Grzimek's
Animal Life Encyclopedia

Second Edition

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Volume 1
Lower Metazoans and Lesser Deuterostomes

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In association with the American Zoo and Aquarium Association

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Grzimek's Animal Life Encyclopedia, Second Edition

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Foreword

Earth is teeming with life. No one knows exactly how many distinct organisms inhabit our planet, but more than 5 million different species of animals and plants could exist, ranging from microscopic algae and bacteria to gigantic elephants, redwood trees and blue whales. Yet, throughout this wonderful tapestry of living creatures, there runs a single thread: Deoxyribonucleic acid or DNA. The existence of DNA, an elegant, twisted organic molecule that is the building block of all life, is perhaps the best evidence that all living organisms on this planet share a common ancestry. Our ancient connection to the living world may drive our curiosity, and perhaps also explain our seemingly insatiable desire for information about animals and nature. Noted zoologist, E. O. Wilson, recently coined the term "biophilia" to describe this phenomenon. The term is derived from the Greek *bios* meaning "life" and *philos* meaning "love." Wilson argues that we are human because of our innate affinity to and interest in the other organisms with which we share our planet. They are, as he says, "the matrix in which the human mind originated and is permanently rooted." To put it simply and metaphorically, our love for nature flows in our blood and is deeply engrained in both our psyche and cultural traditions.

Our own personal awakenings to the natural world are as diverse as humanity itself. I spent my early childhood in rural Iowa where nature was an integral part of my life. My father and I spent many hours collecting, identifying and studying local insects, amphibians and reptiles. These experiences had a significant impact on my early intellectual and even spiritual development. One event I can recall most vividly. I had collected a cocoon in a field near my home in early spring. The large, silky capsule was attached to a stick. I brought the cocoon back to my room and placed it in a jar on top of my dresser. I remember waking one morning and, there, perched on the tip of the stick was a large moth, slowly moving its delicate, light green wings in the early morning sunlight. It took my breath away. To my inexperienced eyes, it was one of the most beautiful things I had ever seen. I knew it was a moth, but did not know which species. Upon closer examination, I noticed two moon-like markings on the wings and also noted that the wings had long "tails", much like the ubiquitous tiger swallow-tail butterflies that visited the lilac bush in our backyard. Not wanting to suffer my ignorance any longer, I reached immediately for my *Golden Guide to North American Insects* and searched through the section on moths and butterflies. It was a luna moth! My heart was pounding with the excitement of new knowledge as I ran to share the discovery with my parents.

I consider myself very fortunate to have made a living as a professional biologist and conservationist for the past 20 years. I've traveled to over 30 countries and six continents to study and photograph wildlife or to attend related conferences and meetings. Yet, each time I encounter a new and unusual animal or habitat my heart still races with the same excitement of my youth. If this is biophilia, then I certainly possess it, and it is my hope that others will experience it too. I am therefore extremely proud to have served as the series editor for the Gale Group's rewrite of *Grzimek's Animal Life Encyclopedia*, one of the best known and widely used reference works on the animal world. *Grzimek's* is a celebration of animals, a snapshot of our current knowledge of the Earth's incredible range of biological diversity. Although many other animal encyclopedias exist, *Grzimek's Animal Life Encyclopedia* remains unparalleled in its size and in the breadth of topics and organisms it covers.

The revision of these volumes could not come at a more opportune time. In fact, there is a desperate need for a deeper understanding and appreciation of our natural world. Many species are classified as threatened or endangered, and the situation is expected to get much worse before it gets better. Species extinction has always been part of the evolutionary history of life; some organisms adapt to changing circumstances and some do not. However, the current rate of species loss is now estimated to be 1,000–10,000 times the normal "background" rate of extinction since life began on Earth some 4 billion years ago. The primary factor responsible for this decline in biological diversity is the exponential growth of human populations, combined with peoples' unsustainable appetite for natural resources, such as land, water, minerals, oil, and timber. The world's human population now exceeds 6 billion, and even though the average birth rate has begun to decline, most demographers believe that the global human population will reach 8–10 billion in the next 50 years. Much of this projected growth will occur in developing countries in Central and South America, Asia and Africa—regions that are rich in unique biological diversity.

Finding solutions to conservation challenges will not be easy in today's human-dominated world. A growing number of people live in urban settings and are becoming increasingly isolated from nature. They "hunt" in supermarkets and malls, live in apartments and houses, spend their time watching television and searching the World Wide Web. Children and adults must be taught to value biological diversity and the habitats that support it. Education is of prime importance now while we still have time to respond to the impending crisis. There still exist in many parts of the world large numbers of biological "hotspots"—places that are relatively unaffected by humans and which still contain a rich store of their original animal and plant life. These living repositories, along with selected populations of animals and plants held in professionally managed zoos, aquariums and botanical gardens, could provide the basis for restoring the planet's biological wealth and ecological health. This encyclopedia and the collective knowledge it represents can assist in educating people about animals and their ecological and cultural significance. Perhaps it will also assist others in making deeper connections to nature and spreading biophilia. Information on the conservation status, threats and efforts to preserve various species have been integrated into this revision. We have also included information on the cultural significance of animals, including their roles in art and religion.

It was over 30 years ago that Dr. Bernhard Grzimek, then director of the Frankfurt Zoo in Frankfurt, Germany, edited the first edition of *Grzimek's Animal Life Encyclopedia*. Dr. Grzimek was among the world's best known zoo directors and conservationists. He was a prolific author, publishing nine books. Among his contributions were: *Serengeti Shall Not Die*, *Rhinos Belong to Everybody* and *He and I and the Elephants*. Dr. Grzimek's career was remarkable. He was one of the first modern zoo or aquarium directors to understand the importance of zoo involvement in *in situ* conservation, that is, of their role in preserving wildlife in nature. During his tenure, Frankfurt Zoo became one of the leading western advocates and supporters of wildlife conservation in East Africa. Dr. Grzimek served as a Trustee of the National Parks Board of Uganda and Tanzania and assisted in the development of several protected areas. The film he made with his son Michael, *Serengeti Shall Not Die*, won the 1959 Oscar for best documentary.

Professor Grzimek has recently been criticized by some for his failure to consider the human element in wildlife conservation. He once wrote: "A national park must remain a primordial wilderness to be effective. No men, not even native ones, should live inside its borders." Such ideas, although considered politically incorrect by many, may in retrospect actually prove to be true. Human populations throughout Africa continue to grow exponentially, forcing wildlife into small islands of natural habitat surrounded by a sea of humanity. The illegal commercial bushmeat trade—the hunting of endangered wild animals for large scale human consumption—is pushing many species, including our closest relatives, the gorillas, bonobos and chimpanzees, to the brink of extinction. The trade is driven by widespread poverty and lack of economic alternatives. In order for some species to survive it will be necessary, as Grzimek suggested, to establish and enforce a system of protected areas where wildlife can roam free from exploitation of any kind.

While it is clear that modern conservation must take the needs of both wildlife and people into consideration, what will the quality of human life be if the collective impact of short-term economic decisions is allowed to drive wildlife populations into irreversible extinction? Many rural populations living in areas of high biodiversity are dependent on wild animals as their major source of protein. In addition, wildlife tourism is the primary source of foreign currency in many developing countries and is critical to their financial and social stability. When this source of protein and income is gone, what will become of the local people? The loss of species is not only a conservation disaster; it also has the potential to be a human tragedy of immense proportions. Protected areas, such as national parks, and regulated hunting in areas outside of parks are the only solutions. What critics do not realize is that the fate of wildlife and people in developing countries is closely intertwined. Forests and savannas emptied of wildlife will result in hungry, desperate people, and will, in the long-term lead to extreme poverty and social instability. Dr. Grzimek's early contributions to conservation should be recognized, not only as benefiting wildlife, but as benefiting local people as well.

Dr. Grzimek's hope in publishing his *Animal Life Encyclopedia* was that it would "...disseminate knowledge of the animals and love for them", so that future generations would "...have an opportunity to live together with the great diversity of these magnificent creatures." As stated above, our goals in producing this updated and revised edition are similar. However, our challenges in producing this encyclopedia were more formidable. The volume of knowledge to be summarized is certainly much greater in the twenty-first century than it was in the 1970's and 80's. Scientists, both professional and amateur, have learned and published a great deal about the animal kingdom in the past three decades, and our understanding of biological and ecological theory has also progressed. Perhaps our greatest hurdle in producing this revision was to include the new information, while at the same time retaining some of the characteristics that have made *Grzimek's Animal Life Encyclopedia* so popular. We have therefore strived to retain the series' narrative style, while giving the information more organizational structure. Unlike the original *Grzimek's*, this updated version organizes information under specific topic areas, such as reproduction, behavior, ecology and so forth. In addition, the basic organizational structure is generally consistent from one volume to the next, regardless of the animal groups covered. This should make it easier for users to locate information more quickly and efficiently. Like the original Grzimek's, we have done our best to avoid any overly technical language that would make the work difficult to understand by non-biologists. When certain technical expressions were necessary, we have included explanations or clarifications.

Considering the vast array of knowledge that such a work represents, it would be impossible for any one zoologist to have completed these volumes. We have therefore sought specialists from various disciplines to write the sections with which they are most familiar. As with the original *Grzimek's*, we have engaged the best scholars available to serve as topic editors, writers, and consultants. There were some complaints about inaccuracies in the original English version that may have been due to mistakes or misinterpretation during the complicated translation process. However, unlike the original *Grzimek's*, which was translated from German, this revision has been completely re-written by English-speaking scientists. This work was truly a cooperative endeavor, and I thank all of those dedicated individuals who have written, edited, consulted, drawn, photographed, or contributed to its production in any way. The names of the topic editors, authors, and illustrators are presented in the list of contributors in each individual volume.

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy or biosystematics. Taxonomy is the science through which various organisms are discovered, identified, described, named, classified and catalogued. It should be noted that in preparing this volume we adopted what might be termed a conservative approach, relying primarily on traditional animal classification schemes. Taxonomy has always been a volatile field, with frequent arguments over the naming of or evolutionary relationships between various organisms. The advent of DNA fingerprinting and other advanced biochemical techniques has revolutionized the field and, not unexpectedly, has produced both advances and confusion. In producing these volumes, we have consulted with specialists to obtain the most up-to-date information possible, but knowing that new findings may result in changes at any time. When scientific controversy over the classification of a particular animal or group of animals existed, we did our best to point this out in the text.

Readers should note that it was impossible to include as much detail on some animal groups as was provided on others. For example, the marine and freshwater fish, with vast numbers of orders, families, and species, did not receive as detailed a treatment as did the birds and mammals. Due to practical and financial considerations, the publishers could provide only so much space for each animal group. In such cases, it was impossible to provide more than a broad overview and to feature a few selected examples for the purposes of illustration. To help compensate, we have provided a few key bibliographic references in each section to aid those interested in learning more. This is a common limitation in all reference works, but *Grzimek's Encyclopedia of Animal Life* is still the most comprehensive work of its kind.

I am indebted to the Gale Group, Inc. and Senior Editor Donna Olendorf for selecting me as Series Editor for this project. It was an honor to follow in the footsteps of Dr. Grzimek and to play a key role in the revision that still bears his name. *Grzimek's Animal Life Encyclopedia* is being published by the Gale Group, Inc. in affiliation with my employer, the American Zoo and Aquarium Association (AZA), and I would like to thank AZA Executive Director, Sydney J. Butler; AZA Past-President Ted Beattie (John G. Shedd Aquarium, Chicago, IL); and current AZA President, John Lewis (John Ball Zoological Garden, Grand Rapids, MI), for approving my participation. I would also like to thank AZA Conservation and Science Department Program Assistant, Michael Souza, for his assistance during the project. The AZA is a professional membership association, representing 215 accredited zoological parks and aquariums in North America. As Director/William Conway Chair, AZA Department of Conservation and Science, I feel that I am a philosophical descendant of Dr. Grzimek, whose many works I have collected and read. The zoo and aquarium profession has come a long way since the 1970s, due, in part, to innovative thinkers such as Dr. Grzimek. I hope this latest revision of his work will continue his extraordinary legacy.

Silver Spring, Maryland, 2001
Michael Hutchins
Series Editor

How to use this book

Grzimek's Animal Life Encyclopedia is an internationally prominent scientific reference compilation, first published in German in the late 1960s, under the editorship of zoologist Bernhard Grzimek (1909–1987). In a cooperative effort between Gale and the American Zoo and Aquarium Association, the series has been completely revised and updated for the first time in over 30 years. Gale expanded the series from 13 to 17 volumes, commissioned new color paintings, and updated the information so as to make the set easier to use. The order of revisions is:

Volumes 8–11: Birds I–IV
Volume 6: Amphibians
Volume 7: Reptiles
Volumes 4–5: Fishes I–II
Volumes 12–16: Mammals I–V
Volume 3: Insects
Volume 2: Protostomes
Volume 1: Lower Metazoans and Lesser Deuterostomes
Volume 17: Cumulative Index

Organized by taxonomy

The overall structure of this reference work is based on the classification of animals into naturally related groups, a discipline known as taxonomy—the science in which various organisms are discovered, identified, described, named, classified, and catalogued. Starting with the simplest life forms, the lower metazoans and lesser deuterostomes, in volume 1, the series progresses through the more complex classes of animals, culminating with the mammals in volumes 12–16. Volume 17 is a stand-alone cumulative index.

Organization of chapters within each volume reinforces the taxonomic hierarchy. In the case of the volume on Lower Metazoans and Lesser Deuterostomes, introductory chapters describe general characteristics of all organisms in these groups, followed by taxonomic chapters dedicated to Phylum or Class. Species accounts appear at the end of the taxonomic chapters. To help the reader grasp the scientific arrangement, each type of chapter has a distinctive color and symbol:

■ = Phylum Chapter (lavender background)

⬟ = Class Chapter (peach background)

Introductory chapters have a loose structure, reminiscent of the first edition. Chapters on taxonomic groups, by contrast, are highly structured, following a prescribed format of standard rubrics that make information easy to find. These chapters typically include:

- Opening section
  - Scientific name
  - Common name
  - Phylum
  - Class (if applicable)
  - Number of families
  - Thumbnail description

- Main chapter
  - Evolution and systematics
  - Physical characteristics
  - Distribution
  - Habitat
  - Behavior
  - Feeding ecology and diet
  - Reproductive biology
  - Conservation status
  - Significance to humans

- Species accounts
  - Common name
  - Scientific name
  - Order
  - Family
  - Taxonomy
  - Other common names
  - Physical characteristics
  - Distribution
  - Habitat
  - Behavior
  - Feeding ecology and diet
  - Reproductive biology
  - Conservation status
  - Significance to humans

- Resources
  - Books
  - Periodicals
  - Organizations
  - Other

Color graphics enhance understanding

Grzimek's features approximately 3,000 color photos, including nearly 110 in the Lower Metazoans and Lesser Deuterostomes volume; 3,500 total color maps, including approximately 130 in the Lower Metazoans and Lesser Deuterostomes volume; and approximately 5,500 total color illustrations, including approximately 350 in the Lower Metazoans and Lesser Deuterostomes volume. Each featured species of animal is accompanied by both a distribution map and an illustration.

All maps in *Grzimek's* were created specifically for the project by XNR Productions. Distribution information was provided by expert contributors and, if necessary, further researched at the University of Michigan Zoological Museum library. Maps are intended to show broad distribution, not definitive ranges.

All the color illustrations in *Grzimek's* were created specifically for the project by Michigan Science Art. Expert contributors recommended the species to be illustrated and provided feedback to the artists, who supplemented this information with authoritative references and animal specimens from the University of Michigan Zoological Museum library. In addition to illustrations of species, *Grzimek's* features drawings that illustrate characteristic traits and behaviors.

About the contributors

Virtually all of the chapters were written by scientists who are specialists on specific subjects and/or taxonomic groups. Dennis A. Thoney reviewed the completed chapters to insure consistency and accuracy.

Standards employed

In preparing the volume on Lower Metazoans and Lesser Deuterostomes, the editors relied primarily on the taxonomic structure outlined in *Invertebrates*, edited by R. C. Brusca, and G. J. Brusca (1990). Systematics is a dynamic discipline in that new species are being discovered continuously, and new techniques (e.g., DNA sequencing) frequently result in changes in the hypothesized evolutionary relationships among various organisms. Consequently, controversy often exists regarding classification of a particular animal or group of animals; such differences are mentioned in the text.

Grzimek's has been designed with ready reference in mind, and the editors have standardized information wherever feasible. For **Conservation Status,** *Grzimek's* follows the IUCN Red List system, developed by its Species Survival Commission. The Red List provides the world's most comprehensive inventory of the global conservation status of plants and animals. Using a set of criteria to evaluate extinction risk, the IUCN recognizes the following categories: Extinct, Extinct in the Wild, Critically Endangered, Endangered, Vulnerable, Conservation Dependent, Near Threatened, Least Concern, and Data Deficient. For a complete explanation of each category, visit the IUCN Web page at <http://www.iucn.org/themes/ssc/redlists/categor.htm>.

In addition to IUCN ratings, chapters may contain other conservation information, such as a species' inclusion on one of three Convention on International Trade in Endangered Species (CITES) appendices. Adopted in 1975, CITES is a global treaty whose focus is the protection of plant and animal species from unregulated international trade.

In the species accounts throughout the volume, the editors have attempted to provide common names not only in English but also in French, German, Spanish, and local dialects..

Grzimek's provides the following standard information on lineage in the **Taxonomy** rubric of each Species account: [First described as] *Actinia xanthogrammica* [by] Brandt, [in] 1835, [based on a specimen from] Sitka, Alaska. The person's name and date refer to earliest identification of a species. If the species was originally described with a different scientific name, the researcher's name and the date are in parentheses.

Readers should note that within chapters, species accounts are organized alphabetically by order name, then by family, and then by genus and species.

Anatomical illustrations

While the encyclopedia attempts to minimize scientific jargon, readers will encounter numerous technical terms related to anatomy and physiology throughout the volume. To assist readers in placing physiological terms in their proper context, we have created a number of detailed anatomical drawings that are found within the particular taxonomic chapters to which they relate. Readers are urged to make heavy use of these drawings. In addition, many anatomical terms are defined in the **Glossary** at the back of the book.

Appendices and index

In addition to the main text and the aforementioned **Glossary,** the volume contains numerous other elements. **For further reading** directs readers to additional sources of information about lower metazoans and lesser deuterostomes. Valuable contact information for **Organizations** is also included in an appendix. An exhaustive **Lower Metazoans and Lesser Deuterostomes order list** records all orders of lower metazoans and lesser deuterostomes as recognized by the editors and contributors of the volume. And a full-color **Geologic time scale** helps readers understand prehistoric time periods. Additionally, the volume contains a **Subject index.**

Acknowledgements

Gale would like to thank several individuals for their important contributions to the volume. Dr. Dennis A. Thoney, topic editor for the Lower Metazoans and Lesser Deuterostomes volume, oversaw all phases of the volume, including creation of the topic list, chapter review, and compilation of the appendices. Neil Schlager, project manager for the Lower Metazoans and Lesser Deuterostomes volume, and Vanessa

Torrado-Caputo, associate editor at Schlager Group, coordinated the writing and editing of the text. Dr. Michael Hutchins, chief consulting editor for the series, and Michael Souza, program assistant, Department of Conservation and Science at the American Zoo and Aquarium Association, provided valuable input and research support.

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Topic overviews

What are lower metazoans
and lesser deuterostomes?

Evolution and systematics

Reproduction, development, and life history

Ecology

Symbiosis

Behavior

Lower metazoans,
lesser deuterostomes, and humans

Conservation

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What are lower metazoans and lesser deuterostomes?

Introduction

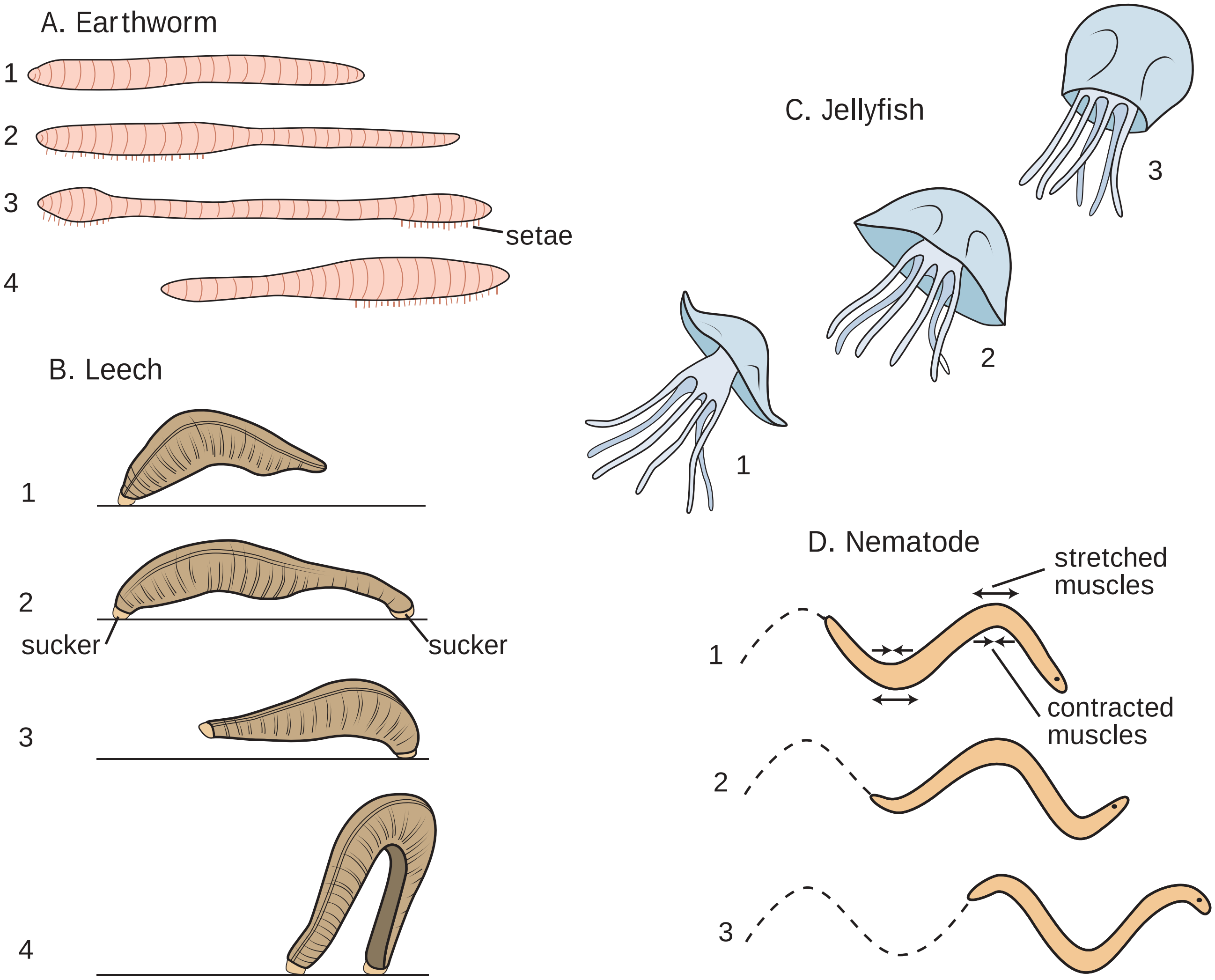
The Metazoa, today taken as a synonym of Animalia, comprises a large grouping of organisms that may be characterized as being multicellular and heterotrophic, i.e., they do not synthesize their own food, but obtain it from external sources. While there has been some debate in the past, it now seems overwhelmingly likely that the metazoans are monophyletic, and thus that all living examples are descended from an animal that lived some time in the Proterozoic (probably at least 600 million years ago [mya]). Even this statement is controversial, however. Molecular evidence suggests that metazoans had emerged up to one billion years ago or more; but the fossil record is most reasonably read as implying a much later origin, with definitive metazoans not appearing before 600 mya, and perhaps even later. Unfortunately, most "lower" metazoans today lack substantial hard parts such as mineralized shells, so their fossil record is correspondingly very poor. Telling the true time of appearance of such animals just from the fossil record may therefore well be inaccurate.

Animal evolution

Because of their long history and enormous adaptability, animals are organized in a remarkable number of different ways, ranging from simple sponges with only a few cell types through to the vertebrates with their complex nervous and immune systems. Indeed, it is possible to arrange animals in a broad series, from organisms that do not possess true tissues (e.g., sponges), through organisms with tissues but no organs (e.g., cnidarians), into the bilaterally symmetrical animals (the Bilateria) with both. The Bilateria typically also possess a central nervous system and muscles; some of them are segmented; and some possess a body cavity called a coelom.

The evolution of the animals has long been a contentious issue that has generated a huge number of theories. Nevertheless, at the heart of the issue is whether or not the organizational gradient that can be erected tells anything at all about animal evolution, or whether it merely reflects different adaptive needs of each organism. To put it more simply: are all the simple animals more basal than the more complex ones, or is animal evolution less tidy than that? The traditional assumption has been that organization is indeed a reflection of animal relationships and evolution, although the more thoughtful authors have refrained from definitively stating this. In this view, it makes sense to talk about animal evolution being a more or less stately progress from simple to complex; thus, one can label the simple animals, which are at the bottom of the tree, the "lower" metazoans, and the more advanced ones, the "higher" metazoans. To be more precise, animals without coeloms or segments are typically thought of as being "lower." These sorts of organisms show a variety of functional adaptations. Sponges and cnidarians typically have some sort of central fluid-filled cavity, which is critical to many roles including support, nutrition, excretion, and reproduction. Small bilaterians, on the other hand, have typically no need of any such system, as they are small enough to

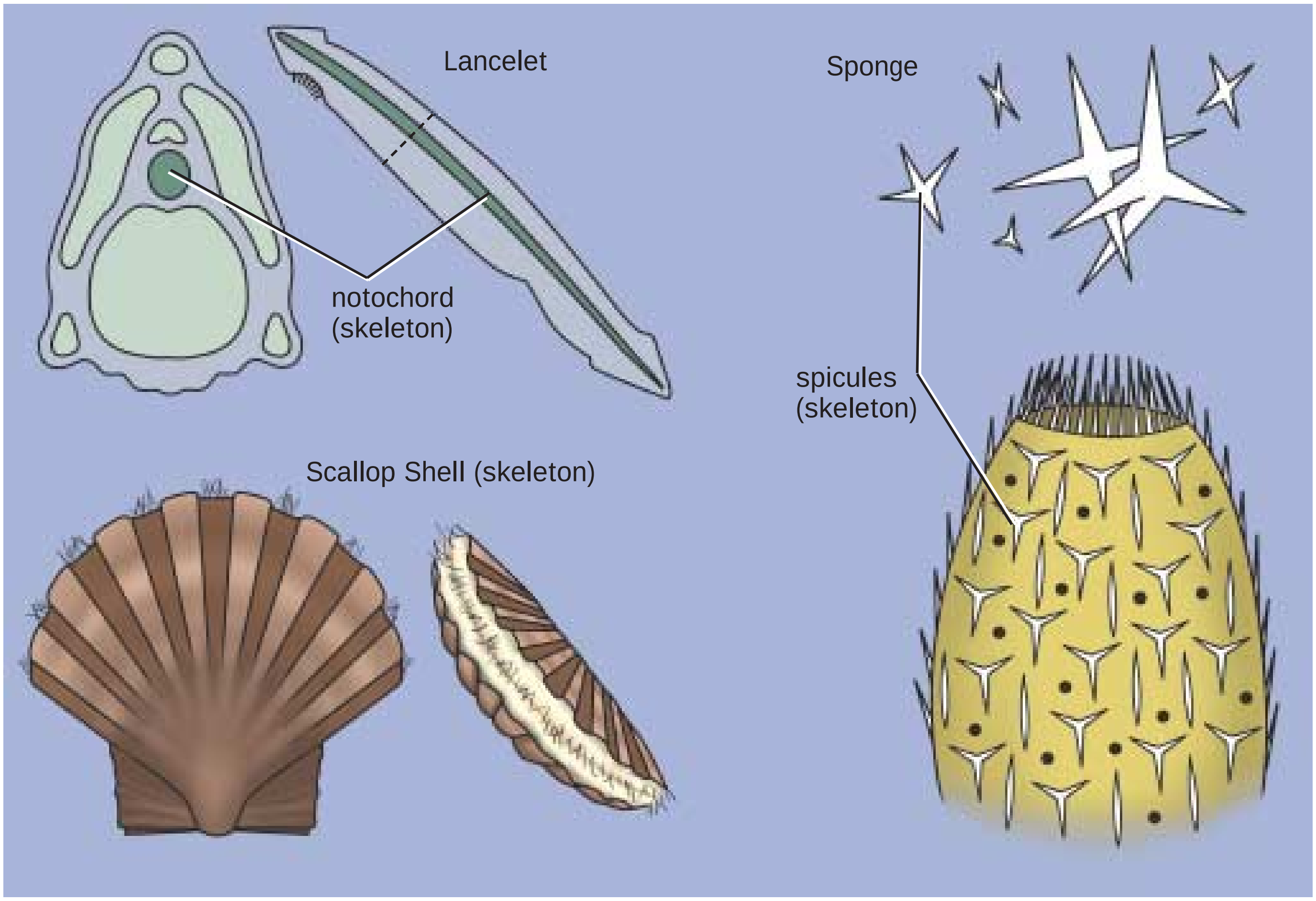
A three striped flatworm (*Pseudoceros tristriatus*) showing aposematic coloration. (Photo by ©A. Flowers & L. Newman/Photo Researchers, Inc. Reproduced by permission.)



Locomotion in different animals: A. Earthworm (a protostome); B. Leech (a protostome); C. Jellyfish; D. Nematode. (Illustration by Patricia Ferrer)

allow diffusion directly to and from the body tissues. Although lower metazoans by the definition here lack a true coelom, which can be used as a hydrostatic skeleton, such a tack is replaced either by the use of a rather solid array of muscles, or by some other type of body cavity, such as the so-called pseudocoelom. It should be stressed that this "lower" terminology is a remnant of certain types of eighteenth century views of the world that are in many ways entirely inappropriate to the modern evolutionary ways of thinking about animals. Furthermore, modern systematic practice forbids the use of taxonomic units that are defined by exclusion—lower metazoans defined by being everything except the higher metazoans, which are usually taken as deuterostomes, arthropods, mollusks, and perhaps annelids, together with their close allies. Nevertheless, the central issue of the relationship of overall form to evolution remains unsolved, and, indeed, has been in hot contention since the last years of the twentieth century.

The debate has become sharp because of the introduction of entirely new sources of data that have bearing on the problem, i.e., evidence from molecules. Analysis of the nucleic acids allows a view of animal evolution that is completely, or largely, independent from that provided by classical morphological studies, and the results have sometimes been surprising. The sponges, with their relatively poorly organized morphology, remain basal within the tree, followed by the cnidarians (jellyfish, corals, and allies) and the ctenophores (the comb jellies), although the exact relationships between these three is contentious. All other animals fall into the Bilateria, but the relationships within this group remain highly debated. On a strictly "progressionist" view, the most basal bilaterians would be the flatworms, followed by animals that possess a body cavity that is not fully bounded by mesodermally derived epithelium (i.e., the coelom), followed by the coelomates themselves. However, this view, prevalent among scientists in Great Britain and the United States until a few years ago, was always rejected by many zoologists in Ger-



Different types of skeletons. (Illustration by Kristen Workman)

many and elsewhere. In their view, the basal metazoans already possessed a coelom and segments, and the bilaterians that lack these features have therefore lost them secondarily. Therefore, there are at least two radically differing views of what a "lower metazoan" is, at least as applied to the bilaterians: one, a relatively simple organism with no through-gut, blood vascular system, or coelom, and another with all of these features present.

The advent of molecular systematics has had a dramatic effect on the view of animal relationships, especially within the Bilateria. Two important features stand out. First, the group of lower metazoans referred to collectively as pseudocoelomates, possessing a body cavity that does not fall under the definition of the coelom, is seen to be a highly heteregeneous group. The most surprising aspect of their reassignment has been the proposal that some of them, notably the nematodes and priapulids, are close relatives to the arthropods (forming the Ecdysozoa), displacing the annelids that are traditionally placed in this position. Secondly, at least some of the flatworms have been largely displaced from the base of the tree to form a group loosely related to the annelids and mollusks in a remnant of one of the old branches of the bilaterians, the protostomes. Both these developments lend support to the idea that the ancestral bilaterians were rather complex. Nevertheless, at least some of the flatworms, the acoels, have now been reinstated at the base of the tree. Are their simple features primitive for all of the bilaterians, or have they simply lost their

Sea squirts in the South Pacific. (Photo by ©Nancy Sefton/Photo Researchers, Inc. Reproduced by permission.)

A northern sea star (*Asterias vulgaris*) feeding on sea urchin. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

complex features, as have the other flatworms by implication of their higher position? One further line of evidence has come from the shared developmental mechanisms between the bilaterians. Genes that control the layout of the complex morphology, including segments, eyes, and the development of the heart, are all highly conserved between the "higher" metazoans such as the arthropods and chordates. The implication is that these genes are present in the lower bilaterians (and indeed, this has been shown in some cases), and that they may originally have functioned as they do today—implying the very deep origin of the structures these genes now regulate. Such conclusions are controversial, and have by no means been accepted by all, especially morphologists.

Summary

The lower metazoans comprise animals that are thought to lie relatively close to the evolutionary root of animals as a whole. While they all have their own specializations, it is possible, and to be hoped for, that they retain some features that were characteristic of the very earliest stages of metazoan and bilaterian evolution. Although it is widely accepted that the sponges are basal within the animals, broadly followed by the ctenophores and cnidarians, the relationships of the bilaterians remain highly controversial. Molecular systematics places the bilaterians into three groups: the Deuterostomia (including, among others, echinoderms and chordates); the Ecdysozoa (principally arthropods and nematodes), and the Trochozoa (annelids, mollusks, most flatworms, and several other small groups, including the brachiopods). At least one group of the flatworms may still be basal within the bilaterians, but the implications this position may have for the evolution of the lower metazoans are presently unclear. The fundamental questions about bilaterian evolution, including the origin of the coelom and segmentation, remain unanswered, and, indeed, as vigorously contested as ever.

Resources

Books

Nielson, C. *Animal Evolution: Interrelationships of the Living Phyla.* Oxford: Oxford University Press, 2001.

Periodicals

Budd, G. E., and S. Jensen. "A Critical Reappraisal of the Fossil Record of the Bilaterian Phyla." *Biological Reviews* 75 (2000): 253–295.

Graham Budd, PhD

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Evolution and systematics

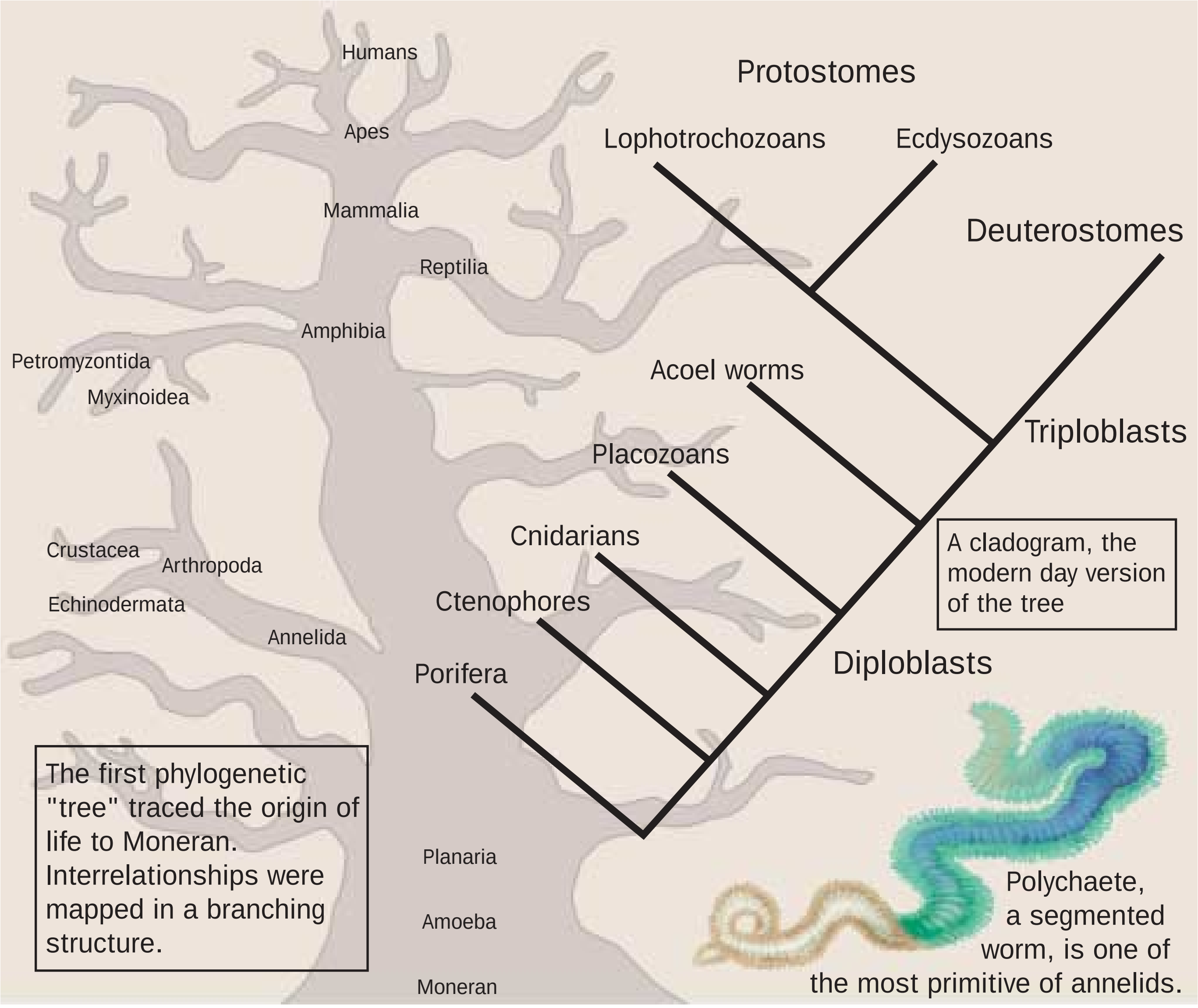
Origin of lower Metazoa

The lower Metazoa comprises a diverse assemblage of animal phyla traditionally considered primitive by most biologists in the nineteenth and twentieth centuries. Despite claims about their primitive appearance (e.g., simple anatomy, small size), the lower Metazoa collectively displays some of the greatest morphological and developmental diversity within the Animalia. There is also mounting evidence to suggest that the primitiveness of many lower metazoans is a secondary phenomenon, i.e., the lack of complexity is interpreted as a loss of derived features of more complex ancestors. Moreover, many animals once thought to have simple anatomy are now regarded as morphologically complex by way of advanced techniques to explore their organ systems (electron microscopy, immunofluorescence, and molecular probes). Still, debate exists over the evolutionary relationships of many of the lower Metazoa, and a proper examination of metazoan origins is necessary to discern the basis of these arguments.

The evolutionary origin of the Metazoa has long been a source of major controversy, and several theories have been proposed to explain the phylogenetic jump from unicellular organism to multicellular animal. Ernst Haeckel (1874) was the first biologist to speculate that animals share a common ancestry with unicellular protists, and his subsequent theories on metazoan origins revolve around the perceived similarities between unicellular protists and the process of animal embryology. In Haeckel's 1866 penultimate work, in which he formulated his fundamental biogenetic law, he posits that embryonic development (ontogeny) recapitulates evolution (phylogeny), or rather, that the development of individuals (from zygote to larva) is a stepwise progression through adult ancestral forms. While the idea of recapitulation (one-to-one correspondence between ontogeny and phylogeny) has in the ensuing period been rejected, developmental characters still play an important role in reconstructing metazoan evolution. Two of Haeckel's theories on the origin of the Metazoa have relied almost exclusively on developmental characters and the biogenetic law: the cellularization theory and the colonial theory.

In Haeckel's cellularization theory, a ciliate-like ancestor became multicellular through a process of cellularization, i.e., cytokinesis that results in the synchronous formation of many cells. This organism, variously regarded as planula larva-like (phylum Cnidaria) or even an acoel flatworm (Platyhelminthes, Acoela), served as a model of the metazoan ancestor and was subsequently championed in numerous theories on metazoan evolution (e.g., planula or planuloid-acoeloid theory of von Graff in the 1880s and Hyman in the 1950s; the syncytial or ciliate-acoel theory of Hadzi in 1953 and Steinböck in 1963). The implications of these theories are threefold: first, the cnidarian planula larva or adult acoel flatworm represents the most primitive metazoan; second, that acoel flatworms are the link between Cnidaria and the rest of the animal kingdom (Bilateria); and third, that the acoelomate body organization is primitive within the Bilateria. Recent findings using ultrastructural and molecular sequence data have essentially disproved these theories.

Haeckel's second theory, and one that has received more widespread acceptance, is the colonial theory (1874), which states that the most primitive metazoans were derived from a colonial amoeba-like organism (synamoebium) that later became ciliated, similar in appearance to modern-day *Volvox* (phylum Chlorophyta). While protists such as *Volvox* are colonial flagellates, and not amoeba-like (phylum Rhizopoda) or ciliated (phylum Ciliophora), they nonetheless have a characteristic hollow, spherical appearance analogous to the blastula stage of metazoan embryos. Haeckel coined this metazoan precursor a "blastaea." Following his biogenetic law, Haeckel suggested the blastaea evolved into a "gastraea," a two-layered sac with two germ layers, corresponding to the gastrula stage of animal embryogeny. This theory is important for two reasons: first, it introduced comparative embryology into phylogenetic discussions that would later have prominence in the creation of Protostomia and Deuterostomia; and second, it presupposed the ancestral metazoan to have had primary radial symmetry, as is the case for some primitive metazoans (e.g., Cnidaria). Adding further support to this theory was the discovery of choanoflagellates (phylum Choanoflagellata), a group of protists that possesses a collar complex (a forwardly directed flagellum surrounded by an inverted cone-shaped collar of 30–40 retractile microvilli). The collar complex is interpreted as a synapomorphy uniting Choanoflagellata and Metazoa (=Animalia) because a homologous structure is present in basal metazoans (e.g., the choanocyte layer of sponges). In 1880, the British protozo-


Humans
Apes
Mammalia
Reptilia
Amphibia
Petromyzontida
Myxinoidea
Crustacea
Arthropoda
Echinodermata
Annelida
Planaria
Amoeba
Moneran
The first phylogenetic "tree" traced the origin of life to Moneran. Interrelationships were mapped in a branching structure.
Protostomes
Lophotrochozoans
Ecdysozoans
Deuterostomes
Acoel worms
Triploblasts
Placozoans
Cnidarians
Ctenophores
Porifera
Diploblasts
A cladogram, the modern day version of the tree
Polychaete, a segmented worm, is one of the most primitive of annelids.

Phylogeny of lower metazoans, lesser deuterostomes, and protostomes. (Illustration by Christina St. Clair)

ologist Saville-Kent went so far as to consider the sponges (phylum Porifera) as colonial protists derived directly from choanoflagellates. The existence of colonial choanoflagellates such as *Proterospongia* (Greek: *protero* = earlier or former) has added fuel to this theory, and since this time, it has remained conventional wisdom that Choanoflagellata is the most likely sister-group of Metazoa.

The early radiation of the Metazoa still remains a major puzzle in animal evolution. The earliest known metazoan fossils were once thought to extend only as far back as the Cambrian Period, 540 million years ago (mya). The Cambrian marks a time when most of the major animal phyla first appear in the fossil record. The period of time over which much of this diversification appeared, approximately 30 million years, is relatively rapid compared to the known age of metazoan life (low estimate: 600 million years based on paleontology; high estimate: 1,100 based on molecular clock). Consequently, it is often referred to as the Cambrian explosion. However, intriguing evidence suggests that there was a cryptic Precambrian metazoan history. Some of the most recent finds (Xiao et al., 1998) include the smallest known fossils, in the form of embryos and early larval stages, dating back to the Neoproterozoic (570 mya). These fossils clearly indicate the existence of a fauna prior to the Cambrian explosion, and perhaps allude to the presence of small, planktonic or interstitial organisms that did not readily fossilize. While molecular and fossil evidence verifies Precambrian existence, most of the larger animal phyla clearly diversified during the Cambrian. Some of the earliest molecular studies (Field et al., 1988; Christen et al., 1991) also provided evidence to suggest that the Metazoa was diphyletic, and that two subkingdoms, Radiata and Bilateria, arose independently from flagellated protozoa in the Precambrian. Both terms allude to the ani-

Artist's rendition of Precambrian life forms based on fossils from the Ediacara Hills of South Australia. Prominent in the diorama are jellyfish (*Ediacaria flindersi*), *Mawsonites spriggi*, *Kimberella quadrata*, sea pens (*Charniodiscus arboreus*), pink paddles (*Charniodiscus oppositus*), flat worms (*Dickensonia costata*), and algae. (Photo by ©Chase Studios, Inc/Photo Researchers, Inc. Reproduced by permission.)

mals' primary axis of symmetry, and though the terms remain active in the literature, there is conclusive evidence to support monophyly of the Metazoa; synapomorphies include multicellularity, cell junctions, collagen, gametic meiosis with haploid egg and sperm, sperm with acrosome, and fundamentally radial cleavage. These ground-pattern characteristics are still found in basal and derived metazoans, despite up to one billion years of animal evolution. As of recent times, most phyla are considered monophyletic, i.e., a clade consisting of an ancestral species and all its descendants and all sharing a characteristic combination of specific anatomical features (Nielsen, 2003).

Systematics of lower Metazoa

Molecular, morphological, and paleontological evidence suggests the most primitive phyla are found within two paraphyletic groups, Parazoa and Radiata. The Parazoa includes two phyla, Porifera and Placozoa, which display the most primitive grade of organization and are at the base of the evolutionary tree. The Radiata contains the radiate phyla, Cnidaria and Ctenophora, the first true metazoans prior to the evolution of the bilateral body plan in the Precambrian. Some enigmatic groups with questionable affinities to either Radiata or Bilateria include the Monoblastozoa, Orthonectida, and Rhombozoa, often included under the name Mesozoa. The largest assemblage of animals is found within the Bilateria, a monophylum consisting of two large clades, Protostomia and Deuterostomia. Branching order within these clades is unresolved, though molecular evidence indicates the Protostomia may be subdivided into Ecdysozoa (molting animals) and Lophotrochozoa (ciliated animals). Lophotrochozoa contains several phyla, including the Lophophorata, a superphylum of Brachiopoda, Ectoprocta and Phoronida, still considered by many authors to be deuterostomes. Additionally, subordinate clades within the Protostomia define certain groups of lower Metazoa. These groups go by a variety of names, including Aschelminthes, Nemathelminthes, Gnathifera, Cycloneuralia, Introverta, and Cephalorhyncha. Nemathelminthes and Aschelminthes are older terms proposed in 1859 and 1910, respectively, to consume a variety of acoelomate and pesudocoelomate taxa; neither group is considered monophyletic.

The monophylum Gnathifera was erected in 1995 to include three phyla, Gnathostomulida, Rotifera, and Acanthocephala. The Micrognathozoa, discovered in 2002, is now included in this clade, and some biologists also place the Chaetognatha within Gnathifera. Cycloneuralia includes six acoelomate and pseudocoelomate taxa: Gastrotricha, Nematoda, Nematomorpha, Kinorhyncha, Loricifera, and Priapulida. The Introverta makes up a subset of Cycloneuralia, and Cephalorhyncha is yet a smaller subset of Introverta. Phyla of uncertain taxonomic affinity include the Entoprocta and

Cycliophora. Some biologists consider entoprocts closely related to ectoprocts or a sister taxon of Cycliophora. Within Deuterostomia, subordinate clades include Lophophorata (also considered protostomes), Neorenalia, and Cyrotreta. The animal, *Xenoturbella bocki*, is perhaps the most enigmatic bilaterian to date, being variously regarded as a species of protobranch bivalve (Mollusca), member of the Acoela (Platyhelminthes), relative of acorn worms (Enteropneusta) and Holothuroidea (Echinodermata), or as the most basal bilaterian; *Xenoturbella's* affinities remain undetermined.

The Parazoa (Greek: *para* = beside, *zoa* = animals, Metazoa) includes animals with the most primitive grade of organization: they lack definable nervous systems, true tissues, or organ systems, and epithelia do not rest on a basement membrane. Sponges (phylum Porifera) are the most basal parazoans. According to some researchers, sponges are little more than colonial choanoflagellates, but arguments can be made to classify sponges as more advanced than colonial, heterotrophic eurkaryotes such as *Proterospongia*. Sponges contain many more specialized cell types (including sex cells similar to other metazoans), have at least a rudimentary ability to form tissue-like epithelia via septate junctions (between choanocytes), and undergo an embryonic process of tissue formation (though probably not homologous to gastrulation of eumetazoa). The Porifera is a well-defined monophylum characterized by two synapomorphies, cellular totipotency and acquiferous systems of choanocyte chambers. Nearly all sponges are benthic, sessile suspension-feeders with the exception of *Asbestopluma*, a carnivorous demosponge. More than 5,000 living species of sponge are known globally, and many more fossil species exist, some dating as far back as 600 mya. Four sponge-like fossil groups are well known to have produced massive reef-like structures back in the early Paleozoic (550–480 mya): archaeocyathans, stromatoporids, sphinctozoans, and chaetetids.

Unlike Porifera, the phylum Placozoa has no known fossil record. Discovered in 1883, *Trichoplax adhaerens*, the only known member of Placozoa, is best characterized as a minute (0.07–0.11 in [2–3 mm]), flattened bag of epithelial cells with dorso-ventral polarity and no anterior-posterior polarity or symmetry. The outer epithelium is composed of monociliate cells (one cilium per cell) interconnected with belt desmosomes and perhaps septate junctions. The narrow space between epithelial layers is filled with a gel-like mesenchyme. Asexual and sexual reproduction is known, but details of sexual reproduction are incomplete. The existence of striated ciliary rootlets in the monociliate cells suggests an evolutionary link to eumetazoans, and the lack of autapomorphies defining the placozoan body plan suggests a placozoan-like ancestor may have given rise to the Eumetazoa.

Eumetazoa (Greek: *eu* = good) refers to the remaining animal groups, approximately 30 phyla. Eumetazoans share several synapomorphies, including a synaptic nervous system, gap junctions between cells, a basal lamina, striated myofibrils, organized gonads, definable germ layers (ectoderm, endoderm), and body symmetry. The Cnidaria is the most basal eumetazoan phylum and contains approximately 10,000 extant species and several thousand fossil species. The fossil record extends back to the Precambrian (540 mya), though many fossils, especially those of Ediacara and Burgess Shale, have questionable affinities to the Cnidaria. The phylum is defined by at least three synapomorphies: cnidae (nematocysts), planula larva, and coelenteron with mouth surrounded by tentacles. Other synapomorphies might characterize the group, depending on one's view of the interrelationships. The phylum is traditionally divided into four classes: Hydrozoa, Scyphozoa, Cubozoa, and Anthozoa. Body morphology is highly variable within the classes but is generally a variation on one or two basic body plans: polyp and medusa. Polyps are generally sessile, benthic forms with a ring of tentacles around the mouth, although some polyps have become colonial and taken up a pelagic existence (e.g., *Velella velella*). The medusa, or jellyfish, is often a flattened disc-shaped animal that lives in the water column, though some species have adopted a polypoid form and become benthic (*Haliclystus*). The polyp may be a sexual form that produces gametes (e.g., Anthozoa) or an asexual form that produces medusae (e.g., Cubozoa, Schyphozoa, Hydrozoa). Only polyps within Anthozoa form large reefs in mostly tropical seas. Interrelationships within the phylum are contentious.

Two prominent theories on the origin of Cnidaria have become established: the medusa theory and the polyp theory. The medusa theory postulates that the cnidarian ancestor was a planula-like animal that first gave rise to the medusoid form, subsequently followed by evolution of the polyp stage. Such a scenario places the trachyline hydrozoans as basal cnidarians, and therefore the medusoid body form would be a synapomorphy of the phylum. The polyp theory states that the polypoid form is ancestral, and therefore the Anthozoa is the most basal group within the phylum. In this scenario, Anthozoa is a paraphyletic taxon and the medusoid form is a synapomorphy of more derived clades within the Cnidaria. These theories have played important roles in the understanding of metazoan evolution, particularly regarding the origin of flatworms, the origin of the coelom, and the origin of mesodermal muscles (Rieger, 1986).

The triploblasts, or Triploblastica (Greek: *triplo* = three, *blast* = bud), refer to phyla that possess three embryonic germ layers (ectoderm, mesoderm, endoderm) formed during gastrulation, though mesoderm is probably not homologous between protostomes and deuterostomes. Prior to 1985, the phylum Ctenophora was generally considered a diploblastic phylum because true mesoderm (entomesoderm) was not found; however, subsequent studies have revealed the presence of mesoderm during embryogeny. Ctenophora is considered the most primitive of the triploblastic phyla because it is hypothesized to have originated prior to the evolution of the bilateral body plan. Ctenophora is a small phylum of approximately 80 gelatinous animals known as comb jellies and sea gooseberries. Their paleontological history extends back to the Cambrian. The phylum is well defined by the presence of adhesive colloblasts, eight rows of ciliary plates, a unique apical sense organ, and a cydippid larval stage. Interrelationships among the seven inclusive orders are not well resolved, and there is disagreement around which form of ctenophore is most primitive, the tentaculate or atentactulate form. The ctenophore body plan has played a historical role in various theories on metazoan evolution (e.g., ctenophore-polyclad theory, ctenophore-trochophore theory).

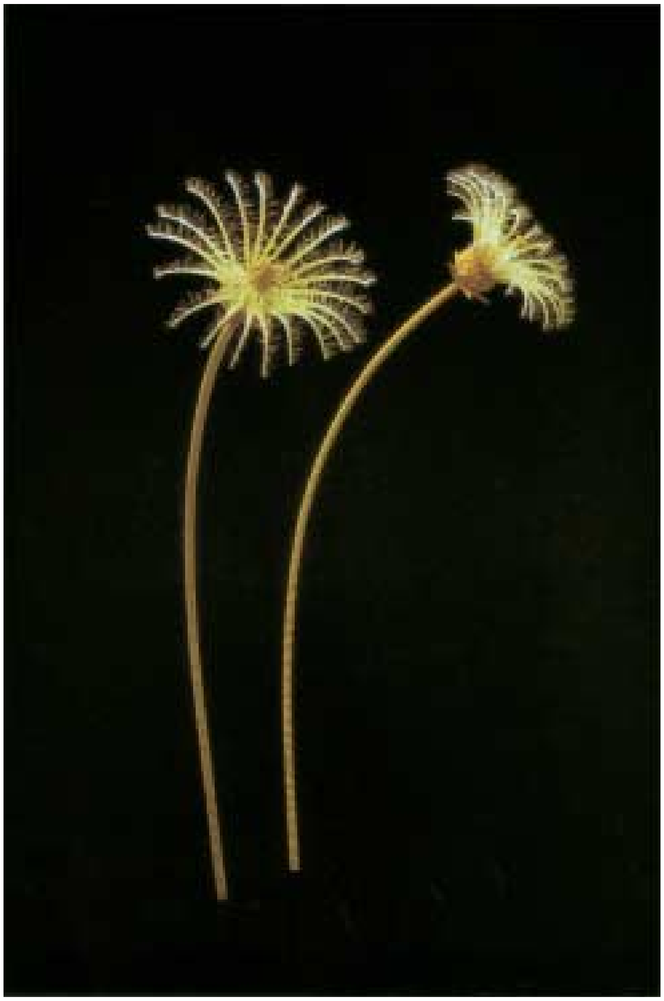
The Bilateria (Greek: *bi* = two, *latus* = side) is a well-defined monophylum characterized by a bilaterally symmetric body plan, a pronounced antero-posterior axis, and cephalization (brain). The phylum Platyhelminthes has figured prominently in nearly all discussions of the origin and relationships of the Bilateria. Originally classified within the taxon Vermes by Linnaeus in his 1735 book, *Systema Naturae*, the Platyhelminthes has since had a contentious history. In 1851 Vogt was first to isolate the phylum (with the nemerteans) into a single taxon called Platyelmia, later changed to Platyelminthes (now Platyhelminthes) by Gregenbaur in 1859. Platyhelminthes was subsequently erected to phylum-level status containing four classes: Turbellaria, Nemertea, Trematoda, and Cestoda. Minot (1876) later dropped Nemertea from this taxon. As of recent times, the Platyhelminthes contains close to 20,000 species of free-living and parasitic flatworms, with very little fossil record. The phylum is divided into three monophyletic clades: Acoelomorpha, Catenulida, and Rhabditophora. The terms Acoelomorpha and Rhabditophora are recent systematic additions to the platyhelminth literature (Ehlers, 1985). Acoelomorphs include the subclades (orders) Acoela and Nemertodermatida, and Rhabditophora includes all remaining groups (free living and parasitic), with the exception of Catenulida.

Historically, the Catenulida, both acoelomorph taxa, and all free-living groups of Rhabditophora (approximately nine orders) made up class Turbellaria; however, since recently, the Turbellaria is considered paraphyletic and there is little agreement on its precise composition because of the lack of well-defined synapomorphies. Turbellarian worms are best characterized as lower platyhelminths with a ciliated epidermis and most use cilia for locomotion. The remaining parasitic classes within the Rhabditophora are often referred to together as Neodermata (Latin: *neo* = new, *derm* = skin), in reference to their tegument. Class Trematoda historically contained all parasitic flukes (endo- and ectoparasites), but has subsequently been changed to include only the digenetic and aspidogastrean flukes. Class Monogenea contains only monogenetic flukes, and class Cestoda contains the tapeworms.

Relationships among all major clades and classes are unknown and highly speculative. Morphological and molecular data argue for a major restructuring of the Platyhelminthes, particularly in the removal of the taxon name Turbellaria, recognition of its (potentially) evolutionary independent clades, and a search for synapomorphies to unite the major taxa. Arguments based on molecular data, mostly sequence data in the form of 18S rDNA, assert a polyphyletic Platyhelminthes, with complete removal of the Acoelomorpha and its transference to a position at the base of the Bilateria. Morphologists recognize the uniqueness of the Acoelomorpha, but contend removal from the phylum is not yet warranted. They emphasize the search for shared, derived characters to unite the three main clades, and assume a cladistic stance that accentuates the similarities that unite taxa (synapomorphies), not the differences that separate them. Potential synapomorphies exist at different levels within the phylum. According to Rieger and Ladurner (2001), the mode of epidermal replacement during growth or general maintenance appears to be unique to the Platyhelminthes. New epidermal cells arise from neoblasts below the body wall, instead of from dividing epidermal cells as occurs in all other metazoans. Tyler (2001) mentions the unregionalized sac-like gut as a potential autapomorphy of the phylum, and the structure of the hermaphroditic reproductive system and presence of biflagellate spermatozoa may be synapomorphies of Acoelomorpha and Rhabditophora. Within the Rhabditophora, the exclusively parasitic classes, Trematoda, Monogenea, and Cestoda, are related by the shared presence of a syncytial tegument that arises through the developmental replacement of the larval epidermis. Relationships among the smaller clades of free-living and symbiotic "turbellarians" are still a work in progress. The phylogenetic position of the Platyhelminthes remains unknown and will likely prevail as the main topic of discussion among biologists interested in the origins and early radiation of the Metazoa. Enigmatic animals such as *Xenoturbella* and the turbellariomorph annelid, *Lobatocerebrum*, along with enteropneust models proposed by Tyler (2001), may also figure prominently in understanding platyhelminth evolution.

The phylum Nemertea is a small group of approximately 900 predatory worms occupying marine, freshwater, and terrestrial habitats. There is no reliable fossil record. Nemerteans have been known since 1758, but it was not until 1876 that they were recognized as a group distinct from the turbellarian flatworms. The monophyletic nature of Nemertea is confirmed by the presence of their unique proboscis apparatus, but other synapomorphies may exist depending on their accepted theory of origin. Two classes exist, Anopla and Enopla, based on the structure of the proboscis and the position of the proboscis pore. The Anopla is generally considered primitive to the Enopla and may be a paraphyletic taxon since the defining features are symplesiomorphies. Relationships to other metazoans are less well known. Spiral cleavage and the presence of a true coelom place the nemerteans within the Protostomia, but questions have been raised as to the homology of the nemertean coelom (rhynchocoel, bloodvessel system) with other protostomes. The traditional placement of Nemertea close to the Platyhelminthes is often favored because both groups are functionally acoelomate, though no synapomorphies are evident.

The clade Gnathifera contains four phyla defined by the ultrastructure of jaw-like elements in the mouth, though the orientation and number of elements are phylum specific. Historically, Rotifera is the best-known group of gnathiferans, containing approximately 2,000 species of exclusively microscopic, pseudocoelomate animals with a ciliated wheel-like organ on their head (Latin: *rota* = wheel, *fera* = bearer). The fossil record is sparse and only dates back to the Eocene epoch (54 mya) where animals are preserved in Dominican amber. The phylum is monophyletic and characterized by the ciliated corona, a retrocerebral organ, and unique jaw structure. Some researchers prefer to include the phylum Acanthocephala within the Rotifera based on the shared presence of an intracytoplasmic lamina and anterior flagellum on the sperm. The name Syndermata is often used to refer to both phyla together. Acanthocephala consists of approximately



Middle Silurian crinoids (*Calliocrinus cronutus*) based on fossils from the Racine Dolomite of the Chicago-Milwaukee area. Although they resemble flowers, crinoids are animals related to starfish. With a net of delicate, feathery arms splayed out in the current, crinoids were able to trap microscopic food particles. The food was transported down the arms into the mouth, centrally located on the bulb-like calyx. The long stem-like column served to lift the animal above the sea floor, exposing it to currents for feeding. (Photo by ©Chase Studios, Inc/Photo Researchers, Inc. Reproduced by permission.)

1,100 species of obligate intestinal parasites of vertebrates. Traditionally, acanthocephalans were closely aligned with turbellarians or Aschelminthes, but recent studies support the sister-group relationship of Acanthocephala and Rotifera. If considered part of Gnathifera, acanthocephalans must be considered highly derived, having lost the main gnathiferan characteristic (jaws) in their evolution towards parasitism.

Autapomorphies of Acanthocephala include a hook-bearing proboscis with unique ligament system and the absence of a gut. The phylum is traditionally divided into three classes, though relationships among the classes are poorly known. Gnathostomulids were first described in 1956 by Peter Ax as turbellarians, but later raised to phylum status in 1969. The phylum is small, containing approximately 100 species divided into two monophyletic classes and characterized by the unique jaw structure. A fossil record is lacking. Micrognathozoa is the most recent group of gnathiferans to be discovered, described by Reinhardt Kristensen and Peter Funch in 2000. The group consists of microscopic, ciliated, jawed worms found in a cold spring at Disko Island, Greenland. Only a single species has been described, *Limnognathia maerski*. The authors chose to treat Micrognathozoa as a class within the phylum Gnathifera, relegating the phyla Rotifera, Acanthocephala, and Gnathostomulida to classes within Gnathifera. Gnathostomulida is the sister group to the clade containing Micrognathozoa, Acanthocephala, and Rotifera.

Cycloneuralia is a morphologically defined clade containing Gastrotricha, Nematoda, Nematomorpha, Priapula, Kinorhyncha, and Loricifera. Molecular evidence indicates the clade is paraphyletic, but several potential synapomorphies exist: terminal mouth, radial pharynx, and tripartite peripharyngeal brain. The phylum Gastrotricha is the most primitive group of cycloneuralians, and the one often considered having the weakest affiliation with the clade. Gastrotrichs are microscopic (0.003–0.11 in [0.1–3 mm]) ciliated worms that bear cuticular adhesive organs. There is no fossil record. Synapomorphies defining the small phylum of approximately 600 species include a multilayered cuticle that covers the cilia, tube-like dual-gland adhesive organs, the unique structure of their sensory cilia, and helicoidal muscles that surround the digestive tract. The two orders within the phylum are monophyletic. Relationships of gastrotrichs to specific clades within the Protostomia are uncertain; the possession of both a cuticle and external cilia places gastrotrichs in an intermediate position between Ecdysozoa and Lophotrochozoa.

