they believed may have been the original chemical elements of the earth in a closed container into which they discharged an electrical pulse, thereby attempting to replicate lightning. The experiment produced amino acids, one of the essential building blocks of life.

isting system, he continued, was completely inadequate to deal with the platypus and echidna (or spiny anteater), the monotremes that alone, in the class Mammalia, lay eggs.[2] "Already the *Ornithorhyncus* and the *Echidna*", he wrote, "seem to indicate the existence of animals intermediate between birds and mammals. How greatly natural science would profit if the vast region of Australia and many others were better known to us!" (Lamarck 1809a, p. 23)

A Major Revision: *Le Règne Animal* of Cuvier

In 1795, two years after Lamarck's appointment, his colleague, professor of vertebrate zoology Étienne Geoffroy Saint-Hilaire (1772–1844), invited Georges Cuvier (1769–1832), who had begun to acquire a reputation as a naturalist, to the Muséum as an assistant. A dominant personality with well-developed diplomatic skills, Cuvier was promoted in 1802 to the chair of comparative animal anatomy, and worked amicably throughout his life under successive revolutionary, Napoleonic and monarchic governments. He produced an impressive body of publications of which the epitome was his comparative anatomical taxonomy of the entire animal kingdom then known. The first edition of *La Règne animal* (*The Animal Kingdom*) appeared in 1816, and a revised 606-page edition 12 years later.

Like Lamarck, Cuvier was dissatisfied with the *Systema naturae* of Linnaeus, commenting that it was unusable, having subsequently been "disfigured by an unfortunate editor" with many "species grouped or dispersed contrary to all reason". Therefore, he explained, he resolved to begin anew with "anatomy and zoology, dissection and classification" in order to arrive at "a body of anatomical doctrine fitted to develop and explain the zoological system" underlying all animal taxonomy (Cuvier 1816, p. xi–xii). His approach, consequently, by means of empirical observation, mainly of gross morphology and intensive anatomical dissection, was to establish "on positive relations [the full range of] well-authenticated species". From there, he would be able "to construct this great scaffolding of genera, tribes, families, orders, classes and primary divisions which constitute the entire animal kingdom" (Cuvier 1816, p. xiv), subsequently renaming the primary divisions as phyla (sing. phylum), from the Greek *phylon* (a race).

Central to his great taxonomic programme was a conviction that all taxonomies are human constructs, and that there is no natural system in the organic world. From the outset he criticized previous attempts to arrange animals in a "single line, in order to mark their relative superiority", and scornfully dismissed the "supposed chain of being" (*la chaîne des êtres pretendue*) as a "chimerical project" (Cuvier 1816 p. xvii).

As a Protestant Christian born into a Francophone community in the German region of Lutheran Württemburg, which was later incorporated into France, he believed fervently, in contrast to the growing materialism among many intellectuals in post-revolutionary France (including Lamarck, whom he secretly despised[3]), that all life began by divine creation. From his extensive studies in "positive" comparative anatomy, he argued that the different structural forms of various animals were separately designed for adaptation to the environment, which resulted in four independent subkingdoms he termed *embranchements*, and that each *embranchement* had been specifically created by God, with no possibility of overlapping. From their structure, they were described as Vertebrata (flexible), Mollusca (Lat. *mollis*, "soft" [bodied]), Articulata (Lat. *artus*, "jointed") and Radiata (Lat. *radiatus*, "ray-like") for those with symmetrically radial bodies.

Although discoveries of extinct fossils convinced Cuvier that life forms exhibited progressive development and that successive epochs had ensued following catastrophes that occurred unpredictably over immense periods of geological time, and he recognized, unlike most of his contemporaries, that species had become extinct, he steadfastly refuted to the end Lamarck's belief that it indicated some type of transformism. Nonetheless, even his choice of the term *embranchement* for the four taxa reveals confusion, because in French it means "a branching off" or "road junction", which implies some form of development.

Having retained the four classes of Linnaeus for the vertebrates, when Cuvier came to cover the other three great *embranchements* of Mollusca, Articulata and Radiata, in the *Preface* to the first edition of *La Règne animal*, he stated explicitly that in order to complete his great scaffolding, he drew almost entirely from other authors, mentioning the eminent biologists Carl Rudolphi and Friedrich Tiedemann specifically. With respect to shells and corals, he added that he could depend on Lamarck's *Histoire naturelle des Animaux sans Vertèbres*, particularly as both "the Corals and the Infusoria, offering no field for anatomical investigations, will be briefly disposed of" (Cuvier 1816, p. xii, xx).

In the *embranchement* of Radiata, he placed "all those animals known under the name of Zoophytes [which] may be designated *Animalia* radiate", because, unlike the other invertebrates (molluscs, crustaceans, spiders and insects) whose structures are organized bilaterally along a central axis, the Radiata "are disposed as rays around a centre". That taxon, however, had less precision, because he extended it to

[2] Whereas the other three classes of vertebrates—birds, fish, reptiles—have a single gastrointestinal canal terminating in a cloaca, in all animal vertebrates there are two exit places, urethra and anus, except in the *monotremes* (Gk. *mono*, one + *trema*, hole).

[3] Cuvier's hostility was revealed in his "Eulogy" on the death of Lamarck.

five families: Echinodermata (sea stars, urchins, holothurians), Entozoa (minute worms), Acalepha (Gk *akaléphe*, "sea nettles" or stinging jellyfish), Polypi (coral animals) and Infusoria, all of which, by an exercise of the imagination, can be visualized in cross-section as "radiate".

Cuvier's main contribution to coral theory, consequently, came from his identification of the Radiata. A decade later, his views had not changed and he continued to ignore the Radiata, and maintained his belief that they exhibited the least complex morphology and physiology. They only "approximate to the homogeneity of plants", he asserted, "having no distinct nervous system, nor organs of particular senses: there can scarcely be perceived, in some of them, the vestiges of a circulation; their respiratory organs are almost on the surface of the body; the greater number have only a sac without issue for the whole intestine; and the lowest families present only a sort of homogenous pulp, endowed with motion and sensibility" (Cuvier 1828, p. 21–22).

Although Lamarck could describe individual coral polyps as the most imperfect of all animals, and infusorians as nothing more than "animated particles", and Cuvier could equally dismiss the Radiata as "offering no field for anatomical investigations", those judgements, in fact, were assumptions from ignorance. On even the most cursory inspection, the so-called zoophytes displayed an enormous variety of species, none of which at the time had received extensive investigation. Cuvier had based his entire *Règne animal* on the comparative anatomy of adult forms, with very little use of the microscope, which was a seriously limiting factor. Like Lamarck, he had almost no knowledge of embryology and apparently was completely unaware of the contemporaneous research into embryology by Karl Ernst von Baer, Martin Rathke and others in Germany that was beginning to revolutionize biology and completely reconstruct all taxonomies, with major implications for invertebrates.

Even so, in its final second edition of 1828, Cuvier's *Règne animal* marked a great forward development in taxonomy: from a disordered assortment appended to the *Systema naturae*, his new taxon of Radiata was readily accepted and its investigation in coral reef science began to draw increasing attention in the immediate decades following publication. That position, which he presented in *La Règne animal*, however, was to erupt into the most intense scientific *cause célèbre* of the decade in a violent verbal conflict between Cuvier and Geoffroy Saint-Hilaire. In opposition to Cuvier's position on structural adaptation resulting in totally separate classes, Geoffroy's anatomical research into vertebrate anatomy—animals already classified by Linnaeus as mammals, birds, reptiles and fish—led him to believe that all vertebrates were built on the same skeletal plan.

The two opposing views were part of an intense religious debate that was raging at the time, which reached a climactic phase in the French Revolution and influenced scientific investigation profoundly. By then, widespread doubt had been generated about the existence of God, at least in the traditional Biblical anthropomorphic image. Deism, while acknowledging a Creator, had emerged as a reasoned understanding of the world from the interaction of everyday physical processes, while Pantheism was an even more imaginative response, attempting to bridge both worlds, divine and existent. Where Pantheism went beyond Deism by identifying God and Nature as a single entity, however, was in suggesting a conception of God as a continually evolving spiritual force, which opened the way for a major revisionist conception of religion.

By 1809, that changed conception had become extensively developed in the philosophy of Friedrich Wilhelm von Schelling (1755–1854) in his major work *Ueber das Wesen der Menschlichen Freiheit* (On the Nature of Human Freedom), which attracted considerable following during the wave of German Enlightenment promoted by Wolff and Kant. The naturalist Lorenz Oken (1779–1855), Schelling's colleague, created a name for that metaphysical process the following year in his *Lehrbuch der Naturphilosophie* (Manual of Naturphilosophy), in which he presented the Philosophy of Nature as "the science of the eternal transformation of God into the world". "It is", he wrote, "the history of the evolution of the cosmos from nothingness through primitive organisms to the appearance of man and reason" (Lovejoy 1936, p. 320).

Influenced by *Naturphilosophie*, which drew in part from the Neoplatonism of Plotinus, the skeletal plan of vertebrates, Geoffroy believed, came from a divine archetype. Their corresponding parts he therefore considered to be "analogous", although that term was later replaced in 1843 by Richard Owen, recently appointed professor of comparative anatomy in the Hunter Museum of the Royal College of Surgeons, with "homologous" (Gk *homologos*, "in agreement") in his lectures on the "Comparative Anatomy and Physiology of the Invertebrate Animals". Geoffroy's "analogy", and its adjectival form "analogous", then became applied to corresponding structures in vertebrates and invertebrates with similar functions: for example, the legs of mammals and crustaceans. Owen's "homology" was to become the standard term, and a crucial concept as various types of evolutionary theories were proposed to explain the manifest changes visible in the stratigraphic column.

By early 1830, the conflict between Cuvier and Geoffroy regarding taxonomy and structural form had become so acrimonious that an attempt was made to resolve it in weekly debates between the two antagonists before an assembly of scientists and the public in the *Académie des Sciences* (see Appel 1987, p 143 f). Neither, however, gained wide support because each viewpoint had its adherents, and those issues were soon overtaken by developments in embryology and palaeontology that became the way of the future for most biological research, particularly with respect to marine invertebrates.

One of the most intriguing aspects of early 19th-century biology was the infectious enthusiasm of numerous investigators to pursue such anatomical investigations: to construct a more thorough understanding of the Radiata and to map, in detail, every species within the class of Polypi. Although one of the lowest forms of life, according to Lamarck, the humble polyp was responsible for creating some of the most extensive and baffling structures in the natural world.

Zoophyte Taxonomy and Reef Formation

Probably the first attempt at a synoptic view of reef formation came in the 1816 publication of *Histoire des Polypiers coralligènes flexible* by Jean Vincent Fèlix Lamouroux (1779–1825), professor of natural history at the University of Caen, close to the English Channel, from whom Cuvier had been able to draw much information. His was an early attempt to classify every polyp form, from the cold waters of the North Sea to the tropical Caribbean and the Red Sea.

Lamouroux began his taxonomy of coralline polyp structures with a lengthy *Introduction*, setting out his descriptive criteria for arranging them in four classes, with a caution that it was an early work since, of "those Polypidoms which people the vast empire of the deep…only a small number of their polypi have been observed, and entire orders still exist, whose animals have not to this moment been discussed" (Lamouroux 1816, p. v). In that statement, introducing the term "*polypidom*" as a synonym for the compound, colonial structures, and "flexible" for supple or pliant, characterizing the soft-bodied form of most polyps with which he was familiar in European waters, he was careful to comment that "*polypidom*" did not imply the analogy of the "beehive" of the previous century, already dismissed by Linnaeus in the *Systema naturae* and Ellis in his 1786 *Natural History*. Even so, its provenance from the Latin *domus* (house), as already noted created an etymological confusion that irritated other naturalists and lasted for several decades.

Working entirely from external appearances, only observable at the time by rudimentary microscopes, Lamouroux described a considerable number of species, separating them into four categories based on their structural forms as "celluliferous" (Lat. *cellula*, "box"), such as Flustra (moss animals); "calciferous" (Lat. *calcarius*, "lime" or "chalky" in composition) for the hard, rock-like lithophytes; "corticiferous" (Lat. *cortex*, "rind, bark") for organisms such as sponges and gorgonians; and "carnoid" (Lat. *carnosus*, "fleshy"), an indeterminate class characterized by "a fleshy mass, wholly animated…possessing no central axe, and of which almost nothing is known" (Lamouroux 1816 p. vii–viii). Clearly, his carnoid class (possibly ascidians, the sea squirts) was the "homogenous pulp" of Cuvier, an equivalent dumping ground to the Vermes of Linnaeus.

It was the particular taxon of calciferous polyps found in Indo-Pacific tropical regions that he believed responsible for the formation of coral reefs, because there we find "madreporic islands" that "curve in the form of a circle…[that] elevate by slow degrees their rocky dwellings to the surface of the waters". Obviously describing, but not naming them as atolls, and most likely having read of Laval's disaster in the Maldives and almost certainly the French translation of Cook's collision in the "Labyrinth", he introduced that vivid image employed by adventure travel writers of the period of "the navigator confidently sailing in a sea that his predecessors have indicated as free from rocks, [but who, unfortunately,] dashes his prow on an unexpected shelf whose sides are so perpendicular…[and which] from the depths of the oceans emerge those immense reefs" (Lamouroux 1816, p. xi–xiii). Lamouroux's taxonomy of corals, however, which depended in large part on the ideas and categories of Lamarck and Cuvier, found little acceptance in the decades following because he described mainly from external appearances and failed to introduce any defining criteria for his classes based on the interior structures of the animals that he described in detail.

It is important, however, to take a more appreciative view of the work of Lamouroux, pioneer that he was in attempting to organize the immensity of Cuvier's class of Radiata. At the time, like all of his colleagues, Lamouroux was severely hampered by the imperfections of the microscope. The single-lens instrument in 1816 (basically, a simple magnifying glass) created considerable distortion of the object because it could not focus light rays evenly. Significant improvements came by 1834 when the first commercially successful lenses were being produced in France by Charles Chevalier (1804–1859), and also by a number of competing manufacturers: by the late 1830s, the achromatic compound lens and its rapid widespread adoption completely revolutionized microscopy. Not only did it allow increased magnification and a sharply focused field of view, even more significantly, the all-important resolving power, the ability to observe two points only micrometres apart, was strengthened immeasurably, opening an entirely new world for investigation.

The New Microscopy: Zoophyte Morphology Pursued

With more powerful and accurate lenses, the study of zoophyte anatomy advanced rapidly, and Christian Gottfried Ehrenberg (1795–1876), professor of medicine in the University of Berlin from 1839, was a pioneer. Becoming one of the period's most renowned investigators of microscopic life, Ehrenberg began researching corals in the Red Sea during an expedition from 1820 until 1825, and in 1834 presented his findings in a four-volume study entitled *Corallenthieren des rothen Meeres* (Coralline Animals of the Red Sea). In that work, he finally identified the essential differences between Flustra (moss animals or sea mats) and coral polyps, with his discovery that Flustra, unlike polyps, had a complete digestive system, which he assigned to the class of Bryozoans (Gk *bryos*, "moss"), today Ectoprocta. He also identified and named the columella, the central calcified pillar in the skeletal framework of many coral formations.

His really significant contribution came later from his expedition to the North Sea island of Helgoland which he reported in his classic 1838 study, *Die Infusionsthierenchen als vollkommene organismen* (The Organic Perfection of Infusoria). Through brilliant microscopy which resulted in superbly accurate drawings, his description of more than 350 species of single-celled organisms, such as diatoms and foraminiferans, revealed that, despite their apparently primitive character, they exhibited "perfect biological development", although he was mistaken in ascribing developed gastric systems within them. In that study, Ehrenberg emphatically dismissed Lamarck's description of infusorians as mere "animated particles" as well as Cuvier's cavalier contempt for the lower zoophytes because they "offered no field for anatomical investigations".

Notwithstanding the achievements of Ehrenberg, and of an increasing number of other German investigators, the main centre for investigation into zoophyte morphology remained Paris, under the new dominating influence of Henri Milne-Edwards (1800–1885), who succeeded Cuvier in 1838, with his innovative school of physiological zoology. Born of a French mother in Bruges, then part of France, Milne-Edwards, as he styled himself by always prefixing his second given name to his English father's surname, had first practiced as a medical doctor before being drawn to the attractions of the natural history of the marine environment. After moving to the Muséum, he was appointed in 1841 to the chair of entomology, becoming dean of the faculty of science, and in 1864, Director of the entire Muséum, and an undisputed leader of French biology.

From 1828 to 1844, Milne-Edwards pursued extensive research with Victor Adouin, one of Lamarck's former assistants, along the Atlantic coastline of France, their findings appeared in two volumes released between 1832 and 1834 as *Recherches pour servir à l'Histoire naturelle du littoral de la France*. Several years later, again in collaboration with Adouin and others, Milne-Edwards began another major expedition to the coast of Algeria between 1834 and 1836; the discoveries from that mission led to a stream of articles in the *Annales* and *Archives du Muséum*.

Milne-Edwards then began a productive period of research with the zoological polymath Jean Louis Armand de Quatrefages de Bréau (1810–1892), professor of natural history at the Lycée Napoléon. Five years later in 1844, along with several companions, they set off on a grand biological investigation of the Bay of Biscay, sections of the French and Spanish Atlantic coastline, and then southern Italy and Sicily.

In those years before the mid-20th-century development of self-contained underwater breathing apparatus (scuba) equipment by Jacques Cousteau and Émile Gagnan, corals were observed *in situ* through long tubes with a glass lens on the lower end, and in the laboratory after surface net sweeps for plankton, dredging and gathering from exposed cliff crevices and reef platforms at low tide. While in Sicily, Milne-Edwards created an historical precedent by collecting specimens wearing a novel diving apparatus. Before departure, he had a helmet constructed similar to an apparatus used by the Paris Fire Brigade to descend safely into smoke-filled cellars, possibly based on an 1823 English design by John and Charles Deane to fight fires in the holds of ships. As described by de Quatrefages in *Souvenirs d'un Naturaliste (sur les côtes de Sainthonge)* (Rambles of a Naturalist), a record of that expedition, with no seeming knowledge that the Deane invention had been further developed into a diving version in 1828, Milne-Edwards wore "a metallic helmet, provided with a glass visor, [which] encircled the head of the diver, and was fastened round the neck by means of a leather frame supported by a padded collar…[connected] by flexible tube with the air-pump, which was worked by two of our men". Secured to a harness and lifeline from the fishing boat *Santa Rosalia*, and wearing sandals with "heavy lead soles…kept in their places by strong straps", he descended into the Bay of Messina, near Milazzo. Despite some mishaps and awkward moments, de Quatrefages recorded that on one descent "we saw him, at a depth of upwards of twenty-five feet, below the surface of the water, working for more than three-quarters of an hour to detach with a pickaxe some of those large Panopeas of the Mediterranean which are only known by their large bivalve shells". On another occasion, he "returned from the bottom of the sea, his box…richly laden with Molluscs and Zoophytes" (De Quatrefages 1854, II, pp. 17–19).[4]

The Great United States Exploring Expedition of 1838–1842

Simultaneously with Milne-Edwards' research of the coastlines of Europe and North Africa, a most unusual naval expedition had been surveying the entire Pacific, and it came to influence reef science profoundly. The infant nation of the USA, composed mainly of the eastern states and territories—barely extending beyond the Mississippi River into

[4] English translation of 1857.

Missouri, Arkansas and Louisiana—began a challenge to French and English dominance in the Pacific, as well as an increasing Russian presence after the voyages of Otto von Kotzebue (1815–1818, 1823–1826), Fabian Bellingshausen (1819–1821) and Fedor Petrovitch Lütke (1826–1829).

In 1838, the USA dispatched a fleet of six vessels from its small navy, with the grandiose title of United States Exploring Expedition, whose primary function, as set out by Secretary of the Navy, James K. Paulding in his "instructions" to the commander, was "not for conquest, but discovery". In particular, given the "important interests of our commerce embarked in the great whale fisheries…in the great Southern Ocean", he stated, the expedition was to explore, survey and "determine the existence of all doubtful islands and shoals, as to discover and accurately fix the position of those which lie in or near the track of our vessels in that quarter, and may have escaped the observation of scientific investigators". As the Fiji group was a major centre for whalers, an important task was also to select "a safe harbor, easy of access and in every respect adapted to the reception of the vessels of the United States engaged in the whale-fishery, and the general commerce of the seas" (Wilkes 1845, p. 360–363). Although the chief object was "the promotion of commerce and navigation", it was also incumbent on the commander "to extend the bounds of science, and promote the acquisition of knowledge" and for "the more successful attainment of these, a corps of scientific gentlemen … will accompany the expedition". In all, nine men were assigned to the expedition: a philologist, two naturalists, a conchologist, a mineralogist, a botanist, two draftsmen and a horticulturalist (Wilkes 1845, p. 362).

Under command, as events transpired, of the erratic psychopath Lieutenant Charles Wilkes aboard the flagship *Vincennes*, accompanied by another sloop-of-war as well as a store ship, a smaller brig and two small schooner-rigged tenders, the expedition sailed from its base in Norfolk, Virginia, on 18 August 1838. For the next 4 years, less 1 month, it rounded Tierra del Fuego and traversed the coasts of Chile and Peru, then in turn, the Tuomotu archipelago, the Tahiti group and Samoa. Continuing to Australia, after a short stay in Sydney in 1840, where the scientists remained temporarily to further their research, Wilkes departed for Antarctica where he surveyed what is now known as Wilkes Land on the edge of that continent. The expedition then returned to Sydney, and with the scientists back on board, headed to the Fiji group where it remained for some time, then on to Hawaii and finally the western coast of North America, to survey the Columbia River and the Straits of Juan de Fuca where the Russians and British were contesting US interests. The instructions completed, the expedition returned to New York via the Philippines, Singapore and the Cape of Good Hope.

After one of the most extensive surveys of the Pacific, certainly by the largest fleet of any nation at the time, when the four surviving vessels (one sloop-of-war, the *Peacock* having been wrecked and one of the tenders rendered too unseaworthy to continue) sailed into New York Harbour in July 1842. Almost immediately, Wilkes had to face a court martial for his brutal and indifferent cruelty to the seamen; his arrogant, condescending attitude to his officers, including his dismissal of some during the voyage and his paranoid quest for vainglory.

Despite Wilke's unpredictable leadership, a great advance in knowledge of coral reefs was achieved. Two of the scientists, zoologist and conchologist Joseph Couthouy, and geologist James Dana, had made extensive species collections while in the major coral reef regions of Fiji, Hawaii, Tahiti and Samoa, and Dana, officially the mineralogist, was simultaneously involved in his main task of geological surveys of all reefs visited. After one of Wilkes' intemperate outbursts over the smell of zoological material set out on the decks to dry, Couthouy ceased scientific work and left the expedition at Honolulu (Philbrick 2004, pp. 124, 237). Dana immediately undertook Couthouy's duties on top of his own, because he had become experienced in many aspects of conchology and coral zoology as part of his wide-ranging geological interests.

James Dana: Structure and Classification of Zoophytes

James Dwight Dana (1813–1895) was born into a devout Christian middle-class Utica family in upstate New York, and he soon developed a passion for nature that never left him. In 1830, he enrolled at Yale College under the tutelage of Professor of Natural History Benjamin Silliman—later, his father-in-law—where he followed an eclectic programme of studies, mainly chemistry, mineralogy, mathematics and botany. However it was mineralogy, and the emerging science of geology in particular, that attracted him and for whom it became a lifelong career. By the time the Exploring Expedition sailed, Dana had read most of the foundation literature in coral science, and following the lead of Cuvier who exerted a strong formative influence, palaeontology had become one of his special interests, especially the fascinating and contentious history of reef formation advanced by Darwin.

Dana's immediate task after the return of the expedition in 1842 was the preparation of his scientific report, which appeared in 1844 under the title *Structure and Classification of Zoophytes*. An enormous work of 700 pages of text, with an accompanying *Atlas* in 1849 with 61 folio plates of 1008 drawings by Dana himself, all of which had been written from his collection of 300 fossils, 400 coral species and 1000 crustaceans, along with 208 jars of preserved specimens (Philbrick 2004, p. 332). He advanced knowledge of coral species distribution immeasurably, and today is recognized as having "described 18 per cent of coral species in currently operational taxonomy" (Veron 1995, p. 63). Of the coral species retrieved from dredging and littoral collecting, Dana recorded that "among the Feejees, I have taken hold of the corals, and figured 175 species, with the animals of most of them" apparently at the time unknown to science (Gilman 1899, p. 123).

Divided into two main parts, his *Report on Zoophytes*, as he named the taxonomic section, summarized everything published so far by previous investigators including Marsigli, Imperato, Peyssonnel, Boccone, Pallas, Cuvier, Linnaeus and Ellis, along with an outline of the latest research of his contemporaries, mentioning Ehrenberg, de Blainville, Milne-Edwards, Adouin and Grant specifically. Like all those before him, Dana had to struggle with a mass of confusing terminology, particularly the exact meaning of the word "coral". For some it remained limited to the calcareous structure, for others it referred either to the polyp animal or both the animal and the structure.

At the same time, there was still no agreement on how the zoophytes were to be separated into different classes, or of their affinities. Particularly elusive was the status of the numerous species which secreted no calcium and remained solitary, such as sea anemones and medusae, yet were identical in morphology with the main objects of his research, those he designated "reef-building" species. With an explicit acceptance of Cuvier's division of Radiata, Dana dealt with such difficulties in his opening pages, rejecting a number of "objectionable" terms, chiefly "*polypidom*", and presenting his own definition for the work that followed: "We have then the term *Zoophyte* for the whole polyp mass, whether simple or compound, coral-making or not; the term *polyp* for the individual animals; and *Corallum* for the framework or skeleton secreted by polyps. To express the fact that certain polyps secrete a corallum, we use the expression *coral-forming* or *coralligenous*. The animals of a coral zoophyte are *coral-animals* or *coral-polyps*" (Dana 1846, p. 15). The polyp itself he defined as an animal with "a simple visceral cavity, with the single opening to it placed at the centre above, with traces of a radiated structure around it … having no glands to aid digestion … no system of vessels in any part for circulation—imperfect nervous system, if any—no distinction of sex—and no senses but those of taste and touch [with most] attached by their lower surface or extremity to the rocks or some other support, where they live on such chance-bits as are thrown in their way" (Dana 1846, pp. 11–12).

His report then expanded the description of the polyp, one of the first to appear in the literature, going well beyond Lamarck's brief account of "a sac of greater or lesser length with only one opening—at once both mouth and anus". The polyp body, which can be quite large in the case of solitary anemones and medusae, and barely a few millimetres for the smallest, is certainly sac-like with a base attached to a firm substratum and a mouth at the top surrounded by tentacles, and often likened to a coronet. The interior, Dana described as the visceral cavity, where food is captured by the tentacles and digested with the aid of gastric juices known as "chyle" by some then unknown process, the residue then being expelled back through the mouth. The visceral cavity, however, is quite complex with vertical folds or lamellae (Lat. *lamina*, "plate"), some of which generate reproductive ovules.

With that general description, his taxonomy, presented in Chapter 7 of *The Structure and Classification of Zoophytes* (1846) with descriptions in Latin and parallel English translations, identified two basic orders, Hydroidea and Actinoidea, which he considered the "primary subdivisions of zoophytes", all other radiates having been excluded, notably from the earlier research of Milne-Edwards and Adouin in 1828 and Ehrenberg in 1834. As the Hydroidea reproduced only by "ovules pullulating [budding] from the sides of the parent" and their "visceral cavity…[was merely] a simple tubular sac", they were clearly morphologically distinct from the Actinoidea. Originally named by Ellis from the resemblance of their radial tentacles to the rays of the sun (Gk *aktis*, "ray, beam"), the interior of the Actinoidea was described as "divided vertically by fleshy lamellae, proceeding from the walls and forming a radiate series around the cavity" within which their ovules were generated and expelled orally (Dana 1846, p. 16).

The bulk of the *Report on Zoophytes* described in considerable detail the main features of Actinoidea morphology, nutrition and habitats. Reproduction was either by "ovules" or budding, in the latter case with their outgrowths creating the colonial structures where, "although their visceral cavities are distinct, there are numerous communications between those of adjoining polyps, and the fluids pass more or less freely" (Dana 1846, p. 4), whereas the corallum, the calcified skeleton of each polyp, arises from internal secretion. Nutrition came from the particles of animal "chance-bits" in the water column seized by the tentacles armed with what he called "lasso cells" which possessed a yet not understood "stinging power".

Once Dana had completed his work on zoophytes, he plunged ever more energetically into writing. In 1848, he wrote a *Manual of Mineralogy* in which he made valuable contributions to crystallography, and a few years later, in 1853, from the extensive wealth of geological data he had collected, mainly from Fiji, but also from Hawaii, Tahiti, Samoa and Tonga, he produced *Coral Reefs and Islands*. Presented as a comprehensive theory of coral reef origins and geomorphology, he depended throughout on many of the ideas in Darwin's *Structure and Distribution of Coral Reefs* of 1842, with specific acknowledgement that "Mr. Darwin has happily and successfully pursued, and has arrived, as we have reason to believe, at the true theory of Coral Islands" (Dana 1853, p. 88). In contrast to Darwin's work, however, which dealt entirely with the geology and geomorphology of reef formation, Dana's also went into biological detail concerning the structure and habits of coral zoophytes, drawn from his earlier *Report on Zoophytes*.

His continuing taxonomic output made Dana a celebrity in the world of marine science with the award of the Royal Society's Copley Medal. Milne-Edwards wrote several letters in French from Paris, the first as early as 20 September 1847, advising that he had also been awarded the Diploma of La Société Philomatique de Paris, which welcomed him as a Corresponding Member, and expressing joy that at last "the natural sciences are being cultivated with equal success on both sides of the Atlantic". Following his later publications, Charles Lyell wrote from London, and Asa Gray, America's leading botanist, from Harvard. Perhaps the greatest compliment came in a letter from Samuel Morse, of telegraph fame, dated 25 August 1856 from Berlin. While visiting Baron Alexander von Humboldt, Morse informed him that Humboldt described "the science of America as commanding at the present time much admiration in Europe, and in connection with the subject, he spoke most enthusiastically of your work, characterizing it as the most splendid contribution to science of the present day" (see letters in Gilman 1899, p. 356).

In significant contrast to Darwin's descriptive study, however, Dana's work was also suffused with his theist beliefs, well illustrated in his conviction that it is impossible to speculate on "the growth of coral zoophytes and coral formations" because "it is vain to hope to understand fully the works of Him who is himself infinite and incomprehensible". Going far beyond the conceptual ideas of natural theology, the task of the scientist, he believed, was primarily to employ the "scrutinizing eye of science [which] penetrates with far-reaching sight the system of things about us", but always having to recognize the constraints of mankind's "dim limits of vision [which] reads everywhere the word mystery" (Dana 1853, p. 46). As he continued to explain the formation of reefs and their geographical distribution, when he came to discuss atolls and the theory of earth oscillation, he described them as "permanent registers, planted in ages past in the tropics", thereby informing the reader that it is "Divine wisdom [which] creates and makes the creations inscribe their own history; and [for the scientist] there is a noble pleasure in deciphering even one sentence in the Book of Nature" (Dana 1853, p. 124).

Three years later, he followed with a much more controversial study *On the Origin of the Geographical Distribution of the Crustacea* in which he attempted to hold the line for divine design as various evolutionary theories were being hypothesized. In place of development and adaptation of species to the environment, he asserted that the characteristics of crustaceans are not of "climatal origin", but are of divine creation and exhibit "the impress of the Creator's hand, when the species had their first existence in those regions calculated to respond to their necessities" (Dana 1856, p. 43).

Then, in 1872, Dana issued a revision of his 1853 book, re-titled *Corals and Coral Islands*, with the same chapters and structure, but expanded to twice its length from the incorporation of greater detail previously garnered during the exploring expedition. The original edition had neither preface nor bibliography, and relatively few acknowledgements appeared, as needed, within its pages. The short bibliography, apart from several memoirs on polyps and corals by Professor A. E. Verrill, America's leading coral scientist, from the period 1860–1870, drew entirely from works published before 1853, and demonstrated that Dana had not kept up with advances in marine science. He seemed completely unaware of the remarkable biological discoveries in cell theory, embryonic growth and polyp histology. By then, however, Dana had become seriously debilitated, having entered a physical, and almost certainly mental, collapse, from which he never recovered, becoming reclusive, virtually house-bound and aggressively hostile to the increasing reception by scientists of Darwin's 1859 theory of evolution by natural selection in *The Origin of Species*. To the end of his life, Dana never faltered in his unshakeable faith in the overarching providence of God and the visible evidence of divine design everywhere. In one representative passage he wrote that the beholder's joy in the beauty of "coral gardens" arises because "in the beginning…the Spirit of God moved on the face of the waters…and man finds delight therein inasmuch as he bears the image of his Maker" (Dana 1872, p. 57).

The Polyp Defined: Cnidarian Phylum "Coelenterate"

Dana's taxonomy—from a strictly scientific standpoint—was immediately integrated into the literature. Milne-Edwards in particular came to benefit considerably from *Structure and Classification of Zoophytes*, noting explicitly that *dans ces dernières anneés, les progrès de la zoophytologie sont dus principalement aux travaux de M. Dana* (in recent years the progress of zoophytology [has been] due principally to the efforts of Dana). In particular, he singled out Dana's meticulous studies of polyp morphology, the modes of aggregation of colonial species, and the important changes he made in coral systematics, in respect of which he stated that his own arrangement of the Actinoidea followed Dana's methods (Milne-Edwards 1857, xxxiii, p. 2).

Although Dana never studied zoophytes directly again, and concentrated on his academic concerns with geology and writing numerous tracts on religion, coral research continued unabated under Milne-Edwards at the Muséum. Soon after the return of the United States Exploring Expedition, in the mid-1840s in fact, Milne-Edwards had begun collaborating with Jules Haime, his most promising student, and from 1848 until 1854 they jointly published an impressive 15 research papers, mainly in the Muséum's *Annales, Archives* and *Comptes rendus* ("*Reports*") to the *Académie des Sciences*. These were then followed by two major monographs: the identification and description of British fossil corals at the invitation of the Palaeontographical Society in London (founded in 1847 as fossil collecting expanded rapidly) and a request by the Paris encyclopaedia publisher Nicolas Roret for an extended study of the polypi based on their research over the previous decades. In 1854, their joint monograph *British Fossil Corals* was published, Milne-Edwards remarking in the Introduction, rather curiously, that he wrote in English, "a language with which I am not so familiar as I could wish", because translation from his native French could "lend itself to a lack of accuracy of meaning" (Milne-Edwards and Haime 1850–1854, p. 1). In that work, they gave a far more detailed description of polyp morphology than Dana did, and published the criteria employed for description of the carbonate corallum of fossil corals and their taxonomic arrangement which, in general, are followed to the present day for all species.

After that project was completed, they began in 1855 to work intensively on the Roret commission, but before long Haime was taken seriously ill and after a debilitating 18 months, died in 1856. Milne-Edwards laboured on to complete the task, expressing his profound grief in a most touching Preface to the first volume, making it clear that Haime had been, in every sense, his highly talented collaborator, not only in the preliminary research stages but also in actively drafting the first volume (Milne-Edwards 1857, Preface, pp. vii–viii).

That publication, *Histoire naturelle des Coralliaires, ou Polypes proprement dits*, was a comprehensive work, which brought together everything that went before. Finally issued in three volumes between 1857 and 1860, with a supplementary *Atlas*, the biology and taxonomy of the simple polyp itself, indicated in the title by the French idiom "*proprement dits*", meaning "properly so-called", became available to all coral researchers. Although it never appeared in translation, it is evident from the literature of the period that scientists, in Germany and England in particular, used it extensively and followed Dana's lead.

The express intention of his "*chef d'oeuvre*" was to coordinate and consolidate everything so far definitely determined about the coral polyp itself—"*proprement dits*"—from antiquity to the then present day. Opening with a short, 33-page section, it presented a richly informative survey of the main achievements in polyp research from European scientists, mainly in the decades since Peyssonnel, along with generous recognition to Dana. The body of the text of Volume 1 which followed, headed *Considérations Générales sur les Coralliaires* (*A General Account of Corals*), provided a very detailed 92-page section on the anatomy of the polyp, followed by the bulk of the text in Part 2 headed *Classification des Coralliaires*. Starting his taxonomy was the primary definition that "*La classe des coralliaires…se compose des Animaux Radiares*" has the following characteristics: a central mouth, surrounded by tentacles, a cavity freely communicating with the outside, and the generative organs lining it (Milne-Edwards 1857, p. 93).

One of the most interesting results from the anatomical study of the polyp came with a solution to the long-standing puzzle of the cause of the notorious stinging powers, first described by Aristotle, in the sea nettles (Gk. *akalephe*, Lat. *urtica*), which came from lengths of cells that trailed behind. Polyps also had similar cells in their tentacles, and so, as an American, Dana had looked to the cattle-ranching frontier and named them "lasso-cells" from their ability to capture prey, while other scientists, because of their structure, designated them "thread cells". From close microscopic analysis and exhaustive research, Jules Haime had discovered that each so-called "thread cell" was composed of a spiral array of toxic stinging barbs ("*corps uticants ou spicules filifères*"), each within an individual sac.

Haime's major achievement was recorded in Milne-Edwards' gracious tribute to the investigation carried out entirely "by my brilliant, young collaborator" ("*tirés d'un travail fait entièrement par mon jeune et savant collaborateur, J. Haime*") with a neologism that has passed permanently into the universal language of marine science. Describing Haime's accomplishment, and turning to traditional Greek for appropriate terms (Gk *nema*, "thread" + *kystis*, "bladder"), Milne-Edwards declared that "*nous appellerons par abréviation nematocysts* (we shall call them by a single word—nematocysts) (Milne-Edwards 1857, p. 19, note 1).

Having completed the lengthy opening section on the anatomy of the polyp, Milne-Edwards presented in Part 2 an exhaustive taxonomy of all species of the order Alcyonaria, the so-called soft corals, *malacodermés* (Gk. *malakía*, "soft" + *dérma*, "skin"), and the order Zoantharia, the hard corals, *corallières sclérodermés* (Gk. *skleros*, "hard"). To describe that distinctive structure he adopted a recent neologism devised by Rudolf Leuckart a decade earlier. In 1847, Heinrich Frey (1822–1890) and Rudolf Leuckart (1822–1898) of the University of Göttingen had published the results of their North Sea expedition to the island of Helgoland as *Beiträge zur Kenntnis wirbelloser Thiere norddeutschen Meeres* (*Contribution to Our Knowledge of Invertebrates in the North Sea*). To identify the unique morphological character of the simple polyp, Leuckart combined the Greek *koilos* for "hollow" and *enteron* for "stomach", and latinized the compound to "coelenterons", thereby introducing the neologism "coelenterate" (Frey and Leuckart 1847, p. 37). With specific acknowledgement, Milne-Edwards adopted it as his primary taxonomic term: *la classe des Coralliaires se compose des*

ZOOPHYTES RADIARES COELENTÉRÉS (Milne-Edwards 1857, p. 4). Thereafter, Coelenterata became the defining taxon for all polyps, composed of the two phyla Cnidaria and Ctenophora (comb jellies).

With those achievements, Milne-Edwards then made yet another innovation in coral taxonomy. With the identification of nematocysts as an essential characteristic of all coral polyps, he took the Greek *knidé*, meaning "stinging", and classified the two orders of alcyonaria and zoantharia in *Histoire naturelle des Coralliaires* as cnidarians: "*la sous-classe des cnidaires*" (Milne-Edwards 1857, p. 325).[5]

Consequently, with the comprehensive publications of Dana and Milne-Edwards, and an increasing series of contributions from a rising number of investigators, understanding of polyp biology and coral taxonomy had advanced considerably since the days of Ellis and Lamarck. What remained a major taxonomic obstacle, however, was Cuvier's class of Radiata, which still lacked any detailed histological analysis and depended solely on gross morphology. Major revisions were to come in subsequent decades as advances were made in understanding epigenetic (growth and development) processes, in the first instance from the publication in 1849 of an astonishing contribution to coral science from a completely unknown tyro: a 23-year-old assistant naval surgeon and amateur biologist.

[5] Today the former Phylum 'coelenterate' is the Phylum Cnidaria, and the coelenterates consist of the Cnidaria and the nematocyst-free Ctenopora.

6 Embryos, Archetypes and Evolution

One of the major problems facing the Australian colonial government in the early decades of settlement was the frequent losses of ships travelling to Britain, India, Asia and North America while navigating the extremely dangerous Great Barrier Reef that borders the northern half of the eastern coast for 1000 nautical miles. As the colony expanded, remembering that the only effective transport was by sea, accurate charts, both of hazards and safe anchorages, were essential for settlement, trade and naval defence. In response to this problem, and mainly to ensure the safety of the shorter and less turbulent inner route to Asia, India and North America throughout the early decades, extensive surveys were conducted. Following the initial voyage by Matthew Flinders in command of *Investigator* from 1801–1803, five more hydrographic surveys were commissioned to complete the task. Quite unexpectedly, from the three survey cruises of HMS *Rattlesnake* between 1846 and 1850 came a taxonomic report that changed coral science and remains one of its most defining discoveries.

Thomas Henry Huxley: Microscopy and the Polyp

On 21 June 1849, the Earl of Rosse, President of the Royal Society of London announced at one of its regular meetings that a paper would be read *On the Anatomy and Affinities of the Family of the Medusae* by Thomas Henry Huxley, Esq., who has had "numerous and peculiar opportunities for the investigation of these animals during a cruise of some months along the eastern coast of Australia and Bass's Strait" (Huxley 1849, pp. 432–433).

Son of George Huxley, a country schoolmaster in rural Middlesex, Huxley (1825–1895) passed the University of London medical examinations with honours in anatomy and physiology in 1845, and the following year received assignment as assistant surgeon to the *Rattlesnake* that was being prepared for the voyage to the Great Barrier Reef. Very little is known of Huxley's activities throughout the 3½ years of the three consecutive *Rattlesnake* surveys: he is mentioned, almost always incidentally, in a supporting role by the ship's naturalist John MacGillivray in the official record of 1852, the *Narrative of the Voyage of HMS Rattlesnake* (MacGillivray 1852). The mystery is heightened by the fact that although Huxley departed with the express intention recorded in his diary of making a "careful study of all matters relating to coral and corallines" along the Great Barrier Reef, the greatest region in the world for such a project and with an unrivalled opportunity, he evidently made no specific coral studies at all (Huxley 1935, p. 52). Instead, he became preoccupied with other coelenterates, especially the medusae or scyphozoans (jellyfish) and the hydrozoans (stinging corals, the Portuguese man-o-war or bluebottle, *Physalia physalis*), and similar colonial animals, collecting specimens by townetting on the way out from England, supplementing them with varieties found in reef waters. His published descriptions and skilful drawings, however, reveal meticulous study and dissection, indicating most likely that he spent most of his scientific time aboard the ship at the microscope.

In March 1848, while relaxing in Sydney after the first cruise, Huxley was again welcomed at the Elizabeth Bay mansion, considered the finest residence ever built in Australia, and now part of the National Trust, of chief administrator Colonial Secretary Alexander Macleay and his son William Sharp Macleay (1792–1865), who were particularly enthused by his dramatized recounting of adventures in biological collecting along the Great Barrier Reef. During that visit, he showed a paper he had written from his painstaking dissections of medusae to William Sharp, himself an enthusiastic naturalist who was attempting to develop a new taxonomy (the "quinary system"), one safely within the orthodoxy of Divine Design.

William Sharp Macleay, who succeeded his father as chairman of the boards of trustees of both the Australian Museum and the Sydney Botanical Gardens when Alexander died in 1848, was so impressed with the quality of Huxley's paper that he took the initiative of sending it, in government dispatches, to the Zoological Society of London after Huxley

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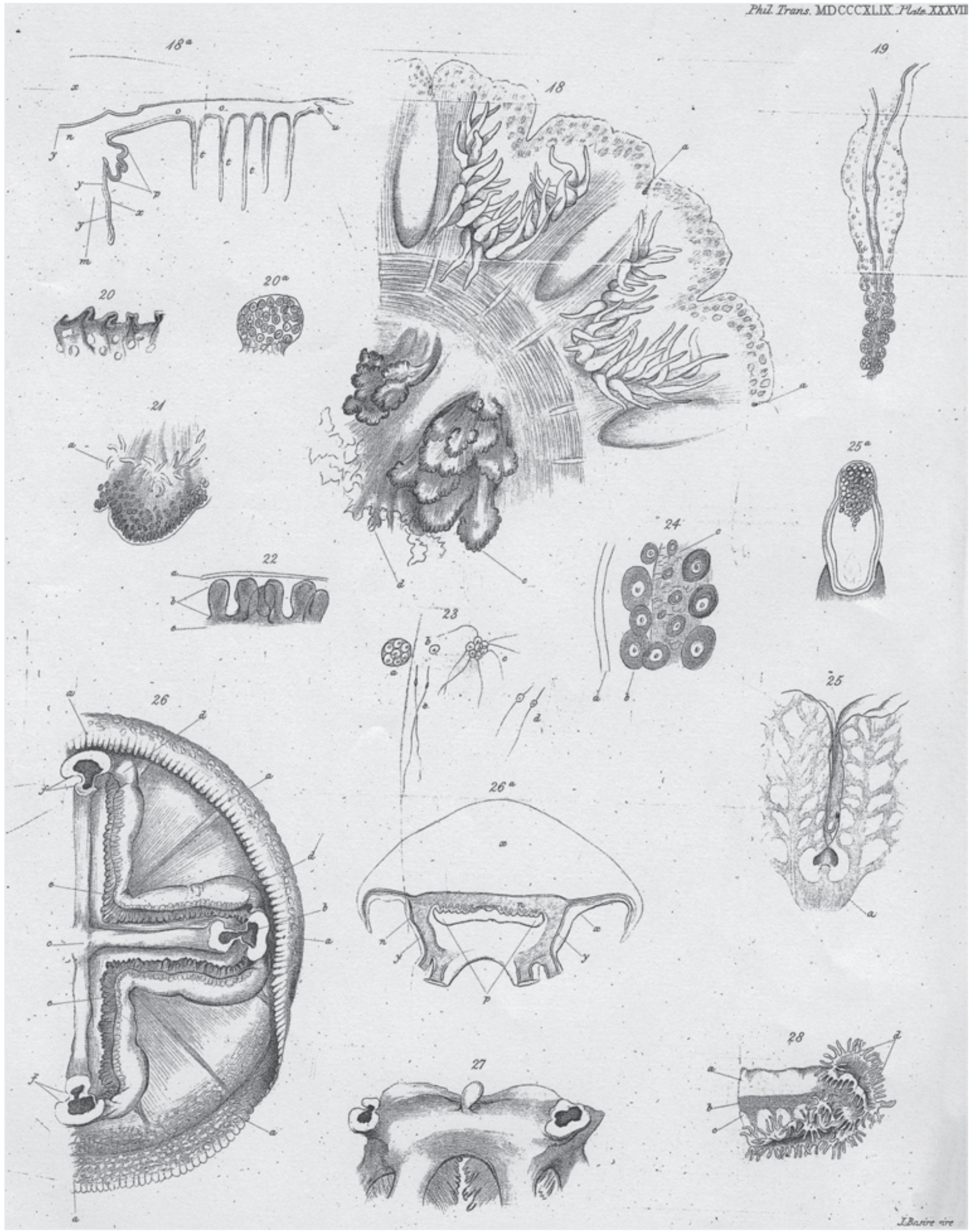

Medusa dissections by Huxley during the Great Barrier Reef survey by HMS *Rattlesnake*. (Reproduced from the *Philosophical Transactions*, 1849: Plate 36)

had departed on the second survey cruise. Not only was it published in the *Philosophical Transactions*, it also led in June 1851 to his election as a Fellow of the Royal Society and the award of their Royal Medal the following year.

Apparently unknown to all on board, however, Huxley kept a secret diary in which he recorded his thoughts throughout the voyage, and that diary was eventually discovered in family papers nearly a century later by his grandson, himself to become a distinguished biologist. From the publication of the diary in 1935, edited by Julian Huxley, we are able to gain some understanding of the formative scientific years of one of England's greatest biologists of the 19th century. In a passage the young assistant surgeon penned inside the back cover of the diary, there is a most intriguing indicator of his future vigorous, and often controversial, career. Headed with an epigram in early nineteenth century German, "*Thätige Skepsis*", it is followed by his personal elaboration: "An Active Scepticism is that which unceasingly strives to overcome itself and by well directed Research attain to a Kind of Conditional Certainty".[1]

To appreciate the full impact of Huxley's groundbreaking paper on the Medusae, it is necessary to sketch the background that guided his thinking. As a student, he had studied the prevailing theory of medical treatment developed in the

[1] Facsimile in Huxley 1935, p. 352.

Paris hospitals by surgeon Marie-François-Xavier Bichat (1771–1802) and described in his *Traité des Membranes en générale, et diverse Membranes en particulier* of 1800 (English translation 1813, *A Treatise on the Membranes*). From dissection of some 600 cadavers, Bichat proposed that the study of visible pathologies in the various tissues of the human body held the key to diagnosis. In all, 21 types of tissue (cartilaginous, muscular, fatty, skeletal, etc.) were identified, and in his doctrine, the scientific discipline of histology (Gk *histos*, "web, network") has its origins. The potential of the microscope for tissue analysis was hence advanced considerably, notably in the emerging field of embryology that would become central to the development of coral science.

Some decades previously, in his doctoral thesis of 1759, *Theoria generationis* (Theory of Generation), Caspar Friedrich Wolff (1733–1794) had completely discredited the theory of preformation, which began with the microscopy of Leeuwenhoek and led to the belief that the spermatozoon was a miniature adult, a "homunculus". From microscopic analysis of the unincubated zygote (fertilized egg) of the domestic hen, Wolff established that no vital organs were visible at conception, and that they only appeared later during the developmental process. In 1817, his observations were taken a stage further by Christian Pander (1794–1865) who observed the initial appearance of "agglomerations" of "unstructured, gelatinous substances" in chick development during incubation, which he named the blastoderm (Gk *blastema*, "offspring") and described its subsequent structure as consisting of three germ layers (Lat. *germen*, "to sprout"). "At the twelfth hour", he wrote, "the blastoderm consists of two entirely separate layers, an inner one, thicker, granular and opaque, and an outer one, thinner, smooth and transparent. The latter…we may call the serous layer [Lat. *serum*, 'watery fluid'] and the former the mucous layer [Lat. *mucus*, 'nasal discharge'].… Then arises between the two layers of the blastoderm, a third middle one in which the blood-vessels are formed, which we therefore call the vessel-layer".[2]

In the same period, understanding of coral polyp morphology was advanced by Martin Heinrich Rathke (1793–1860) who, stimulated by the research of Pander, applied the same methods to invertebrates and reported in 1825 that initially only two germ layers are formed. Then, "after the blastoderm has divided into two layers, each of these proceeds by itself towards its final goal", the outer, serous layer giving rise to the nervous and muscular systems and the inner, mucous layer developing into the intestine. In 1829, in a follow-up paper, Rathke reported a further discovery that the two initial layers of the invertebrates are similar to those of the vertebrates in the early stages of development, one corresponding "to the mucous layer of vertebrates…the other…essentially comparable to the serous layer of the vertebrate".[3]

The new discipline of embryology was advancing rapidly, and in 1827 came the momentous publication of *Epistola de ovo mammalium et hominis genesi* ("Concerning the Mammalian Ovum and Human Origins") by Karl Ernst von Baer (1792–1876) from Königsberg, where he identified the mammalian ovum in a dog. In 1828 came Volume 1 of von Baer's even more definitive two-volume masterwork, *Über Entwickelungsgeshichte der Thiere* ("On the Developmental History of Animals") (Baer 1828–1837), which revolutionized embryology. An Estonian of Prussian ancestry and the Russian aristocracy (Estonia was then part of the Russian Empire), von Baer moved in 1830 to the Imperial Academy in St Petersburg, closer to his ancestral home, where he remained until retirement in 1867. Unfortunately, with his temporary inability to access essential research publications, and despite the publisher's exhortations, the second volume did not appear until 1837 (see Groeben 1993, p. 94, note 106).

Accepting Cuvier's fourfold division of the animal kingdom into "*embranchements*", each of which followed a separate predetermined developmental pattern, von Baer's intensive investigations described the initial stage of fertilization of the ovum as the growth of a globular mass of granular tissue, which, from its similarity to a blackberry, was given the equivalent Latin name, *morula*. The morula then developed into a hollow ball, or *blastula*, around which the serous layer formed, basically a very fine molecular sheet barely 10 nm (10^{-8} m) thick. In the final stage, von Baer described how in the central "vessel-layer" membrane, a fine thread of cells appears as the notochord, which in higher animals develops into the spine. The next task was to describe the process of gastrulation, that is, the actual behaviour of cells in the course of proliferation as they separate into tissue layers, enclosing what becomes the alimentary cavity, the *enteron*. The possibility that cells themselves, first described in the 17th century by Robert Hooke as "a great many little boxes" could play an active epigenetic role during embryonic growth had been first suggested by Matthias Schleiden (1804–1882) and given a label as "cell theory" in 1839 by his colleague Theodor Schwann (1810–1882). In his cytoblastema theory (Gk *kytos*, "vessel"), Schwann theorized that cells were somehow generated from the "unstructured, gelatinous substances" within which dark granules appeared (named "nucleoli" by Gabriel Gustav Valentin in 1836) which in turn fused into nuclei, earlier identified by Robert Brown in 1833 as the "kernel" or nucleus of the cell, by some unspecified precipitation process.

With the embryological discoveries of von Baer, completed in the second volume of his *Developmental History of Animals*, and the contemporaneous suggestion of Schwann

[2] Pander 1817, translation by Oppenheimer 1967, p. 258.

[3] Rathke 1829, translation by Oppenheimer 1967, p. 260.

that the cell could well be the fundamental building block of life, a new avenue of investigation was opened. Hooke, of course, had only identified the outer cell casings in a slice of cork, the content having dried out: exactly what made up the viscous protoplasm within living plant and animal cells remained to be discovered. Once tissues could be studied and discrete cells observed through the much-improved microscope, however, it had become certain that in some way they were essential to the formation of living tissue of both plants and animals. Exactly how was to occupy histologists for the rest of the century. Not until the 1850s did Robert Remak (1815–1865) at the University of St Petersburg discover the process of cell division by binary fission, and hence of tissue growth and development (Remak 1855).

At the time of the *Rattlesnake* cruise, though, germ layer theory and histology were infant sciences: cell division and function remained unknown, and Huxley's ideas on epigenesis were directed by his reading of Bichat, Rathke, von Baer, Schleiden and Schwann, among others. It was the discovery by Rathke of the primary formation of the outer and inner membranes in the invertebrates that directed Huxley's research into the medusae and led to the next major advance in coral science.

Anatomy and Affinities of the Family of the Medusae

Medusae are known around the world as the ubiquitous jellyfish, global travellers in a huge range of nearly 1000 species, riding the ocean currents, and distressing bathers with their stinging cells. Contact with the extremely toxic trailing tentacles up to 50 cm long on the tiny 2-cm-wide body of the Irukandji (*Carukia barnesi*) and up to 3 m long on the larger 20-cm-wide box jellyfish (*Chironex fleckeri*) of the Great Barrier Reef proved in some cases fatal to humans, and if not immediately treated could result in the equivalent of third-degree burns. Classified today in the phylum Cnidaria, within the class Scyphozoa (from the resemblance of their bell-shaped body to the *skyfos*, the ancient Greek drinking cup), their name was taken by Linnaeus from the mythical female monster Medusa, whose hair was a mass of writhing snakes, as a vivid metaphor for the numerous tentacles attached to their gelatinous bell.

That of course raises a puzzle in reading Huxley's research report read to the Royal Society in June 1849. If he really had intended to make a "careful study of all matters relating to coral and corallines" in Great Barrier Reef waters, why did he spend most of his 3 years on the medusae? As his personal diary reveals, Huxley was highly ambitious for acclaim, and his talent for "active scepticism" while reading von Baer and Rathke suggests an intriguing thesis he may have decided to explore during the survey of the Great Barrier Reef.

By the 1840s, comparative anatomy had become an intensively investigated field as palaeontology and histology attracted ever more scientists. Lamarck's theory of transformism and Cuvier's belief in the progressive development of species were continuing as very active concepts, now given fresh impetus from von Baer's work in "developmental history". In addition, coming from a completely unexpected direction, and vigorously stimulating speculation on human origins, was the anonymous, sensational publication in 1844 of *Vestiges of the Natural History of Creation*. Following the theory of Pièrre Laplace, it argued that the earth had been formed from inchoate clouds of nebulous gases on which life subsequently appeared, beginning with invertebrates, then the lower animals and finally humans, among whom the "Negro, Malay, American and Mongolian nations", were "simply representations of particular stages in the development of the highest or Caucasian type" (Chambers 1844, p. 307). Evolutionary theory—Lamarck's "transformism" at the time—was certainly in the air.

Huxley's starting point was the taxon Radiata within which Cuvier had separated the polypi from the other four families of Echinodermata, Entozoa, Acalephi and Infusoria on the basis of a blind gut. All other life forms in the Radiata, from the lowly bryozoans, as Ehrenberg had demonstrated, through the vertebrates to mankind, have a complete alimentary canal, with a third intermediate membrane. The research of von Baer consequently enabled Huxley to identify the polypi as unique in the animal kingdom: in fact, they were out of place even in the Radiata.

In a developmental and physiological sense, the polypi were anomalous, and that suggests the thesis Huxley may have planned to pursue: to account for what seemed aberrant forms and to discover their relationships with each other and with all other taxa in the animal kingdom. Huxley's intentions, in fact, are set out succinctly, with a considerable dash of hubris, in his opening sentence: "Perhaps no class of animals has been so much investigated with so little satisfactory and comprehensive result as the family of the Medusae" (Huxley 1849, p. 413).

What prompted that comment about the substantial body of published research on the Medusae, which he had read thoroughly? In the opening page, he identified Ehrenberg, Milne-Edwards, de Blainville, Péron and Lesueur: a roll call of the most significant contemporary marine invertebrate scientists. In 1810, the naturalist François-Auguste Péron (1775–1810) and artist Charles-Alexandre Lesueur (1778–1846), in large part from their research during the voyage of *Le Géographe* under the command of the ill-starred Baudin, had published *Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce* *jour* (Genera and Species of all Known Medusae to the Present Day). Ehrenberg's studies in the Red Sea covered the Medusae; Henri Marie Ducrotay de Blainville (1778–1850), who followed in Cuvier's chair of Comparative Anatomy, made a major study of medusae as part of his 1825–1827 *Manuel de Malacologie et Conchyliologie* ("Handbook of Molluscs and Shells").

Why too did Huxley want to study the medusae specifically? In terms of general morphology, they are simply very large inverted polyps, although entirely pelagic and with a slightly more complex metamorphosis. In his opening section, he described their basic structure as a central disc, surrounded by tentacles, containing a stomach and canals, and "generative organs, either ovaria or testes", in effect, the essential features of coelenterates. Not mentioned is one possible reason: being larger, they would have been more easily dissected with the microscopes of the time aboard a ship at sea in often-agitated waters. At first glance, that might seem a quite practical explanation for his interest, but an additional, deeper motivation can be discerned in his opening comments. The limitations he found in the work of those he mentioned was because "they have contented themselves with stating matters of detail concerning particular genera and species, instead of giving broad and general views of the whole class, considered as organized upon a given type, and inquiring into its relations with other families". He then continued: "My present research has done much towards suggesting a clue in unravelling many complexities, at first sight not very intelligible" (Huxley 1849, p. 413), the "clue" being contained in the phrase "organized upon a given type". Although von Baer and Rathke are never mentioned, it is abundantly clear throughout the pages that follow that Huxley had suspected that the primary stage of blastogenesis when the inner cavity begins expanding inside the morula was of major taxonomic importance, and that it had not been examined in sufficient detail by those he cited.

The entire paper, consequently, is one sustained examination of germ layer theory applied to the anatomy of the medusae. "I would wish to lay particular stress", he emphasized in his opening comments, "upon the composition of [the stomach] and other organs of the Medusae out of two distinct membranes, as I believe that it is one of the essential peculiarities of their structure, and that a knowledge of the fact is of great importance in investigating their homologies" (Huxley 1849, p. 414).

Of profound significance here is Huxley's introduction of the term "homology" that was to create much of the controversy following publication of his paper. The concept itself, as mentioned before, had been introduced in 1843 by palaeontologist Richard Owen in his Hunterian Lectures. To give it greater precision than the earlier term "analogy" devised by Geoffroy, he defined it as "the same organ in different animals under every variety of form and function",[4] in order to describe nothing more than similar structural relationships. Huxley, however, primarily a surgeon and anatomist, and familiar with the work of Bichat, von Baer, Rathke, Schlieden and Schwann, was searching for similarity based on physical structure from a "given type".

In a methodical analysis of the numerous genera and species he was able to dissect, Huxley's paper dealt, in sequence, with the four major features of the medusae: the stomach, the disc (or bell), the tentacles and the generative organs of ovarium and testis. The major organ identified was the stomach, attached to the disc, which he called a "common cavity". Its inner lining consisted of internal canals containing the generative organs (the ovarium with "immense multitudes of ova" and the testis with "a vast number of pyriform sacs" full of spermatozoa "in every stage of development") and some of the stinging thread cells, other thread cells being located within the outer membrane of the tentacles (Huxley 1849, p. 422). For every specimen dissected, Huxley discovered the same basic plan: "a Medusa consists essentially of two membranes enclosing a variously shaped cavity", within which were the generative organs, with "thread-cells universally present" (Huxley 1849, p. 425).[5]

That constituted a remarkable achievement. Despite their vast range of shapes, sizes, and global distribution, today known to number at least 1000 species, with many still undescribed, Huxley's concentration on their morphology and the "two foundation membranes" led to his generalization that the medusae, in all their variety, were "organized upon a given type…[and were] by no means so distinct as has been hitherto supposed, but…are members of one great group, organized upon one simple and uniform plan, and even their most complex and aberrant forms [are] reducible to the same type". Then came a suggestive comment: discovering that their organs were obviously homologous, Huxley speculated that all polyps in "their various families are traceable back to the same point in the way of development".

Huxley's most prescient observation, however, was drawn from the earlier researches of Rathke and von Baer. "It is curious to remark", he commented, "that throughout, the inner and outer membranes appear to bear the same physiological relation to one another as the serous and mucous layers of the germ; the outer becoming developed into the muscular system and giving rise to the organs of offense and defense; the inner, on the other hand, appearing more closely subservient

[4] Because the legs of crabs and horses have the same function but different structures, they are considered "analogous". In contrast, because the flipper of a dolphin, the foreleg of a horse and the arm of a human all have the same skeletal structure, they are described as "homologous".

[5] The term "nematocyst" was still a decade away in 1857.

to the purposes of nutrition and generation" (Huxley 1849, p. 426). That observation remained a sleeper for 20 years!

Defence of Nature's Chain

At the time of Huxley's paper in mid-century, with rejection of the Great Chain of Being by Lamarck and Cuvier, yet another increasingly confrontational debate began. As "transformist" and evolutionary theories began appearing, such as *Vestiges of the Natural History of Creation* in 1844 and the elaborately contrived arguments of "*Naturphilosophie*", defence of the traditional orthodox position became intensified, strongly expressed by Dana in his belief that Divine Creation underlay all nature. Even more outspokenly, theism was defended by Gosse who declared in *Omphalos* (Gk "navel") his weird attempt to reconcile geological evidence with Mosaic creation, that the characters of all present species were "as definite at the first instant of their creation as now" (Gosse 1857, p. 111). Even Adam, Gosse asserted confidently, came with a navel, which gave the name for his book.

An even more dedicated apologist for Mosaic creation was America's most prominent biologist, Louis Agassiz. Born Jean Louis Rodolfe Agassiz (1807–1873) in Francophone Switzerland, he was appointed on the recommendation of Alexander von Humboldt to a chair in the Lyceum of Neuchâtel. In 1846, he migrated to the USA and 2 years later accepted a professorship at Harvard College, founding the Museum of Comparative Zoology in 1859, where he rapidly established an influential reputation. His strong support for the creationist cause appeared in 1857 in his *Essay on Classification* as Volume I of his four-volume *Contributions to the Natural History of the United States of America* (1857–1862).

Volume I is organized into two sections, the first a descriptive account of the "the fundamental relations of animals to one another and the world in which they live as the basis of the natural system of animals", and the second, of approximately equal length, a survey and critical discussion of the various taxonomies then being proposed. Although he declared that he was "not writing a didactic work" and would "simply recall the leading features of the evidence" then available from "the affinities or the anatomical structure of animals, or from their habits and their geographical distribution, from their embryology, or from their succession in past geological ages", he ended that short statement of intent with his belief that, because the available evidence consisted of "isolated and disconnected facts", they were in themselves of "little consequence in the contemplation of the whole plan of creation" (Agassiz 1857–1862, I, pp. 12–13).

The necessary steps needed to explain the "isolated and disconnected facts" of natural history, Agassiz declared, lay in understanding that taxonomy cannot be a human invention but, in essence, a search for "an ideal connection in the mind of the Creator…which had not grown out of the necessary action of physical laws, but was a free conception of the Almighty Intellect, matured in his thought, before it was manifested in tangible external forms". By accepting divine "premeditation prior to the act of creation, we have done once and for ever with the desolate theory that refers us to the laws of matter as accounting for all the wonders of the universe and leaves us with no God but the monotonous, unvarying action of physical forces, binding all things to their inevitable destiny" (Agassiz 1857–1862, I, p. 10). Concluding his lengthy opening chapter on the "Fundamental Relations of Animals", Agassiz drew it together with his unequivocal statement that nature "proclaims aloud the One God…and Natural History must in good time become the analysis of the thoughts of the Creator of the Universe" (Agassiz 1857–1862, I, p. 137).

An even more outspoken defence of Divine Design came from Dublin-born Frederick McCoy (1817–1899), who became foundation professor of natural history in the then new University of Melbourne in 1855. In a series of public lectures over the period 1869–1870 (McCoy 1869, 1870), McCoy explained to his audience that the significance of investigation into Australian biota, much of which did not exist on other continents, lay in finding evidence to complete the picture of God's creation. The visible world we experience, he declared, "the whole of the vegetables, the whole of the animals, are part of one, great, complete, universal, perfect plan, which was conceived by the Almighty, in the beginning while as yet there were none of them, and that all of the separate parts were brought into existence at His own different times, following laws some part of which we may dimly perceive". As those missing separate parts were discovered in Australia, he explained, naturalists were able to work on completing the overall design. At first there were many empty spaces, he declared, but, as exploration and collections continue, when "you go to look at some other country you find many of the creatures that were wanted to fill your gaps, to make up the perfect sequence" which will lead you to "find that many of them follow in such exact succession that admiration is excited at the beauty and continuity of the chain" (McCoy 1870, pp. 23–32).

Problem of the "Archetype": Platonic Form or Taxonomic Term?

Meanwhile, as supports for divine governance were increasingly promoted while Huxley was aboard the *Rattlesnake*, the debate was becoming even more confrontational. In 1848, Owen moved to develop more precisely his earlier ideas on homology of 1843 concerning the invertebrates in a report to the British Association for the Advancement of Science (generally shortened to the "British Association" or the

BA), under the title *On the Archetype and Homologies of the Vertebrate Skeleton*. In that lengthy work, he advanced a number of contentious issues that came to embroil him in extensive dispute with Huxley and Darwin.

The key words homology and archetype were the catalysts to argument, and, in essence, fundamental to the current direction of scientific investigation. Homology in Owen's original definition of 1843 was simply descriptive: in contrast, when Huxley adopted it for his article, he had precise developmental processes in mind, suspecting that homologous species could have descended from a common ancestor, as the etymology of homology (Gk *homologos*, "in agreement") indicates. Unwittingly, perhaps, he was feeling for some kind of time pattern in species affinities. Owen, however, had subsequently formulated a revised definition of "archetype" that was to encounter far more sustained opposition. Reasoning from his universally acclaimed reconstructions of fossil discoveries as they were increasingly unearthed throughout the world, he moved to identify the common vertebrate structure revealed in comparative studies specifically as an "archetype". Using it for the first time in his 1848 publication as a "primary pattern", Owen went much further than in 1843. An avowed theist, like Dana and Gosse, Owen had conceived his "archetype" (Gk *arché*, "origin" or "first cause" + *túpos*, "figure" or "image") as a pre-existent metaphysical entity: an ideal "otherworldly" form that underlies the material existence of all animals and which, in his view, was confirmed by homology. That was where his difficulties multiplied as he entered deeper water than he realized. The Platonic legacy of the archetype, as Owen conceived it, although he was probably unaware of its origin, was distinctly Neoplatonic, based on the writings of Plotinus. For Owen, the skeletal plan of all vertebrates was one of the "thoughts of God", one of the archetypal ideas emanating from the "will of the Divine Creator".

