



*Encyclopedia of Caves*  
AND *Karst Science*

*John Gunn, Editor*

# *Encyclopedia of Caves and Karst Science*

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*Encyclopedia of Caves and Karst  
Science*

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Front cover illustrations:

Looking out of the 100 m deep “Lost World” entrance to Mangapu Cave, Waitomo, New Zealand. (Photo by John Gunn) Stalactites and stalagmites in “Castle Grotto”, Hollow Hill Cave, Waitomo, New Zealand. (Photo by John Gunn) A fine polygonal karst of dolines each about 100 m across in the gypsum karst of Sivas, Turkey. (Photo by Tony Waltham) Camel cricket (*Ceuthophilus cunicularis*), a troglone in central Texas caves. (Photo by Steve Taylor)

Back cover illustrations:

Solution pocket developed along a joint in the ceiling of Gruta de Torrinha, Brazil. (Photo by John Gunn) Classic hand silhouettes in the cave of Ujung Bulu in Sulawesi, Indonesia. (Photo by Tony Waltham) The troglomorphic crab *Cancrocaeca xenomorpha*. (Photo by Didier Rigal) Tower karst near Guilin, China. (Photo by Tony Waltham)

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# CONTENTS

Board of Advisers	ii
Editor's Introduction	vi
Alphabetical List of Entries	xi
Thematic List of Entries	xx
<b>Encyclopedia of Caves and Karst Science</b>	<b>1</b>
Notes on Contributors	1683
Index	1724

## EDITOR'S INTRODUCTION

This is the first encyclopedia of Caves and Karst Science and provides a unique, comprehensive, and authoritative reference source that can be used both by subject-specialists who wish to obtain information from outside of their immediate area of knowledge and by non-specialists who wish to gain an understanding of the diverse and multi-disciplinary nature of caves and karst science. It will also be useful to cavers who wish to learn more about the environments in which they undertake their sport and to conservationists, engineers, planners, and others who are charged with developing and managing in a sustainable manner complex karst environments. The 351 entries were selected by a multi-disciplinary Advisory Board of leading scholars, all of whom are cavers. The entries cover a wide range of topics and each entry also includes both references and further reading to enable deeper study. While not intended as an atlas, there is a wide geographical coverage of all scientifically important karst areas, the level of detail (continent, country, region, or individual site or cave) reflecting the Advisory Board's opinions as to the importance of the locality. It is the first encyclopedia to cover all the disciplines involved in cave and karst science—archaeology, biology, chemistry, ecology, geology, geomorphology, history, hydrology, paleontology, and physics as well as exploration, survey, photography, literature, and art. The resources found in caves and in karst areas are outlined, including the underground water that supplies around a quarter of the world's population. Caves and karst environments are fragile and special places so there is appropriate consideration of conservation and management, including protected areas. Contributors are all leading authorities in their area and all entries were subject to review by the Editor, members of the Advisory Board, or other subject specialists.

The term "cave" is commonly applied to natural openings, usually in rocks, that are large enough to permit entry by humans. The term is also sometimes applied to openings constructed by humans but this encyclopedia is confined to natural caves. The majority of these form parts of a wider landscape known as karst, defined by Derek Ford in this volume as "terrain with distinctive hydrology and landforms arising from the combination of high rock solubility and well-developed solution channel (secondary) porosity underground". As well as distinctive landforms and drainage, karst areas have distinctive biological attributes and provide a wide range of resources, together with particular problems for humans who wish to exploit them. Caves are natural museums, preserving important archaeological evidence as well as sediments and deposits that provide clues to past environments. They also present many challenges for explorers. Although several thousand kilometres of cave have been explored, it is certain that many passages have yet to be entered and these represent the only truly unknown parts of the Earth outside of the oceans. Each year several well-equipped teams undertake major expeditions to discover new cave but it remains the case that individuals and groups working steadily on smaller projects also succeed

in becoming the first humans ever to set foot in a particular passage. While the thrill of discovery drives many, caving has also become a popular recreational activity in many countries and many thousands more enjoy visits to commercially developed tourist caves.

To discover new cave it is usually necessary to have an understanding of the scientific contexts in which caves are formed while the discovery of new caves provides opportunities for new scientific discoveries. This synergy between science and exploration is one of the factors that makes the study of caves and karst so exciting. Caves are widely distributed, from within the Arctic Circle to the Antarctic and from below sea level to altitudes of several thousand metres. Karst is also widespread and it has been estimated that about a quarter of the world's population draw their water from karst rocks. Cave and karst science is multi-disciplinary, being undertaken by archaeologists, biologists, chemists, ecologists, geologists, geographers, historians, hydrologists, and physicists. It is also applied as conservationists, consultants, engineers, environmental managers, and planners require an understanding of the special characteristics of karst in order to manage and sustainably develop the many resources of karst areas.

### **Choosing the entries and authors**

Given the above it is perhaps surprising that this is the first encyclopedia devoted to Caves and Karst Science. As such it seeks to describe all of the world's important karst areas and the most important caves. However, it is not an atlas and coverage is not, and could not have been, exhaustive. Instead, an initial list of sites was drawn up with the assistance of an appointed board of advisers who have very wide subject expertise and caving experience (see page ii and Notes on Contributors). The list was then widely publicized and suggestions for additional/ alternative sites sought from the cave and karst community before a final list was agreed. This comprises 100 entries on the world's most significant cave and karst sites, and regional discussions of the world's largest areas of caves and karst. In addition to assisting in the choice of important sites and areas the Advisory Board helped to draw up a list of topical entries considered to be of primary importance to their particular branch of science. Again there was wide discussion of the lists both between the Advisory Board and also via the encyclopedia web site.

Following the consultative process a final list was produced broken down by themes, although some entries fall into more than one field:

*Archaeology, Art in Caves and Paleontology:* 29 entries, from dating methods to major sites, and regional discussions of art in caves

*Biospeleology:* 78 entries on ecology and ecological processes, habitats, cave ecology & man, subterranean fauna, subterranean biodiversity, regional faunas, the world's richest cave faunas, evolution of subterranean fauna, and important subterranean taxa

*Caves and Caving:* 23 entries on cave media, caving, and the uses of caves

*Cave and Karst Regions:* 75 entries on the world's largest and most important areas of caves and karst together with 28 entries on individual caves and cave systems



*Conservation and Management:* 19 entries on topics such as environmental impact assessment, groundwater pollution, and tourist caves

*Geoscience:* 78 entries on caves and speleogenesis, climate of caves, deposits in caves, karst settings and landforms, processes and techniques, and pseudokarst

*History:* 27 entries on key events and personalities in the history of cave and karst science together with the history of cave exploration in particular regions of the world

*Resources and Development:* 22 entries on the resources of karst regions and some of the key problems in their exploitation

The next stage was to allocate a word limit for each entry and to seek suitable authors. Most entries were planned at 1000 words, although it was recognized that some would need to be longer, up to a maximum of 4000 words. The Advisory Board suggested some possible authors who were invited individually. Other authors were approached in more general terms and invited to offer to write entries that remained unassigned. The objective was to include the leading authorities on each topic from a range of different countries. All entries were read by the Editor and by selected members of the Advisory Board or other reviewers.

The finished work has a total of 351 entries on a wide range of topics. A thematic list, an extensive index, and cross-references are provided to help readers explore themes systematically. All the entries have bibliographies and/or suggestions for further reading, pointing the reader toward original research and textbooks that augment the overview approach to which an encyclopedia is inevitably limited. Most entries have either line diagrams expanding on explanations given in the text, or photographs illustrating type examples. There is also a section of colour pages illustrating the range of themes.

## **Entries and structure**

The 351 entries appear in alphabetical order and are of several kinds (for the complete list of entries see page xi). Although each entry is self-contained, the links between entries can be explored in a number of ways. The Thematic List on page xv groups the entries within broad and more specific categories and provides a useful summary of related entries. Almost all of the entries have “See Also” links, both within the text and at the end of the entry, so the reader is encouraged to browse outwards from a starting node. Finally the Index provides a detailed listing of topics, organisms, and sites or countries that do not have their own entry but are discussed within the context of broader entries.

One aspect which came as a surprise to the Editor was the difficulty of deciding the exact titles of several entries and hence the point at which they would appear in the alphabetic listing. Following much discussion it was decided that all organisms would appear alphabetically by scientific name (hence “Chiroptera” not “Bats”, and “Pisces” not “Fish”) and that where the common name for a site commences with a local word for a cave or geographical feature then the entry should be under the location (hence “Draenen, Ogof Draenen, Wales” and “Encantado, Sistema del Rio, Puerto Rico”). We recognize that this may initially cause some confusion but if you cannot find an entry on a topic you expected to find you should be able to use the Thematic List or Index to locate the title of

the entry that contains the topic you are looking for. Thus, for the examples above the Index will contain cross references for Bats, Fish, Ogof Draenen, Rio Encantado, and Sistema del Rio Encantado.

### **Acknowledgements**

My thanks are due to all the contributors who provided excellent material, adhered to length guidelines and submitted their work on time. I also thank those who caused me angst by submitting overlong scripts that needed serious pruning and those from whom the script was finally extricated months after the deadline. You know who you are...

Particular thanks are due to fellow cavers who supplied photographs for no reward other than seeing their work in print. Commitment to the wider good of caving is one of the marks of our sport.

The Editorial Advisory Board played a vitally important role in helping to decide what entries should be included and who should write them, as well as in reviewing the submitted essays. Special thanks are due to Paul Wood who reviewed all of the biology entries, many of which were written by scientists who do not have English as their mother tongue. Also to Tony Waltham who reviewed all of the entries on individual cave systems and on the world's largest and most important areas of caves and karst. Tony also edited many of the maps and photographs to ensure consistency and provided new maps and many photographs for entries where the author was unable to do so. As we approached the production phase Tony also provided a great deal of constructive advice on the choice of illustrative material, particularly in the colour section.

From start to finish the project has been overseen in an incredibly efficient manner by Gillian Lindsey, first at Fitzroy Dearborn and then at Routledge in New York. Without her commitment and drive the work may never have come to fruition and on behalf of myself and the members of the Advisory Board I offer her our very grateful thanks.

Special thanks for personal support during the editorial process are due to Ernest, Doreen, Cathy, Eilíse, and Owain Gunn, to Paul Somers and Lian, caver of the future, and to Sarah Davies.



# ALPHABETICAL LIST OF ENTRIES

## A

### Accidents and Rescue

Adaptation: Behavioural

Adaptation: Eyes

Adaptation: Genetics

Adaptation: Morphological (External)

Adaptation: Morphological (Internal)

Adaptation: Physiological

Africa, North

Africa, South: Archaeological Caves

Africa, Sub-Saharan

Africa: Biospeleology

Aggtelek and Slovak Karst, Hungary-Slovakia

Aggtelek Caves, Hungary-Slovakia: Archaeology

Akiyoshi-dai Karst and Caves, Japan

Alpine Karst

Altamira Cave, Spain: Archaeology

America, Central

America, Central and Caribbean Islands: Biospeleology

America, Central: Archaeological Caves

America, North: Archaeological Caves

America, North: Biospeleology

America, North: History

America, South

America, South: Biospeleology

America, South: History

Amphibia

Amphibia: *Proteus*

Anchialine Habitats

Annelida

Antarctica

Appalachian Mountains, United States

Arachnida

Arachnida: Aranae (Spiders)

Arachnida: Acari (Mites and Ticks)

Arachnida: Minor Groups

Archaeologists

Archaeology of Caves: History

Ardèche Caves, France: Archaeology

Art in Caves  
Art in Caves: History  
Art Showing Caves  
Art: Cave Art in Australasia  
Art: Cave Art in Europe  
Art: Cave Art in the Americas  
Asia, Central  
Asia, Northeast  
Asia, Northeast: History  
Asia, Southeast  
Asia, Southeast Islands  
Asia, Southeast: Archaeological Caves  
Asia, Southeast: Biospeleology  
Asia, Southeast: History  
Asia, Southwest  
Asiago Plateau, Italy  
Atapuerca Caves, Spain: Archaeology  
Australia  
Australia: Archaeological and Paleontological Caves  
Australia: Biospeleology  
Australia: History  
Aves (Birds)

## **B**

Bambuí Karst, Brazil  
Bauxite Deposits in Karst  
Bear Rock Karst, Canada  
Belgium: Archaeological Caves  
Belize River Caves  
Biodiversity in Hypogean Waters  
Biodiversity in Terrestrial Cave Habitats  
Biofilms  
Biokarstification  
Biology of Caves  
Biospeleologists  
Blue Holes of the Bahamas  
Boa Vista, Toca, Brazil  
Books on Caving  
Britain and Ireland: Archaeological and Paleontological Caves  
Britain and Ireland: Biospeleology  
Britain and Ireland: History  
Burials in Caves  
Burren Glaciokarst, Ireland

## C

Calcareous Alps, Austria  
Canada  
Canary Islands: Biospeleology  
Cape Range, Australia: Biospeleology Carbon Dioxide-enriched Cave Air  
Carbonate Karst  
Carbonate Minerals: Precipitation  
Caribbean Islands  
Caribbean Islands: History  
Carlsbad Cavern and Lechuguilla Cave, United States  
Carmel Caves, Israel: Archaeology  
Castleguard Cave, Canada  
Caucasus, Georgia  
Caves  
Caves in Fiction  
Caves in History: The Eastern Mediterranean  
Cerknica Polje, Slovenia: History  
Cheju-do Lava Caves, South Korea  
Chemistry of Natural Karst Waters  
Chillagoe and Mitchell-Palmer Karsts, Australia  
China  
China: Archaeological Caves  
Chiroptera (Bats)  
Climate of Caves  
Coastal Karst  
Cockpit Country Cone Karst, Jamaica  
Colonization  
Communications in Caves  
Condensation Corrosion  
Cone Karst  
Conservation: Cave Biota  
Conservation: Protected Areas  
Construction on Karst  
Crevice Caves  
Crimea, Ukraine  
Crustacea  
Crustacea: Amphipoda  
Crustacea: Copepoda  
Crustacea: Decapoda (Shrimps, Crayfish, Crabs)  
Crustacea: Isopoda (Aquatic)  
Crustacea: Isopoda: Oniscidea (Woodlice)  
Crustacea: Ostracoda  
Crustacea: Syncarida  
Cuba  
Cupp-Coutunn Cave, Turkmenistan

## **D**

- Dams and Reservoirs on Karst
- Dating Methods: Archaeological
- Dating of Karst Landforms
- Dent de Crolles Cave System, France
- Di Feng Dong, China
- Dinaric Karst
- Dinaric Karst: Biospeleology
- Dinaride Poljes
- Disease
- Dissolution: Carbonate Rocks
- Dissolution: Evaporite Rocks
- Dissolution: Silicate Rocks
- Diving in Caves
- Dolines
- Draenen, Ogor Draenen, Wales

## **E**

- Edwards Aquifer, United States
- Edwards Aquifer, United States: Biospeleology
- Encantado, Sistema del Rio, Puerto Rico
- Entrance Habitats
- Environmental Impacts Assessment
- Erosion Rates: Field Measurements
- Erosion Rates: Theoretical Models
- Europe, Alpine
- Europe, Balkans and Carpathians
- Europe, Central
- Europe, Central: Archaeological Caves
- Europe, Central: History
- Europe, Mediterranean
- Europe, Mediterranean: Archaeological and Paleontological Caves
- Europe, North
- Evaporite Karst
- Evolution of Hypogean Fauna
- Exploration Societies
- Exploring Caves
- Extraterrestrial Caves

## **F**

- Films in Caves
- Floral Resources
- Fluviokarst
- Folklore and Mythology
- Food Resources
- Forests on Karst

France: Biospeleology  
France: History  
France, Southern Massif Central  
Frasassi Caves, Italy

## **G**

Geophysical Detection of Caves and Karstic Voids  
Geoscientists  
Gibraltar Caves: Archaeology  
Glacier Caves and Glacier Pseudokarst  
Glacierized and Glaciated Karst  
Golondrinas and the Giant Shafts of Mexico  
Grand Canyon, United States  
Groundwater in Karst  
Groundwater in Karst: Borehole Hydrology  
Groundwater in Karst: Conceptual Models  
Groundwater in Karst: Mathematical Models  
Groundwater Pollution: Dispersed  
Groundwater Pollution: Point Sources  
Groundwater Pollution: Remediation  
Groundwater Protection  
Guano  
Gunpowder

## **H**

Ha Long Bay, Vietnam  
Hawaii Lava Tube Caves, United States  
Hawaiian Islands: Biospeleology  
Highways on Karst  
Hölloch, Switzerland  
Hongshui River Fengcong Karst, China  
Huanglong and Jiuzhaigou, China  
Huatla Cave System, Mexico  
Human Occupation of Caves  
Hydraulics of Caves  
Hydrocarbons in Karst

## **I**

Ice in Caves  
Inception of Caves  
Indian Subcontinent  
Insecta: Apterygota  
Insecta: Coleoptera (Beetles)  
Insecta: Pterygota  
Interstitial Habitats (Aquatic)  
Interstitial Habitats (Terrestrial)



Invertebrates: Minor Groups

Iran

## **J**

Jeita Cave, Lebanon

Journals on Caves

## **K**

Kaijende Arête and Pinnacle Karst, Papua New Guinea

Kanin Massif, Slovenia-Italy

Karren

Karst

Karst Evolution

Karst Hydrology: History

Karst Resources and Values

Karst Water Resources

Khammouan, Laos-Vietnam

Kras, Slovenia

Krubera Cave, Georgia

## **L**

Limestone as a Mineral Resource

Littoral Caves

## **M**

Madagascar

Mammoth Cave Region, United States

Mammoth Cave, United States: Biospeleology

Marine Cave Habitats

Mendip Hills, England

Microbial Processes in Caves

Microorganisms in Caves

Military Uses of Caves

Minerals in Caves

Mineral Deposits in Karst

Mollusca

Mona, Puerto Rico

Monitoring

Morphology of Caves

Morphometry of Caves

Morphometry of Karst

Movile Cave, Romania

Mulu, Sarawak

Music in and about Caves

Myriapoda (Centipedes and Millipedes)

## **N**

- Nahanni Karst, Canada
- Nakanai Caves, Papua New Guinea
- New Zealand
- Nullarbor Plain, Australia

## **O**

- Organic Resources in Caves
- Organisms: Classification
- Ornamental Use of Limestone

## **P**

- Paleoenvironments: Clastic Cave Sediments
- Paleoenvironments: Speleothems
- Paleokarst
- Paleontology: Animal Remains in Caves
- Paleotectonics from Speleothems
- Palynology
- Pamukkale, Turkey
- Paragenesis
- Patagonia Marble Karst, Chile
- Patterns of Caves
- Peak District, England
- Photographing Caves
- Phytokarst
- Picos de Europa, Spain
- Pierre Saint-Martin, France-Spain
- Pinega Gypsum Caves, Russia
- Piping Caves and Badlands Pseudokarst
- Pisces (Fishes)
- Pisces (Fishes): Amblyopsidae
- Plitvice Lakes, Croatia
- Poljes
- Ponors
- Postojna-Planina Cave System, Slovenia
- Postojna Planina Cave System: Biospeleology
- Pseudokarst

## **Q**

- Quarrying of Limestone
- Quartzite Caves of South America

## **R**

- Radiolocation
- Radon in Caves
- Ramsar Sites—Wetlands of International Importance

Recreational Caving  
Religious Sites  
Restoration of Caves and Speleothem Repair  
Russia and Ukraine

## S

Salukkan Kallang, Indonesia: Biospeleology  
Sediments: Allochthonous Clastic  
Sediments: Autochthonous Clastic  
Sediments: Biogenic  
Sedom Salt Karst, Israel  
Selma Plateau Caves, Oman  
Sewu Cone Karst, Java  
Shanidar Cave, Iraq: Archaeology  
Shilin Stone Forest, China  
Siberia, Russia  
Siebenhengste, Switzerland  
Silicate Karst  
Škocjanske Jama, Slovenia  
Sof Omar Cave, Ethiopia  
Soils on Carbonate Karst  
Soil Erosion and Sedimentation  
Solution Breccias  
Soviet Union: Speleological History  
Spannagel Cave, Austria  
Speciation  
Speleogenesis  
Speleogenesis Theories: Early  
Speleogenesis Theories: Post-1890  
Speleogenesis: Coastal and Oceanic Settings  
Speleogenesis: Computer Models  
Speleogenesis: Deep-Seated and Confined Settings  
Speleogenesis: Unconfined Settings  
Speleologists  
Speleothem Studies: History  
Speleothems: Carbonate  
Speleothems: Evaporite  
Speleothems: Luminescence  
Speleotherapy  
Springs  
Stamps and Postcards  
Stripe Karst  
Subterranean Ecology  
Subterranean Habitats  
Sulfide Minerals in Karst  
Surveying Caves

## Syngenetic Karst

### T

#### Talus Caves

Thermal Water Habitats

Tourism and Caves: History

Tourist Caves

Tourist Caves: Air Quality

Tourist Caves: Airborne Debris

Tourist Caves: Algae and Lampenflora

Tower Karst

Travertine

Tunnelling and Underground Dams in Karst

Turkey

### U

#### Ukraine Gypsum Caves and Karst

United States of America

### V

#### Valleys in Karst

Vercors, France

Vézère Archaeological Caves, France

Villa Luz, Cueva de, Mexico

Vjetrenica, Bosnia-Herzegovina: Biospeleology

Volcanic Caves

Vulcanospeleology: History

### W

#### Walsingham Caves, Bermuda: Biospeleology

Water Tracing

Water Tracing: History

Wilderness

Wind and Jewel Caves, United States

World Heritage Sites

### Y

#### Yangshuo Karst, China

Yorkshire Dales, England

Yucatán Phreatic, Mexico

# THEMATIC LIST OF ENTRIES

## **Archaeology, Paleontology, and Cave Art**

Africa, South: Archaeological Caves

Aggtelek Caves, Hungary-Slovakia: Archaeology

Altamira Cave, Spain: Archaeology

America, Central: Archaeological Caves

America, North: Archaeological Caves

Ardèche Caves, France: Archaeology

Archaeologists

Archaeology of Caves: History

Art in Caves

Art in Caves: History

Art: Cave Art in Australasia

Art: Cave Art in Europe

Art: Cave Art in the Americas

Asia, Southeast: Archaeological Caves

Atapuerca Caves, Spain: Archaeology

Australia: Archaeological and Paleontological Caves

Belgium: Archaeological Caves

Britain and Ireland: Archaeological and Paleontological Caves

Burials in Caves

Carmel Caves, Israel: Archaeology

China: Archaeological Caves

Dating Methods: Archaeological

Europe, Central: Archaeological Caves

Europe, Mediterranean: Archaeological and Paleontological Caves

Gibraltar Caves: Archaeology

Human Occupation of Caves

Paleontology: Animal Remains in Caves

Shanidar Cave, Iraq: Archaeology

Vézère Archaeological Caves, France

## **Biospeleology (Speleobiology)**

*Ecology and Ecological Processes*

Biodiversity in Hypogean Waters

Biodiversity in Terrestrial Cave Habitats

Biofilms

Biology of Caves

Biokarstification

Food Resources

Guano

Microorganisms in Caves

Paleontology: Animal Remains in Caves

Sediments: Biogenic

Subterranean Ecology

*Habitats*

Anchialine Habitats

Entrance Habitats

Interstitial Habitats (Aquatic)

Interstitial Habitats (Terrestrial)

Marine Cave Habitats

Subterranean Habitats

Thermal Water Habitats

*Cave Ecology and Man*

Biospeleologists

Conservation: Cave Biota

Folklore and Mythology

Groundwater Pollution: Dispersed

Groundwater Pollution: Point Source

Tourist Caves: Algae and Lampenflora

*Regional Subterranean Faunas*

Africa: Biospeleology

America, Central and Caribbean Islands: Biospeleology

America, North: Biospeleology

America, South: Biospeleology

Asia, Southeast: Biospeleology

Australia: Biospeleology

Britain and Ireland: Biospeleology

Canary Islands: Biospeleology

Dinaric Karst: Biospeleology

France: Biospeleology

*Richest Cave Faunas*

Cape Range, Australia: Biospeleology

Edwards Aquifer, United States: Biospeleology

Hawaiian Islands: Biospeleology

Mammoth Cave, United States: Biospeleology

Mobile Cave, Romania

Postojna-Planina Cave System, Slovenia: Biospeleology

Salukkan Kallang, Indonesia: Biospeleology

Vjetrenica, Bosnia-Herzegovina: Biospeleology

Walsingham Caves, Bermuda: Biospeleology

*Evolution of Subterranean Fauna*

Adaptation: Behavioural

Adaptation: Eyes

Adaptation: Genetics

Adaptation: Morphological (External)

Adaptation: Morphological (Internal)  
Adaptation: Physiological  
Colonization  
Evolution of Hypogean Fauna  
Organisms: Classification  
Speciation  
*Important Subterranean Taxa*  
Amphibia  
Amphibia: *Proteus*  
Annelida  
Arachnida  
Arachnida: Acari (Mites)  
Arachnida: Araneae (Spiders)  
Arachnida: Minor Groups  
Aves (Birds)  
Chiroptera (Bats)  
Crustacea  
Crustacea: Amphipoda  
Crustacea: Copepoda  
Crustacea: Decapoda (Shrimps, Crayfish, Crabs)  
Crustacea: Isopoda (Aquatic)  
Crustacea: Isopoda-Oniscidea (Woodlice)  
Crustacea: Ostracoda  
Crustacea: Syncarida  
Insecta: Apterygota  
Insecta: Coleoptera (Beetles)  
Insecta: Pterygota  
Invertebrates: Minor Groups  
Mollusca  
Myriapoda (Centipedes and Millipedes)  
Pisces (Fishes)  
Pisces (Fishes): Amblyopsidae

## **Caves and Caving**

### *Cave Media*

Art Showing Caves  
Books on Caves  
Caves in Fiction  
Films in Caves  
Folklore and Mythology  
Journals on Caves  
Music about and in Caves  
Stamps and Postcards  
*Caving*  
Accidents and Rescue  
Communications in Caves

Diving in Caves  
Exploring Caves  
Photographing Caves  
Radiolocation  
Recreational Caving  
Surveying Caves  
*Uses of caves*  
Burials in Caves  
Human Occupation of Caves  
Military Uses of Caves  
Music about and in Caves  
Religious Sites  
Speleotherapy  
Tourist Caves

## **Caves and Karst Regions**

### *Caves and Cave Systems*

Belize River Caves  
Blue Holes of Bahamas  
Boa Vista, Brazil  
Carlsbad Cavern and Lechuguilla Cave, United States  
Castleguard Cave, Canada  
Cheju-do Lava Caves, South Korea  
Cupp-Coutunn Cave, Turkmenistan  
Dent de Crolles Cave System, France  
Di Feng Dong, China  
Draenen, Ogor Draenen, Wales  
Encantado, Sistema del Rio, Puerto Rico  
Frasassi Caves, Italy  
Golondrinas and the Giant Shafts of Mexico  
Hawaii Lava Tube Caves, United States  
Hölloch, Switzerland  
Huatla Cave System, Mexico  
Jeita Cave, Lebanon  
Kruber Cave, Georgia  
Mammoth Cave Region, United States  
Movile Cave, Romania  
Nakanai Caves, Papua New Guinea  
Postojna-Planina Cave System, Slovenia  
Siebenhengste, Switzerland  
Škocjanske Jama, Slovenia  
Sof Omar Cave, Ethiopia  
Spannagel Cave, Austria  
Villa Luz, Cueva de, Mexico  
Wind and Jewel Caves, United States

### *Karst Regions*



Africa, North  
Africa, Sub-Saharan  
Aggtelek and Slovak Karst, Hungary-Slovakia  
Akiyoshi-dai, Japan  
America, Central  
America, South  
Antarctica  
Appalachian Mountains, United States  
Asia, Central  
Asia, Northeast  
Asia, Southeast  
Asia, Southeast Islands  
Asia, Southwest  
Asiago Plateau, Italy  
Australia  
Bambuí Karst, Brazil  
Bear Rock Karst, Canada  
Burren Glaciokarst, Eire  
Calcareous Alps, Austria  
Canada  
Caribbean Islands  
Caucasus, Georgia  
Chillagoe and Mitchell-Palmer Karsts, Australia  
China  
Cockpit Country Cone Karst, Jamaica  
Crimea, Ukraine  
Cuba  
Dinaric Karst  
Dinaride Poljes  
Edwards Aquifer and the Texas Karst, United States  
Europe, Alpine  
Europe, Balkans and Carpathians  
Europe, Central  
Europe, Mediterranean  
Europe, North  
France, Southern Massif Central  
Grand Canyon, United States  
Ha Long Bay, Vietnam  
Hongshui River Fengcong Karst, China  
Huanglong and Jiuzhaigou, China  
Indian Subcontinent  
Iran  
Kaijende Arete and Pinnacle Karst, Papua New Guinea  
Kanin Massif, Slovenia-Italy  
Khammouan, Laos-Vietnam  
Kras, Slovenia

Madagascar  
Mendip Hills, England  
Mona, Puerto Rico  
Mulu, Sarawak  
Nahanni Karst, Canada  
New Zealand  
Nullarbor Plain, Australia  
Pamir and Tien Shan Karst, Asia  
Pamukkale, Turkey  
Patagonia Marble Karst, Chile  
Peak District, England  
Picos de Europa, Spain  
Pierre Saint-Martin, France-Spain  
Pinega Gypsum Caves, Russia  
Plitvice Lakes, Croatia  
Quartzite Caves of South America  
Russia and Ukraine  
Sedom Salt Karst, Israel  
Selma Plateau Caves, Oman  
Sewu Cone Karst, Java  
Shilin Stone Forest, China  
Siberia, Russia  
Turkey  
Ukraine Gypsum Caves and Karst  
United States of America  
Vercors, France  
Yangshuo Karst, China  
Yorkshire Dales, England  
Yucatán Phreas, Mexico

## **Conservation and Management**

Carbon Dioxide-enriched Cave Air

Conservation: Cave Biota

Conservation: Protected Areas

Environmental Impact Assessment

Groundwater Pollution: Dispersed

Groundwater Pollution: Point Source

Groundwater Pollution: Remediation

Groundwater Protection

Karst Resources and Values

Monitoring

Ramsar Sites—Wetlands of International Importance

Religious Sites

Restoration of Caves and Speleothem Repair

Tourist Caves

Tourist Caves: Air Quality

Tourist Caves: Airborne Debris  
Tourist Caves: Algae and Lampenflora  
Wilderness  
World Heritage Sites

## **Geoscience**

### *Caves and Speleogenesis*

Caves  
Extraterrestrial Caves  
Hydraulics of Caves  
Inception of Caves  
Morphology of Caves  
Morphometry of Caves  
Paragenesis  
Patterns of Caves  
Speleogenesis  
Speleogenesis: Coastal and Oceanic Settings  
Speleogenesis: Computer Models  
Speleogenesis: Deep-seated and Confined Settings  
Speleogenesis: Unconfined Settings  
Speleogenesis Theories: Early  
Speleogenesis Theories: Post-1890

### *Deposits in Caves*

Carbonate Minerals: Precipitation  
Ice in Caves  
Minerals in Caves  
Palaeoenvironments: Clastic Sediments  
Palaeoenvironments: Speleothems  
Palynology  
Sediments: Allochthonous Clastic  
Sediments: Autochthonous Clastic  
Sediments: Biogenic  
Speleothems: Carbonate  
Speleothems: Evaporite  
Speleothems: Luminescence

### *Karst Geomorphology*

Alpine Karst  
Carbonate Karst  
Coastal Karst  
Cone Karst  
Dolines  
Evaporite Karst  
Fluviokarst  
Glaciated and Glacierized Karst  
Karren  
Karst

Karst Evolution  
Morphometry of Karst  
Paleokarst  
Phytokarst  
Poljes  
Ponors  
Silicate Karst  
Solution Breccias  
Springs  
Stripe Karst  
Syngenetic Karst  
Tower Karst  
Travertine  
Valleys in Karst  
*Processes and Techniques*  
Biokarstification  
Carbon Dioxide-enriched Cave Air  
Chemistry of Natural Karst Waters  
Climate of Caves  
Condensation Corrosion  
Dating of Karst Landforms  
Dissolution: Carbonate Rocks  
Dissolution: Evaporite Rocks  
Dissolution: Silicate Rocks  
Erosion Rates: Field Measurements  
Erosion Rates: Theoretical Models  
Geophysical Detection of Caves and Karstic Voids  
Groundwater in Karst  
Groundwater in Karst: Borehole Hydrology  
Groundwater in Karst: Conceptual Models  
Groundwater in Karst: Mathematical Models  
Microbial Processes in Caves  
Palaeotectonics from Speleothems  
Radon in Caves  
Water Tracing  
*Pseudokarst*  
Crevice Caves  
Glacier Caves and Glacier Pseudokarst  
Littoral caves  
Piping Caves and Badlands Pseudokarst  
Pseudokarst  
Talus Caves  
Volcanic Caves

## **History**

America, North: History

America, South: History  
Archaeologists  
Archaeology of Caves: History  
Art in Caves: History  
Asia, Northeast: History  
Asia, Southeast: History  
Australia: History  
Biospeleologists  
Britain and Ireland: History  
Caribbean Islands: History  
Caves in History: The Eastern Mediterranean  
Cerknica Polje, Slovenia: History  
Europe, Central: History  
Exploration Societies  
France: History  
Geoscientists  
Gunpowder  
Karst Hydrology: History  
Soviet Union: Speleological History  
Speleogenesis Theories: Early  
Speleogenesis Theories: Post-1890  
Speleologists  
Speleothem Studies: History  
Tourism and Caves: History  
Vulcanospeleology: History  
Water Tracing: History

## **Resources and Development**

Bauxite Deposits in Karst  
Construction on Karst  
Dams and Reservoirs on Karst  
Disease  
Floral Resources  
Forests on Karst  
Guano  
Gunpowder  
Highways on Karst  
Hydrocarbons in Karst  
Karst Resources and Values  
Karst Water Resources  
Limestone as a Mineral Resource  
Mineral Deposits in Karst  
Organic Resources in Caves  
Ornamental Use of Limestone  
Quarrying of Limestone  
Religious Sites

Soils on Carbonate Karst  
Soil Erosion and Sedimentation  
Sulfide Minerals in Karst  
Tunnelling and Underground Dams in Karst

# A

## ACCIDENTS AND RESCUE

Cave exploration is, by its nature, a potentially hazardous activity, although the relative risk of an accident, and its severity, clearly vary from cave to cave. In all but the simplest of cases, rescue of an injured person from a cave poses problems that are different from those encountered on the surface. A cave is a relatively hostile environment in which to perform a rescue: it is completely dark beyond the entrance zone and there may be other potential hazards, including water, low temperatures, constricted passages, and vertical shafts. Hence, there is a need for specialist rescue teams who are aware of the latest rescue techniques.

The French Cave Rescue Organization has records that have been kept from the early 1900s but it is believed that the world's first formally organized cave rescue team was founded in Yorkshire, England, in 1934 (Eyre & Frankland, 1988). At present, over 20 nations have active cave rescue organizations. The International Cave Rescue Commission within the International Union of Speleology provides a forum for cave rescue organizations to communicate with each other at their congresses and through the internet at <http://netdial.caribe.net/~emercado/uis.htm>.

Rescue organizations have training seminars and extensive practice rescue from caves. At the training seminars, often international events, experience gathered from real and practice rescues is exchanged and rescue equipment and techniques are demonstrated. Rescue records are published in national journals, often with full details and analysis. In addition, many organizations keep detailed records of their rescues and hence it is possible to generate statistics on the diversity of caving accidents that require rescue. Statistics from the United States show that the majority of incidents (*c.* 30%) involve vertical caving and rope work. This is followed by individuals who have become lost or have experienced light failure (18%); water problems including being trapped by flooding (14%); entrapment (10%); and explosion, rock fall, bad air, and medical problems, each making 5% or less (Hempel & Fregeau-Conover, 2001). Frankland (1991) gives statistics for the causes of injury or death to British cavers: falls (61%), rock fall (15%), drowning (12%), bad air (21%), and others (10%). A more detailed analysis of cave rescue statistics for the Yorkshire Dales area (Forder, 2001) showed that half of the incidents between 1935 and 2000 involved floods or falls and that falls accounted for a quarter of all fatalities, and floods 13%. Standing (1976) showed that 80% of British rescue incidents involved novices and in the United States, 90% of call-outs were for inexperienced or poorly equipped cavers (Hempel & Fregeau-Conover, 2001).

The above statistics illustrate that inexperienced and poorly equipped cavers are most at risk and that falls, usually off short, unprotected climbs or while vertical caving with ropes and ladders, are the most common accidents. In such falls lower limb fractures are the most common injury, followed closely and perhaps surprisingly by spinal fractures, almost entirely without spinal cord damage. Spinal injuries pose particular difficulties for the rescue team.

Rescue of the lost caver requires that the rescue teams have substantial local knowledge and the resources for rapid systematic searches of complex caves or several caves in an area. Speed in any rescue is critical because even if the cavers are not injured they are in danger from hypothermia. Lloyd (1964) found that death from hypothermia could occur within half an hour of the onset of symptoms. The prevention of hypothermia in the lost, trapped, or accident victim is a major consideration of the rescue team, who typically carry equipment such as thick neoprene exposure bags, heat packs, insulating systems, and warm-air rebreathing apparatus.

When a person is injured a factor critical to successful rescue is the time taken to alert the rescue organization. Nevertheless, the difficulty of the cave and the depth of the accident site mean that there may be hours or even days between an injury and the arrival of the rescue team. Hence, the availability of basic survival equipment and knowledge of first aid among the victim's group enhances the probability of a successful rescue.

Many cave systems flood and often flash flood. Special care is required in the lowest levels of caves and close to sumps as in these regions back-flooding can cause water levels to rise exceptionally rapidly. When floodwaters prevent safe exit the only option is to seek a position above the maximum water level, which can sometimes be deduced from foam or mud-coated walls or vegetation lodged in cracks and crevices. Some caves that experience frequent flooding of their entrance passages have designated points where trapped cavers may safely await rescue (e.g. Peak Cavern, England). It is usually advisable to wait until the rescue team arrives unless absolutely certain that the water levels have dropped sufficiently for a safe exit. It is not wise to move with or against a flood, and exceptionally hazardous to attempt to ascend or descend ropes or ladders when the cave is flooding. The worst caving disaster in Britain was in Mossdale Caverns in 1967 when six cavers lost their lives as a result of an unexpected flash flood. Guide books often contain information as to which caves are known to flood and a wise caver will check the weather before entering such caves. However, intense precipitation is not always predictable and in the Mossdale area on 3 May 1986, another flash flood resulted in six separate rescue call-outs. This time there was only a single fatality.

Rock fall or movement can trap a caver, especially when they are negotiating breakdown. Rescue of the trapped can be a frightening experience for the rescue team if the area remains unstable. Rescue of a person from bad air requires both a fast response and great care as accidents in bad air could result in the deaths of the rescuer as well as the victim. Rescue and recovery teams use breathing equipment or wait until the hazardous atmosphere has cleared. Bad air can arise from a number of sources: partial combustion of fuel in fires, stoves, or generators can result in accumulations of carbon monoxide as well as carbon dioxide, and explosives release a variety of exceptionally toxic gases. Less obviously, respiration in a confined space results in hazardous increases of carbon dioxide and reduced oxygen. For example, in England in 1976 six cavers were free diving a c.8 m sump in Langstroth Pot with a small air bell where a breath could be



taken halfway. Unfortunately they used up the oxygen in the air bell, replacing it with expired carbon dioxide, and there were three fatalities.

Every rescue situation is different and there is no formula for exactly what must be done. On expeditions in remote areas and in most vertical caves emphasis is placed on self-rescue, which in this context means that members of the victim's party organize the rescue. The cavers performing self-rescue must assess the degree of injury and the availability of outside rescue before attempting to remove the victim from the cave. Some rescues cannot wait for an outside team; for example, if the victim is trapped on rope hanging in a harness they should be released as fast as possible as death occurs rapidly to both the conscious and unconscious. If the cavers are trained in first aid and techniques of rescue, especially those needed for rescue in vertical caves (Warild, 1994), then the probability of a successful self-rescue is increased. However, an untrained group would probably fail to rescue a severely injured victim from deep in a cave. It should be emphasized that the death of a victim can be a harrowing experience for all. The most experienced rescuer should adequately package the body such that the object being handled by the recovery team is minimally visibly human.

Flooded passages (sumps) pose particular problems. Only fellow divers can rescue cave divers who have equipment failure or an accident; divers have also been used to bring out uninjured cavers trapped beyond flooded cave passages. Probably the earliest such rescue was in 1969 when a trapped and unconscious caver in Merigill Hole, England, was brought through a sump with a diving mask held onto his face. He survived the dive, but died of hypothermia shortly afterwards. Subsequently there has been considerable research into the development of equipment for transporting injured or trapped cavers safely through flooded passages. Unfortunately very few cave diving incidents result in a successful rescue, and body recovery poses its own problems. In the United States the International Underwater Cave Rescue and Recovery team assists local law enforcement agencies and other rescue organizations by supplying specially trained divers to aid in rescues or recoveries.

Modern rescue teams have the benefit of state-of-the-art equipment; the ability to call out cave, mine, and other specialist rescue teams, and to transport experts and victims thousands of kilometres if necessary. No expense is spared if it is believed the cavers are still alive. For example, probably the world's longest, largest, and most expensive cave rescue took place in France in November 1999 when seven cavers were trapped by floods. Shafts were drilled to locate air spaces in which the cavers were likely to be waiting (a first) and the successful rescue took ten days.

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## ADAPTATION: BEHAVIOURAL

Of all phenotypic traits, behaviour plays the most immediate role in determining the ability of a group of individuals to survive during colonization of the subterranean (hypogean) environment. Changes in behaviour as a response to environmental change are thus crucial to understanding the phenomenon of adaptation to hypogean environments. In the following overview of current understanding of behavioural adaptations in caves, most of the examples presented come from studies of fish, the taxon on which most behavioural experiments have been performed.

Numerous animals colonize the hypogean environment by developing entirely new behaviours such as echo-location (e.g. bats and the nocturnal oilbird *Steatornis caripensis*), bioluminescence (e.g. the New Zealand glow-worm—actually a fly larva—*Arachnocampa luminosa*), or hibernation (e.g. a carp from China, *Varicorhinus [Scaphistes] macrolepis*). However, these types of behavioural modifications are the exception, not the rule. Most can be grouped into one of the following categories: feeding, reproduction, social behaviour (including aggregation, responses to alarm substances, and antagonistic behaviour), photoresponses, and circadian rhythms.

### Feeding

Many cave animals have enlarged sensory systems that allow them to sense the presence of food. To improve their ability to find food, many cave animals move continuously in their environment; for example the troglomorphic form of the fish *Astyanax fasciatus* swims continuously. In studies, these fish also decrease the angle of their body relative to the bottom of the aquarium in order to increase the area of contact between food on the bottom and areas of their skin where there are larger numbers of chemoreceptors (Schemmel, 1980). Similar adaptations have been reported for the toothless blindcat *Trogloglanis pattersoni*, the Somalian cave fish *Phreatichthys andruzzii*, and the catfish *Trichomycterus itacarambiensis*. Coprophagy (feeding on excrement) is not uncommon in caves, and some animals specifically choose such environments. For example, larvae

of the pyralid moth *Aglossa pinguinalis* are found inside caves in densities 700 times greater than at the surface. This is apparently due to the fact that in more exposed excrement they cannot compete with other coprophagous specialists, owing to a lack of parental care and slow growth rates for this species (Piñero & López, 1998).

### **Reproductive Behaviour**

The use of chemicals to attract mates has been reported in a number of cave organisms, ranging from crickets to fish. This behaviour has yet to be studied thoroughly in natural conditions. Aggressive behaviour associated with reproduction has been observed to decrease, probably due to a lack of visual information (Parzefall, 2000) (see below).

### **Aggregation/Schooling**

In general, all hypogean animals show a tendency to reduce organized forms of aggregation, from insects (Christiansen, 1970) to fish (Romero, 2001). Romero (1984, 1985a), for example, observed that individuals of *A. fasciatus* morphologically identical to the epigeal populations of the same species actively entered a cave in Costa Rica for both feeding and to escape from predators (the fishing bat *Noctilio leporinus*). However, unlike the typical epigeal *A. fasciatus*, the population did not form schools.

### **Responses to Alarm Substances**

Many bony fishes contain an “alarm substance” in their skin that is released into the water when the skin is damaged, for example by biting. It is believed that this substance is sensed by conspecifics (members of the same species) of the individual that has been harmed, and thus they use the information to escape or seek refuge. Although the substance is produced by many hypogean fishes, the response to its release is either highly reduced or lost (Fricke, 1988).

### **Aggression and Antagonistic Behaviour**

Aggression has been reported for many cave fishes, and some amphibia and crustaceans (Parzefall, 2000). Aggression is usually reduced, but antagonistic (confrontational behaviour without fighting) behaviour persists in many species, including amblyopsids (where the rituals decrease in complexity in parallel with the degree of cave adaptation, Bechler, 1983), the Ceguinho catfish *Pimelodella kronei*, and the Cueva del Guácharo blind catfish *Tricomys conradi*.

### **Responses to Light**

Many blind, depigmented hypogean animals do show behavioural responses to light. Photoresponses are mediated by the pineal organ and—to a certain extent—by extrapineal organs (Langecker, 1992; see Adaptation: Morphological-Internal). They are termed scotophilia (the tendency to stay in the dark side of an aquarium under experimental conditions) and have been reported for many species of hypogean fishes (Romero, 2001). The behaviour of staying away from light is usually more common among recent invaders of the hypogean environment than among more troglomorphic species (Green & Romero, 1997). Also, the degree of scotophilia (in which the fish moves away from light) increases with development, as it does for epigeal forms (Romero, 1985b). Although earlier authors made much of this behaviour as an indication

that these species maintain such responses in order to stay in caves, all available evidence suggests that such behaviour is an inherited relic from their epigeal ancestors (Romero, 1985b).

### **Circadian Rhythms**

This is a system also known as a “biological clock”, which controls a series of physiological and behavioural responses in an organism. The rhythmicity generated by these clocks is usually triggered by light and temperature changes in the environment. Many cave animals show a reduction or total loss in their ability to generate biological rhythms even when exposed to light under experimental conditions (Lamprecht & Weber, 1992). As with the photoresponses mentioned above, circadian cycles are more reduced (or totally absent) in the more troglomorphic species (see also Adaptation: Eyes).

### **Acoustic Behaviour**

Hoch (2000) found that the cave planthopper, *Oliarus polyphemus*, utilizes communication systems similar to those of its epigeal ancestor, by communicating using substrate-borne vibrations, and also found that the cave environment seems to be especially suited to low-frequency sound transmissions. No acoustic communication has been demonstrated for hypogean fish, despite the obvious advantage of such behaviour. More research is needed in this area.

In summary, with the exception of a few very specialized types of behaviour, most cave animals tend to reduce or eliminate many of the typical responses of their epigeal ancestors. To understand the role played by behaviour during hypogean colonization, ethological studies on hypogean organisms that have yet to achieve a troglomorphic state are probably the most important avenues to explore.

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*See also* **Colonization**

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## ADAPTATION: EYES

The lightless regions of caves, referred to as “the deep zone” by Howarth (1993), can harbour aquatic, terrestrial, and even flying organisms. Although troglophiles—and even some animals that occasionally visit caves—often show adaptations involving photoreceptors and sight, few generalizations can be made regarding their eyes. Cave animals such as bats generally possess poor eyesight, but are never blind; other animals that simply visit caves may have grossly enlarged eyes with highly sensitive photoreceptors (Jamaican cave frogs, for instance) or, as in the case of some millipedes, may lack eyes altogether. On the other hand, obligate cave-dwellers frequently have eyes that are reduced in size, and some have lost their eyes entirely. Thus, eyelessness has traditionally been regarded as a sure sign of a “troglitic” lifestyle. However, with the discovery in New Zealand of cave harvestmen (*Hendea myersi cavernicola*) that possess large, functional eyes but display other typically troglitic features such as a pale, nonpigmented body, it has become clear that troglites need not necessarily be blind. The New Zealand cave harvestmen prey upon the luminescent larvae of the so-called glow-worm fly, *Arachnocampa luminosa*, which is a troglophile. For a predatory animal

like the cave harvestman, to be able to see its luminescent prey is an obvious advantage. Therefore, as with the occurrence of bioluminescence in mesopelagic organisms, an adaptation which has prevented the widespread evolution of eyelessness in the deep sea—only a few bathypelagic fishes completely lack eyes—provided that light sources still exist and sight still has a role to play, then even a troglobite need not be eyeless.