Once considered closely related to Gastrotricha, phylum Nematoda (also Nemata) is the largest phylum of cycloneuralians, containing greater than 20,000 described species. Together with its sister group Nematomorpha, these two phyla form a basal group within the Introverta, a subclade of Cycloneuralia defined by the loss of external cilia, a molted cuticle, and an introvert (an anterior part of the head than can be invaginated). The Nematoda is monophyletic and well defined by the presence of sensory organs called amphids and a unique form of excretory system (renette cells). The presence of an introvert is not often considered part of the ground pattern of the phylum (only known in *Kinonchulus*), so relationships to other Introverta are tenuous based on this character. The fossil record is sparse and dates back only to the Carboniferous Period (354–290 mya). Molecular evidence suggests the class of predominantly marine, free-living nematodes, Adenophorea, may be paraphyletic as it includes the ancestors of Secernentea, the class of terrestrial parasites. The closely related phylum, Nematomorpha, contains approximately 325 species of exclusively parasitic worms, often called horsehair worms. The phylum is defined by the presence of a unique larval stage that parasitizes arthropods, and an adult body devoid of a gut. The fossil record is sparse and extends only back to the Eocene (15–45 mya). Nematomorphs share several characteristics with nematodes that suggest a sister-group relationship: collagenous cuticle without microvilli, absence of circular muscles, and ectodermal longitudinal cords. According to some zoologists, nematomorphs may have evolved from the mermithoid nematodes that they resemble.

The Cephalorhyncha, a sub-clade of Introverta within the Cycloneuralia, contains the phyla Priapula, Kinorhyncha, and Loricifera. These phyla are united by the shared presence of chitin in their cuticles, of rings of scalids on their introverts, flosculi, and two rings of introvert retractor muscles attached through their brains. Phylum Priapula is the most primitive of the cephalorhynchs, contains fewer than 20 extant species, and has an extensive fossil record. Recent species range in size from minute to inches (millimeters to centimeters) and are exclusively benthic predators. Autapomorphies of Priapula include a large body cavity containing amoebocytes and erthryocytes, and perhaps the unique structure of their urogenital system. The fossil record for priapulans is unique within the Cycloneuralia because it extends back to the Cambrian: *Ottoia prolifica* is the most abundant fossil species and closely resembles the extant *Halicryptus spinulosus*. The two remaining phyla, Kinorhyncha and Loricifera, are closely united by the structure of their introvert, which actually protrudes out rather than evaginates out (turns inside out by eversion of an inner surface) as in priapulans. The Kinorhyncha is a small phylum of approximately 150 species, all microscopic with a body composed of 13 segments, and with an internally segmented musculature and nervous system. Despite the tough cuticle, no fossilized kinorhynchs have been found. Reinhardt Kristensen, the co-discoverer of Micrognathozoa and Cycliophora, first described Loriciferans in 1983. The Loricifera is a small phylum of 100 species characterized by scalids (spines) with intrinsic muscles and a lifecycle with a Higgins larva. No fossils are known.

The phyla Entoprocta and Cycliophora comprise a monophylum, according to cladistic studies. Phylum Entoprocta consists of 150 extant species and few fossilized forms that extend back to the Upper Jurassic (200 mya). Species are either individual or colonies of globular polyps with ciliated tentacles on a short stalk. Entoprocts are functionally acoelomate but may have small pseudocoelic sinuses. Embryonic cleavage is clearly of the spiral pattern and results in a trochophore larva, placing entoprocts within the Protostomia. Traditionally, entoprocts were allied with ectoprocts in the phylum Bryozoa, but a lack of synapomorphies led to their eventual separation in 1921. Danish biologist Claus Nielsen (2001) still supports a close relationship between the taxa and suggests several possible synapomorphies: myoepithelial cells in the apical organ, similar metamorphosis, and the ultrastructure of larval eyes. Cladistic studies have pointed out a potential relationship to Cycliophora, a recently discovered phylum of symbiotic micrometazoans that live on the mouthparts of lobsters (Funch and Kristensen, 1995). The phylum is characterized by a highly complicated lifecycle involving asexual female stages, sexual female stages, sexual dwarf males, and a variety of larval forms (pandora larvae, chordoid larvae). The chordoid larva is thought to be homologous with the typical protostome trochophore larva, and may have developed neotenically from entoprocts, according to some researchers. A single synapomorphy unites the two phyla: mushroom-shaped extensions from the basal lamina into the epidermis.

The Deuterostomia is a morphologically well-defined group with a long fossil history. Traditionally, the Deuterostomia is characterized by embryological criteria such as radial cleavage (a symplesiomorphy), blastopore becomes the anus, enterocoelous archenteric mesoderm, and a tripartite coelom. The deuterostome clade generally includes the Chaetognatha, Lophophorata (Brachiopoda, Ectoprocta, Phoronida), Hemichordata (Enteropneusta, Pterobranchia), Echinodermata, and Chordata. Several phyla, namely Chaetognatha and the lophophorate groups, share characteristics with both protostomes and deuterostomes, and their phylogenetic affinities are muddled. The advent of molecular phylogenetics in the 1990s also raised several questions regarding traditional deuterostome relationships. The hemichordates, echinoderms, and chordates make up a characteristic clade of derived deuterostomes defined by at least five synapomorphies, depending on views about their evolutionary origins: glomerular complex, epithelia that binds iodine and secretes iodothyrosine, separate gonoducts, pharyngeal gill slits, and a dorsally concentrated nervous system. The Hemichordata is a small phylum of a few hundred species, with a fossil record dating back to the Cambrian, and generally considered monophyletic by the presence of an anterior evagination of the gut called the stomochord. Brusca and Brusca (2002) consider the glomerulur complex, an excretory organ comprising a heart and blood vessel network in the prosome of the proboscis, an additional synapomorphy, but Nielsen (2001) regards it as a synapomorphy of Neorenalia (= Deuterostomia: Hemichordata + Echinodermata + Chordata). Nielsen also considers the Hemichordata to be polyphyletic with pterobranchs forming the sister group of Echinodermata. Alternatively, molecular studies suggest that enteropneusts and echinoderms are sister groups, or echinoderms are the closest sister group to the chordates.

Despite their extensive fossil record extending to the Cambrian, echinoderms and chordates have been notoriously difficult in terms of identifying a closest sister group. Echinoderms are defined primarily by the endoskeletal system of plates with a stereom structure, and external ciliary grooves for suspension feeding. Two extinct groups, the Carpoids and Helicoplacoids, are basal groups with the phylum. According to some authors, the Carpoids represent the ancestor to most fossil and modern echinoderms, but the lack of radial symmetry and evidence of a water vascular system make their presence within the phylum debatable. The Helicoplacoids, however, had triradial symmetry and water vascular systems with open ambulacral grooves, and are so considered basal echinoderms. The six remaining classes are united by the characteristic pentaradial symmetry, with mouth and anus on oral surface, and attachment to the substratum by the aboral surface.

According to the paleontologist R. P. S. Jefferies (1986), a group of extinct echinoderms called calcichordates gave rise to the chordate lineage. Jefferies claims to have identified chordate-like structures such as gill slits, a brain, notochord, and dorsal nerve cord in fossils of calcichordates. This calcichordate theory is still hotly contested, although many paleontologists have rejected the theory because they do not accept Jefferies' identification of the chordate features in these extinct echinoderms. The traditional branching of the chordate line is generally well accepted with Urochordata arising first, followed by Cephalochordata and Vertebrata. The cephalochordate-vertebrate line is hypothesized to have evolved via paedomorphosis from a urochordate-like ancestor. Some zoologists even prefer Garstang's theory (1928) that vertebrates evolved directly from a larval urochordate by paedomorphosis. However, lately, the model cephalochordate, *Branchiostoma* (Amphioxus), is considered to be the closest living relative of Vertebrata. Synapomorphies uniting Cephalochordata and Vertebrata include segmental muscles (myomeres), a ventral pulsating blood vessel (homologous with the vertebrate heart), an intestinal diverticulum (embryonic precursor of the vertebrate liver), and separate dorsal and ventral roots of the spinal cord.

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Rick Hochberg, PhD

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Reproduction, development, and life history

What is a life history?

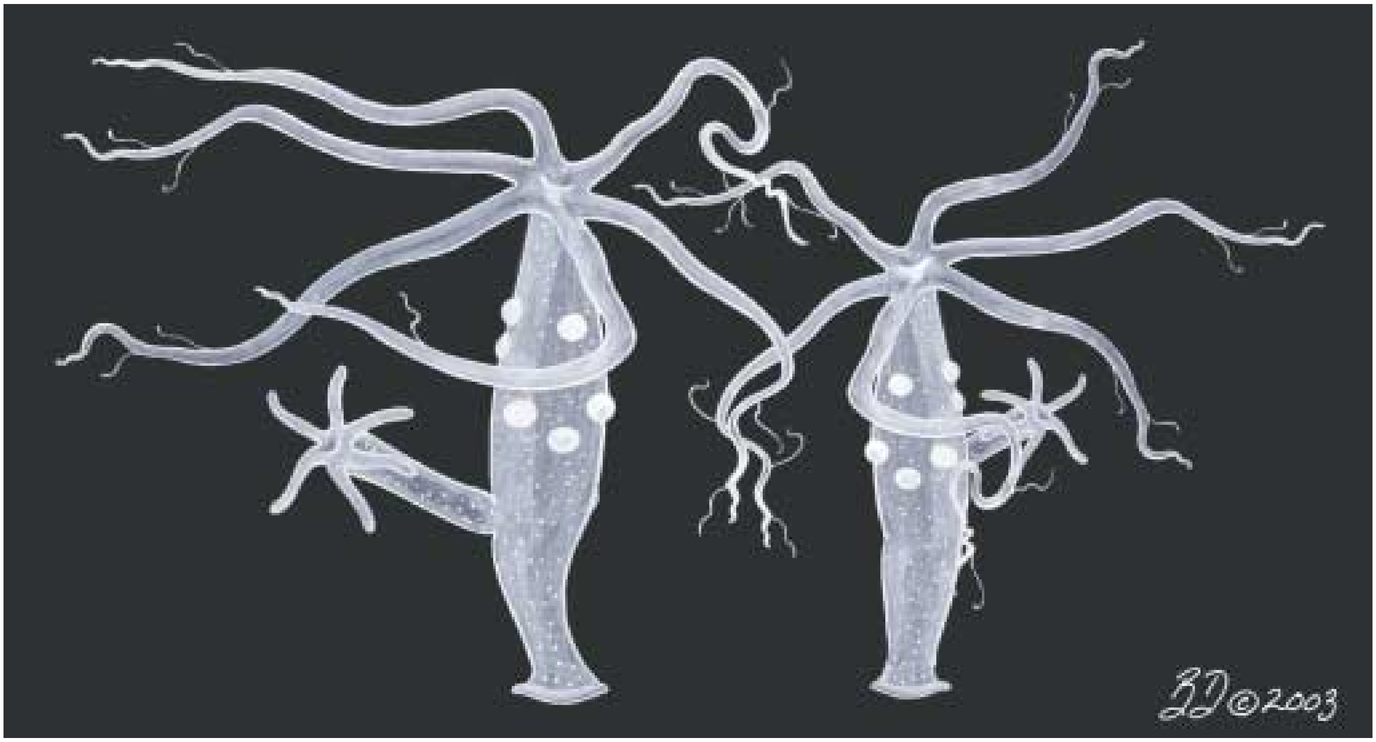
Each animal species can be viewed as a collection of individuals, all sharing a common pool of genes. The genes determine all of the animal's characteristics, and are made of the complex molecule known as DNA. The genes are exchanged among the members of the species through a variety of mechanisms, all of which are related in some way to the process of reproduction. For this reason, the ability to reproduce is often considered to be one of the most important defining characteristics of life. But reproduction, like most basic biological functions, occurs primarily at the level of a single individual that may interact with another individual to exchange genetic information through the transfer of DNA. This individual parent animal reproduces to form another new individual offspring. The offspring, however, begins its individual life as a single cell rather than as a multicellular animal like its parent. If it is to reproduce, it must usually become multicellular as well, and must ultimately mature to be anatomically similar to its parent. This entire cycle of development is generally known as the life history of an individual animal. In other words, the life history of any individual animal comprises the processes of reproduction and development; in turn, each of these processes is broken down into other more specific processes, each designed to accomplish a particular function.

Asexual reproduction

Fundamentally, reproduction is the copying of an individual animal's DNA combined with transferring the copy into a newly formed individual. In some cases, the copy of the DNA is nearly exact, and the offspring develop from a single parent. This is typically the case in what is known as asexual reproduction. In its truest form, asexual reproduction involves simple cell division, or mitosis, without any reorganization of DNA fragments during the process. Asexual reproduction also involves only one parent, and thus involves no new combinations of genes resulting from mixing complementary genes from two parents. Asexual reproduction has the advantage of allowing a very fast rate of reproduction, with a resulting rapid increase in the population of a given species. The primary disadvantage of asexual reproduction is that it does not permit much genetic variability; as a result, the population as a whole is relatively unable to adapt to diverse or changing environmental conditions.

Sexual reproduction

In most cases, the DNA copy is not exact, so that the genetic makeup of the newly formed offspring differs from that of its parent. This programmed variability is accomplished primarily by sexual reproduction. The genetic process that defines sexual reproduction occurs only during a very brief specialized phase of cell division, and only within cells belonging to the germ cell line. A germ cell is defined as a cell belonging to a cellular lineage that, at some point, will deviate from normal cell division (i.e., mitosis, which results in exact duplicate copies of DNA) to engage in meiosis. Meiosis is often known as reductional division, because it results in reducing the number of chromosomes by half in preparation for an exchange with the complementary chromosome of a mating partner that restores the full set. The most important aspect of meiosis, however, occurs long before this reduction of chromosome number, which occurs late in meiosis. Early in meiosis, gene segments are actually recombined by the exchange of DNA sequences, so that the individual chromosomes are transformed into genetically unique combinations of genes. This process is known as crossing over; it is the defining event that distinguishes sexual from asexual reproduction. In this way, germ cells become genetically unique while they are still in the parent animal, long before they become fully formed sperm or oocytes, and even longer before they fuse with gametes from another parent. At the later point of gamete fusion, the recombined genes in the chromosomes from two parents will fertilize each other to produce new chromosome combinations. Thus, the genetic recombination that takes place during meiosis, combined with the reaggregation of the chromosomes that occurs during fertilization, results in the distinctive offspring that characterize most animals. It is important, however, to recognize that sexual reproduction does not require either fertilization or two parents. If meiosis takes place, the reproduction is sexual. In some lower metazoans, a single parent animal may produce gametes by meiosis, which can then develop into fully formed offspring by various processes known collectively as sexual parthenogenesis.



Hydras reproduce by budding. (Illustration by Barbara Duperron)

Reproductive duality

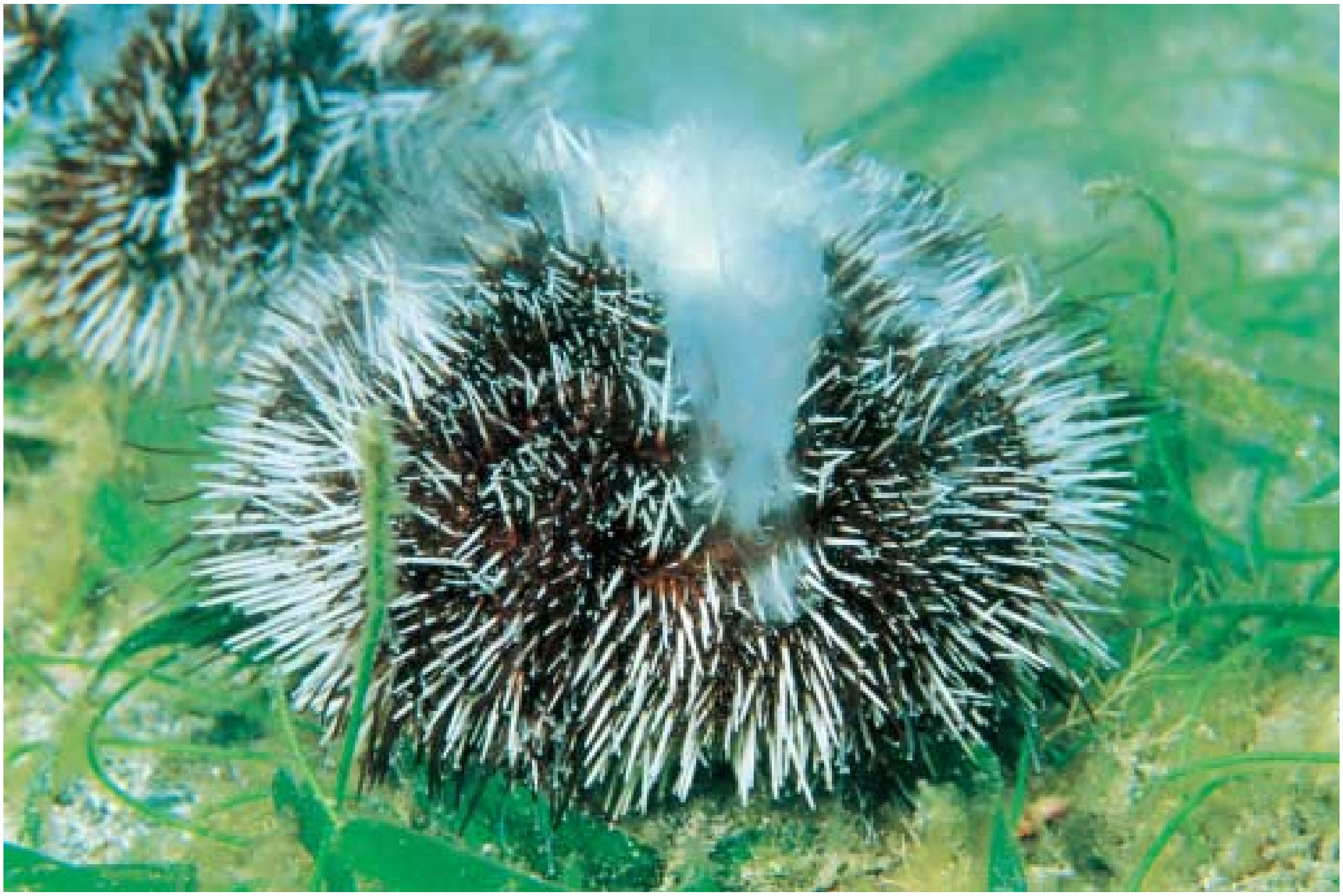
Many animals, particularly the lower metazoans, actually use both asexual and sexual reproduction at various times. This reproductive duality gives them the advantages of both modes. It is rare for both asexual and sexual reproduction to occur simultaneously, however. In many lower metazoans, the asexual and sexual processes are cyclical, occurring in different seasons. Examples include many marine sponges (phylum Porifera), in which a single individual may alternate between reproductive modes. Another example may be seen among the freshwater rotifers (phylum Rotifera), in which the two reproductive modes will be restricted to sequential generations that are otherwise anatomically similar. In other lower metazoan groups, asexual and sexual processes are segregated into two distinct stages in the life history, with radically different anatomical and behavioral traits, or even different habitats. The best examples of these stages are found among the hydroids and jellyfishes (phylum Cnidaria), and among the parasitic flatworms (phylum Platyhelminthes). Since the life history stages responsible for asexual and sexual phases are so distinctive in these groups, and occur in a regularly alternating pattern, this general reproductive strategy is often called alternation of generations.

Gametogenesis

During sexual reproduction, each parent animal must form specialized cells known as gametes, which are genetically recombined and in which the chromosome number is reduced by half from a diploid double set to a haploid single set. Both processes occur during meiosis, which is the first stage of gamete formation, or gametogenesis. In virtually all animals that reproduce sexually, the gametes occur in two morphologically distinct forms corresponding to male and female. These distinctions in form and structure are related to the specific functions of each gamete. The differences become apparent during the latter stages of spermatogenesis (for male gametes) and oogenesis (for female gametes).

After spermatogenic meiosis, the morphological transformation of the male gamete generally includes development of a small motile sperm. The sperm's function is to move toward and ultimately meet the female gamete, beginning a sequence of events that ends in the fusion of the two gametes. After the gametes fuse, the sperm's role is essentially complete except for the final genetic contribution from its half of the new offspring's genome. Thus, the primary structures developed by the sperm are concerned with movement and with engaging the female gamete and its coatings. The specific locomotory structures of sperm vary among the lower metazoans, ranging from pseudopodia (temporary extensions of cell material) resembling amoebas in the roundworms (phylum Nemata) to flagella (long whiplike projections) in most other groups.

After oogenetic meiosis, the morphological transformation of the female gamete generally includes development of a large oocyte that does not move around. The oocyte's functions are far more numerous than those of the sperm. For most lower metazoan groups, they include equal or greater participation in the process of gamete fusion. Following fusion, however, the oocyte must provide the coordination of and materials for all the early stages of embryo and larval de-



A West Indies sea egg (*Tripneustes ventricosus*) releasing sperm into water. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

velopment. To carry out these functions, the oocyte must build up large stores of energy-rich nutrients (e.g., carbohydrates in the form of glycogen, and lipid or proteinaceous yolk); phospholipid stores for membrane synthesis; extra nucleotides or redundant DNA; transcripts of RNA for protein synthesis; extra regulatory and structural proteins; and occasionally materials for eventual eggshell formation. In most cases, the oocyte must fulfill all these functions by itself. Some animals, however, use other germ cells to assist the oocyte. Perhaps the best example of this assistance is found among the parasitic flatworms (phylum Platyhelminthes). These organisms have special vitelline (resembling yolk) germ cells that never become gametes but instead supply the gametes with needed materials. The oogenic stage that is most often involved in fertilization is the oocyte; however, there are some exceptions to this generalization. The ambiguous term "egg" is often applied to oocytes and other fertilizable stages of female gametes. "Egg" may, however, also refer to fully formed embryos or juveniles within various embryonic coverings, so the word should be avoided in most instances.

Spermatogenesis and oogenesis most often occur in different individual animals known as males and females respectively. This differentiation of sexes is known as gonochorism. Alternatively, it is quite common for the same individual to produce both sperm and oocytes. This condition is known as hermaphroditism; it may involve either simultaneous or sequential production of sperm and oocytes. Oogenesis and spermatogenesis may occur in different gonads, namely ovaries and testes, or may occur in a single hermaphroditic gonad. Such lower metazoans as sponges (phylum Porifera) may lack distinct gonads, with gametes developing in normally somatic regions of the body. Whether through gonochorism or hermaphroditism, gametogenesis may occur throughout the adult life of the animal, as in parasitic flatworms (phylum Platyhelminthes). The more common pattern among the lower metazoans, however, is one of seasonal reproduction.

Gamete exchange

Gametes come together in a variety of ways among the animals in the lower metazoan groups. Sperm are generally motile and engage in oocyte-seeking behavior of some sort. The small size and short-term motility of the sperm, however, mean that their efforts are effective for only a very short time; thus sperm motility is only effective for meeting the oocyte within very small spaces. Bringing the sperm and oocyte into these small spaces depends on the behavior of the parent animal, which must engage in some form of gamete exchange.

Adult animals fall into two broad categories in relation to gamete exchange: spawners and copulators. Lower metazoans demonstrate a broad range of variations within both of these categories. The vast majority of spawners release their gametes directly into the surrounding water, an activity known as broadcast spawning. Broadcast spawning is the most common method of gamete exchange in free-living marine invertebrates, but is rare among most freshwater groups. In the very lowest phyla (e.g., Porifera, Placozoa, Cnidaria) spawning is the only method of gamete exchange. In some groups, only the males spawn while the females take up the sperm while retaining their oocytes for internal fertilization. In others, both sperm and oocytes are spawned, resulting in external fertilization. For broadcast spawning with external fertilization to be successful, the parent animal must use some strategy to increase the chances of the gametes coming together. The most common strategy involves simultaneous spawning, in which all gametes are released at the same time by all members of a population. Other strategies include producing gametes with similar densities, adhesive properties, or other features that cause them to settle out into the same general parts of the water column or substrate.

Copulation occurs in many groups, and varies considerably among the lower metazoans. In all cases, there is some mechanism for transferring sperm directly from the male to the female. This transfer may occur by direct injection or by transfer of sperm packets known as spermatophores. Most copulators have specialized genital structures for transferring the sperm. Most often these structures inject the sperm directly into the female's reproductive system, but they may also inject them through the body wall, as in the hypodermic traumatic insemination seen in some turbellarian flatworms (phylum Platyhelminthes).

In many animals, the males and females are morphologically distinct, thus exhibiting sexual dimorphism. Sexual dimorphism is, however, more common among higher animals. The males and females of many lower metazoans are sexually monomorphic, and thus are distinguishable only microscopically by the nature of their gametes. Generally speaking, most broadcast spawners are sexually monomorphic, while copulators tend to be sexually dimorphic. The dimorphism may relate only to differences in copulatory structures or genitalia, but in some cases it may relate to differences in other habits or roles of the two sexes. Marked somatic dimorphism is much more common among higher animals, but does occur in some lower metazoans; examples include the schistosomatid flukes (phylum Platyhelminthes) and certain roundworms (phylum Nemata). In both of these cases, the dimorphism reflects differences in size as well as form.

Fertilization

After the gametes come together, they must fuse with one another to form a diploid zygote, which is the genetically complete new animal in a unicellular (single-celled) form. Fertilization is not a single event; rather, it is a complex series of events in which both sperm and oocyte actively participate. It begins with simple recognition among the sperm and oocytes of a given species, and concludes with the fusion of the haploid pronucleus of the sperm and the haploid pronucleus of the oocyte. Between these two events, there is considerable variation among the lower metazoans. In some cases, the oocytes have a covering that must be penetrated by the sperm. In most cases, the sperm must initiate the actual process of fusion of the cell membranes of the two gametes; however, it is the oocyte that generally is most active in directing the fusion and actually incorporating the sperm into its cytoplasm. The actual fusion of the two cells, known as syngamy, is accomplished largely by the oocyte. After syngamy occurs, pronuclear fusion may follow rapidly or be delayed up to several days, depending on the species. At this point, the new genetically unique and genetically complete animal, in the form of a single-celled zygote, is ready to complete the development of its body.

Embryogenesis

The development of a fully functional animal body begins with the transformation of the single-celled zygote into a multicellular embryo. Part of the definition of an animal (i.e., a metazoan) is that it possesses true multicellularity, which it acquires during the process of embryogenesis. True multicellularity is defined not only as the possession of multiple cells in the body, but also a specific division of labor among those cells. In particular, the body of an animal must have somatic (body) cells separated from the reproductive (germ) cells. But, beyond that the somatic cells must be differentiated into different functional groups. During the process of embryogenesis, the new individual first develops numerous cells, then differentiates them according to space, structure, and function. Among the lower metazoans, we find a range of structural complexity, from simple double-layered groups of cells in the phylum Placozoa to complex organ systems in such phyla as the Platyhelminthes, Nemertea, and Nemata. Many other lower metazoan phyla fall at various places along this spectrum.

The first stage of embryogenesis is cleavage, which creates the simplest form of multicellularity. Cleavage is simply a series of mitotic cell divisions that take the new individual from a unicellular zygote to a multicellular mass of cells generally known as a morula. Depending on the phylum and species, this cell mass may consist of a few dozen to hundreds of cells. The actual pattern of cleavage varies in terms of the cells' spatial relationships to one another, the plane of the cell axis at which cleavage occurs, and the degree to which the cytoplasm is divided. The subject of cleavage is complex, but the type of cleavage is important in defining a group's evolutionary relationships to other groups. There is also great variation in the degree of cellular differentiation at this stage. In most lower metazoans, however, the cells do differentiate during cleavage into large macromeres and small micromeres; some groups also have intermediate-sized mesomeres. In most cases, these classes of cells are destined to become specific layers within the later embryo. In turn, each layer will give rise to certain tissues of the adult body. Prior to forming layers, most embryos go through a stage of minor reorganization known as blastulation, which provides the spatial framework in which the actual layering takes place.

The vast majority of animals develop either two or three layers of cells, known as germ layers. These germ layers develop out of the dramatic reorganization of the cells that were formed during cleavage and slightly reorganized during blastulation. The stage of radical reorganization is called gastrulation. Possession of two or fewer germ layers is found only in certain lower metazoan phyla. A very few simple phyla (e.g., the Placozoa, Monoblastozoa, Orthonectida, and Rhombozoa) do not have specific germ layers. Sponges (phylum Porifera) are often interpreted as having no germ layers, but some biologists regard them as having two. Members of the phyla Cnidaria (jellyfishes, corals, etc.) and Ctenophora posses two well-developed germ layers, and thus are described as diploblastic. All other lower metazoans, and indeed all other animal phyla, possess three well-developed germ layers, and are correspondingly described as triploblastic. The actual mechanisms of layering vary widely among different phyla; they range from the migration of cells into the interior of the cell mass to the infolding of an entire hemisphere of the spherical blastula. In all cases, however, the embryo is left with an endoderm layer on the inside and an ectoderm layer on the outside. In triploblastic phyla, a layer of mesoderm forms between the other two. The endoderm typically develops into the digestive system of the adult animal, while the ectoderm develops into the epidermis and nervous system. The mesoderm, if one is present, gives rise to such structures as excretory systems and the tissues that line body cavities. Other organ systems develop from various layers, depending on the phylum, and most often involve contributions from two germ layers working cooperatively.

At the end of gastrulation the embryo is fully formed; embryogenesis is complete. The new organism now looks a bit like an animal with a skin and a gut; all the basic layers are present, ready to differentiate further into a more definitive animal having the recognizable characteristics of its taxonomic group.

Most higher animals, above the platyhelminthes, can be divided into two groups based primarily on embryonic features. These two major branches are known as the protostomes and the deuterostomes. Protostomes undergo determinate cleavage or mosaic development, in contrast to the indeterminate cleavage or regulative development of deuterostomes. The determinate cleavage of protostomes results from a plane of cell division, usually visible after the second division, that cuts diagonally across the original zygote axis, thus compartmentalizing different regulative and nutritive chemicals in each of the resulting cells. This is referred to as spiral cleavage, since the cells dividing diagonally appear under the microscope to spiral around the original axis. In contrast, the indeterminate cleavage of deuterostomes results from a planes of cell division that cut alternatively longitudinally along the zygote axis, then transversely across the axis, thus leaving each resulting tier of cells with similar regulative and nutritive chemicals. This is referred to as radial cleavage, since the cells dividing at alternating parallel and right angles to the original axis appear under the microscope to radiate in parallel planes from that axis. The most important thing is not whether the resulting cell masses appear to spiral or to radiate, but that only the spiraling cells of the protostomes show determination of specific germ layers as early as the first cell division, and almost universally by the third. Thus, at the very earliest stages of cleavages, specific cells of protostomes have already been determined to a fate of forming a specific one of the three germ layers. During gastrulation, the embryo is left with an opening to the outside called the blastopore, which will develop into an opening into the gut in the adult animal. The precise nature of the opening is the second major feature differentiating deuterostomes from protostomes. In protostomes, the blastopore becomes the adult mouth, whereas in deuterostomes, the blastopore becomes the anus. Shortly or immediately after gastrulation is complete, higher animals form their body cavity, the coelom. By definition, the true coelom is always a body cavity within mesodermal tissue. The mechanism by which the coelom is formed is the third primary distinction between protostomes and deuterostomes. In most deuterostomes, the coelom forms by outpocketing from the original archenteron, a process known as enterocoely since the coelomic cavities are thus derived directly from embryonic enteric cavities. In protostomes, the coelom forms from a split in the previously solid mass of mesodermal cells, a process thus known as schizocoely. There are some exceptions to this rule, but it applies well to most.

Postembryonic development

Most animal embryos look rather similar to one another up through the stage of gastrulation. It is during the important stages of postembryonic development, however, that the characteristic features of specific phyla, classes, and orders finally emerge. For this reason, much of postembryonic development is said to involve morphogenesis, or the establishment of the animal's definitive body form. Along with the completion of form comes the establishment of function, so that the end result is a fully functional animal. For some species, this fully functional individual will be a juvenile, which resembles an adult in form but lacks a mature reproductive system. Development that proceeds from embryo to juvenile with no intervening stage is known as direct development. Direct development occurs in some lower metazoans, including the nematodes, gnathostomulids, rotifers, and gastrotrichs. In contrast, most lower metazoans undergo indirect development, in which a larval stage is inserted between the embryo and the juvenile or adult.

A larva is a fully functional animal, generally feeding and moving about independently. The larval form of a given species is generally as characteristic of the species as the adult, and may complete some critical parts of the life history strategy for its species. The most common task of larvae is long-distance migration in order to colonize new environments for the species. This phenomenon, known as planktonic dispersal, is especially critical in marine species whose adult forms have limited or no mobility, such as corals, sponges, ribbonworms, and polyclad flatworms. Larvae may also make use of food resources that differ from those needed by the parent, thus avoiding competition within the species. Because of the critical and distinctive attributes of larvae, their formation is frequently referred to as larvigenesis, and represents a discrete (separate) stage of postembryonic morphogenesis.

Mating flatworms (*Pseudoceros bifurcus*) with insemination marks. (Photo by ©A. Flowers & L. Newman/Photo Researchers, Inc. Reproduced by permission.)

By definition, larvae and adults are dissimilar in structure and function. For this reason, the transition from larva to adult requires radical changes in the morphological, behavioral, and physiological characteristics of the animal. This transformation between successive postembryonic forms is known as metamorphosis. As with cleavage and gastrulation, the exact mechanism of metamorphosis varies widely among different lower metazoan phyla. In all, it involves the loss of some specifically larval structures and the development of new adult structures from groups of undifferentiated cells.

Sexual maturation

After the embryo or larva is transformed into a juvenile form, all that remains for the individual is maturation of its sexual reproductive systems, accompanied or followed by meiotic maturation of the gametes to form fully functional and fertilizable sperm and oocytes. The mechanisms for maturation vary widely among animal phyla, but are especially diverse among the lower metazoans. Such phyla as placozoans and sponges have no discernible gonads; the gametes simply form out of previously undifferentiated somatic cells. In such others as the diploblastic cnidarians, the gametes develop from specialized cells within one of the germ layers, but no other gonadal tissues are present. At the other end of the scale of complexity, such animals as roundworms and flatworms develop elaborate gonads and ducts; these structures include discrete testes with sperm ducts, discrete ovaries with oviducts, and even numerous types of specialized reproductive glands. In some respects, the parasitic flatworms have the most structurally sophisticated reproductive systems in the animal kingdom, even though as a group they are considered primitive organisms.

Another variation that occurs among the lower metazoa relates to reproductive seasonality. While some groups, such as tapeworms and flukes, reproduce continually and thus retain all of their sex organs, such others as hydroids and turbellarian flatworms reproduce only temporarily, but repeatedly. These organisms often lose their reproductive organs during their nonreproductive periods and redevelop them during the next mating season.

Structural maturation of the sex organs and gametes is often accompanied by certain changes in behavior as well as the development of special structures that are not gonadal but are nonetheless related to reproduction. The most obvious behavioral changes involve mate-seeking and copulatory behaviors. Structural changes include the development of special genitalia for coupling. The latter includes the copulatory cirrus (flexible penis) of parasitic flatworms and the copulatory spicules of many roundworms. Other related behavior may include various forms of brooding or other parental care strategies. While parental care is not generally as common or as well developed among lower metazoans as in higher animals, some examples do exist. Among the lower metazoans, most of these are more structural than behavioral. Examples include the maintenance of amphiblastula larvae within specially adapted radial canals of calcareous sponges; the development of special egg-enclosure organs in several tapeworms; the retention of fully-formed juveniles within the uterus of some roundworms; and the retention of successive generations as colonies in many hydroids and other cnidarians.

Phylum summaries

Brief summaries of the primary reproductive and developmental strategies of each lower metazoan and deuterostome phyla follow. The variations are within each phylum are great, however, and the short summaries below are intended only to situate each phylum within the overall context of reproductive strategies and processes discussed earlier. Interested readers should consult the references listed for further details and analyses.

Phylum Placozoa

The limited information on *Trichoplax adhaerens*, the only known species of Placozoa, indicates that the organism has no capacity for sexual reproduction. Asexual reproduction, however, is very effective and diverse, occurring in three distinct modes. Simple fission, or division of the simple body by cell separation, is the most common mode. More rarely, two types of budding occur. In one form, hollow swarmers bud off the parent organism and may swim to remote locations to develop further. In other individuals, the attached buds may stretch and attach themselves to adjacent substrates before detaching from the parent. In both cases, cellular rearrangements similar to gastrulation occur.

Phylum Monoblastozoa

This phylum, represented only by the single genus *Salinella*, has been observed and described by only one author, and some researchers question its existence. The original description is vague, but describes asexual reproduction by a sort of transverse fission similar to that of placozoans.

Phylum Porifera

Sponges may be either gonochoristic or hermaphroditic, but most undergo some form of sexual reproduction. The exact origin of germ cells varies somewhat among species, but most sperm and oocytes develop from undifferentiated cells known as archeocytes in the central mesohyl (connective tissue) layer. In some species, sperm may develop through transformation of the flagellated collar cells that line the sponge's chambers and create the water currents responsible for the exchange of all materials within the sponge. Males are broadcast spawners, but most sponges undergo internal fertilization. Fertilization is followed by internal brooding of larvae in many sponges, including most marine calcareous sponges and the spongillid family of freshwater sponges. Whether sponges have true germ layers is often debated, since some cells can transform into any cell type even in the adult; however, cellular rearrangements comparable to gastrulation take place at the end of embryogenesis. Sponges are perhaps the most efficient phylum in the animal kingdom for asexual reproduction. They employ a number of different strategies ranging from simple fragmentation of the adult body to formation of specialized gemmules (reproductive buds), the latter being more common in the overwintering stages of freshwater species.

Phylum Cnidaria

Sexual reproduction is well developed throughout the phylum. Gonochoristic and hermaphroditic species are known to occur; however, the true jellyfishes (class Scyphozoa) and colonial hydroids (class Hydrozoa) are primarily gonochoristic. Germ cells develop in either the ectoderm or endoderm, depending on the class, but always originate from undifferentiated cells known as interstitial cells. Most species of cnidarians are broadcast spawners, but in some, such as the freshwater *Hydra*, the oocyte may be retained for internal fertilization. In most species, embryonic development leads to a planula larva that settles to the substrate for metamorphosis into the adult cnidarian. Asexual reproduction is very common and takes many different forms. Many species undergo alternation of generations, with asexually produced medusae (free-swimming jellyfish) alternating with sexually produced polyps attached to the substrate. Sexual and asexual mechanisms of reproduction may occur in either stage, however, depending on the species.

Phylum Ctenophora

Comb jellies are primarily hermaphroditic, with only a few gonochoristic species. They have simple gonads resembling those of the closely related cnidarians. Most are broadcast spawners, but some are fertilized internally and may even brood their larvae. Embryogenesis results in a cydippid larva that swims freely during its metamorphosis into an adult. Asexual reproduction is not known to occur in this phylum.

Phylum Rhombozoa

The dicyemid mesozoans are all parasites, and alternate between sexual stages in the adult host and asexual stages in the juvenile host. The sexual forms are hermaphroditic. These animals are structurally simple, barely qualifying as truly multicellular. They lack layers comparable to the germ layers of other animal phyla.

Phylum Orthonectida

Orthonectids are parasites that alternate between sexual and asexual stages within their host animal. Asexually produced plasmodia may develop into sexual forms, most of which are gonochoristic, with a few hermaphroditic species. Copulation is followed by internal fertilization, and the larva ultimately leaves the parent to seek a new host.

Phylum Platyhelminthes

The vast majority of flatworms are hermaphroditic, but some gonochoristic forms occur, including the medically important schistosome flukes. The reproductive systems of predominantly free-living turbellarians are simple and transient (temporary), whereas those of the parasitic tapeworms and flukes are complex and permanent, with many specialized organs. Copulation is the rule for reproduction in this phylum, followed by internal fertilization and either internal or external development. Fertilization generally involves incorporation of the full sperm into the oocyte. Internal development often takes place within specialized structures for maternal care of the larvae. Cleavage and embryogenesis occur in patterns unique to this phylum, especially among the tapeworms and flukes; there are many different forms of larvae and patterns of metamorphosis in this group. In addition, the tapeworms and flukes engage in regular alternation of sexual and asexual generations, perhaps producing the greatest number of progeny in the animal kingdom.

Phylum Nemertea

Nemerteans are primarily gonochoristic (except for the few freshwater and terrestrial species), with large but simple gonads. Most species are marine, and reproduce by broadcast spawning followed by external fertilization and embryonic development. They undergo spiral cleavage, and thus are generally considered to be related to the protostomes. Postembryonic development leads to formation of a pilidium larva in most nemerteans. Some species may reproduce asexually by fragmentation, but this pattern is uncommon.

Phylum Nemata (Nematoda)

Sexual reproduction is the rule among the roundworms; most species are gonochoristic with some sexual dimorphism. Some hermaphroditic species do exist. Reproductive systems are tubular; in copulation, the male introduces amoeboid sperm into the vagina of the female. The embryogenetic process begins with an unusual form of bilateral cleavage, which ends with the direct development of a juvenile form (often incorrectly called a larva) that is structurally like a miniature adult. There are five juvenile molts before the adult form is reached. Asexual reproduction is extremely rare, and only involves the mitotic division of female germ cells.

Phylum Nematomorpha

Horsehair worms are exclusively sexual and gonochoristic. The gametes develop in long strands attached to support cells.

Adult nematomorphs copulate, often in large masses; fertilization is either external or internal, depending on the species. Little is known about embryogenesis in this phylum, but it culminates in a distinctive free-swimming larva that must invade an arthropod host before it can transform itself into a juvenile. The juvenile in turn must leave the host before maturing into an adult. Asexual reproduction is unknown in this phylum.

Phylum Priapulida

Priapulids are all gonochoristic, with no known mode of asexual reproduction. Their reproductive systems are poorly described, but are similar to those of nematomorphans in being formed as strands of oocytes attached to a common stalk. Most priapulids are broadcast spawners, with external fertilization and embryogenesis. Postembryonic development involves a distinctive larva that undergoes metamorphosis to become an adult.

Phylum Acanthocephala

Thorny-headed worms are gonochoristic, with complex reproductive systems, copulation, and internal fertilization. They develop through an intricate series of stages, including an acanthor larva and a cystacanth juvenile. The various stages of development occur inside different hosts of these parasitic animals. Asexual reproduction does not occur in this phylum.

Phylum Rotifera

As a group, rotifers exhibit a variety of reproductive strategies, with the three classes distinguished by either hermaphroditic or gonochoristic sexuality. Some species, especially in freshwater habitats, alternate between generations produced by parthenogenesis, in which no fertilization occurs, and typical generations produced by copulation and fertilization. The gonads of these tiny animals consist of only a few gametes enclosed by a thin sac. Embryogenesis culminates in direct development of a juvenile that quickly matures into an adult.

Phylum Gastrotricha

Gastrotrichs are generally hermaphroditic, with sperm and oocytes generally forming within the same gonad. Adults reciprocally inseminate each other during copulation. Fertilization is internal, but embryonic development is external. Postembryonic development is direct, and there is no known example of asexual reproduction in this phylum.

Phylum Loricifera

The loriciferans are exclusively sexual and gonochoristic in their reproduction. Little is known about their embryonic development, but it ends with the formation of a distinctive Higgins larva, or perhaps juvenile, that is similar to the adult.

Phylum Kinorhyncha

All known kinorhynchs are sexual and gonochoristic. Copulation, fertilization, and embryonic development are poorly known. Postembryonic development appears to be direct.

Phylum Gnathostomulida

Gnathostomulids are primarily hermaphroditic, and none are known to reproduce asexually. Simple reproductive systems, copulation, and internal fertilization characterize this group. The spiral cleavage is similar to that of protostome animals, and development progresses directly into a juvenile and then an adult form.

Phylum Chaetognatha

Adult arrow worms are hermaphroditic, with well-developed male and female gonads in separate body cavities. Fertilization is internal, but development of the embryos is external, though some species brood their young. Cleavage is radial, and the coeloblastula undergoes gastrulation similar to that of echinoderms and other deuterostomes. Asexual reproduction is not known to occur.

Phylum Hemichordata

Acorn worms are gonochoristic, and gametes are spawned into the open seawater. Fertilization and embryonic development, beginning with radial cleavage, occur in the plankton, and are similar to the patterns of echinoderms. Embryos develop directly or through a distinctive tornaria larva. Some species may reproduce asexually by fragmentation.

Phylum Echinodermata

Starfishes, sea urchins, sea lillies, and their relatives are extremely diverse, and exhibit a variety of reproductive and development modes. In all, however, typical deuterostome development is the rule, beginning with radial cleavage. Larval forms are varied, and tend toward different forms in different classes. Both sexual and asexual reproduction occur within the phylum, but broadcast spawning and planktonic development are the most common patterns.

Phylum Chordata

The invertebrate chordates, including tunicates, lancelets, and their relatives, generally reproduce by spawning and development planktonically in the seawater. Sexual and asexual reproduction may occur in the urochordates, but cephalochordates only undergo sexual processes. Cleavage is generally radial, but may be more mosaic than that of other deuterostomes.

Phylum Entoprocta

Various entoprocts may be either gonochoristic or hermaphroditic, depending on the species. A few may reproduce asexually by budding. Males generally spawn into open water, but the sperm are usually taken up by females for internal fertilization. Cleavage is spiral, possibly indicating some relationship to protostomes.

Phylum Ectoprocta (Bryozoa)

Most bryozoans are hermaphroditic. As colonial animals, all reproduce by asexual means as well. Males spawn sperm, which females take up for internal fertilization. Cleavage is radial, and most species have planktonic larvae.

Phylum Brachiopoda

Lampshells are primarily gonochoristic. Fertilization is variable, but cleavage is always radial. Depending on the class, they may undergo planktonic development through a larva, or may develop directly. Asexual reproduction has not been described for the group.

Phylum Phoronida

The vast majority of phoronids are hermaphroditic, with female and male gonads functioning simultaneously. Fertilization is usually internal. Cleavage is radial, followed by planktonic development in most species, generally through a distinctive actinotroch larva. Asexual reproduction by budding or fission occurs in a few species.

Phylum Cycliophora

Cycliophorans alternate between sexual and asexual stages. They are gonochoristic, and the male attaches to the female for insemination followed by internal fertilization and development. The modified trochophore larva is somewhat similar to that of some protostome groups.

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Ecology

Introduction

The ecology of invertebrates consists of all the external factors acting upon that organism. These factors may be either physical or biological. The physical or abiotic environment consists of the nonliving aspects of an organism's surroundings, including temperature; salinity; pH (a measurement of acidity or alkalinity); exposure to sunlight; ocean currents; wave action; and the type and size of sediment particles. The biotic environment consists of living organisms and the ways in which they interact with one another.

Invertebrate species have colonized all types of aquatic habitats. For example, sponges of the class Calcarea are restricted to firm substrates. They are also restricted by physical factors that affect their skeletons, limiting their habitats to shallow zones. Hexactinellida sponges colonize soft surfaces; they prefer to live in deep water. Demosponges can live on such different substrates as rock, unstable shell, sand, and mud; in some cases they burrow into calcareous material. They are found in a variety of underwater habitats ranging from upper intertidal to hadal depths (below 20,000 ft or 6,100 m). The ecological dominance of the Demospongiae reflects their diversity in form, structure, reproductive capabilities and physiological adaptation. Cnidarians and ctenophores are mostly marine; however, a few groups have successfully made their way into freshwater habitats.

Most lower metazoans are either sessile polyps, which means that they are attached at the base to the surface that they live on, or planktonic carnivores. Some, however, employ suspension feeding and many species harbor symbiotic intracellular algae that supply them with energy. Hydroids, scyphozoans, and anthozoans live in seas around the globe, from polar to tropical oceans. Most lower metazoans, however, live in coastal waters.

Physical factors

Light

Sunlight has an important role in both terrestrial and marine environments, powering the process of photosynthesis that provides energy either directly or indirectly to nearly all forms of life on earth. The diel, or 24-hour cyclical migrations of epipelagic species, are at least in part active responses to changing light levels. Epipelagic refers to the upper levels of the ocean that are penetrated by enough sunlight for photosynthesis to occur. *Aurelia aurita* approaches the surface during the day, at both midday and midnight, or only at night, and becomes scattered throughout the water column at night or during the sunlit days. Diel migrations probably do not occur in the bathypelagic zone (about 3,280–6,562 ft or 1–2 km); migration in the mesopelagic zone (about 656–3,280 ft or 200–1,000 m) depends on the levels of available light in that zone. Sunlight is necessary for vision as well as photosynthesis. Many animals rely on their vision to capture prey, avoid predation, and communicate with one another.

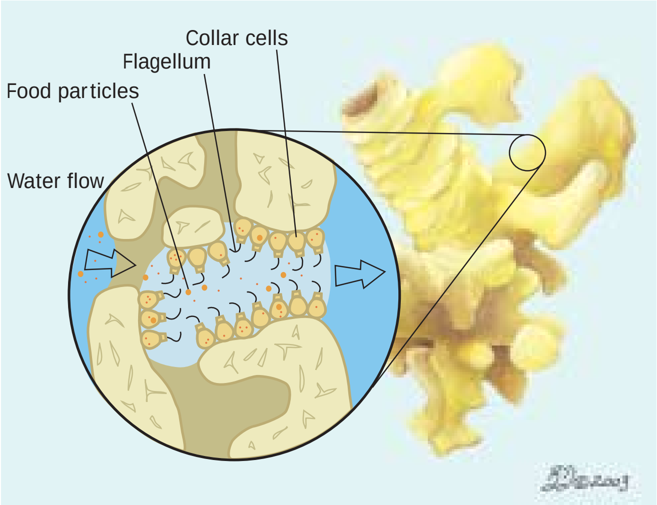
Bioluminescence is a type of visible light produced by marine animals such as scyphozoans, hydrozoans, ctenophores, squids, thaliaceans, and fishes. It may be used for counterillumination or as ventral camouflage. Another possibility is that bioluminescence is a useful defense mechanism against potential predators.

Turbidity

Turbidity refers to the cloudiness of sea water caused by the suspension of sediment particles and organic matter. High concentrations of suspended particles in the water over offshore coral reefs are considered a stress factor for coral colonies because they reduce the amount of light for photosynthesis and smother coral tissues. Nevertheless, many reefs with large growths of coral are found in relatively turbid waters, such as the fringe reefs around the inshore continental islands in the Great Barrier Reef lagoon. This finding suggests that turbid water is not necessarily harmful to coral. Fine, suspended particles provide a large surface area for colonization by microorganisms that produce organic nutrients. By limiting light penetration, turbid water also limits the distribution of both benthic algae and phytoplankton, which are at the base of the web.

Temperature

All lower metazoans are ectothermic (sometimes referred to as "cold-blooded"), which means that they retain the same temperture as their surroundings. Because of this restraint; invertebrate physiology has evolved to operate in a specific temperature range for each species. Most organisms can tolerate only a narrow range of temperatures; changes above or below this critical range disrupt their metabolism, resulting in a lowered rate of reproduction, injury, or even death. Since temperatures change less rapidly in the open sea than in shallow waters, species in shallow waters can tolerate a wider range of temperature than deep water species. Temperature often influences the distribution, reproduction, and morphology (form and structure) of these organisms. Colonies of *Obelia geniculata* and *Silicularia bilabiata* living in cold water develop long, branching hydrocauli (stalks), whereas colonies of these species living in warm waters have short stems with few branches. Gametogenesis in the hydrozoan *Sertularella miuresis* begins when the temperature reaches 50°F (10°C) and stops when it reaches 64°F (18°C). *Coryne tubulosa* reproduces asexually at around 57°F (14°C), but produces medusae when the temperature falls to 35°F (2°C). The acclimation temperature of *Chrysaora quinquecirrha* polyps is about 51°F (10.50°C), but the upper lethal temperature dose, defined as the temperature at which 50% of the test animals die (LD-50), is 95°F (35°C).



A sponge feeding. (Illustration by Barbara Duperron)

Salinity

Salinity, or the level of salt content in seawater, can affect invertebrates. Species that have evolved to live in freshwater can rarely live in salt water, and few marine species can tolerate low salinities or freshwater. This becomes quite apparent when one studies species richness (number of species) as one moves down a river into an estuary. Species richness (number of species) is relatively high in freshwater, then decreases considerably as salinity increases to about 5ppt, where most freshwater species cannot exist. Species richness then increases with salinity as more low-salinity-tolerant species are encountered. Species richness is at its greatest at the mouth of the estuary, where fully marine species occur with estuarine species.

Salinity can effect the morphology of organisms. For example, the shape, number, and size of tentacles of *Cordylophora caspia* polyps is affected by salinity. The scyphozoan medusae of *Rhopiena esculenta* can survive at levels of salt concentration as low as 8 parts per thousand (ppt), the scyphistomae to 10 ppt and the planulae to 12 ppt. The estromatolites of *Phylloriza peronlesueri*, however, form in hypersaline (very salty) waters. A rise in the salt content of the Baltic Sea allowed *A. aurita* and *C. capillata* to expand into northern waters, and allowed *Rhizostoma pulmo* and *A. aurita* to move from the Azov Sea into the Black Sea. The hydroid *Laomedea flexuosa* increases its production of gonozooids when the seawater concentration is around 30–40 ppt; at higher concentrations, however, the colonies begin to degenerate. The cephalochordate *Branchiostoma nigeriense* becomes opaque above salinities of 13 ppt.

Ocean currents and turbulence

Moving water is essential to lower metazoans because it supplies food and dissolved gases; prevents the accumulation of sediment; and disperses waste products, medusae, and larvae. *Aglaophenia picardi* resorbs the tissues of its hydrocauli into the hydrorhiza when the surrounding water is relatively stagnant, but regenerates them when the water begins to move more rapidly. The speed and direction of current flow affect the form and size of some lower metazoans. The size of hydroids is usually inversely related to the speed of water movement; large specimens are found in calm water and smaller specimens in rougher water. *Aglaophenia pluma* develops unbranched hydrocauli about 0.6 in (1.5 cm) tall in shallow, turbulent water, but produces branched hydrocauli as high as 19.6 in (50 cm) in deeper water with bidirectional currents. Planar (flat) forms such as *A. pluma*, *Plumularia setacea*, and *Eudendrium rameum* are most abundant where the current tends to flow in one direction, while radial or arborescent (treelike) forms such as *Lytocarpia myriophyllum*, *Nemertesia antenna*, and *E. racemosum* flourish in bi- or multidirectional currents. The distribution of species that inhabit coral reefs and display highly specific patterns of tolerance is greatly affected by water movement. Morphological differences in hydroids and anthozoans are also regarded as indicators of distinct patterns in water movement.

Water depth

The majority of organisms are not able to survive in great depths (below 3,281 ft or 1,000 m). In general, the number of invertebrates is highest in shallow water communities and decreases as water depth increases. However, species diversity may be quite high at great depths on the abyssal plain where the environment has been extremely stable for millennia. Though diversity can be high, biomass may be low in these deep benthic habitats, because the lack of light prevents any primary production. Therefore, these habitats are usually limited by food and depend on organic input from sunlit seas above.

The lack of mixing and primary production result in oxygen-minimum layers in the ocean, and many species are either adapted to lower oxygen concentrations or avoid these areas. The scyphozoans *Periphylla periphylla* and *Nausithoe rubra* show high levels of the anaerobic enzyme lactate dehydrogenase, probably as an adaptation to moving at depths between 1,312 and 4,921 ft (400–1,500 m), which has minimal levels of oxygen.

Aerial view of the reef complex of Heron and Wistari Reefs at low tide, showing an extensive reef system with a deep channel and coral cay, southern Great Barrier Reef, Australia. (Photo by A. Flowers & L. Newman. Reproduced by permission.)

Environmental contaminants

Pollution may result from contamination by sewage, hydrocarbons, polyvinyl biphenals (i.e., PCBs), pesticides (e.g., DDT), and heavy metals such as cadmium, copper, lead, mercury, and zinc. Experiments have revealed that exposure to pollutants can lead to sublethal effects in hydroids, including changes in the curvature or branching of the hydrorhiza; loss of hydranths; stimulation of gonozooid production; or changes in the rate of growth. Low concentrations of metal ions such as copper and mercury may inhibit growth regulation in hydroids while increasing the growth rate in *Laomedea flexuosa* and *Clavopsella michaeli*. In Elefsis Bay, a polluted area of Greece, populations of *Aurelia aurita* have multiplied to rates of more than 1,500 medusae per 10 m^3. Certain species of *Rhizostoma* have survived in parts of Madras Harbor that have been polluted by diesel oil; however, the presence of crude petroleum in the waters of Alaska has caused a reduction or cessation in the strobilation in the polyps of *A. aurita*, and the production of ephyra and polyps with both morphological and behavioral abnormalities. *Pelagia noctiluca*, a scyphozoan from the Mediterranean Sea, acquires high concentrations of cadmium, lead, mercury and zinc. Individuals of the species *Chrysaora quinquecirrha* have been found to have highly concentrated levels of the herbicide pendimethalin in their tentacles; they show no change in behavior at concentrations of the pesticide that are lethal to fishes such as perch. The dumping of raw sewage in may tropical areas of the world destroys coral reefs by increasing turbidity that prevents light penetration, increasing sediment loads that smother corals, and increasing nutrient loads that encourage algae growth that can out-compete corals.

Species interactions

Competition occurs when organisms require the same limited resources, such as food, living space, or mates; or when two groups of organisms try to occupy an ecological niche in the same location at the same time. Competition may either be interspecific (between different species) or intraspecific (within the same species). Hydroids, which have a stoloniferous growth pattern, demonstrate two different growth strategies. The first, a guerrilla strategy, is characterized by extensive hydrorhizal growth with little branching and sparsely spaced hydrocauli or polyps; this pattern is exhibited by *L. flexuosa*. Guerilla behavior is an opportunist-style strategy for reducing interspecific competition for space and the possibility of overgrowth by other organisms. The second strategy, phalanx; results in highly branched hydrorhizae with dense hydranths carried on large hydrocauli. The phalanx strategy is exemplified by *Podocoryne carnea* and *Hydractinia* *echinata*, which grow on the shells of hermit crabs. Intraspecific variation in the allocation of resources that lead to hydrorhizal growth can be observed in the colonies of *H. echinata*. This species usually shows either little outward hydrorhizal growth combined with a high rate of reproduction, or extensive hydrorhizal growth combined with a lower rate of reproduction and correspondingly greater competitive ability. Contact with another colony leads the hydrorhiza to produce an abnormally large number of stolons (shoots or runners) armed with nematocysts, which sting and kill the tissue of other hydroids. Guerrilla growth strategies have adaptive value in situations where there is relatively little space available, as on shells occupied by other hydroids, while the phalanx strategy is more advantageous for expanding the colony to shells that are inhabited by hydroids.

Competition for space is of prime importance in the coral reef ecosystem. Most of the aggressive species are small and have slow growth rates, while the less aggressive coral species have faster growth rates and are able to outpace their competitors through rapid growth. The ability to maintain either rapid growth or aggressively dominative practices, but never both, explains why no single species of coral is able to dominate a coral reef. One possible outcome of competition is the extinction of the less successful competitor.

A niche can be subdivided into two or more small niches with minimal overlap, allowing competing organisms to share a resource. Examples of resource partitioning may be found on coral reefs. Small ecological niches can be occupied by similar species if the anatomy, feeding behavior, and territory of each species are only slightly different from those of another. The hydrozoans *Hydractinia* (retained gonophores), *Stylactis* (medusoids), and *Podocoryne* (medusae) have similar morphologies but different reproductive strategies, which allows them to occupy similar niches on the shells of hermit crabs. The competitive ability of colonies may also depend on their size. *Podocoryne carnea* hydroids show a greater selective advantage in aggressiveness in relation to *H. echinata* in interspecific competition. In instances of intraspecific competition among different colonies of *P. carnea*, however, the colony most likely to lose out is the one with the slowest rate of growth.

Feeding mechanisms and behavior

Suspension feeding

Lower metazoans demonstrate a remarkable variety of feeding mechanisms. Most sponges are suspension feeders that subsist on such fine particles as bacterioplankton and dissolved organic matter. Sponges acquire food and oxygen from water that flows through them; this flow is actively generated by sponges beating their flagella (microscopic whiplike structures). This process also acts as a means of waste removal for sponges. The movement of water through sponges is aided by ambient currents passing over raised excurrent (providing outward passage) openings, which creates an area of low pressure above these openings. Sponges are also capable of regulating the amount of flow through their bodies by narrowing or partly closing off various openings. The volume of water passing through a sponge can be enormous—as much as 20,000 times its volume over a 24-hour period.

Sponges are size-selective particle feeders. Their aquiferous systems create a series of “sieves” of varying mesh size. The largest diameter of incurrent openings is usually around 0.002 in (50 μm), which keeps larger particles from entering the aquiferous system. A few species have larger incurrent pores, reaching diameters of 0.006–0.0069 in (150–175 μm). Some sponges trap roughly 90% of all bacteria in the water they filter. Other sponges also take significant amounts of dissolved organic matter into their aquiferous systems. In some demosponges, 80% of the organic matter that is filtered through their aquiferous system is too small to be seen by light microscopy. The other 20% is composed primarily of bacteria and dinoflagellates. Other sponges harbor symbionts such as green algae, dinoflagellates (zooxanthellae), or cyanobacteria, which also provide them with nutrients.

Predation

Many invertebrates are predators that feed on protozoans, other invertebrates, and fishes. The discovery of several Mediterranean species of sponges that capture and digest entire animals came as a surprise to marine biologists. These species of the family Cladorhizidae have no choanocytes or aquiferous systems, but anatomic and biological analysis revealed the presence of spiky filaments with raised hook-shaped spicules. These carnivorous sponges capture and hold small crustaceans with their spicules, which act like Velcro® tape when they come in contact with the crustaceans’ exoskeletons. Once captive, the crustaceans cannot free themselves. They struggle for several hours, which indicates that the spicules do not produce any paralyzing or toxic secretions. Cells then migrate around the helpless prey, and digestion takes place outside the cell walls.

Most cnidarians are carnivorous, using cnidocytes on their tentacles to capture prey. Polyps, the sessile stage of cnidarians, are generally believed to be passive predators, feeding on animals that blunder into their tentacles. Some cnidarian medusae possess sensory structures resembling primitive eyes; they are active predators. Many corals and anemones feed by suspending thin strands or sheets of mucus over the surface of their colony. The sticky mucus collects fine particles of nourishment from the water; cilia present on the organisms drive the food-laden mucus into the mouths of coral or anemones. Many species have developed complementary adaptations such as ectodermal ciliary currents on their tentacles, oral discs or columns, or the ability to position themselves strategically within the water’s flow pattern.

In sea anemones, the presence of nearby food evokes behavior that has two phases: a prefeeding, and a feeding response that leads to the ingestion of prey. The prefeeding response consists of the expansion of the oral disc, the movement of its tentacles, and both the extension and swaying of the column. This prefeeding behavior increases the chances of catching nearby food. The feeding response, which takes place after the prey has made contact with the anemone’s tentacles or oral disc, includes the discharge of nematocysts and ingesting movements. Sea anemones are able to detect prey from the prey’s emission of small dissolved molecules of

Flatworms (class Turbellaria) feed on smaller animals such as this water louse, or on dead animals. They help to keep the ecosystem in balance. (Photo by Animals Animals ©G. I. Bernard, OSF. Reproduced by permission.)

amino acids, tripeptides, and vitamins. The cnidae, which ensure the capture of the prey, are spirocysts and nematocysts. The numerous spirocysts on the tentacles of sea anemones appear to have an adhesive function. The contact of solid food with the tentacles leads to a massive discharge of spirocysts, which hold the prey while the nematocysts inject their toxin. Ingestion is directed by the chemical and mechanical stimuli produced by the immobilized prey. After ingestion, the prey is enclosed by filaments whose cnidoglandular tracts contain nematocysts but no spirocysts. The penetrating filaments of these nematocysts inject more toxin. The prey is then subject to the action of secretory cells that ensure its extracellular digestion.