This is not the context for further presentation of the complex philosophical and theological thought of that period; it is, however, highly relevant to making it clear that nowhere in the *corpus Platonicum* do we find unambiguous evidence that Plato himself actually held the view that the *eide* (Gk "ideas") are substantial.[6] What we do find is the assertion, even more forcefully in Aristotle,[7] that ideas have reality as linguistic universals that allow classification and predication, nothing more.

[6] Developed in Phaedo (100b–101d) where they are merely hypothesized and in Parmenides (130a–134e) where they are vigorously criticized.

[7] *Metaphysics* 1036a, 1084b.

Increasing Speculation: Persistent Types and Incremental Change

As science advanced in the 1850s, Owen's assumption of unchanging archetypes became ever more unsustainable as palaeontology progressed rapidly and the stratigraphic column revealed evidence of incremental change for many species, as well as the disappearance of others. Neither Huxley nor Darwin could tolerate Owen's notion of archetype and the arcane metaphysical conception of species as material evidence of the "thoughts of God". Writing to Huxley on 23 April 1853, Darwin readily accepted the concept of a "type or idea for each great class, [which] I cannot doubt is one of the highest ends of Natural History". In the same letter, however, he interpolated in parenthesis that "I detest the word as used by Owen, Agassiz & Co".[8] For Huxley, as for Darwin, ideas were simply taxonomic devices for describing affinities. "I make no reference to any real or imaginary 'ideas' upon which animal forms are modelled", Huxley recorded in his *Scientific Memoirs* on the morphology of the molluscs he had described previously from collecting on board the *Rattlesnake:* "All that I mean is the conception of a form embodying the most general propositions that [can] be affirmed respecting the Cephalous Mollusca, standing in the same relation to a geometrical theorem, and like it at once imaginary and true" (Huxley 1853a, p. 176).

The concept of progressive development of a temporal sequence of changes in species since the earlier work of Lamarck and Cuvier that had suggested some form of transmutation was becoming increasingly discussed. Huxley had already intimated as much in his study of the Medusae, a few years after Chambers' anonymous publication of *Vestiges*. For him, solving the mystery of taxonomic affinities had become an even more pressing issue, having already been convinced from his investigation of the medusae that the process of blastogenesis had to be directed by some "organizing or vital force", and that almost certainly all polyp forms had developed from a simpler, common ancestor. In his 1853 lecture "The Cell Theory", Huxley speculated that because "the organism exists before its organs and tissues, and evolves from them itself,—is it not probable that the organs and tissues also, are not produced by the coalescence of the cells of which they are composed, in consequence of their peculiar forces, but contrariwise, that the cells are a product of something which existed before them?" (Huxley 1853b, p. 254)

With his anticipatory use of the concept "evolves itself", Huxley continued his speculations, one of which foreshadowed a major new direction in biological thought. In a

[8] All Darwin documentation of letters, here and in following chapters, refers to the number assigned in the Darwin Online Database. This reference is *Letter* 1480.

lecture before the Royal Institution on 3 June 1859 entitled "Persistent Types of Animal Life" (Huxley 1859), he surveyed the progress of geology and palaeontology which revealed that "certain well marked forms of living beings have existed through enormous epochs…persisting comparatively unaltered, while other forms of life have appeared and disappeared. Such forms may be termed 'persistent types' of life; and examples of them are abundant enough in both the animal and vegetable worlds". For instance, "among the Coelenterata, the tabulate corals of the Silurian epoch are wonderfully like the Millepores of our own seas".

Given the persistence of types being revealed almost daily by palaeontologists, Huxley continued, "it is difficult to comprehend the meaning of such facts as these, if we suppose that each species of animal and plant, or each great type of organization, was formed and placed on the surface of the globe at long intervals by a distinct act of creative power,… if, on the other hand, we view 'Persistent Types', in relation to that hypothesis which supposes the species of living beings at any time to be the result of the gradual modification of pre-existing species…their existence would seem to show that the amount of modification which living beings have undergone during geological time is very small in relation to the whole series of changes they have suffered" (Huxley 1859, pp. 92–93).

For some time too, Darwin had also been pondering the problem posed by "persistent types", and had incubated the idea of drawing together nearly 30 years of investigation. Beginning with his field studies in South America and across the Pacific during the cruise of the *Beagle*, notably in the Galapagos Archipelago, he was considering a new explanation of the most pressing biological—and theological—issue of the day: the origin of species. Having married his cousin Emma Wedgwood and settled in Down House in rural Kent in September 1842, Darwin commenced his experimental research. From wide-ranging correspondence with numerous scientists, exhaustive reading of learned journals, mainly French and German as well as English, and continued support from three of the most eminent scientists of the day—geologist Charles Lyell, botanist Joseph Hooker and zoologist Huxley—he began to gather data, using the 20 acres (8 ha.) of his property for intensive experiments in plant and animal propagation. Utilizing his global network of colleagues, for plants he dispatched seeds to study their dispersal and biogeographic distribution; for animals, he researched variations and species in considerable detail, notably barnacles as invertebrates, and pigeons and dogs as vertebrates on account of their numerous varieties bred by fanciers under domestication.

As a significant part of his research into variation of species, Darwin began a study of the barnacles, the most enigmatic of all arthropods and placed within the subphylum Crustacea on account of their shell. Barnacles in themselves have no more significance in marine science than any other organism, but because of their enormous diversity they were ideal for taxonomic study, particularly because they were also believed to be hermaphrodites as no males could be discovered. That obviously raised the issue of sexual selection in the descent of species. Darwin simultaneously engaged in extensive correspondence with the large number of naturalists who were also researching barnacles, read voraciously the increasing number of scientific memoirs on the topic and spent uncountable hours in fine dissection of the animal inside, reporting in the most discriminating detail the structures observed. In 1855, the Ray Society published his 684 page, two-volume research as *A Monograph on the Sub-class Cirripedia*, one of the most remarkable studies in the history of marine science, in any branch of science for that matter. Never intended to appeal to the general reading public, it is a comprehensive study of barnacles as animals for descriptive analysis, intended solely for the cognoscenti.

The sheer complexity of the data Darwin presented defies presentation of anything but a short example, with an intriguing discovery. Central to that project was an examination of every possible feature of barnacles, where his description of the female *Alcippe lampas* is illustrative of his intense scrutiny and attention to detail. For that species, he was unable at first to identify any males. As he continued to search, on every female when first examined, he described how, in the course of his microscopy, he "found some minute parasites (or epizoons) attached to the lateral edges of the upper part of the horny disc" which at first he discarded, thinking they were bryozoans. Only later, after examining 30 similar specimens of "these cirripedial parasites" did he discover them to be males of the species when he observed as many as five or more—each measuring around 25/1000ths of an inch (0.0635 cm)—attached to the female, inseminating with a minute "probosciformed penis" (Darwin 1855, p. 555). More than any other single study, that monograph on the Cirripedia offered no intimations to those who used it as a taxonomic guide of what was to come from Darwin's next biological venture.

In complete contrast, a year later in 1856, Darwin began to compose a detailed, descriptive account of the means by which he believed the manifold species then currently known had appeared. Focusing throughout on the evidence for organic evolution by natural processes, he was able in April 1859 to send his first five chapters to publisher John Murray who, initially, was sceptical about the soundness of the science and planned a short print run of 500. The completed pages finally went to proof, Darwin revising and returning them, and sending a prepublication copy to Huxley. On 23 November 1859, Huxley replied with a letter of strong support, and some reservations, indicating that he yet had to "read the book two or three more times before I presume to begin picking holes", although he continued to urge Darwin not to be "disgusted or annoyed by the considerable abuse and misrepresentation which unless I greatly mistake is in store for you … [from] the curs which will bark & yelp", concluding with a final note that all Darwin's friends were "endowed with an amount of combativeness which…may stand you in good stead". Then, in typical Huxley style, he ended with an assurance to Darwin that "I am sharpening my claws & beak in readiness".[9] For some next decades, no one rose to Darwin's defence so pugnaciously, and Huxley came to be known as "Darwin's bulldog".

By October 10, when the manuscript was ready for printing, Murray had overcome his earlier doubts and took a gamble on 1250 copies.

The Most Dangerous Man in England

With the subtitle "The Preservation of Favoured Races in the Struggle for Life", *The Origin of Species by Means of Natural Selection* (Darwin 1859) was published the following day, 24 November 1859. When it sold out immediately, Murray and the reading public of Britain were astounded. Just a few weeks later, in December, having encountered Darwin in the British Museum, entomologist Roland Trimmer related that he had been warned against him by a clergyman friend who he met earlier, as "the most dangerous man in England" (de Beer 1963, p. 161). That indeed was the general reaction of the conservative classes, alarmed by the threat to the security of their society living under Divine Governance as John Murray rapidly issued a reprint: 3000 copies 2 weeks later on 7 January 1860; followed by 2000 more in April 1861, and further revised editions in 1869, 1871 and 1872, totalling 12,500 copies in all.

No book on science, before or since, has had such an impact across the globe: reviled as threatening the divine architecture of the heavens and the moral fabric of the nation, it was equally praised for finally explaining the processes of change being recorded by palaeontology. Similar transformist ideas had already been presented in Russia in the 1850s in lectures by Karl Rouillier that had created profound alarm. The aristocracy and Orthodox theologians, insisting on the inviolability of Genesis, recognized a threat to their God-given authority and sought the repression of such ideas, even though Rouillier had been careful to state that humankind had been a separate creation (Rogers 1973, p. 495). Even a century later, in 1950, Pope Pius XII issued the Encyclical *Humani generis* ("Concerning False Opinions") warning the faithful that "Some will contend that the theory of evolution, as it is called—a theory which has not yet been proved beyond contradiction even in the sphere of natural science—applies to the origin of all things whatsoever" (Fremantle 1956, p. 284).[10] Notwithstanding the considerable authority of the Catholic Church and the opposition of numerous intellectually fossilized communities of religious fundamentalists, Darwin's book irrevocably changed humankind's view of the natural world.

Science and *The Origin of Species*

Apart from the intense furore created by various churches and the affronted bourgeoisie, the main influence of the *Origin* was exerted initially on embryology and comparative anatomy, and, quite importantly, on coral reef science and polyp histology. There was a strong mutual interaction between Darwin's hypothesis, which provided a stimulus to invertebrate histologists, with histological discoveries in return providing convincing evidence to confirm the soundness of his evolutionary argument. It is necessary then, to understand the advances that were to be made in biology, initially in coral reef science, to consider the *Origin*, which, in the words with which he opened his final chapter, had turned out to be "one long argument".

What actually was the cause of the violent disruption to British and European social stability, reaching as far as St Petersburg and Moscow? In short, Darwin was attempting, in easily understood language characteristic of the entire text, to present evidence that the world of plants and animals had not been created according to the Mosaic revelation. Rather, they came from the entirely material processes of natural selection, which he defined as "the preservation of favourable variations and the rejection of injurious variations".[11]

The central theme of the "one long argument" was stated explicitly in the opening pages of the "Introduction" where Darwin began by recounting his experiences during the voyage of the *Beagle* that led him to consider that "a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and such other facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species" (Darwin 1968, p. 66). In a pithy conclusion to the "Introduction", Darwin made eminently clear his belief that "the view which most naturalists entertain, and which I formerly entertained—namely, that each species has been independently created—is erroneous" (Darwin 1968, p. 69).

[9] Darwin *Letter* 2544.

[10] Fremantle (1956, p. 284). That edict has since been moderated to accept the possibility of material evolution within a world created by God out of nothing, but with all souls separately created by God, and absolute proscription of atheistic evolution.

[11] This definition is in the opening pages of Chapter 4 of *Origin*, entitled "Natural Selection". The page references to Darwin that follow are from the widely accessible 1968 Penguin Edition of *Origin of Species*.

Following an exhaustive presentation of the evidence, Darwin finally brought his argument into focus in Chapter 13 of *Origin*, entitled "Mutual Affinities of Organic Beings" with the subheading "Classification", where he stressed that his research was to clarify exactly what is meant by the "Natural System" of taxonomy. His opening pages began by commenting that "many naturalists think that…the Natural System…reveals the plan of the Creator; but unless it be specified whether order in time or space, or what else is meant by the plan of the Creator, it seems to me that nothing is added to our knowledge…. I believe that…propinquity of descent—the only known cause of the similarity of organic beings—is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications" (Darwin 1968, p. 399). According to Darwin's argument, plants and animals could no longer be considered divinely created as separate species: all life had evolved over deep geological time through slowly acting processes of natural selection. As "our classifications are often plainly influenced by chains of affinities", he continued, "community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation" (Darwin 1968, p. 404).

When he came to the contentious issues of homology and archetype, Darwin again invoked natural selection as the causative agent. Homology simply means that "members of the same class, independently of their habits of life, resemble each other in the general plan of their organization. This resemblance is often expressed by the term 'unity of type', or by saying that the several parts and organs in the different species of the class are homologous" (Darwin 1968, p. 415). As natural selection makes "successive slight modifications, each modification being profitable in some way to the modified form, but often affecting by correlation of growth other parts of the organization", it seems obvious that those modifications have been derived from some hypothetical "ancient progenitor, the archetype as it may be called" or "existing general pattern" (Darwin 1968, p. 416). Nothing more was intimated: no ideal "otherworldly" forms. *The Origin of Species* was uncompromisingly materialistic with its emphasis on natural processes.

The circumstances surrounding the interaction between Darwin and Alfred Russell Wallace concerning their simultaneous co-discovery of the theory, which appeared in the *Journal of Proceedings* of the Linnean Society on 1 July 1858, and the subsequent tumultuous hostility to the initial reception of the *Origin*, have generated an enormous literature, one of the largest in the history of science. Receiving the greatest coverage at the time was the four hour uproar in a meeting of the British Association at Oxford on 30 June 1860, seven months after publication, with the heated argument between a hostile Bishop Wilberforce and protagonist Huxley, exacerbated by Wilberforce's insolent taunt, to the consternation of distressed ladies at the meeting, asking Huxley whether it was through his grandfather or his grandmother that he had descended from a monkey. Having been presented in numerous articles and books ever since, often in considerable detail, there is no need to repeat them yet again here.[12] What does need airing, though, is the bizarre review of the *Origin* that appeared in the *Edinburgh Review* for April 1860, at the time one of the most influential literary magazines in Britain. Although printed as coming from an anonymous author, it was transparently written by Richard Owen, by then one of the establishment's most respected scientists and supporters, in a sustained attack on Darwin's theory, and a strong defence of his own scientific achievements and theist beliefs. Unfortunately for Owen, he was "hoist by his own petard": the grenade he attempted to plant in the review blew his own position to pieces and virtually guaranteed the eventual acceptance of Darwin's theory.

Opening with an *ad hominem* jibe that "our younger naturalists have been seduced into the acceptance of the homeopathic form of the transmutative hypothesis now presented to them by Mr. Darwin" (Owen 1860, p. 487), the review went into considerable detail quoting numerous paragraphs from the *Origin* that, although offering praise for "important original observations", asserted that they were "few indeed and far apart, leaving the determination of the origin of species very nearly where the author found it…and having now cited the chief, if not the whole, of the original observations adduced by its author in the volume now before us, our disappointment may be conceived" (Owen 1860, pp. 494–496). Owen's assault on Darwin then began with a statement of the painfully obvious that "the origin of species is the question of questions in Zoology", and continued by asserting that Darwin had simply failed to prove his case by committing the "fundamental mistake…of confounding questions, of species being the result of secondary cause or law, and of the nature of that creative law" (Owen 1860, p. 496). Any reading of the *Origin* makes it clear that Darwin never attempted to discover causation: even in the final pages, he stressed that in considering the entire panorama of natural history, it is hopeless to speculate on original creation: "we can only say that so it is; that it has so pleased the Creator to construct each animal and plant" (Darwin 1859, p. 416). In using the term "Creator", it was clear that Darwin had accepted some kind of "First Cause", even though he did not see it in terms of religious dogma.[13]

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[12] One of the most succinct, informative, readable, and probably accessible accounts for the modern reader appears in Chapter 8, "Reception of the Origin" in de Beer (1963, pp. 157–179).

[13] Not until Darwin's granddaughter Nora Barlow edited and published an unexpurgated edition of his Autobiography in 1958 was Darwin's agnosticism fully revealed.

Owen, however, was definitely thinking in orthodox Biblical terms, of a divine Mosaic creation of individual species as recorded in *Genesis:* in Platonic concepts, a *plenum formarum*. Certainly, he admitted, the advances of science had revealed progressive changes in nature, but they were not the consequence, as Darwin argued, of natural selection, the struggle for survival and the emergence of new species. On the contrary, Owen claimed, they were all the result of "a constantly operating secondary creational law…the law of vegetative repetition…the law of unity of plan or relations to an archetype". Owen then referred to his own convictions. Writing as an anonymous author, in support of his argument, he cited "Professor Owen [who] does not hesitate to state 'that perhaps the most important and significant result of palaeontological research has been the establishment of the axiom of the continuous operation of the ordained becoming of living things'" (Owen 1860, p. 500).

In attempting to sustain his belief in the primacy of Platonic archetypes, Owen floundered further throughout the review, asserting that the Divine Creator had implanted "innate tendencies" which provided for "secondary causation". To bolster his case, he pointed out that all the great investigators had deliberately "kept aloof from any hypothesis on the origin of species", and one investigator in particular, referring to himself, "in connexion with his palaeontological discoveries, with this development of the law of irrelative repetition and of homologies, including the relation of the latter to an archetype, has pronounced in favour of the view of origin of species by a continuously operative creational law", at the same time setting forth "some of the strongest objections or exceptions of the nature of the law as a progressively and gradually transmutational one" (Owen 1860, p. 504). Owen's was an attempt to hold the line for creation by divine fiat: for the progressive changes in species from "secondary" processes, and not the result of evolution by natural selection.

Immovable Objects or Irresistible Forces?

For the next decade, the debate over Darwin's theory raged, but idealist philosophy was waning rapidly and creationist arguments were simply pushed aside. Apart from continued resistance by a dwindling number of recalcitrants, led by Owen and Agassiz, progress in embryology, particularly in Germany, had already begun to support Darwin's theory. Owen's obscure reference to developmental changes in nature being attributable to "the ordained becoming of living things", with its teleological—even eschatological—overtones, was seen for what it was: nonsense. His was a desperate attempt, in opaque language, to invoke metaphysical forces for the obvious changes in species that were being documented by empirical, positivist studies, in the first instance from palaeontology and embryology, and later in field and population studies. Despite Owen's frantic efforts, the tsunami of support for evolution by natural selection was bearing down with increasing speed. Time, space, descent: those were the key concepts that rapidly took hold and enthused the minds of the new generation of professional scientists—a neologism of William Whewell as early as 1840 to distinguish contemporary experimentalists from earlier gentleman "cabinet collectors", none of whom had been "seduced" by Darwin's hypothesis and were equally convinced that life had a progressive character and were seeking an explanatory mechanism.

One of the strongest statements of support for the new era in biology came from Edinburgh-born William Haswell (1854–1925), professor of biology at the University of Sydney, at the conference of the Australasian Association for the Advancement of Science in Christchurch in 1891 with his ringing endorsement of the new direction in which biology was heading. His paper *Recent Biological Theories* declared a vigorous research programme for the future and swept away any possibility of a continuation of the cabinet collecting era intended to display the plenitude of divine creation exemplified by the Macleays and McCoy that had dominated colonial natural history throughout previous centuries.

In his opening paragraph, Haswell delivered a devastating broadside at the preceding era with his central argument that "the word 'theory' was almost anathema to the vast majority of students of plant and animal life. The naturalist of the old school went plodding along, accumulating his descriptions of species and his records of remarkable and interesting facts, without much thought of theoretical explanation". Great changes, he declared, have been made in the life sciences as "new theories or new modifications of old theories have found the light in the course of the last year or two". Then followed his emphatic declaration: attributable "mainly to the influence of Darwin's writings…a very important change has come over biological research…in the nature of an illumination, and the illuminating influence has been theory, and more especially the theories of descent and modification by natural selection" (Haswell 1891, p. 173).

As in Britain, the *Origin* was resisted strenuously across Europe by the privileged classes, although it was accepted rapidly by many leading scientists. Von Baer was ambivalent, writing in retirement from Dorpat in Estonia to the committed evolutionist Anton Dohrn in Naples on 10 January 1875 that "I have become half a Darwinist, or rather a transformist; but I can become neither a full adherent nor a full opponent. I have been left behind on the old sandbank which bears the heading: *Nescimus* [Lat. *ignoramus*]" (Groeben 1993, pp. 72–73).

Despite opposition from the Orthodox Church, the *Origin* was welcomed even more enthusiastically in Russia by the restless political radicals who, chafing under the restrictive regime of the autocratic Tsar Alexander II, labelled Darwin the "Newton of Biology" and read into the *Origin* a powerful ideology for social change (Rogers 1973, p. 502). Two Russian scientists in particular were inspired: the brothers Alexander and Vladimir Kovalevsky, professors of embryology and palaeontology, respectively, in the Imperial Academy of St Petersburg. Early in 1862, Vladimir Onufrievich Kovalevsky (1842–1883) began writing to Darwin, and in 1867 visited him at Down House, where he requested approval to translate the *Origin* into Russian. He then exchanged continuing correspondence with Darwin over the ensuing 5 years until the translation was completed. In the same period, Alexander Kovalevsky had begun reporting his investigations into invertebrates from the Bay of Naples and which held promise of corroborating Darwin's hypothesis.

As evidence continued to arrive to strengthen Huxley's introduction of homology into his study of the medusae, the concept "unity of type" had a compelling logic. If histology revealed that all plants and animals demonstrated a common pattern of early growth following conception, then it was definitely possible to discover and chart that elusive "community of descent" suggested in the diagram Darwin included in his chapter "Natural Selection". In Germany in particular, the challenge for an enthusiastic number of embryologists rapidly developed into a quest to find the Holy Grail of evolution: *das Urbild*, the "primary form" from whence, it was believed, all plants and animals had subsequently evolved, and from which lines of descent could be identified.

7 Darwinism: The New Driving Force in Biology

The quest to identify the earliest life forms had actually begun some decades earlier with the efforts of Johann Peter Müller (1801–1857). After he was appointed to the German Confederation's most coveted chair of physiology, comparative anatomy and microscopy at the University of Berlin in 1833, Müller recognized from the discoveries of Pander and Rathke the significance of marine invertebrate research as the primary means for tracing the history of life from its origins in the sea. Through comparative anatomy, he planned to create the long-sought goal of a genuinely "natural" taxonomy. With the publication of his *Handbuch der Physiologie* (1833–1840), which became adopted as the standard text in embryology, he dominated all German biology as a charismatic, stimulating innovator until his early death in 1857 from an overdose of laudanum (a commonly employed pain-relieving opiate medication) prescribed for his exhausting, insomniac lifestyle.

The French had extensive coasts on the Atlantic Ocean and the Mediterranean Sea, as well as easy access to the invertebrate-rich waters of the Bay of Naples and the Straits of Messina between Sicily and the Italian mainland, and, like the British, to the seas surrounding their numerous colonial possessions. For German scientists, however, a major problem was the terrestrial character of the nation: their only readily accessible waters were the North Sea and the Baltic. Both had limited potential: the North Sea is stormy and unpredictable and the Baltic is shallow and brackish and, east of Rügen, a small coastal island north of Berlin, almost an inland sea and a biological desert, impoverished in nitrogen, an element vital for the growth of algae and marine biota. Neither sea has a rocky coastline, essential to invertebrate habitat, and collecting is possible only at low tide when sessile and crevice-dwelling fauna are accessible. Initially, therefore, the Germans were compelled to travel mainly to the Red Sea or the waters bordering the west coast of Italy.

The only convenient alternative was the island of Helgoland in the North Sea, some 60 km northwest of the estuary of the River Elbe where Hamburg is situated. Seized by the British from Denmark, an ally of France, during the Napoleonic Wars in 1807, it was ceded to Britain in 1814 by the Treaty of Paris. On the same latitude as the English holiday town of Scarborough on the east coast of North Yorkshire, in order to build a viable economy once peace had been restored, the German-speaking inhabitants had created a vacation resort on the plateau-topped island known as "The Rock", along with its adjoining sandy island, "The Dunes"; it had become a popular venue for enjoying the beach and bathing, with waters warmed in summer by the Gulf Stream. It also became attractive to German biologists in the 1830s.

To increase research opportunities beyond the limited potential of the North Sea, Müller extended his studies to Europe's most productive area for invertebrates: the seas around the Straits of Messina where, for his efforts in tracing the development and systematics of echinoderms, he was awarded the Copley Medal of the Royal Society in 1854. The "ultimate ancestor", however, remained elusive.

Das Urbild: The Ultimate Ancestor

Within a decade, the search became strongly focused in the University of Jena, situated in a small market town in Thuringia, close to Weimar, known for its excellence in biological research, particularly given the stimulating influence of one of Müller's outstanding students, the comparative anatomist Carl Gegenbauer (1826–1903).

No sooner had the *Origin* been published, with Darwin's evocative concept of the "existing general pattern", than pursuit of the ultimate ancestor and the promotion of Darwin's theory of evolution became the obsessive preoccupation of Gegenbauer's most productive and controversial protégé, Ernst Haeckel (1834–1919). Born in Potsdam, son of a judge and Privy Counsellor to the Prussian Court, Haeckel completed his medical doctorate in Würzburg under Albert von Kölliker (1817–1905), also one of Müller's distinguished students, who had become the greatest microscopist of the day. In addition, Haekel studied under Rudolf Virchow (1821–1902), renowned throughout Europe for his theories of the cellular basis of organic life. Following Remak's

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discovery of the process of cell division by binary fission, Virchow, in 1855, advanced that achievement by demonstrating that the cell is the basis of all organic development, which he expressed in the terse dictum that *omnis cellula e cellula:* "Every cell comes from a cell".

Moving to Berlin in 1854, Haeckel originally became enthused by Müller during a collecting expedition to Helgoland, and it was therefore under his guidance that Haeckel hoped to complete his studies. That ambition, unfortunately, was frustrated by the death of his "great, highly revered master", which Haeckel suspected to have been a suicide. He was forced to seek a new adviser and moved to Jena to study under Carl Gegenbauer—previously a lecturer (Privatdozent) in Müller's department—under whose guidance he completed his studies in zoology.

Having been taught by Müller the technique of collecting the vast range of microscopic plankton in the sea (Gk. *planktos*, "wandering") using long-handled butterfly-style nets or surface sweeps from a small vessel, Haeckel went on his first Messina expedition in 1859, where he discovered 144 new species. Describing the area as "an Eldorado of zoology", he decided to concentrate on the Radiolaria, a group of marine plankton protists with an intricate, symmetrical skeleton of siliceous spicules. Taking his specimens with him to the Berlin Zoological Museum, having earlier attended art school with youthful enthusiasm to become a professional painter, he described and illustrated them himself.

In 1861, he was appointed Privatdozent in Jena. Barely a year later in 1862, his publication of the 570-page text *Die Radiolarien*, with a supplementary volume of 35 superb coloured plates, took academia by surprise. Haeckel was almost immediately promoted to *ausserordenlicher Professur* (associate professor) of Comparative Anatomy and Director of the University Zoological Institute. Scarcely had he settled into that new position than his life was shattered. On 16 February 1864, just as he was advised that *Die Radiolarien* had been awarded the gold medal of the Berlin Academy of Science, his much-loved wife Anna Sethe, like Darwin's Emma Wedgwood, his first cousin, after a mere 18 months of marriage, died suddenly of a mysterious fever. Haeckel collapsed in a paroxysm of grief that lasted for more than a week, but after a lengthy convalescence in Nice on the shores of the Ligurian Sea, he recovered sufficiently to continue his research in a personal chair specially created for him in 1865. Sadly, despite his remarriage 2 years later to Agnes Schultze, he remained tragically haunted to his final days (see Richards 2008).

Haeckel's determination to promote Darwinism came in his first major monograph, *Generelle Morphologie* of 1866. In a frenetic episode of intense writing to assuage his grief, he recalled "I made the first attempt to apply the Theory of Evolution to the entire classification of organisms, including Man". Taking the *Origin* as the base text, he endeavoured to determine finally what had frustrated taxonomists throughout biological history and what Müller had tried to address previously; to create a genuine natural system based on genetic descent (Haeckel 1879, p. 102).

The stimulus came from a commentary on the *Origin* written by Johann Friedrich Theodor Müller (1821–1897), who gained his science doctorate in Berlin under his namesake, during which time, to distinguish himself from Johann Peter, he adopted the diminutive of Friedrich, becoming known as Fritz Müller. As he progressed through medical studies with the intention of becoming a doctor, Fritz became profoundly influenced by Ludwig Feuerbach's treatise of 1841, *Essence of Christianity* (Feuerbach 1841, translated and reprinted 1957), which asserted "God is [only] the reflection of human thoughts and aspirations". With further deep thought, he became a convinced atheist, which led to a conflict with authority when, on completion of his studies, as a matter of high moral principle, he refused to take the required concluding graduation oath "…so help me God and his sacred Gospel". Although Jews were excused the "sacred Gospel" words, Fritz was denied his medical degree despite his entreaties.

Those were also years of political turmoil that led to revolutions in Paris, Vienna and Berlin in which Fritz Müller had been involved as a student radical. As a result of the ruthless repression that followed the revolution of 1848 in Germany, and with no medical qualifications in Germany, he left in 1852 for a German colony in Brazil, founded by Hermann Blumenau and 17 other migrants in 1850. In 1856, he settled for a time in a small village of Desterro on the nearby adjoining coastal island of Santa Caterina, some 600 km south of São Paulo. There, Fritz began to investigate intertidal life thoroughly, with particular attention to crustaceans and their earliest larval stage as nauplii and the subsequent development of each nauplius into adult form. When he received the German translation of the *Origin* mailed by his friend Max Schultze in 1861, he was instantly enthralled because he discovered an explanation for a phenomenon he had already noted. In an excited letter to his brother Hermann in Germany, he wrote on 16 December 1862 that "If Darwin's theory is correct…all higher Crustacea will probably be traceable back to a zoëa [ancestor]" (West 2003, pp. 117–118).[1] So complete was his acceptance of Darwin's theory of evolution that in 1863 he began drafting an adulatory monograph entitled *Für Darwin* that was published the following year in Leipzig and reviewed favourably.

When that monograph came to Darwin's attention, he described Fritz Müller as the "prince of observers" and helped have it translated into English and published by John Murray in 1869 as *Facts and Arguments for Darwin*. Correspondence continued, with Darwin writing in relation to his

[1] Müller's astonishing career, long lost in the English language literature, has been recently brought back in this scholarly biography.

observations on the Crustacea "that many of your arguments seem to me to be excellent, & many of your facts wonderful…nothing has convinced me so plainly what admirable results we shall arrive at in Natural History in the course of a few years" (West 2003, p. 119).

Fritz Müller's studies of morphogenesis in the crabs on Santa Caterina revealed two modes of crustacean development: either the nauplius changes direction from that taken by their parents, or, by following them, moves on to a new form. It was Müller's conclusion that "the common nauplius form was the ancestor of the whole class" of crustaceans that inspired Haeckel, enthused by Darwin's comments in the *Origin*, to continue his search for the ultimate ancestor in his massive three-volume *Das Kalkschwämme* (*The Calcareous Sponges*) in which he explored the evolutionary history of the sponge.

In that study, Haeckel introduced his most contentious idea, which engendered decades of controversy, asserting that in the beginning of animal evolution there had been "a primitive extinct organism from which all the higher animals descended", which he hypothesized as the *gastraea* (Haeckel 1872, 1874). During the primary stage of development, after the digestive tract is formed by invagination of the cell mass, which he proposed should be called the coelom (Haeckel 1872, I, p. 468),[2] subsequently reproduced in the life history of all species, his later discredited theory of "recapitulation", it would be possible, he believed, to discover the ultimate ancestor (Haeckel 1872, I, p. 468; 1904, p. 142).

Embryology and the *Origin*: The Coelenterate Foundation of Life

The stimulating possibilities suggested in the *Origin* were multiplying rapidly, and while Fritz Müller was seeking the *zoëa*, and Haeckel the *gastraea*, in the same year as *Das Kalkschwämme* came yet another startling discovery. A series of research projects by Alexander Onufrievich Kovalevsky (1840–1901) published in the *Mémoires de l'Académie des Sciences de St Petersbourg*—possibly first mentioned during Vladimir's visit to Down House in 1867—immediately attracted Darwin's attention and eclipsed everything reported thus far. From studies of holothurian (sea slug or bêche-de-mer) eggs in the Bay of Naples, a favoured location for the study of marine life as the need for permanent marine stations began accelerating, came his epochal observation in 1867. In the earliest stages of fertilization he described how a small "invagination becomes visible at one pole of the egg… [which] progresses gradually farther and farther and after a few hours forms a deep sac" (Oppenheimer 1967, p. 265; the translation of *Mémoire* Series 7, T16, no. 6).

In a second, follow-up study on a primitive marine organism 5 cm long (*Amphioxus*; today *Branchiostoma*) came yet another major observation with future significance for understanding the evolution of reef life. From a row of cells that form a simple notochord (or protospine), *Amphioxus* was believed to be the archetypal ancestor of the subphylum Cephalochordata, and it is still considered the key to understanding the origin of the Vertebrata (see the exhaustive list of references in Shimeld and Holland 2005). Having observed the invagination of the morula and formation of the primary membrane, Kovalevsky recorded that subsequently "the embryo now consists of two sheets of germ layers which are the same for birds, turtles and mammals", which indicated that "the first formation of the embryo would be quite in agreement for all these different animals" (Oppenheimer 1967, p. 266; the translation of *Mémoire* 4 of 1867).

The consequences were stunning: Alexander Kovalevsky, as Huxley had intimated in 1849, had established that all animals, from invertebrates to mammals, have exactly the same developmental origin, from a single initial membrane by invagination into two, then three separate germ layers, each then, in the words of Rathke in 1829, "proceeding by itself towards its final goal".

Further correspondence with Alexander continued, Darwin recording on 25 July 1870 that "M. Kovalevsky writes to me from Naples that he has now carried these observations further, and should his results be well established, the whole will form a discovery of the very greatest value. Thus, if we may rely on embryology, ever the safest guide in classification, it seems that we have at last gained a clue to the source whence the Vertebrata were derived" (Darwin 1872, p. 159; quotations taken from the 2003 reprint of that work). In fact, Alexander Kovalevsky had made yet another startling discovery in his research into the developmental history of ascidians that Darwin was able to introduce as further supporting evidence in his succeeding book on evolution, *The Descent of Man*, the first edition appearing in 1871 and a revised version a year later. As Darwin summarized Kovalevsky's research (Darwin 1872, p. 159), in the early stages of development "the larvae of the Ascidians are related to the Vertebrata…in possessing a structure closely like the *chorda dorsalis* [spinal chord] of vertebrate animals". Darwin then made the daring inference that, as that such may be the case, "we should be justified in believing at an extremely remote period a group of animals existed, resembling in many respects the larvae of our present Ascidians [sea squirts], which diverged into two great branches—the one retrograding in development and producing the present class of Ascidians,

[2] "In place of the unwieldy nine-syllable word *Pleuroperitonealhöhle*", Haeckel wrote, using the Greek spelling for *coelom*, "it would be more convenient to take the Greek word for 'cavity' (*τό κοίλωμα*) which is found only among the higher species (… *findet sich nur bei den höheren Thierstammen*…)".

the other rising to the crown and summit of the animal kingdom by giving birth to the Vertebrata" (Darwin 1872, p. 160).

Finally, in the same year, after half a century of intense creativity, facilitated in large measure by progress in embryology, the long quest to understand the growth and development of the animal kingdom, and in particular the taxonomic status of the coral polyp, reached a moment of climactic achievement. That came with Nikolai Kleinenberg's monograph on *Hydra* that dealt with the Divine Creation theory and its *coup de grâce*. He built on Kovalevsky's critical finding that all three germ layers develop from a single membrane around the morula, and that in all animals, vertebrate and invertebrate, the initial stages are histologically identical. "If we follow the developmental history…backwards", Kleinenberg wrote, from his research in St Petersburg and the Bay of Naples, "we arrive, finally, in the Vertebrates and probably in all animal groups, to forms which correspond essentially to those of the Coelenterates". From that position, Kleinenberg concluded that "the resultant great simplicity and uniformity of the whole body structure distinguishes the Coelenterates from all other animal groups", so "the constant type of the Coelenterate is passed through as a developmental stage by all higher animals. The simple type of the Coelenterate is the common ground form to which all the infinitely rich and manifold configurations of the animal body can be directly or indirectly referred" (Kleinenberg 1872, pp. 87–88; in translation in Oppenheimer 1967, p. 267). The humble polyp was finally discovered, as Lamarck had believed more than half a century earlier, to be the ancestor of all multicellular animal forms, with the vertebrates later branching off to pursue their own pathways.

Ecology: Haeckel's Enduring Contribution

Despite the failure of the *Gastraea Theorie* to take hold, and what eventuated as an enduring controversy over the search for the ultimate ancestor which continues to the present day (see Leys and Eerkes-Medrano 2005), Haeckel's enduring impact which became one of the central ideas driving modern coral reef and environmental science, was his concept in 1869 of "the community of relationships within nature". In his 1857 *Essay on Classification*, Louis Agassiz had strongly criticized what he considered were the excesses of "comparative anatomy [which had begun] to absorb almost entirely the attention of naturalists [and which] has been very unfavourable to the investigation of the habits of animals, in relation to one another and to the conditions under which they live" (Agassiz 1857–1862: II, p. 65). Haeckel was the first to follow the implications of that challenge, and a decade later, proposed yet another avenue for research, that of the interaction of plants and animals with each other and their habitats. The idea of organic interaction, however, was not an original creative thought of Haeckel; on the contrary, it was first expressed by Linnaeus in his 1749 Latin essay *Oeconomia naturae*, where he introduced the concept of nature as a circular chain of mutual dependency, a theme he repeated in 1760 in *Politia naturae*, wherein each link exists for the sake of all others. Those two concepts, the "economy of nature" and the "polity of nature" soon became currency for natural historians in that era, one of the most outstanding observers being Gilbert White (1720–1793), vicar of Selborne, about 80 km (50 miles) southwest of London.

In 1789, White's collection of 110 letters written between 1781 and 1787 were published as *The Natural History of Selbourne*, necessarily for a cleric of that era set within the context of the "Great Chain of Being". An outstanding work of descriptive natural history, it became widely read throughout the century, profoundly influenced Darwin, and served as an exemplar for naturalists throughout the 19th century. A contemporary of Linnaeus, White was strongly influenced by *Oeconomia naturae* from which he came to appreciate that "in *zoology* as it is in *botany*: all nature is so full" (White 1789, p. 58). Recognizing the infinite creative wisdom of God who had filled every space within the universe, he believed that the task of the naturalist was to reveal the manifold beauty of that creation.

Specifically acknowledging his debt to White in earlier writings, the idea of the economy of nature then came to underlie Chapter 4 (Natural Selection) in the *Origin*, where Darwin began with an admonition to "let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life". With that understanding of the "intimate and complex manner in which the inhabitants of each country are bound together", he wrote, we come to recognize that "any change in the numerical proportions of some of the inhabitants, independently of the change of climate itself, would most seriously affect many of the others". Once change takes place, he continued, vacant places in "the economy of nature" would certainly be taken up in the struggle for existence (Darwin 1859, p. 131).

Haeckel developed the same theme in his *General Morphology*, where in a footnote on p. 8 in the opening chapter of Vol. 1, in discussing the interaction of plants and animals, he described the process in German as *Ökologie*, i.e. the science of the economy, habits and external relations of organisms to each other. Some 50 pages later, he expanded the concept in a section where he set out to discuss "two special branches of physiology which so far have been largely neglected, namely, the ecology and chorology of organisms", with a footnote to explain the Greek etymology of *ökologie* from *oikos*, "a household", and "chorology" from *chora*, "a dwelling place".

Continuing, Haeckel elaborated his ideas by defining ecology as "the whole science of the relations of the

Anton Dohrn, founder of *La Stazione Zoologica di Napoli*, 1898. (Reproduced courtesy Christiane Groeben)

organism to the environment including, in the broad sense, all the 'conditions of existence'. These are partly organic, partly inorganic in nature". The inorganic conditions he described as "the physical and chemical properties of its habitat, the climate, the inorganic nutrients, nature of the water and of the soil, etc." He then proceeded to list the organic conditions of existence as "the entire relations of the organism to all other organisms with which it comes into contact, and of which most contribute to its advantage or harm", dealing with basic issues such as predator/prey relationships, and making the strong statement, with Lamarckian overtones, that the "organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic". Then followed an unequivocal statement of his materialist conception of nature in which "all the infinitely complicated relations whereby each organism occurs in relation to the environment, how the steady reciprocal action between it and all the organic and inorganic conditions of existence are not the premeditated arrangements of a Creator fashioning nature according to a plan but are the necessary effects of existing matter with its inalienable properties and their continual motion in time and space. Thus, the theory of evolution explains the housekeeping relations of organisms mechanistically as the necessary consequences of effectual causes and so forms the monistic groundwork of ecology" (Stauffer 1957, pp. 140–141; a translation from Haeckel 1866: II, pp. 286–287).

Three years later, in *The Science of Life*, Haeckel set out a "Synopsis of the Chief Branches of Biology", which, in modern terms, encompassed anatomy, morphology, phylogeny, ontogeny, kinesiology, biogeography and ecology. In his explanatory notes, he repeated his definition of ecology as "the science of domestic life; biological economy; relations of the organism to the environment, and to other organisms with which it lives". Since then, ecology has superseded biology and become the overarching concept in today's era of heightened environmental concern, with biology reduced to one of its contributing branches.

To the end, Haeckel remained an indefatigable proponent of the theory of evolution, and a pantheistic view of nature which he first expressed as an opening epigram to *General Morphology* with a quotation from Goethe "There is in nature an eternal life, becoming, and movement". That belief helped sustain his tortured emotions that had endured since the death of Anna, which came through very clearly in his final work, *The Wonders of Life*, a few years before his retirement in 1908. Throughout his scientific life, like Darwin, he explained, he denied the guiding role of any divinity, but retained a vision "of one great harmonious working universe—whether you call this Nature, or Cosmos, World or God" (Haeckel 1904, xii).

The Marine Research Station: Concept and Gestation, 1859–1871

Embryology, and the quest for the ultimate ancestor, believed by Kovalevsky to have been the polyp, however, was still being held back by simple logistics. The most frustrating aspect of all invertebrate research at the time was its episodic character. Field studies could only be pursued during inter-semester breaks, exacerbated by the problem that once the animals had been collected they had to be kept alive and taken to laboratories for developmental studies and histological analysis, often over long distances. During his graduate studies, Haeckel had become annoyed with that difficulty, which he first expressed in 1859 during an early expedition to Helgoland. With four other students, in a moment of exasperation, he discussed the problem and recorded in his notes the idea of a permanent marine station there, which became the next significant development in the advancement of biological science and knowledge of coral reefs (Groeben 2005, p. 293).

One of Haeckel's colleagues on Helgoland in 1859 had been Anton Dohrn who, after Haeckel introduced him to Darwin's *Origin* in 1862, became infatuated with the hypothesis. Almost immediately, Dohrn envisioned that a way to further its cause could be achieved by founding a

La Stazione Zoologica di Napoli, 1898. (Reproduced courtesy Christiane Groeben)

permanent experimental marine station with an aquarium, preferably near the invertebrate-rich waters of Messina. In such a location, embryological processes could be monitored closely and would attract to one location all those who were researching animal development. There a community of scientists would be able to generate a powerful body of knowledge to support the evolutionary cause.

Born in Stettin into a wealthy, cultivated German family close to the Baltic Sea, in the Prussian region of Pomerania (today, Szczecin in Poland), Dohrn (1840–1909) had also come to Jena to study under Gegenbauer for a period as part of his studies for a lectureship programme. During his student years he concentrated on the phylum Arthropoda under the supervision of Eduard Grube in Breslau (then in Prussian Silesia, today Wroclaw in Poland), where in November 1865 he completed a doctoral thesis, *Zur Anatomie der Hemipteren*, on an order of blood- or sap-sucking insects, most commonly known as bugs. After that critical period in Jena where he became aware of the new developmental theory of the *Origin*, his final research programme (*Habilitationsschrift*) for appointment as a Privatdozent in a German university was completed in 1868 with the publication of *Studien zur Embryologie und Genealogie der Arthropoden* (Groeben 1993, p. 38, note 19). Towards the end of the decade, however, Dohrn had lost interest in the routine procedures of marine science and began to redirect his energies, having also parted company with Haeckel, who he believed was too heavily under the influence of *Naturphilosophie* and had strayed from Darwin's version of evolution based on strict, empirically verified evidence.

Dohrn's preoccupation with promoting Darwinism soon developed into an almost incurable obsession, one he later described in a letter to von Baer as his "innermost drive" (*innerstem Drange*; Groeben 1993, p. 45) which led to his first effort in 1867 to contact Darwin by sending his paper on *Morphology of Arthropoda* for comment and advice. Darwin replied courteously on 26 November, to which Dohrn responded 4 days later thanking him, explaining that his personal ambition was to reform zoology using Darwin's principles (Darwin *Letter* 5701 of 30 November 1867).

Further encouragement to create a dedicated marine research station had come at the same time from a visiting Russian scientist in Jena, Baron Nikolai Nikolaievich Miklouho-Maclay (1846–1888). From a minor branch of the aristocracy ennobled by Catherine the Great in the previous century, and with an ancestor from Scotland whose name he was proud to retain, Miklouho-Maclay had embarked on a career in natural history. Having been one of the student radicals in St Petersburg during the reign of the autocratic Tsar Alexander II, he was excluded from the university, and to continue his biological studies, moved across the border into Germany. Beginning in Heidelberg, he finally reached Jena where he began his acquaintance with Haeckel, their scientific relationship beginning in 1866 when he acted as Haeckel's assistant on an extended field trip to Madeira, the Canary Islands and Morocco.

In 1868, Miklouho-Maclay joined Dohrn on an expedition to Messina where the two men rented rooms, and while engaged in relentless collecting from first light to late evening, discussed the dream of establishing in Messina not only one permanent research station but also a network of similar institutions across the globe. Moreover, it seemed by then that Dohrn had resolved to undertake total management of the initial venture himself, despite it requiring considerable funding. Creative thoughts come easily, but practicalities have a way of intruding. How exactly could the dream be realized?

Although Messina was ideal for invertebrate studies, it was not, as Miklouho-Maclay reminded him, part of the European tourist circuit and could not support an aquarium that would depend on admission charges. In contrast, Naples at the time was capital of the Kingdom of the Two Sicilies and the second largest city in Europe, with a substantial tourist trade. As an equal incentive, as Miklouho-Maclay also advised, it was a splendid collecting location for invertebrates. With those suggestions, Dohrn became convinced of the possibilities of the Bay of Naples and decided to approach the city authorities with the audacious proposition that were he granted a waterfront site on which to build a research station and an aquarium, the complex would come at no cost to the city.

La Stazione Zoologica di Napoli: Foundation and Influence

More determined than ever, Dohrn forged ahead by contacting as many scientists as possible with details of the proposal. Being also an astute politician who recognized the value of friends in high places, and already assured of the assistance of Huxley and several other English scientists, he decided to seek the support of Darwin and von Baer, both of whom he hoped would lobby on behalf of the proposal. He was not disappointed, as the continuous stream of correspondence between Dohrn, Darwin and von Baer testifies.[3]

Towards the end of 1869, Dohrn wrote directly to Darwin with a description of his proposal for a totally independent institution directed specifically towards furthering the cause of evolutionary theory by sustained research. Moving beyond the prevailing descriptive zoology, he informed Darwin that the activities at the station would be to observe animals through various morphological stages with a full range of equipment, and a continuing supply of experimental organisms. Darwin replied in two separate letters on 4 January, 1870, urging care, with the encouraging comment that such an institution will get "the good wishes of every naturalist in Europe", but with a warning to go slowly and circumspectly: "caution is the soul of science", he advised (Darwin *Letters* 7070 and 7071).

Dohrn had considerable funds of his own, as well as a promise of more from his father, but there was still a shortfall to be made up, along with numerous issues yet to be resolved, paramount among which was persuading the city authorities to accept such an imaginative proposal. Dohrn realized that the aquarium would be an important drawcard for the city, given that other aquaria being constructed in major European cities were enhancing their civic reputations. As part of his preliminary survey, a few months before the epochal August 1870 meeting of the British Association, he visited Berlin in January to inspect its new aquarium where he learned that entrance fees contributed substantially to meeting running costs. Six months later, he went to London to confer with William Alford Lloyd, who had been commissioned to design and superintend construction of the new Crystal Palace Aquarium based on an improved version of the one he had built in Hamburg. With 38 separate, connected viewing tanks which drew supply from a massive underground 100,000 gallon (454,000 l) tank, that aquarium opened 18 months later on 22 August 1871.

To manage the project more effectively, Dohrn moved permanently in October 1871 to Naples; however, negotiations with the Council did not prove easy because they had to be conducted against the background of the recent Franco-Prussian War of 1870/71, when French armies were defeated and Paris was occupied by the German army in January 1871. Italy and Austria had allied themselves with Emperor Napoleon III against the German Confederation and, although Italian troops were not engaged in the conflict, subsequent relations between Italy and the new Germany were tense. Nonetheless, after some difficult months, Dohrn finally received approval to begin construction. Not that it was an easy task for him because, despite being a permanent resident in Italy, he was still considered to be a Prussian. For some time to come, therefore, the process remained challenging, leading him to write to Darwin that construction was "advancing slowly". In a letter to von Baer on 8 February 1873, Dohrn actually accepted some of the blame himself, attributable to "the novelty of the affair, from the peculiar situation of the City of Naples, and in particular from my personal inexperience" (Groeben 1993, p. 45).

Financing was the greatest problem with the project because Dohrn had already calculated that the principal research function would be far more costly than entry charges to the aquarium under construction could defray. He devised an innovative idea: to request the various nations of Europe to fund worktables (*Arbeitstische*) for their scientists. In a figurative sense, he described the "table system" specifically as "the supply of all those tools and provisions, except the microscope, which a zoologist needs at the seaside, i.e. chemicals, scalpels, needles, drawing and writing equipment, aquaria for experiments, permanent provision of living animals, eggs, larvae, [supplemented by] an extensive and very soon a complete library" (Groeben 1993, p. 45).

The historical record of that struggle to make the project a success is convoluted and does not need extended reporting here, although some of the most noteworthy features in the correspondence of Darwin and von Baer, which reveal their unwavering support throughout the critical decade of the 1870s, certainly deserve appreciative comment, beginning when finances began to falter in early 1873. Immediate

[3] The von Baer German correspondence, with English translations, are contained in Groeben (1993), with translations made by Christiane Groeben and Jane Oppenheimer.

relief came from the newly founded Deutsches Reich with a subvention of 10,000 taler to assist the completion of the main building.

When Huxley was informed of the project, he rallied other English scientists (among whom Ray Lankester and Francis Balfour were active) to campaign for funds, with the list headed by Darwin's personal donation of £75, and 4 months later a further £120 from himself and his sons George and Francis. By April 1874, the English contribution alone amounted to > £1000. Through the efforts of von Baer, the tables were also subscribed by individual German states as well as by Russia. Both Darwin and von Baer were staunch supporters of the project during those difficult early years, particularly by encouraging nations to subscribe to their tables and scientific societies to offer copies of their publications to build the essential reference library. Darwin, in particular, was very generous, writing to John Murray in August 1872 requesting him to forward copies of all his publications to Naples.

As further money came in slowly, infrastructure material was also arriving. The library increased steadily with publications from the Royal Society of London and others from scientific academies in Copenhagen, Berlin, Amsterdam, Vienna, St Petersburg and the Smithsonian Institution in Washington D.C., later followed by some from other organizations, and tables were being subscribed in burgeoning numbers. By 1875, as the *Stazione* became increasingly self-sufficient with 24 rented tables and a second subvention of 10,000 taler from the Reich, Dohrn could inform Darwin in February that "the crisis is nearly over" and that the station was "flourishing". Gradually, with his incessant travelling and promotion, tables were being funded, in many cases in multiple numbers, by most of the German states as well as by Cambridge University, Italy, Austria–Hungary, Switzerland, Russia, Holland, Denmark, Belgium, Romania and the USA, augmented slowly as more nations joined the system. In this respect, a remarkable advance in marine science was achieved when, of the five tables subscribed from the USA, one each from Columbia University and the Smithsonian, two from the Carnegie Institution, the fifth was subscribed by the Association of American Women and reserved solely for female investigators (Fischer 1980, p. 228, note 9). Then, in 1877, the Prussian Ministry of Education made the generous gesture of providing funds for the purchase of a small research steamship that was proudly named *Johannes Müller* in honour of the founding father of marine invertebrate research.

To project the image of the *Stazione* even more widely, in 1879 the *Reports* of the station, *Mittheilungen aus der Zoologischen Station zu Neapel*, were commenced, followed by a sequence of monographs on *Fauna und Flora des Golfes von Neapel* along with the almanac *Zoologischer Jahresbericht*. Yet another important research tool became available when Ernst Abbé, the physics genius who enabled Carl Zeiss to become the premier optics manufacturer in Europe, offered discounted microscopes to the *Stazione* which, in a clever advertising stratagem, brought them to the notice of scientists from around the globe.

The long struggle was drawing to a close. In a moment of exhilaration, as he reflected on surmounting a decade of difficulties, Dohrn, who had dedicated his life to the role of administrator and facilitator of Europe's greatest marine research station in the cause of advancing evolutionary thought, described himself in a letter to his wife Marie von Baranowska in 1888 as the "Statesman of Darwinism". By 1890, after a decade of almost superhuman effort, Dohrn had realized his dream, with the complex cleared of all debt: by 1909 the total number of subscribed tables had approached 60 (Groeben 1985, p. 10).

Today the *Stazione Zoologica* is a huge, beautifully constructed complex of several three-storey permanent, dressed-masonry buildings, expanded through time with improved additions, with handsome arched colonnades along its facades and set in landscaped, palm-grove grounds. In honour of its founder, it is known today as *Stazione Zoologica Anton Dohrn*. However, once the *Stazione* had begun to operate without difficulty in the 1880s, a new era in marine invertebrate science was heralded, the most vigorously fertile phase yet experienced. With Naples as a role model, two stations were founded almost immediately: Tokyo's Misaki Marine Biological Laboratory in 1882 and the Woods Hole Marine Biological Laboratory on the site of a former guano-processing plant near Boston in 1886. In the same period, Huxley and Lankester helped found the Marine Biological Association of the UK in 1884, which subsequently organized the building of the Plymouth Marine Laboratory in 1888 that Huxley hoped would become active in experimental research, an area where he believed that Britain was lagging.

Germany, however, despite its European leadership in embryology, still lacked its own marine station. Concerned about that deficiency, at their annual meeting in Hamburg in 1876, and with strong support from Haeckel and Leuckart, the *Gesellschaft Deutscher Naturforscher und Ärzte* (German Society of Naturalists and Physicians) passed a resolution urging the government to establish a marine station on Helgoland. Germans had always considered that island their occupied territory because, with a resident German population, its only British characteristic, apart from the Governor and a few civil servants, was Queen Victoria's image on the postage stamps. A way forward soon arose as a result of a new international development. Late in the grab for empire, Germany moved in 1884 to West Africa and occupied Kamerun (today Cameroon), and followed by annexing part of East Africa in 1885 (the part that is now Tanzania). When the British East Africa Company moved into the east coast of Africa in 1888 and the British colony of Kenya was founded, in a territorial treaty of 1890, Germany ceded the nearby island of Zanzibar and the coastal chiefdom of Witu, both formerly part of German East Africa, to Britain in exchange for Helgoland. Two years later, the Reich agreed to fund the establishment there of a marine station, and in 1892 Germany's own marine station was opened as *Die Biologische Anstalt Helgoland*, and in 1992 that station celebrated its centenary (Florey 1995, p. 96 f).

French Chauvinism: Resistance to European Cooperation

France, however, not only remained outside the cooperative network of marine research, but continued in active opposition as a consequence of the hostile attitude of the politically powerful Félix Joseph Henri de Lacaze-Duthiers, who had a strong antipathy to Prussia following French humiliation during the Franco-Prussian War. Originally, a medical specialist in chest and lung disorders, Lacaze-Duthiers (1821–1901) had been forced to resign his government post after refusing to swear allegiance to the new emperor Louis-Napoléon Bonaparte following the *coup d'État* of December 1851. Deciding to change his occupation, he moved into marine biology in 1853, his first field expedition taking place in 1854 as an assistant to Jules Haime in the Balearic Isles. Soon after, with Haime's endorsement, Milne-Edwards recommended Lacaze-Duthiers for a chair in zoology at Lille. He then climbed the ladder of opportunity rapidly, with a monograph in 1864 on the natural history of coral and its commercial harvesting in Algeria (*Histoire naturelle du Corail*; Lacaze-Duthiers 1864), the same year being appointed professor in the *Muséum national d'Histoire naturelle* and the following year a professor of invertebrate zoology at the Sorbonne. In 1871, Lacaze-Duthiers was elected to the *Académie des Sciences* at the same time as Dohrn was beginning his foundation of the *Stazione* in Naples.

When Dohrn offered European nations the opportunity to subscribe to tables, France did not simply decline: it refused outright. At first Dohrn was puzzled, but it was not long before he learned that Lacaze-Duthiers, from his premier position in Paris, was in active opposition. Once Dohrn became aware of the situation, he wrote a letter to von Baer on 8 February 1873, canvassing subscriptions, and stating that although he would like to "make the same offer to France", he knew that he would "certainly meet with a refusal, the more so since Monsieur Lacaze-Duthiers has already behaved very improperly [*ungeziemend*] on my behalf" (Groeben 1993, p. 46, *Letter* 8).

Apart from his intense French chauvinism, Lacaze-Duthiers was also attempting to safeguard his own research interests because France had already established an enviable reputation with the record of its marine scientists from Peyssonell through Cuvier, Adouin and de Quatrefages to Haime and Milne-Edwards. In addition, a few small research facilities had been established on the French Atlantic coastline at Concarneau in 1859 and Arcachon in 1863, followed by Wimereux on the Pas-de-Calais coast of the English Channel in 1874. Moreover, Lacaze-Duthiers was planning his own research station at Roscoff in Brittany, which he opened in 1876, and made it known that he disapproved of French scientists supporting the *Stazione*: he threatened that anyone who did so would be banned from the research stations in France.

The situation erupted openly in 1878 when Dohrn offered a table to Jules Henri Barrois (1852–1943), professor of biology at Lille. In a reply dated 21 March 1878, the first official record of the conflict, Barrois replied to Dohrn that he was pleased with the invitation and would dearly like to accept, although, in guarded language, explained that acceptance was currently impossible and that he deplored the extraordinary stubbornness of "certain influential scientists in Paris" who were opposing the request: "*...et ai deplore l'entêtement singulier des savants influential en Paris qui nous empêchent d'avoir une table à un laboratoire devenu Européen*" (French text in Fischer 1980, p. 228).

As Barrois on his own initiative had been unable to take advantage of Dohrn's offer, Jules Ferry, as Minister for Public Instruction, in a conciliatory gesture and in an attempt to soothe Franco-German relations 4 years later, planned to fund a table at Naples. That action drove Lacaze-Duthiers into a paroxysm of rage, which amounted to what can only be described as an infantile tantrum with the outburst that if the government dares accept a table from that "Prussian in Naples" I will demolish my station at Roscoff completely, resign my chair at the Sorbonne and return all my decorations! In Lacaze-Duthiers' exact words that were relayed to Dohrn, and he in turn recorded a decade later in a letter to his sister, Lacaze-Duthiers expostulated that "*je détruirai toute mon institution de Roscoff, je donnerai ma demission comme professeur à la Sorbonne, et je renverrai mes decorations*" (Heuss 1940, p. 284).

Jules Ferry chose not to provoke such a confrontation, but in order to circumvent French isolation from the wider marine science community, decided to establish an international marine station inside the French border at Villefranche, on the Mediterranean coast close to Italy near Nice and Monaco, with Barrois as director. Even that act could probably provoke Lacaze-Duthiers to another outburst, and to mitigate yet another ugly confrontation, Barrois sent a short note to Darwin on 6 March 1882 asking for a letter of support because "I believe that all foreign scientists would be extremely happy to know that you approved…the establishment of an international laboratory at Villefranche sur mer". He ended with his belief that the location was ideal because numerous foreign scientists had already pursued their research there, so it would be open to all applicants with no distinction of nationality (*aucun distinction de nationalité*) and solely motivated by the desire to be useful to everyone.

Darwin replied soon after, in his inimitable handwriting (in an undated letter) with the very diplomatic opening that he was heartened to hear of the proposal because "many naturalists have already gained experience in Dohrn's Institute in Naples and in the laboratory founded by your Lacaze-Duthiers on the shores of France". He ended his letter with the warm comment that "Foreigners of every country ought to be grateful for the liberality of the French government which is willing that all should profit by their new foundation. Nor is there any danger of too many Laboratories being founded, for the amount of scientific work which has to be done in the several great invertebrate classes is almost infinite. Permit me to add that I am convinced that the Laboratory at Villefranche is eminently fortunate in having acquired your services as Director".

Barrois then wrote to Dohrn on 26 April 1882, informing him of the Villefranche project and expressing regret at the isolation of France from all other scientists, although with the hope that in time the new station would help bridge the wide gulf. Lacaze-Duthiers, for his part, remained utterly intransigent and to counter the Villefranche development, almost immediately founded one under his own direction at the opposite end of the Mediterranean coast at Banyuls-sur-Mer, near Perpignan, close to the Spanish border. The impasse dragged on through the following decade, and as French opposition to cooperation with Naples was becoming a national scandal, it prompted Lacaze-Duthiers to defend his position in a speech entitled *Le monde de la mer et ses laboratoires*, presented on 4 February 1888 in a meeting of the *Association française pour l'Avancement des Sciences*. Not only had France already established an enviable record in marine research, he asserted proudly, but also had all its stations free. Unlike fee-charging Naples, which was preoccupied with experimental embryology on the German model, he claimed that the French approach was forward-looking because it focused on "systematics, anatomy and comparative physiology" and, most importantly, collecting and studying organisms in the environment within which they had evolved (Fischer 1980, p. 230). Lacaze-Duthiers, however, did not have it all his own way: opposition slowly began to form and several leading scientists began a campaign to end French isolation, with one scientist, Henri Bouquet, recording that Lacaze-Duthiers was a "morose, sarcastic character…who rejected any new idea he did not think of first" (Fischer 1980, p. 229, note 12).

The slow, convoluted interplay of hostility and rapprochement continued, and even after Lacaze-Duthiers died in 1901, his personal effects were interred in the station walls surrounding Roscoff; the isolation of France continued, much to the irritation of Alfred Giard (1846–1908), a leading professor of science at the University of Paris who had founded the French station at Wimereux. On 20 December 1903, Giard wrote supportively to Dohrn with an assurance that all French scientists were seeking the same goal and that he soon hoped to send several young French zoologists to "your splendid station in Naples". Dohrn replied on Christmas Day, writing that he, like Giard, wished to see all French scientists united with their European colleagues, working collaboratively in a genuine international scientific effort to the same end: "…*et que nous travaillerons tous ensemble, une vraie Internationale Scientifique, pour le même but*" (Fischer 1980, p. 232).

The government, however, prevaricated on the grounds that France already had sufficient research stations, and in any case, the annual rental in 1905 of 2500 francs was excessive. Four years later, Anton Dohrn died and management of the *Stazione* passed to his son Reinhard, who continued negotiations. Further developments were basically political and need no elaboration here, having been well documented by Jean-Louis Fischer from the archives of the *Académie des Sciences* from which this account has been drawn (Fischer 1980, p. 229, note 12). Suffice it to record, however, that by 1909 many French scientists were becoming extremely restive over their exclusion from Naples and in 1911 a petition by 18 leading zoologists was presented to Théodor Steeg, Minister for Public Instruction, who was favourably disposed to their call.

By then, however, relations between France and Germany were again becoming tense, with the French still angered over the loss of their territories of Alsace and Lorraine from the 1870 conflict and anxiously preoccupied watching the gathering storm clouds that heralded the Great War of 1914–1918. Only after peace was restored and France had regained its territories east of the Rhine, therefore, did the French government feel disposed to deal with the *Stazione*, which they still saw as a predominantly German foundation. The stalemate over what had always been a distressing situation to all concerned, not the least for Lacaze-Duthiers, was finally settled after the Great War on 3 June 1919, when France subscribed to its first table at the *Stazione Zoologica*.

8 Reef Construction and Symbionts

The quest for the ultimate ancestor remained a preoccupation for many German zoologists, and provided a wealth of information regarding invertebrate development, but a more comprehensive understanding of both the geological and biological processes of reef formation remained elusive. Darwin's 1842 geological solution presented in *The Structure and Distribution of Coral Reefs* continued to be disputed, and biological advancement was hampered by the patently inadequate taxonomy inherited from Cuvier. The strange miscellany collected into his *embranchement* of Radiata in which he had placed infusorians, foraminiferans, sponges, scolecoid (sucking) worms, echinoderms, polyzoans, hydrozoans and actiniarians, on no other criteria than their external radial morphology, was hardly an effective basis for further research.

A Radical Taxonomy of Invertebrates

One of the first to express disquiet with Cuvier's subkingdom Radiata had been Huxley, who, during the third survey cruise aboard the *Rattlesnake*, wrote from Cape York in October 1849 to his mentor Edward Forbes (1815–1854) at the Geological Survey that, having examined a very large number of invertebrates, he had reached an important conclusion. As all acalephs and polyps from their unique "two membrane" structure constituted a discrete "great family", he believed accordingly that "the total re-arrangement of the Radiata" was imperative.

The total re-arrangement finally came in a series of lectures Huxley delivered in 1863 and published the following year as *Lectures on the Elements of Comparative Anatomy*, ranging from Infusoria to mammals, where he presented a radical revision of the invertebrate subkingdom as described by Cuvier in *Règne Animal*. In the opening pages, he stressed that his classification was highly specific: "not physiological, nor biographical", but treating animal structures as "fabrics, each of which is built upon a certain plan" (Huxley 1864, p. 2). Acknowledging Cuvier's earlier taxonomy of four separate subkingdoms or "embranchements" and conceding that "it is possible and conceivable that every animal should have been constructed on a plan of its own", he immediately counter-asserted "no such mutual independence of animal forms exists in nature. On the contrary, the different members of the animal kingdom, from the highest to the lowest, are marvellously interconnected". There were, therefore, he continued, two aspects to classification: identifying the features that every animal has "in common with all its fellows", and the ways in which "it differs but little from them" (Huxley 1864, p. 3).

As he worked through the five lectures, progressing from protists to vertebrates, the influence of the *Origin* and recent progress in embryology, including his own discoveries from the Medusae, came through clearly. Having covered the single-celled Protists in *Lecture 1*, he moved in *Lecture 2* to the (multicellular) Metazoans, beginning with the two closely related classes of Hydrozoa and Actinozoa: collectively, hydroid polyps, Medusae, anemones and "coral polyps". Kleinenberg's discovery that the Coelenterata were the "common ground form" through which all animals pass in their developmental processes was unknown in 1864, but as a taxon it had been intensively investigated, and Huxley, drawing from the considerable literature and with his genius for popularization as well as scientific achievement, described their "common and diagnostic" characters.

Some years earlier, while dissecting the Cordylophora (tubularian hydroids) "for greater precision in description" of the two foundation membranes, Prof. James Allman had named "ectoderm" for the external layer and "endoderm" for the internal. As Huxley was arguing that the fundamental structural "fabric" of all organisms lay in the fact that "the body always exhibits a separation into two distinct layers", he seized on those two neologisms and passed them into permanent usage (Allman 1853, pp. 367–371).

