The Natural History of Santo

edited by
Philippe Bouchet, Hervé Le Guyader, Olivier Pascal

PATRIMOINES NATURELS

PUBLICATIONS SCIENTIFIQUES DU MUSÉUM
IRD ÉDITIONS
PRO-NATURA INTERNATIONAL

The Santo 2006 expedition was organized,
with the support, among others, of

STAVROS NIARCHOS FOUNDATION

FONDATION TOTAL

Liberté • Egalité • Fraternité
RÉPUBLIQUE FRANÇAISE
FONDS PACIFIQUE

and

CENSUS OF MARINE LIFE

EDIT European Distributed Institute of Taxonomy

NATIONAL GEOGRAPHIC

tvl Telecom Vanuatu Ltd

Vrai d'agriculture biologique

fondation d'entreprise VEOLIA ENVIRONNEMENT

SOLVIN

RICOH

Universal Sodexho REMOTE SITES

Représentation de l'Union Européenne au Vanuatu

The Natural History of Santo

edited by
Philippe Bouchet, Hervé Le Guyader & Olivier Pascal

Institut de recherche
pour le développement

Contents

Foreword by Edward Natapei, Prime Minister of Vanuatu 10

Introduction. The Natural History of Santo: An Attempt to Bridge the Gap between Academic Research and Consevation and Education 11

Vanuatu in the South Pacific 13
Benoît Antheaume

ESPIRITU SANTO IN SPACE AND TIME 17
coordinated by Bruno Corbara

The Late Quaternaty Reefs 19
Guy Cabioch & Frederick W. Taylor

The Holocene and Pleistocene Marine Faunas Reconsidered 25
Pierre Lozouet, Alan Beu, Philippe Maestrati, Rufino Pineda & Jean-Louis Reyss

Geography of Santo and of the Sanma Province 34
Patricia Siméoni

Drainage, Hydrology and Fluvial Geomorphology 46
James P. Terry

The Climate of Santo 52
James P. Terry

Large-scale Climatic and Oceanic Conditions around Santo 57
Christophe Maes & David Varillon

A Brief History of Biodiversity Exploration and Scientific Expeditions on and off the Island of Santo 62
Bruno Corbara & Bertrand Richer de Forges

Deforestation on Santo and Logging Operations 67
Rufino Pineda

The Impact of WWII on Infrastructures and Landscape 69
Laurent Palka & Rufino Pineda

Conservation Efforts in Santo 71
Samson Vilvil-Fare

VEGETATION AND FLORA 73
coordinated by Jérôme Munzinger & Porter P. Lowry II

Exploration by the Santo 2006 Botany Team 75
Porter P. Lowry II & Jérôme Munzinger

Principal Types of Vegetation Occuring on Santo 76
Jérôme Munzinger, Porter P. Lowry II & Jean-Noël Labat

- **Phytogeographic Relationships** 77
  Gordon McPherson
- **How Old are the Kauri (*Agathis microphylla*) Trees?** 83
  Jonathan Palmer

The Flora of Santo 89

- **Some New, Characteristic or Remarkable Species** 89
  Gordon McPherson & Jérôme Munzinger
- **Focus on Araliaceae: Several Genera Exemplify Santo's Melanesian Biogeographic Relations** 90
  Porter P. Lowry II & Gregory M. Plunkett
- **Focus on *Geissois* (Cunoniaceae): Another Example of the Melanesian Connection** 93
  Yohan Pillon
- **Focus on Pandans** 94
  Thomas Haevermans
- **Focus on Orchids** 97
  Marc Pignal

Focus on Palms 102
Jean-Michel Dupuyoo

Focus on Ferns 105
Germinal Rouhan

Focus on Bryophytes 110
Elizabeth A. Brown

Fungi, the Forgotten Kingdom 113
Bart Buyck

TERRESTRIAL FAUNA 117
coordinated by Bruno Corbara

IBISCA-Santo Biodiversity Along an Altitudinal Gradient 119
Bruno Corbara on behalf of the IBISCA network