Notwithstanding the exceptions discussed above, it is clear that lack of light—especially sunlight—is a powerful feature of most cave environments and, undoubtedly, has led to the reduction and even disappearance of eyes and their constituent elements in many cavernicolous vertebrate as well as invertebrate species. In the dark it is energetically demanding to maintain a functioning eye with its photopigments, optical structures, dark/ light adaptational mechanisms, nerve connections to the brain, and the ability to integrate and interpret visual signals. Moreover, it is a luxury that can become a handicap, because eyes can become injured, infected, or become a hindrance in locomotion. Consequently, eye degenerations in cave vertebrates are common among troglobitic fishes (see Table and Figure in Pisces: Amblyopsidae) as well as cave newts and salamanders, but nevertheless, tiny eye rudiments under the skin—often invisible from the outside—are usually present.

Embryologically, the eyes of cave fishes and amphibia at first develop quite normally, but then begin to exhibit developmental retardation. Arrested growth and differentiation follows, and finally programmed cell deaths occur. The grafting experiments of the French biospeleologist Jacques Durand showed elegantly and convincingly that this scenario does not depend on the presence or absence of light. He exchanged the larval eyes of the hypogean, aquatic cave salamander *Proteus anguinus* with those of the epigean *Euproctes asper* and observed that in both cases the donor eye behaved in the way that it would have done in the specimen of origin. The degeneration of the eye appears to be controlled by a cascade of regulatory genes; eight to ten genes are now thought to be involved specifically in the eye regression of the cave fish *Astyanax fasciatus*. Eye regression in cave vertebrates is mostly centripetal, which means that it commences peripherally with the cornea and lens, then affects retinal and perceptive structures, and finally engulfs nerves and the optic centres of the brain. Interestingly, cave fish are known to compensate for the loss of their visual system with enhancements to their lateral line organ and taste buds. Eyeless cave arthropods frequently exhibit elongated limbs, antennae, and body hairs, presumably to facilitate the detection of tactile stimuli, water or air currents. In arthropods with compound eyes, reduced eye size and a smaller number of facets are usually the first signs of eye regression: approximately 30 ommatidia are present in the eye of the cave opossum shrimp *Heteromysoides cotti*, three in the cave shrimp *Typhlatya garciai*, and none in *Troglocaris anophthalmus*.

Apparently the more rudimentary the eye, the more variable its appearance: the percentage of misshapen or malformed ommatidia increases, pigmentation becomes irregular, and cellular outlines as well as photoreceptive elements become increasingly less uniform. Such multifariousness in a rudimentary organ has been interpreted as support for Darwin's theory of natural selection, since organs deemed unnecessary—and which have therefore undergone regression—ought to be less and less affected by selection. Functionally, loss of colour-, shape-, and form-vision precede changes in the ability to detect flickering lights, to adjust the visual system to changes in ambient light intensity, and to protect the eye against photic damage. However, whether the latter

occurs as a consequence of the cave environment or has prompted a species to establish itself in the cave, needs to be examined from case to case. An entire book has been devoted to one species of cave crustacean, the amphipod *Gammarus minus*. It is interesting that numerous totally eyeless species of terrestrial cave insects and aquatic crustaceans exist, but that almost no cave crab is completely eyeless, either exhibiting only reductions in eye size or lack of pigment and facetation around the eye region as well. Eyeless cave arthropods need not necessarily be completely insensitive to light: extra-ocular photoreceptors (for example, the so-called tail photoreceptor in the sixth abdominal ganglion of the crayfish), may be able to convey information on ambient light levels.

Without daylight, the most important time-keeper to coordinate circadian or seasonal rhythmicities is absent in caves, and many troglobitic animals, whether with or without rudimentary eyes, are indeed non-rhythmic. However, strictly clock-controlled locomotion rhythms are known from some troglobites. Since eyes and photoreception cannot be involved, secondary or even tertiary signals, such as daily movements of cave bats; periods of increased production of faeces; or activity periods of bat guano flies probably are. The question of how long it would take an animal species to lose its eye in total darkness is hard to answer. Fruitflies kept in total darkness for more than 600 generations showed little change in eye size. However, selective pressures were absent in that particular experiment, and undoubtedly the presence of predators would have had some impact. It was estimated that the total loss of the compound eye in a troglobitic arthropod could require some 100000–1000000 generations. However, in view of the fact that deep-water hydrothermal vent shrimps apparently underwent a near-total loss of the dioptric (lens and corneal) elements (but not the photoreceptive cells) of their eyes in only 10000 generations, estimates for the time-scale of morphological changes in the eyes of cave organisms may need to be revised.

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## ADAPTATION: GENETICS

Any particular feature of an organism results from the interplay of genetics and the environment, but it is the genetic component that is passed on to succeeding generations, forming the raw material of evolution, which is, by one definition, simply the change in gene frequency through time. For a trait—whether behavioural, demographic, or morphological—to be adaptive in the cave environment, it must satisfy several requirements (Brandon, 1990), the most important of which are: (1) that some types are better adapted than others in the cave environment; (2) that selection has occurred; and (3) that trait differences are genetically determined. For many of the traits shared by obligate cave animals, the selective advantage is obvious. Thus, any increase in size or complexity of extra-optic sensory structures confers an apparent advantage in the darkness of caves, and any decrease in number of eggs produced confers an apparent advantage in the food-poor environment of caves. The third requirement—that trait differences are genetically determined—is more difficult to document. Purely environmental effects can mimic some of these adaptive changes. For example, colour differences between cave-dwelling and surface-dwelling crayfish (*Procambarus simulans*) are related to the availability of carotenoid pigment precursors, not genetic differences (Maguire, 1960). Starvation can also mimic some effects. Starving animals become emaciated, sometimes giving the appearance of a true cave animal. Even egg production is affected by starvation (Charlesworth, 1980).

There have been two studies that document the genetic basis of adaptation—Fong's study of the heritability of relative antennal length in cave and spring populations of the amphipod *Gammarus minus* (Fong, 1989; Jernigan, Culver & Fong, 1994) and Schemmel's study of taste-bud density and feeding behaviour in river and cave populations of the Mexican characin fish *Astyanax fasciatus* (Schemmel, 1974a, 1974b).

Schemmel found that density of taste buds was high in cave populations, low in surface river populations, and intermediate in phylogenetically young cave populations. In river populations the only area of dense taste buds is at the tip of the mouth, and this is enlarged in all cave populations, especially to the ventral side of the head (Wilkins, 1992). For the most part these differences were shown to be genetic because he measured the differences on long-term captive populations raised under identical conditions. Taking advantage of the captive populations at the Zoological Institute in Hamburg, Schemmel crossed several cave populations in order to learn more about the genetics of tastebud density differences. By considering the variability of the offspring of these



crosses, Schemmel showed that the differences in taste-bud density between river fish and cave fish were due to at least two or three taste-bud genes. The polygenes show an additive manner of expression, but there was a threshold effect, where the density increases abruptly, indicating gene interaction.

Fong studied a series of antennal characters in two spring and two cave populations of *Gammarus minus*. He measured both relative lengths and number of segments in 60-day-old individuals raised under constant darkness and constant temperature. As expected, all relative lengths and number of segments were larger in cave populations than in spring populations. Because he compared groups of siblings, Fong was able to measure heritability, the fraction of the variation that is attributable to genetic as opposed to environmental variation. Fong measured what is called broad-sense heritability (because it does not eliminate the variance due to the common environment of sibs, e.g. the maternal effect). Nevertheless, his results were striking. For the six antennal traits measured in four populations, heritabilities averaged 0.6, and in only one case in 24 was there no statistically significant heritability (Fong, 1989).

If these results are typical of cave organisms, then almost all cases of morphological change associated with isolation in caves have a strong genetic component. The kinds of morphological changes associated with starvation and the absence of pigment precursors listed above only mimic adaptation at a superficial level, and are not a general explanation for the adaptation of animals to the cave environment.

Fong and his colleagues (Jones, Culver & Kane, 1992; Culver *et al.*, 1994; Culver, Kane & Fong, 1995), were able to push the analysis of the genetic basis of adaptation much further because they were able to demonstrate that animals with larger antennae or more antennal segments had larger numbers of eggs and/or were more likely to mate than animals with smaller antennae or fewer antennal segments. Both mating propensity and egg number are components of fitness. This reconnects with the criteria for showing that a trait is adaptive—the differences must be genetic and selected for. In this case, the agent of selection is clearly life in darkness.

Eye reduction has a strong genetic basis in those species that have been carefully studied, including *Astyanax fasciatus* and *Gammarus minus* (Culver & Wilkens, 2000). However, the adaptive nature of these losses is not at all certain. At least in part, eye loss occurs due to the relaxation of selection in favour of maintaining eyes and the accumulation of selectively neutral, structurally reducing mutations. The work of Fong and his colleagues on *Gammarus minus* cited above also indicates that there is a selective advantage to eye loss, due to either energy conservation or simplification of neurological connections.

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*See also* **Evolution of Hypogean Fauna; Speciation**

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## **ADAPTATION: MORPHOLOGICAL (EXTERNAL)**

Morphological adaptation is used to mean evolutionary modifications of the external morphology of lineages of organisms, which are associated with their existence in caves. While some of these modifications may be non-adaptive, most putatively increase their chances of survival or competitiveness in caves. Selected works describing such adaptations in specific groups and reviews of general cave adaptation are listed in the references and further reading. A good example of morphological changes can be seen in cave Collembola of the family Entomobryidae where members of the genera *Pseudosinella* and *Sinella* go through very similar evolutionary changes in the caves of Japan, North America, Central America, and Europe (Christiansen, 1961; see Figure 1). These involve increase of adult size, expansion of mesothorax and elongation of furcula, and associated muscle changes producing an enlarged mesothorax, all associated with increased jumping ability. They also involve elongation of legs (also probably associated with increased predation escape), elongation of antennae, and enlargement of antennal sensory organs (both probably associated with increased olfactory and tactile sensitivity). The most studied changes are major changes in the foot complex. These have been shown to be associated first with adhesion on smooth wet rock surfaces and penetration into wet clay, and then with movement over water surfaces. In addition, there is the much-debated loss of eyes and pigment.

Other excellent descriptions of morphological changes involved in lineages of cave-adapted organisms have been given for a number of groups, all of which include eye and pigment reduction or loss. In each case there are more specialized changes. In Amblyopsid fishes (see Pisces: Amblyopsidae) these include hypertrophy of free motion sensing neuromasts and flattening of the head (see Figure 2D in that entry). Specialized changes in beetles of the family Cholevidae and the subfamily Trechinae include wing loss, cuticle thinning, elongation of appendages, narrowing of the prothorax, physogastry or (in some Cholevidae) narrowing of abdomen (see Insecta: Coleoptera). In Crustacea of the family Crangoncytidae (Amphipoda) the special changes include elongation of appendages (see Crustacea: Amphipoda).

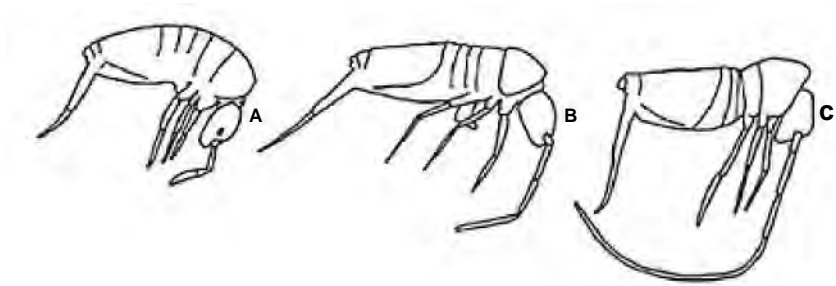
It is notable that while earlier works suggested non-neoDarwinian explanations for adaptation in cave animals (Vandel, 1965) almost all recent work has been undertaken with the clear assumption of the applicability of the Darwinian core tenets. A possible recurrence of a view similar to that held by Vandel can be seen in the emphasis on phenoplastic adaptation put forward by Romero (see Evolution of Hypogean Fauna).

### **Troglomorphy**

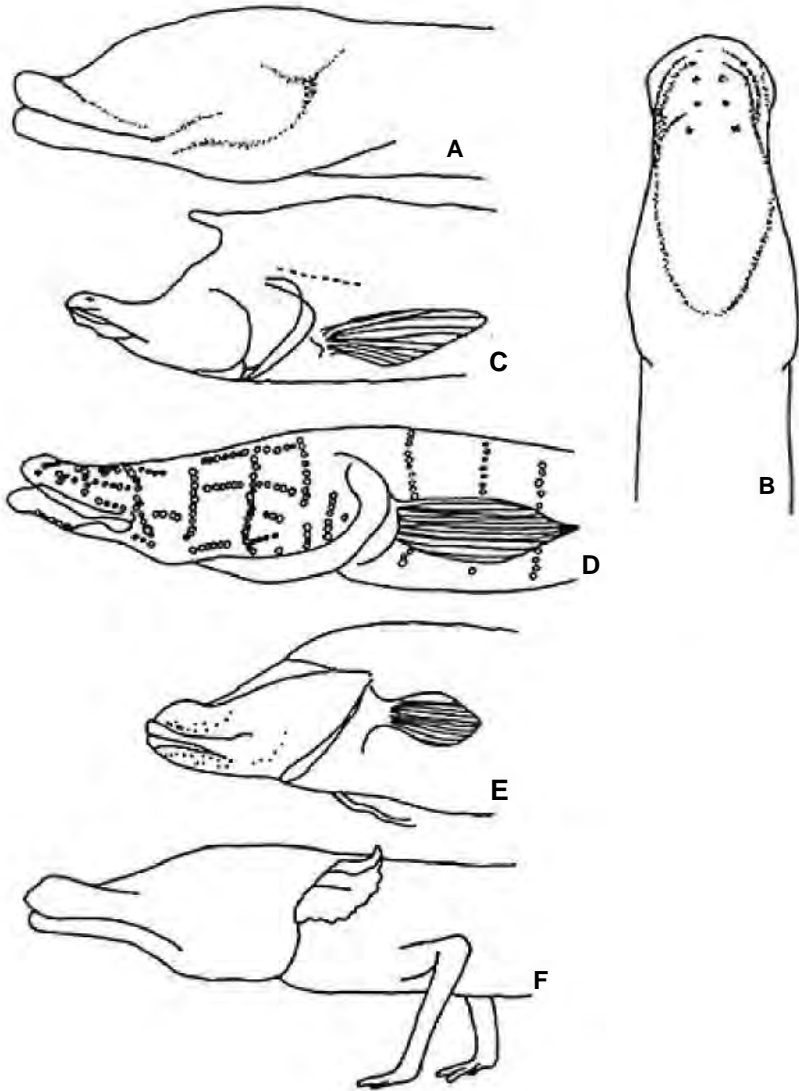
The term “troglomorph” (Christiansen, 1962) was created to designate phenotypic features that are characteristic of cave animal evolution, and served to identify cave-adapted organisms without the unprovable and often erroneous assumption that they live only in caves implied by terms such as troglobite. While the term was originally used for morphological features, subsequent work has shown that it applies equally well to

behavioural and physiological features. The Table summarizes some of the major morphological troglomorphic features.

Questions as to the adaptive nature of troglomorphic features are putatively answered by their convergent nature but many recent works have furnished more direct evidence (e.g. Christiansen, 1965; Culver, Kane & Fong, 1995 and references within).



**Adaptation: Morphological (External): Figure 1.** Stages of increasing troglomorphy in Collembola Entomobryinae. A. *Pseudosinella octopunctata*; B. *P. hirsuta*; C. *P. christianseni*.



**Adaptation: Morphological (External): Figure 2.** Various troglomorphic vertebrates showing head flattening. A. lateral and B. dorsal view of head of *Ophisternon infernale* (Synbranchidae), after Vandell (1965); C. *Synocyclocheilus hyalinus* (Cyprinidae); D. *Speoplatyrhinus*

*poulsoni* (Amblyopsidae), C. and D. modified after Weber in Wilkins *et al.* (2000), with permission from Elsevier Science; E. *Lucifuga subterraneus* (Bythitidae); F. *Typhlomolge rathbuni* (Plethodontidae), E. and F. after Eigenmann (1909).

Trogomorphy is not universal among cave organisms. In order for it to occur two factors have to be present: 1) a strong selection pressure for the development of a particular characteristic, and 2) the genetic and physiological or behavioural ability of the organism to respond to this pressure. Many cave organisms lack one or both of these factors. The phreatobite entomostracan crustacea and the extremely edaphic Collembola, such as the members of the family Onychiuridae, rarely show morphological troglomorphy. In many other groups, troglomorphy is questionable or inconsistent (Culver, 1982). It is also absent in cave environments such as guano piles or large masses of organic debris which are extremely energy rich. Peck has pointed out that troglomorphy should not be expected in these cases since troglomorphy only occurs when organisms are exploiting large volume spaces such as the surface of cave walls or floors (Peck, 1973), or large bodies of water. Indeed it has been long noted that the troglomorphic features of cave Entomobryidae are most closely approached in two very different surface habitats. The foot structure is closest to that seen in aquatic Collembola but the body shape features are most similar to those seen in forms (largely tropical) which live above the litter or soil, in trees. It is interesting that something similar to troglomorphy has been found in phreatobites where small size and elongate body form are developed convergently (Boutin & Coineau, 2000).

Where troglomorphy does occur, it allows for a separate analysis of those features clearly affected by the cave environment and those which are unaffected by it. It also gives clear polarity for phylogenetic analysis and permits a measure, or least an indication, of the degree of cave adaptation of different groups of organisms (Christiansen, 1961; Poulson, 1986).

Troglomorphy also shows varying degrees of taxonomic localization. In all cases there is some degree of convergent or parallel evolution in different regions and taxonomic groups. This is

**Adaptation: Morphological (External): Common troglomorphic characteristics.**

Morphological	Reference
Specialization of sensory organs (touch, chemoreceptor, hygroreceptor, thermoreceptor, pressure receptors)	Vandel, 1964; Weber, 2000
Elongation of appendages	Weber, 2000; Christiansen, 1961; Harvey, Shear & Hoch, 2000; Vandel, 1964
Pseudophysogastry	Vandel, 1964

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Reduction of eyes, pigment, wings	Vandel, 1964; Weber, 2000
Compressed or depressed body form (hexapods)	Harvey, Shear & Hoch, 2000
Increased egg volume	Vandel, 1964
Increased size (Collembola, Arachnida)	Christiansen, 1961; Harvey, Shear & Hoch, 2000
Unguis elongation (Collembola)	Christiansen, 1961
Foot modification (Collembola, planthoppers)	Christiansen, 1961, Howarth <i>et al.</i> , 1990
Scale reduction or loss (Fish)	Weber, 2000
Loss of pigment cells and deposits	Numerous
Cuticle thinning (terrestrial arthropods)	Numerous
Elongate body form (Teleost fishes, Arachnids)	Weber, 2000
Depressed, shovel-like heads (Teleost fishes and salamanders)	Weber, 2000
Reduction or loss of swim bladder	Romero & Paulson, 2001

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usually transgeneric or even transfamilial, as in the case of the foot structure of European, Japanese, and American members of the genera *Pseudosinella* (Figure 1) and *Sinella* of the family Entomobryidae. In this case, as well as in the case of the similar changes in the family Orchesellidae, the adaptive significance of these changes is well known (Christiansen, 1965). In many cases, as with the flattening of the heads of troglomorphic fish and Amphibia (Figure 2), this is not so. Some troglomorphic features are so general (elongation of appendages, loss of pigmentation) as to be considered virtually universal.

Studies of troglomorphic evolution have produced a number of interesting ideas. Most exciting of all are the works of Culver, Kane, and their collaborators on *Gammarus minus*, which unites genetic, population genetic, population dynamic, and ecological analysis to answer the question of whether troglomorphic changes are in fact adaptive (e.g. Kane & Culver, 1992; Richardson & Kane, 1988). These works indicate that the troglomorphic features which have been studied are subject to selection and are in fact adaptive.

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*See also* **Evolution of Hypogean Fauna**

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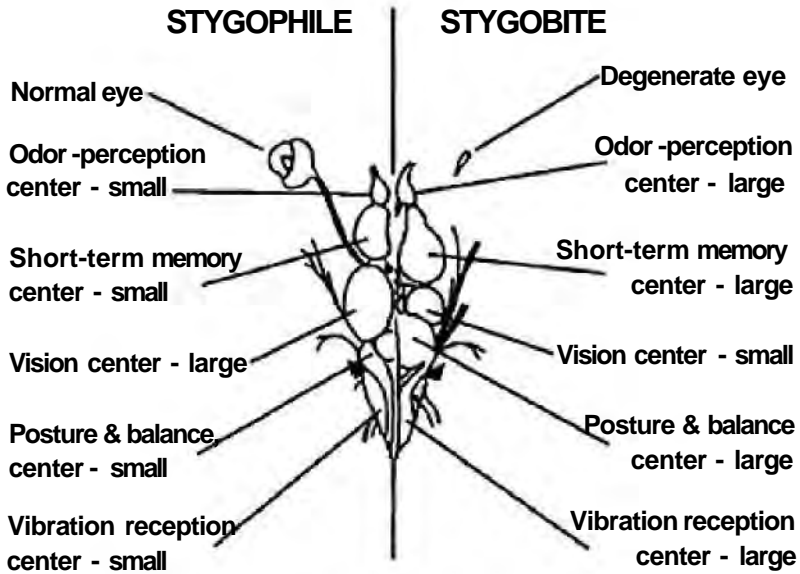


## **ADAPTATION: MORPHOLOGICAL (INTERNAL)**

Anatomical adaptations are the internal reflections of the morphological and behavioural modifications of subterranean animals. Total darkness, almost unique to the subterranean environment, favours those organisms that have developed or are in the process of developing non-visual sensory structures. These are represented by any structure employed in any kind of sensory reception: mechanical (air currents, touch), olfactory (smell), gustatory (taste), or auditory (sounds). These sensory structures tend to be more highly developed in cave animals compared to epigeal organisms.

In the brains of cave fish the nervous centres responsible for non-visual sensations, memory, learning, and spatial orientation are hypertrophied and can be used to estimate the degree of eye regression, and of sensorial compensation in cave vertebrates. Telencephalon hypertrophy is the most homogenous feature in the cerebral development of hypogean fishes. The cerebellum of many subterranean fishes is larger and its dimension is related to the time since cave colonization. This part of the brain receives information from the lateral line, free neuromasts, and other nerve pathways. The degree of development reflects the locomotory activity of cave species. Sometimes, related stygobitic and stygophilic fishes co-exist in the same pool within a cave. American researchers who compared the brain of the highly adapted *Typhlichthys* sp. and the less adapted *Chologaster* sp. from the River Styx in Mammoth Cave (Kentucky) found obvious differences (Mohr & Poulson, 1966) (see Figure 1). The inner ear structures of hypogean fishes are also modified, generally being larger, and are used to maintain equilibrium by perception of body motion and position.

The pineal organ has a photoreceptive function in fishes and amphibians. It contains many photosensitive cells, similar to receptors within the eye, but also has neuroendocrine cells that synthesize and release the hormone melatonin in the presence of light. Thus, the absence of light in caves will induce the degeneration of the exterior parts of pineal photoreceptors of stygobitic animals. Some cavernicolous species with completely



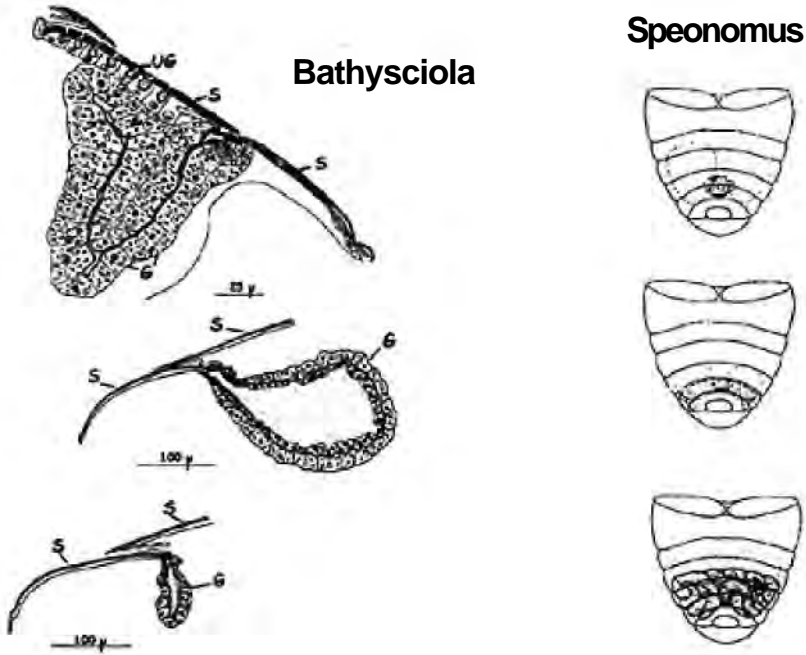
**Adaptation: Morphological (Internal): Figure 1.** Differences between the brains of the stygobitic fish *Typhlichthys* sp. and the stygophilic *Chologaster* sp. (after Mohr & Poulson, 1966, modified).

reduced eyes can still have functional pineal cells. This has been clearly demonstrated in the fish *Astyanax fasciatus* (Langecker, 2000).

The development of sensory structures in the dark is relatively well documented for some subterranean species. In contrast, the development of other organs not directly linked to sight has been very poorly studied, for example exocrine glands, producing pheromones. Cave beetles from the sub-family Leptodirinae that possess several types of glands with varying degrees of development or involution (depending on the phyletic line) have been described. The sternal gland is a multicellular gland present in the males of several Leptodirinae species. The *Speonomus* spp. are characterized by enhanced development of this gland but in marked contrast, *Batysciola* spp. are characterized by reduction of the sternal gland (Juberthie-Jupeau & Cazals, 1984; Moldovan & Juberthie, 1998) (see Figure 2). In the latter case, there is also a change from a secretion with less volatile particles to a very volatile secretion. However, this gland is absent in beetles highly adapted to life in subterranean habitats.

In subterranean environments, food input is not uniformly distributed in space or time and the primary adaptation of animals living in hypogean habitats is the improved ability to accumulate and store large energy reserves. Their lipids contain twice the energy per unit weight compared to proteins and carbohydrates. The adipose tissue can increase

through excessive feeding, increased feeding efficiency, and improved metabolic pathways favouring lipid deposition during food-rich periods (Hüppop, 2000). This has also been observed in epigeal animals, for example hibernating birds and mammals. In several terrestrial and aquatic cave animals an increase in fat content has been observed. Exceptional development of the adipose tissue has been recorded



**Adaptation: Morphological**

**(Internal): Figure 2.** Evolution of the sternal gland in two subterranean genera: *Bathysciola*—a soil species (top) and a cavernicolous species (bottom), and *Speonomus*—from different cavernicolous species: *S. delarouzei*: (top), *S. pyrenaus* (middle), and *S. hydrophilus* (bottom). UG=unicellular gland, S=sternite, G=sternal gland.

in springtails, Leptodirinae beetles, remipedes, and shrimps. For example, cave beetles can survive for several months without feeding. In cave decapod crustaceans, the hepatopancreas, a major lipid storage organ, is larger than that of other decapods and lipids are also deposited in oleospheres, specialized compartments within the

hepatopancreas. An interesting example is that of the larvae of the most highly adapted cave beetles from the Leptodirinae family that hatch from large, yolk-rich eggs, do not feed at all, have an atrophied and non-functional digestive apparatus, and break down the lipid reserves to protein (Deleurance-Glaçon, 1963). The adult digestive apparatus of soil and cave species only display differences linked to the presence of the chitinous spines in proventricular and mesenteric caecums. Cave animals accumulate large volumes of fat reserves in the internal spaces occupied by other structures in epigeal species, such as the wing muscles and the sternal gland, and which are completely absent in subterranean species.

The storage of lipids in fish has been extensively studied. The primary organs used for storage are the subcutis, muscles, viscera, orbit of the reduced eyeball, and cranium. An interesting example is provided by two Texas cave fishes *Trogloglanis pattersoni* and *Satan eurystomus* (Siluriforme), whose swim bladders are totally reduced and their place filled by fat deposits (Langecker & Longley, 1993). This allows the maintenance of a small body, which is advantageous for animals living in subterranean crevices.

Food scarcity and stability of the environment also help explain the tendency for paedomorphosis and neoteny in some subterranean vertebrates. Besides the morphological features that characterize this retardation of somatic development, some anatomical changes have been observed in cave fish and amphibians, including reduced muscles and ossification. Together with a reduced metabolic rate, oxygen consumption and accumulation of lipids are all characteristic of hypothyroidism. In some subterranean fish underdevelopment of the thyroid has been recorded. However, in *Proteus anguinus* the thyroid is highly developed and in this instance we probably observe the insensitivity of the tissues to thyroxin, the hormone secreted by the thyroid (Langecker, 2000).

There have been relatively few detailed studies of anatomical adaptations to subterranean life and much remains to be learnt from the organisms that inhabit hypogean habitats.

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## ADAPTATION: PHYSIOLOGICAL

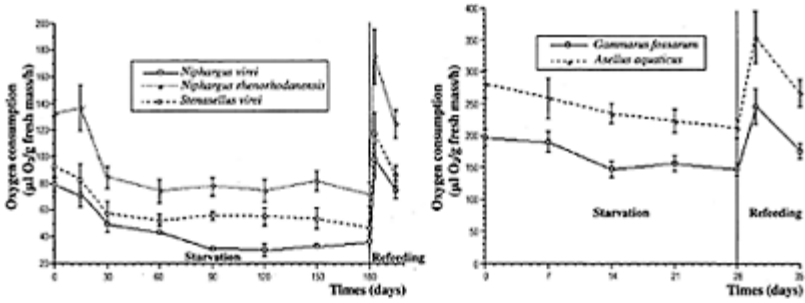
In subterranean ecosystems, the main environmental factors influencing physiological adaptations in cave organisms are darkness, lack of food, and also hypoxic conditions. These factors have a high selective value in regard to adaptive features such as a drastic reduction in eye size and a reduced metabolic rate compared with that of surface-dwelling relatives. To study the physiological adaptations of cave organisms to the subterranean environment, it is necessary to compare troglobites with troglophilous and epigeal species. Studies have been carried out on aquatic and terrestrial invertebrates and vertebrates by investigating oxygen consumption and metabolic responses.

### Oxygen Consumption

The most meaningful information on metabolic rate is given by measuring the oxygen consumption of the organism's whole body rather than just part of it. In most comparisons, hypogean species show generally lower metabolic rates than their epigeal relatives. For example, the hypogean crustaceans *Stenasellus virei*, *Niphargus virei*, and *N. rhenorhodanensis* have a reduced metabolic rate because they show O<sub>2</sub> consumption rates in normal oxygenation 1.6–4.5 times lower than the epigeal *Asellus aquaticus* and *Gammarus fossarum* (Hervant *et al.*, 1998). The same was found with salamanders, among which the obligate cave-dweller *Proteus anguinus* has an oxygen consumption as low as one-eighth that of the facultative cave-dweller *Euproctus asper* (Hervant *et al.*, 2000).

Reduced activity and decreased metabolic rates are a response to a selection pressure to economize on energy use because food and oxygen are in short supply (Culver, 1982; Malard & Hervant, 1999). Usually, cave animals have a higher basal metabolic rate than interstitial fauna. Culver & Poulson (1971) showed that individuals of *Stygobromus emarginatus* inhabiting more open water have higher activity rates than those of *S. spinatus* living deeper in the gravels of the stream bed. In the same way, Mathieu (1980, 1983) found interstitial *N. rhenorhodanensis* to be less active than cave-adapted ones.

A low metabolic rate is also an adaptation to a dysoxic environment. During periods of hypoxic stress, hypogean crustacean species possess a lower critical pO<sub>2</sub> (oxygen partial pressure) than epigeal ones, which may indicate that these organisms are better adapted to low O<sub>2</sub> tensions (Hervant *et al.*, 1998), and probably maintain a more efficient aerobic metabolism for a longer time in declining pO<sub>2</sub> pressure instead of partly switching to anaerobic metabolism. Post-hypoxic recovery results in a high oxygen debt (the excess O<sub>2</sub> consumed during post-hypoxia). The main expla-



**Adaptation: Physiological:** Oxygen consumption of the epigean *Gammarus fossarum* and *Asellus aquaticus*, and of the hypogean *Niphargus virei*, *N. rhenorhodanensis*, and *Stenasellus virei* during long-term starvation and subsequent feeding at 11°C and in darkness. Values are means ± standard deviation for  $n=8-10$  animals (modified from Hervant *et al.*, 1997).

nation for the smaller O<sub>2</sub> debt shown by hypogean species is the lower energetic expenditure during hypoxia, due to a decrease in movement and ventilation rates.

During long-term starvation, the respiratory—but also locomotory and ventilation—rates are drastically reduced in hypogean crustacean species, whereas epigean species show a smaller decrease in these rates and respond by a marked and transitory hyperactivity (Hervant *et al.*, 1997) (see Figure). During such a long-term starvation, the troglobite vertebrate *Proteus anguinus* shows a slight increase in oxygen consumption, after which its respiratory rate decreases. By contrast, the epigean *Euproctes asper* shows an immediate and high increase in its rate of respiration, which decreases later to a value similar to that for well-fed individuals (Hervant *et al.*, 2001).

### Metabolic Adaptations

The physiological adaptations of cave animals may also be understood by examining intermediary and energy metabolism. Both epigean and hypogean animals respond to long-term severe hypoxia with classic anaerobic metabolism, characterized by a decrease in ATP and phosphagen, the use of glycogen, and the accumulation of lactate (Hervant *et al.*, 1995; 1996). Compared with epigean crustaceans, the hypogean amphipod *N. virei*, which uses coupled fermentation of glycogen and amino acids, stores large amounts of glycogen and arginine phosphate. After severe hypoxia, *N. virei* appears to implement a strategy of lactate removal quite different from that observed in epigean crustaceans, favouring lactate-supported gluco- and glyconeogenesis and rapid glycogen replenishment, instead of rapid lactate removal via oxidative pathways.

The metabolic response to prolonged food deprivation in epigeal amphipods appears to be monophasic, showing an immediate and large decline in all energy reserves. In contrast, hypogean amphipods display successive periods of glucidic, proteo-glucidic, and then lipidic-dominant catabolism during food deprivation. Lipids and proteins are the most metabolized substrates, whereas glycogen contributes little energy (Hervant *et al.*, 2001).

This high degree of storage, the rapid restoration of fermentable metabolic fuel without feeding, and the ability to reduce glycolytic flux and energy expenditure due to a decrease in locomotion and ventilation activity, allow hypogean species to survive harsh conditions, and consequently are very good adaptations to the subterranean environment.

### Sensory Functions

It is generally assumed that the distinctive morphology of cave animals results from selection for increased sensory organs on appendages, which in turn results in lengthened appendages to compensate for eye and pigment cell degeneration (Culver, 1982). A good example of such adaptations is given by the amphipod *Gammarus minus*, which can be found in large caves and in springs in Virginia. Cave-dwelling *G. minus* populations have smaller eyes and longer antennae than surface populations, and they also have smaller optic ganglia and larger olfactory lobes in their central nervous system. In some other species of arthropods, the antennae of hypogean species are relatively short compared to those of their epigeal relatives (Culver, 1982). It has also been demonstrated that the blind crayfish *Orconectes australis packardii* learns about its environment using both tactile and chemosensory cues, mainly located on the antennae but also elsewhere on the body (Li & Cooper, 2001).

A classic example of sensory compensation and cave adaptation in general is also provided by primitive vertebrates, one obvious feature being the hypertrophy of the lateral line system observed in cave fishes or amphibians. This is clear in the amblyopsid cave fishes, where, because of differences in neuromast morphology, some species are more sensitive to general water movement, and others are more sensitive to the direction of the current (Poulson, 1963). Hypertrophy and differential sensitivity certainly confer an increased ability to find food and detect predators in an environment where food is scarce.

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## AFRICA, NORTH

The African continent is poor in limestone outcrops in general, but the northern zone has abundant karst and Algeria has the longest and deepest cave systems in Africa (Boll Maza, 18.6 km, Anou Ifflis, –1170 m, Anou Bousouil, –805 m). For a long time Morocco had the continent's deepest cave (Kef Toghobeit, –722 m) and one of the longest cave networks (Wit Tamdoun, 17.5 km). There is very good potential for further discoveries in both countries. Tunisia has only a few karstified massifs, which are not very well known. Libya possesses a few areas of interesting gypsum karst, and Egypt has very few caves. Climates of North Africa vary with annual rainfalls ranging from >1000



mm in high mountains (Rif and Atlas ranges) to <150 mm in the Sahara. Karst morphology is equally variable.

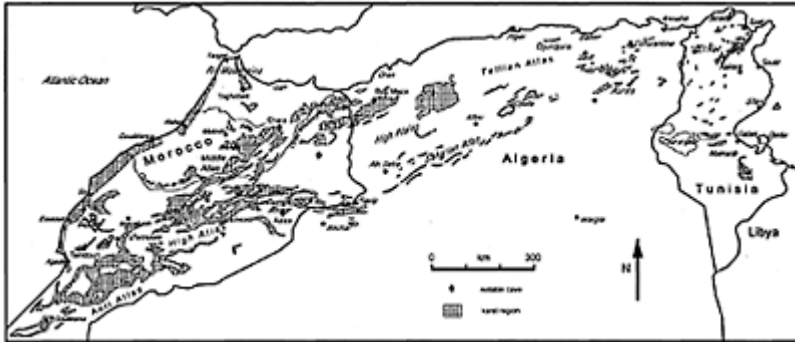
### Morocco

In Morocco, less than 1000 caves have been discovered, but the country has more than 100000 km<sup>2</sup> of karst terrain (see Figure 1). There are three geological domains north of the Saharan border, which correspond to three orogenic phases: (1) the Anti-Atlas domain near the Saharan border has folded Precambrian rocks forming mountains ranging from 2000 to 3000 m in elevation; (2) the Atlas domain is a second range with Caledonian, Hercynian, and Alpine structures; it is the largest of the three domains and has very different stratigraphies and lithologies; and (3) the Rifin domain, the smallest and youngest domain from the late Alpine. These three domains are separated by major fault zones. Karst landscapes, especially on limestone, are well represented in these three domains. Paleozoic limestone occurs in the Anti-Atlas domain (18000 km<sup>2</sup>) where it is more than 300 m thick in the western part, becoming thinner in the east. Superficial karst forms are developed, but caves are rare.

Lias limestone and dolostone form the largest karst terrain in Morocco, 30000 km<sup>2</sup> in extent, mainly in the Middle and High Atlas ranges. These formations are large reservoirs that sustain the base flow of Morocco's major rivers. They measure up to 500 m thick in the calcareous High Atlas. Alpine karst is well developed with karren, dolines, poljes, and shafts in the higher altitudes of the High Atlas with good rainfall (600 to 1000 mm annual rainfall) and snow cover during winter. One of Africa's deepest caves, Kef Toghobeit (-722 m), is also developed in this formation, in the Rif (Northern Morocco). In the Middle Atlas, lower than the High Atlas, the karst landforms are also dense and various, but the limestones facies are not very

**Africa, North: Table 1.** Major Caves of Morocco.

Name	Region	Length/Depth
Wit Tamdoun	Tazroukht, Agadir	17500 m
Rhar Chara	Middle Atlas, Taza	7650 m
Kef Aziza	Central Atlas, Bou Denib	3950 m
Kef Toghobeit	Rif, Bab Taza, Chaouene	3918 m
Rhar Chiker	Middle Atlas, Taza	3865 m
Kef Toghobeit	Rif, Bab Taza, Chaouene	-722 m
Kef Tikhoubai	Middle Atlas, Taza	-310 m



**Africa, North: Figure 1.** The main karst regions and locations of the major caves in the Moroccan and Algerian sectors of the Atlas Mountains in North Africa.

good for cave development. The more frequent landforms are poljes developed upon the limestone plateaus. Among the other types of closed depressions are “issianes”, shallow basins due to superficial corrosion following the truncation of paleovalleys, and large dolines whose origin lies in the dissolution of underlying Triassic salt beds. In the fresh volcanic landscapes, rugged holes are scattered across the outcrops of basaltic sheets. Some may be related to the collapse of lava tunnels, but most are interstratal karstic collapses into the underlying limestones (Martin, 1981, and see photo in Dolines entry).

Middle and Upper Jurassic limestones are also very common in the High Atlas, Middle Atlas, and Eastern Morocco (c. 20000 km<sup>2</sup>). They are thinner and are less homogenous. Some interesting karst landforms have been described on these limestones including “wave karst”, a succession of small parallel dry valleys with asymmetrical dolines on the Ait Abdi plateau (Azilal), which are aligned with the main wind direction due to control by snow accumulations (Couvreur, 1974; Perritaz & Monbaron, 1998). On this plateau, an ancient cave network with vertical shafts suggests that climates were wetter in the past. Radiometric dating of speleothems yielded ages between 3200 and 220000 years, and some beyond the range of the U-Th method (>400000 years). The lateral flow is conducted by an interstratal network, inactive and dry in the upper part, but active at the base near the regional aquiclude, attesting three karstification phases. Morocco’s longest cave, the Wit Tamdoun underground river, is developed in Malm limestone, in the Western High Atlas, near Agadir.

Nearly everywhere in Morocco, karst springs are associated with calcareous tufas. Some deposits are very large and form attractive landforms, especially where they obstruct valleys. The Ouzoud cascades and the Imi n’Ifri natural bridge (Azilal) are well-known examples.



**Africa, North: Figure 2.** The Ighi bou Ilaghamane is a clean shaft in the floor of a dry valley in the Moroccan karst. (Photo by Pete Hart)

### Algeria

In Algeria people have used caves over a long period of time as shelters, sanctuaries, and sheepfolds. Cave wall paintings have been discovered in the shelters in Tassli N'Ajjer, in the southern part of Algeria. Many caves are still used today by shepherds (Collignon, 1997). The first modern cave explorations were by French scientists and speleologists at the beginning of the 20th century. In 1948, Anou Boussouil, then 505 m deep, was briefly the world's second deepest known cave, and the Tafna underground river was Africa's longest known cave in 1933. During the war for independence (1954–62), explorations could not be made, but caves were widely used as refuges, arsenals, or small hospitals. Systematic explorations by French and Belgian immigrants began again after 1973. Expeditions were organized by European cavers and geologists, and Algerian caving groups were founded, but the civil war that began in 1991 again stopped exploration. There are many small limestone ranges scattered throughout northern Algeria, and four terrains have been found to contain significant karst—the Oran Meseta (plateau), the Tell mountain ranges, the Constantine tabular massifs, and salt and gypsum diapirs.

The Oran Meseta are large karstic plateaus in western Algeria comprising some 6000 km<sup>2</sup> of mostly Jurassic limestone and dolostone between 800 m and 1500 m in elevation. Large underground rivers, siphons, and the main Algerian poljes are found there. In the Tlemcen and Saïda mountains, about ten streamsinks and springs have been dived, from which the country's largest underground rivers can be reached (including Tafna, 18.6 km of large galleries). These rivers are generally of low gradient and represent some of the region's main water resources, especially during the dry summer season. Some caves are used as pumping stations and speleologists have significantly contributed to their exploitation at Rhar El Khal and Hassi Dermam.

The Tellian Atlas contains many small karst areas, of which Djurdjura and Babors, composed of Jurassic and Eocene limestones folded into one another, are the most spectacular. The highest parts (c. 2300 m) are all composed of limestone. Classical high mountain range karst landforms (karren, snow pits, dolines, perennial underground ice) are well developed, in areas with the highest rainfalls in the country (more than 1000 mm a<sup>-1</sup>). In 1950, Anou Boussouil, a large pit in the Djurdjura, was explored to a depth of 505 m (the world's second deepest pit at that time). In 1980 it became Africa's deepest cave (-805 m). New groups of cavers came to Djurdjura and discovered Anou Ifflis (-1170 m, Africa's only cave >1000 m deep) and about 20 other pits, of which three are over 200 m deep.

In the Constantine region, Cretaceous neritic limestone with many dolines and shafts forms small anticlines that overlook the surrounding eastern Algerian plains in a terrain of 18000 km<sup>2</sup> where it is more than 300 m thick in the western part, becoming thinner in the east. Superficial karst forms are developed, but caves are rare.

In most of northern Algeria, Jurassic limestones overlie Triassic sequences with abundant salt and gypsum layers in anticlines,

**Africa, North: Table 2.** Major caves of Algeria.

<b>Name</b>	<b>Region</b>	<b>Length/Depth</b>
Rhar Bou Maza (Tafna)	Tlemcen	18600 m
Kef El Kaous	Traras	4160 m
Anou Boussouil	Djurdjura	3200 m
Anou Ifflis	Djurdjura	-1170 m
Anou Boussouil	Djurdjura	-805 m
Anou Achra Lemoun	Djurdjura	-323 m



**Africa, North: Figure 3.** The AA4 shaft on the Ait Abdi plateau in Morocco's Central High Atlas, that descends into a cave is rich in speleothems that are evidence of more humid climates in the past. (Photo by Luc Perritaz)

diapirs, or salt domes. The Djebel Nador, in the east of the country, possesses one of the largest diapiric structures in Africa. In such zones there are abundant dolines and pits. The rock is weak and roofs are often collapsed in many places, dividing long galleries into many smaller caves. In Algeria some of the world's deepest gypsum caves (e.g.

Dahredj Ghar Kef in Djebel Nador, 2450 m long, 212 m deep) and salt caves (El Outaya, –55 m) have been discovered. Salt outcrops are quickly dissolved by rainwater, and caves exist only in very dry regions with active diapiric uplift.

Algeria is tectonically active and has many thermal springs. Some of these hydrothermal flows cross the limestone massifs, where they have produced caves with cupolas and calcite and gypsum encrustations (especially when water contains carbon dioxide and hydrogen sulfide). The small Biban massif in the Tellian Atlas has some wonderful caves (Rhar Es Skhoun, Rhar Amalou, Rhar Medjraba) with very rare speleothems, but exploration is hindered by the high temperatures.

### **Tunisia**

In spite of the fact that a large portion of the Tunisian landscape is composed of limestone (or dolomite), there are only a few karstified ranges (for example djebels Zaghouan Oust, Ben Saïdane, and Fkirine, see Figure 1). In addition to this, the carbonates are relatively thin, except in the djebels Serdj, Bargou, Taboursouk, and Cap Bon. The Djebel Serdj (1357 m high) has been extensively explored and contains the country's largest cave networks: the Rhar Ain et Tsab cave (2700 m long, 160 m deep) and the Mine cave (also called Rhar Djebel Serdj cave, 1700 m long, 267 m deep). Lhopiteau (1980) grouped Tunisian caves into oasis caves (mainly short and dry); many types of southern djebel caves (in climatic transition zones); northern Tunisia caves (very similar to European ones); gypsum caves (small and not deep, with good mineral concretions); and thermal springs and caves.

### **Libya**

In spite of the desert climate, which is unfavourable for karstification, some remarkable caves have nonetheless developed. A gypsum karst is associated with the Upper Jurassic Bir al Ghanam formation, extending 100 km southeast of Tripoli to, and beyond, the border with Tunisia. The formation, which is 400 m thick and horizontal, consists of two gypsum beds separated by an essentially dolomitic bed. Both the upper and lower gypsum beds are karstified and contain numerous caves. Some 7 km of passage has been surveyed, including Umm al Masabih cave (3593 m long). The caves are mainly linear, carrying ephemeral streams (active several hours a year during rain-generated floods), and they display vadose morphology. Bedding planes and joints both play a role in passage development. In the karst, the upper gypsum is removed by erosion and the plateau surface lies on the more resistant dolomite. Underlying caves cause collapse features, and many of these contain cave entrances and swallets (Klimchouk *et al.*, 1996).

### **Egypt**

About half the area of Egypt is on outcrops of limestone and chalk, but there is minimal karst development in the harsh desert climates. A low plateau of Mesozoic and Tertiary limestones separates the Nile Valley from the sand seas of the Western Desert, and the same limestones extend eastwards to the north end of the Gulf of Suez. Across most of these areas, karst landforms are barely seen in terrains of bare rock escarpments and aeolian dune fields (Stringfield, LaMoreaux & LeGrand, 1974). The few small springs and caves are known because they provide water and shelter in the desert; typically, the location of St Antony's Monastery, east of Cairo, is due to its karstic spring and caves

(only a few metres long). In the Western Desert, the Farafra oasis is famed for its spectacular “White Desert”, a basin 100 km across distinguished by thousands of pinnacles of snow-white chalk that stand clear of the orange desert sand (Waltham, 2001). These are relict karst features, mostly pinnacles 2–4 m tall, but there are small areas of towers 10–15 m tall. They were formed in wetter climates of the late Tertiary, and are now being degraded by thermal shattering and aeolian sand abrasion. Travertines in the nearby Kharga oasis, which are now dry and largely predate 750000 years ago, are probably contemporary with the pinnacle and tower karsts. In the Eastern Desert, about 70 km southeast of Beni-Suef city, an unusual cave in alabaster was intersected by blasting. Sannur Cave is a crescent-shaped chamber which at 275 m is the largest cave in Egypt (Günay *et al.*, 1997).