The prey of sedentary cnidarians is composed of small motile animals such as zooplanktonic larvae, isopods, amphipods, and polychaetes. Sea anemones found closer to shore may complete their diet with larger sessile prey dislodged by wave action or foraging predators. The size of the prey is generally small considering the diameter of the sea anemone, and many species may be considered microphagous. Of the nine common species of Caribbean reef sea anemones, seven are planktivores. *Condylactis gigantea* and *Stoichactis helianthus*, which eat macroscopic prey such as gastropods and echinoids, probably depend on heavy wave action in the reef to supply them with prey.

Comb jellies are entirely predatory in their habitats. The long tentacles of ctenophores have muscular cores with an epidermal cover that contains colloblasts, or adhesive cells. The tentacles trail passively through the water or are twirled about by various circular movements of the body. Upon contact with the prey, the colloblasts burst and discharge a strong sticky material. In ctenophores, which bear very short tentacles (orders Lobata and Cestida), small zooplankton are trapped in mucus on the body surface and then carried to the mouth by ciliary currents (along ciliated auricular grooves in ctenophore lobates and ciliated oral grooves in cestids). Under conditions of starvation in an aquarium, lobate adults often swim vertically through the water only to descend with their lobes extended; in this position the width of the lobes may be as much as 116% of the animal's length. The lobe width decreases to about 79% of the body length after food is placed in the aquarium and the animal begins to feed. Once the digestive tract is full, these adults still continue to feed by entangling their prey in mucus, which produces a bolus or clump near the mouth. Quite frequently they will either spit out this ball of food or completely empty their digestive tract and continue to feed. This behavior pattern can continue for several hours until the concentration of food is reduced to the point at which all the prey that have been captured can be ingested.

Most pelagic ctenophores and cnidarians feed primarily on copepods. There are a few intriguing examples of pelagic cnidarians that feed exclusively on one type of prey. The siphonophore *Hippopodius hippopus* feeds only on ostracods; the hydromedusae *Bougainvillia principis* feeds mainly on barnacle nauplii; and *Proboscidactyla flavicirrata* eats only veligers (mollusk larvae). Some cnidarians and ctenophores feed specifically on gelatinous prey or fishes. Ctenophores of the genus *Beroe* offer well-known examples of selective feeding on gelatinous prey: *B. cucumis* feeds exclusively on the ctenophore *Bolinopsis vitrea*, and *B. gracilis* feeds only on *Pleurobrachia pileus*. When beroids prey on animals larger than themselves, they appear to attach themselves to the prey and suck its tissues into their mouths. Beroids lack tentacles; however, they do possess some 3,000 macrocilia that are hexagonally arranged and form a ciliary band around the inside of the mouth that beats inward, and forcing tissue from the prey into the beroid's pharynx. Gelatinous species that include high proportions of soft-bodied prey in their diets often eat fish eggs and larvae when they are available.

The diets of gelatinous predators generally show some selectivity, and are dependent on factors including the prey's size; the width and spacing of the predator's tentacles; the predator's swimming behavior and speed; water flow; and the prey's ability to escape. In general, species that catch large prey have few and widely spaced tentacles, while those that feed on small prey have numerous closely spaced tentacles. Most gelatinous predators move while feeding, which allows them to make use of water currents that will bring prey toward their tentacles. Cnidarians that are ambush predators are able to catch large, fast-moving prey; cruising predators prefer small, slow-moving prey. For example, siphonophores, which are ambush predators, tend to select large and relatively swift prey, while *Aurelia aurita*, which is a cruising predator, selects slow-moving organisms. Swimming offers the advantage of allowing predators to scan larger volumes of water; however, it also has the disadvantage of alerting the prey to the predator's presence. Some predators deal with this disadvantage by remaining stationary while they are "fishing."

Swimming is not the only way for prey to escape. Bivalve veligers will close themselves off when they are disturbed by the medusae of *Chrysaora quinquecirrha*; 99% of captured veligers are ingested alive.

Ecological significance of predation

The feeding rate of predators can be expressed in terms of clearance rate (volume of water × predator −1 × time −1), or in terms of numbers or biomass of prey captured (predator −1 × time −1) and are often combined with estimates of predator and prey densities in order to estimate the effects of predation on prey populations. One characteristic of gelatinous predators is that clearance rates tend to be constant even at extremely high prey densities. In species with few tentacles (e.g., *Pleurobrachia* spp.), however, ingestion is limited by prey handling. Saturation feeding at typical prey densities rarely occurs in situ. Gelatinous predators feeding on small prey seldom fill themselves at natural prey densities. They may not reduce populations, but they do keep them in check. Predators that consume ichthyoplankton often appear in areas of intense spawning activity and are major causes of fish egg and larva mortality. In some areas large schyphomedusae consume high numbers of commercially important fish larvae, and they also compete with fishes for food. Swarms of jellyfish may be so dense that they clog and damage fishing nets. Many hydromedusae species, including *Porpita* spp., *Velella* spp., and *Physalia* spp., also occur in huge concentrations, particularly in tropical seas.

Some species have such a significant ecological effect that they are considered "keystone species." If these species disappear or appear in an environment, the entire habitat can shift dramatically. For example, active predation by sea stars can significantly affect prey populations. The crown-of-thorns sea stars (*Acanthaster* spp.) feed on coral polyps in tropical reef habitats worldwide. Occasionally, population explosions of *A. planci* occur that can have devastating effects on coral reefs. Thousands of square miles (kilometers) of bare coral skeletons can result. Species composition and diversity of other inhabitants are affected secondarily as algae and other organisms colonize the reef. Organisms that depend on live coral for survival either leave the area or die.

Aggressive and defensive behavior

Gastropods, pycnogonids, sea stars, sea urchins, fishes, and sea turtles are predators that feed on invertebrates. Moreover, jellyfishes and comb jellies can be predators of other cnidarians and ctenophores. Sea turtles, especially *Dermochelys coriacea*, feed on scyphomedusae such as *A. aurita*. In addition, birds may add scyphozoans to their diets. Some benthic animals like the nudibranchs may feed on the scyphistomae of *Cyanea capillata* and *A. aurita*. A single nudibranch can consume as many as 200 polyps per day; however, not all nudibranchs are able to eat scyphozoans. As in the pelagic environment, scyphozoans in their benthic stages may eat one another; for example, the scyphistomae of *A. aurita* eat the planulae larvae of *C. capillata* as well as the larvae of their own species. In addition to natural predation, scyphozoans may be affected by fisheries.

In general, these species defend themselves against predators by the production of physical structures or the emission of various chemicals. Sponges are the most diverse source of marine natural products; some of these compounds offer potential pharmacological benefits. Compounds isolated from sponges vary widely in structural complexity; they include sterols, terpenoids, amino acid derivatives, saponins, and macrolides. The toxins produced by temperate and tropical sponges have been shown to deter predation by fishes, asteroids, and gastropods. The organic component of sponges consists primarily of NaOH-soluble and insoluble protein, NaOH being the chemical formula for sodium hydroxide, or lye. About 56% of Antarctic sponges are toxic. *Leucetta leptorhapsis* and *Mycale acerata* are highly toxic; however, the asteroid *Perknaster fucus antarcticus* is a specialist and is able to feed on *M. acerata* without succumbing to its toxins. This finding suggests that some asteroids have evolved physiological mechanisms that neutralize or sequester (compartmentalize) sponge toxins. In many cases these secondary metabolites are not necessarily toxic, but may make the sponge distasteful to predators and may be more effective in deterring predation. These compounds not only help the sponges avoid predators, but also prevent infection by microorganisms. In addition, they allow the sponges to compete for space with other sessile invertebrates such as ectoprocts, ascidians, corals and even other sponges. Clinoid sponges are among the most common and destructive endolithic (living embedded in rock surfaces) borers on coral reefs worldwide. *Cliona*, *Anthosigmella*, and *Spheciospongia* of the order Hadromerida; and *Siphonodictyon*, of the order Haplosclerida are siliceous sponges known to bore into hard substrates. Such sponges are able to excavate galleries in calcareous material by removing small fragments of the mineral by specialized archaeocyte cells. The cells secrete chemicals that dissolve the calcareous substrate. When infested corals are split open, clinoid sponges appear as brown, yellow, or orange patches lining the corroded interiors of the coral skeleton.

The sponge *Cinachyra antarctica* has distinctively long spicule tufts that emerge from the spiral conules on their surface. This species, found throughout Antarctica at depths of 59–2,496 ft (18–761 m), uses its spicules to protect itself from predators. When spicules are removed, *C. antarctica* is made vulnerable to predators.

Defensive and feeding activities are closely associated in most cnidarians; the tentacles of most anemones and jellyfishes serve both purposes. In some cases, however, both functions are performed by separate structures. Sea anemones and corals have developed several specialize structures used to defend against territorial invasion. Three of these structures, namely acrorhagi (special fighting tentacles), catch tentacles, and sweeper tentacles, are modified feeding tentacles. The mesentenic filament is another modified defensive structure. The acrorhagi are located at the margin of the anemone's body column. When these anemones make physical contact with one another, usually with their tentacles, the acrorhagi expand and apply themselves on the target organism. The ectodermal tissue of the acrorhagus lifts away from its underlying mesenclyme (cellular jellylike material) while the acrorhagus discharges its nematocysts, and the ectoderm then clings to the target organism. This process is called peeling. As a result of continued discharges from the nematocysts, the victim's tissue beneath the acrorhagial peel becomes necrotic and dies. Catch tentacles (in sea anemones) and sweeper tentacles (in scleractinian corals) develop from feeding tentacles that undergo a morphological change when the organism comes into contact with appropriate other species. In response to weeks of contact, the feeding tentacles alter their form, structure, and complement of cnidae. Catch and sweeper tentacles do not adhere to potential food objects; when they are touched by prey, they actually retract. Sweeper tentacles emerge at night; as their name implies, they flail about or undulate. They can reach 5–10 times the length of feeding tentacles. The coral *Montastrea cavernosa* is a mildly aggressive coral, capable of destroying the tissue of a variety of subordinate coral species with its mesenterial filaments. But its own mesenterial filaments can be destroyed by *M. annularis* when both are placed together. These species have sweeper tentacles, which are multipurpose structures with the capacity to regulate the distance between colonies, thus functioning as organs of competition.

Although the ability of hydroids to resist predation is often attributed to their nematocysts and associated toxins, the chemical compounds make them much less attractive to a potential hydroid predator. Some species of hydroids secrete chemicals that deter feeding by the pinfish *Lagodon rhomboides*. After having been treated with potassium chloride, which forces them to discharge their nematocysts, both *Halocordyle disticha* and *Tubularia crocea* become palatable; this suggests that these species rely on nematocysts to defend themselves against predators. However, species such as *Corydendrium parasiticum*, *Eudendrium carneum*, *Hydractinia symbiologicarpus*, and *Tridentata marginata*, remain unpalatable after their nematocysts have been discharged.

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Symbiosis

Introduction

Symbiosis is an association between two or more different species of organisms. The association may be permanent, the organisms never being separated, or it may be long lasting. Life is complex and often involves a delicate balancing act between hosts and symbionts, in associations that range from parasitism to mutualism. In the long history of life on Earth, symbionts have evolved many protective strategies in their attempts to overcome a host's defenses, including molecular camouflage, deception, mimicry, and subversion. By studying symbiosis one gains a wider evolutionary perspective on the extent and nature of biological interactions between species.

Symbiosis and modern biology

The recognition of symbiotic relationships has had a revolutionary impact on modern biological thought. The idea that mitochondria and chloroplasts are transformed by symbiotic bacteria provides a common thread to the biological world and raises hope of finding other symbiotic wonders among life's diversity. Plants and animals have acquired new metabolic capabilities through symbioses with bacteria and fungi. Mammalian herbivores and termites digest cellulose with the help of microbial symbionts. The luminescent bacteria contained in the specialized light organs of some fishes and squids produce marine bioluminescence. Diverse animal life around deep-sea vents is based on symbiosis with bacteria that oxidize hydrogen sulfide and chemosynthetically fix carbon dioxide into carbohydrates. Associations between fungi and algae have resulted in unique morphological structures called lichens. Early land plants formed associations with mycorrhizal fungi, which greatly facilitated their phosphorous uptake and thus played a significant role in the plants' ability to colonize terrestrial habitats. Evolutionary changes in organisms and their gene pools are not restricted to nuclear events and sexual mechanisms. Horizontal gene transfer between species has been documented in all forms of life. Bacterial cells possess plasmids and viruses that transfer new genetic properties from one cell to another. Many virulence factors in pathogenic bacteria are expressed through plasmid-borne genes. Similarly, bacteria become resistant to antibiotics when they incorporate plasmids with genes for antibiotic resistance. Horizontal gene transfer has been suggested in the evolution of flowers, fruits, and storage structures from gall-forming insects and viruses. The role of viruses as genetic engineers is gaining importance in evolutionary biology. The *Rhizobium*-legume symbiotic relationship is an excellent example of how host cells and bacterial symbionts within root nodules undergo transformation, which allows the bacterial cells to fix nitrogen-converting atmospheric nitrogen into a chemical form that can be taken up by plants. Within the host cells, Rhizobia acting as bacteroids behave as temporary cell organelles that fix nitrogen. Intragenomic conflict is an evolutionary force. The evolution of sex was a form of genomic conflict management. Uniparental inheritance of cytoplasmic genes, mating types, and many features of sexual behavior may have evolved as a result of evolutionary conflict. The two-sex model that is widespread throughout the diversity of life may have been the result of ancient intracellular symbiosis. The Red Queen hypothesis suggests that harmful parasites and virulent pathogens exert selection pressure on their hosts so that sexual selection is maintained. Parasites, pathogens, and their hosts are involved in a microevolutionary "arms race" and in time, the symbionts' offense and the host defenses produce cycles of coadaptations.

Types of symbioses

The term "symbiosis" was, in a broad sense, originally intended by Anton de Bary in 1879 to refer to different organisms living together. Proposals to change this definition and redefine symbiosis, such as equating it to mutualism, have led to confusion. Various types of symbioses, whether beneficial or harmful, are described by the terms commensalism, mutualism, and parasitism.

The term "commensalism" was first used by P. J. van Beneden in 1876 for associations in which one animal shared food caught by another animal. An example of a commensalistic symbiosis is the relationship between silverfish and army ants. The silverfish live with the army ants, participate in their raids, and share their prey. They neither harm nor benefit the ants.

In mutualistic symbiosis, both partners benefit from the relationship. The extent to which each symbiont benefits, however, may vary and is generally difficult to assess. The complex interactions that take place between the symbionts may involve a reciprocal exchange of nutrients. For example, in the symbioses of algae and invertebrates (such as corals, anemones, and flatworms), the algae provides the animals with organic compounds that are products of photosynthesis, while the animals provide the algae with waste products such as nitrogenous compounds and carbon dioxide, which the algae use in photosynthesis. Unfortunately, in many academic circles, the terms symbiosis, mutualism, and cooperation have similar meanings and are often used interchangeably. Mutualism has also been widely used to describe intraspecific cooperative behavior in various animal species. The study of cooperation has enjoyed a resurgence during the past several decades. The evolution of cooperation via byproduct mutualism is generally found in the context of interspecific associations.

Parasitism is a form of symbiosis in which one symbiont benefits at the expense of its host. Parasitic symbioses affect the host in different ways. Some parasites are so pathogenic that they produce disease in the host shortly after parasitism begins. In other associations, the host and parasite have coevolved into a controlled parasitism in which the death of the host cells is highly regulated. Associations among many species are not clear and are more difficult to define categorically. For instance, when in their larval form, flukes might be considered parasites to snails because they harm their host; but, adult flukes have a commensal relationship with snails because when present in the alimentary tract of invertebrates they only share digesting food.

Classification of symbioses

Many scientists have attempted to standardize the many conflicting terms that have been used to describe different symbioses, including:

- Ectosymbiosis: The partners remain external to each other, such as in lichens.
- Endosymbiosis: The smaller symbionts are inside the host, but remain extracellular. Most of the time endosymbionts are in the digestive tract, or inside particular organs.
- Endocytobiosis is intracellular symbiosis. Symbiosome membranes are the host cell's vacuoles that enclose the symbiont.
- Obligate symbionts are so highly adapted to a symbiotic experience that they cannot live outside of it.
- Facultative symbionts, however, can live in a free-living condition.

Some examples of symbiosis in lower metazoans and tunicates

Commensalistic associations

Sharing of food and the provision of shelter are two main features of commensalistic relationships. Many species that display commensalistic relationships inhabit the internal spaces of sponges, clams, and sea cucumbers. The symbionts are often smaller and more streamlined than their free-living relatives and show evidence of long-term associations. For example, there are crab and shrimp species that live in the mantle cavities of bivalve mollusks; the pearl fish, *Corpus*, shows both structural and behavioral modifications that adapted in order to live in the cloacal spaces of sea cucumbers. These adaptations include a dramatic shift of the anal opening to just beneath the head, and the loss of both scales and the pelvic fins. In tropical water the hat-pin urchin *Diadema*, with its long needle-like spines, provides protection to fish such as *Aeoliscus* (the shrimpfish) and *Diademichthys* (the clingfish). These elongated fish species hide among the host's spines, which are constantly moving, by orienting themselves parallel to the spines. Another common example of commensalism is the relationship that exists between fishes and jellyfish. Fishes of the family Nomeidae congregate among the tentacles of jellyfish for protection. The anemonefishes keep the surface of their host anemones free of debris and may also lure fishes into the tentacles, thus providing food to the host.

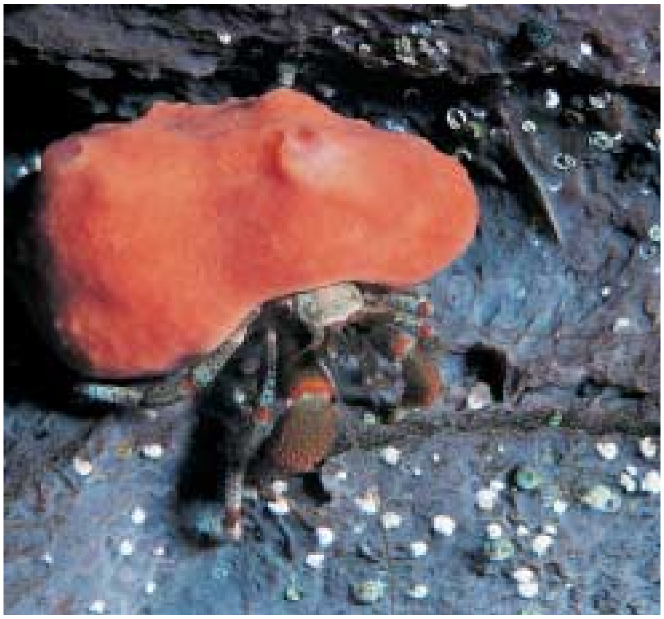
Sponges

Marine sponges contain a variety of endosymbionts, including bacteria, dinoflagellates, diatoms, and cryptomonads. Symbionts are especially common among tropical sponges. Many sponges contain endosymbiotic cyanobacteria that are intercellular (in sponge tissue). The sponge obtains nutrients from the digestion of bacteria or from the excretion of compounds such as glycerol and nitrogen from bacteria. In turn the bacteria receives nutrients and a place to live.

Phytosynthetic associations

Green hydra-*Chlorella* symbiosis

Hydra are common inhabitants of freshwater lakes and ponds, where they feed on small animals. *Hydra viridis* contains the green alga *Chlorella*. Algae reproduces asexually within the gastrodermal cells and a single hydra may contain about 150,000 algal cells. Under normal conditions, symbiotic algae are not digested by hydra. There are two reasons for this: first, the cell wall of algae contains sporopollenin, a protein that resists digestive enzymes; second, vacuoles containing algae do not fuse with lysosomes, the organelles that contain digestive enzymes and normally fuse with food particles. But if a digestive cell takes in more algal cells than normal, the extra cells are either digested or ejected. A bilateral movement of nutrients takes place between the symbionts. Algae supplies the animals with photosynthetic products such as maltose. At an acidic pH level, almost 60% of the carbon fixed by the algae is excreted as maltose, but at a neutral pH level, very little maltose is excreted. The rapidly hydrolyzed maltose is converted to glucose, and then glycogen is produced. Algae also provide the animal with oxygen, which they produce during photosynthesis. Hydra provides the algae with nutrients, including precursors of proteins and nucleic acids, and a protected place to live. As digestion is avoided and the host cells are able to regulate algal reproduction, the sym-



A sponge (*Suberites ficus*) gets more food by travelling with a hermit crab (*Pagurus beringanus*). The hermit crab profits from the sponge's protective cover. (Photo by ©Tom McHugh/Photo Researchers, Inc. Reproduced by permission.)

biosis that exists between *H. viridis* and *Chlorella* appears to be a finely tuned, nonpathogenic equilibrium.

Marine algal-invertebrate symbioses

Many marine invertebrates, such as sea anemones, coral, and flatworms have formed mutualistic symbioses with the photosynthetic algae known as the dinoflagellates. Their chloroplasts have efficient light-harvesting complexes that include chlorophyll a, chlorophyll c, and large amounts of xanthophylls. A common dinoflagellate of marine invertebrates is *Symbiodinium microadriaticum*, and this is greatly modified when it lives inside animal cells. The algal cell wall becomes thinner, loses the groove and flagella, and divides only by binary fission. In the host animal the algae excrete large amounts of glycerol, in addition to glucose, alanine, and organic acids. When the algae are isolated from animals and grown in culture, they stop excreting these substances.

Sea anemones and jellyfish

The sea anemone *Anthopleura xanthogrammica*, contains two types of symbiotic algae: zoochlorellae and zooxanthellae. The relative proportion of each algal symbiont in the animal depends on the water temperature. The anemones position themselves in ways to increase the exposure of their symbionts to light.

Cassiopea xamachana is a jellyfish that has been used to study how an invertebrate selects its algal symbionts. The lifecycle of *Cassiopea* includes a sexual medusoid stage, which contains algae that does not swim freely, but rather lies upside down in shallow waters, a behavioral adaptation that allows the algae in its tentacles to receive maximum daylight for photosynthesis, and gives the animal its common name, the upside-down jellyfish.

Anemone-clownfish symbiosis

Fishes of the genera *Amphiprion*, *Dascyllus*, and *Premnas*, commonly called clownfish, form mutualistic associations with giant sea anemones that live in coral reefs throughout the Pacific Ocean. The association is obligatory for the fish, but facultative for the anemones. The anemones eat prey that have been paralyzed by means of poisonous nematocysts discharged from specialized cells in their tentacles. The clownfishes are immune to the stinging nematocysts and can nestle among tentacles without harm. Some clownfish go through a period of acclimation before they become immune to the anemones' poison. Symbiosis with the anemone changes the mucous coating around the fish and the fish is no longer recognized as prey by the anemone. Clownfishes are brightly colored and marked, and attract larger fish to the anemone. These fish, if they come too close, are stung by the tentacles and eaten by the anemone. The clownfish share in the meal. A similar relationship exists between the Portugese man-of-war (*Physalia physalia*) and the horse mackerel (*Trachurus trachurus*). The bright blue and silver color of the fish, as well as its small size, attract prey for the man-of-war.

Reef-building corals

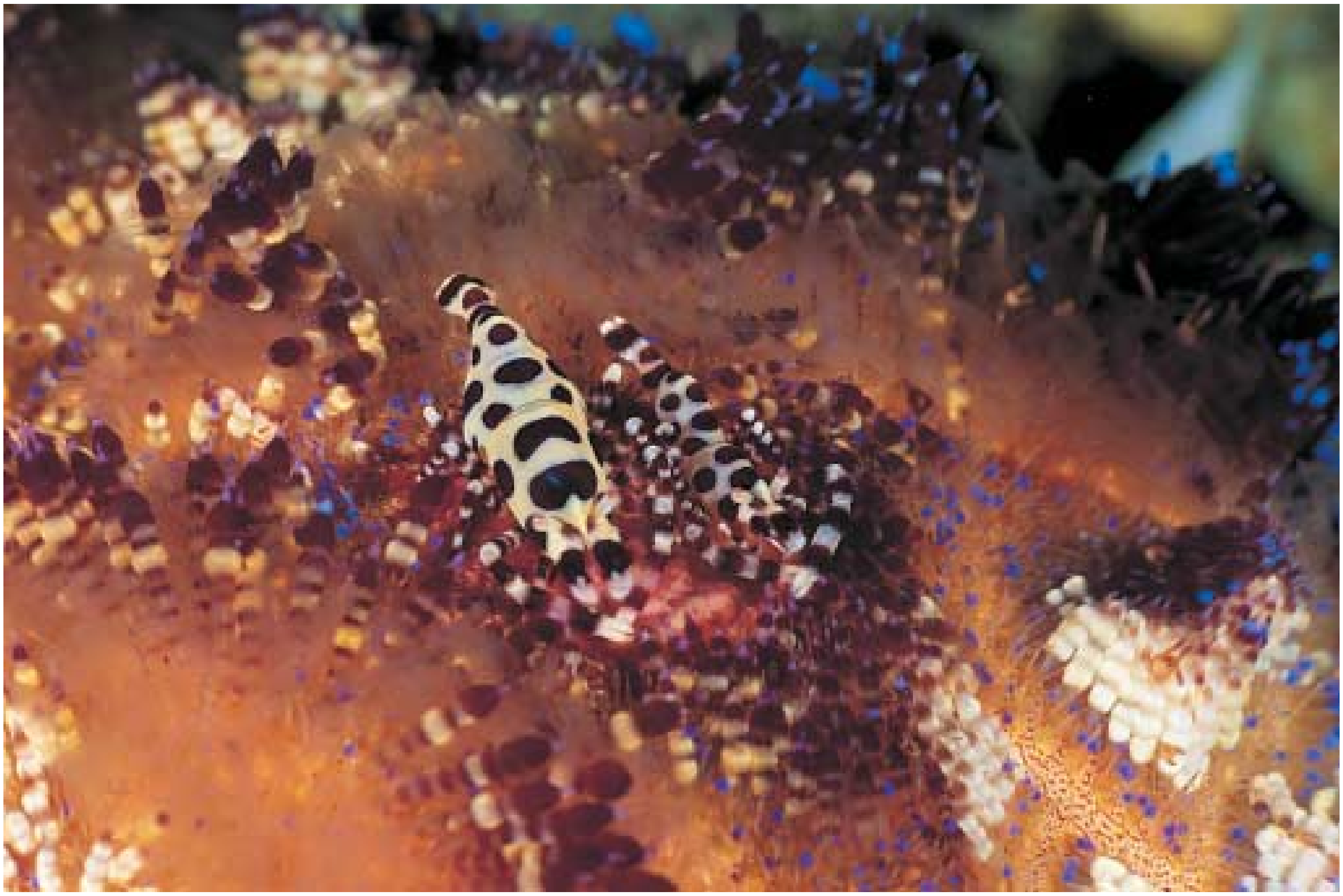
The symbiotic association between *Symbiodinium*-reef-building corals (Scleractinia) is of great importance in marine tropical ecosystems and has been the subject of many studies. Coral reefs support large communities of organisms. Coral polyps excrete a calcium carbonate shell around their body. As the polyp dies, the shells harden, and new polyps grow over them. After many years of this process, coral reefs are formed. Symbiotic dinoflagellates live inside nutrient-rich cells of the gasterodermis of the coral polyp. In some corals more than 90% of photosynthate may be released by the symbiont to its host cell. The algae supply the coral with oxygen, carbon, and nitrogen compounds. The animal obtains vitamins, trace elements, and other essential compounds from the digestion of old algal symbionts. Animal waste products such as ammonia are converted by the algae into amino acids, which are translocated to the animals. Such a recycling of nitrogen is an important feature in the nitrogen-poor habitats of coral. Coral bleaching is caused by the loss of symbiotic algae from the host and may be caused by environmental stresses such as global warming, pollution, and increased ultraviolet radiation.

Green flatworms

Convoluta roscoffensis is a small marine flatworm that lives in the intertidal zones of beaches in the Channel Islands of the United Kingdom and in western France. The worms are 0.08–0.16 in (2–4 mm) long and deep green in color from the algae they contain. During high tide, the worms are buried in the sand, but at low tide, during daylight, they move up to the surface. During this time the green algal symbiont, *Tetraselmis convolutae*, photosynthesizes until the next high tide. The *Convoluta*-algal symbiotic relationship is an early example of detailed studies (1910) that attracted public attention to the broader significance of symbiosis in nature.

Tunicates

Some marine tunicates contain an unusual photosynthetic symbiont, *Prochloron*, that has characteristics of both cyano-



Coleman's shrimp (*Periclimenes colemani*) lives exclusively with the venomous fire urchin (*Asthenosoma varium*). They are found often as a male/female pair on a bare patch that they have created by removing the urchin's tube feet and spines. They can move through the venomous spines without being harmed. (Photo by ©David Hall/Photo Researchers, Inc. Reproduced by permission.)

bacteria and green algae. In some tunicates the symbionts lie within a cellulose matrix that surrounds the outer surface of the animal, whereas in other tunicates symbionts are loosely attached to the cloacal wall. The larvae of some tunicates have specialized pouches that carry *Prochloron* cells that they obtain from the parent.

Symbiosis and animal parasitism

Scientists estimate that up to 50% of all animal species are parasitic symbionts. Some phyla such as the Platyhelminthes, Nematoda, and Arthropoda contain large a number of parasitic species. Hosts and parasites have coevolved together and under natural conditions many have become mutually tolerant. Host organisms can live independently, but, in most cases, the parasite's association with its host is obligatory. Animal parasites affect the health of humans and domesticated animals throughout the world. In most warm climates parasitic infections from flukes, nematodes, and arthropods greatly diminish the quality of life for people.

Helminths are widely distributed parasites of vertebrates. Infections caused by helminths such as schistosoma, hookworms, and filarial nematodes are a major cause of sickness of humans inhabiting the tropics. Helminths have complex lifecycles. They live for a long period within host animals, and they often possess a remarkable ability to evade the host's defense mechanisms. The prevalence of helminthic infections in some areas is high; however, only a few hosts develop disease. Helminths do not multiply in humans, and therefore the severity of the disease depends on the extent of the original infection. However, some helminthes may accumulate after repeated infection of a host.

Some fluke symbioses

Flukes (including the liver fluke, lung fluke, and human blood fluke) are obligate endoparasites of vertebrates as adults. After mating, the female fluke produces eggs into the host environment which are then are passed out of the host with feces or urine. There is a series of larval stages that multiply asexually in snails, serving as the first intermediate hosts. A larval stage (cercaria) with a characteristic tail emerges from the snail and either penetrates a vertebrate host immediately, encysts on to vegetation, or is eaten by a second intermediate host such as a crab or a fish, which may then be ingested by a vertebrate. *Fasciola hepatica*, the sheep liver fluke, commonly inhabits the bile duct, liver, or gallbladder of cattle, horses, pigs, and other farm animals. The Chinese liver fluke, *Clonorchis sinensis*, is an important parasite of humans and other fish-eating mammals in Far Eastern countries. Fish farming in east Asia is a major source of fluke infections in people. In other areas, dogs and cats serve as reservoir hosts of *C. sinensis*. *Paragonimus westermani*, the lung fluke, infects humans, cats, dogs, and rats. Occurences of this fluke are extremely prevalent in the people of China, the Philippines, Thailand, and other Asian countries.

Next to malaria, schistosomiasis is the most important parasitic disease in the world, affecting more than 200 million people in more than 75 countries. Schistosomes are blood flukes, and they reside in the mesenteric blood vessels of humans. Adult flukes are elongated and wormlike, and the female fluke is permanently held in the ventral groove of the male fluke. The presence of blood fluke eggs in various host tissues triggers an immune response, causing the affected person to show symptoms of disease that include enlargement of the liver and spleen, bladder calcification, and kidney disorders. Three important blood flukes that infect humans are *Schistosoma mansoni*, *S. japonicum*, and *S. haematobium*. *Schsitosoma mansoni* has been known to cause intestinal bilharziasis among people in South America, Central America, and the Middle East. Urinary schistosomiasis is caused by *S. haematobium* and is thought to occur in about 40 million people in Africa and the Middle East.

Cestodes: Tapeworms

Tapeworms represent the ultimate example of biological adaptation in order to live in another organism. All tapeworms are obligate symbionts of vertebrates and arthropods. Sexually mature tapeworms live in the intestines of vertebrates; in their larval stages they develop in the visceral organs of an alternate host, which may be a vertebrate or an arthropod. Serious diseases are caused by the progressive larval stages that take place in the muscles and nervous tissue of the vertebrate host. Some scientists view the adult tapeworms in the alimentary canal as endocommensals living in a nutrient-rich environment. Tapeworms lack a digestive system and absorb all their nutrients through their tegument, which is remarkably similar to that of flukes. *Diphyllobothrium latum*, the fish tapeworm, is a common inhabitant of the alimentary canal of fish-eating mammals, birds, and fishes. In temperate climates, people who eat raw fish often carry *D. latum*. The fish tapeworm is well known for its ability to absorb vitamin B^{12}, thereby causing the host to be deficient in a vitamin that is essential for the development of red blood cells. Humans become infected with pork tapeworm (*Taenia solium*) when they eat undercooked meat. Humans acquire the beef tapeworm, *Taenia saginata*, by eating raw or undercooked beef. *Hymenolepis diminuta*, the rat tapeworm, has been a favorite experimental subject to investigate the nutrition, biochemistry, immunology, and developmental biology of tapeworms.

Nematodes

Roundworms are second only to insects as the most abundant animals on earth. Most nematodes are free living. They occur in freshwater, marine, and soil habitats, feeding on microorganisms and decaying organic matter. Many nematodes are adapted for a parasitic lifestyle in plants, fungi, and animals. Scientists estimate that every kind of animal is inhabited by at least one parasitic nematode. Many nematodes live in the alimentary canals of their hosts, while others parasitize organs such as the eyes, liver, and lungs, often causing destruction to the host tissue. *Ascaris lumbricoides* is one of the largest intestinal nematodes present in humans and is prevalent throughout warmer climates. The two most important hookworms are *Ancylostoma duodenale*—the oriental hookworm of China, Japan, Asia, North Africa, the Caribbean Islands, and South America, and *Necator americanus*—which is primarily in South and Central America but also present in Africa and Asia. An estimated one billion people who live in the warmer climates of the world are infected with these nematodes, but most are asymptomatic. *Trichinella spiralis*, one of the most common parasites of vertebrates, has been studied extensively by physicians, experimental biologists, and ecologists.

Young brittle stars on sea lettuce. (Photo by Animals Animals ©G. I. Bernard, OSF. Reproduced by permission.)

Filarial nematodes are obligate parasites with complex lifecycles involving humans, other vertebrates, and arthropod vectors. *Wuchereria bancrofti* and *Brugia malayi* occur in the lymphatic system and cause the elephantiasis disease. The filarial worm, *Onchocerca volvulus*, causes skin tumors and blindness and is prevalent among the people of Africa and the Middle East. A typical filarial lifecycle begins when humans acquire the parasite from the bite of an infected bloodsucking insect. Once in the bloodstream or lymphatic system the nematode larvae become sexually mature. The mature female gives birth to larval stage microfilariae, which infest the biting insects that continue the lifecycle. Symptoms of filarial diseases are the result of host immune response and the physical blockage of ducts.

Nematode-insect symbioses

Insects are the dominant form of life on earth, and nematodes have successfully evolved symbioses with many of them. Nematodes that are symbionts of insects have intricate lifecycles that are synchronized with those of their hosts. *Heterorhabditis* and *Steinernema* are nematodes that parasitize insects and transmit bacteria that kill the hosts. The possibility of developing a biological control for mosquitoes has heightened interest in the mermithid nematode, *Romanomermis*, which kills mosquito larvae.

Most nematodes that attack plants are obligate parasites and include root-knot nematodes (*Meloidogyne* spp.) and cyst nematodes (*Globodera* and *Heterodera* spp.) that cause destructive infections in crop plants. There are more than 2,000 species of plant-parasitic nematodes, but few species are pests. Cell proliferation, giant cell formation, suppression of cell division, and cell wall breakdown are some of the host responses to nematode parasitism.

Bursaphaloenchus exylophilus is a nematode that lives in weakened or dead pine trees. A beetle that may carry up to 15,000 juvenile nematodes to a new location spreads the nematode, which feed on wood tissue and are suspected of killing pine trees. The relationship between the plant-parasitic nematode and the bark beetle is thought to be an example of mutualistic symbiosis.

Resources

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Organizations

International Society of Endocytobiology.
Web site: <http://www.endocytobiology.org/>

International Symbiosis Society.
Web site: <http://www.ma.psu.edu/lkh1/iss/>

Surindar Paracer, PhD

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Behavior

Behavioral characteristics of invertebrates

This chapter will familiarize you with issues and examples related to the behavior of invertebrates. The large number and sheer diversity of invertebrates requires a restriction in the types of behaviors (and species) that can be discussed. The behaviors selected were based in part on their importance to the survival of an individual organism. Since there is little known about the behavior of many of the lower invertebrate and deuterstome phyla, examples of insects and other protostomes were used to illustrate the various kinds of behavior mentioned.

All animals are metazoans and are characterized by being multicellular. The principles of behavior discovered in unicellular organisms are fundamentally the same in multicellular organisms. The similarities that exist between both forms of organisms are fascinating because the evolution of multicellularity has led organisms to develop a fantastic array of complex activities and modifiable behavior. Consider, for instance, the behavior of the marine sponge *Sycon gelatinosum* (phylum Porifera). During the larval stage it is a free-swimming animal that moves toward light at the water's surface. As it develops, it lives near the substrate and eventually becomes a sessile adult. The adult sponge is no longer a free-swimming animal and is entirely incapable of active movement. Reactive behavior is elicited from the adult sponge when individual cells are stimulated directly. The resulting responses are localized, slow, and uncoordinated. The inability to hunt food items such as bacteria, plankton, and detritus requires the sponge to develop specially designed feeding structures that bring food to it.

Contrast the poorly coordinated behavior of sponges with the more active behavior of animals in the phylum Cnidaria, which includes multicellular marine animals such as jellyfish, corals, sea anemones, and the freshwater *Hydras.* In cnidarians, cells performing the same function are grouped into tissue. The creation of tissue allows cnidarians to behave in more complex ways than sponges. *Hydras,* for example, coordinate their tentacles to grasp prey, contract their entire bodies in response to strong mechanical stimulation such as predatory attacks, and move a single tentacle in response to a non-threatening organism or passing shadow.

A great advance in behavior is seen in worms of the phylum Platyhelminthes. This phylum contains animals such as planarians, flukes, and tapeworms. In these animals we find the first evidence of characteristics critical for the development of complex behavior. These characteristics include bilateral symmetry, the appearance of a brain, polarized neurons, and definitive anterior and posterior ends—with the anterior end containing a head, and eyes. The advances present in this phylum make complex orientation possible. The first examples of complex learning are also present in flatworms. An example of this development is the flatworm's ability to to discriminate between two signals—one of which leads to a biologically relevant stimulus. This organism's ability to modify its behavior based on the possible consequences of an encounter in order to avoid dangerous situations moves an existing reflex into a new context. Although primitive types of behavior modification are possible in members of the phyla Porifera and Cnidaria, they are not as complex as those found in flatworms, nor are they retained for as as long as they are in worms.

The advances first seen in members of the phylum Platyhelminthes and elaborated by worms in the phylum Annelida (e.g., polychetes, earthworms, leeches) and reach their apex in members of the phyla Mollusca (e.g., snails, clams, squid, octopus) and Arthropoda (e.g., spiders, crabs, crayfish, lobsters, honey bees, wasps, ants). For example, the cephalopods' neural development, problem solving capability, sensory apparatus, and ability to modify behavior is unsurpassed among the invertebrates. Among the arthropods, social insects such as the honey bee and ant have astonishing examples of defensive, social, and learned behavior patterns. What is behavior, and who studies it? Behavior is not easy to define and various definitions exist. For example, physiologists might describe the "behavior of a neuron," but some comparative psychologists would find this objectionable. Generally speaking, behavior is defined as "what organisms do." Behavior is the action an animal takes in order to adjust, manipulate, and interact with its environment. Actions such as moving, grooming, and feeding can be referred to as maintenance behavior. Action that influences members of the same and/or different species can be called communication behavior. Behavior that is modifiable is known as learned behavior. In general, each of these three types of behavior defines or "orientates" the animal in space.

Various disciplines have contributed to the study of invertebrate behavior. These disciplines include comparative psychology, ethology, physiology, ecology, and entomology.

A stalked jellyfish (*Haliclystus auricula*) attaches to kelp and eelgrass near British Columbia. (Photo by ©Neil G. McDaniel/Photo Researchers, Inc. Reproduced by permission.)

Scientists engaged in the study of behavior often do so from an interdisciplinary approach in which psychologists, ethologists, physiologists, and entomologists all work alongside each other. Comparative psychologists have a special interest in searching for similarities and differences in behavior.

Orientation behavior

Over the years various classification systems have been developed to describe orientation, and the terminology used within these systems is confusing. Popular systems in which orientation can be described are kinesis and taxis. Orientation behavior represents an example of the type of behavior referred to as maintenance behavior.

Kinesis

The simplest response through which invertebrates find a suitable location to live is referred to as kinesis. The response is not directed toward or away from a stimulus, but nevertheless places the animal in an optimum location. Changes in activity, rate of movement, and/or turning is non-directional and directly related to the intensity of the stimulus from moment to moment. Kinetic responses often occur when the source of the stimulus cannot be sensed at a distance. Several types of kinesis are recognized including: barokinesis, hygrokinesis, orthokinesis, photokinesis, thigmokinesis, and klinokinesis. Theories regarding kinesis are made more confusing when describing orientation using two kineses. For example, an animal that changes its rate of movement under illumination is said to exhibit "photo-orthokinesis." The words negative and positive also can be added to these terms in order to further adapt their meaning; an animal that is active under little or no illumination is said to exhibit "photo-negative kinesis."

Examples of kinesis:

BAROKINESIS

Various classes of invertebrates react to pressure changes, including increased locomotion because of changes in barometric pressure. Larvae of the crab genus *Carcinus* swim toward the water's surface when pressure increases. Copepods, adult and larval polychaetes, and jellyfish medusae are other examples of animals that increase their activity in response to pressure changes.

HYGROKINESIS

Increased locomotion in reaction to changes in humidity is referred to as hygrokinesis. Some species of nematoda are stimulated to move due to conditions of low humidity and are less active when there are high degrees of humidity. The increase in activity under dry conditions increases the chances of finding a suitable damp environment. Increasing locomotion based on fluctuations in humidity levels is important among terrestrial invertebrates (e.g., planaria) because, with the exception of insects, very few have developed methods of conserving significant amounts of water.

PHOTOKINESIS

Increased locomotion resulting from changes in levels of light is called photokinesis. Flatworms (e.g., *Dugesia dorotocephala*, *Dugesia tigrina*) all increase their activity depending on the intensity of illumination that surrounds them. Other examples of organisms that exhibit photokinesis include gill and skin fluke larvae (monogenea), jellyfishes, and rotifers. Not all invertebrates respond to increases in illumination. When conducting studies on the effect of light on activity levels it is important to separate the role of illumination from the temperature increases produced by light.

THIGMOKINESIS

This form of kinesis is defined as increased locomotion in response to changes in contact with the immediate physical environment. Some invertebrates are more active in open spaces than in closed spaces. Examples of closed spaces include cracks and crevices. For example, the contraction of longitudinal muscles in nematodes produces a whiplike undulatory motion that relies on environmental substrata for the body to push against; when they are placed in fluid without substrata they thrash around.

OTHER FORMS OF KINESIS

Orthokinesis refers to changes in the speed or frequency of movement in reaction to changes in the intensity of a stimulus. Stimuli that produces a change in direction (such as turning) is known as klinokinesis. Movement influenced by gravity is known as geokinesis, and changes of movement caused by water currents is known as rheokinesis. Kinetic responses also can be in reaction to chemical and temperature stimuli (chemokinesis and thermokinesis, respectively). The oncomiricidia (larvae) of the Monogenea have been shown to change speed and direction in reaction to gravity, current, and light stimuli.

Taxis

Taxis is a more complex response through which invertebrates find a suitable location to live. The response is directed toward or away from a stimulus to place the animal in an optimum location to inhabit. Changes in activity, rate of movement, and/or direction are related to the intensity of the stimulus gradient from moment to moment. Taxis differs from kinesis in that taxic responses allow invertebrates to engage in specific activity as opposed to general activity, relative to a stimulus source.

Taxis can be characterized by:

1. Whether the animal moves toward or away from a stimulus.
2. The way in which the animal moves.
3. The complexity of the sensory structures used to detect the stimulus.

An invertebrate with a single visual receptor can determine the direction of a light source simply by moving the receptor (such as turning its head) and sampling the stimulus gradient produced by the light. If the animal is attracted to light, its receptor becomes more active the closer it moves toward the light source. The majority of invertebrates have at least two receptors; the second receptor allows the animal to make simultaneous comparisons from each side of its body from moment to moment as it moves through a stimulus gradient.

Several different types of taxis are recognized including, phototaxis, klinotaxis, phototropotaxis, and phototelotaxis. Moreover, movements toward the source of stimulation are called positive, and movements away from the source are called negative. For example, movements toward a source of light is called "positive phototaxis," while movement away from light is referred to as "negative phototaxis."

Examples of various form of taxis include:

PHOTOTAXIS

An animal that moves toward (positive phototaxis) or away (negative phototaxis) from light is exhibiting phototaxis. Movement is parallel to the direction of light. Examples of animals that exhibit this type of behavior are jellyfishes, oncomiricidia (monogenea larvae), and some echinoderms (sea stars and sea urchins). Planarians are negatively phototoxic in that they seek less illuminated areas.

KLINOTAXIS

A change in directed movement based on successive comparisons of a stimulus is referred to as klinotaxis. The larvae of many flies, including the common house fly, *Musca domestica*, find the location of a light source by moving their head left and right in order to compare the relative intensity of a stimulus. Derivatives of this behavior also occur to many lower invertebrates, including planaria and echinoderms.

PHOTOTROPOTAXIS

Animals that display phototropotaxis undergo movement toward a source of illumination based on a comparison of information gathered by their eyes. The animal orientates toward the direction of light (assuming it exhibits positive phototropotaxis) and moves in a direction that keeps the eyes equally stimulated. Phototropotaxis is best demonstrated experimentally in what is known as a "two-light experiment." In this design, an animal is placed between two light sources. Phototropotaxis is indicated if the animal follows a path between the two light sources thereby stimulating the photoreceptors equally. Phototropotaxis also can be detected by preventing visual information reaching one eye. This test can be done by removing or painting an eye. Phototropotaxis is indicated if the animal begins to engage in "circus movements." For example, when the honey bee (*Apis mellifera*) is blinded in one eye it will perform "circus movements" (sideways movements) toward a light source. Positive phototropotaxis can be detected if the animals continuously turns toward a light source; if an animal is negatively phototropotaxic it will continuously turn away from a light source (i.e., it will turn so that its blind side faces the light).

PHOTOTELOTAXIS

Movement directed toward one of two sources of illumination is known as phototelotaxis. This form of behavior is dependent upon the type of sophistication present in the visual receptors. If the eye is capable of forming an image that will allow the animal to identify the source of illumination, the animal can move directly toward the source without the need for comparing two sources of illumination. Phototelotaxis is found in invertebrates possessing compound eyes (arthropods such as insects and crustaceans) including hermit crabs, isopods, and mysid crustaceans. There are no known examples of this behavior among the lower invertebrate and invertebrate deuterostomes.

GEOTAXIS

Geotaxis refers to movement along lines of gravitational force. As with all forms of taxic behavior, the direction of movement can be either positive or negative. Geotaxis is observed on surfaces (especially inclines), in water, air, sand, or mud. The most pronounced examples of geotaxis are found in invertebrates that live in sand or mud. Many examples of geotatic behavior occur in animals with statocysts, although there are examples where statocysts are not involved. The statocyst is a heavy object (statolith) located in a fluid-filled chamber used to detect gravitational forces. When the statocyst is moved, the statolith induces movement by activating various sensory and motor systems that return the animal back to its normal balance. Geotaxis is most readily studied in invertebrates by having an animal crawl on a vertical glass plate that is gently rotated or inclined. In order to test burrowing animals such as polychaetes the animal can be sandwiched

A common or edible sea urchin (*Echinus esculentus*) on the move, with tube-feet extended. (Photo by Jane Burton. Bruce Coleman, Inc. Reproduced by permission.)

between two glass plates filled with sand, or on a rotating table or centrifuge. Examples of geotactic behavior can be found in medusa (e.g., *Cotylorhiza tuberculata*), planaria (e.g., *Convoluta roscoffensis*), and polychaetes (e.g., *Arenicola grubei*). There are many cases of invertebrates that exhibit geotatic behavior without statocysts, including *Helix*, *Limax*, the sea anemone *Cerianthus*, monogeneans, starfishes, and sea urchins.

RHEOTAXIS

Rheotactic behavior involves movement directed by water flow, and can be found in most classes of invertebrates that inhabit water. Examples of organisms that display rheotaxis include anemones, planarians, monogeneans, and many protostomes (gastropods, crustaceans, and both nymphs and larvae of insects).

OTHER FORMS OF TAXIS

Thigmotaxis is defined as movement when direction is determined by a stimulus making contact with an animal's body. Turbellarians are positively thigmotactic on their ventral sides, and negatively thigmotactic on their dorsal sides, which keeps their ventral side against the substrate. Movement influenced by air currents is known as Anemotaxis. Taxic responses also are created by chemical and temperature stimuli (referred to as chemotaxis and thermotaxis respectively).

Learned behavior

Learned behavior is another class of behavior exhibited by invertebrates. The reasons for studying learning in invertebrates are varied and include gaining further knowledge of how biochemistry and physiology affect the process of learning, searching for similarities and differences within and between phyla, and using learning paradigms to explore applied and basic research questions (e.g., how pesticides influence the foraging behavior of the honey bee).

The term learning, like the term behavior, has several definitions. When reviewing studies of learning, the reader should be aware that definitions may vary from researcher to researcher. For example, a researcher may consider behavior controlled by its consequences (i.e., behavior that is rewarded or punished) as an example of operant behavior, while others believe that it depends upon the type of behavior being modified. Moreover, some believe that any association between stimuli represents an example of Pavlovian conditioning, while others believe that the "conditioned stimulus" must never elicit a trained response prior to the process of association.

We will define learning as a relatively permanent change in behavior potential that comes as a result of experience. This definition contains several important principles. First, learning is inferred from behavior. Second, learning is the result of experience. Third, temporary fluctuations are not considered learning; rather, the change in behavior identified as learned must persist as such behavior is appropriate. This definition excludes changes in behavior produced as the result of physical development, aging, fatigue, adaptation, or circadian rhythms. To better understand the process of learning in invertebrates, many behavioral scientists have divided the categories of learning into non-associative and associative.

Non-associative learning

This form of behavior modification involves an association developing from one event, as when the repeated presentation of a stimulus leads to an alteration of the frequency or speed of a response. Non-associative learning is considered to be the most basic of the learning processes and forms the building blocks of higher types of learning in metazoans. The organism does not learn to do anything new or better; rather the innate response to a situation or to a particular stimulus is modified. Many basic demonstrations of non-associative learning are available in scientific literature, but there is little sustained work on the many parameters that influence such learning (e.g., time between stimulus presentations, intensity of stimulation, number of repeated trials). There are two types of non-associative learning: habituation and sensitization.

HABITUATION

Habituation refers to a reduction in the response elicited by a stimulus as it is repeated. For a decline in responsiveness to be considered an instance non-associative learning, it must be determined that any decline related to sensory and motor fatigue do not exert an influence.

Studies of habituation show that it has several characteristics, including the following:

1. The more rapid the rate of stimulation is, the faster habituation occurs.
2. The weaker the stimulus is, the faster habituation occurs.

3. Habituation to one stimulus will produce habituation to similar stimuli.
4. Withholding the stimulus for a long period of time will lead to the recovery of the response.

SENSITIZATION

Sensitization refers to the augmentation of a response to a stimulus. In essence, it is the opposite of habituation and refers to an increase in the frequency or probability of a response. Studies of sensitization show that this process has several defining characteristics, including the following:

1. The stronger the stimulus is, the greater the probability that sensitization will be produced.
2. Sensitization to one stimulus will produce sensitization to similar stimuli.
3. Repeated presentations of the sensitizing stimulus tend to diminish its effect.

Associative learning

A form of behavior modification involving the association of two or more events, such as between two stimuli, or between a stimulus and a response is referred to as associative learning. This form of learning allows a participant to aqcuire the ability to perform a new task, or improve on their ability to perform a task. Associative learning differs from non-associative learning by the number and kind of events that are learned and how the events are learned. Another difference between the two forms of learning is that non-associative learning is considered to be a more fundamental mechanism for behavior modification than those mechanisms present in associative learning; examples of these differences can easily be found in the animal kingdom. Habituation and sensitization are present in all invertebrates, but classical and instrumental conditioning seems to occur first in flatworms (phylum Platyhelminthes). In addition, the available evidence suggests that the behavioral and cellular mechanisms uncovered for non-associative learning may serve as building blocks for the type of complex behavior characteristic of associative learning. The term associative learning is reserved for a wide variety of classical, instrumental, and operant procedures in which responses are associated with stimuli, consequences, and other responses.

CLASSICAL CONDITIONING

Classical conditioning refers to the modification of behavior in which an originally neutral stimulus—known as a conditioned stimulus (CS)—is paired with a second stimulus that elicits a particular response—known as the unconditioned stimulus (US). The response which the US elicits is known as the unconditioned response (UR). A participant exposed to repeated pairings of the CS and the US will often respond to the originally neutral stimulus as it did to the US. Studies of classical conditioning show that it has several characteristics, including the following:

1. The more intense the CS is, the greater the effectiveness of the training.
2. The more intense the US is, the greater the effectiveness of the training.
3. The shorter the interval is between the CS and the US, the greater the effectiveness of the training.
4. The more pairings there are of the CS and the US, the greater the effectiveness of the training.
5. When the US no longer follows the CS, the conditioned response gradually becomes weaker over time and eventually stops occurring.
6. When a conditioned response has been established to a particular CS, stimuli similar to the CS may elicit the response.

INSTRUMENTAL AND OPERANT CONDITIONING

Instrumental and operant conditioning refer to the modification of behavior involving an organism's responses and the consequences of those responses. In order to gain further understanding of this concept it may be helpful to conceptualize an operant and instrumental conditioning experiment as a classical conditioning experiment in which the sequence of stimuli and reward is controlled by the behavior of the participant. Studies of instrumental and operant conditioning show that they have several characteristics, including the following:

1. The greater the amount and quality of the reward, the faster the acquisition is.
2. The greater the interval of time between response and reward, the slower the acquisition.
3. The greater the motivation, the more vigorous the response.
4. When reward no longer follows the response, the response gradually becomes weaker over time and eventually stops occurring.

Non-associative and/or associative learning has been demonstrated in all the invertebrates in which it has been investigated, including planarians and many protostomes (polychaetes, earthworms, leeches, water fleas, acorn barnacles, crabs, crayfish, lobsters, cockroaches, fruit flies, ants, honey bees, pond snails, freshwater snails, land snails, slug, sea hare, and octopus). While there is no general agreement, most behavioral scientists familiar with the literature would suggest that the most sophisticated examples of learning occur in several of the protostome taxa (crustaceans, social insects, gastropod mollusks, and cephalopods). Many of the organisms in these groups can solve complex and simple discrimination tasks, learn to use an existing reflex in a new context, and learn to control their behavior by the consequences of their actions.

Defensive behavior

Defensive behavior represents a class of behavior referred to as communication behavior. Metazoans must defend themselves against an impressive array of predators. To survive against an attack, various strategies have evolved. These

Forbes' common sea star (*Asteruas firbesii*) regenerating arms that have been lost. This ability is a type of defense mechanism, enabling the sea star to stay alive even if a predator takes an arm. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

strategies include active mimicry, flash and startle displays, and chemical/physical defense.

Physical and chemical defense

A common behavior exhibited by invertebrates in response to danger is the adoption of a threatening posture. For example, when the long-spined sea urchin (*Diadema* sp.) is threatened it will point its spines toward the predator or threat. Aquatic organisms found in the order Decapoda, such as the cuttlefish and squid, defend themselves by discharging an ink that temporarily disorientates the predator, allowing the organisms time to escape. Some decapods (such as the octopus) in the order Octopoda have a similar ink defense system. At least one case has been observed in which *Octopus vulgaris* was recorded holding stones in its tentacles as a defensive shield against a moray eel. When sea cucumbers are threatened they expel their intestines to confuse a predator and allow them to escape.

In general, organisms during early ontogenetic development approach low-intensity stimulation and withdraw from high-intensity stimulation (e.g., light intensity). Sessile invertebrates like anemones, corals, and tunicates will contract or withdraw to protect their most vulnerable body parts. Mobile invertebrates can usually escape an aggressor's high intensity stimulation by engaging in kinesis and/or taxis such as crawling, swimming, flying, or jumping. Such behavior is easily observed in the cephalopod *Onychoteuthis* (protostome) popularly known as the "flying squid." The flying squid can escape aggressors by emitting strong water bursts from its mantle, which propels the animal into the air where finlike structures allow it to glide for a brief period of time. Most other nonsessile invertebrates—like flatworms, echinoderms, and arrow worms—crawl away to hide under a rock, or change direction and swim away to escape predatory stimuli.

MIMICRY

There are various forms of mimicry and only a few can be mentioned here. Some of the more well-known invertebrates that engage in mimicry are butterflies. The species *Zeltus amasa maximianus* (Lycaenidae) presents a "false head" to aggressors that is made more attractive to the predator by the motion of its wings. False-head mimicry requires not only morphological adaptations but also an ability to engage in behavior patterns that force the predator to focus its attention on the false structure. By presenting a predator with a convincing false target the probability of surviving an attack is increased. A similar strategy is also common in caterpillars. Species of *Lirimiris* (Notodontidae) actually inflate a head-like sac that is found posteriorly. The resulting fictitious appendage draws the attention of the predator away from the actual head and toward the comparatively tough posterior end. An interesting version of false-head mimicry exists in crab spiders (*Phrynarachne* spp.), and longhorn beetles (*Aethomerus* spp.), which both mimic the appearance of bird feces, and the Anaea butterfly caterpillar (Nymphalidae), which mimics the appearance of dried leaf tips. Mimicry and false mimicry—where animals mimic another animal—are not well developed among the invertebrate taxa.

STARTLE DISPLAYS AND FLASH COLORATION

When some invertebrates are stimulated by an aggressor they quickly modify their posture in an attempt to make it appear larger, and at the same time their body will quickly present a "flash" of color. This type of behavior has evolved mostly in protostomes. However, many combjellies and jellyfish can produce flashes of bioluminescent light that deters or confuses predators.

Migratory behavior

Migration is a second example of communication behavior. Migratory behavior refers to the movement of entire populations. For invertebrates such movement can range from one or two meters to hundreds of meters. Some well known examples of migratory behavior can be found among insects such as the monarch butterfly, *Danaus plexippus* (Danaidae) and the locust *Schistocerca gregaria* (Tettigoniidae).

During migration, activities such as foraging for food and engaging in mate selection are reduced or suspended altogether. The separation of movement from vegetative activities such as feeding, defense, and reproduction is one criterion used to determine if migratory behavior is occurring.

Migratory behavior is usually confined to animals living in temporary habitats. The ability to leave a particular habitat is important for those animals that feed on vegetation or plankton that is seasonal or limited, and that live in unstable environments. Leaving aversive conditions related to crowding or food shortages is one hypothesis that explains migratory behavior in invertebrates. Examples of lower invertebrate migrations are few. While it is known that several species of jellyfish often congregate in groups of thousands, the mechanism that brings them together is largely unknown.

Many species that do not or are not capable of migration (i.e., sessile forms) may encyst, or produce encysted formations or eggs that can withstand seasonal variation in food and other environment conditions. Many sponges, flatworms, rotifers, nematodes, and gastrotrichs can produce resistant eggs or other forms that are capable of withstanding temporary environmental fluctuation.

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Lower metazoans, lesser deuterostomes, and humans

Marine organisms from all marine phyla have been a source of food since humans first began to explore marine environments. In stark contrast to terrestrial plants and animals that have been widely used for remedies of human disorders—the World Health Organization (WHO) estimates that 60–80% of the world's population relies primarily on plants for their basic health care—only a small number of marine species have been used for medicines, mostly due to human's limited access to marine resources.

Perhaps the earliest industrial application of components of marine organisms is Tyrian purple or royal purple, a brilliant dye produced from marine gastropods (protostome) of the superfamily Muricacea, which dates back to 1600 B.C. Phoenicians processed the dye from the mucus in the hypobrachial glands of such mollusks as *Murex trunculus* at many dyeing factories located on the coast of Lebanon. However, only 0.03 oz (1 g) of the dye could be obtained from 10,000 animals and was worth as much as 0.35–0.7 oz (10–20 g) of gold. Actually, the mucus contained in the hypobranchial glands is colorless, which turns purple by enzymatic, oxidation, and photochemical reactions during processing.

Regarding the medicinal application of marine organisms, though, there were only a few examples, including using the red alga, *Digenea simplex*, to treat ascariasis in Asian countries. No one had seriously thought about this issue until the early 1950s when a professor at Yale University discovered unusual nucleosides, spongouridine and spongothymidine, from the Caribbean sponge, *Tectitethya crypta* (=*Chryptotethya crypta*); these nucleosides are composed of arabinose in place of ribose or deoxyribose found in those of RNA or DNA. This discovery was unprecedented and impressed researchers with the uniqueness of marine metabolites. Nearly 15 years later, Ara-A (arabinosyl adenine) and Ara-C (arabinosyl cytosine), antiviral and anticancer drugs, respectively, were developed from these sponge-derived nucleosides. Obviously, this development was the most significant driving force for organizing the symposium entitled "Drugs from the Sea," which was held at University of Rhode Island in 1967. The 1969 discovery of a large amount of prostaglandins from the Caribbean gorgonian, *Plexaura homomala* further stimulated research into marine metabolites. These achievements occurred largely due to scuba diving, which allowed researchers not only to observe but also to collect exotic marine creatures.

A new research field of marine natural products was created in the early 1970s, and many researchers from academia as well as industry embarked on exploring medicinally active compounds from marine organisms. This resulted in the isolation of more than 10,000 new compounds over the next 30 years, including a number of structurally unusual and biologically interesting compounds. Clinical trials on more than 30 marine natural products and their derivatives have since been conducted.

More than any other organism, sponges have been the most actively exploited sources for drugs, because they con-

In Greece sponges are gathered from the ocean and sold, often to tourists. This practice is common around the world. (Photo by ©Margot Granitsas/Photo Researchers, Inc. Reproduced by permission.)