Insects on Santo 123

Focus on Orthoptera 123
Laure Desutter-Grandcolas, Sylvain Hugel & Tony Robillard

Termites in Santo: Lessons from a Survey in the Penaoru Area 128
Yves Roisin, Bruno Corbara, Thibaut Delsinne, Jérôme Orivel & Maurice Leponce

Focus on Bees and Wasps 131
Claire Villemant

Myrmecophily in Santo: A Canopy Ant-Plant and its Expected and Less Expected Inhabitants 143
Bruno Corbara

Beetles in Saratsi Range, Santo 146
Alexey K. Tishechkin, Jürgen Schmidl

Lepidoptera in Vanuatu: Fauna, Geography and the IBISCA-Santo Project 155
Roger L. Kitching

Other Invertebrates 161

Diversity of Spiders 161
Christine Rollard

Some Arthropods as Expressed in the Words of Penaoru Villagers 167
Bruno Corbara

Indigenous Land Snails 169
Benoît Fontaine, Olivier Gargominy & Vincent Prié

The Vertebrates of Santo 179

Terrestrial Bird Communities 179
Nicolas Barré, Thibaut Delsinne & Benoît Fontaine

Amphibians and Reptiles 187
Ivan Ineich

RIVERS AND OTHER FRESHWATER HABITATS 237
coordinated by Philippe Keith

Freshwater Habitat Types 239
Philippe Keith & Clara Lord

Freshwater Biota 242

Focus on Fish, Shrimps and Crabs 242
Philippe Keith, Clara Lord, Philippe Gerbeaux & Donna Kalfatak

Focus on Aquatic Insects 251
Arnold H. Staniczek

Focus on Freshwater Snails 257
Yasunori Kano, Elen E. Strong, Benoît Fontaine, Olivier Gargominy, Matthias Glaubrecht & Philippe Bouchet

CAVES AND SOILS 265
coordinated by Louis Deharveng

The Karst Team 267
Louis Deharveng & Anne-Marie Sémah

Karst and Caves 269
Bernard Lips, Franck Bréhier, Denis Wirrmann, Nadir Lasson, Stefan Eberhard, Josiane Lips & Louis Deharveng

Caves as Archives 278
Denis Wirrmann, Jean-Christophe Galipaud, Anne-Marie Sémah & Tonyo Alcover,

Ni-Vanuatu Perception and Attitudes Vis-à-Vis the Karstic Environment 284
Florence Brunois

Karst Habitats of Santo 288

- **Focus on Soils** 288
  Anne Bedos, Vincent Prié & Louis Deharveng
- **Focus on Cave Terrestrial Habitats** 296
  Louis Deharveng, Anne Bedos, Vincent Prié & Éric Queinnec
- **Focus on Guano** 300
  Louis Deharveng, Josiane Lips & Cahyo Rahmadi
- **Focus on Blue Holes** 306
  Stefan Eberhard, Nadir Lasson & Franck Bréhier
- **Focus on the Loren Cave** 310
  Franck Bréhier, Sephan Eberhard & Nadir Lasson
- **Focus on Anchialine Fauna** 312
  Geoff Boxshall & Damià Jaume

Karst Biota of Santo 316

- **Focus on Bats** 316
  Vincent Prié
- **Fish and Shrimps of Santo Karstic Systems** 323
  Marc Pouilly & Philippe Keith
- **Focus on Springtails** 327
  Louis Deharveng & Anne Bedos
- **Focus on Microcrustaceans** 331
  Damià Jaume, Geoff Boxshall & Eric Queinnec

MARINE ECOSYSTEMS 335
coordinated by Philippe Bouchet

Benthic Algal and Seagrass Communities from Santo Island in Relation to Habitat Diversity 337
Claude E. Payri

The Position of Santo in Relation to the Centre of Maximum Marine Biodiversity (the Coral Triangle) 369
Bert W. Hoeksema & Adriaan Gittenberger