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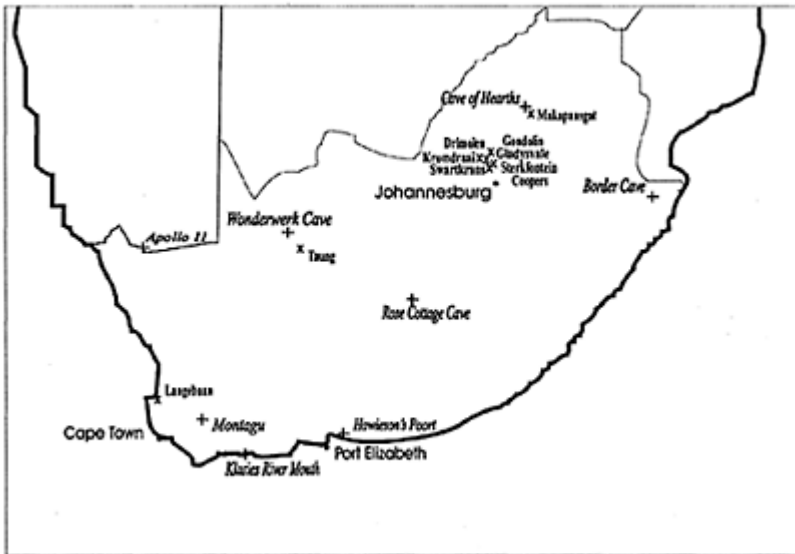
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## AFRICA, SOUTH: ARCHAEOLOGICAL CAVES

The archaeological caves of South Africa are remarkable in that together they contain a long history of evolution of hominids (hominins, by some authorities), beginning with the Australopithecines at over three million years ago, through to the first tool users in the early Stone Age (ESA; 2.5 million to 250000 years ago), the middle Stone Age (MSA; 250000 to 22000 years ago), *Homo sapiens* in the MSA (at least 100000 years ago) and the late Stone Age (LSA; 22000 to 2000 years ago) and up to the historical period (see Figure 1). The Iron Age in southern Africa is marked by the arrival of the taller Bantu-type peoples—farmers—into an area that had been predominantly bushman territory. The bushmen, mainly hunter-gatherers, are also noted for their rock art, and they currently live in the drier areas of southern West Africa.

The first Australopithecine to be uncovered was the Taung child skull found at the Buxton Lime Quarry, in the Kalahari Desert, near the Namib border in 1924. This site is not a cave but a very large set of tufa (travertine) deposits, and the skull was unearthed by blasting operations, along with fossil baboons and other fauna. Raymond Dart at Witwatersrand University, Johannesburg, assigned the skull to a new genus, *Australopithecus africanus* (meaning “southern ape” for the genus and “of Africa”



**Africa, South: Archaeological Caves: Figure 1.** Southern Africa locations of caves mentioned in the text. “X” marks the Australopithecine



sites north of Johannesburg. “+” signs represent *Homo* and later cave sites. Langebaan is an open-air site that has provided a rich source of mammalian fauna for the late Miocene. It has been used to aid faunal dating of Makapansgat and other Australopithecine sites.

for the species name) claiming a “missing-link” status for it. It took more than 30 years for the skull and similar finds to be accepted by British authorities, such as Sir Arthur Keith (of Piltdown fame), as being germane to the evolution of humans. By the association of the faunal remains at the site to similar dated fauna of East Africa, the Taung skull is currently reckoned to be about 2.4 to 2.6 million years old. Berger & Clarke (1995) have reconstructed an interesting story of how the skull and other fauna may have resulted from eagle predation.

The Australopithecine caves of South Africa formed in Proterozoic dolomites and, in addition to the usual clastic infill, originally contained massive amounts of pure speleothems in the form of stalagmites and flowstones. In the early part of the 1900s these speleothems were mined for gold extraction in the Witwatersrand goldfields around Johannesburg and Pretoria. The Australopithecine fossils turned up with the speleothems and with the unwanted breccias. Among the hominid finds was the skull, “Mrs Ples”, at Sterkfontein, blasted out of a flowstone in two pieces. Robert Broom, who came to be in charge of the acquired site, assigned it to *Plesianthropus transvaalensis*. Later, Robinson reassigned it to *Australopithecus*. Sterkfontein has turned out to be a rich site: the latest find, by Ron Clarke and Nkwane Molefe, being an almost complete skeleton known as “Little Foot” from the Silberberg Grotto near the bottom of a shaft inside the cave (Clarke, 1998). By magnetostratigraphy, the skeleton is currently assigned an age of between 3.30 and 3.33 Ma BP (Partridge *et al.*, 1999).

Across the shallow valley from Sterkfontein lies the mined site of Swartkrans. The fossil hominid sites of Sterkfontein, Swartkrans, and Kromdraai were declared a World Heritage Site in 1999. Swartkrans too contained *Australopithecus* remains, although the skulls of many of the finds are more robust than the early finds at Sterkfontein. The Swartkrans skulls possess a sagittal crest, more robust jaws and more massive molar teeth, indicating a more powerful masticatory action than the gracile Australopithecines of Sterkfontein and Makapansgat. The robust species are referred to either as *Australopithecus robustus* or to a new genus, *Paranthropus robustus*. There are active debates as to how distinct these genera are from each other and which of these or the East African Australopithecines is a direct ancestor to the *Homo* lineage. The later, long, excavation at Swartkrans was largely the work of C.K. “Bob” Brain, of the Transvaal Museum, Pretoria, who went about reconstruction of the stratigraphy in a painstaking enterprise (see Figure 2). Brain also tested Dart’s ideas about the nature of the remains at another site, the Makapansgat Limeworks Cave. This huge cave is in the Northern Province (old Transvaal) about 300 km north of the Johannesburg group. Dart had been shown shattered animal long bones that seemed to have been burned artificially. From

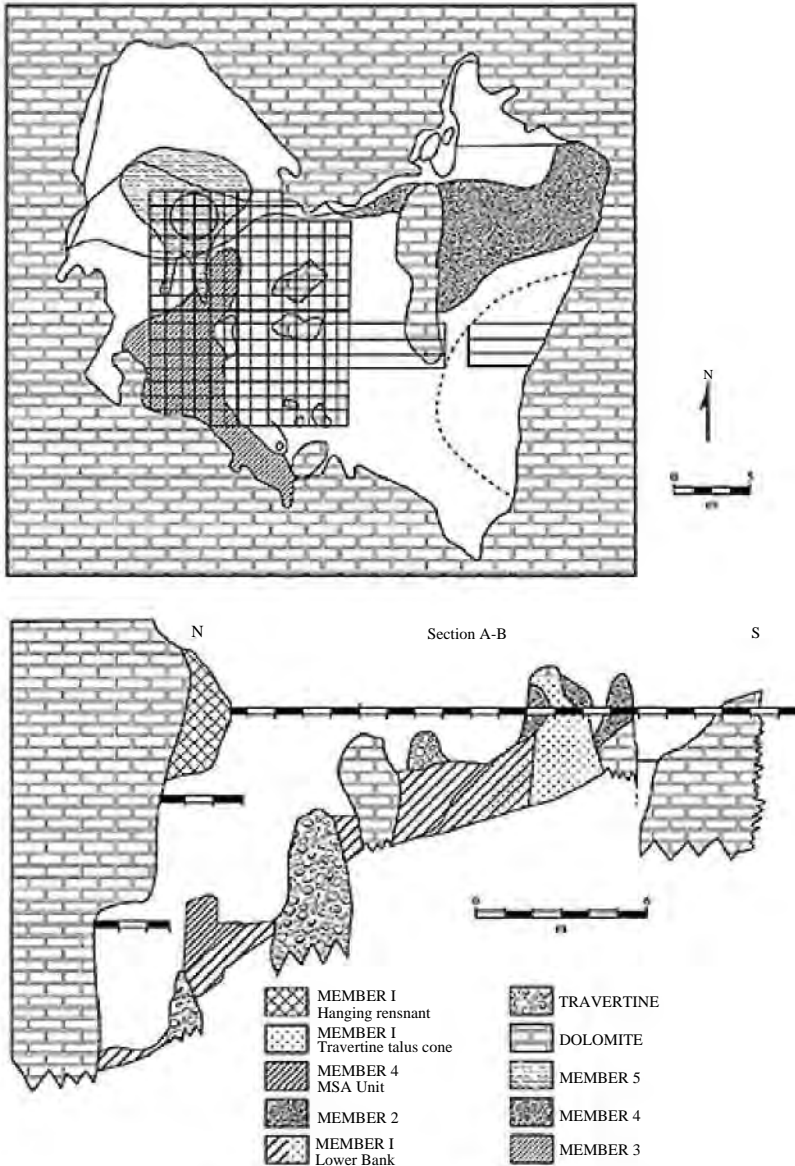
these, he pictured a savage Australopithecine culture using bones, teeth, and horns as weapons and tools and using fire inside the cave, and he coined the term “osteodontokeratic” (bone-teeth-horn) culture. It was later shown that the burnt appearance was due to infiltration by manganese dioxide, which is black. Brain carried out a series of heating experiments on bone to show how different stages of burning might appear on site. He and others also investigated hyena dens to show, firstly, that the thick bone accumulations at the Limeworks Cave and elsewhere were due to animal denning and, secondly, that the marks on the bones (when properly prepared from the matrix in the laboratory) were due to hyena tooth marks and the gnawing of other animals such as porcupines.

The study of how buried bones and artefacts result in their present state is known as taphonomy, and Dart and Brain are thus two of the earliest researchers to promote cave taphonomy. As an interesting example of a story in taphonomy, Brain showed fairly convincingly that the puncture marks on one of the juvenile Australopithecine skulls resulted from being dragged by a leopard to the cave site. The upper canines of a leopard closely fit the puncture marks in the top of the skull cap (calvaria). This in turn has implications on whether the cave functioned as an Australopithecines’ “home” site, in the way that baboons often use caves, or was a leopard (or felid) lair (Brain, 1981).

The later deposits of Sterkfontein, Swartkrans, and other caves have yielded remains of tool-making *Homo*, variously suggested to belong to either *H. habilis*, *H. erectus*, or *H. ergaster*. The remains occur together with some of the earliest ESA stone tools in the form of simple choppers of Oldowan type (Clark, 1993).

How are the remains and artefacts dated? The two main problems with all these sites is that they are very difficult to unravel stratigraphically and the deposits in which they lie are not readily amenable to direct, radiometric, dating. This is in contrast to their East African Rift, and Ethiopian, counterparts where there is often simple “layer-cake” stratigraphy and where there is often recognizable inter-site stratigraphic correlation. Riverine and lake sediments can be dated by magnetostratigraphy, and ash horizons are datable by potassium-argon (K-Ar) dating (or Ar-Ar dating).

The Johannesburg group of Swartkrans, Sterkfontein, Drimolen, Kromdraai, Gondolin, Coopers, and Gladysvale are mainly eroded rift systems to the surface (avens from below), with complex collapse phases of breccias and flowstones with uncertain contacts and rapid lateral changes of facies. Sterkfontein and other caves still possess streams flowing sluggishly under a low gradient. In most cases, the miners got there before the archaeologists, and their excavations reveal some relationships but obscure and confuse others. Magnetostratigraphy of the sediment and flowstone successions is also an uncertain game, since the various polarities that are recorded in the deposits are stretched and compressed due to different depositional rates and can therefore be fitted to almost any part of the global polarity time-scale (GPTS). As for radiometric methods, there are no ash deposits (no nearby volcanoes) and so Ar-Ar cannot be used. The hominid-bearing speleothem deposits are not less than 500000 years old, and so they are beyond the range of the U-Th method. Electron spin resonance (ESR) techniques have been tried at Sterkfontein, but the ages are thought to be tentative, mainly because of the difficulty of estimating reliably the longterm dose rates (see Dating Methods: Archaeological) (Schwarz *et al.*, 1994).



**Africa, South: Archaeological Caves: Figure 2.** Plan and section of Swartkrans Cave (from Brain, 1993, with permission). The section shows the cave in its present state of partial excavation.

The Makapansgat Limeworks Cave is different in that it appears to have operated as a huge resurgence to a mountain river system, probably in the late Miocene (ending at about 5.1 million years ago). Toward the end of its life about 3–3.5 million years ago, it contained an estimated 60000 tonnes of speleothems and thick layers of sediments and breccias. The present 2 ha cavern is an eroded remnant estimated to be about half its original height, revealing speleothems at the surface. Nearly all the speleothems have been mined out, although, interestingly, some distinctive subaqueous, mammillary, deposits are still in place. A number of Australopithecine remains were retrieved from miner's breccia dumps, and a 1 m thick bone breccia band, known as the "Grey Breccia" contained a dense assemblage consisting of over 80% bovid bones, the rest being baboons, equids, large felids, hyenas, Australopithecus, and smaller animals.

At about the same time as the Limeworks dumps were being sorted, from about 1945 to the 1960s, some of the Witwatersrand researchers (Van Riet Lowe, Kitching, Tobias, Hughes, Malan, and others) were working at another mine site about 1 km up the valley—the Cave of Hearths. Under the direction of Revil Mason, a long sequence of early *Homo* occupation layers were uncovered, containing stone tools from the ESA, MSA, LSA, and up to historic times. The Cave of Hearths, together with Wonderwerk Cave, Northern Cape, and Montagu Cave in the Western Cape, is one of the few South African caves to contain artefacts of the Acheulian culture (MSA) (Deacon & Deacon, 1999). As Mason blasted his way down through the calcite-hardened breccias he uncovered hearth-like structures firstly in the upper layers and then toward the base. Tentative claims were made for the earliest known use of fire although this still remains to be substantiated. This site has undergone recent reappraisal, chiefly by a team from Liverpool University (England). The lowermost archaeological layers are normally magnetized, showing that they are less than 780000 years old. The sediments contain no associated speleothems in the unexcavated sediment left as a witness section that might lend themselves to U-Th dating, and they are probably too old for thermoluminescence or optically stimulated luminescence dating. In comparison to Wonderwerk Cave, the Cave of Hearths has a much lower density of faunal material, and this suggests that it probably did not operate as a home base in the way that was once thought likely.

In 1925, a poorly excavated skull, with a brain capacity of 1280 ml and with some Neanderthal-like features, was unearthed from a fissure in a dolomite cave at Kabwe (the Broken Hill lead-zinc quarry), in Zambia. The maxilla shows dental caries and abscessing, and Bartsiokas & Day (1993) have suggested that the skull displays evidence of lead poisoning.

Those sites of the Middle Stone Age that contain not only artefacts but also human remains are relevant to the question about the transition of *Homo erectus*, associated with the Acheulian hand-axe technology, to *Homo sapiens* associated with the Upper Paleolithic (in Europe) and more sophisticated stone tools of the preformed core type (in Europe, the Levallois technique). Migration of *Homo erectus* out of Africa (the migration known popularly as "Out of Africa I") is thought to have occurred between 1.5 and 2 million years ago. In Europe, these hominids were succeeded, probably ancestrally, by the Neanderthals. When and where the first anatomically modern humans appeared also finds its answers in Africa. Several DNA studies suggest that humans appeared in Africa at about 200000 years ago. In South Africa, there are several caves containing modernlooking skeletal remains, including Klasies River (Mouth) Cave and Border Cave.

Klasies River Cave, near Port Elizabeth, is a set of openings, 6 to 18m above sea level. It was excavated by Wymer and Singer from 1967 to 1968 (Singer & Wymer, 1982) and then again by H. Deacon in the 1990s. The human remains uncovered included jaws, teeth, and fragments of crania (Rightmire & Deacon, 1991) that have been dated faunally and by ESR to between about 115000 to 60000 years ago (Klein, 1999). In Europe, by contrast, the first anatomically modern humans (AMH; old term, Cro-Magnon) succeeded the Neanderthals from about 40000 to 30000 years ago (Eastern Europe to Iberia). It should be realized that although this discussion restricts itself to evidence from cave sites, there is a broader picture of hominid evolution and culture from all African sites. Although many archaeologists and paleoanthropologists are persuaded by the origin of modern humans by replacement out of Africa (“Out-of-Africa II”) there is a sizeable minority that thinks that modern humans evolved more or less in every region of the Old World (including, possibly, Australia which appears to have witnessed the first entry of humans about 40000 to 60000 years ago). Milford Wolpoff is the chief dissenting voice on the Out-of-Africa II migration, but see also, for example, Smith (1992) and, for the argument itself, see Delson *et al.* (2000).

Near the Cape, around 1910, John Hewitt excavated a rock shelter at Howiesons Poort and uncovered a fine, small, and distinctive stone tool technology of the MSA that was not to be approximated till the late Stone Age (22000 to 2000 years ago; Deacon & Deacon, 1999). The fine blades appear to have supported hafted tools, and the Howiesons Poort technology has been found at many other sites in southern Africa, including Klasies River Mouth Cave and in Nelson’s Bay Cave, between the Cape and Port Elizabeth. At Rose Cottage Cave, excavated currently by Lyn Wadley of Witwatersrand Archaeology Department, there was occupation before and after Howiesons Poort times. Dated to between 70000 and 60000 years ago (Vogel, 2001), the Howiesons Poort culture is used as a marker horizon in southern African sites as far north as Lake Eyasi in central Tanzania and west to the Apollo 11 Cave in Namibia (Deacon & Deacon, 1999).

Many archaeologically important cave sites are situated on the southern coast, and they are important as recorders of the use of seafood. Sea levels were high around 125000 years ago during interglacial isotope stage 5e, and this appears to have resulted in the scouring of the Klasies River Mouth Cave openings. After that, as sea levels fell, the evidence suggests that the caves were occupied sporadically by hunter-gatherers who scavenged and hunted seals and penguins and also lived off shellfish.

The fact that the MSA human skeletal remains are thought to be modern has suggested to some anthropologists that fully modern humans came out of Africa at least by 120000 years ago (the “Out-of-Africa II” event—see Carmel Caves, Israel: Archaeology). The aforementioned Howieson’s Poort MSA technology has also featured in this issue (Parkington, 1990). A reconstruction of ash layers, tools, various adornments, and other cultural evidence on site, has prompted Deacon & Deacon (1999) also to suggest that, “They were probably the direct ancestors of the Later Stone Age peoples”—and that must include the Bushmen of today. In effect, the Bushmen of southern Africa may well be the direct descendants of the earliest humans. This adds impetus to the great interest in old and new Bushman wall paintings.

ALF LATHAM

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### Further Reading

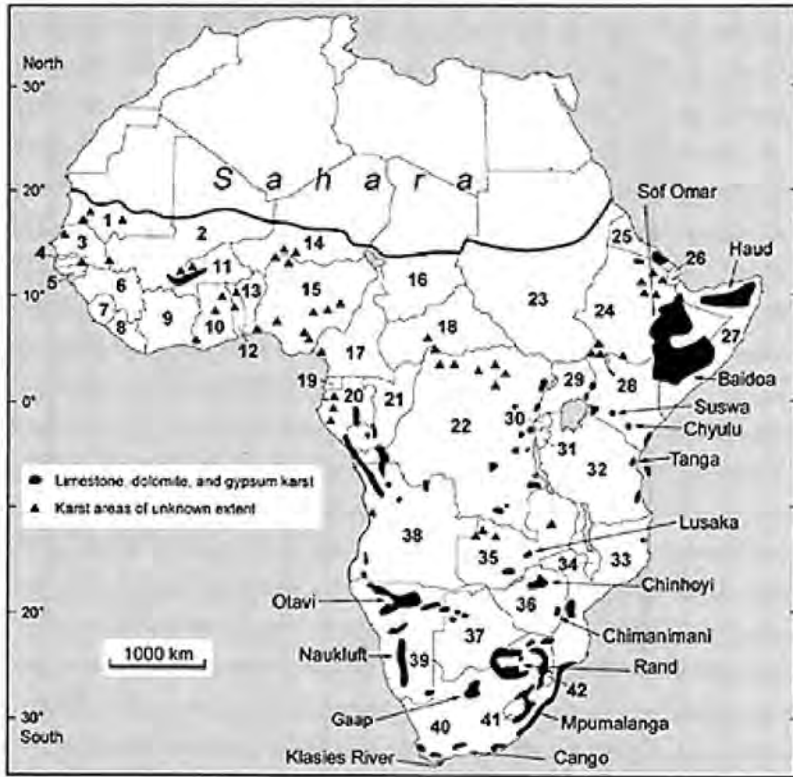
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## AFRICA, SUB-SAHARAN

Sub-Saharan Africa has 42 countries, climates ranging from humid tropical to arid, and a predominance of ancient Precambrian rocks. Although only a small proportion of the area is karst, and many of the karst areas have never been fully explored, the subcontinent has many significant sites: caves with early hominid remains dating to 4.5–5.0 Ma, the largest underground lake in the world and the fourth deepest siphon, a 305 m deep cave in quartzite, the sixth and ninth longest lava tube caves in the world, caves in pyroclastics that are frequented by elephants and buffalo to lick salt from their walls, and a cave with 5 m speleothems in the floor of an active volcanic crater. It also has an example of the rare labyrinth karst landform, human-induced subsidence into karst cavities as a result of gold-mining activities, and a sea cave in quartzite with large carbonate speleothems and the remains of the first modern humans.

**Caves:** The two longest caves in sub-Saharan Africa are Sof Omar in Ethiopia and Apocalypse Pothole in South Africa, both of which are maze caves. Sof Omar (see separate entry) is 15.1 km long but only 1.2 km of this is river passage, the remainder being in a maze formed near the resurgence, giving the cave a total of 42 entrances. Apocalypse Pothole in dolomite has 12.1 km of mapped passages. The deepest caves are Mwenga Mwena (Zimbabwe) in quartzite (–305 m), and Bushmangat (South Africa) in dolomite (–295 m). Congo Cave (5.3 km long) in the Western Cape of South Africa is the most important tourist cave and is possibly the best decorated.

The sub-continent has spectacular cenotes, as well as caves with large underground lakes. In the Otavi Mountains of Namibia are the cenotes of Aikab, Aigamas, Guinas Lake, and Otji-



**Africa: Sub-Saharan: Figure 1.** The main karst areas of sub-Saharan Africa. Nations are numbered:

- 1=Mauritania.
- 2=Mali. 3=Senegal.
- 4=Gambia. 5=Guinea Bissau.
- 6=Guinea. 7=Sierra Leone.
- 8=Liberia. 9=Ivory Coast.
- 10=Ghana. 11=Burkino Fasso.
- 12=Togo. 13=Benin. 14=Niger.
- 15=Nigeria. 16=Chad.
- 17=Cameroon.
- 18=Central African Republic.



- 19=Equatorial Guinea. 20=Gabon.  
21=Congo. 22=Zaire. 23=Sudan.  
24=Ethiopia. 25=Eritrea.  
26=Djibouti. 27=Somalia.  
28=Kenya. 29=Uganda.  
30=Rwanda.  
31=Burundi. 32=Tanzania.  
33=Mozambique. 34=Malawi.  
35=Zambia. 36=Zimbabwe.  
37=Botswana. 38=Angola.  
39=Namibia. 40=South Africa.  
41=Lesotho. 42=Swaziland.

koto Lake (see Figure 2), and also underground lakes at Harasib and Dragon's Breath. The latter, discovered in 1986, may have the largest underground lake in the world, 260×180m, more than 90 m deep, and 60 m below ground. Harasib Cave is the fourth deepest cave on the subcontinent (-210m) with a lake 135×35m and 90 m deep. Lakes in Aikab, Guinas, and Aigamas



**Africa: Sub-Saharan: Figure 2.**  
Otjikoto Lake, a cenote in the Otavi  
Mountains of Namibia. (Photo by  
Tony Waltham)

are 120×100×63m deep, 145×70×120 m deep, and 115 ×0×40 m deep. Guinas is one of two sites with the multicoloured indigenous fish, *Tilapia guinasana*, while Aigamas is the only site with the catfish, *Clarias cavernicola*. Otjikoto Lake, 100 m in diameter and 75 m deep, is a National Monument because during World War I German troops dumped Krupp ammunition wagons and field guns into the lake before surrendering to British troops. Today this military equipment is an underwater museum at depths of 48–52 m. Divers have recovered speleothems up to 130 ka old from depths up to 40 m in the Otavi lakes, indicating much lower ground water levels in the past. The Wonderhole at Chinhoyi Caves, northwest of Harare, Zimbabwe, is a circular cenote 46 m in diameter and 190 m deep, with a 144 m deep lake—the Sleeping Pool. Bushmangat in the Gaap Plateau dolomites of the Northern Cape, South Africa, contains a lake 30×12 m at the surface and 264 m deep, making it the fifth deepest siphon in the world. The lake widens to 247×75 m in plan extent at a depth of 100m.

Three of the five deepest caves in sub-Saharan Africa are in the Chimanimani Mountains of eastern Zimbabwe in quartzite: Mawenga Mwena (–305 m), Jungle Pot (–221 m), and Bounding Pot (–194 m). Big End Chasm has the world's largest chamber in quartzite: 90 m high and 70×15 m in plan. The famous Klasies River Mouth sea caves on the South African Tsitsikama coast are also in quartzite. They contain the oldest remains of anatomically modern humans, dating to more than 100 ka (see entry Africa, South: Archaeological Caves), and also house carbonate speleothems up to 1 m in diameter and 4 m high, deposited by dripwaters draining from shell-rich aeolian sands on the surface above the cave.

The largest and most important caves in East Africa are in volcanic rocks. Kenya has the sixth longest lava tube cave in the world, Leviathan Cave, 12.5 km long and 3–10 m in diameter; the ninth longest, Mount Suswa, at 11.0 km; and six of the top 60. Almost 100 lava tube caves are known in the Chyulu Range between Nairobi and Mombasa, while Mt Suswa has 40 caves in an area of 3 km<sup>2</sup> that are segments of a complex braided tube system with up to 3 levels of passages, and 67 entrances. Passages are 6–10 m in diameter increasing to 20–30 m where collapse has occurred. The 19th longest lava tube cave in the world is Ubuvomo bwa Musanze on Mt Ruhengeri in Rwanda at 4.6 km and 210m deep, while nearby Ubuvomo bwa Nyrabadogo is 1.5 km long. All are developed in pahoehoe lava flows and various caves have lavafalls 10m high, lava stalactites and flowstones, rare silica dripstones and flowstones, calcium phosphate deposits beneath bat guano, and bones of rhino, giraffe, leopard, baboon, and antelope.

In 1990, Hades Cave was discovered in the crater floor of Oldoinyo Lengai in northern Tanzania, the world's only active carbonatite volcano. The cave, 20–30 m in diameter and 5–8 m deep, was formed by the collapse of the 0.5–1.0 m thick roof of an old spatter cone. Pale yellow stalactites 1–4 cm in diameter and up to 5 m long stretched from the ceiling, probably formed from lava spatters that stuck to the roof of the void. As there was considerable volcanic activity within 100 m of the cave, it probably did not survive for long.

There are also numerous small caves in tuffs and agglomerates; these are up to 300 m long but have breakdown chambers up to 100 m wide, the best known being Kitum and Makingen caves on Mt Elgon in Kenya. The entrances to these caves are behind waterfalls and are frequented by elephant and buffalo for the salt they contain, as seen by tusk marks on the walls.

Many dolomite caves in southern and eastern Africa are water-table caves formed by solution in the upper part of the phreatic zone. Lowering of the water table focused solution deeper in the dolomite and left upper passages aerated and open to the surface via vertical shafts allowing the influx of soils and making them death traps for animals falling into them. In Botswana, Angola, Namibia, and South Africa caves of this kind contain fossiliferous, cemented breccias of middle Miocene to Holocene age that include baboon, hominoid, and hominid remains. At Berg Aukas, Namibia, remains of two hominoids, 13 and 9–10 Ma old, were recovered from sediments in dolomite fissures. Several dolomite caves northwest of Johannesburg, South Africa, including Sterkfontein, and Makapansgat Limeworks near Potgietersrus, contain important fossils. Basal breccias at Sterkfontein in the upper, older part of the cave are more than 4 Ma old, and an almost complete hominid skeleton recovered from the cave is 3.30–3.33 Ma old.

**Surface karst** varies considerably across the region in response to both the climate and the rock lithology. In the humid tropics, rare labyrinth karst has formed in the Tanga limestone of Tanzania, with fissures up to 15 m deep and 1–2 m wide isolating sharp pinnacles and ridges and in places coalescing to form internal closed depressions. Cone and tower karst with depressions occurs in an area including parts of south Congo, western Zaire, and Angola. Elsewhere on the subcontinent doline karst is more typical with occasional uvalas and poljes. Coastal limestones in Western Cape, South Africa, have closed depressions up to 20 km long, dry valleys, large springs, and extensive dry phreatic cave systems. Hundreds of shallow dolines, dry valleys, and depressions up to 8 km long dot the covered karst near Alexandria, Eastern Cape. The Gaap Plateau, Northern Cape Province is pockmarked by closed depressions with ephemeral lakes typically 3–5 m deep and 100–500 m long, while strings of dolines 5–10 m deep mark old stream drainage lines. There is also doline karst in calcrete 5–10 m thick in the upper catchments of the Tsondab, Gaub, and Kuiseb rivers of the central Namib Desert where annual rainfall is only 150–250 mm. This karst extends from the escarpment westwards for 40–50 km with dolines up to 25 m across and 2–3 m deep.

Lusaka, the capital of Zambia, sits atop a marble plateau with dolines 10–100 m across and up to 10 m deep. Almost everywhere the marble is buried beneath a shallow layer of lateritic gravel. As there is no surface drainage, the marble surface is susceptible to flooding after very heavy rains when infiltration capacity is exceeded. The worst flooding was in 1926 when the whole township was flooded and boats were rowed down Cairo Road in the city centre. Despite construction of flood drains the city was flooded again in 1978–79. In areas where the lateritic gravels have been excavated, marble pinnacles 3–10 m high have been exposed (see Figure 3). The pinnacles are disappearing rapidly as they are being broken into pieces for sale on the street as aggregate.

The Rand gold mining area of South Africa, west of Johannesburg, is perhaps the best-known area of karst in the subcontinent. Gold is found in beds of quartzite and conglomerate overlain by 1220 m of dolomite largely hidden beneath 9–150 m of unconsolidated sediment. The dolomites are divided into water compartments by a series of vertical syenite dikes. To facilitate mining, groundwater was pumped from the Venterspost compartment in 1955, and from the Oberholzer and Bank compart-



**Africa: Sub-Saharan: Figure 3.**  
 Marble pinnacles exposed from  
 beneath lateritic gravel in Lusaka,  
 Zambia. (Photo by George Brook)

ments in 1960 and 1972, the watertight nature of the dikes making it possible for each compartment to be de-watered independently. By 1957 sinkholes appeared in the Venterspost compartment by compaction of surficial sediments (up to several km long) and by their collapse into subsurface cavities. In 1962 a vertical-sided sinkhole, 55 m across and 30 m deep, formed in the Oberholzer compartment, engulfing the crushing plant of the West Driefontein mine and causing 29 deaths. As sinkholes continued to develop, some small towns had to be evacuated. In 1964 the West Driefontein mine was extended into the Bank compartment which had not been de-watered. On 26 October, 1968 a fissure opened up in the roof of the workings beneath the Bank compartment and a torrent of water flowed in. Fortunately, 13500 men were evacuated safely but it took 26 days to stem the flow of water. The source of the inrush was the saturated, cavernous dolomites of the Bank compartment with 850 m head. Following the disaster the Bank compartment was de-watered.

Evaporite karst is unusual in sub-Saharan Africa but is well developed in gypsum and anhydrite on the northern Haud Plateau in Somalia. Shallow solution dolines up to 100 m in diameter are common, while many collapse dolines up to 50 m in diameter and 15m deep lead into caves 0.5–20 m below the surface, such as Ail Afwein (1275 m long) and Las Anod (1455 m long). Many caves contain water that is used for camels and goats.

Gypsum speleothems and crystals are common, and hyenas occupy many entrances. On the limestone Baidoa Plateau in southern Somalia there are several 1–3 km long structural/erosional basins with lakes including those at Ted, Moragavi, and Burdo. In the east, the plateau has a thick soil cover and some of the numerous shallow depressions contain perched water bodies.

Quartzite karst has developed in eastern Mpumalanga Province, South Africa (see Silicate Karst) where dolines with pinnacled slopes occur along abandoned streamlines in 20–25 m of quartzite resting on granite. Seventeen caves up to several hundred metres long are known, some with vertical shafts to 20 m deep and chambers 60×25 m and 15 m high. Most have water flowing through them, disappearing and reappearing several times. Small limonite stalactites and flowstones are present. Quartzite karst has also developed in the Cape Peninsula of South Africa including numerous small caves, with Ronan's Well the longest at over 700 m.

**Spring and waterfall tufas** occur in semiarid and arid parts of sub-Saharan Africa. Notable are the massive, relict, perched spring and waterfall tufas in South Africa, Namibia, and Somalia, and there are smaller examples in southeastern Zimbabwe. Since the Miocene, thick masses of tufa have accumulated along the dolomite Gaap Escarpment of South Africa, particularly in gorges cut back into the scarp. Individual tufa masses such as Gorrokop are 1.8 km long and average about 30 m thick. At Buxton-Norlim, in 1924, the famous type specimen of the species *Australopithecus africanus* was discovered in the Thabaseek tufa carapace, which was being quarried for lime. Smaller waterfall tufas about 45 m across and 10m high, but up to 1200 m across and 30 m high, occur as plugs in incised valleys of dolomite areas in Northern and Mpumalanga Province. Numerous massive waterfall tufas occur at different elevations in the Naukluft Mountains of Namibia, a dolomitic nappe complex. The Blässkranz tufa, 500 m long and 150m high, becomes a huge waterfall after uncommon heavy rains. Large waterfall tufas also occur in Kaokoland near Warmquelle, in the Kuiseb River Valley where average annual rainfall is less than 50 mm, and in the Swartkloof Mountains of southwest Namibia. The largest tufas in Somalia are around the southeastern edge of the Baidoa plateau at Deileb Wane and Isha Baidoa. At Isha Baidoa the tufa is more than 20 m thick and extends for hundreds of metres along the escarpment. In northern Somalia relict spring and waterfall tufas up to 300 m long and 40 m high are found at several locations in the Golis Mountains and on the Gulf of Aden coast.

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## AFRICA: BIOSPELEOLOGY

Africa spans temperate to tropical latitudes, with a great variety of different ecosystems, making it an extremely varied continent with high levels of biodiversity. Few zones have been explored from a biospeleological perspective, nonetheless the results obtained so far show considerable subterranean diversity. Biospeleological research began in the first decades of the 20th century and was concentrated in eastern (Ethiopia, Kenya, and Somalia), northern (especially Morocco), and southern (Namibia and South Africa) Africa, and on Madagascar. Several researchers explored these territories and collected a large amount of zoological material.

The French zoologists C.Alluand and R.Jeannel were among the first to research in detail the subterranean fauna of Africa. In 1911–12 they visited several African countries where they collected a large amount of troglobitic material, and the first African stygobites. The results of their research were published in *Biospeologica* (Jeannel & Racovitza, 1914), where the first review of several African caves and their fauna can be found. In the 1950s, French scholars led extensive research in Madagascar, while more recently activity has been re-established in northern Africa by French and Moroccan researchers and, in southern Africa, by Namibian and South African researchers. At the beginning of the 20th century and later, in the 1970s, Italian researchers collected and presented data on biospeleological aspects of Ethiopia and Somalia. In the rest of the continent biospeleological research has been sporadic and scattered.

African caves host almost all animal taxa, with many troglaphiles and troglaxenes, but only a few troglobites. Stygobites, stygophiles, and stygoxenes on the contrary are numerous and are primarily restricted to karstic areas developed in the limestone deposited during Cretaceous (*c.* 100 million years ago) marine invasions. In some cases,

such as Amphipoda and Isopoda of eastern and southern Africa, these are apparently the only representatives of the taxa in the region.

Although the continent has not been extensively explored from a biospeleological perspective, the list of African subterranean-dwelling animals is long. Excluding Protozoa, flatworms, worms, and all hyporheic (interstitial spaces within the sediments of a stream bed) and marine interstitial (living in the spaces between sand grains) taxa, the subterranean African diversity is presented below by taxa.

### **Mollusca**

A number of terrestrial and aquatic snails and clams are reported from African caves, although no true troglobitic species are known.

### **Crustacea**

The presence of Copepoda in subterranean waters in Africa has been reported from almost every explored area; however the reports are scattered and fragmentary. Ostracoda is a widely distributed taxon in subterranean waters, although few species are strictly stygophilic or stygobitic. A single stygobitic species has been found in Zaire and several others in the wells of Somalia. Of the Malacostraca, several African forms of Bathynellacea have been described, mostly interstitial. Several species of Thermosbaenacea are reported from African subterranean waters (Morocco, Somalia, South Africa, and Tunisia). The first to be described was *Thermosbaena mirabilis* from the El Hamma hot springs in Tunisia. No stygobitic Mysid (Mysidacea, or Opossum shrimps) is present in Africa, though stygophilic species are reported from Kenya, Madagascar, Aldabra, and Zanzibar Islands. A single species of Spelaeogriphacea, *Spelaeogriphus lepidops*, has been described from South Africa.

There are many stygobitic Isopoda species distributed in eastern, western, northern, and southern Africa belonging especially to the Cirolanidae and Stenasellidae families. Some of them show a striking aspect such as the *spiny Acanthastenasellus forficuloides*, known from a single female specimen collected in Somalian subterranean waters. Subterranean species of African terrestrial Isopoda are mostly troglomorphic. Only termitophilous taxa show true troglobitic adaptations.

Amphipoda has many stygobitic species, belonging to several families (Hadziidae, Salentinellidae, and Gammaridae being the most represented), distributed in eastern, western, northern, and southern Africa.

Of the Order Decapoda (shrimps), several stygobitic and stygophilic species of the Athyidae family are found in Kenya, Madagascar, Somalia, Tanzania, and Zaire. One species of the Palaemonidae, *Typhlocaris lethaea* from Libya and several stygoxene decapods of the Penaeidae and Athyidae families are also present in African caves.

### **Onychophora**

Only two true troglobitic species of velvet worms exist in the world, of which one, *Peripatopsis alba*, lives in a South African cave.

### **Arachnida**

The best-represented arachnid orders in African caves are the Scorpiones (scorpions), Pseudoscorpiones (pseudoscorpions), Solifugae (sun-spiders), Araneae (spiders),

Opiliones (harvestmen), Amblypigi (whip spiders), and Acari (ticks and water mites). It is impossible to enumerate all the Arachnida that can be found waiting for their prey in African caves. Numerous parasitic ticks live on bats, and terrestrial taxa that are associated with guano, predate on eggs or insect larvae, feed on fungi, or scavenge are common in caves. Several water mites (Halacarids and Hydracarids) can be found in subterranean waters.

### Myriapoda

Centipedes (Chilopoda) are often present in caves, although no troglobites are reported so far from Africa. Millipedes (Dipolopoda) are present with a few troglphilic and troglxene species in caves. In Somalia specimens of *Graphidostreptus gigas* were found in Showli Berdi cave.

### Hexapoda

Although numerous species of springtails (Collembola) have been found in African caves, only two species from Madagascar are described as true troglobites: *Cyphoderopsis madagascarensis* and *Troglobius coprophagus*. Only one Diplura genus, *Anysocampa*, is reported from the Ethiopian region. A single species is truly troglobitic in Zaire, *Austrjapyx leleupi*.

### Insecta

Only one species of silver fish (Thysanura) is reported from South Africa as troglobitic, *Lepidospira makapaan*. Cavernicolous or troglphilic Orthoptera (crickets) are present in most African caves, they are mostly scavenger and detritus feeders. They belong to only two families, the Phalangopsidae and Rhabdiphoridae. The fleas (Siphonaptera) are well known to any speleologist and to those working in African caves in particular. They cannot be considered true cavernicoles because they are all parasites of vertebrates such as bats, and belong to the subterranean world only because of this specialization. No troglobitic species of wasps or bees (Hymenoptera) are known but many nest at the cool and dark entrance of many caves in Africa. They are quite aggressive, especially the bees, thus making some caves a risky place to enter. Beetles (Coleoptera) are the most diversified insect taxon to have colonized the subterranean environment. They are present in African caves especially with many carabids (ground beetle), cholevids, curculionids (snout beetle), pselaphids, staphilinids (rove beetle), and even with aquatic forms of the Hydrophilidae and Dytiscidae families (diving beetle). Only one earwig (Dermaptera) species is known from Africa. This is the first ever described species of a troglobitic earwig, *Dyplatis milloti*. Of cockroaches (Blattodea), only the family Nocticolidae has troglobitic species in Africa, where several troglphilic species are present. Cicadas and aphids (Homoptera) have very few cave representatives in Africa: one species of Hypochthonellidae in Zimbabwe and only one troglobitic species of Cixidae in Madagascar. Only a few species of moths (Lepidoptera) of the families Oecophoridae, Plutellinae, Alucitidae, and Noctuidae have been so far reported from African caves, but they cannot be considered troglobitic species. The four reported African species of troglobitic flies (Diptera) have guanophagous (feeding on bat guano) larvae and haematophagous (blood-sucking) adults.



## Fish

Eight species of cave-dwelling fish were described in Africa between 1921 and 1959: *Caecobarbus geertsii* (former Zaire); *Uegitglanis zammaranoi* (Somalia); *Phreatichthys andruzzii* (Somalia); *Barbopsis devecchii* (Somalia); *Typhleotris madagascariensis* (Madagascar); *Clarias cavernicola* (Namibia); and *Typhleotris pauliani* (Madagascar). The first cave-dwelling fish, a small cyprinid discovered in 1921 in the Belgian Congo, was the first subterranean fish in the world to be officially protected (by the Belgian colonial authorities). Somalia has the highest cave fish diversity in Africa, with three species. Italian interest has remained strong and these species have been extensively studied in recent years.

## Amphibia and reptiles

Several toads and frogs searching for cool, humid places rich in insects, can be easily found in African caves. No troglobitic snake or lizard has been recorded in any African cave. Most of the reptiles enter the caves to feed on bats, bird eggs, or mice as is the case with *Naja* sp. (cobra), *Bitis* sp. (puff adder), and *Varanus* sp.

## Birds

Several species of swallows (*Apus* sp.) inhabit the entrances of African caves, but so far none is reported to have adaptations like those observed for Asian species, which use echolocation deep in the cave. Only one other bird has been reported to nest inside caves in Africa, *Picathartes orea* (bald picathartes) of Gabon.

## Mammals

Several species of mammals spend part of their time in caves. Bats are certainly the best-represented group: several insectivorous and frugivorous bats roost in African caves, often forming huge colonies. Other mammals, especially the Insectivora and Rodentia such as the Hystricidae (Old World porcupines), may be found in caves, even in the deeper zones. The signalled presences of Carnivora especially felids such as the African wildcat (*Felis lybica*) or the leopard (*Panthera pardus*) are numerous. The African elephant *Loxodonta africana* has been documented to enter the Kitum Cave (Mt Elgon, Kenya) and to dig with its tusks the salt that can be found there.

GIUSEPPE MESSANA

## Further Reading

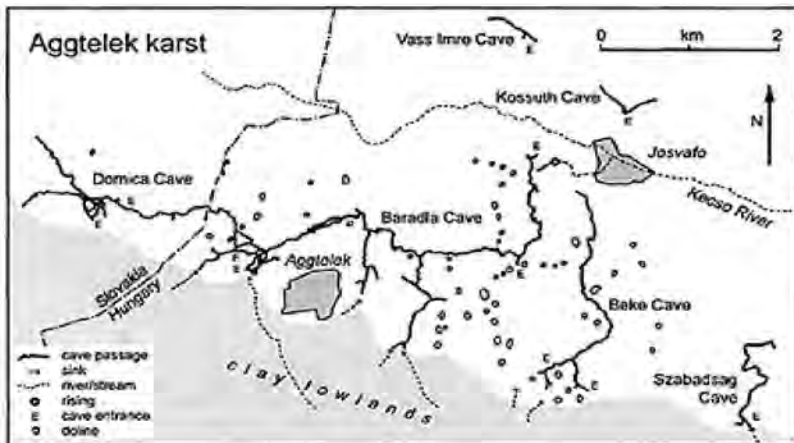
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## AGGTELEK AND SLOVAK KARST, HUNGARY-SLOVAKIA

The Aggtelek and Slovak area comprises a major karst region, in which the caves have been designated as a World Heritage Site, approved in 1995. It straddles the southern foothills of the Carpathians, and consists of the Aggtelek National Park and Biosphere Reserve in Hungary (19708 ha) and the Slovak Karst Protected Landscape Area and Biosphere Reserve in Slovakia (36165 ha), together with the nearby Dobšina Ice Cave. Topographically, the main block comprises a series of rolling plateaux in thick limestones and dolostones, dissected by a few deep river valleys. Relief ranges from altitudes of 200 to 900 m. Geologically, it is a part of the Szilice Overthrust in the Carpathians, displaying complex, highly deformed structure. More than 700 solution caves are known. The climate is humid continental, with mean annual temperatures between 5 and 12°C and 600–1000 mm precipitation, depending on altitude. Natural vegetation is an oak, hornbeam, and beech deciduous forest.

### Aggtelek-Domica Region

The principal karst area is shown in Figure 1. The limestone (Wetterstein Formation) and dolostone (Guttenstein Formation) are platform deposits of Triassic age, uplifted and deformed during the Cretaceous. Denudation commenced in the late Cretaceous under tropical or subtropical conditions, forming *terra rossa* soils, with some bauxites in karst depressions. In the mid-



**Aggtelek and Slovak Karst: Figure 1.** Outline map of the cave systems within the Aggtelek karst beneath the border between Hungary and Slovakia.

Tertiary (Miocene), the region was partly buried by deposits of the Pannonian Inland Sea, chiefly sands and clays from the mountains further north. Erosion has since exhumed the higher ground, which now forms a rounded massif to altitudes of 450–500 m, above remaining clay lowlands at *c.* 300 m. Kecso River (Figure 1) entrenched the massif, permitting early springs to drain to it, at an altitude of *c.* 270 m. A knickpoint has receded through the Kecso valley, lowering modern spring levels to 220–230 m. The region experienced severe cold at times during the Quaternary, with solifluction and other periglacial features indicating periodic loss of natural forest cover, although there was no growth of glaciers (Zambo, 1993).

It is important to appreciate that the modern (post-Pannonian) karst has developed upon an older, well-fissured subtropical karst that remains partly buried. The principal surface karst landforms are shapely solution dolines, 10–100 m in diameter and up to 30 m in depth. Larger examples retain Pliocene sediments at their bases, covered by a few metres of colder climate brown or black earths, with up to one metre of man-induced erosional detritus on top. A few have become blocked, creating ponds. Modern dissolutional activity is studied intensely in Beké Doline, a major karst monitoring site (Zambo & Ford, 1997). There are also extensive subsoil karren, frequently exposed by erosion.

The principal caves are excellent examples of dendritic river cave development of the water table-shallow phreatic type (Ford, 2000). Baradla-Domica Cave (24 km long) is the lengthiest, an underground linking of six streams that collect on the clays and sink at the limestone contact (Figure 1), plus rivulets from the overlying karst. The entrance galleries at Aggtelek and Domica have a complex, multi-level structure, apparently due to Quaternary episodes of clastic filling, with paragenesis and incomplete re-excavation (Bolner-Takacs *et al.*, 1989). The main trunk passage is slightly sinuous and *c.* 7 km long. It descends through the highly deformed strata, at a regular gradient of 4–8 m km<sup>-1</sup>. Its cross-sectional area *decreases* downstream, despite the addition of tributary streams, due to progressive undercapture to modern springs downstream of the Kecso River knickpoint. Flood overflow now reaches a sinkpoint in a boulder pile beneath the Oriasokterem (Giants' Hall) breakdown chamber, on average once every two years. The spring cave is constricted; flood discharge there is *c.* 20 m<sup>3</sup> s<sup>-1</sup>.

The cave is profusely decorated with calcite speleothems, including stalagmites and bosses up to 10 m or more in height or girth. U-series dating has established that most growth is no older than the last interglacial (*c.* 125000 years BP); the cave was partly filled with alluvial debris during the succeeding Würm cold phases and some larger stalagmites were toppled by extreme flooding. There is also significant condensation corrosion damage to speleothems in tall chambers, which can function as cave climate chimneys.

Beké Cave (6.4 km long), Szabadsag (3.4 km long), Kossuth (1.3 km long), and Vass Imre (1 km long) are similar, low gradient river caves but with lesser catchments and smaller passages. Beké Cave is noted for the erosional effects of aggradation that it displays, such as multiple, undulating corrosional-corrosional notching in the rock walls. Beké, Kossuth, and Vass Imre are sites of long-term hydrologic, hydrochemical, and cave climatic studies.