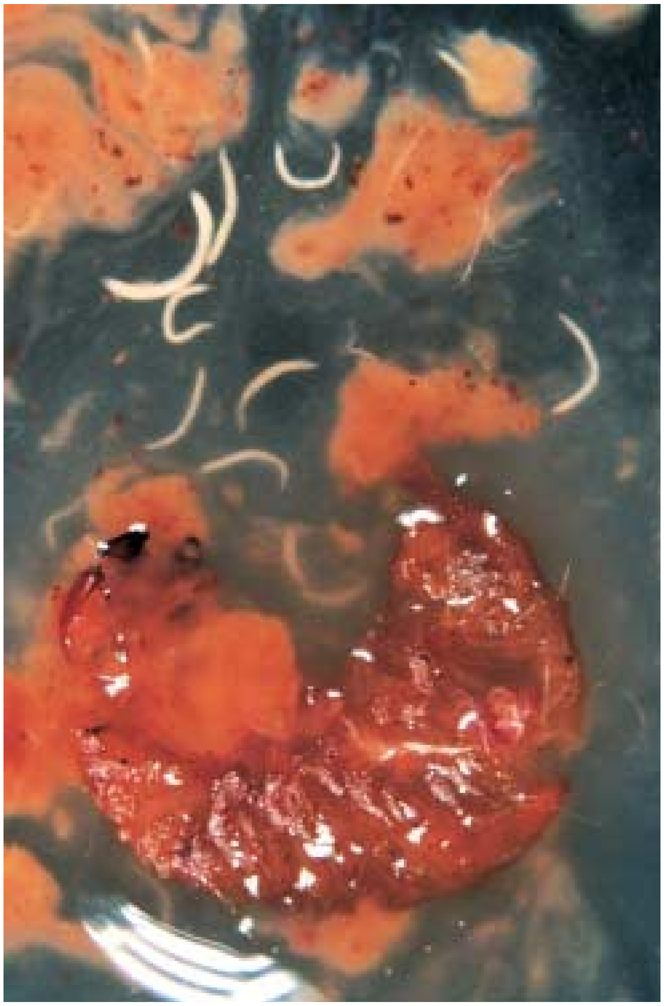
tain not only metabolites of unique structures, but also of potent biological activities. It is widely believed that symbiotic bacteria or other microbes are responsible for the production of biologically active sponge metabolites. In fact, sponges contain numerous compounds reminiscent of microbial metabolites (e.g., sponge peptides often embrace D-amino acids and unusual amino acids). Increasing evidence for the involvement of bacteria in production of unusual sponge metabolites has been obtained; highly unusual antifungal cyclic peptides, theopalauamides, were found to be contained in the new δ-proteobacterium *Entotheonella palauensis* isolated from the Palauan sponge, *Theonella swinhoei*.

Among sponge-derived compounds, halichondrin B, an unusual polyether macrolide originally discovered from the Japanese marine sponge, *Halichondria okadai*, is highly promising as an anticancer agent. However, its low contents (10% based on wet weight) and its complex structure are the most serious obstacles for the development of drugs, as is the case for other marine-derived drug candidates. Fortunately, a New Zealand sponge, *Lissodendoryx* sp., inhabiting depths of 279–344 ft (85–105 m) off the Kaikoura Peninsula, South Island, was found to contain larger amounts of halichondrin B and analogues. To guarantee sponge supplies required for clinical trials, aquaculture of this sponge has been initiated. Small pieces of the sponge were cultured on lantern arrays in shallow waters; small explants grew rapidly, 50-fold in six weeks in some areas. Although the bath sponges have been cultured in the Mediterranean and other regions for more than 80 years, this is the first sponge aquaculture for the production of drugs.

Another promising sponge-derived anticancer agent is discodermolide, discovered from *Discodermia dissolute* collected at depths of 656 ft (200 m) off the Bahamas. It causes anticancer activity by stabilizing microtubules, as in the case of the bestselling anticancer drug, Taxol, which is extracted from the Pacific yew tree. Again, large amounts cannot be supplied by extracting the sponge that inhabits deep sea, but its relatively simple structure indicates the possibility of chemical synthesis.

Cnidaria usually harbor symbiotic dinoflagellates that are thought to be responsible for the synthesis of cnidarian metabolites such as terpenoids. Diterpenoid glycosides called pseudopterosins, which are isolated from the Caribbean sea whip, *Pseudopterogorgia elisabethae*, have been added to skincare creams because of their anti-inflammatory properties.

Opisthobranch mollusks (protostome) are unique animals that have abandoned their protective shells in the course of evolution. Instead, they have developed chemical defenses, which are extracted from their prey organisms. For example, the Spanish dancer, *Hexabranchus sanguineus*, extracts powerful antifeedants, trisoxazole-containing macrolides from sponges. Similarly, the sea hare, *Dolabella auricularia*, accumulates numbers of bioactive compounds from cyanobacteria such as *Lyngbya majuscula*, among which dolastatin 10, an unusual linear peptide, is highly promising as an anticancer drug (under Phase II clinical trials in 2003). *Elysia rufescens*, a Hawaiian sacoglossan mollusk, extracts a cyclic peptide, kahalalide F, from a green alga, *Bryopsis* sp. (actually derived from an epiphytic cyanobacteria, most likely *Lyngbya* spp.). The peptide entered Phase I clinical trials in 2002 as an anticancer drug.



A vine weevil larva (*Otiorhynchus sulcatus*) infected with a parasitic nematode of the genus *Heterorhabditis* shows the contents of its body cavity containing immature nematodes. This nematode is watered into the soil in commercial greenhouses and market gardens to contol vine weevils. (Photo by H. S. I. (Nigel Cattlin/Photo Researchers, Inc. Reproduced by permission.)

Cone snails (protostome), comprising 500 species, hunt fishes, mollusks, and worms using venomous harpoons, which is a very rare adaptation for marine animals. Unexpectedly, the venom glands contain hundreds of small biologically active peptides. For example, *Conus geographus*, a fish-hunting species that occasionally causes death in humans, contains peptides, tabbed conotoxins, that act on Na+ channels, Ca2+ channels, acetylcholine receptors, and others. Consequently, conotoxins are considered potential drugs for the treatment of neurological disorders. In fact, Ω-conotoxin MVIIA derived from *C. magnus*, an N-type Ca2+ channel blocker, is promising as a painkiller for cancer and HIV patients; it is 50 times more potent than morphine.

Colonial ascidians often contain compounds of highly unusual structures with potent biological activities, which perhaps is due to the presence of microbial symbions such as prochlorons. *Ecteinascidia turbinate*, which grows on mangrove roots in the Caribbean, was first reported to be highly antitumoral in 1967, but the active components were not unveiled until 1990. Interestingly, ecteinascidin 743, an active component, is closely related to saframycins, antibiotics isolated from terrestrial actinomycetes. This alkaloid is shortly expected to become the first marine anticancer drug. It should be noted that echteinascidins are likely produced by symbiotic microbe(s). The Mediterranean tunicate, *Aplidium albicans*, contains a depsipeptide, aplydine (dehydrodidemnin B), which showed good results in clinical trials as a anticancer drug.

Cephalostatin 1, a highly unusual dimeric steroid discovered from the hemichordate, *Cephalodiscus gilchristi*, collected at depths of 197–262 ft (60–80 m) off East Africa, proved to inhibit the growth of P388 murine leukemia cells at incredibly low concentrations. Interestingly, closely related ritterazines were isolated from the Japanese ascidian, *Ritterella tokioka*, thus indicating the involvement of symbiotic microbes in synthesis of this unique dimeric steroid.

Increasing numbers of marine natural products have been found to have promising properties for the treatment of human medical disorders. Obviously, marine organisms, particularly benthic invertebrates, are an important source of drugs.

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Nobuhiro Fusetani, PhD

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Conservation

Need for conservation

The conservation of habitat and species poses an enormous challenge for humans in the twenty-first century. As the earth's population grows, human use of natural resources increases. Municipalities, reservoirs, aqueducts and roads impinge upon natural habitat, fragmenting it into smaller pieces. As people burn fossil fuels, remove minerals, harvest commercial species, or convert wild land into farms, they necessarily compel other species to adapt to or emigrate from shrinking habitat or other changes in the environment. As humans consume more of the world's natural resources, they are faced with environmental concerns that range from acid rain, carbon emissions, and ozone depletion to starvation and the emergence of previously unknown diseases. The loss of a species—unlike pollution, unlike hunger, unlike global warming—cannot be reversed. Once a species is gone, it is gone forever.

In a seminal scientific paper first published in 1968, Garret Hardin pointed out that such areas as the open ocean that are not considered private property inevitably suffer from overuse resulting from their being common to all. Hardin argued that because they belong to no one in particular, they do not benefit from anyone's stewardship; no one wants to make personal sacrifices in order to increase the profits of others. He called this phenomenon the "tragedy of the commons." Hardin's article began as a retiring president's address and later appeared in the prestigious journal *Science.* Subsequently his paper was discussed in academic contexts ranging from engineering to political science; his 600 reprints were exhausted in a matter of months. Hardin began his original essay with this citation from a 1964 article published in *Scientific American* by J. B. Wiesner and H. F. York: "Both sides in the arms race are confronted by the dilemma of steadily increasing military power and steadily decreasing national security. It is our considered professional judgment that this dilemma has no technical solution. If the great powers continue to look for solutions in the area of science and technology only, the result will be to worsen the situation." Today, this citation remains uniquely pertinent.

Wiesner and York's observation led to Hardin's incendiary suggestion that there are problems for which science has no solution. Scientists do their work under the explicit or implicit assumption that the questions they address have technical and logical answers. To suggest otherwise is to strike at a collective Achilles heel. Wiesner and York were speaking of the potential for nuclear war in their original article, but Hardin thought their words were equally relevant to ecological concerns. He applied their reasoning to the social goal first proposed by the nineteenth-century English philosopher Jeremy Bentham: acquiring the greatest good for the greatest number of people. In essence, Hardin was talking about human population control; he wanted to know if humans could have their cake and eat it too.

Deductively and simply he showed that the optimum population is less than the maximum, although he admitted that the latter term is difficult to quantify. Humans want the maximum good for the maximum number of people, but differ among themselves in their definitions of "the good." Hardin used the term "tragedy" in its original Greek sense of downfall caused by a remorseless and inexorable fate rather than its modern connotation of personal unhappiness. He used the example of a herdsman who shares a pasture open to all herdsmen in a specific community. Since all who are using the pasture want to graze as many sheep as they can on it, the pasture eventually reaches its carrying capacity. Thereafter, when any herdsman adds another sheep to his flock, the result is that that herdsman has a net gain of almost +1. Because of the shared overgrazing, all others realize a net loss of some fraction of 1. The mathematics and illustration are simple but the results inarguable. Certainly the tragedy of the commons led to the near extirpation of the American bison, many cetaceans, tigers, rhinoceros, and the list continues. Dugongs and dodo birds were less fortunate. Moreover, the example of the commons can be readily extended to the use of rivers and streams for agriculture, hydroelectric power, or fishing (upstream = benefit, downstream = impoverished). It also may be applied to any contemporary marine fishery.

Hardin's logic extends further, but in the opposite direction, when he addresses such issues as the pollution of air or water and the disposal of wastes in leaky landfills or at sea. The tragedy of the commons includes putting certain things into the natural world as well as taking them out; thus it encompasses the release of carbon dioxide and other greenhouse gases by industrialized nations that cause warming worldwide. When the herdsman states his case to a board of inquiry, few could argue with his rationale; he merely wants to add one more animal to his herd. Tragically, that is the conclusion reached by each and every herdsman. Hardin was speaking directly to the issue of human overpopulation that exacerbates the tragedy of the commons, but implicit throughout his message is the need for conservation.

Rate of extinctions

The condition of rarity generally precedes extinction of a species, even though passenger pigeons numbered in the millions less than a century before they died out entirely. Endangered species tend to have the smallest populations and are hence the most likely to die out in the short term. While extinctions can occur for a host of reasons, they can be broadly categorized into two types: systematic pressures and random events. The former include such human activities as habitat destruction, overharvesting, and behaviors that affect the rate of climate change—all of these are factors that can systematically push a species toward extinction. Random pressures, however, are stochastic and may be less obvious. They include such catastrophic events as fires and floods; disease; or demographic fluctuations caused by genetic drift, bottlenecking or inbreeding depression, often acting in combination.

Of course, extinctions are not new events. Fossils provide a clear record of many terrestrial and marine species that once lived on earth and do so no longer. The naturalist Alfred Russell Wallace wrote over a hundred years ago that "...we live in a zoologically impoverished world, from which all the hugest, and fiercest, and strangest forms have recently disappeared...." For Wallace, "recent" meant the Quaternary period, about 12,500 to 11,000 years ago; and the animals he referred to varied according to the continent on which they lived. In the global ocean and in Africa and Asia, there were relatively few Quaternary extinctions; in the Americas, Madagascar, and Australia, however, extinction was nothing short of cataclysmic in its reach. Almost three-quarters of the genera that weighed over 97 lb (44 kg) died out from North America. Australia fared even worse; the continent lost every terrestrial vertebrate species larger than a human being. These included carnivorous kangaroos, a horned tortoise the size of a small automobile, and a monitor lizard almost 22.9 ft (7 m) long. Many small mammals, reptiles, and flightless birds also died out. In fact, eggshells from the giant flightless bird *Genyornis newtoni* indicate that it went extinct simultaneously in three disparate locations. These extinctions occurred during a time in the Quaternary when climate change was relatively mild. They also happened to coincide with the coming of humans to Australia.

Of course, species extinctions also predate human influence and have occurred throughout history as the consequence of climate change, natural selection, and evolution—a fact erroneously used as evidence that conservation is unnecessary. Unfortunately, a consensus exists among many scientists that the earth's species are vanishing at an alarmingly fast rate when compared to background levels of extinction. Sobering warnings come from esteemed scientists like Paul Dayton, Paul Ehrlich, Jane Lubchenco, Stuart Pimm, Michael Soulé, and E. O. Wilson, who have each worked for decades in their respective fields. We dismiss their opinions at grave risk. E. O. Wilson, professor and curator of entomology at Harvard University's Museum of Comparative Zoology, predicts that as many as 20% of the species alive today will be extinct by the year 2030 if conservation measures are not implemented.

Conservation biology

Conservation biology is an interdisciplinary science that attempts to integrate the fields of biology, ecology, economics, and conservation. Scientists Michael Soulé and Bruce Wilcox held the First International Conference on Conservation Biology in the United States in 1978 to address such problems as extinction and habitat loss. Those who attended were ecologists and population biologists already studying these issues. The discipline of conservation biology was founded on the principle that advances in population biology could be applied to conservation issues and put into practice by managers of protected areas. Organizations like the World Conservation Union's (IUCN) Species Survival Commission (SSC) had emerged from the improved quantification of biological diversity as well as the need for conservation. As of 2003, the SSC is a clearinghouse for information on the health and status of species worldwide. Toward that end, the SSC publishes a Red List that uses set criteria (population size, distributional range, rates of decline) to assess and manage extinction risk. As of the year 2000, the Red List included all known birds and mammals on its inventory of 18,000 species. Of these, 11,000 are designated as threatened. The reader should bear in mind that there are about 1.5 million species of insects alone that have been described in the scientific literature. Plants have evolved together with insects, and their species numbers are similarly diverse. Conservative estimates place the total number of eukaryotic (multicelled) species at somewhere near 7 million, so the compilers of the Red List have much information to gather.

Need for biodiversity

When a species is commercially important and goes extinct, its loss can be assigned a dollar value. Atlantic cod, American mahogany, and great auks are listed by the IUCN Red List as Vulnerable, Endangered and Extinct species respectively. All are or were harvested commercially, and all could be ascribed some worth by the industries that made use of them. Such large organisms as whales, tigers, bison, and manatees are mammalian megafauna that, while not commercially important, hold symbolic or aesthetic values for humans. But what about the lower metazoans, the species described in this volume of *Grzimek's*? Most people would not know that an ophiuroid is related to a sea star or that ascidians in their early life possess a structure very like a human notochord, let alone value these organisms. "Priapulan" is harder to pronounce than to describe, but few people will have even seen the word. Loriceferans were described for the first time in 1983 as resembling tiny "ambulatory pineapples." People might realize that sea cucumbers do not improve either the taste or the appearance of garden salads, but if one refers to them as holothuroids, most will respond with blank stares. When the poor name recognition of some of the lower metazoans is combined with their lack of commercial value, the fact that some of their populations are close to the vanishing point makes their value seem questionable.

The loss of any species, however, goes beyond its monetary worth. Certainly the morality of allowing species, including many that have been evolving longer than humans have, to suffer extinction as the result of human interference is indefensible. But a more scientific and impartial reason to prevent extinction exists: biodiversity. First coined by E. O. Wilson in 1986, the term "biodiversity" refers to the sum of all diversity, all the variability in a given area that is genetic, conferred by other species, or inherent in the ecosystem itself. Simply put, biodiversity is the natural variability among living organisms and everything that fosters that variability.

From a strictly anthropocentric standpoint, humans have benefited directly and greatly from biological diversity. Penicillin comes from the mold *Penicillium* sp. The tree *Calophyllum lanigerum* was found to produce a substance that inhibits replication in the AIDS virus. Aequorin, collected from the jellyfish *Aequorea victoria*, is a common fluorescent marker used in medicine and microbiology. Studies of the venom of a South American pit viper led to the discovery of the angiotensin system that regulates human blood pressure. Venom from marine cone snails has given rise to a synthetic analgesic and is used to keep nerve cells alive following ischemia. The compound cytarabine is more effective at inducing remission in one form of leukemia than any other drug. The polymerase chain reaction (PCR), a technique that revolutionized the field of microbiology, was made possible because of an enzyme discovered in a bacterium in the hot springs of Yellowstone, Wyoming. PCR enables us to perform rapid DNA testing of criminal suspects. It allows microbiologists to modify the genomes of bacteria, insert specific genes into them, and ultimately produce genetic modifications of other plants and animals. The thermophilic bacteria found in those hot springs are more similar to bacteria found at hydrothermal vents in the deep sea than to common bacteria like *Escherichia coli*; scientists have classified them in their own kingdom, Archaea.

As we find new organisms or look more closely at familiar ones, we discover more human uses for those organisms. This fact underscores the very tangible benefits to humans of conservation—even if it is based on aesthetic values, as was the inception of Yellowstone National Park over a century ago. Moreover, conservation offers emphatic demonstrations of the value of biological surveys because scientists continue to find new organisms even at the most general level of classification, the animal kingdom.

Yet even species that have no present or apparent commercial use benefit humans in ways that are taken for granted. Processes as fundamental as natural selection and evolution depend on genetic variability. Plants require nitrogen to grow. Although nitrogen is the largest single component of the air humans breathe, most plants cannot use it in its stable atmospheric form N_2. Some bacteria and blue-green algae help to "fix" atmospheric nitrogen into forms that can be used by plants. Different species of bacteria form different types of nitrogenous byproducts. Some bacteria are even endosymbiotic and live in the root tissues of legumes. As organisms die and then decompose into their elemental components—mostly water, carbon, nitrogen and some minerals—which are eventually recycled, the very mechanics of nutrient and energy transfer are dependent upon a diversity of plant and animal species. Humans do not ascribe a monetary value to such ecosystem services as decomposition, carbon, or nitrogen cycling. They are, however, invaluable because life as we know it would not exist without them.

Risk assessment

On a practical level, it is difficult to assess which species are most at risk. Because biodiversity encompasses the range of variation, from individuals to populations to habitats themselves, it is virtually impossible to enumerate and quantify. Nevertheless, it is precisely that complexity that is worth conserving. In the absence of long-term data and exact numbers for such ecological parameters as abundance and diversity, conservation efforts usually focus on surrogate species and assume that the protection of some species will include others. Generally, surrogate species fall under three categories: flagship species, umbrella species, and biodiversity indicators. The first group includes well-known or well-publicized species that appeal to the general public. Umbrella species are those that require such large tracts of habitat that their protection envelops other species; for example, large mammalian carnivores. The third surrogate category includes sets of species or taxa whose presence indicates a rich variety of other species. For example, a species of bee may indicate several species of plants it pollinates and they, in turn, may provide habitat to a number of species of birds, invertebrates or mammals. In this particular example, the bee functions as a "keystone" species, since its activities support the well-being of others.

Species are often interdependent in ways that are less apparent. For example, white wartyback mussels (*Plethobasus cicatricosus*) are dependent on a fish host in their larval phase. When rivers in which the mussels and fishes lived were dammed, the fishes could not survive in the colder river water released from those dams and died out. Thus, although white wartyback mussels can still be found, the population cannot reproduce and is functionally extinct, a "living ghost." Such rare species as white wartyback mussels run a higher risk of extinction than common species.

Endemic species are restricted to a given area and are rare by definition; that is, they are found nowhere else. Endemism is common among island flora and fauna because they have evolved more or less in isolation from other populations. Over time, natural selection acts to mold such species into what are often very specific niches; they adapt themselves to very narrowly defined habitats. The many shapes of bills found on the finches of the Galapagos Islands may serve as a common example. Endemic species are commonly used surrogates in conservation strategies.

Habitat conservation

Organisms have evolved to live in certain habitats. It stands to reason, then, that the most severe problem in protecting global biodiversity concerns habitat destruction and fragmentation. Habitats are generally defined by myriad physical parameters like temperature, rainfall, elevation, topography, salinity, soil type and many others. For tuna, habitat might be generally defined as the pelagic ocean within a certain temperature range. For tiny tardigrades, or moss bears, habitat may be forest moss, lichen, beach sand or arctic tundra. For gnathostomulids, the interstices between silt-sized sand grains in the deep sea comprise their habitat. Flightless birds and many herptiles (reptiles and amphibians) may not require much physical space but may be highly specific regarding the space they can inhabit because of such factors as predators, food availability, or breeding sites. An organism's habitat is thus defined by a combination of physical and biological factors.

Biodiversity is not equally distributed but varies from ocean to tidepool, entire rainforest to one strangler fig tree, from temperate zones to tropical. Ecologists and conservationists understand that biodiversity is unrelated to aesthetics or the sweeping vistas of national parks. In fact, habitats with some of the highest numbers of species ("species-rich") include such places as streams, wetlands, coastal mangroves, rainforests, sloughs and estuaries—places often targeted by farmers and developers.

Hotspots are found in areas where the habitats of several rare species overlap. Because so much diversity is concentrated within relatively small areas they are, in fact, hot spots for extinction. The tropics have an inordinate number of hotspots because both species diversity and endemism increase as one travels from the poles to the equator. By way of example, the southeastern Appalachian mountains and all of southern California have many endangered species, but the vast majority of endangered species in the United States occur in the much smaller area of the Hawaiian Islands.

As of 2003, habitat has been already greatly reduced within biodiversity hotspots. This fact is of great concern to scientists. Worldwide, approximately two-thirds of all eukaryotic (multicellular) species occur in humid tropical forests. As the twenty-first century begins, these same forests are being cleared at a rate of approximately 386,100.5 mi^2 (1 million km^2) every 5–10 years. Logging and burning account for several times that loss. From the time a species' habitat begins to decline to the time when the population of that species also declines there will usually be a lag. Thus, the loss of habitat may initially cause only a few extinctions as small pockets of habitat remain; then, however, as habitat is lost entirely or so fragmented that some species cannot survive, individuals die out and the number of extinctions rises. The concern here in this "fewer extinctions now, more later" scenario is that by the time scientists have quantified the loss, it will be too late to stop it.

Consequently, designating and protecting hotspots may be a logical first step in conservation. Myers and colleagues calculate that a staggering 46% of all plant diversity involves endemics. They also estimate that 30–40% of all terrestrial vertebrates could be protected in 24 hotspots. Moreover, those 24 hotspots would span only about 2% of the earth's surface. Protecting hotspots makes economic sense as well. Although the expense of conservation per unit area varies hugely, from less than a cent in United States currency to over a million dollars per 0.4 mi^2 (1 km^2), costs are generally lower in less developed countries. More importantly, these same countries often have the most left to conserve. Furthermore, as habitat becomes fragmented through development or exploitation, the costs of mitigation and conservation rise. Pimm and Raven agree that the selective protection of hotspots is necessary but caution that it is insufficient for long-term conservation of biodiversity. Usually conservation biologists favor increasing the size of protected areas as a means of including more organisms and as safeguarding against some of the random causes of extinction discussed previously. In some cases less diverse but cheaper habitats can be purchased, ultimately conserving the same number of species on larger or more numerous tracts of land.

Marine conservation and shifting baselines

The conservation strategies outlined above are based largely on terrestrial research. This bias may result in part from the fact that the marine environment was long considered less at risk for environmental degradation because of its sheer immensity and the "unlimited bounty" of the seas. Many marine invertebrates and vertebrates have planktonic larvae capable of spreading over great distances in ocean currents; such species would be less likely to suffer from genetic bottlenecks, inbreeding, or the risk associated with endemic status. Yet in fact the ocean's bounty is limited. Many scientists are concerned that we may be seeing those limits breached.

Overfishing refers to fishing practiced unsustainably. Overfished species are species that have had their numbers so depleted that stocks may never recover. In most coastal ecosystems, manatees, dugongs, sea cows, monk seals, crocodiles, swordfish, codfish, sharks, and rays are functionally or formally extinct. The data compiled by these authors are impressive and cause for foreboding. In order to detect ecological trends a baseline for comparison is necessary, as is a distinction between natural and human-caused changes. As a starting point for such a baseline, Jackson and Kirby gathered paleoecological data, beginning about 125,000 years ago, together with archeological data from human coastal settlements from about 100,000 years ago. To augment these data, they made use of historical records from documents, charts and journals from the fifteenth century. Ecological records from scientific literature spanning the twentieth century completed their data set. Based on these data the authors found that from the onset of overfishing, lag times of only decades to centuries preceded large-scale changes in ecological communities.

In some cases, such time lags existed because other species filled in the gap left by the overfished species. For example, sea otters were all but eliminated from the northern Pacific by fur traders in the 1800s. Because the voracious appetite of sea otters kept sea urchin populations in check, sea urchin numbers increased and decimated kelp forests. Sea otters off the southern California coast were similarly wiped out at approximately the same time as those in the northern Pacific; however, the California kelp forests did not begin to disappear until the 1950s. Diversity across trophic levels was the reason for the lag time between overharvest and threshold response. Predatory fishes like sheephead also ate sea urchins, and spiny lobsters and abalone competed with urchins for kelp. Together these animals effectively "shifted over" to occupy a portion of the ecological niche formerly occupied by the sea otters. Since sea urchins have become a popular fishery, some well-developed kelp forests have returned. Unfortunately, they now have only a vestige of their former complexity. Kelp forests off southern California now lack the trophic diversity of sea otters and such predatory fishes as sheephead, black seabass, and white seabass that they once possessed. Unregulated fisheries exist for echinoids like sea cucumbers, for crabs, and for small snails. The numbers of abalone—greens, reds, whites, and blacks—have dwindled from overharvest and disease. The once diverse southern California kelp forest community has been reduced to a community of primary producers. Thus overfishing affects not only the target species, but dramatically alters ecosystem diversity when "keystone" species are removed.

Nor are coastal ecosystems the only habitats affected. Pelagic longlines are the most widespread fishing gear used in the ocean and threaten many open ocean species. Some species form legitimate fisheries; such others as sea turtles constitute by-catch. Because many pelagic animals have such extensive habitat and evolved to swim great distances often at high speeds, they can be extremely difficult to study. Nevertheless, we know that billfishes, tuna, and sea turtles are in need of conservation because they have been subjected to such intense exploitation. Relatively less is known about open ocean sharks, but with the exception of makos their numbers are estimated to have declined by at least half in less than two decades. Such large animals as these generally bear fewer young, reproduce less often, and do so at an older age. In ecological terms, they have a low intrinsic rate of increase. This low rate means that their ability to rebound if fishing pressures are decreased is slim, and that conservation efforts will have to be long-term if their numbers are to increase.

Jellyfish, medusae, ctenophores and siphonophores are invertebrate predators that typically feed on the same prey as larval and adult fishes do. Concern exists that jellies may be sliding over to fill the void left by declining pelagic predators. Although Carr and his colleagues studied fishes, their field experiments provide insight as to how such "cascading negative consequences" occur. They found that by removing important predators (groupers or jacks) and other highly competitive fish (territorial damselfishes), as is often done by fishermen as well as by the aquarium trade, species interactions changed. As species interactions decreased, population fluctuations increased. As fish populations grew more unstable, the likelihood of extinction increased locally and regionally. In part, jellies are able to shift and fill the ecological "holes" left by declining fish stocks because they can reproduce quickly and in great numbers. *Mnemiopsis leidyi*, a tiny comb jelly, was introduced into the Black Sea, probably when a grain ship pumped out her ballast. The *Mnemiopsis* population was able to take advantage of habitat conditions that were unfavorable to potential competitors; as a result, *M. leidyi* populations peaked in the late 1980s and 1990s. Over this same time *Mnemiopsis* consumed most of the zooplankton production that had previously been taken up by commercial fisheries. Consequently commercial fisheries in the Black Sea went virtually extinct themselves. This example illustrates both the shift in keystone species as well as the devastating effect that introduced species can have at the level of an entire ecosystem.

A diver with a camera looking at a coral reef near Lizard Island in the Great Barrier Reef. (Photo by A. Flowers & L. Newman. Reproduced by permission.)

In addition, fisheries suffer because the fishing industry is a powerful political lobby. Ample scientific evidence exists that illustrates the need for change in fisheries management. The industry itself, however, continually clamors for additional proof, unable or unwilling to listen to the nails being driven into its own coffin. If a dearth of evidence exists, it is any that can demonstrate that fisheries are harvested sustainably. In part, fisheries may be slow to acknowledge problems because, as the numbers of fish decrease, technological development has advanced in the fishing industry—such as satellite imagery that can be downloaded to computers; sensitive sonar that can locate fish schools; large fleets of fast boats—disguising diminishing stocks by more efficiently harvesting what remains.

Aquaculture is commonly believed to relieve pressure on fisheries. It is true that between 1986 and 1996 the global production of fishes by aquaculture more than doubled. Aqua-

The calm mangroves of the Florida Keys are a protective network of canals for manatees and a diverse range of marine flora and fauna. (Photo by A. Flowers & L. Newman. Reproduced by permission.)

culture alone, however, is not an answer; by reducing wild fish supplies for seedstock collection or for feed, aquaculture can in many ways be detrimental. Hundreds of thousands of Atlantic salmon raised in pens in the Pacific have escaped to locations where they can hybridize and genetically weaken native stocks. Atlantic salmon escaped from Atlantic pens can also interbreed with wild stocks and interfere with the latter's ability to find their spawning grounds, which is a trait that is passed on genetically. Other problems posed by aquaculture include the spread of diseases amongst pens and to wild stocks as well as the discharge of untreated effluent and nitrogenous wastes that result in eutrophication.

Marine reserves are controlled-take areas that have been helpful in restoring depleted fish and invertebrate populations. Because open ocean species as well as fishing fleets move around, however, the effectiveness of reserves to help species living in the open ocean is equivocal. Reserves, although helpful, are not enough; effective conservation will require intelligent consumer choices. The Monterey Bay Aquarium is making an attempt to educate the public regarding sustainable harvesting of fishes. Toward this end the aquarium offers a free "Seafood Watch Card" that takes into account the sustainability of the fishery as well as the ecology of the species; then rates that species accordingly. Informed consumers can make more intelligent purchasing decisions and use their buying power to encourage conservation and improved management of fisheries.

Global warming

Aside from being responsible for causing the most species extinction worldwide, tropical deforestation creates 20–30 percent of global carbon emissions, with the burning of fossil fuels accounting for most of the remainder. Although it is commonly thought that carbon dioxide emissions are to blame for the rapid warming trends observed in recent decades, such other noncarbon greenhouse gases as chlorofluorocarbons and nitrous oxides contribute as well. Aerosols are tiny particles emitted into the air as pollution, which we see as visible smog or haze. Aerosols alter the brightness of clouds and increase solar heating in the atmosphere. These changes serve in turn to weaken the earth's hydrologic cycle, reducing rainfall and fresh water supplies.

Biological indicators for global warming abound. Species from butterflies to marine invertebrates show a tendency to migrate northward; by so doing, they act as indicators of climate change. Like extinction, global warming predates human influence; however, the global effects that humans can and do have on the earth's climate are facts that cannot be dismissed. As with concerns over extinction, global warming is not an unfounded notion propounded by aging hippies or ecoterrorists. Rather, it is a measurable phenomenon that concerns scientists around the world. Warming has been shown to increase the spread of infectious diseases; and in concert with the overharvesting of resources terrestrial, freshwater or marine, temperature change can have synergistic affects that lead to more extinctions and loss of biodiversity. Warming causes bleaching in coral reefs as well as some sea anemones. Coral reefs fringe no less than a sixth of the world's coastlines. They are species-rich and more biologically diverse than any other shallow-water marine ecosystem.

An obvious way to decrease human contribution to global warming is to restrict the release of greenhouse gases. Now, as we contemplate using the deep sea to store excess carbon dioxide, scientists are asked to assess the risks. Certainly sequestering carbon in the deep sea seems a logical way to decrease atmospheric input and concomitant warming. This approach, however, is only a bandage solution because it fails to address causative agents. Moreover, many of the lower metazoans discussed in this chapter live in the deep sea. Deep sea organisms generally have slow metabolism and difficulty dealing with even minor changes in the acidity or alkalinity of sea water. Dumping carbon dioxide into the deep sea causes pH changes of a little to a lot depending on proximity. It impairs the metabolism of deep sea animals and weakens their exoskeletons, either of which causes increased mortality. As a pool of carbon dioxide forms in the deep sea, such destructive changes are not limited to the benthic fauna living on top but extend to the benthic infauna as well—the habitat occupied by gnathostomulids, loriciferans and their metazoan kin.

Humans claim to cherish our natural environment, yet each year we lose between 14,000 and 40,000 species from tropical forests alone. Between one-third to one-half of the land surface has been transformed by our species; we use more than half of the accessible freshwater. Gone with those species may be life-saving medicines, models for research, or services to the ecosystem that sustain our quality of life. Not that of future generations, but our own. Through it all we must remember the importance of biodiversity and conservation. Conservation is not a luxury; rather, it has been a luxury for humankind to progress as far as the twenty-first century without putting proper emphasis on conservation. Designating reserves can no longer be an opportunistic action performed at the whim of politicians with financial ties to business and industry. Can conservation be a priority for the twenty-first century? Humans are too knowledgeable for excuses and too skilled to do nothing. What is biodiversity worth? What price conservation? Are these questions that science can answer? When it does, are we willing to listen?

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Organizations

IUCN Species Survival Commission. Rue Mauverney 28, Gland, 1196 Switzerland. Phone: +41 (22) 999 0000. Fax: +41 (22) 999 0002. E-mail: ssc@iucn.org Web site: <http://www.iucn.org>

Rob Sherlock, PhD

◆

Calcarea

(Calcareous sponges)

Phylum Porifera

Class Calcarea

Number of families 22

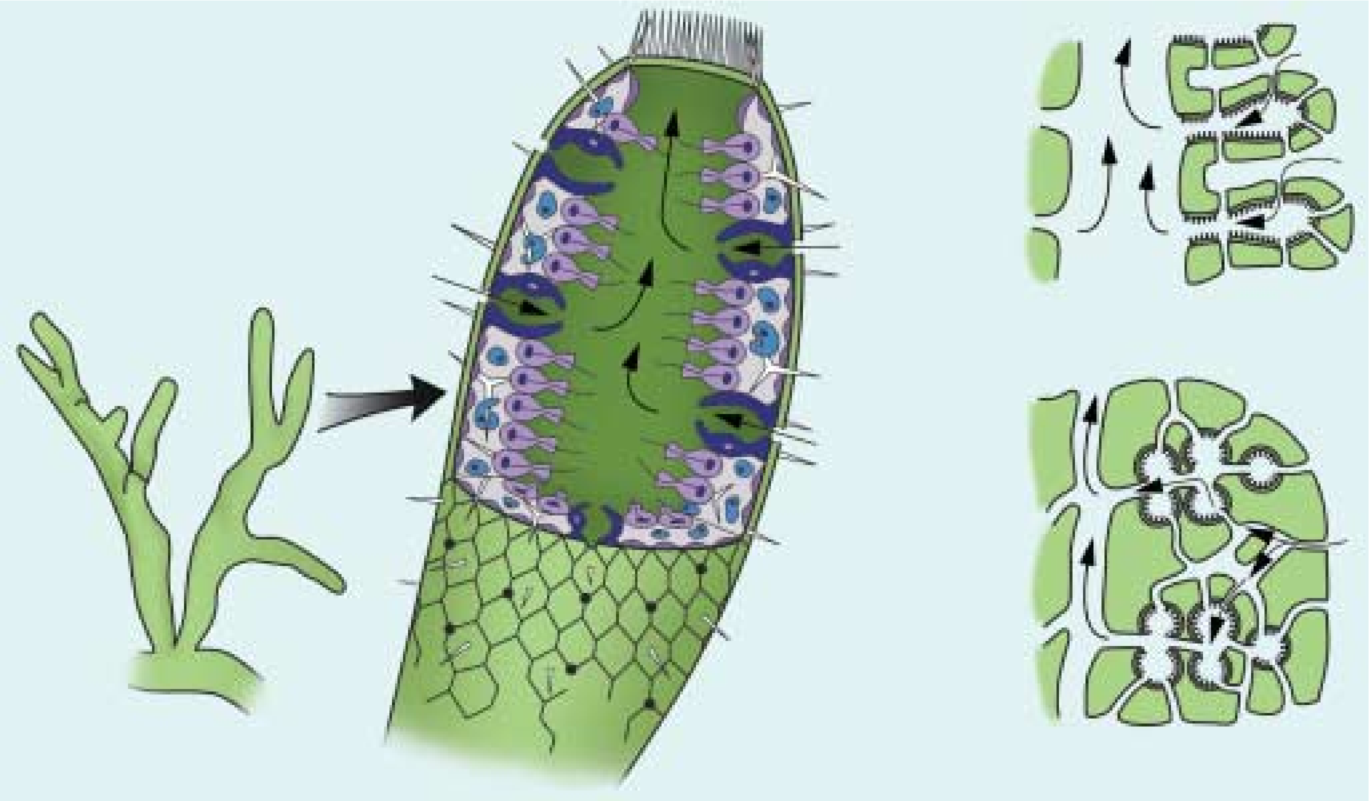
Thumbnail description
Marine sponges with calcareous skeletal elements (spicules)

Photo: A calcareous sponge in a cryptic reef environment in waters near the Little Cayman Islands, at a depth of 82 ft (25 m). (Photo by ©Gregory G. Dimijian, M. D./Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The fossil record of unambiguously identified Calcarea is relatively poor and fragmented. Most calcareous sponges in the fossil record were classified as either stromatoporoids, chaetetids, archaeocyaths, inozoans, pharetronids, or sphinctozoans. They are common in the Paleozoic and Mesozoic, however, rare in the Cenozoic. It is now established that many of these forms actually belong to several groups of demosponges because of the possession of primary siliceous spicules, and only few to Calcarea (pharetronids and some sphinctozoans). Identification of "true" calcareous sponges in the fossil record is difficult because fossil remains often lack diagnostic spicules at all. Heteractinida, characterized by a spiculate (consisting of six-rayed heteractinid octactines, polyactines) and aspiculate calcitic skeleton, are now regarded as an extinct order of Calcarea, restricted to the Paleozoic. The oldest probable calcareous sponge with affinities to modern subclass Calcaronea (*Gravestockia pharetroniensis* Reitner, 1992) was described from the lower Cambrain of South Australia. The assignment of many records of so-called "Pharetronida," calcareous sponges with a rigid calcareous skeleton, to subclasses Calcaronea or Calcinea is difficult if they do not possess characteristic spicules to allow precise assignment. However, most Pharetronids probably belong to subclass Calcaronea. The majority of modern spiculate calcareans would be found as dissociated spicules in the fossil record; there is only one record from the middle Jurassic at King's Sutton, Northamptonshire, where the form and arrangement of a calcareous sponge was preserved (*Leucandra walfordi* Hinde, 1893).

Calcarea are regarded as one of four classes of the phylum Porifera (three extant [Demospongiae, Hexactinellida, Calcarea] and one fossil [Archaeocyatha]), distinctive in possessing a spicule skeleton composed exclusively of calcium carbonate and being the only poriferan taxon realizing all three stages of development of the aquiferous system (asconoid-syconoid-leuconoid). There is still dispute about the true phylogenetic relationships of the three extant sponge classes, including also the relationship of the class Calcarea to other (higher) diploblastic taxa like Ctenophora and Cnidaria. Two competing hypotheses group a) Hexactinellida + Demospongiae more closely together based on the possession of silicious spicules ("Silicea") in contrast to Calcarea ("Calcispongia") and b) Demospongiae more closely with Calcarea based on the possession of a cellular pinacoderm ("Cellularia"/"Pinacophora") to the exclusion of Hexactinellida, which possess a cyncitial tissue structure ("Symplasma"). Both proposals, however, assume poriferan monophyly. More recently, several authors have suggested from ribosomal DNA sequence data that Calcarea might be more closely related to the phyla Ctenophora/Cnidaria than to the other two extant classes of Porifera, rendering phylum Porifera paraphyletic. Class Calcarea was elevated to phylum status ("Calcispongia," a term that was already used in the mid-nineteenth century) (Zrzavy, et al., 1998; Borchiellini, et al., 2001), but as yet without robust statistical support (e.g., Medina, et al., 2001). However, this proposal is not followed in the most comprehensive systematic treatment of sponges to date, the *Systema Porifera* (Hooper and Van Soest, 2002) and the issue of sponge paraphyly is at the time of writing (2003) far from being resolved. Therefore, it should be regarded as still contentious until further corroboratory data, such as a molecular multi-locus approach, is presented. However, new chemotaxonomic data from lipid biomarkers (Thiel, et al., 2002) support a closer relationship of Hexactinellida and Demosponges. Although this



Calcareous sponge anatomy. (Illustration by Kristen Workman)

confirms that Calcarea are chemotaxonomically different from "Silicosponges" or "Silicea" (Demospongiae + Hexactinellida), it does not necessarily imply sponge paraphyly.

Number of classes and families: 1 class (Calcarea); 2 subclasses (Calcinea, Calcaronea); 5 orders (2 in Calcinea: Clathrinida, Murrayonida; 3 in Calcaronea: Leucosoleniida, Lithonida, Baeriida); 22 families; 75 genera; about 500 described species.

Physical characteristics

Calcareous sponges are mostly small and inconspicious; they occur in a variety of forms, as single tubes, sometimes vase shaped, a mass of small tubes ("cormus"), a bushy arrangement of single tubes, or sometimes massive without any apparent symmetry. Three types of aquiferous system are realized in Calcarea: asconoid, all internal cavities are lined by choanocytes (flagellated cells) without folding of the choanoderm; syconoid, simple folding of the choanoderm; and leuconoid, choanocytes are arranged in discrete "choanocyte chambers."

Calcareous sponges range from minute size an inch or less (few millimeters), to about a maximum of about 12 in (30 cm) (*Pericharax heteroraphis*). They are mostly colorless (whitish to beige), sometimes bright yellow (*Leucetta chagosensis*), dark greenish-brown (*Pericharax heteroraphis*), or fluorescent red/orange (*Leucetta microraphis*, sometimes).

Calcareous sponges have a skeleton that is made of calcium carbonate (calcite), composed of free diactines, triactines, tetracines, and/or polyactine spicules, to which a solid basal calcitic skeleton may be added, with either cemented basal spicules or which is fully embedded in an enveloping calcareous cement. Calcareans are viviparous and have blastula larvae.

Distribution

Calcareous sponges are found globally in all oceans, from intertidal to the deep sea, but not the abyss.

Habitat

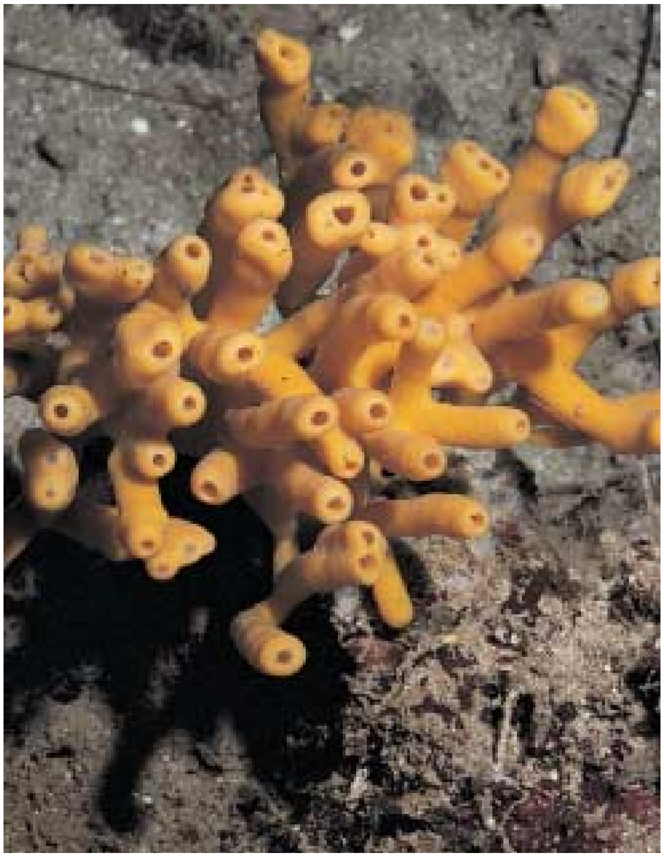
Calcareous sponges live in diverse habitats. In tropical coral reefs, they dwell mainly in shaded and/or cryptic habitats and prefer calmer waters.

Behavior

Not applicable; calcareous sponges are sessile filter feeders.

Feeding ecology and diet

Calcareous sponges are sessile filter feeders, whose main diet is dissolved organic matter and small particulate matter (bacteria) filtered from seawater by pumping activity.



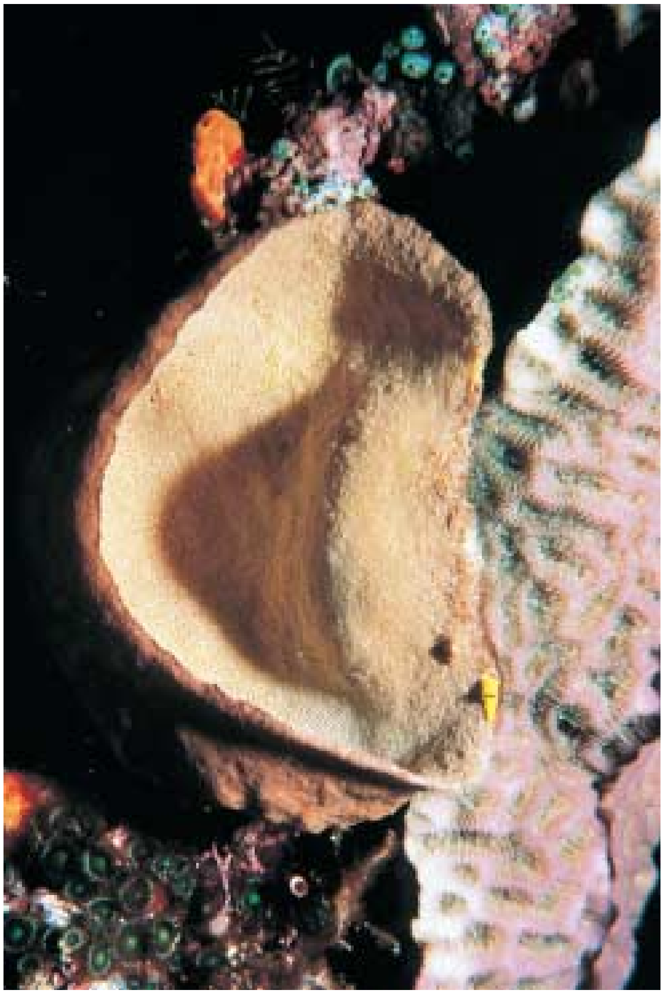
Clathrina sponges are usually dull colored and less than 0.16 in (4 mm) long. These were seen in Papua, New Guinea. (Photo by Ron and Valerie Taylor. Bruce Coleman, Inc. Reproduced by permission.)

Reproductive biology

Calcareous sponges have internal fertilization, with egg size ranging from 25 to 100 μm. They are sexual and viviparous, with some species probably asexual by budding.

Conservation status

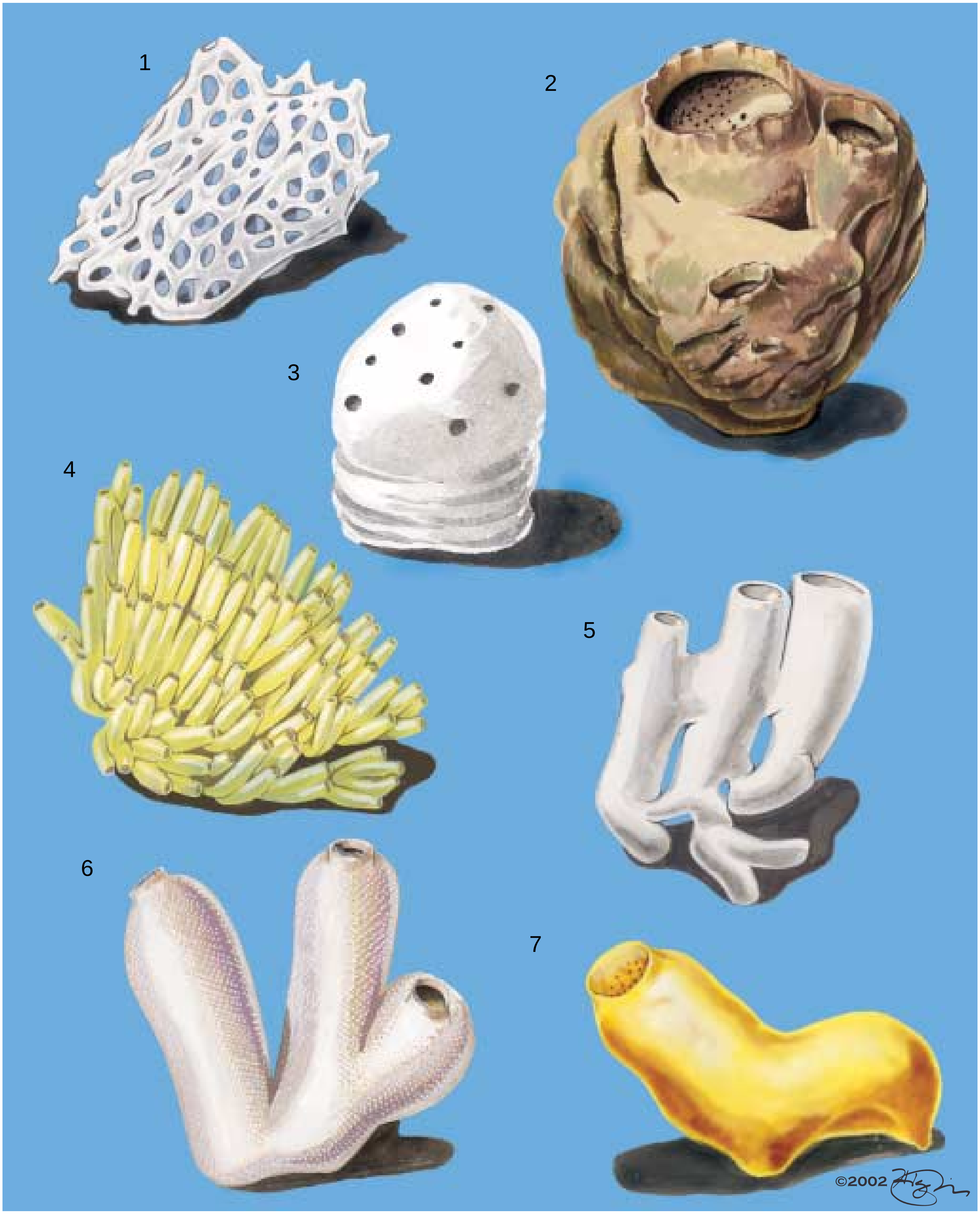
No species are listed by the IUCN.



This calcareous sponge *Pericharax* sp. has been eaten by nudibranchs *Notodoris*. (Photo by Bill Wood. Bruce Coleman, Inc. Reproduced by permission.)

Significance to humans

There is no known significance of calcareous sponges to humans.



1. *Clathrina heronensis*; 2. *Pericharax heteroraphis*; 3. *Petrobiona masselina*; 4. *Soleneiscus radovani*; 5. *Grantiopsis heroni*; 6. *Sycon capricorn*; 7. Lemon-sponge (*Leucetta chagosensis*). (Illustration by Jonathan Higgins)

Species accounts

No common name

Clathrina heronensis

ORDER

Clathrinida

FAMILY

Clathrinidae

TAXONOMY

Clathrina heronensis Wörheide & Hooper, 1999, Heron Island, at Wistari Channel, Great Barrier Reef.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

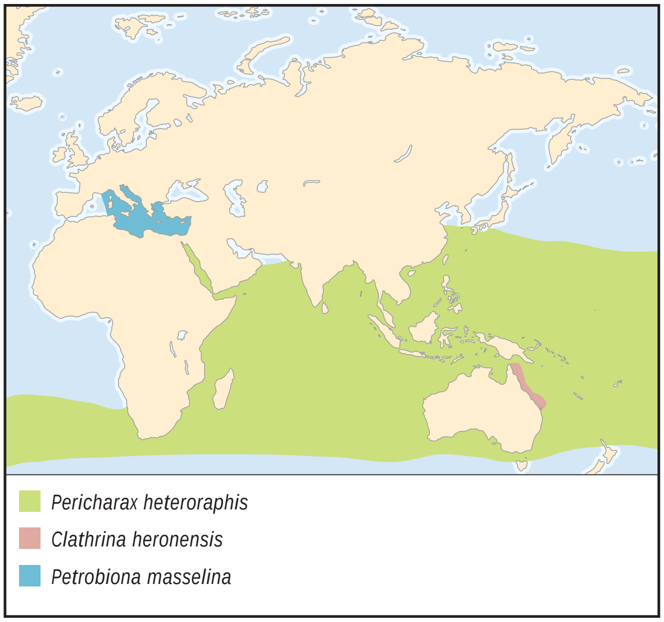
Mass of loosely anastomosing tubes, approximately 0.04 in (1 mm) diameter, with fairly large space between tubes, whole sponge 1.2 × 0.8 in (3 × 2 cm), flat. Life color white. No visible oscules nor distinct exhalant system. With soft, compressible, and delicate texture, smooth surface. Skeleton consists solely of a layer of irregular triactines. Triactines tangentially orientated, actines sometimes overlap. No differentiation or zonation of skeleton, appears to be uniform throughout cormus (sponge body). Asconoid grade of aquiferous system. One type of triactines, with a more-or-less blunt tip, actines measuring 80–130 × 8–12µm.

DISTRIBUTION

Currently only known from the Great Barrier Reef, Australia. Putative member of the cosmopolitan species group *Clathrina coriacea.*

HABITAT

Cryptic, under rubble at reef crest, intertidal.



BEHAVIOR

Sessile.

FEEDING ECOLOGY AND DIET

Sessile filter feeder.

REPRODUCTIVE BIOLOGY

Viviparous, not much known.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Lemon-sponge

Leucetta chagosensis

ORDER

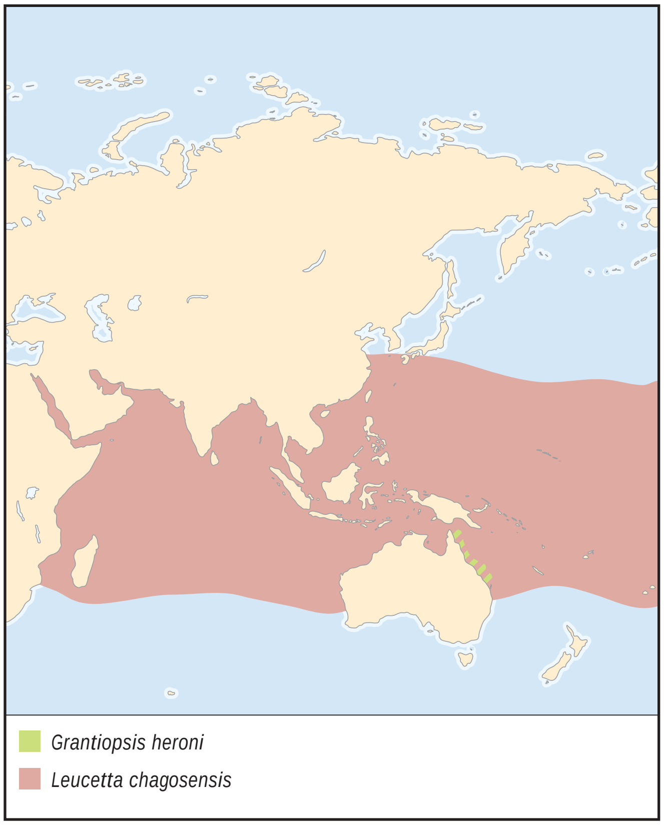
Clathrinida

FAMILY

Leucettidae

TAXONOMY

Leucetta chagosensis Dendy, 1913, Chagos Archipelago, Indian Ocean.



OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Massive, globular, slightly elongated-globular to pyriform or elongate growth form. Specimens range from 0.39–2.0 in (1–5 cm) in size. Bright yellow color in life (while alive). Globular specimens with one prominent osculum with a naked "lip." Elongated specimens with a few oscules with a naked "lip" on the ridge of the sponge body. Firm and smooth, with slightly translucent surface. With a distinct thin cortex, up to 50 µm thick, sustained by tangentially arranged small regular triactines (three rayed "mercedes-star" spicules), with some large triactines also scattered tangentially in the cortex. Small subdermal cavities present (50–150 µm diameter). Choanocyte-chamber free zone of sub-dermal cavities with a thickness of up to 250 µm. Large regular triactines also found here. A peculiar, special, small sagittal triactine only found in the oscular rim ("lip"). Dense irregular meshwork of small regular triactines form choanoskeleton. Larger triactines occasionally irregularly scattered in the choanosome in small numbers. Small tetractines (four-rayed spicules) concentrated around exhalant canals. Leuconoid aquiferous system. Spicules small: larger regular triactines about 250–500 × 25–50 µm, smaller regular triactines 100–200 × 10–25 µm; regular tetractines of the excurrent canals 90–125 × 10–20 µm.

DISTRIBUTION
Probably circum Indo-Pacific, from (southern) Red Sea to French Polynesia in most tropical coral reefs. Recorded from Indo-West Pacific, in Western Australia (Houtman Abrolhos, Fremantle), Queensland (Great Barrier Reef); also Indian Ocean (Chagos) and western Pacific (New Caledonia, Fiji, Vanuatu, French Polynesia).

HABITAT
In crevices and under overhangs of coral bommies, also abundant in illuminated reef habitats.

BEHAVIOR
Sessile.

FEEDING ECOLOGY AND DIET
Sessile filter feeder.

REPRODUCTIVE BIOLOGY
Viviparous, not much known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Pericharax heteroraphis

ORDER
Clathrinida

FAMILY
Leucettidae

TAXONOMY
Pericharax carteri heteroraphis Poléjaeff, 1883, Tristan da Cunha (South Atlantic).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Massive, bulbous, rarely clavate growth form. Small and young specimens pyriform, with external surface not folded; older and larger specimens with characteristic irregularly folded external surface. Maximum size of about 12 in (30 cm) in height. Yellow greenish to dark greenish brown color in life, one large terminal osculum always present, mostly with a "lip." Firm, harsh texture, surface smooth but brittle, large triactines protruding through the surface readily visible. With a thin but distinct, up to 50 µm thick, cortex consisting of tangentially aligned small, characteristic tripod-like triactines, but small and large triactines also present. Sub-dermal cavities present in most areas below the cortex (50–200 µm diameter), devoid of choanocyte chambers. Sub-dermal cavity zone up to 400 µm thick. Dense irregular meshwork of mainly regular small triactines forms the choanosomal skeleton. Some small tetractines also. Many large "giant" triactines irregularly dispersed throughout the choanosome. Small tetractines concentrated at, but not restricted to, excurrent water canals. Leuconoid aquiferous system. Large regular triactines 500–1,600 × 70–200 µm; smaller regular triactines 120–200 × 15–25 µm; tetractines 90–180 × 10–20 µm; tripod-like cortical sagittal triactines 45–130 × 7–15 µm.

DISTRIBUTION
Widely distributed, allegedly nearly cosmopolitan. From tropical coral reefs (e.g., Great Barrier Reef) to the Subantarctic, also south Atlantic, Indian Ocean, and Indo-Malayan region.

HABITAT
Widely distributed in exposed and semi-shaded habitats, sometimes under overhangs.

BEHAVIOR
Sessile.

FEEDING ECOLOGY AND DIET
Sessile filter feeder.

REPRODUCTIVE BIOLOGY
Viviparous. Not much known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

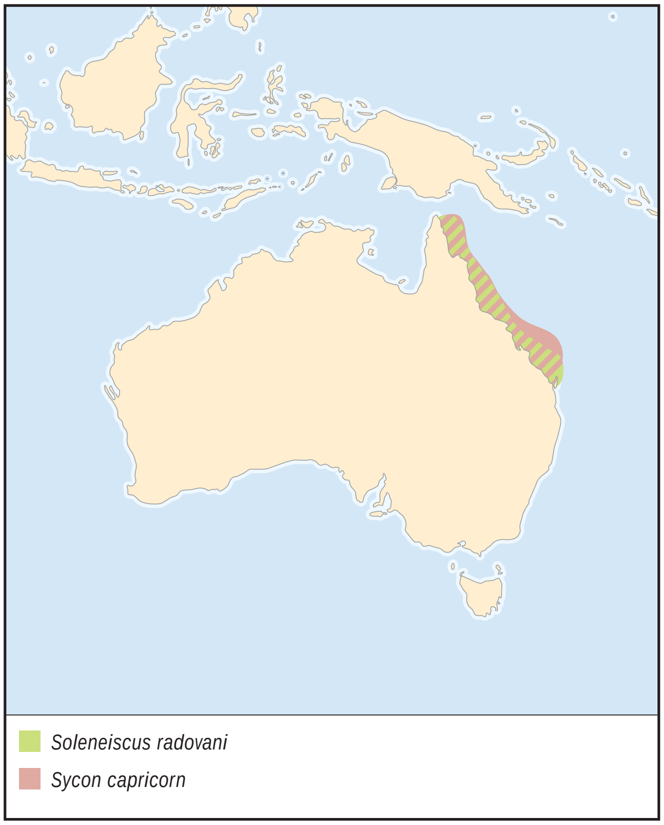
No common name
Soleneiscus radovani

ORDER
Clathrinida

FAMILY
Soleneiscidae

TAXONOMY
Soleneiscus radovani Wörheide & Hooper, 1999, south side of Wistari Reef, Great Barrier Reef, 56 ft (17 m) depth.

OTHER COMMON NAMES
None known.



PHYSICAL CHARACTERISTICS

Aborescent, bushy, with single, delicate tubes branching dichotomous and polychotomous from a few central tubes. Bright yellow color. Central, proximal tube larger than the distal tubes; tubes ramify only in the lower part of the sponge "bush." Distal parts of tubes mostly longer than ramified parts. Single tubes approximately 0.08 in (2 mm) in diameter. Size of the sponge "bush" is less than 4 in (10 cm). One naked osculum on top of each tube. Soft and delicate texture, easily torn. Sagittal tetractines only make up skeleton. Tangentially arranged facial plane of tetractines forms wall of tubes, with the longer ray of basal triradiate system pointing in direction of central tube (growth axis). The curved and free actines of tetractines protrude into tube, tips of the free actines bent in direction of osculum. Asconoid grade of aquiferous system. Only one spicule type is present. Non-curved, longer unpaired actine of basal triradiate system approximately 120–200 µm × 8–12 µm, the paired shorter (curved) actines of pseudosagittal basal plane approximately 85–130 × 8–12 µm.

DISTRIBUTION

Currently only described from the Great Barrier Reef, probably wider distribution in the tropical western Pacific.

HABITAT

Small patches of coral, under overhangs.

BEHAVIOR

Sessile.

FEEDING ECOLOGY AND DIET

Filter feeder.

REPRODUCTIVE BIOLOGY

Viviparous, details not known.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

No common name

Sycon capricorn

ORDER

Leucosoleniida

FAMILY

Sycettidae

TAXONOMY

Sycon capricorn Wörheide & Hooper, 2003, south side of Heron Island, Great Barrier Reef.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Tubular and mostly branching growth form. If small, only a single tube with a few smaller branches arising from a narrower base. Otherwise bushy, with multiple dichotomous or occasionally polychotomous branching digits. Apical oscule of each branch always fringed. Digitations with a diameter of 0.2–0.4 in (0.5–1 cm). Beige color in life. Smooth, soft, tesselated texture. No defined cortex (i.e., with tangentially arranged spicules). Ectosomal skeleton (forming the external surface) consists of characteristic "tufts" of bundled free actines of t-shaped sagittal triactines and two types of microdiactines. Tufts, with a diameter of 100–150 µm, form minute tessellation of external sponge surface, located over radially arranged choanocyte chambers. Long, thin diactines around the osculum, sustaining the oscular fringe, with a size of 200–600 × 7–15 µm. Choanosomal skeleton composed of two types of sagittal t-shaped triactines in articulated arrangement. First type (shorter unpaired actines) builds walls of tubular choanocyte chambers, with size of unpaired actines 69–170 × 5–15 µm, the paired actines are 40–95 µm long. Second type only found in the distal parts of the choanocyte chamber-tubes, with size of unpaired actines 150–290 × 4–15 µm, length paired actines 40–80 µm. Their longer, unpaired actines contributes to ectosomal tessellation, with brush-like tufts of microdiactines arranged around them. Sinuous fusiform diactines of spicule tufts with a size of 70–180 × 3–12 µm, and smaller microdiactines with a characteristic "ball"-type thickening, with a size of 55–75 × 7–12 µm. Atrial skeleton of sagittal triactines and tetractines, their elongated free unpaired/apical actines protruding into atrium, with a size of 45–230 × 6–15 µm. Syconoid grade of aquiferous system.