Focus on Selected (Micro)Habitats 373

- **Sulfide Rich Environments** 373
  Yasunori Kano & Takuma Haga
- **Marine Interstitial** 375
  Timea Neuser
- **Mangroves Environments of South East Santo** 377
  Jean-Claude Plaziat & Pierre Lozouet

Focus on Selected Biota 383

- **Checklist of the Fishes** 383
  Ronald Fricke, John L. Earle, Richard L. Pyle & Bernard Séret

Unusual and Spectacular Crustaceans 410
Tim-Yam Chan, Masako Mitsuhashi, Charles H.J.M. Fransen, Régis Cleva, Swee Hee Tan, Jose Christopher Mendoza, Marivene Manuel-Santos & Peter K.L. Ng

The Marine Molluscs of Santo 421
Philippe Bouchet, Virginie Héros, Pierre Lozouet, Philippe Maestrati & Rudo von Cosel

A Rapid Assessment of the Marine Molluscs of Southeastern Santo 431
Fred E. Wells

Molluscs on Biogenic Substrates 438
Anders Warén

Marine Partnerships in Santo's Reef Environments: Parasites, Commensals and Other Organisms that Live in Close Association 449
Stefano Schiaparelli, Charles Fransen & Marco Oliverio

Seaslugs: The Underwater Jewels of Santo 458
Yolanda E. Camacho & Marta Pola

MAN AND NATURE 465
coordinated by Michel Pascal

Pre-European Times 467

Vertebrate Pre-Human Fauna of Santo: What Can we Expect to Find? 467
Joseph Antoni Alcover

The Prehistory of Santo 469
Jean-Christophe Galipaud

Introduced Biota 476

Overview: Introduced Species, the "Good", the "Worrisome" and the "Bad" 476
Michel Pascal, Olivier Lorvelec, Nicolas Barré, Michel de Garine-Wichatitsky & Marc Pignal

Focus on Synanthropic Mammals 480
Olivier Lorvelec & Michel Pascal

Focus on Feral Mammals 483
Michel de Garine-Wichatitsky & Anthony Harry

Focus on Alien Birds 488
Nicolas Barré

Focus on Introduced Amphibians and Reptiles 490
Olivier Lorvelec & Michel Pascal

Focus on Introduced Fish 494
Philippe Keith, Clara Lord, Donna Kalfatak & Philippe Gerbeaux

Focus on Alien Land Snails 495
Olivier Gargominy, Benoît Fontaine & Vincent Prié

Endemic, Native, Alien or Cryptogenic? The Controversy of Santo Darkling Beetles (Insecta: Coleoptera: Tenebrionidae) 500
Laurent Soldati

The Case of Two Invasive Species: *Mikania micrantha* and *Merremia peltata* 503
Marc Pignal

Man Santo in his Environment 508

Food-Garden Biodiversity in Vanuatu 508
Sara Muller, Vincent Lebot & Annie Walter

At the Junction of Biological Cycles and Custom: the Night of the Palolo 515
Laurent Palka

Ni-Vanuatu Perceptions and Attitudes Vis-à-Vis Biodiversité 516
Florence Brunois & Marine Robillard

THE SANTO 2006 EXPEDITION 523

The Santo 2006 Expedition from an Ethnologist's Point of View 525
Elsa Faugère

The "Making of" Santo 2006 ..... **529**
Philippe Bouchet, Hervé Le Guyader, Olivier Pascal

Santo 2006 Expedition in the Classroom **549**
Sophie Pons & Alain Pothet

Santo 2006 Expedition Participants List **550**

Acknowledgements **553**

Bibliography **557**

Addresses of the Authors **564**

in BOUCHET P., LE GUYADER H. & PASCAL O. (Eds), *The Natural History of Santo*. MNHN, Paris; IRD, Marseille; PNI, Paris. 572 p. (Patrimoines naturels; 70).