Higher on the plateaux, 162 steep swallet caves or vertical shafts beneath dolines are known, reaching depths of 100–250 m. Sixty collapse caves are also recorded. Miners

discovered relict hydrothermal caves in some isolated limestone blocks at the extremities of the karst, including the spectacular Ochtina Aragonite Cave (in Slovakia) and Rákóczi Cave, which are open to tourists.

Baradla Cave was one of the earliest centres of biospeleological research. More than 500 troglobite and troglophile species and sub-species are now known from here and other caves of the region, some of them unique. There are 21 species of bats, many of which winter in the caves.

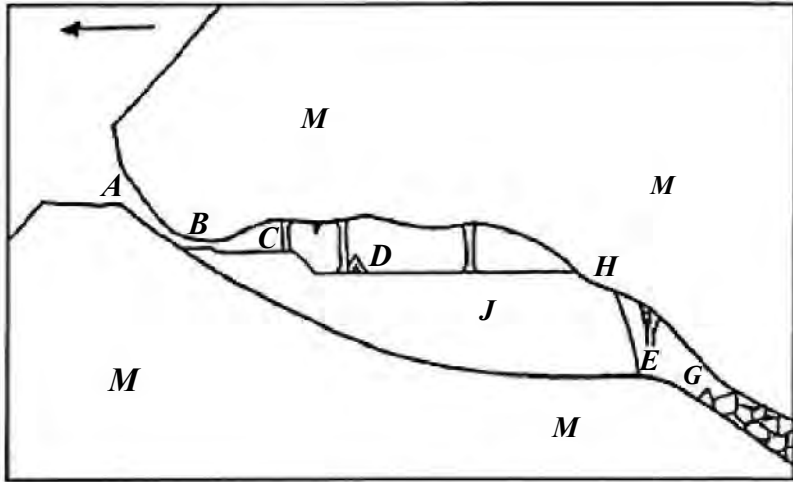
### History

The earliest surviving published reference on Baradla Cave is from 1549 AD. Guided visits took place quite frequently during the 18th century. The first accurate map, 1794, showed 2170 m of passages from the Aggtelek entrance. In 1825, the county engineer, Imre Vass, passed a downstream obstacle to extend the known cave, publishing a striking map, with 7.9 km of galleries, in 1829. Tourism increased vigorously in the following years. A partly artificial entrance was engineered alongside Voros-to (Red Lake, a pond doline) in 1890, permitting 6 km through-trips from Aggtelek. A second tunnel, in 1930, allowed entrance or exit at the downstream end of the cave, at Jósvafő. The connection between Baradla and Domica Cave was discovered in 1932.

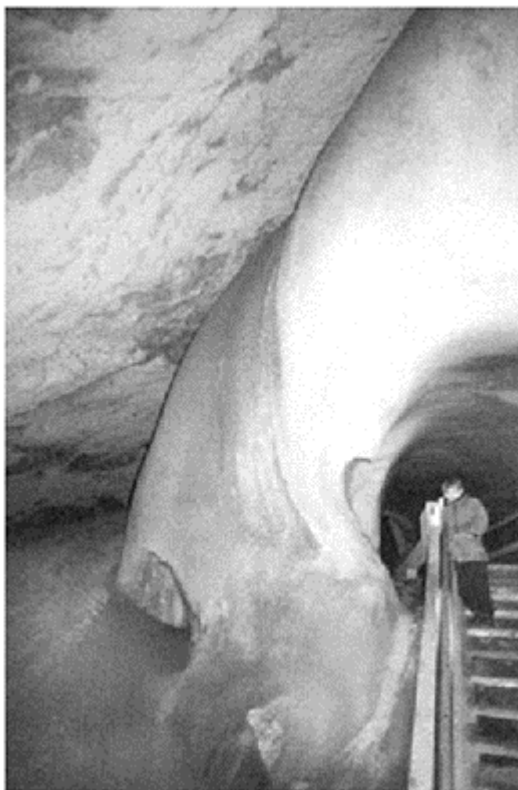
### Dobšina Ice Cave

Dobšina (German: Dobschau) Ice Cave is first known to have been entered in 1870, via a small collapse doline at an altitude of 969 m in a north-facing slope. This gave access to a series of breakdown chambers containing large, perennial ice masses and descending to a depth of *c.* 110 m (Figure 2). The discovery attracted great attention, was opened for tourists the following year, and fitted with electric lighting as early as 1884. In 2000, it was added to the World Heritage List, as an adjunct of the Slovak Karst. The cave is the truncated, relict, upstream end of the Stratenska Cave system, an 18.3 km, multi-level river cave in the Wetterstein limestone (Tulis, 1986). Breakdown and sedimentation have separated the Dobšina end (1232 m of passages) from the remainder with a seal that is nearly airtight and watertight, although there is limited through drainage.

The main ice body is a “textbook” example of a *glacière*. It largely fills two chambers, has a volume of *c.* 110 000 m<sup>3</sup> and a maximum thickness of 26.5 m, making it the largest compact



**Aggtelek and Slovak Karst: Figure 2.** A sketch long section of Dobšina Ice Cave drawn by Dr. Johann E. Pelech (1879). It indicates the principles of the *glacière* or cold trap very well. The direction of the arrow indicates north. (A) External visible hollow in the limestone. (B) Actual entrance. (C, D) Upper portion of the Cavern with the three Ice Pillars, the Ice Saloon, Ice Tent, and Ice Hillock. (E) Lower portion of the Cavern, the Corridor with the Ice Wall. Near (G) the Cavern contracts, and is filled with fragments of rock; through these the water flows away. (J). The great Ice Mass. (M) The Limestone Rock. At (H) the top of the ice is in contact with the roof of the Cavern, thus dividing it into two parts, the Upper and Lower Stages. (Pelech, 1879)



**Aggtelek and Slovak Karst: Figure 3.** Tunnel cut through the ice in Dobšina Ice Cave. (Photo by John Gunn)

glacière in a show cave. It has an extensive flat floor, sometimes used for skating parties, and large ice stalagmites, columns, and draperies. The glacière accreted from films of flowing water in regular wet season layers because the sealed cavity is a cold trap, receiving dense cool air in winter that cannot be displaced by the warmer air of other seasons. Measurements in the 1880s found that the annual range of air temperature was  $-0.15$  to  $-0.86^{\circ}\text{C}$  around the glacière, in contrast to a mean annual temperature of approximately  $+6^{\circ}\text{C}$  outside the cave.

There are 515 m of tourist paths to display the ice, including a tunnel cut through it that reveals the layered structure (Figure 3). Modern ice behaviour is closely monitored to prevent degradation due to visitors. Between 1981 and 1990, floor ice was observed to increase by  $3\text{--}115\text{ mm a}^{-1}$  at different locations, much of the water deriving from the melt of nearby wall ice at  $1\text{--}27\text{ mm a}^{-1}$ . The mass was also deforming plastically (flowing) at rates of  $\sim 10\text{ mm a}^{-1}$  horizontally and up to  $27\text{ mm a}^{-1}$  vertically downwards (Lalkovic, 1995).

See also **Aggtelek Caves: Archaeology; Ice in Caves**

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## AGGTELEK CAVES, HUNGARY-SLOVAKIA: ARCHAEOLOGY

The Baradla-Domica Cave System, one of the most important archaeological sites in Central Europe, where artefacts of the Neolithic Bükk culture have been found, straddles the boundary between northeastern Hungary and southern Slovakia. The cave system is almost 25 km long and is the most important landform of both the Aggtelek (Hungary) and the Slovak karst. It was excavated by the erosive activity of the underground Styx River, mainly in Middle Triassic (Ladinian) Wetterstein limestone. However, there are substantial cave deposits consisting of gravel and cave loam. The Baradla-Domica caves probably served as temporary or permanent dwellings for paleolithic hunters. In the

Middle Ages they also provided sanctuary from the invading Tartars and Turks. But the people of the Bükk culture inhabited the caves for the longest period—during the Middle Neolithic, *c.* 6000–4500 BC.

The Bükk culture derives its name from the Bükk Mountains in northeastern Hungary, which was the main centre from which it spread. The people subsisted by farming, animal husbandry (especially sheep and goats), the obsidian trade, and textile and ceramic production. Their ceramics include some of the finest examples of Central European Neolithic pottery. Apart from their settlements on the river terraces and hillsides, the people also favoured caves as dwelling-places. From this point of view, the Baradla-Domica Cave System (especially the Domica Cave in Slovakia) represents the most important archaeological site for the Bükk culture.

The first archaeological discoveries in the Domica Cave sediments were made in 1926. However, the first archaeological research only began in 1932–33, about 50 years later than in the Hungarian Baradla Cave, where Jenő Nyári had already begun work in 1876–77. Jaroslav Böhm led the research at Domica Cave in the 1930s, in cooperation with American archaeologists (V.J.Fewkes and his team). The Hungarian scientists Hubert Kessler and Maria Mottl also excavated in this cave during World War II (in 1940). New research into the cave settlement was initiated by the Archaeological Department of the Slovak Academy of Sciences in 1956 (by Juraj Bárta) and continued in 1963 (Bárta, 1965; Lichardus, 1969).

A large quantity of new data on the occupancy of the Domica Cave have been collected during this research. The finding of paleolithic leaf-shaped stone “spike” (tool) of the Szeletian culture in allochthonous sediments was especially noteworthy. This is evidence of the presence of prehistoric hunters in the cave or nearby. However, a substantial proportion of the cave artefacts date back to the Neolithic Period. In the cave, six cultural horizons (Domica Ia, Ib, IIa, IIb, III, and IV) have been found (Lichardus, 1969). These horizons cover the time span from the end of the Early Neolithic to the Middle-Late Neolithic boundary. The painted ceramics of the older Neolithic cultures (a sphere from the Starčevo-Karanovo-Kriš culture and pottery shards from the Gemer painted ceramics culture) have been found in the Domica Ia to IIa horizons, whereas artefacts of the Bükk culture have been excavated only from younger horizons (Domica IIb to IV) (Bárta, 1965; Lichardus, 1969).

Unlike the painted ceramics, the basic motif of the Bükk culture line pottery is a spiral, sculpted decoration, often encrusted with white, yellow, and red pigment. Round vessels predominate, with amphora-like vessels being less common. Bone tools (awls, smoothers, comb-like tools, grinders, rods, a bone ring, pendants, needles, and daggers), stone tools (polished axes and splintered blades), and earthen spindles (evidence of the textile production) have also been found here. Post-holes, connected with the Bükk culture and also known from the Baradla Cave, suggest that dwellings were constructed inside the caves. Several fireplaces were also found, some of which served as sources of charcoal for radiometric dating. On the basis of radiocarbon analysis, the Bükk culture charcoal layer was dated to  $6122 \pm 75$  BP ( $4120 \pm 75$  BC). This is in good agreement with the age ( $6492 \pm 100$  BP,  $4490 \pm 100$  BC) obtained by radiocarbon dating of samples from the Bükk culture settlement of Arkatul, near Korfát in Hungary (Bárta, 1965).

The unique discovery of three geometrical Neolithic charcoal drawings in 1931 was the most important find both in the Domica Cave (Benický, 1945) and the whole cave



system. These drawings (see Figure)—the only prehistoric murals found in Central Europe—may represent symbols of fertility, and a stylized female figure. They are situated in the back of the cave section known as the “Sacred Corridor”, which has a shape of a female lap. The way in which the drawings are located in this part of the cave is presumably related to a sacred site in which religious ceremonies could take place. The corridor was separated from the other cave spaces in two places, probably by some kind of curtains fastened to wooden beams. Traces of post-holes on the cave floor tend to confirm this theory (Bárta, 1965).

From the anthropological point of view, only two human jawbones (one of which belonged to an elderly individual) have been found in the Domica Cave, whereas a Neolithic burialground with 13 human skeletons has been discovered in Baradla Cave. The individuals were buried in a crouched position, face down, and were covered by large flat stones. Along with these



**Aggtelek Caves: Archaeology:** One of three charcoal drawings in the “Sacred Corridor” of the Domica Cave. (Reproduced by the permission of the Slovak Museum of Nature Protection and Speleology in Liptovský Mikuláš, Slovakia.)

human bones, footprints of Neolithic people were preserved on the floors of both caves. Unfortunately, these footprints were inadvertently destroyed during the first exploration of the cave system.

It is known that the Domica Cave was settled by the Bükk people, especially during the winter, when it was warmer in the cave than outside (the average temperature in the cave is 10°C). The cave could have served as a religious site and/or a ceramics production centre. Artefacts of the Bükk culture have also been discovered in other caves of the Baradla-Domica system (e.g. Baradla Cave, Čertová pec Cave, etc.), but their importance is not as great as those in Domica Cave. However, because of the presence of unique karst phenomena and rare archaeological finds, the Baradla-Domica Cave System was registered as a UNESCO World Heritage Site in 1995.

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*See also* **Aggtelek and Slovak Karst; Art: Cave Art in Europe**

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## AKIYOSHI-DAI KARST AND CAVES, JAPAN

The Akiyoshi-dai (plateau) karst is located in Yamaguchi Prefecture, in the western part of mainland Honshu, the largest of the Japanese islands, and is the most famous and largest karst plateau in Japan. Permo-Carboniferous limestones crop out over an area of some 130 km<sup>2</sup> in one of the main caving regions in Japan. The limestone plateau is shaped like a parallelogram, measuring 17 km in an eastnortheast-westsouthwest direction and 8 km in a northnorthwest-southsoutheast direction, and is surrounded by mainly clastic facies of Permo-Carboniferous age. The western part is covered by Triassic and the northern part by Cretaceous rocks.

The limestone plateau is at altitude of 100–400 m with a gently undulating surface and is mostly surrounded by steep marginal slopes. The valley of the Koto River cuts through the central part of the area from north to south, and divides the Akiyoshi-dai (plateau) into two areas: Higashino-dai in the east and Nishino-dai to the west. About 2200 dolines have been located, and the mean doline density for the total area is *c.* 20 per square kilometre on the plateau. The highest doline density is 140–160 per square kilometre in the central part of the Higashino-dai (Miura, 1991). There are also 81 karst springs and 429 caves distributed all over the plateau. About 45 km<sup>2</sup> of the Akiyoshi-dai Plateau was designated a Quasi-National Park of Japan in 1955, and 13.8 km<sup>2</sup> was designated a Special National Monument of Japan in 1964, based on its great significance to the geological sciences.

The Akiyoshi Limestone Group, which forms the Akiyoshidai Plateau, has a total thickness of *c.* 770 m, ranging in age from early Carboniferous (late Tournasian) to late Permian (Guadalupian), and yields abundant fusulinids, bryozoans, crinoids, brachiopods, corals, and other fossils. There is no terrigenous clastic material in any part of the succession. The limestones were deposited in five main environments: talus slope, true reef, beach, marginal lagoon, and central lagoon. The limestone rests conformably on a greenstone succession of alkaline volcanoclastic rocks. The reef complex was formed above a ridge as the result of submarine volcanic activity (Ota, 1977). The northwestern part of the Akiyoshi limestone complex is inverted (recumbent folded and subsequently overturned structures) and the southwestern part displays the normal succession (Schwan & Ota, 1977). In the Carboniferous limestone belonging to the upper part of the *Millerella yowarensis* zone, emergence surfaces with evidence of paleokarst are known to occur (Nagai, 1993).

The caves developed in the Akiyoshi-dai limestone plateau can be divided into three groups on the basis of elevation: high-altitude (higher than 250 m above sea level), middle altitude (250–130 m above sea level) and low-altitude (lower than 130 m above sea level) caves. The high-altitude caves are mostly pits at altitudes of 320–280 m on the Choujagamori Plain. The middle-altitude caves range from an altitude of 160 to 180 m, and occur mostly on the Wakatakebara Plain. The lower-altitude caves mostly open at the foot of the plateau (Kawano, 1983).

Akiyoshi-do Cave is the longest cave in the plateau and is designated a Special Natural Monument of Japan. It is one of the lower-altitude caves, with a natural entrance at the foot of a 50 m high limestone cliff; the entrance is 20 m high and 8 m wide. Before the 1960s, the known passageway of Akiyoshi-do Cave was *c.* 2 km long including the tourist route, but underwater explorations by various teams have since revealed that it is more than 7.5 km long. A connection was also found between Akiyoshi-do Cave and Kuzuga-ana Cave, and the combined cave system is currently over 8.5 km long. The tourist route, 1 km long, in Akiyoshi-do Cave runs parallel to an underground stream, and passes a complex of 500 terraced rimstone pools (see Figure), large stalagmites, and large columns.



**Akiyoshi-dai Karst and Caves,  
Japan:** The terraced gour pools of  
Hyakumai-zara in the main stream  
cave of Akiyoshi-dai. (Photo by  
Akiyoshi-dai Museum)

Taisho-da Cave lies in the northern part of Higashi-dai Plateau and opens at an altitude of 159 m of the northern foot of Mt Mana. Taisho-do Cave is designated a Natural Monument of Japan. The cave is complex, developed with three passage levels and is 1000 m in total length. The upper-level passage (at an altitude of 180–175 m) includes a large chamber containing many speleothems and notches at an altitude of 178 m on the cave walls. The middle level (at an altitude of 175–160 m) is a labyrinthine passage. The lower-level passages (at an altitude of 160–120 m) reach to the water table. Within these three levels, many phreatic solution features (bore passage, natural bridges, pillars, pockets, and anastomoses) are developed. Taisho-do Cave consists of a phreatic cave system linked with Sano-ana Cave, Inugamori-no-ana Cave, and Current-mark-no-ana Cave. The total length of these caves is *c.* 2200 m. (Nakagawa *et al.*, 1979).

Takaga-ana Cave is located on the northern part of Nishinodai Plateau. The vertical entrance shaft of 42 m in a collapse doline is located at an altitude of 241.6 m. Takaga-ana Cave lies in the middle-altitude group and is the second-longest cave in the Akiyoshi-dai Plateau. It is a complex cave with shafts and passages on four levels at heights of 180 m, 170–160 m, 140–130 m and 90 m levels. The main cave passages are more than 1500 m long, developed at the 170–160 m level. The total surveyed length including the 41 branch caves is 4525 m, and the volume is *c.* 120000 m<sup>3</sup>, developed along many fissures. The cave is decorated with numerous speleothems of various types. *Macaca* (macaques), *Lutra* (river otters), *Paleoloxodon naumani* (an extinct elephant), and other vertebrate remains have been obtained by surface collection of the cave deposits (Shuho-cho *et al.*, 1981).

Recently, polluted waste waters have sometimes been detected in the groundwaters of the Akiyoshi-do Cave. It is obvious that the pollution is derived from domestic waste water from the tourist hotels and installations built on the surface of the Akiyoshi-dai Plateau. It is essential that the pollution is prevented by dealing with the waste-water problem and periodically monitoring the groundwater in the caves.

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*See also map in Asia, Northeast*

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## ALPINE KARST

Alpine karst is the solutional landscape occurring at high altitudes throughout the mountains of the world. It is distinctive primarily by virtue of localized colder conditions resulting from the altitude, often resulting in restricted vegetation, seasonal snow and snow melt, and past and present glaciers. Exceptionally steep hydraulic gradients develop between upland recharge areas and adjacent valleys. Alpine conditions do not particularly favour karst development: runoff is seasonal, dissolution subdued by reduced biological activity, and past and present geomorphic processes compete and hinder evolution of karst.

### Hydrology

Alpine environments are characterized by strong climatic gradients; average temperatures decline by about 6°C per km elevation and upland areas capture additional precipitation, much of which may be in the form of snow. Many alpine karsts therefore experience a strong spring-summer freshet, supplemented only so far as snow patches, glacier ice, and summer rainfall sustain runoff. Meltwater from snow and ice initially contains little dissolved gas or minerals and hence does not have much inherent capacity to dissolve limestone. Carbon dioxide solubility is higher under cold conditions, but partial pressures of gases are reduced under lower atmospheric pressures. Furthermore, poorly developed or skeletal soils combined with a limited growing season result in little enhancement of solutional capacity from soil CO<sub>2</sub> during infiltration.

Groundwater hydraulics under mountains are strongly influenced by relief. Saw-tooth (dissected cuesta) terrain characterized by continuous slopes between peak and valley tends to develop recharge in the upper fraction and discharge throughout the lower fraction with respective linkage of the highest and lowest components. More classical alpine terrain of cirques, dissected plateaus, and entrenched valleys exhibits much deeper circulation and strong groundwater convergence in valleys below.

### Processes

Alpine karst processes reflect the seasonal hydrology and subdued chemistry. For much of the year cold conditions may limit runoff, and lack of soil water storage may result in intermittent rather than sustained summer flows. Alpine snow banks are important in sustaining infiltration and stream flow. Closed depressions preferentially accumulate and sustain snow into the summer, and the resulting meltwater may enhance their development in otherwise dry summer conditions.

Much solutional potential may be expended on preferential dissolution of fine carbonates generated by glacial abrasion, and present in glacially derived soils. Evapotranspiration losses are low in comparison with many other environments and hence the runoff percentage tends to be high, although this is more than compensated for by low pCO<sub>2</sub> in the absence of biogenic sources. Hence, karst denudation rates are not high, and alpine karst generally develops quite slowly, unless there is substantial runoff or a supplementary source of acidity. Oxidation of crushed pyrite to produce sulfuric acid is one such process. Two factors, currently poorly understood, are the impact of initial freshet water that is chemically enriched (especially where acidic air pollution is high),

and the very rapid kinetics of dissolution arising from water containing no dissolved minerals.

Cold conditions, seasonally abundant water, rapid runoff, and steep gradients strongly sustain other geomorphic processes, most of which can be viewed as competing with karst development. Frozen ground may allow accumulation of massive ice and perennial snow in surface shafts. This effectively cuts off the water supply and may prevent exploration, although in the Julian Alps explorers have been able to penetrate over 200 m down ice-filled shafts by following narrow routes at the contact between ice and the rock walls. Frost shattering of susceptible materials can devastate surface karst forms and choke closed depressions. Mass movement by solifluction, creep, rockfall, and debris flows may also obscure karst features, or restrict groundwater recharge.

Glaciers play an ambiguous role in alpine karst where many closed depression are both karstic and glacial in development. Closed depressions tend to be preferred sites for snow accumulation and glacier development, and glacier erosion at valley heads tends to produce overdeepened (closed) cirques that may function in a similar way to dolines following ice-melt. The bed temperature of most alpine glaciers is fixed at melting point. As a result, glaciers protect the ground from freezing and so permit groundwater recharge at altitudes otherwise sustaining permanently frozen ground. They may also prevent frost shattering, and scour accumulated debris from surfaces. As a result the finest alpine karst terrain is largely found in areas recently exposed by glacier retreat. Small cirque glaciers may coexist with active karst, as they produce little debris. However, more active, extensive glaciers generate large quantities of till that accumulates in lower reaches as moraines. Much alpine karst is obscured by a mantle of such glacial deposits that not only neutralize solutional erosion, but may also preclude groundwater recharge, and support lakes which act as sustained traps for fine sediments. Glacial action is particularly enhanced by the steep topographic and climatic gradients of alpine regions. At higher altitudes, erosion dominates, generally disrupting surface catchments (especially closed depressions) and truncating shallower karst systems. At lower altitudes, glaciers tend to deposition and the resulting glacial, fluvio-glacial, and glaciolacustrine sediments occupy valley floors, raising local base levels and often burying karst springs.

### **Karst Landforms**

The composition of carbonate mountain ranges reflects the regional geological history. As most mountains are developed at plate margins, the carbonates of mountain ranges may be considerably thicker than is found in plate interiors. Intense folding, faulting, and alteration of rocks are common in mountain ranges, resulting in varied juxtaposition of various grades of carbonate with insoluble silicates, and sometimes containing exotic minerals arising from hydrothermal and volcanic activity. Many of the features of alpine karst may be linked to the active tectonics associated with mountain development. Valleys and poljes may occupy down-faulted blocks or zones of weakness; horizontally bedded blocks form plateaus. Tilted blocks tend to generate saw-tooth ridges that may be separated by strike-aligned valleys developed in weaker strata; regional karst drainage is often along the strike of such blocks discharging into larger, cross-cutting glacial valleys. Carbonate tectonic units in the European Alps



**Alpine Karst:** View across the dipping limestone pavements on the Slovene side of Monte Kanin. (Photo by John Gunn)

may contain independent karst systems isolated from adjacent rocks by the impermeable fault surface.

The paucity of surface vegetation due to glacial erosion, soil erosion, and the harsh climate renders alpine karst features more easily seen and appreciated than in other environments. Solutional features like karren are often well developed in suitably massive, pure carbonates, and the resulting lapiaz or limestone pavements can cover many square kilometres (see figure). Such surfaces are composed of numerous, structurally controlled closed depressions, indicating highly fragmented recharge. Larger closed depressions may occupy tectonic structures, or may occupy cirque floors or valleys previously overdeepened by ice. However, many alpine closed depressions act as agents of their own burial. They are filled with clastic deposits generated by weathering, mass movement, glaciation, and runoff, and the sink points are unable to carry the coarse materials involved. In time, if the terrain stabilizes, suffosion dolines may develop in the fill, eventually leading to reopening of the ponor. For example, Medicine Lake, Jasper National Park, Canada occupies a karst depression blocked by a rock slide, glacial deposits, and river sediments. It has failed to develop a significant ponor due to continuous infilling of nascent openings.

### **Alpine Caves**



The fundamental features of alpine caves are those of any cave system, although there may be considerably greater vertical development and longer preservation of ancient passages. Vertical shafts are common underground, and are often exposed at the surface, truncated by glaciation and filled with shattered rock and sediment. They are the most common alpine cave entrance, but relatively few provide access to a cave system. Vadose channels may downcut rapidly, rather than widening, creating narrow meandering canyons linking sequences of shafts, as at Krubera Cave (see separate entry). Phreatic sections may also develop considerable vertical range, including dramatic upwards flowing segments to phreatic loops, reflecting the fracture frequency, and the tendency to deep groundwater circulation in alpine terrain.

Mountains are dynamic landscapes at the time scale of karst development. Tectonic, climatic, and geomorphic patterns may change many times during evolution of cave systems. Changes to the alpine terrain and base level will alter patterns of recharge and discharge, disrupting the fundamental trajectories of cave system development. Recharge shafts may entirely lose their surface catchment and become relict. Springs developed at the valley floor may become perched above base level as a consequence of later entrenchment, and the associated passages become progressively abandoned. Passage infill and overflows may develop in response to alluvial infilling of the valley floor, for example the more than 60 separate springs recognized in and below Maligne Canyon, Jasper National Park, Canada. Within the cave system, phreatic conduits may be abandoned and reactivated as a response to cycles of valley deepening and infilling, or glaciation of the recharge surface and valleys. Reorganized surface recharge may form new vertical shafts, graded to a new local base level and cutting directly through former passage networks. These are type examples of invasion vadose caves (see *Speleogenesis: Unconfined Settings*). Backfilling in valleys may result in these shafts becoming flooded, and overflows may reactivate ancient phreatic or choked conduits. Such rejuvenation and reactivation are normal in many karst regions. However, in alpine karst, thick carbonates, the great vertical range of cave development, and the marked transitions in controls over time may result in more radical changes and permit greater preservation of cave systems than in lower relief regions. Multilevel passages, shaft complexes, and a wide suite of clastic and mineral deposits provide a tantalising record of the past environment.

### **Exploration**

The great relief of alpine regions permits development of the great deep caves of the world, and the complex history of many alpine caves makes them extraordinarily extensive. In many cases, active streams occupy relatively few of the known passages. The possibility of ever greater depths of exploration has attracted considerable interest from speleologists. However, apart from relief, there is no common form for deep alpine caves. Some are simple shafts (e.g. Epos Chasm, Astraka Plateau, Greece), or are developed along simple contacts or fractures (e.g. Krubera). Some are developed into complex horizontal networks, linked by shafts (e.g. Gouffre Berger, see *Vercors* entry). Others are trunk systems gathering water from a number of distinct subcatchments (e.g. Pierre Saint-Martin, see separate entry). The challenge is often to gain entry to the system, for the recharge surface may be disrupted. In fact, many great caves are not entered by hydrologically prominent depressions, for these are often infilled. Rather, inconspicuous shafts, lacking any surface catchment often survive to permit explorers to

enter (e.g. Yorkshire Pot, Alberta, Canada). A number of alpine caves have been explored from the lower entrance. In some (e.g. Castleguard Cave, see separate entry) exploration has required only persistence, as all the large shafts are descents, despite penetrating upstream. In others, extraordinary technical virtuosity has been required to push exploration up vertical shafts (for examples see entries on Dent de Crolles and on Siebenhengste). Fortunately, upward exploration, often pursuing the cave wind, may reveal upper entrances, permitting more ready access to the inner reaches of the system (e.g. Hölloch, see separate entry, and Nettlebed Cave, New Zealand).

Alpine cave exploration is almost always highly technical, requiring skill and equipment to tackle the vertical sections. Not only is there a considerable quantity of equipment to transport, but the length of many trips demands establishment of underground camps. In many systems, water also poses a challenge, in some cases by the intensity of flow, in others by closure of passages by floods. Exploration may be restricted to wintertime when there is much less runoff. Low temperatures mean that ice may form, preventing access, or possibly converting a difficult wet section to a straightforward frozen pool.

### Resources

Alpine karst aquifers may be used in water supply and power generation. For example Vienna (Austria) obtains at least 60% of its water from alpine karst. However, the strong seasonality of flow, lack of quality protection, and poor moderation of recharge may render the water resource of limited value. Quarrying poses a threat in some regions as many alpine caves are developed in carbonates attractive to the aggregate and cement industries. Much alpine karst lacks surface expression, but retains its hydrological function. Reservoirs may prove ineffective, if built on such terrain. Surface karst is often extremely fragile, although nature may be the primary vandal. However, economic development of alpine terrain often results in wholesale destruction of karst surfaces for development of roads and alpine resorts, and significant compromise of water quality.

CHRIS SMART

*See also* **Asiago Plateau, Italy; Caucasus, Georgia; Europe, Alpine; Glacierized and Glaciated Karst; Kanin Massif, Slovenia/Italy; Picos de Europa, Spain**

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## ALTAMIRA CAVE, SPAIN: ARCHAEOLOGY

Located 2 km south of the village of Santillana del Mar (Santander), near the north coast of Spain, the cave of Altamira, nicknamed the Sistine Chapel of Cave Art, was decorated at various times between *c.* 16000 and 14000 years ago. First discovered by a hunter in 1868, it was visited in 1876 by a local landowner, Don Marcelino Sanz de Sautuola, who noticed some black painted signs on a wall at the back, but thought little of them. In 1879 he returned to do some excavating and, while he was digging in the cave floor, searching for prehistoric tools and portable art of the kind he had recently seen displayed at a Paris exhibition, his 8-year-old daughter Maria was playing in the cavern. Suddenly she spotted the cluster of great polychrome bison paintings on the ceiling.

Her father, at first incredulous, became more interested when he found that the figures seemed to be done with a fatty paste, and noticed a close similarity in style between these huge figures and the small portable depictions from the Ice Age which he had seen at the Paris exhibition; he therefore deduced that the cave art was of similar age, but his attempts to present his views and his discovery to the academic establishment met with widespread rejection and accusations of naivety or fraud. Sanz de Sautuola died prematurely in 1888, a sad and disillusioned man (see Art in Caves: History).

Altamira Cave is 296 m long, comprises a series of chambers and passages, and ends in a very long, narrow section known as the “Horse’s Tail”. Although the site is best known for its magnificent decorated ceiling, its galleries contain an abundance of engravings, including some particularly fine deer heads identical to some engraved on deer shoulder-blades in the cave’s occupation layers. There are also some meandering finger tracings, some of which form a bovine head. One remarkable feature is a series of masks, where natural rock-shapes were turned into humanoid faces by the addition of eyes and other details; most of these masks can only be noticed when one is leaving, rather than entering, the “Horse’s Tail”.

The great hall, with its high vault, has engravings and also some red compartmentalized quadrilateral signs, similar to those of the cave of El Castillo in the same region. The cave also has black paintings (black figures often occur in different zones from red figures), some stencilled hands, and some (far rarer) positive painted hand prints.

To the left, as one enters Altamira, is the great hall of paintings, measuring about 20 m by 10 m. The floor has been lowered in order to allow visitors easier access and viewing of the very low ceiling on which a score of large painted animals are spread: there are 18 bison, a horse and a hind, the latter being 2.5 m in length—the biggest figure in the cave. They are polychromes, done in ochre, manganese, and charcoal. Most animals are standing, but a few natural bosses in the ceiling are occupied by curled-up bison, which thus appear three-dimensional. Two or three painted figures on the ceiling have often been described as boars (a very rare animal in Ice Age art) but they are now seen as streamlined bison (especially since one has horns).

The curled-up bison on the bosses have been described as sleeping, wounded or dying, falling down a cliff, or as clear pictures of females giving birth. Currently the dominant

view is that they are males, rolling in dust impregnated with their urine, in order to rub their scent on territorial markers, even though one of them has udders! In fact, they may simply be bison drawn to fit the bosses—they have the same volume, form, and dorsal line as those standing around them, but their legs are bent and their heads are down. Some researchers see this chamber as a symbolic pound, with a bison-drive depicted on the ceiling (the curled-up animals at the centre are dead, while those around them stand and face the hunters—there are male humans engraved at the edge); another interpretation is that the ceiling is a depiction of a bison herd in rutting season.

Although the Altamira ceiling has sometimes been taken as a single accumulated composition, it actually comprises a series of superimpositions: researchers have distinguished five separate phases of decoration, beginning with some continuous-line engravings, followed by figures in red flat-wash, then some multiple-line engravings, some black figures, and finally the famous polychromes. The multiple-line figures are identical to some portable specimens from the cave, dated to 14480 years ago, so it is clear that the two earlier phases pre-date them, while the black figures and polychromes are younger. Charcoal used in some polychrome bison on the painted ceiling has produced radiocarbon dates from 14820 to 13130 years ago. The cave was probably blocked shortly after this period.

Sanz de Sautuola saw the ceiling as a unified work, and many subsequent researchers have declared that one artist of genius could have done all the cave polychromes. Recent detailed observations have confirmed these intuitions that one expert artist was probably responsible for at least all the polychrome bison on the ceiling. The different radiocarbon dates, if accurate, may indicate subsequent retouching.

The occupation layers at Altamira have yielded material from the Mousterian; the Solutrean, including classic shouldered-points and the engraved deer shoulder-blades; and the early Magdalenian, with perforated antler batons, and antler spear-points with complex decorative motifs. The Magdalenian fauna is dominated by red deer, and has abundant seashells reflecting the cave's proximity to the coast; seal bones occurred in the Solutrean layers. Between the Solutrean and Magdalenian periods, the cave was used by cave bears for hibernation. Altamira's wealth of occupation material and of portable and parietal art (literally art on walls) suggests strongly that it was an important regional focus at times, perhaps the scene of seasonal or periodic aggregations when people from a wide area might meet for ritual, economic, and social activities.

Altamira became a World Heritage Site in 1985. In July 2001, a magnificent facsimile of Altamira Cave, constructed a few hundred metres from the original, was opened to the public; it not only contains a perfect replica of the decorated ceiling, with every crack, engraving and painting on it, but places it in its original context by reconstructing the whole of the cave entrance chamber and its gaping mouth, which has not been seen since it collapsed towards the end of the Ice Age.

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*See also Art: Cave Art in Europe*

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## AMERICA, CENTRAL

Central America, here defined as the isthmus between the United States and South America including the Yucatan Peninsula, contains many significant carbonate karst landscapes, with a regional karst area totalling about 431300 km<sup>2</sup>, or 17% of the total land area (Figure 1). Over 90% of Central America's karst is in Mexico, particularly in the southern and eastern states of Oaxaca, Guerrero, Chiapas, Pueblo, and Tamaulipas, and on the Yucatán Peninsula. Significant karst also occurs in Guatemala, Belize, and Honduras.

Geologically, the bulk of Mexico, excluding the Yucatan, is related structurally to North America and not to the remainder of Central America. The carbonate rocks of Central America range in age from Quaternary to Jurassic, representing discontinuous carbonate deposition over more than 200 million years. Considerable geologic, topographic, and environmental heterogeneity characterizes the region, but Central America contains a number of dramatic karst landscapes. These include cockpits, towers, dry valleys, dolines of various types and sizes, cenotes, and extensive cave systems,

together with an impressive marine karst landscape (Table 1). The world's second longest barrier reef is located off the Caribbean coast of the Yucatan, Belize, and Honduras.

Karst landscapes in Central America have been, and still are, influenced by tectonic, eustatic, and climatic changes (Gardner, 1987) and they have also undergone significant alterations as the result of human activity (Day, 1993).

The most extensive Central American carbonate karst areas are in Mexico, in the Sierra Madre Oriental, in the Yucatan Peninsula, and in the Southern Mountains. The Sierra Madre Oriental includes some 130000 km<sup>2</sup> of rugged, mountainous



**America, Central: Figure 1.** The main karst regions in Central America, and the location of significant caves referred to in the text.

karst with extensive dolines and deep shafts punctuating an elevated plateau, bounded by steep escarpments and dissected by deep canyons. The Southern Mountains are a structurally complex range that extends into Guatemala. They include the Huautla Plateau and the Chiapas Highlands, in a karst area extending over 60000 km<sup>2</sup>, and a similarly sized area further west in northern Guerrero. In the Yucatán, over 115000 km<sup>2</sup> of Tertiary and Quaternary carbonates give rise to a subdued karst landscape, characterized by shallow dolines, low residual hills, cenotes, and flooded cave systems.

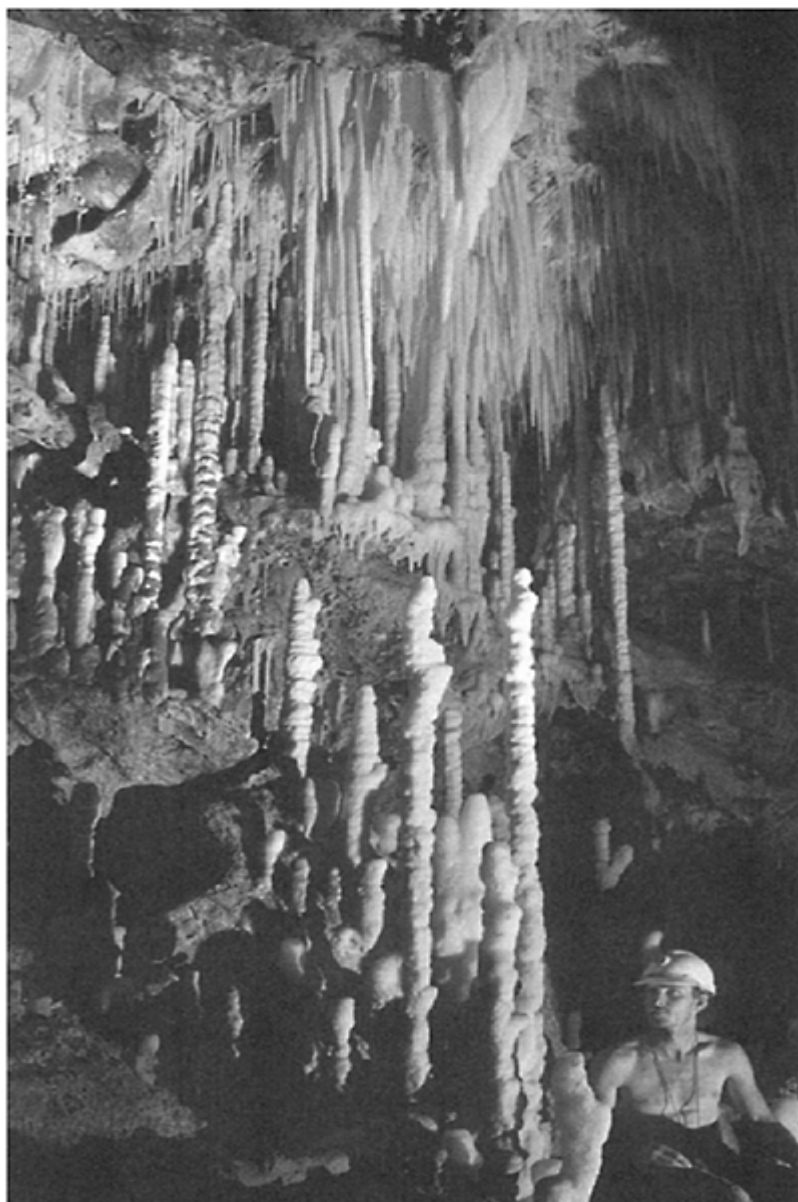
Another extensive karst area, including cockpit and tower karst developed in Cretaceous and Tertiary carbonates, extends through the Peten of east central Guatemala into western Belize, covering nearly 15000 km<sup>2</sup>, and there are also significant elevated karst areas in the Alta Verapaz and Huehuetenango Departments of Guatemala. Honduras

has three major karst areas, covering approximately 10000 km<sup>2</sup>: the Montana Santa Barbara in the northwest, the Cordillera Agalta in central Honduras, and the Sierra de Colon and Cordillera Entre Rios in the southeast bordering Nicaragua. The karst in Montana Santa Barbara and Cordillera Agalta has received only moderate scientific attention, and the karst on the Sierra de Colon has received little attention, due to its remoteness and dense vegetation. The folded limestone mountains of the Sierra de Colon extend across the border into neighbouring Nicaragua. The Cretaceous carbonates of the Atima Limestone of the Yojoa Group are several hundred metres thick and are heavily karstified. There are also significant carbonate karst areas elsewhere in Nicaragua and throughout Costa Rica (Mora, 1992; Peacock & Hempel, 1993; Troester *et al.*, 1987). In Panama, there is karst in the northwest along the border with Costa Rica, in the Archipielego de Bocas del Toro, in central Panama in the Maje Mountains near the Rio Chepo o Bayano, and in the eastern Darien Department (Reeves, 2000). El Salvador has less than 300 km<sup>2</sup> of karst, located along the border with Honduras and Guatemala, south of Anguiatu.

Considerable topographic variation characterizes the karst of Central America as a whole, although three distinct karst terrain styles—doline, polygonal (cockpit/cone), and tower—are recog-

**America, Central:** The areas of karst and significant landforms in Central America.

Country/Area	Karst Area (km <sup>2</sup> )	Towers	Cockpits	Dolines	Fluviokarst	Marine
Belize	5000	✓	✓	✓	✓	✓
Costa Rica	2000			✓	✓	✓
El Salvador	300			✓		
Guatemala	15000	✓	✓	✓	✓	
Honduras	10000		✓	✓		✓
Yucatan Peninsula	115000			✓		✓
Rest of Mexico	276700	✓		✓	✓	
Nicaragua	5000			✓		
Panama	2000			✓		✓



**America, Central: Figure 2.** A corner of the extensive calcite dripstone deposits in the Gruta del Palmito in the Bustamente karst of northern Mexico. (Photo by Andy Eavis)



nized. Dry or underdrained valleys and subdued depressions or dolines occur throughout the region but have received little scientific attention. Cockpit, cone, and tower karst occurs in southern Mexico, Belize, Guatemala, Honduras, and Nicaragua. Variations of these types occur throughout Central America and are not restricted to the areas described above. Flooded shafts, cenotes, are the characteristic surface landform across the northern Yucatán Peninsula.

The karst rocks range from pure, dense, hard, fractured, crystalline limestones, some much altered from their original state, to impure, powdery, soft, porous, amorphous carbonates. Their depositional environments were highly variable, but the low-lying limestones of the Yucatán Peninsula were formed as extensive carbonate platforms and reefs analogous to those off the Caribbean shore today. Some interior karstlands, especially in mountainous areas adjacent to volcanoes, are mantled by volcanic ash. Some carbonates, particularly in Belize and Guatemala, are brecciated as a result of extreme tectonic disruption or meteoric impact. Others have been extensively folded and faulted as a consequence of orogenic mountain building. Karst landscape elevations range from sea level to an altitude of 3000 m; some are mountainous and restricted in area, others planar and extensive; some are hydrologically isolated, while others receive allogenic surface drainage from higher, adjacent non-karst terrains.

There has been considerable but disparate cave exploration and scientific karst research in Central America. Some of the longer and deeper cave systems have been explored and studied extensively, but other potentially significant karst areas have received little attention. The history of cave exploration dates back to the pre-Hispanic Maya, who penetrated some caves for considerable distances as part of ceremonial and ritual practices, and made extensive and varied uses of caves. Modern cave research started in the 19th century with, for example, the exploration of the Gruta de Palmito in Nuevo Leon, Mexico, between 1835 and 1875. Exploration of the Guerrero caves began in earnest in the 1930s, with the traverses of the underground rivers of Chontalcoatlán and San Jeronimo. More recently, the Grupo Espeleológico Mexicano, which was formed around 1960, and the Association for Mexican Cave Studies, formed in 1962, have promoted cave and karst research throughout Mexico, increasingly with international cooperation. The Yucatán karst (see separate entry) has received considerable attention in the context of differential dissolution in groundwater mixing zones and has become famous for its very long underwater cave systems.

Widely published scientific research has been conducted in some other Central American karst areas, notably in Belize (see Veni, 1996) and Costa Rica (Peacock & Hempel, 1993; Troester *et al.*, 1987), but overall the regional karst offers considerable scope for future research. The karst areas of Honduras and Nicaragua warrant further study, although this may be hindered by problems of access.

Extensive cave systems occur through Central America, although the best known are those in the Sierra Madre Oriental, the Southern Highlands, the Yucatan Peninsula, Guatemala, and Belize. The Sierra Madre Oriental includes many famous deep and long cave systems, including Sistema Purificacion, 94 km long. Sistema Cuetzalan is an extensive, dendritic river cave system with over 35 km of passage and as much again in adjacent caves not yet connected. Sótano de Las Golondrinas (see separate entry, Golondrinas and the Giant Shafts of Mexico) is the most famous of many large bell-shaped daylight shafts. In Puebla, at the southern tip of the Sierra Madre Oriental, there is

another group of significant deep cave systems including Akemati (1130 m deep) and Ocotempa (1063 m deep).

The Southern Mountains, including the Huautla Plateau, the Chiapas Highlands and northern Guerrero, constitute another of the world's premier cave areas. Sistema Huautla (see separate entry) is 56 km long and at 1475 m deep the deepest cave in the western hemisphere, while, on the opposite side of the Santa Domingo Canyon, Sistema Cheve is 1386 m deep and drains to a canyon-floor resurgence 2540 m below the Cheve entrance (Hose, 2000). Spectacular river caves in Chiapas include the resurgence system of Veshtucoc (5 km long and 380 m deep), while the Sumidero Yochib is a challenging system over 3 km long and over 200 m deep with polished canyons containing waterfalls and deep plunge pools. The Guerrero karst includes well-known caves, such as hoyo de San Miguel (455 m deep), the very well decorated show cave grutas de Juxtlahuaca (5 km), and the river caves of Rio Chontalcoatlán (6 km), and gruta del Rio San Jeronimo (6 km). In Quintana Roo, the extensive water-filled conduit caves of the coastal Yucatan have been a focus of research into carbonate dissolution in freshwater-seawater mixing zones (Back *et al.*, 1986).

In Belize the caves of the Chiquibul River System are particularly well known (see separate entry, Belize River Caves). The Chiquibul Cave System contains four segments, three in Belize (Cebada Cave, Actun Tun Kul, and the Kabal Group), and the fourth (Xibalba) in Guatemala, with a total length exceeding 50 km. There are also extensive river caves in Guatemala, including the Sistema del Rio Candaleria in Alta Verapaz, with 12 km of passages in seven segments and at least 55 entrances (Bordier, 1976).

Central America's natural karstland vegetation varies from xerophytic scrub to wet tropical broadleaf forest, including both deciduous and evergreen trees, although much of the original forest has been cleared, with only fragments remaining in remote karst areas. The region also supports one of the world's most diverse wildlife assemblages, and specifics of the regional karstland ecology warrant additional studies. Regionally, levels of endemism and species diversity are high, particularly in terms of plant species and terrestrial vertebrates.

Human impacts on Central American karst landscapes and caves have been long-term and severe, in particular through forest clearance, species introduction, agriculture, degradation of water resources, and industrial activities, including mining, quarrying, and construction (Day, 1993). Important archaeological sites, both surface and subterranean, are significant facets of karstlands throughout Central America. Mayan archaeological sites within karst areas include Tikal (in Guatemala), Caracol (in Belize), and Chichen-Itza (in Yucatan). The Mayan cave art in Naj Tunich, Guatemala is less well known but no less significant. Pre-Hispanic influence on regional karst areas was extensive, particularly in terms of forest clearance and agricultural activities.