Both classes were built on the same basic plan of "two distinct layers of tissue", but their essential difference lay in the fact that in the Hydrozoa, the digestive cavity and generative organs were "developed as outward processes of

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the body wall", whereas the "*Actinozoa*, polyp-like as they are in external appearance, differ from the *Hydrozoa* by a very important further progress towards complexity". In the Actinozoa, the alimentary cavity and generative organs are enclosed within the body and connected to the walls "by means of membraneous partitions, the so-called mesenteries, which pass radially from the stomach to the side walls of the body and divide the 'perivisceral cavity' into a number of chambers".[1] Following von Baer's research that had established that they are "absolutely unique" in the animal kingdom, the coelenterates, he summarized, stand alone as a "sub-kingdom": they are "as sharply defined and devoid of transitional forms as that of the *Vertebrata* from the rest of the Animal Kingdom" (Huxley 1864, p. 82).

Having examined all other invertebrates comprehensively, making clear the common features of each taxon and their essential differences on the basis of a "very great advance in complexity of structure", and unlike the acalephs and polyps, the possession of a complete gastrointestinal tract, in his final *Lecture 5*, Huxley explained the rationale underlying his "total re-arrangement" of the invertebrata.

Cuvier, who himself admitted that he knew little of the lowest groups, Huxley argued, had simply thrown them "into one great heterogeneous assemblage—the Radiata" that was manifestly inadequate and confusing. That taxon, he asserted, was indeed manifestly inadequate and confusing, because we now know that "the whole of the Animal Kingdom is divisible into eight primary categories … defined by characters which shall be at once common and diagnostic" which are the Vertebrata, Mollusca, Molluscoida, Annulosa, Annuloida, Coelenterata, Infusoria and Protozoa".[2] Given the "progress of our knowledge since Cuvier's time", and the evidence available at present, he believed it was mandatory for the Radiata to be "altogether remodelled and rearranged". Then came his brusque dismissal: "Whatever form the classification of the Animal Kingdom may eventually take, the Cuverian *Radiata* is, in my judgment, effectually abolished" (Huxley 1864, pp. 85–86).

Coral Reefs and Madrepores: The Search for Definition

As invertebrate zoology advanced rapidly, Huxley subsequently revised several of his *Lectures* of 1864 as a major textbook, appropriately called *A Manual of the Anatomy of Invertebrated Animals*. In that extensive survey of 1877, he provided more detailed analyses of the three Hydrozoan orders of Hydrophora, Discophora and Siphonophora, and the two major divisions of the Actinozoa (later renamed Anthozoa): the Ctenophora and the Coralligena. The Ctenophora (comb jellies; Gk *kteis*, "comb"), being without nematocysts, were in a division of their own; the Coralligena, however, were distinctly different.

Ever since 1599 when Imperato devised the term "madrepore" for clustered coral formations, the term began to be used for many polyp species, whether reef-building or not. It first achieved wide recognition in the *Systema Naturae* where Linnaeus established three genera of Lithophyta consisting of eight species of *Tubipora* with a corallum composed of cylindrical tubes (*Corallium tubis subcylindricus*), nine species of *Millepora* with a rounded, top-shaped corallum *(Corallium tubis turbinatis teretibus*) and 25 *Madrepora* whose tubular corallum was composed of star-shaped plates: *Corallium tubulis stellato-lamellosis* (*Systema Naturae* 1757, pp. 793–798). As research progressed, however, his taxonomy was revised: the *Tubipora* were moved to the Alcyonaria, the *Millepora* to the Hydrozoa and many of the madrepores relocated elsewhere.

The first account of coral reef formation following Linnaeus had appeared in 1832 in Vol. 2 of Charles Lyell's trilogy, *Principles of Geology*, in which he used the current terms, writing that the "new rock-formations continually in progress are most conspicuously displayed in the labours of the coral animals", which he termed "zoophytes of the oceans". Although he was able to name some of the genera involved (*Meandrina*, *Caryophyllia*, *Astrea*), on the following page he was compelled to revert to "the branched madrepores, which live at a considerable depth, [that] may form the first foundation of a reef, and raise a platform on which other species may build" (Lyell 1830–1833, II, pp. 283–286).

Huxley was just as unclear as Darwin and failed to use a consistent term for reef-building corals, which is not entirely surprising because the relevant genera were yet to be identified, although he did demonstrate an awareness of the problem by including the *Octocoralla* and *Hexacoralla* in the taxon of "coralligena". To recognize the reef-building animals, Huxley employed the compound "coral polyps", although in his *Manual* he described them more generally as "stone-corals", which "have a wide range, both as respects depth and temperature, but are most abundant in hot seas…forming what are called coral reefs" (Huxley 1877, p. 166).

The need for an accurate descriptor was clearly evident, but in default of any precise understanding of the actual processes involved in coral reef formation, for the remaining decades of the 19th century and into the 20th, the term "madrepore" continued to be used by coral scientists as synonymous with "reef-building". Not until the mid-20th century were the specific processes involved in building atolls and barrier reefs, and the particular genera concerned, finally identified.

[1] Huxley 1864, pp. 23–24 ("mesenteries": Gk *mesos*, "mid" + *enteron*, "intestine").

[2] Molluscoida: "mollusc-like"; Annuloida: "segmented, worm-like".

By the mid-19th century, however, to progress further there was still a problem to solve that had never been considered in any detail: What, exactly, is a coral reef?

The Recognition of "Reef" Identity

The first stages of identification had commenced in the early 19th century when navigators and shipboard naturalists began a closer scrutiny of reefs during their voyages of colonial exploration and settlement. As the Pacific and Indian oceans and the seas of Southeast Asia came under investigation more intensively, a wide-ranging body of observations began to build up that were described in British *Admiralty Reports* and published in scientific journals. Reefs, it was being realized, could no longer be considered the simple "constructions of insects" on rocky substrata with some mysterious inner power, which, in Forster's words of 1778, allowed them to resist "the rage and power of the ocean". Accumulating evidence was beginning to indicate that they were far more complex structures, consisting of a wide range of materials, mineral and organic, and inhabited by an extensive number of marine species, both plant and animal.

After Cook's second voyage when Forster first made his notes, further observations were made in the early 19th century by a number of explorers. During the 1815–1818 cruise of the Russian ship *Rurik*, naturalist Adelbert von Chamisso had recorded that, despite "the unremitting fury of the ocean … the larger species of corals…prefer the more violent surf on the external edge of the reef", and that the surface of the reef when exposed at low tide was discovered to consist of "sea-shells, fragments of coral, sea-hedgehog shells and their broken off prickles, united by the burning sun through the medium of the cementing calcareous sand" (Chamisso 1821, III, pp. 321–323). In the same years during the voyage of the French corvette *l'Uranie* from 1817 to 1820, Jean René Quoy and Joseph Paul Gaimard confirmed from their investigations in Philippine and Hawaiian waters that "there are no islands of any size … which are entirely formed by corals" (Quoy and Gaimard 1823, p. 273). Those comments were supported by geologist William Fitton, who, while aboard the *Mermaid* survey of the Great Barrier Reef in 1827, described "marine shells in cemented masses" that had become "agglutinated in coral rock".[3] It was also becoming evident that plant life was an integral feature of reef construction that initiated yet another line of inquiry.

Although coral reefs had been compared with attractive gardens, Flinders describing them in his *Voyage to Terra Australis* as resembling "wheat sheaves, mushrooms, stag horns, cabbage leaves and a variety of other forms, glowing under water with vivid tints of every shade betwixt green, purple, brown and white; equalling in beauty and excelling in grandeur the most favourite *parterre* of the curious florist" (Flinders 1814, II, p. 88), there remained one aspect of reef construction that hitherto had not been widely considered by zoologists: the relationships between corals and plants on reefs.

Because of his inability to create a natural plant taxonomy based on the visible male and female reproductive parts in *Species Plantarum* of 1753, Linnaeus classified those whose sexual characteristics could not be readily identified into four orders, which included algae and lichens. As some algae were also calcareous and at the time superficially indistinguishable from corals, in default they had been collectively located within the heterogeneous taxon of "Corallines", so creating considerable uncertainty until plants could finally be separated from animals, a task that continued to occupy reef scientists for many decades.

Following the efforts of Linnaeus, with most of the plant and animal species yet to be placed in systematic order, renewed vigour came from the emerging botanical science of phycology (Gk *fukos*, "seaweed"), starting with the studies of Lamouroux, Philippi and Harvey. In 1812, Lamouroux identified and named the Melobesia (after Melobosis, daughter of the god of the sea Okeanos in Greek mythology) as an important reef-encrusting alga, and presented the first algal taxonomy by arranging them into groups based on colour. He was followed by the German botanist Rodolfo Amando Philippi (1808–1904), who, from his research in the Mediterranean, finally established in 1837 that all corallines are algae, and named two such genera as *Lithophyllum* (Gk "stony plant") and *Lithothamnion* (Gk *thamnos*, "bush", and hence "stony bush").

Progress in marine botany then accelerated with the unfortunately short lifetime research of Philippi's contemporary William Henry Harvey (1811–1866), an indefatigable systematist who ranged widely in his search for scientific evidence. One of his earliest efforts in 1836 was to follow the colour approach of Lamouroux and to classify algae into the four discrete groups red, brown, green and earthy, and this landmark finding is still followed today under the names Rhodophyta (red), Phaeophyta (brown), Chlorophyta (green) and Chrysophyta (diatomaceous and golden). Harvey's research contributed a massive number and volume of publications on marine algae: from a 7-year period (1835–1842) in South Africa came *Genera of South African Plants and Flora Capensis*, following which, from a year in 1849 at Harvard, he published definitive studies of North American algae. Then, in the period 1853–1856, following investigations in India, Australia and the South Pacific, he produced *Nereis Australis*, *or Algae of the Southern Ocean*,[4] along with a five-volume *Phycologia Australica* and *Phycologia*

[3] Fitton, in King 1827, II, pp. 592–593.

[4] Nereis, daughter of the sea god Nereus; granddaughter of Okeanos.

Britannica, also in multiple volumes, which led to his appointment in 1856 as professor of botany at Trinity College Dublin.

In *Phycologia Britannica*, Harvey set reef studies on a new direction with his definitive assertion that "the question of the vegetable nature of Corallines, among which the *Melobesia* [crustose algae] take rank, may now be finally set at rest, by the researches of Kützing, Philippi and Decaisne".[5] It was following his extensive studies that tropical reefs were finally being understood as extremely complex ecological assemblages: Harvey's recognition of the Melobesia as the most important of the algal reef genera marked a major advance. The tribe Melobesiae, with a wide range of species, is found throughout the seas of the world, from the Arctic around 80°N to the Antarctic at 70°S. Able to attach themselves to any firm base, tropical species only thrive on rocky coasts with vigorous windward wave fronts, where they grow quickly from nutrients brought by surging waters, and the calcareous red algal forms, *Porolithon*, *Lithothamnion* and *Lithophyllum*, create the pink cemented masses that had been noted by the earlier explorers. The metabolism of calcium from seawater by encrusting algae was now becoming appreciated as the initial process in the formation of the firm surfaces on which coral polyps themselves later became established.

The first extended account of reef composition came from Darwin after he consolidated his geological discoveries during the voyage of the *Beagle* (1831–1836) in *The Structure and Distribution of Coral Reefs* where he described the processes of atoll and lagoon construction on the Keeling Islands from his observations in April 1836. From "information provided by Mr Liesk", a resident there, Darwin recorded that corals die if exposed to the air and strong sunlight during low tides. Consequently, he inferred, "being thus checked in its upward growth, [the coral] extends laterally, and hence most of the masses, especially a little further inwards had flat dead summits", all growth consequently taking place on the ocean side where "the Porites and Millepora [corals] alone seem able to resist the fury of the breakers on its upper and outer edge…[although, he added] at the depth of a few fathoms (5–7 m) other kinds of stony corals live" (Darwin 1842, pp. 6–7).

In his cross-sectional diagram of one of the 27 small islets of the Keeling group, Darwin described the first line of defence against "the fury of the breakers" as a "convex mound … two or three feet in thickness" along the wave front that seemed "like [an] artificial breakwater", which he assumed had been built up from successive growth layers. Integrated with *Porites* and *Millepora* corals, he noted further that "three species of *Nullipora* flourish", some growing as thin sheets, others as stony knobs, of considerable strength and, because they are on "the part most exposed to the breakers … this must effectually aid in preserving [the atoll] from being worn down", so explaining how reefs could resist the power of the oceans (Darwin 1842, pp. 9–10). Then, immediately behind the "convex mound" on the reef flat, today known as an algal ridge, and obviously thrown up by storms, he observed "rounded particles, generally almost blended together, of shells, corals, the spines of echini, and other such organic bodies" which "become firmly cemented together by the percolation of calcareous matter [and consequently are able] to resist the daily tides longer, and hence project as a ledge" (Darwin 1842, p. 12). Behind the protective barrier of the algal ridge in the sheltered waters of the lagoon where, in the world's most coral-productive waters of Indonesia, the Philippines and the Great Barrier Reef, there is a wider range of coral species, more than 500 species have now been described.

As Darwin continued his observations, of considerable significance was the discovery from FitzRoy's line soundings that the first 12 fathoms (18 m) of reef slope revealed various species of madrepores (retrieved from the tallow inserts in the lead bell), but below, to a depth of 20 fathoms (36 m), "every one [of the soundings] shewed that the bottom was covered with sand". Then, from the deck of the *Beagle* standing farther out to sea at 2200 yards (2 km), "Captain Fitzroy found no bottom with a line 7200 ft [2.2 km] in length", leading Darwin to comment, without further explanation, that "hence the submarine slope of this coral formation is steeper than any volcanic cone" (Darwin 1842, pp. 6–8).

Darwin made further comments on algae, for instance, "at a greater depth than 90 fathoms (164 m, 540 ft) off this coral island", that the bottom was "thickly strewed with joints of Halimeda and small fragments of other Nulliporae, all but dead". After making similar observations later in Mauritius, where the beaches were covered with "vast quantities of fragments of Nulliporae", he inferred that these simply organized bodies, which are "the lowest classes of the vegetable kingdom" are also "amongst the most abundant productions of the sea".[6]

Darwin continued to defend his volcanic subsidence hypothesis with the assertion that "reefs may possibly rise from very great depths through the means of small corals, first making a platform for the growth of the stronger kinds" (Darwin 1842, pp. 86–87), he recognized that reef construction at the surface could no longer be considered a solitary activity by "saxigenous lithophytes" (Lat. *saxeus*, "stony"), but was only one aspect of a more complicated process of bi-

[5] Harvey 1846–1851, I, fasc. 13, Plate 73.

[6] Halimeda, a calcareous green alga (Gk *halimures*, "of the sea"), Phylum Chlorophyta; Nullipores (Lat. "no pores") is an overall term for encrusting coralline algae of the family Corallinaceae in the same phylum.

otic interaction in which algae have an essential role. Slowly the evidence was beginning to create an overall synoptic view of what exactly a "reef" is, evidence that would later become more explicable within the context of Haeckel's concept of ecology.

Animal Life in the Marine Environment

Yet another element of reef ecology came to be introduced that had been noted in 1801 by Matthew Flinders in his passage through the Great Barrier Reef when he likened coral growths to luxuriant gardens. If Darwin's theory of speciation were due to natural selection, what then was the cause of so many different forms and varieties that occupied reef flats and reef fronts at different depths as far down as 90 m? That issue was not finally examined in detail until 1995.[7]

The first attempt to investigate coral reefs as a total assemblage within the framework of "the economy of nature" was undertaken by Carl Gottfried Semper (1832–1893), a student of the famous microscopist Albert von Kölliker at Würzburg. Immediately after completing his studies, he travelled during the years 1857–1865 throughout the Spanish Philippines, spending a year in 1862 on Peleliu and the other five major atolls in the Pelew group (present-day Palau). Some 800 km (500 miles) due east of the island of Mindanao, at around 7° N 135° E, he made the first in-depth field investigation of animal life in the natural marine environment of coral reefs. Somewhat unexpectedly, he came to the conclusion that the irregular configuration of the Pelew island chain with its areas of both elevation and possible subsidence created serious problems for Darwin's theory of reef formation. Accordingly, he sent a short 12-page *Reisebericht* (travel report) to a German zoological journal in 1863 with his dissenting observations.

On his return to Würzburg, Semper was appointed *Privatdozent*, and having wholeheartedly accepted the Darwinian theory of evolution and being aware of Haeckel's 1866 neologism of ecology to encompass the "relations of the organism to the environment, and to other organisms with which it lives", recognized its potential for presenting his preliminary Philippine findings. These were published in 1868 as *Reisen im Archipel der Philippinen* (*Travels in the Philippines*), in which he asserted that the next major task for biologists was to investigate experimentally "the influence of temperature, light, heat, humidity, nutrition, & c., on the living animal", and to determine the "ecological laws affecting organic forms and their functioning".[8]

In 1869, Semper was promoted to professor and director of the zoological institute at the University of Würzburg and began organizing his Philippine experiences into a major ecological study, which he first presented in 1877 when invited to Boston to present his research to the Lowell Institute, a philanthropic foundation that sponsored lectures by distinguished persons. Those lectures, essentially a textbook in animal ecology, were published in Leipzig in 1880 under the title *Die natürlichen Existenzbedingungen der Thiere*, which he translated into English the same year as *The Natural Conditions of Existence as They Affect Animal Life*, developed from the plan adumbrated in his 1868 *Travels in the Philippines*. In that work, he dealt sequentially with the physiology of marine organisms and the influences on animal life of nutrition, light, temperature, atmosphere, water, species distribution and other organisms. Of particular relevance to coral reefs were his chapters on "The influence of water in motion" and "The influence of light", in which he discussed the formation of coral reefs as the natural habitat of polyps and the entire range of associated marine life.

A Major Discovery: Chlorophyll and Photosynthesis

In Chapter 3, "The influence of light", Semper made a forward-looking contribution to coral reef theory when he brought into the literature for the first time a critical issue: the presence of chlorophyll in plants. He therefore initiated a quest that came to dominate much of reef science for the following century. Barely 50 years earlier, two French chemists, Pierre Pelletier and Joseph Caventou, first isolated *la matière verte des végétaux*, the green substance in plants that gave them their colour, and indicated in their *Report* to the *Annales de Chimie* that *nous proposons de lui donner le nom de chlorophyle*, their neologism derived from the Greek for "greenish-yellow" (*chloros*) and "leaf" (*phyllon*) (Pelletier and Caventou 1818, p. 195). The function of chlorophyll in plants, however, remained obscure until 1845, when the German physicist Julius Robert von Mayer (1814–1878), from his studies of living organisms during a period as ship's surgeon in the Dutch East Indies, hypothesized that the energy requirements of animals come from plants. In some way, he hypothesized that they are able to convert solar radiation into energy, possibly through unidentified chemical processes in their leaves stimulated by chlorophyll.

Although most, but not all, plants contain chlorophyll, it was still debated at the time whether it also existed in animals. It had always been obvious that green leaves and sunlight were essential to healthy plant growth, but even when the green substance had been isolated and named chlorophyll, the biological action involved remained unidentified. Following general acceptance of Mayer's ideas, biochemistry continued to advance until it became established that plants synthesize carbonic acid (H_2CO_3) as their basic meta-

7 Veron 1995: 49 f.

8 Semper 1868, p. 228 (reproduced in translation by Nyhart 1995, p. 179).

bolic process from water (H_2O) in the soil and carbon dioxide (CO_2) from the atmosphere. Once created, carbonic acid is decomposed through the (then unknown) action of chlorophyll, to make organic compounds that are broadly known as sugar or starch or, more generally, carbohydrate (CH_2O), the primary source of animal energy. One consequence of its decomposition through respiration is the release of oxygen (O_2), a process that accounts for most of the oxygen in the atmosphere.

By the late 1870s, Semper was able to confirm that although "the chlorophyll bodies of plants are…microscopic and elementary bodies of peculiar structure and definite function, their principal property is that they decompose carbonic acid under the influence of light, and form organic compounds by the combination of three or four elements". Animals, in distinct contrast he pointed out, are "absolutely incapable of decomposing carbonic acid, but are, nevertheless, frequently of a green colour", although the colouration of green animals, particularly insects and reptiles, came from certain pigments other than chlorophyll.

At the same time, it became clearly evident that some invertebrates also contained chlorophyll, specifically *Hydra viridis* and some of the Coelenterata. Semper therefore suggested that it could "be possible that the green constituents are not integral elements of the animal, but foreign bodies living within it—commensals or 'messmates' as they are called". In raising the presence of commensals or "messmates", Semper was referring to the theory of Simon Schwendener (1829–1919), professor of botany at the University of Basel. At the annual general meeting of the Swiss Natural History Society on 10 September 1867, Schwendener presented a controversial paper with the revolutionary hypothesis that lichens are not a single primitive encrusting plant, but a curious combination of two totally separate organisms: algae and fungi. Moreover, the two are joined in an obligate (compulsory) union which Pierre-Joseph van Beneden (1809–1894), professor of zoology at Louvain University in Belgium, described in 1873 as "mutualism".

When Semper introduced the concept of commensals in lichens, he did so to strengthen his own observations that had been corroborated by the Russian protistologist Leon Cienkowski, who, "from his very careful labours [has] recently proved that these [greenish] yellow cells in the Radiolarians are in fact nothing more than one-celled Algae living as messmates [*Tischgenossen*] with the animal in the same sort of community as certain Fungi and Algae which, as is well known, combine to form the apparently simple vegetables as Lichens, which, however, are still generally classed as a distinct group of plants".[9]

Drawing that section of his discussion to a close, Semper noted that "Sponges and Polyps frequently take up dead or living foreign bodies and utilize them as normal elements of the tissue", which led to a speculative element that changed coral reef research dramatically. "If we find true chlorophyll in animal tissues", he declared, "we will be obliged to recognise in its presence a singular and interesting case either of parasitism or the community of two organisms so different as an animal with true tissues and organs, and a one-celled plant".[10] The question immediately arises: What exactly does "mutualism" mean, and, further, how is it related to "commensal" and "messmate"?

The term commensal first appeared in the 16th century from the Latin "com" (a variant of *cum*, "with") and *mensa*, a table, used colloquially to refer to persons eating "with each other at the same table". By the 18th century, it had entered English informal speech as "'messmate" (from Late Latin *missus*, "a course of food"), which in German became *Tischgenossen*. Following the increasing research into botany, with the appearance of van Beneden's "mutualism" and his 1875 study of *Les Commensaux et les Parasites dans le Règne animal* (*Commensals and Parasites among Animals*), at least three different versions of mutualism became current: "parasite" from the original Greek *parasitos*, meaning an "uninvited guest who imposes on the table" and thereby creates difficulties for the unfortunate host, in cases causing serious harm by reducing vital efficiency, even death; "commensal" for those in relatively harmless cohabitation, such as barnacles on whales or on crab carapaces; and "mutualistic" in which there is believed to be some form of beneficial exchange, although the exact meaning of that, which became rather loosely used, was not clear.

Yet another neologism appeared when in 1879 the ardent mycologist Heinrich Anton de Bary (1831–1888) concerned, among other issues, with problems of fungal blight in food crops, published *Die Erscheinung der Symbiose* (*The Phenomenon of Symbiosis*), in which he expanded the term "symbiolismus" that Albert Bernhard Frank had devised in 1877 to avoid the presumption of parasitism. Intended to mean some form of mutualism, de Bary's shortened French term, "symbiose", which he took straight from the Greek *symbios* ("companion", "partner"), simply denoted the "living together" relationship of microorganisms such as fungi and moulds. Once launched into the scientific domain, "symbiosis" developed a life of its own that stimulated a period of intense, decidedly controversial research (see Sapp 1994, Ryan 2002). Coral reef science eventually became involved following publication of several reports that would assist in providing a key to help unlock the mysterious puzzle of the actual processes by which coral polyps build reefs.

[9] Semper (1868, pp. 71–74 of the 1880 translation).

[10] Semper (1868, p. 76 of the 1880 translation).

The Strange Case of "Vegetating Animals"

Meanwhile, the apparent presence of chlorophyll in invertebrates was being pursued in what eventuated as a crucial investigation by Patrick Geddes (1854–1932), one of Huxley's students in the London Royal College of Mines, publication of which appeared in the 1879 *Proceedings of the Royal Society of London* as "Observations on the physiology and histology of *Convoluta schultzii*". His opening words set the question with admirable brevity: "Chlorophylloid green colouring matters are known to exist in the tissues of a not inconsiderable number of animals belonging to various invertebrate groups—Protozoa, Porifera, Coelenterata, Vermes and even Crustacea; but all information as to the function of chlorophyll in the animal organism is wanting" (Geddes 1879, p. 449). In particular, because chlorophyll was observed in some of the coelenterates, especially the Actinians, did it exert any influence on reef formation?

The difficulty at the time was one of making a clear distinction between animals and plants. It had already been established, as Semper noted, that plants were entirely self-supporting—in biological language, they are autotrophs (Gk *autos*, "'self"+*trophos*, "nourishment")—from the metabolic process of respiration in which carbonic acid by the action of sunlight creates carbohydrates, generally known as starch, to meet their energy and growth requirements. To illustrate this ambiguous difficulty, Geddes cited "Schmidt [who] had prepared from [the protist] *Euglena viridis* a body isomeric with starch…but these facts seemed as much to point to the algoid [plant-like] nature of these long disputed organisms as to warrant our supposing a more or less vegetable mode of life in animals so well organized, and so evidently carnivorous as Coelenterates and Turbellarians".[11] Therein lay the problem to solve: could some invertebrates, because they exhibit autotrophic behaviour, really be algae, or even, with overtones of the zoophyte issue, a curious hybrid "plant-animal"?

Throughout the summer of 1878 at the biological station in Roscoff on the far northwestern tip of Brittany, in the same years that Lacaze-Duthiers was involved in hostile confrontation with Anton Dohrn, Geddes had been attracted to start his investigations with a most unusual biological phenomenon that occurs only on the beaches of that Atlantic coastal region. They are the habitat of a minute Planarian, an unsegmented free-living worm 4 mm long, one of several species in the genus *Convoluta*. Densely packed with chlorophyll, during intertidal hours on bright sunny days, the worms rise in their millions into the surface film of water, creating large patches of spinach-green sand. For his experiment, Geddes focused on the species *Convoluta schultzii* by asking two simple questions: Does the chlorophyll in them "have its ordinary vegetable functions" when exposed to sunlight, so leading to the emission of oxygen? Further, if such proved to be the case, and it could be demonstrated that the worms actually do "decompose carbonic acid … one naturally enquires whether they do not still more completely resemble green plants in fixing the carbon in the same way" (Geddes 1879, p. 452). The implication of that suggestion was, in fact, that fixed carbon, as Schmidt had previously demonstrated, would give rise to energy-giving carbohydrate.

In a series of laboratory experiments throughout the summer, Geddes was able to collect gases "evolved by the animals [that did] not contain less than 45–55 per 100 of oxygen", which Ray Lankester of University College London documented in 1879 to be "the first direct proof of the evolution of oxygen gas through the agency of the chlorophyll contained in the tissues of animals of so high an organisation as the Planarian worms" (Lankester 1879, p. 434). Further chemical analysis revealed that in the process they had synthesized an even more complex carbohydrate, "ordinary vegetable starch" ($C_6H_{10}O_5$), and when dead specimens in sufficient quantity were incinerated, their ash revealed iodine, "another analogy to the algae", all of which indicated incontrovertible proof of plant character. That discovery led Geddes to speculate that perhaps "these Planarians may not unfairly be called Vegetating Animals, for one case is the precise reciprocal of the other" (Geddes 1879, p. 453).

Ingeniously simple as Geddes' experiment was, nothing was really settled; instead, it initiated yet a further line of inquiry. What could explain Schmidt's comment on the "algoid nature" of *Euglena viridis*, and Geddes' discovery that the worm *Convoluta schultzii* contained iodine, a characteristic of plants? An answer came 2 years later. On 11 November 1881, a late entry was appended to the agenda of a Berlin Physiological Society meeting with the title *Ueber das Zusammenleben von Thieren und Algen* by K. Brandt. That short speech, recorded in their *Transactions* (*Verhandlungen der Berliner Physiologischen Gesellschaft*) and published in a four-page article in the *Archiv für Physiologie* for December 1881 (Brandt 1881, pp. 570–574), was disarmingly influential in determining the next century of coral reef investigation. Its brief title, "Concerning the coexistence of animals and plants", came from the growing interest of marine biologists in the many vexed problems regarding symbiosis and the puzzle of understanding the interaction of algae and chlorophyll in small, almost microscopic invertebrates, particularly given that von Mayer had suggested that an unidentified chemical reaction between chlorophyll and algae could be the source of animal energy.

Virtually unknown in biological circles at the time, the author of that article was to become one of the most cited in literature, through to the present day. His article, in ef-

[11] *Euglena viridis* is today classified as Phylum Euglenophyta in the Kingdom Protista. Isomeric: same atomic elements arranged differently.

fect, became the datum point where all papers and books on modern coral reef taxonomy find their origin.[12] The citation beginning such discussion always carries the simple reference "Brandt 1881", although it is rarely evident that modern authors have had any acquaintance with the text itself.

Karl Brandt and his Yellow Algal Cells

Karl Andreas Heinrich Brandt (1854–1931) was born in Magdeburg and studied natural science in the University of Berlin with a strong interest in marine invertebrates. In 1879, from the Berlin Academy of Science table at the Stazione Zoologica di Napoli, his research resulted in the 1881 article, written in somewhat obscure 19th-century German and motivated in part by Semper's *Die natürlichen Existenzbedingungen der Thiere*. In the opening section, Brandt commented that Semper had many stimulating thoughts, including an overview of the three existing opinions regarding chlorophyll in animals: Do animals contain the same chlorophyll as plants? Is the chlorophyll a parasite? Or, is the "green mass" (*grünen Massen*) something that has been eaten and is merely in process of being digested? Obviously, he stated, the first step would be to make a careful biological examination in order to determine whether the "green bodies" (*grünen Körper*) consist solely of chlorophyll, have a cell nucleus and are bounded by a cellulose membrane. It is also necessary, he continued, to determine whether the "green bodies" have an independent existence, and whether they can "infect a chlorophyll-free animal": *Chlorophyllführenden Thier zu inficiren*. In that short phrase, Brandt's suggestion of "infection" by algae with its pathological overtones was carried forward for several decades as coral biologists sought to resolve the issue.

Brandt began his meticulous research with hydra, sponges and turbellarians (free-living flatworms) and "numerous other infusorians" (stentor, paramecium, stylonchyia and various vorticellae) in order to extract the "green bodies", named chloroplasts in 1884 as a shortened form of the German "chloroplastid", an organelle containing chlorophyll. He then subjected them to intensive morphological, microscopic and chemical analysis, and concluded that they were not completely and evenly green, but consisted of hyaline (translucent) protoplasm along with the "chlorophyll bodies" proper, each of which is "a morphologically independent single-celled creature". Following that discovery, he identified them experimentally as algae, and with that confirmation gave his enduring contribution to coral reef science by writing that "since no algal genus [*Algengattung*] has yet been described to whom these green bodies could be assigned", specific names have to be devised. Turning in standard taxonomic style to the Greek *zōon* for "animal" and *chloros* for "greenish-yellow", he described the three green species he had identified with the generic name *Zoochlorella*, creating yet another hybrid in the same mode as "zoophyte" (Brandt 1881, p. 571).

Brandt's paper then discussed, briefly, the yellow cells that Cienkowski, Hertwig and he had already discovered to be single-celled algae with both nucleus and chlorophyll, cohabiting as messmates in radiolarians and "certain Hydrozoa and Actinia", with a "morphological and physiological independence from the animals with whom they lived". As they also had not been described, another generic descriptor was needed to distinguish them from the zoochlorellae. With a claim to taxonomic priority, he decided to "permit himself to assign corresponding genus names", so, along with the zoochlorellae, from the Greek diminutive *xanthellos* for yellow-brown, those algal species (*gelben Zellen*) were named, in the plural, *zooxanthellae*.[13] One of the species of zooxanthellae found in Radiolarians, Hydrozoans and reef-forming Actinian corals was discovered almost a century later to be a crucial missing link that would help in decoding the enigma of reef formation.

Further advances were reported in Brandt's article. In addition to the morphological independence of the zoochlorellae, he established their physiological independence, observing that even when isolated "they continued to manufacture starch grains" (*so treten Stärkekörner in ihnen auf*), a clear "sign they do not lose an ability to process their functions". In addition, infection (Ger. *infizieren*) experiments were conducted, and many of the Infusoria did not retain the zoochlorellae. It was, however, possible to infect some with zoochlorellae from dead *Hydra viridis*. He made no mention of attempts to infect other animals with zooxanthellae.

Brandt then moved to the parasite problem. Animals do not create chlorophyll at all, he confirmed, and when it is found in them, he stated somewhat hesitantly, it enters, thanks to parasites ("*Wenn as bei Thieren findet, verdankt es eingewanderten Parasiten sein Dasein*") (Brandt 1881, p. 572), immediately modifying that inference by stating that the "parasite" allusion did not carry any pathological implication. In fact, unlike parasites which "extract substances from their host", and Brandt seems to be the first zoologist to use the term "host", using the German equivalent "der Wirt" to describe the hapless recipient, both algal genera of zoochlorellae and zooxanthellae are capable of producing an organic substance, i.e. carbonic acid, from water and carbon dioxide.

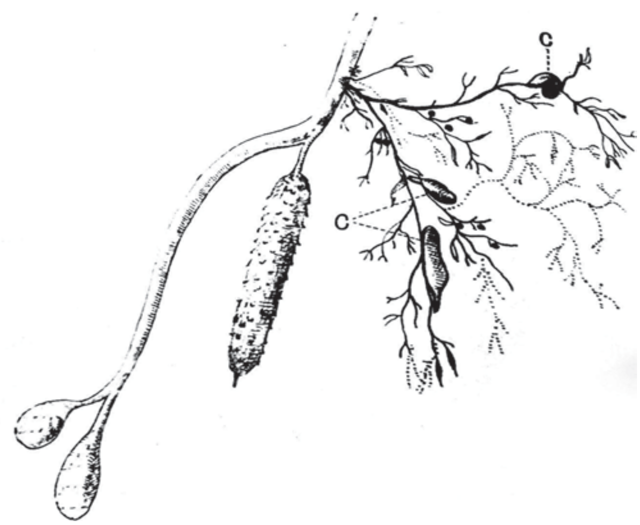
[12] The assistance of diving companion Niels Feldman of Darmstadt, Germany, with this section, and especially with the translation of the Brandt (1881) article, is gratefully acknowledged.

[13] Zooxanthellos is pronounced correctly as "Zoh-oh-zan-thell-oss", and the plural, zooxanthellae, as "zoh-oh-zan-thell-eye". The suffix "xanthellos" is a Greek diminutive of "yellowish-green".

Unlike lichens, where it is a one-way process with "the algae supplying nutrition to the parasitic fungus", both zoochlorellae and zooxanthellae could keep their hosts alive indefinitely. In the case of algae and animals, he concluded, there is genuine symbiosis (*Symbiose*), with the caveat that "once the green or yellow algae have moved into the animals and have reproduced themselves enough, the animals give up their independent life and let themselves feed by their parasites only". Brandt concluded with a wry twist: "The co-existence of algae and animals is quite peculiar. From a morphological perspective the algae are parasites, from a physiological perspective the animals are the parasites" (Brandt 1881, p. 574).

At least Brandt had solved the problem that confronted Geddes by demonstrating experimentally that the green appearance of a large number of invertebrates comes from their symbiotic algae, so minuscule that several million can occupy a square centimetre of surface tissue,[14] and had introduced into scientific discourse the two neologisms of zoochlorella and zooxanthella. Following publication of his 1881 article, he returned to the *Stazione Zoologica* as a scientific assistant where, in 1885, he published *Fauna und Flora des Golfes von Neapal*, following which he was invited in 1886 to Königsberg by Prof. Carl Chun to conduct experimental research on symbiosis, part of which he also did at the *Stazione'*s Berlin Academy of Science table. Leaving chlorophyll research, the baton Brandt accepted from Geddes was passed to others, among whom Frederick Keeble was to continue research into the still problematic issues of mutualism and parasitism.

Convoluta roscoffensis after Keeble (1910). At extreme right, the central dotted line refers to an otocyst (today, statocyst), with two others, central and far left, that provide a sense of gravity to assist movement up and down. Dotted lines above and below the otocyst on the right point to the eyes



Convoluta paradoxa, labelled C, from Keeble (1910), showing their attachment to seaweeds in the paradoxa zone

Mutualism Resolved: Obligate Parasitism

The identification of zoochlorellae and zooxanthellae by Brandt, in conjunction with the results of the work of Geddes, presented some intriguing challenges: the suggestion of a "vegetating animal", like the puzzle centuries before about the hybrid "zoophyte", could not be left at rest. Further investigation was demanded, and it engaged the curiosity of Frederick William Keeble (1870–1952), professor of botany at Reading University College, who pursued a 10-year research programme on the beaches of Roscoff from his summer vacation home at nearby Trégastel. Throughout those 10 years, he continued experiments in exhaustive detail on two species of planarian, *Convoluta roscoffensis* and *Convoluta paradoxa*, "infested" with zoochlorellae and zooxanthellae, respectively.

His absorbing and authoritative investigations were finally published in 1910 under the title *Plant-Animals: A Study in Symbiosis*, in which he attempted to solve, once and for all, the puzzle of ambiguous behaviour by animals that acted more like plants. It had already been confirmed experimentally by Geddes and Brandt that within the host animals, algal cells create carbohydrate in the form of starch and emit oxygen. Geddes could only suggest that the *Convolutae*, consequently, were some borderline genus of "vegetating animal", whereas Brandt was of the opinion that algae and hosts were locked into some kind of mutualistic parasitism. From that point, Keeble resumed investigation in much closer detail, beginning with histological analysis of the two species. Certain they were animals, because they had a mouth and ingested food at their juvenile stage, he was unable to account for the green and yellow-brown cells, which he described as "puzzling objects because, whilst they seem to be just as much integral parts of the bodies of the animals as any

[14] Considerable interest in algal densities was generated when high levels of solar irradiance were linked with zooxanthellae loss during episodes of coral bleaching that became prominent in the 1980s and thereafter (McCowan et al. 2011, p. 31 report densities between 3.85×10^6 and 2.77×10^6 cm^2; see Chapter 13).

other tissue elements, they have nevertheless a foreign and plant-like appearance" (Keeble 1910, p. 118). At the same time, Keeble observed in his extended studies of the developmental stages over the 10 years that adult forms never eat, neither species had an alimentary canal to dispose of waste, and no traces of food could be found in their bodies.

The aptly named *Convoluta paradoxa*, whose zooxanthellate cells were also found in reef-forming madrepores and their close relatives, the anemones, "from the time of hatching to the period of maturity…feeds voraciously", he reported, although on reaching the adult stage, they also cease eating, because Brandt had noted earlier that they "give up their independent life and let themselves feed by their parasites only". That led Keeble to believe that the green and yellow-brown algal cells provided all the nourishment required. At that point, he turned to the emerging concept of photosynthesis, "a process as yet imperfectly understood" (Keeble 1910, p. 78), a term devised in 1893 by Charles Barnes, professor of plant physiology at the University of Chicago, to describe the light-dependent process by which plants reduce CO_2 to organic matter.[15] Unaware at the time of the processes involved, Keeble inferred that their nutrition came from some inner pressure exerted by the phototropic algae for replenishment by radiant sunlight, and that it could explain their unusual behaviour of rising from under the sand during sunlit hours to form extensive deep green patches in what could easily be described as mass sunbathing.

With the process of carbonic acid decomposition now understood to result from photosynthesis, Keeble engaged in a lengthy sequence of experiments to be certain that the green cells were not organically part of the worm and were genuinely of "intrusive origin", and whether they could be "identified with any known, free-living alga". At first, he attempted to isolate and cultivate the chloroplasts, the green organelles containing photosynthetic cells within the algae, but had to admit defeat. His only recourse was to undertake a close, painstaking study of all stages of larval development to maturity. The technique he adopted was to collect the egg capsules of gravid hermaphrodite worms (although the sperm always came from another hermaphroditic worm) and allow them to hatch in filtered water. The details are lengthy and meticulously described. Here, it is simply relevant to report that after numerous failures to completely eliminate algae from the filtered water, he discovered that they had been present in the mucilaginous (sticky) coating of the egg capsules. Once that source of error was corrected, he succeeded in reporting that from one batch incubated in filtered water, "not a single animal of a total of forty-seven was found to contain any trace of green cell or colourless precursor" (Keeble 1910, p. 118).

The next stage was to "test the hypothesis" by transferring the uninfected worms to normal seawater. Almost immediately, green cells started to appear in the bodies of the worms with uniform regularity, he observed, as each one newly hatched began "swallowing eagerly all the minute particles that come its way; [and] as it grows it seeks the light and takes on its green algal appearance". Keeble, thereby, confirmed "that the green [and yellow-brown] cells of *C. roscoffensis* are algae; that the species to which they belong exists as a free-living, independent, marine plant … [and] that it is ingested with the food … where it multiplies and forms the green tissue". A corollary followed: some of the waste products of animal nutrition are nitrogen compounds, chiefly urea (CH_4N_2O) and uric acid ($C_5H_4N_4O_3$). Plants, however, cannot manufacture the essential nitrogen needed for their growth themselves: they have to find it, so from animal waste the nutritional needs of algae are partly provided. The ingestion of algal cells was therefore assumed to be of fundamental importance because it led to the conclusion that "forces itself upon us that the green cells and yellow-brown cells constitute the excretory organs of *C. roscoffensis* and *C. paradoxa* respectively" (Keeble 1910, p. 118). Consequently, "it cannot escape its destiny. A colourless or green [or yellow-brown] cell is taken into its body and the plant-animal is formed" (Keeble 1910, p. 128). His only inference was to conceive them "as an animal which lives like a plant, in other words, a plant-animal".

As the *Convoluta* had come to rely totally on passing nitrogen to the resident algae, which functioned as their excretory organs, Keeble observed that unfortunately "this handing of nitrogen-containing substances to and from animal to plant and from plant again to animal cannot go on indefinitely without loss. Sooner or later, the animal finds itself lacking in essential nitrogen-containing food-materials". As the algae can no longer meet supply demand, "the animal is under the dire necessity of digesting its algal cells", and moves into a saprophytic (offal-eating) mode (Gk *sapros*, "stale", "putrid") and begins digesting the algae, necessarily leading to its own doom (Keeble 1910, p. 147). Accordingly, with echoes of Brandt's summary, and from whose seminal paper Keeble had drawn, although without specific reference, to label the association between plant and animal as symbiosis is to miss its significance: "from the standpoint of the animal it is one of obligate parasitism. Apart from their algal cells, *C. roscoffensis* and *C. paradoxa* are unable to live … the existence of either species depends upon the infection of the individuals of each successive generation. …From the standpoint of the ingested algal cell, the association with the animal means a successful solution of the nitrogen problem. It sacrifices its independence for a life of plenty. This uni-

[15] Barnes' original term was the simpler and etymologically debated "photosyntax" (Gk *syntaxis*, "systematic arrangement". The description is from Gest (2002, pp. 7–10).

versal nitrogen-hunger is a misery which makes strange bedfellows" (Keeble 1910, p. 153).

Keeble finally suggested that saprophytic feeding among the *Convoluta* "will rank high in interest among organisms as suggesting the route along which far-reaching evolution has travelled". His intimation here is that speciation has developed, at least in part, from various parasitic and mutualistic liaisons, although in the case of the *Convoluta*, they did not complete the transitional process to full vegetative status. Where they missed out, he wrote in the style for which he became so highly regarded in his day, is the ability to cultivate their "highly productive gardens". If only they "could but learn how to bequeath packets of vegetable seed to their descendents, they might lose their animal characteristics altogether and become *C. roscoffensis* a green plant, and *C. paradoxa* a yellow-brown plant. As it is, the garden has to be replanted by the individuals of the successive generations and so they remain plant-animals" (Keeble 1910, p. 157).

Keeble continued to an illustrious career as a Fellow of the Royal Society, including being chair of botany at Oxford from 1920 to 1927, and he received a knighthood in 1922 for his substantial contributions to both fundamental and applied botanical research. However, it is significant that his 1953 Royal Society obituary placed considerable emphasis on his study of *Convoluta* (Blackman 1953, pp. 492, 496, 497).

Part II

A New Era In Reef Science

9 Field Studies and Taxonomic Revision, 1901–1945

Throughout the decades, from Cuvier to Keeble, biological knowledge advanced considerably and elements were being assembled that would contribute to a more accurate understanding of coral reefs. After Huxley had effectively demolished the taxon of Radiata containing Cuvier's miscellany of incompatible organisms, and following the work of Haime and Milne-Edwards, the independent phylum Cnidaria was finally created, which today, with the comb jellies forming the nematocyst-free phylum Ctenophora, are known collectively as the coelenterates.

Within the Cnidaria were all the reef-creating hard corals known generally in the 19th century as madrepores, and thereafter, reefs could no longer be identified as mere aggregates of coral species. It was clear, in large part from the rapid progress of marine botany, particularly the discovery of the role of encrusting coralline algae as the necessary foundation for coral establishment and the formation of lagoons, reef flats, atolls and islands, that coral reefs are complex ecological assemblages. Moreover, with the contributions of Semper, Brandt, Geddes and Keeble, and the respective roles of chlorophyll, algae and zooxanthellae within the context of symbiosis, a new element had been introduced into reef research, one that germinated slowly and began to tantalize and frustrate scientists for many years.

In terms of geological investigation, the publication of Darwin's *The Structure and Distribution of Coral Reefs* stimulated great scientific interest and vigorous opposition from Alexander Agassiz and John Murray. Between 1896 and 1898, surveys and drilling attempts to either confirm or deny Darwin's subsidence hypothesis were made in sequence jointly by the Royal Society and Australia on Funafuti Atoll in today's Tuvalu, and by Alexander Agassiz in Fiji in 1896. All were unsuccessful, including four inconclusive final attempts by Reginald Daly and Alfred Mayor in Samoa between 1917 and 1920, the deepest only reaching 166 ft (50 m) (Bowen 2002, pp. 210–212).

There was, however, still a missing element that was becoming evident: all research up to then had consisted of separate, isolated projects that, although valuable in themselves, were not advancing a synoptic overview of reefs as ecological systems.

Mayor in Torres Strait 1913: The Paradigm Study

In 1913, the first of several notable biological investigations of a single coral reef location over a sustained period by the Department of Marine Biology in the Carnegie Institution of Washington was commenced in Torres Strait, between Australia and New Guinea, and it became a paradigm model for ecological research into reefs. Under the leadership of the director of the Department of Marine Biology, Alfred Goldsborough Mayer, later changed from the German spelling to Mayor as the Great War raged, and including zoologist Frank Potts of Trinity Hall, Cambridge, the expedition arrived at Thursday Island. Their plan was to comprehensively study the coral reef at Thursday Island, part of a complex of islands 35 km (22 miles) northwest of Cape York. Finding the location unsuitable because of heavy silting at the time, however, the project was moved 200 km (124 miles) northeast to Murray Island (indigenous Mer).

The most northerly island of the Great Barrier Reef itself (8°S 144°E), Mer is a volcanic structure 2.6 km long (1.6 miles) and 1.6 km (1 mile) across at its widest place, with its main axis lying southwest to northeast. In the southern centre of its symmetrically elliptical shape, there is a small extinct volcano that rises 122 m (400 ft), ringed at a distance by an elliptical arc southwest of several ash-filled minor craters. The studies were conducted at its northeastern end, where it is surrounded for half its circumference by a reef flat some 600 m (0.4 miles) long. Throughout October that year, the small team pursued a thorough investigation that was published in 1918 under the title *Ecology of the Murray Island Coral Reef*. In using the concept of ecology possibly for the first time in reef literature, Mayor sought to investigate, record and analyse what he considered to be the

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major interactions that led to the formation and continuing sustainability of a coral reef.

As they were primarily biologists, the Carnegie team concentrated on the corals themselves: range of species, distribution, along with the environmental parameters of air and water temperature, water chemistry and circulation. In addition, in common with most other investigators up to that time, they had planned a geological survey to compare the rival hypotheses of Darwin and his opponents, chiefly John Murray (Bowen 2002, pp. 193–196). They were concerned too about testing an alternative hypothesis suggested a decade earlier by Ernest Andrews of the New South Wales Geological Survey. In 1901, in company with Charles Hedley, Andrews had surveyed the central section of the Great Barrier Reef around the Whitsunday Islands between 20° and 21°S, and the findings were published in the *Proceedings of the Linnean Society of New South Wales* in 1902. Focus had been on the wide continental shelf, which extends from north to south of the entire eastern coast, where Andrews conjectured that originally there had been a fringing reef on the northern sections, broken in places by river outflow. Since the Pleistocene Epoch 1.6 million years ago, he wrote, there had been a period of subsidence that allowed water to cover much of the former land, leading in turn to water-caused erosion, "during which a uniform coast and smooth offshore bottom had been formed". He then explained that "the sinking of this uniform area allowed the sea to trespass far over the old coast sands into the ranges, and corals…[which then] proceeded in the clear waters of the shelf margin, now removed far seaward, to invest the whole width of the smooth offshore deposits with their masses, and establish themselves as the Barrier reef" (Andrews 1902, p. 177). In the subsequent geological phase, there was a moderate uplift, so accounting for the elevated strata observed by Jukes during the survey by HMS *Fly* between 1842 and 1846 (Jukes 1847), so the pre-Pleistocene river estuaries, once drowned during subsidence, probably accounted for the maritime passages in the outer Reef.

All the geological conclusions reached by those who conducted surveys favoured the Darwin hypothesis. Mayor believed that "the best working hypothesis so far proposed for living coral reefs" was the development of Darwin's theory in subsequent studies, as confirmed by Andrews, Canadian-born Harvard geologist Reginald Daly and the American palaeontologist Thomas Wayland Vaughan (Mayer 1918, p. 14). Moreover, they concluded that "the entire visible reef belongs to the recent period subsequent to the cessation of volcanic activity and has evidently grown seaward over its own talus" (Mayer 1918, p. 16). Exercising caution, however, their report stressed that "the subject of the formation of barrier reefs and atolls is far from being settled in the minds of its students" (Mayer 1918, p. 12).

For the month of October, however, their primary concern was with biological observations: various species were mapped *in situ*, and daily measurements were made of air and sea water temperatures at stations across reef transects, tidal movements and seawater circulation, the chemical composition of seawater and the rate of solution of $CaCO_3$. In addition, laboratory experiments were conducted on various species of coral polyp of the effects of sunlight deprivation, changes in water temperature, silting, dilution of seawater by freshwater and drying out.

Although Murray was not mentioned by name in the laboratory experiments, it is clear that one aspect of the programme was to test his hypotheses on the solution of calcium in seawater and the influence of tidal action in forming reefs. As a determined opponent of Darwin, Murray had proposed two alternative agencies to account for reef formation. First, emergent volcanoes, once extinct, had been degraded below the surface by wave action and had thereby created a large body of surrounding rock debris that formed a suitable platform. Second, deposition on that platform of the skeletal and shell remains of the billions of microscopic plankton (foraminifera, radiolaria, diatoms, etc.), which built up faster than the carbonic acid present in seawater could dissolve them. Once "the accumulation of the dead silicious and calcareous shells" had formed a foundation, he asserted, numerous species of marine organism became established, and "eventually coral-forming species attach themselves to such banks, and then commences the formation of Coral Atolls" to the extent that "it is in a high degree probable that the majority of atolls are seated on banks formed in this manner".

His argument opposed the opinion of Darwin: "it is a much more natural view", Murray argued, "to regard these atolls and submerged banks as originally volcanoes reaching to various heights beneath the sea, which have subsequently been built up towards the surface by accumulations of organic sediment and the growth of coral on their summits" (Murray 1880, p. 513). Murray's theory fared badly; however, from tests conducted by Mayor on pieces of *Cassis* gastropod seashells, the conclusion was that "it would take at least 1,000,000 years to dissolve a layer one fathom [6 ft or 1.8 m] thick", the calcium carbonate thickness of many established reefs. An alternative theory advanced in 1880 by Carl Semper from his observations in Palau was judged to be no better when his observations revealed that "scouring by currents and disintegration are…of limited efficacy in the deepening of lagoons in the Murray Islands" (Mayer 1918, pp. 42–43; Bowen 2002, p. 194).

In their section on corals, the team reported that species were distributed in horizontal zones across the reef flats, so presenting isopan generic contours that they believed were attributable to a gradient of changes in air and water temperature. Experiments were conducted in glass aquaria by manipulating changes to the salinity of the water and silt cover which, not surprisingly, led to conclusions that corals thrive best in clean seawater. One of the most interesting observations, from a present day perspective, concerned the abundance of species and density on the outer reef fronts and their progressive decline in number towards the shore. In particular, there was a need to estimate the rate of growth, and an ingenious method was devised in one instance. Using a photograph from Saville-Kent's magnum opus of 1893 of a large coral head of the *Symphyllia* genus on a reef flat on Thursday Island as reference datum, they located the same head 23 years later.[1] Saville-Kent had measured its diameter as 30 in. (76 cm), and Mayor found it to have increased to 74 in. (1.9 m), so concluding growth to have been at "the rate of 1.88 in. [48.75 mm] per annum" (Mayer 1918, p. 18). Mayor's studies on Mer reached four main conclusions in terms of the ecology of the reef, defined in terms of distribution of species, that it depended on temperature, silting, moving water and other mechanical effects, plus, with a Darwinian touch, "the struggle for existence" (Mayer 1918, p. 44).

By then, particularly given that the Great Barrier Reef had become a major locale for investigation by overseas scientists, Australians were anxious to become involved. In response to their approaches, it was decided that the 84th meeting of the British Association would be held in Adelaide and Melbourne in August 1914. A large number of delegates left Britain in late June and early July, along with a number of distinguished foreign scientists, but, while still at sea, came a tragic turn of events: Germany declared war on Russia on 1 August and on France 2 days later, so leading Europe into World War I. Scientific fieldwork by the belligerent powers, especially in the war theatres of the Indian and Pacific oceans, ceased until 1920.

The Pan-Pacific Union and Scientific Congresses, 1920–1926

After the Great World War ended in 1918, major developments in reef research slowly began to resume, in part as a result of worldwide concern over the unprecedented carnage from the war and the consequent resolve for international peace and harmony to be secured. Considerable idealistic initiative was displayed by US President Woodrow Wilson with his vision of a League of Nations, which was enacted at the Paris Peace Conference in 1919 as an association of nations that would seek to provide guarantees of political independence and territorial integrity for all nations, regardless of size. Throughout the 1920s, the Pacific region became an arena where the search for peace and international cooperation was kept alive, and significant progress in reef science was achieved under the sponsorship of the Pan-Pacific Union.

The prime mover was Alexander Ford (1868–1945), a prominent newspaper publisher in Honolulu, who, in the same idealistic spirit that motivated President Wilson, dreamed of a fellowship of Pacific nations, united in a common bond of "friendly and commercial contact and relationship". To that end, he worked tirelessly to create a formal organization to further his vision, and to promote Hawaii as a centre of Pacific cultural and research activity. Ford's efforts were rewarded when, in 1919, the government of the Territory of Hawaii, as it then was, incorporated the Pan-Pacific Union as a trusteeship of 21 nation members appointed by Pacific governments with a comprehensive charter "to unite the races and countries in and about the Pacific in closer bonds of fellowship". The central activity envisaged was to promote knowledge of regional resources and opportunities by means of periodic conferences.

In the same years as the USA became active in reef research, a separate movement was initiated by William Morris Davis from Harvard, one of the more accomplished of the visitors invited to the 84th British Association meeting in Adelaide and Melbourne in 1914. A world authority on coral reefs at that time, Davis had taken the opportunity during his voyage to Australia to survey numerous Pacific reefs between February and July of that year, and visited the Great Barrier Reef on a short post-conference trip in September. On his return to the USA, he proposed that more extensive coral reef work be organized by all interested Pacific nations on a cooperative basis. That proposal was pursued in 1919 when the American Association for the Advancement of Science, which had been founded in 1848, set up a Committee for the Exploration of the North Pacific and began negotiations with the Pan-Pacific Union about a possible conference.

As a result of Ford's energetic lobbying, the Hawaiian legislature appropriated funds in April 1919 for the Pan-Pacific Union to organize a Pan-Pacific Scientific Congress in 1920. In July 1919, the dream of Ford and the proposal of Davis came together when planning was undertaken by the Committee on Pacific Exploration of the American National Research Council. The first of the projected congress series would be held in Honolulu under the auspices of the Pan-Pacific Union, the main purpose being "to outline the scientific problems of the Pacific Ocean region and suggest methods for their solution".

Participants from all learned societies rimming the Pacific met in Hawaii from 2 to 20 August 1920 "to take stock of our present knowledge" in an agenda covering race relations, anthropology, botany, fisheries, biological research stations and desirable investigations for the future. The Congress concluded with a number of resolutions that stressed the need for a marine biological survey and raising the problem of sustainable resource management. That particular concern

[1] Saville-Kent 1893, Plate II facing p. 6.

came from the fact that the need for "conservation of natural resources has become imperative, since, in the case of the Pacific Ocean, certain economic marine species have been exterminated and others are in peril of extinction or grave depletion. Measures for such conservation must be based on an exact knowledge of the life histories of marine organisms". Terrestrial fauna were not ignored: the resolution also noted that, in many places, as a direct result of human impact, many species were "fast disappearing or likely to become extinct in the near future".[2] An educational resolution was also passed, stressing the need to promote and train young men in science by means of fellowships and exchanges among institutions, and concluding with a decision to reconvene in Australia three years later.

Adhering to the Congress resolution, the Second Pan-Pacific Scientific Congress met in Melbourne from 13 to 22 August 1923 and in Sydney from 23 August to 3 September, with overseas attendance mainly from the USA and Japan. In opening the Congress, Prof. David Masson of the University of Melbourne expressed the hope that it would help "the public demand for science in Australia grow", both in its fundamental and applied areas for the economic benefit of the whole community and that Australian governments and sponsors would provide support comparable with that in America "where the organization and endowment of scientific work are now on a scale that arouses universal admiration".[3] After their deliberations, the Congress concluded in an atmosphere of rising enthusiasm to expand Pacific Ocean research generally, and with a resolution to continue meeting triennially.

The Third Pan-Pacific Science Congress, as it was redesignated at that meeting, met in Tokyo in October and November 1926, with representation from eight nations: Australia, France, Great Britain, Japan, the Netherlands (for the Dutch East Indies), New Zealand, the Philippines and the USA. In its final plenary session of 11 November, several major resolutions were passed that focused on coral reef research specifically, the most significant being the Seventh, which read in full:

"Whereas, Coral reefs are symbiotic entities whose origin and growth relations have received too little attention, and whereas Coral reefs differ widely and the methods of investigation are complicated and costly";

"Be it resolved, that this Congress institute a Committee consisting of biologists, oceanographers, and geologists to consider and draw up a plan for a comprehensive investigation of the coral reefs of the Pacific Ocean".[4]

Wayland Vaughan, then Director of the Scripps Institution of Oceanography, was elected chair of the planning committee with the task of implementing the resolution. He began organizing as soon as he returned to Scripps and was able to enlist some of the world's leading coral reef scientists: from the USA, chiefly William Morris Davis, Reginald Daly and Edward Hoffmeister, along with Vaughan himself; from Britain, Stanley Gardiner of Cambridge; from Australia, Henry Richards.

While implementation of the Congress resolutions was still being considered, Henry Casselli Richards (1884–1947), professor of geology at the University of Queensland, already had in progress his own research programme to make a geological survey of the Great Barrier Reef, and it required considerable support. In 1922, he had been instrumental in forming a Great Barrier Reef Committee in Brisbane, to provide financial and logistical assistance, and in 1926 was able to persuade the committee to finance the drilling of a small coral cay northeast of Cairns in order to confirm Darwin's theory of reef formation, and, he anticipated, discover sedimentary oil-bearing deposits. Unfortunately, it was unsuccessful. Following the Congress, however, given the resolution for a committee of biologists, oceanographers and geologists to be set up to devise a plan for wide-ranging investigation of Pacific coral reefs, Richards sensed the opportunity to direct attention to the Great Barrier Reef, where he was anxious to continue drilling. In addition, his colleague Ernest Goddard, professor of biology at the University of Queensland, was determined to establish Australia's first marine biological station on the Reef. His ambition was to begin training young Australians in what then, despite its total dependence on the sea for coastal and overseas communications, and the considerable economic benefits gained from fisheries, pearling and whaling, was the largely undeveloped field of marine science.

Not at all disheartened by the failure of his 1926 Michaelmas Cay drilling attempt, Richards, to further his planned geological exploration of the Great Barrier Reef, sought help after the Tokyo Congress from John Stanley Gardiner, professor of biology at the University of Cambridge, head of its Zoological Laboratory and director of Scientific Investigations for the British Ministry of Fisheries. Gardiner already had extensive knowledge of coral reefs as a 28-year-old student of Caius College, Cambridge, and a supernumerary member of the 1898 Funafuti expedition, along with subsequent intensive field studies in the Indian Ocean: the Laccadives and Maldives between 1899 and 1890, followed by a second study aboard the survey ship HMS *Sealark* in 1905, and of the western Indian Ocean between the Chagos Archipelago, the Seychelles and Mauritius in 1908, all of which led to a stream of authoritative reef studies. In addition, as a Fellow of the Royal Society, he exercised considerable influence in Britain. Gardiner raised the proposal with Vaughan, who, after further discussions, became receptive to Richards' suggestion of the Great Barrier Reef as an ideal location for

2 Pan-Pacific Scientific Congress Honolulu 1920, III, p. 31..

3 Pan-Pacific Scientific Congress Melbourne and Sydney (1923, I, pp. 18, 25). Note that name changed thereafter to "Science Congress".

4 Pan-Pacific Science Congress Tokyo (1928) s.v. *Resolutions*.

implementing the Congress resolution to investigate Pacific coral reefs.

From that stimulus was formed an English Barrier Reef Committee, with support and funding from the Royal Society of London and several philanthropic foundations. After considerable political searching in Britain to find a suitable team to undertake the project, Gardiner included in a letter to Vaughan a detailed programme devised by the combined British committees for intensive research of the Great Barrier Reef.

The Great Barrier Reef Expedition of 1928–1929

The site chosen was the Low Isles, a small vegetated coral cay near 16°S, logged by Cook in 1770 and named in the plural because it had an adjoining semi-submerged crescent-shaped lagoonal cay covered with almost impenetrable mangroves, first investigated by MacGillivray and Huxley on the voyage of the *Rattlesnake* in 1848, and conveniently close to the mainland city of Cairns some 65 km to the southwest. Gardiner thereby became the principal actor in devising what eventuated as the greatest coral reef field study ever undertaken up to then. Nothing on such an extensive scale had ever been planned before in the history of coral reef science. Although Carnegie expeditions to Mer and Samoa had achieved notable results that advanced ecological investigation of various aspects of coral reefs, the Low Isles expedition was designed to yield much more than any previous investigation: nothing less than recording every possible biological and geomorphological feature of the Great Barrier Reef.

The team leader selected by Gardiner was a 29-year-old specialist in marine invertebrates named Charles Maurice Yonge (1899–1986) of the Plymouth Marine Biological Laboratory, who until arriving on the Low Isles in 1928 had never seen a coral reef.[5] In close collaboration with Frederick Russell, also from Plymouth, Yonge (pronounced Young) selected a support team of six men and four women from marine laboratories in Edinburgh, Cambridge, Plymouth, London and Millport, who would be able to come together early in 1928 to complete the necessary planning. They were to set sail for Australia in the vanguard for a full year (July 1928 to July 1929), to be joined, or replaced, by others in the course of the expedition, with support from the relatively few Australian scientists with marine interests from the Australian (Sydney) and Brisbane Museums.

The expedition was characterized by meticulous, comprehensive planning from the start, and it requires some detail here to indicate the magnitude of the operation. Prefabricated timber buildings were erected on the site in advance, with a laboratory the centrepiece, equipped with all essential scientific equipment. A considerable amount of this was shipped from Britain, including microscopes and bench appliances, trawling and temperature recording apparatus, plus a centrifuge for plankton analysis. For recording, a professional camera was included to photograph the various field sites and coral colonies at which the specimens were collected, and those were processed in one of the huts. In addition, an extensive library of scientific books was brought and housed on shelves in the laboratory. Equally essential to the project were suitable vessels. For marine surveying, a 39-ft (12-m) ketch with a 26-hp engine was chartered, but for close-in work around the cay, a small 12-ft (3.6 m) dinghy with a 2.5-hp outboard motor was purchased. For underwater collecting, in the days before scuba, a “dustbin style” helmet was constructed, apparently based on the model used in Messina by Milne-Edwards in 1844, to be supplied with air from a motor tyre pump operated by two men. It allowed descent to some 20 ft by a brave volunteer: a north-country Englishman, chemist and hydrographer, A. P. Orr, who had never learned how to swim and descended with a signalling and rescue safety line attached.

In addition to their own resources and the assistance offered by visiting Australian scientists and workers, other agencies were more than willing to help what had developed into a great international enterprise that attracted excited and sustained press coverage throughout the year, particularly in London and Sydney. Supplementing the considerable cooperation extended by the Commonwealth Navigation Department in authorizing the use of two lighthouse service vessels, as Yonge described in his popular discursive account of *A Year on the Great Barrier Reef*, the Royal Australian Navy lent a “Lucas sounding machine, sounding lines and leads, binnacle compass, station pointer, sounding sextants, Douglas protractor, patent log, Admiralty charts, and much other material”. The Royal Australian Air Force sent an amphibious Seagull III seaplane to take aerial photographs of the Low Isles for accurate mapping of the region and transect evaluation, and “the Commonwealth Meteorological Bureau supplied standard instruments: barograph, thermograph, hygrograph, sunshine recorder, anemometer, and maximum and minimum and wet and dry bulb thermometers” (Yonge 1931, p. 10).[6]

[5] The complex details of one of the most devious plots in coral reef history to ensure the most suitable leadership and outcomes are given by Bowen (2002, pp. 255–258).

[6] That document, plus a set of the progressive field mimeographed copies by Yonge from which citations have been taken while in the author’s possession, have since been donated to the archives of the Oxley Library, Brisbane (see Footnote 7 for an explanation of how the field mimeographed copies are cited).

YEAR ON WEIRD REEF.

GREAT BARRIER AND ITS SECRETS.

LONDON BANDS BY RADIO FOR DANCES.

A HANDFUL of young people, men and women, living for over a year in wooden huts on a lonely island in the Coral Sea, *and, as one method of keeping fit, dancing to the music of London's bands.*

Never before has there been a scientific expedition of which it has been possible to paint quite so unorthodox a picture. But the expedition to the Great Barrier Reef of Australia, which sailed from Tilbury on Saturday, is in many respects unique.

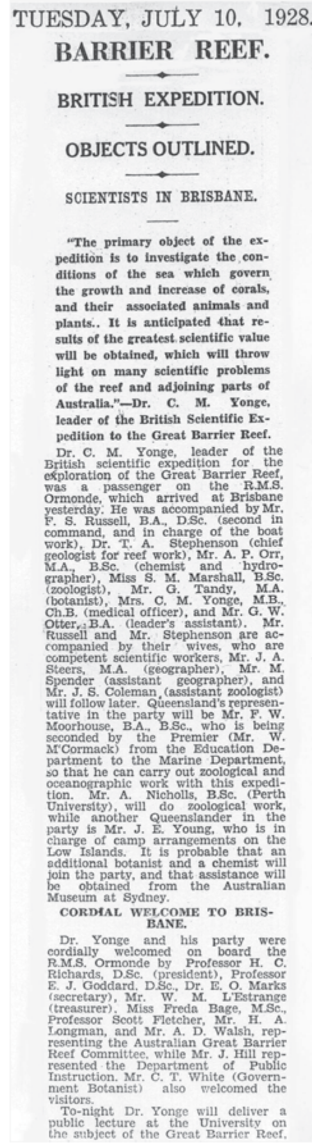
Even in such weird and desolate surroundings as those of the 1,200-mile-long reef, whose secrets the expedition is to probe, explorers need no longer be cut off from a homeland 12,000 miles and more away. The B.B.C. short-wave station at Chelmsford, 5 S W, which is conducting continuous experiments in Empire broadcasting, will tell them the time by Big Ben, give them the news, and teach them the latest fox-trots, too.

In 1925, when the Hamilton-Rice Expedition, amid the forests of the Upper Amazon, kept the outside world informed of its progress by short-wave wireless, the importance of this latest development of radio was first realised by explorers. It should now play a big part in banishing tedium from the remarkable expedition which Dr. Yonge is taking out "to show what youth can do when given a chance."