FOCUS ON ANCHIALINE FAUNA

Geoff Boxshall, Damià Jaume

Around the coastal zone of tropical and subtropical islands like Santo it is possible to find flooded marine caves, particularly in karstic areas that represent raised fossil coral reefs. Some of these flooded caves show a unique layering of the water within them, and have a surface layer of fresh water sitting above a deeper layer of dense salty water that penetrates through the porous rock separating the cave from the adjacent sea. Habitats which have this double layer of fresh water on top of sea water are known as anchialine habitats and they tend to be inhabited by unusual organisms. On Santo we found only one such habitat, Loren Cave, located just South of the village of Lotoror. Loren Cave has many of the characteristics of a true anchialine cave: it has a superficial freshwater layer which overlies a deeper seawater layer. There is also a marked tidal effect — with tidal rise and fall of about one meter, and there seems to be considerable exchange of water during the tidal cycle. The physical characteristics of the cave and the structure of the water column of this cave system are described in the earlier text "Focus on the Loren Cave".

Cave lakes in anchialine caves are inhabited by unique organisms that have become accessible for study only since the advent of specialized cave diving techniques and equipment (Fig. 384).

Caves are extreme environments for aquatic organisms for several reasons; firstly there is no light, so there is no photosynthesis by green plants. This means the only sources of energy to support the community of organisms in the cave lake are either bacterial production or the inflow of organic material carried into the cave in the inflowing water. These sources of energy usually cannot support dense populations of animals. Secondly the layered water column is often characterised by low oxygen levels, especially in the deeper marine water layer, and oxygen is required by most organisms for their normal respiration. Animals adapted for life at low oxygen levels typically do not survive well outside of these conditions. So aquatic animals that are cave adapted, often have highly localised or restricted distribution patterns.

Anchialine organisms are highly specialized yet many retain extremely primitive features and some, especially those living in and around the Caribbean region, have been classified as living fossils. Specializations that are common in anchialine animals include loss of eyes, enhancement of chemosensory systems, tolerance of low oxygen levels and physiological adaptation to extremely low energy systems.

Figure 384: Member of cave diving team in Loren Cave preparing baited traps before diving.

Just inside Loren Cave is a shallow pool of fresh water which is dimly lit by light from the cave entrance. It contained a few shrimps belonging to a crustacean genus called *Macrobrachium*. Its Latin name means "long arms" and this shrimp has the most amazing elongate claws, often brightly coloured. There are more than 200 species of *Macrobrachium* known and they can be found in warm tropical and subtropical fresh waters around the world. In addition to some small fish, which were not caught, the pool contained some other small crustaceans known as copepods. These are tiny relatives of the shrimps and crabs, but their adult size is often only one millimeter or even less (Fig. 385). The pool contained copepods belonging to the genus *Halicyclops*. The name *Halicyclops* refers to the fact that these species prefer to live in very slightly salty water (known as brackish water) and that they belong to the group typified by Cyclops, the mythical monster with only one eye.

Halicyclops species, like most copepods, have only one eye, a tiny spot located in the middle of the front of their heads. The eyespot is a simple structure which only allows the copepod to detect light and dark, but enables them to see a predatory fish by its passing shadow and to make the appropriate escape reactions. *Halicyclops* frequently swims away from the bottom of the pool and up into the water. This behaviour helps to distinguish *Halicyclops* from the harpacticoid copepods which were present in the same pool. Harpacticoids have elongate slender bodies with short antennules and move rapidly over the sediment and stones on the floor of the pool, rarely venturing up into the water. Harpacticoid copepods typically consume small particles of organic material that they find in the sediment; some scrape off and feed on the film of bacteria that is present on the surface of sediment particles.