DISTRIBUTION

Currently only known from the Great Barrier Reef, Australia. Member of the allegedly more widespread *Sycon gelationosum/arborea* species group.

HABITAT

Cryptic, mostly in caves and under overhangs, rarely in the open.

BEHAVIOR

Sessile.

FEEDING ECOLOGY AND DIET
Sessile filter feeder.

REPRODUCTIVE BIOLOGY
Viviparous, amphiblastula larva.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Grantiopsis heroni

ORDER
Leucosoleniida

FAMILY
Lelapiidae

TAXONOMY
Grantiopsis heroni Wörheide & Hooper, 2003, northern side of Wistari Reef, Great Barrier Reef.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Mass of branching and anastomosing tubes, about 2 × 1.2 × 0.8 in (5 × 3 × 2 cm) in size. Tubes anastomose in proximal part of cormus at the base, but become unified and only partly branching in distal part. With a terminal osculum of about 0.20 in (5 mm) diameter. White color in life, soft texture, no surface ornamentation. With a distinct cortex of tangentially arranged thick sagittal triactines, with more-or-less cylindrical actines and an unpaired angle of up to 160°. Paired actines with a size of 220–350 µm, unpaired actines 210–370 µm, maximum thickness 15–40 µm. Ectosomal membrane (exopinacoderm) supported by perpendicularly arranged micro-diactines, restricted to the ectosomal (distal) part of cortex, 40–100 µm long, often finely spined. Sometimes small subcortical cavities, with diameter of 50–100 µm. Inarticulated choanoskeleton only supported by two (non-articulated) spicules, apical actines of sub-atrial sagittal tetractines and nail-shaped triactines (with totally reduced paired actines). With a size of 140–350 × 4–12 µm. Nail-shaped triactines pointing with "unpaired" actines towards cortex, unpaired actines of the sub-atrial triactines do not extend to the cortex. Subatrial sagittal tetractines delimit choanosome towards atrial skeleton with their regular basal triradiate system, their elongated apical actine forms proximal part of choanoskeleton. Actines of basal triradiate system 30–80 µm long, longer apical actine 130–330 µm long. The atrial skeleton is supported by sagittal tetractines with their curved free actines pointing towards and into the atrium. Spicule with a "plough-like" shape. Apical actine, with a size of 65–120 µm, bent towards unpaired actine of basal triradiate system. Basal triradiate actines are 30–75 µm long, with maximum thickness of 2–12 µm. Syconoid grade of aquiferous system.

DISTRIBUTION
Currently only known from the Great Barrier Reef, Australia. Putative member of the allegedly more widespread *Grantiopsis cylindrica* species group.

HABITAT
Overhangs, swim throughs and crevices between coral bommies at the reef edge.

BEHAVIOR
Sessile.

FEEDING ECOLOGY AND DIET
Sessile filter feeder.

REPRODUCTIVE BIOLOGY
Viviparous.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Petrobiona masselina

ORDER
Lithonida

FAMILY
Petrobionidae

TAXONOMY
Petrobiona masselina Vacelet & Levi, 1958, Mediterranean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Massive, subspherical or multi-lobate growth form, encrusting in high energy habitats or dead stalk in calm habitats. Maximum size of up to 2.4 in (6 cm) in diameter when encrusting, if not, living "head" of 0.39–0.47 in (1.0–1.2 cm) in diameter with a stalk 0.79 in (2 cm) long. Stony texture, white color, smooth surface. In subspherical specimens apical oscules, 600–800 µm in diameter. Living tissue only located at the surface and between crests of basal skeleton, with a choanosome 600 µm thick. Spicules are sagittal triactines (with actines 25–200 × 6–40 µm), tuning-fork (diapason) triactines (basal actines 30–70 × 5–8.5 µm, apical actines 20–50 × 4–7 µm), two size categories of tetractines (pugioles) (apical actines 40–130 × 22–28 µm and 16–40 × 5.5–8.5 µm, actines of basal triradiate system 8–100 × 10–28 µm and 30–70 × 5.5–8.5 µm), spined microdiactines 30–60 × 2–3 µm. Elongate, irregular skeletal elements, with a radial orientation of the crystals giving them a pseudo-spherulitic appearance, form solid calcareous basal skeleton of Mg-calcite, with crests and depressions on the surface. Some spicules entrapped in basal skeleton, randomly arranged. Leuconoid grade of aquiferous system.

DISTRIBUTION
Mediterranean: eastern basin (Adriatic, Ionian Sea, Crete, Malta, Tunisia), western part of the eastern basin (not recorded west of the Rhone delta and Algeria).

HABITAT
Common near the entrance of dark caves, more rarely on the under surface of stones, 1.6–82 ft (0.5–25 m) depth.

BEHAVIOR
Sessile.

FEEDING ECOLOGY AND DIET
Sessile filter feeder.

REPRODUCTIVE BIOLOGY
Viviparous. Amphiblastula larva.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

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Gert Wörheide, PhD

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Hexactinellida

(Glass sponges)

Phylum Porifera

Class Hexactinellida

Number of families 17

Thumbnail description
Deepwater marine sponges with a glass skeleton, and typically six rays; unusual because of their multinucleate tissues and ability to conduct electrical signals in the absence of nerves

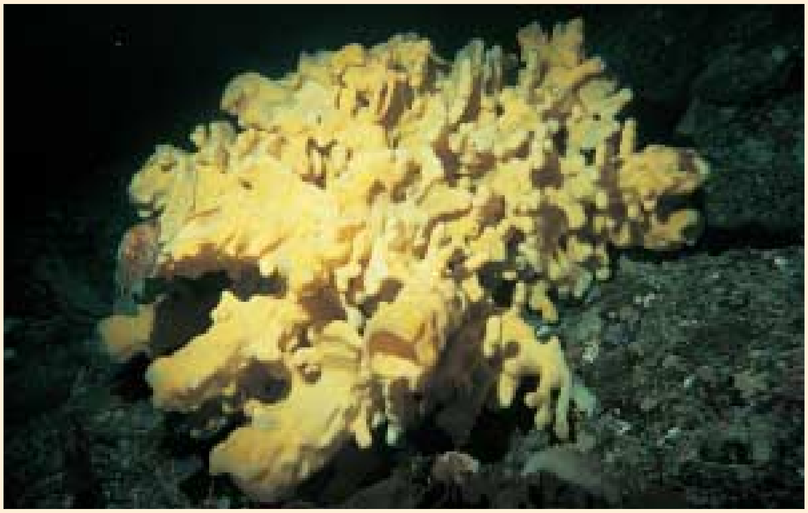


Photo: A glass sponge (*Aphrocallistes vastus*) living in deep waters off of British Columbia. (Photo by ©Neil G. McDaniel/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

Hexactinellids (glass sponges) are deepwater marine sponges that have skeletons of siliceous (glass) spicules with a distinctive triaxonic (cubic three-rayed) symmetry. Unlike the other two main classes of sponges (Calcarea and Demospongiae), glass sponges lack either a calcareous or organic skeleton. Furthermore, glass sponges are highly unusual in that their major tissue component is a giant "syncytium" (see below) that ramifies throughout the entire body, stretching like a cobweb over the glass skeleton. As their skeletons are both made of glass rather than calcium, early classification schemes grouped hexactinellids with the demosponges; however, at present hexactinellids are separated from cellular sponges (the Calcarea and Demospongiae) in the subphylum Symplasma because of their unique (syncytial) structure. Nevertheless, recent molecular evidence suggests that whereas modern hexactinellids are descended from the most ancient multicellular animals, they are more closely related to demosponges than either group is to the calcareous sponges or other metazoans. There are approximately 500 species of hexactinellids in two subclasses containing five orders, 17 families, and 118 genera.

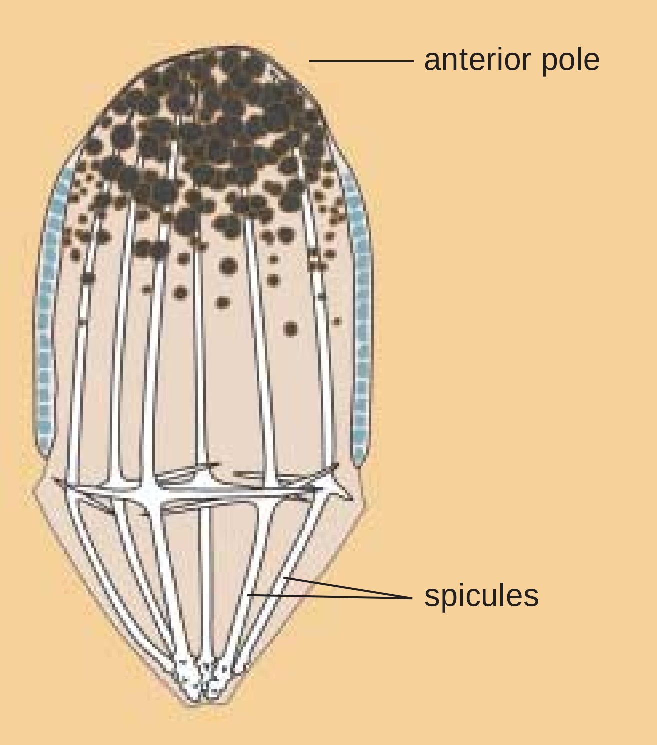
Hexactinellids have left the oldest fossil record of multicellular animals on Earth. Their triaxonic spicules are known from the Late Proterozoic of Mongolia and China. The group thrived during the Middle Cambrian and reached its maximum radiation and diversity during the Cretaceous, when hexactinellids formed vast reefs in the Tethys Sea. Their fossilized skeletons now make up the stony outcrops upon which many castles are built from southern Spain through France, Germany, and Poland to Romania.

Physical characteristics

Within each of the two subclasses of hexactinellids are sponges with loose skeletons—spicules held together by living tissue—and sponges with fused skeletons. Sponges of both designs are essentially vase-shaped, with a large central or atrial cavity, usually with one opening, the osculum. The species with fused skeletons often have mittenlike or fingerlike protrusions of the body wall, and some form platelike structures; these species have oscula on each of the projections. The tissue of hexactinellids generally is creamy yellow to white. Some animals are quite clean, so that the whiteness of their tissue looms out of the darkness of their deepwater habitats. Others tend to accumulate particulate matter on the outside and can look quite dirty. The diverse species of hexactinellids vary in length from 0.2 to 5 ft (0.5 cm to 1.5 m); many of the largest hexactinellids are as wide as they are tall.

The body wall is composed of three parts: both the inner and outer peripheral trabecular networks, and the feeding region, which is called the choanosome. Large incurrent and excurrent canals meet at the choanosome, where the fine, branchlike endings of the incurrent canals contact oval, flagellated chambers that create the feeding current through the sponge.

While sponges of other groups are constructed of single cells, each with a single nucleus, the greater part of the soft tissue in a hexactinellid consists of the trabecular reticulum, which contains thousands of nuclei and cytoplasm that is free to move as it is unimpeded by membrane barriers (the "syncytial" condition). The trabecular reticulum hangs from the skeleton in thin strands, resembling a cobweb, and stretches from the outermost layer, termed the dermal membrane, to the innermost layer, the atrial membrane. Single cells, specialized for particular functions, are also present. Cells are attached to one another and the trabecular reticulum by a unique type of attachment structure referred to as the "plugged junction," which is called so because it is slotted into the neck of cytoplasm between two regions, resembling a plug. It is not an extension of the lipo-protein cell membrane, but is a multi-



The larva of a hexactinellid sponge. (Illustration by Emily Damstra)

laminar proteinaceous structure. While it undoubtedly serves as a partial barrier to the free exchange of materials, electric currents can flow through it and transport vesicles are able to move through pores in its structure. Between cellular and syncytial components of the sponge there is a very thin collagen layer, the mesohyl. This layer is believed to be too thin for cells to migrate within, as is the case with other sponges. Instead, transport of nutrients and other materials appears to occur along vast networks of microtubules within the multinucleate tissue.

Distribution

Hexactinellid sponges are known at depths from 30 to 22,200 ft (9.14–6,770 m) in all oceans. There are no records of this class in freshwater. The fossil record suggests that their historical range was similar.

Habitat

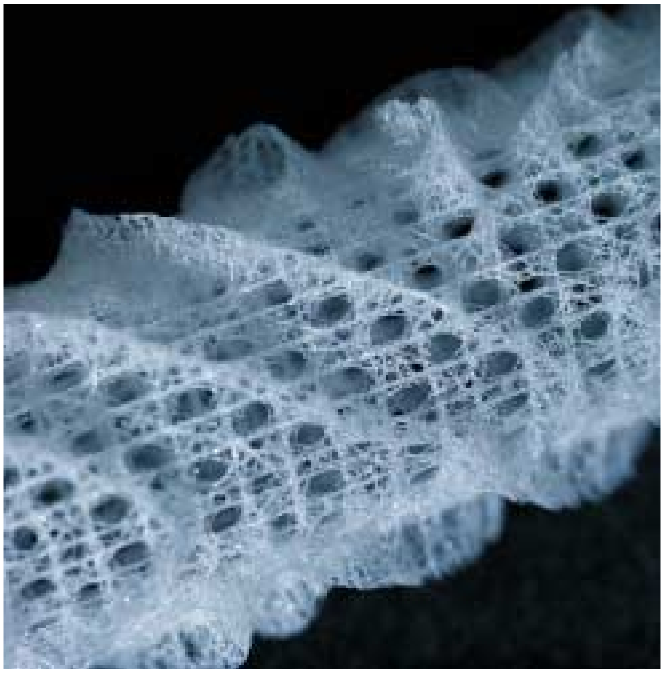
The vast majority of hexactinellids live at depths greater than 1,000 ft (304.8 m). In a few coastal locations, however, such as Antarctica, the northeastern Pacific, New Zealand, and some caves in the Mediterranean, species are found at depths accessible by scuba divers. These habitats have in common cold water (35–52°F, or 2–11°C), relatively high levels of dissolved silica, and low light intensity. Although many hexactinellids require a firm substratum, such as rocks, for attachment, others grow on fused skeletons of dead sponges, and still others live over soft sediments. The latter group, though not numerous, support themselves on struts made of bundles of long spicules that project down into the sediment.

Behavior

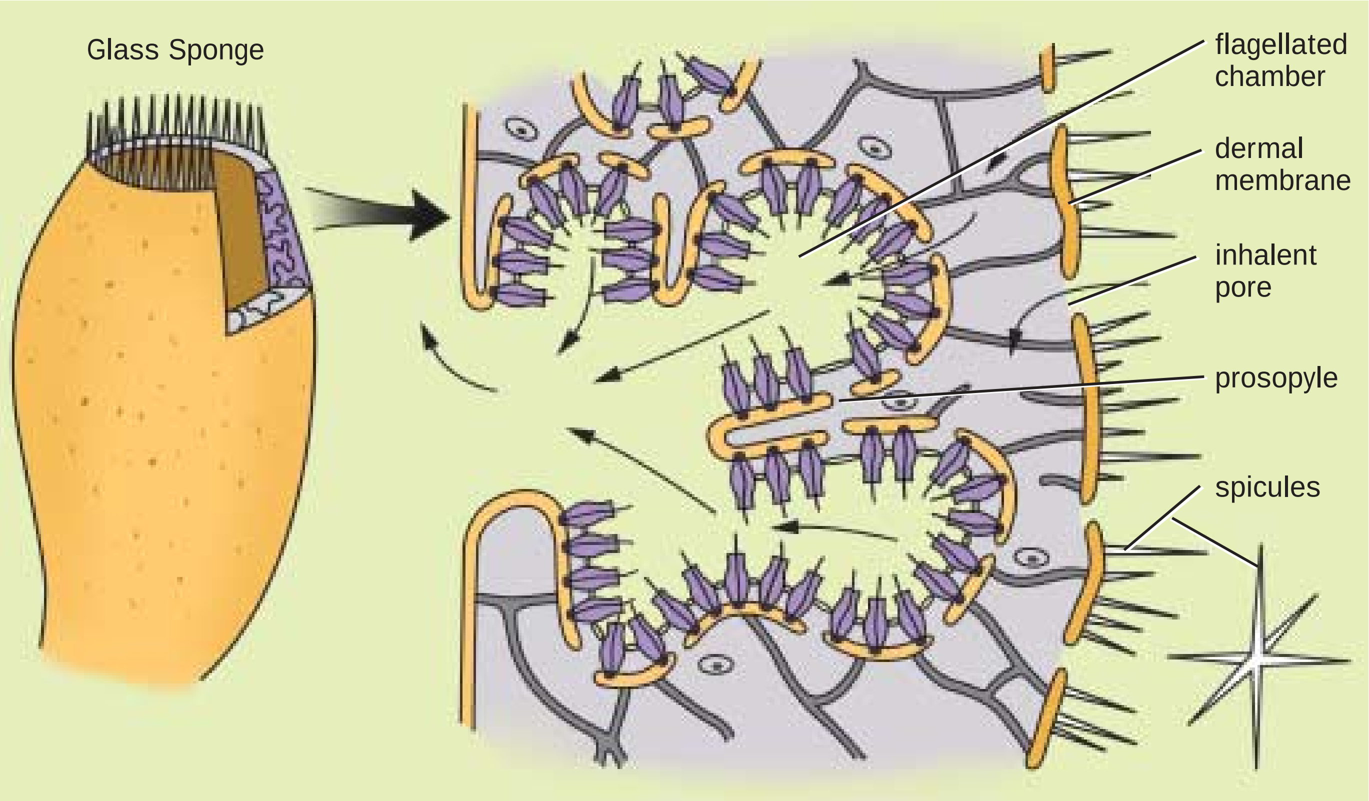
Sponges are not noted for their complex behavior. Nevertheless, hexactinellids can respond to mechanical or electrical stimuli by instantly shutting down the feeding current. The explanation for this unusual ability lies in their possession of a trabecular reticulum, which acts like a nervous system, conveying impulses to all parts of the body. Sponges of other groups lack any such system and show no evidence of an ability to conduct electrical impulses. Electrical signals traveling at 0.07 in per second (0.26 cm per second) have been recorded from slabs of the body wall of *R. dawsoni*. It is presumed that when the signals reach the flagellated chambers, the pumping stops. No rhythmic pattern has been found in the cessation of pumping. It is thought that since glass sponges lack motile cells that would otherwise remove unwanted material from the sponge, shutting down the feeding current may prevent the clogging of the canal system with large amounts of debris.

Feeding ecology and diet

Like the majority of sponges, glass sponges are thought to filter food from the water that they pump through the choanosome. Two in situ studies confirm this to be true for sponges that lack debris on their outer surfaces. Studies comparing the content of inhaled and exhaled water showed that both *Aphrocallistes vastus* and *Sericolophus hawaiicus* retain particulate matter—mostly bacteria—and rely little on dissolved organic carbon. The results of one study that compared such water samples from a sponge covered in debris (*Rhabdocalyptus dawsoni*) suggest that particulate matter is not retained and that the sponge instead relies for nutrition entirely on the uptake of dissolved organic carbon. It is thought that the organisms coating the sponge produce sufficient organic carbon for



A glass sponge (*Aphrocallistes vastus*) skeleton. (Photo by ©Ken M. Highfill/Photo Researchers, Inc. Reproduced by permission.)



Glass sponge anatomy. (Illustration by Kristen Workman)

themselves and their host. Nevertheless, *R. dawsoni* can phagocytose both bacteria and latex beads in laboratory preparations.

Laboratory experiments with *R. dawsoni* and *Oopsacas minuta* (also a rosellid sponge, but one with a clean exterior) have shown that uptake of particulates occurs in the trabecular syncytium near to and in the flagellated chambers, not in choanocytes, as is normally the case in cellular sponges. In hexactinellid sponges the structure equivalent to a choanocyte, the collar body, lacks a nucleus, and in most species examined so far the collar body is enveloped by extensions of the trabecular syncytium (the primary and secondary reticula), which do most of the particulate capture and uptake. The siliceous skeleton may protect hexactinellids from many predators, but at least one asteroid species is not deterred. *Pteraster tesselatus* frequently can be found digesting the soft tissues off the skeleton of *R. dawsoni.*

Reproductive biology

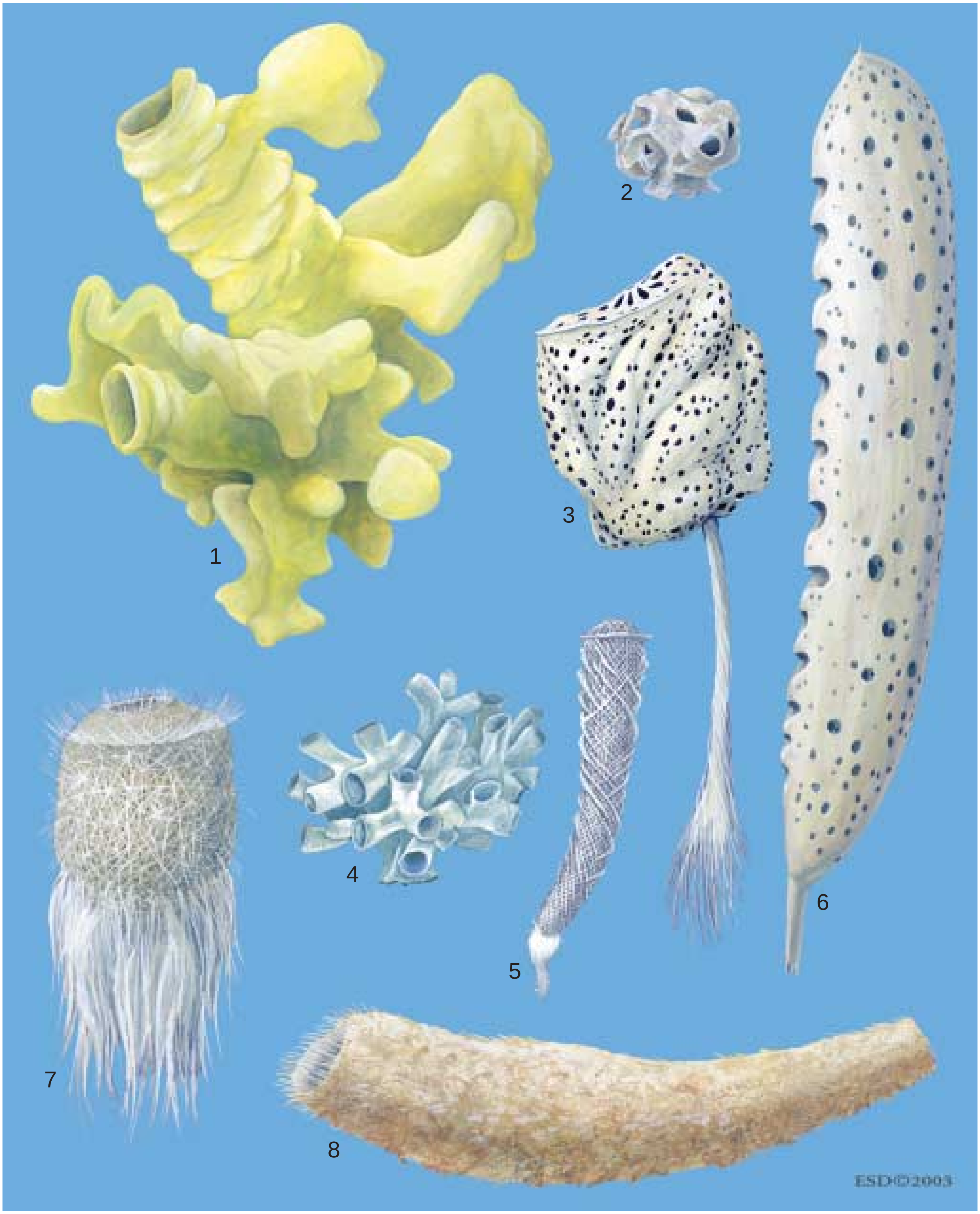
It is generally thought that most hexactinellids lack a seasonal reproductive period because of their deepwater habitat. Nevertheless, because of the difficulty in collecting and preserving these sponges there is little information on reproduction in most deepwater populations. Our knowledge of their development comes from studies done on only a handful of species. Hexactinellid sponges are viviparous. Eggs arise from cells within groups of archaeocytes, a type of pleuripotent cell found in all sponges. The first cell divisions that occur are equal and result in the formation of a hollow ball of cells (a blastula). Gastrulation (the formation of two cells layers during embryonic development) is said to occur by delamination. The larvae are top-shaped with a girdle, band, or cilia around their middle. The tissues are already syncytial, although it is not yet known how the multinucleate tissue arises. When the larva matures, it is released through the osculum. The species *Oopsacas minuta*, which is reproductive throughout the year, produces the only known live larvae. When studied in a laboratory setting larvae swim slowly to the surface of dishes in left-handed rotations (clockwise, as seen from the anterior pole); although they can swim for several days, they begin to settle and transform into juvenile sponges within 12 hours of release from the parent sponge.

Conservation status

In general, most hexactinellid sponges inhabit areas well out of the reach of human activity. However, on the continental shelf of the northeastern Pacific in British Columbia, reefs of hexactinellid sponges several city blocks in area have been damaged by trawlers. New legislation for the establishment of marine protected areas around these reefs is under development. No species of hexactinellid is listed by the IUCN.

Significance to humans

Euplectella aspergillum, which harbors a pair of crustaceans within its enclosed atrial cavity for life, is commonly given to newlyweds in Japan as a symbol of bonding.



1. Cloud sponge (*Aphrocallistes vastus*); 2. *Neoaulocystis grayi*; 3. Glass-rope sponge (*Hyalonema sieboldi*); 4. *Farrea occa*; 5. Venus's flower basket (*Euplectella aspergillum*); 6. *Monorhaphis chuni*; 7. Bird's nest sponge (*Pheronema carpenteri*); 8. Sharp-lipped boot sponge (*Rhabdocalyptus dawsoni*). (Illustration by Emily Damstra)

Species accounts

Glass-rope sponge

Hyalonema sieboldi

ORDER
Amphidiscosida

FAMILY
Hyalonematidae

TAXONOMY
Hyalonema sieboldi Gray, 1835, Japan.

OTHER COMMON NAMES
English: Glass plant; Japanese: Hoshi-gai.

PHYSICAL CHARACTERISTICS
Truncated oval body, 3–6 in (75–155 mm) long by 2.2–6 in (55–155 mm) wide, which is borne on a compact, twisted bundle, 16–26 in (400–650 mm) long, of 200–300 coarse, siliceous root spicules. Flat body top is covered by perforated sieve plate. Spicules are never fused.

DISTRIBUTION
Known only from entrance of Tokyo Bay, Japan.

HABITAT
Restricted to soft-bottom habitats; anchored in sediments by long root tuft. No reliable depth record is known.

BEHAVIOR
Nothing known.

FEEDING ECOLOGY AND DIET
Presumably filter feeds.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This hexactinellid, the first to be described, is displayed in museums worldwide. ◆

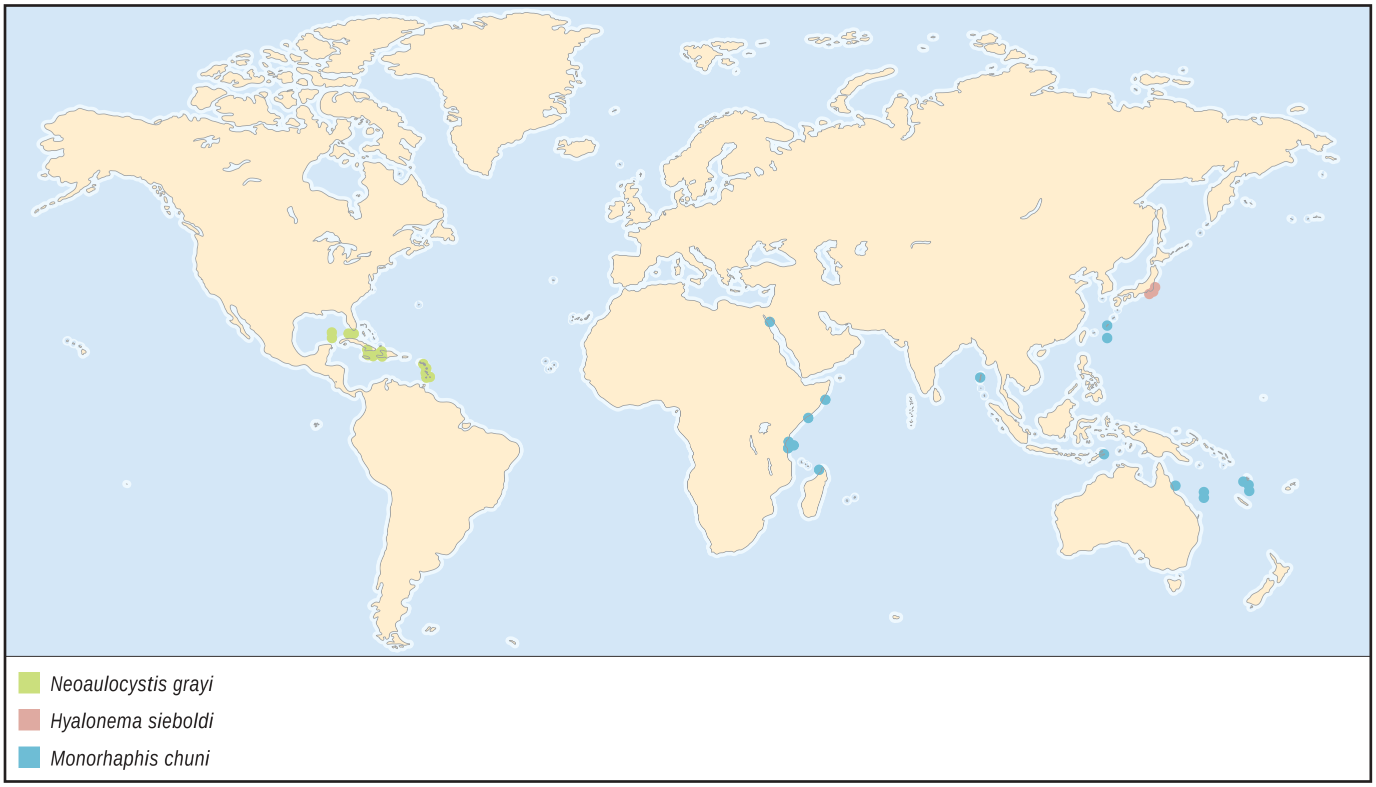
No common name

Monorhaphis chuni

ORDER
Amphidiscosida

FAMILY
Monorhaphididae

TAXONOMY
Monorhaphis chuni Schulze, 1904, eastern Indian Ocean north of Madagascar.



OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Cylindrical body, 41 in (105 cm) long and 6 in (15 cm) wide, supported on a single large anchor or basal spicule; the largest siliceous structure formed by any organism (excluding humans), which may reach 9.8 ft (3 m) in length and 0.4 in (10 mm) in width.

DISTRIBUTION

Indo-West Pacific from eastern Africa to New Caledonia.

HABITAT

Lives suspended over muddy bottoms on long anchor spicule at depths of 1,604–6,553 ft (489–1,998 m).

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Presumably filter feeds.

REPRODUCTIVE BIOLOGY

Nothing is known.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Bird's nest sponge

Pheronema carpenteri

ORDER

Amphidiscosida

FAMILY

Pheronematidae

TAXONOMY

Holtenia carpenteri Thomson, 1869, northeastern Atlantic off northern Scotland.

OTHER COMMON NAMES

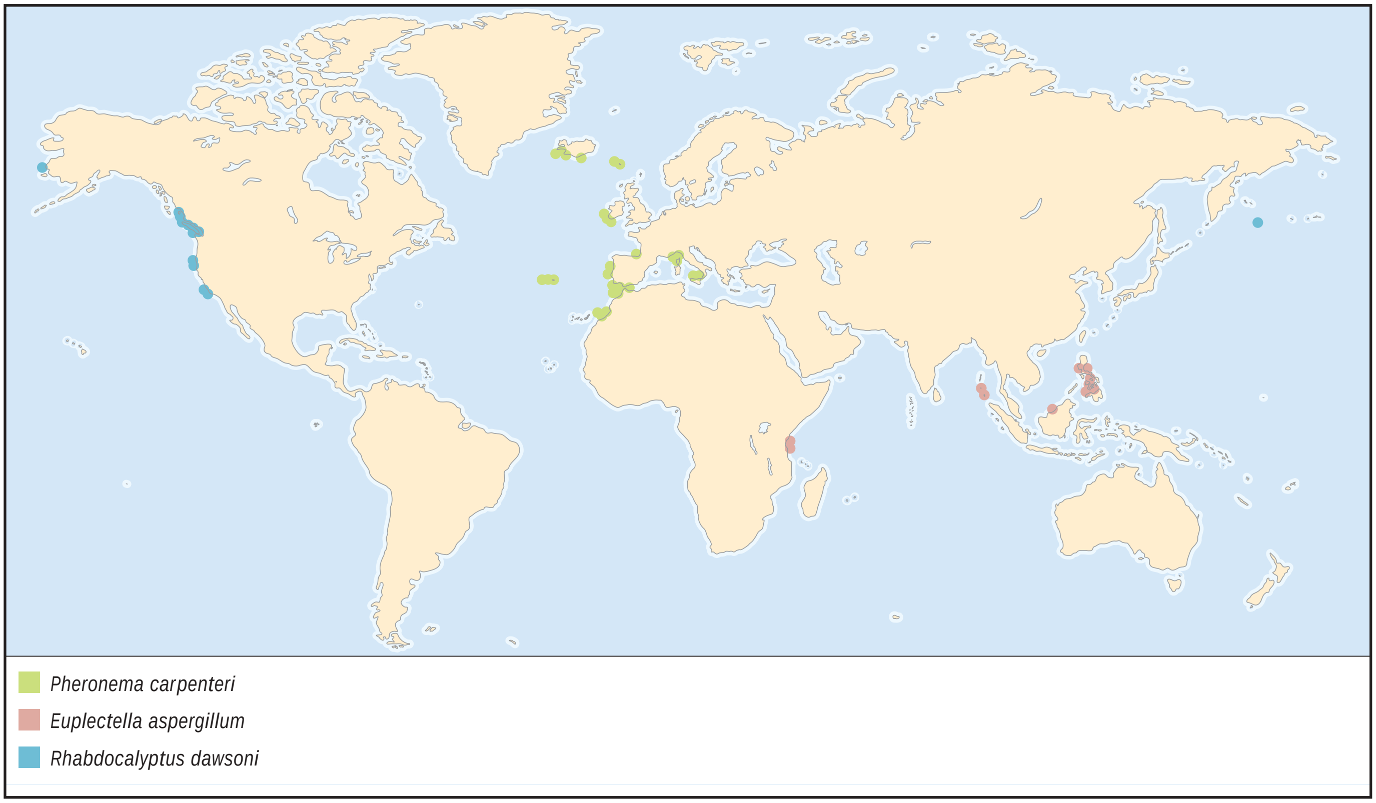
Portuguese: Ninhos de mer.

PHYSICAL CHARACTERISTICS

Ranges in shape from tall and narrow with a deep interior cavity (resembling a barrel), to a squat shape that is broader than it is tall with a shallow depression on top (resembling a cake). Grows to 10 in (25 cm) tall and 8 in (20 cm) wide. Thick, cavernous body wall tapers to single sharp-edged upper opening, which leads to narrow internal atrial cavity. Thin, hairlike siliceous spicules project from annulus around upper third of body and over entire lower third of the body, where they serve as attachment anchors in soft mud. Spicules are never fused.

DISTRIBUTION

Northeastern Atlantic from Iceland to northern Africa, including the Mediterranean Sea. Reports from Brazil and eastern Africa are dubious.



HABITAT
On soft, muddy bottoms at depths of 1,007–7,118 ft (307–2,170 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumably filter feeds.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The reasons for the surprisingly high population density and biomass of this species at bathyal depths, usually poor in animal abundance, has been a focus of oceanographic research. ◆

Cloud sponge

Aphrocallistes vastus

ORDER
Hexactinosida

FAMILY
Aphrocallistidae

TAXONOMY
Aphrocallistes vastus Schulze, 1886, Sagami Bay, Japan.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
An expanding hollow cone, usually with mittenlike external projections. Grows to more than 3 ft (1 m). Rigid siliceous skeleton of body wall is 0.4 in (1 cm) thick and composed of honeycomb array of small tubes, 0.25 in (1 mm) in diameter, oriented perpendicular to the surface and passing through the entire body wall.

DISTRIBUTION
Northern Pacific Ocean west to Japan and east to Central America.

HABITAT
Attached by cementation to hard bottom at depths of 16–10,500 ft (5–3,000 m).

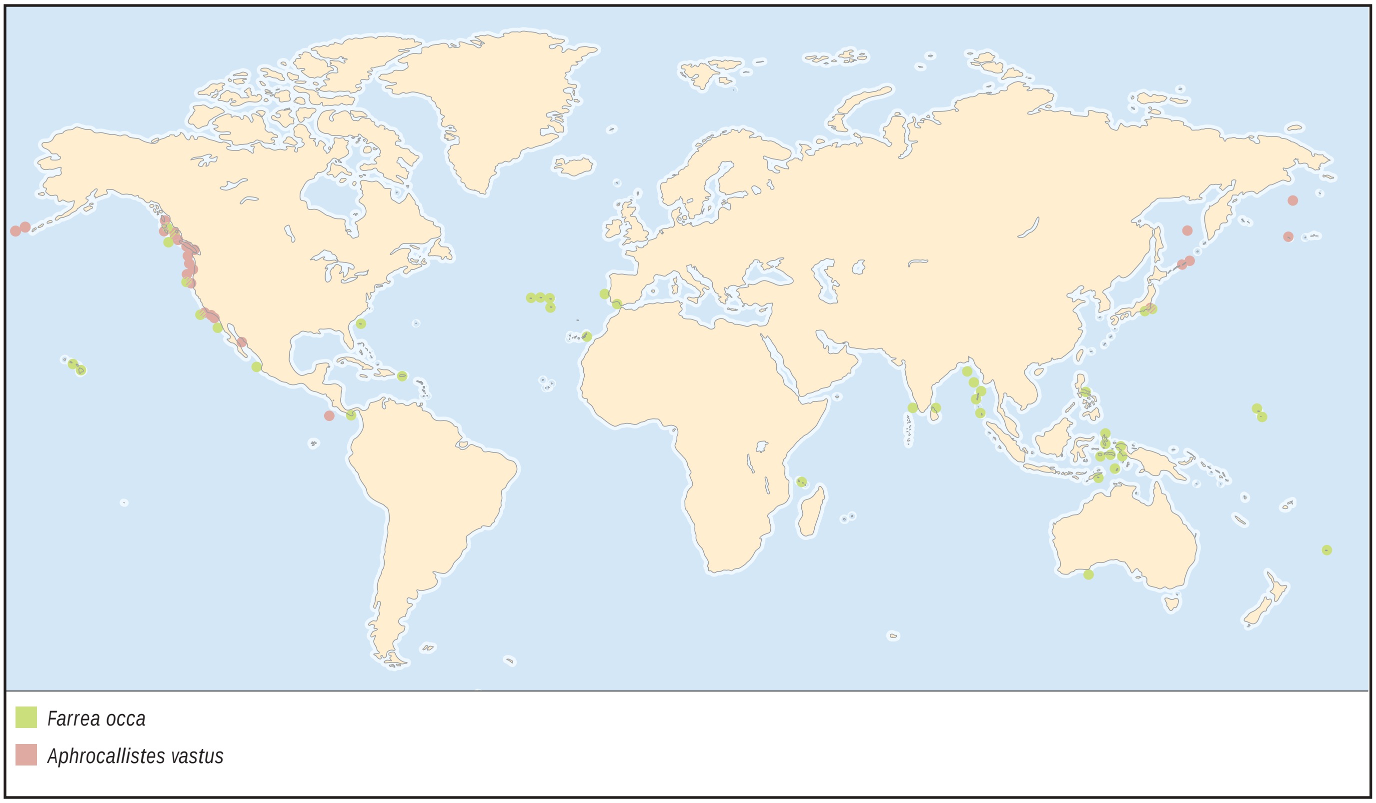
BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Filter feeds on bacteria easily visible with normal laboratory microscopes and smaller, microscopically invisible particles (colloids, viruses).

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
One of few hexactinellids living within scuba range along the coast of British Columbia, Canada, and thus available for *in*



situ and laboratory study. One of three hexactinellids that build unique living glass sponge reefs, which in 2002 were proposed for designation as marine protected areas by the Canadian Parks and Wilderness Society. ◆

No common name

Farrea occa

ORDER
Hexactinosida

FAMILY
Farreidae

TAXONOMY
Farrea occa Bowerbank, 1862, Comoro Islands, Indian Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Network of thin-walled, branching and fusing tubules, 0.2–0.8 in (0.5–2 cm) in diameter. Skeletal framework of tubule wall consists of single layer of fused six-ray spicules, forming a rectangular lattice. Loose spicules include pin-shaped forms.

DISTRIBUTION
Cosmopolitan between latitudes of 48° north and 35° south.

HABITAT
Attached by cementation to hard bottom at depths of 282–6,235 ft (86–1,901 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumably filter feeds.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
One of three hexactinellids that build unique living glass sponge reefs on the coast of British Columbia, Canada, which in 2002 were proposed for designation as marine protected areas by the Canadian Parks and Wilderness Society. ◆

No common name

Neoaulocystis grayi

ORDER
Lychniscosida

FAMILY
Aulocystidae

TAXONOMY
Myliusia grayi Bowerbank, 1869, Saint Vincent, West Indies.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hemispherical; grows to 4.7 in (12 cm) in diameter. Composed of a network of branching and fusing tubules, 0.10–0.24 in (3–6 mm) in diameter. Skeletal frame of tubule wall consists of two to five layers of six-ray spicules fused into a rigid lattice. Intersections of this framework have 12 supporting struts and are called lantern nodes.

DISTRIBUTION
Gulf of Mexico and West Indies.

HABITAT
Attached by cementation to hard bottom at depths of 348–4,536 ft (106–1,383 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumably filter feeds.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The first and most well known of the few surviving members of the order Lychniscosida, a once dominant reef-building group during the Jurassic and Cretaceous periods. ◆

Venus's flower basket

Euplectella aspergillum

ORDER
Lyssacinosida

FAMILY
Euplectellidae

TAXONOMY
Euplectella aspergillum Owen, 1841, Philippines.

OTHER COMMON NAMES
Spanish: Regadera de filipinas; Norwegian: Venuskurv.

PHYSICAL CHARACTERISTICS
Thin-walled tubular body up to 9.5 in (240 mm) long by 2 in (50 mm) wide, with numerous holes through sides and an upper terminal, colander-like sieve plate. External ridges occur obliquely on the sides and as a circular cuff around edge of sieve plate. Skeletal spicules are fused into rigid network in mature specimens. Attached to soft bottom by root of thin, hairlike glass strands, ending in microscopic anchors.

DISTRIBUTION
Indo-West Pacific from the Philippines to eastern Africa.

HABITAT
Lives on soft, muddy bottoms at depths of 144–1,520 ft (44–463 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Presumably filter feeds.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
In Japan and the Philippines it traditionally is given as a marriage gift symbolizing fidelity, because a pair of crustaceans often live imprisoned inside the hollow sponge. This demand and its desirability as a beautiful curio have supported a Philippine fishery for hundreds of years. ◆

Sharp-lipped boot sponge

Rhabdocalyptus dawsoni

ORDER
Lyssacinosida

FAMILY
Rossellidae

TAXONOMY
Bathydorus dawsoni Lambe, 1893, Vancouver Island, British Columbia, Canada. The recent transfer of this species to the genus *Adanthascus* is not recognized here.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Soft, thick-walled tube, often J shape; grows to more than 33 in (1 m) in length. Has large terminal hole (osculum) that opens into wide, deep atrial cavity. External surface is shaggy, owing to a thick veil of five-ray spicules projecting to 0.4 in (1 cm) fouled by dense community of small animals and bacteria. Attaches to hard bottom by grappling spicules; direct cementation is not reported. Spicules are never fused.

DISTRIBUTION
Northern Pacific Ocean from southern California to the Bering Sea.

HABITAT
Lives at depths of 33–1,433 ft (10–437 m) on rock surfaces and adjacent silt bottoms, to which it presumably falls after detachment from original site.

BEHAVIOR
Stops water pumping for short periods at irregular intervals when undisturbed or immediately when subjected to mechanical or electrical stimulus. Sheds outer spicule veil seasonally.

FEEDING ECOLOGY AND DIET
Captures and presumably digests small algae and bacteria in the laboratory; field study suggests that it captures primarily dissolved organic matter.

REPRODUCTIVE BIOLOGY
Presumed embryos found in adult tissues year-round but are more common in late summer; mature sperm and larvae are unknown.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
This is the most intensely studied hexactinellid, because of its occurrence within scuba range on the coast of British Columbia, Canada, and its high rate of survival in the laboratory. ◆

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Sally P. Leys, PhD
Henry M. Reiswig, PhD

◆

Demospongiae

(Demosponges)

Phylum Porifera
Class Demospongiae
Number of families 80

Thumbnail description
Soft, elastic, but also tough, friable, or hard, frequently brightly colored sponges; varying in shape from encrusting, massive, tubes, or branches to cups or vases; the body reinforced by spongin, siliceous (containing silica) spicules, or a combination of both

Photo: A row pore rope sponge (*Aplysina cauliformis*) seen near the Cayman Islands. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

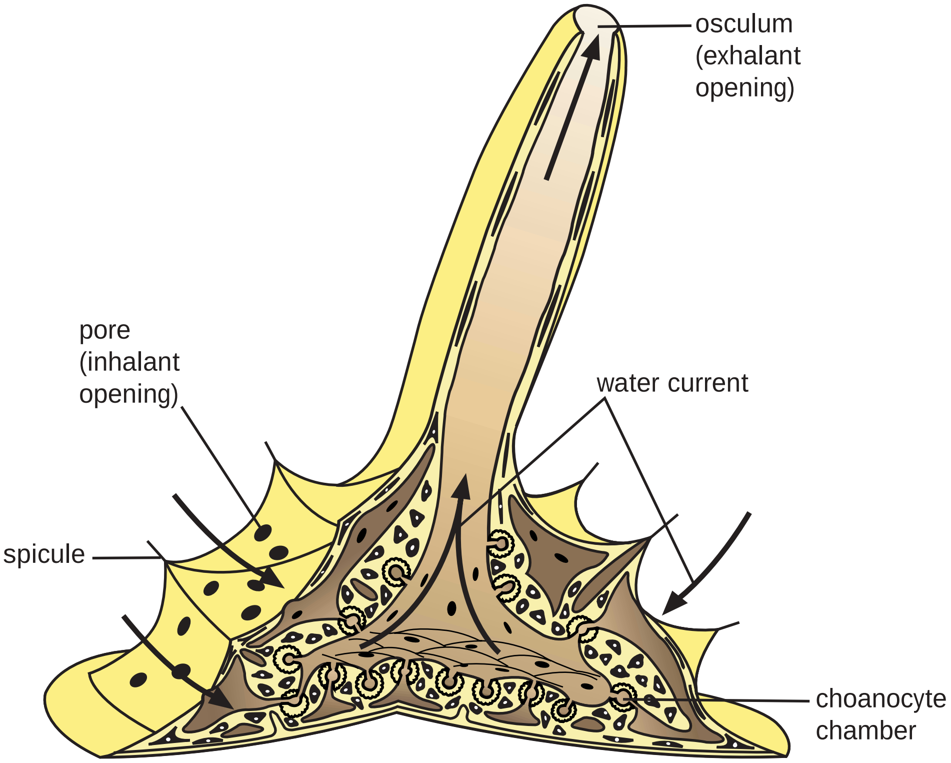
The demosponges originated in the Cambrian period and form the largest class of the phylum Porifera, containing about 85% of all described Holocene species. The class Demospongiae is divided into three subclasses:

1. Subclass Homoscleromorpha, with one order, Homosclerophorida; one family; and about 60 species.
2. Subclass Tetractinomorpha, with four orders, Astrophorida (also known as Choristida), Chondrosida, Hadromerida, and Spirophorida; 22 families; and several hundred species.
3. Subclass Ceractinomorpha, with nine orders, Agelasida, Dendroceratida, Dictyoceratida, Halichondrida, Halisarcida, Haplosclerida, Poecilosclerida, Verongida, and Verticillitida; 57 families; and several thousand species.

The names of these subclasses have been in use for several decades. As of 2002, however, with the publication of *Systema Porifera*, several changes in classification have been made and definitions refined. These changes have made the subclasses more homogeneous, though still not completely so.

The subclass Homoscleromorpha is a small and well-defined group of sponges with or without a skeleton, characterized by viviparous reproduction and a unique incubated cinctoblastula type of larva. If skeletal elements are present, they are relatively small, consisting of tetraxonic (four-rayed) siliceous spicules without a clear distinction between megascleres (large spicules) and microscleres (small spicules). The Tetractinomorpha have monaxonic (single-rayed) spicules in addition to large tetraxonic spicules; asterose (star-shaped) microscleres; a skeleton that is usually radial or axially compressed; predominantly oviparous reproduction and parenchymellar (solid) or blastular (hollow) larvae. Ceractinomorpha is the largest and most diverse subclass, with a wide variety of monactine megascleres and various kinds of microscleres, with the exception of asterose forms. In general, sponges in this subclass have skeletons made of spongin and spicules in different proportions, with a variety of skeletal structures. Their reproduction is predominantly viviparous and their larvae are parenchymellar.

The former class of Sclerospongiae, which was proposed in 1970 (“sclerosponges”), together with the former order Ceratoporellida, formed a polyphyletic (descended from more than one line of ancestors) group of coralline sponges that included several Holocene species as well as fossil sponges. The Sclerospongiae are hard, stony sponges with a rigid calcareous basal skeleton in addition to an otherwise “normal” demosponge type of skeleton and spicule complement. Since 1985 the class name Sclerospongiae has been discarded and its fam-



Demosponge anatomy. (Illustration by Laura Pabst)

ilies reassigned to different orders on the basis of characteristics reflecting common ancestry.

Another polyphyletic group is the former order Lithistida, which included many fossil and several Holocene species characterized by a special type of spicules called desmas. Most species in this group were deep-water sponges. The evolutionary history of these sponges is still far from resolved; some appear to be related to the Astrophorida and others to the Hadromerida. Most taxa (categories) in this group, however, have been classified as an artificial fifth order (Lithistida) in the subclass Tetractinomorpha.

Axinellida, another polyphyletic group, is no longer defined as an order. Its families have been reassigned to various orders of Tetractinomorpha and Ceractinomorpha.

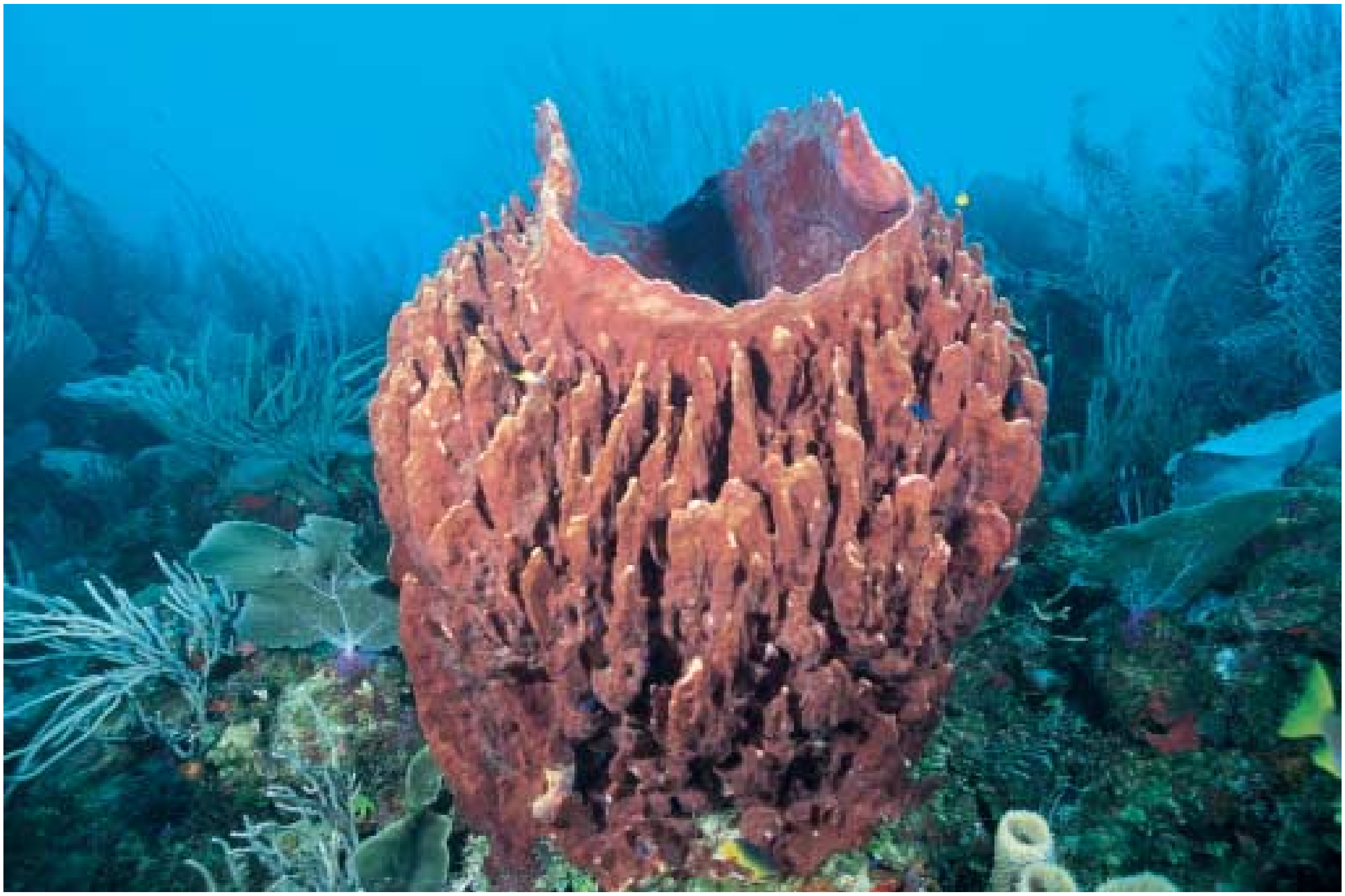
Verticillitida consists of the fossil family Verticillitidae. It belongs to an unrelated assemblage of mainly calcified fossil sponges with chambered structures known as Sphinctozoa. One Holocene genus, *Vaceletia*, which has one known polymorphic species and possibly other “living fossil” species, has been assigned to this order.

Physical characteristics

The demosponges as a group display a wide variety of shapes, colors, textures, skeletal architectures, and spicule morphology. There are species that are capable of hollowing out limestone, penetrating deep inside rocks, coral heads, and shells. Most demosponges have skeletons made of siliceous spicules, spongin fibers, or a combination of both; one group, however, has no skeleton at all. The architecture varies widely among the different groups; it may be reticulate (netlike), confused, radial (spreading outward from a common center), plumose (feathery) or axially compressed. The spicules are usually divided into two size categories (megascleres and microscleres) with a distinct morphology.

The order Poecilosclerida is the largest and most diverse order, with 25 families and several thousand species. Although this group displays a wide variety in form and skeletal architecture, it has a unique feature— chelae, which are meniscoid (crescent-shaped) microscleres with a curved shaft and recurved, winglike or broadly rounded structures at each end. These chelae are extremely diverse, and new ultrastructural characteristics are still being discovered.

The order Haplosclerida comprises 13 families and hundreds of species. All freshwater sponges belong to this order as the suborder Spongillina. They are frequently cushion-shaped; however, encrusting, branching, tubular, vase-, and fan-shaped forms are also quite common. Their coloring is not very intense; most sponges in this order come in delicate shades of purple, lavender, light brown or blue. Most freshwater sponges are green. They are rather soft and easily squeezed except for species of the suborder Petrosina, which are firm and cannot be compressed. All haplosclerids have a netlike skeleton of smooth, single-rayed, one-pointed short megascleres bound together by different amounts of spongin. Most



A giant barrel sponge (*Xestospongia muta*) in the Lighthouse Reef, Belize. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

marine haplosclerids have no microscleres. Where microscleres are present, they are very simple in structure and none are unique to the order. The spicules of the Spongillina are more elaborate, with smooth or variably ornamented megascleres and several kinds of microscleres. The simple structure of the spicules, combined with a very high degree of variability in skeletal architecture in some species, make the marine Haplosclerida among the most difficult sponges to identify.

The Dendroceratida, Dictyoceratida, and Verongida, also known as Keratosa, are sponges with a skeleton made up only of spongin without spicules. All commercial bath sponges belong to the Dictyoceratida. Taken together, these orders contain 10 families and about 450 species. The sponges are often rather tough and flexible; in one family, the Spongiidae, both the surface and the spongin fibers may be heavily coated with foreign spicules and detritus. Species of the order Verongida are easily noticed tube-, fan-, or vase-shaped sponges, frequently colored a deep sulphur yellow. When these sponges are damaged or exposed to air, their color changes rapidly to a deep purple or black.

Distribution

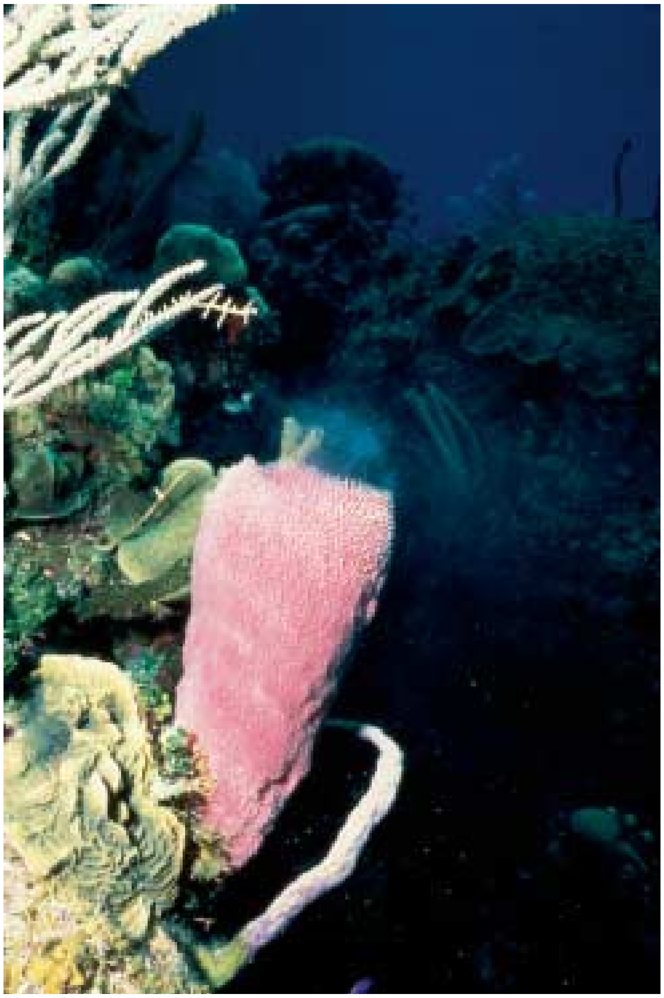
The Astrophorida, Chondrosida, Hadromerida, Halichondrida, both the marine and freshwater Haplosclerida, the Homoscleromorpha, Poecilosclerida and most Spirophorida have a worldwide distribution. The Agelasida, Dictyoceratida, and the sclerosponges, however, are found mostly in the tropics. The Verticillitida; the spirophorid family Spirasigmidae; and two families of the Verongida, the Pseudoceratinidae and the Aplysinellidae, are restricted to the Indian and Pacific Oceans; while the Halisarcida, the dendroceratid family Dictyodendrillidae, and the dictyoceratid family Thorectidae are not found in the polar regions.

Habitat

Most demosponges occur in all habitats at all depths. The Homoscleromorpha, Chondrosida, Agelasida, Dendroceratida, Halisarcida, and most Dictyoceratida occur mainly in the shallower parts of the oceans. The sclerosponges prefer cryptic (hidden) habitats.

Behavior

Most demosponges are immobile animals attached at the base to a substrate, or surface on which they live. Some species, however, successfully compete with corals and other sponges for space by releasing toxic chemicals.



A *Niphates digitalis* releasing sperm. (Photo by ©Nancy Sefton/Photo Researchers, Inc. Reproduced by permission.)

Feeding ecology and diet

Like all other sponges, the Demospongiae are filter-feeders. One genus consists of carnivorous species that engulf and digest small crustaceans.

Reproductive biology

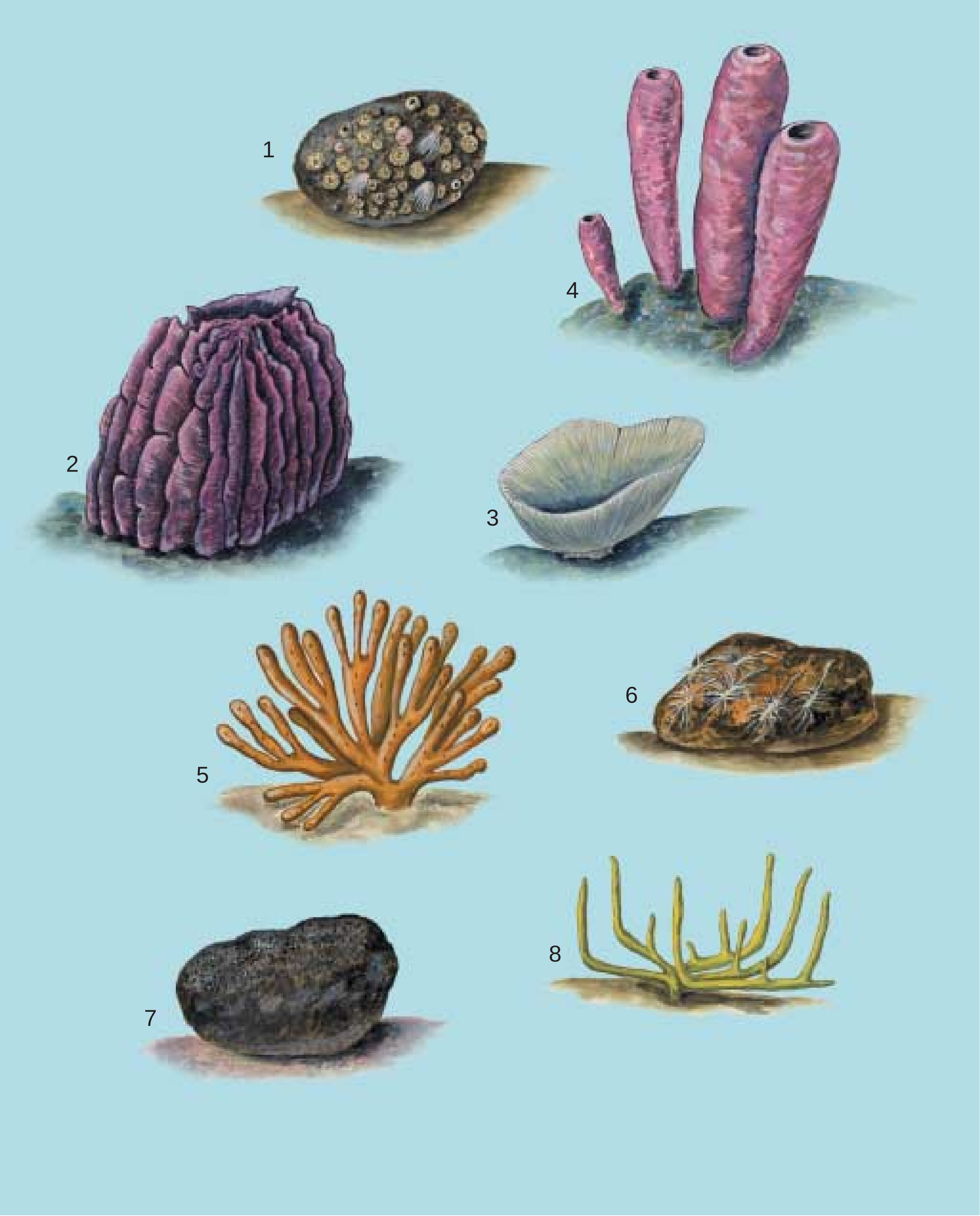
Some demosponges are hermaphroditic while others have distinct sexes. Their reproduction may be viviparous, oviparous, or asexual. Asexual reproduction occurs by means of budding, fragmentation, or the production of resistant globular bodies called gemmulae. Demosponge larvae are partly or completely ciliated, usually somewhat elongated blastulae (hollow larvae) or parenchymellae (solid larvae) about 300 µm long. The larvae swim or crawl around for a few hours or days at most, after which they settle on a substrate and metamorphose into an adult sponge.