The *Westminster Gazette* of 28 May 1928 announcing the Low Isles research project

Reef Construction: The Zooxanthellae Problem

In planning the expedition, Yonge and Russell knew that all possible parameters contributing to the biological complexity and geological features of the Reef, as then understood, had to be investigated. The main focus of interest, however, was the overall biology of reef-building corals, and specifically the physiological processes that supported the formation of those immense limestone structures over geological eons. Throughout the year, consequently, the team members had their particular areas of responsibility that covered feeding, digestive enzymes, calcium carbonate metabolism, responses to variations in light, temperature, water chemistry (salinity, dissolved oxygen, carbonic acid), plankton density and variety, current flow and tidal fluctuations. In addition, it was necessary to gain accurate knowledge of the circulation and chemistry of seawater and the availability of calcium carbonate to build the corallum.



TUESDAY, JULY 10, 1928.

BARRIER REEF.

BRITISH EXPEDITION.

OBJECTS OUTLINED.

SCIENTISTS IN BRISBANE.

"The primary object of the expedition is to investigate the conditions of the sea which govern the growth and increase of corals, and their associated animals and plants.. It is anticipated that results of the greatest scientific value will be obtained, which will throw light on many scientific problems of the reef and adjoining parts of Australia."—Dr. C. M. Yonge, leader of the British Scientific Expedition to the Great Barrier Reef.

Dr. C. M. Yonge, leader of the British scientific expedition for the exploration of the Great Barrier Reef, was a passenger on the R.M.S. Ormonde, which arrived at Brisbane yesterday. He was accompanied by Mr. F. S. Russell, B.A., D.Sc. (second in command, and in charge of the boat work), Dr. T. A. Stephenson (chief geologist for reef work), Mr. A. P. Orr, M.A., B.Sc. (chemist and hydrographer), Miss S. M. Marshall, B.Sc. (zoologist), Mr. G. Tandy, M.A. (botanist), Mrs. C. M. Yonge, M.B., Ch.B. (medical officer), and Mr. G. W. Otter, B.A. (leader's assistant). Mr. Russell and Mr. Stephenson are accompanied by their wives, who are competent scientific workers, Mr. J. A. Steers, M.A. (geographer), Mr. M. Spender (assistant geographer), and Mr. J. S. Coleman (assistant zoologist) will follow later. Queensland's representative in the party will be Mr. F. W. Moorhouse, B.A., B.Sc., who is being seconded by the Premier (Mr. W. M'Cormack) from the Education Department to the Marine Department, so that he can carry out zoological and oceanographic work with this expedition. Mr. A. Nicholls, B.Sc. (Perth University), will do zoological work, while another Queenslander in the party is Mr. J. E. Young, who is in charge of camp arrangements on the Low Islands. It is probable that an additional botanist and a chemist will join the party, and that assistance will be obtained from the Australian Museum at Sydney.

CORDIAL WELCOME TO BRISBANE.

Dr. Yonge and his party were cordially welcomed on board the R.M.S. Ormonde by Professor H. C. Richards, D.Sc. (president), Professor E. J. Goddard, D.Sc., Dr. E. O. Marks (secretary), Mr. W. M. L'Estrange (treasurer), Miss Freda Bage, M.Sc., Professor Scott Fletcher, Mr. H. A. Longman, and Mr. A. D. Walsh, representing the Australian Great Barrier Reef Committee, while Mr. J. Hill represented the Department of Public Instruction. Mr. C. T. White (Government Botanist) also welcomed the visitors.

To-night Dr. Yonge will deliver a public lecture at the University on the subject of the Great Barrier Reef.

The Brisbane *Courier* report the day after the arrival of Low Isles Expedition scientists

Exerting a continuing, hovering presence over the entire biological project, however, was the still intractable problem of explaining the supposed function of zooxanthellae ever since the chlorophyll issue had been raised. Throughout the previous 50 years, the growing body of research evidence had been starting to suggest that zooxanthellae were far more than harmless commensals, and conflicting opinions were being circulated in scientific journals that were creating considerable tension, mainly about the influence of light on polyp respiration and the metabolic processes of oxygen and carbohydrate production.

First triggered by Brandt's suggestion that zooxanthellate algae were an infestation, their presence in a large range of marine creatures, including anemones and clams, presented an intriguing challenge for researchers, made even

THE BRISBANE COURIER.

BRITISH SCIENTISTS WHO HAVE COME TO QUEENSLAND TO INVESTIGATE THE BIOLOGICAL PROBLEMS AND ECONOMIC POSSIBILITIES OF THE GREAT BARRIER REEF.

Back row (left to right):—Mr. G. Tandy, M.A. (botanist), Dr. T. A. Stephenson (Chief Geologist for reef work), Miss S. M. Marshall, B.Sc. (zoologist), Mr. A. P. Orr, M.A., B.Sc. (chemist and hydrographer).

Front row:—Mr. F. S. Russell, B.A., D.Sc. (second in command), Mrs. T. A. Stephenson, Professor Richards (president of the Great Barrier Reef Committee), Mr. C. M. Yonge, D.Sc., D.Ph. (leader of the expedition), Mrs. C. M. Yonge, M.B., Ch.B. (medical officer), Mr. G. W. Otter, B.A. (leader's assistant), Mrs. F. S. Russell.

The Low Isles party on their arrival in Brisbane at 09:00 on 9 July 1928

The Low Isles project's prefabricated library

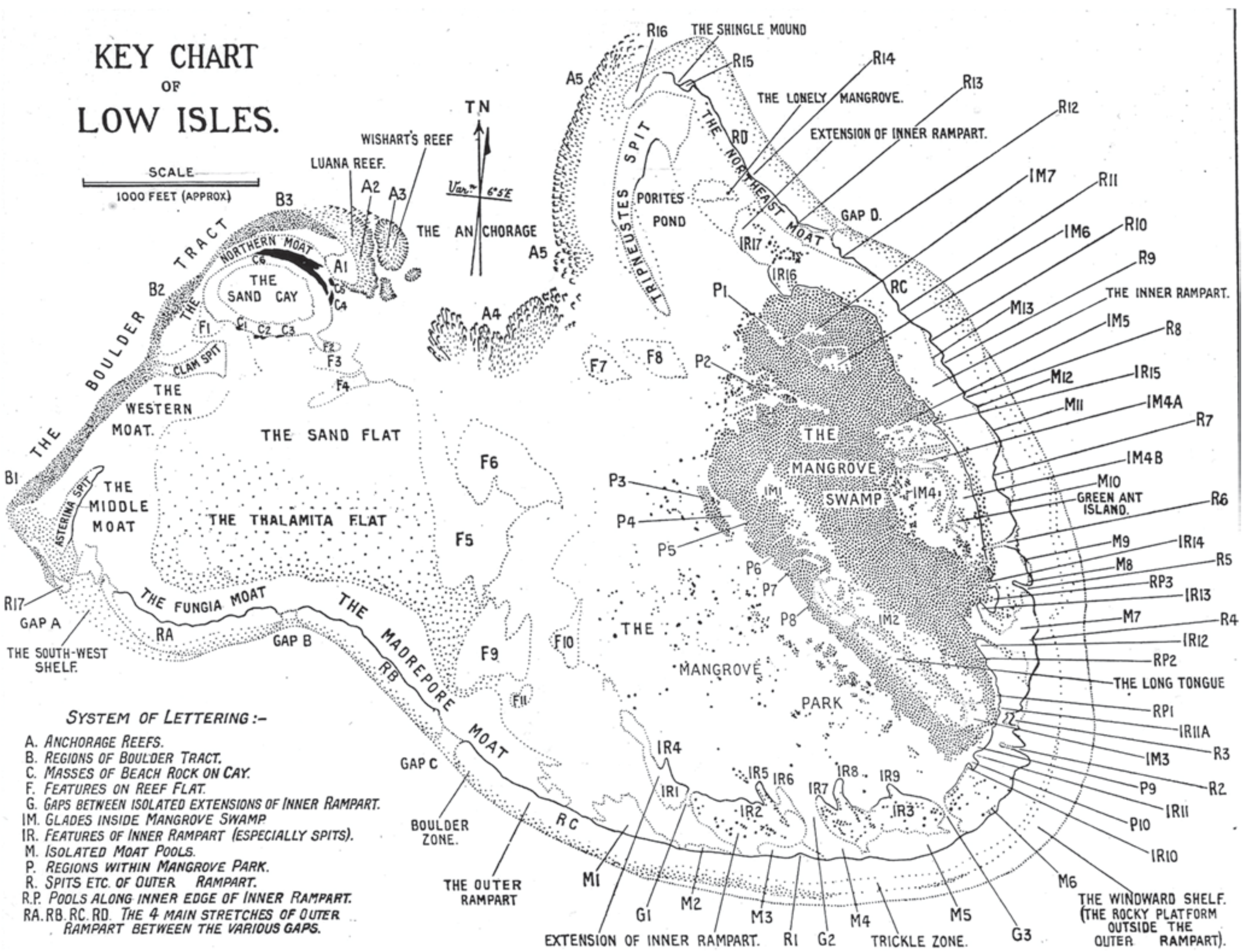
more complex when Geddes and Keeble confirmed that two invertebrates, *Euglena viridis* and *Convoluta roscoffensis*, actually depended on the algal chloroplasts in their tissues to synthesize carbohydrate that was translocated to the host. Keeble, however, rejected the term symbiosis and stated explicitly that the relationship between *C. roscoffensis* and algae was one of obligate parasitism that inevitably led to saprophytic behaviour by the host. New questions emerged:

The Low Isles project's prefabricated laboratory

for instance, was that also the case with corals? Already it had been suggested that because reefs lay in vast open expanses of oligotrophic water where plankton are scarce that autotrophy might be essential. How else could polyps produce excess oxygen from their respiration? If the zooxanthellae generated sufficient quantities of carbohydrate for the algae to utilize for energy, they could be at least partly autotrophic, which might be an element contributing to reef construction.

Extensive literature had been produced on the issue, and one of the most prolific witers was the Friesian scientist Hilbrand Boschma, who made extensive investigations throughout the Netherlands East Indies. His 1925 article "On the feeding reactions and digestion in the coral polyp *Astrangia danae*, with notes on its symbiosis with zooxanthellae" exerted a major influence on thinking, both for and against. In the same year, he published what is essentially a three-page synopsis from experiments in the Woods Hole biological station in Bermuda which presented the central argument that "the food of reef-corals consists in large part of the zooxanthellae which live in great abundance in the entoderm", citing Gardiner's experiences in Funafuti and Rotuma Island, Fiji, in support. The evidence, he stated, "lies in the fact that the food-remnants found in the gastric cavity of the living coral-polyps always contain a large number of zooxanthellae in various stages of disintegration, as a result of digestive action on them" (Boschma 1925, p. 65).

That was the main issue that Yonge attempted to resolve. Before his departure, in a single-page planning document, he outlined his objectives: specifically "to examine a sector of the Great Barrier Reef off Cairns, from the shore to the open ocean…studying the associations of plants and animals" along with an investigation into the physiology of growth and reproduction of corals, in an effort to understand the "relative importance of plankton and commensal algae". From the outset, Yonge assumed, like Dana nearly a century before who described their food as coming from "such chance-bits as are thrown their way" (Dana 1846, p. 12), that all corals are carnivorous predators by virtue of their cnidarian tentacles, i.e. they are totally heterotrophic (Gk *heteros*, "other" + *trophos*, "food supply"). However, because they fed on zooplankton from the surrounding water, in what possible way could zooxanthellae contribute to coral nutrition? That question raised the issue of the role of light in stimulating algal photosynthesis and how any product could be utilized by the coral itself. The first extended discussion of light on coral growth had appeared almost two decades earlier in a study by Frederic Wood-Jones based on his research in the Seychelles, the Solomon Islands and along the Malabar coast of India, supported by evidence from other investigators, in all cases gained from laboratory observation of corals maintained in tanks, dredged from as far down as 45 fathoms (82 m), and in the case of one particular solitary species, *Caryophyllia clavus*, from 380 fathoms (695 m). Additional



Map of the Low Isles based on RAAF aerial surveys by an amphibious *Seagull* aircraft. The site of the research station was on the small area of ~1 acre labelled "The sand cay" in the *upper left* northwest corner, *below* "The northern moat" and the adjoining "Anchorage"

direct observation and collecting was supplemented by Yonge's lantern-lit walks across reef flats at night.

While serving as medical officer in charge of the Australian cable station on Keeling Island, Wood-Jones published *Coral and Atolls* in 1910; it was a comprehensive account in the same style as Dana's *Coral Reefs and Islands* from half a century earlier. Drawing on a wide range of historical reports and his own research, Wood-Jones' review of reef development in Darwin's *Structure and Distribution of Coral Reefs* continued to stimulate controversy when he rejected the subsidence theory. Although accepting that "coral reefs are definitely established on a sunken basis", he argued that it was "not the same thing as saying that the sinking caused their present disposition" (Wood-Jones 1910, p. 236). He believed, like John Murray before him, that reefs originated on submerged platforms, and in attempting to explain their development, denied strenuously that the resident algae made any contribution to either the growth or nutrition of the carnivorous corals, or that they influenced the depth to which various species grew on reef fronts.

Wood-Jones asserted dogmatically from the fact that reef-building corals expand their tentacles only at night that "light is not essential for their feeding". Even more emphatically, he emphasized that "corals are not entirely dependent on their commensal algae for their food-supply, for anyone can see the reaching out of tentacles, and the engulfing of particles, when a crushed-up shell-fish is dropped upon a colony at night". After that declaration, he concluded that "on the strength of this evidence, I therefore discard light as being the determining cause of the bathymetrical limit of distribution of the reef-builders" (Wood-Jones 1910, pp. 241–242). As additional evidence, he reported his experiments in depriving corals of light for extended periods; the algae died but the corals remained unaffected, though bleached from the loss of algae. That result, he added, had also been confirmed by Vaughan in similar experiments in the Tortugas.

Within the same conceptual framework, and influenced by the conclusions of Wood-Jones, the research programme was directed by Yonge's concern expressed in his planning document mentioned above to investigate "the relative importance of plankton and commensal algae", based on the assumption that polyps captured food from the only available source, the vagrant zooplankton, within specific levels of sea temperature and light. From the outset, however, Yonge and his assistant, graduate student Aubrey Nicholls from Perth, approached the still unsubstantiated nutritive function of zooxanthellae with great scepticism. In the opening sentence of the general introduction to his *Studies on the Physiology of Corals*, Yonge made a statement about the investigative programme that had been pursued throughout the year: "Few subjects of such obvious zoological importance are so obscure as the nutrition of corals and the significance of their zooxanthellae". At the present moment, he continued, "considerable controversy exists regarding the food of Madreporaria which possess zooxanthellae, that is the reef builders", between those scientists who believe that algae form at least part of the food, and those who insist that "corals are specialized carnivores", leading to "such discordant conclusions" with excessive "emphasis laid on the supposed inability of some, if not all, genera of corals to capture living prey", that "the fullest possible survey of the manner of feeding of corals and the type of food which they are capable of securing was clearly of primary importance" (Yonge 1930a, p. 14).

Throughout his field notes and the *Scientific Reports* from the expedition, Yonge continued to exhibit a manifestly critical attitude to the zooxanthellae nutrition argument and resolutely supported the "specialized carnivore" theory. This can be illustrated in a few representative cases describing experiments conducted on corals taken from his 2-monthly mimeographed reports for the team and the Great Barrier Reef Committee. One experiment to test the carnivore hypothesis consisted of feeding *Favia* and *Galaxea* corals with zooplankton up to 3 mm long. With the discovery that the plankton were "completely digested and the empty skeletons ejected within a period of twelve hours or less, he believed that fact confirmed their carnivore nature".[7]

To determine more accurately the role of zooxanthellae, several experiments were conducted to measure the oxygen production that allowed the creation of carbohydrate, necessary for polyp respiration and calcification. Yonge's method was to contain them in sealed glass jars and to measure oxygen levels at the end of specified periods. His conclusion, which he found no reason to alter even 10 years later, was that "the significance of the oxygen produced by the algae must remain undetermined" (Yonge 1940, p. 367).

Experiments on the effects of both starvation and darkness on corals of the *Favia*, *Fungia*, *Galaxea* and *Psammacora* genera were even designed to prove that zooxanthellae are not essential to reef health. To counter claims by other investigators, chiefly the 1925 Caribbean evidence of Boschma that in response to starvation, polyps digest their zooxanthellae, Yonge's own experiments led him to conclude that if "fed they remain in good condition whether in light or darkness, paling in colour slightly in the dark, but when starved their tissues quickly begin to shrink, undamaged algae are expelled in large numbers and the remaining tissue turns pale as a result". The only interpretation that can be placed on these results, he concluded, is that "the algae are not and cannot be used as food by the corals, a conclusion which agrees entirely with the results of the feeding and enzyme experiments".[8]

To pursue that line of investigation more intensively, Yonge subsequently had "a large light-tight box…cemented on the reef flat and placed a number of corals in it" which confirmed earlier findings that after several months they showed "a high degree of paling but [were] still healthy, the death of the algae apparently not affecting the corals".[9] In his final report of 25 September 1929, he stated categorically that "corals kept for 5 months in the dark box on the reef flat survived to a large extent, those dead having been mainly killed by sediment".[10]

Running through Yonge's mind as he conducted his experiments was the evidence of Keeble's studies of *C. roscoffensis*, which confirmed its dependence on commensal algae for the translocation of carbohydrate nutrients, and it continued to cast a long shadow. Experiencing a phase of insecurity back in Plymouth in summer 1930, before he began to draw his experimental results together in his lengthy six-part *Studies on the Physiology of Corals*, Yonge travelled to Roscoff to repeat Keeble's procedures. Although able to confirm their accuracy, he argued in his report that the nature of the relationship between the animals and their resident plants was totally different because, unlike the algal symbiont *Clamydomonas* in *Convoluta*, the zooxanthellae in the Madreporaria were "surrounded by a thick cellulose wall which effectively prevents any such transference" (Yonge 1930b, p. 207). In summarizing his experiments on starvation and light deprivation on "all species of forty genera of Madreporaria examined", Yonge stated emphatically that every one was "adapted in various ways for the capture of zooplankton". Despite Gardiner's belief that zooxanthellae assisted coral growth through the processes of photosynthesis, which Gardiner later presented in a short article to *Nature* (Gardiner

[7] LIE, Low Isles Expedition. Copies of the six mimeographed progressive field Reports to the Great Barrier Reef Committee by Yonge are referred to as follows: Yonge LIE, followed by the sequence in Roman numerals from I to VI, followed by month and year, and finally page number. This reference: Yonge LIE 2/29, p. 8. In May 2010, these documents were transferred to the archives of the Oxley Library in Brisbane.

[8] Yonge LIE III 2/29, p. 9.

[9] Yonge LIE IV 5/29, p. 6.

[10] Yonge LIE IV 9/29, p. 7.

1931, pp. 857–858) and was confirmed by Siro Kawaguti in Palau (known as Palao during the Japanese occupation period) in 1937 (Kawaguti 1940, p. 15), Yonge insisted that his evidence confirmed that each species fed entirely on "living animal prey, capturing it by means of the nematocysts on the tentacles" which led to his final conclusion that "Corals are carnivores with highly developed feeding mechanisms" (Yonge 1930a, pp. 51–55).

Results and Significance of the Expedition

Results from the year were progressively published by the Natural History division of the British Museum between 1930 and 1950 as individual pieces, and later collected into six volumes entitled *Great Barrier Reef Expedition 1928–1929: Scientific Reports*.[11] Altogether, 62 reports were produced, along with a belated seventh volume on *Crustacea, Decapoda and Stomatopoda* by Frank McNeill of the Australian Museum, which appeared in 1968. In all, 32 were published in the first few years from 1930 on by the original participants, of which 25 were by individuals and 7 were co-authored. The other 30 reports, all with a strong systematic character, were written by other specialists to whom the collected material and field notes had been sent; they appeared between 1935 and 1950. In his considerable contribution to Volume 1 of the official *Reports*, Yonge wrote six papers individually on experimental physiology and four with Aubrey Nicholls, three being highly influential studies on the unresolved controversy about the significance of zooxanthellae in coral polyps. In addition, a continuing sequence of occasional articles was sent to various scientific journals by individual members along with more popular accounts to semi-scholarly magazines, and further reflections on the expedition continued to be published into the 1970s and 1980s.

Another important outcome of the expedition was a description of the extensive range of other research activities conducted by Alan Stephenson, who was responsible for the "shore party" whose operations were to investigate the intertidal zone and reef slopes around the cay, and the other reefs they visited for comparative data. In his report on *The Structure and Ecology of Low Isles and other Reefs*, Stephenson stated that the main purpose of the expedition was to move coral reef science away from its preoccupation with geology and turn "the centre of interest back towards the biological side". In a surprisingly advanced view for the times, perhaps an early expression of the growing importance of population biology, he described the specific aim of the shore party as moving "towards the elucidation and problems which have a direct bearing on ecology (i.e. towards a study of conditions and food-supply in the sea, and the feeding and metabolism of corals, of the growth and breeding of marine organisms and so forth)…[in order that] we should acquire a knowledge of what organisms form the bulk of these populations, and in what manner they arrange themselves with respect to one another and to their environment". Stressing accurate measurement and instrumentation, he indicated that they were seeking "a true conception of the inter relation of the parts of a reef, both in the horizontal and vertical senses; and to describe accurately the distribution of organisms on it, especially as regards their zonation according to level and their relation to states of the tide" (Stephenson et al. 1931, pp. 19–20).

Once the immense volume of data had been collected, the central issue of the entire expedition in seeking a clear understanding of the formation of coral reefs and the physiological properties of the Madreporian corals that allow them to create such immense assemblages took innumerable scientists decades to digest and evaluate, and to become assimilated into the literature. In his own final scientific report entitled *The Biology of Reef-Building Corals* (Yonge 1940), Yonge surveyed the entire output of 60 reef scientists over the previous half century and distilled his conclusions into an 18-point, two-page summary: "Coral reefs are marine communities occurring in shallow waters within the tropics, the dominant organisms being Madreporaria containing zooxanthellae (i.e. reef-building corals)", their "horizontal distribution" being controlled by the temperature of warm waters, and their "vertical distribution…primarily by light, acting possibly both directly on the corals and by way of its effect on the zooxanthellae". He also made it clear that "Reef-builders certainly exhibit phototropism, and there is evidence that they are also influenced by light in both speed and solidity of growth", although he advanced no suggestions for the specific functions of particular processes involved.

Given his acceptance of the necessary effects of light on the symbiotic algae to generate oxygen for the essential respiration of the polyps, Yonge completely dismissed zooxanthellae from the reef-building scene with the rather astonishing statement that the "association between corals and zooxanthellae is essential to the zooxanthellae which never occur free in the sea". That comment, which implied obligate parasitism, was immediately followed by the assertion that the association "is not essential to the life of individual coral colonies". Following a decade of reflection on the achievements of the expedition, during which he was the dominant personality, Yonge declared with absolute conviction that "Corals are specialized carnivores feeding on zooplankton, for the capture and digestion of which they are highly specialized". In a curt dismissal of the autotrophic, self-sufficient nature of coral polyps, he summarized one important theme from his personal year's research in but ten words:

[11] Great Barrier Reef Expedition 1928–29 (1930–1940).

"the zooxanthellae play no part in the nutrition of corals" (Yonge 1940, pp. 384–385).

Despite Yonge's insistence on the heterotrophic nutrition of corals, which came to generate decades of controversy and prove him seriously mistaken, the significance of the expedition cannot be overstated: it was the greatest marine science venture on a global magnitude since the *Challenger* oceanographic voyage more than 50 years earlier. It is to Yonge's credit that he organized his colleagues so efficiently that they were able to assemble the massive volume of research data in the *Reports* that commanded close attention and respect within the scientific community. For subsequent investigators, those findings were to become a major source for reef studies to the present day and were to have their greatest impact in creating an entirely new avenue of research into the biological activity of zooxanthellae in reef formation.

Vaughan and Wells: A Major Taxonomic Revision

While the Low Isles Expedition was in progress and its results were appearing throughout the 1930s and thereafter, significant developments were being made in taxonomic revision by two American palaeontologists, Thomas Wayland Vaughan and John West Wells. Following the early phase of commercial exploitation of petroleum oil in the USA in the 1850s, palaeontology and chronostratigraphy had become important related sciences in the quest to determine with greater accuracy the evolution of the earth's crust and the location of oil-bearing sedimentary strata. Essential to both of those disciplines was the study of relict reefs and fossilized corals.

Wayland Vaughan (1870–1952), as he preferred to be known, was one of the leading palaeontologists of his era. Following completion of his doctoral degree at Harvard in 1903, he continued his position with the US Geological Survey, working on fossil corals of the American coastal plain bordering the Caribbean, then expanding to other areas until 1924 when he was appointed Director of the Scripps Institution of Oceanography in La Jolla, close to San Diego. By that time he had also achieved an impressive reputation in the taxonomy of reef-forming corals, chiefly from Florida, the West Indies and the Gulf of Mexico, and was recognized as a world authority, even being asked to identify part of the collection of the Emperor of Japan (Cole 1952, p. 46).[12] On retirement in 1936, he moved to Washington, DC, where he continued investigations into the foraminifera until forced to reduce his workload after an attack of pneumonia led to impairment of his eyesight. Fortunately for reef science, however, during that phase of his career, he made the acquaintance of a neophyte prodigy with whom he was to collaborate in revising the taxonomy of the Madreporaria to new levels of accuracy.

John West Wells (1907–1994), although born in Philadelphia, spent his early years in the village of Homer, New York State, 20 miles from Cornell University in Ithaca. After graduating with his basic science degree from the University of Pittsburg, he received his first academic position in 1928 at the University of Texas as an instructor in geology, where he began intensive research into reef-forming corals, many of the Cretaceous Period (144–165 Mya). Demonstrating considerable promise, in 1931 he was awarded a geological sciences Storrow Fellowship which resulted in a monumental article of 292 pp. entitled *Corals of the Cretaceous of the Atlantic and Gulf Coastal Plains and Western Interior of the United States*, published in 1933 in the *Bulletins of American Paleontology*. His references and descriptions to "146 species and varieties representing 68 genera, 22 families, and the 3 suborders of the order Madreporaria" covered not only North American fossils but also drew comparisons with species from Cretaceous limestone deposits in the Caribbean, France, Italy, Spain, East Africa, Japan and Venezuela (Wells 1933, pp. 86, 88).

Introduced quietly into the *Bulletin* in his discussion of the facies (geological deposits) of the Early Cretaceous Period—known by palaeontologists as the Albian Stage (c. 100 Mya)—he made a clear distinction between shallow water facies on today's North American mainland and the deepwater specimens found in Mexican and West Indies deposits. As only the neritic (shallow water) species are reef builders, he rejected the current term "deepwater type" for the latter Caribbean facies. Comparing specimens from two separate formations, he described one as a colonial form "of the hermatypic type", so devising a new descriptor for reef-forming corals, which he elaborated on in an extended footnote to that discussion. Because "true reef corals are exclusively neritic", he suggested adoption of the term "hermatypic", from [the Greek] *herma*, "a sunken reef" and *tupos*, "type", to describe corals of the reef-building type, the living species of which possess symbiotic zooxanthellae within their tissues. In contrast to that term, ahermatypic was proposed to describe the corals of the non-reef-building type, the living forms of which do not possess zooxanthellae, and which live under greatly varying conditions of depth, temperature and light. The use of these terms eliminates the inaccurate expression "deep-sea corals". Ahermatypic corals include both the deep (bathyal) and shallow (neritic) water forms that do not build reefs (Wells 1933, p. 109, note 41).

Finally, after several centuries of searching, a substantively specific word came into reef studies to replace such vague descriptions as "madreporic", "coralligenous", "stony", "saxigenous" and "reef building". Hermatypic came to be

12 The Emperor recognized his scholarship with the award of an Order of the Rising Sun.

accepted description, although not without yet further qualification to distinguish the deep-water scleractinian species without zooxanthellae from the hermatypic zooxanthellate corals within the photic zone of the surface layer (see, Schumacher and Zibrowius 1985).

Soon after that exceptional publication, especially for a novice, Wells gained his doctorate in geology from Cornell in 1933 and was awarded an American National Research Council fellowship that allowed him to continue his studies in the geological divisions of the British Museum, the Paris Musée National and the Berlin Humboldt Museum. On his return from Europe and temporarily without an academic position, he visited Washington in 1936 and met Vaughan, and the meeting led to a most unusual relationship: Wells was the only palaeontologist with whom Vaughan ever collaborated on hermatypic corals. In 1938, Wells moved to Ohio State University and stayed there until 1948, when he made his final move to Cornell, and it was during that decade that he and Vaughan produced the next major advance in the understanding of reef-building corals with their impressive *Revision of the Suborders, Families and Genera of the Scleractinia*, published in 1943.

The stimulus to the "*Revision*", despite many advances throughout the previous century, was the conviction of both that classification of "the stony corals" remained "in a very unsatisfactory condition" (Vaughan and Wells 1943, p. v). That problem was one of long standing, and in an effort to clarify the still-confusing range of species described as Madreporaria, the British Museum, which held the world's greatest collection of coral species, published as early as 1893 a comprehensive *Catalogue of the Madreporian Corals* in seven volumes. In his introductory preface, general editor and taxonomist George Brook began with a detailed historical account of the entire range of perplexing usages of Madrepore in an attempt to finally determine the true reef-building corals and to explain the pressing urgency to eliminate unnecessary duplication and misleading description.

That monumental catalogue was followed in 1900 by an equally immense encyclopaedic eight-volume *Treatise on Zoology*, edited by Sir Edwin Ray Lankester (Lankester 1900, 1909), by then director of the British Museum, in which Gilbert Bourne, Lecturer in Comparative Anatomy and Fellow of New College, Oxford, presented yet another revised taxonomy of corals. In his chapter on the Anthozoa, Bourne proposed two suborders: Malactiniae for soft-bodied corals (Gk *malakos*, "soft" + *aktis*, "ray of the sun", for the star-shaped pattern of the tentacles), and Scleractiniae (Gk *skleros*, "hard") for the stony corals, as a more accurately descriptive term to replace Madreporaria. The major descriptive change suggested by Vaughan and Wells, consequently, because the term Madreporaria then included both the extinct tetracorals and contemporary hexacorals, was to abandon it "as a systematic term and to substitute for the stony corals the term Scleractinia of Bourne" (Vaughan and Wells 1943, p. 9).

Following that introductory terminological change, and drawing from the earlier taxonomy of Milne-Edwards and Haime, the revision of Vaughan and Wells identified five suborders of hermatypic coral, starting with a careful general account of polyp anatomy and morphology, all described and illustrated with line drawings in meticulous detail. Their taxonomic endeavour attempted to classify every available type and topotype (specimen from the locality of the original type) of coral, extinct and extant, amounting to some 500 genera, primarily on the structure of the vertical septa (sing. *septum*) and what they believed was the "most useful unit of the scleractinian skeleton", namely the distinctly different arrangements of the trabeculae (Lat. *trabecula*, "mini-beam"), which are the transverse calcified supporting structures reaching between the outer corallum and the vertical partitions of muscular mesentery. In addition, in 293 pp. of text, they covered, where possible, reproductive behaviour, growth form, morphogenesis of the corallum, ontogeny and relevant ecological factors, which they supplemented with 51 black-and-white plates depicting 401 species, along with a bibliography of 1024 titles, from Peysonnell to the *Scientific Reports* of the Low Isles Expedition, which gives an indication of the intense scientific study of coral over two centuries.

In describing the anatomy and morphology of the scleractinia, passing attention was given to the still-puzzling zooxanthellae and, clearly influenced by the arguments of Yonge, with the particular observation that, whereas they are found only in hermatypic corals, "there is no evidence that they can live apart from the corals" and that they reach their maximum density "at depths between 4 and 7 meters, decreasing upward and downward from this narrow range". When deprived of their zooxanthellae, Vaughan and Wells noted, with a degree of uncertainty, that corals "live perfectly well, although the fact that reef corals kept in darkness soon lose their zooxanthellae and eventually die seems to indicate they are not altogether independent of these algae". With that brief discussion, the two concluded with the more explanatory comment that if corals are exposed to abnormally high temperatures, they soon lose their zooxanthellae and eventually die because the necessary supplies of CO_2, nitrogen and phosphorus for the algae can no longer be obtained as a consequence of the lowered metabolism of the polyps. Like previous researchers, they implicitly accepted the concept of obligate parasitism in which the zooxanthellae function as little more than efficient excretory organs (Vaughan and Wells 1943, pp. 30–31).

The discussion of ecological factors, in a brief 16 pages, dealt only with major statistical parameters for the scleractinia, with transitory reference to non-hermatypic corals, covering depth and temperature of the water, which for hermatypes they found to be limited to a maximum of 46 m for active growth and a temperature range of 18.5–29 °C (65.3–84.2 °F). However, higher temperatures, they noted, could be endured for longer periods than cold. Having previously considered the role of zooxanthellae, Vaughan and Wells commented that "strong light is essential for vigorous growth of hermatypic corals" which constitutes "the principal relationship with the zooxanthellae" because light "is necessary for photosynthesis, the chief life process of these algae, from which the coral benefits by the released oxygen and the consumption of the waste products of the algae". No link, however, was made with actual nutrition of the polyp by the algae because, relying mainly on the LIE reports of Yonge, "coral polyps, so far as has been definitely proved, are wholly carnivorous… [and their food] consists of small floating and swimming animals which they capture by their tentacles and the action of nematocysts" (Vaughan and Wells 1943, p. 59).

Corallum Construction: The Calcification Puzzle

As the "*Revision*" was primarily a palaeontological and morphological endeavour, the study provided extensive detail on the formation and composition of the skeleton, and the century-long puzzle, still unresolved, of exactly how the coral polyp built its structure from the dissolved calcium in the surrounding water. By the mid-19th century, the science of mineralogy and the basic structure of constituent crystals was developing rapidly, considerably facilitated from the invention in 1828 by William Nicol of his "Nicol prism" which, used with a polariscope and a beam of light, allowed the determination of the axes of crystals and hence their structural properties. Two crystal systems in particular were relevant to understanding the precipitation of calcium into its two forms of calcium carbonate ($CaCO_3$): the relatively unstable aragonite (the type location is the village of Molina de Aragón in Spain, where it was first discovered in limestone cave speleothems in 1797), which is characteristic of scleractinian corals, and the more durable calcite polymorph found in coral skeletal fossils resulting from diagenesis (deterioration) of aragonite through steady continuous processes. Those processes begin a few years after secretion of the skeleton and continue over millennia from changes in pressure and temperature (Perrin 2004, p. 95).[13]

Early speculation on the processes of calcification had been made by Milne-Edwards and Haime, who considered the madreporian skeleton to be a calcified mesoderm. In 1881, the Austrian biologist A. von Heider described a layer of rounded cells underlying the corallum of a genus of *Cladocora* and described them as "calicoblasts" with the suggestion they could be the calcifying element, a suggestion confirmed the following year by G. von Koch, who had published numerous articles on calcification and reported that the calicoblast layers came from secretions in the basal ectoderm. Those reports attracted the attention of Gilbert Bourne, whose microscopic studies indicated that von Heider's interpretation was wrong and that calcification took place as a secretion from the mesogloea (gelatinous layer)[14] between the two walls of the mesenteries, beginning with the calicoblasts at the base. Bourne was criticized in turn by the talented Scottish biologist Maria Ogilvie (1864–1939), who reported her own microscopic findings in 1895 and used them as the basis for yet another taxonomy of the Madreporaria in which she asserted that "the skeleton of the Madreporaria takes its origin from an actual calcification of the calicoblasts" from calcareous deposits laid down within the ectoderm that crystallize into spicules, the common calcified form in Alcyonarians, as aragonite, then fuse into "a connected calcareous lamina" (Ogilvie 1895–1896, p. 9).

While preparing his definitive article on the Anthozoa for Lankester's great eight-volume *Treatise on Zoology*, Bourne published a spirited refutation to Ogilvie in which, while praising "her excellent memoir on the structure of Madreporian corals", re-asserted his former position that the calcified corallum is not composed of spicules but is simply "a secretion product of a definite layer of cells derived from the ectoderm, which I have called, like those of the Madreporaria, calicoblasts" (Bourne 1900, p. 518). In that lengthy paper, however, he was careful to make it clear that a final solution was not yet attainable: "we are as ignorant of the laws which govern the formation of these organic crystalline growths as we are of the molecular laws which determine why a given mineral solution shall crystallize out according to a given system" (Bourne 1900, p. 541).

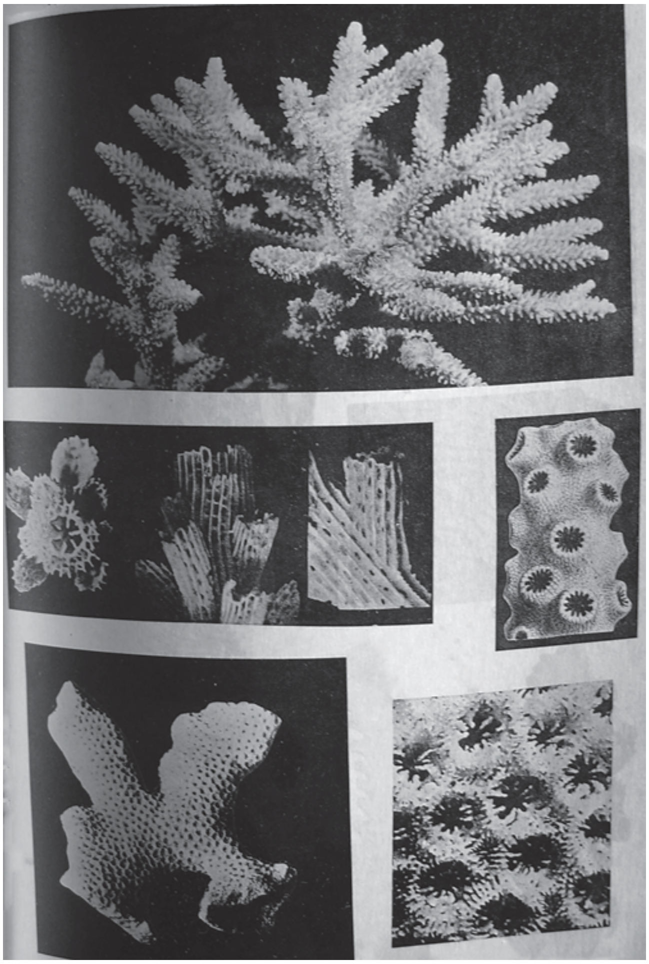
With that frank admission of the current state of knowledge concerning the calcification of the scleractinia, there was little further development over the ensuing decades, and when Vaughan and Wells came to discuss skeletonization, they relied on papers by Ogilvie and Vaughan. They concluded, as had Bourne, with the disclaimer that "the exact method by which the skeleton, consisting of $CaCO_3$ crystallized as fibrous aragonite, is deposited by the polyp is not thoroughly understood, and it has been supposed that it is carried out within (intraprotoplasmic) certain specialized cells of the 'calicoblast layer' of the ectoderm of the body wall and that the result is to be considered an exoskeleton" (Vaughan and Wells 1943, p. 31).

Decades of Despair: The World at War

In retrospect, it is astonishing that Vaughan and Wells could produce such a splendid advance in coral science by 1943 with their *Revision of the Scleractinia*. The 1930s and

[13] Aragonite has an orthorhombic crystal structure with three axes of symmetry, one vertical and two horizontal, at right angles to each other. Calcite has a trigonal structure with a vertical axis and three lateral axes at 120° to each other.

[14] Gk *gloios*. "gelatinous substance"; Bourne (1899).



Page from *Revision of the Scleractinia* by Vaughan and Wells (1943)

1940s included some of the most horrendous times that modern society has ever experienced, beginning in September 1929 when a staggering blow fell on the world economy. In late October that year, the New York stock market began to falter; on 29 October 1929, known universally as "Black Tuesday", came the massive crash that began the worldwide economic depression that lasted a decade. The immediate collapse of the American economy was profound: its gross national product sank by one-third and one-quarter of the labour force became unemployed.

Science was severely influenced by these events and research became increasingly limited, so throughout the 1930s, the steady progress of coral reef research that had been achieved during the 1920s ground almost to a halt. Although the Fourth Pan-Pacific Congress of 1929 was held in Bandung, as scheduled, little attention was paid to coral reefs: the Congress was preoccupied with agriculture and economic recovery of the Pacific region. Despite the devastating international economic depression, an immense body of organized knowledge had been achieved by 1940, in large part from the Low Isles Expedition, as well as the final identification of the scleractinians as reef builders and full acceptance of their descriptor as hermatypic. Many of the long-standing coral reef problems had been solved, although some details remained to be finalized, mainly relating to the exact processes of calcification and a solution to the still intractable dispute over the role of zooxanthellae in polyp physiology.

At the same time, Europe was becoming convulsed by disturbing political events with the rise of Nazism in Germany and Communism in Russia, which led to the outbreak of World War II. Immediately following the onset of hostilities in Europe with the German invasion of Poland on 1 September 1939, the Indo-Pacific region became an active war zone between European Allied and Axis powers, which effectively halted all reef research in the field. There were greater convulsions thereafter as German armies occupied much of Europe and then invaded Russia in June 1941.

Meanwhile, although it had been one of the victorious Allied nations in the Great World War of 1914–1918, Japan had become throughout those ominous decades of drifting towards war, in the 1930s increasingly hostile towards its former allies as a result of what it believed was inferior treatment during the 1921 Washington International Conference on Naval Limitation, by which it was restricted to smaller warship tonnages than Britain and the USA. Feeling humiliated in March 1933 by an almost unanimous condemnation from the League of Nations for its invasion of Manchuria in 1931 and in a final act of defiance and ultra-nationalism, Japan left the League. Exhibiting a progressively more belligerent attitude towards the outside world, Japan accelerated its preparations for war. In 1937, it invaded and ravaged China and fortified the Pacific atolls of Kwajalein and Enewetak as part of its far eastern defence perimeter, close to the US naval base at Midway Island and the International Date Line (longitude 180°).

Six months later, on 7 December 1941, a Japanese carrier aircraft attacked the American naval base at Pearl Harbor, destroying most of the US Pacific battleship fleet in an attempt to establish maritime hegemony over the western Pacific. Grossly mistaken in the deluded belief that the USA had lost its will to fight from the impact of the Great Depression and its proclaimed isolationist policy, which precluded it from ever joining the League of Nations following the horrendous bloodshed from World War I, the peoples of the USA rallied behind President Roosevelt and began mobilizing for war.

Four years later, on 7 May 1945, the European War ended with Germany's unconditional surrender. Three months later, following the nuclear devastation of Hiroshima on 6 August 1945 and of Nagasaki 3 days later, Japan capitulated to the Allied powers on 14 August, ending the Pacific War. On 2 September in Tokyo Bay, Japan's representatives signed the Instrument of Surrender aboard the USS *Missouri*, so concluding those dreadful 6 years and its appalling loss of an estimated 61 million lives.

Ecosystem Analysis and Nuclear Technology

10

To begin reconstruction after the extensive devastation of both the built and natural environments during World War II (WWII), there was a gargantuan task ahead of the international community. Almost immediately, in 1945, the United Nations Organization was founded. Soon thereafter the same year, two specialized agencies were created, the UN Educational, Scientific and Cultural Organization (UNESCO) and the Food and Agriculture Organization (FAO), followed by the World Meteorological Organization (WMO) in 1951.

The defeat of Japan in August 1945 did not end world conflict; however, at the Yalta Conference in February 1945, when victory was clearly in sight, Britain and the USA agreed, reluctantly, that the Soviet Union could retain a post-war sphere of influence in eastern Europe. Stalin went further and ordered Soviet forces to occupy the ravaged nations along its European borders. Events were becoming ever more ominous for the democracies, and a year later at a speech in Missouri on 5 March 1946, Winston Churchill gave the sombre warning that "from Stettin in the Baltic to Trieste in the Adriatic, an iron curtain has descended across the continent". The term "iron curtain" resonated around the free world, nowhere with more alarming effect than in the USA which, having emerged from the conflict as the world's most industrially powerful nation, stepped up its defence preparations as an era began of even greater tension than existed during the rise of Nazism in the 1930s. The military "hot war" was replaced by the more sinister "cold war". Still the only nuclear power at the time, the USA, with its ingrained fear of communism and repelled by the collectivist and seemingly brutal regime established by Stalin in the Soviet Union and its occupied eastern European satellites, began an accelerated programme to improve the destructive capabilities of its nuclear weapons. On 1 July 1946, it commenced a series of atomic bomb tests in the Marshall Islands, which, in an irony of history, finally decided Darwin's theory of reef formation.

Reef Formation Problem: Bikini and Enewetak

The Marshalls are a chain of 1225 mostly uninhabited atolls and reefs in Micronesia—east of the Philippines in the mid-Pacific Ocean centred around 10°N 165°E—named after a British ship's captain who visited them in 1788. In 1885, they became a German protectorate until the outbreak of WWI in 1914, when they were seized by Japan as an ally of Britain and France. Following the Peace Settlement of 1919, the Marshalls became Japan's mandated territories. Unfortunately for reef science, however, the Japanese closed the region to all foreigners and access was denied for any investigation until after the Pacific War.

Soon after the outbreak of hostilities in December 1941, Japanese forces had advanced rapidly throughout the western Pacific in a great arc reaching from the Aleutians in the northeast to New Guinea and the Solomon Islands in the southwestern Coral Sea. Two years later, in November 1943, when the American carrier and battle fleets began their Central Pacific counteroffensive, the atolls of Kwajalein and Enewetak were the first to be captured.

Becoming a United Nations trusteeship in 1945, and because it was remote from the main centres of world population, Bikini Atoll in the Marshalls, with its lagoon 35 miles long and 20 miles wide (56 × 32 km) seemed an ideal place for further experiments on the detonation of nuclear devices. With its indigenous population of barely 1000 living on its four main island surfaces temporarily relocated 124 miles (200 km) east to uninhabited Rongerik Atoll in Operation Crossroads, two plutonium fusion bombs similar to those dropped on Nagasaki were exploded in 1946 on 95 redundant American and Japanese target vessels moored in the lagoon of Bikini Atoll.

Following the first nuclear tests, in the Bikini Scientific Resurvey of 1947, in preparation for testing the more destructive thermonuclear (hydrogen) bombs, but with uncertainty surrounding the strength of the geological substratum, the Atomic Energy Commission began with three inconclusive test holes drilled by the US Geological Survey, the deepest

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reaching 775 m. Later that year, the testing site was relocated 180 miles due west to Enewetak (10°N 160°E), of a similar size to Bikini, with a nearly circular lagoon some 20 miles (32 km) diameter, where a larger number of bores were made between 1950 and 1952. The three deepest, coded K-113, E-1 and F-1, descended to 390, 1287 and 1411 m, respectively. Both E-1 and F-1 located a volcanic foundation, each retrieving a 5 m olivine (igneous) core, establishing a world depth-drilling record.

For reef scientists, the news was massively exciting. In the 1953 *Bulletin* of the American Association of Petroleum Geologists, consultant geologist Harry Ladd reported that the cores disclosed "a basaltic foundation beneath Enewetak Atoll [and thereby] substantiated Darwin's subsidence theory of atoll formation" (Ladd et al. 1953), his findings later being quoted in the final 1987 report of the US Office of Scientific and Technical Information (Ristvet 1987, p. 39). In stark contrast, all previous efforts at Funafuti and in Fiji, as well as Murray's rival hypothesis of reef formation, paled into insignificance. Immediately, a century of debate over the formation and structure of coral reefs ceased: Darwin's theory had been confirmed.

To permit preliminary assessment of the Bikini explosions, a field research station was created to study the radioactive aspects of testing during and after the 43 nuclear detonations between 1948 and 1958. In conjunction with the University of Hawaii, delegated responsibility for supervision, the first stage was established on 3 June 1954 with the title Enewetak Marine Biological Laboratory (EMBL). Given security demands, only male US scientists with high-level clearances were allowed to conduct studies on both biological and geological aspects of the Pacific war zones, and to the benefit of reef science, the results were published in standard journals.[1] With the addition of Laboratory 2 in 1961 and Laboratory 3 in 1969, along with greater infrastructural support, the EMBL was redesignated in 1969 as the Mid-Pacific Marine Laboratory (MPML). That laboratory continued to operate until 1982, when the cleaning up of the atoll had been completed, and it was restored to its indigenous inhabitants as part of an independent nation, Republic of the Marshall Islands, in free association with the USA.

During the same period, another major advance in reef knowledge came when the Geological Society of America published the initial volume of a vast synopsis of more than a century of coral reef research in its wide-ranging *Treatise on Invertebrate Paleontology*. Under the general editorship of Raymond Moore (1892–1974), director of the Kansas State Geological Survey and professor of geology at the University of Kansas, preliminary planning of the *Treatise* began in 1948. In the opening words to his editorial preface, Moore declared that it would "present the most comprehensive, and authoritative, yet compact statement of knowledge concerning invertebrate fossil groups that can be formulated by collaboration of competent specialists in seeking to organize what has been learned of this subject to the mid-point of the present century…[and] which may be expected to yield [a much] needed foundation for future research" (Moore 1953–1962, p. viii).

Moore brought together ten of the leading palaeontologists of the era, including John West Wells, collaborating with Dorothy Hill of the University of Queensland (the leading Australian authority on reef geology), to describe the general features of the phyla Cnidaria (Hill and Wells 1956) and Anthozoa. Wells alone was responsible for the exhaustive 114-page section on the Scleractinia in which he examined in detail their anatomy, skeletal morphology, reproduction and colony formation, morphogenesis of the corallum, ecology, stratigraphic and geographic distribution, evolution and classification, followed by their systematic description. With the now well-established palaeontological foundation provided by Moore's *Treatise*, and the confirmation of Darwin's volcanic foundation theory, reef science began a new chapter in its intriguing quest to solve yet other aspects of the coral reef enigma.

Ecosystems and Energy Flow: The "New Biology" Begins

With the formation of EMBL in 1954, major changes were being made in biology as a reaction to 19th-century approaches, when biologists were preoccupied with attempts to create a coherent understanding of life forms and processes in terms of natural selection. In the last decades of the 19th century, efforts were riddled with controversy and speculation, unlike the mathematically based disciplines of physics and chemistry that had been making spectacular advances. With their stress on quantification, objectivity and exactness, the physical sciences had become assumed by the general public to be "real science" whereas biology appeared quite the opposite: when it did receive recognition, it was often for its applied value in advancing medical, veterinary or horticultural knowledge.

In the early decades of the 20th century, the successes of the physical sciences and their research protocols began to influence some of the more inventive minds within the rising generation of biologists, among whom one of the first to exert a strong influence was the American statistician Alfred Lotka (1880–1949) with his 1924 publication of *Elements of Physical Biology*. His approach was to consider natural processes as dependent upon energy flow, with their

[1] The published findings reported for the period 1946–1955 are listed in the references in Odum and Odum (1955).

transformation formulated in causal laws, presented statistically. Others exemplified the same mathematical style, particularly Oxford University zoologist Charles Elton (1900–1991), who in *Animal Ecology*, published in 1927, led the emerging discipline of population biology. Elton's influence was pervasive, mainly through the *Journal of Animal Ecology*, which he founded in 1932 and edited thereafter, and his directorship of the Oxford Bureau of Animal Population, established the same year. Two of his most enduring concepts were those of food chains, the trophic dynamics through which radiant solar energy from photosynthesis is transferred between organisms, and his popularization of the term "ecological niche", developed at length by George Evelyn Hutchinson (Hutchinson 1978, p. 246).

When Elton retired in 1968, in a foreword to a celebration issue of the *Journal of Animal Ecology*, his Oxford University colleague Alister Hardy (1896–1985) described the early years of their generation as young biologists. "What we all rebelled against", he recollected, with memories of the research of Huxley, Haeckel and Kleinenberg, "was the great emphasis on comparative anatomy and descriptive embryology that held zoologists fascinated for half a century. The original attraction had been the wrestling with intricate puzzles of possible homologies which it was believed could establish the actual course of evolution". However, he continued, Elton "set out to turn natural history into science, and that, of course, is what ecology is: the quantitative and experimental study of living organisms in relation to their environments". In that pursuit, he continued, Elton had asserted that there are two faces to natural selection: that "which may be called the *selection of the environment by the animal*, as opposed to the *natural selection of the animal by the environment*. In evolution there are two variables—variations of the outer environment in place and time, and variations of the characters of species in place and time" (Hardy 1968, pp. 3, 5; *emphasis* as in original).

From that striking suggestion emerged a concept in 1935 that became entrenched in all biological thinking thereafter when Oxford professor of botany Arthur Tansley (1871–1955) conjoined animals, plants and their environment into a single collective concept as an "ecosystem". Tansley had been active in promoting the new biology since the turn of the century, founding the innovative journal *New Phytologist* in 1901 and a decade later, in 1913, the British Ecological Society and its journal *Ecology*. He edited both those journals for many years, and it was there where the concept of an ecosystem first entered the literature. A composite of "ecology" and the physical sciences term "system" to connote an organized, integrated structure of empirical evidence, Tansley brought the issue to attention specifically in his 1935 article on "The use and abuse of vegetational concepts and terms". His main complaint was the widespread failure of ecologists to extend the concept of "biome" or "community" beyond the animals and plants that are instrumental in vegetation succession to include the physical environment within which are all the biological processes. Following his critical observations on the limited outlook of his botanical contemporaries, Tansley developed his central message in a final section headed "The Ecosystem". In rejecting the common use of the term "biotic community", which he considered uninformative, what needed to be taken into account, he argued, "as it seems to me, is the whole *system*—in the sense of physics—including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system" (Tansley 1935, pp. 299–300). Moreover, his concern to develop the concept of natural selection beyond Darwin's original formulation comes through a few paragraphs later with his statement that "There is in fact a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest".

Two decades later, Tansley's comprehensive concept of the ecosystem and the climax community received its first full-scale application in coral reef science by scientists brought in to staff of EMBL. Among the many studies undertaken, one into the trophic structure and productivity of Enewetak Atoll by brothers Howard and Eugene Odum in 1954 came to exercise a major influence on coral reef studies worldwide. For the first time since Mayor in Samoa in 1924 and Yonge on the Low Isles in 1928/1929, the brothers Odum employed the radical innovation of ecosystem analysis.

Trophic Dynamics of an Atoll: The Enewetak Study

When approached by the Atomic Energy Commission, Howard and Eugene Odum had already established sound reputations in ecology, mainly from their involvement in limnology, and specifically the inland lakes of North America as self-contained ecosystems. Howard Odum (1924–2002) had written his 1950 doctoral thesis at Yale on *The Biogeochemistry of Strontium* and its global circulation, following Lotka's ideas of energy flow. In the same year, he presented a paper to the Ecological Society of America in which he suggested that there was some type of underlying energy force driving living organisms, analogous to electrical circuits. To develop his theory further, he conducted the first complete analysis of an ecosystem in the Silver Spring inland lake in north-central Florida where he was able to describe the energy processes that enabled its steady-state maintenance. The two brothers then led the way in 1953 with their pioneering *Fundamentals of Ecology* in which Howard's chapter expounded his central concern with the "Principles and concepts pertaining to energy in ecological systems".

The brief handed to the Odum brothers by the Atomic Energy Commission, they reported, was to assess how, apart from minor fluctuations, coral reefs "seem unchanged year after year, and apparently persist, at least intermittently, for millions of years". With obvious thoughts of the conflict that had shattered so much of the world as well as many Pacific atolls, their aim was to contrast natural processes with "mankind's great civilization [which] is not in steady state and its relation with nature seems to fluctuate erratically and dangerously". Specifically, "since nuclear explosion tests are being conducted in the vicinity of these inherently stable reef communities, a unique opportunity is provided for critical assays of the effects of radiations due to fission products *on whole populations and entire ecological systems in the field*", and presented in statistical measurements, as required by the Atomic Energy Commission, "which will aid future comparisons between the normal and the irradiated reef ecosystems" (Odum and Odum 1955, p. 291).

Over a 6-week period during July/August 1954 before the reef had been directly disturbed by nuclear explosions, their joint aim was "to show that systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a corresponding low but optimum efficiency". In their final report, where they used the nonindigenous spelling of the atoll's name, "Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll",[2] Howard's input is clearly evident in the statement that their hypothesis could be confirmed with relative ease "due to rapid advances in metabolic and productivity measurement in recent years", by calculating "the relationship between the standing crop, defined as the dry biomass of existing organisms per area, and productivity, defined as the rate of manufacture of dry biomass per area" (Odum and Odum 1955, pp. 291–292).

To achieve that goal, the brothers Odum established six investigation quadrats on Japtan, one of the four small islands on the atoll rim, which, on the southeastern windward section, had a continuous unidirectional water flow across the reef. That location was important because the reefs around the other three islands on the atoll rim, and in earlier similar studies, where the water broke onto the reef front, then returned along the same path as an undertow, allowed them to gain measurements as accurately as possible of daytime production of energy and oxygen, and night-time respiration from consumption of oxygen.

With that preliminary planning, the brothers surveyed all possible corals and algae with the pertinent observation that "the coral reef is like most known self-sufficient ecosystems in having a much greater weight of plant biomass than animal biomass" (Odum and Odum 1955, p. 301). Their primary task was, therefore, to survey the relative proportions of plant and animal components in living coral. As anticipated, they found that plants dominated, although, unexpectedly, most of the algae were not zooxanthellate but a wide range of other species, including considerable quantities of "the bright green filamentous algae growing in the pores of the inert skeleton" discovered in all species of hermatypic corals "in abundance". The two also examined planktonic algae from the open sea, all of which, when extracted, dried and measured, revealed that the non-zooxanthellate algae produced most of the plant protoplasm. When they assessed the algal component in polyp tissues, they measured a much smaller mass, equalling just one-third of that in plants, in the ratio 0.021:0.063 g cm^{-2}, all of which results they presented in great detail in numerous statistical tables for each coral species identified (Odum and Odum 1955, p. 298).

As their focus was on the nutritional features of the ecosystem, the brothers Odum were keen to investigate the conviction, strongly held by Yonge among others, that polyps are carnivores. Their caution on that controversial issue was expressed carefully, because their evidence from samples taken across the reef at various stations indicated the "relative sparsity of true plankton", which they recorded in detail (Odum and Odum 1955, p. 312, Table 13). Although polyps "catch zooplankton, especially at night", they ventured that if other researchers are correct, "a coral animal is very much an herbivore because of nutrition received from symbiotic algae" (Odum and Odum 1955, p. 305). Their extensive and careful measurements indicated the "predominance of producer algae", although they could not be certain whether the reef subsisted entirely on its own primary production. It was likely, they suspected, that it also derived critical nutrients from the strong, continuous, one-way ocean flow over the community.

The findings led to their further speculation on trophic structure: because "symbiotic zooxanthellae were found in the tissues of the animal polyp", it seemed most probable "that, metabolically, corals might be part-plant and contribute to the primary production of the community". That possibility, of course, was contrary to Yonge's vigorous opposition to Boschma's research belief and his continued insistence in 1940 that zooxanthellae play no part in the nutrition of corals. However, the brothers Odum recorded, their observations "suggest the hypothesis that [the filamentous] skeletal algae, as well as zooxanthellae, have a symbiotic relationship with coral animals", although at the time, as Eugene

[2] In the early phases of investigation, the non-indigenous spelling of Eniwetok was used on US naval maps and by American scientists, including the brothers Odum, and it appears in that form in their journal article. The correct Marshallese spelling as Enewetak is documented in Devaney et al. (1987, p. xi).

Reef flat, Heron Island, c. 1928, illustrating the wide range of coral species at low tide. Barely intruding on the upper right corner is the wreck of His Majesty's Colonial Ship *Protector*, the only vessel in South Australia's navy in the 19th century. Taken to Heron, it was used as a block-ship before the construction of a jetty. Its remains continue to intrigue tourists

Odum recalled in 1998, they were unable to demonstrate it conclusively. From their extensive measurements, the two were able to create "trophic pyramids" for all six quadrats, the algae providing a wide base as energy producers for the decreasingly smaller levels above of polyps, algal grazers and other marine animals (molluscs, echinoderms, holothurians, urchins, anemones, sea stars and fish). In their analysis of the data collected, the brothers concluded, "tentatively, that the Japtan reef is a true climax community…[which is] highly productive and not far from a steady state balance of growth and decay … the algal-coelenterate complex, therefore, comprises a highly integrated ecological unit—comparable to the algal–fungal complex of a lichen, which permits cyclic use and reuse of food and nutrients necessary for vigorous coral growth in tropical 'desert' waters having a very low plankton content. The coral is thus conceived to be almost a whole ecological unit in itself with producer, herbivore (utilizing food from symbiotic algae) and carnivore (plankton feeding at night) aspects".

In finishing their summary, the bothers made it clear that "the sessile part of the community is primarily autotrophic with relatively few plankton feeders other than coral polyps", whereas "production on the reef seems to about balance the respiration of the reef" as confirmed by their phosphorus and nitrogen analyses … [which] "indicates a true ecological climax or open steady state system" (Odum and Odum 1955, p. 316, Table 17, and p. 319).

Strong support for the conclusions of the brothers Odum came from two other significant staff members of EMBL. In preparation for atomic testing, extensive surveys of Marshall Islands atolls had been made by the US Geological Survey covering not only the geology but also numerous biological aspects. One significant study a decade before the Odum brothers had been conducted in July 1946 by Scripps oceanographer Marston Sargent and Hawaiian Pacific Oceanic Fisheries investigator Thomas Austin, along with some colleagues, at three locations on Rongerik Atoll where the residents of Bikini had been relocated before nuclear testing began. In a report entitled "Biologic economy of coral reefs", finally released in 1954 at the time of the Enewetak findings, the two dealt intensively with the zooxanthellae issue that had set Yonge at odds with Gardiner, Boschma and Siro Kawaguti. Their studies were conducted at three locations, with eight stations having one-way vigorous current flows on Rongerik, two in the east and one in the west during July 1946. Measurements were made of current strength, water temperature and the concentrations of oxygen and dissolved phosphorus. The results were compared with those of earlier investigators, including Yonge's reports of the Great Barrier Reef Expedition, and they provided a striking, unambiguous contrast. "The most fundamental conclusion drawn from the observations recorded here", they stated, "is that atoll reefs are essentially self-sufficient communities, producing as much organic matter as they consume, or more" (Sargent et al. 1954, p. 293). They further indicated that the "most striking oxygen-producing organisms … are undoubtedly the zooxanthellae of numerous corals", and that the production rates "reported by Yonge et al. (1932, pp. 224–228)" were all lower than those obtained on Rongerik.

In support of their findings, Sargent and his colleagues cited the evidence of Kawaguti in a 1937 paper entitled "On the oxygen exchange of reef corals" in the Palao Tropical Biological Station Studies (Kawaguti 1937).[3] Kawaguti found oxygen production "as high as those we have observed. Therefore, our values for maximum oxygen production by corals probably are dependable", the two reported. Further, the picture that emerges of "the reef as a self-supporting community, depending on the current only for dissolved nutrients (in a broad sense), and not particulate or dissolved matter, is reasonably clean cut". This conclusion had previously been reached by Kawaguti who found that "the zooxanthellae of corals produce organic matter at a rate quite comparable with its rate of consumption by the coral colony, [and] under favorable circumstances probably exceeded it" (Sargent et al. 1954, p. 299). Given the evidence they discovered in support, Sargent and his colleagues concluded that "we can find no other ultimate reason for the flourishing of coral atolls in an empty ocean".

[3] Although cited by other investigators, only one set of these papers survive in Guam, and despite intensive investigation, I was unable to find them. The Siro Kawaguti Working Group of the Japanese Coral Reef Society are in the process of translating the full set of Kawaguti's Reports into English, but as yet this is incomplete. Consequently, I have relied on the comments by Sargent et al. (1954).

Developments in Ecosystem Analysis: Radioactivity Experiments

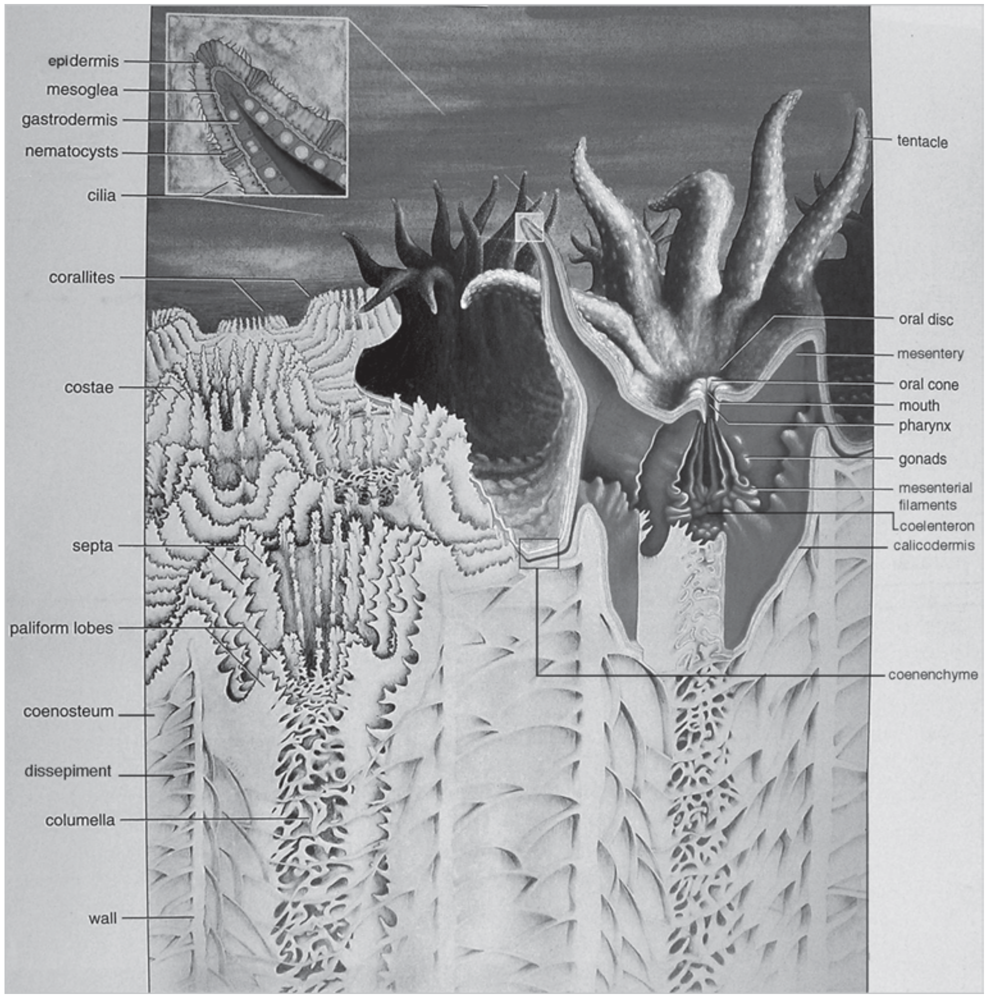
Following publication of their lengthy paper in 1955, the method of ecosystem analysis introduced into coral science by the brothers Odum during their investigation of Enewetak became the dominant paradigm for field studies in the second part of the 20th century. The atomic era also entered peaceful scientific activity when the journal *Science* printed an announcement on 14 June 1946, from the Manhattan Project (the US nuclear authority at the time) entitled "Availability of radioactive isotopes", which stated that they were "cognizant of its peacetime potentialities … and that therefore the supply of radioactive isotopes can begin to meet demand" (Anon. 1946, p. 697). A little more than a decade later, the first use of such isotopes in coral reef science was made by ecologist Tom Goreau in Jamaica.

In 1933, Fritz Goreau (1901–1986), a Jew and newspaper editor in Munich, had been forced by the Nazis to cease publication. Fortunately, before the rising tide of genocidal anti-Semitism became a flood, he was able to leave for France, accompanied by his family. Three years later, they arrived as migrants in the USA where, as Fritz Goro, he became a celebrated nature photographer for *Life* and *Scientific American* magazines and one of the photographers for the Manhattan Project at the Los Alamos Trinity Test site of the first nuclear detonation on 16 July 1945. His son Thomas (Tom) Fritz Goreau (1924–1970), while a medical student in the University of Pennsylvania, became involved in the early nuclear experimental period in Bikini in 1947 as a chemical analyst, where he collected radioactive specimens by scuba diving in the lagoon.