Using baited traps laid in the cave lake we caught numerous larger crustaceans, mainly crabs and shrimps, which were attracted to the smell of the bait. Two kinds of crabs were found in the

Figure 385: Copepods are very small and it is best to pick them out from samples while they are still alive, using a field microscope.

submerged passages of the cave, a species of *Orcovita* and *Laubuanium trapezoideum* both provisionally identified by Professor Peter Ng, a crab expert from Singapore. There was also a surprising variety of shrimps species present; we found at least two species of the family Palaemonidae and three more species of the family Atyidae. Cave shrimps typically have extremely long antennae which are supplied with sensors that allow them to detect traces of chemicals as well as mechanical disturbances in the water caused by swimming of other organisms. They use these sensors to find their food and to detect possible predators.

The divers also swam holding hand-nets and collected samples down to a maximum depth of 28 m, into the deep saline water below the halocline (the zone of rapid salinity change marking the boundary between the upper freshwater and lower seawater layers). In the deep samples we found a single adult male copepod nearly 2 mm in length, belonging to the order Calanoida. Calanoid copepods dominate the plankton community of the world's oceans and this male is a member of the family Centropagidae. Centropagid copepods, particularly those belonging to the genus *Centropages*, are common in shallow coastal waters around the world but members of some other genera in the same family have colonised freshwater habitats in Australia and South America. The male we found in Loren Cave represents a new species of the marine genus *Centropages* (Fig. 386), most closely related to species described from Australian waters. This is the very first *Centropages* to be found in an anchialine cave, and it is an interesting discovery as it leads us to conclude that this *Centropages* probably colonised Loren Cave from the coastal waters surrounding Santo.

Centropages copepods feed on small particles like single celled algae and protozoans which they detect in the water and catch by grasping them with their finely branched mouthparts.

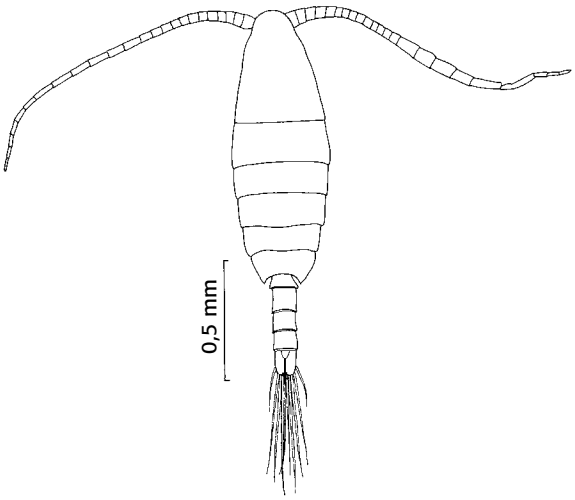
They typically have long paired antennules armed with fine sensitive hairs (setae) for detecting their food as well as for detecting the vibrations made by potential predators, such as swimming fish. This male has asymmetrical antennules, with the left hand antennule normal but the right one modified for grasping onto the female during mating.

About 50 m away from the entrance of Loren Cave is a small pool into which an active spring discharges water. Although it is about 30 m from the sea, at high tide the water flow is greatly reduced and the water is slightly brackish (3.2 parts per thousand). As well as being indirectly connected to the sea, this pool is probably also connected to the Loren Cave system. The floor of the pool is formed from coarse coral rubble and it is surrounded by trees. Samples taken by passing a hand net through the water in the pool (Fig. 387) and brushing it firmly across the surface of the stones contained a small amphipod shrimp, in large numbers. Amphipod shrimps are typically flattened from side to side and can be found on and under rocks and stones in most freshwater habitats around the world. The species found here, belongs to the family Sebidae and was described as *Seborgia sanctensis* in 2009.

The adult female of the new *Seborgia* species (Fig. 388) is just less than 2 mm in length. Specimens were observed alive under the stereo-microscope in the field laboratory and we found that the animals moved ventral side down, not upside-down or on one side. This posture is quite unusual for an amphipod, more closely resembling a typical isopod due to their slightly dorso-ventrally depressed body. The females also tended hold the hind end of the body (the pleon or abdomen) bent forwards underneath the anterior part (the pereon), giving the animal a short and "tail-less" appearance when seen in dorsal view. Female amphipods carry their developing embryos in a marsupium, or brood pouch, located ventrally under the body, and in this species each brooding female carried only two embryos in its brood pouch.