Conservation status

In response to the overfishing of commercial sponges, patrimonial interest, and rare and remarkable characteristics of certain sponges, eight Mediterranean sponges are protected under the Bern Convention of 1998, and an additional seven species are protected in Italy.

Significance to humans

Several species are of pharmacological interest because of the production of bioactive compounds with antiviral (spongothymidine) and antibacterial (polybrominated diphenyl ethers) properties. Mediterranean and Caribbean horny sponges have commercial value as bath sponges.



1. Yellow boring sponge (*Cliona celata)*, boring stage; 2. Barrel sponge (*Xestospongia testudinaria)*; 3. *Carteriospongia foliascens*; 4. Stove-pipe sponge (*Aplysina archeri)*; 5. Eyed finger sponge (*Haliclona oculata)*; 6. Carnivorous sponge (*Asbestopluma hypogea)*; 7. Bath sponge (*Spongia officinalis)*; 8. Freshwater sponge (*Spongilla lacustris)*. (Illustration by Michelle Meneghini)

Species accounts

Eyed finger sponge

Haliclona oculata

ORDER

Haplosclerida

FAMILY

Chalinidae

TAXONOMY

Haliclona oculata Pallas, 1766, British Isles.

OTHER COMMON NAMES

Dutch: Geweispons.

PHYSICAL CHARACTERISTICS

Clusters of thin, commonly somewhat flattened branches, up to 12 in (30 cm) high, arising from a common stalk and attached to the substrate with a small pedicel or foot. In places with strong water currents, branches may fuse to the point of becoming flabellate, or fan-shaped. Oscules (small mouthlike openings) are small and circular, regularly distributed along the narrower sides of the branches. Sponges have a soft, velvety consistency and are light-brown or pinkish-brown in color.

DISTRIBUTION

Arctic-boreal.

HABITAT

Infralittoral to about 328 ft (100 m), on shores with rocky or sandy bottoms.

BEHAVIOR

Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET

Filter-feeder, like all other sponges.

REPRODUCTIVE BIOLOGY

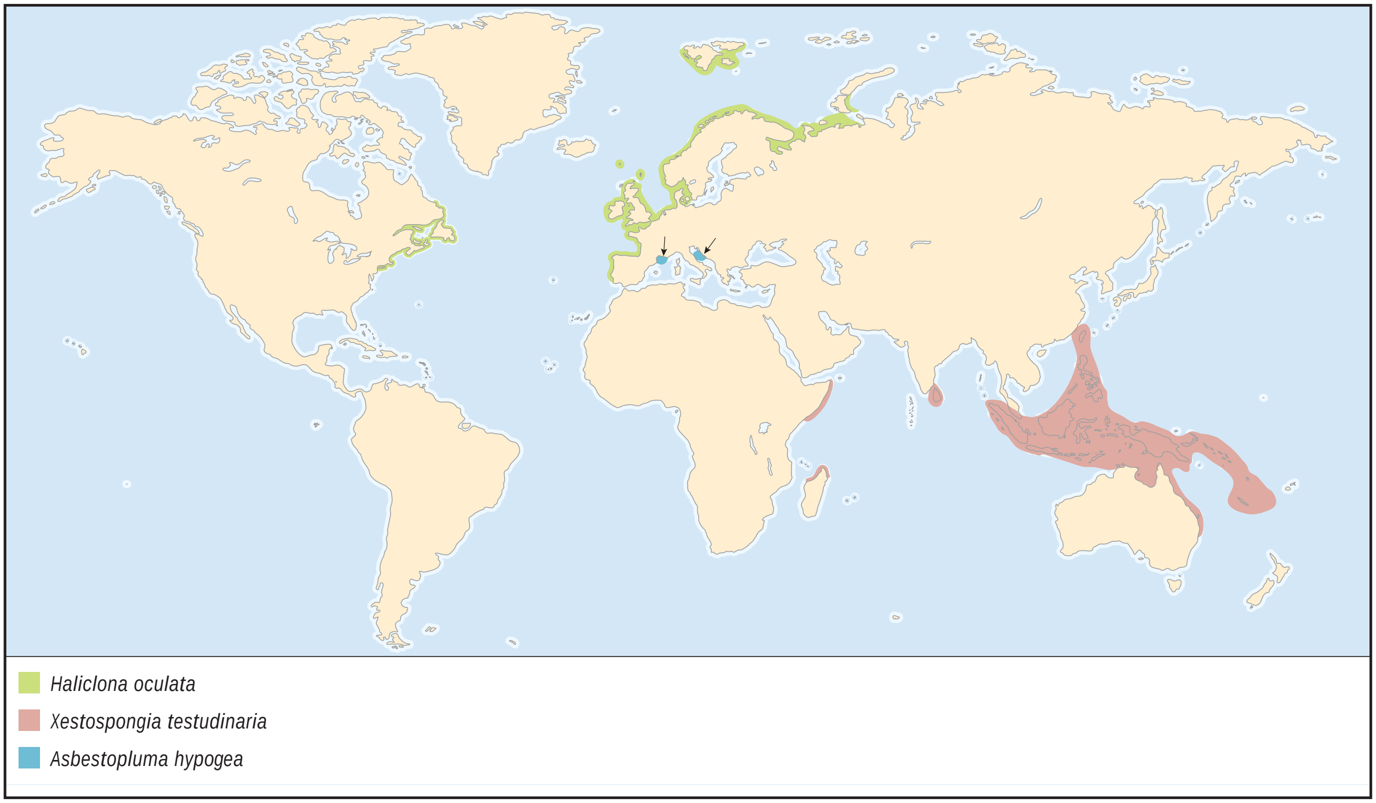
Viviparous. White oval larvae are produced from July to November. Asexual reproduction occurs occasionally by means of gemmules attached to the base of the stalk.

CONSERVATION STATUS

Not threatened.

SIGNIFICANCE TO HUMANS

An elegant, attractive sponge; as such, a pleasure for snorklers and divers to collect. ◆



Barrel sponge

Xestospongia testudinaria

ORDER
Haplusclenda

FAMILY
Petrosiidae

TAXONOMY
Xestospongia testudinaria Lamarck, 1815, Cape Denison, Queensland, Australia.

OTHER COMMON NAMES
English: Great vase sponge, volcano sponge; German: Grosser Vasenschwamm.

PHYSICAL CHARACTERISTICS
A large erect reddish brown, barrel- or cup-shaped, thick-walled sponge as much as 4.92 ft (1.5 m) high, with prominent ridges or knobs at the surface. The upper edge of the cup is irregularly indented; the cup itself forms a conspicuous central cavity occupying as much as a third of the total height of the sponge. The sponge is firm and slightly compressible in consistency.

DISTRIBUTION
Western and Central Indian Ocean, Indo-Malesia, northeastern Australia, New Caledonia.

HABITAT
Reefs and lagoons, on rock or dead coral substrates.

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter-feeder like all other sponges.

REPRODUCTIVE BIOLOGY
Individual sponges are of separate sexes. Mass release of the gametes takes place in September ('smoking' sponges), after which fertilization occurs in the sea water.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A pleasure for snorklers and divers to find or collect. ◆

Stove-pipe sponge

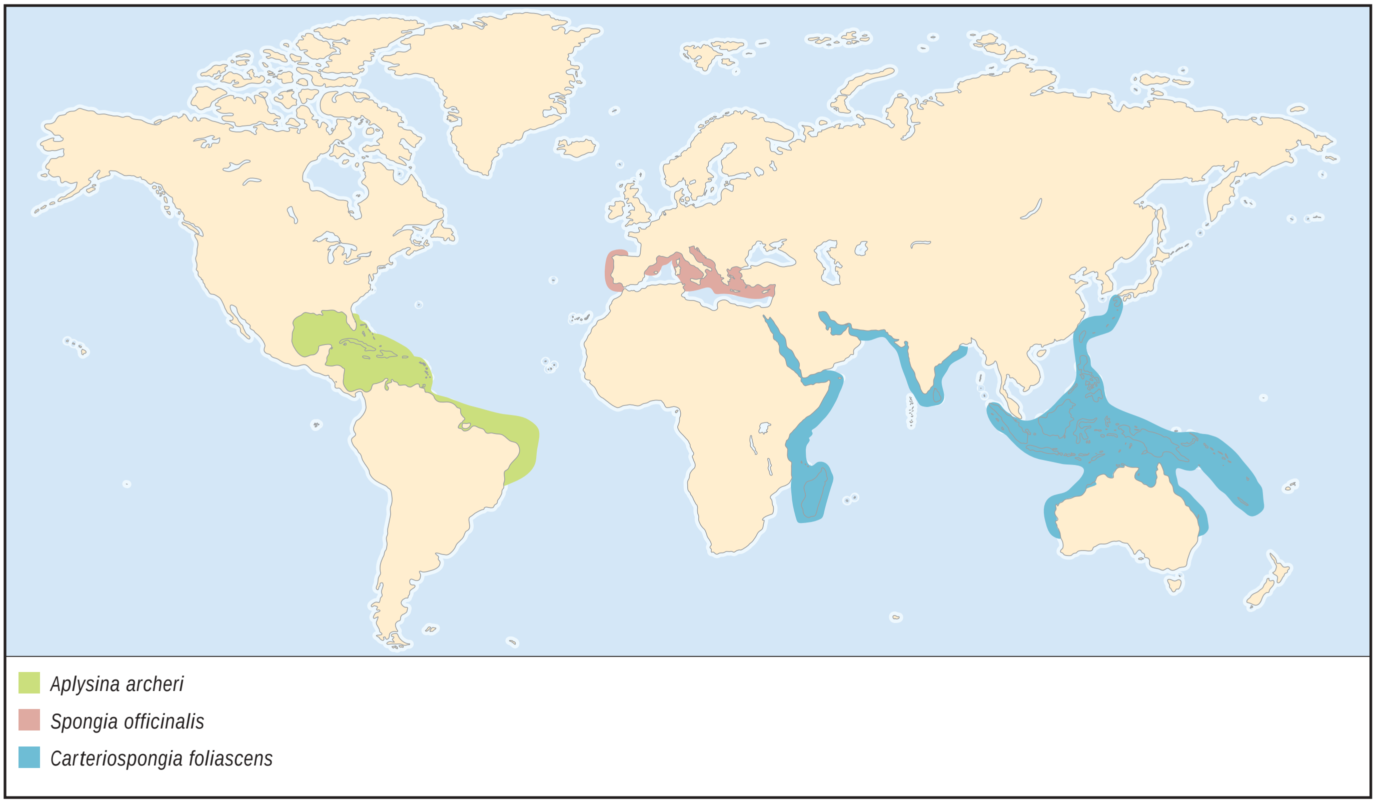
Aplysina archeri

ORDER
Verongida

FAMILY
Aplysinidae

TAXONOMY
Aplysina archeri Higgin, 1875, Yucatán, Mexico.

OTHER COMMON NAMES
Italian: Spugna a tuba di stufa.



PHYSICAL CHARACTERISTICS
Large pink or purplish gray tubes, growing in groups of several isolated tubes arising from a common base, gradually tapering towards a terminal thick-walled vent. Individual tubes as large as 5 ft (1.5 m) high and 3 in (8 cm) thick. Surface finely conulose (cone-shaped), commonly with a pattern of rounded disc-shaped elevations.

DISTRIBUTION
Caribbean.

HABITAT
Grows in reef localities, 6.5-130 ft (2–40 m) in depth.

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter-feeder, like all other sponges.

REPRODUCTIVE BIOLOGY
Oviparous, separate sexes, simultaneous spawning during a short period.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
An attractive sponge to snorklers and divers. ◆

Yellow boring sponge
Cliona celata

ORDER
Hadromerida

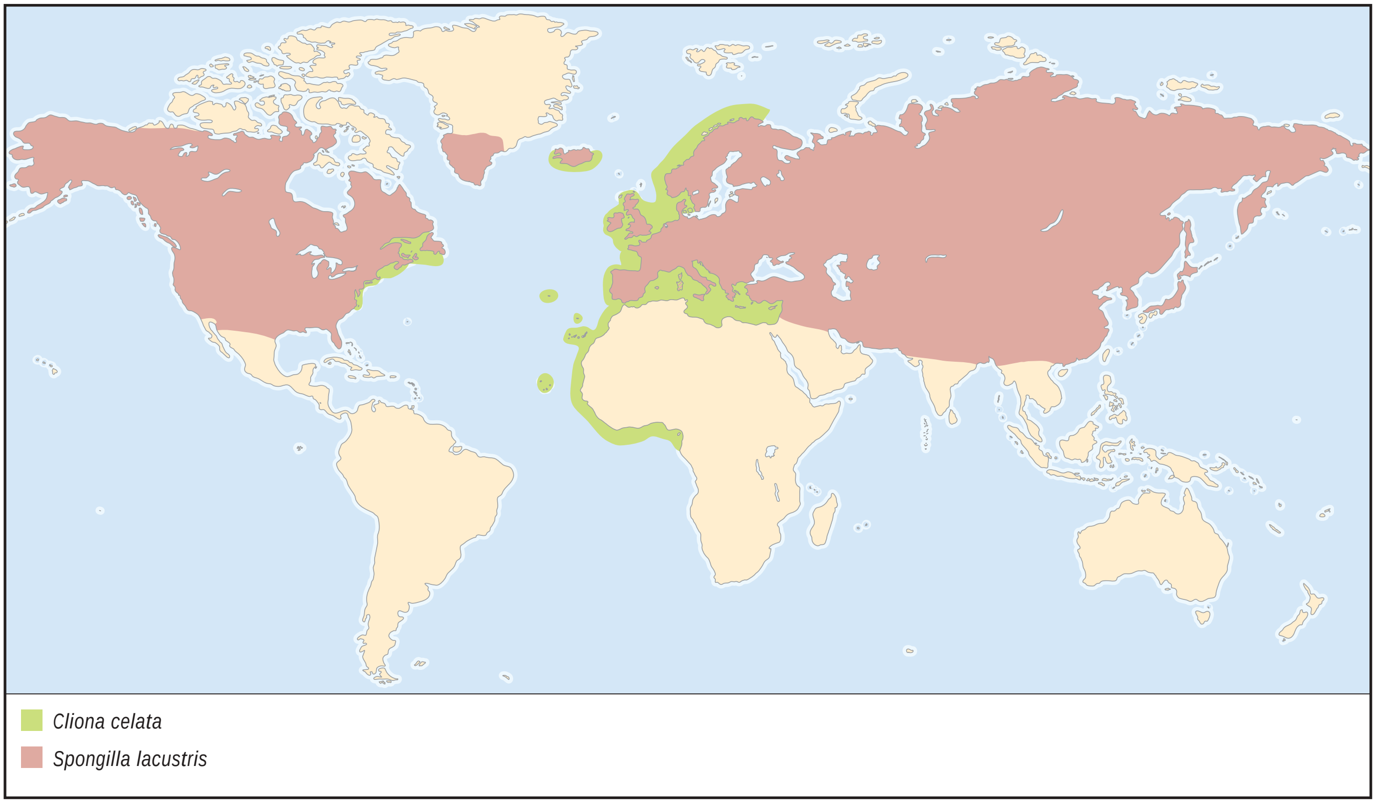
FAMILY
Clionaidae

TAXONOMY
Cliona celata Grant, 1826, Firth of Forth, Scotland.

OTHER COMMON NAMES
Spanish: Esponja perforadora

PHYSICAL CHARACTERISTICS
An excavating, bright yellow sponge occurring in two different forms: a boring stage appearing as low, rounded papillae sticking out from such limestone substrates as calcareous rocks and shells; and a so-called gamma stage that consists of massive lobes as large as 3 ft (1 m) across and 20 in (50 cm) high. Lobes have raised rounded ridges and small round nodules spread over the surface.

DISTRIBUTION
Northeastern Atlantic from Norway south to the Gulf of Guinea; Mediterranean; eastern coast of North America from Newfoundland south to North Carolina.



HABITAT
Infralittoral zone, 0-650 ft (0–200 m).

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter feeder, like all other sponges.

REPRODUCTIVE BIOLOGY
Hermaphroditic; oocytes and sperm develop between June and November. Occasionally reproduces by means of asexual buds.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
A pest to oyster growers. ◆

Bath sponge
Spongia officinalis

ORDER
Dictyoceratida

FAMILY
Spongiidae

TAXONOMY
Spongia officinalis Linnaeus, 1759, Mediterranean.

OTHER COMMON NAMES
German: Meerschwamm; Greek: Fino, Matapas; Italian: Spugna da bagno.

PHYSICAL CHARACTERISTICS
Globular-massive sponges, usually over 4 in (10 cm) in diameter, varying in color from white to black depending on environmental circumstances, with a finely conulose (cone-shaped) surface and spongy-elastic consistency.

DISTRIBUTION
Atlantic coasts of Spain; Mediterranean.

HABITAT
On rocks and in caves from the shoreline to the edge of the continental shelf.

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter-feeder, like all other sponges.

REPRODUCTIVE BIOLOGY
Viviparous; separate sexes. The parenchymellar larvae are large (to 500 µm) and elliptical in shape with short cilia over most of the body.

CONSERVATION STATUS
As of 1986 populations declined as a result of an epidemic disease; protected under the Bern Convention 1998.

SIGNIFICANCE TO HUMANS
Regarded as the finest quality bath sponge in Europe. ◆

No common name
Carteriospongia foliascens

ORDER
Dictyoceratida

FAMILY
Thorectidae

TAXONOMY
Carteriospongia foliascens Pallas, 1766, India.

OTHER COMMON NAMES
German: Blattschwamm.

PHYSICAL CHARACTERISTICS
Lamellate (thinly layered) or foliose (leaflike) greyish-blue sponges, the surface heavily coated with foreign debris, with a characteristic pattern of mounds or ridges. Consistency coarse and flexible.

DISTRIBUTION
Indo-Pacific, Red Sea.

HABITAT
Shallow waters around reefs.

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter-feeder, like all other sponges.

REPRODUCTIVE BIOLOGY
Viviparous.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Produces cytotoxic chemicals named sesterterpenoids with biomedical properties. ◆

Carnivorous sponge
Asbestopluma hypogea

ORDER
Poecilosclerida

FAMILY
Cladorhizidae

TAXONOMY
Asbestopluma hypogea Vacelet & Boury-Esnault, 1996, La Ciotat, Mediterranean.

OTHER COMMON NAMES
French: Éponge carnivore.

PHYSICAL CHARACTERISTICS
Small white sponge with an ovoid body as large as 0.25 in (6.5 mm) high and 0.04 in (1.2 mm) thick, attached to the substrate with a long, thin stalk up to 0.5 in (14 mm) long and .007 in (0.18 mm) in diameter. The body bears 30–60 filaments up to 2.3 in (60 mm) long and 50–80 µm in diameter. The filaments are sticky and shaggy because of their dense cover of tiny raised hook-shaped microscleres (anisochelae).

DISTRIBUTION
Known from two caves near Marseille, France, and one in La Croatia, (Mediterranean).

HABITAT
Rocky surfaces in caves where water is trapped all year long and thus has a constant low temperature of 55-58° F (13–14.7° C), 50-195 ft (15–60 m) away from the entrance, at a depth of 55-75 ft (17–23 m).

BEHAVIOR
Their carnivorous feeding behavior makes these sponges unique.

FEEDING ECOLOGY AND DIET
These sponges have no aquiferous system or choanocyte chambers. Their diet consists of small crustaceans that they capture in their filaments. The prey is completely surrounded by new filaments and digested within a few days.

REPRODUCTIVE BIOLOGY
Viviparous; however, little is known as of 2003 regarding the exact time of reproduction and structure of the embryos.

CONSERVATION STATUS
Known only from La Ciotat; protected under the Bern Convention of 1998 due to its patrimonial interest.

SIGNIFICANCE TO HUMANS
None known. ◆

Freshwater sponge
Spongilla lacustris

ORDER
Haplusclenida

FAMILY
Spongillidae

TAXONOMY
Spongilla lacustris Linnaeus, 1759, Lake of Småland.

OTHER COMMON NAMES
French: Éponge d'eau douce; German: Süsswasserschwamm.

PHYSICAL CHARACTERISTICS
Encrusting, branched, arborescent or massive sponges with a fragile, soft consistency and whitish or green color, with irregularly scattered and inconspicuous oscula. Surface uneven and roughened by tiny spines. Gemmules subspherical to oval, occurring in dense clusters or irregularly scattered in the skeletal network.

DISTRIBUTION
Palaearctic.

HABITAT
In standing and running fresh water.

BEHAVIOR
Little is known besides feeding ecology and reproductive biology.

FEEDING ECOLOGY AND DIET
Filter-feeder, like all other sponges.

REPRODUCTIVE BIOLOGY
Overwinters as gemmules, the dormant stage. Viviparous, with sexual reproduction during the summer.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Books

Bergquist, Patricia R. *Sponges.* London: Hutchinson; Berkeley and Los Angeles: University of California Press, 1978.

Hooper, John N.A., and Rob W. M. van Soest, eds. *Systema Porifera: A Guide to the Classification of Sponges.* New York: Kluwer Academic/Plenum Publishers, 2002.

Hooper, John N. A., and Felix Wiedenmayer. "Porifera." In *Zoological Catalogue of Australia.* Vol. 12, edited by A. Wells. Melbourne, Australia: CSIRO, 1994.

Moss, David, and Graham Ackers, eds. *The UCS Sponge Guide.* Ross-on-Wye: The Underwater Conservation Society, 1982.

Other

van Soest, Rob W. M., Bernard Picton, and Christine Morrow. *Sponges of the North East Atlantic.* [CD-ROM] World Biodiversity Database CD-ROM Series. Windows version 1.0. Amsterdam: Biodiversity Center of ETI, Multimedia Interactive Software, 2000.

Wallie H. de Weerdt, PhD

Placozoa

(Placozoans)

Phylum Placozoa

Number of families 1

Thumbnail description

A large, flat, amoeba-like creature up to 0.078 in (2 mm) in diameter; the grayish white body of the organism consists of several thousand cells that form two epithelia (thin layers of tissue composed of closely apposed cells) but are not organized into tissues and organs

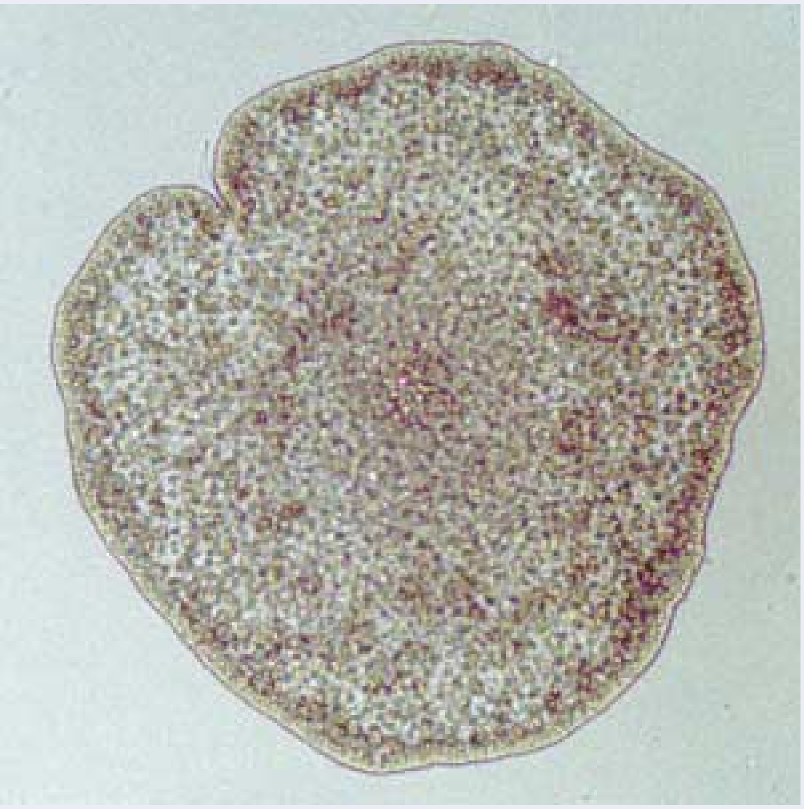


Photo: Dorsal view of *Trichoplax adhaerens.* (Photo by Hidetaka Furuya. Reproduced by permission.)

Evolution and systematics

Phylum Placozoa includes only one species, *Trichoplax adhaerens*. Because this phylum is so small, it has no classes or orders assigned to it. There is one family, the Trichoplacidae. Little is known about this organism because it has never been observed in the wild; it has been studied from samples cultured in laboratory aquaria around the world. *Trichoplax adhaerens* was first discovered in the aquarium of the Graz Zoological Institute in Austria in 1883. A second species, *Trichoplax reptans*, was found in 1896. This species, however, has never been seen since it was first described, causing some researchers to doubt its existence.

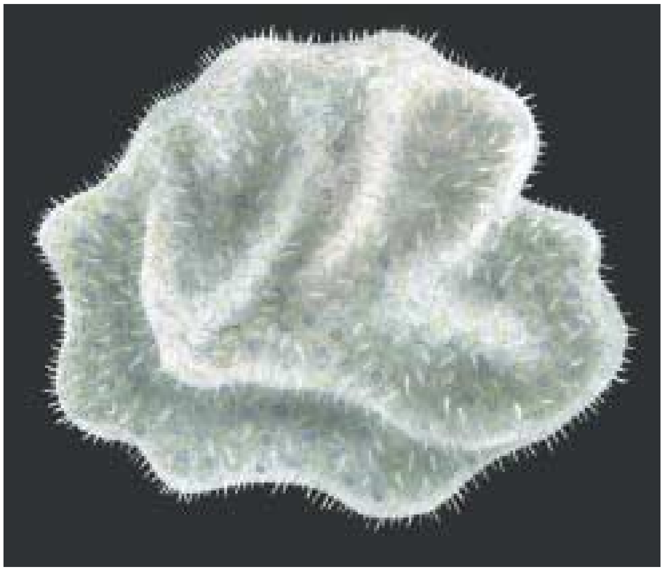
The placozoans were formerly assigned to the phylum Mesozoa together with the dicyemids, orthonectids, and *Salinella* on the basis of their simple body organization. It became evident, however, that placozoans are not like other mesozoans and do not fit into any other metazoan phylum. As a result, phylum Placozoa was established in 1971. Since that date, specimens of *T. adhaerens* have been found in aquaria around the world. It is not known whether placozoans are cosmopolitan (widely distributed around the world); they are, however, so cryptic (hidden) that their diversity may be much greater than we realize.

Some zoologists have inferred that placozoans may represent the earliest form of animal life. Others regard them as a modified form of the planula stage of a cnidarian. Recent molecular phylogenetic studies suggest that the placozoans are closely related to cnidarians. If this finding is confirmed, it would imply that the placozoans are a secondary simplification of more complex ancestors that possessed fully differentiated tissues and organs, including muscles and nerves.

The taxonomy for this species is: *Trichoplax adhaerens* Schulze, 1883, aquarium of the Zoological Institute in Graz, Austria.

Physical characteristics

Placozoans are extremely simple multicellular animals, with no anterior-posterior (front to rear) polarity or bilateral (right to left) symmetry. They have only dorsoventral (upper surface to lower surface) polarity. The bodies of placozoans consist of several thousand cells but only four cell types. The dorsal epithelium is thin and loosely constructed of cover cells that bear a single flagellum (microscopic whip-like appendage), and contain droplets of fatty material that refract light. The ventral epithelium is composed of a thicker, denser layer of nonflagellated gland cells and columnar cylindrical



Trichoplax adhaerens. (Illustration by Dan Erickson)

cells with a single flagellum. A fluid-filled space lies between the two epithelia. It contains mesenchyme, a network of loosely organized cells known as fiber cells. The fiber cell is a syncytium, or mass of protoplasm containing many nuclei. Fiber cells are star-shaped, and connected to one another and to both epithelia by branched extensions. Microtubules and microfilaments can be seen within the cytoplasm of the fiber cells; they may be associated with the contraction of cells. Each fiber cell has a synapse-like structure at the point of its attachment to neighboring cells. The fiber cells are thought to function as both muscle and nerve cells. An additional feature of the fiber cells is the presence of symbiotic bacteria within the space of the endoplasmic reticulum.

Distribution

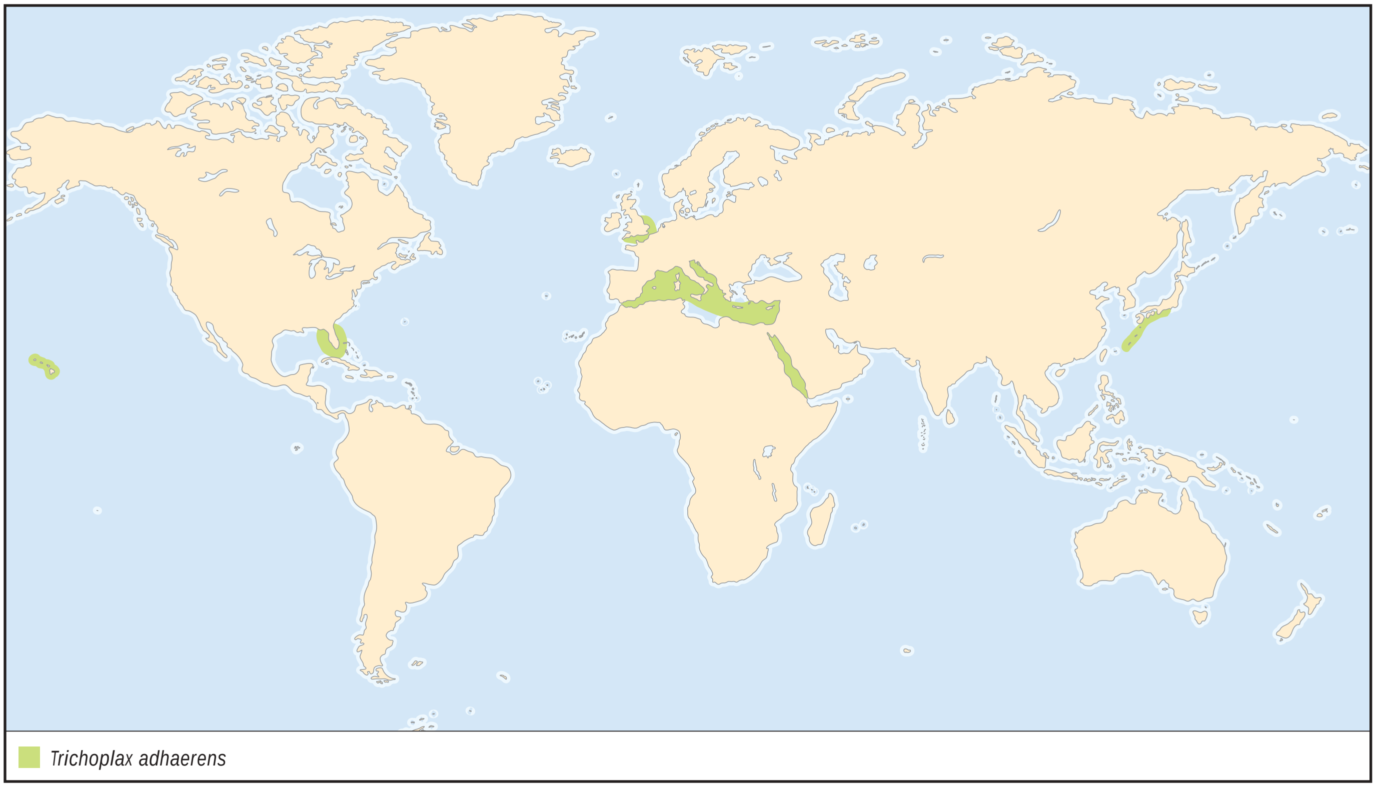
Placozoans are distributed in aquaria located in the littoral zones of tropical and subtropical seas.

Habitat

As of 2003, nothing is known about the biology of placozoans under natural conditions. They may occur on the surface of underwater rocks and benthic marine organisms with shells.

Behavior

Placozoans move around by waving or beating their cilia (tiny hairlike projections), and their outer shape changes continuously. Feeding behavior depends on the amount of available food. When food concentration is low, the organisms move rapidly with frequent random changes in shape. At high concentrations, however, they flatten themselves and move around less.



Feeding ecology and diet

In aquaria and laboratory cultures, placozoans have been observed to creep over the substrate by beating the cilia on their ventral surface. They often lift themselves off the substrate, forming a digestive bag in which they can digest their food more efficiently. They are able to digest detritus, living protozoans, and algae by extracellar digestion. The ventral epithelium absorbs the digested material by phagocytosis.

Reproductive biology

Placozoans appear to undergo asexual reproduction in three ways: fission, in which the body divides in half; fragmentation, in which small parts separate from the body; and budding. Sexual reproduction has occasionally been observed in laboratory vessels containing two different clones of placozoans.

Conservation status

This species is not listed by the IUCN.

Significance to humans

There is no known significance to humans.

Resources

Books

Grell, Karl G., and A. Ruthmann. "Placozoa." In *Microscopic Anatomy of Invertebrates*, vol. 2, edited by Frederick W. Harrison and J. A. Westfall. New York: John Wiley and Sons, 1991.

Periodicals

Grell, Karl G. "Einbildung und Forschung von *Trichoplax adhaerens* F. E. Schulze (Placozoa)." *Zeitschrift für Morphologie der Tiere* 73 (1972): 297–314.

Grell, Karl G., and G. Benwitz. "Die Ultrastruktur von *Trichoplax adhaerens* F. E. Schulze." *Cytobiologie* 4 (1971): 216–240.

Kim, Jihee, W. Kim, and C. W. Cunningham. "A New Perspective on Lower Metazoan Relationships from 18S rDNA Sequences." *Molecular Biology and Evolution* 16, no. 3 (1999): 423–427.

Hidetaka Furuya, PhD

Monoblastozoa

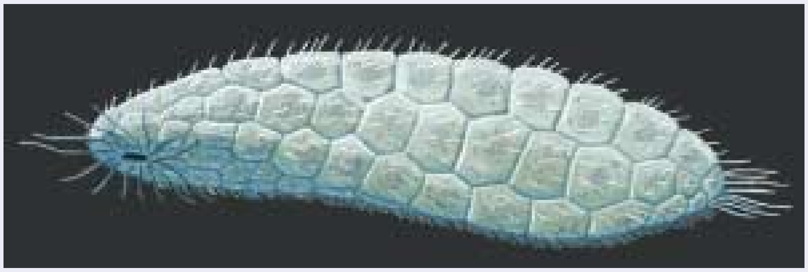
(Salinella)

Phylum Monoblastozoa

Number of families 1

Thumbnail description
A small organism consisting of a single cell layer and lacking tissues and organs

Illustration: *Salinella salve*. (Illustration by Dan Erickson)



Evolution and systematics

Phylum Monoblastozoa includes only one species, *Salinella salve*. Because this phylum is so small, it has no classes or orders assigned to it. *Salinella salve* was found in 1892 in a culture of 2% saline solution made from material taken from the salt beds of Cordova, Argentina. According to Frenzel, the author of the only published record of the organism, the body of *Salinella* consists of a single cell layer and lacks tissues and organs. *Salinella*, however, has never been observed since its discovery. As a result, some zoologists doubt that it really exists.

Salinella has been classified within the phylum Mesozoa, together with the dicyemids, orthonectids, and *Trichoplax*. The body of *Salinella*, however, differs from those of any other metazoans in lacking internal cells. Its body organization is clearly different from the usual pattern of relegating some cells to the interior of the organism to form endoderm. In this regard, *Salinella* appears to be more closely related to unicellular (one-celled) organisms than to living multicellular animals. If contemporary researchers are able to find new specimens of *Salinella* and study them in detail, they might find that the organism represents an intermediate stage between unicellular and multicellular animals.

The taxonomy for this species is: *Salinella salve* Frenzel, 1892, in a culture made from materials taken from the salt beds of Cordoba, Argentina.

Physical characteristics

The body of *Salinella* consists of about a hundred cells and a single cell layer enclosing a digestive cavity. The cavity is open at both ends, with the openings functioning as a mouth and anus respectively. Distinct bristles can be seen around the mouth and anus. The organism's dorsal surface carries a sparse collection of bristles. The ventral surface is somewhat flattened but is heavily ciliated. The cell walls facing the inner cavity are also heavily ciliated.

Distribution

Salinella salve has been identified only in Argentina.

Habitat

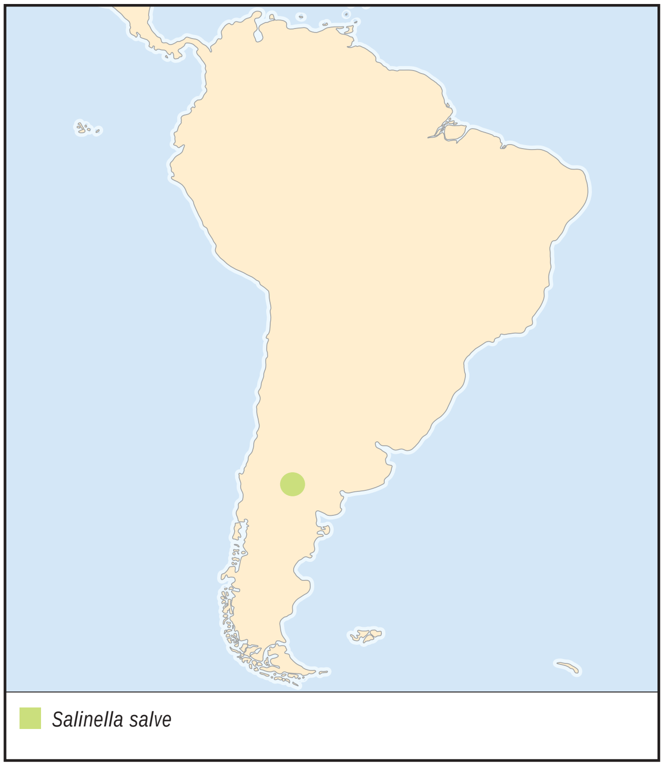
As of 2003, nothing is known about the biology of *Salinella* under natural conditions.

Behavior

Salinella is reported to move by ciliary gliding in the manner of ciliates and small flatworms.

Feeding ecology and diet

Salinella appears to feed by ingesting organic detritus in its internal cavity. Undigested materials are carried to the anus by the movement of the cilia.



Reproductive biology

Asexual reproduction occurs by transverse fission; however, another mode of reproduction was frequently seen in culture. *Salinella* appears to form a cyst by the conjugation or coupling of two individuals. Although the details of the process are unknown, a unicellular individual that possibly came from the cyst was found in the culture. It is not known whether sexual reproduction takes place within the cyst.

Conservation status

The species is not listed by the IUCN.

Significance to humans

There is no known significance to humans.

Resources

Periodicals

Frenzel, Johannes. "Untersuchungen über die mikroskopische Fauna Argentiniens." *Archiv für Naturgeschichte* 58 (1892): 66–96.

Hidetaka Furuya, PhD

Rhombozoa

(Rhombozoans)

Phylum Rhomobozoa

Number of families 3

Thumbnail description
Characteristic parasites of the kidney of benthic cephalopod mollusks; the body consists of only 8–40 cells, which are fewer in number than in any other metazoans and are organized very simply

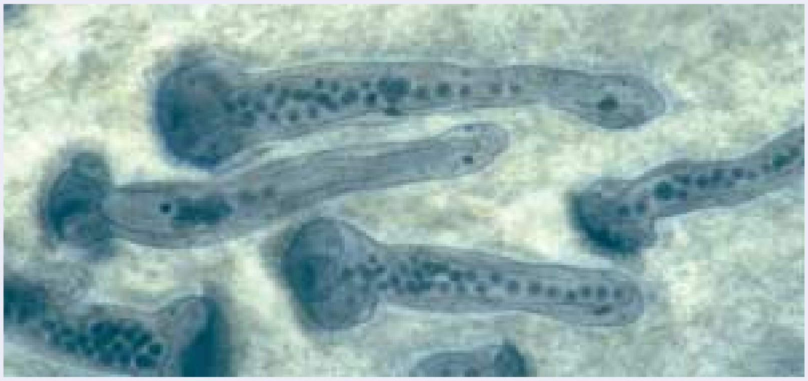


Photo: *Dicyemodeca deca* within its host *Octopus dofleini*. (Photo by Hidetaka Furuya. Reproduced by permission.)

Evolution and systematics

The phylum Rhombozoa includes three families, eight genera, and approximately 150 species. The three families are Conocyemidae, Dicyemidae, and Kantharellidae.

Édouard van Beneden proposed the name Mesozoa for these organisms as an intermediate between Protozoa and Metazoa in body organization. Later zoologists considered rhombozoans degenerated from metazoans such as trematodes because of adaptation for the parasitic lifestyle. Results of phylogenetic studies with nucleotide sequences of 18S recombinant DNA and Hox gene have suggested rhombozoans are spiralians (protostomes) such as turbellarians, nemerteans, annelids, and mollusks. Many scientists now place this group within the phylum Dicyemida.

Physical characteristics

Rhombozoans have two phases of body organization—the vermiform stages of vermiform embryo and adult (nematogen, rhombogen) and the infusoriform embryo. The body of vermiform rhombozoans consists of a central cylindrical cell called the axial cell and a layer of 8–30 ciliated external cells called peripheral cells. The number of peripheral cells is fixed and species specific. At the anterior region, 4–10 peripheral cells form the calotte, the cilia of which are shorter and denser than in more posterior peripheral cells. The calotte comprises two tiers of cells—propolar cells and metapolar cells. Calotte shape varies with species.

Infusoriform embryos consist of 37 or 39 cells, which are more differentiated than those of vermiform organisms. Inside the embryo are four large cells called urn cells, each containing a germinal cell that may give rise to the next generation. At the anterior region of the embryo is a pair of unique cells called apical cells, each containing a refringent body composed of magnesium inositol hexaphosphate. At the posterior region, external cells are ciliated.

Distribution

Temperate and subtropical continental waters. Okhotsk Sea; Sea of Japan; northern, eastern, and western Pacific Ocean; New Zealand; Australia. Mediterranean Sea; northern, eastern, western Atlantic Ocean; Gulf of Mexico; Antarctic Ocean.

Habitat

Vermiform stages of rhombozoans are restricted to the renal sac of cephalopods. In decapods, rhombozoans are also found in the renopancreatic coelom. Some rhombozoans are found in the pericardium of decapods. On the surface of the renal appendage, vermiform rhombozoans insert their heads into renal tubules and folds.

Behavior

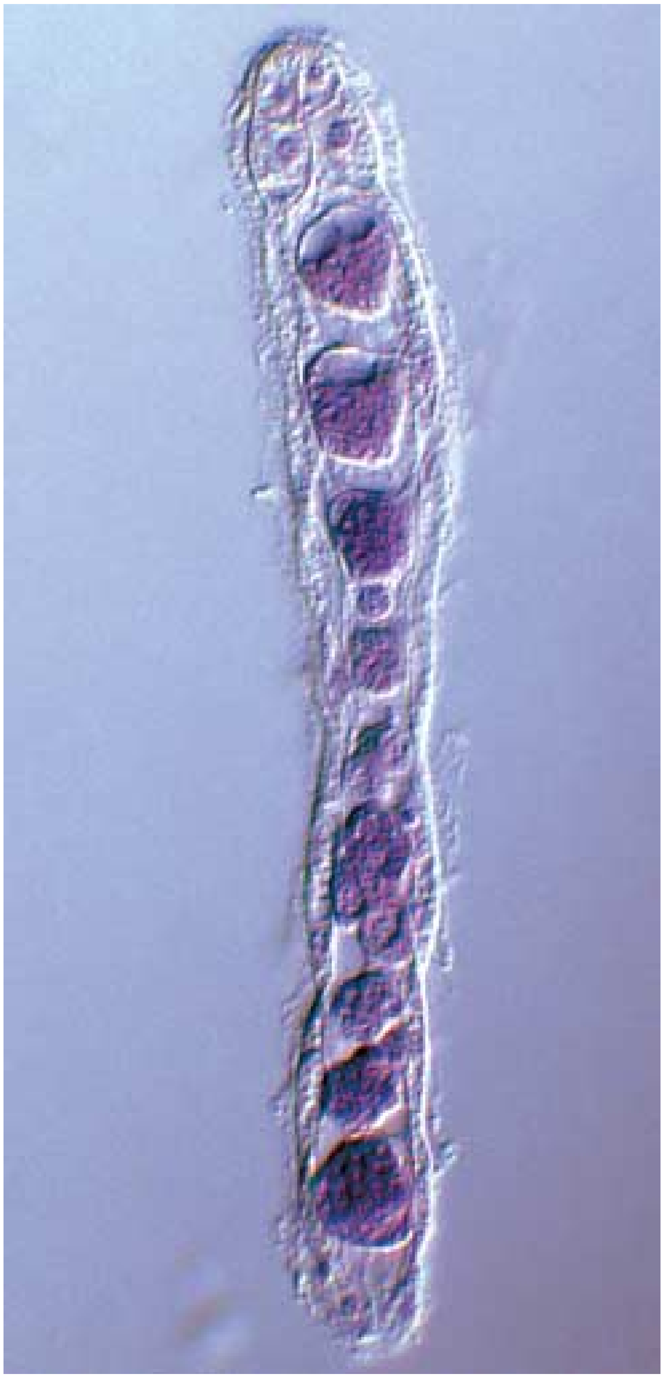
Vermiforms and infusoriform embryos swim with their cilia. There appears to be positive thigmotaxis to renal appendages in the vermiform stages.

Feeding ecology and diet

The surface of the rhombozoan body possesses numerous cilia and has a folded structure believed to contribute to absorption of nutrients from the urine of hosts.

Reproductive biology

The vermiform embryo develops asexually from an agamete (axoblast) and grows into an adult. A high population density in the host renal sac can cause a shift from an asexual mode to a sexual mode of reproduction. The functionally hermaphroditic gonad, the infusorigen, forms at high population density. Mature spermatozoa without tails fertilize the pri-



Dicyema acuticephalum taken from its host *Octopus vulgaris.* (Specimens in McConnaughey collection, Santa Barbara Museum of Natural History. Photo by Hidetaka Furuya. Reproduced by permission.)

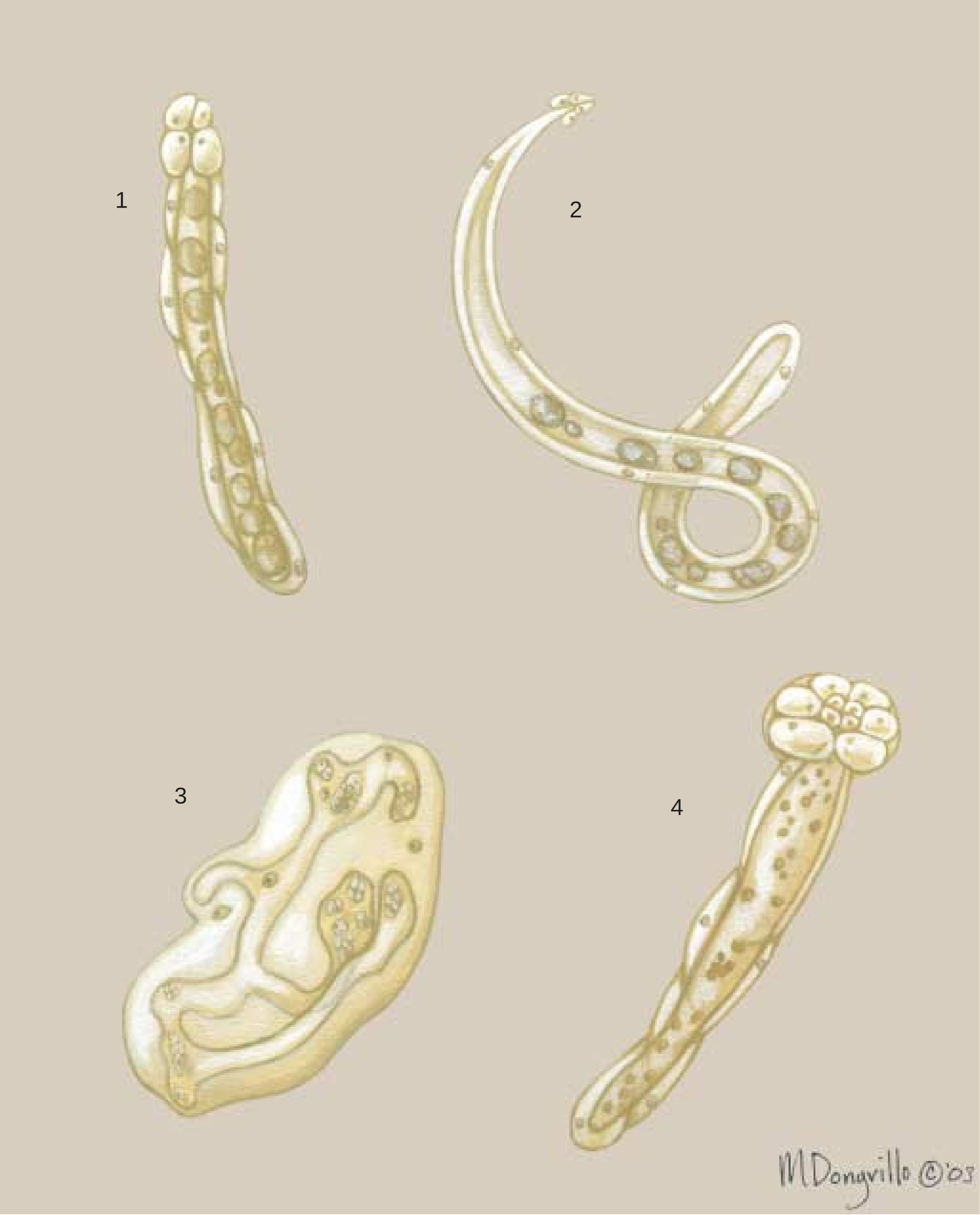
mary oocytes. A fertilized egg develops into an infusoriform embryo. It remains to be understood how infusoriform larvae infect the new host and develop into vermiforms.

Conservation status

No species is listed by the IUCN.

Significance to humans

None known.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1. *Dicyema acuticephalum*; 2. *Dicyemennea antarcticensis*; 3. *Microcyema vespa*; 4. *Dicyemodeca deca*. (Illustration by Marguette Dongvillo)

Species accounts

No common name
Dicyema acuticephalum

FAMILY
Dicyemidae

TAXONOMY
Dicyema acuticephalum Nouvel, 1947, Japan.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Dicyema acuticephalum is characterized by the presence of four propolar and metapolar cells. In this genus, cells of the propolar tier are opposite cells in the metapolar tier. Adults are up to 0.03 in (800 µm) long. Vermiform embryos are approximately 0.002 in (50 µm) long. There are 16–18 peripheral cells. The calotte is bell shaped. Infusoriform embryos consist of 37 cells and are approximately 0.001 in (30 µm) long.

DISTRIBUTION
Japan.

HABITAT
Renal sacs of *Octopus vulgaris.*

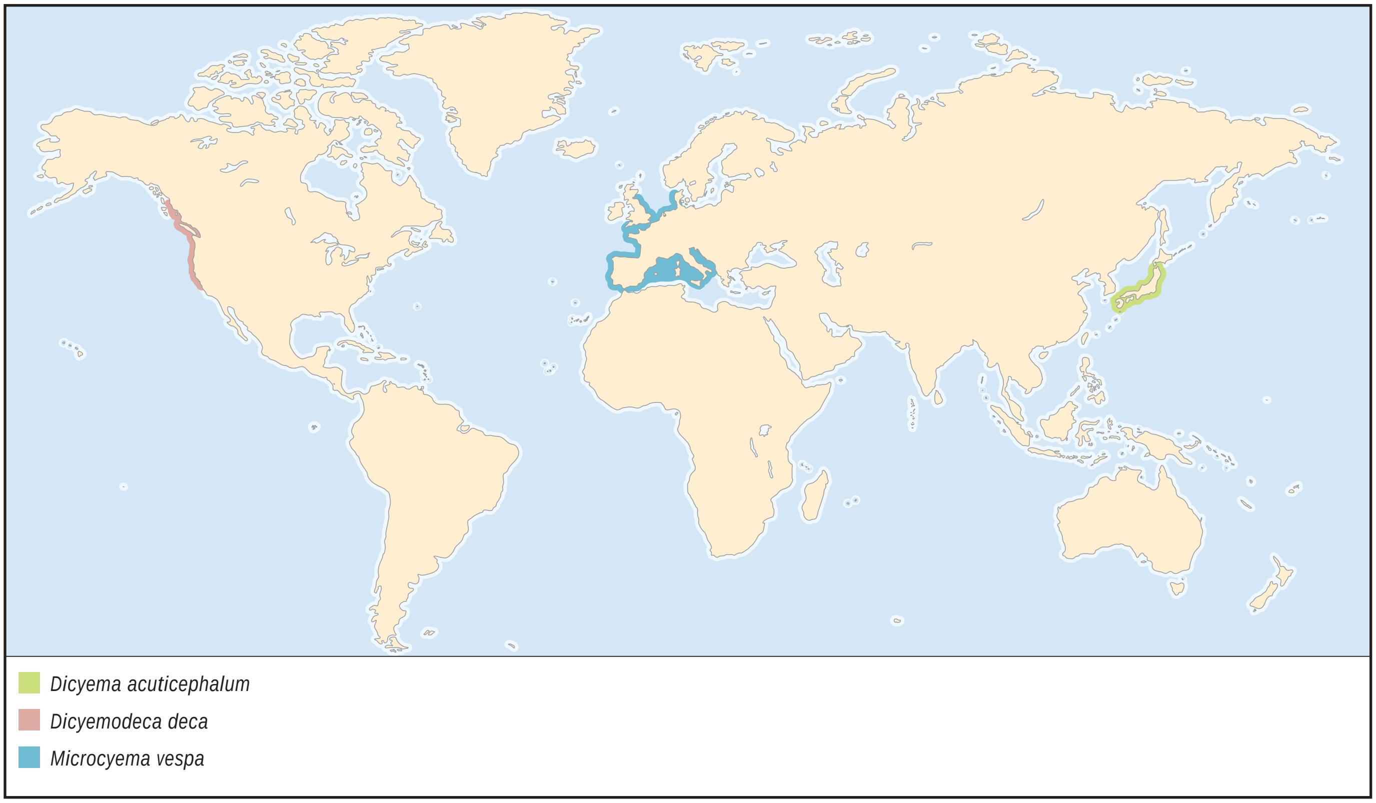
BEHAVIOR
Vermiform rhombozoans and infusoriform embryos swim with their cilia. There appears to be positive thigmotaxis to renal appendages in the vermiform stages.

FEEDING ECOLOGY AND DIET
Absorption of nutrients from the urine of hosts.

REPRODUCTIVE BIOLOGY
Adults have a single hermaphroditic gonad, the infusorigen. Approximately nine egg-line cells (oogonia primary oocytes) and 16 sperm-line cells (spermatogonia, primary spermatocytes, secondary spermatocytes, sperm) usually are found in an infusorigen.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



No common name
Dicyemennea antarcticensis

FAMILY
Dicyemidae

TAXONOMY
Dicyemennea antarcticensis Short and Hochberg, 1970, Antarctic Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Dicyemennea antarcticensis is characterized by the presence of four propolar and five metapolar cells. The body length of adults is up to 0.2 in (5,500 µm). The body length of vermiform embryos is approximately 0.01 in (300 µm). There are 34–36 peripheral cells. The calotte is triangular in the side view and pointed to rounded in the anterior view. Infusoriform embryos consist of 39 cells. The body length of infusoriform embryos is approximately 0.002 in (51 µm).

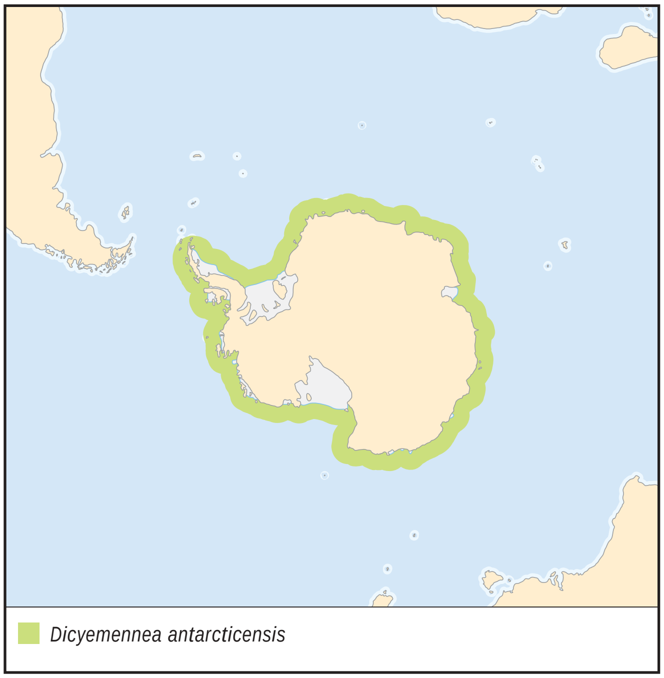
DISTRIBUTION
Antarctic Ocean.

HABITAT
Renal sacs of the Antarctic octopus (*Pareledone turqueti*).

BEHAVIOR
Vermiform rhombozoans and infusoriform embryos swim with their cilia. There appears to be positive thigmotaxis to renal appendages in the vermiform stages.

FEEDING ECOLOGY AND DIET
Absorption of nutrients from the urine of hosts.

REPRODUCTIVE BIOLOGY
Adults have a single hermaphroditic gonad, the infusorigen. Approximately 10 egg-line cells (oogonia primary oocytes) and four sperm-line cells (spermatogonia, primary spermatocytes, secondary spermatocytes, sperm) usually are found in an infusorigen.



CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Dicyemodeca deca

FAMILY
Dicyemidae

TAXONOMY
Dicyemodeca deca McConnaughey, 1957, northeastern Pacific Ocean (Washington, United States).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Dicyemodeca deca is characterized by the presence of four propolar and six metapolar cells. The body length of adults does not exceed 0.04 in (1,000 µm). The body length of vermiform embryos is approximately 0.002 in (40–60 µm). There are 23 or 24 peripheral cells. The calotte is disk shaped. Infusoriform embryos consist of 35 cells and are approximately 0.001 in (33 µm) long.

DISTRIBUTION
Northeastern Pacific Ocean.

HABITAT
Renal sacs of *Octopus dofleini.*

BEHAVIOR
Vermiform rhombozoans and infusoriform embryos swim with their cilia. There appears to be positive thigmotaxis to renal appendages in the vermiform stages.

FEEDING ECOLOGY AND DIET
Absorption of nutrients from the urine of hosts.

REPRODUCTIVE BIOLOGY
Adults have two infusorigens. Approximately 16 egg-line cells (oogonia primary oocytes) and 15 sperm-line cells (spermatogonia, primary spermatocytes, secondary spermatocytes, sperms) usually are found in an infusorigen.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Microcyema vespa

FAMILY
Conocyemidae

TAXONOMY
Microcyema vespa van Beneden, 1882, English Channel.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Microcyema vespa is characterized by an irregular shape in adults; they lack external cilia and have a syncytiumal peripheral cell. The body length of adults is up to 0.03 in (800 µm). The body length of vermiform embryos is approximately 0.001 in (25 µm). There are 10 peripheral cells.

In vermiform embryos the calotte is a syncytium containing six nuclei. Infusoriform embryos consist of 39 cells. The body length of infusoriform embryos is approximately 0.001 in (26 µm).

DISTRIBUTION

English Channel, Mediterranean Sea.

HABITAT

Renal sacs of *Sepia officinalis.*

BEHAVIOR

Vermiform embryos and infusoriform embryos swim with their cilia. There appears to be positive thigmotaxis to renal appendages in the vermiform stages.

FEEDING ECOLOGY AND DIET

Absorption of nutrients from the urine of hosts.

REPRODUCTIVE BIOLOGY

Adults have approximately 10 infusorigens. Approximately 9 egg-line cells (oogonia primary oocytes) and 8 sperm-line cells (spermatogonia, primary spermatocytes, secondary spermatocytes, sperms) usually are found in an infusorigen.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

Hochberg, F. G. “Diseases Caused by Protistans and Mesozoans.” In *Diseases of Marine Animals.* Vol. III, edited by Otto Kinne. Hamburg: Biologische Anstalt Helgoland, 1990.

Periodicals

Furuya, Hidetaka. “Fourteen New Species of Dicyemid Mesozoans from Six Japanese Cephalopods, with Comments on Host Specificity.” *Species Diversity* 4 (1999): 257–319.

McConnaughey, Bayard H. “Two New Mesozoa from the Pacific Northwest.” *Journal of Parasitology* 43 (1957): 358–61.

Nouvel, Henri. “Les Dicyémides. Systématique, générations, vermiformes, infusorigène et sexualité.” *Archives de Biologie, Paris* 58 (1947): 59–220.

Short, Robert B., and F. G. Hochberg. “A New Species of *Dicyemennea* (Mesozoa: Dicyemidae) from Near the Antarctic Peninsula.” *Journal of Parasitology* 56 (1970): 517–22.

van Beneden, Édouard. “Contribution à l’histoire des Dicyémides.” *Archives de Biologie*, *Paris* 31 (1882): 195–228.

Hidetaka Furuya, PhD

■

Orthonectida

(Orthonectidans)

Phylum Orthonectida

Number of families 1

Thumbnail description
Minute dioecious and dimorphic or hermaphroditic parasites found in tissues of a wide variety of marine invertebrate phyla.

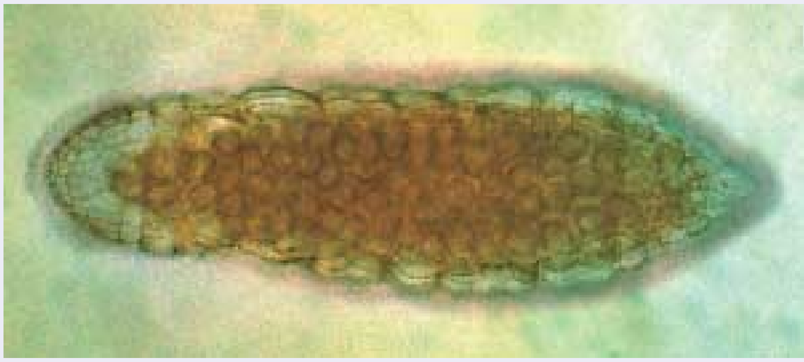


Photo: A female *Rhopalura ophiocomae*. (Specimens in Nouvel collection, Santa Barbara Museum of Natural History. Photo by Hidetaka Furuya. Reproduced by permission.)