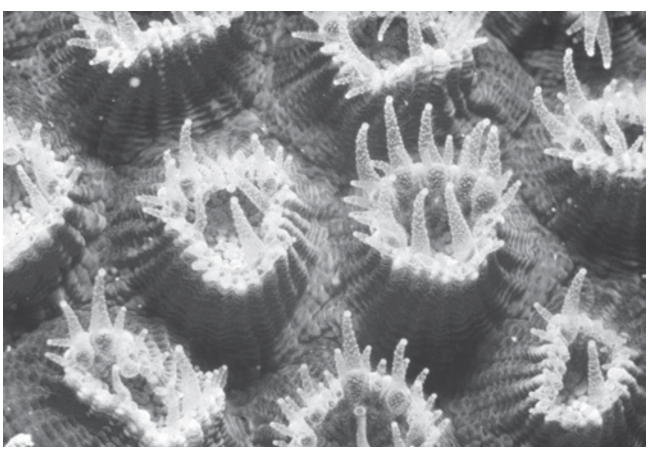
In 1951, Tom Goreau was appointed to the Department of Physiology in the University College of the West Indies, where he continued his research into corals and established a small marine research facility in Discovery Bay on the central northern coast of Jamaica. Over the ensuing decade, he continued with the pioneering work of the brothers Odum in ecosystem analysis as related to the role of zooxanthellae in coral physiology, which first appeared in his doctoral dissertation at Yale in 1956 entitled *A study of the biology and histochemistry of corals*. A 3-year research programme immediately followed on the ecology of Jamaican coral reefs; it was the first rigorous analysis of an important facet of reef ecology attempted by a single scientist, rivalling the results achieved at the Low Isles or on Enewetak. Its explicit aim was to compare the zonation and species composition of Jamaican reefs with the greater complexity and abundance of Indo-Pacific reefs, particularly those on which Goreau had already dived in the Marshall Islands, the Great Barrier Reef and the Red Sea. Employing the new methods of underwater recording by photography and plexiglass noteboards while swimming with mask and snorkel, as well as scuba and self-contained oxygen recirculating diving equipment, the project covered the entire perimeter of the Caribbean island, some 150 miles (240 km) in east–west length, and 50 miles (80 km) across at its widest in the south. He surveyed reef systems along horizontal transects at right angles to the shore, intersected by vertical sounding lines, from the deep outer slopes through the fore-reef, over the crest and reef flat into the lagoon and the beach.

It had been well known to investigators for a century that Caribbean reefs were less luxuriant than those of the Indo-Pacific, but the precise reasons for this had not made it into reef literature at the time Goreau was working, so a short explanatory comment is required. In 1915, while in military hospital recovering from war injuries, German meteorologist and Greenland explorer Alfred Lothar Wegener (1880–1930) had published a controversial and much-ridiculed theory in the book *Die Enstehung der Kontinente und Ozeane*, which sought to explain the origins of the continents and oceans. His hypothesis was based on the supposition that originally the earth's masses had been a single continent he named Pangaea (Gk *pan*, "one" + *gaia*, "land"), surrounded by the primeval waters of the great ocean (described in Homeric legend as the god Okeanos, "the great encircling river") which, over geological time through the processes of continental drift, had split into separate parts that began moving into new locations. Tragically, Wegener died of starvation on his fourth exploratory trek across Greenland before geophysical research later in the 20th century confirmed his theory. Eventually, from continued subterranean activity, Pangaea broke apart into great underlying tectonic plates that were carried in continuous, generally imperceptible, motion by convection currents in the molten siliceous magma beneath, with the visible continents merely their surface features. Plates only became detectable later using advanced meteorological instrumentation when periodic collisions and fractures, indicated by volcanic eruptions, earthquakes and tsunamis, revealed their activity.

Palaeontological research has since confirmed that the epicentre of scleractinian reef evolution began during the Anisian Stage of the Triassic Period some 240 million years ago in the specific palaeogeographic region known as the Tethys Sea—named after the wife of Okeanos and mother of Melobosis by the great Austrian geologist Eduard Suess in 1893—between the separate land masses of Africa and Asia. The evidence of palaeontological remains indicates that it was then the richest centre of marine life on the planet. Some ten million years ago, as tectonic activity continued moving the plates, Africa and Asia came together where today's Suez Canal is now located, the Tethys Sea becoming the smaller enclosed Mediterranean. Then, about 3 million years ago when the hitherto unconnected continents of South and North America fused at the Isthmus of Panama, two separate oceans were formed. Free circulation of marine



Section of a zooxanthellate polyp with explanatory details. (Drawn by Geoff Kelly and reproduced courtesy John Veron)



Coral polyps in feeding mode

life in the tropical waters of the globe throughout the Tethys hence ceased, and at the same time, with tectonic activity continuing, the Atlantic and Caribbean contracted and the Indo-Pacific expanded rapidly (geologically speaking), and coral species evolved prolifically (see Veron 2008a, pp. 113–125).

With that geological development, the Caribbean became almost an enclosed sea with a chain of semi-submerged islands from Cuba and the Greater Antilles to the Lesser Antilles, ending at Trinidad near the coast of Venezuela. Since then, that submarine barrier has hindered the flux of deeper, cooler, nutrient-rich upwelling Atlantic waters from reinvigorating reef life. Unfortunately, those geophysical reasons for the depauperate condition of Caribbean reefs were unknown to Goreau and other reef scientists at that time. Goreau's results did, however, provide further precise information with his discovery that "Jamaican waters were remarkably homogenous … with no important regional differences", and that coral's composition, with 41 species belonging to 25 genera, compared favourably with Florida and the Bahamas, and better than Barbados and Bermuda. The larger reefs, he reported, "are of the fringing barrier type with scleractinians as the most important hermatypic organisms" (Goreau 1959a, p. 83).

Jamaican corals were later revised by John West Wells up to 64 species, including ahermatypes, but even so, by comparison, the epicentre of the Indo-Pacific around Indonesia has >500 species. This number then decreases in

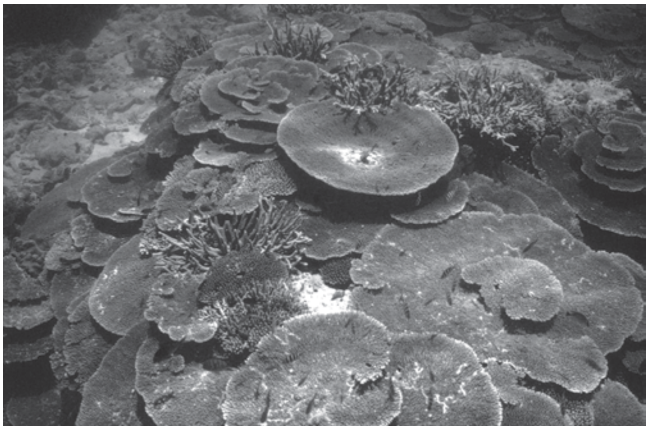


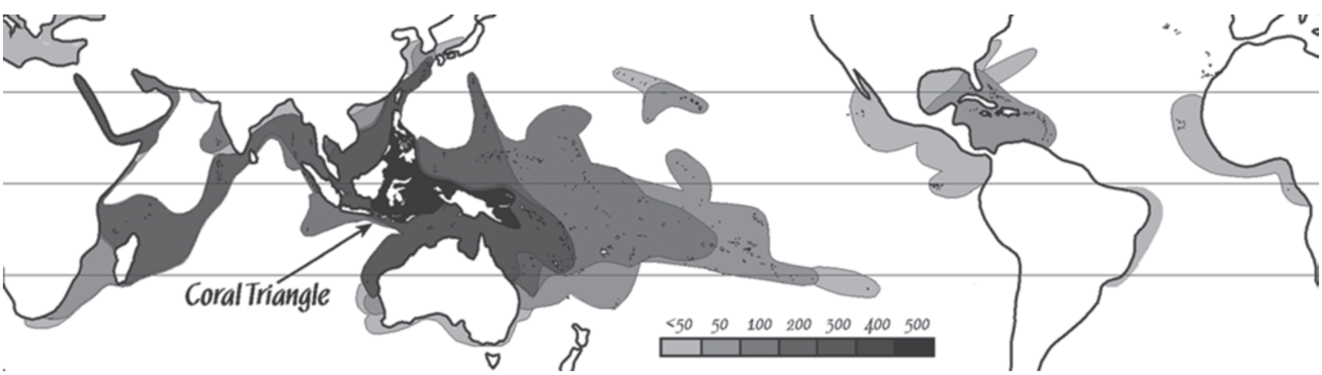
Plate (or tabletop) corals, a commonly seen species

isopan generic contours towards the outer far eastern limits to just 40 species in the region of Clipperton Atoll, 650 miles (1046 km) southwest of the Pacific coast of Mexico, and to 51 species of scleractinian, including 45 hermatypes, in the reefs of the Indian Ocean's far western Seychelles. Although Goreau's survey solved none of the outstanding coral reef issues, it was an important milestone in reef research with its comprehensive analysis of reef zonation that set a standard for subsequent coral ecosystem analyses, most importantly for the Caribbean, one of the most turbulent cyclonic regions on Earth.

In the same year, Goreau published results of his innovatory radioactivity experiments in the *Biological Bulletin*, which made a major contribution to understanding the problem of hermatypic reef formation. As he first reported at a conference in Puerto Rico in 1957, his aim, with the later assistance of his Panamanian-born wife Nora, was "to determine calcification rates in the different parts of coral colonies, and to estimate quantitatively the effect of light and darkness, zooxanthellae and carbonic anhydrase inhibitors [which hinder conversion of carbon dioxide to organic carbon during photosynthesis] on skeletogenesis". His technique was to utilize the new availability of radioactive isotopes, which are variant forms of the same chemical element, but with a different atomic weight. In his experiment, he placed the radioactive isotope calcium-45 (^{45}Ca) in the compound form of calcium chloride ($^{45}CaCl_2$) into seawater vessels containing 14 species of zooxanthellate coral, and that compound could be detected later in the skeleton and measured by means of a Geiger–Müller radiation counter. He consequently developed "a rapid and precise method for measuring the incorporation of calcium into the coral skeleton under controlled laboratory conditions" (Goreau 1959b, pp. 59–60).

Throughout the experiment, a careful protocol was followed, described and illustrated graphically in precise detail, focusing on the still controversial process of polyp nutrition by zooxanthellae, along with the effects of light and darkness on calcium deposition. Finding it diplomatically necessary at the time "to agree with the conclusions of Yonge and Nicholls that reef corals are specialized carnivores", he assumed in his experiments that, because zooxanthellae are absent from deep sea and cold water corals, "zooxanthellae *per se* are not necessary to individual coral polyps, nor do they appear to be directly linked with the calcification process". Even so, his indecisiveness is evident in his comment that "although the zooxanthellae seem to play an important role in determining calcification rates in reef-building corals, certain as yet unknown physiological factors operate to control the basic mineralization process" (Goreau 1959b, pp. 67–68).

In his *Biological Bulletin* paper, Goreau explained in great detail the complex biochemical processes involved that led to the notable discovery that "there was a slow but appreciable isotopic exchange between the coral skeleton and sea water", and "in many of the reef-building corals tested so far, the calcification rate was significantly lowered by the exclusion of light". Those observations led to Goreau's



Isopan generic contours of species diversity ranging from 500 in the Coral Triangle around Borneo to 400 in the Coral Sea and the western Indian Ocean. Species habitats require warm currents that move clockwise above the equator and counter-clockwise in the southern hemisphere. This explains the paucity of species in the cooler Pacific waters of Mesoamerica and the Atlantic coast of Africa. (Illustration courtesy John Veron) final conclusion that calcium is adsorbed from seawater and promoted ten times faster in light which "in part was mediated through the zooxanthellae", with the qualification that it was not clear whether the results he obtained in the laboratory "can be compared to those found in open reefs under natural conditions" (Goreau 1959b, pp. 71–73). Two years later, he amplified those conclusions at a conference with the declaration that "photosynthesis appears to be in some way essential in reef formation", and although "zooxanthellae do not themselves calcify, their presence results in a very powerful enhancement of calcification in the coral host as soon as photosynthesis begins".[4]

Simultaneously with Goreau's calcium-45 studies, a similar research initiative was being undertaken with radioactive carbon-14 (^{14}C) by Leonard Muscatine (1932–2007), a doctoral student at the Berkeley campus of the University of California, who hoped to resolve finally the highly disputed issue of the translocation of nutrients within symbioses. Under the guidance of his supervisor Prof. Cadet Hand, who suggested the use of radioactive carbon as a tracer, Muscatine's thesis proposal was a direct challenge to the views of the time with his two objectives: "to establish the existence of a nutritional relationship between algae and host, and to characterize the chemical basis of this relationship".[5] In collaboration with Hand, the first experiments by Muscatine with $^{14}CO_2$ were on starvation of the zooxanthellate sea anemone *Anthopleura elegantissima*, which he compared with zooxanthellae-free specimens that grew under Californian wharves in the absence of sunlight, in order to determine weight loss over time. The results were encouraging when he was able to conclude that "the lower rate loss by symbiotized anemones is related to the presence of algae".[6]

The next step was to investigate plant–animal symbioses with other zooxanthellate organisms, beginning with the common laboratory experimental organism *Chlorohydra viridissima*. From data collected on different occasions in the Marshalls by several EMBL scientists (the brothers Odum, Sargent and some colleagues), which showed that corals there grew quite well with minimal food supply, Muscatine's results with starvation of hydras yielded similar results. These suggested "in the case of *C. viridissima* that symbiotic algae can account for this by promoting efficient utilization of available food" in the form of organic fixed carbon.[7] Finally, in an exhaustive landmark co-authored paper of 1969, Muscatine was able to state unequivocally that in separate experiments by himself and others with four species of coelenterate, *Pocillopora damicornis*, *Anthopleura elegantissima*, *Zoanthus confervus*, *Fungia scutaria*, that the carbohydrate glycerol was released from algal symbionts to their hosts (Smith et al. 1969, p. 26). Muscatine's research at Berkeley continued to make a remarkable number of contributions to invertebrate zoology, of which only a short synopsis is presented here.

Several years after his experiments with anemones, but relevant to the coral reef problem of massive carbonate formations and their long-term stability, was Muscatine's investigation in collaboration with Elsa Cernachiari of the transfer of photosynthate products from algae to the host. For their laboratory experiments on the widely distributed Pacific coral species *Pocillopora damicornis*, they used radioactive sodium carbonate ($Na_2{}^{14}CO_3$) to measure the effects of darkness and light over periods of 24 hours. The results were significant, showing that "of the total ^{14}C fixed photosynthetically by the zooxanthellae, some 35–50% is released and incorporated into host coral constituents" (Muscatine and Cernachiari 1969, p. 507). Their conclusion was unequivocal and established not only that light was essential to nutrition of corals but also that "the skeletal organic matrix also acquires ^{14}C" (Muscatine and Cernachiari 1969, p. 522). That led him, as expressed in a profound obituary tribute from seven of his colleagues in 2007, to "a life-long passion for the symbiosis between algae and invertebrates" (Hoegh-Guldberg et al. 2007a, p. 732).

The concomitant discovery of the acquisition of radioactive carbon by the corallum immediately raised a closely related question that also demanded an answer, unresolvable earlier by Bourne, Ogilvie, Vaughan or Wells. How does calcium become available to the coral skeleton? The obvious inference is from dissolved calcium in the seawater. However, given the results of Goreau's ^{45}Ca tracer studies and the subsequent work by Muscatine and Cernachiari with sodium carbonate, which confirmed that coral skeletons acquire ^{14}C, another possibility was suspected by Vicki Pearse of Stanford University that, in addition, "skeletal carbonate originates from metabolic CO_2" that is, in part, from the photosynthetic process whereby the algae create carbohydrate (CH_2O). After an experiment feeding mouse tissue impregnated with radioactive carbon to the coral *Fungia scutaria*, she recorded "direct evidence that metabolic CO_2 was incorporated into the skeletal carbonate". Her conclusions, however, had not completely solved the issue of corallum calcification because "the relative contributions of carbonate from seawater and from metabolism are still unknown" (Pearse 1970, p. 363). To the present day, despite continuing research, the exact processes of calcification remain unclear, but they are generally believed to come from continuing precipitation of aragonite crystals in a fine cellular sheet of calicoblastic epithelium lining the polyp interior (see Constantz 1986).

While the nutrition debate continued, Tom and Nora Goreau, collaborating with Maurice Yonge, made a further assessment of the carnivore status of corals and of the role

[4] Goreau et al. (1961), cited in Lenhoff and Loomis (1961, p. 279).

[5] Muscatine (1961), cited in Lenhoff and Loomis (1961, p. 255).

[6] Muscatine (1961), cited in Lenhoff and Loomis (1961, p. 259).

[7] Muscatine (1961), cited in Lenhoff and Loomis (1961, p. 264).

of plankton. By that stage, Yonge had become less dogmatic than several decades earlier and had reached the equivocal position that "the question whether any of these diverse organic particulates are available as food to the corals is still undecided". As research by a number of scientists, he stated, had "abundantly established that material does pass from zooxanthellae into the tissues of the host coelenterate … the precise significance of this, in the context of the nutrition of the animal remains to be determined" (Goreau et al. 1971, pp. 251, 257). Tragically for Tom Goreau, the paper was written during 1969 while his primitive Discovery Bay Marine Laboratory was being expanded into a modern institute, and publication came after he died in 1970 at the age of 46 from radiation-induced cancer, believed to have been initiated in Bikini lagoon.

The summary to their joint paper with "the assumption that reef corals are wholly autotrophic due to the presence of zooxanthellae is questioned" would be resolved when the remaining experimental gap concerning translocation of nutrients led Muscatine, along with James Porter of the University of Georgia, to ask the quantitative question: "To what extent does translocation satisfy coral animal tissue carbon requirements for daily maintenance respiration?" (Muscatine and Porter 1977, p. 456). Working from the data subsequently established by Porter and other researchers, they attempted to establish a mathematical formula to estimate the "contribution made by zooxanthellae to animal respiration". That research, known by the acronym CZAR, was completed in 1984 by Muscatine, in association with three colleagues, into the symbiotic coral *Stylophora pistillata.* Their evidence was unequivocal: they established quantitatively that "the balance of net fixed carbon (more than 95%) is translocated to the host", and "the contribution of translocated carbon to animal maintenance respiration (CZAR) was 143% in light corals and 58% in shade corals". In conditions of abundant light, they concluded, corals could be almost entirely autotrophic whereas shade-adapted corals, which need to retain nearly half their carbon output for individual growth, remain obligate heterotrophs (Muscatine et al. 1984, p. 181).

Taxonomic Status of Zooxanthellae: Confusion Clarified

During those early post-WWII years of exciting developments in reef science, another series of what may be considered less remarkable but equally important investigations were proceeding into the microworld of protists. Protists are single-celled eukaryotic organisms that include the dinoflagellates, marine organisms with a whirling motion (Gk *dinos*, "whirling") propelled by two flagellae (Lat. *flagellum*, "whip"), first classified in 1885 by the eminent protozoologist Otto Bütschli at the University of Heidelberg as the order Dinoflagellida. Ever since the pioneering work of Antony van Leewenhoek and the numerous advances that stemmed from fascination with the invisible world revealed by the microscope, protozoology had been advancing from the discoveries by Ehrenberg in the 1830s, with his influential study of protists "The organic perfection of Infusoria". Protozoology continued to attract a highly specialized coterie of scientists who were intrigued by that incredible abundance of microorganisms existing between the plant and animal kingdoms, among which were the enigmatic zooxanthellae, with their uncertain taxonomic status.

One of the great, stimulating leaders of protozoology in the immediate post-war years was Richard Pinkham Hall (1900–1969) of New York University, who attracted ambitious young students to his department and to its privately endowed research institute, the Haskins Laboratory (since moved to New Haven and affiliated with Yale). One of his innovative research programmes, in which he developed entirely new methods, was the preparation of suitable media for cultivating marine flagellates and ciliates axenically (Gk *axenos*, "inhospitable to strangers"), i.e. in a culture medium free of contamination from other microorganisms, symbionts and parasites. One such student was Hugo Freudenthal who, having graduated in pharmacy from Columbia University and like so many before him, was drawn to marine science; after studies at Woods Hole, he enrolled under the tutorship of Hall. The consequences led to a remarkable achievement in reef science.

With his strong background in chemistry, and casting around for a suitable doctoral thesis, Freudenthal was approached by John McLaughlin, another of Hall's students, who had recently succeeded in isolating zooxanthellae from one of the species of the jellyfish *Cassiopoeia* in an axenic medium. As the taxonomic status of the zooxanthellae was still in a state of confusion, and with a pure culture of that alga now obtained, an interesting topic might be to study those dinoflagellates further and to describe their life history and taxonomic status. Such a result would make a great contribution to the ecological knowledge of corals and other zooxanthellate organisms in the photic zone.

That suggestion was a remarkable case of serendipity. In 1959, the neophyte 29-year-old Freudenthal, following the procedures established by John McLaughlin and his colleague Paul Zahl, submitted his doctoral thesis on the taxonomy, life cycle and morphology of the zooxanthellae. Three years later, a synopsis was published in the *Journal of Protozoology* giving an absorbing account of the reconstruction of the life cycle of the zooxanthellate symbiont within the scyphozoan (jellyfish) *Cassiopoeia xamachana*. What emerged from his investigations was of first-order significance: a careful description of the various stages of zooxanthellate

Coral spawning under the full moon, showing gametes broadcast into the night, Outer Barrier Ribbon Reef No. 2, 2005, during a research project carried out by Anya Saleh and the author

Porites (boulder or brain) corals

development to maturity, including the gymnodinioid stage as "naked dinoflagellates" (Gk *gymnos*, "naked"), noting the influence of photoperiodicity.

Initially, Freudenthal experienced great difficulty in determining the specific identity of the alga he had isolated from *Cassiopoeia*, particularly its close similarity to *Gymnodinium microadriaticum*. However, he noted, *G. microadriaticum* was much larger and "continued study of the morphology and life cycle may not be as strong as previously suspected". As "none of the existing genera of free-living or parasitic algae are wholly applicable to this organism", he concluded that "for this reason the zooxanthella from *Cassiopoeia* sp. is here labelled a new species, with the specific name *microadriaticum* chosen to maintain the relationship with the earlier report" (Freudenthal 1962, p. 50). Following his carefully detailed discussion, he decided that "a new genus seems the only tenable classification for this zooxanthella, to be called *Symbiodinium* (Gr *symbion*, 'living together') in the family Blastodiniaceae" (Freudenthal 1962, p. 52).

Freudenthal's description of the new genus of *Symbiodinium* and its species *S. microadriaticum* was not readily accepted initially, and controversy followed with some taxonomists asserting that it should be placed within the genus *Gymnodinium*. Freudenthal, however, responded by arguing that the dividing line between parasites and symbionts in some cases is very fine, and on balance he continued to defend his judgement. Finally, as the widespread acceptance of his new descriptor indicates, "*S. microadriaticum* Freudenthal 1962" became firmly established in coral science literature.

By 1984, a satisfactory understanding of coral–algal nutritional and calcification interaction had been achieved. Many intricately detailed problems remained to be solved, but from extensive experimentation and complex reasoning by many, the century-old question about the role of zooxanthellae in coral reef ecology that allowed the construction of massive natural features was brought at least to temporary finality. With that achievement, research focused on the active photosynthetic dinoflagellate *S. microadriaticum*, which became one of the most significant organisms in the ensuing decades of coral reef science. In particular, the dissenting views of Rudolf Blank and Robert Trench stimulated intensive research that yielded a completely new understanding of the fascinating complexity of the coral reef enigma when the molecular structure of *S. microadriaticum* began to be investigated by DNA analysis, beginning with the pioneer work of Rob Rowan (Rowan 1991).

11 A Changing Global Environment: International Response

The scientific activities of the USA in advancing reef knowledge in Bikini, Enewetak and the Mid-Pacific Marine Laboratory throughout the 1950s and later had been accompanied in the same years by a much broader international response to post-war development. To begin reconstruction after the extensive devastation of both the built and natural environments during World War II (WWII), the task for the international community was gargantuan.

Democratization of Science and the Explosion of Research

In an attempt to meet the tremendous challenges ahead, President Harry Truman announced in 1947 the urgent need for the USA to accelerate scientific "research and development". Opportunities multiplied rapidly for aspiring scientists, and stimulated by the nuclear studies in the Marshall Islands, with increasing funds from the US Office of Naval Research and grants from other bodies such as the American National Academy of Sciences, plus university allocations, coral reef research and publication burgeoned.

Quickly, some essential infrastructure was created. Simultaneously, with the revolutionary change in biology early in the 20th century from the approaches of Elton and Tansley, carried through by *inter alia* the brothers Odum, Goreau and Muscatine, scientific research was being democratized radically. Coral reef science was soon a major beneficiary resulting in the USA becoming the dominant coral reef science nation, but accompanied by the world-leading achievements of many Australian tropical reef scientists in Great Barrier Reef centres.

Until the 20th century, throughout the 17th, the 18th and into the early 19th centuries, virtually all scientists came from either the nobility or the wealthier, privileged classes. There were relatively few journals available for publication of research output, and the existing few were mainly within the cloistered confines of established societies such as the venerable 1665 foundations of the *Journal des Sçavans* in Paris and the *Philosophical Transactions of the Royal Society of London*, or in the various publications of museums and universities.

Slowly, the democratizing process, along with the foundation of scientific societies, gathered pace as university access was broadened with the burgeoning demands of an industrializing economy. In contrast to the Neoclassical and Georgian architecture of the privileged, private European sandstone and American Ivy League foundations, the "redbrick" regional universities in Great Britain, which grew out of technical institutes, and the Federal Land-Grant Colleges of Agricultural Arts and Sciences in the USA, established by the Morrill Act of 1862, came into being.

In response to the groundswell for change, the British Association had been founded in 1831 on the model of the *Deutscher Naturforscher und Ärtze* (German Nature Society of Researchers and Physicians). Across the Atlantic, the similar American Association for the Advancement of Science, today the world's largest, was founded in 1848.

After 1950, the small number of journals that had been founded progressively to accommodate the increase in scientific knowledge could not cope. As journals appeared in increasing numbers, including *Nature* in Britain in 1869 and the AAAS journal *Science* in 1880, and reef knowledge exploded, it became apparent that greater coordination of both research and publication was needed. Consequently, in January 1969, the First International Coral Reef Symposium was held in Mandapam, India. Resolutions were passed to reconvene the event every 4 years, and the next took place in 1974 aboard the liner *Marco Polo* while cruising the Great Barrier Reef. That led to the foundation of the International Society for Reef Studies in 1980 at Churchill College, Cambridge, to coordinate research, which 2 years later began publication of its quarterly journal *Coral Reefs* as "a focal point for multidisciplinary literature of analytical and theoretical papers across the broad fields of reef studies". As editor David Stoddart noted in his 1982 *Editorial*, the publication was designed to "play a central role in the emergence of reef studies as a unified discipline" by coordinating

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
DOI 10.1007/978-3-319-07479-5_11,

research and ensuring "the rapid and efficient flow of information between [coral reef and other] scientists".

When personal computers became more widely available in the 1980s, scientists were able to mobilize previously unimaginable volumes of information and seek instant confirmation from colleagues and other sources electronically over the internet and by email. Soon, masses of data and underwater photographs appeared on a scale that could never have been attempted by individuals just two or three decades earlier. Between 1986 and 2002, several important books on coral reefs were published, drawn from the wealth of consolidated data and underwater photography. The first was the large landmark publication *Corals of Australia and the Indo-Pacific* by Chief Scientist John Veron at the Australian Institute of Marine Research (Veron 1986). For the first time in coral reef history, a descriptive account of all species within the 22 families of reef-building scleractinians and 12 non-reef-building scleractinia and non-scleractinian corals became available in 644 informative pages. Illustrated with full-colour images of every species depicted, along with coloured and black-and-white diagrams of inner structure, and distributional maps across the Indian and Pacific oceans, a ready reference work was at scientists' fingertips.

Two years later, in 1988, the United Nations Environment Programme (UNEP) and the International Union for the Conservation of Nature (IUCN) jointly published a three-volume descriptive atlas of *Coral Reefs of the World*, covering the Atlantic and eastern Pacific oceans, the Central and West Pacific, the Indian Ocean, the Red Sea and the Persian Gulf, with extended verbal descriptions, line diagrams and maps (IUCN Conservation Monitoring Centre 1988). An even more comprehensive *World Atlas of Coral Reefs* was published in 2001 by the World Conservation Monitoring Centre of UNEP, a sumptuous 424-page full colour record of the 81 discrete reef complexes in the world, with accompanying descriptive accounts and aerial images from National Aeronautics and Space Administration (NASA) spacecraft. Not only did it feature reefs to a depth of 15 m but it also showed other areas of interest, including adjacent landforms, human settlements, sediment plumes from estuaries, shallow banks and remote independent atolls. An indispensable reference work, it provides yet another example of international cooperation to promote the knowledge and study of coral reefs.

While that volume was in course of publication, in 2000, Veron published his masterwork, the massive three-volume *Corals of the World* (Veron 2000). In 1081 pages, that work distils everything yet discovered about corals into accounts of reef geological and biogeographic history, with keys to genera and species. In addition, it examines the vexing issue of the evolution of species, dealt with previously in his 1995 taxonomic account of *Corals in Space and Time.* Then follows the main text: descriptive accounts of the global coral families with colour images of every species, many identified for the first time, described and photographed by Veron. It includes a massive amount of information and data, organized and lucidly presented by Veron, edited by marine scientist Mary Stafford-Smith. Subsequently, as a vital reference work for scientists, with laptops and electronic notebooks as a part of essential working kit at sea, Veron's CD of 2002, *Coral ID*, with images of every species likely to be encountered, was released to meet the need for instant data retrieval to identify and confirm discoveries, and to document future investigations. In 2004, at the International Coral Reef Symposium in Okinawa, John "Charlie" Veron was awarded the International Coral Reef Society Darwin Medal.

Dr John "Charlie" Veron

The Industrial Heritage: A Degraded Environment

With the democratization of science and an established context for future reef research, global reconstruction remained a perplexing prospect for some of the nations most affected. Despite the grand ambitions expressed in the early post-war years for a new era to be created, the natural landscape had already suffered badly throughout the 19th century as unregulated industrialization in Britain, Europe and the USA gathered pace. Not until Britain's Alkali Act of 1862 was the world's first industrial environmental legislation passed, prohibiting the discharge of waste sulphuric acid and hydrogen sulphide gas into streams and the atmosphere from factories producing commercially essential soda ash in its industrial northwest. Throughout all industrial areas, numerous environmental disasters, crises and flashpoints continued to accumulate. Examples abound, but just a few indicate the spread of degradation.

One of the most appalling episodes was experienced in Belgium's Meuse Valley in 1930, when more than 60 died and several thousand suffered pulmonary attacks from poisonous fluorine emissions from 15 factories in the region. There was a similar occurrence in Donora, Pennsylvania, during Halloween 1948, when a temperature inversion trapped poisonous carbon monoxide emissions from the zinc works of US Steel, killing 20 and injuring hundreds. An even greater mass tragedy was only averted by the sudden onset of heavy precipitation. In 1952, London experienced a catastrophic episode when more than 6000 died of respiratory failure one winter from sulphur-laden smoke discharged from domestic coal fires inside a blanket of fog, creating the phenomenon known as smog. The following year, smog killed some 260 in New York alone and a year later forced the closure of schools in Los Angeles. In tardy response, following an Air Pollution Congress in New York City, the US passed its first Air Pollution Control Act in 1955; the following year, the British Clean Air Act was proclaimed.

Around the world, similar incidents continued to be reported on an even more horrific scale, the most distressing at that time being numerous inexplicable cases of crippling neurological diseases and deaths in Minimata, Japan. By 1956, that epidemic had become an international scandal, and it caused outrage in Japan when it was discovered to have arisen from the continuous discharge of toxic methyl mercury wastes into the water from battery factories along the foreshores of Minimata Bay on Japan's southern island of Kyushu. More than 3000 people were poisoned there by the shellfish that were a major component of the local diet; many died. Even so, the issue was ignored for decades by the Japanese government, health authorities and Chisso Corporation, the company involved. Then, in 2004, the Supreme Court of Japan found in favour of the plaintiffs in the class-action.

As other disasters were reported to be coming together in a pattern of connection, the situation reached a focus in the US in 1962 in Rachel Carson's *Silent Spring*, the greatest indictment ever of rapidly accelerating environmental degradation from widely promoted and available organochlorine pesticides such as DDT. No work before or since has so triggered international awareness and concern, and it remains a definitive record of humankind's heedless destruction of the natural habitat of life. Fortunately, it was written by a highly competent scientist at Woods Hole Marine Laboratory in Massachusetts, and it immediately entered the best-seller lists, in part, ironically, because it was pilloried with massive protests from the manufacturing and agrichemical industries that were being exposed.

Public alarm about the seas was also heightened when the world's first supertanker, BP's Liberia-registered *Torrey Canyon* and its cargo of 120,000 t of crude oil crashed into submerged rocks off the coast of Cornwall in March 1967 and spilled 31 million gallons (80 million litres) across the English Channel. Reaching the shores of Brittany and Normandy as well as the British recreational coastline, it resulted in massive destruction of wildlife. Two years later came drilling blowouts in the Californian Santa Barbara Channel, which fouled the silver beaches of Los Angeles and the Gulf of Mexico, accompanied by devastating wildfires in 1969.[1]

The United Nations Stockholm Conference of 1972

By 1972, the unprecedented scale of dangerous levels of pollution from the rapid growth of science and technology was seriously transforming the environment in countless ways, with major changes to the ecological balance of the biosphere. In particular, the accelerating deterioration of the marine environment and the rapidly increasing pollution of freshwater had become a major international problem. In response, in June of that year, the United Nations convened a Conference on the Human Environment in Stockholm.

With the distinguished Canadian politician and diplomat Maurice Strong being appointed Secretary-General, one of his preparatory acts was to commission a background briefing paper by French microbiologist and humanist philosopher René Dubos and British economist Barbara Ward. With the evocative title *Only One Earth: the Care and Maintenance of a Small Planet* (Ward and Dubos 1972), their paper was later published as a popular 302-page book by Pelican. That landmark publication expanded on Dubos' apt phrase of "think globally, act locally", and the concept of sustainable development Barbara Ward presented in her 1966 book, *Spaceship Earth*, the title believed to be the first use of that powerful image.

From the final plenary session of that Conference came the Stockholm Declaration of 26 "principles", which stressed the need for all nations to maintain the health of the natural resources of the earth, including the air, water, land, flora and fauna. In particular, it focused on representative samples of natural ecosystems, along with the need to safeguard and manage wisely the heritage of wildlife and its habitat, gravely endangered by a combination of adverse factors.

The inherent conflict between the need to safeguard the biosphere on the one hand and post-war enthusiasm for rapid progress in science and technology on the other was a matter of huge concern. Restraint was urged in the discharge of toxic substances that could cause serious or irreversible

[1] Described exhaustively by Bowen (2002, pp. 317–343). Similar disasters have continued, e.g. the *Exxon Valdez* tanker wreck in Prince William Sound, Alaska, in March 1989 that spilled up to 119,000 m^3 of crude oil, and the BP drilling explosion in the Gulf of Mexico in April 2010 that allowed oil to gush out at some 9900 m^3 per day until it was finally brought under control three months later.

damage to ecosystems by releasing heat in quantities or concentrations exceeding the capacity of the environment to render them harmless. The marine environment was covered in a recommendation for all nations to "take all possible steps to prevent pollution of the seas by substances liable to create hazards to human health, to harm living resources and marine life; to damage amenities or to interfere with other legitimate uses of the sea". The immediate outcome of the Conference was the founding of the United Nations Environment Programme to deal with emerging problems in the atmospheric, marine and terrestrial ecosystems.[2]

Soon after that 1972 Conference, an equally pressing issue urged the United Nations into action: the inexcusable continuation of world hunger and malnutrition in the least developed nations. In response, the General Assembly of the United Nations convened the World Food Conference in Rome in 1974, conducted, as noted in its *Proceedings*, "in the shadow of the world food crisis of famine and mass starvation in Bangladesh, India and Ethiopia during 1972/1973".

The World Climate Conference of 1979

Deliberations from the two conferences of Stockholm and Rome were beginning to raise concern among governments, with the growing recognition that problems in the environment and food supply were linked by a common, but not explicitly recognized factor: threatening changes taking place in the world climate. Despite the various Clean Air Acts being enacted, less visible and even more polluting industrial chemical discharges into the atmosphere were proliferating, foremost among which was that of carbon dioxide. Immediate action was needed and the World Meteorological Organization (WMO), with support of other specialized UN agencies, mainly Food and Agricultural Organization (FAO), UN Educational, Scientific and Cultural Organization (UNESCO) and the World Health Organization (WHO), called a World Climate Conference in Geneva from 12 to 23 February 1979.

With American meteorologist Robert White in the chair, his preparatory briefing describing it as a "conference of experts on climate and mankind", was quite specific. The agenda for delegates was to respond "to the growing world-wide concerns about the impacts of natural variations in climate upon world food supply and demand, water resources, land use, and other aspects of society". He continued with a dire warning: "It is also a response to the ominous and significant changes in climate. There are now sufficient indications that some of these potential changes, such as those that might result from increased amounts of atmospheric carbon dioxide, could have a pervasive impact upon the nations of the world and may require unprecedented forms of international action to deal with them effectively" (White 1978, p. 233).

One of the major outcomes of that Conference, in response to the urgency for greater understanding of climate, was the creation 2 months later, at the Eighth WMO Congress in Geneva, of the World Climate Research Programme (WCRP), to operate in conjunction with the International Council for Science (ICSU) and UNESCO's Intergovernmental Oceanographic Commission (IOC). Its express purpose was to focus on two major issues: climate predictability and human influence on climate (WCRP 2006, p. 12).

Carbon Dioxide: The Atmospheric Pollution Issue

One scientist particularly concerned in the early post-war period with climate predictability and human impact was Roger Revelle (1909–1991). Following naval service, he became a vigorous director of the Scripps Institution of Oceanography from 1950 to 1964, when he organized extensive surveys of the Pacific and showed an intense interest in the problems looming from the accumulation of CO_2 in the atmosphere.

In 1896, Swedish scientist Svante Arrhenius, who was awarded the Nobel Prize for chemistry in 1903, reported in the English *Philosophical Magazine* based on quantitative calculations that climate change may be attributable to fluctuations in the carbonic acid content of the air and hence account for measured increases in surface air temperature (Arrhenius 1896). Stimulated by that work, Revelle began researching the accumulation of CO_2 in the atmosphere, and in collaboration with chemist Hans Eduard Suess, grandson of Eduard Suess who had hypothesized and named the Tethys Sea, they published the results of a project funded by the US Office of Naval Research in 1957. Their paper was specific in stating that, because of increasing levels of combustion of fossil fuels as the industrial era progressed, carbon dioxide had been steadily increasing in the upper atmosphere and had exceeded the 19th century total by an additional 15 %. The immediate consequence was that it "would lower the mean level of back radiation in the infrared and thereby increase the average temperature near the earth's surface" (Revelle and Suess 1957, p. 18).

In that observation, we find the origin of the concept of the "greenhouse effect", now part of common understanding as an underlying contributor to climate change (Weart 2003). The term itself, however, is not an accurate analogy because the principle of the greenhouse is to retain warm air generated by solar radiation. In the outside environment, in contrast,

[2] Throughout the post-war years of urgency for reconstruction and industrial development, the need to protect the global environment had prompted the UN in the same year as its foundation in 1945 to create two specialized agencies: UNESCO and the FAO. The WMO followed in 1951.

incoming ultraviolet (UV) shortwave solar radiation, most of which is normally returned to space as longwave infrared radiation, is retained in large part by a mantle of water vapour in its various forms: moisture, clouds, rain, snow. These act to keep the planet habitable some 30 °C warmer than would be the case if it did not exist.

Unfortunately, whereas water vapour, which can amount up to two-thirds of the mantle, is short-lived and exchanges rapidly, the increasing volumes of carbon dioxide and other industrial chemicals being discharged into the atmosphere (nitrous oxide, methane, ozone and fluorocarbons) also collect in the mantle as so-called greenhouse gases (GHGs) and prevent some of the outgoing energy returning to the troposphere (Weart 2003, p. 27). Unlike water vapour, they remain in the mantle for long periods, in some cases for centuries. Consequently, the balancing return of radiant heat back into space is restricted, contributing to the increase in global temperatures. Although the description as a greenhouse is not strictly exact, it has sufficient rhetorical force to remain as a useful analogy.

Anticipating the profoundly deleterious effects of industrial GHGs and the future consequences, Revelle and Suess based their analysis on the table of *World Requirements of Energy 1975–2000* from the 1955 UN International Conference on the Peaceful Uses of Atomic Energy, held in Geneva. Constructed to show the predicted percentages of CO_2 added to the atmosphere each decade until 2000–2009, the amount of CO_2 added in the decade 1950–1959 was 3.9%, but the increase from 1950–1959 to 2000–2009 was estimated to reach a predicted cumulative total of 73.5%. Most disconcertingly, more than half the CO_2 in the atmosphere would be added after 1975, the figures having been calculated on the assumption that “fossil fuel consumption remains constant at the estimated 1955 rate”. The potentially disastrous consequences of that rate of utilization, they asserted, is that “human beings are now carrying out a large scale geophysical experiment of a kind that could not have happened in the past nor be reproduced in the future. Within a few centuries, we are returning to the atmosphere and oceans the concentrated organic carbon stored in sedimentary rocks over hundreds of millions of years” (Revelle and Suess 1957, p. 19; Table I).

Following an intensive mathematical analysis of the possible sources of CO_2 in the atmosphere, including exchange from the oceans, they concluded that since 1950–1959, for the decade 2000–2009, “a total increase of 20–40% in atmospheric CO_2 can be anticipated”. As a disclaimer, though, they stated that “present data on the total amount of CO_2 in the atmosphere, and the rates and mechanisms of CO_2 exchange between the sea and the air, and between the air and the soils, are insufficient to give an accurate base line for measurement of future changes in atmospheric CO_2”. Not included in their article was the disconcerting fact that the world’s population had risen from 2.5 billion in 1950 to more than 4 billion in 1975, and that it was projected to increase by some 1.2% per year to about 6 billion in the year 2000, adding a further significant increase in CO_2.

Their final sentence indicated the direction Revelle intended to proceed: “An opportunity exists during the International Geophysical Year [IGY] to obtain much of the necessary information” (Revelle and Suess 1957, p. 26). Revelle, who had been instrumental in promoting the IGY in 1957/1958, had already begun such planning by persuading Charles Keeling, a promising young post-doctoral student in geochemistry at the California Institute of Technology (Caltech), to join his team at Scripps.

Charles David Keeling (1918–2005) spent his entire professional life at Scripps, starting in 1956. Initially, he began the collection of atmospheric CO_2 on the windy elevated central Californian coastline at Big Sur near Carmel, north of Scripps. In 1957, with funding from an IGY grant, Keeling established the world’s first CO_2 monitoring base at Mauna Loa on “Big Island”, the largest volcanic island of the Hawaiian chain, regarded as an ideal mid-ocean location in the northern hemisphere with minimum CO_2 contamination arising from vegetation and human activities. Since Keeling began his monitoring programme of hourly air samples, the station has been upgraded as technology improved, and it now holds the longest continuous record on the planet. His measurements of the molecules of CO_2 in carefully calibrated parcels of dry air, expressed as parts per million (ppm), to provide whole numbers and so avoid the lengthy fractions after the decimal point, completely vindicated Revelle’s beliefs. Levels of CO_2 in the atmosphere were rising continually, with small annual downward fluctuations in the boreal spring as vegetation burst into life and drew in CO_2 for growth. The increasing quantities, when plotted, revealed an exponential graph known as the Keeling Curve. These were augmented by southern hemisphere records from 1976 on, when the Australian Government established the Cape Grim Baseline Air Pollution Station on the northwestern tip of Tasmania, in the path of the “Roaring Forties”, even more free of terrestrial contaminants than Mauna Loa.

Instability in the Stratosphere: The Ozone Hole

In the stratosphere, between 10 and 50 km above the surface of the earth, is the ozone layer, which absorbs most of the shortwave UV radiation from the sun before it reaches the earth. It is that stratum of sparsely diffused molecules of ozone (O_3)—1 in 100,000 parts of oxygen (O_2)—that absorbs solar UV radiation and makes the planet habitable. Without it, the consequences for humankind would be lethal: melanomas of the skin and eye cataracts. In the wider environment, UV radiation would damage food crops and marine ecosystems, particularly coral reefs in the vulnerable surface photic zone, where even fish have been detected recently with melanomas (Sweet et al. 2012). In the lower troposphere enclosing the surface of the earth, moreover, where it is generated by hydrocarbon emissions from industrial and vehicle exhausts, ozone has a dangerous side.

At the surface of the earth, ozone captures heat, as it does in the stratosphere, moderating incoming radiation, and acts as a GHG; low-level ozone, in fact, is quite a large contributor to global warming. The threat from ozone, however, first became significant around 1970 when British and American chemists became concerned that the ozone layer in the stratosphere would be damaged by the various nitrogen compounds emitted from the exhaust gases of proposed Boeing supersonic aircraft, the Anglo-French Concorde and the Soviet Tupolev. In March 1971, the US Department of Commerce convened a workshop of specialists in atmospheric chemistry in Boulder, Colorado, one of whom was Harold Johnston from the University of California at Berkeley, an expert on the reaction mechanisms of various nitrogen compounds, collectively designated NO_x. Following the workshop, Johnston presented his evidence in an article that received wide exposure in the journal *Science*, its major impact arising from his startling claim that the projected increase in oxides of nitrogen from SST exhaust could “reduce the ozone shield by about a factor of 2, thus permitting harsh radiation below 300 nm to permeate the lower atmosphere” (Johnston 1971).

At that time, Paul Crutzen, a Dutch chemist, motivated by Johnston’s paper, was investigating the possible effects of excessive nitrogen compounds on the ozone layer in the upper atmosphere. In 1973, he submitted his research to the University of Stockholm in a doctoral dissertation entitled “On the photochemistry of ozone in the stratosphere and troposphere by high-flying aircraft”. Several months later, as he reported in a later autobiography (Crutzen 1995), two American chemists, Sherwood Rowland and Mexican-born Mario Molina, sent him an offprint of their paper to *Nature* in 1974 entitled the “Stratospheric sink for chlorofluoromethanes: chlorine catalysed destruction of ozone”. That paper dealt with ozone depletion by chlorine, a component of the chlorofluorocarbons (CFCs) used extensively as a refrigerant in cooling systems and as a propellant in the newly developed aerosol sprays, which, once liberated into the atmosphere, was suspected of causing even greater damage to the ozone layer than nitrogen oxides. Patented by the DuPont Corporation in 1928, CFCs are man-made chemicals (CF_2Cl_2 and $CFCl_3$ were two of the most common) and, because they are chemically inert, were also widely used as rocket fuel in the early decades of space exploration.[3]

[3] See Meadows et al. (2004) for an account of the ozone disaster.

What the research by Rowland and Molina revealed was the process whereby the complex CFC molecules, once free in the atmosphere, whether from spray cans, decommissioned refrigerators, hypersonic jet exhausts, rocket fuel or numerous other industrial applications, are split by UV radiation into their constituents and begin to release chlorine atoms into the ozone layer. Once free, the vagrant chlorine atoms attach themselves to ozone molecules to create the chlorate ClO_3 that in turn becomes broken apart by UV radiation, releasing the chlorine atoms and forming chlorine monoxide (ClO) and O_2. The chlorine monoxide in turn is broken apart by UV radiation, which releases the chlorine atom that bonds onto another O_3 molecule, and the process continues as the chlorine atoms continue progressively to thin the ozone layer.

That paper created shockwaves. The problem it identified is that because CFCs are entirely synthetic, there are no natural processes by which they can degrade and be rendered harmless soon after release. The indisputable facts were that CFCs can remain in the atmosphere for a very long time: “lifetimes in excess of more than 10 and 30 years”, Molina and Rowland reported, “can already be estimated from the known industrial production rates and atmospheric concentrations” (Molina and Rowland 1974, p. 811). Using the metaphor of a “sink” down which discarded matter can be flushed and biodegraded to its constituent elements, they pointed out that in the atmosphere there are “no obvious rapid sinks for their removal”. The only possibility, they continued, would be “stratospheric photolytic dissociation… at altitudes of 20–40 km”. Furthermore, because CFCs are insoluble in water and cannot be degraded by rainout in the troposphere or by dissolution in the ocean, “a major oceanic sink cannot be inferred”. Continuing, with a sombre concluding comment, the two stated that “it seems quite clear the atmosphere has only a finite capacity for absorbing chlorine atoms produced in the stratosphere, and that important consequences may result” (Molina and Rowland 1974, p. 812).

Building on that paper, which presented evidence that production rates of CFCs had been increasing by 8.7 % per year in the US alone, and in other parts of the world at proportionally alarming rates, Crutzen began an intensive investigation. Finally, he calculated “a model analysis of the potential ozone depletion resulting from continued use of the fluorocarbons (CFCs) which indicated the possibility of up to 40 % ozone depletion as a result of continued use of these compounds at 1974 rates” (Crutzen 1995, p. 209). Those findings by Molina, Rowland and Crutzen eventuated in their shared award of the Nobel Prize for Chemistry in 1995.

After continuing media and scientific speculation, accompanied by intensive research activity by National Oceanic and Atmospheric Administration (NOAA) and the US National Center for Atmospheric Research (NCAR), the US Department of Energy in 1982 established the Carbon

Dioxide Information Analysis Center at the Oak Ridge National Laboratory. Functioning as the World Data Center for Atmospheric Trace Gases from 53 monitoring stations in 30 nations across the globe, Alaska to Antarctica, an even more extensive range of information on other GHGs, including methane (CH_4) and nitrous oxide (N_2O), was collected in addition to data on ozone. The findings provided compelling evidence for the United Nations to convene a conference of member nations in Vienna to consider the serious consequences of "the potentially harmful impact on human health and the environment through modification of the ozone layer".[4]

Following the deliberations, on 22 March 1985, the Vienna Convention for the Protection of the Ozone Layer concluded with a pledge by all nations to exchange observational and research data on the physics and chemistry of the atmosphere, on health, biological and photodegradation effects, and influences on climate. In addition, attention was directed more broadly to the wider range of "chemical substances of natural and anthropogenic origin…thought to have the potential to modify the chemical and physical properties of the ozone layer", namely, carbon monoxide, carbon dioxide, methane, nitrous oxide, nitrogen oxides and halogenated alkanes.[5] Signature by member nations was scheduled for Vienna between 22 March and 21 September 1985, and for UN Headquarters in New York between 22 September and 21 March 1986.

Well before many member states could sign, however, a virtual bombshell exploded in the political and industrial domains in May 1985. Under the leadership of Joe Farman, the British Antarctic Survey at its Halley Research Station (73° S 26° W) discovered among the measurements they were making that the protective ozone layer had thinned to barely 30 % of its normal cover, far worse than Crutzen's prediction of a 60 % ozone remainder. "We were sitting on top of one of the biggest environmental discoveries of the decade…or even perhaps of the century", Farman recalled in a BBC World Service broadcast in July 1999. In their report to *Nature* in 1985, soon after the discovery, his team stated that their instruments indicated unquestionably "that the spring values of total O_3 in Antarctica have now fallen considerably…and possible chemical causes must be considered", particularly because the Antarctic stratosphere is "uniquely sensitive to growth of inorganic chlorine" (Farman et al. 1985, p. 207).

The monthly measurements from late 1959 to mid-1980 (Farman et al. 1985, p. 208, Fig. 2) showed a dramatic decline in O_3 concentrations, starting in 1970, just when CFCs were coming into increasing production. In their opinion, an intensive programme of studies was needed to improve understanding of stratospheric chemistry, "and thereby improve considerably the prediction of effects on the ozone layer for future halocarbon releases" (Farman et al. 1985, p. 210).

With convincing proof by Farman's team in Antarctica of the formation of a huge popularly labelled ozone hole in the southern atmosphere, UNEP, the WMO and the ICSU before the year was out and with a sense of great urgency, convened a joint meeting of 29 climate scientists in Villach, Austria, in October 1985. Their task, at the time, was "to assess the role of increased carbon dioxide and other radiatively active constituents of the atmosphere…[since] it is now believed, from their earlier modelling experiments that indicated a doubling of CO_2 concentration, along with an increase of surface temperature of between 1.5 and 4.5 °C and a potential sea-level rise of 20–140 cm…in the first half of the coming century a rise of global mean temperature could occur, which is greater than any in man's history".[6] Even more threateningly, in their concluding remarks, the group stated that the potential for GHGs other than CO_2 in changing climate was already about as important as that of CO_2.

Their recommended actions, known as the Villach Declaration, stressed the need for priority to be given to the World Climate Research Programme, with long-term monitoring and interpretation of radiatively important atmospheric constituents in addition to CO_2, including aerosols and solar irradiance, as well as recording rises in sea levels. In addition, the scientists urged UNEP, the WMO and the ICSU to establish a small task force on GHGs and to help ensure that appropriate agencies and bodies follow up the recommendations of Villach 1985.

There was an immediate result: by 2050 at the current rate of production and emission into the atmosphere, ozone depletion would have risen to at least 50 % in the northern hemisphere's mid-latitudes and 70 % in southern mid-latitudes. Recognizing the need for stronger measures, a world conference adopted the Montreal Protocol on Substances that Deplete the Ozone Layer, in September 1987 (UNEP 2003). The Protocol was a comprehensive agreement that set schedules for phasing out not only CFCs but also more dangerous halogen pollutants: those containing carbon, chlorine and bromine.[7] Even so, the target dates, with concessions to developing countries, ranged from 1994 for the worst pollutants to 2020 for hydrobromofluorocarbons. Barely 6 months later, on 4 March 1988, DuPont chairman Richard Heckert wrote to US senators maintaining his opposition to the Protocol with the claim that present "scientific

[4] Preamble to the *Proceedings* of the Vienna Convention for the Protection of the Ozone Layer.

[5] Annex I of the *Proceedings* of the Vienna Convention for the Protection of the Ozone Layer.

[6] *Introduction* to the Villach Statement.

[7] The pollutants specified in the Montreal Protocol were halo-carbons, carbon tetrachloride, methyl chloroform, hydrofluorocarbons, hydrobromofluorocarbons, methyl bromide and bromochloromethane. *Halogen*, from Gk *halys*, "the sea", so "salt generating".

evidence does not point to the need for dramatic CFC emission reductions”.[8]

Despite corporate intransigence and the continuing manufacture of CFCs in Third World countries, from that encouraging start, international action maintained the search for acceptable policies to reduce proliferation of other GHGs with the formation in 1988 of the Intergovernmental Panel on Climate Change (IPCC). Managed jointly by the WMO and UNEP, its task was to continue monitoring changes, not only to climate but also in the biosphere. The disturbing evidence of the continued rise of GHGs, which produced more stringent regulations in the Montreal Protocol, led to the Second World Climate Conference from September to November 1990 and including delegates from 137 nations, to review WMO and UNEP policy recommendations. The Conference regrettably failed to secure any specified targets, mainly because of the inflexibility of many industrialized nations to accept the plan of the European Community to maintain carbon dioxide emission levels for 1990 to the year 2000.

Two years later, the 1992 UN Conference on Environment and Development, known popularly as the “Earth Summit”, was convened in Rio de Janeiro to consider a revised Protocol in yet another quest for international agreement during the forthcoming attempt to formulate an agreement to stabilize global emissions. Meeting in Kyoto in December 1997, after sustained resistance by some of the most dangerous CO_2-emitting nations, targets were finally set for the reduction of GHG emissions: carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), sulphur hexafluoride (SF_6), fluorocarbons and perfluorocarbons. Even so, as the world’s climate continued to deteriorate, exacerbated by the increasing range of nitrogen oxides, the Kyoto Protocol to the UNFCCC Conference was not set to come into force until 16 February 2005. Assuming total international compliance with the provisions of the Montreal and Kyoto Protocols, unfortunately for the atmosphere and the moderation of global warming, numerous studies of dangerous emissions by NASA scientists in its Goddard Institute for Space Studies (GISS) indicated that although CFCs have now been banned internationally, the damaged ozone layer is not expected to recover until around 2050 (Tabazedeh and Cordero 2004, p. 649). The greater significance of the ozone problem and research to solve it came with international recognition of the fragility of the atmosphere as industrial pollutants were being discharged progressively, with minimal controls.

By the time of the Kyoto Protocol, from which developing nations continued to be exempted, and noting that the US Senate did not ratify it even though the USA was producing 36 % of world emissions at the time, climate change had been recognized by all other responsible nations as a reality. The forebodings of coral reef scientists, who had been documenting serious disturbances in the marine biosphere as possibly attributable to rising global temperatures, were becoming evident, not as alarmist but fully justified early indications of dangerous developments that had been taking place in the world’s climate that introduced a new concept into climatic discourse: global warming.

The Discovery of Global Warming

While scientists were preoccupied with atmospheric pollution issues, international politics had been becoming increasingly threatening. Back in June 1948, as the Soviet Union strengthened its “Iron Curtain”, the Russian army blocked Allied access to Berlin in an attempt to bring the divided, occupied city under sole communist control. As confrontation between the USA and the Soviet Union in the ensuing decade moved dangerously close to nuclear war, in 1959 in project Iceworm, the US Army established a secret missile base in far northwestern Greenland near its early warning missile radar installation at Thule. Their public press cover described it as an “Army Polar Research and Development Center”, with a designation as Camp Century. An extensive network of tunnels was excavated within which a military camp was laid out from prefabricated steel and corrugated iron buildings. These were then buried under the snow and powered by a portable nuclear reactor to accommodate 200 men over the following years.

To find bedrock through the ice, three bores were drilled: in 1961, 1962 and 1963, the third successfully reaching bedrock at 1387 m in July 1966. As the nuclear threat began to ease, however, the project was discontinued and the base abandoned. To retrieve the valuable climatic data, a Danish–American team under the leadership of Willi Dansgaard continued analysis of the Camp Century ice cores (Dansgaard et al. 1971). To extend coverage in the Greenland Ice Sheet Project (GISP), other bases were established by 1960 as part of the Distant Early Warning missile defence system (the DEW Line), among which Dye-3 became significant, with its cores being analysed by Swiss glaciologist Hans Oeschger.

The evidence was perplexing. Despite concern over the increasing CO_2 content in the atmosphere, scientific debate was equally concerned from palaeo-records revealed in ice cores by the disturbing finding that a cooling trend seemed to be developing, which even became magnified into a possibility that the earth could be entering a new ice age. However, a decade later, the findings stimulated internationally renowned geoscientist Wallace Broecker at the Lamont–Doherty Earth Observatory of Columbia University to question the inference that “the O_2 record in the Greenland ice cores strongly suggests the present cooling as one of

[8] Greenpeace Position Paper, prepared for the 9th meeting of Parties to the Montreal Protocol, September 1997.

a long series of similar natural climate fluctuations" which followed 80- and 180-year cycles (Broecker 1975, p. 460). His doubt that cooling was in progress came from Keeling's Mauna Loa records and additional evidence in further cores. Although scientific and public discussion had been covering the manifold possibilities of climate change for several decades, that possibility stimulated Broecker to ask the critical question: "Are we on the brink of a pronounced global warming?" When that idea appeared as the title of his 1975 article in *Science*, it was the first explicit use of the term "global warming". Since then, like "greenhouse gases", it has become a fixture in all environmental debate, and in 2003 a book by Spencer Weart (Weart 2003) presented a descriptive survey of environmental politics over the past half century.

In his 1975 discussion of global warming, Broecker dismissed the cooling possibility and put in its place a stark future: even if the observed cooling "bottoms out" during the next decade or so, "by the first decade of the next century, we may experience global temperatures warmer than any in the last 2000 years". Not only atmospheric saturation by CO_2 but also the increasing density of "dust" coming from "man-made particles" (industrial aerosol emissions of colloidal dimensions) is a climate threat because "the response of the global temperature to atmospheric CO_2 content is not linear. As the CO_2 content rises, the absorption of infra-red radiation will "saturate" an ever greater portion of the band". That led Broecker to warn in 1975 that "global temperature would begin a dramatic rise which would continue for about four decades (i.e. half the 80-year cycles). The warming would by the year 2000 bring average global temperatures beyond the range experienced during the previous 1000 years. Until chemical fuel consumption is dramatically reduced, global temperatures would continue to rise" (Broecker 1975, p. 462).

Carbon Emissions: The Consequences

In the decades following and as research progressed, evidence was accumulating to indicate that an unseen consequence of the unremitting discharge of carbon dioxide into the atmosphere is reef collapse. Throughout geological and pre-industrial times over the past 420,000 years, as revealed from ice-coring projects in Greenland and Antarctica, carbon levels in the atmosphere for most of Earth's history had been falling and had remained below 300 parts per million (ppm).

Palaeographic evidence certainly reveals fluctuating carbon levels, as the Antarctic Vostok study confirmed empirically in 1999, but they have never been as high as today. By 2007, however, Mauna Loa Observatory data disclosed that the world's atmospheric concentration of CO_2 had climbed to 380 ppm, the highest in 740,000 years (Hoegh-Guldberg et al. 2007b, p. 1737), of which more than 30 % has been taken up by the oceans and on present indications is considered a danger point for reef survival. In August 2012, NOAA reported that Mauna Loa readings had reached 392.41 ppm with no sign of slowing, and in July 2013 it had reached 397.41 ppm.

Measured in terms of mass from NASA Earth Observatory data, the atmosphere held 550 billion t (550 GtC) of carbon in 1800: by 2008, that had climbed to 750 GtC, an increase of more than 36 %. As Australian National University earth and palaeoclimate scientist Andrew Glikson citing those data has observed trenchantly, to date, the oceans have long been tacitly accepted as a carbon sink for atmospheric emissions without any thought to the consequences. Today, he warned, the oceans "contain about fifty times the current CO_2 inventory of 750 GtC, which…is already beginning to retard the growth of calcifying organisms, including corals and plankton" (Glikson 2008, pp. 2–065, 2–125).

A major consequence from the reaction of carbon dioxide with seawater is the formation of carbonic acid that in turn dissociates (breaks apart) the dissolved carbonate and decreases the available carbonate ion concentrations from which polyps and all marine organisms build their skeletons or shells to create the reef biosphere. The variety is extensive, and includes not only the 600 or so species of hard and soft corals and hydrozoans but also some 25 % of all species of bony fish, reptiles such as sea snakes and turtles, crustaceans, gastropod and cephalopod molluscs and echinoderms. Even further, there are calcified plants, particularly green halimeda and crustose red coralline algae which form part of the basic reef foundations, as well as the extensive range of calcifying protists such as diatoms, forams (foraminiferans) and coccoliths (coccolithophoroids).

One of the most discerning summaries of reef disturbance from the unremitting discharge of carbon dioxide into the atmosphere, with predictions of future events affecting coral reefs from an ecological perspective, was made as early as 2000 at a National Academy of Sciences colloquium by Scripps marine biologist Nancy Knowlton (Knowlton 2001b). In her presentation, she surveyed the unprecedented change in reefs during the Cenozoic Era following the great extinction event 65 million years ago, known as the K/T boundary,[9] when the dinosaurs perished, the Cretaceous Period came to a close, and the Tertiary Period of the Palaeogene Epoch began when all modern coral reef families appeared.

[9] K for German *Kreidzeit* (Cretaceous, Lat. *creta*, "chalk") because C designates the Cambrian Period, and T for the ensuing Tertiary Period. Cenozoic derives from the Latin *recens*: "recent". An alternative term seen is "Cainozoic" from the Greek *kainos*, also meaning "recent". The impact on reefs is discussed in Veron (2008a, pp. 81–88).

As reefs have increasingly degraded, she explained, biodiversity has continued to decline, and bleaching has severely affected symbiosis and reduced the ability of zooxanthellae to provide nutrients to their polyp hosts. Worse, as reefs collapse, their reproductive capability is weakened from lowered gamete densities during the brief summer spawning episodes when sperm and ova are broadcast into a water column often contaminated by increasing quantities of chemicals and pollutants. A further most disturbing consequence she identified is likely to follow from the Allee effect—proposed in 1931 by ecologist Warder Clyde Allee—whereby reproductive capacity is lowered as population size decreases, which leads to inbreeding, hybridization and stunted, impoverished "weedy" coral colonies with shorter lifespans. As many herbivores, mainly fish and urchins that maintain the ecological balance of reefs by grazing on infiltrating algae, begin to disappear, coral cover diminishes and major changes continue. That situation is already manifest in the Caribbean, as discussed earlier, where the almost complete loss of the urchin *Diadema antillarum*, despite some recovery in places such as St Croix (Miller et al. 2003, p. 182), has allowed aggressive algae to invade, preventing newly hatched coral planulae from finding firm substrata for settlement and growth.

The inevitable outcome, as biologists have been observing for several decades since reef degradation became manifest, and as Knowlton explained, is an accelerated loss of habitat for many other animals. That then leads to chain reactions affecting the biodiversity of other biota, such as flatworms, segmented worms, chordates and sponges, which exist in various symbioses and mutualisms with them. "The recent history of coral reefs", Knowlton concluded, "suggests that collapse is not impossible, and indeed, that we may be closer to worldwide collapse than we realize" (Knowlton 2001b, p. 5424).

The processes described and foreshadowed by Knowlton are the classical symptoms of ecological succession as spaces or seres (Lat. *seresco*, "to become dry") are created, and marine habitats become haloseres, which provide opportunities for invaders on degraded reefs. The future of turtles, which are obligate reef dwellers, is particularly precarious because global warming of coastlines has already begun to affect their sex ratios. In 2006, David Booth at the University of Queensland reported the results of his study of rising sea temperature on turtle fecundity at the Great Barrier Reef, which revealed that mostly males are incubated in nests where the sand temperature is 22.5–27 °C, whereas at > 29 °C, females are incubated. With rising temperature, a predominance of females is being recorded that will lead inevitably to reduced population sizes (Booth 2006, p. 274). That in turn will lead to further reef changes as ecological succession continues.

Hoegh-Guldberg expanded on the calcification issue with the stark warning that the quantities of carbon dioxide entering the oceans today are irreversible on human timescales (Hoegh-Guldberg et al. 2007b), and if they continue at present rates, the escalating discharge of CO_2 into the atmosphere and oceans will alter its chemical balance permanently. As Hoegh-Guldberg described the present situation, reinforcing Knowlton's comments, corals with reduced calcium may respond by building shorter, smaller branches, have less skeletal density and hence be more fragile to wave action in stormy weather. Alternatively, in an effort to maintain greater skeletal density, they will need to sacrifice reproductive capacity.

To heighten awareness, Hoegh-Guldberg introduced a concept that has been receiving greater attention recently: that of the "tipping point" when continuing sequences of subliminal actions attain a certain stage and begin to initiate changes that become irreversible. The great tragedy is that even when the tipping point or critical threshold is reached, it is not recognized, and contributing actions are not moderated or ceased in time to preclude further disaster. From his extensive experience, Hoegh-Guldberg believes that we have moved closer to that stage. "If pushed far enough", he speculated, "the ecosystem may exceed a 'tipping point' and change rapidly into an alternative state with its own inherent resilience and stability, often making the possibility of returning to a coral-dominated state difficult" (Hoegh-Guldberg et al. 2007b, pp. 1738–1739). To strengthen his warning on the consequences of passing that threshold, in an article with two colleagues, Hoegh-Guldberg could not have been more direct: as those processes continue, he asserted, repeating Knowlton's warning, coral reefs as we know them will simply disappear (Eakin et al. 2008, p. 29).

That stern warning was repeated in a submission by the Inter-Academy Panel representing 70 scientific academies around the world to the Bonn Climate Change talks in June 2009, preparatory to the Copenhagen Climate Change Conference in December 2009 charged with drafting a successor agreement to the then superseded Kyoto Protocol. If CO_2 continues to be released into the atmosphere at current rates without radical controls by all emitting nations, the Panel warned, once 450 ppm is reached, some 95 % of tropical reefs will be unable to support coral growth. That situation becomes potentially fatal because at 550 ppm, coral reefs could start dissolving as the CO_2 lowers pH and reduces the calcium carbonate ion saturation state beyond minimum levels.