Contemporary threats to the Yucatan karst include hotel expansion along the coast, illegal quarrying activities, and the potential impacts of inappropriate attempts to restore quarried areas. Groundwater contamination, as a result of inadequate sewage disposal practices, is a perennial problem in the Yucatan (Back, 1999). In Belize, adverse impacts range from agricultural expansion to increasing tourism. Forest reserves continue to be logged, despite local opposition, and quarrying of limestone for construction projects is ongoing. In Guatemala and Honduras, major threats include the exploitation of floral and faunal resources, the establishment of settlements within protected areas, and unclear or

ineffective legislation. Overall, about 10% of the Central American karst has been designated as some form of protected area, including 68% of the karst in Belize. However, no karstlands are yet designated as protected areas in Nicaragua or El Salvador, and much of the most significant Mexican karst is not protected.

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*See also* **Caribbean Islands; Cone Karst; Tower Karst; Villa Luz, Cueva de**

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## AMERICA, CENTRAL AND THE CARIBBEAN ISLANDS: BIOSPELEOLOGY

Central America (including Mexico) and the Caribbean Islands encompass a vast area ranging from the temperate zone in the north to the tropics in the south. The hypogean fauna is highly diverse and contains species derived from northern and southern elements and from freshwater and marine ancestors. The subterranean fauna of much of this area is poorly known with large areas still essentially unexplored. This is especially true of south

ern Central America where remoteness and a long history of political instability have prevented any comprehensive study of the fauna.

Volcanic deposits cover much of southern Central America but extensive limestone outcrops occur in Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. Lava tubes occur in all of the countries of this area except for Belize. No biospeleological studies have been conducted in Nicaragua and only a few guano-associated species have been reported from El Salvador. The only cave system in Panama that has been extensively surveyed is the Chilibrillo Caves. This large bat cave contains no troglobitic fauna. Several studies have been conducted in Costa Rica, but only one troglobite (a phalangodid harvestman) and one stygobite (a pseudothelphusid crab) have been described from caves. Studies in the caves of Honduras have produced a few troglobites but only one collembolan has been described. The interstitial habitat has produced stygobitic mites in Costa Rica and copepods in El Salvador and Honduras.

American, Canadian, French, and Italian biospeleologists have studied areas of Guatemala. A few caves have been investigated in the provinces of Izabal and Petén but no troglobites or stygobites are known here. However, the highland provinces of Alta Verapaz and Huehuetenango have a rich fauna of troglobites and stygobites. The troglobitic fauna includes pseudoscorpions, spiders, millipedes, collembolans, entotrophs, crickets, and carabid and leiodid beetles. All have close affinities with the fauna of southern Mexico. The stygobitic fauna includes triclاد planarians, amphipods, isopods, and crabs. The triclاد and amphipods are of marine origin, whereas the isopods and crabs are derived from freshwater ancestors.

The troglobites of Belize are closely related to the fauna of the Yucatan Peninsula, but include an unusual endemic millipede and two genera of Opiliones not otherwise represented by troglobites in Mexico. Other troglobites include schizomids, spiders, pseudoscorpions, and crickets. The stygobitic fauna includes two species (a pseudothelphusid crab and a pimelodid catfish) of freshwater origin. These genera also contain species in southern Mexico. The remaining stygobites have been obtained from anchialine habitats off the coast of Belize and include Remipedia, copepods, and cirolanid isopods. These species have affinities with other anchialine species from the coast of Yucatan and the Caribbean Islands.

Reddell (1981) detailed the history of biospeleological studies in Mexico. The Association for Mexican Cave Studies continues study in various parts of Mexico. Recent work under the direction of José Palacios-Vargas from Mexico City has resulted in major faunal discoveries. Approximately 300 troglobites and 140 stygobites have been described from Mexico but many more will probably be recorded. Few areas of the country have been adequately sampled and large areas remain unexplored. In particular, many of the numerous isolated mountain ranges in northern Mexico have yet to be visited. One lava tube in Veracruz contains a prolific fauna and other volcanic caves probably contain fauna of interest. Recent discoveries of endemic stygobites in caves and springs in northern Mexico suggest that many additional species await discovery and description.

The distribution and composition of the cavernicole fauna of Mexico is a result of a combination of past climatic and geological history and the complex physiography of the country. The majority of the terrestrial fauna is composed of species closely related to taxa still inhabiting the surface. A few species in the extreme north of Mexico are

identical to or congeneric with species found in Texas to the north. Numerous species in northern Mexico occupy caves in isolated mountain ranges surrounded by desert. Of special interest are two families of millipede, the Cambalidae and Trichopetalidae, which are common elements of the southeastern United States fauna but occur only in caves in Mexico. These appear to be relicts derived from leaf litter inhabitants of forests that once extended along the Gulf Coast south into Veracruz. These forests are now restricted to high elevations in Mexico, but some species of these families are now restricted to caves at both high and low elevations, with the more highly cave-adapted species found in lowland caves.

The aquatic fauna in Mexico is derived both from freshwater and marine ancestors. The freshwater groups include some dugesiid flatworms, hydrobiid snails, asellid and stenasellid isopods, crayfish, palaemonid shrimps, pseudothelphusid crabs, dytiscid beetles, and fishes. Two species of earthworm and one trichoniscid isopod appear to have become secondarily adapted to freshwater in caves. The marine derivatives include species that are apparently relicts of the vast Cretaceous marine embayment that covered much of Mexico. These species presumably became adapted to freshwater as the seas retreated. This fauna includes amphipods, isopods, mysids, and alpheid shrimp. A large number of species have been described from the caves of the Yucatan Peninsula (see separate entry), largely as the result of diving. Although some of the species inhabiting groundwater in this area are fully adapted to freshwater, others have been found only in anchialine habitats. These latter species have their closest affinities with the fauna of the islands of the Caribbean. Among notable groups inhabiting these waters are remipedes, copepods, ostracods, cirolanid isopods, mysids, amphipods, and fishes.

The nutrient-rich caves of the lowlands in the eastern foothills of the Sierra Madre Oriental, Oaxaca, Veracruz, and Tabasco contain a preponderance of troglaphiles, many associated with bat guano. The troglobitic fauna include species apparently derived from taxa inhabiting leaf litter and include large isopods, arachnids, centipedes, millipedes, thysanurans, and histerid beetles. The spiders (particularly the Pholcidae) are well represented, but troglobitic schizomids, pseudoscorpions, and ricinuleids are also known. One tarantula from the family Theraphosidae is a troglobite in the lowland caves of Oaxaca. The stygobitic fauna includes species of both freshwater and marine origin. The freshwater derivatives include snails, palaemonid shrimp, crayfish, and fish. The marine derivatives include dimarcusid flatworms, cirolanid isopods, mysids, and alpheid and atyid shrimps. Of special interest are several species of fish. Two species of the ictalurid genus *Prietella* have been found in caves along the eastern slopes of the Sierra Madre Oriental and one in the extreme north of Mexico near the border with Texas. One pimelodid catfish of the genus *Rhamdia* has been found in caves in Oaxaca. Two species that possess troglomorphic populations are of special interest. The poeciliid *Poecilia mexicana* displays varying degrees of eye and pigment reduction within Cueva de Villa de Luz, a remarkable sulfur-based chemoautotrophic cave ecosystem (see separate entry). The characid *Astyanax fasciatus* has apparently colonized caves many times in the states of San Luis Potosí and Tamaulipas and has become the best-studied cave fish in the world. This reflects the ability of subterranean populations to fully interbreed with surface ancestral populations and the ease with which it can be raised in captivity.

High elevation caves throughout Mexico are typically more nutrient-poor and contain a much more diverse troglobitic fauna than caves at lower elevations. The fauna of the

Sierra Madre Oriental includes trichoniscid isopods, scorpions, schizomids, amblypygids, pseudoscorpions, opilionids, numerous species of spider, centipedes, millipedes, collembolans, campodeid entotrophs, silverfish, phalangopsid crickets, and beetles. Troglobitic beetles, which are absent from lowland caves, are especially speciose with numerous species of carabid beetles belonging to several genera. The family Leiodidae also contains troglobites in this area. Many genera reach their northern limits in the isolated mountain ranges of Durango, Nuevo León, and Coahuila. Several schizomids, ricinuleids, spiders, pseudoscorpions, opilionids, centipedes, millipedes, thysanurans, and carabid beetles are now relicts at higher elevations on mountains surrounded by desert. Stygobites found at higher elevations include dugesiid flatworms, earthworms, amphipods, isopods, and dytiscid beetles. The troglobitic fauna of the highlands of southern Mexico typically contains the same groups as that of the Sierra Madre Oriental but includes several families of spider and millipede that reach their northern limits of distribution in extreme southern Mexico. Pseudothelphusid crabs have also been found in Chiapas. The stygobitic fauna includes a number of unusual species, including a polychaete worm from a cave in Guerrero.

The troglobitic fauna of the Yucatan Peninsula includes trichoniscid isopods, scorpions, amblypygids, pseudoscorpions, spiders, millipedes, collembolans, and phalangopsid crickets. The stygobitic fauna is particularly rich and includes remipedes, copepods, ostracods, thermosbaenaceans, mysids, amphipods, cirolanid isopods, and fish. The fish *Ogilbia pearsei* is a marine relict, whereas the eel *Ophisternon infernale* is presumably of freshwater origin.

Numerous species of bat inhabit Mexican caves. These include carnivorous, piscivorous, insectivorous, and haematophagous species. Attempts to eradicate vampire bats in southern Mexico have led to the destruction of many colonies of all species. Other vertebrates occurring as troglloxenes in Mexican caves include frogs, salamanders, lizards, snakes, and rodents.

The cavernicole fauna of the Caribbean islands is generally poorly studied although the fauna of Cuba has been fairly well documented and research in Jamaica and Puerto Rico has considerably extended our knowledge of the troglobitic fauna of these islands (Peck, 1999; Peck *et al.*, 1998). Very little is known about the terrestrial cave fauna of the island of Hispaniola. The aquatic fauna of many of the islands is now well understood due to the extensive studies by a number of researchers studying the interstitial and subterranean fauna. Extensive diving in many caves has greatly expanded our knowledge of the anchialine fauna (Illiffe, 2000; see also Walsingham Caves, Bermuda: Biospeleology). A troglobitic onychophoran from Jamaica is only one of two in the world, the other being in South Africa. The only troglobitic isopod recorded from the Caribbean Islands is an undescribed species from Jamaica. With few exceptions, the troglobitic arachnids from the Caribbean islands are represented by endemic genera. Troglobitic schizomids are known from Cuba and Jamaica, amblypygids from Cuba, pseudoscorpions from the Dominican Republic, Cuba, and Jamaica, opilionids from Jamaica, and spiders from Cuba, Jamaica, and Mona Island. Of special interest are troglobitic mygalomorph spiders from Cuba (Barychelidae) and Jamaica (Dipluridae). Two species of troglobitic centipede are known from Cuba. The absence of troglobitic millipedes from the Caribbean islands is puzzling. The troglobitic insect fauna of the Caribbean islands is far more limited than on the mainland. Collembola are known from

Cuba, Guadeloupe, Haiti, and Jamaica, thysanurans on Cuba, pentacentrid and phalangopsid crickets on Cuba, roaches on Cuba, Jamaica, and Puerto Rico, fulgoroid homopterans on Jamaica and possibly Mona Island, and carabid beetles on Jamaica.

The stygobitic fauna in the Caribbean is almost entirely derived from marine ancestors. The only exceptions appear to be some copepods and crayfish on Cuba and elmld beetles on Haiti. Many mites have been sampled from the interstitial zone below rivers in Cuba and Haiti. There is a remarkable diversity of species inhabiting both freshwater and anchialine habitats in the Caribbean islands. With the exception of triclad planarians on Jamaica and in the Venezuelan Islands, polychaetes in the Bahama Islands and Netherlands Antilles, and a chaetognath in the Bahama Islands, the invertebrates all belong to the Crustacea. Remipedes have been found in the Bahama Islands and Turks and Caicos Islands; themosbaenaceans in Cuba, República Dominicana, Guadeloupe, Jamaica, Puerto Rico, Venezuelan Islands, and Virgin Islands; ostracods in the Bahama Islands, Cuba, Haiti, Jamaica, and Turks and Caicos; copepods in the Bahama Islands, Barbados, Cuba, Guadeloupe, Haiti, Jamaica, Netherlands Antilles, and Venezuelan Islands; cumaceans in the Bahama Islands; isopods in the Bahama Islands, Cayman Islands, Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, and Netherlands Antilles; amphipods in the Bahama Islands, Barbados, Cayman Islands, Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Leeward Islands, Netherlands Antilles, Puerto Rico, Turks and Caicos, Venezuelan Islands, and Virgin Islands; mysids in the Bahama Islands, Cuba, Dominican Republic, Jamaica, and Puerto Rico; grapsid crabs in the Bahama Islands and Jamaica; and shrimps in the Bahama Islands, Cayman Islands, Cuba, Dominican Republic, Guadeloupe, Jamaica, Leeward Islands, Mona Island, Netherlands Antilles, Puerto Rico, and Turks and Caicos. Stygobitic fish, all belonging to the genus *Lucifuga*, have been found only in the Bahama Islands, Cuba, and Jamaica.

The stygobitic fauna of the Caribbean islands exhibits many puzzling distributional patterns, with some genera endemic to a particular island whereas others are widespread throughout the Caribbean, including Belize and the Yucatan Peninsula. Some genera also occur in the Galapagos Islands, some on both sides of the Atlantic Ocean, and a few have recently also been found in Australia. The distribution of many of these taxa clearly indicates a great age for some lineages.

The subterranean fauna of Central America and the Caribbean islands is severely threatened by a variety of pressures. The greatest threat in many areas is deforestation with resultant erosion, loss of habitat for bats, and reduction in sources of nutrient input into caves. The construction of extensive resorts along the Caribbean coast of Mexico and on many of the islands of the Caribbean has destroyed some caves and led to severe problems with pollution from inadequate sewage disposal facilities. Many caves in Mexico lie in or near small villages that routinely dispose of trash and raw sewage directly into entrances. A proposal to dispose of sewage from cities into wells in northern Yucatan threatens the entire water supply of the Peninsula. Overpumping, especially along the Caribbean coast of the Yucatan Peninsula and some Caribbean islands, threatens to diminish groundwater supplies but also increase the salinity of caves that open onto the coast. Although national parks and other nature reserves exist in some areas, these form only a limited part of the area needed to protect the natural subterranean biodiversity of this region.

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## AMERICA, CENTRAL: ARCHAEOLOGICAL CAVES

The geographical area discussed here corresponds with the region known to archaeologists as Mesoamerica. It includes the area of pre-Columbian high cultures in central and southern Mexico, all of Guatemala, Belize, and the western portions of Honduras and El Salvador.

For Mesoamerican cultures, caves were perhaps the most sacred features in the natural landscape. Their importance is a reflection of a basic Amerindian religious focus on the Earth as a sacred and animate entity. Growing out of that focus was a fundamental concern with place. In central Mexico, the Nahuatl word for community, *altépetl*, literally means “water-filled mountain”. The glyphic rendering is a mountain with a cave at its base. A people were identified with their place, their sacred mountain, and its cave. In many Maya languages the name for the principal indigenous deity translates as “hill-valley”, and the deity is considered to be the owner of that “hill-valley”. In a very real sense, the landscape is personified and deified. The word for cave in many indigenous languages translates as “stone house” because caves were seen as the residence of the deities. This may be the reason that 16th-century Yucatec Maya used the term *actun* for both caves and stone buildings like temples. Neither is this the only case. In Maya inscriptions, pyramids were called “hills” and represented sacred mountains. Thus, place



and its surrounding landscape were so important that the dominant human constructions, pyramids and temples, were models of mountains and caves.

### **Historical Development of Cave Archaeology**

The archaeological investigation of caves in Mexico and Central America has a long history, dating back to the travels and descriptions of John Lloyd Stevens and Frederick Catherwood in the 1840s. Formal archaeological investigations that met or exceeded the standards of the day were initiated before the end of the 19th century at a number of sites in the Maya area. Henry Mercer published *Hill-Caves of Yucatan* in 1896, Edward Thompson wrote *Cave of Loltun* (1897), the *Caverns of Copan* was published by George Gordon (1898), and Eduard Seler reported on Quen Santo (1901) in the Guatemalan Highlands.

During the period between the world wars, cave studies languished, with the only noteworthy studies being the British Museum Expedition to Pusilhá in the Maya area (Gruning, 1930; Joyce *et al.*, 1928; Joyce, 1929) and the Cueva Encantada, Morelos (Arellano & Müller, 1948; Müller, 1948) in Central Mexico. During this period, cave studies disappeared as an important element of the archaeological literature and never again approached the discipline's highest standards of field methodology.

After World War II, the situation slowly improved, with sound scientific studies being produced by the Carnegie Institution of Washington's Mayapan Project and by David Pendergast in Belize. At the same time, a number of high-profile discoveries focused attention on the often-spectacular cave remains. The most impressive was the opening of a blocked passage at Balankanche near Chichen Itza, which revealed dozens of elaborate incense burners and other artefacts, all in their original context. The study of the cave was noteworthy for the recording of a modern Maya cave ritual that coincided with the beginning of the study (Andrews, 1970). Two caves containing Olmec paintings were discovered in Guerrero, but unfortunately no archaeological study accompanied the recording of the artwork. Finally, the discovery of a cave beneath the Pyramid of the Sun at Teotihuacan was probably the single most important cave discovery in Central Mexico, because it engendered a great deal of rethinking of the importance of caves. In the Maya area, the discovery of Naj Tunich served to launch cave archaeology as a recognized subdiscipline (Brady, 2000).

While cave investigation has a 150-year history, no attempt was made to synthesize the data and produce a coherent statement on the function of caves until the publication of J.Eric Thompson's *The Role of Caves in Maya Culture* in 1959. Thompson's views, however, were not widely circulated until the appearance of a revised version of his original article (Thompson, 1975). Thompson's synthesis is noteworthy because, with the exception of the use of cenotes as sources of drinking water, all of his major functions are religious. Furthermore, habitation, the function most frequently proposed by field archaeologists, was discarded completely. That same year, Doris Heyden (1975) published the first synthesis in English on Central Mexican cave use. Heyden's discussion is noteworthy because she is the first to propose that a cave was of such importance that it determined the placement, size, and orientation of one of the largest structures in all of Mesoamerica. Interestingly, neither Thompson nor Heyden ever did archaeological work in caves. By the late 1980s a new trend was notable as

archaeologists specializing in caves began to dominate theoretical discussions, using data that they had collected in the field (Bonor Villarejo, 1989; Brady, 2000; Stone, 1995)

### **The Role of Caves in Legitimizing Settlement**

The founding of a new settlement in Mesoamerica was a matter of great cosmological importance and was always accompanied by ritual. After their conquest, the Spanish found that the easiest way to map a community's boundaries was to have the foundation ritual reperformed, because this ceremony formally established those boundaries. As a result, there are many descriptions of such rituals. It is clear from these descriptions that indigenous people searched for a particular landscape configuration that had cosmological significance and in which caves were central. Angel García-Zambrano (1994:218) notes that these caves, "when ritually dedicated to the divinities, became the pulsing heart of the new town, providing the cosmogonic referents that legitimized the settlers' rights for occupying that space and for the ruler's authority over that site."

From 1990 to 1993 a cave survey was carried out at the Maya site of Dos Pilas in the Peten area of northern Guatemala, in order to determine if a relationship between surface architecture and caves could be detected. The study found a far more pervasive pattern of locating site architecture in relation to caves than reported for any other site. Relationships are present on three levels. Two of the site's three large public architectural complexes are built directly over caves. Hieroglyphic inscriptions at the largest complex appear to refer to the cave in the toponym, or place name. The third complex may be aligned with a cave feature (springs), and there is the possibility that a cave also runs below it. At a nearby site, a cave runs beneath the central plaza, and the architecture was laid out so that a skylight entrance could be utilized as an important religious feature. A number of important, but secondary, complexes also appear to be formed around large caves. Finally, small residential complexes and even individual house structures are associated with small caves generally less than 10 m in length (Brady, 1997; Brady *et al.*, 1997). Thus, it appears that the caves at Dos Pilas structured the site layout from the largest public architectural complexes down to individual house mounds.

While the Dos Pilas data are the most systematic and compelling, a number of examples of cave/architecture relationships have been recorded. The earliest example was Edward Thompson's discovery in 1896 of a cave beneath the centre of the Ossario at Chichen Itza (Thompson, 1938). Other early examples were reported at Tulum (Lothrop, 1924:109), Cozumel (Mason, 1927:278), and Polol (Lundell, 1934:177). Because the importance of the caves was not appreciated, no attempt was made to interpret what appears to be a clear and widespread pattern.

### **Artificial Caves**

As noted above, within Mesoamerica there is a widely shared conceptual landscape in which caves are a major feature. Interestingly, most of the volcanic areas of Mesoamerica have few if any natural caves. In these areas the conceptual landscape is imposed on and reproduced in local landscapes by the excavation of artificial caves. In recent years, large numbers of these have been documented in the Maya Highlands (Brady & Veni, 1992) and in Central Mexico (Manzanilla, López & Freter, 1996; Medina Jaen, 2000).

Artificial caves offer clear proof that the relationship between architecture and natural caves noted at Dos Pilas and other sites was deliberate, because artificial caves replicate

the same patterns. These features are also important because their form reflects the decisions of their makers. Several of the elaborate artificial caves appear to be models of the seven-chambered cave of origin, suggesting that this may be what all the caves in site centres are meant to represent. The association of other artificial caves with sacred locations and pilgrimage sites adds another dimension to our understanding of the role of caves. The presence of the cave would appear to be one of those markers that alerts visitors to the fact that this is a place of supernatural power.

Artificial caves appear to be constructed along fairly regular plans, so they are clearly an architectural form in their own right. Some of the caves reflect construction on a monumental scale, requiring as much or more labour input as pyramidal structures. The truly massive scale of some constructions is of central importance, because the lavish expenditure of resources should alert archaeologists to the fact that the focus of such attention is somehow central to the concerns of the society.

### **Caves and Ritual**

The preceding sections have dealt with caves that were located in political core areas and so were the focus of large-scale public rituals. To this could be added the many pilgrimage caves. The vast majority of all caves, however, are located in peripheral areas, but these almost invariably show some type of ancient utilization. This suggests that these features, no matter how small or how remote, were never overlooked.

What type of rituals were carried out in these caves? The rural Mesoamerica religious tradition, which is still very much alive, suggests that the rituals revolved around the agricultural cycle. Villages often make processions to ask the permission of the Earth Lord before clearing and burning fields, and perhaps again at the time of planting. The discovery of small corn cobs, four to five centimetres long, at many caves indicates that ceremonies for the offering of the first young ears may have been widely practised. The Day of the Cross (3 May) is celebrated throughout Mesoamerica. Occurring just before the onset of the rainy season, the celebrations traditionally include petitions for rain. The ceremonies are often made in a cave, because rain is considered to be a terrestrial rather than a celestial phenomenon. Rain, clouds, and lightning are formed within caves and then sent by the rain deities into the sky. Special rituals are undertaken in cases of drought, which are usually interpreted as a supernatural punishment for some oversight or infraction. Thus, rituals involving caves appear to occur at every significant point in the agricultural cycle.

Besides providing rain and fertility, the earth is also the source of disease and pestilence. In Yucatan, rituals are performed to keep the evil airs from escaping from caves/cenotes. Curing ceremonies often involve cave rituals. In many cases, the disease-causing agent may be removed by a shaman passing an egg over the person's body or sucking out a poisonous intrusion. The disease-bearing object will then be returned to its source in the cave. Not surprisingly then, caves are often thought to be places of witchcraft where disease can be given to an enemy.

Caves appear to have been used by all segments of society in pre-Columbian Mesoamerica. These features carried a variety of meanings. As the place of human origin they were connected to the miracle of creation and were the focus of group identity. The association with the earth made them sacred places where earth deities could be propitiated and petitioned for the basic necessities of agrarian life. They were frightening

places as well. From caves, the deities could send drought and disease to punish humans for misconduct. The huge artefact assemblages recovered from caves suggest that the visitation for all these purposes was heavy and prolonged.

### **Show Caves**

There are a number of show caves open to the public in the region but only a few of the better developed can be mentioned here, and many of the large caves, such as the Chiquibul System, have not been excavated professionally. In northern Mexico near Ciudad Madera, Chihuahua, the Cuartena Casas (Forty Houses) Archaeological Zone is formed around a series of cliff dwellings related to Southwestern rather than Mesoamerican culture. The sites were occupied from about 950 AD until perhaps the 14th century and appear to be related to Casas Grandes (Paquimé).

In Central Mexico, the most famous cave is the man-made tunnel under the Pyramid of the Sun at Teotihuacan, which has been discussed in detail by Heyden (1975). Special permission is needed, however, to get access. Another man-made cave at the site of Xochicalco, Morelos, is open to the public. The main cave appears to have been used as a solar observatory. The position of the sun was charted by sunlight entering through a hole in the ceiling.

In the Maya area, Balankanche Cave near the World Heritage Site of Chichen Itza has regular tours in an assortment of languages. Both the cave and the original context of many of the artefacts were heavily modified in opening the cave to tourism. Loltun Cave, near Oxkutzcab is one of the most impressive caves with large passages. The site is noteworthy for its rock art (Thompson, 1897) as well as a sequence of use dating back to the end of the Pleistocene. Finally, the Cave of Bolanchen, Campeche, made famous by Frederick Catherwood's painting of the use of a huge ladder in the 1840s, has been the subject of a good deal of archaeological investigation (Zapata Peraza, Benevides Castillo & Peña Castillo, 1991).

In Guatemala, the Cueva de las Pinturas, 20 km south of Flores, Peten, contains a large polychrome inscription and substantial architectural modifications dating to the Preclassic. Just across from Flores in Santa Elena, parts of Actun Kan are open to the public. The cave, formerly known as Jobitzina, is quite extensive with another entrance on the opposite side of the hill in which the cave is located. In Alta Verapaz, Lanquin Cave has long been a tourist destination but is also sacred to the Q'eqchi' Maya. Finally, the man-made caves at Uatlan can be visited but are often in use by the K'iche' Maya.

In Honduras, Tauleve, a show cave near Lake Yojoa, is sacred to the Lenca who conduct ceremonies at the cave on April 24. The Talgua Cave (Cave of the Glowing Skulls) near Catacamas is now open to tourism but visitors are not allowed to enter the chambers containing archaeological material. In Belize, visitors can see many intact vessels in their original context at Actun Chichem Ha, near San Ignacio.

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*See also* **Art: Cave Art in the Americas**

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## AMERICA, NORTH: ARCHAEOLOGICAL CAVES

Archaeological cave sites in North America occur from Alaska to the Yucatan Peninsula. The only significant area lacking archaeological caves is the Canadian Shield. The two most significant areas of prehistoric deep cave use occur in the karst regions of the Central Lowlands of the United States and the Mayan cave region of southern Mexico and Central America (see America, Central: Archaeological Caves). Most archaeological caves are prehistoric habitation sites, where people sought shelter under cliff overhangs, or rock shelters and cave entrances. A significant number of cave sites, however, contain evidence of human activity far beyond the reach of daylight, that includes the mining of minerals and stone resources, drawing pictographs and petroglyphs, placement or burial of the dead, and performance of rituals.

In North America, as in all parts of the world, humans have used the natural shelter afforded by cave entrances for everyday activities: processing food, cooking, making tools and clothing, and, undoubtedly, other social activities. Many cave entrances contain deeply stratified deposits, some dating to the earliest, well-accepted occupation of the Americas, *c.* 10000–12000 years BP. Deeply stratified cave deposits were used to define regional cultural chronologies in many regions of North America, thus making them important sites in the history of archaeology.

Two important cave sites, with late Pleistocene Paleoindian occupations, are Wasden/Owl Cave, Idaho, and Bluefish Caves, Yukon. Owl Cave is a collapsed lava tube with a large bison bone bed, stone tools, and worked bone,  $^{14}\text{C}$  dated between 8200 and 7800 BP. Underlying this strata, is a bone bed of broken and modified mammoth, bison, and camelid remains, with a fluted, Paleoindian point association (Miller, 1982). Bluefish Cave I contains an early deposit of stone tools and other artefacts, with the remains of mammoth, bison, horse, and other mammals. Bone collagen  $^{14}\text{C}$  dates range from 25000–12000 BP, and the tool assemblage is similar to late Pleistocene tool traditions known from Siberia (Cinq-Mars, 1978). The association between the human artefacts and Pleistocene animal bone, however, is still problematic.

Three important stratified cave sites in the western United States are Ventana Cave, Arizona, Danger Cave, Utah, and Bat Cave, New Mexico. Ventana Cave is a deep rock shelter formed by a seep spring in volcanic agglomerate. Completely excavated in the 1940s (Haury, 1950), the cave yielded stratified deposits from the late Pleistocene to historic Tohono O'odham (Papago) Indians. The earliest deposit contained bones of extinct Pleistocene fauna and a few human artefacts, suggesting a possible Paleoindian occupation. Later  $^{14}\text{C}$  dating of this layer established that it was early Holocene (*c.* 10600–8800 years BP) in age, and that the early tool industry was more closely related to later Archaic occupations than Paleoindian. Danger Cave is a dry cave that has a long history of excavation, beginning in the 1930s (Jennings, 1957). A stratified sequence of occupations dating from 10500 BP up to historic Indian occupations, was used to define the Desert Archaic tradition, a successful hunting and gathering way of life adapted to the desert and mountain environments of western North America. Bat Cave also has a long sequence of occupation (*c.* 10500 BP to historic times); however, it is best known because it contains the earliest association of maize with human occupation outside of Mesoamerica (Dick, 1965). Re-analysis of the deposits, and direct  $^{14}\text{C}$  dating of the maize remains, confirmed its spread into North America by 3500–3000 BP.

In central and eastern United States, three important stratified cave sites are Russell Cave, Alabama, Dust Cave, Alabama, and Graham Cave, Missouri. Russell Cave is a true limestone cave that is now a US National Monument. Excavated in the 1950s and 1960s, archaeological deposits in the entrance were more than 9 m deep, dating from 9000 to 400 BP (Griffin, 1974). The deposits yielded a wealth of chronological information on tool and artefact manufacture, especially during the Archaic Period (*c.* 9000–3000 BP). Ongoing excavations at nearby Dust Cave, with deposits dating from 10500 to 3250 BP, are yielding new information on the depositional context, paleoenvironment and human subsistence during this early time period, as well as more traditional information on prehistoric tool manufacture and use. Graham Cave is an unusual cave, formed in sandstone, which also contains early archaeological deposits, primarily dating from 9700 to 7000 BP (Logan, 1952). Prehistoric occupation spans the transition from the late

Paleoindian to Archaic Period hunters and gatherers in an important ecotone between the western prairies and eastern hardwood forests.

In the eastern United States, the first evidence of deep cave exploration by prehistoric Indians is dated *c.* 4600 BP. In a remote passage of a cave in Tennessee, approximately 1.5 km from the entrance, were found some 275 foot impressions in a soft mud floor. A thin scatter of cane torch charcoal (*Arundinaria* sp.), and charcoal smudges on the walls and ceiling of the passage, were used to date this prehistoric exploration. It appears from the footprints that nine individuals (possibly in two separate trips) travelled to the end of this passage and then returned. A number of other cave sites in Tennessee, Kentucky, and Indiana, contain evidence of prehistoric exploration dating prior to 3000 BP. Based on the limited remains found in these caves, the objective of these early cave trips appears to be simply exploring. However, these early prehistoric cave explorers were apparently adept at penetrating remote and demanding cave passage and successfully returning to the entrance.

A number of new activities begin to appear *c.* 3000 BP, in the record of prehistoric cave use in the eastern United States. Third Unnamed Cave, Tennessee, contains evidence for quarrying chert cobbles from a remote sandy-floored passage, testing and reducing the cobbles by knapping, and the engraving of petroglyphs onto the limestone ceiling and walls (Simek, Franklin & Sherwood, 1998). The petroglyphs are primarily geometric: rayed circles, semi-circles, checkerboards, chevron patterns, and numerous other enigmatic groups of lines. Wyandotte Cave, Indiana, was explored in prehistoric times and variously mined for chert and aragonite. The exploration and possibly chert mining occurred earlier, *c.* 4150–2200 BP, but the mining of a large aragonite stalagmite appears to date *c.* 2200–1150 BP (Munson & Munson, 1990). Artefacts made of Wyandotte Cave aragonite have been identified at several sites in the Midwestern United States, suggesting that this cave resource was widely valued.

The most extensive prehistoric mining activity in the caves of North America is found in Mammoth Cave and Salts Cave, Mammoth Cave National Park, Kentucky. Dating *c.* 3000–2200 BP, several kilometres of both caves were systematically mined for gypsum ( $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ ) in the form of crusts and flowers battered from the walls and ceiling, and selenite needles dug from the floor sediments. In more limited quantities, mirabilite ( $\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$ ) is also present in the caves and appears to have been collected in prehistoric times. It is not clear why so much effort was spent mining sulfate minerals, although gypsum may be made into a white paint or paste and the crystals themselves can be quite spectacular. Mirabilite, if ingested in sufficient quantities, is a medicinal cathartic.

The archaeology of Mammoth and Salts caves is well known for the perishable remains preserved in the dry passages: unburned torch material, cordage, woven foot wear, twined textile fragments, gourd containers, wooden bowls, digging sticks, mussel shell scrapers, and climbing poles are commonly found in the mined passages (Watson, 1969; 1974). Historically, at least two desiccated prehistoric bodies were found in the cave, both appearing to be mining accident victims. One is a *c.* 45-year old man killed by rock fall, and the other a *c.* 9-year old boy who appears to have died from a fall. Also among the dry remains preserved in the caves, are hundreds of human paleofaeces (hence the strong suggestion that mirabilite was consumed in the cave for its cathartic effect), which is an unparalleled source of material for the study of prehistoric diet and parasitic



infection during this time period. There are also a small number of enigmatic charcoal pictographs and petroglyphs found in Mammoth and Salts caves, associated with the mining, although the rendering of glyphs appears to have been a minor activity.

During later prehistoric periods in North America (c. 2000 BP to historic times), native groups appear to have used caves increasingly for ceremonial or ritualistic settings, including use as burial sites and decoration of the walls and ceilings with glyphs. The Copena culture of northern Alabama and Georgia used caves to inter individuals with elaborate burial items, including artefacts made of imported copper, galena, mica, marine shell, and steatite (Beck, 1995). Vertical shafts or pit caves, with surface openings, were used to deposit bodies in many areas of North America. This is not a very well-studied phenomenon, but the greatest concentration of burial pit caves is reported from southwest Virginia and east Tennessee. Human remains, incorporated into talus cones at the base of pit openings, are complex depositional environments awaiting more detailed, systematic study.

So-called “cave art”, in the dark zone of caves, is turning out to be widespread in the eastern United States. Pictographs, petroglyphs, and mud-glyphs, found in numerous caves, contain an array of geometric shapes, but increasingly zoomorphic, anthropomorphic, and iconographic elements dominate the art. Some of the art appears related to motifs found on artefacts widespread in the southeastern United States, and mythological figures of historic Indian groups, such as Cherokee underworld creatures (Faulkner, Deane & Earnest, 1984). The performance of rituals or shamanistic acts, associated with the drawing of cave art, has been inferred for many of these late prehistoric deep cave sites.

One of the best archaeological examples of the use of an inner cave setting for ritual behaviour, is Feather Cave, New Mexico. An inner room of the cave, rediscovered in 1964, contained some 400 perishable artefacts in their original position, thought to be at least 600 years old. The room contained a large assortment of miniature bows, reed arrows, crook pahos (prayer sticks) and other artefacts, along with pictographs adorning some walls (especially hand prints outlined in white clay-like pigment). The site was interpreted, with the help of elders from the nearby Pueblo Indians, as a Mogollon sun and earth shrine visited during biannual solar ceremonies, similar to Pueblo ceremonial caves still in use today (Ellis & Hammack, 1968). Parallels may also be drawn between Pueblo ceremonial caves and concepts regarding caves and supernatural beings in Mesoamerican cultures. It is debatable whether parallel beliefs between cultures are due to diffusion of religious ideas, or similar geological features (in this case caves) influence similar concepts among different cultures.

The ritual use of caves is also a renewed topic of interest in Mesoamerican archaeology. Classic Maya sites (c. 1700–1050 BP) appear to be associated with important caves, often incorporating local caves into the settlement layout. From these new cave discoveries, a more complete picture of ancient Maya ritual practice is emerging. As in the case of the historic Cherokee in the eastern United States, and Pueblo groups in the southwestern United States, belief systems of modern Maya Indians provide a link between sacred cave use and ritual knowledge in the present to the beginning of prehistoric concepts of caves a millennium or more in the past.

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*See also Art: Cave Art in the Americas*

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## AMERICA, NORTH: BIOSPELEOLOGY

### Faunal Distributions: a Result of History

North America—Canada and the continental United States (northern Mexico is discussed in the entry on America, Central & the Caribbean Islands: Biospeleology) contains a diverse and widely distributed cave fauna. The current distribution of cavernicoles is the result of interwoven historical parameters such as glaciation, shifting of vegetative communities, moisture (or aridity), and the rise and fall of shallow inland seas.

Continental drift (elements of the North American cave fauna have holarctic affinities) and the availability of suitable caves—typically in limestone, but also lava tubes and other types of caves—play a role in explaining the current biogeographic setting.

Pleistocene glaciation is a factor limiting the northern extent of the range of many North American troglobites and stygobites, especially terrestrial taxa. Most terrestrial cavernicoles see their greatest diversity south of the maximum reach of Pleistocene glaciation (see biodiversity map of United States in colour plate section). Notable exceptions occur, such as Castleguard Cave in western Canada where a troglobitic mite (*Robustocheles occulta*) is thought to have survived the Pleistocene in this cave beneath the Columbia Ice Field. Distributions of aquatic faunas, too, are sometimes limited by the glacial history—for example, the troglobitic flatworms of the genus *Sphalloplana* are found almost exclusively to the south of the maximum extent of Pleistocene glaciation. Among the aquatic taxa there are a number of lineages that seem to have survived the episodic advance and retreat of glaciers in the groundwater. Distributions of various amphipod crustaceans (e.g. species of *Stygobromus* and *Bactrurus*) are especially indicative of such a history.

The Pleistocene climatic fluctuations have influenced not only through the direct impacts of glaciers, but also through shifts in vegetative zones. Much of the North American terrestrial troglobite fauna has affinities with epigeal leaf-litter/soil communities. Faunal elements associated with moist leaf litter typical of cooler montane forests may have entered caves during cooler periods when such forests extended further south and to lower elevations. As the forests retreated north and to higher elevations some taxa—especially those with features that preadapt them to life in caves—were isolated from their epigeal ancestors.

The relatively depauperate fauna of western North America is explained only in part by somewhat lower densities of caves. Here, the more extreme aridity of the climate may have had much the same influence on terrestrial troglobites as glaciation had on the cave fauna of the northern parts of eastern North America. Arid western caves may have historically lacked the capacity to sustain populations of terrestrial troglobites because of both insufficient moisture and a lack of suitable energy input in the form of organic debris entering the caves from the more sparse vegetative communities in this arid climate. Finally, forest leaf litter communities in the southwestern United States are thought to have historically lacked a diverse community of cool/ moist adapted invertebrates through most of the Pleistocene. Such ancestral, pre-adapted, taxa are thought to have been precursors to many of the terrestrial troglobitic arthropods of the eastern United States.

The aquatic fauna of North American caves is also influenced by ancient seas. Stygobitic freshwater isopods of the largely marine family Cirolanidae occur in southern Texas caves (and southward into Mexico) and an endemic cirolanid (*Antrolana lira*) is also known from a small area in Virginia. These taxa may be relicts that were able to adapt to the freshwater cave environment as ancient shallow seas receded. Other aquatic cavernicoles have clear links to extant epigeal aquatic taxa which co-occur in the same region. Stygobites in these groups may represent more recent invasions from the surface.

### Richness and diversity of the fauna

There are approximately 1300 to 1500 described species of troglobites and stygobites in North America (north of Mexico). Approximately 70% of these are terrestrial, the remainder aquatic. Recent estimates as high as 6000 species have been made when undescribed taxa are included. Such estimates generally ignore microbes, protozoa, and fungi. The richness of the North American stygobite and troglobite faunas is not equally distributed among major taxonomic groups.

Among the vertebrates, troglobites and stygobites are found only among the fish (six or seven species) and salamanders (at least ten taxa). Several species of stygobitic fish occur in the family Amblyopsidae with several species across the eastern United States (*Amblyopsis rosae* in the Ozark Plateau and *Amblyopsis spelaea* and *Typhlichthys subterraneus* in the Interior Low Plateaux). The most extremely troglomorphic species among them is *Speoplatyrhinus poulsoni*, endemic to a very small area in northern Alabama. Two small catfish species are known from the large aquifer of the Edward Plateau. The grotto sculpin, *Cottus* sp. (Cottidae), of southeastern Missouri is likely to be described as a species distinct from a closely related surface relative.

The salamander fauna of North American caves includes a number of troglophiles and troglobites, dominated by members of the family Plethodontidae. Among these are *Haidetriton wallacei* (Florida and Georgia), *Typhlotriton spelaeus* (Ozark Plateau), two species and several subspecies of *Gyrinophilus* (Interior Low Plateaux and Appalachians), the Cave Salamander, *Eurycea lucifuga*, and several plethodontid salamanders in the Edwards Plateau (see Edwards Aquifer: Biospeleology, and photo of Texas Blind Cave Salamander in Amphibia).

Many North American bats are troglaxenes, and utilize caves as roost sites for overwintering, for migration stopovers, as maternity sites, and as bachelor roosts. Those species that roost in large colonies produce large deposits of guano that serve as an energy-rich food source for a guanophilic community that includes a variety of flies, beetles, mites, millipedes, and other invertebrates. Among the more significant large-colony bat species are two eastern North American species, the Indiana Bat and the Gray Bat, and, further south, the Mexican Free-Tailed bat. All three species can congregate in large colonies which sometimes number many thousands of individuals. A variety of other bat species, especially in the genera *Myotis*, *Pipistrellus*, and *Eptesicus*, are frequent inhabitants of North American caves.

Other troglaxenic vertebrates regularly utilizing caves include packrats (*Neotoma* spp.), mice, Turkey Vultures (*Cathartes aura*), and Eastern Phoebe (*Sayornis phoebe*), all of which commonly nest in or near the entrances or twilight zones of caves. Raccoons (*Procyon lotor*), who commonly venture deeper into caves, may leave behind significant deposits of faeces which can comprise an important energy input into some caves.

North America's invertebrate cave fauna includes a variety of insect, myriopod, arachnid, and crustacean species. Other groups of cavernicolous organisms—generally less well studied than the macroinvertebrates and vertebrates—include aquatic oligochetes (Annelida), branchiobdellidans, horsehair worms, entocytherid ostracods, copepods, and a variety of bacteria, fungi, and protozoans. Among the flatworms (Turbellaria), stygobites are known in several genera, including *Macrocotyla* and *Sphalloplana*.

Few molluscs are adapted for life in caves. Several groups contain stygobites, and the hydrobiid genus *Fontigens* is notable among these, as it includes several stygobites found in caves of the eastern and southeastern United States.

The arachnid fauna of North America is diverse and fascinating. Several genera of opilioniids are troglobites, including *Phalangodes* and *Bishopella* in the eastern United States, *Texella* species in the Edwards Plateau and Guadalupe Mountains, and *Cryptobunus* in the west. Some of these species are troglobites and others are troglaphiles. A number of other opilioniids may be found in caves, such as the Holarctic genus *Sabacon*. The common genus *Lieobunum* includes troglaxenes that occur in caves from Canada to Texas (and into Mexico). A southwestern species, *Lieobunum townsendii*, frequently occurs in huge aggregations of many hundreds of individuals in or near cave entrances. This species forages above ground at night, and thus may function as an important energy source for some caves.

Mites of caves are not well studied. The family Rhagidiidae occurs in caves across much of North America and includes several troglobites. Pseudoscorpionida is one of the more diverse cavernicolous arachnid groups. There are more than 20 troglobitic pseudoscorpions in the Appalachians alone. Some cave pseudoscorpions are notably larger than their surface relatives. Troglobites occur in several families. *Apochthonius* (Chthoniidae) is one of the more diverse genera, with troglobites found in caves across the United States. As with many of the arachnid groups, there are a number of species that are endemic to one or few sites.

Across much of the United States the spider families Linyphiidae, Leptonetidae, and Nesticidae contain troglobites. Other families (e.g., Telemidae and Dictynidae) contain numerous cave-adapted species in certain regions. In the eastern United States there are several cave-limited *Islandia* and *Nesticus* species. In Texas, the genera *Eidmanella*, *Neoleptoneta*, and *Cicurina* contain a variety of troglobites, and the genus *Cicurina* (Dictynidae) includes epigeal species, troglaphiles, and narrowly endemic troglobites. In the western United States (California), the genera *Telema*, *Blabomma*, and *Cybaeozyga* each contain several troglobites. The most commonly encountered troglobitic/troglyphic spider in the eastern United States is the widespread linyphiid, *Phanetta subterranea*. Several pholcids are common troglaphilic spiders. The common troglaphilic spider *Meta ovalis* is one of the more obvious arachnid inhabitants of caves in eastern North America, and is closely related to a European species.

The stygobitic crustaceans include more than 30 decapods—primarily crayfish species (especially *Orconectes* and *Procambarus*) but also three narrowly endemic species of freshwater paleomonid shrimps. Troglobitic crayfish are known from the Ozark Plateau and the Interior Low Plateaus, but the group is most diverse in the aquifers of Florida, where up to three species coexist. One notable decapod community outside of Florida is the faunal assemblage of Shelta Cave (Huntsville, Alabama) where three species of crayfish and a shrimp (one of the three stygobitic *Palaemonias* species) are known.

The amphipod fauna of caves and other groundwater in North America is diverse and dominated by crangonyctid and gammarid taxa. Among the genera frequently encountered are *Crangonyx*, *Stygobromus*, *Bacetrurus*, and *Gammarus*. Detailed studies of *Gammarus minus* and other Appalachian cave fauna are the basis for some of the theoretical framework of current studies of aquatic cavernicoles in North America.

Several other amphipod families occur in North American caves and groundwater, most notably in the Edwards Aquifer of Texas.

In addition to the cirrolanid isopods mentioned above, there are many stygobitic or phreatobitic species of the asellid isopod genus *Caecidotea*. *Salmasellus* occurs in a few caves of western North America. Cave-adapted terrestrial isopods of the family Trichoniscidae may also be found in caves of the southeastern and western United States.

Of the myriopods, only the millipedes contain an abundance of troglobites. Troglobitic millipedes are frequently encountered in caves throughout the eastern United States and occur in caves across the country. Genera with troglobites include *Pseudotremia*, *Cambala*, *Tingupa*, and *Scoterpes*, but there are a number of others. The centipedes commonly encountered in North American caves are troglaphiles.

Among the hexapods, there are a number of troglobites among the springtails (*Arrhapolites*, *Tomocera*, *Sinella*, *Pseudosinella*, and *Oncopodura* are examples of genera containing troglobites) and diplurans (e.g. *Litocampa*, *Haplocampa*, *Eumesocampa*).

Troglaphiles and troglonexes are found in several insect orders. The colourful moth *Scolioptrix libatrix* over-winters in caves, and other moths are associated with guano deposits. Flies of the families Heleomyzidae, Phoridae, Sphaeroceridae, and Mycetophilidae are frequent in caves. In the eastern United States the larval stage of the fungus gnat *Macrocera* builds webs to entrap prey. Mosquitoes (Culicidae) of several genera over-winter in caves across much of North America.

Cave crickets (e.g. *Haedenoecus* spp.) and camel crickets (*Ceuthophilus* spp.; Figure 1) are important components of many North American cave communities, and several species may co-occur in a single cave. Troglonexic *Ceuthophilus* species forage outside of caves at night and rest in the caves during the daytime. Faeces, bodies, and eggs of these animals comprise an important energy source for terrestrial cave communities. In the western United States, some lava tube caves contain another interesting orthopteran, *Grylloblatta* (Grylloblattodea).

Hymenoptera are generally not important components of North American cave communities, with the exception of the Red Imported Fire Ant (*Solenopsis invicta*). This introduced species forages in caves of the Edwards Plateau (and perhaps elsewhere in the southeastern United States) and is thought to have a negative impact on cave communities.