Figure 387: Fishing for tiny amphipod and tanaid shrimps using fine mesh plankton nets in the pool near Loren Cave.

The biogeography of *Seborgia* is remarkable. Even though this genus displays an extremely broad but discontinuous distribution, its members live only in subterranean waters. The ten species known thus far appear scattered in very localised sites across tropical-subtropical latitudes, stretching from an inland aquifer in Texas (USA) to anchialine habitats of the Andaman Islands, Vietnam, the Salomons, Loyalty Islands and Vanuatu. In trying to understand the distribution pattern of these species, we assume that they were all derived from shallow-water marine ancestors and that they are unable to disperse across wide and deep oceanic



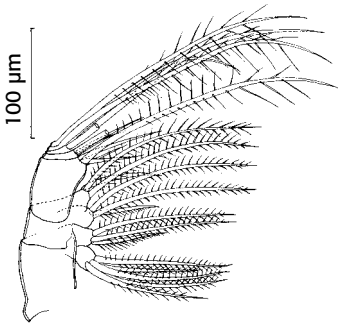


Figure 386: The adult male of a new species of *Centropages* — a calanoid copepod — with inset figure showing one of its specialised mouthparts used for catching the small particles that it feeds on. (Drawings by G. Boxshall).

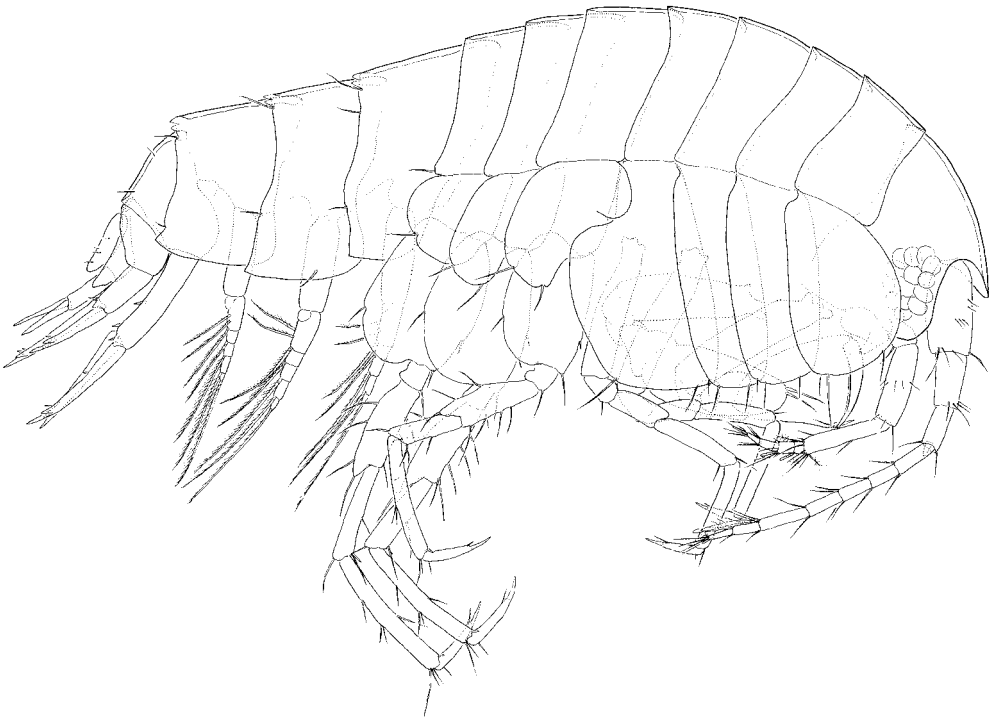


Figure 388: Side view of an adult female of the new species of tiny amphipod shrimp *Seborgia*, collected in the pool near Loren Cave. This female is 1.9 mm long. (Drawing by D. Jaume).