However, there are precedents in the geological record for extreme changes. In an investigation published in 2010, a team of scientists from several universities, led by Jonathan Payne of Stanford, suspected that sustained volcanic eruptions during a period up to several million years had changed the CO_2 composition of the atmosphere, which then led to massive increases in acidification of seawater. Their research led them to extensive volcanically formed limestone cliffs in Guizhou Province in southeast China, where they analysed calcium isotopes extracted from the deposits. They identified an "abrupt shift in style of carbonate sedimentation and… the carbon isotope $\delta^{13}C$ composition of carbonate minerals which reflected a change in [the] global $\delta^{44/40}Ca$ composition of seawater".[10] The inference they drew was that alterations to the carbonate in seawater from CO_2 saturation had lowered pH values, which increased carbonic acid content. That disruptive variation to the ocean, they hypothesized, was the final event that caused the greatest mass extinction ever known. Although a repetition is highly unlikely, the dire consequences of further increases in atmospheric CO_2 were brought to international attention on 22 April 2010, when the US National Research Council released its Report to Congress *Ocean Acidification: A National Strategy to Meet the Challenges of a Changing Ocean*. With a million tonnes of CO_2 an hour being absorbed by the oceans, the latter are 30 % more acidic than in 1800, and "the rate of change exceeds any known to have occurred for the past hundreds of thousands of years. The consequences will be that unless anthropogenic CO_2 is controlled by some other means, the average pH [alkalinity index] of the ocean will continue to fall".

The term "acidification", however, is not entirely accurate, even if it sends a strong warning signal. Like the earlier neologism of "greenhouse gases" that contribute to atmospheric warming, acidification has acquired similar rhetorical usage in climate discussions. To be clear, the seas at present are not acidic: they are alkaline (or basic), and they will remain so while ever-dissolved carbonate from terrestrial sources continues to accumulate on the seafloor.[11] Even so, there is no comfort in that. During the 17th century, seawater had an alkalinity reading of ~8.2, whereas today it is almost 8.179: on current indications, it is projected to decrease to around 7.9 (Veron et al. 2009, p. 1430). That is a serious decline of some 25 % as measured on the pH logarithmic scale.

In its report to Congress, the US National Research Council stressed the risk of "ecosystem changes which threaten coral reefs, fisheries, protected species, and other natural resources of value to society".[12] With decreasingly alkaline seas, if atmospheric CO_2 levels continue to rise to a critical 450 ppm, then the availability of carbonate for calcifying organisms will fall below minimum levels and in combination with warming waters already causing extensive bleaching, reefs will be unable to sustain their former condition.

At the International Coral Reef Society conference in Cairns in July 2012, it was reported that the IPCC predicts that "by 2030, the Great Barrier Reef will be functionally extinct". The Consensus Statement from the 2500 participants issued by the International Coral Reef Symposium (ICRS) Secretariat made it clear that "this combined change in temperature and ocean chemistry has not occurred since the last reef crisis 55 million years ago. A concerted effort to preserve reefs for the future demands action at global level, but will also benefit hugely from continued local protection". Wistfully, Research Director of Australian Institute of Marine Science (AIMS) Peter Doherty commented that on present indications, Australia appeared to be "losing the war" to save the Great Barrier Reef.[13]

Levels of apprehension must inevitably rise if the Queensland Government ignores UNESCO's warning on 1 June 2012 that the Reef's World Heritage listing may be lost if it continues current plans to increase coal export facilities from Curtis Island and the Port of Gladstone. Not only does dredging seabed channels and overdeveloping the region disturb the already delicate balance of its ecology but also putting more coal into circulation will exacerbate atmospheric pollution. Further evidence came as recently as June 2012 from my own investigation since a previous expedition in 2006. Surveys of the Outer Barrier Ribbon Reefs (16° N) and the Low Isles closer to Port Douglas (16.30° N) revealed the widespread formation of haloseres leading to dominance of soft corals and significant loss of biodiversity. The same picture emerged in mid-reef locations east of the Whitsunday Islands group (~20° S): considerable storm damage and markedly diminished biodiversity.

The cumulative evidence presented so far is starting to provide a possible future for reefs if human activity continues to overload the atmosphere with carbon. The world will not end, but it will certainly change beyond its present condition, with farm and grazing lands even more impoverished from reduced rainfall as aridity spreads. That will almost certainly lead to major conflicts over access to already diminishing freshwater for rural people dependent on glacial melt, aquifers, lakes and flowing rivers, as the dispute between Pakistan and India over Indus River water illustrates. Similarly threatening are supplies for the growing masses in ever-increasing urban concentrations for which water has to be piped in, often over considerable distances, from desalinization plants or recycled water reservoirs. In terms of reefs, the processes already in train worsening their crisis condition will continue to a point in the not-too-distant future when living reef colonies will collapse in places, and crumbling calcium mounds overgrown by algae will become more common.

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[10] Payne et al. 2010. The symbols $\delta^{13}C$ and $\delta^{44/40}Ca$, known as "delta values", indicate the ratios of normal carbon and calcium to their particular isotopes. During violent earth movements, isotope proportions change, and the resulting delta (δ) ratios which indicate abnormal conditions are expressed as parts per thousand (‰). See next chapter.

[11] Described by Veron (2008a, pp. 214–216), as a "giant antacid tablet".

[12] NRC Report to Congress, 22 April 2010.

[13] Ben Cubby, *News Review*, *Sydney Morning Herald*, 14–15 July 2012, p. 5.

Climate Anomalies and the *El Niño* Phenomenon

12

Well before coral scientists found evidence to link warming waters with pollution and outbreaks of disease, many had become deeply concerned about rising sea surface temperatures (SSTs) from their individual laboratory and field research activities. Reef-building corals are environmentally restricted to the tropical photic zone, the relatively uniform layer of wave-mixed surface water warmed by the sun to between 22 and 28 °C (71.6–82.4 °F) and bounded by a transitional thermocline zone between 100 and 200 m below, where an accompanying pycnocline zone of increasing density (Gk *pyknos*, "dense") begins. These form the halocline layer (Gk *halys*, "the sea"), an intermediate zone of increasing salinity down to 2000 m, where temperatures decrease rapidly until they become close to zero.

Paul Jokiel and Steve Coles recorded the thermal tolerance range of corals as early as 1969 in laboratory experiments to evaluate the effects of rising water temperature when a nuclear power plant was proposed for Kane'ohe Bay in Hawaii (Steve Coles, pers. comm.). Although the proposal never eventuated, their results established that corals die within two weeks in temperatures below 18 °C, and after a few days when they rise above 32 °C (Jokiel and Coles 1977, pp. 201–208). Outside that range, corals cease to flourish and higher water temperature over an extended period can be fatal to several species. Consequently, when some scientists reported a marked increase of 4–6° in Galapagos surface waters in 1982, barely 650 miles (~ 1000 km) due west on the equator from Ecuador, it foreboded a serious disturbance.

Because December in Hispanic cultures is colloquially referred to as the month of *El Niño*, in Spanish the "Little Boy" and by inference, the "Christ Child", when meteorologists in the mid-20th century began to investigate the phenomenon of irregular warming of eastern Pacific waters, they adapted that term. The December phases of periodic higher SST became known as *El Niño* events, so a new, enduring concept entered reef literature to become essential to understanding climate change and its impact on the future of coral reefs.

Particularly sensitive to warming waters are the coastal regions of Ecuador and Peru, and when an *El Niño* event appeared imminent, it threatened their economies. In most years, as strong coastal winds push surface waters west and allow upwelling of the deep, cool, phytoplankton-rich waters of the north-flowing Peru current, enormous shoals of anchoveta (*Engraulis ringens*), a species of the family Engraulidae, generally some 20 cm (8 in.) long fuel one of the world's most productive fisheries. In the 1950s, factories were established all along the coast, and by 1970, Peru caught one-quarter of all fish taken worldwide and was the market leader for processing the anchoveta into fishmeal for export to the aquaculture and poultry industries. The harvest, however, was not always assured: fishers had known for at least two centuries that periodically, usually in a cycle between 2 and 7 years, the cool current originating in the Antarctic was invaded by warmer equatorial waters from the tropical west that suppressed the upwelling-supported phytoplankton blooms and reduced the catch significantly.

The Barometric See-Saw: The *El Niño* Puzzle

First steps towards understanding *El Niño* and climate anomalies (scientists employ that term to describe departures from fixed long-term averages) and, consequently, the causes of contemporary global warming and reef disturbance, arose from disasters during the occupation of India by the British Raj in the later decades of the 19th century.

Droughts are tragically repeated events in India, often occurring simultaneously in the neighbouring Indian Ocean regions of Ethiopia, South Africa, Australia and China. Following the horrifying death toll in the Calcutta cyclone of 1864 that killed 70,000, the British Government established the India Meteorological Department (IMD) to predict the onset of cyclones that come out of the Bay of Bengal at intervals of approximately 5–7 years. In 1867, Henry Francis Blanford (1834–1893), geologist and professor of science in Calcutta, was appointed Meteorological Reporter for Bengal

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with instructions to provide long-term weather forecasts and predict the arrival of the summer monsoon rains. From the Portuguese *monção*, a seasonal wind, monsoons can be either life-giving or life-threatening, depending on when they come. Soon after the establishment of the IMD came the horrendous drought of 1876–1879 that killed 6–10 million in India and 10–20 million in China. There was a similar devastation in Abyssinia (today, Ethiopia), where one-third of its 4 million people died, and Russia registered ~500,000 deaths. In the next global drought of 1896–1902, 12–29 million died in India and 10–30 million in China (Davis 2001, p. 7).

Blanford, who must have been appalled as the death and disease reports came in, collected weather data across India from the Himalayas to islands in the Indian Ocean, which, from correlation of monthly air pressure readings with precipitation, revealed that heavy snowfalls on the Himalayas resulted in decreased rainfall on the plains. By that time, telegraph cables had connected the world, and when the monsoon failed to arrive in 1877, and having collected the barometric data for India, he contacted a southern colony of the Empire for additional information. The reply from Charles Todd, Government Meteorologist for South Australia in Adelaide, was surprising; Blanford discovered that, like India, Australia was also experiencing extremely high pressures. The same result came from correspondents in Shanghai, then a British Treaty Port.

The Indian Ocean, encompassing a great arena from eastern Africa to Mauritius, Australia and across to Indonesia was, given the barometric readings from several other meteorological centres, clearly a single zone of high pressure, as also was Siberia near the Aral Sea. As Blanford's theory was based on a belief that the air pressure is governed by sunspot flares that increase solar radiation and that occur in cycles of 11 years, which seemed to match the frequency of some famines, that condition contrasted with the usual low pressure systems observed in the monsoon season. Consequently, he sent a note to *Nature* in 1878 (Blanford 1882, pp. 477–482) that provided an instantly recognizable descriptive term for the phenomenon he developed in detail in his official 1882 *Report on the Meteorology of India* to the government. Monsoons are generated under low-pressure systems, which enable the warm seas to pass moisture into the troposphere and form the dense rain-giving cloud masses, so Blanford had found the first clue to interpreting the mystery of weather irregularities. Unwittingly, perhaps, he began the new interface science of ocean/atmosphere interaction that has become essential to 21st century understanding of rising SSTs and climate change impacts on coral reefs.

In 1889, the mathematician Gilbert Thomas Walker (1868–1958) was appointed Director-General of Observatories for India. Following the disastrous famine created by the drought of 1896–1902, Walker was requested to investigate more exhaustively the causes of monsoon failure, and to offer predictions. In effect, his task was to discover the pattern underlying the alternating global droughts that moved eastbound from Nigeria and Ethiopia to India, China and Australia, and then across the Pacific to Ecuador and Peru. In a rigorously mathematical way, he began by investigating the relationships between air pressure and rainfall, two of the conditions underlying all weather events.

By that time, a number of meteorologists had attempted to solve the monsoon failure problem and, from the accumulation of data on barometric pressure differences, Walker employed the statistical technique of regression equations through which the behaviour of variables could be predicted. From past weather records and atmospheric measurements obtained between 1923 and 1928 across the Indian and Pacific oceans (Cairo and South Africa to Buenos Aires), Walker established that the see-saw phenomenon described by Blanford was not caused by sunspot cycles but by a periodic movement of pressure and rainfall centres along the Equator. In 1924, he named that phenomenon the Southern Oscillation, to distinguish it from the North Pacific and North Atlantic Oscillations, two similar phenomena he discovered from regression equations applied to other datasets.

What emerged from Walker's discoveries was an almost unbelievable possibility at that time: in some way, monsoon weather over southern Asia that oscillated across the Pacific at irregular annual cycles was linked to weather patterns in parts of Africa and Australia, and even in western Canada and the USA. In 1924, Walker moved to the chair of meteorology at Imperial College, London, having made his great contribution: the significant discovery that the failure of monsoons over India always coincided with high pressures in the Indian Ocean and low pressures in the mid-Pacific at Tahiti.

Discovery of the Southern Oscillation and the Walker Circulation

Walker's work was not followed up until renewed interest in the meteorological implications of the global pressure differentials he described as the Southern Oscillation were revived in Batavia (today Djakarta) by Hendrik Petrus Berlage (1896–1968), and in Los Angeles by Jacob Bjerknes (1897–1975). Both men, instead of using the complex mathematical method of Walker, adopted the approach of analysing pressure differences between two stations.

Berlage first investigated the monsoon issue in 1926 when in charge of the Meteorological Observatory in Batavia, coming across a curious verbal tradition of Peruvian fishers dating from 1791 about a warm, east-moving equatorial countercurrent which had been recorded in 1894 by the politician Victor Eguiguren.[1] The irregular *contracorriente El Niño*, as Peruvian fishers called it, provides a balancing return of water during *El Niño* events between the westbound North Pacific and South Pacific equatorial currents, each part of the two great circulating Pacific gyres where the Coriolis force from the earth's rotation moving them is minimal. Its effects were also experienced in the northeastern Pacific when it reached San Diego, where Wayland Vaughan at Scripps had a personal interest because he was building his oceanographic network, in part through strong support from the Pan Pacific Scientific Congresses with their concern for a better understanding of climatic activity in the Pacific basin.

At the 1926 Pan-Pacific Science Congress in Tokyo, an account of the personal observations of the 1925/1926 *El Niño* warming event by American ornithologist Robert Murphy (1887–1973), who had been in Peru recording birdlife, was presented at Vaughan's request by Scripps oceanographer George McEwen (1882–1972). In some way McEwen had secured copies of Eguiguren's records of 1894 which had been passed on to Berlage, supplemented by SST data collected by merchant ships travelling between Valparaiso and New York via the Panama Canal. As historian Gregory Cushman has recorded "Berlage made the crucial connection between Peruvian events and climate anomalies on the other side of the Pacific…and determined that they correlated almost exactly with the 6–7 years cycle in the 'east monsoon' since 1864…and announced his results at the 1929 Pacific Science Congress held in Batavia to showcase Dutch colonial science" (Cushman 2004, p. 70).

When Berlage revived his interest in the Southern Oscillation to create barometric maps of the Pacific, he used the pressure differentials between Batavia, now Jakarta (06°S 107°E), and three distant Pacific locations: Santiago (33°S 70°W), the island of Juan Fernandez (33°S 80°W) off the Chilean coast, and Easter Island (27°S 109°W). Berlage was able to infer, from "the availability of data from the 1957/1958 and 1965/1966 *El Niño* events", that most Dutch East Indies monsoonal droughts occurred when the eastern Pacific region was experiencing high SST and heavy rainfall (Kiladis and Diaz 1986, p. 1038). Consequently, "a new wave of concerted research on the Southern Oscillation occurred" in which Berlage was able to incorporate mean sea level pressure data (MSLP) into his analysis of the oscillation (Allan et al. 1996, p. 17).

In 1966, with Berlage's maps of the Southern Oscillation showing the worldwide distribution of inverse correlations between eastern Pacific annual pressure anomalies and those in Djakarta, Jacob Bjerknes made a significant contribution to explaining the action of the Southern Oscillation and its relationship with the *El Niño* phenomenon of the east monsoon. Son of the leading Norwegian meteorologist Vilhelm Bjerknes (1862–1951), Jacob was born in Stockholm when his father was professor of mathematical physics at the university. In a most fortuitous decision in July 1939, Vilhelm took his family to the USA for a lecture tour and, while there in April 1940, Norway was invaded and occupied by Nazi forces. Although not yet combatants, the US military was keeping a close watch and invited Jacob to remain and help train meteorologists in the event of war. Choosing the University of California at Los Angeles, Jacob Bjerknes began extending his knowledge of meteorology based on his father's work, which allowed him to start explaining the puzzle of the *El Niño* event in the eastern Pacific, based on an impressive body of knowledge he brought to bear on the problem.

Aware that weather is a global phenomenon and that individual manifestations are part of integrated sequences that encompass the earth from pole to pole, Bjerknes began his study of the eastern monsoon phenomenon with the relevant information on pressure, rainfall, SST and atmospheric condition from the *El Niño* of 1957/1958. From sea temperature readings, mainly collected by the California Cooperative Oceanic Fisheries Investigations (CalCOFI), he discovered that eastern Pacific surface waters had registered high positive sea temperature anomalies, up to 4 °C above the average 26 °C (79 °F), across the equatorial zone from the mid-Pacific to South America, with the warm water thermocline boundary nearly 180 m (600 ft) deep (Bjerknes 1966, p. 824). Those temperatures consequently provided the necessary warm pool for the formation of cloud masses and heavy eastern Pacific rains that flooded Peru and diminished the harvest of anchoveta.

To pursue investigations and confirm his tentative hypothesis for the periodic alternation of warm water between west and east, Bjerknes began a time-series of air and sea temperature readings from measurements provided by merchant ships sailing between Samoa and Hawaii and that passed close to the mid-Pacific atoll of Canton (today, Kanton) in Kiribati (03°S 171°W). He supplemented those readings with others from Djakarta and Singapore. In explaining the process whereby the warm water moved a distance of some 2500 sea miles from the west Pacific near New Guinea at 165° E to north of Tahiti at 160° W, he described how the driving force behind all atmospheric activity is solar radiation in the equatorial belt. Atmospheric warming then causes air to rise and flow polewards in both hemispheres in a complex overturning movement known as the Hadley Circulation.

As the air cools in the troposphere and then descends in temperate latitudes, it returns to the equatorial zone as the

[1] The account that follows is based on the publication of Cushman (2004).

easterly trade winds, which keep equatorial waters banked up in the western Pacific. Periodically, however, the trade winds ease because of changing atmospheric activity in the northern Pacific, and conditions for the *El Niño* event are created that allow the warm Equatorial Countercurrent (at 5°N owing to the unequal heating of the North and South Pacific) to flow east and generate rain. When the trades resume their usual strength from subsequent atmospheric changes, the warm equatorial waters are again pushed west and the *El Niño* event ceases. Although he had explained the action of the weather phases between west and east and the "never-ending succession of alternating trends by air–sea interaction in the equatorial belt", he was not at all sure "just how the turnabout takes place" (Bjerknes 1969, p. 169).

To recognize Walker's description in 1926 of the periodic phenomenon of the Southern Oscillation whereby air pressure reversed between west and east, Bjerknes named the process of cloud formation and accompanying rainfall the "Walker Circulation" (Bjerknes 1969, p. 167). In 1935, his colleague Anders Ångström had devised the term teleconnections to suggest the global interconnectedness of weather (Ångström 1935). Bjerknes, therefore, re-introduced the term into weather forecasting, stressing the need for more detailed meteorological maps at the time of the "turnabouts" to help clarify the "remarkable fact of organized teleconnections", although that task, he suggested, "may have to be developed by the science of dynamic oceanography" (Bjerknes 1969, p. 170).

Climate Prediction: Searching the Archives

The *El Niño* phenomenon soon began to assume increasing importance, not only because it was linked to threatening changes in the atmosphere that were affecting coral reefs but also because meteorologists were increasingly troubled by its unpredictability and varying intensity. The major difficulty they encountered was the lack of a widely available, verified database as a context for analysing and predicting variations in the earth climate system, a deficiency that prompted creation of the World Climate Research Programme (WCRP) in 1980. The unseen presence at that time, paradoxically, was the immense volume of data already in existence: millions of records made since 1854 by merchant, naval, fishing and whaling vessels, and stored in meteorological archives in Europe, were almost completely uncoordinated and relatively inaccessible.

A start to predicting weather changes and moderating their impacts had commenced in 1960 with the foundation by UNESCO of the Intergovernmental Oceanographic Commission (IOC) which, to deal specifically with maritime issues of climate predictability, created its subsidiary International Oceanographic Data and Information Exchange in 1961 to collaborate with, and contribute to, the needs of all member states. Until those organizations became fully functioning in the 1980s, the main data source for studying *El Niño* phenomena continued to be the weather records compiled by meteorologists from Blanford to Bjerknes, and the Southern Oscillation Indices (SOI) of air pressure differences between Darwin and Tahiti collected by the Australian Bureau of Meteorology since 1876.

Calculated from a mathematical formula designed to eliminate minor fluctuations causing deviations from long-term averages, the monthly indices range across a zero midpoint (indicating a theoretical stationary air system throughout the equatorial Pacific) from + 35 to −35, which are the hypothetical limits. Positive numbers are associated with strong Pacific trade winds, warm seas and rainfall over the north of Australia in the western Pacific, and negative indices with weakened trade winds, warm water and low pressure over the eastern Pacific, signalling the likelihood of an *El Niño* event.

In practical forecasting applications, the value of the Bureau's records lies in the evidence they provide regarding the onset and frequency of *El Niño* events for more than 130 years. The first such occasion was recorded in 1877/1878 at the time of the horrendous Indian drought and consequent famine, when millions perished. That was followed by minor events in 1884/1885 and 1888/1889 until the equally devastating drought of 1896/1897, during which many more millions died. Altogether, over the following century, the Australian SOI archives recorded a total of at least 21 *El Niño* events of varying intensity to the recent episodes of 2006/2007 and 2009.[2]

From 1960 onwards, the search for elusive *El Niño* Southern Oscillation (ENSO) teleconnections were pursued actively in a number of ways: more frequent field measurements of SST, mapping of bleached and damaged areas of coral reefs, and the identification of those species particularly affected. On the ground, wide-ranging investigations to supplement the SOI were sought for evidence of past climates by meteorologists, palaeontologists and geologists from early archival weather records, as well as empirical evidence from existing artefacts known as proxies (adapted from the legal sense of one person acting for another with written authorization: Lat. *proximus*, nearness).

Palaeoclimatologists gain much of their information about earlier conditions from annual accretions in ice cores,

[2] *El Niño* events occurred in the years beginning 1900, 1905, 1911, 1914, 1919, 1925, 1929, 1940, 1952, 1958, 1965, 1969, 1972, 1977, 1982, 1987, 1991, 1997, 2003 and 2006.

tree rings, fossilized plant pollens and lake and sea floor sedimentary strata from varying annual layers of sediment known as varves (Swedish, literally full circle) which can indicate droughts, floods, rainfall, atmospheric temperatures and gas concentrations. Geochemical analysis of proxies, which includes radiocarbon and potassium argon dating, as well as optical and thermoluminescence methods, are also used when necessary. One widely employed chemical method measures isotopes extracted from the artefact. From the Greek *isos* (same) and *topos* (place), these are elements with the same atomic number and similar chemical properties, but different atomic weight. Many artefacts have isotopes incorporated in them, so their ratios yield dateable information and conditions obtaining at that time.

An early use of isotopes as proxies for dating palaeoclimates came in the research of Willi Dansgaard at Camp Century, when he extracted isotopic O^{18}/O^{16} delta (δ) ratios (parts per thousand, per mil, ‰) from the cores (see Chapter 14). As the lighter ^{16}O is more easily vaporized, low O^{18}/O^{16} delta ratios with a preponderance of ^{16}O indicate warmer climate conditions prevailing. As the heavier ^{18}O is less able to vaporize and becomes trapped in ice, high numbers of ^{18}O indicate colder climates (for more details, see Chapter 14). Similarly, the ratio of stable, non-radioactive carbon isotopes ^{12}C to ^{13}C allows measurement of the energy flow through ecosystems; in marine analysis, ratios of $^{15}N/^{14}N$ provide a means of assessing trophic levels and exchanges in animal diets.

In the case of coral reefs, an important source of proxy evidence comes from *Porites* (boulder) and several other species of coral, along with relict reefs from past epochs that are often far inland as a consequence of ancient plate tectonic action (continental drift). A world leader in this area is Australian Institute of Marine Science scientist Janice Lough, whose coral core collection provides environmental and climatic histories reaching back several centuries. The fundamental nature of reefs arises from "the rapid formation of calcium carbonate skeletons (calcification) fuelled by the coral–algal symbiosis", and Lough's special interest is in the measurement of various geochemical tracers incorporated into the dateable $CaCO_3$ density bands that allow the reconstruction of past climate conditions (Lough 2010). As she describes them, "each band is a page in an environmental archive that reveals past responses of growth (linear extension, skeletal density and calcification rate) and provides a basis for prediction of future growth". All current reef research is focused on future outcomes as the planet warms, so beyond geochemical analysis, the study of growth bands provides the third fundamental dimension of time, and yields "immensely valuable aids in unravelling the consequences of anthropogenic climate change on coral reefs" (Lough and Cooper 2011, p. 170).

An American Initiative: A Comprehensive Ocean and Atmosphere Dataset

During the 1960s, some meteorologists had been suspecting that ocean/atmosphere interaction in the waters of the Southern Hemisphere, as suggested by Blanford in his see-saw-theory, was the fundamental force driving global climate. Equal in area to all of the continents combined, along with an additional area equivalent to another Africa, that concept captured the imagination of US meteorologist Joseph Fletcher (1920–2008), an Assistant Administrator for Ocean and Atmospheric Research in the Environmental Research Laboratory (ERL) within the National Oceanic and Atmospheric Administration (NOAA). With extensive wartime experience in the US Army Air Corps and subsequent years as commander of the 58th Strategic Reconnaissance Squadron based in Alaska, Fletcher joined NOAA in 1963 and became the motivating force for construction of a Comprehensive Ocean and Atmosphere Data Set (COADS).

Fletcher's theory, which he described in a short recollection at the opening of an International COADS Workshop in Boulder, Colorado, in 1992, demonstrated his conviction, which came to exercise such a powerful effect on climate research. Specifically, he theorized, "one of the strongest thermal forcing features of the global system is Antarctica and the most steady energetic dynamical feature is the southern hemisphere westerlies". The meteorological need he programmed ahead, therefore, was to look for "variability of the Antarctic heat sink and the wind field". That, he believed, could be best accomplished by "looking backward in time" for the "surface marine record [which] provides the spatial and temporal extent to help understand climate behaviour; this is the Rosetta Stone for interpreting the longer proxy records that can be extracted from countless other sources" (Fletcher 1992).

Deciphering the Rosetta Stone, however, turned out to be a long, painstaking task and it was many years before COADS became operational. To look backwards, Fletcher had become aware, from his early research into US Navy records, of the massive volume of completely uncoordinated and relatively inaccessible meteorological data in existence, dating from the 1853 foundation of the International Maritime Organization in Brussels. At that conference, some seafaring nations agreed to exchange observations with the intention of devising a world maritime standard. Immediately thereafter, starting in 1854, measurements were recorded in ships' logs of sea surface and atmospheric temperatures and pressures, current movements from drifting buoys, wind velocities, humidity, cloud cover and rainfall. Those records, in turn, were passed either to the British Meteorological Office, the Royal Netherlands Meteorological Institute (KNMI) or the German Maritime Observatory (Deutsche Seewarte).

After Herman Hollerith devised the punch-card system to tabulate the vast quantity of data from the US 1890 census, ships' records were recorded on similar decks of what became known generically as Hollerith cards. A more efficient method of transmission from ships came in 1906, by wireless telegraphy, and from 1921, by direct radio communication, although the Hollerith cards, once developed further by the IBM Corporation for a wide variety of business applications, continued into the 1970s where they were stored as "card decks". During the Second World War, the belligerents collected huge amounts of meteorological data that became augmented when the Americans captured a valuable deck from the Germans with records spanning the years 1853–1939. At the time, unfortunately, the separate observations that had accumulated into millions had no standardized form; the SSTs from bucket and cooling intake ports, for example, differed as much as 0.5 °C (Woodruff et al. 1987, p. 1239 f).

Beginning soon after Fletcher joined NOAA, as described by Scott Woodruff (one of Fletcher's team), the initial task confronting the ERL to progress to a better understanding of the relationships between global weather, climate change and the ENSO phenomenon was the need to collate early manual records and the Hollerith card decks into a single, accurate database. Faulty readings and biases from different methods of collection, duplicate entries and difficulty in reading the handwritten entries in ships' logbooks and meteorological reports in various languages and scripts had to be overcome. With diligent application, he recorded, those demanding tasks were completed "by the 1960s [when] 15 different decks had been converted into a single Tape Data family at the National Climate Data Centre" (NCDC; Woodruff et al. 1987, p. 1240).

As work progressed steadily throughout the 1970s, a Mercator map of the world was constructed by NCDC as a rectangular grid of 648 boxes (36 × 18), each measuring 10° square, into which the data were plotted as they emerged to create an Atlas File. In October 1978, NOAA augmented the Atlas File with deployment into space of an Advanced Very High Resolution Radiometer (AVHRR) aboard the TIROS-N satellite, to record a wider range of data from the infra-red spectrum, including day and night cloud and surface mapping, snow and ice cover and SSTs.

With publication of the Atlas File, which allowed ready identification of global circulation patterns, COADS finally came into operation. As data continued to arrive and faulty entries were corrected, the File was upgraded. By 1981, the NCDC completed a revision of the Atlas Files covering the decade 1970–1979 which included new information from ocean buoys and the Global Telecommunication System, including a more powerful six-channel AVHRR/3 satellite sent into orbit in 1998. Innovations in communication technology had also been adopted progressively: the Hollerith data were transferred to magnetic tapes, and they in turn to digital computer files, with continuing improvements in filtering for quality control and storage compression.

It had also become unnecessary for maritime nations to work independently and the American initiative morphed into an international relationship, renamed ICOADS, which continues today with the ongoing consolidation of reliable, accurate, weather and climate data consisting of information on SST, air temperature, surface humidity, pressure, wind measurements, cloud cover and wave behaviour. The measurements have been released in phased updates, the first in 1985 for the period 1854–1979. Data collection has since been extended significantly, and in May 2009, ICOADS published Release 2.5 for the years 1662–2009, which is readily available online.

The Elusive *El Niño:* The Ecological Disaster of 1982/1983

Meanwhile, and with that laborious task in progress, the unpredictability of ENSO episodes continued to defy understanding. In a major effort to establish a functional hypothesis by coordinating as many available Southern Oscillation data as possible, in 1980, Eugene Rasmussen and Thomas Carpenter at the NOAA Climate Analysis Centre in Washington DC began intensive historical research into the years 1949–1981. For their study based on SST records retrieved by the NCDC from the "unseen archives" spanning the years 1854–1976, they selected six representative episodes. Three major (1957, 1965, 1972) and three minor (1951, 1953, 1969) episodes were from a shore station on the coast of Peru at Puerto Chicama (07°S 79°W), and 26 separate maritime sources made by vessels from seven nations over more than a century. A serious limitation at the time, though, was the irregular nature of the readings collected over varying periods by volunteer merchant ships travelling regular commercial routes along with whaling and tuna fisheries vessels and naval ships.[3]

With considerable care to make corrections for the variations and errors in readings from different depths and techniques of collection, and the absence of data for much of the Pacific, Rasmussen and Carpenter constructed composite wind and SST anomaly maps for the sequences from onset to peak phase. These confirmed previous barometric SOI evidence that the forcing mechanism for *El Niño* events was an "intensification and subsequent relaxation of the trade winds in the central equatorial Pacific" (Rasmussen and Carpenter 1982, p. 375). An even more significant finding was that the Walker Circulation could no longer be interpreted as a

[3] To render earlier records more reliable for modern analysis of climate change, a method was proposed by Folland and Parker (1995).

"standing oscillation": on the contrary, it is a dynamic movement of the atmosphere/ocean surface, which demanded more-thorough study. In their concluding comments, the two were able to report that their study of the composites drawn from all six episodes "are surprisingly consistent and in good agreement with many other sources of information" (Rasmussen and Carpenter 1982, p. 381). Although the pattern of anomalies conformed to the expected irregular rhythm of the Southern Oscillation, no extreme variations were revealed.

Rasmussen and Carpenter submitted their paper for consideration to *Monthly Weather Review* in December 1981 and the final version had barely appeared in print in May 1982 when an unpredicted occurrence suddenly caught everyone by surprise. The SOIs had been relatively steady since a minor *El Niño* event in 1977, but in June 1982, the index fell steeply to –20.1 and continued hovering around that level until January 1983, when it plunged again to –30.6 and then to –33.3 in February. That final index approached the theoretical limit and the lowest ever recorded, far surpassing the negative indices recorded during the horrendous famines and droughts in 19th century India.

The global ecological consequences of that *El Niño* event of 1982/1983, described by Peter Glynn and 31 other reef scientists in 1990 in a comprehensive, authoritative volume edited by Glynn, were devastating for reefs, marine and birdlife, and also for the anchovy harvest (Glynn 1990). Coastlines were seriously eroded in places, there were tropical storms and floods in southern California and Peru, and a million died of famine in Ethiopia. Simultaneously, droughts and wildfires were experienced in Australia, Indonesia and Southeast Asia and NOAA recorded some 2000 human fatalities and an estimated 13 billion equivalent US$ in damage.

In the issue of *Science* for December 1983 Rasmussen, in collaboration with University of Washington meteorologist John Wallace, examined that completely unanticipated *El Niño* event by comparing it with the six selected episodes reported in May 1982. In framing their discussion, they commented on the two prevailing approaches to interpretation: that of the meteorologist who sees the Southern Oscillation as a response to changes in SST, and the oceanographer who treats *El Niño* events as a response to a prescribed wind stress at the sea surface (Rasmussen and Wallace 1983, p. 1196). Both approaches were valid, they observed, but limited in explanatory power: the problem was to integrate the two with the critical recognition that "ocean circulation plays the role of a flywheel in the climate system and is responsible for the extraordinary persistence of the atmospheric anomalies from month to month" (Rasmussen and Wallace 1983, p. 1195). Clearly, more data than SOIs would be required to understand the ENSO phenomenon, and more importantly, to predict its onset with greater accuracy along with its relationship within the wider climate system and its impact on reefs.

Reefs in Real-Time by Remote Sensing

Although a remarkably comprehensive database had become available in the first stage by 1985, and despite upgrades as new information arrived, ICOADS remained basically an historical record with little immediate forecasting value. Triggered by the intensity of the 1982/1983 *El Niño*, however, the critical need was for the essential missing element: direct measurements in real time of oceanic and atmospheric behaviour, to enable meteorologists to issue warnings the moment change seemed imminent. Consequently, to determine the pattern of teleconnections and the likely onset of future weather problems, the WCRP began in 1984 what is known as TOGA (the Tropical Ocean Global Atmosphere study). The fundamental idea was simplicity itself: an array of automated deep-ocean moored buoys across Pacific equatorial waters from the Galapagos to New Guinea. These were to be deployed over several years to record surface wind patterns and sea and subsurface water temperatures and currents, and to transmit the data as they were recorded via satellite for processing by the Pacific Marine Environmental Laboratory (PMEL), a NOAA facility in Seattle.

The first trial array of four Tropical Atmosphere Ocean (TAO) Atlas buoys was moored by PMEL in 1984/1985 south of Clipperton Atoll (10°18′N 109°13′W) along the 110° W meridian between 10° N and 10° S. Following satisfactory performance of that array, further arrays were placed progressively to the west in depths varying between 1.5 and 6 km until the full number of 70 buoys was completed in 1994, reaching to the Solomon Islands and covering most Pacific equatorial waters, in company with five subsurface current-meter recorders spaced along the equator itself. Throughout that decade, data recovery received a major enhancement after the launching of the TOPEX/Poseidon (Topography Experiment over the Ocean) satellite in 1992 as a joint venture between NASA and the Centre National d'Études Spatiales (CNES) in Paris. With astonishing precision, its two altimeters produced topographical maps of all ice-free ocean surfaces, revealing images of hills and valleys with an accuracy of 3.3 cm. Combined with TOGA data, the main interpretation centre at PMEL was finally in a position to record and predict the onset of ENSO phenomena.

With the TAO system offering considerable promise, the WCRP continued to establish a far-reaching network of information-gathering sites and, in 1990, began an ambitious World Ocean Circulation Experiment (WOCE) to collect data on a broad range of physical and chemical parameters by satellites, TAO arrays, drifting buoys with satellite transmitters, and ships. In 1994, TAO was incorporated into a more comprehensive programme to study climate variability and predictability and the impact of anthropogenic forcing, suitably named Climate Variability and Predictability (CLIVAR).

Valuable as those data were for predicting ocean behaviour on a seasonal and annual basis, the IOC also recognized the need for much greater understanding of how the ocean actually functions as a single body of water and stores and moves great volumes of heat (potential energy) around the globe. In addition, there was a need to explain the operation of ENSO phenomena that were affecting not only the equatorial Pacific but also places at higher latitude. Consequently, in a separate programme in collaboration with the WCRP, the IOC commenced a Global Ocean Observing System (GOOS) in 1991. With the cooperation of many nations with ocean coastlines, ongoing records are made of temperature, salinity, water level and sea-ice cover from observing networks of moored and drifting buoys, ocean satellites, archive records and weather forecasts, and observations from cooperating merchant ships of opportunity. To provide international awareness of the ocean's heat content as waters circulate in real time, or as close as possible to it, those continuous observations are sent to the IOC Secretariat in Paris, where they are coordinated and made available on the Internet by GOSIC (Global Observing Systems Information Center).

1997/1998: The Most Destructive ENSO Event Ever

In the early 1990s, there was a feeling of confidence that all possible steps had been taken to prepare for serious weather disturbances. Following the disastrous 1982/1983 *El Niño*, negative SOIs were only recorded on two occasions, in 1986/1987 and again in 1992/1994, signifying relatively minor *El Niño* events, but with no indications to create alarm. However, when the TAO array began recording a build-up of heat content in the waters of the western equatorial Pacific in 1996 with extremely high SSTs, uncertainty, even anxiety, was again confronting ENSO scientists. The exceptionally strong easterly trade winds forcing surface waters towards the Solomon Islands and New Guinea were suggesting the potential for an imminent major *El Niño* episode when atmospheric fluctuations would ease them. However, none of the impressive equipment could indicate exactly when it might arise.

Suddenly, in early 1997, atmospheric behaviour became erratic, the trade winds ceased unexpectedly and strong westerly winds and ocean currents began to push the elevated pool of warm water east. The SOIs began falling rapidly: in March 1997, the index registered –8.5 and then continued downwards until it bottomed at –28.5 in March 1998. In the words of Michael McPhaden, senior scientist in charge of PMEL operations, an "*El Niño* developed so rapidly that each month from June to December 1997 a new monthly record high was set for SSTs in the eastern equatorial Pacific, based on measurements dating back to the middle of past century…[which] caught the scientific community by surprise" (McPhaden 1999, p. 950). The index rose slightly to –24.4 in April and then, quite abruptly, climbed to +0.5 in May when the equatorial zone became tranquil and increasingly positive indices and lower SSTs were registered for the remainder of the year.

Despite the inability of PMEL to issue advance warnings to potentially affected places until "April–May 1997 after the first appearance of warm SST anomalies", subsequent data analysis allowed detailed reconstruction of the course of what was the most destructive ENSO event ever experienced (McPhaden 1999, p. 952). It was inferred that a combination of fast-moving eastbound waves propagated by a sudden cessation of the trade winds had pushed the warm pool towards South America and further depressed the thermocline boundary another 90 m. That warm pool had thereby minimized the cold upwelling necessary for the anchoveta harvest and provided an extensive pool of energy for the formation of rain-bearing cloud formations. Termination of the event came unexpectedly with the sudden resumption of the trade winds, but the cause could not be identified. What is known for certain is that "the predictability of ENSO is ultimately linked to large-scale wave dynamics that redistribute heat and mass on seasonal to inter-annual time scales" (McPhaden 1999, p. 953).

The devastating impact of the 1997/1998 *El Niño* event was far greater than that of the 1982/1983 event. In an account published by World Meteorological Organization (WMO), the calamity was described as having wrought immense destruction along the tropical coasts of both Americas: from California to Ecuador and Peru. Those regions received ten times their annual average rainfall with widespread flooding, erosion and mudslides causing loss of life, crops and roads. Southern Brazil, Paraguay and Uruguay were flooded by torrential rains that crossed the Andes, and Mexico, Panama and Columbia were seriously impacted: Acapulco was battered by cyclone Pauline that brought further destruction as it crossed the Rockies, bringing record rainfall into the southeastern USA. From the American coastline to the mid-Pacific, island economies experienced a record number of tropical cyclones, with destruction of habitations and crops.

In the western Pacific, there were reciprocal disasters: Australia suffered extensive agricultural crop losses from one of its most severe droughts ever, particularly the wheat harvest; Indonesia and the Philippines had reduced rice crops and in New Guinea, the basic yam and other staples failed and international food aid was necessary to feed the starving population. Nor were Africa or Asia spared, the entire Indian Ocean feeling its effects with devastation of the 26 atolls and 1190 islets of the sea-level archipelago of the Maldives in the mid-Indian Ocean along with the uninhabited reefs of the Chagos Archipelago to the south and the lightly populated Seychelles Islands northeast of Madagascar. The Maldives suffered extensive losses to its essential tourist economy, and East Africa had periods of heavy flooding and associated damage to infrastructure and crops, particularly in Zimbabwe where the staple maize crop was ruined. Tibet had record snowfalls and southern China received flooding rains at record levels, which gouged out parts of the Yangtse Basin with considerable loss of life and infrastructure. Northern China, in contrast, experienced extremely high temperatures and reduced agricultural output.

The far-reaching disasters described in the WMO report, discovered for the first time from the TOPEX/Poseidon satellite and TAO arrays, was the extent of the pool of warm water that moved from west to east. Its greatest spatial coverage in November 1997 was 1½ × that of the continental US and the sea level was 35 cm (14″) higher around the Galapagos than in the western Pacific near the Solomon Islands and New Guinea. Equally astonishing is the volume of warm water recorded, with SSTs up to 30 °C (86 °F), some 30 × the volume of all five North American Great Lakes combined and holding as much potential solar energy as 93 × the total energy from fossil fuels consumed by the US in 1995.[4] An assessment by the NOAA Office of Global Programs calculated the direct loss at US $34 billion, total human mortality at 24,000 and morbid illnesses as affecting 533,000. Some 6 million persons were displaced, another 111 million were directly affected, and 56 million acres (22.6 million ha) of land were damaged.[5]

Preparedness became the watchword for the future and the WMO commenced a Voluntary Cooperation Programme to assist developing countries preserve their climate records and establish computer-based archives as well as make more systematic meteorological observations that could be shared widely to permit better prediction of weather and climate extremes and provide more precisely targeted warnings. Climate enquiry became even more intensified in 1999 when WMO, IOC and United Nations Environment Programme (UNEP) began planning the cooperative Global Climate Observing System (GCOS) foreshadowed in 1991 at the 11th International WMO Conference.

To extend ENSO observation coverage, the Japanese Agency for Marine–Earth Science and Technology (JAMSTEC) signed a Memorandum of Understanding with NOAA to monitor waters in the Federated States of Micronesia west of Kiribati (Gilbert Islands) at 165° E. To commence operations, the Triangle Trans-Ocean Buoy Network with 4 Triton moorings was deployed along 156° E, around 300 km east of Truk (today Chuuk) Atoll (07° N 151° E) from the Equator at 0°, 2°, 5° and 8° N from March to June 1998. Subsequently, another eight Triton buoys were installed eastwards, later replaced with improved NextGeneration buoys, the task being completed in November 2001 with the American and Japanese data merged into a common file, available online.

With the successful installation of the Pacific TAO arrays, ENSO behaviour across the Pacific became monitored in real-time directly by the NOAA website and can provide advance warnings of potentially serious disturbances with forecasts, potential impacts and prediction benefits.

Extension of TAO Arrays: Indian and Atlantic Oceans

The failure of PMEL to recognize the impending disaster of the 1997/1998 ENSO event and the various disasters across both the Pacific and Indian oceans was an indication of still inadequate knowledge. Events similar to ENSO were becoming recognized in the Indian and Atlantic oceans, and an obvious need was extension of the TAO system within the Global Ocean Observing System (GOOS).

Stimulus came in 1999 when a weather event in the Indian Ocean similar to the Pacific *El Niño* oscillation was observed and described by Toshio Yamagata of the Climate Variations Research Programme (CVRP), affiliated with JAMSTEC. Monsoonal conditions in India and related weather events were occasionally reaching Madagascar in the southwest Indian Ocean, whereas in the northeast at the same time, Indonesia, Australia, the Philippines and Japan were experiencing extremely dry conditions. From data gathered by satellites on sea-level changes, ocean circulation patterns, upper SSTs and outgoing infrared longwave radiation, Yamagata believed the change to the anomalous positive phase of warm waters in the eastern Indian Ocean was being caused by equatorial ocean dynamics and zonal winds.

To explain periodical reversals of water temperature and rainfall in the Indian Ocean, Yamagata described the phenomenon as the Indian Ocean Dipole (IOD), an analogy borrowed from physics, which describes opposing positive and negative electrical charges. Adopting the same SOI conventions of plus in the west and minus in the east, the positive phase refers to the irregularly warm monsoonal waters in western regions closer to Africa and the negative phase to the normally cooler waters in the eastern regions of the Indian Ocean around Indonesia, northern Australia and New Guinea.

The IOD oscillation prompted Australian meteorologists to begin their own investigation into its causes and any possible coupling with ENSO. Although the palaeographic record indicates its existence for at least the past 6000 years, evidence was lacking for more recent behaviour. As climatic data for the Indian Ocean are still scarce, to gain proxy

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[4] Internet release by Goddard Space Flight Center (GSFC), Jet Propulsion Laboratory (JPL) and Centre National d' Études Spatiales (CNES): LG-1998–05-004-GSFC.

[5] See *The 1997–1998 El Niño Event* issued by the World Meteorological Organization.

evidence, palaeoclimatologist Nerilie Abram from the Australian National University began a search for the background history of the IOD. In 2008, a drilling team led by Abram extracted a 3 m coral core from a massive *Porites* coral in the Mentawai Islands group, 200 km southwest of Sumatra in the Indian Ocean. Isotope data for $CaCO_3$ formation taken from the core provided evidence for the past 160 years that eastern Indian Ocean waters were becoming cooler in recent decades, and in the five major cooling events identified, four had arisen since 1961, and three of those since 1994 (Abram 2009, p. 26).

As indications of cooling in the eastern positive phase were associated with minimal rainfall in the eastern Indian Ocean, Abram inferred that it was possibly "connected to climate changes caused by man-made greenhouse warming" which strengthened Monsoon trade winds along the Sumatran coast and pushed the warm waters into the western regions and allowed cooler waters to rise around Indonesia. That process, still in its early investigative phases, suggested to her that the Indian Ocean "plays an increasingly important role in determining rainfall patterns in our region, and can be used to improve long-term rainfall forecasts". Furthermore, because the "impacts of continued intensification of the Indian Ocean are likely to be severe…[such] climate variability should also be seen as a further impetus for urgently reducing greenhouse gas emissions".

A second IOD project with direct relevance to countries bordering the Indian Ocean is currently being undertaken by a team from the University of New South Wales (UNSW), the Commonwealth Scientific and Industrial Research Organization (CSIRO) and the University of Tasmania. The focus is to investigate the links between ENSO, the IOD and droughts in Australia, with a hypothesis suggested in a preliminary report of 2009 by Caroline Ummenhofer from UNSW. Her thesis is that the IOD "is the key factor driving major south-east Australian droughts over the past 120 years",[6] and that Australia's extreme droughts are "driven by Indian Ocean variability, not Pacific Ocean conditions as traditionally assumed. Specifically, a conspicuous absence of Indian Ocean temperature conditions conducive to enhanced tropical moisture transport had deprived south-eastern Australia of its normal rainfall quota. In the case of the decade-long 'Big Dry' of 1988–1998, its unprecedented intensity is also related to recent higher temperatures" (Ummenhofer et al. 2009).

Research into the behaviour of the IOD and teleconnections with ENSO, she commented, may well contribute to a more useful understanding of global weather patterns such as the terrible *El Niño* event of 1982/1983 and the even more horrendous event of 1997/1998. She suggested that they had a strong teleconnection with the IOD, which awaits further investigation in relation to the global warming and higher SSTs believed to be responsible for coral disease and the explosive growth of pathogens.

In a search for further evidence of ENSO/IOD interaction, NOAA extended the TAO project into the Indian Ocean in 2000 with project RAMA, for the Research Moored Array for African–Asian–Australian Monsoon Analysis that was completed in 2008. Yet a further need for understanding ENSO-type events began when NOAA extended the TAO system to the Atlantic as a joint venture between Brazil, the USA and France, covering the ocean between the Amazon and the Gulf of Guinea. From the Pilot Research Moored Array in the Tropical Atlantic (PIRATA), consisting of Atlas buoys and current meters on 18 sites, with an initial delivery of 132 files in 1999, data had increased rapidly to 61,492 files online by 2007.

The ENSO phenomenon soon began to assume even greater importance because it appeared, in some still obscure way, to be of critical involvement not only to SSTs, but also more ominously to the warming of the entire planet that was being associated with increasing atmospheric pollution.

[6] UNSW media release.

13 Bioturbation: Unpredictable Expansion

Early signs of serious disturbance in coral reefs came more than 30 years before the Kyoto Protocol, with a mass invasion by a seastar in Western Pacific waters that rapidly achieved an international reputation as a voracious corallivore threatening the viability of tropic reef resorts. At the time, however, there was no understanding that it could be related in any way to toxic atmospheric emissions and global climate change, or that it would become a serious threat. With its Biblical allusion as Crown-of-Thorns, the *Acanthaster planci* infestation appeared silently on Australia's Great Barrier Reef (GBR) in 1960 when they were noticed around Green Island, a popular tourist resort near the city of Cairns. The second largest seastar in the world, and known popularly as a starfish, it reaches 1 m or more across (3 + ft), with as many as 21 arms covered in spines up to 5 cm (2 in.) long, which are highly toxic when they puncture flesh.

Early Arrivals: The Seastar Invasion

Originally described and named by Linnaeus after Janus Plancus, the pseudonym of anatomist Simon Giovanni Bianchi (1693–1775), its generic name came from the Greek *Akantha*, prickly plant, familiar as the floral decoration atop Corinthian columns, and *aster*, a star. Although its spines have been found in the palaeographic column, the earliest observations only began in accounts of explorers in the 18th century. Not until the mid-20th century, however, did it enter the literature of concern, no doubt stimulated by the swift increase in popularity of scuba by scientists and recreational divers, which augmented the number of sightings. First seen in the Ryukyus in 1953, it was noted in Okinawa in 1955, Rabaul in 1962 and Guam in 1965. In 1968, Richard Chesher, a young New York marine biologist, mobilized scientists along with navy and recreational divers at the Guam University Marine Laboratory to physically remove the seastar, to begin a study of its behaviour, and to raise international awareness (described in Sapp 1999, pp. 13–34).

The abundant populations described in the historical record were periodic sightings in the Philippines and the Palau (Belau) islands, and even on the GBR before the Green Island outbreak. Thomas Goreau had observed them in the Red Sea in 1963 (Goreau et al. 1979) and with his experience in Jamaican reef zonation and ecological distribution, suggested that such outbreaks were possibly natural fluctuations.

Australia at the time had few marine scientists and no research organizations with tropical expertise: consequently, there was no appreciation of what was to become a virtually intractable problem. By 1965, numbers on the GBR had increased alarmingly as a consequence of the exceptionally fertile females being able to release up to 60 million eggs annually. When they changed their position on the reef, white patches were evident that were discovered to be feeding scars where the seastars had released digestive enzymes onto the corals from their everted stomachs and absorbed the liquefied tissue during night-time feeding. Once sucked dry, the coral did not regenerate: the skeletons became overgrown by brown filamentous algae, giving a dreary, lifeless appearance.

After they appeared on yet more reefs, some media reports claimed the frequency was approaching plague proportions. Initial concern at Green Island is understandable because the GBR is one of the world's most alluring tourist destinations, and it became essential for management to destroy them, or at least to contain the spread. Following several ineffective attempts at control, such as physical removal by divers, injection of formalin by scuba divers from a hypodermic apparatus, such as a needle tip to a fishing spear, was found to be both fatal and environmentally responsible, because formalin is biodegradable in water and leaves no toxic residue. Notwithstanding, the overwhelming numbers made it a virtually impossible task to eradicate them. Soon, many of the premier tourist reefs were losing their visual beauty and, in an effort to find a solution, Robert Endean of the University of Queensland, a biologist with expertise in marine toxicity, began a 2-year study. By April 1968, Endean offered two

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
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possible explanations for the outbreak: either breakdown of predator–prey relationships through heavy poaching by Taiwanese and Japanese fishing fleets of the giant clam, *Charonia tritonis*, or toxic pollution in reef waters by organochlorine biocides from adjacent coastal cane farming and other forms of agricultural run-off. The DDT-type residues, he argued, had also travelled through the currents in the planktonic food chain and killed the natural predators of seastar larval planulae in the water column.

With the Queensland Government and tourism operators in a state of heightened anxiety and international concern being aroused, a number of other reef scientists began to investigate the issue. Publications began appearing that indicated that the seastars were common on coral reefs of the Red Sea along the coast of Sudan, and throughout the tropical zone of the Indian and Pacific oceans up to the Gulf of Chiriqui on the west coast of Panama. At Cambridge University, a Coral Starfish Research Expedition was formed for a survey of the reefs of Sudan in 1970, and their findings were reported by participant Peter Vine (Vine 1971). Reduced predation by the giant clam (*C. tritonis*) was dismissed as a cause of the outbreak by most investigators because it is a scarce and sluggish predator and the main lines of evidence suggested that much broader factors were operative, *Acanthaster* only preying on certain corals, mainly the genera *Pocillopora*, *Goniastrea*, *Turbinaria*, *Montipora* and *Acropora*. Following an outbreak off the Pacific coast of Panama in the Gulf of Chiriqui, Peter Glynn reported in 1985 that cores drilled from *Gardineroseris planulata* on Uva Reef indicated that *A. planci* had been present there for at least 200 years (Glynn 1985, p. 298).

A second Cambridge expedition to the Red Sea led by Rupert Ormond 2 years later was directed at investigating ecological determinants in Indo-Pacific waters. Those efforts discerned a pattern of clustering of the organism in densities of hundreds, which suggested a possible chemo-attraction that guides *Acanthaster* to its prey, in the same manner as other seastars, and that one of the possible controlling factors was the predatory behaviour of certain species of fish (Ormond et al. 1973, p. 168).

Towards the end of the 1960s, the mass outbreaks on Green Island had subsided, but cause for alarm came again in 1979 and then in 1982 when aggregations were recorded off nearby Innisfail, coinciding with devastating outbreaks on the Okinawan island of Iriomote-Jima, where most of its reefs were destroyed by 1986. Australia, meantime, had finally moved towards effective deterrence and policing of foreign poaching on the GBR with passage of the Continental Shelf (Living Natural Resources) Act No. 149 of 1968, under provisions of the Geneva Convention that provided for Australian sovereignty over its continental waters. As a result of an election pledge by a seriously embattled Federal conservative government 2 years later, Australia moved towards scientific monitoring and research of tropical waters with the creation of the Australian Institute of Marine Science (AIMS). That institute was established near Townsville in the centre of the GBR in 1970, specifically to develop tropical marine science, opening at Cape Ferguson in 1978. Subsequently, in December 1985, the Australian Government announced that it had arranged for the world's greatest single marine research and expenditure project on the GBR to be undertaken by AIMS, to coordinate ecological investigations. In all, 58 projects were initiated, requiring the collaboration of some 70 senior scientists, including some from overseas institutions who had also been investigating the *Acanthaster* puzzle, for the ensuing 4 years. Main research effort was on population dynamics, prey and ecosystem context, predator–prey relationships and technological methodology.

After the first year of intense investigation, no conclusive results were reached. By the end of the 1980s, there had been outbreaks over nearly 21 % of the Reef, but although > 300 scientific papers had been published by then, scientists were still no closer to a real solution to the problem. Graeme Kelleher, chair of the Great Barrier Reef Marine Park Authority (GBRMPA) in 1987 commented "attempts to eradicate the starfish on a wide scale have proved futile", so the Authority decided that the best management approach would be to channel expenditure into research in a quest for conclusive evidence (Kelleher 1987, p. 14). Subsequently, and despite extensive research and millions of dollars in funding for almost 15 years, a report to the Australian Science and Technology Council (ASTEC) by GBRMPA on the state of research in 1991 concluded that "It seems very likely there will be further outbreaks in the future. It is vital that research be continued to determine whether human activities cause or exacerbate such outbreaks" (Lassig and Kelleher 1991). With no firm evidence to settle the controversy, AIMS created a specialist long-term monitoring program (LTMP) in 1992, with responsibility for field surveys of 50 selected core sites to measure outbreaks, defined as occurring when corals are eaten faster than they can regenerate.

Possibly, the most informative results came from University of Queensland scientists Ann Cameron, Robert Endean and Lyndon DeVantier in their 1991 conclusion to an exhaustive 20-year study of *Acanthaster*. From the known growth rates of major reef species, they inferred that "repeated outbreaks of the intensity of those of the past 20 years could not have occurred in the century prior to the 1960s on reefs in the central third of the GBR, otherwise, the reefs would not carry the numbers and size structures of massive corals observed during this study". Their final comments brought yet further evidence to support the growing belief that "outbreaks on the GBR are novel events, peculiar to the latter half of the 20th century and coincident with large-scale human activities on the GBR, rather than integral features of reef ecology in the region" (Cameron et al. 1991, p. 257).

In 1999, the entire issue of reef bioturbation received significant international attention when Canadian historian Jan Sapp brought the *Acanthaster* decades together in a comprehensive historical survey that examined the history of global concern with the behaviour of the seastar. From Green Island, Guam and across the Pacific to Panama, he dealt with the inevitable responses and controversies as to whether such outbreaks were part of the greater mystery of natural cycles or could be assigned incontrovertibly to human activities. With the subtitle *Coral Reef Crisis*, his book title asked the question that continues to the present day in respect of environmental change, which he was unable to answer: *What is Natural?*

As the foregoing history of reefs and their place in the entire biosphere of the planet illustrates, disasters and catastrophes have been essential aspects of geophysical evolution and the formation of coral reefs. Indeed, it could not have been otherwise, and will continue to the end of time. Where we of the Holocene epoch need to take pause and assess the present situation relates to concerns regarding the accelerating changes to the essential nature of coral reefs coming from our intensifying impact on them, which has been increasing noticeably in recent decades. As its ecosystem becomes disturbed by human activities that are accelerating the length of the GBR with an incompatible mix of agriculture, land clearing, trawling, resort building, mass tourism, port development and dredging seabed access channels, its correction will continue to be equally difficult, if not impossible.

The *Acanthaster* investigation efforts revealed how complex reef ecosystems are, and how limited is our current understanding of the steady accretion of subliminal processes of disturbance from human actions. There is now growing conviction among scientists that the end is foreseeable. In 2008, John "Charlie" Veron published a detailed overview of the impacts of climate change on coral reefs, a book about the GBR, but one that sent echoes around the world (Veron 2008a). As recently as October 2012, destruction by *Acanthaster* seastars was continuing unabated, and it was listed along with coral bleaching and cyclone scouring in a report by the AIMS to the *Proceedings of the National Academy of Sciences* as one of the three main causes of continuing GBR decline (De'ath et al. 2012).

Death in the Caribbean: The Sea Urchin Epizootic

With the Crown-of-Thorns infestation remaining a serious threat to the ecological structure of the GBR and all other tropical reefs, and a problem specific to the tourism industry, there was disturbance on an equally severe scale in the Caribbean. With an epizootic outbreak that was threatening to eliminate the sea urchin *Diadema antillarum*, a startling paradox was created regarding two species of echinoderm: anxiety at the abundance of *Acanthaster* and the absence of *Diadema*.

Sea urchins have been identified as early as the upper Ordovician Period (460–439 million years ago) and some 940 species have been described, although none is as important in the Caribbean as *D. antillarum*. A relentless predator and algal grazer, it has an essential role in maintaining ecological balance by preventing overgrowth of the solid substratum by the algae which can smother corals. Its name comes from Middle English "urchon", derived from late Latin *ericius*, the hedgehog, so the marine form is sea hedgehog. Its basic morphology is a calcified test (Lat. *testa*, shell) some 10 cm (4 in.) in diameter enclosing the body, covered with long, black toxic spines up to 20 cm long. Like its echinoid relative, the Crown-of-Thorns, these spines can break off easily and puncture human skin, which led in the 16th century to the word being applied to the prickly behaviour of excessively unruly children. It moves by locomotion from its mobile spines and, although preferring shallow waters down to 10 m where photosynthesis assures abundant algae, in the Indo-Pacific it has been recorded down to 70 m.

The urchin's disappearance was first noticed on the coast of Panama in January 1983 by marine scientist Harilaos Lessios of the Smithsonian Tropical Research Institute in Balboa. During that year, observations from a number of other scientists alerted by Lessios recorded mass mortality throughout the Caribbean in a generally clockwise progression northwards following the prevailing currents along the coast of Yucatan, around Cuba, Hispaniola, the Bahamas and Bermuda, then southeast along the Antilles chain of islands, reaching Tobago near the Venezuelan coast in December. Collectively, the group assembled a large databank, which revealed the scale of the problem: within a year, *D. antillarum* had reached near-extinction levels, with population densities "reduced to 1.1–5.8% of their previous levels in Panama to 0.6% in Jamaica" (Lessios et al. 1984, p. 335). It was, in the words of Nancy Knowlton of Scripps, one of the scientists who investigated the problem, "immediately recognized for what it was: biological disturbance of unprecedented scale with potentially enormous ecological effects.… By February 1984, *D. antillarum* had been virtually eliminated from all of its range, apart from populations in the eastern Atlantic, making this the most extensive and severe mass mortality ever reported for a marine organism" (Knowlton 2001a, p. 4822).

From the progressive movement of urchin mortality in the absence of a specific causative agent, it was assumed that it came from "a waterborne pathogen transported by ocean currents" and was specific to *D. antillarum* because none of the other six species of coexisting urchins was affected. Sensing significant change, Lessios and two colleagues at the Balboa Institute moved proactively by constructing five permanent 25 m^2 quadrats in shallow-water habitats in May 1983 at Panama before disappearance there had been noted, and a sixth nearby after dead tests were discovered. Over 10 years of continuous monitoring the collapse continued, and in 1995 Lessios reported "little recruitment and no population recovery", despite the high monthly fecundity of around 10 million eggs per female (Lessios 1995, pp. 333–335).

Accelerating Disturbance: Coral Disease

Reef scientists were now beginning to confront increasingly numerous and difficult challenges. Although the two almost overwhelming issues of *Acanthaster* outbreaks and *Diadema* population collapse seemed unsolvable, evidence was beginning to accumulate of another form of reef disturbance, which from its appearance was initially described as black band disease (BBD). First observations were made on Glover's Reef in Belize around 1972 when University of Vienna marine scientist Arnfried Antonius observed strange black spots on boulder (*Porites* spp.) corals, several millimetres deep and around 1 cm wide. He noted that they began to expand radially and form a dense circular black mat that moved outwards, up to 1 cm per day, in warm summer temperatures (faster than coral can regenerate) killing the polyps and leaving behind a bald chalky surface that became colonized by filamentous algae (Antonius 1977).

Alarm soon spread throughout the reef science community and following investigation by Klaus Rützler of the University of Vienna in collaboration with mycologist D. L. Santavy, BBD was recognized in 1983 as a cyanobacterial infection, the main pathogen being *Phormidium corallyticum*. Once recognized, its presence was then noted around the tropical reef systems of Florida, on other Caribbean reefs, and later in accounts from the Gulf of Oman, the Red Sea, the Philippines, the Indo-Pacific and the GBR. The main scientific problem, although the pathogen had been identified, is that its cause remains unknown. Various factors have been suspected, particularly the frequently polluted waters in which the diseased corals were found, along with other environmental stressors, and because the bacteria are photosynthetic, elevated sea surface temperatures during warm periods also became a matter for investigation.

Soon after the discovery of BBD in 1973, Philip Dustan reported an equally alarming disease from the Florida Keys that he named "White plague" and which he observed on six species (Dunstan 1977). Characterized by the appearance of a line of necrotising tissue that spreads relentlessly several millimetres a day, it has since been noted on >30 scleractinian species. At around the same time, William Gladfelter of the Fairleigh Dickinson University Marine Laboratory at Saint Croix in the US Virgin Islands found what seemed to be another kind of coral disease. As every diver knows, branching Acroporid corals have pale tips that gain colouration as they grow. What Gladfelter observed, however, was that two particular species of staghorn coral, *Acropora palmata* and *A. cervicornis*, were exhibiting pale sections at their bases, and in some cases in the central parts of the stems, causing the loss of tissue as cells died and fell away, leaving behind a bare calcium surface that also became colonized by filamentous algae. Described as white band disease (WBD), despite much effort, no pathogen for WBD-I has been found and its etiology remains a mystery.

It was then recognized throughout the Caribbean and a particular variant designated WBD-II was found in the Bahamas, which progressively reduced *A. palmata* to 5 % of its former cover (Gladfelter 1982). Results were finally obtained for WBD-II when its pathogen was identified as the bioluminescent marine bacterium *Vibrio harveyi* (Gil-Agudelo et al. 2006, p. 59). The accelerating pace of various forms of coral disease in the Caribbean during the final two decades of the 20th century had developed into an ecological disaster with some 80 % of coral cover killed. WBD was also discovered throughout the tropical oceans from the Gulf of Oman and the Red Sea to the Philippines and Australia. Along the GBR, a number of different appearances of WBD causing the death of coral species led the LTMP of the GBRMPA to substitute on 1999 the more generic descriptor "White syndrome" because the seven or eight forms they identified were different from those encountered in the Caribbean. Like the Caribbean WBD-I, the varieties encountered in GBR waters all manifest the sloughing of diseased zooxanthellate tissue, leaving only denuded coral skeletons. No pathogen has been observed either, but from surveys by the LTMP came the discovery that White syndrome disease increases progressively on table-type coral species towards the outer shelf.

As global concern with reef disturbance increased, more pathological diseases were identified as more and more scientists became involved and more accurate diagnoses could be made. Following an outbreak of corallivorous gastropods in the Red Sea, specifically the marine snail *Drupella cornus*, Arnfried Antonius and Bernhard Riegl conducted an intensive investigation in the Gulf of Aqaba where they also encountered an abnormally high proportion of dead corals, which they attributed to white syndrome. In their report, they listed other diseases causing coral mortality that had been identified in various locations well before their survey: BBD, black overgrowing Cyanophyta (BOC), WBD, white plague and white pox, tissue bleaching, shut-down-reaction (in aquaria) and skeleton eroding band (SEB; Antonius and Riegl 1997, pp. 1, 3). In addition, other disorders were listed, including brown band disease (BrB) and pink spot disease, along with two lethal diseases of coralline algae, one being infection by *Aspillergus* fungus in gorgonian sea fans (Sutherland et al. 2004, pp. 274).

The increasing frequency of coral disease in those decades had become a serious indicator of increasing reef instability, and efforts to discover the causes were intensified around the world. Some successes were achieved: following identification of *Phormidium corallyticum* as the cause of BBD, the LTMP traced SEB, which penetrates and disrupts coral tissue, on the GBR and other reefs in the wider Indo-Pacific, to the ciliate protist *Halofolliculina corallasia*. Pink Spot Disease, which typifies swollen coral polyps on *Porites* boulder corals, was discovered to be caused by a parasitic flatworm, and the black necrosing syndrome that infected the Gorgonacea family of soft corals came from an unidentified fungal infection. Unfortunately, the causes of the widespread white syndrome disease as well as coral tumours, which exhibit abnormal growth rates and subsequent death, remain unknown, nor have any cures been identified.

For several decades, the continuing spread of coral diseases and the uncharacteristic growth of algae throughout the tropic reefs seemed to indicate that transition to "coralgal" reefs, particularly in the Caribbean, was becoming a matter of ecological fact. Many scientists were beginning to strengthen their earlier suspicions that warmer summer temperatures, exacerbated by the polluted waters that surround what were becoming more densely settled islands, activated the outbreaks of deadly viruses that destroy the vital processes of coral polyps. Between 1950 and 1975, in addition to increased movement by American residents to the retirement state of Florida, throughout Caribbean, Polynesian, Melanesian and Indian Ocean waters, the human population had doubled from 30 to 60 million, with the Caribbean Islands alone providing an additional 15 million, i.e. half the population increase (McEvedy and Jones 1978).

Unlike developed countries where townships have efficient sanitation systems, many tropical islands discharge sewage directly or minimally treated into surrounding waters, which in most cases are lagoons enclosed by encircling reefs. The outcome was labelled eutrophication (Gk *eu*, "good" + *trophos*, "nourishment") from the now abundant essential plant nutrients of nitrogen and phosphorus. As coral reefs have evolved in turbulent, well-fluxed, oligotrophic (Gk *oligos*, "little, few" + *trophos*, "nutrition") waters, the consequences since 1969 in those nutrient-rich waters was the explosive growth of various kinds of space-competitive algae, prompting a number of investigations into the progressive decline in water quality and into coral diseases.