**America, North: Biospeleology:**

**Figure 1.** *Ceuthophilus cunicularis*, a troglaxene in central Texas caves.

Cave crickets are important components of many North American cave communities. (Photo by Steve Taylor, courtesy of Natural Resources Branch, Fort Hood, Texas)

Insect troglobite diversity is greatest in the beetles. Several staphylinids occur in caves, with the troglophile genus *Quedius* being the most frequently encountered. Spider beetles (Ptinidae) include some troglobitic species (e.g. *Niptus*), and the mold beetle family Pselaphidae is rich in troglobites, especially in the widespread genus *Batrisodes*, but also several other genera. Mold beetles occur in many caves of the Appalachians, Interior Low



**America, North: Biospeleology:**

**Figure 2.** *Rhadine reyesi*, a predatory troglobitic beetle that feeds on the eggs of cave crickets. (Photo by Jean Krejca and Steve Taylor, courtesy of Natural Resources Branch, Fort Hood, Texas)

Plateaux, and Edwards Plateau. Aquatic beetles occur in the Edwards Aquifer. The Leiodidae is one of the important cave beetle families, with more than 18 troglobites in the genus *Ptomaphagus* in the southeastern United States. Much of the cavernicole diversity in the Coleoptera occurs in the Carabidae, with many troglophilic and troglobitic species especially in the genera *Pseudanophthalmus* which is especially rich in species in the Appalachians and Interior Low Plateaus and *Rhadine* (Figure 2) which is most diverse in the Edwards Plateau and occurs in caves throughout much of the southwestern United States. Several species of beetles in each of these two genera are closely associated with cave or camel crickets, and prey upon the eggs of those crickets.

North America's cave fauna is threatened by a variety of environmental problems associated with human activities. These problems, discussed in greater detail in the entry



Conservation: Cave Biota, include 1) microbial contamination and organic enrichment of karst aquifers through inadequate treatment of human, livestock, and poultry waste; 2) increased sedimentation of subterranean streams resulting from deforestation, agricultural activities, and development; 3) spills of toxic materials (e.g. petroleum and acids) from pipelines, tanker trucks, and freight

**America, North: Biospeleology.** Endangered species utilizing caves in the continental United States (excludes spring and groundwater taxa). Modified after Elliott (2000).

Common Name	Scientific Name	Year listed as Federally Endangered	Occurrence
<b>Snail:</b>			
Tumbling Creek Cavesnail	<i>Antrobia culveri</i>	2001	Missouri
<b>Arachnids:</b>			
Bee Creek Cave Harvestman	<i>Texella reddelli</i>	1988	Texas
Bone Cave Harvestman	<i>Texella reyesi</i>	1988	Texas
Robber Baron Cave Harvestman	<i>Texella cokendolpheri</i>	2000	Texas
Tooth Cave Pseudoscorpion	<i>Tartarocreagris texana</i>	1988	Texas
Tooth Cave Spider	<i>Neoleptoneta myopica</i>	1988	Texas
Madla's Cave Spider	<i>Cicurina madla</i>	2000	Texas
Robber Baron Cave Spider	<i>Cicurina baronia</i>	2000	Texas
cave spider*	<i>Cicurina venii</i>	2000	Texas
Vesper Cave Spider	<i>Cicurina vespera</i>	2000	Texas
Government Canyon Cave Spider	<i>Neoleptoneta microps</i>	2000	Texas
<b>Insects:</b>			
Coffin Cave Mold Beetle	<i>Batrisodes texanus</i>	1988	Texas
Helotes Mold Beetle	<i>Batrisodes venyivi</i>	2000	Texas
Kretschmarr Cave Mold Beetle	<i>Texamaurops reddelli</i>	1988	Texas

Tooth Cave Ground Beetle	<i>Rhadine persephone</i>	1988	Texas
ground beetle*	<i>Rhadine exilis</i>	2000	Texas
ground beetle*	<i>Rhadine infernalis</i>	2000	Texas
<b>Crustaceans:</b>			
cave crayfish*	<i>Cambarus aculabrum</i>	1993	Arkansas
cave crayfish*	<i>Cambarus zophonastes</i>	1987	Arkansas
Lee County Cave Isopod	<i>Lirceus usdagalun</i>	1992	Virginia
Alabama Cave Shrimp	<i>Palaemonias alabamae</i>	1988	Alabama
Kentucky Cave Shrimp	<i>Palaemonias ganteri</i>	1983	Kentucky
Illinois Cave Amphipod	<i>Gammarus acherondytes</i>	1998	Illinois
<b>Fish and Amphibia:</b>			
Alabama Cavefish	<i>Speoplatyrhinus poulsoni</i>	1977	Alabama
Salamander			
Texas Blind Salamander	<i>Typhlomolge rathbuni</i>	1967	Texas
<b>Bats:</b>			
Gray Bat	<i>Myotis grisescens</i>	1976	southeastern US
Indiana Bat	<i>Myotis sodalis</i>	1967	eastern US
Lesser Long-Nosed Bat	<i>Leptonycteris curasoae yerbabuena</i>	1988	Arizona and New Mexico, to
Mexican Long-Nosed Bat	<i>Leptonycteris nivalis</i>	1988	Central America New Mexico, Texas, to Central America
Ozark Big-Eared Bat	<i>Corynorhinus townsendii ingens</i>	1979	Arkansas, Missouri, Oklahoma
Virginia Big-Eared Bat	<i>Corynorhinus townsendii virginianus</i>	1979	Kentucky, North Carolina, West Virginia, Virginia

\* no common name

trains; and 4) reductions in recharge, resulting from increased impervious cover (buildings, roads, parking lots). Continued human population growth also increases impact visitation to caves (habitat degradation), as well as increased rates of cave destruction through quarrying and filling of caves. In the continental United States, 23 troglobitic invertebrates, one fish, one salamander and six bats—all taxa that utilize caves—are currently listed as federally endangered (see Table). In addition, a variety of other cave-dependent species have been proposed as candidates for federal recognition.

STEVEN J. TAYLOR

*See also* **Edwards Aquifer: Biospeleology; Mammoth Cave: Biospeleology**

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## AMERICA, NORTH: HISTORY

Canada and the United States have karsts and pseudokarsts in many differing terrains, with differing landforms, and with differing spelean histories. In broad terms, the United States has about a dozen major calcareous karst areas and one in gypsum. Canada has almost as many in carbonate rocks, and several in gypsum (see entries on Canada and United States of America). The density and types of caves and other features vary markedly between the areas, and many of their subordinate units have their own history of exploration and study, and of significant events.

The study of cave exploration in the United States and Canada began in the 18th century with a simple mention of caves as curiosities. Longer accounts followed, largely in locally oriented tourist guides and early travel books and articles. Gazetteers pulled together scattered accounts, but these tended to be oriented toward specific localities. Eventually, caves were studied as interesting features of natural history; the study of caves for their own sake came relatively late. When a distinctly American speleology began to arise in the 19th century, it too was oriented toward local caves and their specific patterns and features. Thus it was largely independent of evolving European concepts, and perhaps somewhat suspicious of them.

In 1832 the erratic genius Constantine Rafinesque chose an inopportune time to utilize some of these European concepts. In the first systematic effort in American speleology (a classification of the caves of Kentucky) he began with his own observations on swallow and resurgence caves, rock shelters and crevice caves, and saltpetre caves with huge passages. To these he added Buckland's theology-based antediluvial concepts of bone caves, and a brand-new concept of limestone as a lava-like rock extruded from caves through crater-like dolines. At least in part, Buckland soon abandoned the antediluvial theory, and hardly anyone else ever thought of limestone as an extruded rock.

At the north end of the Appalachian Highlands karst area, Kastning has shown how a host of little-remembered figures contributed significantly to American speleology through local observations and reports (Kastning, 1981). To some degree, similar unsung participants contributed to equivalent progress in other karstic areas. Benchmark papers (e.g. those of Nathaniel Shaler, William M. Davis, and other well-known later speleologists) thus evolved naturally from a broadly based continuum, rather than as isolated studies.

Shaw (1992) mentions several writers who, in addition to Constantine Rafinesque, merit special note in this period: W.S. Blatchley, H.C. Hovey and his son E.O. Hovey, Edmund Lee, David Owen, Louisa Owen, and Charles Wright. These notables were a small fraction of the potential list. Not all were obscure. Not all were academics. But all were fluent in English. Early French and Spanish reports (for example, on what now is Florida Caverns, in 1693), were almost entirely unknown to pioneer American speleologists.

In the United States, the first wave of interest in caves was based largely on the pioneers' need for nitrates to manufacture gunpowder. The second wave began in Kentucky, Indiana, Virginia, and New York in the 1880s, peaked around the turn of the century, and ebbed at the time of World War I. The third began to gain momentum in the 1930s and 1940s and achieved unprecedented success after World War II.

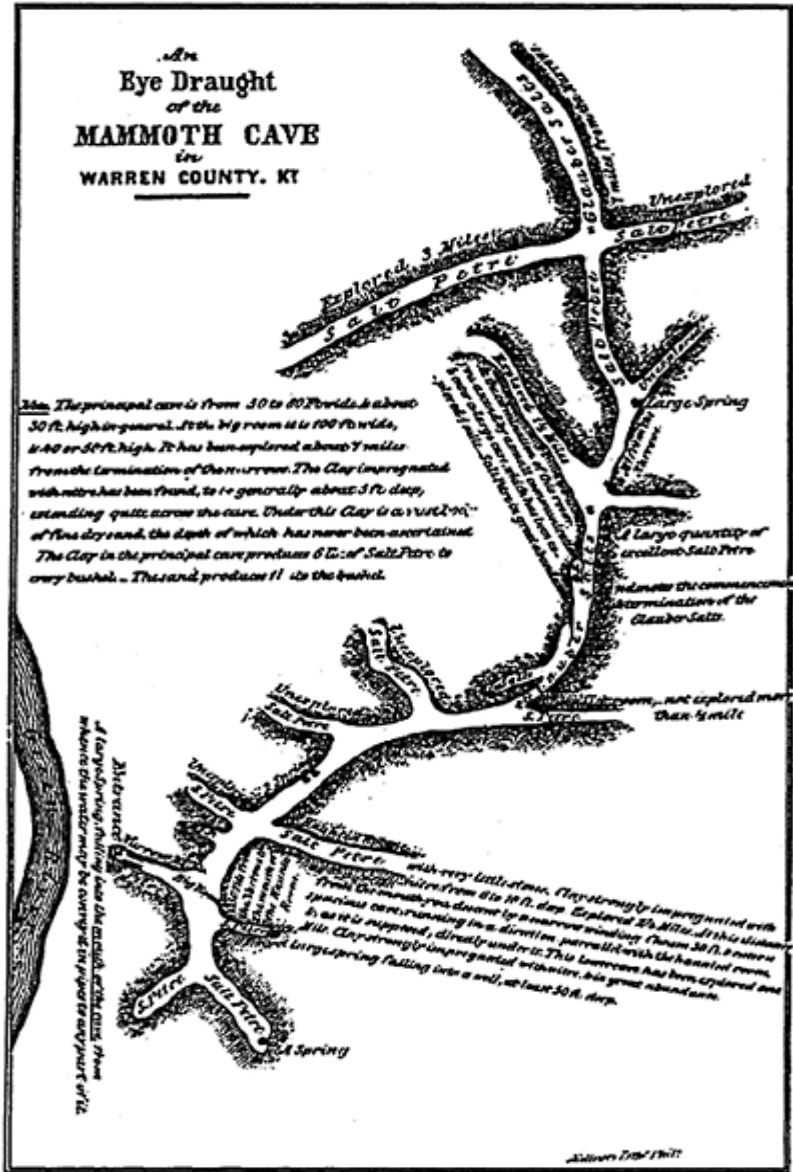
The Europeans founded their initial settlements along the Atlantic coast and its rivers, with littoral and riverside caves being the first to be found. Important riverside caves included Cave-in-Rock on the Ohio River, Indian Cave on the Tennessee River and the largely forgotten Carver's Cave in what is now St Paul, Minnesota. Away from the rivers, small caves in Pennsylvania and in the Virginia highlands were recorded in the 1740s and 1750s.

The names of well-educated “founding fathers” of the United States are prominent in this early period. George Washington left his signature in a small cave near what is now Harpers Ferry, West Virginia. Thomas Jefferson made the first map of a US cave (Madison's Cave, Virginia) and a later edition of his celebrated book (1853) *Notes on the State of Virginia* reproduced the third and fourth American cave maps—of Madison's Cave and what now is Grand Caverns, Virginia, and of Mammoth Cave, Kentucky (Figure 1). Jefferson consistently used scientific principles to evaluate aspects of caves. His studies of remains of a ground sloth from Organ Cave, West Virginia—the first ever discovered—led to its scientific name: *Megalonyx jeffersoni*.

In the mid-18th century, “long hunters” (hunters from pioneer settlements who stayed away from home for up to several months at a time) and a few hardy settlers began making gunpowder from nitrates in caves in what was then western Virginia (see Gunpowder). During the American Revolution, several of these caves were briefly pressed into full production. Around the turn of the century, Mammoth Cave and dozens of others were explored for nitrates, with production eventually reaching a very large scale until the Kentucky producers were devastated by the New Madrid earthquakes. Then the entire nitrate market collapsed at the end of the War of 1812.

American cave explorers followed in the footsteps of early cavers of the French and Spanish eras, but apparently without learning anything from them. Constructive plagiarism by fledgling American literary and scientific journals and travel books kept literate Americans somewhat informed about European caves and concepts. But 20 years after the collapse of the nitrate industry, “cave hunting was little else than a bizarre and venturesome underground diversion” (Clarke, 1914).

Canadian caves were even less celebrated. One cave near Lake Ontario was mentioned (fancifully and apparently second hand) in Winterbotham's 1796 *View of the United States of America*. Two others were reported in Quebec, in 1822 and 1823, with a new discovery in Ontario in 1824 and a flowery account of a cave in Nova Scotia in 1836. Gibb's landmark: *On Canadian Caverns*, however, did not appear until 1861. The now-famous Steam Cave at Banff was not seen by a European until 1875 and most of the other long-famous Canadian Rockies caves were not encountered until after 1900. The hell-roaring Nakimu Caves were discovered in 1904; within a few years they were developed in an early version of ecotourism. Alpinist A.O. Wheeler led North America's first real alpine cave exploration in 1911, down 76 m of pitches in Arctomys Cave.



America, North, History: Figure 1. 1811 sketch map of Mammoth Cave, Kentucky, as reproduced in the 1853 edition of *Notes on the State of Virginia* by Thomas Jefferson. William R. Halliday Collection.



**America, North, History: Figure 2.**  
Horace C.Hovey, father of American  
speleology. From an 1871 portrait by a  
photographer named Thompson.  
William R.Halliday Collection.

In the rebel southern states of the United States, the American Civil War (1861–65) precipitated a renewed wave of exploitation of saltpetre caves, and interest heightened throughout the reunited nation. Notable academic geologists, archaeologists, and biologists like Nathaniel Shaler and A.S.Packard, published landmark reports in 1876 and 1888.

However, it was a middle-aged clergyman, Horace C.Hovey, who triggered the second major wave of American speleology. Beginning in 1878, his writings had an impact unmatched in American spelean history. Hovey began caving as a youth but pursued it only intermittently. Nevertheless he dominated American speleology for 35 years. To the public he brought genial, unexaggerated accounts with which each reader could identify. His timing was fortunate: cave diggers broke through into Virginia's magnificent Luray Caverns shortly after publication of his 1878 article. When the news broke, *Scientific American* magazine rushed him to Luray for a scoop, and suddenly Hovey had enough material for his famous 1882 book *Celebrated American Caverns*. It became the most influential American cave book of all time. Almost overnight he became "final in experience and judgment in that phase of science now designated by the unlovely term speleology" (Clarke, 1914).

Hovey never travelled west of Arizona's Grand Canyon, but his wave of enthusiasm swept across the entire country. Show caves sprang into existence as far away as California. Back home in Indiana, W.S.Blatchley published the first state-wide report on caves. In 1900, E.S.Balch followed with *Glacières, or Freezing Caverns*, the first exhaustive American work on cave meteorology.

The Hovey wave ebbed during World War I, but a new wave of interest began in 1925 when Floyd Collins died in a detached part of Mammoth Cave. Later that year, members of the Explorers Club light-heartedly sought the end of Virginia's Endless Cavern, with considerable publicity. Publicity also was building at Carlsbad Cavern, where the ill-fated Nicholson Expedition of 1930 provided another prolonged media event—and triggered the creation of Carlsbad Caverns National Park. Raconteur Russell Trall Neville lectured widely in the 1930s, and Clay Perry's books and articles about American caves brought still further cave consciousness to a wide audience.

In the scientific world, notable papers by Weller (1927) and William M.Davis (1930) strongly stimulated speleogenetic thought in the United States. Within a few years, Swinnerton, Gardner, and Malott all provided the beginnings of a new, ongoing flood of papers expanding Davis's concepts in specific localities. That of J Harlen Bretz in 1942 was especially significant. From it, ordinary American cavers learned to read the silent language of speleogenetic sequences. More recently, contributions by William B.White, Arthur Palmer, and Ernst Kastning are among many meriting special mention.

State-wide cave reports began to appear. Ralph Stone's *Caves of Pennsylvania* was published in 1930. Soon it was followed by McGill's *Caves of Virginia* and W.E.Davies's *Caves of West Virginia* and *Caves of Maryland*. Bretz's *Caves of Missouri* and many others followed.

The word "speleogenesis" broke into print in 1960 at a symposium where the old concept of speleogenetic cycles was laid to rest (Halliday, 1960). (Kyrle had used its German equivalent by 1923.) Also advanced at that symposium was a then-heretical concept: not all karstic caves have precisely the same origin.

Extensive US participation in international speleological congresses accelerated in 1981 when the 8th was convened in Kentucky. The purely American brand of speleology became more and more internationalized. With an extensive publication programme culminating in the appearance of the internationally edited book *Speleogenesis* in 2000, the National Speleological Society took on a leadership role in international speleology.



The National Speleological Society was founded in 1941. After World War II, the third wave of American speleology rose to new heights. The number of recorded caves skyrocketed; 8000 are now listed in the state of Tennessee alone. New US depth records were repeatedly broken in the Rocky Mountains, then surpassed by Lechuguilla Cave at 478 m (the vertical ranges of long lava tube caves don't count; see Volcanic Caves). That depth wasn't much by world standards, but the Cave Research Foundation of especially dedicated explorers (an offshoot of the National Speleological Society) pushed the mapped length of Mammoth Cave to 587 km by 1996, by far the greatest in the world. And a barely separate segment of its system—Fisher Ridge Cave—reached 161 km in 2001.

Opened in 1986 by two years' digging, the crystalline magnificence of Lechuguilla Cave somewhat distracted attention from its statistics. With 176 km currently mapped, it became the third longest in the United States.

The explored length of "little" Jewel Cave in South Dakota increased rapidly to 204 km, surpassing neighbouring Wind Cave (just over 160 km). Even California, not renowned for its caves, was found to have a long cave: Lilburn Cave at 27 km and another which is 367 m deep (Bigfoot Cave).

Progress in conservation has been no less important. Most Americans think in terms of national parks and monuments rather than World Heritage Sites, but three caves or groups of caves have been designated as national parks (Mammoth Cave, Carlsbad Caverns, and Wind Cave). Four others are national monuments: Jewel Cave, beautiful little Timpanogos Cave in Utah, Oregon Cave, and Russell Cave in Alabama (primarily an archaeological reserve, but also with notable karstic features). When Mount St Helens National Volcanic Monument was created, the Caves Basalt Lava Flow comprised one of its three units, and many other American and Canadian national parks and monuments are karstic or pseudokarstic.

In Canada, cave studies in the 20th century followed a somewhat different route. The arrival of Derek Ford and other keen British cavers at McMaster University provided an international scientific flavour long lacking in the United States. They also brought in their special skills and determination, and experience in alpine karsts. Soon a secondary Canadian centre of speleology was spun off to Calgary, and the famous Nakimu Caves soon lost their status on the list of deep Canadian caves. In the 1960s and 1970s, three of the five deepest caves in Canada were discovered, explored and/or studied in the Canadian Rockies: Arctomys Cave, Castleguard Cave, Yorkshire Pot, and later, Close to the Edge Cave. Castleguard Cave—Ford's speciality and Canada's longest—was mapped for 20.1 km. A member of his team found that it ends with ice plugs from a major glacier overhead. Even in the remote Northwest Territory, Quebec cavers and members of Ford's group found several caves over 1 km long in the isolated Nahanni National Park. Here, Grotte Valerie is notable for its exceptionally diversified underground climate.

Meanwhile in Québec, the vigorous and well-organized Société Québécois de Spéléologie was formed in the early 1970s, with a distinct French flavour (Beaupré & Caron, 1986). It soon became noted for excellent scientific and educational programmes, but found itself frustrated by the lack of large caves in Québec. Its activities soon became thoroughly international.

Another caving centre developed in and near Victoria, British Columbia. With an initial impetus in the early 1960s from Clarence Hronek in Vancouver and Seattle's

Cascade Grotto of the National Speleological Society, several vigorous groups emerged in the 1960s, 1970s, and 1980s. Vancouver Island now has the greatest number and density of caves in any Canadian region, including five each from the dozen longest and dozen deepest caves in Canada.

Cave diving in the continental United States began to come of age in 1953, in enormous underwater cave passages in Florida. Pleistocene mastodon and other paleontological remains were found at the start of a huge underwater borehole at Wakulla Spring. Here, current explorations are more than 5 km from the entrance, with an average depth of nearly 100 m *en route*. Garry Salsman and Wally Jenkins are acclaimed for early achievements here. The nearby Woodville Karst Plain system may be far larger, with more than 20 interconnected spring entrances and a claimed underwater length of 32.9 km in 2001. The longest recorded underwater traverse in Florida appears to be 4268 m, between Big Dismal Sink and Cheryl Sink. Elsewhere, cave diving in the remarkable karstic springs of the Ozark Plateau has shown that several are outlets of other huge karstic conduits at depth, reached by underwater corridors sloping uniformly downward from the swirling springs. In Nevada, however, the National Park Service forbids diving in the amazing Devil's Hole, so its remarkable depth remains unmeasured. The late Sheck Exley is widely credited with the primary role in advancing American cave diving, with Bill Stone noted for technological advances.

Biologists initiated systematic study of gypsum caves in Kansas in the mid-20th century. In the great gypsum karst of Texas, David Belski subsequently began an extensive geomorphological project, still ongoing. Interest in crevice caves and other limestone landforms resulting from deeply buried gypsum karst in northeastern Arizona is largely recent. In Canada, gypsum caves are widespread but interest in them has been desultory. An apparently world-class example in Wood Buffalo National Park is full of very cold water, and the others all seem to be less than 300 m long (D.Ford, personal communication, 2001).

Interest in American and Canadian pseudokarst and pseudokarstic caves has been sporadic. William R.Halliday, Donald Davis, Louise Hose, and the Colorado, San Diego and Southern California Grottoes (Chapters) of the National Speleological Society have provided notable leadership. The smooth, waterpolished surfaces of Greenhorn Cave and other granite stream caves of California have been appreciated by local cavers, but the talus caves in the Pinnacles National Monument have received more publicity. Regions especially noted for piping caves include Oregon's John Day country, Texas's Palo Duro Canyon, and the Anza-Borrego area of southern California.

More than a century ago, Israel Russell found lengthy glacier caves in Alaska, with a subglacial river about 50 km long coursing beneath the entire width of the Malaspina Glacier's piedmont. Direct scientific observation in Alaskan glacier caves shows a lack of progress since the 1970s. The Paradise Ice Caves—large glacier caves on Mount Rainier—were commonly visited by 1908, and its summit geothermal firn caves saved the lives of the first party to ascend it. The geothermal summit caves of Mount Rainier and Mount Baker were primarily investigated by Eugene Kiver in the 1970s. The glacier containing the Paradise Ice Caves shrivelled, re-expanded, and then disappeared completely during the last decades of the 20th century, though in 2001, the caves were reported to be re-forming in firn.

WILLIAM R.HALLIDAY

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## AMERICA, SOUTH

Compared with other continents, South America contains relatively small areas of carbonate, probably less than 2% of its total surface. Carbonate karst is concentrated within the ancient plateaux of central Brazil and in a few scattered areas of the Andean countries, although some small bodies of carbonate rock are dispersed throughout the continent (Figure 1). Nevertheless, there are some important South American karst areas with significant caves (see Table), including the world's best-developed quartzite karst (see Quartzite Caves of South America).

Venezuela is second only to Brazil in the area covered by karst scenery. The Roraima quartzite occupies a major part of the country's southern sector, hosting impressive vertical caves on the top of quartzite towers (known locally as tepuis), which rise abruptly from the rainforest. Many deep fissure-like caves and massive shafts occur in this area. Carbonate karst is concentrated in the northern coastal mountains of the Andean zone, the location of *c.* 95% of all caves recorded in Venezuela. In this area, karst is developed in carbonate rocks of Jurassic-Tertiary age, mostly as isolated outcrops usually of local extent, surrounded by noncarbonate rocks. The most significant karst is developed in five areas: Oriental, Central, Falcon, Andes, and Perija. In the Oriental area, the best-developed karst occurs in the Caripe-Mata de Mango area in the state of Monagas, where about 30 caves are developed in Cretaceous limestone. Venezuela's most celebrated cave, the 10 200 m long Cueva del Guácharo is located in this area, protected since 1949 by the Alejandro de Humboldt Natural Monument. The central part of this area hosts significant caves in the metamorphosed limestones of the Cordillera de la Costa (Coastal Range), for example, the 4292 m long Cueva Alfredo Jahn.

In the Falcón area, karst occurs in the San Luis and Serranía Churuguara mountains. The former area shows well-developed karst topography on Oligocene reefal limestones. Many deep caves occur within this zone, such as the 305 m deep Haitón del Guarataro. The Andes area shows Cretaceous reefal limestone at Humocaró, La Azulita, and Guaraque. The karst region of the Sierra Perijá, close to the Colombian border, has recently yielded major caves. In this area, lower Cretaceous limestones outcrop in a very wet rainforest environment. Many active caves exist in the area, including Venezuela's longest known cave, the 18200 m long Cueva del Samán and many other important caves such as Cueva Sumidero La Retirada (6080 m long), Cueva los Encantos (4600 m), and Cueva los Laureles (4300 m).



**America, South: Figure 1.** Main areas of carbonate and quartzite karst in South America.

Little is known about karst in Surinam, Guyana, and French Guyana. Carbonate rocks appear to be absent, although the Roraima quartzite does extend towards Guyana. Short caves in granite and under laterite (ferricrete) layers have been noted in French Guyana.

Over a hundred caves have been recorded in Colombia. Carbonate karst occurs mainly within the Cordillera Oriental, where isolated karst areas contain a number of significant caves. The best-known area lies in the Santander Department, where some major vertical caves have been recorded, among them the renowned Hoyo del Aire, a 120 m deep, 100+m wide pit which gives access to a massive passage terminating at a depth of 270 m, and the 4926 m long Sistema Hermosura, Colombia's longest cave. In southern Colombia, a small karst area hosts the Cueva del Indio (3507 m long) and the important Cueva de los Guácharos (1000 m long), both of which have been protected since 1960 by the Cueva de los Guácharos National Park. One significant sandstone cave has been explored in the Tolima area—the Cueva del Cunday, which is 850 m long and 160 m deep.

Carbonate karst in Ecuador is concentrated mostly in the Oriental sector of the Andes. The Cretaceous limestones of the Napo, Pastaza, and Morona Santiago provinces host most of

### **America, South:** The longest and deepest caves of South America, as at January 2003.

Longest caves			Deepest caves		
Cave	Country	Length (m)	Cave	Country	Depth (m)
1. Toca da Boa Vista	Brazil	97000	1. Sima Pumacocha	Peru	638
2. Toca da Barriguda	Brazil	28700	2. Gruta do Centenário	Brazil	481
3. Cueva del Samán	Venezuela	18200	3. Millpu de Kaukiran	Peru	407
4. Gruta do Padre	Brazil	16400	4. Gruta da Bocaina	Brazil	404
5. Boqueirão	Brazil	15170	5. Sima Aonda	Venezuela	383
6. Lapa do Angélica	Brazil	14100	6. Perte du Futur	Chile	376
7. Gruna da Água Clara	Brazil	13880	7. Sima Auyán-tepui Noroeste	Venezuela	370
8. Lapa São Mateus III	Brazil	10610	8. Sima Aonda 3	Venezuela	335
9. Cueva del Guácharo	Venezuela	10200	9. El Tragadero	Peru	334
10. Lapa São Vicente I	Brazil	10130	10. Sima Aonda 2	Venezuela	325

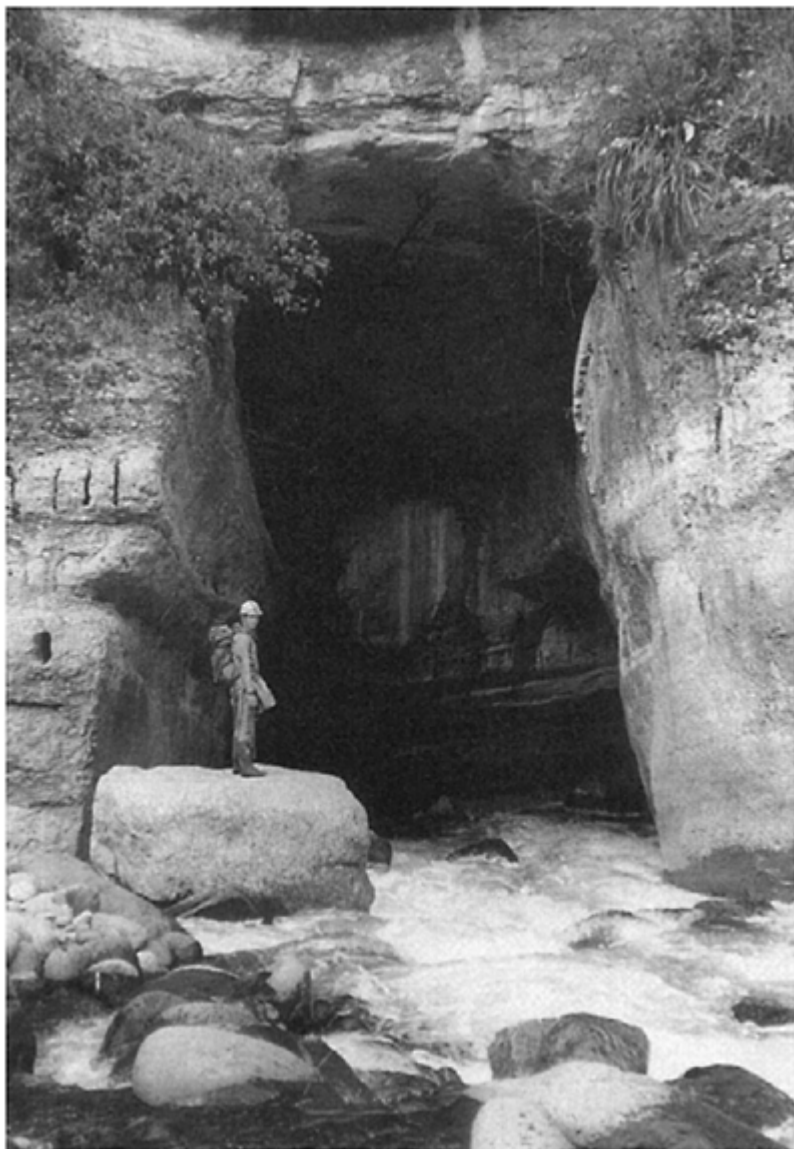
the c. 400 caves known so far. The Napo Province hosts many caves, including the 2460 m long Cueva de San Bernardo. The Pastaza Province is home to several caves, but difficulties of access have precluded systematic exploration. The deepest and longest caves in Ecuador are located in the Morona Santiago area. The Cueva de los Tayos de

Coangos is 4800 m long and 201 m deep. The same region contains the 2305 m long Cueva de Shimpiz. Important lava caves occur in the volcanic Galápagos Islands. Most of the 67 caves that were recorded up to 1988 are concentrated in Santa Cruz Island, including the 3010 m long Cueva del Cascajo and the partially commercialized 2331 m long Cueva de Gallardo, the most important lava tube cave in South America.

Carbonate crops out in many areas of Peru, although some of the best-developed karst lies in the northern and central region. The country is noted for its high-altitude karst, some of which occurs as high as 4800 m in altitude. In the northern portion of the country, significant caves occur in the Cajamarca area, one of the most important being the hydrological system known as Uchkopisjo, with a combined length of 2350 m. The San Andrés de Cutervo area has been a National Park since 1961 and contains, among other caves, the Gruta de los Guácharos (1134 m long and 180 m deep) and the 334 m deep El Tragadero (Figure 2). Southeast of the town of Cajamarca there is a high-altitude karst area (4000–4200 m in altitude) with an extraordinary collection of deep pits, many with depths around 200 m. The area near the town of Tarma (Central Peru) hosts the Millpu de Kaukiran, the second deepest carbonate cave in South America (407 m deep and 2141 m long). Its resurgence is the Gruta Huagapo, the longest Peruvian cave at 2396 m in length. Ongoing exploration in an area in south-central Peru has yielded South America's deepest carbonate cave, Sima Pumacocha, which is 638 m deep.

There are only a few karst areas in Bolivia, but the most well-known area is the Torotoro Karst near Cochabamba, which comprises Cretaceous limestones hosting the Gruta Umajalanta, the deepest and longest cave in the country at 4.6 km long and 164 m deep. Other nearby caves include the resurgence of Chiflonkkakka and the 154 m deep Caverna Huayllas. The area belongs to the Torotoro National Park, which was established in 1989. There are some areas of gypsum and sandstone karst in the country, which host respectively the 413 m long Gruta de San Pedro and the 350 m long Gruta San Miserato. Precambrian carbonates also occur near the border with Brazil, at Puerto Suarez. These outcrops have received little attention to date and no significant caves have yet been noted.

The most important karst zone in Paraguay is located near the border with Brazil, where Precambrian dolomites form a



**America, South: Figure 2.** The large open sink of the Rio Charcay at the Tragadero de San Andes in the high Andean karst of Peru. (Photo by Chris Birkhead)

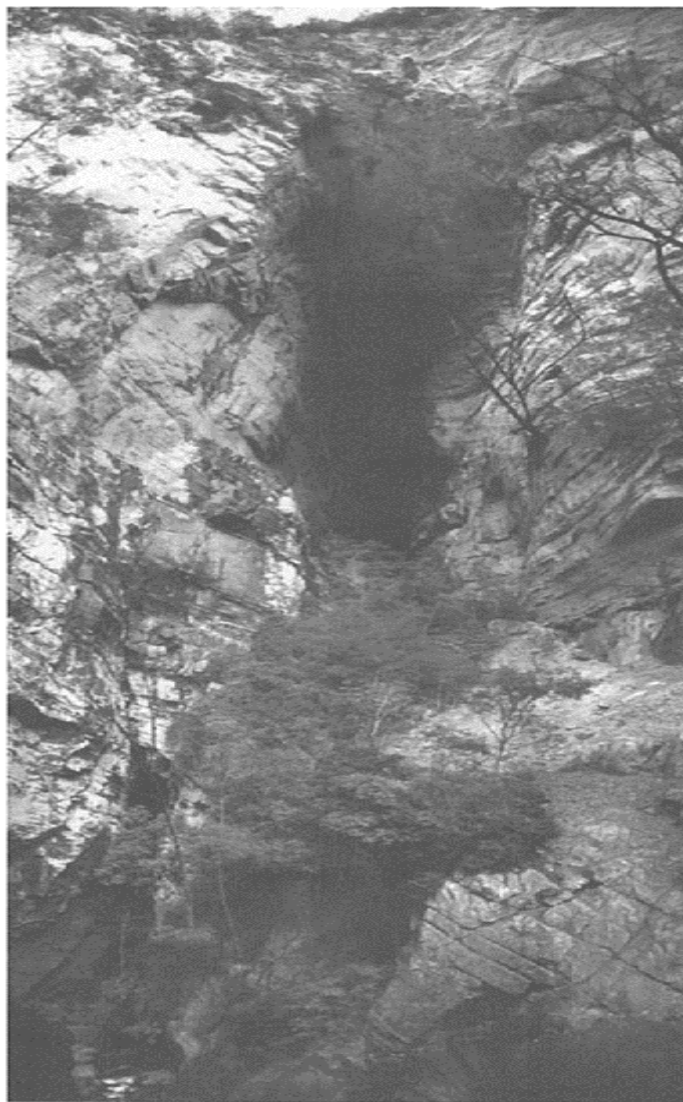


cone karst with isolated hills above the alluvial plain of the Paraguay River and its tributaries. A number of caves have been explored in this area, none of which is of a significant length. Uruguay is of little speleological importance due to the near absence of carbonates. The best-known cave in the country is the 41 m long Cueva de Arequita, developed in granite and located near the town of Minas.

The Chilean karst is characterized by extreme climatic conditions. Limestone, gypsum, and salt are known to outcrop in the hyper-arid Atacama Desert (precipitation of around  $1 \text{ mm a}^{-1}$ ) in northern Chile. Surface karst features have been noted in these rocks, and the Cueva del Valle de la Luna, in salt, comprise two separate caves respectively 500 and 250 m in length. At the southern end of Chile, the Patagonian region hosts some spectacular marble karst, especially on the islands of Diego de Almagro and Madre de Dios (see Patagonia Marble Karst, Chile), under high precipitation (*c.*  $7000 \text{ mm a}^{-1}$ ) and extreme conditions of wind and temperature. Unique wind-controlled karren have been observed, and recent exploration in the Madre de Dios has yielded the 376 m deep Perte du Futur. Near Puerto Natales, the celebrated Cueva Mylodon is probably South America's best-known paleontological site. The cave is a massive passage 200 m long and 100 m wide, developed in conglomerate, where well-preserved ground sloth and human fossil remains have been studied since the end of the 19th century.

Only  $1000 \text{ km}^2$  of Argentina is made up of karst, which is a fairly small area for such a large country. The most important carbonate and gypsum areas occur in the provinces of Mendoza and Neuquén. The two most important carbonate areas are the Las Brujas region, near Malargüe, Mendoza, with the 1343 m long Cueva de las Brujas, a cave of supposedly hypogene origin (Forti, Benedetto & Costa, 1993), and the Cuchillo Cura area in Las Lajas, Neuquén, home of the country's longest cave, the 3433 m long Sistema Cuchillo Cura. Gypsum karst occurs in La Yesera del Tiromen and Curymil, both in the Neuquén Province, and at Sierra de Reyes and Sierra de Cara Cura in the Mendoza Province. The most significant gypsum cave in Argentina is the 853 m long Cueva del León in Las Lajas, Neuquén. Some lava caves also exist, such as the Cueva de Doña Otilia in Malargüe, Mendoza, at 838 m in length.

Brazil contains the largest area of karst in South America. Carbonate karst occupies *c.*  $200000 \text{ km}^2$ , mostly distributed in the southern half of the country. The majority of the karst develops over Precambrian carbonates, under a seasonal climate (with a rainfall of between 500 and  $2000 \text{ mm a}^{-1}$ ). The Bambuí karst (see Bambuí Karst, Brazil) is the largest carbonate area in the country, hosting about half of the *c.* 3500 known caves, including some of the country's most significant caves. The Una Karst, located mostly within a semi-arid area, in northern Bahia State, is home to the longest cave in South America, the 97 km long Toca da Boa Vista (see entry on Boa Vista, Toca, Brazil) besides significant caves in the vicinity of the town of Iraquara. In southern Brazil, the outcrops of the Açungui Group contains many major active caves in tropical rain forest, including the world's tallest cave entrance at Gruta Casa de Pedra (215 m, Figure 3). Caves in this area are generally very well decorated (Figure 4), and most of this area is protected by the Upper Ribeira and Jacupiranga State Parks (Karmann & Ferrari, 2000). In western Brazil, many caves have been identified in the isolated carbonate hills of the Corumbá and Araras Groups, including important



**America, South: Figure 3.** Part of the entrance to Casa de Pedra cave, Ribeira karst, Brazil. The entrance is thought to be the highest in the world at 215 m. The stream-sink at the bottom left leads to a fine river passage. (Photo by John Gunn)

flooded caves near the town of Bonito. Other important carbonate areas include Cretaceous limestones of the Apodi Group in the northeasternmost part of Brazil, and karst developed over freshwater carbonates of the Caatinga Formation, in northern Bahia State.

Brazilian quartzite caves occur mostly in the eastern portion of the country (see Quartzite Caves of South America), and comprise the deepest and longest caves known in this type of rock. Sandstone karst is widespread throughout Brazil, from the



**America, South: Figure 4.** Fallen stalactite block in Casa de Pedra cave, Ribeira Karst, Brazil. The block appears to have detached slowly and rotated through 180° landing upside down on the floor. (Photo by John Gunn)

southern provinces to Amazonia. The best-developed areas lie in rocks of the Furnas and Botucatu formations, including the 1400 m long Caverna Aroe Jari at Chapada dos Guimarães, Mato Grosso State. In Amazonia, the Prainha area has some long sandstone caves, such as the 1297 m long Gruta Planaltina. The longest sandstone cave in Brazil is currently the 1633 m long Toca das Confusões in the semi-arid region of the state of Piauí. Another cave of note is the 1600 m long Caverna dos Ecos, developed in mica schists (Karmann, Sánchez & Fairchild, 2001). Caves in granite, talus, bauxite, and under laterite have also been recorded.

AUGUSTO AULER

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## AMERICA, SOUTH: BIOSPELEOLOGY

South America, with an area of 17800000 km<sup>2</sup> mostly within the tropical zone and a high diversity of physiography from lowland forests to semi-desert high mountains, encompasses several regions of biological megadiversity. The subterranean fauna was therefore predicted to be accordingly rich and diversified due to the diversity of potential

colonizers. Intensive, systematic biospeleological studies started late in comparison with Europe and North America. However, rapid progress has been made in the last 30 years.

In 1799, the naturalist Alexander von Humboldt made the first written reference to a South American cave animal, the oilbird or “guácharo” (*Steatornis caripensis*), from caves in Venezuela. Other naturalists travelling throughout the continent in the 19th century occasionally mentioned cave animals, especially bats and birds. By the end of that century, the first South American troglobite, the blind catfish—*Pimelodella kronei*, was described from caves in southeastern Brazil. During the first half of the 20th century, biospeleology in South America was mainly restricted to occasional descriptions of taxa from caves scattered across the continent. Extensive studies started in the 1950s and 1960s, with foreign expeditions to several countries in addition to efforts by some native biologists, especially in Venezuela, and later in Brazil. Brazil currently has the best-studied cave fauna in South America, following intensive studies starting in the 1980s that ranged from faunistic surveys to community studies and to investigation of the biology of different taxa.

Based on such studies, ecological and evolutionary patterns began to emerge, revealing that differences with respect to temperate cave ecosystems were less than previously assumed. Although the taxonomic composition of subterranean communities differ as a consequence of biogeographic factors, ecological and evolutionary mechanisms and processes appear to be similar. Caves with huge amounts of guano produced by very large colonies of bats and echo-locating birds, frequently cited as characteristic of tropical regions, are not as common in South America as generally assumed. As observed in temperate areas, many caves studied in South America are oligotrophic, with food resources for cavernicoles represented by vegetal debris, relatively small guano piles, and dead and living epigeal organisms accidentally entering caves or carried in by water (streams or percolating water).

The most frequent subterranean taxa found in continental South America are presented here, organized by ecological affini-ties. Some taxa are distributed throughout the continent, whereas others are restricted either to fully tropical, warm caves (>22°C) to the north of Tropic of Capricorn, or to subtropical to temperate caves in southeast Brazil, Uruguay, and Chile.

South America is remarkable for its chiropteran (bat) diversity, only equalled by that in Southeast Asia. Many bat species frequently use caves, especially phyllostomids that include frugivorous, nectarivorous, insectivorous, carnivorous, and haematophagous species. In inhabited karst areas with livestock, vampire bats may be particularly numerous in some caves. Different kinds of bat guano support distinct communities of invertebrates; it is noteworthy that vampire bats, with their distinctive black guano due to their specialized diet based on blood, are exclusively neotropical. Other troglone mammals include didelphids (e.g., the four-eyed opossum, *Philander opossum*, the river otter (*Lontra longicaudis*), and rodents such as the water rat (*Nectomys squamipes*), spiny rats (*Proechmys*), and agouti (*Agouti paca*). In northwest South America, oilbirds form large, noisy colonies nesting in some caves. Their “guano”, actually a mixture of faeces and regurgitated, partially digested fruits, supports rich communities of detritivorous invertebrates. Barn owls and some other birds are observed in caves throughout South America, but never far from entrances. Among invertebrates, it has been shown that large

opilionids (harvestmen) of the genus *Goniosoma* form troglaxene populations in southeast Brazil, reproduce near the entrances, and leave caves regularly to feed.

Most terrestrial invertebrates regularly found in South American caves are troglaphiles. Conspicuous omnivorous/detritivorous macroinvertebrates include phalangopsid crickets, mainly *Endecous*, cockroaches (in warm caves), harvestmen, and millipedes; rhabdiphorid crickets, typical of North temperate caves, have been found in Chile. Their predators are mainly spiders, which present a high diversity in South American caves—33 out of 54 families occurring in the neotropical region have been recorded in Brazilian caves. The most frequent are large wandering ctenids (mainly *Ctenus*), sicariids (*Loxosceles*), and web-building pholcids, theridiosomatids (mainly *Plato*), and theridiids. Additional predators are centipedes, reduviid bugs and, in fully tropical caves, amblypigids (especially the large *Heterophrynus*) and scorpions. Among detritivores, cave millipedes are also diversified in South America, including Polydesmida (e.g., chelodesmids), pseudonannolenids, and spirostreptids. Most cave harvestmen are gonyleptids, especially pachylines; cosmetids, agoristenids, and cranids are found in fully tropical caves.

Soil animals are typically found in sediment banks, concentrating in plant debris and animal matter deposited on these banks or on rocky surfaces. These include earthworms (e.g., enchytraeids), the ubiquitous springtails (isotomids, paronellids, entomobryids, arrhopalitids) and mites, campodeid diplurans, oniscidean isopods (mainly phylosciids, platyarthrids, and styloniscids), millipedes, larvae of tineid moths, larvae and adults of beetles such as cholevids (usually on animal matter), and ptilodactylids. Their predators include predaceous mites, beetles (e.g., carabids, pselaphids, histerids, staphylinids), pseudoscorpions (mainly chernetids), small spiders (e.g., ochyroceratids, hahniids), centipedes, and, in tropical caves, schizomids. Some species are mainly found in guano, certain taxa being restricted to or showing strong preference for particular kinds of guano (e.g., *Acherontides* springtails, larvae of *Drosophila*, *Fannia*, and *Psilochaeta* flies in vampire bat guano; cydnid and lygaeid homopterans, and lithobiomorph centipedes in frugivorous bat guano).

As expected in view of their overall diversity, beetles and flies are the most diversified cave insects in South America. Several families of small to medium-sized predaceous and detritivorous beetles have been recorded. As in temperate karst areas, the predaceous carabids and the detritivorous cholevids are among the commonest cave beetles; however, the subgroups that contribute with the highest diversity in most temperate caves—trechines within carabids, bathysciines within cholevids, including many troglotitic (exclusively subterranean) species—are rare in South American caves. Several families of dipterans have been recorded in South American caves, including psychodids, chironomids, keroplatids, sphaerocerids, phorids, milichiids and muscids.

Nymphs and larvae of flying insects such as chironomid flies, mayflies, and caddisflies live in cave streams. Their adults, which may attain very high population densities at certain times of the year, are captured in the webs of spiders and of larvae of keroplatid flies. In addition to immature insects, the aquatic fauna includes adult heteropterans (e.g., veliids) and beetles (e.g., elminthids, dytiscids), molluscs such as hydrobiid gastropods, and crustaceans. Among crustaceans, amphipods, mainly bogidiellids and hyalellids, are frequent in both streams and phreatic water bodies throughout South America. Other crustacean taxa have more localized distributions:

spelaogriphaceans in phreatic water bodies from southwest Brazil; Calabozoa isopods in phreatic waters from Venezuela and northeast Brazil; the anomuran *Aegla* in cave streams of southeast Brazil; and crabs mainly in northwest South America. Shrimps are rare in South American caves, usually as accidental or troglone occurrences.

The total diversity of terrestrial troglobites in South America is moderate, much lower than the observed in Northern hemisphere temperate caves especially for some groups such as spiders and beetles. The great majority of South American terrestrial troglobites evolved from soil animals—several springtails, isopods, a few campodeid diplurans, rare thysanurans, chthoniid pseudoscorpions, a few, generally small spiders, beetles (mainly pselaphids and carabids), and polydesmida diplopods. Other terrestrial troglobites are harvestmen (gonyleptids in Brazil, agoristenids in Venezuela, a triaenonychid in Argentina), a few cockroaches (Venezuela and Brazil) and a cixiid homopteran (Argentina).