Evolution and systematics

The phylum Orthonectida encompasses one family, four genera, and 20 species. Twenty nominal species have been described and variously placed in four genera. Genera are separated on the basis of body shape and the number and arrangement of egg cells in the axial region of the females. Species are separated on the basis of body size; the number, size, and arrangement of rings of ciliated and unciliated jacket cells; the presence and location of pigment and refringent granules in jacket cells; and host specificity. One family, the Rhopaluridae, contains all four genera: *Rhopalura*, *Intoshia*, *Ciliocincta*, and *Stoecharthrum*.

The orthonectids were previously placed in the Mesozoa because of their simple body organization, but recent phylogenetic studies suggest the orthonectids are closer to myxozoans and nematodes. Many scientists now classify Orthonectida at the order level. A more traditional classification; with Orthonectida at the phylum level, is followed here.

Physical characteristics

Depending on the species, orthonectids are either dioecious and dimorphic, or hermaphroditic. The adults are minute, ranging in length from 0.002 to 0.031 in (50 to 800 µm). The body of the adult consists of a jacket of ciliated and unciliated somatic cells arranged in rings around an internal axial mass. Contractile muscle cells differentiate to pack the gonad with longitudinal, circular, and oblique orientations.

Distribution

Orthonectids occur in coastal regions of the English Channel, the Dover Strait, the Strait of Kattegat, the Barents Sea, the White Sea, the northwestern Pacific Ocean (Japan), and the northeastern Pacific Ocean (United States).

Habitat

Orthonectids are found in tissues of organisms in the marine invertebrate phyla Platyhelminthes, Nemertea, Annelida, Mollusca, Echinodermata, Bryozoa, and Urochordata. In the host, infective orthonectid germinal cells penetrate a host cell, and embryos develop and grow into adults within the cytoplasm of the host cell (the "plasmodium").

Behavior

The name Orthonectida means "straight swimming," because orthonectids swim in a straight line, but they generally swim in a spiral motion.

Feeding ecology and diet

Orthonectids may absorb nutrients within the host's cytoplasm.

Reproductive biology

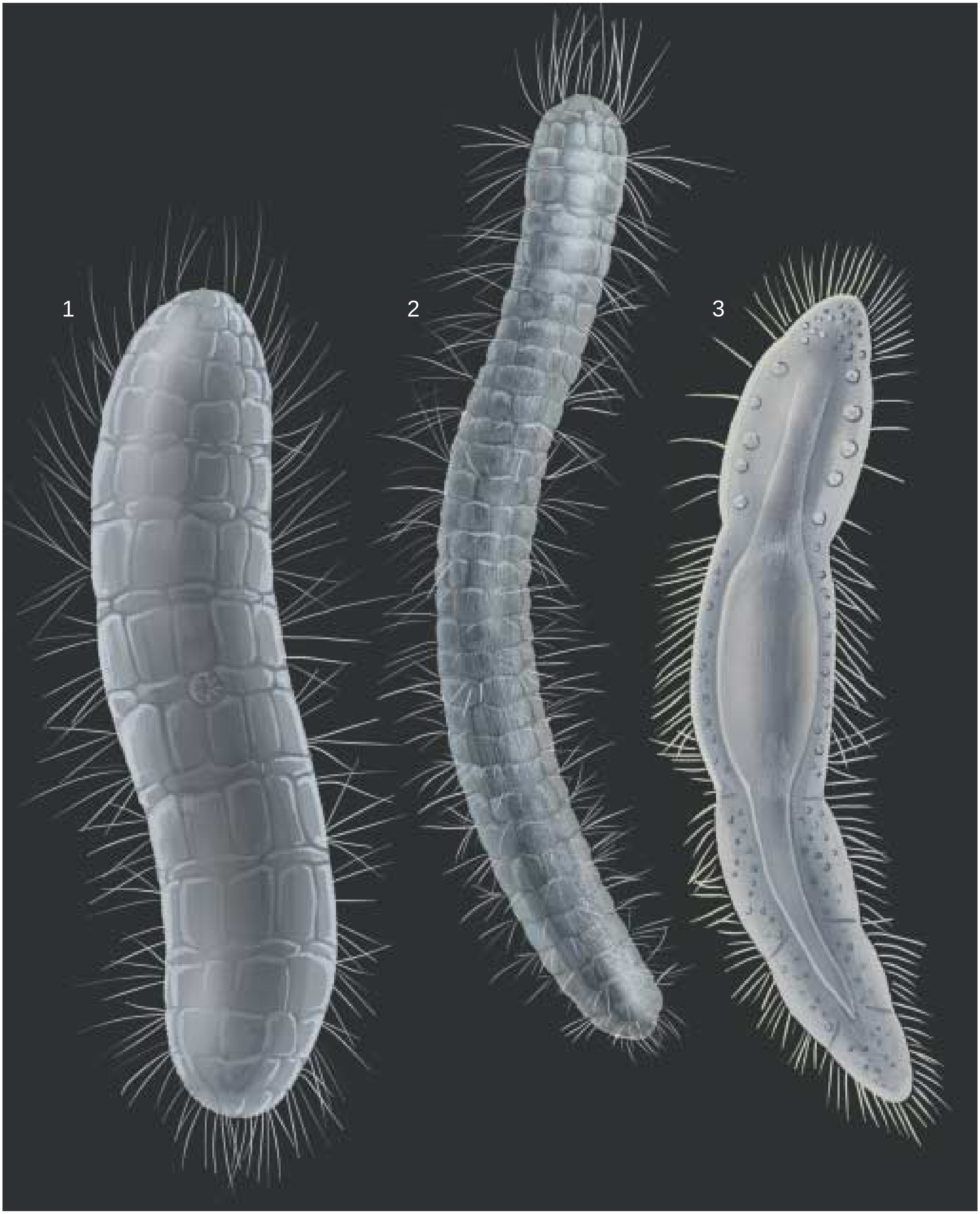
During mating, males make brief contact with females when sperm are released. Fertilization is internal in females. Embryos form about 22 hours after the first cleavage of eggs. When the embryos are fully developed, the female ruptures and dies, releasing ciliated larvae that disperse and enter a new host.

Conservation status

No species of orthonectid is listed by the IUCN.

Significance to humans

None known.



1. *Intoshia linei*; 2. *Ciliocincta sabellariae*; 3. *Rhopalura ophiocomae*. (Illustration by John Megahan)

Species accounts

No common name

Rhopalura ophiocomae

FAMILY
Rhopaluridae

TAXONOMY
Rhopalura ophiocomae Giard, 1877, Wimereux, France.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Reaches length of 0.01 in (260 µm) in females, 0.005 in (130 µm) in males. This genus is characterized by sexual dimorphism, the demarcation of the body into regions being much sharper in males than in females. Males possess conspicuous crystalline inclusions in some epidermal cells. In females, the numerous oocytes form a compact mass that occupies most of the body; in males, the sperm mass is located in the middle third of the body.

DISTRIBUTION
Widely distributed. The usual host species, *Amphipholis squamata*, occurs off the coasts of France, Great Britain, and Italy, and Washington and California in the United States.

HABITAT
The perivisceral coelom are closely associated with the walls of the genital bursae or the gut of a parasitized brittle star.

BEHAVIOR
Generally swims by a spiraling motion.

FEEDING ECOLOGY AND DIET
May absorb nutrients in the host cytoplasm.

REPRODUCTIVE BIOLOGY
In males, the genital pore is located between epidermal rings 12 and 14; in females, in ring 19. The male and female may bring their genital pores together long enough for sperm transfer to be effected.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Ciliocincta sabellariae

FAMILY
Rhopaluridae

TAXONOMY
Ciliocincta sabellariae Kozloff, 1965, San Juan Archipelago, Washington, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body length of females up to 0.01 in (270 µm); usually 38 or 39 rings of epidermal cells. Males up to 0.005 in (130 µm); usually 30 rings of epidermal cells. This genus is characterized by slight sexual dimorphism. Males are smaller than females, but the arrangement of epidermal cells and the pattern of ciliation are similar in both sexes. Males have no crystalline inclusions in epidermal cells comparable to those of male *Rhopalura*. In females, oocytes are in a single series.

DISTRIBUTION
The host is the sabellid polychaete *Sabellaria cementarium*, which occurs in the San Juan Archipelago, off the coast of the state of Washington, in the United States.

HABITAT
Epidermal tissues of the body wall and dorsal cirri of the parasitized polychaete.

BEHAVIOR
Generally swims in a spiral motion.

FEEDING ECOLOGY AND DIET
May absorb nutrients in the host cytoplasm.

REPRODUCTIVE BIOLOGY
In males, the genital pore is located in the boundary between epidermal rings 15 and 16; in females, in ring 14. The male and female may bring their genital pores together long enough for sperm transfer to be effected.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

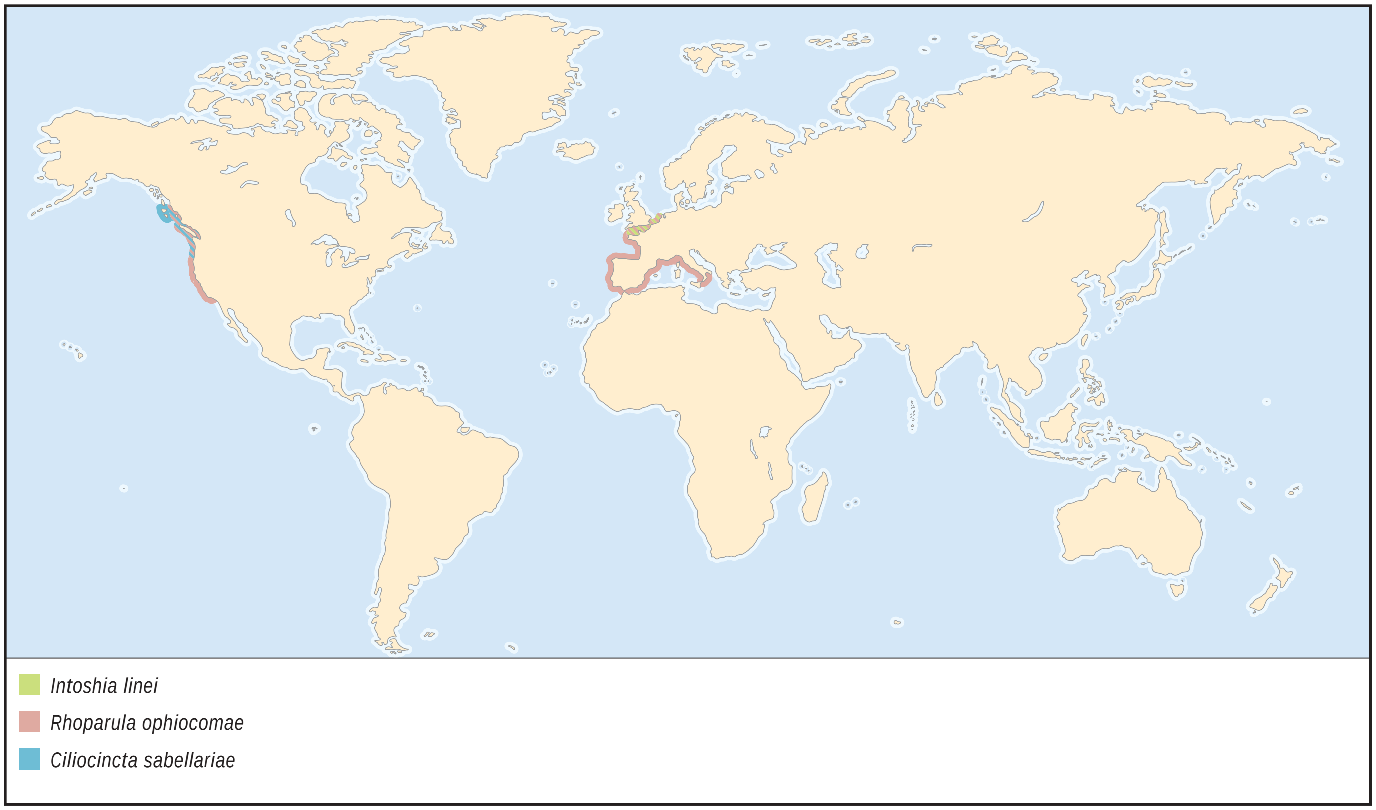
Intoshia linei

FAMILY
Rhopaluridae

TAXONOMY
Intoshia linei Giard, 1877, Wimereux, France.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body length up to 0.006 in (160 µm); usually 24 rings of epidermal cells. In males, the body of the largest individual is not over 0.0016 in (41 µm) in length. In this genus, more than half the rings of epidermal cells are completely ciliated; the rest lack cilia. Sexual dimorphism usually occurs. Males are much smaller than females, are ovoid, and have two genital pores. Males have no crystalline inclusions in epidermal cells compa-



rable to those in male *Rhopalura*. In females, the oocytes fill most of the axial mass, and are packed together so they seem to form two or three rows.

DISTRIBUTION
The hosts are the nemerteans *Lineus viridus*, *L. sanguineus*, and *L. rubber*, which occur on the English Channel coast of France at Wimereux and Roscoff.

HABITAT
Tissues of a parasitized nemertean.

BEHAVIOR
Generally swims in a spiraling motion.

FEEDING ECOLOGY AND DIET
May absorb nutrients in the host cytoplasm.

REPRODUCTIVE BIOLOGY
In males, there are two genital pores, located in epidural rings 8 and 16; in females, in ring 12. The male and female may bring their genital pores together long enough for sperm transfer to be effected.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Books

Kozloff, Eugene N. “Phyla Placozoa, Dicyemida, and Orthonectida.” In *Invertebrates.* Philadelphia: Saunders College Publishing, 1990.

Periodical

Kozloff, Eugene N. “The Genera of the Phylum Orthonectida.” *Cahiers de Biologie Marine* 33 (1992): 377–406.

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Hidetaka Furuya, PhD

Anthozoa

(Anemones and corals)

Phylum Cnidaria

Class Anthozoa

Number of families 130

Thumbnail description

Exclusively polypoid cnidarians. Tubular body with hollow tentacles around the mouth; has a pharynx that opens into a digestive cavity subdivided by infoldings of the gut wall. May be solitary or colonial, with or without an internal or external skeleton.

Photo: Jeweled anemone (*Corynactis californica*) (©Shedd Aquarium. Photo by Patrice Ceisel. Reproduced by permission.)

Evolution and systematics

Anthozoa is the largest class in the phylum Cnidaria, with over 6,000 extant species divided among nine orders and classified in two subclasses. The nine orders are as follows:

Subclass Octocorallia (= Alcyonaria)

- Order Pennatulacea, the sea pens and sea pansies; 16 families
- Order Helioporacea, the blue corals; two families
- Order Alcyonacea, the soft corals, sea fans, and sea whips; 29 families

Subclass Hexacorallia (= Zoantharia)

- Order Actiniaria, the sea anemones; 42 families
- Order Scleractinia (= Madreporaria), the true (stony or hard) corals; 25 families
- Order Corallimorpharia, the mushroom (false) corals (also known as mushroom anemones or disc anemones); 4 families
- Order Zoanthidea (= Zoanthinaria), the zoanthids; four families
- Order Antipatharia, the black (thorny) corals and wire corals; five families
- Order Ceriantharia, the tube anemones; three families

Some authors classify the Ceriantharia and Antipatharia together in a third subclass, the Ceriantipatharia, but genetic evidence does not support this grouping.

Molecular evidence places the Anthozoa as the earliest branch of the phylum Cnidaria. Since anthozoans exist exclusively as benthic (sea bottom) polyps, whereas the remaining cnidarians have life cycles that alternate between benthic polyp and pelagic medusoid stages, this evidence indicates that the polyp stage is the ancestral condition among Cnidaria. Within the Hexacorallia, additional evidence suggests that actiniarians, and more recently corallimorpharians, may have evolved from a scleractinian ancestor, accompanied by the loss of a skeleton.

Fossils resembling anthozoans, including sea pens, are known from as early as the Precambrian eon (>540 million years ago [mya]), but it wasn't until the Ordovician period (about 465 mya) that stony coral fossils became common. Two groups of corals dominant among Ordovician fossils—the Tabulata and Rugosa—became extinct at the end of the Permian period (about 248 mya). The earliest scleractinian fossils come from the middle Triassic period (about 230 mya).

Physical characteristics

Anthozoans are polypoid cnidarians. As in all cnidarians, the body wall is composed of two cell layers—the outer ectodermis (or epidermis) and the inner gastrodermis—separated by a layer of gelatinous material known as mesoglea or mesenchyme. Tentacles bearing stinging cells surround the mouth, which is the only opening to the digestive system. A polyp is essentially a tubular sac, with the mouth and tentacles on a flattened upper surface called the oral disk. The mouth leads to a pharynx, a short tube projecting into the closed gut (the coelenteron or gastrovascular cavity). The pharynx typically has one or more ciliated grooves (siphonoglyphs) that funnel water into the coelenteron. The coelenteron is subdivided into chambers by vertical septa (or mesenteries), infoldings of the gut wall that may or may not

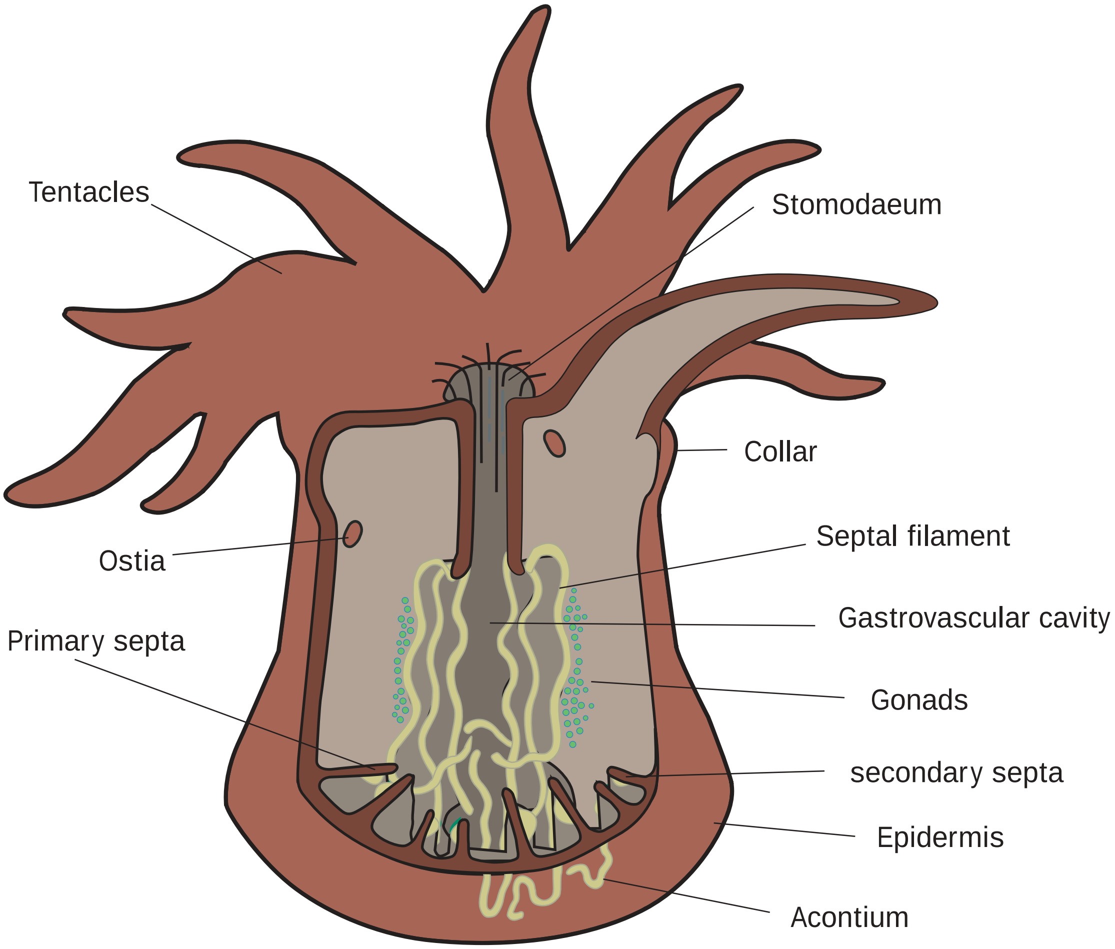
Frogspawn coral (*Euphyllia cristata*). (©Shedd Aquarium. Photo by Edward G. Lines, Jr. Reproduced by permission.)

attach to the pharynx. Below the pharynx, the free edges of the septa are thickened to form septal, or mesenterial, filaments that contain cells involved in digestion, including nematocysts. The tentacles are hollow and continuous with the coelenteron.

Octocorals have eight pinnate (parts arranged on each side of a common axis) tentacles and eight septa; hexacorals have septa and tentacles—usually simple—in multiples of six. Cerianthids have two circlets of tentacles, one around the mouth and the other around the edge of the oral disc. There are a number of other details of polyp anatomy that are used to distinguish the orders of Anthozoa.

A unique characteristic of cnidarians is the cnida, a complex intracellular capsule containing an eversible hollow tubule that can be released to sting or trap prey. Eversible means that the structure can turn inside out. There are three basic types of cnidae, and all can be found in the class Anthozoa. Nematocysts, which contain toxins and are typically armed with spines for penetrating the tissues of other organisms, are possessed by all anthozoans. Spirocysts are sticky rather than penetrating and are found only in the hexacorallians. Ptychocysts are unique to the cerianthid tube anemones and are used to construct their tubes.

Species in the orders Scleractinia, Octocorallia, and Antipatharia produce skeletons. In the Scleractinia, the living tissue essentially lies above an external skeleton made of calcium carbonate secreted by the ectodermis. Scleractinian skeletons can take on a variety of shapes, generally described as massive, columnar, encrusting, branching, leaflike or platelike. It is these skeletons that form the framework of tropical coral reefs. Antipatharians secrete an internal horny skeleton that is flexible, black in color, and equipped with thorns on its surface. Octocorals secrete an internal skeleton composed of a protein called gorgonin, calcium carbonate, or a combination of both. Octocorallian and antipatharian skeletons are usually branching treelike or whiplike forms. Unlike other octocorals, helioporaceans produce a massive skeleton that is blue in color and resembles those found in the stony corals. Oc-



Anthozoa anatomy. (Illustration by Christina St. Clair)

tocorals also secrete small calcareous sclerites (hardened plates) of a variety of shapes and colors that are embedded in the mesenchyme and that may give a spiny or scaly appearance to the colony. Octocorallian soft corals lack a supporting internal skeleton and can inflate or deflate the fleshy colony by funneling water into or out of their polyps. With the exception of the zoanthid genus *Gerardia*, species in the remaining anthozoan orders do not secrete a skeleton. A few actiniarians secrete a chitinous tube, and one genus is able to form a chitinous coiled shell, similar in shape to a snail shell, that is inhabited by a hermit crab. Cerianthids build soft, feltlike tubes from fired ptychocysts.

Anthozoans may be either solitary or colonial. In colonial species, the polyps are united by living tissue, the coenenchyme, and their gastrovascular cavities are joined by canals or tubes. Actiniarians and ceriantharians are exclusively solitary, and the octocorals and antipatharians are exclusively colonial, but the remaining orders have both types of morphologies. Solitary polyps are commonly 0.5–2 in (1–5 cm) in diameter at the oral disk, but the largest species grow to 3 ft (1 m) across. Polyps of colonial species are typically much smaller (<0.4 in (5 mm)), but the colonies themselves can be quite large. Octocorallian and antipatharian colonies may grow >8 ft (2.5 m) tall, and some scleractinian corals may reach a size of 19.5 ft (6 m) in height and width. Colonial anthozoans may reach a great age. For example, many octocorals are 100 or more years old, and the deep-sea zoanthid *Gerardia* has been estimated to be 1800 years old.

Distribution

Anthozoans are found worldwide in all oceans.

Habitat

Anthozoans are restricted to marine habitats, but can be found from the intertidal zone to over 19,500 ft (6,000 m) deep. Solitary forms may be attached to a hard substrate or burrowed into soft bottom mud or sand. Colonial forms grow as an encrusting or stoloniferous form on other substrates, or build massive skeletons; tree-like colonial forms are attached by the base of the main stem. Sea pen colonies are anchored into soft bottoms by the base of the primary polyp. Reef-building corals are most typically found in clear, shallow, warm tropical waters, although a few species are known from the cold, dark deep sea.

Crimson anemone (*Cribinopsis fernaldi*). (©Shedd Aquarium. Photo by Patrice Ceisel. Reproduced by permission.)

Behavior

One of the most spectacular of anthozoan behaviors is the synchronous release of sperm and eggs by many colonies over a wide area of coral reef. Mass spawning events have been observed in octocorallian and zoanthid species, but are best known in the scleractinian corals of the Great Barrier Reef, Australia. In some cases, many species release gametes on the same night, and there is considerable evidence that hybridization between species may occur. Synchrony is achieved by timing gamete release with the lunar cycle, and many corals spawn shortly after sunset following a full moon. Eggs and sperm may be released separately into the water column; or, in some hermaphroditic species, may be combined into gamete bundles that float to the surface and break apart there. During these mass spawning events, huge slicks of gametes and developing larvae can be observed on the water surface, attracting a variety of predators that feed on the spawned gametes.

Anthozoans engage in aggressive interactions to defend space from neighboring individuals of the same or different species. A number of specialized structures may be used to repel encroachers. Sea anemones may possess acrorhagi, inflated saclike structures bearing nematocysts that ring the collar below the tentacles. Acrorhagi can be elongated to come into contact with an intruder, whereupon they cause tissue death. Scleractinian, octocorallian, and antipatharian corals may develop specialized tentacles ("sweeper tentacles") after prolonged contact with foreign species. These tentacles are five to ten times longer than normal feeding tentacles and have a greater number of stinging nematocysts. The tentacles search and sweep an area around the polyp and cause tissue death in neighboring species upon contact. Similar structures found in some sea anemones are called "catch tentacles." Some scleractinian corals and corallimorpharians also may extrude their septal filaments to digest the neighboring species' tissues.

Several octocorallian species can produce light when contact with the colony is made. This bioluminescence may be in the form of a bright green flash from a polyp, or a wave of light across the colony as polyps flash sequentially from the point of contact. It is likely the light is meant to startle visual predators.

Feeding ecology and diet

Most anthozoans are suspension feeders whose diet consists of small planktonic invertebrates, phytoplankton, bacterioplankton, or other suspended organic matter. Their methods of prey capture are generally, though not exclusively, passive. Drifting prey may be captured when it comes in contact with the extended tentacles of anthozoan polyps. Prey capture may also involve the firing of cnidae. Many scleractinians produce a slimy mucus that covers the polyp and traps floating and sinking food particles. The mucus is moved around by cilia (small hairlike projections), and eventually enters the mouth. Large sea anemones may feed on crabs, bivalves and fishes, while ptychodactarian anemones have been observed preying upon gorgonian octocorals. In 1997, colonies of the soft coral *Gersemia antarctica* were first reported to bend over and feed in the soft sediments of the Antarctic. Researchers proposed that this feeding strategy may be employed where suspended organic material is in low supply, as it is in the deep sea. Some anthozoans also may absorb dissolved organic matter directly from the seawater into their cells.

Another source of nutrition for many anthozoans comes from symbiotic photosynthetic algae living within cells of the gastrodermis. Like other plants, these algae produce energy-rich organic molecules through photosynthesis; between 20% and 95% of this production is transferred to the host. These

Bubble coral (*Pleurogyra sinuosa*). (©Shedd Aquarium. Photo by Edward G. Lines, Jr. Reproduced by permission.)

symbionts are usually dinoflagellates, called "zooxanthellae"; however, green algae symbionts ("zoochlorellae") are also known. Most shallow-water, reef-building corals contain zooxanthellae, and they also may be found in tropical gorgonians, anemones, and zoanthids. The zooxanthellae are additionally thought to increase the rate at which scleractinian reef corals produce their calcium carbonate skeleton.

The predators of anthozoans include nudibranchs, sea stars, crabs, polychaetes, and fishes.

Reproductive biology

Anthozoans display a wide range of reproductive strategies. Asexual clones may be produced in a variety of ways. Polyps may undergo fission in either a longitudinal or transverse direction. Many sea anemones produce clones by pedal laceration, wherein pieces of the pedal disk tear off or break free and develop into new individuals. The growth of anthozoan colonies may be considered a mode of asexual reproduction. After a free-living larva settles, it metamorphoses into a polyp that repeatedly divides to give rise to additional polyps, all of which remain connected by living tissue. In some species, budded polyps may be released from the parent colony, and these then settle and develop a new colony. Anthozoans, particularly colonial species, also may reproduce by fragmentation. For many scleractinian corals, damage caused by storms or strong wave action may produce fragments that lead to new colonies.

Anthozoans may be gonochoristic (having separate sexes) or hermaphroditic. In colonial species, gonochoristic colonies are composed entirely of male or female polyps, whereas hermaphroditic colonies may have both male and female polyps ("monoecious") or hermaphroditic polyps. Polyps lack well-defined gonads; rather, the gametes accumulate in the gastrodermis of some or all mesenteries. The gametes are typically shed into the gastrovascular cavity and are either released through the mouth for external fertilization ("broadcast spawners"), or eggs are retained for internal fertilization and the embryos released through the mouth at a later time ("brooders"). Brooding species may hold the embryos internally within the gastrovascular cavity or externally in a coat of mucus on the polyp's surface. Anthozoan embryos develop into ciliated planula larvae that may or may not feed, and that can stay in the water column for days to weeks. Contrary to initial assumptions, some species also can produce larvae asexually.

Conservation status

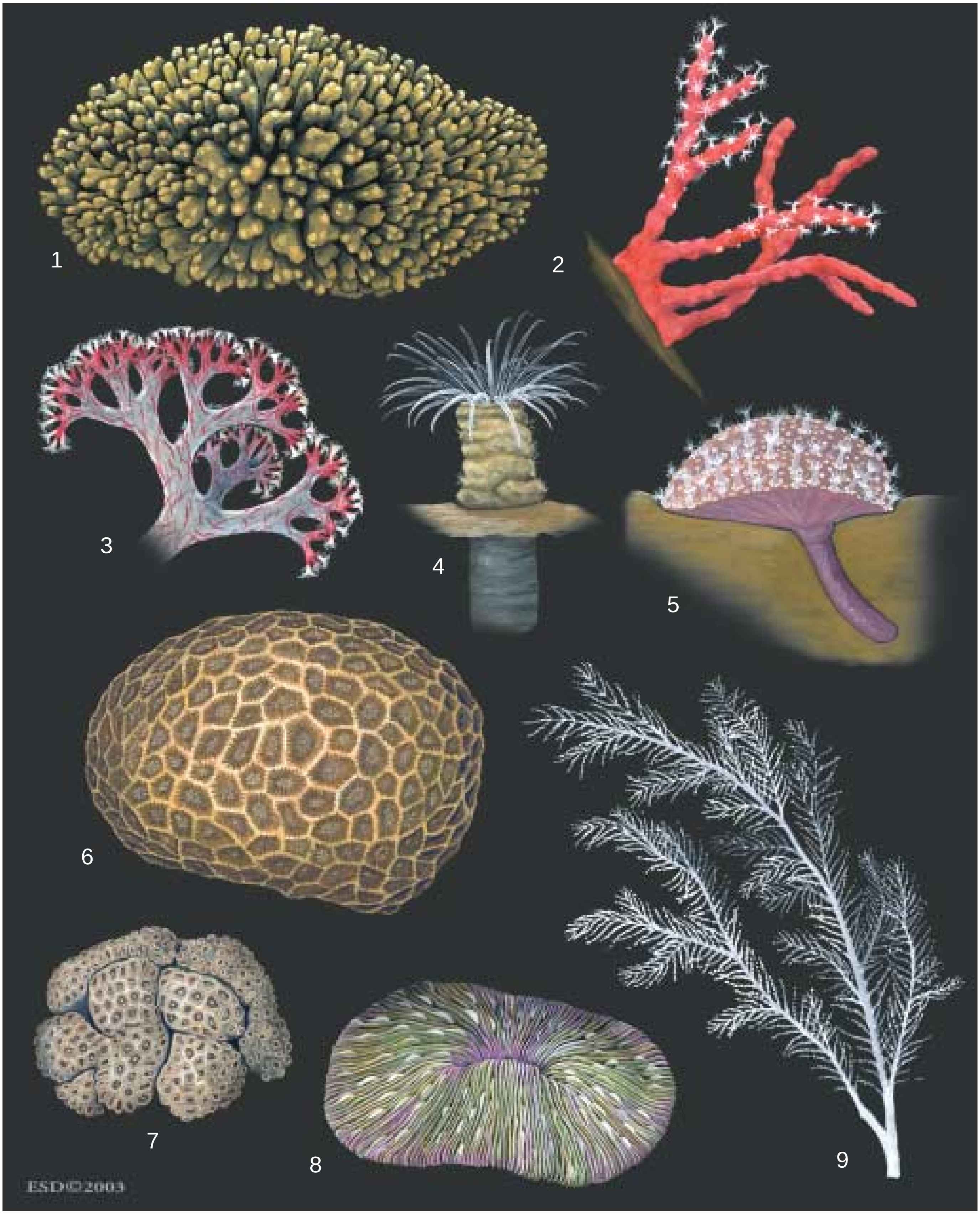
Some of the largest concentrations of anthozoans, in terms of both numbers and species diversity, occur on coral reefs. Such human activities as fishing, coastal development, terrestrial runoff, and marine pollution have had dramatic negative impacts on coral reefs, as have coral diseases that have increased in frequency and severity over the last decade of the twentieth century. Despite a ban in most countries, cyanide is still commonly used to collect reef fishes for the aquarium trade. The cyanide stuns the target fishes, allowing for easy collection, but kills many of the anthozoans and other invertebrates living on the reef. In 1998, the World Resources Institute estimated that more than half of the world's coral reefs are threatened by these and other human activities. As of 2002, however, only two anthozoan species were listed on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species: the broad sea fan, *Eunicella verrucosa*, and the starlet sea anemone, *Nematostella vectensis*. All scleractinian corals, antipatharian black corals, and octocorallian blue corals and organ-pipe corals, are listed on Appendix II of the Convention on International Trade in Endangered Species (CITES). This listing means that "trade must be controlled in order to avoid utilization incompatible with their survival." A number of other treaties have been established to protect coral reef organisms, such as the International Coral Reef Initiative and the U.S. Coral Reef Initiative. Most recently, there has been concern over the impact of deep-sea fisheries trawling on slow-growing deep-water corals. Norway and Australia have created conservation areas to protect reefs within their territorial waters.

Significance to humans

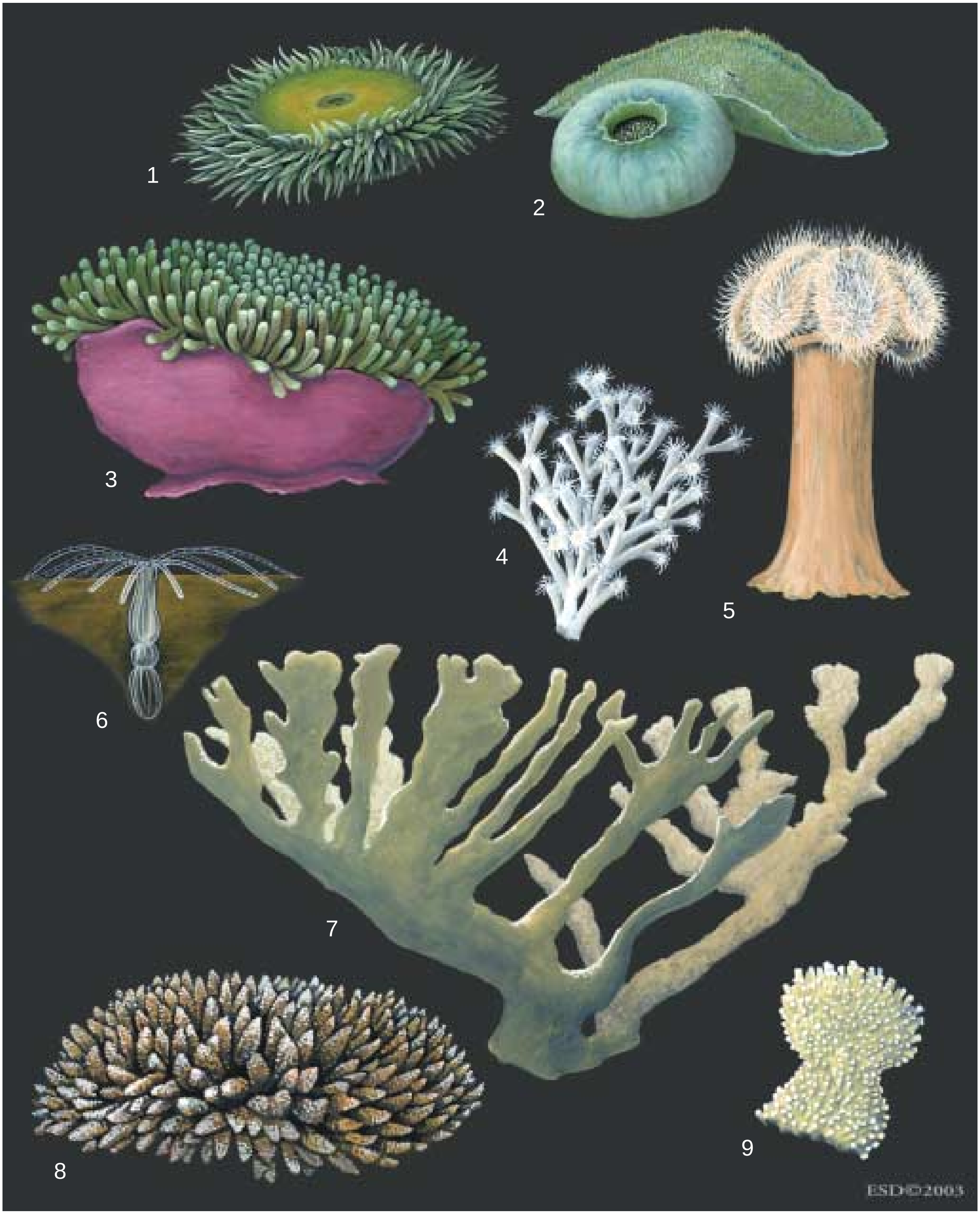
Coral reefs, which are largely a framework of scleractinian skeletons glued together by sponges and other organisms, are a major tourist destination and source of recreation. Corals provide a habitat for a variety of organisms that humans use for food, including fishes, urchins, mollusks and crustaceans. It is estimated that approximately 50% of U.S. federally-managed fisheries depend on coral reefs for part of their life cycle, at an annual worth of over $100 million. Anthozoans of all orders (except Antipatharia) are sold in the aquarium trade, and octocorallian and antipatharian skeletons are used to make coral jewelry. Scleractinian skeletons are used as building material and in bone grafts, as the structure of the coral skeleton is similar to that of human bone. Black

Sea anemone seen near Cozumel, Mexico. (Photo by AP/Wide World Photos/University of Wisconsin-Superior. Reproduced by permission.)

coral skeleton was once thought to have medicinal properties, and the name "*Antipathes*" is a Latin word that means "against disease." A variety of natural products have been isolated from anthozoans for commercial use, from suntan lotions to antifoulants. In particular, octocorals produce a range of bioactive compounds; some of these have been harvested for molecular biological and pharmaceutical applications, including anticancer and anti-inflammatory agents.



1. Cauliflower coral (*Pocillopora damicornis*); 2. Red coral (*Corallium rubrum*); 3. Red soft tree coral (*Dendronephthya hemprichi*); 4. American tube dwelling anemme (*Ceriantheopsis americanus*); 5. Sea pansy (*Renilla reniformis*); 6. *Goniastrea aspera*; 7. Rubber coral (*Palythoa caesia*); 8. Mushroom coral (*Fungia scutaria*); 9. Black coral (*Antipathella fiordensis*). (Illustration by Emily Damstra)



1. Giant green anemone (*Anthopleura xanthogrammica*); 2. Elephant ear polyps (*Amplexidiscus fenestrafer*); 3. Magnificent sea anemone (*Heteractis magnifica*); 4. Deep water reef coral (*Lophelia pertusa*); 5. Frilled anemone (*Metridium senile*); 6. Starlet sea anemone (*Nematostella vectensis*); 7. Elkhorn coral (*Acropora palmata*); 8. *Acropora millepora*; 9. Close-up of *A. palmata.* (Illustration by Emily Damstra)

Species accounts

Giant green anemone

Anthopleura xanthogrammica

ORDER
Actiniaria

FAMILY
Actiniidae

TAXONOMY
Actinia xanthogrammica Brandt, 1835, Sitka, Alaska, United States.

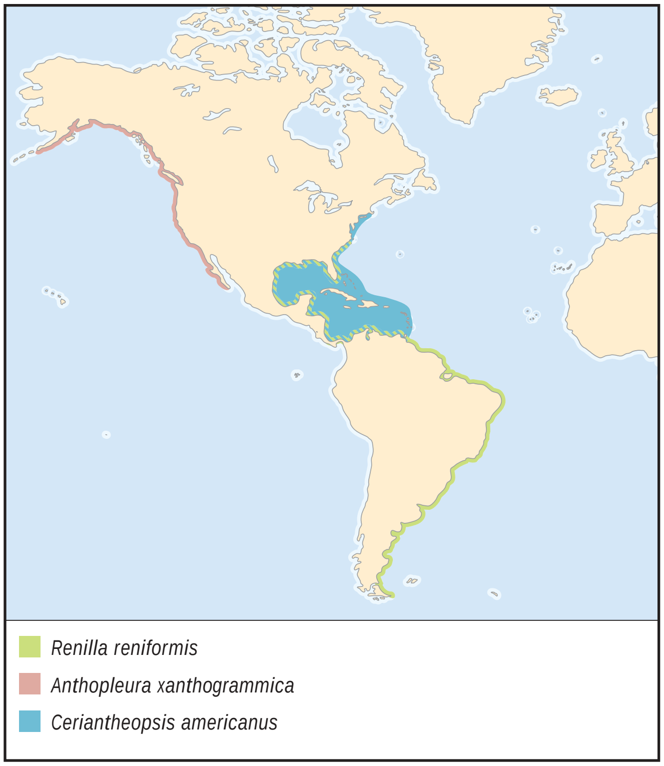
OTHER COMMON NAMES
Portuguese: Anémona-verde-gigante.

PHYSICAL CHARACTERISTICS
Large, flat oral disk up to 9.8 in (25 cm) diameter; column densely covered with hollow adhesive wartlike protuberances known as verrucae; tentacles and disk are emerald green, column is olive or brownish.

DISTRIBUTION
Western coast of North America from Alaska south to Baja California.

HABITAT
Low intertidal to shallow subtidal zones on exposed coastlines where it is subject to strong wave action; it often forms carpets of individuals in surge channels.

BEHAVIOR
Nothing is known.



FEEDING ECOLOGY AND DIET
Feeds on sea urchins, crabs, and mussels dislodged by floating debris. One study found that *A. xanthogrammica* benefits when urchins fleeing from predatory seastars fall into the anemone's tentacles. Mussels that are detached by wave action also are eaten. Also derives nutrition from symbiotic association with zooxanthellae and zoochlorellae.

REPRODUCTIVE BIOLOGY
Gonochoristic; reaches sexual maturity in 5–10 years; planktotrophic larvae feed on algae. No asexual reproduction known.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Produces toxins known as anthopleurins that stimulate heart muscle and that were considered for medical use. ◆

Starlet sea anemone

Nematostella vectensis

ORDER
Actiniaria

FAMILY
Edwardsiidae

TAXONOMY
Nematostella vectensis Stephenson, 1935, Isle of Wight, England.

OTHER COMMON NAMES
English: Athenarian burrowing anemone; dwarf mud anemone.

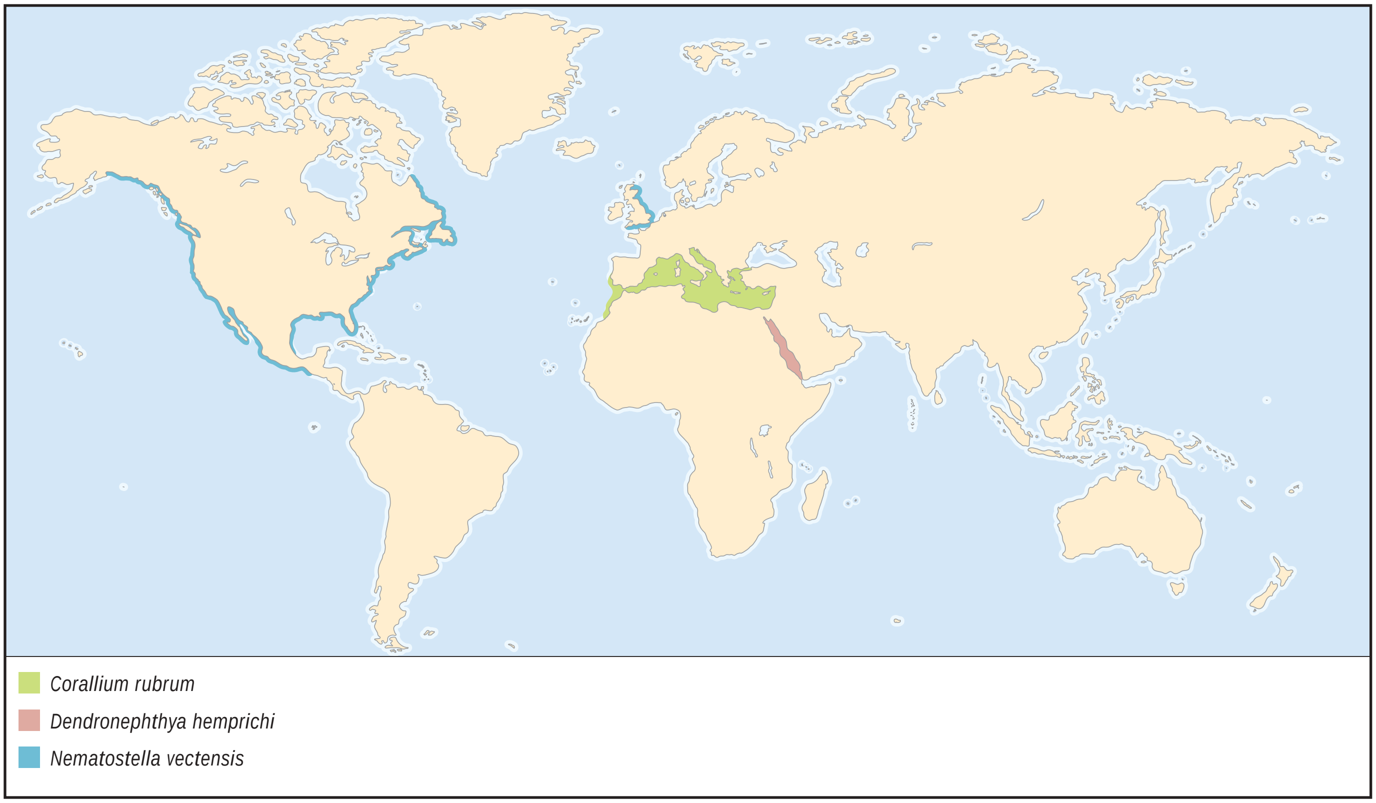
PHYSICAL CHARACTERISTICS
Tiny worm-like anemone, rarely more than 0.6 in (15 mm) in length, with 9–18 relatively long (up to 0.4 in [10 mm]) tentacles arranged in two rings; column is smooth with a rounded base called a physa; largely translucent with white bands on the tentacles.

DISTRIBUTION
Atlantic and Pacific coasts of North America; southern and eastern coasts of England. It is thought to have been introduced to England from North America.

HABITAT
Intertidal to shallow subtidal zones; burrows in mud of estuaries and salt marshes. Tolerates a broad range of salinities (8.96–51.54 ppt) and temperatures (30 to 82°F [-1 to 28°C]).

BEHAVIOR
When disturbed, the anemone can completely withdraw into its burrow. It may also move completely out of the burrow and climb onto algae and aquatic vegetation.

FEEDING ECOLOGY AND DIET
Feeds mainly on snails; however, copepods, ostracods, insects, and nematodes also have been found in the coelenteron.



REPRODUCTIVE BIOLOGY

Gonochoristic, broadcast spawner; females release gelatinous egg masses that contain as few as five or as many as 2000 ova and hundreds to thousands of nematosomes, which are spherical, flagellated bodies containing nematocysts and are unique to this species. Planktotrophic larvae may settle in 7 days. Asexual reproduction may be more common than sexual reproduction. Several unisex populations have been discovered in North America, while no males have been observed in England. The starlet sea anemone is one of only five anemone species known to reproduce asexually by transverse fission and is the only anemone known to release gelatinous masses of eggs.

CONSERVATION STATUS

Although as many as five million individuals have been found in a single pond, this species is listed as vulnerable on the IUCN Red List. It is considered rare and endangered in the United Kingdom, largely because of its restricted habitat.

SIGNIFICANCE TO HUMANS

Used in laboratory studies of developmental genetics. ◆

Frilled anemone

Metridium senile

ORDER

Actiniaria

FAMILY

Metridiidae

TAXONOMY

Priapus senilis Linnaeus, 1761, Baltic Sea.

OTHER COMMON NAMES

English: Plumose anemone (Britain); French: Anémone plumeuse; German: Seenelke; Norwegian: Sjønellik.

PHYSICAL CHARACTERISTICS

Tall, to 11.8 in (30 cm), with hundreds to thousands of small, slender tentacles on a lobed crown giving a feathery or plume-like appearance; column smooth with a distinct collar below tentacles; with numerous threadlike acontia arising from bases of septa that can be discharged through column pores known as cinclides; color varies from white to brownish-orange.

DISTRIBUTION

Circumpolar, boreo-Arctic; found as far south as New Jersey, United States, in the western Atlantic; Bay of Biscay in the eastern Atlantic; southern California, United States, in the eastern Pacific; and South Korea in the western Pacific. Introduced populations have been found in South Africa and the Adriatic Sea.

HABITAT

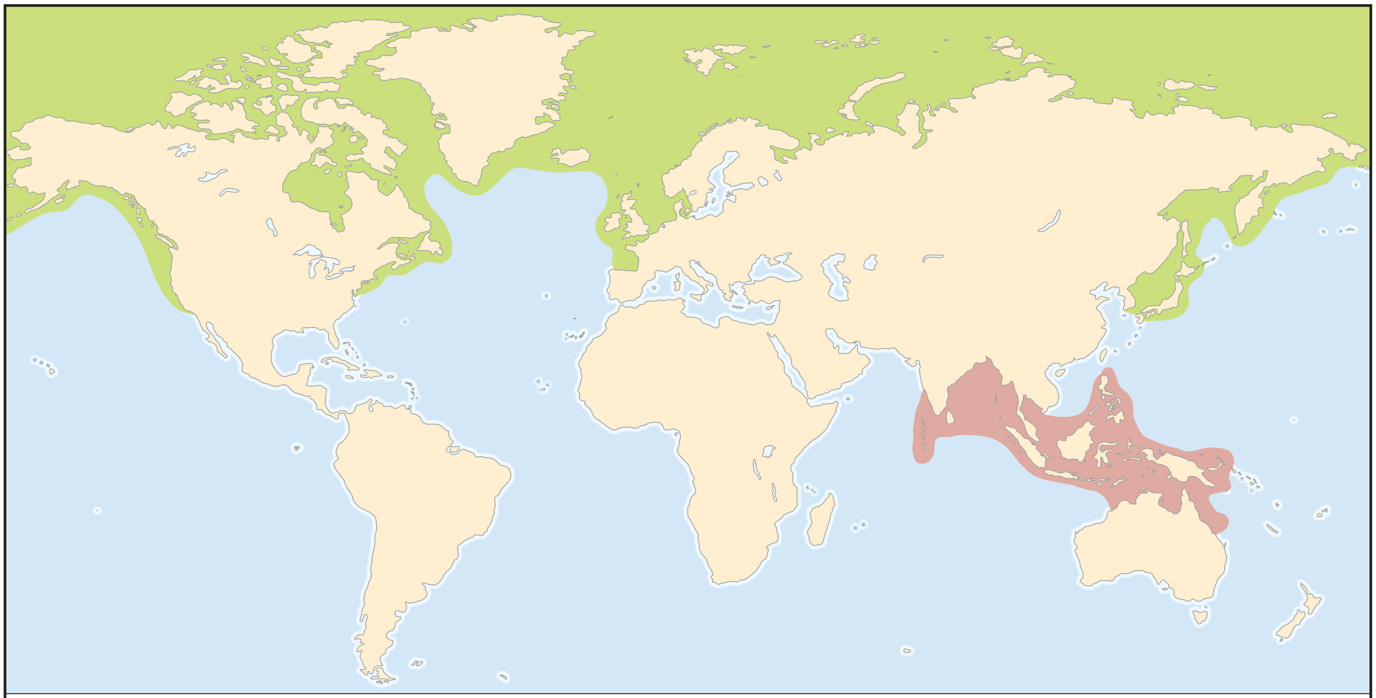
Attached to rock, shell, wood, and other hard substrates from the intertidal zone to 540 ft (166 m) deep; tolerates temperatures between 32–80°F (0–27°C).

BEHAVIOR

Adjusts the length of the body column according to current flow. Uses catch tentacles equipped with specialized nematocysts to attack other species in competition for space; tips of the catch tentacles remain attached to the victim.

FEEDING ECOLOGY AND DIET

Passive suspension feeder that traps prey in mucus-coated tentacles; these particles are carried to the mouth by ciliary action.



Prey items include copepods and polychaetes; and decapod, bivalve, and gastropod larvae.

REPRODUCTIVE BIOLOGY
Gonochoristic, broadcast spawner; planktotrophic larvae feed primarily on dinoflagellates, but also on copepods, chaetognaths and other cnidarian larvae. Asexual reproduction by pedal laceration and fission.

CONSERVATION STATUS
Not listed by the IUCN or CITES.

SIGNIFICANCE TO HUMANS
None known. ◆

Magnificent sea anemone

Heteractis magnifica

ORDER
Actiniaria

FAMILY
Stichodactylidae

TAXONOMY
Actinia magnifica Quoy and Gaimard, 1833, Vanikoro, Santa Cruz Islands, New Hebrides.

OTHER COMMON NAMES
English: Bulb-tip anemone, maroon anemone, Ritteri anemone; German: Prachtanemone; Local dialects: Rambu-rambu (Indonesia), Burin (Malaysia)

PHYSICAL CHARACTERISTICS
Oral disc up to 39 in (1 m) in diameter; column as much as 8 in (20 cm) tall and wide at the base; tentacles 3 in (7.5 cm) long, of uniform thickness with blunt or slightly bulbous tips. Brightly colored column may be avocado green, magenta, cerulean blue, or white, with yellow, green, or white tentacles.

DISTRIBUTION
Tropical Indo-Pacific seas.

HABITAT
From less than 3–65 ft (1–20 m) deep on or near coral reefs, often perched on prominent structures in strong currents.

BEHAVIOR
Host to clownfish (*Amphiprion*) and damselfish (*Dascyllus*) that chase off potential predators. The fishes are protected from their predators by the anemone's nematocysts, but are themselves unaffected because of a coating of mucus that they pick up from the anemone.

FEEDING ECOLOGY AND DIET
Feeds on plankton that it traps from the water using nematocysts and mucus on the oral disc; digestion of prey begins prior to ingestion. Also derives nutrition from symbiotic zooxanthellae harbored within cells lining the inside of the tentacles and oral disc.

REPRODUCTIVE BIOLOGY
Capable of asexual reproduction by longitudinal fission. Sexual reproduction is presumed but data are lacking.

CONSERVATION STATUS
Not listed by the IUCN or CITES.

SIGNIFICANCE TO HUMANS
Reportedly one of the most frequently photographed anemones because of its coloration, shallow-water location, and tolerance of disturbance. Sold in the aquarium trade. ◆

Red coral
Corallium rubrum

ORDER
Alcyonacea

FAMILY
Coralliidae

TAXONOMY
Madrepora rubra Linnaeus, 1758, "Mari Numidico ad la Calle".

OTHER COMMON NAMES
English: Precious coral; French: Corail rouge; German: Rote Edelkoralle; Italian: Corallo rosso; Spanish: Coral rojo.

PHYSICAL CHARACTERISTICS
Arborescent colonies with red calcium carbonate skeleton up to 19.5 in (50 cm) tall; feeding polyps with eight pinnate tentacles can be completely withdrawn into tissue; also possesses tiny non-feeding polyps (siphonozooids) that lack tentacles and contain the gonads; red calcareous spicules embedded in mesoglea.

DISTRIBUTION
Central and western Mediterranean Sea, with a few records from the eastern Mediterranean; Atlantic coast of southern Portugal and northern Africa.

HABITAT
Cave walls, vertical cliffs, and overhangs from a depth of 32–812 ft (10–250 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Captures small zooplankton from water column with tentacles. Also may directly absorb dissolved organic carbon from the water through epidermis.

REPRODUCTIVE BIOLOGY
Gonochoristic; male colonies release sperm that swim and are carried by currents to female colonies; eggs are fertilized internally and brooded for up to 30 days. Nonfeeding larvae are released from June through October and swim for up to 15 days before settling. Limited capacity for asexual reproduction.

CONSERVATION STATUS
Not listed by the IUCN or CITES. Population sizes are large but dominated by smaller, younger colonies, as larger colonies have been preferentially harvested. Commercial yields of precious coral declined from 100 tons (91,000 kg) in 1875 to 40 tons (36,000 kg) in 1989 and 27 tons (25,000 kg) in 1996. Underwent mass mortality in the northwestern Mediterranean in 1999 associated with abnormally high water temperatures.

SIGNIFICANCE TO HUMANS
The skeleton is highly valued for coral jewelry and has been harvested since Paleolithic times. It is commonly used by Navajo and other Native American craftspeople in the southwestern United States for inlays in fine handmade jewelry. The ancient Phoenicians, Egyptians and Romans used coral for trade. According to Greek legend, it confers such magical powers as overcoming evil, protecting crops, warding off epilepsy, defending ships against lightning, and eliminating hatred from the home. Powdered coral skeleton is sold as herbal or homeopathic medicine to be used as an antacid, astringent, emmenagogue, nervine tonic, laxative, diuretic, emetic, or antibilious agent. The traditional Indian Ayurvedic herbal medicine presents the following applications for *C. rubrum* skeleton: "Coughs, wasting, asthma, low fever, urinary diseases, carbuncles, scrofula, spermatorrhoea, gonorrhea and other genital inflammation with mucus discharge, nerve headaches, giddiness, vertigo, chronic bronchitis, pulmonary tuberculosis, vomiting, dyspepsia, bilious headache, weakness, and debility. It is added to tooth powders as an astringent. "

The term "coral" was originally applied to this species, and only subsequently to black corals, stony corals, and soft corals. ◆

Red soft tree coral
Dendronephthya hemprichi

ORDER
Alcyonacea

FAMILY
Nephtheidae

TAXONOMY
Spongodes hemprichi Klunzinger, 1877, Red Sea.

OTHER COMMON NAMES
German: Hemprichs Schleierbäumchen; Italian: Alcionario rosa.

PHYSICAL CHARACTERISTICS
Highly-branched, fleshy, arborescent (treelike) colony lacking an axial skeleton; large embedded sclerites are visible in branches and are conspicuous in polyps, producing a spiky appearance; polyps are not retractile and are mainly clustered in bundles at the end of branches; translucent, colors vary from red to pink, orange, or violet.

DISTRIBUTION
Red Sea.

HABITAT
Found only in strong currents, often on vertical surfaces. Dominant organism on artificial reefs and oil platforms in the Red Sea.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Suspension feeder almost exclusively on phytoplankton, a mode of nutrition considered rare among corals. Very small numbers of zooplankton also have been found in the gut. Lacks zooxanthellae.

REPRODUCTIVE BIOLOGY
Gonochoristic, broadcast spawner releases gametes year round. Eggs may remain attached to the mouth by a thread of mucus for several minutes after spawning; when released, the eggs

sink to the bottom. Larvae can metamorphose as soon as 27 hours or as long as 65 days after fertilization, and can live as long as 100 days. *Dendronephthya hemprichi* has a unique method of asexual reproduction: clusters of 4–12 polyps grow from the surface of the colony and autotomize (self-amputate) within two days; the detached polyp fragments have root-like processes that allow for rapid attachment to substrates. There may be hundreds of these fragments in a single colony, allowing for rapid clonal reproduction.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Dendronephthya corals are very popular attractions for divers and underwater photographers. ◆

Black coral
Antipathella fiordensis

ORDER
Antipatharia

FAMILY
Myriopathidae

TAXONOMY
Antipathes fiordensis Grange, 1990, Doubtful Sound, New Zealand.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Densely branched tree-like colonies grow to over 16 ft (5 m) tall. Tiny polyps, arranged in rows, are white with six tentacles surrounding a mouth that is raised on an oral cone. Proteinaceous black skeleton is covered with spines.

DISTRIBUTION
Endemic to southwestern New Zealand.

HABITAT
Attached to the walls of fjords from 13 to over 325 ft (4 to over 100 m) in depth (but most abundant between 32–114 ft [10–35 m]). This habitat range is unusually shallow for black coral, which are typically found in deeper waters.

BEHAVIOR
Produces sweeper tentacles, which are up to eight times longer, and more densely covered with nematocysts, than normal tentacles. Sweeper tentacles are used in aggressive interactions with other cnidarians in competition for space.

FEEDING ECOLOGY AND DIET
Diet consists of zooplankton, primarily copepods, which are captured by direct contact with the tentacles.

REPRODUCTIVE BIOLOGY
Gonochoristic; broadcast spawns annually during the summer to produce free-swimming planula larvae.

CONSERVATION STATUS
Endemic to the fjords of Fiordland in southwestern New Zealand. Population size has been estimated at more than seven million colonies. Black coral is a protected species in New Zealand, and all black corals are listed on CITES Appendix II.

SIGNIFICANCE TO HUMANS
The skeleton of black coral is used to make jewelry; however, no known fishery exists for *A. fiordensis* as of 2003. ◆

American tube dwelling anemone
Ceriantheopsis americanus

ORDER
Ceriantharia

FAMILY
Cerianthidae

TAXONOMY
Cerianthus americanus Agassiz in Verrill, 1864, Charleston, South Carolina, United States.

OTHER COMMON NAMES
English: Burrowing mud anemone, North American tube anemone, tube sea anemone.

PHYSICAL CHARACTERISTICS
Solitary, elongate, worm-like anemone up to 14 in (36cm) long and 0.79 in (2 cm) wide. Two rings of thin tentacles: up to 125 long ones around the outer edge of the oral disk, and an inner ring of short ones surrounding the mouth. Produces a soft, slippery, felt-like gray tube formed of ptychocysts, mucous, and debris. Colors range from brown or tan to maroon or purple.

DISTRIBUTION
Eastern coast of United States from Cape Cod south into the Gulf of Mexico; Caribbean; West Indies.

HABITAT
Intertidal zones up to 227 ft (70 m) deep; builds tube in vertical burrow as much as 18 in (45 cm) deep in muddy or sandy bottom; only the oral end emerges from the tube.

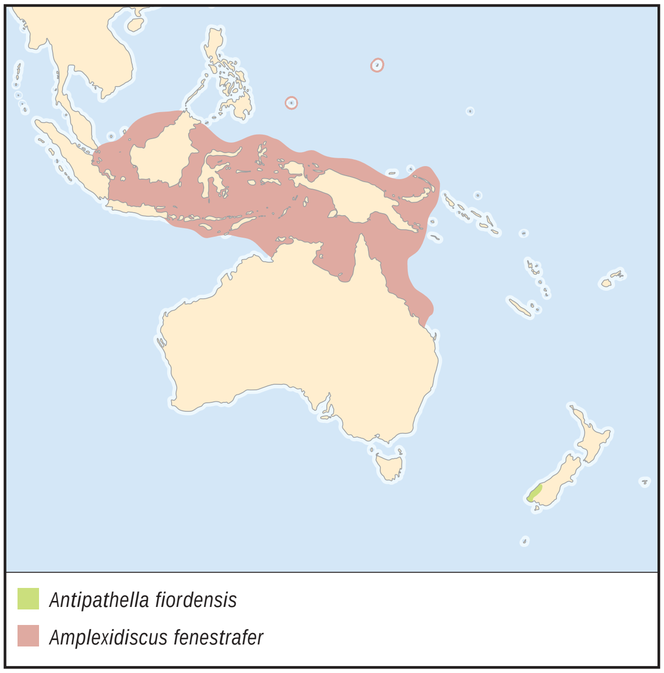
BEHAVIOR
Will withdraw rapidly to bottom of tube when disturbed.