In addition to rising sea surface temperatures, bleaching and pollution, equally disturbing evidence of an ailing ecosystem was becoming evident in the expanding number and spread of diseases among zooxanthellate corals described in detail earlier, particularly throughout the Caribbean and to a lesser extent in Indo-Pacific waters. In 1999, a team of 13 investigators led by Drew Harvell, ecologist of Cornell University, published their distressing findings on the continuing rise of emerging marine diseases that were causing mass mortality among not only coral reefs and sea grasses but also in fish, cetaceans (whales) and pinnipeds (seals, sea lions, walruses). Vectors were a number of pathogens, mainly bacteria, viruses and fungi, although other agents were identified, such as slime moulds and nematodes (unsegmented worms), which placed the blame directly on climate change and warming seas, in a world of anthropogenic factors (Harvell et al. 1999). The main problem in dealing with what was termed "the rising tide of ocean diseases", from the first reported disease of skeletal anomalies in 1965 to the 19th disorder of *Vibrio corallyticus*-induced bacterial bleaching identified by DNA sequencing in 2002 (Ben-Haim et al. 2003, p. 314), were the poorly developed diagnostic tools available. After the survey by her team, Harvell urged the use of molecular technology to detect the origins and reservoirs of marine diseases, particularly their transport from land into the sea. Equally important was the need to classify all pathogens by longevity and to identify the role of anthropogenic causes in incubating and conveying diseases, with the aim of creating epidemiological models to facilitate analysis and possible correction (Harvell et al. 1999, p. 1508).

The dramatic rising tide of marine diseases also attracted the attention of Kathryn Sutherland, James Porter and Cecilia Torres from the Institute of Ecology at the University of Georgia, who began an exhaustive review of the evidence, which they published in 2004. Particularly disturbing were marked variations in global distribution: "Of the approximately 400 coral species then known in the Indo-Pacific", they reported, "only 98 (25 %) have been documented with one or more diseases, while at least 52 of the 66 (82 %) Caribbean coral species are known to be susceptible to disease" (Sutherland et al. 2004, p. 296). Even more distressing was the discovery that "the scale and severity of coral loss in many Caribbean reefs is unprecedented in the paleontological record" (Selig et al. 2006, p. 112). With further support from accumulating evidence, they concluded that "human activity in the watershed may be causally related, along with elevated sea surface temperatures, nutrient sewage and sediment loading" which may "deliver potentially pathogenic organisms to the marine environment" (Sutherland et al. 2004, p. 297).

Some 40 years after the first observations of a cyanobacterial infection of corals was reported from Belize, a new, previously undiagnosed disorder was discovered in 2011 in the clear, highly protected, unpolluted waters of the GBR between the Heron Island and One Tree Island Research Stations. In that case, the victims were the highly prized coral trout (*Plectropomus leopardi*) which manifested very unusual, dark lesions on their skin, covering between 10 % and 100 % of the surface of individual fish. Scientists from AIMS collected a random sample of 136 coral trout in waters no deeper than 20 m on four separate occasions. Of those, 20 showed signs of skin abnormalities, a number that was statistically significant. Specimens of the lesions were sent to Michael Sweet, an internationally recognized expert heading

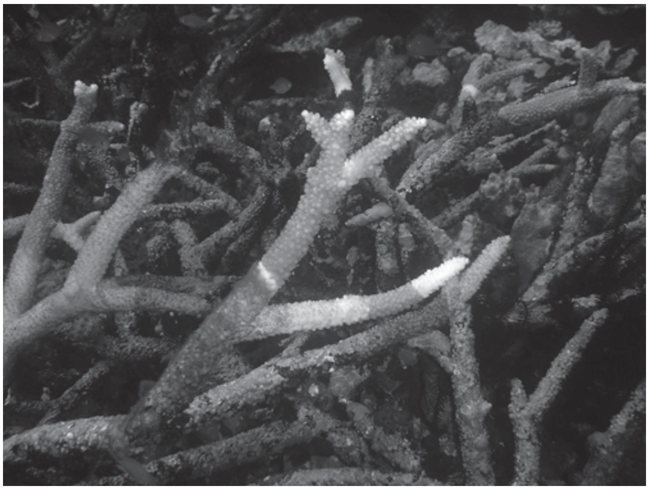
One Tree Island research station. Sketch by the author during the ENCORE experiment, 1994

the Coral Health and Disease Laboratory at the University of Newcastle upon Tyne in the UK. After an exhaustive battery of tests, including gel electrophoresis for ribosomal ribonucleic acid (rRNA) analysis and both scanning and transmission electron microscopy for microbial analysis and histological examination, results were uncompromising: "No known microbial pathogen sequences were found in lesion samples". What they found, however, were "Melanin-containing cells (melanosomes) … in higher density and with a deeper distribution within the lesions than compared to healthy tissue sections". In simple terms, the specimens exhibited an early phase of skin cancer. "Along with a lack of any evidence for a pathogenic cause", the research team concluded that "this represents the first case of melanoma in a wild fish population", although they were unable to determine "whether this type of melanoma is benign or malignant". Furthermore, "as the sampled fish were collected offshore in a marine protected area with no reports of pollution, the likelihood of potential carcinogenic pollutants being the causal factor is low, at least in this reported case" (Sweet et al. 2012, p. 4).

As potentially lethal ultraviolet-B (UV-B) radiation reaches a depth of 30 m, and the life expectancy of the cancer-induced experimental laboratory fish *Xiphophorus hellerii* was reduced from 4 years to 6 months, a crucial and challenging task will confront GBR park management. In particular, "it will have implications for the fish population as a whole and the commercial and recreational fisheries that exploit this species". To add another dimension of concern, Michelle Heupel, the AIMS scientist in the team, advised that "current information suggests this syndrome is present throughout the GBR", and "highest in the southern GBR", but previously not analysed to the present level of detail. The final words echoed the universal thoughts of all who strive for the survival of reefs: "It is unclear whether future changes in the ocean environment or climate will similarly exacerbate the effect of melanoma in wild *Plectropomus leopardi* populations, but clearly further research is urgently needed to understand the distribution, prevalence, ecological and fisheries significance of this syndrome" (Sweet et al. 2012, p. 5). One statement made in the Abstract of the paper is significant. As the ozone hole hovers over the Southern Hemisphere, they suggested that "research of the potential links of this syndrome to increases in UV radiation from atmospheric ozone depletion needs to be completed".

Increasing Global Anomalies: Hurricanes and Tornadoes

Finally, after years of hesitation, in 2009 the LTMP focused attention on the often-suspected cause: ocean warming attributable to climate change. Their finding was that steadily rising water temperatures increased the frequency of the common Indo-Pacific disease of white syndrome, and by 2003 they reported that "high coral cover (>50 %) and anomalously warm water appear to be necessary for white syndrome outbreaks to occur and these two risk factors explained nearly 75 % of the variance in disease cases". "Although the mechanisms are not known", they concluded, "this study found a strong correlative relationship between



White disease of acroporid corals. (Illustration courtesy John Veron)

white syndrome and warm temperature anomalies" (Selig et al. 2006, pp. 112, 122).

Yet another serious concern being generated by global warming is escalating cyclone activity, now believed to be causally connected as warming waters increase the likelihood of rainfall. Those known in the Caribbean as hurricanes are the most destructive of all natural forces exerted on coral reefs, where their history has been one of extreme violence. From records since 1900, the National Oceanic and Atmospheric Administration (NOAA) documented 35 major Caribbean hurricanes and five extremely violent ones up to the overwhelmingly infamous Katrina in 2005, which at the time ravaged New Orleans beyond any previous human experience. Fortunately, there is no evidence at present that frequency has increased. Equally devastating in terms of human life and property damage have been the tornadoes, or twisters, generated in the Caribbean and leaving a trail of damage throughout the Mississippi Valley, the US Midwest and southern coastal states. On "Super Tuesday", 5 February 2008, when 87 documented tornadoes killed 57 persons, they caused more than a billion dollars in damage. Less than 2 years later between 14 and 16 April 2011, more than 200 confirmed tornadoes rampaged across 16 US states killing at least 43 persons, and an even more violent twister came 2 weeks later leaving 344 dead.

Since then came two more closely documented cyclones, starting with Hamish, which caused tremendous destruction along the GBR in March 2009 by travelling from the Coral Sea and moving south along most of its length, severely battering it as it went. Damage was severe and in places coral cover had been reduced by up to 70% through "scouring" (the stripping and fragmentation of surface layers) and "exfoliation" (the complete destruction of the reef matrix and everything on it), mainly by cyclone-generated waves. Damage has been estimated to take around 15 years to recover, provided there are no more cyclones in the intervening years (media release by H. Sweatman of AIMS in 2009). Then, in February 2011, the Fiji-generated cyclone Yasi devastated the GBR with equal ferocity to Katrina and left a trail of shattered homes, plantations, marinas and commercial buildings. Unfortunately, cyclones do not only destroy the coral structure or the built environment, they also create considerable collateral damage from intense agitation of reef waters by rainfall, which reduces salinity and increases bleaching as well as creating massive river outflow flooding that smothers corals with sediment. In 2011, large numbers of green turtles (*Chelonia mydas*) were also killed by the enormous volumes of sediment and debris discharged from extensive flooding across the central Queensland basin.

Coral Reef Watch and the Caribbean Warm Event of 2005

Although the effects of disease and death observed in coral reefs provided convincing evidence that increasing water temperatures were intimately involved, they were becoming impossible to explain from individual investigations. A more coordinated response from a wider range of observations at an international level was clearly needed, as urged by Glynn (1984). That need was finally met in 1998 when Presidential Executive Order 13089 created the US Coral Reef Task Force (USCRTF) "to preserve and protect coral reef ecosystems". Composed of 12 Federal Agencies, it also included American states with coral reef ecosystems in their waters, along with American Samoa, Guam, Puerto Rico and the US Virgin Islands. Immediately following, in 2000, the USCRTF adopted the "National Action Plan to Conserve Coral Reefs", to grapple with what had become an almost overwhelming international crisis. Two years later, the US Coral Reef National Action Strategy was initiated to provide the guiding framework for the priorities, strategies and actions of the USCRTF and its members.[1]

To provide information on threatening weather developments, in addition to the remote sensing instruments already in operation in climate variability and predictability (CLIVAR), the USCRTF established Coral Reef Watch (CRW) in January 2000 to give almost instantaneous warnings of anomalously high temperatures liable to result in mass coral bleaching and mortality. From Pathfinder satellite data that identified threatening increases in water temperature, in a term borrowed from plate tectonics as "HotSpots", the empirical measurement of degree heating weeks (DHWs) was devised. One DHW was defined by NOAA as 1 week of sea surface temperature values above the expected summer maximum by 1 °C, 2 DHWs as equivalent to 1 week of 2 °C

[1] CoRIS: Coral Reef Information System.

above, or 2 weeks at 1 °C above. As the CRW system became operational in September 2000, in order to have a more substantial starting point for prediction, sea surface temperature archives since 1985 were incorporated into its database. Periods of sustained heating are then determined from intensity and duration of heating to map affected areas and predict likely outcomes. DHW values ≥4 °C-weeks generally resulted in bleaching, and >8 °C-weeks caused widespread bleaching and significant mortality.

The system soon received its first major test when warm waters began building up in midsummer June 2005 in the Caribbean and adjacent Atlantic waters, lasting until mid-autumn in October. In some places, 16 DHWs were recorded by NOAA with temperatures as much as 1.2 °C above, which contributed to "the most active Atlantic hurricane season on record and the most severe and extensive mass coral bleaching event observed in the Caribbean". To gather *in situ* information, CRW alerted reef scientists by Internet to monitor developments as heat built up, and to forward reports. The results were both surprising and disturbing. In a wide-ranging summary of the course of the episode, Mark Eakin of CRW coordinated data from 56 observers and 2575 field surveys that were finally published in 2010 (Eakin et al. 2010). From 2005 to 2007, it was revealed that mortality exceeded 50% in several locations, and that increased temperatures were "quickly followed by a loss of resistance to pathogenic disease and an increased abundance of microbial pathogens in *A. palmata*". In addition, bleached corals suffered greater disease-associated mortality than unbleached colonies.

Human disturbance, the report mentioned, had increased substantially over the 20th century and it is "unlikely that natural climate variability was the cause of declines in Caribbean reefs during recent decades [since] coral reef community composition has remained remarkably stable [since the last glacial cycle]". By 2010, in contrast, "Major bleaching events have returned to the Caribbean every five years or less, with growing intensity. With no sign of real recovery… these repeated events are likely to have caused reef decline that will extend beyond our lifetimes" (Eakin et al. 2010).

Warming Waters and Climate Change Confirmed

By 2012, there was a near-universal agreement that warming waters were the cause of much global ecological disturbance. In March that year, the South East Climate Change Program of the Australian Government recorded that the East Australian Current, which flows south along the GBR and passes the northern half of the New South Wales coast, had strengthened by 20% over the previous 50 years, and was 2.3 °C warmer. One consequence was that the long-spine sea urchin *Centrostephanus rodgersii*, a voracious temperate climate predator, had migrated from New South Wales waters down to Victoria and was ravaging the productive fishing waters of the cooler coastal zone of eastern Tasmania around 42°S to a depth of 20 m.[2] Yet another serious impact was reported by Australian Government (CSIRO) marine ecologists: some of the giant kelp forests of southwestern Tasmania, rising 25 m from the seafloor and dependent on cold waters, had been diminished by >95% as temperatures rose.

Also in March 2012, James Hansen, Director of the National Aeronautics and Space Administration (NASA) Goddard Institute for Space Studies, felt compelled to affirm the present global situation in a peer-reviewed co-authored article that provoked immediate, critical and in some cases, ill-informed responses. Choosing 1951–1980 as the base period, because it was "a time of relatively stable global temperature" and "within the Holocene range", he argued from existing empirical data that the ensuing years, 1981–2010, were "probably outside the Holocene range" because of melting of polar ice sheets and anomalously high land temperatures. This situation was clearly confirmed by "extremely hot outliers, more than three standard deviations warmer than the climatology of the base period of 1951–1980" (Hansen et al. 2012, p. 1). Copiously illustrated with coloured boreal temperature anomaly graphs and normal distribution bell curves showing progressive displacement to the right on the *x*-axis up to three standard deviations, the article concluded with a survey of the broader implications of extreme climate change. Natural ecosystems, he pointed out, are adapted to the Holocene climate, but, with ubiquitous surface heating and elevated greenhouse gas levels, in already prone regions we might expect more frequent droughts and unusually heavy rainfall and floods. Many animal species can migrate to more equitable zones but that would be difficult for vegetation in the short-term, particularly given that continued heavy land conversion is creating habitat destruction, species overharvesting, homogenization of biota and widespread toxins. The way ahead, he suggested, was political: "a rising price on carbon emissions sufficient to spur transition to a clean energy future without burning all fossil fuels" (Hansen et al. 2012, p. 8).

Disease, Pathogens and the Causes of Coral Death

In the same period as the Caribbean bleaching disaster, the World Bank had commissioned a separate Coral Reef Targeted Research Program (CRTRP) to conduct a specific global investigation into the decline of coral reef ecosystems with the particular aim of assessing the prevalence of disease, the

[2] Australian Government, Fisheries Research and Development Corporation, *FISH* 20.2, June 2012, 17: 24–25.

environmental drivers, the causative pathogens and the resistance capabilities of corals. Although rising sea surface temperatures were the centre of interest, the CRTRP working hypothesis was to determine whether coral death "is facilitated by opportunistic infectious pathogens whose virulence is enhanced by increased temperatures" (Harvell et al. 2004, and 2007, p. 174). As the environmental driver of coral disease was accepted as "high temperature anomalies", the task of the working group was to discover the causative agents. How exactly does warm water lead to the explosive growth of pathogens and the death of large colonies, and what is the impact of heat stress on each polyp?

Under the leadership of Drew Harvell, and supported by seven internationally respected reef scientists, four monitoring centres were established in the Yucatan, the GBR, the Philippines and East Africa. Their primary data collection established that there are at least 19 major diseases, mostly bacterial and fungal: 12 in Caribbean HotSpots, where >70% of major diseases are found, in contrast to 7 in the Indo-Pacific. Unfortunately, most of the disease identities are not known, and in a number of cases, several are present simultaneously in various species (Harvell et al. 2004, and 2007, p. 188). Among these diseases, the most frequent by far is white plague II (found in 41 species), followed by black band (in 19 species). The remaining 17 species range in frequency from 13 to 1, with Indo-Pacific–Mediterranean occurrence much lower, between 5 and 1 species. Equally significant are the victims, with >250 species of acroporid infected, followed by some 125 species of faviid and some 90 species of poritid.

As all diseases begin as small lesions on the outer membrane of the coral, which increase in surface area until the colony dies, investigation soon assumed a dermatological character to examine the surface mucopolysaccharide layer (SML). Consisting of a carbon-based gel-like layer of glycol-protein, it varies in thickness from 1 mm or less in some scleractinians to several centimetres in certain soft corals. Within the SML is "an impressive diversity of microbial communities", whose function apparently is to maintain an immune response to invading pathogens, although, unfortunately, many coral pathogens are still unknown and some are complexes of different bacterial types. Regrettably, the CRTRP has to date been unable to understand much about the SML's function, although, using the analogy of the skin, they believe that it acts as a protective barrier against invading microbes (Harvell et al. 2007, p. 190). Clearly, considerable investigation is needed to determine why its protective function is failing in many cases.

During the 2005 Caribbean bleaching event, one interesting study by Marilyn Brandt and John McManus provided evidence of a positive correlation between bleaching and incidence of mainly white plague, dark spot and black band diseases in certain species. As they reported, both bleaching and disease are independently capable of altering the structure of coral populations through loss of living tissue, and the composition of the SML becomes significantly changed during bleaching which affects its physiological function negatively (Brandt and McManus 2009). With that finding, which indicated that warmer waters were the stimulus to infection, in the concluding remarks to the CRTRP report in 2007, Harvell stated that they were unable to assign causation because at present in coral biology, there is little understanding about "the interactions between host immunity and pathogenesis in nature". Consequently, it is difficult to determine "whether warmer temperatures inhibit coral defences by altering the immune response because of bleaching, or whether temperature enhances the virulence of pathogens" (Harvell et al. 2007, p. 191).

At the time the CRTRP report was submitted, no firm conclusions could be reached, and the same litany of anguish that had been running through much research during the previous two decades over human-induced climate change and warmer waters as the cause of reef loss was presented. "If habitat deterioration and climate warming continue at the same rates", Harvell wrote, "we are faced with unprecedented challenges in managing coral reef communities". Furthermore, "we are still far away from any miracle vaccine or remediation protocol against any of the current coral reef diseases". Even the establishment of marine protected areas (MPAs) as defined by IUCN, at present numbering almost 7000 globally, she believed, did not seem to offer much hope. "Currently, the only viable management option is to trace the origin of coral disease and attempt to shut off any known inputs". Then came her unanswerable comment. "It is unrealistic to think that we can restore a 1000-year-old coral reef without restoring the original environmental conditions. Without a concerted effort among researchers, governments and all stakeholders, the future of coral communities is in jeopardy" (Harvell et al. 2007, pp. 192–193).

Reefs at Risk: Threats to Biodiversity

Whereas atmospheric forcing of world climate has become a matter of great concern, efforts have been ongoing for several decades by a number of international organizations to deal with the other face of reef collapse. With people increasingly being forced off their land and onto the already crowded coastlines in Indonesia, the Philippines and the Caribbean, as well as in Madagascar and the Seychelles, East Africa and various Pacific nations, reefs are being degraded as a result of the excessive pollution and destruction by their indigenous inhabitants. Least educated and income poorest, the burgeoning populations of those tropical regions are exerting massive pressure on coral reefs in a desperate need for protein. That pressure is particularly heavy in Indonesia and the Philippines because of destructive fishing practices with home-made bottle bombs, as well as the release of cyanide into the surrounding water to stun fish for capture. Although now banned in most countries, it is still practiced illegally to meet restaurant demand, and most destructively for the aquarium trade in which some 20 million fish and other reef species are captured each year, along with decorative corals, anemones and other ornamental varieties.[3] Although defended on the grounds of helping developing communities climb out of poverty, the final effect can be a reciprocal impoverishment of the tropical ecosystem.

Such practices destroy habitat and affect marine population density heavily in coastal waters already polluted by inadequate village sanitation. Great damage is also exerted by large profit-motivated corporations, in collusion with corrupt local politicians and business groups in clearing rainforests and mangroves for timber milling and establishing large plantations for such activities as oil-seed harvesting. Other injurious practices include blasting reefs to create harbour access, whereas mangroves, the nurseries of reef life, are dredged and seagrass beds cleared for resort developments and housing estates. Exacerbating the loss of habitat further is the continuing deliberate damage of coral reefs for other kinds of economic gain. Around tropical coasts, their limestone content continues to be mined for building blocks and cement manufacture, and as an industrial flux for smelting iron ore, and their sedimentary substrata are explored for petroleum deposits. Further despoliation and impoverishment of reef productivity comes from fishing by trawlers and factory ships for overseas markets.

Those destructive practices make a significant impact on biological diversity. To deal with that growing problem of sustainability, the American National Research Council, an organization designed to facilitate government action on issues of technology and the environment, convened a National Forum on Biodiversity in Washington DC in September 1986. That meeting led to the creation in 1991 of an Intergovernmental Negotiating Committee to help moderate damage to coral reefs, particularly in developing regions. In May 1992, that Committee held its first session in Nairobi to prepare a negotiating text for a UN Convention on Biological Diversity for presentation to the Rio Earth Summit, the same year that it had been hoped to reach a successor agreement to the Kyoto Protocol.

During the Summit, where the Convention was signed by 168 nations, one of its most enduring concepts was formulation and promotion of the precautionary principle to exercise some control over such environmentally hostile plans as the intention of DuPont chairman Heckert in 1988 to continue chlorofluorocarbon (CFC) manufacture in the face of evidence for ozone depletion provided by Crutzen, Molina and Rowland. In order to counter the common commercial denial of impacts as a consequence of the lack of scientific evidence, such as climate change itself, the Conference declared that "where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation". Following the Summit, from 6 to 17 November 1995, a conference of 181 parties in Jakarta passed a resolution as a result of their "deep concern at the serious threats to marine and coastal biological diversity caused by factors including physical alteration, destruction and degradation of habitats, pollution, invasion of alien species, and over-exploitation of living marine and coastal resources". Known as the Jakarta Mandate, to strengthen its influence in heavily impacted regions, it has since had continuing revisions at meetings in Bratislava in May 1998 and Nairobi in 2000. Then, in January 2002, the parties adopted the Cartagena Protocol to protect living biodiversity from the potential risks posed by deliberate human activity in gene transfer and genome dynamics, because high levels are currently affecting the pattern of evolution by natural selection. Although in everyday language the Protocol refers to the range of visible species, it also encompasses the higher levels of ecosystem, genetic, and even molecular organization from which an enormous literature of disquiet has been generated.

Community Cooperation: Saving Reefs and Ecosystems

During the deliberations, growing evidence of the degradation of reefs and mangroves also prompted the United Nations Environment Programme (UNEP), the Intergovernmental Oceanographic Commission (IOC), the World Meteorological Organization (WMO) and the International Union for the Conservation of Nature (IUCN) to convene a meeting of experts in Monaco in 1991 to devise local response strategies for such a serious issue, and the following year on the closely related implications of climate change for coral reefs. Soon thereafter, at the 1994 UN Global Conference on the Sustainable Development of Small Island Developing States in Barbados, the International Coral Reef Initiative (ICRI) was established as a partnership among governments and other interested organizations, specifically to preserve coral reefs and related ecosystems.

The following year in its Framework for Action, the ICRI established the Global Coral Reef Monitoring Network (GCRMN) as its operational organization. In 1996, Clive Wilkinson from AIMS was appointed Global Coordinator and in 1997, the GCRMN Strategic Plan was made public.

[3] UNEP World Conservation Monitoring Centre, BBC media report 30 September 2003. There are several online websites with detailed information.

Its main objective was defined as linking governments, organizations and local communities into a network for collecting information on the deteriorating condition of coral reefs around the world, and improvement of the educational level of local communities regarding the ecosystems on which their livelihoods depend.

From a careful survey by 32 ecologists of the tropical Americas (Caribbean and Pacific Panama waters), the Indian Ocean, the Middle East (Red Sea and Persian Gulf), East Asia and the Pacific Ocean, the ICRI issued a grim warning in 1998. From "the deteriorating condition of coral reefs around the world", the report made it clear that they continue to be a source of grave concern, and that over the past decade the "state of coral reefs and associated marine ecosystems has worsened significantly". Their distressing findings disclosed that 58 % of the world's reefs are potentially threatened by direct, destructive human activity and that those of Southeast Asia, the most species-rich on earth, are also the most threatened, at 80 %. In contrast, Pacific reefs and other areas are in a lower risk category, at some 70 %, their main problems being coral bleaching and destructive fishing. Lowering of risk factors unfortunately has had to be accepted as a slow educative process, although it is now finally beginning to show some signs of progress (ICRI 1998).

The same problem was being observed with dismay not only by UNEP but also by non-governmental and voluntary organizations (NGOs), particularly the World Resources Institute (WRI), an environmental issues research centre founded in 1982, and the WorldFish Centre (formerly ICLARM, the International Centre for Living Aquatic Resources Management). In 1998, the first of these produced their first global assessment in *Reefs at Risk,* where risk was defined as "problem areas around the world where, in the absence of good management, coral reef degradation might be expected, or predicted to occur shortly, given ongoing levels of human activity. Such degradation includes major changes in the species composition, relative species abundance, and/or the productivity of coral reef communities, attributable to human disturbance" (Bryant et al. 1998, p. 17). In 2002, the same organization focused on reefs in Southeast Asia (Burke et al. 2002), and in 2004 on Mediterranean reefs (Burke and Maidens 2004), and the same principles in terms of risk were applied.

In 1998, the GCRMN published its first *Status of Coral Reefs of the World* report, now a biennial publication drawing evidence from as many as 372 experts in 96 countries. Unfortunately, each account continues to advise that coral reefs of great significance as global centres of biodiversity "are being damaged by a combination of direct human impacts and global climate change" coming from increasing sea temperatures resulting in higher acidification levels and lower concentrations of seawater carbonate needed for calcification. If present trends continue, the 2008 report warned, with global warming unabated, "the potential for a 4 °C rise could make bleaching an annual event". Even a 2 °C rise, if permanent, would mean that "coral dominated reefs [which support at least 25 % of all marine life] are expected to largely disappear from many shallow coastal regions of the world" (Wilkinson 2008, p. 31).

14 A New Enigma: Deciphering the Synergism

As bioturbation increased, scientific opinion had become totally convinced that it was related to elevated sea surface temperatures and *El Niño* Southern Oscillation (ENSO) events. In the same period, human population had been increasing steadily, consuming ever more resources, although, despite the evidence of global warming, public opinion remained divided on the question of responsibility and remediation.

The rapid increase in coral disease across the tropics, and most disastrously in the Caribbean, was becoming a matter of ever greater concern when entire sections of reefs began losing their attractive colours and turning white, with many then dying. There was also considerable confusion between death from white-band disease, or predation as in the case of *Acanthaster*, which left a white skeleton, and loss of colour, usually of a temporary nature whenever localized areas were heated by short, occasional warm phases, especially in shallow waters, that was generally described as bleaching. By the early 1980s, though, as numerous tropic-wide bleaching incidences were reported, and it became evident that large tracts of corals were turning white and dying, it was being interpreted with alarm as a possible epizootic that threatened the ecological health and even the survival of coral reefs.

Although there was widespread recognition that reefs were becoming seriously endangered, there was less knowledge of what was causing coral reef disorders on such a global scale. It was an enigma whose solution defied easy answers. The need to understand and, if possible, to control the synergistic interaction of these various factors, and to separate causes from effects, became a major challenge.

Background to Bleaching: The Historical Record, 1928–1980

One of the earliest discussions of bleaching, originally described as paling, appeared in the reports of the Low Isles Expedition of 1928/1929 when various coral genera (*Favia, Fungia, Galaxea* and *Psammacora*) were starved in various experiments to prove that zooxanthellae are not essential to coral reef health. Yonge's procedures, described earlier, were designed to refute claims by other investigators, such as the 1930 Caribbean findings of Hilbrand Boschma, discussed in Chapter 9, that in response to starvation, polyps digest their zooxanthellae. Yonge's results indicated quite the opposite. If corals are fed, they remain in good condition whether in light or darkness, [although] paling in colour slightly in the dark, but when starved their tissues quickly begin to shrink, undamaged algae are expelled in large numbers and the remaining tissue turns pale as a result". The only interpretation that could be placed on these results, he decided, is that "the algae are not and cannot be used as food by the corals, a conclusion which agrees entirely with the results of the feeding and enzyme experiments".[1]

To pursue that line of investigation more intensively, Yonge subsequently had "a large light-tight box …cemented on the reef flat and placed a number of corals in it", which confirmed earlier findings that after several months the corals showed "a high degree of paling but [were] still healthy, the death of the algae apparently not affecting the corals".[2] In his final report of 25 September 1929, he stated categorically that "corals kept for 5 months in the dark box on the reef flat survived to a large extent, those dead having been mainly killed by sediment" (Yonge 1930b).[3]

Coral bleaching subsequently seems not to have created further scientific interest until 1964, when Thomas Goreau published a report describing the impact of Hurricane Flora on Jamaican coral reef communities. At the time, bleaching was simply a visual description of changes in the colour of corals from loss of the algal symbionts in polyps and all other marine organisms with zooxanthellae in their tissues, including anemones, sponges, clams and other molluscs. Once the zooxanthellae go, the coral tissues become transparent and

[1] Yonge LIE III.2/29: p. 9.
[2] Yonge LIE IV.5/29: p. 6.
[3] Yonge LIE IV.9/29: p. 7.

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
DOI 10.1007/978-3-319-07479-5_14,

the white skeleton is visible. There was little awareness then of the issue of rising sea surface temperature, and his article suggested that "mass expulsion [of zooxanthellae] from the tissues of Millepora, Scleractinia, Zoanthidea and Actinaria living in the shallow reef zone" had been caused by "lowered osmotic pressure on the surface of the sea, rather than by sedimentation or fouling". Although regeneration was slow, Goreau reported that "many of the bleached colonies survived well despite the near total absence of zooxanthellae from their tissues for over 2 months" (Goreau 1964, p. 383).

A decade later, several instructive accounts were published by Paul Jokiel and Steve Coles, beginning with their 1969 experiments, described earlier in this book, to determine the range of thermal tolerance of corals, as part of an environmental impact assessment for a nuclear power station in Hawaii. Several years later, they made a similar investigation of the effects of heated effluent on hermatypic corals at Kahe Point in Hawaii, preparatory to the construction of an electricity steam-generating station. As the facility was to draw cooling water from the ocean around Oahu, and to discharge heated effluent back, the need was to establish the extent of reef damage. One of their most interesting analyses was probably the first attempt to grade the level of bleaching in corals. In the immediate vicinity of discharge, nearly all corals in water 4–5 °C above upper-ambient temperature died, and then in a widening range came the "bleached" ones which had lost most of their zooxanthellar pigment. Next, away from the warm water were the "pale" corals with sufficient pigment to show some colour, and farthest out were the "normal" corals, which "displayed the opaque yellow-greens and browns characteristic of healthy coral" (Jokiel and Coles 1973, p. 3). Unsurprisingly, they noted that "when generating capacity of the plant was increased from 270–360 MW, the area of dead and damaged corals increased from 0.38 ha (0.94 acre) to 0.71 ha (1.76 acre)" (Jokiel and Coles 1973, p. 1).

To continue their investigations of thermal tolerance levels and stress leading to loss of zooxanthellae, the two then focused on coral metabolism as affected by respiration and photosynthesis under ambient temperature conditions. Their most interesting discovery, following a visit to Enewetak Marine Biological Laboratory (EMBL) in the Marshall Islands, was a comparison between corals in Hawaii and Enewetak, where they concluded that "corals resident in these two areas have become physiologically adapted to different temperature regimes". The Enewetak corals, they discovered, could cope with ambient temperatures "2–5 degrees higher than for Hawaiian corals". Their final inference looked forward to the issue of adaptation: "These results", they concluded, "indicate that tropical and subtropical corals are rigorously adapted to their ambient water-temperature conditions" (Jokiel and Coles 1977, pp. 209–216). However, they stressed that more investigation was needed to determine whether that was a consequence of natural selection.

Background to Bleaching: Field Observations, 1981–1990

During the spread of the *Acanthaster* corallivore throughout the 1960s and 1970s, some had appeared in the Gulf of Chiriqui on the Pacific coast of Panama, where Peter Glynn, then with the Smithsonian Tropical Research Institute in Balboa, Panama, had been investigating coral community structure and the "feeding preferences of *Acanthaster* in relation to prey availability". From his study sites on reefs around Secas Islands and Uva Island, he reported that the most consumed corals (between 50 and 85 %) were the *Pocillopora* species, although he considered that factor more the result of availability because he noted that less abundant, non-branching corals were preferred (Glynn 1976, p. 432).

One of Glynn's interesting observations was that widespread *Acanthaster* predation contributed to changes in coral communities, mainly in deeper water, by lowering species diversity. At the same time, other factors needed to be recognized, mainly the disruptive effects of bioturbation from other predators—fish, boring molluscs, crustaceans, worms—and cyclones, endemic in tropical regions. From his investigations, Glynn foreshadowed future issues for intensive research by commenting, "it is clear that any predictions of the effects of *Acanthaster* on reef structure will have to be framed in the context of numerous physical and biological processes" (Glynn 1976, p. 454). Concerned by the large-scale bleaching and death of reef-building corals off the Pacific coast of Panama, Glynn began fresh studies of disturbances to coral reefs in his *Acanthaster* research areas. Uncertain of the causes of the problem, he exercised caution in those early days by placing quotes around the word "bleaching" throughout the entire article (Glynn 1983, p. 149). The first signs came early in 1983 where many species of coral populations and entire reefs that had undergone "bleaching" had died, and similar events had been reported from French Polynesia, the Tokelau Islands north of New Zealand, southern Japan, the Indonesian Java Sea and the Florida Keys.

Alerted by other scientists to further widespread bleaching in the tropical Pacific and the western Atlantic following the warming event of the 1982/1983 *El Niño*, and "a growing body of evidence that modern coral reefs, and many of their constituent populations, are perturbed or destabilized more frequently than was formerly believed", Glynn decided to investigate the issue more comprehensively. In February 1983, he began transect studies of reefs in the Gulf of Chiriqui, examining warmer waters by both snorkel and scuba methods to a depth of 20 m. Like Jokiel and Coles before him, he graded bleached corals by appearance. He described four visual conditions: normal, partially bleached (uniform overall fading), bleached (discolouration of an entire colony to white or lemon-yellow) and dead (no living tissues remaining) (Glynn 1984, pp. 133–134).

Bleached corals

By late October, Glynn reported that “no living colonies of *Millepora* spp. or *Porites paramensis* were found on Uva Reef (about 1 ha in extent) to a depth of 18 m. These species, except for one 2 cm branch of *M. intricata*, were also dead on Secas Reef (about 6 ha in extent) where…by the end of October only dead colonies by the hundreds were observed” (Glynn 1984, p. 136). To compound the evident distress, Glynn cited other scientists who had also observed that “Many scleractinian and hydrozoan [non-scleractinian, zooxanthellate] hard corals, as well as gorgonians, sea anemones, and zoanthids [stony corals], began losing their coloration on the Caribbean side of Panamá in the Bahamas during the first half of June 1983 [the boreal summer]” (Glynn 1984, p. 138). With similar observations being made across the entire tropical zone, Glynn raised a thought-provoking issue with his tentative speculation that “the nearly worldwide disturbance to coral reefs in 1983 and the occurrence of the 1982–1983 *El Niño*—probably the strongest warming of the equatorial Pacific this century…may not be entirely independent events” (Glynn 1984, p. 143).

Glynn’s findings were disturbing, and because bleaching was synchronous with the *Acanthaster* outbreaks and the *Diadema* epizootic, he considered the possibility of infection. After discussion with aquatic toxicologist Esther Peters and reef colleague Leonard Muscatine, he was able to report that “no clear evidence has been found that implicates pathogens as a primary cause for coral mortality in Panamá” (Glynn 1984, p. 143). A year later, in a joint study, the three concluded that the causes of “catastrophic coral mortality in Panama” were “some factor other than a disease”. As the reasons for zooxanthellae loss were still little understood in 1985, although high concentrations of herbicide contaminants were detected in the tissues of affected Panamanian corals, the contributing causes, they reiterated, were likely to be the results of environmental stress from the “prolonged ocean warming during the severe 1982/1983 *El Niño* event” (Glynn et al. 1985, p. 36).

A major contribution to understanding the proliferating problem of numerous reef disturbances appeared in 1990 in a challenging article by Ernest Williams and Lucy Bunkley-Williams of the University of Puerto Rico Aquatic Animal Health Project. Using their own observations, published literature and a questionnaire sent in 1988/1989 to coral reef researchers around the world, they collated a large number of observations covering bleaching events, coral diseases and sea surface temperatures. The replies concerning three “coral reef bleaching complexes” between 1979 and 1988 led them to assert that “We believe the worldwide coral reef bleaching complex “cycle” is caused by increased global temperatures of the 1980s. In an ominous conclusion, they stated from the evidence gathered that the bleaching cycles may recur “possibly with more intensity, and will probably continue and increase until coral dominated reefs no longer exist” (Williams and Bunkley-Williams 1990, p. 1). Despite continued belief that “the severe 1982/1983 *El Niño* event” was the cause of bleaching death, an indication of the uncertainty surrounding the global warming issue at the time was Glynn’s comment on a draft of the Williams and Bunkley-Williams paper, published the same year, that their prediction was a “provocative though unfounded proposal” (Glynn 1990, p. 111).

Goreau’s account in 1964 of the “mass expulsion of zooxanthellae” in Jamaican reefs had already brought to notice the fact that bleaching was closely related to the algal symbionts in coral tissues. That raised an important question: What exactly does “expulsion” mean? The verb “to expel”, *sensu stricto*, means “to drive out forcefully”. Goreau’s thoughts of expulsion obviously came from the impact of Hurricane Flora, although he clearly used the word with a generalized meaning. As concern with rising sea temperatures and bleaching stress intensified in the decades following, attention was directed to seeking a clearer understanding of whether the loss of zooxanthellae was a response by the coral polyp or by the symbiont, and in establishing a detailed analysis of the mechanism of expulsion. At the time, however, there was little knowledge of the size of the problem: Specifically, what is the normal density of zooxanthellae in coral tissues? Brandt had described them broadly as “green bodies”, but gave no statistics. As zooxanthellae are closely associated with fatty acids, a start was made in 1970 when RE Johannes and WJ Wiebe introduced a method for the determination of coral tissue biomass and comparison (Johannes and Wiebe 1970). That opened a way to test for changes in symbiont density among various coral species, which was soon applied by Philip Meyers in 1973 and published the following year.

As episodes of coral bleaching became increasingly prominent in the 1980s, intensified research established that the density of zooxanthellate symbionts in coral endoderm tissue was in the order of millions per square centimetre, and, consequently, an approximate sequential rate of symbiont loss could be calculated. In 1997, Ross Jones and David Yellowlees from the University of Sydney gave a "stable state" density count of more than 2 million per cm^2 (2.1×10^6 cm^{-2}) (Jones and Yellowlees 1997, p. 457). Concerned to measure as precisely as possible the extent and severity of bleaching, in 2011, Dominique McCowan and four colleagues at James Cook University when using the WaterPik technique of tissue blasting, and a newer method by decalcification of host tissues, discovered "highly significant differences in zooxanthellae estimates" in *Acropora millepora*. The latter method yielded densities up to a "maximum mean density of zooxanthellae" of 3.85×10^6 cm^{-2} (McCowan et al. 2011, p. 31).

The reason for the loss of zooxanthellae was not understood at the time although one possibility was believed to be some kind of metabolic imbalance, which led either to active expulsion of the algae by the polyp or else their voluntary migration to open waters. That theory, however, was replaced by later research in 1992 by Roberto Iglesias-Prieto and three colleagues who found that at a temperature > 30 °C, the vital photosynthetic processes of carbon fixation and respiration by the symbiont are impaired, and "cease completely at 34–36 °C" (Iglesias-Prieto et al. 1992, p. 10304), which indicated a failure on the part of the algal symbiont. Acceleration of photosynthesis in the zooxanthellae from stronger solar radiation, it was discovered, generates toxic quantities of oxygen, leading in turn to the polyp expelling the algae.[4] The evidence was increasingly coming to focus attention on the vulnerability of algae to rising sea surface temperatures.

Bleaching Research: Evidence from Molecular Genetics

A way forward in dealing with the bleaching problem was advanced rapidly after Alec Jeffreys of the University of Leicester, using the new science of molecular genetics, developed the restriction fragment length polymorphism method (RFLP) for DNA analysis in 1985. Consequently, as the Williams' survey results indicate, research began progressing rapidly on a number of fronts, beginning with the work of Rob Rowan and Dennis Powers, which opened a way for investigation into every possible problem involving genetic identity. The latter's contribution became instrumental in broadening interest not only in the host coral species, on which virtually all previous research had been conducted, but also on their symbionts, which achieved its first success in solving the very questionable status of *S. microadriaticum* (Rowan and Powers 1991a, b).

When Karl Brandt introduced the neologism of zooxanthellae in his paper "Concerning the Coexistence of Animals and Plants" to the Berlin Physiological Society in 1881 to name the algae he found in symbiosis with several hydrozoans and actinians, he was in as yet unfamiliar territory. At the time, he simply described the single-celled dinoflagellates as "cells" and "green bodies", and devised "zooxanthella" and "zoochlorella", based on their respective colours, yellow–brown and green, as convenient genus terms, *Algengattungen*. In several places, Brandt also referred to the "cells" and "green bodies" as "species", using the relevant German term *die Art*, although his text is not clear on how precise he intended it to be.

Some 80 years later, the taxonomy of dinoflagellates was still in confusion when Hugo Freudenthal finally isolated *Symbiodinium microadriaticum*. Consequently, his proposed new genus, *Symbiodinium*, and *S. microadriaticum* as the type species, almost immediately became disputed. At the centre of argument was the continued use of the word "zooxanthella", which led collaborative taxonomists Rudolf Blank, of the University of Erlangen-Nuremberg in Bavaria, and Robert Trench, of the University of California at Santa Barbara, to publish a vigorous objection. Their critical dissent was based on painstaking laboratory investigation throughout the previous decade of cell cultures of four different strains of *S. microadriaticum* which they believed was, at best, a genus and not a discrete species. Their difficulty in the 1980s, they wrote, was that "resolution of the species problem has been hampered by a lack of genetic evidence", because DNA analysis had been in its developmental stages and *S. microadriaticum* was not known to reproduce sexually. Undaunted, they resorted to electron microscopy of each of the four strains and, when their findings and images appeared in *Science*, it was clearly revealed that "the number of chromosomes is different in each strain, suggesting that the different strains are distinct genetic entities". Focusing on *S. microadriaticum*, in 1986 they argued that Brandt's earlier names of zooxanthella and zoochlorella were clearly unacceptable because "the symbionts commonly called zooxanthellae belong to different algal classes" and hence "We therefore propose rejection of "*Zooxanthella* Brandt 1881" under the International Code of Botanical Nomenclature, Art. 69 (Blank and Trench 1985, p. 657).

However, despite that clarification, the term zooxanthella, like *S. microadriaticum*, had become so firmly established that it continued to be used routinely as a generic descriptor for endosymbiotic dinoflagellates, both zooxanthellae and zoochlorellae, in all coral species. Several years later, with the new technology of RFLP genetic analysis, Rowan and Powers were able to go well beyond the "morphological, biochemical, physiological and behavioral observations" of Blank and Trench, and published the first results for zooxanthella identification. Their exciting result revealed that "a sample of 16 cnidarian host species yielded 6 distinct *Symbiodinium* ssRNA genes" (Rowan and Powers 1991a,

[4] Described in Veron (2008a, pp. 56–57). First reported in Jones and Hoegh-Guldberg (1999).

p. 65). Until that discovery in 1991, almost all knowledge of reef biology came from corals, almost nothing from the dinoflagellates nourishing the host species. Throughout the following decade, DNA technology continued to advance rapidly, allowing Rowan to find that zooxanthellae are considerably diverse. By 1993, he reported them as existing among at least seven genera in four orders. Even more interestingly, the questioning by Blank and Trench of Freudenthal's identification of *S. microadriaticum* in 1962 as possibly mistaken, and that it should have been placed within the genus *Gymnodinium*, which is free-living and from which *S. microadriaticum* has apparently evolved, because it is not known as a free-living species in nature, became actively investigated.

Adaptive Bleaching: A Survival Strategy?

With the development of DNA analysis from 1991 on, increasing attention was given to understanding the relationships between host and symbiont, and in particular, the taxonomic diversity of the organisms involved. There was also a strong sense of optimism among many that bleaching was not necessarily a sign of the demise of reefs, but rather an evolutionary response to a changing environment. As first observed at Enewetak by Jokiel and Coles in 1977, they wondered if it was simply acclimatization to higher water-temperature conditions. Even more intriguingly, they puzzled whether it could be a process of natural selection.

In 1993, Robert Buddemeier and Daphne Fautin published a captivating analysis of that particular issue which became known as the "adaptive bleaching hypothesis" (ABH). With DNA research rapidly establishing the "overwhelming diversity" of symbionts which, although certainly not a separate species, regardless of taxonomic status, were considered "functionally distinguishable" as "types", they believed it explained the wide range of responses to bleaching conditions by various species of coral. Different or changing environments, multiple symbionts in the same host, and various types of algae in the same species of coral (conspecific hosts) could all play a role. Central to their argument was the fact that coral reefs have had a long evolutionary existence from the beginning of the Mesozoic era, 250 Mya (Veron 2008b), and "have repeatedly undergone rapid climate-induced environmental changes on time scales of centuries to millennia" (Buddemeier and Fautin 1993, p. 324). If some of the symbionts were proving unable to adapt to high temperature stress, then the symbiont could be expelled and new ones selected from readily available "swarmers" in the water column. That introduced yet another novel concept: symbiont shuffling. Bleaching, they concluded, although it represents instability in the short term, allows a host to be repopulated with a different partner and "promotes long-term stability by enhancing survival chances of both zooxanthellae and host under conditions that are not those of the pre-stress environment" (Buddemeier and Fautin 1993, p. 325).

One of the most important methods for advancing research into bleaching came in 1998, when Rowan reported that "*Symbiodinium* contains three well-represented groups (clades), sometimes called *A, B* and *C*" (Rowan 1998, p. 408). With the introduction of the horticultural concept of clades (Gk *klados*, "a plant slip, or shoot"), a new avenue into symbiont investigation was opened. As research expanded, hundreds of laboratory experiments were reported, all focused on analysing in depth the genetic character of what had become known as the symbiotic dinoflagellate genus *Symbiodinium*. Throughout the following decade, into the 21st century, the literature ramified as the ABH engaged the efforts of numerous investigators. A degree of finality was reached in 2006, however, when a Swiss team led by Xavier Pochon presented the first complete view of *Symbiodium* phylogeny from exhaustive DNA analysis, which revealed that "eight distinctive clades (A–H) form the major taxa of *Symbiodinium*". With the important genetic evidence that the genus is exceptionally diverse, they traced its extant lineages through the palaeographic column to find that it began evolving in the early Eocene, around 56 Mya, and that "the majority of extant lineages diversified since the mid-Miocene, about 15 million years ago" (Pochon et al. 2006, p. 20).

DNA Research: Clades and Symbionts

As bleaching appeared to be increasing in geographic spread, the main areas of enquiry began to focus on the adaptability of different coral species to changes in sea temperature, the impact of radiant energy on their photosynthetic processes, their varieties of symbionts and the capacity for a shuffling response. In particular, as different coral species were exhibiting a range of thermal tolerance levels, great interest was directed towards determining which clades were the most resilient, and therefore their suitability for various management strategies in worst-case scenarios, particularly when declaring marine parks and conservation zones.

One of the earliest attempts to test the ABH theory was made by Andrew Baker who in 2001 published the results of his experiment to assess whether "reef corals bleach to survive change" (Baker 2001, p. 765). Specifically, is bleaching a coral's attempt to rid itself of "suboptimal algae and acquire new partners?" From RFLP analysis, Baker reciprocally transplanted eight species of scleractinian in four clades (A, B, C, D) on the San Blas Archipelago of the Caribbean coast of Panama, between shallow (2–4 m) and deep (20–23 m) locations, then assessed them after 8 weeks for bleaching and after a year for mortality. He believed that his results validated the hypothesis. All 24 colonies that were moved up into shallow waters bleached and had acquired new symbionts to survive increased irradiation. Those moved down failed to bleach, retained their original symbionts and suffered greater mortality, with 7 of the 37 colonies dead.

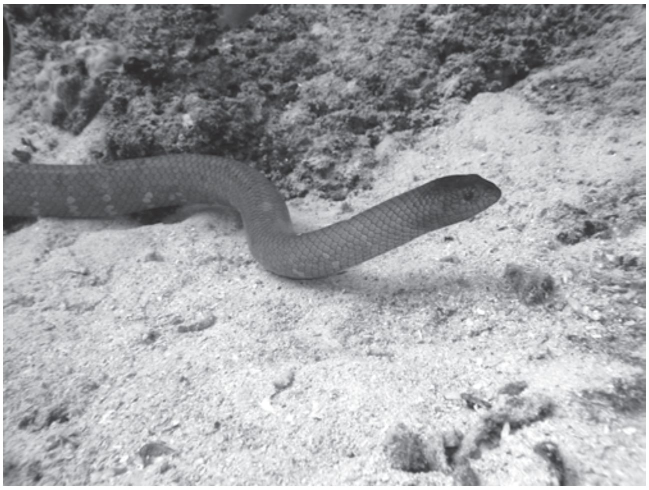
Soon after, in 2003, a critical analysis of the ABH was made by English biologist Angela Douglas when she reviewed the fundamental issue of what exactly causes bleaching, and most importantly, why? Part of the problem, she observed, is that the process was still very obscure, although the ABH theory of an evolutionary advantage, she conceded, "may be correct". However, for the hypothesis to be validated, three processes needed to take place: the displaced symbiont must be inferior to the replacement, the host must have vacant capacity and a replacement symbiont must be available. The 2001 experiment by Baker, she asserted, provided no evidence that "the superior survivorship of the deep-to-shallow transplants was a consequence of their bleaching, and the adaptive bleaching hypothesis remains unproven" (Douglas 2003, p. 390). Although Douglas doubted the ability of corals to make wide-scale adaptation, she stated that the most effective remedy is simply to reduce global warming. Even if the ABH proves to be the case, at present it is only of academic interest and of no "apparent value in mitigating the negative effects on coral reefs of anthropogenic factors that promote bleaching". Despite reefs worldwide being at great risk, she believes that they are capable of tolerating climate change, although "the need for sustained management of the reef ecosystems and protection from local anthropogenic factors is greater than ever" (Douglas 2003, p. 391).

With Baker's positive assessment and the well-argued rejection by Douglas, the efficacy of symbiont shuffling was creating considerable interest. What needed careful examination was Baker's hypothesis that corals deliberately "rid themselves of suboptimal partners" and that there would be "free-living zooxanthellae [swarmers]" waiting in the water column "as colonizers", as the ABH stipulated (Buddemeier and Fautin 1993, p. 322). In 2001, Robert Kinzie and three colleagues published a limited confirmation of the ABH from laboratory experiments on clades A, B and C, which demonstrated that "bleached adult hosts can acquire symbionts from the water column" (Kinzie et al. 2001, p. 51). To go beyond what were generally regarded as inconclusive results, however, the first evidence from field studies to enquire into that possibility was published in 2006 by Tamar Goulet, in a work entitled "Most corals may not change their symbionts". Using all available data on zooxanthellate identity since RFLP methods for symbiont analysis were introduced in 1991, from 43 separate field studies, she located 442 scleractinian and octocoral species, with "a key assumption of algal symbiont change" being "that corals can host multiple zooxanthella genotypes, either concurrently or sequentially" (Goulet 2006, p. 3).

Goulet's results did little to support ABH theory, however. Cladal analysis revealed two distinct categories: only 23 % "can host multiple zooxanthella clades either over depth on the same reef, in different geographic areas, or within the same colony". The majority, 77 %, "host only one zooxanthella clade". From the available data, she concluded that most coral colonies do not switch symbionts over time, even when subjected to stresses from disease or rising temperatures. As most species cannot respond to climate change, she hazarded the opinion that reefs "may be in greater peril than some studies imply…. For the majority of corals, the question is… under which conditions the existing symbiosis may survive" (Goulet 2006, p. 4).

Barely a year later, five scientists from the Netherlands led by JC Mieog released the results of their field investigations on the Great Barrier Reef (GBR) from "a newly developed DNA identification technique of polymerase chain reaction (PCR)", which almost completely reversed Goulet's findings. At 11 mid-GBR locations between Townsville and Rockhampton, a distance of approximately 350 nautical miles (600 km), they tested 82 colonies of four common scleractinian species for background *Symbiodinium* clades. They acknowledged Goulet's conclusions as consistent with the data, but they believed the technology used in the reports she examined lacked sufficient sensitivity. In contrast, their new method of "real-time PCR" analysis, "can detect cryptic or background clades over eight orders of magnitude more sensitive than previously used techniques" (Mieog et al. 2007, p. 454). Those conclusions were both interesting and perplexing. It had been previously established that the least thermally tolerant clade was C and that the most resistant was D, which they were able to confirm. However, although "93 % of the colonies tested were dominated by clade C…76 % of these had a D background", which suggested "that temperature stress can favour clade D and act as a safety-parachute, allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming" (Mieog et al. 2007, p. 455). However, the team puzzled, it is still an open question whether shuffling could act as a mechanism to acclimatize to increasing sea surface temperatures.

The results of their study indicated that the potential for symbiont shuffling is greater than previously thought, later confirmed by James Crabbe and John Carlin (Crabbe and Carlin 2009), but will require prior bleaching before the background symbionts can proliferate. That would cause great mortality in the process, whereas those that survived bleaching may be impaired in growth and reproductive capacity. Even more paradoxically, "if the stressor disappears for a prolonged period of time, the corals may shuffle back to the original symbiont" (Mieog et al. 2007, pp. 455–456).



An olive sea snake, *Aipysurus laevis*, one of the seven species of venomous sea snake endemic to the Great Barrier Reef

By the early years of the 21st century, an enormous literature of research into the genetics of the genus *Symbiodinium* existed, but opinion has turned against the ABH and whether bleaching really indicates natural processes striving for reef survival. At least there is wide agreement that bleaching is a direct response to a warming world.

In 1993, the same year that the ABH appeared, Peter Glynn presented his own scenario for future events. As in 1984, he argued that attempts to explain coral reef disturbance "in terms of possible global change (e.g. greenhouse warming, increased UV radiation flux, deteriorating ecosystem health or some combination of the above)—apart from localized impacts such as pollutants, sedimentation, salinity and light deprivation—have not been convincing" (Glynn 1993, p. 1). Three years later, in 1996, came his considered response: a lengthy analysis of "the facts, hypotheses and implications surrounding coral reef bleaching". He came directly to the root cause: in his view, "the leading factors responsible for large-scale coral reef bleaching are elevated sea temperatures and high solar irradiance (especially ultraviolet wavelengths), which may act jointly" (Glynn 1996, p. 495). Although he did not reject the ABH outright as a strategy for survival, Glynn expressed thoughtful scepticism, because it is now accepted that reefs are predicted to be progressively degraded by sea-level rises and increasing sediment loads within the next 100 years or so. "It is doubtful", he wrote, citing Sir John Houghton's speech at the Intergovernmental Panel on Climate Change (IPCC) 1995 Conference on Climate Change, "that this time frame is sufficiently long to allow evolutionary adaptations in corals or their zooxanthellae to cope with the new conditions" (Glynn 1996, p. 504). "It is probable", he thought, "that a select group of reef-building taxa will survive", and "possible refuge habitats that would be protected from rapid temperature rise might be found at moderate depths, in upwelling centres, on oceanic banks or island shores exposed to vigorous circulation, and some high-latitude sites". Despite that despondent hope, which in any case would take us well into the future, while ever greenhouse warming and higher levels of solar radiation continue to rise, widespread coral mortality and reef decline must be expected in shallow low-latitude areas "for hundreds if not thousands of years as global environmental change continues". Whatever lies ahead, in the present era, it is unavoidable that "coral reef degradation from anthropogenic pollution and over exploitation will continue, a result of unrelenting human population growth" (Glynn 1996, p. 505).

Regardless of the accumulation of scientific knowledge, all studies affirm that bleaching will continue, and the future of coral reefs remains dire (Veron 2008b), most importantly because they are not independent, free-willed ecosystems. On the contrary, their habitat is necessarily in relatively shallow coastal areas that have become increasingly stressed by many influences throughout the 20th century. Whatever the successes of research into bleaching may be, reefs can only survive into the future if they live in healthy waters.

Beyond the ABH: Threats to Water Quality

Elevated sea surface temperatures are only one of the culprits responsible for degrading reefs: their accomplices are water pollution and coral disease. Although reefs are often damaged or even destroyed by natural occurrences, particularly ferocious cyclones, the foremost destructive influence today is the collective activity of an almost infinite variety of anthropogenic causes acting to decrease water quality.

In 1970, the *Marine Pollution Bulletin* commenced publication to deal with that specific issue, which remains its central focus, although gradually it also began publishing articles on related topics such as "Pollution and Degradation of Coral Reef Communities" by Ferguson Wood and Robert Johannes in 1975, which highlighted the paucity of knowledge about the impacts on coral reef communities. Soon thereafter, two zoologists at the University of Newcastle-upon-Tyne, Barbara Brown and L. S. Howard, began one of the most comprehensive studies to that date on the effects of stress on reef corals. Their concern with stress, defined as "a gradient between ideal conditions and the ultimate limits of survival", ranged over an extensive spectrum of both natural and man-made influences recorded in a large number of field studies and laboratory experiments (Brown and Howard 1985, p. 2). The natural influences they presented were abnormally low tides in the Gulf of Eilat, low temperatures, white-band disease, several unexplained cases of coral mortality and cyclones. Anthropogenic influences had a much wider range of degrading influences from fish-collecting for aquaria, land-based sewage discharge, agricultural run-off, excessive river storm flooding, cannery effluents, dredging sediment fluxes, ore loading, geotechnical earth drilling with specialized water- and oil-based muds, and military activities from direct combat operations as well as air-force bombing practice. These were then followed by analyses for growth rate, metabolism, algal loss, altered behaviour, reproductive changes and histological and biochemical conditions (Brown and Howard 1985, Table II, pp. 10–12, and Sect. II, pp. 9–16).

Bleaching did not appear in either category because of "the limited literature to date". However, the authors indicated that "the loss of zooxanthellae in response to a particular stress does give some indication of the relative tolerance of a coral species to parameters such as temperature increase, and salinity change". To that observation, they added a rider that "the value of the response to loss of zooxanthellae by coral tissues as an indicator of stress could be considerably improved by quantification of the magnitude of algal loss, better understanding of the mechanism of expulsion of the algae, and by relating this response to other physiological parameters" (Brown and Howard 1985, p. 34–35).

When this work was published in 1985, although their findings revealed how pervasive various stress factors had been from 14 instances recorded between 1902 and 1933, and continuing escalation as coastal populations increased to 90 episodes by 1979, and a further 78 in the immediate background period to their study between 1980 and 1984, they believed that there was little cause for alarm. Unless reefs were devastated by violent cyclones, extensive toxic or chemical saturation or similar disasters, under less extreme conditions, recovery rates depended on depth of the damage and growth rates of the individual species affected. Reef ecosystems, they commented, were not as fragile as current reports were indicating and that little would be gained from isolated laboratory experiments on pollutants. Investigation, they advised, would require many more data on species diversity from field studies (Brown and Howard 1985, p. 52). Their findings, however, came from a period when remediation of reef stresses had not appeared to be urgent. Although it was a wide-ranging account with a great deal of relevant evidence, what soon became alarming was the subsequent rising number of even graver disturbances: cyclones, *Acanthaster* predation, urchin loss in the Caribbean, and black band, white syndrome and other viral and bacterial coral diseases, in addition to ENSO events. These could no longer be considered isolated incidents by perceptive investigators and were being traced to the relentless processes of the warming and polluting of coastal waters. Once they appeared to form a connected pattern, a new phase of investigation commenced.

The subject of pollution received early attention in Kane'ohe Bay, 12 miles northwest of Honolulu, site of the US Marine Corps airbase, recorded in history as the first target of the 1941 Japanese attack on Pearl Harbor. Since its establishment, minimally treated sewage had been discharged from its septic systems into the bay, encircled by three small barrier reefs, north, central and south, which stimulated the growth of algae and covered the surface of the bay. In 1985, Robert Pastorok and Gordon Bilyard from the environmental engineering firm Tetra Tech, after a site investigation of Kane'ohe Bay, identified the three greatest pollutant threats as nutrients that stimulated the growth of algae and benthic organisms, mainly bryozoans, sponges, sabellid worms and tunicates that rapidly outcompeted the corals, as well as from sedimentation and toxic substances (Pastorok and Bilyard 1985, p. 177). Moreover, some corals, particularly *Porites* boulders, had become smothered by green bubble-alga. Although they also found nitrogen- and phosphorus-rich sewage, the main contributor to eutrophication in the Gulf of Aqaba, Jordan, they discovered that the phosphate mineral fertilizer apatite $[Ca_5(PO_4)_3F]$ had badly polluted the waters around the ore-loading wharves. Not only were coral cover and calcification rates diminished from eutrophication but the variety and biodiversity of species also dropped, leading to weaker coral structures unable to resist cyclone events.

Throughout the years following the urchin epizootic, as major changes in the Caribbean ecosystem became even more disturbing, early in the 1990s, Terrence Hughes from James Cook University began research into the problems afflicting the coral reefs of Jamaica, using the species composition and zonation study of Jamaican coral reefs by Tom Goreau in 1959 as a reference point. When he published his conclusions in 1994 about the disappearance of the sea urchin *D. antillarum*, Hughes inferred that algal proliferation and depletion of coral cover resulted from ecosystem imbalance by excessive clearing of native vegetation for commercial agriculture and land discharge of fertilizers. That led to eutrophication of the water by excessive nutrients and was exacerbated by rural subsistence inhabitants who had been forced off their land onto the coast and into chronic overfishing practices. As a result, "current stocks of herbivorous fish are not capable of reducing algal abundance in the absence of *Diadema*". In what had become a common description of Caribbean reefs, Hughes summarized his argument with the judgement that "the classic zonation patterns of Jamaican reefs, described by Goreau and his colleagues just two to three decades ago no longer exist: a striking phase shift has occurred from a coral-dominated to an algal-dominated system" (Hughes 1994, p. 1549).

In 2001, an ambitious attempt to identify and help prevent coastal zone collapse came from a consortium of 19 scientists led by Scripps biologist Jeremy Jackson. Beginning with the bold assertion that "ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems", their assessment documented historical impact throughout the momentary warm phase of the Holocene Epoch in the three stages of indigenous, colonial and global extraction and the consequences that followed. These were identified as pollution, eutrophication, habitat destruction, disease, microbial outbreaks, species invasion and "human-induced climate change" (Jackson et al. 2001, p. 629). Their article, however, did not discuss causation, foremost among which has been rapidly increasing population pressure. If we survey the *Homo sapiens* scene from the Stone Age, when hunting and gathering were the only mode of subsistence, through the Bronze and Iron Ages into the nuclear present, its most outstanding feature is the exponential rise in world population. Current estimates calculate global population 12,000 years ago to be around 1 million. Not until the year 1800 did it multiply 1000-fold to reach 1 billion. It doubled by 1927, increased to 3 billion in 1960, rose to 4 billion in 1974 and to 6 billion in 1999. From the Industrial Revolution to the beginning of the 21st century, when the Jackson team was preparing their analysis, world population had increased inexorably and astonishingly by a stratospheric 5 billion. A decade later, official UN figures calculated world population in 2011 as 7 billion and continuing to rise.

With no more agricultural land available and the unpredictability of rainfall and climatic regimes, as well as the relentless pressures of modern industrial production methods, one survival alternative is coastal zone hunting and gathering. As Hughes demonstrated in Jamaica, even if it leads to further degradation, what other options do landless indigenous inhabitants have?

The author at Heron Island Research Station, 1994

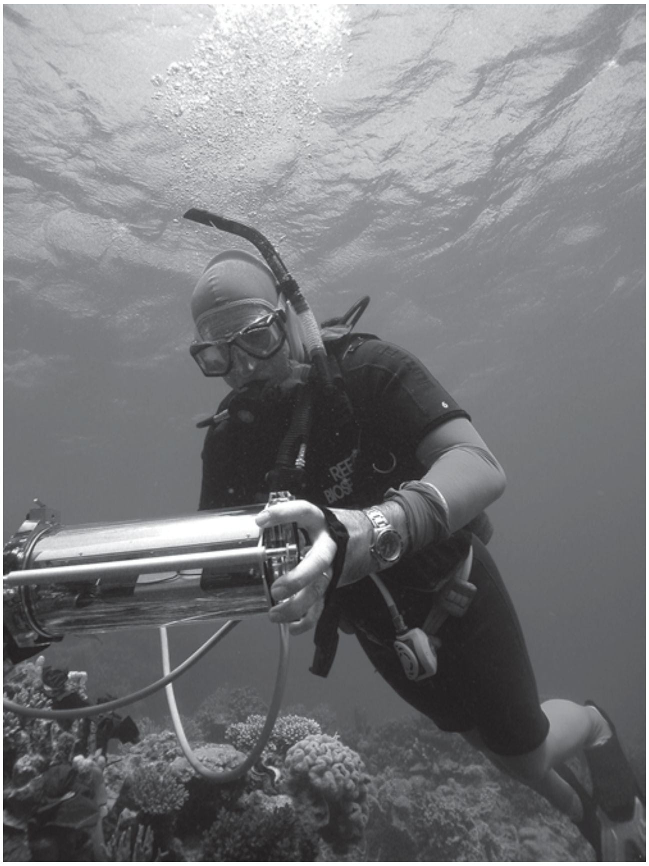
Nutrient Enrichment of Coral Reefs: The ENCORE Experiment

As the relative impacts of top-down disturbance by reduction in algal grazing and bottom-up disturbance from excessive land-discharge pollution by the now abundant essential plant nutrients (nitrogen and phosphorus which stimulate algal growth) were becoming better investigated, Hughes' conclusions came under closer scrutiny. As coral reefs are found in dynamic, low-nutrient waters, his belief that environmental changes in Jamaica had been caused by rampant algal growth resulting from the loss of grazing urchins was seriously questioned. In particular, Hughes was criticized strongly by the Florida biologist Brian Lapointe about his failure to accept nutrient enrichment as "enhancing macroalgal productivity and standing crop", which he dismissed as "without supportive data" (Lapointe 1997, p. 1120).

Simultaneously with Hughes' studies in Jamaica, a team of 18, mainly Australian, scientists was beginning an elaborate field experiment, largely funded by the GBR Marine Park Authority, to provide data on the still limited understanding at the time of the impact of increasing nutrient loads on coral reefs. The site chosen was One Tree Island (OTI), a small restricted-access islet measuring a little over 4×3 km near Heron Island Research Station in the southern waters of the GBR. More than 100 km from land, and traversed by the East Australian Current, it was considered a reasonably unpolluted location for a sustained experiment on eutrophication.

Designated ENCORE as a descriptive acronym for "the effect of nutrient enrichment on coral reefs", the experiment was conducted for 30 months from September 1993 to February 1996. In all, 12 quadrats of coral patch in the lagoon had pontoons moored overhead, nine fitted with automatic nutrient dispensers and the other three acting as controls. Twice daily at low tide, three reefs received measured quantities of inorganic nitrogen, three received inorganic phosphorus and three were given both elements. The experimental design was meticulously and comprehensively described, with numerous detailed tables and graphs showing the effects on phytoplankton, macroalgae, epilithic alga, rhodoliths and animals including stomatopods, reef-building corals and fish. Corals themselves were examined for growth, photophysiology, reproduction and mortality.