On the other hand, South America is relatively rich in aquatic stygobites, including both stream-dwelling and phreatobic crustaceans (syncarids, amphipods, isopods, spelaogriphaceans, decapods such as *Aegla* anomurans, and pseudothelphusid crabs), hydrobiid gastropods, a few planarians, and fishes. South America is distinguished by its richness of stygomorphic fishes. At least 19 exclusively subterranean species are known, mostly Siluriformes (catfishes). The most frequent are catfishes of the genus *Trichomycterus* from Brazil, Venezuela, Colombia, and Bolivia; armoured catfishes of the genus *Ancistrus* from Brazil and Venezuela; and heptapterine catfishes from Brazil. In addition, several epigeal stygomorphic species (with reduction of eyes and pigmentation) have been found in turbid rivers of the Amazon Basin.

While the cave fauna is better known in Brazil, the interstitial aquatic fauna has been better surveyed in countries such as Venezuela, Argentina, and Chile. A diversified stygobitic crustacean fauna including several species of copepods (mainly harpacticoids), ostracods, syncarids, isopods (e.g., protojanirids in Argentina) and amphipods (bogidiellids, ingolfiellids), in addition to hydracarians, have been found in interstitial habitats.

As proposed for temperate karst areas, paleoclimatic fluctuations resulting in periodic elimination of epigeal populations and, consequently, isolation of troglomorphic populations in subterranean habitats (which they colonized during more favourable periods) and subsequent allopatric speciation, have been evoked as a major cause of diversification of the South American troglomorphic fauna, at least for terrestrial taxa. In the case of aquatic troglobites, there is evidence that other isolation mechanisms such as stream capture, or even parapatric or sympatric speciation, may also be important.

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## AMERICA, SOUTH: HISTORY

The relationship between man and caves in South America precedes the arrival of the first Europeans at the end of the 15th century. South American inhabitants did not appear to have strong cultural ties with caves and karst features in the same way as the Maya of Central America and Mexico (see America, Central: Archaeological Caves), but nevertheless there is numerous evidence of use of caves by prehistoric civilizations. Throughout the Brazilian karst, cave entrances were used as shelters from the end of the Pleistocene/beginning of the Holocene, and many of the country's most important archaeological sites are located in karst areas. Some caves were apparently used as burial sites, as large numbers of human remains have been located in selected sites within caves. In Venezuela, the indians of Caripe have hunted the Guácharo or oil bird (*Steatornis caripensis*) inside caves since at least 3500 BP (Perera, 1976). The vocabulary of some indian cultures in eastern Brazil also records a few words that designate karst features, such as *itararé* (“hollow rock”) and *anhonhecanhuva* (“water that sinks”).

Following European colonization there were some sparse references to caves, mostly in Venezuela, during the period 1500–1700. The majority of the descriptions refer to caves with some kind of indian usage. The first recorded reference to a Venezuelan cave dates from 1548 when Diego de Vallejo and others entered a cave in the state of Trujillo (Urbani, 1989). In 1579, in the same area, Alonso Pacheco and others gave a description of Indian rituals in a cave (Urbani, 1993). The Cueva del Guácharo (Venezuela) has the longest and richest history of any cave in South America. It was probably first visited in 1659, and the first published reference dates from 1666 (Urbani, 1996). Since then, numerous visitors of varied scientific relevance have described the cave, among them Tauste (first description of the cave in 1678), Jiménez Perez (1773), Ibarra (1795), Humboldt and Bonpland (1799), Grisel (1834), L’Herminier (1834), Codazzi (1835), Bellerman (first paintings of the cave in 1843), and Lisboa (first sketch of the cave in 1866) (Urbani, 1999).



In 1691, Francisco de Mendonça Mar, a peasant of strong religious inclination established a shrine at a cave by the São Francisco River (presently known as Bom Jesus da Lapa), eastern Brazil, which has since become very popular as a pilgrimage site. Other caves in Brazil became centres of pilgrimage from the 18th century onwards. The Portuguese colonial government in Brazil financed the excavation of saltpetre in hundreds of caves throughout the country for the manufacture of gunpowder. Saltpetre exploitation in Brazil reached its climax during the 18th and 19th centuries, not ending until early in the 20th century.

Numerous naturalists and travellers, mostly Europeans, described caves in South America during the late 18th and 19th centuries, among them Ferreira, Eschwege, Pohl, Spix and Martius, Saint Hilaire, Lund, Liais, Fonseca, and Krone in Brazil; Goudot and Boulin and Cuervo in Colombia; Darwin at Galápagos Islands (Ecuador); Humboldt, Marcoy, Castelnau, and Raimondi in Peru; Berg in Uruguay; and Humboldt, Codazzi, Lisboa, Funk, Goering, Sievers, Scharfernorth, and Marcano in Venezuela. Among them, at least four deserve special mention. Alexander von Humboldt was the forerunner of cave science in Venezuela, following his visit (together with Bonpland) to the Cueva del Guácharo in 1799. Humboldt explored the first 422 m of this famous cave and described scientifically the unique Guácharo in his *Personal Narratives of Travels to the Equinoctial Regions of America during the years 1799–1804*. Humboldt also made a pioneering visit in 1802 to the Uchkupisjo caves in Peru.

In Brazil, the Danish naturalist Peter Wilhelm Lund laid the foundations of Brazilian cave science during intensive research in the caves of central Minas Gerais state from 1834 to 1844. Lund explored over 1000 caves in search of fossil bones. He hired the Norwegian Peter Andreas Brandt, a merchant turned cartographer and painter, who was responsible for surveying the caves and drawing caving scenes. At least 30 cave maps and cave and karst paintings have been preserved in Danish museums. Besides his more immediate interest in vertebrate paleontology, Lund was the first to suggest that cave saltpetre has its origins in nitrates in the soil above the cave, an explanation not adopted again until the 20th century. Lund also published valuable data on karst landscape, cave origin, cave sedimentation, and fossil emplacement in his series of “memories”, published in Danish and translated partially in other languages (Lund, 1840).

The intrepid Father Romualdo Cuervo may well be considered the pioneer of vertical caving in South America after descending suspended in a basket, in 1851, the 120 m deep entrance shaft of Hoyo del Aire in Colombia. The Venezuelan chemist Vicente Marcano was the main explorer of Venezuelan caves in the 19th century, studying over 30 caves between 1883 and 1890. His immediate interest was the study of guano deposits for use as a fertilizer.

The 20th century saw the beginning of organized caving in South America. Several people made important contributions in both exploration and scientific studies of caves, including the first description of a troglobitic fish (in Brazil) by Miranda Ribeiro in 1907. In 1937 the first caving club of South America, the still active Sociedade Excursionista e Espeleológica (SEE), was founded in the town of Ouro Preto, Brazil. Other clubs followed in the 1950s and 1960s, such as the Speleology Section of the Sociedad Venezolana de Ciencias Naturales, formed in 1952, later evolving to the Sociedad Venezolana de Espeleología in 1967. In Brazil, many of these earlier groups were emulated by expatriate cavers of European origin, mainly French. The 1960s also saw the

foundation of national caving bodies, the Sociedad Peruana de Espeleología (now defunct) in 1965 and the Sociedade Brasileira de Espeleologia in 1969.

Cave exploration had a great impetus from the 1960s to the present. Most of the major caves of the continent were explored during this period by enthusiastic local caving clubs and foreign expeditions. The contribution of European expeditions was particularly significant in countries such as Colombia, Peru, Bolivia, and Ecuador, and they are responsible for the majority of what is known about karst and caves in these countries. Argentina also experienced a rapid growth of its speleology from the early 1970s, when many active clubs were formed. In 2000 the Federación Argentina de Espeleología was founded.

The present status of cave and karst research and exploration in South America varies between countries. Well-organized (but small) local caving communities exist in Argentina, Brazil, and Venezuela, with incipient or non-existent local speleology in the remaining countries. Cave and karst research is performed in a few universities and established postgraduate programs allow the regular production of theses on karst related topics. Cave exploration remains restricted mostly to the upper classes of financially debilitated countries, aided by frequent foreign expeditions. Nevertheless, the technical level of both exploration and science is equal with what is done in more developed countries, although performed on a much more restricted scale. Cave preservation is increasingly a topic of concern in South America. Several conservation areas have recently been designated to protect karst resources. In 1997 the Brazilian government created a centre for the protection and management of caves (CECAV), the first of its kind in South America.

AUGUSTO AULER

*See also* **Caribbean Islands: History**

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## AMPHIBIA

The characteristic features of amphibia (frogs, salamanders, and gymnophiona) include a slimy skin that is not well suited to prevent desiccation, and a body temperature corresponding directly to ambient temperature. It is not surprising therefore that amphibia are commonly encountered in the entrance or twilight zone of caves, which are characterized by high air humidity and buffered temperature changes. Many amphibia visit caves occasionally as temporary shelter from unfavourable environmental conditions outside, such as summer drought or winter frost. Caves are also used as breeding sites by some species. However, the impact of those visitors on the cave ecosystem is low since they only make a small contribution to the subterranean food web. More important for biospeleology are the troglophilic salamander species which are rarely found far from caves, and can also feed on subterranean invertebrates. Well-known examples are the Pyrenean salamander *Euproctus asper*, members of the genus *Hydromantes* in southern France, northern to central Italy, Sardinia, and California, the long-tailed salamander *Plethodon longicauda*, the common cave salamander *P. lucifuga*, the slimy salamander *P. glutinosus*, the purple salamander *Gyrinophilus porphyriticus*, all from the eastern United States, and *Eurycea neotenes* from Texas. The high number of amphibian species which can be observed occasionally in caves is in marked contrast to the low number of obligate cave dwellers or troglobites, which cannot survive outside caves. Only ten amphibian troglotic species or subspecies are known and all are salamanders (see Table 1). Troglotic members are restricted to two families, the Proteidae and the Plethodontidae. The Proteidae comprise six species, but only one is troglotic. This is the famous blind

cave salamander *Proteus anguinus* (see Amphibia: *Proteus*) from the Dinaric karst. The family Plethodontidae comprises about 246 species and is distributed mainly from North America down to northern South America, with a few members in Europe. However, the nine troglobitic taxa are restricted to the United States. Cave salamanders share some morphological characteristics with the other group of troglobitic vertebrates, the cave fishes (see Pisces entry). Advanced cave-adapted forms have reduced eyes and body pigmentation, a slender body, and a comparatively large, anteriorly depressed, shovel-like head with a large mouth. Cave plethodontids show a trend to markedly elongated thin legs, giving them a fragile appearance. With the exception of *Proteus* which may reach up to 40 cm in length, all other cave salamanders are small, rarely exceeding 15 cm.

Amphibians are generally characterized by a life cycle with two stages: an aquatic larvae which metamorphoses into a terrestrial adult after some time. With the exception of only two species, *Gyrinophilus subterraneus* and the cave salamander *Typhlotriton spelaeus*, all other troglobitic salamanders usually attain sexual maturity without metamorphosis, i.e. they remain aquatic for the whole life and retain some larval characteristics, such as the feathery external gills and a fin-shaped tail. Because of the blood in the capillaries the external gills appear brightly red and are in sharp contrast to the whitish body. The persistence of a larval body form in the adult is called neoteny. It seems that this life strategy is advantageous in subterranean habitats since approximately half of all known neotenic salamander taxa are troglobitic. However, the reasons for this adaptation are still not fully understood and may even differ between the species. Food scarcity in the caves may play an important role. Salamanders tend to eat any prey they can handle. In caves these are usually crustaceans, insect larvae, snails, and worms, but occasionally also other salamanders—even cannibalism has been observed. Although troglobitic vertebrates are usually small they are nevertheless the largest predators in the subterranean community and therefore at the top of the food chain or web. Hence, the energetic costs of metamorphosis might be too high and selection would act towards prolonging the larval phase. Another argument might be that food scarcity in the terrestrial habitat is usually stronger than in the aquatic habitat. Accordingly, neotenic salamanders that remain aquatic can exploit the more reliable food source. Climate may also have an influence on the development of neoteny. For example, the neotenic troglobite *Eurycea tridentifera* lives in caves of the Edwards Plateau in central Texas.

### **Amphibia:** Troglobitic salamanders (Urodela, Amphibia) and their distribution.

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#### **Proteidae**

*Proteus anguinus* Dinaric karst from Trieste, Italy in the northwest through Slovenia and Croatia to the Trebisnica River in Bosnia-Herzegovina in the southeast

#### **Plethodontidae**

*Eurycea tridentifera* Caves in the Cibolo sinkhole plain and adjacent regions, Comal and Bexar Counties, Edwards Plateau, Texas, United States

*Gyrinophilus gulolineatus* Caves of the east bank of the Tennessee River Valley (Appalachian Valley), Tennessee, United States

*Gyrinophilus nalleucus* Bio Mouth Cave, Elk River drainage, Grundy County, southern

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<i>necturoides</i>	Cumberland Plateau, southern Tennessee, United States
<i>Gyrinophilus palleucus palleucus</i>	Caves of the southern Cumberland Plateau, southern Tennessee and northern Alabama, United States
<i>Gyrinophilus subterraneus</i>	General Davis Cave near Alderson, Greenbrier County, (Greenbrier Valley), West Virginia, United States
<i>Haideotriton wallacei</i>	Subterranean waters of the Dougherty Plain of southwestern Georgia and adjacent northwestern Florida, United States
<i>Typhlomolge rathbuni</i>	San Marcos pool of the Balcones Aquifer, Hays County, Texas, United States
<i>Typhlomolge robusta</i>	Balcones Aquifer to the north and east of the Blanco River, Hays County, Texas, United States
<i>Typhlotriton spelaeus</i>	Southwestern Ozark Plateaus (Springfield and Salem Plateaus) of southwest Missouri, southeast Kansas, northeast Oklahoma, and northwest Arkansas, United States

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This area is not very suitable for amphibians because it is very dry. Therefore, a surface-living close relative, *Eurycea neotenes*, can only survive in damp headwater canyons, springs, and cave entrances. This troglomorphic species exhibits a remarkable plasticity in its life cycle because some populations are completely neotenic while others have a variable proportion of metamorphosed animals. It seems that the reliability of spring discharge is the decisive factor. Only under conditions of a permanently sufficient discharge is metamorphosis an advantageous strategy. Springs with strong discharge fluctuations only support neotenic populations and if the discharge becomes too low the animals retreat into the underground spring. The evolution of the permanent cave dweller *Eurycea tridentifera* potentially started this way. A very remarkable life cycle can be observed in the cave salamander or Ozark blind salamander *Typhlotriton spelaeus*. This species has the largest distribution area of all troglomorphic plethodontids and can be found in food-rich caves of the southwestern Ozark Plateau. *T. spelaeus* still exhibits metamorphosis as a life history characteristic. The larvae possess well-developed functional eyes and a marked body colouration. They usually live in cave entrances or even outside where they feed on small invertebrates. With the onset of metamorphosis after 2–3 years the animals retreat deep into the cave. Colouration becomes pale and the eyes are overgrown by the eyelids. In addition, the photoreceptors in the retina degenerate, i.e. the animal becomes blind. Also as adults the animals stay close to the water. They feed on terrestrial insects, isopods, and snails. It is thought that all troglomorphic salamanders lay eggs instead of giving birth to free-living larvae. The internal insemination probably happens via a spermatophore which has been produced and deposited by the male and is taken up by the female. Not all troglomorphic salamanders live in “real” caves, i.e. in caverns accessible to man. Some, like the Georgia blind salamander *Haideotriton wallacei* or the Texas blind salamander *Typhlomolge rathbuni* inhabit groundwater and are usually found only in wells after pumping activities. *T. rathbuni* is regarded as the most cave-adapted and phylogenetically oldest troglomorphic plethodontid with a supposed Miocene origin. It shows the highest degree of eye reduction and the longest limbs. The animals move very slowly, stalking around on their

thin legs with the large head held high to sense every possible prey organism in the surrounding. Like all aquatic salamanders, *T. rathbuni* possesses well-developed sensory organs for smell, taste, mechanoreception, and even electroreception. If disturbed the animal swims away and tries to hide.

Most salamanders encountered in caves are legally protected and should not be collected. They are potentially at risk due to restricted distribution and low population sizes. Water pollution and excessive groundwater pumping are serious threats for these fascinating animals.

AXEL WEBER

See also **Edwards Aguifer: Biospeleology**

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## AMPHIBIA: *PROTEUS*

*Proteus anguinus anguinus*, popularly called the blind cave salamander or “human fish” due to its pink skin, is the sole species of the genus *Proteus*, and is only found in Europe. It is the largest, most remarkable, and world-famous model for trogllobites. The distribution of *Proteus* is entirely within the Dinaric karst; nearly 200 localities, from the lower reaches of the Isonzo-Soča River in Italy in the northwest through to the southern part of Slovenia to the Trebišnjica River in Herzegovina in the southeast are known (Sket, 1997). As noted in Folklore and Mythology, *Proteus* were once considered to be the offspring of dragons.

*Proteus* is an obligate neotene and preserves some larval or immature characters in adulthood; the major reason for cessation of its metamorphosis, as in other obligate neotenes, probably lies in the insensitivity of its tissues to thyroid hormones. (Neoteny is retention of some larval or immature traits in adulthood; metamorphosis is a series of postembryonic changes involving structural, physiological, biochemical, and behavioural transformations.) *Proteus* retains three pairs of outer gills, two pairs of gill slits, an integument with many larval characteristics, and typical visceral skeletal elements. It has an extended, narrow body and a reduced number of digits, that is three on the anterior legs and two on the posterior legs. *Proteus* shows some general troglomorphic characteristics: specialization of the sensory organs, elongation of individual body parts, especially the disproportionate growth of the head in length, reduced eyes, skin

depigmentation, slow metabolism, resistance to starvation, increased lifespan, and probably the reduction of intraspecific aggressive behaviour. Proteiids characteristically possess no maxillae (i.e. the upper jawbones in vertebrates). Absence of maxillae is clearly paedomorphic (the phenomenon in which larval or immature features of ancestors become adult characteristics of descendants).

*Proteus anguinus parkelj* ssp. nov. from southeastern Slovenia differs from *Proteus anguinus anguinus* in its dark pigmentation, better-developed eyes, and many other morphological characteristics. This black, non-trogomorphic form was discovered in 1986 and has been attributed to a subspecies (Sket & Arntzen, 1994). Further research on the distribution and the racial polymorphism within *Proteus* is in progress. However, allozyme analysis also revealed the probability of speciation within this genus.

The embryonic development of *Proteus* takes about 130 days at 11°C, and larval development takes about 100 days at the same temperature (Durand & Delay, 1981). The water temperature in its natural habitat varies from 8°C during the winter to 11°C in the summer and autumn. They reach sexual maturity in about their 16th year. Owing to their slow metabolism, their lifespan may be as long as 70 years. Nutritional research on *Proteus* in its natural environment has proved that it is carnivorous, and has determined the main organisms on which it feeds, i.e. Crustacea, Insecta larvae, and Gastropoda. Its extraordinarily low metabolic rate, typical of troglobites, reflects its complete adaptation to conditions in cave habitats (Istenič, 1986).

Those sensory organs that have not undergone regression and for which proper stimuli are expected to be found in the underground waters of the Dinaric karst include the inner ear, the lateral line system, and sensory receptors that detect variations in the Earth's magnetic field, all of which are worthy of study (Bulog, 1989a, 1989b; Istenič & Bulog, 1984; Schlegel & Bulog, 1997; Bulog & Schlegel, 2000). In *Proteus*, these sensory organs, including the chemoreceptors, obviously play an important role in orientation, searching for prey, intraspecies communication, and mutual recognition.

Little is known about the hearing of *Proteus*, but occasionally observed reactions to sounds have suggested a hearing capacity, especially underwater. This would be of adaptive value in dark caves—in order to recognize particular sounds and to locate prey. Recently performed behavioural studies on the hearing ability of *Proteus* (Bulog & Schlegel, 2000) indicate that unpigmented specimens showed the greatest sensitivity to sounds at *c.* 1.5 kHz, while the black specimens were most sensitive to sounds at about 2 kHz. The fact that *Proteus* reacts spontaneously and consistently well to sounds demonstrates the biological significance and adaptive value of its underwater hearing.

The lateral-line sensory system is an aggregation of epidermal sensory organs scattered over the head and along the body in fish and aquatic amphibians. It includes ciliary mechanoreceptive neuromasts and electroreceptive ampullary organs. The discovery of ampullary organs in *Proteus* indicated that it is a candidate for passive electroreceptivity, which may play an important role in animals in underground water habitats (Istenič & Bulog, 1984). Behavioural experiments have confirmed that *Proteus* is sensitive to weak electric fields (Schlegel & Bulog, 1997).

Recently, some behavioural evidence of sensitivity to the orientation of the Earth's magnetic field has also been found. It is not yet known whether the magnetic field is detected by electroreceptors, or if the magnetoreceptivity is based on a different sensory mechanism.

The visual system undergoes some degree of regression in most cave animals. Among different changes in the eye structure, such as degeneration of the lens and optic nerve, it often includes changes in the structure of photoreceptor cells. Continuous darkness is known to result in the degeneration of outer segments in the retina as well as in pineal photoreceptors. *Proteus anguinus anguinus* has small eye rudiments, seen as black dots, which lie buried deeply under the skin. The retina, lens, and vitreous body are strongly reduced in size and complexity in comparison to non cave-dwelling salamander species. Although eye development begins normally in the embryo, in the larval stage it is retarded and the degeneration becomes soon evident (Durand, 1971). Light and electron-microscopic studies of the retina of dark-coloured *Proteus* specimens led to the initial comparative analysis of the differentiation of these sensory organs (Bulog, 1992).

*Proteus anguinus anguinus* has a zone of less-pigmented skin on the anterior-dorsal part of its head. This zone is even more obvious on the head of the black subspecies *Proteus anguinus parkelj*. These pale areas are very sensitive to directional pointsource illumination and are located above or in front of the pineal gland. The pineal organ of the lower vertebrates is a photosensitive organ with many functions. Mediated by the pineal hormone melatonin, it controls circadian rhythms, gonadotropic activity, and body colour changes. It contains photoreceptor cells, which in their general features resemble retinal photoreceptors. In cave animals, which live under conditions of permanent darkness and constant temperature, the role of the pineal organ as a circadian pacemaker would be expected to become biologically useless.

*Proteus* has played a significant role in biospeleological study, both in the wild and in captive populations. The comparison of *Proteus anguinus anguinus* with its nontrogomorphic relative, the sighted and black-pigmented *Proteus anguinus parkelj*, is expected to provide new evidence about the development of photoreceptor structures in cave animals. The species is unfortunately threatened by water pollution and unscrupulous international dealers, despite being listed in the CITES convention, which prohibits trade in rare wild animals. The species is also protected under Slovenian law, and listed as vulnerable in the World Conservation Union (IUCN) Red List of Threatened Species.

BORIS BULOG

**See also Dinaric Karst: Biospeleology; Postojna-Planina Cave System, Slovenia: Biospeleology**

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Amphibia web <http://elib.cs.berkeley.edu/aw/index.html>

## ANCHIALINE HABITATS

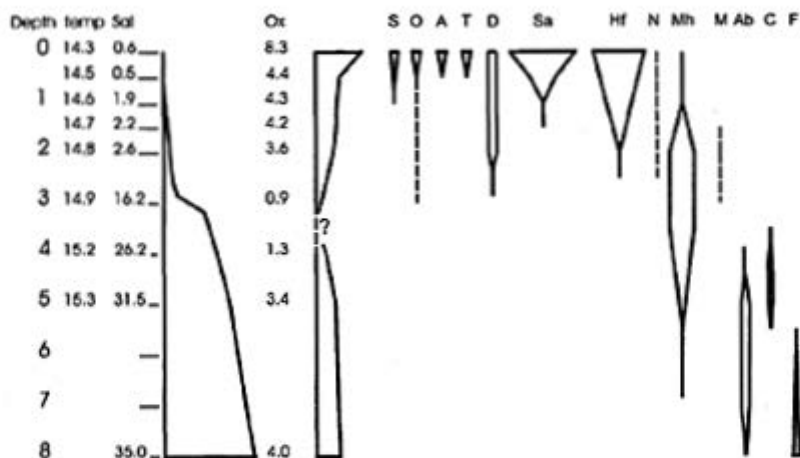
Anchialine (anchihaline) cave habitats are located in water-filled voids near the coast, where there is a demonstrable marine influence shown either by mixohalinity (different brackish salinities) or by the presence of marine-derived animal species (Sket, 1996). The hydrological connections to the sea—as well as to the land—are underground, and there is restricted contact between the water body and the open air. Anchialine cave waters may function as corridors to open anchialine pools (Holthuis, 1973). The distinction between anchialine and marine caves is not always clear. A cave with euhaline (purely marine) water should only be considered as an anchialine habitat if it contains troglomorphic species. Riedl's (1966) concept of the marginal cave also included a theory about its origin, which differs from the archialine cave concept.

Most bodies of anchialine cave water have been observed in tropical to warm-temperate regions. The caves mostly developed during sea-level lowstands in the Pleistocene (see *Speleogenesis: Coastal and Oceanic Settings*); they retained the freshwater influx from the land, while the subsequent sea-water influx changed their ecology. Anchialine habitats in coral reefs and coastal lava fields have a different origin, but a similar morphology. Blue holes, anchialine pools, metahaline pools and some other habitats may exhibit some characteristics of anchialine cave waters. In particular, some stygobites may be present in these habitats, due to a diminished number of competitors in the generally unfavourable conditions of anchialine habitats.

### Ecological Conditions

Besides the mixohalinity itself, one of the most striking abiotic characteristics of anchialine waters is their stratification (Figure 1). The primary stratification is in salinity; the extreme upper and lower layers may be limnic and euhaline (marine) respectively. This depends on the influx intensities of fresh and marine water, and therefore will change throughout the year or even within one day.

Great differences in the densities of waters of variable salinities prevent any mixing of layers, which might otherwise be expected during changes in temperature. Stratification is usually gradual, with a thin layer of rapid transition (the halocline) between the denser and the less-dense layers. This stable salinity and density stratification also allows stratification in other characteristics. Consumption of oxygen by animals and bacteria, particularly on the bottom, causes oxygen depletion. This deficit may be neutralized by exchange with sea water at the bottom and by diffusion from the surface in the uppermost layers, and therefore remains most extreme in the halocline layer, where there is least mixing. Accumulation of hydrogen sulfide may coincide with the oxygen deficit. If the water body is exposed to temperature changes associated with the atmosphere at the land's surface, a temperature inversion may occur in the winter, with the upper layers being the coolest (Sket, 1986).



### **Anchialine Cave Habitats:**

Ecological stratification in the anchialine lake of the cave Šipun near Cavtat, Croatia, in September 1975. Depth in metres; temp, temperature in °C; Sal, salinity in ppt.; Ox, oxygen content in mg l<sup>-1</sup>; S, *Saxurinator sketi* (Gastropoda); O, *Oligochaeta*; A, *Acanthocyclops venustus*, T, *Thermocyclops dybowskii*, and D, *Diacyclops antrincola* (Copepoda); Sa, *Salentinella angelieri*, Hf, *Hadzia fragilis*, and N, *Niphargus salonitanus* (Amphipoda); Mh, *Monodella halophila* (Thermosbaenacea); M, *Metacyclops trisetosus* (Copepoda); Ab, *Ammonia beccarii* (Foraminifera); C, *Caecum glabrum* (Gastropoda); F, *Filigranula annulata*. The population density is measured in estimated relative values.

### **Fauna**

The main biological characteristic of this habitat is the presence of stygobitic species together with species of marine provenance. The unfavourably diverse and variable degree of mixohalinity further reduces the number of species that can colonize these

habitats. On the other hand, contact with the faunistically rich marine ecosystem potentially increases diversity.

The number of species known from anchialine cave waters increased from less than 30 in the 1960s (Riedl, 1966) to *c.* 150 in the 1980s, and close to 400 species in the 1990s. The Table shows species numbers by groups; numbers of known taxa are still increasing rapidly, especially for copepods, but also for amphipods and other groups. Similarly to hypogean waters in general, crustaceans are by far the most prevalent group in anchialine waters. This is evident in the list of known species as well as within any local fauna. Since some crustaceans are larger (except for vertebrates) and more numerous than most other cave inhabitants, Crustacea are also the most important group in relation to biomass. In the Šipun Cave (Cavtat, Croatia; Figure 1) which exhibits a complete salinity range from limnic to polyhaline, nine crustacean species and only six other species have been found. The ratios of individuals and biomass between crustacea and other species is even more striking—at least 10:1. In Cave C-28, on Cape Range Peninsula, Australia, only five species have been found below the pycnocline (the thin layer of a rapid density change), with all but one (a fish) being crustaceans. In the anchialine waters of Quintana Roo, Mexico, 12–14 species have been identified, all of which are crustaceans.

It is difficult to assess exactly the number of anchialine species. While the distinction between anchialine cavernicole and interstitial fauna is seldom ambiguous, it is often questionable if a non- or slightly troglomorphic animal is anchialine or only a marine-benthic generalist. As in freshwater cave habitats, some (here necessarily euryhaline, or able to live in waters of a wide range of salinities) stygoxenes and stygophiles occur in anchialine waters. Another facultative presence—again euryhaline—are stygobitic species from freshwater caves. A very common non-specialized marine species in anchialine caves in the Caribbean is the fish *Eleotris pisonis*, and freshwater species include the copepod

**Anchialine Habitats:** Approximate numbers of essentially anchialine species known in the 1990s (according to Sket, 1996).

Crustacea		Other groups	
Remipedia	11	Porifera	3
Ostracoda	35–40	Turbellaria	1
Copepoda	40–45	Gastropoda	5
Tantulocarida	1	Annelida	10
Leptostraca	1	Chaetognatha	4
Decapoda	45–50		
Thermosbaenacea	30–35	Pisces	10
Mysidacea	30–35		
Mictacea	1		
Tanaidacea	2		

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Isopoda	30–35
Amphipoda	80–95

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*Diacyclops bicuspidatus odessanus* and amphipod *Niphargus hebereri*, both found in anchialine caves on the Dinaric coast. It may be fortuitous that some of these animals may be known only from anchialine caves, without necessarily being confined to them.

Most stygobitic (and usually troglomorphic) species are related to and probably derived from the extant shallow-marine fauna—most amphipods (e.g. Hadziidae) and shrimps (e.g. *Typhlatya* spp.). Representatives of some groups show close phylogenetic relationships to deep-sea species. These include the cavernicole Tantulocarida, Mictacea (*Mictocaris halope* in Bermuda), Decapoda Anomoura (*Munidopsis polymorpha* in the Canary Islands) and some other decapods, and some Ostracoda (*Danielopolina* spp.). The only higher taxonomic group limited to anchialine caves and therefore of a non-identifiable origin seems to be the Remipedia. Some specialized inhabitants of anchialine caves which are unquestionably invaders from fresh waters are known mainly from the Dinaric coast; for example, the amphipods *Niphargus salonitanus* and *N. pectencoronatae*.

### General Comments

Some characteristics of anchialine fauna make them very important for understanding the colonization of less favourable habitats, such as non-marine and hypogean waters. The largely anchialine shrimps *Typhlatya* spp. are among the few members of the mainly circumtropical freshwater family Atyidae, which are still marginally marine. Amphipoda in anchialine waters are globally represented primarily by the family Hadziidae and only a few other species, although a huge variety of amphipod groups come into contact with these habitats. A number of groups are represented circumglobally (resembling the extension of the ancient Tethys ocean), including Remipedia, Thermosbaenacea, genera *Typhlatya* (Decapoda), and *Spelaeomysis* (Mysidacea). The strictly stygobitic species—such as *Niphargus hebereri* from the Dinaric coasts—may build dense populations in sunlit areas if no epigeal competitors are present. Some delicate elements—such as Thermosbaenacea—may show different apparent salinity preferences, depending on the presence or absence of competitors.

BORIS SKET

See also **Cape Range, Australia: Biospeleology; Walsingham Caves, Bermuda: Biospeleology**

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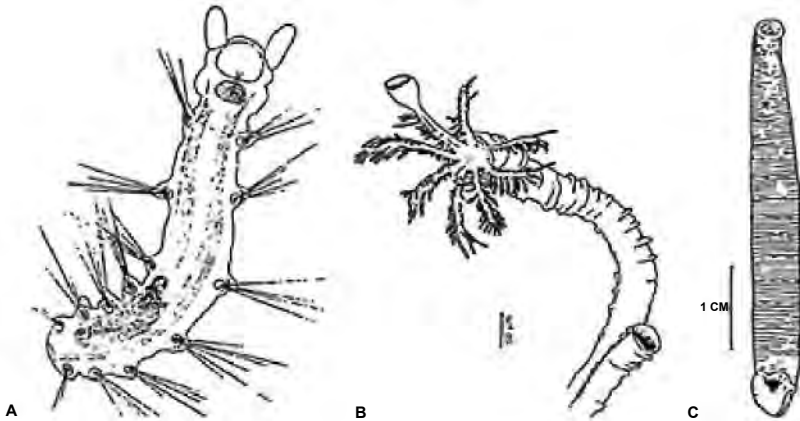
## ANNELIDA

Annelida or annelids are segmented, usually worm-like animals without articulated legs. The body consists of a chain of body segments, or somites; in front of them is the head lobe or prostomium, behind is an anal lobe or pygidium. A paired ventral nerve cord extends along the body with a pair of ganglia in each somite. The mouth and the anus are close to both ends of the body, connected by a straight intestine.

The main groupings of annelids are Polychaeta and Clitellata. The predominantly marine Polychaeta are characterized by pairs of bifurcated limbs or parapodia on each somite, with appendages called rami on the parapodia, each ending with a bundle of chaetae (bristles). Polychaetes are gonochoristic, i.e. they have separate sexes. Clitellata lack parapodia, and are hermaphroditic. The basal subgroup of clitellates is Oligochaeta, where bundles of, or single chaetae, are still present in the wall of each somite and the coelomic cavity is normally segmented. Leeches (Hirudinea) developed from within oligochaetes. They are devoid of chaetae and their coelomic cavity is restructured into a system of tubes that replaces the primary circulatory system. Leeches possess an oral and a caudal sucker, used for locomotion.

Polychaeta or polychaetes are principally a marine group with few freshwater representatives, the latter being mostly hypogean. The free-swimming and worm-like “Errantia” (names within quotation marks are not real taxonomic units) are represented in

marine, anchialine, and fresh cave waters, mostly in the tropics, by representatives of the family Nereididae. Nereids have short antennae and palpi on their prostomia, their evertible mouth cavity has strong, deeply forked, cuticular jaws. *Namanereis hummelincki* is a stygobitic nereid from marine or anchihaline habitats in the Caribbean while *N. beroni* has been recorded from a cave at an altitude of 1600 m in Papua New Guinea. Representatives of the “Archiannelida” family Nerillidae are common in interstitial marine waters and anchihaline caves. They may be a few millimetres long, usually with two palpi on the prostomium and with up to ten somites. Some *Nerilla* species are benthic, others are stygobitic or in the marine interstitial



**Annelida: Figure 1.** (A) Polychaeta: *Troglochaetus beranecki*; (B) Polychaeta: *Marifugia cavatica*; (C) Hirudinea: *Dina absoloni*. Reproduced with permission from Botosaneanu (1986).

habitat. *Troglochaetus beranecki*, 0.5 mm long, is widely distributed in fresh interstitial or cave waters in Europe, from Finland to northern Italy; it has been known since 1921. Similar species have been found in Japan and recently in North America.

The only known stygobitic representative of the substratebound “Sedentaria” group is the cave tube worm, *Marifugia* (*Marifugia cavatica*), the only freshwater species of the family Serpulidae. *Marifugia* secrete a calcareous tube of less than 1 mm external diameter; the first few centimetres are attached to the substrate, while the youngest parts are erect. Apically, feathery ciliated tentacles function as gills for respiration and filter feeding. The ontogeny starts with a ciliated, free-living larva which soon attaches to the substratum and develops a tiny tube. *Marifugia* are present patchily throughout the whole Dinaric karst. While some authors consider it to be an ancient marine relict in caves, it has recently been suggested to have invaded cave waters via extensive Pliocene-Pleistocene freshwater lakes in the region.

Oligochaetes are a group found in the soil, in freshwater, and in marine water. They possess chaetae, whose shape and position are taken into consideration when carrying out a systematic study, as are the position and morphology of the genital organs. Some aquatic (Haplotaxidae, Lumbriculidae, Naididae, Tubificidae, and Parvidrilidae), semiaquatic and terrestrial families (Enchytraeidae, Lumbricidae, and Ocneroдрilidae) are found in caves. The Lumbricidae are found in humid soil, wet guano, and in the sediment of underground watercourses and gours. They are generally considered to be troglonexes. The terrestrial Ocneroдрilidae are found only in South American caves. The Enchytraeidae are common in cave waters with genera such as *Enchytraeus*, *Cernosvitoviella*, and *Marionina*. The Haplotaxidae are also present with the three genera *Delaya*, *Haplotaxis*, and *Villiersia*, *D. bureschi* being largely distributed in Europe. The Naididae are present in caves with ubiquitous species; the *Pristina* and *Pristinella* genera comprise stygophilic species and some stygobitic species, found only in the Antilles. Lumbriculidae and Tubificidae exhibit a high level of diversity and comprise many stygobitic taxa. The presence of freshwater species belonging to the marine genera of Tubificidae (*Tubificoides*, *Spiridion*, *Aktedrilus*, *Abyssidrilus*, *Gianius*, and *Phalldriloides*) highlights the links between some groundwater taxa and their relatives in marine habitats.

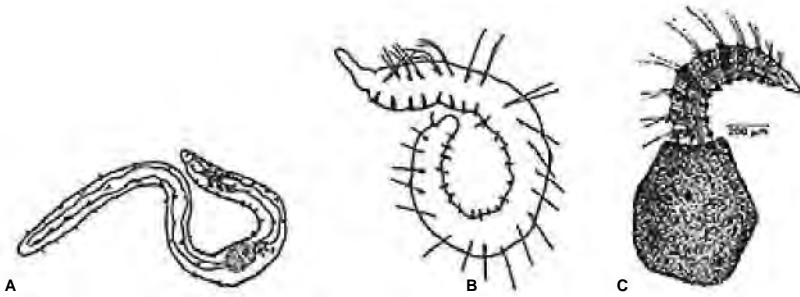
The recently discovered holartic family of Parvidrilidae, which has only two species (the European stygobitic *Parvidrilus spelaeus* and the North American interstitial *P. strayeri*) highlights the relationship between this family and the Gondwanian Pheoдрilidae.

The biodiversity of underground oligochaetes is rather high: up to 100 stygobitic species have been identified worldwide. Some subterranean Oligochaeta show characters probably related to their adaptation to a subterranean way of life, such as a reduction in body size (for example the stygobitic species of Phalldrilinae and Parvidrilidae), or in body diameter on the gonadal region, due to the shifting or the asymmetrical bending of the spermathecae.

Hirudinea (leeches) are represented in caves only by few blood-sucking species. These include troglophilic, mollusc-sucking representatives of the family Glossiphoniidae, such as *Glossiphonia complanata* in the Postojna-Planina Cave System, Slovenia. There are also some land leeches, Haemadipsidae, which suck bats, for example *Leiobdella jawarerenensis* in Papua New Guinea and a *Haemadipsa* sp. in Yunnan, China; both are without skin pigmentation but retain pigmented eyes.

All eyeless cave leeches are predators of small invertebrates, for example *Haemopsis caeca* of Haemopidae in Movile Cave, Romania. Most, however, belong to the family Erpobdellidae, moreover to the genus *Dina* or its phylogenetic vicinity. The epigeal and troglophilic species *D. krasensis* is endemic to southwestern Slovenia and Croatian Istra, with a partially depigmented population in the Postojna-Planina Cave System. The oldest known (by Johansson, 1913) stygobitic leech *D. absoloni*, is eyeless and widespread in southeastern parts of the Dinaric karst. Other stygobitic *Dina* species and probably *Trocheta* species have developed from southeastern France—northern Italy—Dinaric karst—Bulgaria—Georgia. The *Dina*-related *Croatobranchnus mestrovi* from cold (5°C) shafts in the Croatian Mt Velebit is extremely modified. It exhibits unique extendible tentacles around its mouth and c. 10 pairs of finger-shaped gills





**Annelida: Figure 2.** Oligochaeta. (A) the enchytraeid *Marionina argentea*; (B) the naeidid *Pristina aequiseta*; (C) the tubificid *Rhyacodrilus amphigenus*. Reproduced with permission from Timm (1999).

along the trunk. Undescribed stygobitic erpobdellid leeches have been found in Texas and Japan.

BEATRICE SAMBUGAR AND BORIS SKET

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## ANTARCTICA

The first caver on Antarctica was probably Emile Racoviță, who arrived in the Peninsula in January 1898. An ice cave entrance appears in a photo taken during the Scott expedition in 1911, but it wasn't until the mid-1970s that the first cave exploration took place. During the Tazieff expedition to Mount Erebus, some fumarole caves were explored in the volcano, near the US MacMurdo base. In the 1980s, some classic glacier caves, created by water flow, were explored in the Schirmacher Oasis, near the Russian base of Novolazarevskaya (Queen Maud Land). The caves, in the glacier front, consist of some outflow conduits draining internal glacier waters. Later, in 1985, other fumarole caves were explored on Mt Melbourne, by Italian glaciologists. These early explorations were made during the course of research with other objectives and the first caving expedition to Antarctica was in March 2000, when small ice caves (moulin) were explored in the Collins Glacier on King George Island, South Shetlands.

Karst phenomena in glaciers develop where the average yearly temperature is around 0°C, either at high altitudes or at high latitudes (see Glacier Caves and Glacier Pseudokarst). The whole Antarctic continent has an average yearly temperature well below zero; only the edge of the Peninsula and the surrounding islands are not far from the isotherm at 0°C. Hence there are only minor examples of typical glacial karst phenomena, such as moulin and bedières. However, there are also glacier caves in other parts of the continent, that are not formed by simple waterstreams, but by water flow, volcanic heat, local thermal imbalance, and by ice fractures.

### Water Flow

Most glacier caves are formed by runoff, where melt water enters the glacier through a "moulin". These caves are endoglacial because they are excavated inside the glacier core. Antarctica is too cold to allow the formation of large, meltwater rivers. For example, the ablation zone in Collins Glacier (King George Island) has a very limited extension (up to 100 m above sea level) but in spite of this, small (<50 m deep) moulin are formed on the sides of the main ice stream falling into the sea. Also the streams are very small, with a typical discharge of  $11 \text{ s}^{-1}$ . In some regions of the main continent, yet to be explored, the seasonal runoff may be stronger and the interaction of meltwater streams with very cold ice may create morphologies different from the typical temperate glacier karst, in which small water streams can flow away almost everywhere.

### Volcanic Heat

Some glacier caves form by volcanic heat released at fumaroles. These caves are subglacial and are carved on the contact of ice with rock. This cave type is well known in Iceland, where “warm” (0°C) ice tolerates the presence of meltwater. In contrast, the caves seen in Antarctica, on Mt Erebus and Mt Melbourne, formed in ice at -30 to -40°C, and so the water was immediately refrozen. However, strong airflow permits active sublimation, resulting in vapourization of ice in warmer areas and crystallization on cooler zones near the cave entrances. The main interest of these caves, explored for about 100 m, is in their biological material. They are temperate oases surrounded by an extremely adverse environment (the maximum yearly temperature is -20°C) and they host some endemic bacteria. All the areas around these fumarole caves are protected to avoid contamination: visitors are forbidden and special care is necessary to explore the caves.

### **Thermal Imbalance**

Some very large caves have formed at the contact between cold glaciers flowing from the Plateau (-20°C) and warmer sea ice (at -2°C). The contrast in ice temperature results in strong differences in equilibrium vapour pressure in the adjacent atmosphere (~100 Pa at -20°C, and ~500 Pa at -2°C). In a closed cavity, separating two such contrasting ice bodies, the resulting vapour pressure gradient will result in significant sublimation and redistribution of ice. Marine salt probably plays a role, but further studies are necessary to understand these caves that can play a role in the breaking of floating ice tongues.

### **Ice Fractures**

Crevasse in ice are largely tectonic in origin and are not normally classed as glacier caves. Crevasse depth depends upon temperature. For soft, temperate ice (0°C), the ice plasticity is high and the crevasse depths range from 25–30 m. However, when the ice temperature is lower, crevasse may be much deeper: at -50°C (ice temperature of the Antarctic Plateau) the crevasse reach 3–400 m. If these crevasse act as cold traps and are filled with the coldest winter air (-80°C), the depth may increase up to 700–1000 m. However, to date this has not been confirmed by exploration.

Although most of Antarctica is covered by ice, about 3000 m of horizontally bedded sedimentary rocks, ranging in age from Devonian to Jurassic, are exposed in the central Transantarctic Mountains. On the western flank of the Queen Elizabeth Range, beneath Mount Counts, the Lower to Middle Cambrian Shackleton Limestone crops out and is unconformably overlain by the Pagoda Formation (made up of tillite, sandstone, and shale). Lindsay (1970) describes a large depression, thought to be a doline, and a cave up to 6.2 m wide and 5.5 m high, that is completely filled with sediment of pre-Permian age. The site is remote and difficult to access but it is likely that similar paleokarstic deposits, and even open caves, may be discovered in the future.

GIOVANNI BADINO

*See also* **Glacier Caves and Glacier Pseudokarst**

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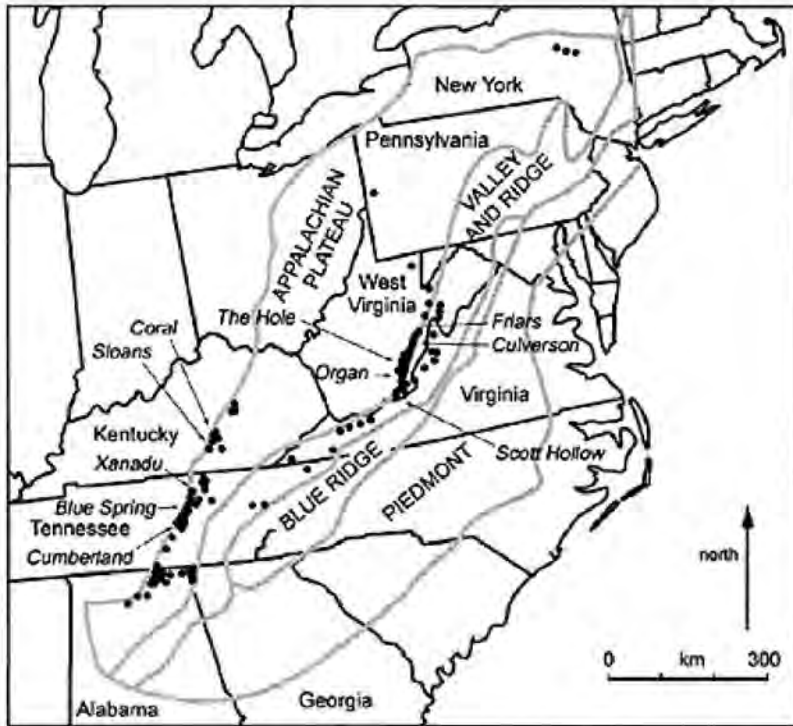
## APPALACHIAN MOUNTAINS, UNITED STATES

The Appalachian mountains extend for 3000 km from Alabama (United States) to Newfoundland (Canada). They contain significant limestone and dolostone formations, especially in western and southern areas, and commonly these are less than 300 m in thickness. There are many sinking streams because of the juxtaposition of carbonates with other rocks, and a large number of extensive cave systems have been found in strata that vary from flat-lying to steeply dipping.

The northern half of the Appalachians, north of New York, consist of relatively flat uplands with isolated mountain ranges. The Proterozoic and Paleozoic strata contain few carbonates and no long caves. The southern half of the Appalachians consist of a series of parallel mountain ranges with local relief of several hundred metres, and is divided into four zones. The eastern two zones, the Piedmont and the Blue Ridge, consist largely of Proterozoic and Lower Paleozoic metamorphosed sedimentary and volcanic rocks, with few carbonates and no long caves. The two western zones, the Valley and Ridge and the Appalachian Plateau, have many extensive caves, and more than 10000 caves have been documented in these two zones. The locations of the caves at least 5 km in length are shown in Figure 1, and are clearly clustered in certain areas.

The Valley and Ridge zone consists of long parallel ridges and valleys. Lower Paleozoic limestones and sandstones form the ridges and shales form the valleys. Stratal dips are often steep, with the result that many caves have linear patterns, being elongated along the strike. The caves of Burnsville Cove in Virginia are typical. Over 80 km of caves have been mapped within a small area in a 230 m sequence of Silurian and Devonian limestones. The principal caves are the Butler—Sinking Creek Cave System (28 km), which is largely formed along a synclinal axis, and the Chestnut Ridge Cave System (22 km), which is partly formed along the adjacent, parallel, anticlinal axis.