basins or continental subterranean waters. The fact that there are species located around the Gulf of Mexico occupying areas not covered by the sea at least since the Late Cretaceous, should be suggests this genus has an ancient origin. However, the existence of several species in the Indo-West Pacific leads us to infer that the origin of the genus is even older, perhaps Early Cretaceous, prior to the opening of the Atlantic, when the fragmentation of the ancient, shallow-water Tethys Sea commenced. This vanished sea once connected the South West Pacific through to the Caribbean Sea, and separated the former northern and southern supercontinents of Laurasia and Gondwana. Its shores were probably already populated by members of the genus *Seborgia*. It leads us to suggest that modern members of *Seborgia* are probably relicts of this ancient tropical shallow-water fauna.
Living in this same pool were many tanaid shrimps. Tanaids are small shrimps which, like the amphipods are characterised by having a ventral marsupium or brood pouch, within which the females carry their eggs and developing young. Tanaids, despite being so small (2-3 mm), have interesting sex lives with each adult male attempting to gather together a harem of numerous females with which to mate. In the pool the tanaids lived within a thick blackish mat of algae or filamentous bacteria that coated the surface of the submerged stones. Tanaids are rarely found in non-marine waters so this is an unusual and interesting discovery.

Loren Cave and its nearby pool contained a fascinating aquatic fauna including several species new to science. In the dry passages of the cave deep into the cave we also found a terrestrial crab (*Discoplax longipes*) which was eventually caught by hand. Its name refers to its relatively long legs (Fig. 389).

Figure 389: A terrestrial crab *Discoplax longipes* was found in dry passages deep inside Loren Cave.

Santo

The Natural History of

The islands of the Pacific are renowned for the high levels of endemism of, and threats to, their unique faunas and floras. Espiritu Santo, affectionately known simply as Santo, is an island of superlatives: the largest and highest in Vanuatu, Santo is an extraordinary geographical and cultural microcosm, combining reefs, caves, mountains, satellite islands, and a history of human habitation going back 3 000 years. In the spirit of famous voyages of discovery of the past, the Santo 2006 expedition brought together over 150 scientists, volunteers and students originating from 25 countries. With contributions by more than 100 authors, *The Natural History of Santo* is a lavishly illustrated homage to the biodiversity of this "planet-island". Bridging the gap between scientific knowledge and conservation and education, *The Natural History of Santo* was written with local stakeholders as well as armchair naturalists from all over the world in mind.

Les îles du Pacifique sont célèbres pour le très haut niveau d'endémisme et la grande vulnérabilité de leurs faunes et de leurs flores. L'île d'Espiritu Santo, ou Santo, cumule les superlatifs : la plus grande et la plus haute du Vanuatu, Santo est un extraordinaire microcosme géographique et culturel, avec récifs, grottes, montagnes, îles et îlots satellites, et une occupation humaine qui remonte à 3 000 ans. Renouant avec l'esprit des "Grandes Expéditions Naturalistes", l'expédition Santo 2006 avait mobilisé sur le terrain plus de 150 scientifiques, bénévoles et étudiants de 25 pays. Petit tour de force éditorial avec plus de 100 auteurs, ce *Natural History of Santo* est un éloge de la biodiversité de cette "île-planète". À la fois beau livre richement illustré et bilan des connaissances scientifiques, *The Natural History of Santo* se veut un outil de connaissance pour sa conservation durable. Il s'adresse autant aux acteurs locaux du développement et de l'éducation qu'aux naturalistes du monde entier.









MUSEUM NATIONAL D'HISTOIRE NATURELLE

IRD
Institut de recherche pour le développement

PRO NATURA INTERNATIONAL

ISSN 1281-6213

ISBN MNHN : 978-2-85653-627-8
ISBN IRD : 978-2-7099-1708-7

9 782856 536278

Prix : 59 € TTC