The formal summary of the experiment concluded that "coral mortality… became evident with increased nutrient dosage", that "linear extension increased in the presence of



Ove Hoegh-Guldberg measuring the photosynthetic efficiency of corals and other photosynthetic organisms with a PAM, a Pulse Amplitude Modulated fluorometer

added phosphorus but skeletal density was reduced", and that "reef organisms and processes investigated in situ were impacted by the effects of elevated nutrients" (Koop et al. 2001, p. 92). The investigative team qualified their conclusions, however, by stressing that establishing reliable bioindicators of nutrient stress would require much more work in order to make the experiment yield results that would be effective management tools in the years ahead when pressure on the world's coral reefs would continue to intensify (Koop et al. 2001, p. 117).

The following year, the ENCORE experiment was trenchantly criticized by marine biologist Alina Szmant from the coral reef research group and nutrient laboratory at the University of North Carolina. Recognizing that "coral reefs are degrading worldwide at an alarming rate", she argued that the reasons for the degradation were far more complex than simple nutrient enrichment, and that eutrophication, the key concept in the ENCORE title, is not a suitable hypothesis from which to generalize on a global scale. Rather, given the major anthropocentric factors affecting reefs today, she suggested that a more appropriate concept would be "nitrification", a process that better describes the complex, increased flux of nutrients now entering coastal waters: "with coral reefs presently declining at a rapid rate, it is important to understand the complexity of these interactions and to place the role of nutrients in perspective" (Szmant 2002, p. 744). However, she added, that would be a difficult task; there is no established criterion of what determines nutrient levels as high or low because these will vary considerably whether close to shore, in lagoons or embayments, or far from human settlement. Consequently, she argued, it is essential to recognize that reefs are highly dynamic ecosystems, which result from a mix of "nutrients (bottom-up) and herbivory–physical disturbance (top-down) factors [which] determine community structure". Excess fishing, for example, removes predators and creates trophic shifts; coral diseases and bleaching provide new niches for algal growths; nutrients can alter polyp physiology and influence calcification and, as a result, growth, reproduction and resistance to storm stress.

Szamant's basic objection was the choice of OTI, which is considered a relatively pristine environment and is closed to the public where even visiting scientists need entry permits from the GBR Marine Park Authority. As OTI has no direct anthropogenic influences from human settlement, land clearing, agriculture, commercial or intense recreational fishing, ship groundings, coral mining and sedimentation, she asserted that it did not provide a representative site for an experiment to predict the future health or decline of coral reefs worldwide. In fact, she stated, many reef problems are locality-specific, because evidence from reefs in the western Pacific, Hawaii, the Indian Ocean, the Red Sea, the Caribbean and the Florida Keys show wide variations in disturbance. It is therefore unwise and unscientific to provide evidence of the effects of nutrient enrichment on coral reefs from a relatively uncorrupted location with results that "are weak and contradictory" and which she believed "make no attempt to…reconcile or explain the inconsistencies in the results [even though] their overall conclusion is that nutrient enrichment reduces coral growth". With serious threats being reported constantly, she considered that the OTI results lacked universal relevance and therefore that "the ENCORE results unfortunately do not constitute a solid basis from which to judge the role of nutrient enrichment on coral health or coral reef decline" (Szmant 2002, p. 751).

This critical analysis of the ENCORE experiment, however, was not the final word on that vexed issue. In 2007, American biologists Peter Bell, Brian Lapointe and Ibrahim Elmetri published a paper entitled "Re-evaluation of ENCORE", in which they supported the eutrophication threshold model for coral reefs. Building their case on the express intention of ENCORE to establish baseline levels of nutrient threshold concentrations (NTC), they made it clear that the OTI experiment was clearly designed to settle a controversy. What was the cut-off point, they asked, at which "nutrient enrichment increased algal growth/organic production rates to the extent that changes in the benthic community structure had begun (e.g. replacement of hermatypic corals with coralline algae, filamentous algae, macroalgae and/or a variety of filter feeders)" (Bell et al. 2007, p. 417) As the problem had originated with Hughes' study in Jamaica a decade earlier, at issue was uncertainty over the impact of elevated nutrient levels on the structure of coral reefs. Although algae were an essential component of reef ecosystems, accelerated growth from the deliberate addition of fertilizers, they argued, would alter that structure permanently with "increased competition for space by other organisms (e.g. algae including coralline algae, filamentous algae, macroalgae and filter-feeders, including octocorals, sponges, bivalves) that can now flourish in the more fertile waters" (Bell et al. 2007, p. 419).

The results from ENCORE, they continued, demonstrated that although elevated inorganic nutrients had several negative impacts on corals, such as increased mortality and reduced reproduction, they "did not cause coral reefs to convert from coral communities to seaweed-dominated reefs, despite contrary reports". With specific reference to Szmant, Hughes and several others, the article by Bell, Lapointe and Elmetri made it very clear that their support for the eutrophication threshold model presented in the ENCORE findings was to counter the "misinterpretation of the results (that) added to the confusion that already permeates through the coral-reef community in relation to quantitative aspects of nutrient dynamics on coral reefs" (Bell et al. 2007, p. 422).

The concluding paragraph of their article, however, is particularly disturbing as a portent for future reef management in marine parks, which have a vital role in providing sanctuaries for reefs as we once knew them. The senior executives of both the GBR Marine Park Authority and the Florida Keys National Marine Sanctuary rejected the eutrophication threshold model in the ENCORE findings. As the evidence indicated clearly that "the overgrowth of the OTI reefs and other reefs in the nearby GBR region suggest that the region as a whole is eutrophic", the authors believed that acceptance of the ENCORE findings "would have meant that they were managers of degraded systems" (Bell et al. 2007, p. 423). The sad fact is that no waters, as with all other natural features on earth, are pristine any more: everything on the planet has been permeated by industrial chemicals, so the word needs to be relegated to the fantasy dictionary of vanished dreams. In the coming decades and centuries, it will be necessary to accept the fact that all environmental management has to be conducted within the context of ailing ecosystems.

Climate Change and the Future of Reefs

15

The most critical period for coral reefs is now, as evidence accumulates to indicate ever more problems arising. Throughout the final three decades of the 20th century, coral reef science developed into a widespread discipline whose practitioners became persistent monitors of reef disturbance, warning of impending decline from the synergistic interaction between bleaching, water pollution, rising sea temperatures, disease and overall global warming. Optimism that reefs will continue, even in changed form, is widespread, but there are other dedicated investigators, devoted to reef survival, who doubt that there will be sufficient political determination to limit global warming and end the downward spiral. Given the relentless population growth, increasing consumption of finite resources by energy-intensive industries and the escalating emissions of carbon dioxide, will it be possible to prevent the ultimate worst-case scenario of reef collapse?

All these are serious questions that cannot be ignored, and which demand a realistic understanding of all the factors influencing the future of coral reef ecosystems. In order to work towards a clear understanding of the issues, we need now to look beyond the specific focus of coral reef science and appreciate the reefs as vulnerable ecosystems in a rapidly deteriorating human-influenced context. It is crucial that we accept the fact that the processes of climate change have radically altered the environmental parameters of both reefs and the entire biosphere in barely 30 years, and that the main factor influencing the future of reefs depends on all nations becoming dedicated to seeking political solutions.

Climate Change: Empirical Evidence

To gain an understanding of the prospects for coral reefs, it is essential to start with the evidence, which became prominent in the public arena in 1999 when Greenpeace published a controversial report entitled "Climate change, coral bleaching and the future of the world's coral reefs". Written by Ove Hoegh-Guldberg, professor of marine studies at the University of Queensland and Director of its Heron Island Research Station, it was also published in *Marine and Freshwater Research*. Its dynamic impact came from existing evidence that sea surface temperatures have already risen "by almost 1 °C over the past 100 years and are currently increasing at the rate of approximately 1–2 °C per century" (Hoegh-Guldberg 1999, p. 839). Although such observations were not welcome news, they were nonetheless incontrovertible facts that had to be taken seriously when examined systematically from the best available sources.

The portents for reef collapse from rising sea surface temperatures had been generated from profoundly disconcerting terrestrial temperatures over the previous decade. As early as 5 March 1984, the Meteorological Office of the Hadley Centre at the University of East Anglia (HadCRUT) reported that 1981 and 1984 were the warmest on record, and that CO_2 emissions had reached a level where they were threatening agriculture and the stability of the polar ice caps. The continued warming of the planet was also confirmed independently in such a reputable journal as *Geophysical Research Letters*, which reported that long-term records, despite periodic downturns, indicate steadily increasing temperatures during the 21st century in close correlation with increasing atmospheric concentration of CO_2 revealed in the Keeling Curve (Easterling and Wehner 2009).

Records continued to be established when both the US National Climatic Data Center and HadCRUT reported in 2008 that the warmest year, since data-keeping by the World Meteorological Organization (WMO) commenced in 1880, was in 1998, and that eight of the ten warmest years have been since that year. The second and third warmest years were in 2002 and 2003 with the remainder almost equally warm; 2007 was the fourth warmest and 2005 not far behind, as recorded by National Aeronautics and Space Administration's (NASA's) Goddard Institute for Space Studies (GISS). The increasing temperature rises were matched yet again in late 2009 when another *El Niño* Southern Oscillation (ENSO) event began, and in equatorial regions, record increases were also measured.

J. Bowen, *The Coral Reef Era: From Discovery to Decline*, Humanity and the Sea,
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Prof. Ove Hoegh-Guldberg

At the start of the United Nations Climate Change Conference in Copenhagen during 7–18 December 2009, which was called to negotiate an acceptable successor to the Kyoto Protocol to moderate global warming, a further disconcerting fact came to light: Michel Jarraud, Secretary General of the WMO, reported that 2009 was possibly the warmest ever. To reinforce that evidence, the Intergovernmental Panel on Climate Change (IPCC) reported the decade 2001–2010 as the warmest on record, with an average temperature 0.46 °C above the previous three decades (Climate Commission 2011, p. 6). Then, in 2013 both NASA and NOAA reported that the ten warmest years recorded were all since 1998, with 2013 continuing the trend.

The reality of climate change, however, was not without considerable controversy that became particularly intense and at times politically acrimonious in the months preceding the Copenhagen Conference. Collectively, polluting industry organizations and their consenting scientists rejected the warming scenario and argued vigorously in defence of coal and oil as fundamental to the continued functioning of the global, and particularly the American, economy. In the USA, the world's greatest carbon emitter until 2008 (now overtaken by China, although Australia leads the world on a *per capita* basis), the number of political lobbyists in Washington DC, mainly for the oil, gas and manufacturing industries, increased fivefold to 2340 between 2004 and 2008, i.e. four times the number of members of Congress.

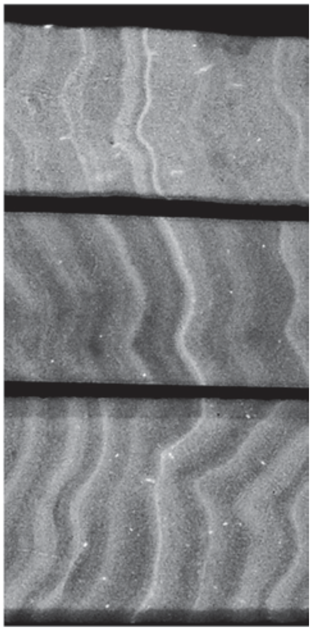
Commercial interests that depended on carbon products and sceptical scientists strenuously reject evidence that rising global warming is attributable to greenhouse gases (GHGs), make unsubstantiated assertions that the IPCC case is based on faulty mathematical modelling, and stress that climate change is actually due in large part to natural processes that they promote by media rhetoric. Even so, how can the denial lobby refute evidence of rising sea surface temperatures now that real-time satellite and remote *in situ* sensing have become employed globally? One recent dramatic development was where serious coral bleaching was recorded in the lagoon of Lord Howe Island off the New South Wales coast, when sea temperatures in December 2009 were 2 °C above normal. This is a serious portent because Lord Howe Island at latitude 31 °54′S has the southernmost coral reefs in the world and bleaching there is yet another indication of the spread of warmer water.[1]

With such concerns becoming increasingly frequent, the need for action had become demanding. Consequently, the briefing document prepared by the IPCC for the 192 nations attending the Copenhagen Climate Change Conference was based almost entirely on existing factual data. Little resort was made to models, prognoses and assumptions: the aim was to facilitate constructive decisions to moderate global warming as much as possible before its inevitable impetus carries the global industrial economy and the biosphere beyond recovery.

In assessing the present situation, two parameters are relevant: a clear definition of "climate" (as distinct from the "weather" that we experience over short time periods) and the geological period within which change is taking place. In its Fourth Assessment Report of 2007, the IPCC defined climate in terms of empirical measurements that can be identified over "an extended period, typically decades or longer … whether due to natural variability or from human activity". That definition contrasted with the specific anthropocentric text issued by the United Nations Framework Convention on Climate Change (UNFCCC), which states that "climate change refers to a change of climate that is attributed directly or indirectly to human activity which alters the composition of the global atmosphere and is in addition to natural climate variability observed over comparable time periods" (IPCC 2008).

Clearly, the entire debate regarding the impact of climate change on coral reefs at present, as in the rest of the biosphere, has been fraught with difficulty over the past few decades in achieving a convincing level of certainty, the main problem being that of separating anthropogenic causation from

[1] From island dive operator records. Serious bleaching, coral fragmentation, and white band disease were since observed by the author in March 2012.



Porites core section, showing luminescence bands of coral density for dating. (Reproduced courtesy Janice Lough)

natural processes. In arriving at a transparent understanding of exactly how climate change evidence is established, and from which the IPCC prepared its report, it is important to be aware of the procedures followed and consolidated from recording stations around the world, starting in 1980 when increasingly serious climate effects were being registered. In that year, the World Meteorological Organization created the World Climate Research Programme (WCRP). In turn, the WCRP established two subsidiary bodies: in 1990, the World Ocean Circulation Experiment (WOCE), and in 1991 the Global Oceans Observing System (GOOS), with both forwarding their findings to the Global Observing Systems Information Centre (GOSIC) in Paris.

In barely three decades, a huge advance had been made in knowledge of reefs, the ENSO phenomenon, and the crucial role of the ocean's influence on climate. Many other aspects of planetary activity were also measured from WOCE after the separate elements of Tropical Ocean Global Atmosphere (TOGA), Tropical Atmosphere Ocean (TAO) and TOPEX were combined into CLIVAR, the Climate Variation Programme, as described in Chapter 12. By 2007, CLIVAR came into full operational status with the deployment of 3000 Argo submerged buoys, increased to 3500 by 16 March 2012, and named after the mythical Greek ship in which Jason set out to find the Golden Fleece. Moored across all oceans as deep as 2 km, they are ingeniously programmed to rise every 10 days to the surface and transmit data on salinity, temperature and pressure to Jason I, the upgraded satellite to Poseidon. Equally valuable is the information gained from the improved Surface Velocity Programme by drifting buoys that had been first deployed in 1988 as part of the TOGA study. Enclosed in small spherical plastic floats 40 cm (16 in.) in diameter with a drogue (a sea anchor) attached for stability, 1250 floats had been placed across all oceans by the year 2005, Arctic to Antarctic, to collect information on sea surface temperature and velocity, which is transmitted to satellites. Today, the extensive range of automated ocean buoys provides instantaneous, accurate records that are received immediately by the Intergovernmental Oceanographic Commission (IOC) secretariat in Paris, where GOSIC processes and posts them on the Internet.

Whereas ocean temperature measurements have arrived at a high degree of precision, those from land sources remain limited because they provide uneven coverage in sparsely settled or empty regions, and satellite sensors cannot penetrate clouds. Consequently, the IPCC projections for the future present a range of possibilities. Measurements from the past are retrieved from proxy isotopic data in ice cores the Rignot team drilled in Antarctica, and the Greenland Ice Core Project (GRIP) by a consortium of eight European nations that delved into 110,000 years of records from a core 3053 m long (UNEP 2010b). Shorter-term weather changes are found in annual growth rings in *Porites* corals as described in Chapter 11 (Lough and Cooper 2011), and in trees such as the Arizona bristlecone pine that can yield data for as much as 8000 years. Temperature variations are also directly measurable from temporary events such as the 1991 eruption of Mount Pinatubo in the Philippines, which discharged an enormous volume of fine aerosol particles into the upper atmosphere and reduced global temperatures by an average of 0.5 °C for the following 2 years. Equally disruptive are *El Niño* and the controversially termed *La Niña.*[2] To eliminate anomalies, records are averaged over at least a decade, and extreme signals are smoothed by statistical techniques.

Constrained to work within those limitations, the IPCC Fourth Assessment Report of 2007, given the criticisms directed to its earlier reports of 1990, 1995, and 2001, is a carefully worded document. From empirical evidence alone, it argues strongly that changes in world climate during the Holocene have been attributable to radiative forcing from greenhouse gas emissions of carbon dioxide, ozone, methane from agriculture and livestock production and halocarbons of industrial manufacture. Additional radiative forcing has been identified from the albedo effect (Lat. *albus*, "white") when part of the incoming energy from the sun that is normally reflected back into space from ice and snow is retained within the greenhouse gas mantle.

[2] Devout Catholics in Latin countries, including some reef scientists, consider the term *La Niña* inappropriate because it implies a female saviour, and prefer the term "anti-*El Niño*".

The Global Water Supply Crisis

In the IPCC Report for the year 2007 (published in 2008), to confirm atmospheric warming, a significant item of evidence indicated a relatively large rise of 1°C in overall global surface temperatures between 1850 and 2000, from 13.5 to 14.5 °C. That rise was accompanied by a corresponding decrease between the years 1920 and 2000 in global snow cover, from a maximum of 40 to 37 million km^2 (the loss approximately equal to the land area of India). It was accompanied by increasing ground instability in permafrost regions, which created rock avalanches in mountainous areas, thinner ice, shorter freezing seasons of lake and river ice, and continuing contraction of the Greenland ice sheet. In addition, some 1800 glaciers, along with great ice sheets more than 50 km^2 in extent, and similar ice shelves attached to land, have been measured and confirmed by the World Glacier Monitoring Service (WGMS) of United Nations Environment Programme (UNEP) to be melting consistently. Estimated to have decreased from 30 % of land area during the Ice Ages to 10 % today, their present volume equals three-quarters of the world's available freshwater resources, and their continued loss will put water supplies at risk for millions of people (UNEP 2010a). In critical locations, that deficit is significantly reducing water flow in populated areas such as the Andes and Mount Kilimanjaro in Africa, where glaciers are an essential source of freshwater.

Almost on the equator in Tanzania and the border with Kenya (03° S 37° E), Kilimanjaro rises to 5895 m from the Masai Steppes, as a free-standing mountain, so is the highest in Africa. Reaching back for millennia, its great glaciers have supported the local populations as they replenish the Pangani and Galana rivers. Since 1912, however, the surrounding forests have been cleared for livestock production, which has lowered woodland transpiration and hence reduced the condensation that formerly contributed to precipitation on its crest, and has since led to steady melting of the ice cap. Records which commenced in 1912 reveal an averaged annual reduction of 1 % to 1953: between 1989 and 2007, when awareness of global warming and monitoring became heightened, and droughts more frequent, that annual rate of reduction rose to 2.5 %.

With the current ice cap estimated to have lost 80 % of its volume from a number of surveys by the universities of Innsbruck in Austria, and Washington and Ohio State in the USA, Kilimanjaro's plight has gained widespread international attention. At current rates, it has been calculated that the ice cap will disappear between 2040 and 2050.[3] Although global warming certainly has contributed to the loss in recent decades, the main cause of ice loss comes from the clearing of land in order to increase agricultural production. In that case, even if not directly attributable to atmospheric carbon, it is a clear consequence of anthropocentric impact.

By far the most threatening loss of glacial meltwater for human populations, however, is in Asia, from Pakistan to China, home to more than 3 billion people, some 44 % of total world population. The major source arises in the region known as the Tien Shan (Celestial Mountains; also referred to as Tian Shan), part of the Himalayan geological upthrust forming the Tibetan Plateau at an altitude of 3800–4500 m. Covering a land area of approximately 1,036,000 km^2 in the western Chinese province of Xianjiang, between 40 and 45° N and 67 and 95° E, it is comparable in extent to Bolivia or Colombia. Alternatively, it is slightly larger than the four topographically similar contiguous states of Idaho, Utah, Wyoming and Colorado, and 3.3 times the land surface of the British Isles. From 16,000 glaciers of varying size, its meltwater augments the Indus River in Pakistan, the Ganges in India and the Brahmaputra, which flows through Nepal, Bhutan and Bangladesh. Waters from the Tien Shan also supply Myanmar from the Salween River; from the Mekong they flow through Thailand, Laos, Cambodia and Vietnam. Waters that run east provide water for the Chinese region of Yunnan from the Lancang River and greater China from the Yangtse. Farther north, some of the Huang He (Yellow River) waters also come from the Tien Shan.

Most of the glaciers provide at least 30 % of irrigation water for densely populated local valleys where the snows collect, but the larger ones are the major sources of supply into the great rivers of Asia. Since 1955, set as a datum point for monitoring by glaciologists in the aptly named Tree Ring Laboratory of the Institute of Geography at the Russian Academy of Sciences, it has been observed that "in the mid-1970s the annual rate of glacier mass balance became more negative". The trends in glacier decline, covering 16 separate investigations between 1955 and 2003, were taken from records at the Tien Shan meteorological station, the "highest in the region with long uninterrupted records from 1930 till now" (Solomina ca. 2000). The Russian study covered the period after the end of the Little Ice Age (LIA), from around 1800 to 2003, which "presented the most comprehensive assessment of fluctuations in the extent of glaciers over the past 150 years in the Terskey–Alatoo Range and the neighbouring glaciated massifs in the inner Tien Shan". Convincing evidence of significant change for the Tien Shan and the adjacent eastern Pamir Mountains in Tajikistan was observed in both regions, where glaciers were receding, with "the largest retreat rates in the northern Tien Shan". There, the Russians recorded, "glaciated areas have declined by 30–40 % during the second half of the 20th century" (Kutuzov and Shahgedanova 2009, p. 59).

The most closely observed glacier in China throughout the past 50 years has been Urumqi No. 1. One of the great

[3] Sources listed in Wikipedia, s.v. Mount Kilimanjaro.

natural wonders of China and a renowned tourist destination, from a temperature increase by 0.7°C from 1987 to 2000 in northwestern China, glaciologists at the World Data Centre for Glaciology and Geocryology in Lanzhou, in central China's Gansu Province, measured a 20 % reduction in mass over the past 45 years (Ye et al. 2005).[4] A year later, in a corroborative study, the UNEP World Glacier Monitoring Service reported that Urumqi No. 1 Glacier had lost 12 m in mass thickness, and an increase in runoff by 30 % between 1983 and 2006 (UNEP 2010b). Quite understandably, the steady, irreversible melting of glaciers rising in the Tien Shan, which climate scientists attribute directly to global warming, is creating great concern in the Chinese Government.

The ramifications of climate change extend beyond the Himalayan boundary with China: to the south, as India's population continues to grow, water supplies from aquifers are becoming a critical issue, which led to an intensive investigation to measure their volume. In 2002, a partnership between NASA and the German Aerospace Centre (DLR; Deutsches Zentrum für Luft-und-Raumfahrt) launched the Gravity Recovery and Climate Experiment (GRACE) twin satellites. These record sequential changes in the earth's gravity field, and hence the volume of water below, as they pass overhead 220 km apart. The data obtained reveal that aquifers are becoming lower by 30 cm (1 ft) a year, and that, consequently, water use by the 114 million farmers in the affected area who withdraw 95 % of their needs from them is now unsustainable because the aquifers hold ancient water that cannot be replenished easily. Confirming that finding, the plight of Indian farmers (where the world's current birthrate is highest) has been heightened from additional evidence gained between 2002 and 2008 by a NASA team of hydrologists at the Goddard Space Flight Center, who recorded a loss of 26 cubic miles (108 km^3) of water in the northern areas of Punjab, Rajasthan, Haryana and Delhi. The decline in water storage is puzzling, however, and is attributed most likely to fast population growth, for which the consequences are particularly disastrous if the glaciers in the Himalayas and the Tien Shan continue to shrink.

An ongoing water rights controversy with potentially threatening consequences arose a decade ago when India began planning a massive dam 75 m high on the Kishanganga River in Indian-controlled, but disputed, Kashmir, where most of the Indus River arises, to send water through a 23-km-long tunnel to power a 969 MW hydroelectric plant. In 2005, Pakistan objected that the water, essential for irrigation downstream where three-quarters of its food is grown, belonged to them, and appealed to the International Court of Arbitration (ICA) in The Hague which issued an interim injunction and began mediation. India made a partial response by reducing the height to 35 m and putting construction on hold. On 17 May 2010, Pakistan instituted proceedings with the ICA, which appointed a team of judges from Pakistan, India, the USA and Great Britain. As at May 2012, the ICA had not reached a final decision beyond restraining India from further works to increase the catchment area. As Pakistan had earlier threatened war over the issue (dispute over Kashmir was the cause of the First Indo–Pakistani War), it is a disturbing indication of future potential conflict over access to water and natural resources as they become scarcer, and is beginning to prompt publication of future scenarios in "climate wars" (see Welzer 2008, Dyer 2010).

With glaciers in China and around the world, and ice cover in Greenland, contracting demonstrably, the situation in Antarctica for a time had been more equivocal. Over the period 1992–2006, French scientist Eric Rignot at the University of California, with six colleagues from NASA's Jet Propulsion Laboratory in Pasadena, studied 85 % of the Antarctic coastline from satellite data to determine the rate of glacier melt and run-off into the ocean. Their conclusions matched those of the IPCC. They discovered that the interior of Antarctica, as in Greenland, has been gaining a small volume of mass from increased snowfall which comes as condensation from warming waters, although not enough to equal melting, and that eastern Antarctica south of Patagonia had a near zero loss along the Filchner and Ross ice shelves. The western regions along the Bellinghausen and Amundsen seas, in contrast, showed a significant decrease in ice sheet cover by 59 % over 10 years, amounting to an estimated 132 Gt (132 billion t) by 2006 (Rignot et al. 2008).[5] Since then, a much more drastic change has been recorded. From GRACE satellite data, a University of Texas team at Austin, led by Jianli Chen, confirmed the Rignot estimate of western Antarctic ice loss to January 2009 to be ~132 Gt annually. That value compared unfavourably with the lesser amount of 83 Gt per decade calculated earlier, whereas eastern Antarctica was also losing ice at an approximate rate of 57 Gt annually.[6]

One further, serious consequence of warming seas recorded separately by the IPCC is that biological impacts in Arctic ecosystems are affecting predators at higher levels of the trophic pyramid as ice sheets melt and habitat disappears for polar bears, sea lions, seals and Arctic foxes. Decline also continues in the Antarctic for seals as well as for Emperor penguins, whose numbers have dropped by 50 %.[7] Also becoming seriously affected as the water temperature rises is the density of krill, the tiny, 2-cm shrimps of the zooplankton

[4] Also, on-site interview by Jonathan Watts, *The Guardian*, Friday, 25 July 2008.

[5] See NASA/JPL online releases 23 January 2008 and November 2009.

[6] Internet release 22 November 2009, BBC News, Green.Blorge.

[7] Internet report by Henri Weimerskirch, Director of the Centre National de la Recherche Scientifique, Villers en Bois, France.

that are essential food for baleen whales and many other Antarctic animals. What is not generally realized is that melting snow also has a direct teleconnection with coral reefs, because it contributes to sea-level rise and warmer waters.

In one of the most thorough climate investigations yet undertaken, strong support for the IPCC position, which, as mentioned, has not yet adopted worst-case scenarios and offers middle-ground possibilities, came from the Russian Vostok Base (*vostok* is Russian for "east") in eastern Antarctica (78° S 106° E). From ice cores drilled to a depth of 3310 m (2 miles) in 1999, Jean Robert Petit and his French, American and Russian research colleagues extracted isotopic climate records from entrapped oxygen and deuterium (a heavy isotope of hydrogen; Gk *isos*, "same" + *topos*, "place", i.e. elements with the same atomic number and similar chemical properties, but different atomic weights) during the four glacial cycles in the mid-Pleistocene Period some 620,000 years ago.

Significant climate changes contained in the ice cores were identified for all three planetary realms: atmosphere, land and ocean. The evidence retrieved of "local temperature and precipitation rate, moisture source conditions, wind strength and aerosol fluxes of marine, volcanic, terrestrial, cosmogenic and anthropogenic origin" was unequivocal, describing both natural occurrences before the evolution of humans and subsequent anthropogenic influences (Petit et al. 1999, p. 429). The main trend, the Vostok team emphasized, was a rising concentration of carbon dioxide and methane in each glacial cycle. Their conclusion could not have been more ominous: the "extension of the greenhouse gas record shows [that] present-day levels of CO_2 and CH_4 are unprecedented during the past 420,000 years". Providing yet further evidence for the close coupling of atmospheric and oceanic processes, the team also reported from their analyses that "similarities between changes in atmospheric CO_2 and Antarctic temperature suggest that the oceanic area around Antarctica plays a role in the long-term CO_2 change" (Petit et al. 1999, pp. 433–435). Undeniably, the primary cause of climate change was identified as atmospheric saturation from emissions of long-lived greenhouse gases, among which CO_2 was the most significant contributor. In conclusion, Petit commented that the greatest significance of the Vostok ice cores is the revelation that "the long stable Holocene is a unique feature of climate during the past 420,000 years with possibly profound implications for evolution and the development of civilizations" (Petit et al. 1999, p. 436). Geologically speaking, the research had confirmed that our present technocratic period is taking place during a relatively warm interglacial phase of world climate.

Despite objections by recalcitrant scientists, the three major datasets available today, compiled at HadCRUT in the UK and in the USA at GISS and the National Climatic Data Center of NOAA, confirm that "the linear trend in globally-averaged annual mean temperatures (the standard yardstick) over the period 1998–2007 remains upward" (Fawcett and Jones 2008, p. 1). Analysis by Robert Fawcett of the Australian National Climate Centre of the Bureau of Meteorology, having made allowances for the extreme 1982–1983 and 1997–1998 *El Niño* events that raised global temperatures markedly, confirmed that "the GISS data show a more consistent warming signal in the past 30 years after the removal of the ENSO signal, particularly in the past ten to fifteen years" (Fawcett 2007, p. 146).

Climate Changes in the Ocean

After Wallace Broecker raised the issue of climate change in his 1975 article "Are we on the brink of a pronounced global warming?", that rhetorical question became the subject of continuing debate. Academic research increased and international organizations and conferences, beginning with the creation of the WCRP in 1980 and finally the IPCC in 1988, demonstrated government response. To assist public understanding, in the November 1987 issue of the American Museum's publication *Natural History*, Broecker wrote a popular article for a "largely lay readership", entitled "The Biggest Chill", on the growing conjecture about abrupt climate change following the last Ice Age. Opening with the words "We, the inhabitants of planet Earth, are performing a gigantic climate experiment", he obviously had in mind Roger Revelle's statement of 1957 that we "human beings are now carrying out a large scale geophysical experiment of a kind that could not have happened in the past nor be reproduced in the future". His intention was to warn of the dangers posed by our present lack of "knowledge of earth's climate system…to predict the effects of [global] heating".

With an ever-swelling volume of research available, Broecker discussed the significance of the oxygen isotope $^{18}O/^{16}O$ values recovered from the Greenland ice cores at Camp Century analysed by Willi Dansgaard, and those from the Dye-3 site by Hans Oeschger. Before the onset of the stable Holocene in which civilization developed, those two scientists independently discovered two abrupt warming periods, since known as Dansgaard–Oeschger events, that were clearly evident in the cores "at ~12,700 and ~10,000 radiocarbon years ago", and, most disturbingly, Broecker exclaimed, "were accomplished in only 50 years!" (Broecker 1991, p. 87).

Well aware that most solar radiation is absorbed by the oceans, or more correctly, "the ocean", because it is a single body of water, Broecker centred his argument on the fact that the ocean carries immense stores of thermal energy, described by Robert Stewart of NOAA as "the engine that drives atmospheric circulation".[8] That led him to conjecture that the two events had been triggered by some massive interference with the ocean/atmosphere relationship that exists in "a curious tie between the two", manifested in "a globe-straddling" ocean current (Broecker 1987, p. 76). Using an analogy, Broecker described it as "conveyor-belt-like", a complex oceanographic process that moves heat around the globe and hence helps to maintain global climatic regimes (Richardson 2007). To inform readers further, a very simplified cartoon of the "conveyor" appeared across pp. 74 and 75 of *Natural History*, with warm currents in red and cold in blue.

Preoccupied with the possibility that global warming could create yet another Dansgaard–Oeschger event from melting Arctic ice interfering with its steady action, which had not altered throughout the 10,000 years of the Holocene, Broecker set out to analyse it in depth. In 1991, he wrote an academic sequel to the *Natural History* article entitled "The Great Ocean Conveyor", in which he described the path it takes around the ocean, where the 1987 cartoon reappeared in monochrome. Some 20 years later, his hypothesis was expanded to monograph length, also titled "The Great Ocean Conveyor", in which he described the situation up to the year 2009. To identify its origin and prime-mover, Broecker began with the chilled waters of the Arctic and an explanation first presented in detail as "the thermohaline circulation" (or THC: Gk *thermos*, "warm" + *halys*, "the sea, salty") by Norwegian pioneer oceanographer Harald Sverdrup in his 1942 landmark publication *The Oceans*. As Sverdrup made clear, "the thermohaline circulation…is responsible mainly for the development of vertical convection currents" in the Arctic, and it is these that initiate and sustain the process.[9]

Convection begins as the surface layer freezes in the Arctic, salt is forced out and ice is formed up to 3 m thick, and the underlying stratum becomes more saline, so denser and heavier. As the heavy Arctic water sinks from the relatively shallow surface layer, around 200–300 m on average, it passes through the halocline layer, an intermediate zone down to 2000 m, composed of the thermocline zone where temperatures decrease rapidly and the pycnocline zone of increasing high density (Gk *pyknos*, "dense"). Below the halocline is the deep-water layer of near zero temperature, several kilometres down. There, a forcing action begins which initiates circulation of the deep layer of the Conveyor, known as North Atlantic Deep Water (NADW), and below 4000 m is "a wedge of Antarctic Bottom Water (AABW) that underrides the NADW mass".

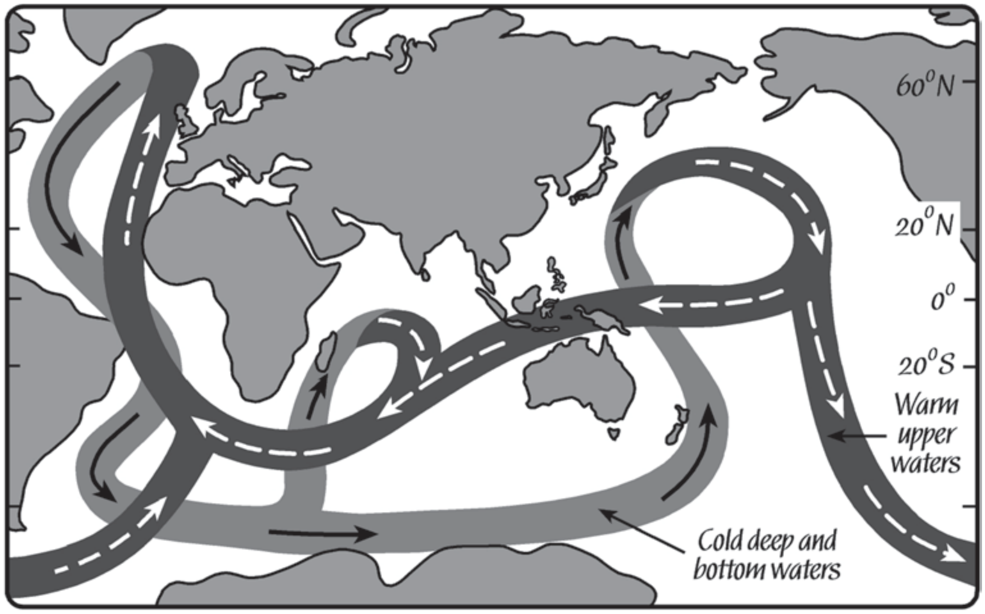
Beginning its passage along the Labrador and Greenland coasts, the Conveyor proceeds southbound through the Atlantic trough until it meets the vigorous eastbound Antarctic Circumpolar Current (ACC) that circulates endlessly around that continent, which Sverdrup described as "the great mixmaster of the world ocean". The process is complicated, although basically it involves low-salt Pacific surface water (32–33 $g\,l^{-1}$) from river inflow and rainfall moving through the Drake Passage into the Southern Atlantic and Indian oceans and overriding the saltier NADW (~34.3 $g\,l^{-1}$) as Antarctic Intermediate Water. As it circulates, the even colder water of the AABW (below zero and $\sim -2\,°C$) continues the forcing action (Broecker 1991, p. 79; but see also Broecker 2010). In a process still not fully understood, and the subject of considerable controversy, the Conveyor then rises and spreads into the Indian and Pacific oceans. In 1991, Broecker described that process as coming from "intense upwelling" in both north and south mid-latitudes, which he illustrated in a sketch map, but without any detailed explanation.

As he made clear in the 2009 Preface to his monograph, the Conveyor was but "a key element of the ocean's operation". Since Sverdrup's time in the 1940s, in more wide-ranging research into climate change, in contrast, from its continuous circulation pole to pole, and the mixing that results, oceanographers in the late 20th century came to describe the Conveyor more specifically as the Meridional Overturning Circulation (MOC). Often used synonymously with the THC because there is a considerable degree of overlap, there are differences of emphasis. Whereas the THC, and particularly Broecker's Conveyor approach, is concerned with the balance between salinity, density, temperature, surface evaporation and the qualities of water chemistry needed to maintain the forcing action, research into the MOC extends into the entire range of forces that determine ocean behaviour and issues of climate change. In addition to ocean warming from solar radiation, the MOC approach considers atmospheric influences, and wind-driven forces that include the Hadley Circulation, the Coriolis effect on current flow, gyres and eddies from the Ekman transport mechanism, which creates downward spirals of water, and wave behaviour from wind stress on coastlines. Where relevant, the physical dynamics of sun, moon and tide, the phenomena of precession and the Milankovitch Cycle, plate tectonics and seafloor topography can also be considered.

Throughout the first decade of the 21st century, the conveyor circulation has been more intensively investigated, and in 2012, oceanographers John Marshall of the Massachusetts Institute of Technology and Kevin Speer of Florida State University proposed a solution drawn from that research. What stimulated them in particular was "the growing realization of the importance of the upwelling branch of the MOC", and that "the Southern Ocean is now taking centre-stage in discussions of processes that drive modern and ancient

[8] R. Stewart 2012 in a NOAA online article entitled "Ocean motion and surface currents".

[9] Sverdrup et al. (1942). The thermohaline circulation: 509–511; 747–755.



The Meridional Overturning Circulation (MOC), or Great Ocean Conveyor, as it appeared in *Natural History* for 1987 and reproduced in Broecker (1991, p. 80). (Illustration reproduced courtesy John Veron)

climate variability". Their study concluded that upwelling is "driven by westerly winds, drawing water up to the surface" in tumultuous gyres and eddies in the South Antarctic Ocean as the MOC passes over the rugged terrain below, contributing what they describe as "topographic steering". From such evidence, they argued strongly that "this upwelling branch roughly balances the North Atlantic downwelling branch, and is much more distributed in space [as it] acts to connect the vast reservoirs of heat and carbon below the Southern Ocean mixed layer with the surface" (Marshall and Speer 2012, p. 171). Consequently, the two scientists asserted that the Southern Ocean upwelling is as equally responsible for the thermohaline circulation as the melting Arctic ice theory proposed by Broecker. In particular, they suggested that the upwelling may have released "abyssal CO_2 into the atmosphere [and] may be indicative of increased exchange between the deep and the surface, and could have contributed, for example, to the transition out of the last ice age" (Marshall and Speer 2012, p. 177).

As the MOC continues into the Indian and Pacific oceans, the surface layer is warmed by solar radiation around 100 $W\,m^{-2}$ to above 10 °C, and absorbs ~1 PW of heat (10^{15} W). With high surface-water evaporation rates that increase salinity and density, it flows above the denser NADW into and through the tropical Atlantic. Near Florida, a subsidiary warm Gulf Stream is created from wind stress, and advection by east-moving air masses above the USA pushes released heat northeastwards. This phenomenon helps to maintain atmospheric temperatures over Europe between 15 and 20° higher than would otherwise be the case (Seager et al. 2002, p. 2563). Flowing on to the Arctic, the MOC freezes and sinks, then continues its steady, relentless pace to repeat the circuit of moving one-third of ocean waters, some 400,000 km^3, around the planet (Maribus 2010, p. 18).

Could the Circulation Collapse?

When first investigated, the bottom water of the MOC was estimated to move slowly with a cycle taking up to 1000 years, that value later confirmed by Broecker from $^{14}C/^{12}C$ radiocarbon measurements (Broecker et al. 1991). In addition, Broecker estimated the residence time of "the entire deep Atlantic to be about 180 years" (Broecker 1991, p. 81). Moreover, in addition to Dansgaard–Oeschger events, Greenland ice cores revealed abrupt rises in temperature, known as Bølling–Allerød warm periods, in which glacial melt from the warmer Allerød, named after the type location in Denmark, stopped saline forcing and closed the MOC down. As anxiety over contemporary global warming began to mount, research intensified from concern that if the MOC became disturbed by a present-day Dansgaard–Oeschger event and its forcing action slowed, it could lead to colder temperatures in Europe. That issue raised a disturbing question: Will the accumulation of CO_2 in the atmosphere begin to slow the MOC down, and even stop it again? That soon became an intensely disturbing possibility.

The first positive reassurance for continuity came when, from the accumulation of research data available from CLIVAR and WOCE, Alexandre Ganachaud and Carl Wunsch of Massachusetts Institute of Technology (MIT) reported to *Nature* that from 1970 to 2000, for the MOC "no statistically significant change in integrated mass transports over the past thirty years was found" (Ganachaud and Wunsch 2000, p. 458). However, observations made soon thereafter suggested that there were significant changes, based on evidence from the Rapid Climate Change Programme (RAPID array) of the Natural Environment Research Council. A consortium of the US Rosenstiel School of Marine and Atmospheric Science in Miami, the UK Oceanographic Data Centre in Liverpool and National Oceanography Centre in Southampton, with assistance from the US National Science Foundation and NOAA, have been observing the MOC closely. In March 2004, three subarrays of 22 moored instruments were deployed across the Atlantic seabed along 26.5° N in the Florida Straits to the Bahamas, in the Western Boundary trough of the Mid-Atlantic Ridge, and the Eastern Boundary trough to the Canary Islands. The Florida Straits array measured Florida Current transport to its overall depth of 800 m. The two major oceanic troughs, descending to 6000 m, are monitored for thermal winds, baroclinic circulation (pressure changes) between water layers, fluctuations in bottom pressure, and changes by surface winds to the behaviour of the Ekman transport phenomenon.

In a short account to *Nature* in 2005, Harry Bryden, Hannah Longworth and Stuart Cunningham of the National Oceanography Centre reported from preliminary RAPID ARRAY data that “the Atlantic Meridional Overturning Circulation has slowed by about 30 % between 1957 and 2004”. While not contradicting the earlier report of Ganachaud and Wunsch, the evidence they advanced indicated that “whereas the northward transport across 25° N has remained nearly constant, the slowing is evident in a 50 % larger southward-moving mid-ocean recirculation of thermohaline waters, and also in a 50 % decrease in the southward transport of lower North Atlantic Deep Water between 3000 and 5000 m in depth”. The implications for climate change, they stressed, are profound “since its heat transport makes a substantial contribution to the moderate climate of maritime and continental Europe” (Bryden et al. 2005, p. 655; see also Rayner et al. 2011).

Intense concern and restless speculation were generated rapidly, in both the oceanographic community and the press. In a public release of 7 December 2005, professor of atmospheric sciences Michael Schlesinger at the University of Illinois in Urbana-Champaign stated that we are witnessing “a dangerous, human-induced climate change” from analysis by his research group that indicated that an MOC shutdown is “a high-consequence, high-probability event”.[10] A year later, however, the IPCC AR4 report dismissed the possibility of a shutdown as mere speculation because, although “it is very likely (> 90 % chance) that the MOC will weaken gradually over the 21st century in response to increasing greenhouse gases, [it is] very unlikely (< 10 % chance) that an abrupt MOC change will occur in that time” (IPCC 2008). Various calculations of the rate of Greenland ice melt and precipitation changes indicate that only relatively small volumes of water into the seas will be released, and take more than 1000 years to dissipate if present CO_2 emissions of 400 ppm do not rise any higher.

The need for stronger evidence of change in the behaviour of the MOC was met in 2012 with publication of the Annual Report Card of the Marine Climate Change Impacts Partnership, which described the findings of the RAPID array between April 2004 and 2007 by five British oceanographers, led by Stuart Cunningham. Studies of a number of modelling simulations revealed a continuing downward trend which “suggests that the MOC will weaken gradually in response to increasing levels of greenhouse gases … and reductions between 0 and 50 % in the MOC by 2100”. However, they qualified that comment with the statement that “no comprehensive climate model … produces a complete or abrupt MOC shutdown in the 21st century,” nor do any models allow for increased Greenland melting. Possibly, if that becomes the case then “such extra fresh water could result in further MOC weakening” (Cunningham et al. 2010/2011, p. 7).

In the same year, 12 oceanographers from the UK, Germany and the USA under the leadership of Darren Rayner also published an extended survey of MOC predictions gained from the RAPID array in *Deep-Sea Research II*. Their investigations led them to infer that the consequences of CO_2 accumulation in the atmosphere “from coupled ocean-atmosphere climate models are in agreement that the Atlantic MOC will decrease as it builds up”. Continuing, they commented that “our best models predict a weakening of the Atlantic MOC under an increase of CO_2 in the atmosphere and suggest that if the MOC abruptly shuts down there would be severe cooling over the northern Atlantic” (Rayner et al. 2011, p. 1745).

A major choke point for Arctic to Atlantic current transport is across a relatively shallow ridge reaching southeast from Greenland, beneath Iceland, to the Faroe Islands, marking the southern boundary of the Norwegian Sea. In an ideal location for measurement of present MOC behaviour, a number of Scandinavian studies have been made of transport through the four available channels, most recently in 2008 by Olsen and his colleagues. From “direct current measurements for the Faroe Bank Channel for 1995–2005”, and an experiment for 1948–2005 using an ocean general model, their results were unequivocal: both field studies and model data show no significant trend in volume transport, which led to the conclusion that “overflow did not decrease consistently from 1950–2005” (Olsen et al. 2008). However, their investigations did reveal “a weakening total Atlantic Meridional overturning circulation as a result of changes

[10] Posted by James Kloeppel, Physical Sciences Editor, UI (Urbana-Champaign) in EurekaAlert! AAAS Science News.

south of the Greenland–Scotland ridge". In the same year, Stein Østerhuis confirmed those results in a short article in the German journal *Klima*, again with the reservation that "even though volume transport has shown no trend, there is a significant change in temperature and salinity in deep water in the [adjoining] Norwegian Sea" (Østerhus 2008).

The observations by Bryden in 2005, and the differing views presented by Olsen and his Scandinavian/German colleagues in 2008 which did not support a weakening MOC, were all considered carefully (Olsen et al. 2008; Holliday et al. 2008). Exercising caution, no final position was reached, but the need to continue MOC research to assist predictability of Atlantic climate change would be of considerable value, Bryden wrote, because at present, variations in movement of the MOC "are not yet fully understood" (Rayner et al. 2011, Abstract). That finely tuned understatement, however, drawn from verifiable, empirical evidence, can be considered further in the light of speculative palaeontological investigations that are beginning to suggest another likely future for present day reefs if the CO_2 content of the atmosphere continues to rise. Triggered by the current debate over ocean acidification, exploration has been intensified in regions of widespread past volcanic activity to determine more precisely the extent to which acidic seas may have been partly responsible for the Permian extinction 250 million years ago when 95 % of all sea life died.

One particular investigation in 2005 by Jeffrey Kiehl and Christine Shields at the National Center for Atmospheric Research (NCAR) in Boulder, Colorado, is exceptionally relevant. Investigating the possible consequences of continued global warming from computer programs correlating atmospheric and ocean temperatures, they discovered that sustained volcanic activity during the Permian Period "which lasted for approximately 700,000 years" had raised atmospheric temperatures between 10 and 30 °C. The massive quantities of CO_2 released simultaneously into the oceans had disrupted the MOC by warming it as far down as 3000 m (10,000 ft), and the resulting combination of oxygen deprivation and water acidification, they inferred, had caused mass extinction of most marine biota.[11] Further palaeographic evidence revealed that on several occasions in the past 100,000 years, the MOC had even completely stopped in times of extreme global warming.

In 2008 came the most speculative, arresting suggestion of our possible future, drawn from the mass extinctions of the past. Written by Peter Ward and published by the Smithsonian Institution, its title "Under a Green Sky" encapsulates the endpoint where all relevant scientific evidence is leading: uncontrolled toxic emissions eventually covering the planet with a greenhouse gas mantle of poisonous hydrogen sulphide, turning the blue sky green. Professor of Biology, Earth and Space Sciences at the University of Washington, Ward's central thesis is that the atmospheric content of CO_2 for the past 200,000 years had remained between 180 and 280 ppm until the year 1800, as revealed in the Greenland and Antarctic ice cores, and Mauna Loa measurements since 1958. Then the volume began climbing steadily until it almost reached 400 ppm in 2012, with no signs of slowing. On the contrary, as China and India, followed by other developing countries, aspire to having energy-intensive appliances for daily living with two cars in every garage, the Keeling Curve will show an accelerating climb at the present rate of 120 ppm per century and reach between 500 and 600 ppm by 2100 (Ward 2008, p. 164 f).

If that increase is allowed to continue, it will create an environment similar to the ice-free Eocene Epoch (56–35 Mya), when CO_2 registered 800 ppm, palms and crocodiles inhabited the Arctic Circle, and sea level was 46 m (150 ft) higher. Under such conditions, the MOC would change dramatically. With no forcing action from the ice-free North Atlantic, its slightly cooler waters would still sink in mid-latitudes, but no longer reach the deep seabed nor carry oxygen to the abyssal deep water benthos, which would become anoxic. Marine life would be extinguished and the changed conditions favour the growth of dense mats of photosynthetic bacteria, particularly green species feeding on sulphur that emit hydrogen sulphide, levels of which would rise far above present-day clouds to form a different type of cloud layer that coloured the sky green. That ghastly scenario has been developed even more radically by David Battisti, Professor of Atmospheric Sciences at the University of Washington, who is convinced on present indications that we will reach 800 ppm by the end of the current century. As described by Ward, such a level will certainly create an Eocene-like world and melting will accelerate, making a green sky possible (Ward 2008, p. 167 f).

Sea-Level Rise

To put such dramatic extrapolations to one side and further complicate prediction of future events, we need to understand that the ocean is not continually at a uniform height: the various seas have different levels depending on location, tides, temperature (warm water is lighter, and rises) and, most particularly, isostatic earth movements. In a process known as eustasis (Gk *eu*, "good", "even" + *stasis*, "level"), as pressure from residual Ice Age sheets is released as they continue to melt along the eastern Swedish coast in the Gulf of Bothnia and in Alaska, in isostatic response the land rises. In addition, sea levels are affected, for example, by subsidence in Louisiana and from the Chandler Wobble as the planet spins erratically, ever so slightly, on its axis.

[11] Kiehl and Shields (2005); press release Helen Briggs, BBC News Science Report, 28 August 2005.

Sea-level changes also vary from the effects of atmospheric pressure, winds, ENSO events, flood discharges from violent inland storms, and the uniform global ocean rise from ice-sheet melting. Further, the five great circulating ocean gyres in the North and South Atlantic, the North and South Pacific and the Indian oceans are at least 1 m higher in the centre than along the coastlines. This is caused by the rotational effects of surface currents (clockwise in the northern oceans, anticlockwise in the southern) forming extensive convex central areas (described from their appearance as "domes" or "lenses") of elevated water from Coriolis forces that create surrounding geostrophic currents which maintain their elevation.

These slow, imperceptible changes are affecting sea levels every day. Consequently, exact measurement is notoriously difficult and variations over time depend too on markers, such as notches in rocks made in earlier periods, to establish the local mean sea level (LMSL) in geologically stable areas, and from weather bureau archives. Considerable reconstruction of past levels also comes from analysis of sedimentary deposits, volumes of water locked up in ice sheets and glaciers and frictional markings in glacial moraines following the Ice Ages, when the seas were 120 m lower. For almost 2000 years up to the start of the 20th century, levels were stable: since the Industrial Revolution, they have risen on average by 3 mm per year.

Present evidence is not encouraging. The IPCC Fourth Assessment Report of 2007 provided six separate scenarios depending on the rise in mean global temperature. With means between 1.8 and 4 °C, the estimated sea-level rises for the 21st century will range from 18 to 38 cm with a 1.8 °C temperature rise, to between 26 and 59 cm from a 4 °C increase. A year later, the World Wildlife Fund (WWF) released an updated estimate by the International Arctic Research Center of the University of Alaska, which revealed that there were much greater changes in Arctic melting than hitherto anticipated. Since 1979 when satellite monitoring commenced, Arctic ice cover had diminished by 39 % to 4.3 million km^2, which led to the WWF conclusion that "there is hardly a component of the Arctic that is not showing signs of change" (WWF 2008, p. 8).

These developments have serious implications for global sea-level rise. From 1880 to 2000, sea levels rose ~2 mm per year, a total of 200 mm (8 in.) over that period. As melting accelerates, particularly in the Arctic, across Greenland and in the Antarctic, increases will be greater and will cause major changes to coastal regions where approximately one half of humanity lives. As each rise of the sea level increases an average encroachment on land by a factor of 100, an increase of 1 m as predicted by the end of the 21st century and an inundation of many major cities, along with their ports, rail and container terminals would result.

Coral Reefs in an Uncertain World: The Anthropocene Epoch

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What future then, lies ahead for coral reefs as the 21st century progresses? Ove Hoegh-Guldberg, their most indefatigable defender living today, made a stark reminder to the world of the consequences of climate change on 17 November 2005, in a speech to the Carnegie Institution of Global Ecology at Stanford University, where he recounted the threats from sea temperature rise. Based on experiments he is directing at Heron Island Research Station on increasing acidification of the oceans, as the threshold of 400 ppm of global CO_2 has almost been reached (indeed it was reached in May 2013), he ventured the disturbing prediction that "beyond 500 ppm coral reefs may no longer exist".[1] In particular, the world's iconic Great Barrier Reef, which he has been studying for the past 30 years, he confirmed, is becoming increasingly vulnerable, and approximately 50 % of coral cover had already been lost from bleaching, *Acanthaster* outbreaks, and other causes.[2]

At the International Coral Reef Society (ICRS) conference in Cairns in July 2012 it was reported that the IPCC predicts "by 2030 the GBR will be functionally extinct". The consensus statement from the 2500 participants issued by the ICRS Secretariat made it clear that "This combined change in temperature and ocean chemistry has not occurred since the last reef crisis 55 million years ago. A concerted effort to preserve reefs for the future demands action at global level, but will also benefit hugely from continued local protection". Rather wistfully, Research Director of the Australian Institute of Marine Science (AIMS), Peter Doherty, commented that, on present indications, Australia appeared to be "losing the war" to save the Great Barrier Reef. [3]

Evidence to confirm that metaphor appeared on 25 September 2012 in an early edition online of the *Proceedings of the National Academy of Sciences* entitled "The 27-year decline of coral cover on the Great Barrier Reef and its causes". The Australian Government announced in 1985 that it had arranged for the world's greatest single marine research and expenditure project on the Great Barrier Reef to be undertaken by AIMS to coordinate ecological investigations into the Crown-of-Thorns starfish. A survey team of four scientists working from AIMS published the results of the 27-year investigation concluded in 2012. From 2258 standardized manta-board survey tows over 214 reefs from northern, central and southern sectors, and incorporating other data collected by the Long Term Monitoring Programme of the Great Barrier Reef Marine Park Authority after its establishment in 1992, the results confirmed reality. Although less degraded than the Caribbean, where coral cover has declined by ~1.4 % $year^{-1}$, the Great Barrier Reef is also on a downward trajectory. Caribbean problems result from disease, hurricanes, overexploitation and phase shifts from coral to algal dominant cover, but the Great Barrier Reef has been largely devastated by the Crown-of-Thorns starfish, cyclone scouring and bleaching. With coral cover loss averaging 22.9 % for 214 reefs over 27 years (1985–2012), there were marked differences between the three sections. Northern and southern regions are more lightly populated and lesser developed, and have higher retention cover values of >35 and >30 %, respectively; the central section with more intense agriculture and grazing, and a progressively developed, bigger population and tourist coastline, revealed a greater loss over 27 years to <20 % (De'ath et al. 2012, p. 1).

These are intensely disturbing figures for the world's greatest reef, and offer few grounds for optimism. The authors conclude that their evidence indicates for the central sector "a major decline in coral cover from 28–13.8 % (0.53 % $year^{-1}$) a loss of 50.7 % of initial coral cover". Moreover, if coral cover on the Great Barrier Reef continues to decline consistently, then "without intervention, it will likely fall to 5–10 % within the next 10 years" (De'ath et al. 2012, p. 1, 4).

Levels of apprehension must inevitably rise if the development-driven ultra-conservative Queensland Government

[1] Hoegh-Guldberg, cited by Rhett A. Butler. mongabay.com/…/1117-corals.html, 17 November 2005.

[2] Jon Brodie and Jane Waterhouse, James Cook University Research Unit, Media Release, 12 April 2012. See also Sweatman et al. 2011.

[3] Ben Cubby, News Review, Sydney Morning Herald, 14–15 July, p. 5.

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ignores UNESCO's warning of 1 June 2012 that the Reef's World Heritage listing may be lost if it continues current plans to increase coal export facilities from Curtis Island and the Port of Gladstone. Not only does dredging seabed channels and overdeveloping the region disturb the already delicate balance of its ecology, but also putting more coal into circulation will continue to exacerbate atmospheric pollution. Further evidence came as recently as June 2012 from investigation by the present author of the Outer Barrier Ribbon Reefs (16° N) and the Low Isles closer to Port Douglas (16.30° N). Since the last expedition of 2006, both revealed widespread formation of haloseres leading to dominance of soft corals and significant loss of biodiversity. As hard corals succumb to warmer waters, there will be ecological succession changes because scleractinian planulae and algae are unable to find firm settlement places, with the further impact of reduced food resources for fish.

The cumulative evidence presented so far is beginning to provide a possible future for reefs if human activity continues to overload the atmosphere with carbon. While the world will not end, it will certainly become further changed beyond its present condition with farm and grazing lands becoming even more impoverished from reduced rainfall as aridity spreads. That will almost certainly lead to major conflicts over access to already diminishing freshwater for rural people dependent on glacial melt, aquifers, lakes and flowing rivers, as the current dispute between Pakistan and India over Indus River water illustrates. Similarly threatening are supplies for the growing masses in ever-increasing urban concentrations for which water has to be piped in, often over considerable distances, in places from desalinization plants or recycled water reservoirs. With respect to reefs, the processes in train already worsening their crisis condition will continue to a point in the not-too-distant future when living reef colonies in places will collapse, and crumbling calcium mounds overgrown by algae will become a more common scene.

Into the Future: The Achievement of Coral Reef Science

In the face of immense obstacles, one can merely marvel at the achievements of reef scientists over four centuries, and particularly their tenacity in attempting to confront the numerous problems presented by changes since the Industrial Revolution, even more so since the beginning of the carbon pollution era. Indefatigably optimistic, every problem presented has received an explanation, and in some cases a positive suggestion for a way forward. Consider the adaptive bleaching hypothesis (ABH), cladal analysis and the discovery of thermo-tolerant clade D and translocation experiments, the creation of marine protected areas, the search for pathogens, the detection of refuges from offshore reefs suggested by Peter Glynn and explored in detail by Bernhard Riegl and Werner Piller of the Institute of Palaeontology at the University of Vienna (Riegl and Piller 2003). Subsequently, in a study of *Acropora cervicornis* in Honduras, Riegl and others sustained that hope for possible refugia for reefs in times of environmental stress in their 2009 chapter on "Monitored and modelled coral population dynamics and the refuge concept" (Riegl et al. 2009).

Irrespective of their endless pleas for international recognition of reef plight and the need for protection, all coral reef scientists recognize the inevitability of change as global warming continues. There is no suggestion of a return to Matthew Flinders' day more than 200 years ago when, in 1802, he was able to describe the corals of the Great Barrier Reef as "glowing under water with vivid tints of every shade betwixt green, purple, brown and white; equalling in beauty and excelling in grandeur the most favourite *parterre* [arrangement] of the curious florist".[4] More appropriate today are Drew Harvell's comments that "It is unrealistic to think we can restore a 1000-year-old coral reef without restoring the original environmental conditions" (Harvell et al. 2007, pp. 192–193). At the same time, though, it is morally reprehensible for us to accept the ultimate scenario of the total dissolution of reefs from the immense pressures we have exerted throughout the past century without making strenuous efforts for their preservation.

Current evidence indicates that we can make the confident prediction that reefs will continue if we try, but in different colonies and locations, as suggested by Paul Sammarco and Kevin Strychar in 2009 in what appears to be one of the best possible scenarios. In a lengthy, comprehensive analysis of "The Effects of Climate Change on Coral Reefs", they discussed the most hopeful signs yet advanced for the future survival of coral reefs through the process of "exaptation". Not mentioned in discussions of cladal change so far, Stephen Jay Gould and Elisabeth Vrba devised the concept in 1982 as a "missing term in the science of form" to identify a process beyond adaptation, which covered "many features of organisms [that] are non-adapted, but available for useful cooptation in descendents" (Gould and Vrba 1982, p. 4). Earlier described as "pre-adaptation" to anticipate the ability of organisms to respond to changes, Gould and Vrba saw the need to avoid the suggestion of pre-existing divine design and to keep to strictly Darwinian evolutionary processes.

Contemporary cladal analysis and symbiont shuffling theory sit comfortably with the concept of exaptation, mainly because corals are relatively long lived, whereas symbionts are ephemeral, with rapid generation times, which provide

[4] Flinders 1814, pp. II, 88. Also, see Bowen 2002, p. 74.

opportunities for more thermally tolerant clades to colonize the surviving hosts. Provided that seas do not continue to warm and rise above the critical ultimate threshold of 36 °C (96.8 °F), even if the less thermally tolerant clade C acroporids finally succumb to warming seas, then the more resistant clade D species, in their numerous varieties, may form new assemblages. It is even possible that those clades not coping well with rising sea surface temperatures may survive on the cooler edges of the tropics. In that event, the acroporids, the branching staghorn species, may continue to help maintain the biodiversity of coral reefs, and there could also possibly be a migration of other species to the margins, if current research output proves correct.

Although “some tropical corals may be lost to local or global extinctions”, Gould and Vrba suggested, “the tropics and sub-tropics will expand poleward, and the other climatic zones will [also] shift poleward at the expense of the polar and sub-polar zones”. Even if the equator itself can no longer support reefs, regions nearby could warm to the point where they become able to support coral reefs and create “hypertropical zones” where “corals will be able to colonize to warmer marginal habitats”. Following the July 2012 International Coral Reef Symposium in Cairns, in a national televised presentation by six participants on the critical issue as to whether coral reefs could survive the 21st century, Jeremy Jackson from the Scripps Institution of Oceanography noted that species of animals and plants are already being recorded as living in waters along coastlines as far as 1000 km from tropical habitats[5]. However, Paul Sammarco and Kevin Strychar have warned that there was also a limiting possibility that it may not necessarily happen “that coral reefs would increase in number or recover with time under global warming conditions”, and also that the density would most probably be lower. If excessively high sea surface temperatures continue, which remains likely, the “overall species diversity of hermatypic scleractinian corals may well decline with time” (Sammarco and Strychar 2009, pp. 31–32).

Undoubtedly, scientists will continue searching for other possibilities for reef survival. One of the most enterprising plans advanced so far is the creation of coral sperm banks by Mary Hagedorn, a reproductive physiologist at the Smithsonian Institution. On 23 July 2012, she created a flurry of media excitement with a report in the *New York Times* of her efforts to collect trillions of gametes and billions of embryonic stem cells from spawning locations in Hawaii, the Great Barrier Reef and the Caribbean for freezing and future use in re-seeding suitable sites if worst-case scenarios eventuate. Being the only such project in progress so far, it is clearly both ambitious and logistically complex, but considering the staggering complexity of global priorities at present, it seems destined to remain in the deep freeze of good intentions. Even the relatively mild suggestion of Angela Douglas that the best way forward is by lowering global temperatures does not provide grounds for optimism, and despite valiant efforts by scientists and politicians so far, we continue to lack a clear vision for the way ahead.

The Challenge Ahead: The Moral Dimension of Climate Change Control

Until effective remediation of the world’s serious climate problems can begin and long-term structural solutions implemented, it is important to recognize, as the Stockholm Nobel Laureate Memorandum of 2011 argued, that we are transgressing planetary boundaries through technological advances that are creating “human pressures [which] are starting to overwhelm the Earth’s buffering capacity” (Stockholm Memorandum 2011). To concentrate on this problem intelligently rules out astute geotechnology that will inevitably create more troubles: rather, it lies necessarily in solving a moral issue, which throughout the 20th century has not been considered seriously at all by the industrialized polluting nations.

The great transformation of human prospects began when the Iron Age dawned. Before the Industrial Revolution and the rise of capitalism around 1800, production was based on agriculture and craft workshops. Throughout the 19th century, starting in England, the ruling classes began the enclosure of smallholdings by Acts of Parliament, which they controlled by means of selective male franchise, thereby legitimizing the formation of large private estates by the powerful and privileged, where land was transformed into a resource to be exploited in the pursuit of profit.

As technology then advanced rapidly throughout the 20th century, the socially cancerous growth of an international culture of competitive capitalist accumulation appeared, driven by the delusion that greed is God, and Nature a resource to plunder. Created in the West, that ethos was rapidly assimilated into the non-Western world, which now makes achieving moral solutions a very difficult, perhaps impossible, task. Philosophical and moral issues have very little place in the world today: this is the crisis point we have reached. How the future eventuates, in seriously realistic terms, will at best be challenging.

Throughout the historical record of scientific investigation into coral reefs described in this narrative, there is little evidence that humans accept the inherent right of reefs to exist as manifestations of Nature’s creation. Rather, they have been seen as hazards to be mastered, or for instrumental uses (food, recreation, development, industrial applications), and not for their own sake. Natural formations such as the giant redwood forests in California, or the Yosemite

[5] Jeremy Jackson, ABC *Future Forum*: “Can coral reefs survive the twenty-first century?”, Cairns, 22 July 2012.

Valley and Sequoia National Park in the USA, and the Great Barrier Reef and Wet Tropics of Queensland in Australia, inspire awe from their overwhelming majesty. Only after the long-term dedicated efforts of resolute campaigners such as John Muir in California and the passionate "Save the Great Barrier Reef" campaigners in Australia to prevent them from exploitation and eventual desolation do they remain.[6] Those examples, unfortunately, along with a relatively small number of other World Heritage sites, stand in bleak contrast to the present state of the global environment. Unfortunately, we do not have the same reverence for the air we breathe, or the waters that support our reefs and marine life.

In drawing this narrative to a temporary, possibly never-ending, conclusion, it seems scarcely necessary to comment that these greatest of challenges to the future of coral reefs are far beyond the province of the historian or of any historical analysis to solve. It is now more essential than ever for us to move beyond recognition of the symptoms of reef decline into an active programme to deal with the major causative factors of climate change: escalating population and economic growth, uncontrolled industrial output, overconsumption of scarce and vital resources and excessive pollution. Those are the most confronting issues in the world today that require the collective energy of every nation and government, in order to reach acceptable solutions. Perhaps the Memorandum of the Third Nobel Laureate Symposium will become our guiding road map.

A warning about sea litter on the dune beachfront produced by kindergarten children in Port Macquarie, New South Wales

In working to that end, the value of the historical record lies in its contribution to an extensive fund of data, which itself provides a reliable context within which political decisions and socially consensual Judgements can be made. It can do nothing more.

[6] The "Save the Great Barrier Reef" campaign is chronicled in detail in Bowen (2002, pp. 317–355).

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1 Quotations from classical authors including Theophrastus, Aristotle, Plato, Pliny, Herodotus, Aquinas, and Plotinus have been taken from standard editions in Oxford, Loeb and similar collections.

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