The Appalachian Plateau is an extensive area of mostly flatlying Carboniferous strata. The plateau is known in the north as the Allegheny Plateau and in the south as the Cumberland Plateau. Upper Carboniferous shales and sandstones outcrop across most of these plateaus, and are underlain by Lower Car-



**Appalachian Mountains: Figure 1.** The four structural zones of the Appalachian karst in the United States, with all caves containing more than 5 km of mapped passage marked by spots, and the ten longest caves named.

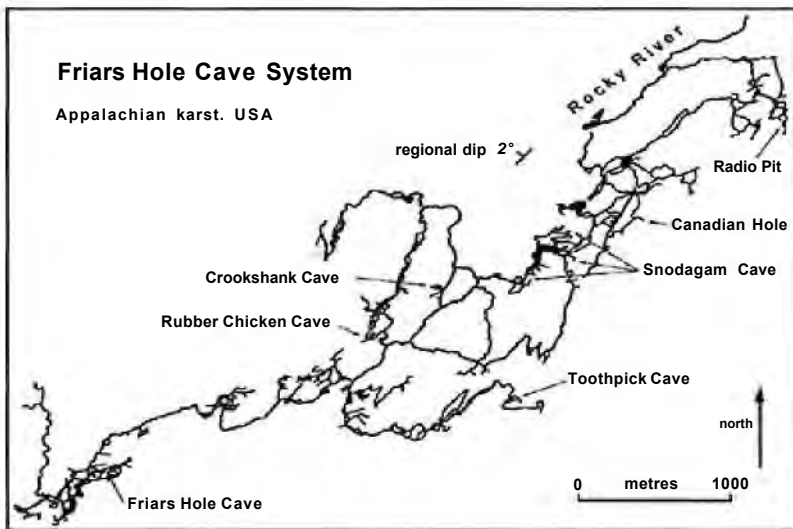
**Appalachian Mountains:** The longest caves in the Appalachians.

Rank	Cave	State	Length (km)
1	Friars Hole Cave System	West Virginia	72
2	Organ Cave System	West Virginia	64
3	Blue Spring Cave	Tennessee	53
4	Cumberland Caverns	Tennessee	44
5	Scott Hollow Cave	West Virginia	43
6	Sloans Valley System	Kentucky	40

7	Xanadu Cave System	Tennessee	38
8	The Hole	West Virginia	37
9	Coral Cave System	Kentucky	36
10	Culverson Creek Cave	West Virginia	33

boniferous strata which include limestones. The most extensive caves have been found in the 40–90 m thick Monteagle Limestone (from Alabama to Kentucky) and the 100–400 m thick Greenbrier Group (in West Virginia). Most of the long caves in the Monteagle Limestone are close to the western edge of the Cumberland Plateau. The outcrop of the Greenbrier Group varies in width from less than 100 m in northern West Virginia to more than 10 km in the south. In the latter area the strata dip gently to the west. Streams that sink along the eastern edge of the limestone have formed distinctive caves at the contact between the limestone and the underlying shale, with vadose passages being incised into the shales. These “contact caves” include Organ Cave (64 km), Scott Hollow Cave (43 km), and The Hole (37 km). Nearby are caves that have been formed by streams sinking at the top of the limestone, and these include Friars Hole Cave System (72 km) and Culverson Creek Cave (33 km).

Friars Hole Cave System is the longest known cave in the Appalachians (Figure 2). It is located close to the boundary of the Valley and Ridge and Appalachian Plateau zones, and bears features typical of caves in both zones. The entrances of the cave are found in a series of small limestone inliers along Friars Hole, a 200 m deep valley. A series of streams flow off predominantly



**Appalachian Mountains: Figure 2.** Outline map of the Friars Hole Cave System in the Appalachian karst.

shales, with minor sandstones and limestones, and drain an area of 86 km<sup>2</sup>. These streams sink where they reach the Union Limestone, a 50 m thick member of the Greenbrier Group, which has a structural dip of 2°. The Union Limestone is composed principally of sparites and micrites, but has four impure beds which are 1–3 m in thickness and have a clay content of about 50%. The 30 m thick Pickaway Limestone underlies the Union Limestone. The sinking streams descend through the vadose zone in a stairstep fashion, descending joints and then flowing downdip to the northwest, perched on the impure beds for distances up to 100 m before descending on another joint. Much of the complexity of the cave is due to the large number of such inlets, and more than 250 have been mapped, of which about 100 currently carry water.

The recharge to the cave throughout its history has been dominated by flow from the sinking streams of Hills Creek and Bruffy Creek, which together provide more than half the recharge of the cave. These streams sink several kilometres to the northeast of the cave, and the water is seen in the cave as Rocky River, a large strike-oriented passage. A second drainage, in the central part of the cave, includes the streams sinking at the Snedegars, Toothpick, Rubber Chicken, and Crookshank entrances. The cave stream descends to the lower Pickaway where it is 80 m stratigraphically below the top of the limestone, but the cave is 188 m deep because it extends almost 2 km downdip from the cave entrances. There is a third major stream in the southern part of the cave, which includes the stream sinking at Friars Hole Cave. All three cave streams flow to a spring which lies 10 km to the southwest on Spring Creek.

The water table has dropped 130 m since the earliest passages in the cave were formed. Uranium series and paleomagnetic dating of speleothems puts the age of the earliest passages at about four million years, and since that time a series of strike-oriented trunk passages has formed in succession. Most of these major passages are roughly rectangular in shape, with heights and widths of 5–10 m. Many were formed at the intersection between low-angle thrust faults and either the Union-Pickaway contact or at the impure bed which is 5 m above it. As the water table dropped, old trunk passages were abandoned and new ones were formed, usually at the same stratigraphic horizon, but several hundred metres downdip and thus at a lower elevation. The exact sequences and interrelations of these major relict passages are difficult to determine because only a small fraction of the passages in the drainage basin have been found. Many major passages in the cave terminate at sediment blockages or breakdown. The complexity in Friars Hole Cave System is caused by multiple sinking streams with their associated loads of clastic rocks, a lithology of interbedded pure and impure limestones, and a long history of karstification, and is typical for major caves in the Appalachians.

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## ARACHNIDA

The Arachnida are one of the most important groups inhabiting subterranean environments. Not only are they extremely abundant and widespread, but also include a large number of species, several of which show troglomorphic adaptations. Most arachnids are active predators and are involved in the ecological equilibrium of the subterranean food web.

The class Arachnida consists of 11 extant orders, nine of which include cavernicolous species. The Orders Araneae and Acari are the main groups and each has a separate entry. They have colonized subterranean habitats worldwide and their adaptation to the hypogean world has yielded a large number of troglomorphic species. An entry on Minor Groups includes the Orders Opilionida and Pseudoescorpionida, which are abundant in most subterranean habitats, but include fewer troglomorphic species, and the Orders Scorpionida, Amblypygi, Schizomida, Palpigradida, and Ricinulei, which are scarce in subterranean environments, although no less interesting. The Orders Uropigia and Solifuga are the only groups that do not have cavernicolous representatives.

Several factors have influenced the adaptation of Arachnida to subterranean environments: the particular physical characteristics of this environment, the scarce energy available, and the fact that Arachnida are primarily predators. This adaptation has involved morphological changes as well as changes related to their life cycles. From a morphological perspective, the main adaptive changes are the reduction and loss of ocular structures, a marked or total loss of pigmentation and the lengthening of appendages. When considering life cycles, adaptation to the subterranean environment is reflected by a reduced metabolic rate, which results in the loss of the nocturnal rhythm, a lengthening of their life cycle, and a low reproductive rate.

CARLES RIBECA



## ARACHNIDA: ARANEAE (SPIDERS)

Spiders are one of the most common groups inhabiting subterranean environments. They are predators, and are usually abundant inside caves, from the entrance to the deepest galleries. Not all species occurring in caves are exclusive to the subterranean environment: around 25–30% are accidentals (troglonexes) and appear in or around the entrance zone; around 50% of the species are regularly found in caves but also occur in the epigeal environment (trogliphiles); and between 20–25% are strictly cavernicolous (troglotitic). These troglotitic species are the most interesting from a taxonomical and evolutionary perspective since they are, in many cases, the living representatives of ancient evolutionary lineages that are now extinct in the epigeal environment.

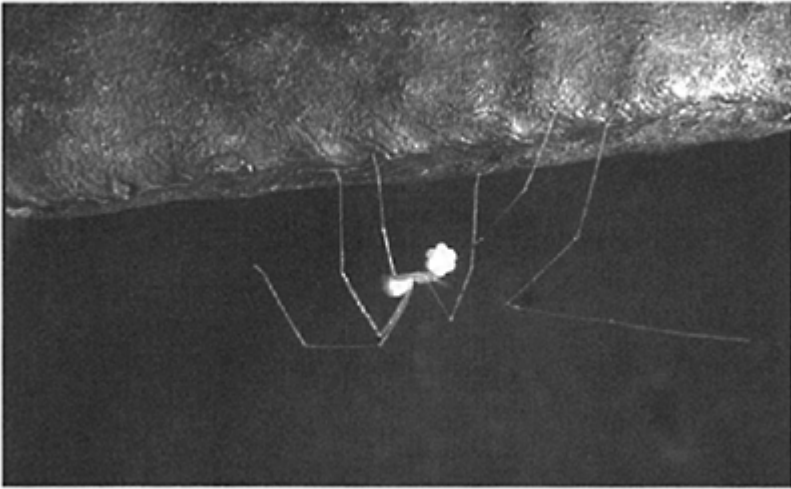
The main morphological adaptations of troglotitic Araneae species are the reduction and loss of eyes, a remarkable or total depigmentation, and the lengthening of appendages. Their adaptation to the subterranean environment also affects their life cycle. Generally, they show a lengthening of their embryonic and post-embryonic development, as well as their adult life. Several interesting studies on this subject have been performed on troglomorphic species belonging to the genera *Phaneta* and *Anthrobia* in the United States (Poulson, 1981) and *Telema*, *Leptoneta*, and *Troglohyphantes* in Europe (Juberthie, 1985; Deeleman-Reinhold, 1978). In general, when compared to their epigeal relatives, cavernicolous species show a low metabolic rate and decreased activity. Their reproductive effort is diminished, the number of eggs per brood is lower, and the eggs are considerably larger. As a result, cavernicolous species have adapted their biological parameters to the environment they inhabit: they regulate their energetic expense according to the amount of energy available in the subterranean environment.

### Distribution

Spiders are very abundant in all subterranean habitats worldwide. Nevertheless, the number of species in each cave varies according to the latitude and biogeographical region. Caves in temperate climates rich in organic matter can host up to ten different species. In contrast, caves in subpolar regions are much poorer in energetic resources as well as in diversity. The areas richest in troglomorphic species are those of temperate climates, mainly Mediterranean: the Mediterranean region, central and southern United States, Mexico, Japan, and Korea. In the southern hemisphere, they are abundant in South Africa, Australia, and in several regions in continental Asia, although these are less known. Tropical areas show a high biodiversity but host a low number of troglomorphic species. Possibly, when the large karst areas in Asia, Africa, and South America are explored, the number of troglomorphic species will increase considerably.

### Main Troglomorphic Groups and Species

The Order Araneae includes three Suborders: Liphistiomorpha, Mygalomorpha, and Arachnomorpha. Currently, there are 40000 spider species known, which are grouped into more than



**Arachnida: Araneae: Figure 1.**  
*Spermophorides justoi* (Araneae:  
 Pholcidae), a troglobitic spider from  
 caves of El Hierro, Canary Islands.  
 The *Spermophorides* genus has other  
 cave-dwelling species occurring in  
 Tenerife and La Palma. (Photo by  
 Pedro Oromi)

120 different families. Half of the families have troglomorphic species, giving just under 1000 troglomorphic species in total.

The Suborder Liphistiomorpha occurs in Southeast Asia, from Japan to Vietnam, and comprises the spiders that are considered the most primitive: they have a segmented opisthosoma (rear part of body). This suborder does not include a large number of species, and only two are troglomorphic: *Liphistius batuensis*, from Batu Cave, Malaysia, and *Liphistius langkawi* from Thailand.

The Suborder Mygalomorpha is common in tropical areas. Some species colonize warm regions in temperate climates, although it is absent from cold climate zones. Species collected inside caves are generally nocturnal, living under rocks found in the entrance zone of caves. Although they may be abundant, most are troglonexes, some are troglophilic, and a few are troglomorphic—all of which occur in tropical regions. Examples from the American continent and the Caribbean area include *Speleoctenizia ashmolei* from Ecuador, *Masteria pecki* from Jamaica, three species of *Euagrus* and six species of *Speleopelma* from Mexico, and *Troglotele caeca* from Cuba. Only one species has been described in Africa: *Aporoptychus stercoricola* (Guinea). From Australia and New Zealand there is *Troglodiplura lowryi* and *Hexatella cavernicola* respectively, and *Masteria caeca* from Asia (Philippines).

The Suborder Araneomorpha comprises most of the known spider species and is well represented in the subterranean environment. Many of its families are cosmopolitan, or worldwide in distribution, such as the Pholcidae, which are abundant in most caves of tropical and temperate regions in both hemispheres. Most Pholcidae species are troglomorphic, but some are troglomorphic. The most common genera that include troglomorphic species are *Pholcus* and *Spermophorides* (see Figure 1) in Europe; *Physocyclus*, *Modisimus*, *Anopsicus*, *Metagonia*, *Pholcophora*, and *Psilochorus* in Mexico, Jamaica, and Belize; *Priscula* in Venezuela; *Coryssocnemis* in Ecuador; and *Artema* in New Guinea.

The Telemidae are an interesting family since their troglomorphic species are distributed across temperate as well as across tropical regions. This fact suggests that the Telemidae are an ancient family, and some of their representatives can be considered as living fossils. *Telema tenella*, one of the most studied troglomorphic species, occurs in the eastern Pyrenees (France and Spain) and is the only Telemidae found in the European continent. Some other troglomorphic species are *T. niponica* from Japan and *T. mayana* from Mexico, *Cangoderces lewisi* and *Apneumonella oculata* from the African continent, and several species belonging to the genus *Usofila* from the United States and New Caledonia.

The Leptonetidae are small spiders inhabiting small rock piles on the floor of caves as well as cracks and rough areas on the walls. Most species are troglomorphic. The most important genera in Europe are *Leptoneta*, *Teloleptoneta*, *Paraleptoneta*, *Protoleptoneta*, *Sulcia*, *Barusia*, and *Leptonetella*, which are distributed across the northern side of the Mediterranean basin, from the Iberian Peninsula to Turkey. In Asia, the main genera are *Leptoneta*, *Saturana*, *Falcileptoneta*, and *Masirana* (occurring in China, Japan, and Korea). American species belong to the genera *Leptoneta*, *Archoleptoneta*, *Neoleptoneta*, *Appaleptoneta*, and *Callileptoneta* (United States, Mexico, and Brazil)

Species belonging to the family Ochyroceratidae are spread across the southern hemisphere and they occupy the same niche as the Leptonetidae in the northern hemisphere. Ochyroceratidae are abundant among fallen leaves and vegetal litter in forest undergrowth, and are also common in caves, where several troglomorphic species have been described. Most of the troglomorphic species belong to the genera *Ochyrocera*, *Theotima*, *Fageicera*, and *Speocera* in South and Central America, the West Indies, and Hawaii; *Speleoderces* from Africa and *Simonicerca*, *Psiloderces*, *Althepus*, *Theotima*, and *Speocera* from Asia.

The Dysderidae are a family with a Palaearctic distribution. They comprise several troglomorphic species belonging to the genera *Dysdera* (see Figure 2), *Speleoharpactea*, *Harpactea*, *Stalita*, *Folkia*, *Stalagtia*, *Minotauria*, *Rhode*, and *Rhoderia*. Troglomorphic species occur on the northern side of the Mediterranean basin, in North Africa, and in the Canary Islands.

The Linyphiidae are one of the most widespread spider families in the epigeal environment. A large number of troglomorphic species are found in the northern hemisphere, most of them belonging to the genera *Troglohyphantes*, *Lepthyphantes*, *Porrhomma*, *Centromerus*, *Caviphantes*, *Thypholyniphia*, *Icariella*, and *Troglodytia* (Europe), *Walkenaeria* (Canary Islands), *Phanetta*



**Arachnida: Araneae: Figure 2.**

*Dysdera unguimmanis* (Araneae: Dysderidae) is by far the most troglomorphic among the eight cave-dwelling species of the genus occurring in Canary Island caves. (Photo by Pedro Oromi)

and *Anthrobia*, (United States), *Meioneta* (Hawaii), *Allomengea* and *Jacsonella* (Korea), and *Dunedinia* (Australia).

The Nesticidae are spread across the northern hemisphere, as the Leptonetidae, but have also been recorded in Brazil. The main genera that include troglomorphic species are *Nesticus* (Europe, United States, China, Japan, Korea, and Ceylon), *Canarionesticus* (Canary Islands), *Typhlonesticus* and *Carpatonesticus* (Europe), *Gaucelmus* and *Eidmanella* (United States and Mexico), and *Nesticiella*, which is distributed across Japan, Russia, China, Vietnam, Central Africa, Hawaii, and Fiji.

The Agelenidae are abundant in tropical regions. Several troglomorphic species have been described in temperate areas: they belong to the genera *Tegenaria*, from the Western Mediterranean region, and *Cicurina* and *Blabomma* from Mexico, United States, Japan, and Korea.

The families Clubionidae, Liocranidae, Gnaphosidae, Lycosidae, and Prodidomidae are poorly represented in subterranean environments, and most species are epigeal. Nevertheless, some extremely troglomorphic exceptions exist, such as *Agraecina cristiani* from Movile Cave in Romania, *Brachyanillus liocraninus* from Spain, *Berlandia tenebricola* from Tanganyika (Clubionidae); two *Lygromma* species from the Galapagos Islands and *Herpsillus suavis* from Cuba (Gnaphosidae); and *Lycosa howarthi* and *Adelocosa anops* from Hawaii (Lycosidae).

The Theridiidae are a set of species closely related to vegetation and ground fauna. They are common in tropical caves. Most species are troglophilic, but there are some troglomorphic species such as *Achaearanea mundula*, and a few more belonging to the genera *Coscinidia* and *Stemops*, from New Guinea, as well as to *Steatoda* and *Pholcomma* from Australia. Some troglomorphic species from the genus *Theridion* have been described in oceanic islands (Azores and Galapagos).

*Hickmania troglodytes*, from Tasmania, deserves special attention: it belongs to the Austrochilidae family, considered the most primitive within the Suborder Araneomorpha.

The genera *Meta* and *Metellina* of the family Metidae are troglophilic, inhabiting caves in temperate regions worldwide. Several species belonging to *Loxosceles* (Loxoscelidae) and the families Theridiosomatidae, Ctenidae, Oonopidae, Tetrablemidae, and Anapidae, are also troglomorphic, inhabiting tropical caves.

CARLES RIBERA

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## ARACHNIDA: ACARI (MITES AND TICKS)

Acari (mites and ticks) and spiders are the most diverse and abundant groups of Arachnida in the subterranean environment. Over 45000 Acari species are recorded, and more than 1000 have been reported from caves. Most Acari found in caves are troglophilic. Considering their environment and their lifestyle, Acari occurring in subterranean habitats can be divided into three groups.

### Acari Terrestria

This group includes those Acari that are totally or optionally free living and they are the most common and abundant group in subterranean environments and occur in most caves. Several species live in close relation to guano deposits, common in many caves. Bat guano may support densities of between tens of thousands and millions of Acari individuals per square metre. These are generally guanobitic, although some species are bat parasites during some periods of their lives, tending to be ecologically and evolutionarily related to the caves they inhabit. Some authors consider them as recent cavernicolous species (eucavernicolous). Another set of species comprises the typical ground species associated with other organic detritus. They are generally predators that consume Collembola and other microarthropods, eggs, and insect larvae, but can also feed on fungi or may be detritophagous or necrophagous. This second group includes many species for which only a few individuals are known and therefore neither their biology nor their ecological requirements have been reported. These forms are considered trogliphilic or troglobitic depending on their external morphological characteristics. A lengthening of appendages and a lack of pigmentation are the most conspicuous adaptations to the subterranean environment.

Among the Acari terrestria the Notostigmata (Opilioacarida) are considered the most primitive group, showing abdominal segmentation. They are cosmopolitan and comprise 20 species, four of which have only been reported from caves (*Opilioacarus orghidani* and *O. vanderhammeni* from Cuba and *Siamacarus dalgeri* and *S. withi* from Thailand).

The Mesostigmata (Gamasida) are common and abundant in most biotopes. All are eyeless and the most common groups in caves are predators, but some are saprophagous or guanophagous. Some species are parasites of small rodents and insectivores. Most species can be considered as trogliphilic, but there are several troglomorphic taxa, such as *Eugamasus cavernicola* (Parasitidae), a European neotroglobitic species, and 31 of the 50 species belonging to the family Uropodidae that have been reported from caves.

The Prostigmata (Actinedida) include seven different families. Most species are trogliphilic, but there are several troglobitic taxa such as *Bonzia brownei* from England and *Ischnothrombium diploctenum* from Cuba. *Proterorhagia ozotloica* (Proterorhagiidae), from Mexican caves, shows an extraordinary adaptation to the subterranean environment. It has lost all pigmentation, its lateral eyes are absent, and its legs and chelicerae are lengthened. It displays highly developed sensorial setae.

The family Rhagidiidae includes 22 troglomorphic species belonging to the genera *Rhagidia* and *Poecilophysis*; they are cosmopolitan and predators. The North American genus *Foveacheles* includes several troglobitic species, as does the genus *Rubostocheles*. *Flabellorhagidia* and *Troglocheles* also comprise troglomorphic species, and *Troglocheles vandeli*, from France, is one of the most highly evolved troglomorphic species.

The Astigmata (Acaridida) also include some cave species. They tend to be saprophagous and/or fungivorous, or associated with bat guano. Most species can be considered trogliphilic, although some are troglobitic. The Cryptostigmata (Oribatida) is the most common group recorded in the subterranean environment.

### **Acari Parasiti**

Parasitic Acari that live in association with bats and other little mammals are common in caves; their evolution is related to that of their hosts. The Acari parasiti can be subdivided into three groups: (i) temporary parasitic species that are only known from caves and are adapted to the subterranean environment; (ii) temporary or periodically parasitic species that do not display any adaptation to the subterranean environment; and (iii) permanent parasites evolutionarily related to their hosts but not to the subterranean environment.

The first group interests us the most and includes ticks, Trombiculids, and some guanobites. They spend most of their adult life in cracks on the walls or in guano and they look for a host only for feeding. Generally, their parasitism is not extremely specific and they parasitize almost any bat species. Most species are well adapted to parasitic life but they do not display adaptations to the subterranean environment. Nevertheless, some species show an extraordinary morphological and physiological adaptation to the subterranean environment. Some Ixodid species, which are parasites of Chiroptera, show a noticeable lengthening of their appendages and develop at a relatively low temperature (15°C). About 30 cavernicolous species are known within the family Argasidae (Metastigmata). The families Spelaeorhychidae (specific Chiroptera parasites), Trombiculidae, and Wenkoekiidae (Prostigmata) include 210 species, most of them trogliphilic.

The second group, comprising temporary or occasional parasitic species that do not display adaptations to the subterranean environment, parasitize rodents and insectivores (Family Laelapidae) or they may be specific Chiroptera parasites. They are exclusively haematophagous. Almost 100 species have been reported, and all of them are considered as trogliphilic.

The third group's occurrence in caves is accidental and they are considered troglonexes. They parasitize hairs, exocuticles, endocuticles, the cornea, nose, mouth, stomach, and intestines. Several authors think their coexistence is very ancient.

### **Hydracarina**

Subterranean Hydracarina (or water mites) are primarily interstitial, although some may also inhabit the water table (Limnohalacaridae and some hydrachnellas). Most species found in the subterranean interstitial environment come into caves from epigeal watercourses. The true subterranean Hydracarina (stygobites) originate from epigeal watercourses but have adapted to the subterranean environment (hyporheic interstitial environment). They are closely associated with the grains of sand that are more or less in contact with the water flow. All subterranean Hydracarina are predators, feeding on insect larvae (mainly Chironomidae), copepods, ostracoda, and other aquatic micro-invertebrates.

Adaptive characteristics shown include absence of visual structures (cornea and retina); a marked diminishment of pigmentation, although in some species the ocular pigment remains; and reduced size but a body elongation—some highly evolved species show a worm-like aspect that helps them move between the grains of sand. Unlike terrestrial cavernicolous species, subterranean Hydracarina show a shortening of the first three pairs of legs; the first pair of legs tend to be used as feelers. The fourth pair, far more robust, are used for moving. The stygobites have also reduced their reproductive effort: they produce fewer eggs per brood.

The Hydracarina (Suborder Actinedida) comprises ten superfamilies. The superfamily Hydrachnellae is the most abundant in the subterranean environment (several hundred species). The superfamily Halacaroidae includes 20 stygobitic species. The superfamily Stygotrombioidea includes 19 species, all of which are stygobitic. Several other superfamilies have subterranean representatives including Trombidioidea, Eylaoidea, and Hydryphantoidea.

CARLES RIBERA

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## ARACHNIDA: MINOR GROUPS

The following section provides a brief overview of Arachnida that occur relatively infrequently or are poorly represented in subterranean environments.

### Scorpionida

The Order Scorpionida includes about 1300 species grouped into nine families, five of which (Chactidae, Vaejovidae, Diplocentridae, Chaerilidae, and Ischnuridae) have troglomorphic representatives. The first records of cave-dwelling scorpions were from Sumatra (*Chaerilus cavernicola*) and Malacca (*Chaerilus agilis*). Three species have been recorded in Europe, although none of these can be considered as troglobitic. *Belisarius xambeui*, endemic to the eastern Pyrenees (France and Spain), shows a slight loss of pigmentation as well as a lack of its central eyes and a marked reduction of laterals, but it inhabits both hyogean and epigeal habitats. The highest number of troglomorphic species is found in the Mexican karst, where ten species have been recorded. In addition, troglobitic species have been recorded from Ecuador, Sarawak, and Australia (the recently described Ischnuridae: *Liocheles polisorum*).

### Pseudoscorpionida

The Order Pseudoscorpionida is composed of about 3000 species distributed worldwide, with the exception of polar areas. Pseudoscorpions are abundant in most subterranean habitats, and a large number of troglomorphic species have been described. Troglomorphic species are not numerous, but they cannot be considered as scarce. The most common families in the subterranean environment are Neobisiidae, Chthoniidae (see Figure), Bochicidae, Vachoniidae, and Syarinidae. A spectacular lengthening of appendages, the absence of eyes, and a complete loss of pigmentation are common adaptations to the



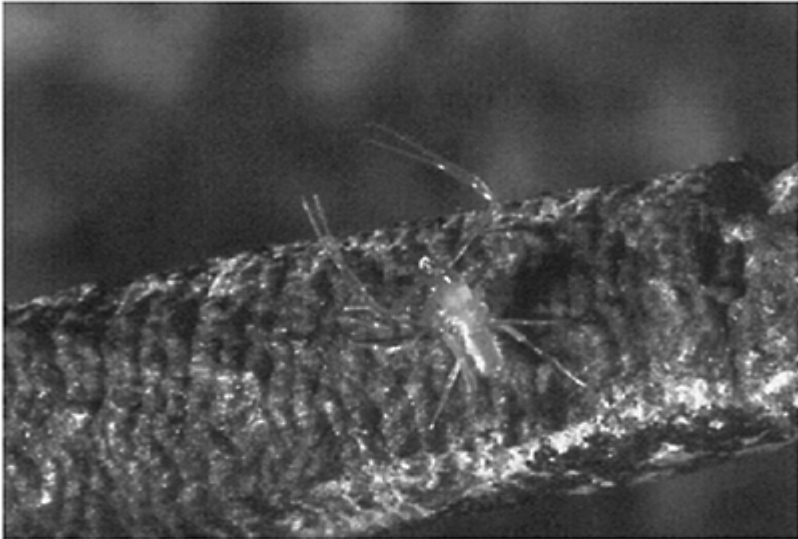
subterranean environment. In some cases, due to the fact that life cycles are unknown, it is difficult to distinguish trogliphilic from troglobitic species.

Troglophobic species are abundant in the Mediterranean climate zone of the northern hemisphere (Mediterranean basin, United States, Mexico, Japan, and Korea). There are also records from South American caves, the West Indies, Australia, and Tasmania, although they seem to be less abundant. The presence or absence of cavernicolous pseudoscorpionida remains unknown in many regions of the world, and therefore the current distribution map will probably be modified in the future.

### **Opilionida**

Harvestmen (Order Opilionida) are common and abundant in many subterranean habitats. About 5000 species are currently known, and 125 of these can be considered as cave dwellers, including 80 troglobitic species. The Order Opilionida is divided into three Suborders: Cyphophthalmi, Laniatores, and Palpatores.

The Cyphophthalmi are small and have similarities with Acari, possessing short legs and hard integuments. Just over 100 species have been described, of which 12 are troglobitic. The main family with cavernicolous representatives is the Sironidae. They inhabit temperate areas in the Northern hemisphere and



### **Arachnida: Minor Groups.**

*Tyrannochthonius superstes*  
(Pseudoscorpiones: Chthoniidae), can be found in the lava tubes of Tenerife, together with other pseudoscorpions well adapted to cave life. (Photo by Pedro Oromí)

include 22 species, all of them eyeless, of which ten troglobitic species occur in Europe. The Pettalidae include 41 eyeless species of Gondwanic distribution, with only one troglomorphic species, *Speleosiro argasiformis* from South Africa. Other families with troglomorphic representatives are Troglосironidae (*Troglosiro aelleni*) from New Caledonia and *Neogovea mexasca* (Neogoveidae) from Mexico.

The Suborder Laniatores is the most abundant, occurring in most regions of the globe, but appears to be more abundant in tropical zones. Its species are humicolous and lapidicolous, with large, spinous, and prehensile pedipalpi. The main groups including troglobitic species are the Phalangodinae (50 troglobitic species), which inhabit temperate and tropical areas in America, Europe, and Asia, and the Assamiidae, distributed across tropical regions of Africa and Southeast Asia. The Triaenonychidae, which includes 20 troglobitic species, have an austral distribution (Australia, New Zealand, Africa, and South America) although they also have a representative in the United States. The Trabunidae, which occur in Europe, United States, and Japan, include some troglomorphic species that are relicts from the ancient fauna that colonized the European continent. Finally, the Gonyleptidae and the Agoristeridae, with a Neotropical distribution, are abundant in South American caves, but they have very few troglomorphic representatives.

The Superfamily Palpatores is cosmopolitan, although it is notably more abundant in the Palaearctic region. The most important groups belong to the families Nemastomatidae, which has nine troglomorphic species in Europe plus two in the United States, and Ischyropsalidae, which has more than ten troglobitic species in Europe.

Finally, the Suborder Phalangodidea is constituted by the typical long-legged harvestmen, with a cosmopolitan distribution. Within this group, there are no troglomorphic representatives, although they are common and abundant in the threshold zone of caves.

### **Amblypygi**

Amblypygi (whip spiders) are largely nocturnal and colonize caves readily. They are distributed across the tropical regions of America, Africa, and Asia. Their main features are a flat body and large, powerful, and spinous pedipalpi. The first pair of legs (antenniform legs) are very long, with sub-segmentation of both the tarsi and the tibia, which are used as feelers. Most genera include epigean and cavernicolous species, some inhabiting both hypogean and epigean environments. Some genera, such as *Stygophrynus*, appear to be restricted to caves. About 40 species, among over 100 Amblypygi species known, have been reported from caves. Nevertheless, only a few can be considered as troglobitic.

There are no real differences between epigean and cave species with the exception of a few cave species that have reduced eyes. In some cavernicolous species, the pedipalpi may be extremely elongated. In others, medial eyes are reduced in size (*Paraphrynus baeops*) or even absent (*P. velame*). Many species of *Paraphrynus* inhabiting Mexican caves show reduced medial eyes. A few *Charinus* species also have reduced eyes. *C. (Speleophrynus) tronchonii* has no median eyes and the lateral eyes partially reduced, and *C. (Speleophrynus) bordoni* is completely blind, both taxa being from Venezuela. A similar eye reduction has occurred in the genus *Tricharinus* from Surinam and Jamaica. The cave-dwelling African *Paracharon caecus* lacks eyes, but also inhabits termite nests.

There are also troglobitic species (*Charinides cubensis* and *C. wanlessi*) in Cuba. Other troglobitic species are known from Venezuela, Guinea, Zanzibar, Tanzania, and Bardera in Somalia.

### Schizomida

The Order Schizomida includes more than 100 species with lucifugous (light-avoiding) and hygrophilic behaviour that are spread across the intertropical region. They are small, between 2 and 8 mm long. Their dorsal scutum is divided into three parts: pro-, meso- and metapeltidium. The opistosome has a long, multiarticulated flagellum that varies between species. They show a marked sexual dimorphism. The first pair of legs is long and thin, and used as feelers. Most Schizomida are endogean (inhabiting the soil zone immediately below the surface) and it is very difficult to tell troglobitic species from endogean ones.

A total of 32 species have been reported from caves, of which 25 can be considered as troglobitic. Most cavernicolous species belong to the genus *Schizomus* and troglomorphic species have been described from Mexico (Chiapas, Tamaulipas, Veracruz, and Yucatan), Guatemala, California, Cuba, Jamaica, Puerto Rico, Ecuador, Venezuela, Tanzania, Zanzibar, Rodriguez Island, and Angola. *Schizomus* is the most diverse and widespread genus. The genus *Agastoschizomus* also includes troglobitic species: *A. lucifer*, from Sierra de El Abra, and *A. huitzomolotitlensis* from El Sotano de Huitzomolotitlam, San Luis de Potosí, both from Mexico. Cave species have also been reported from Africa and Asia: *Trithyreus parvus* from Gabon and *T. pileti* from Batu Caves. Only one species is known from India, and two from Japan.

### Ricinulei

The Order Ricinulei includes only about 30 species that are distributed in tropical and subtropical areas in the American continent and Western Africa. They are small (10 mm), flat, slow, eyeless, and cryptic (coloured to camouflage) and have a preference for humid environments. The only characteristic identifying troglobitic species is a slight lengthening of their appendages, which makes it very difficult to assign them to a clear ecological category.

Known species are grouped into three genera: *Ricinoides* (seven species from Western Africa), *Cryptocellus* (21 species from tropical and subtropical America), and *Heteroricinoides*, (two species from Venezuela and Colombia). There are ten cave-dwelling species, of which nine belong to the genus *Cryptocellus* (eight from Mexico and one from Cuba); the tenth cave-dwelling species is *Heteroricinoides bordoni* from Venezuela. This group has not been reported from African caves.

### Palpigradida

The Order Palpigradida comprises the smallest and most difficult to find Arachnida: they rarely reach 2 mm in length. They are agile and extremely fragile. Their most conspicuous characteristic is a long flagellum used as a feeler. Their pedipalpi are ambulatory and the first pair of legs is antenniform. All palpigradida are blind and totally depigmented. They are thought to be of intertropical origin.

The Palpigradida includes about 80 species, 27 of which have been found only in caves (21 from Europe, one from Cuba and five from tropical Asia). These 27 species can

be considered troglotic: since all palpi-gradida are blind and lack pigmentation, it is difficult to distinguish between endogean and cavernicolous species. Generally, cavernicolous species tend to be bigger than endogean species, and they also show notably longer appendages (particularly the chelicera).

From a taxonomical perspective, the Palpi-gradida are divided into two families: the Protokoeneriidae, with two genera (*Protokoeneria* and *Triadokoeneria*), and the Eukoeneriidae, with four genera (*Eukoeneria*, *Allokoeneria*, *Koenerioides*, and *Leptokoeneria*). With the exception of *Triadokoeneria* and *Leptokoeneria*, the remaining genera are found in caves. The largest and most modified species belong to the genus *Eukoeneria*, which comprises the species that are most adapted to subterranean environments.

CARLES RIBERA

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## ARCHAEOLOGISTS

An archaeologist is defined as one who makes a “study of human antiquities, especially of the prehistoric period and usually by excavation” (*Concise Oxford Dictionary*). This entry reviews the life and work of eight of those who had the greatest influence on understanding the development of the human race before historical records began, using evidence from caves. No aspect could be more crucial than the antiquity of humankind. Until the 1850s, it was normal to believe that humans were a recent addition to the world. There was too little time since the Creation, then thought to have been some 6000 years ago, for humans to have existed at the same time as extinct animals, those destroyed in the biblical Flood. Georges Cuvier, with all his authority, had in 1812 expressly denied the existence of such early humans. So, included here is a succession of people who gradually came to realize that deposits in caves contradicted this belief. None of these researchers were what would now be called archaeologists. They were either geologists, priests, or doctors, taking an interest in this branch of natural history. Nevertheless, the work was archaeological and some of the most important ever to have taken place. Three more conventional archaeologists are also described.

**Johann Friedrich Esper (1732–81)**

Esper (Figure 1) was the parish priest of Uttenreuth, near Erlangen in Germany. Excavating during 1771 in the Bavarian cave of Burggaillenreuth, he found human bones together with those of cave bear and other extinct animals (Esper, 1774, p.26). He considered very carefully whether or not they were contemporary with each other, but concluded that he had insufficient evidence for such a momentous interpretation.

...I do not, however, suppose without adequate reason that these human remains are of the same age as the other animal petrifications. They must have come together with the others by chance.

This extract is translated from the original German version of Esper's book; in the French version published in the same year, the sense was reversed by mistake to say that the human and animal remains were of the same age.

**John McEnery (1796–1841)**

McEnery was the first person to convince himself that early humans were contemporary with extinct animals. His excavations in Kent's Cavern (Devon, United Kingdom) took place between 1825 and 1829, but none of his findings was printed until many years later and even now some of them remain unpublished. What he did and found, however, is known, as are his conclusions and also the opinions of Buckland with whom he was in touch.

McEnery was born in Ireland. Although his name is often spelled as MacEnery, he himself wrote it as McEnery. He was ordained as a priest in 1819 and in 1822 became chaplain to the family living at Torre Abbey in Torquay, where he remained until his early death. The existence of bones in the nearby Kent's Cavern was already known but they had not been seriously studied before McEnery (1825–28?; 1869). He left lengthy notes



**Archaeologists: Figure 1.** J.F.Esper.



**Archaeologists: Figure 2.** William Buckland.



**Archaeologists: Figure 3.** P.C. Schmerling.



**Archaeologists: Figure 4.** William Pengelly.



**Archaeologists: Figure 5.** William Boyd Dawkins.



**Archaeologists: Figure 6.** The Abbé Breuil in 1919 or before.



on his work, which are in the library of the Torquay Natural History Society. Most of them were published in 1869, showing that he had found human bones and teeth, flint tools, pottery, and charcoal, as well as bones and teeth of *Homotherium latidens* (sabre-toothed tiger), rhinoceros, hyaena, and bear.

What is not immediately obvious is McEnery's own opinion. Did he or did he not believe that the human remains were of the same age as the animal bones found with them? What he wrote in his manuscript notes, intended as a basis for publication, conflicts with the opinion he expressed in private letters to Buckland.

It must be remembered that this young (30 years old in 1826) and inexperienced excavator was exposed to two of the world's authorities of the day, both of whom were opposed to the idea. Cuvier, already mentioned, identified some of his specimens and McEnery visited him in Paris. Buckland, with whom McEnery was in close contact, was deliberately cautious, believing that the apparent association at the same level in the deposits could be explained by supposing that humans had dug pits in which their bones and artefacts were found. These two must have been powerful influences on the young man, whose theological training may also have had an effect. This is what he wrote in his manuscript (McEnery, 1869, p.226):

I am persuaded that if due attention is paid to the place in which these remains occur—and the manner that they are intermingled with the soil and bones reputed fossil, it will be in every case found...that they are not coeval neither with one or the other but that they had been added subsequently to the deposition of the former and commingled with them into a common heap by causes such as operated here I mean the visits of man, or according to their position by the disturbing action of running waters.

Had I not devoted so long a period to personal examination of all the circumstances attending this delicate question, in common with others I should have fallen into the error of supposing human remains to be contemporaneous because conjoined with the deposit of mud and bones.

However, what were presumably his true views, forthright and unconstrained by any intention of publication, are contained in two letters written to Buckland in 1828 or 1829 and never previously published (McEnery, 1825–28?):

Nothing could give me greater pleasure than to concur with you in this and in every other point, but it would not be just to truth to give up the impressions of three years observation without the fullest conviction to the contrary.

Hitherto I had rather bowed to your high authority than to evidence. But the matter is now clear as day.

### **William Buckland (1784–1856)**

Buckland (Figure 2) was one of the most influential geologists of the 19th century, but only a small part of his work related to humankind. At Oxford, his lectures were so highly regarded that a new chair of geology was created for him. His sense of fun drew

many listeners and it also prompted humorous drawings relating to his cave interests. Having seen the Burggailenreuth cave where Esper had worked, he was keen to investigate the newly found cave of Kirkdale in Yorkshire, but no human remains were involved. The fact that the cave contained bones of animals too large to get through the entrance and that they were nearly all broken and chewed, led him to conclude that hyaenas, the other occupants, had taken them there as food. This unconventional idea (Buckland, 1822) earned him the Royal Society's Copley Gold Medal. Buckland's only involvement with human remains in caves was in Torquay, as already described. He himself had expected that humankind would be found coeval with extinct animals but he did not accept that the Kent's Cavern evidence was convincing enough for such a contentious conclusion.

### **Philippe Charles Schmerling (1791–1836)**

Although McEnery had been excavating in the 1820s, it was Schmerling who, in 1833, first published a definite statement that the human remains he had found were contemporary with those of extinct animals. Schmerling (Figure 3) trained as a doctor in Belgium and in 1825 began to practise in Liege. Only four years later he gave up medicine as a result of a chance meeting with some fossil animal bones that some of his patients' children were playing with. They came from a cave at Chokier, opened by quarrying and not previously disturbed. Stimulated by these, he spent the next four years exploring more than 40 similar caves. Besides 60 species of animals, he found fossil human bones, together with chipped stone tools and carved bones. They lay beneath flowstone floors, scattered and abraded just like the animal bones that were with them, so they could not have been buried later into an earlier deposit, as Buckland had supposed at Kent's Cavern. At Engis, a child's skull, known now to be a Neanderthal, was next to a mammoth tooth, and a Cro-Magnon skull was with rhinoceros teeth.

Schmerling published his findings in great detail and concluded (1833, p.66): "There can be no doubt that the human bones were buried at the same time and by the same cause as the other extinct species." Charles Lyell visited Schmerling and referred to his discoveries but it was only later that he accepted their significance. At first he had insisted that coexistence could only be proven if the remains were found together in stratified deposits, but he afterwards acknowledged that Schmerling's specimens had been found "under circumstances far more difficult to get over than any I have previously heard of" (Lyell, 1881, 1:401–02).

### **William Pengelly (1812–94)**

Pengelly's great contribution to archaeology was his careful and precisely recorded excavation, carried out in a Brixham cave in Devon in 1858–59, which was sufficient to convince the doubters that humankind and the extinct animals there really were contemporary. The lesson was reinforced by the much more extensive excavations he directed in Kent's Cavern from 1864 to 1879. There is some analogy here with Darwin's achievement, in making evolution generally accepted by means of massive evidence. Darwin, however, had to argue his case; with Pengelly the evidence largely did it for him.

Pengelly (Figure 4) had only an elementary school education and was largely self-taught, yet his researches brought him Fellowship of the Royal Society. He started a school in Torquay and later took private pupils, who included members of European

royal families. He studied geology and also did an immense amount of detailed work on such diverse subjects as dialect and rainfall, and he reprinted all he could find written about Devon caves, amounting to many hundred pages. His publication of the McEnery (1869) manuscript is the most accurate available.

When the Brixham cave was found in 1858, it had been sealed since prehistoric times and its flowstone floor, beneath which the deposits were excavated, was undisturbed. It was this, coupled with his system of excavation, close supervision and accurate recording, which made his findings accepted. A grid system fixed the location of every object and the dig followed the stratification layers (Prestwich, 1874). The Kent's Cavern excavation was less important in that it came second, and previous disturbance of the deposits made it more complex, but the facts and their publication year by year to the wide audience of the British Association for the Advancement of Science members, helped the antiquity of humankind to become generally recognized. McEnery's conclusions of 40 to 50 years before were vindicated and Lyell, who had been sceptical of Schmerling's opinion, was converted.

### **William Boyd Dawkins (1837–1929)**

At last here is someone who was known as an archaeologist who worked in caves, in contrast to the geologists and others, whose crucial evidence for the antiquity of humankind had been archaeological. Boyd Dawkins (Figure 5) was not associated with the same vital breakthrough but he was, on the other hand, better known than many of his predecessors. His work, his writing and his long career, meant that he was regarded as *the* cave archaeologist for much of the 19th and 20th centuries, though more of his work was on Pleistocene animals rather than on humans.

Boyd Dawkins became interested in geology while at Oxford and in 1861 was appointed to the Geological Survey of Great Britain. In 1866, he was elected FRS and from 1874 to 1909 he was Professor of Geology and Anthropology in Owen's College, Manchester, the predecessor of Manchester University. Inspired by Pengelly's results at Brixham, he excavated in the Wookey Hole Hyaena Den, finding Mousterian tools together with extinct animals (Dawkins, 1862–63). His classic book *Cave Hunting* (1874), brought together facts on the physical aspects of caves, as well as their contents in many European countries. He himself carried out many cave excavations until 1903, when he was 66 years old, but still he was more concerned with mammal remains than human.

### **Henri Édouard Prosper Breuil (1877–1961)**

Finally we come to a man who was widely acclaimed throughout his long life, for work in a special field of cave archaeology. It was he who founded, early in the 20th century, the new study of prehistoric cave art (see separate entry, Art in Caves: History). Ordained priest in 1900, the Abbé Breuil (Figure 6) was lecturer in Prehistory and Ethnography in the University of Fribourg 1905–10, Professor of Prehistoric Ethnography at the Institut de Paléontologie Humaine in Paris from 1910, and Professor of Prehistory at the Collège de France 1929–47. He was elected a member of the Institute de France in 1938, received gold medals from the Society of Antiquaries in London and the National Academy of Sciences in Washington, and held honorary degrees from several foreign universities.

While still a young man, he often accompanied Émile Cartailhac (1845–1921), the doyen of prehistory, who had previously denied the antiquity of cave art. Breuil was at the cave of La Mouthe in 1902, when Cartailhac accepted it with his famous “*Mea culpa d’un sceptique*”. He had seen the painted caves of Les Combarelles and Font-de-Gaume, when they were discovered in 1901, and he went to Altamira in 1902. He was also involved in the discovery of Tuc d’Audoubert in 1912 and Les TroisFrères in 1916. His own main contributions were his skilled and laborious copying of the art, its stylistic analysis and interpretation, and its publication in numerous magnificent books. In 1940, it was he who first assessed the Lascaux paintings, but towards the end of his life, he denied the authenticity of those found at Rouffignac in 1956. His bibliography exceeds 793 items (Lantier, 1957).

### Pei Wenzhong (1904–1982)

After graduating in geology from Peking University in 1927, Pei had a long and distinguished career as an archaeologist and paleo-anthropologist, including cave excavations of paleolithic remains in many parts of China. Best known and most significant, was his work at the cave of Zhoukoudian (then spelled Choukoutien), 47 km southwest of Beijing. In 1927, a single tooth from there had been recognized by the Canadian, Davidson Black of Beijing, as coming from a previously unknown hominid called Peking Man, *Sinanthropus pekinensis* at that time and now *Homo erectus pekinensis*. Pei joined the excavation there in 1928, and in the very next year he discovered the first complete skull of Peking Man. It was a predecessor of both Neanderthal and modern man, dated to the middle Pleistocene period. It postdates Java Man and is considered to be more advanced than the other early hominids, with a range of cranial capacity overlapping that of modern man. The discovery of the skull was followed, under Pei’s direction, by stone tools, charred wood, and animal bones, some of which were burnt. The Abbé Breuil visited the site in 1931 and from 1935 to 1937, Pei studied under him in Paris, where he gained his doctorate.

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*See also* **Archaeology of Caves: History**

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## ARCHAEOLOGY OF CAVES: HISTORY

Archaeology was born during the first half of the 19th century through the systematic excavation of deposits found in the caves of Europe. Those excavations were undertaken by inquisitive intellectuals, geologists, and antiquarians, who were delving into the history of the world and especially of humankind. They established a past for humanity by providing great time depth and previously undocumented variation over human history. In the New World, archaeology in caves helped resolve questions about the tenure of Native Americans, establishing the complexity of their cultures and contributing to our knowledge about agriculture in the prehistoric Americas. Cave archaeology has thus been a fundamental part of scientific understandings of human origins and development, and dramatically changed our view of our world and ourselves.

The birth of archaeology was from the mouths of caves in Western Europe, wrapped up in one of the most momentous intellectual changes in human history: the