FEEDING ECOLOGY AND DIET
Spreads tentacles over the surface of the sand or mud to obtain food. Captures its prey with the longer outer tentacles and transfers it to the shorter tentacles surrounding the mouth.

REPRODUCTIVE BIOLOGY
Hermaphroditic; fertilized eggs have been spawned in the laboratory, suggesting self-fertilization is possible.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Sold in the aquarium trade. ◆



Elephant ear polyps
Amplexidiscus fenestrafer

ORDER
Corallimorpharia

FAMILY
Actinodiscidae

TAXONOMY
Amplexidiscus fenestrafer Dunn and Hamner, 1980, Lizard Island, Great Barrier Reef, Australia.

OTHER COMMON NAMES
English: Giant elephant ear mushroom anemone, disk anemone; French: Anémone disque; German: Grosses Elefantenohr; Italian: Anemone orecchio d'elefante.

PHYSICAL CHARACTERISTICS
Short, column up to 2 in (5 cm) tall. Oral disc typically 8–10 in (20–25 cm), but as much as 18 in (45 cm), in diameter; mouth atop a raised cone. 15–20 tentacles around the margin, and many short, conical tentacles arranged in radial rows on the oral disc. A 0.4 in (10 mm) wide tentacle-free "window" rings the oral disc about 0.4 in (10 mm) from the margin. Color is a dull gray to greenish-brown.

DISTRIBUTION
Australia, Indonesia, Palau, and Guam.

HABITAT
In subtidal zones on coral reefs, usually in shallow, quiet water on the inshore side of the reef; attached to vertical walls or coral.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Captures prey by envelopment; the center of the oral disc is drawn down while the edges constrict to form a bowl that closes up like a drawstring within 3 sec, enclosing prey and up to 1 gal (4 l) of water. The prey, which may include zooplankton, shrimp and fishes, continues to swim or crawl within the enclosed space for 10–20 min after envelopment, after which it is swallowed. It has been suggested that *A. fenestrafer* mimics anemones that host anemonefish, thereby attracting anemonefish upon which it can feed. It also derives nutrition from symbiotic zooxanthellae harbored within cells lining the inside of the tentacles.

REPRODUCTIVE BIOLOGY
Capable of asexual reproduction by longitudinal fission, pedal laceration, and budding from the column. Data on sexual reproduction are lacking, although individuals with functional male gonads have been identified.

CONSERVATION STATUS
Not listed by the IUCN or CITES.

SIGNIFICANCE TO HUMANS
Sold in the aquarium trade. ◆

Sea pansy
Renilla reniformis

ORDER
Pennatulacea

FAMILY
Renillidae

TAXONOMY
Pennatula reniformis Pallas, 1766, "Mare Americum."

OTHER COMMON NAMES
English: Atlantic coral.

PHYSICAL CHARACTERISTICS
Colonial; a large primary polyp up to 3 in (7.5 cm) long and wide has a heart-shaped frond arising from a fleshy stalk. Smaller polyps are embedded in the upper surface of the frond: typical octocoral feeding polyps and tiny nonfeeding polyps lacking tentacles. Primary polyp appears purple because of colored sclerites in its tissue. The smaller embedded polyps are transparent.

DISTRIBUTION
Western Atlantic from North Carolina, United States, south to Tierra del Fuego, Argentina.

HABITAT
Stalk anchored in sand with frond lying flat on the surface, from low intertidal to shallow subtidal zones.

BEHAVIOR
Produces bioluminescent bright green waves of light that run across the surface of the colony when disturbed at night. Small tentacle-less polyps act as water pumps, allowing colony to quickly deflate to half its normal size or expand.

FEEDING ECOLOGY AND DIET
Polyps secrete a sticky net of mucus that can trap small zooplankton.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
Bioluminescence is created by a protein called "Green Fluorescent Protein" (GFP). The GFP gene has been isolated and is sold commercially for use in molecular biological studies of gene expression in mammals. Scientists have isolated from the sea pansy unique diterpene lipids known as renillafoulins that prevent fouling organisms (e.g., barnacles) from settling on boats and other manufactured marine structures without killing them. ◆

No common name

Acropora millepora

ORDER
Scleractinia

FAMILY
Acroporidae

TAXONOMY
Heteropora millepora Ehrenberg, 1834, Indian Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial; thick finger-like interlocking branches with upright branchlets form squat colonies. Branch surfaces appear scaly. Tissue color ranges from green with orange tips to bright salmon pink or blue.

DISTRIBUTION
Tropical and subtropical Indo-Pacific waters, from Sri Lanka and Thailand east to the Marshall Islands and Tonga, including Australia.

HABITAT
Common on reef flats, lagoons, and upper reef slopes less than 10 ft (3 m) deep.

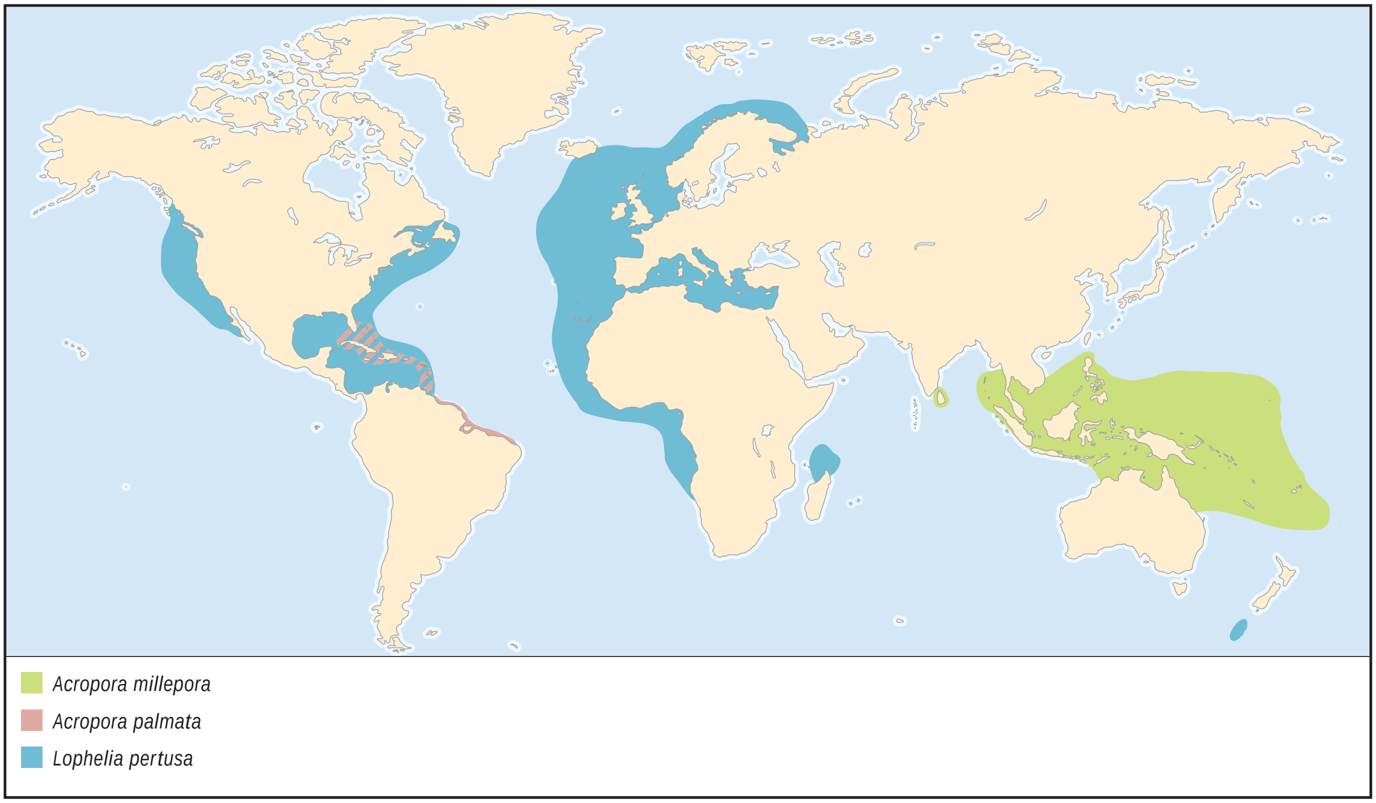
BEHAVIOR
Mass spawning is timed to occur between 4 and 8 days following a full moon.

FEEDING ECOLOGY AND DIET
Feeds on minute zooplankton and derives nutrition from zooxanthellae harbored within cells lining the digestive cavity.

REPRODUCTIVE BIOLOGY
Hermaphroditic polyps release bundles containing both sperm and eggs that float to the sea surface, where they break open and fertilization occurs. Planula larva may be competent to settle 4–5 days after fertilization. Asexual reproduction occurs by fragmentation of colony branches.

CONSERVATION STATUS
All scleractinian corals are listed in CITES Appendix II.

SIGNIFICANCE TO HUMANS
Common reef-builder of Indo-Pacific coral reefs. ◆



Elkhorn coral

Acropora palmata

ORDER

Scleractinia

FAMILY

Acroporidae

TAXONOMY

Madrepora palmata Lamarck, 1816, "American Ocean."

OTHER COMMON NAMES

Spanish: Cuerno de alce.

PHYSICAL CHARACTERISTICS

Colonial; tree-like colonies up to 13 ft (4 m) across and 6.5 ft (2 m) tall, with thick branches broadly flattened near tips to resemble moose or elk antlers; tubular coral cups protrude from branch surface. Tissue tan or pale-brown, with tips of branches white.

DISTRIBUTION

Caribbean; Florida Keys, Bahamas, West Indies to Brazil.

HABITAT

Subtidal zones to 65 ft (20 m); densely aggregated thickets common on windward reef slopes exposed to heavy wave action.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Feed on minute zooplankton and derive nutrition from zooxanthellae harbored within cells lining the digestive cavity.

REPRODUCTIVE BIOLOGY

Hermaphroditic polyps broadcast spawn once a year in August or September. Sperm and eggs are packaged together in bundles that float to the sea surface, where they break open and fertilization occurs. Planula larva are ready to settle 4–5 days after fertilization. Asexual reproduction occurs by fragmentation of colony branches. Damage to colonies caused by hurricanes is in part responsible for the large stands of *A. palmata* as broken branches reattach and produce new colonies.

CONSERVATION STATUS

All scleractinian corals are listed in CITES Appendix II. Population declines across the Caribbean led to a designation as Candidate Species for listing as Threatened or Endangered under the U.S. Endangered Species Act in 1999. Population declines have been attributed to disease outbreaks (white band disease), compounded locally by hurricanes, increased predation, bleaching, and other factors. Poor water quality because of land-derived pollutants, sewage, and sediment may stress elkhorn coral and increase its susceptibility to disease.

SIGNIFICANCE TO HUMANS

Major structural component of Caribbean coral reefs. Provides essential habitat for fishes and other reef invertebrates. Cuts and scratches resulting from contact with elkhorn coral are reportedly slow to heal. ◆

Deep water reef coral

Lophelia pertusa

ORDER

Scleractinia

FAMILY

Caryophyllidae

TAXONOMY

Madrepora pertusa Linnaeus, 1758, type of locality not stated, but probably the fjords of Norway.

OTHER COMMON NAMES

English: Spider hazards, spiders' nests (Nova Scotia); Norwegian: Glasskorall, øyekorall.

PHYSICAL CHARACTERISTICS

Colonial; irregularly branched to form bushy or tree-like colonies up to 2 m tall; brittle tubular branches about 0.5 in (1–1.5 cm) thick; white or pink.

DISTRIBUTION

Most records are from the North Atlantic, but also known from the South Atlantic, northwestern Pacific; Indian Ocean; and waters south of New Zealand.

HABITAT

Cold water (39–53°F [4–12°C]) and deep sea, from 162 to >9750 ft (50 to >3000 m); hard substrates on slopes of continental margins and midoceanic islands. Colonies combine to build reefs and mounds as large as 650 ft (200 m) high, 0.6 mi (1 km) wide, and 3 mi (5 km) long. Studies have found *L. pertusa* associated with methane seeps, although this may simply be because these features represent topographic highs where ocean currents speed up, and not because *L. pertusa* is feeding on methane.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Feeds voraciously on zooplankton, including copepods.

REPRODUCTIVE BIOLOGY

Details of sexual reproduction are unknown. Asexual reproduction of new colonies occurs when the fragile branches break and fragments continue to grow.

CONSERVATION STATUS

Commercial deep-sea fish trawls are likely causing mechanical damage to *Lophelia* reefs. It is unknown what proportion of the coral fragments survive trawling damage. *Lophelia* reefs have received protected status in Norway. All scleractinian corals are listed in CITES Appendix II.

SIGNIFICANCE TO HUMANS

Provides a habitat for a diverse community of invertebrates and fishes. ◆

No common name

Goniastrea aspera

ORDER

Scleractinia

FAMILY

Faviidae

TAXONOMY
Goniastrea aspera Verrill, 1905, Hong Kong.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Massive boulder-like or encrusting colonies; surface has a honeycomb-like appearance. Individual colonies may merge to form plateaus over 16 ft (5 m) across in intertidal zones. Color is usually pale brown; polyps have cream-colored centers.

DISTRIBUTION
Indo-Pacific; Red Sea, Indian Ocean, tropical and subtropical Pacific east to French Polynesia.

HABITAT
Intertidal to shallow subtidal zones; can withstand pounding surf and several hours of exposure to tropical sun and air.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Derive nutrition from symbiotic zooxanthellae harbored within cells lining the digestive cavity, and may feed on minute zooplankton.

REPRODUCTIVE BIOLOGY
Hermaphroditic broadcast spawner; may release buoyant sperm and egg bundles, or eggs may be released moments before sperm. In the latter case, some eggs may be retained, with fertilization and development taking place within the polyp. Spawned larvae may settle within five days, but brooded larvae may remain within polyp for 18 days. Asexual reproduction by colony fission possible, but is not common.

CONSERVATION STATUS
All scleractinian corals are listed in CITES Appendix II. Studies have shown that low concentrations of copper or nickel negatively affect reproductive success. A similar effect is seen with relatively small increases in nutrients, as would occur from eutrophication (algae overgrowth associated with excessive amounts of nutrients in the water) resulting from human activity.

SIGNIFICANCE TO HUMANS
None known. ◆

Mushroom coral
Fungia scutaria

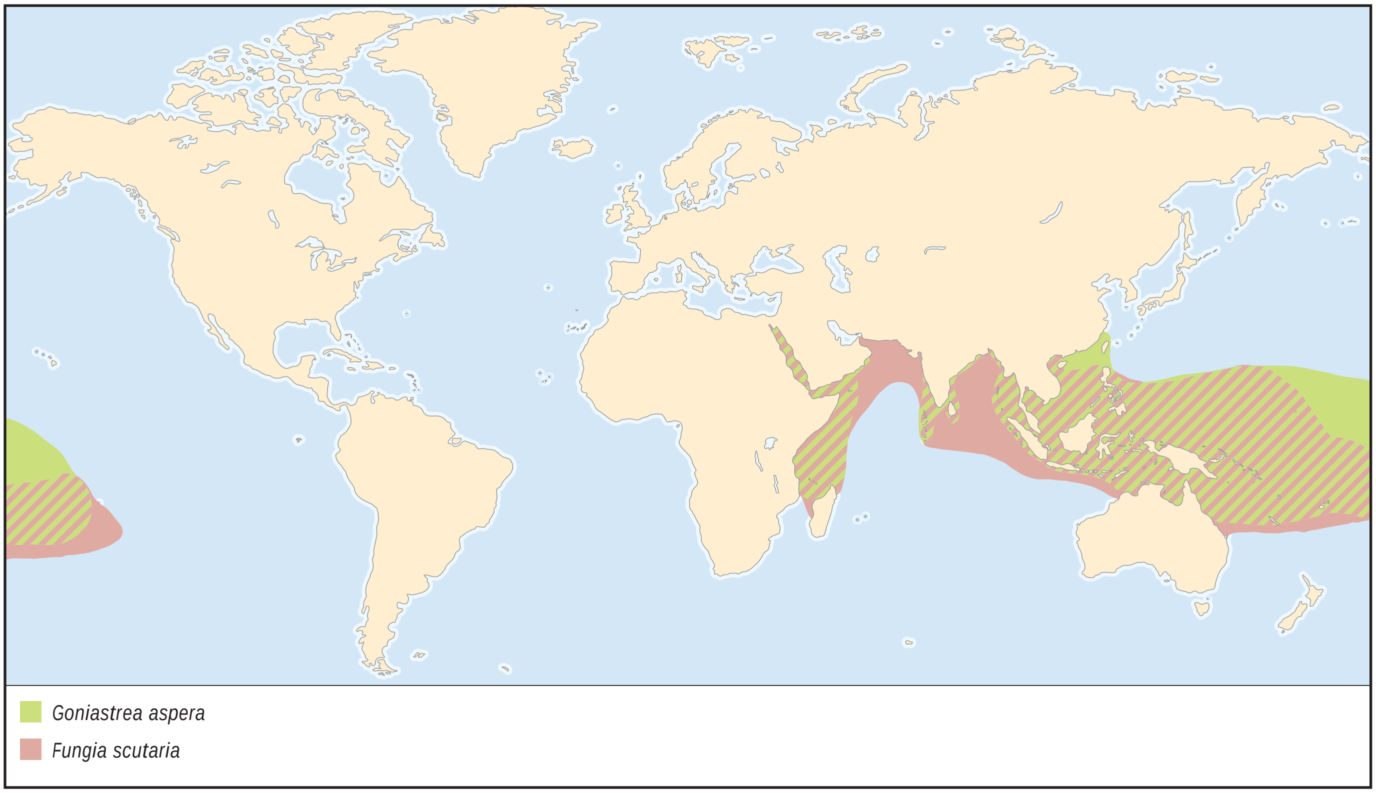
ORDER
Scleractinia

FAMILY
Fungiidae

TAXONOMY
Fungia scutaria Lamarck, 1801, no locality given.

OTHER COMMON NAMES
English: Plate coral; German: Pilzkoralle, Rasiermesserkoralle; Hawaiian: ko'a-kohe

PHYSICAL CHARACTERISTICS
Solitary and free-living (unattached) as an adult; oval to elongate skeleton from 1–7 in (2.5–18 cm) long resembles the underside of a toadstool mushroom; numerous small tentacles



arise from lobes formed by underlying skeleton. Usually brown with irregular pink or violet patches; tentacular lobes often bright green.

DISTRIBUTION
Red Sea, Indian Ocean south to Madagascar, west into Pacific Ocean to Society Islands, north to Hawaiian and Line Islands.

HABITAT
On upper reef slopes exposed to strong wave action or around coral knolls at depths from 1.5–16 ft (0.5–5 m).

BEHAVIOR
In the Red Sea, spawning is synchronized to occur in the late afternoon 1–4 days after a full moon. Free-living, unattached adults that are overturned by wave action can right themselves by taking in water through the mouth to expand one-half of the body. This process may take several hours.

FEEDING ECOLOGY AND DIET
May feed on particulate organic material from water column. Derives nutrition from symbiotic zooxanthellae harbored within cells lining the digestive cavity.

REPRODUCTIVE BIOLOGY
Gonochoristic, broadcast spawners; males are smaller than females. Larvae acquire zooxanthellae in the water column. Larvae attach to the bottom and grow a short, calcareous stalk that eventually breaks, releasing the wide upper disk that becomes the free-living adult. The attached stalk may continue to grow and break off new polyps. Asexual reproduction by budding from adult tissue is also seen.

CONSERVATION STATUS
All scleractinian corals are listed in CITES Appendix II.

SIGNIFICANCE TO HUMANS
Skeleton was used by early Hawaiians as an abrasive for polishing wooden canoes and for removing bristles from pig skins before cooking. ◆

Cauliflower coral
Pocillopora damicornis

ORDER
Scleractinia

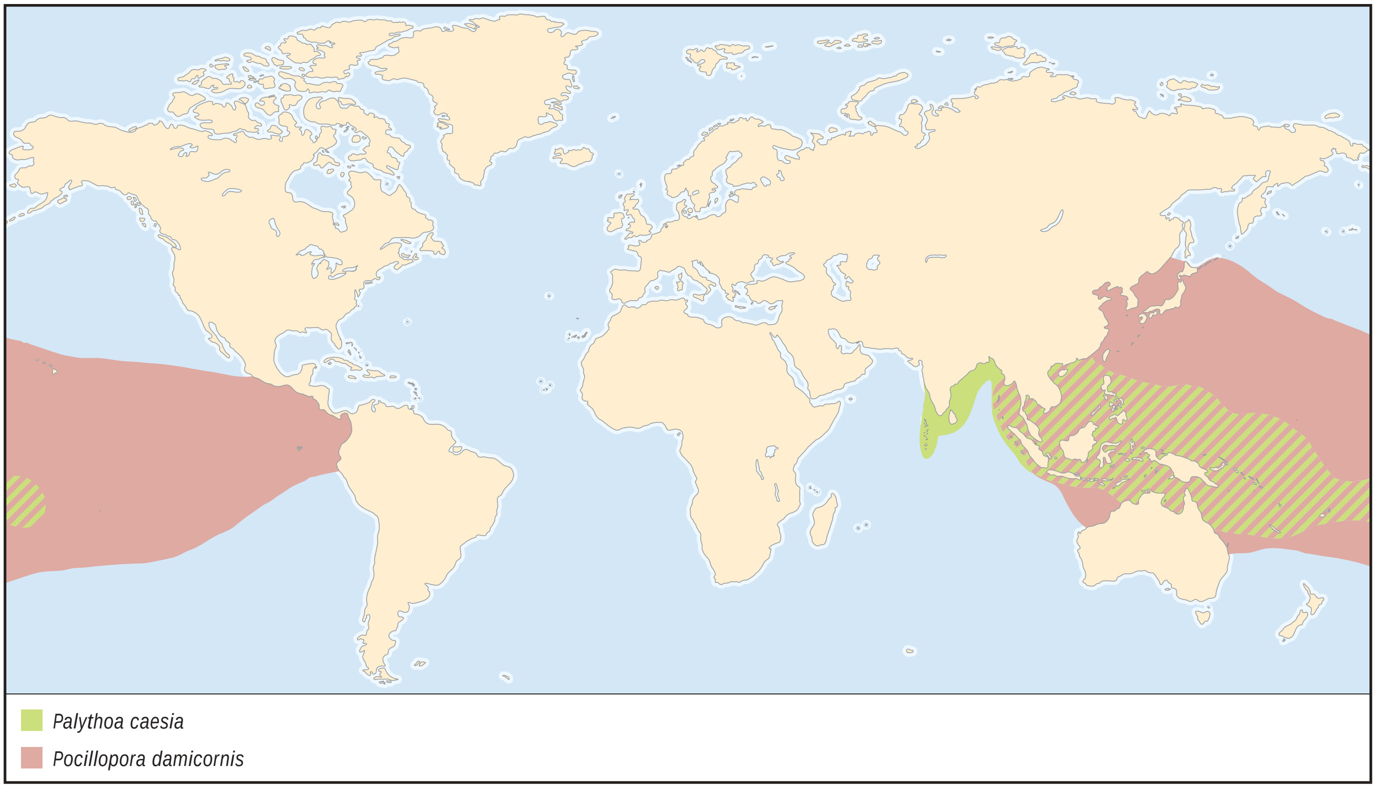
FAMILY
Pocilloporidae

TAXONOMY
Millepora damicornis Linnaeus, 1758, "Oceanus Asiatico."

OTHER COMMON NAMES
English: Bird's nest coral, lace coral; German: Buschkoralle.

PHYSICAL CHARACTERISTICS
Colonial; the colony is a compact clump, up to several meters across, formed of branches; the surface is dotted with verrucae (wartlike bumps) that intergrade with the branches. Growth form varies with environmental conditions and geographic location. Tissue color is pale brown, greenish, or pink.

DISTRIBUTION
Throughout the Indo-Pacific, western and eastern Australia, north to Japan and Hawaii, and east to Central America, Mexico and Ecuador.



HABITAT
Common in all shallow-water habitats, from wharf piles and mangrove swamps to exposed reef fronts; rarely grows deeper than 30 ft (9 m).

BEHAVIOR
Polyp tentacles are usually extended only at night.

FEEDING ECOLOGY AND DIET
Feeds on minute zooplankton and derives nutrition from zooxanthellae harbored within cells lining the digestive cavity.

REPRODUCTIVE BIOLOGY
Polyps are hermaphroditic. Unlike most corals, eggs are fertilized internally and brooded (although in the eastern Pacific, *P. damicornis* is a broadcast spawner). Asexual production of larvae also has been reported. Larvae released from polyps can delay settlement for 100 days or longer, and therefore have the potential to travel great distances. Larvae acquire zooxanthellae from parent.

CONSERVATION STATUS
All scleractinian corals are listed in CITES Appendix II.

SIGNIFICANCE TO HUMANS
Pocilloporids are among the most successful colonizers of coral reefs following disturbance, and are an important framebuilding species. ◆

Rubber coral

Palythoa caesia

ORDER
Zoanthidea

FAMILY
Sphenopidae

TAXONOMY
Palythoa caesia Dana, 1846, "Feejee Islands."

OTHER COMMON NAMES
English: *Palythoa* sea mat

PHYSICAL CHARACTERISTICS
Mat-like colonies appear rubbery in texture; typically form ovoid blobs 2–4 in (5–10 cm) in diameter. Polyps are completely embedded in thick coenenchyme encrusted with sediment; short, simple tentacles with knobbed tips. Color ranges from dark brown to tan.

DISTRIBUTION
Indo-Pacific.

HABITAT
Intertidal or subtidal zones on coral reefs and reef crests. In areas of high abundance, may form mats covering virtually all of the available substrate for tens to hundreds of square meters.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Contains symbiotic zooxanthellae in its tissues. In laboratory studies, *P. caesia* feeds on zooplankton, algae, and bacteria.

REPRODUCTIVE BIOLOGY
Broadcast spawner. Eggs and larvae lack zooxanthellae, so symbionts must be acquired after settlement.

CONSERVATION STATUS
Not listed by the IUCN or CITES.

SIGNIFICANCE TO HUMANS
Palytoxins, which are found in the mucus and gonads of *Palythoa caesia*, are among the most potent toxins known in nature and can be painful and dangerous to humans if absorbed through open wounds. Ancient Hawaiians coated their spear tips with these toxins. ◆

Resources

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Scott C. France, PhD

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Hydrozoa

(Hydroids)

Phylum Cnidaria

Class Hydrozoa

Number of families 114

Thumbnail description

Invertebrates with a body plan that is comprised of a medusa with velum, a muscular projection from the subumbrellar margin that partially closes the subumbrellar cavity, and polyps; life cycles always involve the presence of a planula larva

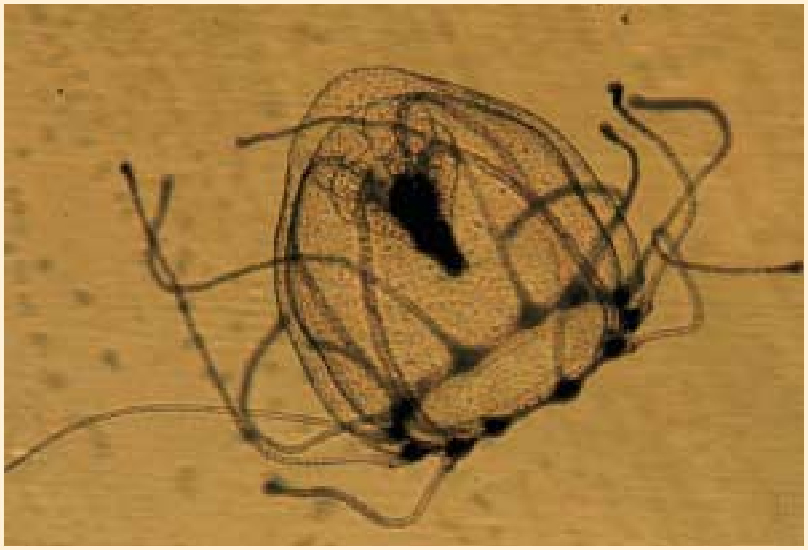


Photo: *A* newly released medusa of *Turritopsis nutricula.* (Photo by S. Piraino [University of Lecce]. Reproduced by permission.)

Evolution and systematics

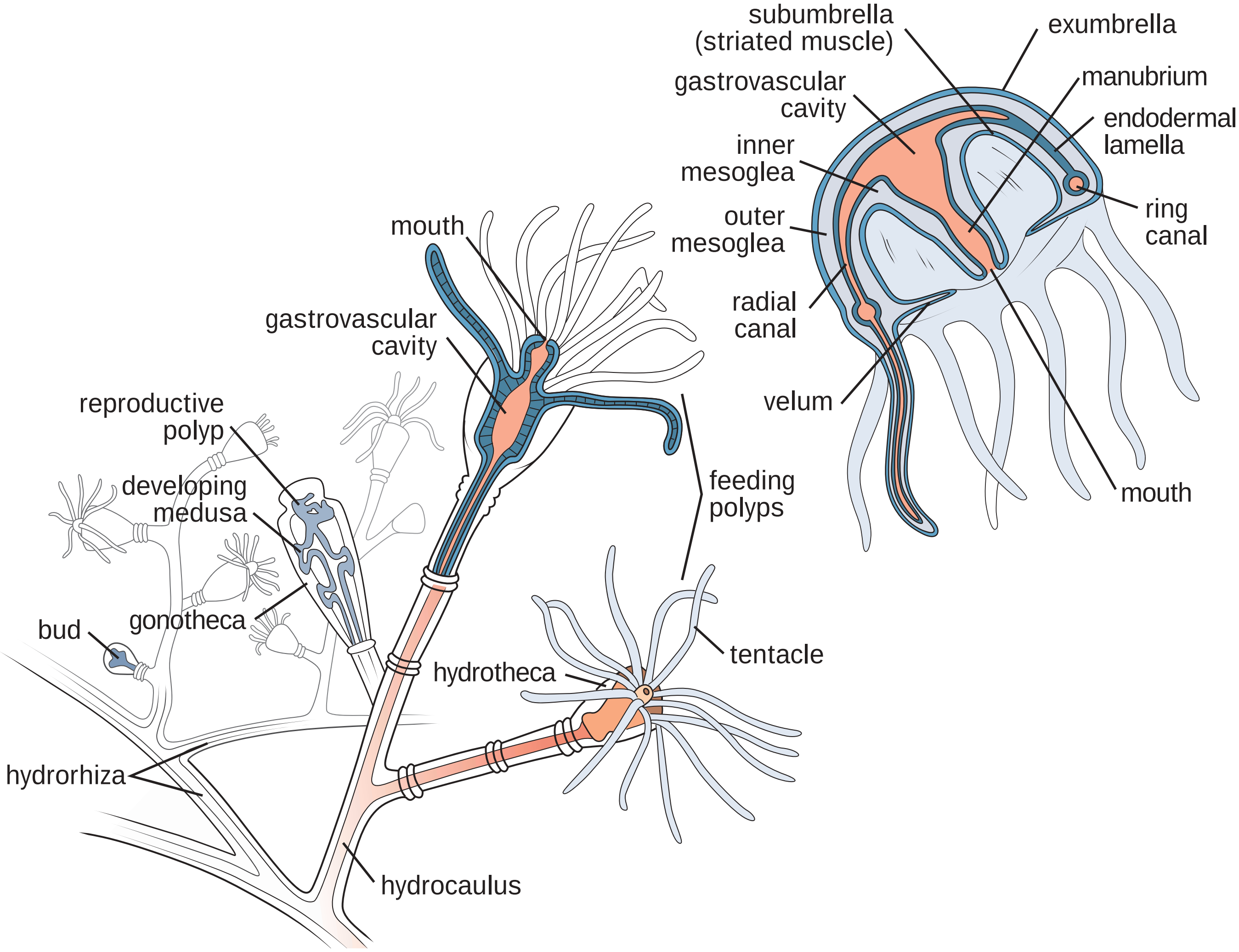
Considered a superclass by some experts, this group has representatives since the Precambrian (velellids). Because of the rarity of skeletal structures, however, the fossil record is fragmentary. Recent interpretations of the medusary nodule (the structure that, from a polyp, gives rise to a medusa by a special type of budding) suggest that the Hydrozoa are triploblastic. The subumbrellar cavity of the hydromedusae, and the layer of striated muscle that lines it, are originated by a morphogenetic pattern very similar to schizocoely, with a third layer of tissue that is formed between ecto- and endoderm and that becomes hollow. The subumbrellar cavity, therefore, is interpreted as a coelom that later becomes open, with the origin of the velar opening. Molecular evidence is now available, showing, for instance, that the genes coding for mesodermic structures in the Bilateria is also present in the Hydrozoa. The polyp stage, thus, is diploblastic, whereas the medusae are triploblastic. If this view is confirmed by further evidence, the transition from diploblasts to triploblasts occurs every time a medusa is budded from a polyp, and one of the great mysteries of metazoan evolution is solved.

Hydrozoa (characterized by medusae with direct development or produced by lateral budding from polyps) are comprised in the subphylum Medusozoa, including also the Scyphozoa (characterized by medusa production by strobilation from polyps), and the Cubozoa (characterized by medusa production by complete metamorphosis of the polyp).

The classes of the superclass Hydrozoa include Automedusa, with the subclasses Actinulidae (one order, two families), Narcomedusae (one order, three families), and Trachymedusae (one order, five families); and Hydroidomedusa, with the subclasses Anthomedusae (two orders, 49 families), Laingiomedusae (one order, one family), Leptomedusae (two orders, 34 families), Limnomedusae (one order, three families), Siphonophorae (three orders, 16 families), and Polypodiozoa (one order, one family).

Physical characteristics

The Automedusa class is represented only by medusae; there are no polyp stages. Development is usually direct, sexes are separated; each fertilized egg leads to a planula that develops into a single medusa, except in some Narcomedusae, in which parasitic stages issued from the egg may give rise to several medusae by asexual budding. Medusae are not formed through a medusary nodule: the subumbrellar cavity and velum are formed by folding and deepening of the oral embryonic ectoderm, being only analogous to the subumbrellar cavity and velum of the Hydroidomedusa. The primary marginal tentacles are always formed before the subumbrellar cavity and the gastro vascular system. The marginal tentacles are deprived of tentacular bulbs. Sensory organs are in the form of ecto-endodermal statocysts, with an endodermal axis, growing out from the circular canal, with sensory cells characterized by numerous kinocilium-lacking rootlets, surrounded by stereocilia, innervated by the upper nerve ring; statoliths are of endodermal origin. Asexual reproduction is present only in "actinula"-like larvae and adults of Narcomedusae. The Actinulidae are all members of the interstitial fauna; they look like actinula-larvae, and the statocysts are the most distinctive medusan feature of these highly specialized medusae. The Narcomedusae have a flattened exumbrella, with lobed margin, incised by deep grooves. Usually with no radial canals, gametes are carried on the wide manubrium. Their intermediate tentaculated post-embryonic stages are juvenile medusae

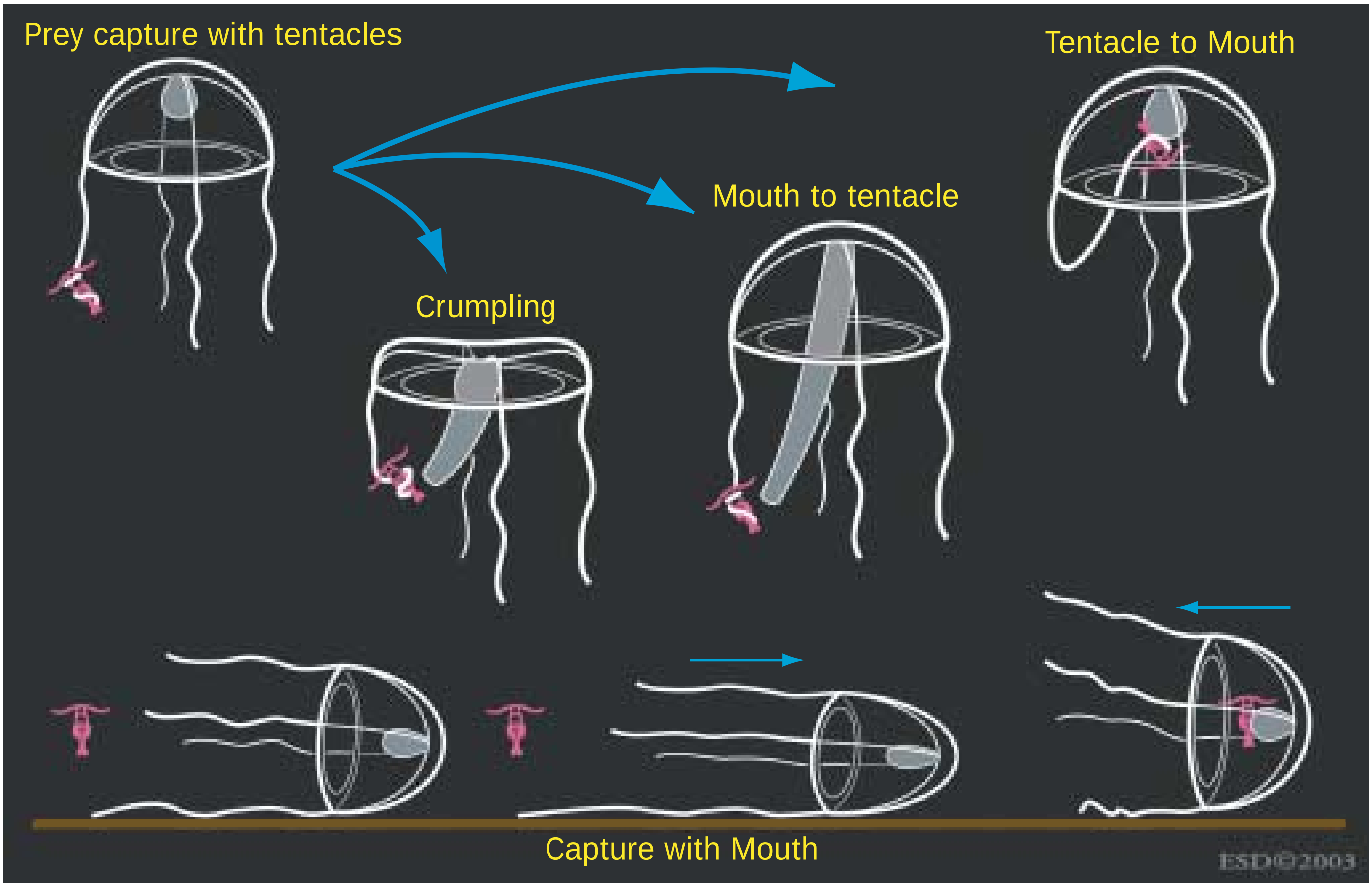

subumbrella (striated muscle)
exumbrella
gastrovascular cavity
manubrium
endodermal lamella
inner mesoglea
ring canal
outer mesoglea
radial canal
velum
mouth
mouth
gastrovascular cavity
reproductive polyp
developing medusa
feeding polyps
bud
gonotheca
tentacle
hydrotheca
hydrorhiza
hydrocaulus

Hydroid anatomy. A. Colony; B. Medusa. (Illustration by Patricia Ferrer)

and are inappropriately called "actinulae," like the juvenile polyps of some Anthomedusae. The Trachymedusae have a bell-shaped umbrella, with circular and radial canals. Gametes ripen on the radial canals. The manubrium is often on a peduncle.

The Hydroidomedusa class is represented by a succession of three stages during indirect development. The planula is a ciliated motile gastrula; it typically develops into a benthic, modular, larval stage, polyp or hydroid (except in the Porpitidae, *Margelopsis* and *Pelagohydra*, where the hydroid is floating). Hydroids can be solitary, but generally form modular colonies by simple budding. Polyps can be specialized for different functions (defensive dactylozooids, reproductive gonozooids, nutritive gastrozooids, etc.). Polyps give rise, by asexual budding, to planktonic, free-swimming, and solitary hydromedusae, representing the sexual adult. The sense organs of pelagic hydroidomedusae, when present, are ocelli (Anthomedusae, some Leptomedusae), or statocysts (Leptomedusae, Limnomedusae); sometimes cordyli of unknown function are also present (Leptomedusae). The Siphonophores have no visible sense organs. Medusae are often reduced to sporosacs (fixed gonophores), so that hydroids, by paedomorphosis, secondarily become the sexual stages. The Hydroidomedusa may also form pelagic, highly polymorphic colonies (Siphonophores). Medusa budding occurs via a medusary nodule or entocodon, forming a coelom-like cavity, the subumbrellar cavity, lined by striated muscle cells; primary marginal tentacles always develop after the subumbrellar cavity and the gastro vascular system. Both embryonic and larval stages, the planula and the polyp, are typically diploblastic; the adult sexual stages, the hydromedusae, acquire a triploblastic kind of organization during embryonic development (medusary nodule formation). Hydroidomedusae are frequently seasonal; the hydroid stage may develop several types of resting stages (frustules, propagules, cysts, stolon system) to overcome unfavorable ecological conditions.

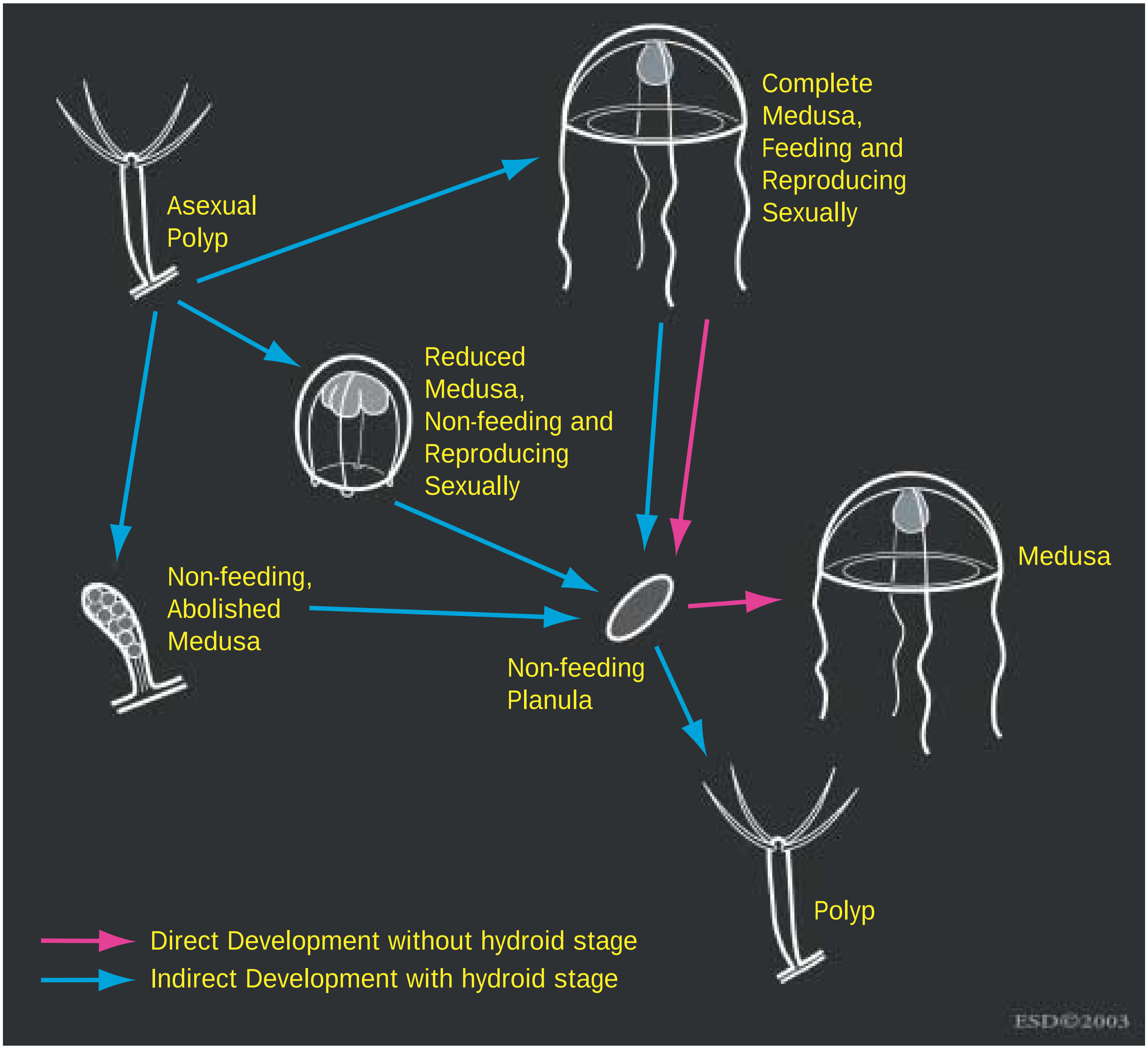
The hydroids of the subclass Anthomedusae do not have a protective perisarc sheath around the polyps and are said athecates; they are usually colonial (but the most famous hy-



Hydroids capture prey with their tentacles and mouth. (Illustration by Emily Damstra)

droid, *Hydra*, is a solitary paedomorphic anthomedusa). The colonies can be either monomorphic or polymorphic, while the structure of the tentacles is in two forms: filiform tentacles do not present particular aggregations of cnidocysts, whereas capitate tentacles have cnidocyst knobs. The medusae are typically bell shaped; their gonads (aggregates of gametes commonly referred to as gonads) are confined on manubrium, sometimes extending on the most proximal parts of the radial canals. Their marginal sense organs, if present, are ocelli; the marginal tentacles are peripheral, hollow, or solid, usually with tentacular bulbs; sexual reproduction occurs through a complex planula. The hydroids of the subclass Laingiomedusae are unknown. The medusae have an almost hemispherical umbrella, with lobed margin, divided by peronial grooves or similar structures. The radial canals are four; there is no typical circular canal but a solid core of endodermal cells around the umbrella margin. The tentacles are solid, inserted above the exumbrellar margin, on the exumbrella. The manubrium is simple, quadrangular, tubular, or conical; the mouth opening is simple, quadrangular to circular; gametes are in four masses on the manubrium or as epidermal lining of interradial pockets of the manubrium. The hydroids of the subclass Leptomedusae are thecate: all parts of the colonies are typically protected by a chitinous perisarcal structure. The hydranth is protected by a hydrotheca, the nematophore by a nematotheca, and the gonophore by a gonotheca. Rarely, hydranths are naked. The medusae are typically with hemispherical or flattened umbrella; the masses of gametes are confined to radial canals, exceptionally extending onto the proximal part of manubrium; when present, the marginal sense organs are ectodermal velar statocysts, rarely cordyli, occasionally adaxial ocelli. The marginal tentacles are peripheral and hollow (except in *Obelia*), with tentacular bulbs. Sexual reproduction occurs through a complex planula. The hydroids of the subclass Limnomedusae are very simple; solitary or colonial; small, sessile; with or without tentacles; often close to planula structure and budding planula-like structures or frustules; there are no perisarcal thecae, but cysts and stolons are covered by chitin. The medusae usually have gamete masses along the radial canals or, exceptionally, on the manubrium. The marginal tentacles are peripheral, hollow, without a true basal bulb; their base is usually with a parenchymatic endodermal core embedded in umbrellar mesoglea. The marginal sense organs are internal, enclosed ecto-endodermal statocysts that are embedded in the mesoglea near the ring canal or in the velum. Exceptionally, medusae can be reduced medusoids. Sexual reproduction leads to simple planulae, without embryonic glandular cells.

The subclass Siphonophorae comprises generally pelagic, free-swimming, or floating species, forming highly polymor-


Asexual Polyp
Complete Medusa, Feeding and Reproducing Sexually
Reduced Medusa, Non-feeding and Reproducing Sexually
Non-feeding, Abolished Medusa
Non-feeding Planula
Medusa
Polyp
Direct Development without hydroid stage
Indirect Development with hydroid stage
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Hydroid life cycles vary by species. Here is shown an example of a "typical" life cycle. (Illustration by Emily Damstra)

phic modular colonies of polypoid and medusoid zooids attached to a stem or stolon supported by a floating and swimming system or nectosome (pneumatophores and nectophores).

The Polypodiozoa class is represented by a single species, *Polypodium hydriforme* Ussow, 1885, the only known metazoan adapted to intracellular parasitism. *Polypodium* has a unique lifecycle, having a succession of a free-living stage and of an intracellular parasitic stage of some Acipenseridae and Polyodontidae eggs. The earliest parasitic stage known is a binucleate cell observed in previtellogenetic fish oocytes. Further parasitic development leads to a didermic stolonal structure, with inverted germ layers, growing at the expense of the egg's yolk and forming numerous inverted buds. Before becoming free at fish spawning, eversion takes place and the germ layers take their normal position (ectoderm out, endoderm inside). Once liberated, the stolon becomes fragmented into individual buds, each originating a free-creeping globular stage that can multiply by longitudinal fission. These stages can move and feed, having an oral mouth-cone and tentacles. Germ cells are endodermal; the females have two kinds of gonads, each with a gonoduct opening in the gastral cavity; the gonads of the males form gametophores carrying cnidocysts. The free-living stage presumably represents the sexual medusae, the parasitic stages being considered as polypoid.

Seen here growing under a ledge near Lizard Island, North Great Barrier Reef, the hydrocoral *Distichopora violacea* is vivid purple in color. (Photo by A. Flowers & L. Newman. Reproduced by permission.)

They differ, however, from all other Hydrozoa by unique features: bilateral symmetry; presence of gonoducts; aberrant gametogenesis; unique structure of cnidocil apparatus; inversion of germ layers during parasitic life; and the complete separation of epidermal and muscle cells.

The umbrella of Hydroido- and Automedusae generally measures between 0.02 in (0.5 mm) and 2 in (50 mm), but in numerous species the size may be greater, reaching 3.9–7.8 in (100–200 mm) (*Aequorea*) and even, exceptionally, 15.7 in (400 mm) of diameter (*Rhacostoma atlanticum*). The colonies of the Hydroidomedusae usually have a reduced size. Most of them do not exceed a few inches (centimeters to a few decimeters) (i.e., *Cladocarpus lignosus* is 27.5 in [70 cm]); the hydranths are usually very tenuous, not exceeding a few inches (millimeters), but there are exceptions (i.e., *Hydrocoryne miurensis*: 2.3 in [6 cm]; *Corymorpha nutans*: 4.7 in [12 cm]; *Monocoryne gigantea*: 15.7 in [40 cm]; *Candelabrum penola*: 33.4 in [85 cm]; and *Branchiocerianthus imperator*: more than 6.5 ft [2 m]). The smallest polyps are those of the Microhydrulidae (Limnomedusae): they are reduced to a spherical or irregular body, ranging from 20 to 480 µm. The longest siphonophore is *Apolemia uvaria*, with colonies reaching 98.4 ft (30 m). The medusae of the hydrozoa are usually diaphanous, as are their polyps. Colored species, however, are frequent. Pigments derive from the diet or are produced directly. The most common color is reddish, deriving from crustaceans; other colors for medusae can be green, white, or orange; whereas polyps can be, according to the species, reddish, pink, white, or blue.

The medusae have typical and easily recognizable body architecture; the main feature that distinguishes them from other medusae is the velum. For this reason, they have also been called Craspedotae (with velum), as opposed to the medusae of the Scypozoa and Cubozoa, which were called Acraspedae (without velum). The polyps are quite varied in architecture, ranging from coral-like colonies (*Millepora* and the stylasterids) to gigantic polyps resembling those of the Anthozoa (*Branchiocerianthus*) to microscopic polyps reduced to a simple ball of tissue (*Microhydrula*).

Distribution

The Hydrozoa are cosmopolitan, and can be found in all water masses of the world, both in marine and in fresh waters. The Hydrozoa are known since the beginning of the modern study of animals; many species are Linnean and were described in the eighteenth century.

Habitat

The medusae of the Hydrozoa and the siphonophores are mostly planktonic; they are seasonal in occurrence and can be present in swarms, transported by the currents. Some medusae and some siphonophores, however, can be benthic. The polyp stages are usually benthic and live attached to the bottom, even though some species can be planktonic, such as the well-known *Velella velella*.

The Hydrozoa occur in all aquatic habitats, from anchialine caves to deep-sea trenches, from lakes and ponds to rocky coasts and the interstices among sand grains. The polyp stages of many species live exclusively on certain types of substrate, usually other organisms such as fishes, tunicates, polychaetes, bryozoans, mollusks, crustaceans, sponges, cnidarians, algae, sea-grasses, etc., with which they have symbiotic relationships ranging from simple epibiosis to commensalisms, mutualism, and parasitism.

Hydrozoa are mostly carnivores, using their habitat to acquire favorable positions to catch their prey. Planktonic stages are transported by currents, but can also move within water masses, searching for food. The position of benthic forms is decided by the planula, at the moment of settlement. Colonies are positioned at locations that will ensure a supply of new, fresh water around the hydranths, enhancing the transport of potential prey.

Behavior

The medusae are sharply individual; they can be gathered by winds and currents to form extensive swarms, but it is not known if they have any kind of social interaction while being

Stinging hydroids (*Lytocarpus philippinus*). (Photo by A. Flowers & L. Newman. Reproduced by permission.)

The species *Turritopsis nutricula* in its hydroid stage. (Photo by S. Piraino [University of Lecce]. Reproduced by permission.)

in close contact. The colonies of Hydrozoa, especially polymorphic ones, have been compared to superorganisms because of the complexity of the functions that they perform through the different types of zooids. The zooids of a colony usually derive from a single planula, thus being interconnected members of a single clone. It is possible, however, that different colonies merge their tissues or that different planulae aggregate to form coalescent colonies. In these cases, different individuals can be in such close connection that they become a single individual, possibly one of the extreme forms of social organization.

Most Hydrozoa have separate sexes. Fertilization is usually internal, with no copulation. Males spawn in the water and the sperm actively swim toward the eggs that are still on the maternal body (either a medusa or a polyp colony). The Hydrozoa are the first animals in which sperm attractants have been demonstrated, with species-specific attraction of sperms by the eggs. For many medusan species, both males and females spawn in the water, where fertilization occurs. Also in this case, however, sperm attractants facilitate gamete encounter.

The members of the same colony perform coordinated behaviors that surely involve communication. In *Thecocodium brieni*, for instance, the dactylozooids catch the prey with their tentacles, while the gastrozooids perceive that a prey is available and stretch towards the dactylozooids, detaching the prey from their tentacles and ingesting it. This division of labor, involving great coordination, is frequent in polymorphic colonies.

Planktonic animals do not show particular territoriality, being, by definition, transported by currents. It is probable, however, that medusae actively prevent being in too close contact to avoid competitive interactions while foraging. Territoriality is very strong in sessile organisms, where competition for the occupation of space is very evident. The arrangement of dactylozooids on the edge of many colonies is related to the defense of the territory from overgrowth by nearby animals. The feeding polyps can eat the settling larvae of potentially competing species, thus preventing competition for space.

When unfed, both polyps and medusae are always in search for food, with species-specific activity patterns. When the coelenteron is full of food, tentacles are usually contracted and do not catch prey, showing some control of cnidocyst discharge. Many medusae perform daily migrations through the water column.

Feeding ecology and diet

Hydrozoa are usually thought to feed on planktonic crustaceans such as copepods. Under laboratory conditions, they mostly survive with a diet based on *Artemia nauplii*. The medusae are mostly voracious carnivores and, when feeding on fish eggs and larvae, can be considered as being at the apex of trophic chains. The polyps are more varied in their food preferences. Recent investigations showed that the few species studied thoroughly feed on a great variety of prey, ranging from gelatinous plankton for the medusae to phytoplankton for the polyps. Some species have symbiotic zooxanthellae and are functionally photosynthetic.

Some medusae can remain immobile in the water, with their tentacles outstretched across the water column, performing ambush predation, whereas others can move across the water to contact prey, performing cruising predation. Polyps can simply extend their tentacles to catch passing prey, but they can also use special sense organs to perceive approaching prey and grab it actively, or they can form currents by moving their tentacles to direct food particles toward the mouth. Symbiotic species are very specialized in their feeding behavior; the most extreme cases are *Halocoryne epizoica* that feed on bryozoan tentacles, and *Polypodium hydriforme* that feed on sturgeon eggs from the inside, being the only intracellular parasitic metazoan.

Hydrozoa use cnidocysts as the main organelles to catch their food. The superclass has the richest variety of cnidocyst types of the whole phylum, with a fine range of adaptations to catch from tiny prey like the single cells of phytoplankton to the crustaceans and larvae of the zooplankton to the animals that live in the sand and mud, such as nematodes. Many species have very restricted diets, being specialized for just one type of food.

Both polyps and medusae are mostly carnivorous, feeding on almost all animals of proper size. In no other metazoan group (with the possible exception of parasitic trematodes) is the lifecycle of such paramount importance in defining the properties of a given species, and this is valid also for the type of prey. Tiny medusae that feed on fish eggs and larvae, sometimes impairing the success of recruitment, can be the most voracious predators of fish. The propensity of feeding on almost all types of larvae (both for polyps and for medusae) includes the Hydrozoa within the predators of almost all Metazoa with an indirect lifecycle.

Reproductive biology

Nothing is known regarding the courtship and mating. The eggs are brought in masses on female medusae or in female gonophores. According to the species, the eggs can be small and in great numbers, or they can be large and few, even a single one per gonophore.

In the Automedusae, with no polyp stages, there is little or no asexual reproduction in larval medusae (known as actinulae in the Narcomedusae) so that each fertilization event leads to one or a few adult medusae. In the Hydroidomedusae, the widespread asexual reproduction of the polyp stage can be considered as a polyembryony or as a larval amplification, as it happens in some parasites such as trematodes. Each fertilization event, therefore, leads to a single planula that produces a polyp colony that, in its turn, will produce many adult medusae. Since the lifespan of polyp colonies can last many years, each planula can lead to the production of hundreds or thousands medusae.

The so-called planula larva is nothing more than a gastrula, thus being more an embryo than a larva. Since gametes are shed before or soon after fertilization, embryonic development takes place outside the maternal body. Planulae can be solid (stereogastrula) or hollow (coeloblastula); usually the species with medusae in the lifecycle have hollow planulae that live part of their life in the water column, swimming with cilia or flagella to reach the settling sites. The species with suppressed medusae usually produce solid planulae that fall to the bottom and settle near the parent colony. Adults, by definition, are the sexually reproductive morphs in a lifecycle; if a medusa is present, it is the adult in the lifecycle. The polyp stage, in this framework, is a specialized (and perennial) larva that produces a great number of adults throughout its long life. In many species, however, the medusa stage can be reduced or even suppressed, so that the larvae, by paedomorphosis, become the sexually mature morphs of the lifecycle. Almost half of the species of Hydroidomedusae have suppressed or reduced medusae; the group is, therefore, the most paedomorphic of the whole animal kingdom.

Some medusae (e.g., *Eleutheria*) have special brood pouches where they safeguard developing medusae. Some hydroids have gonothecae with apical brood chambers that retain the planulae for a certain period.

Many species are sharply seasonal, being active only in narrow periods of time. The medusae can be present for a few weeks or months, completely disappearing from the water column and being represented by the correspondent polyps in the benthos. Polyp colonies can regress to resting hydrorhizae for long periods, reactivating at the onset of favorable conditions. Planulae can become encysted and remain dormant just as the resting hydrorhizae, being covered by a chitinous sheath.

Conservation status

No species are listed by the IUCN Red List. For most Hydrozoa, the distribution and the abundance are not known and only the few remaining specialists know about their presence. Many species are endemic simply because they are not searched for and only the areas of activity of specialists are covered. The only groups mentioned in regional or national red lists are the calcified, coral-like Milleporidae and Stylasteridae, which are also listed by CITES. Inclusion of these taxa on conservation lists is linked to the assessment of species value according to appearance.

Milleporidae and Stylasteridae have been subjected to trade, as are some hydroids (known as “white weeds” in the North Sea). Their decline is linked to habitat degradation.

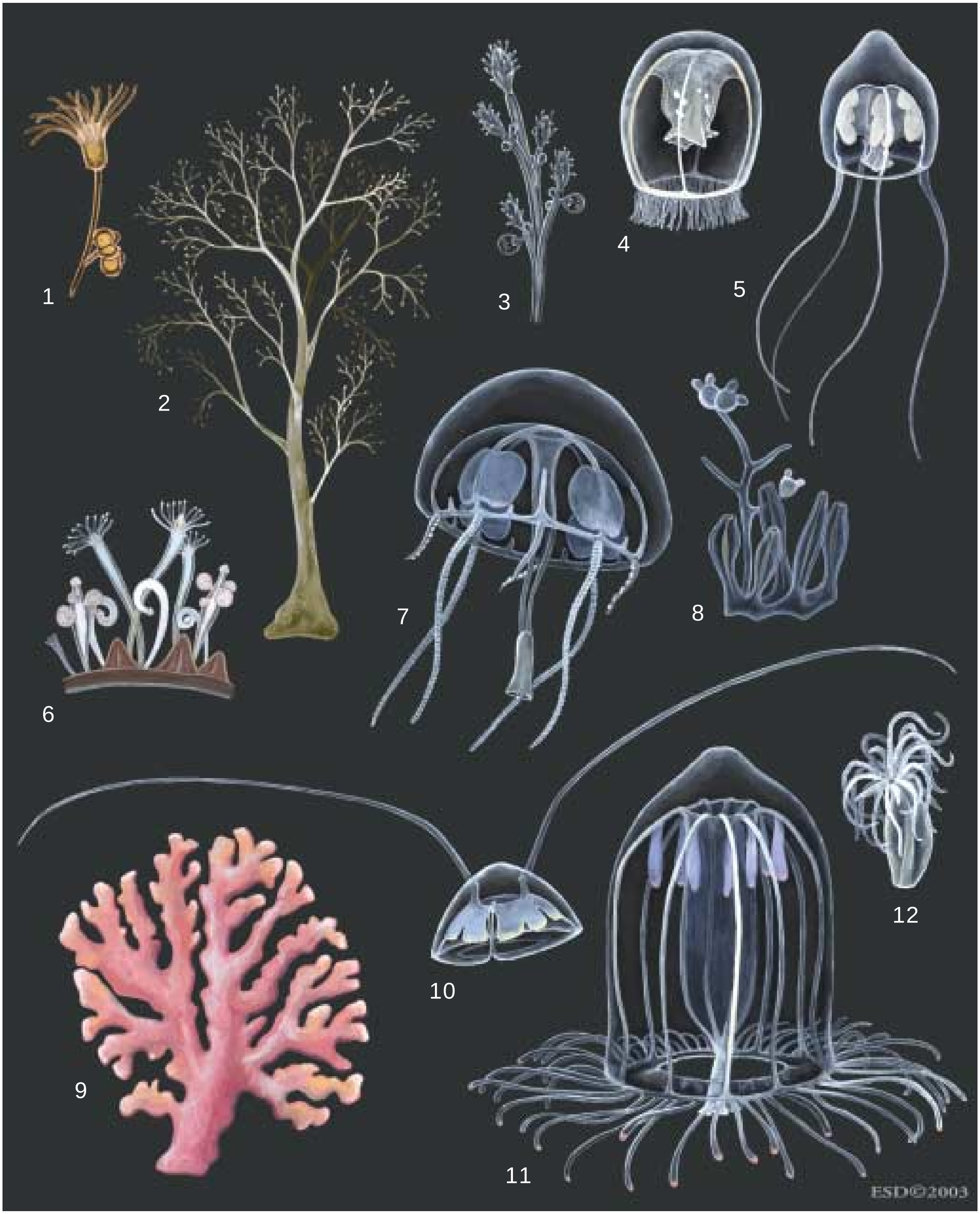
Significance to humans

The Hydrozoa are mostly inconspicuous, both in the polyp and in the medusa stage, and are generally overlooked. The famous treatise by Tremblay, describing transplants in *Hydra*, inspired the fantastic novel *Frankenstein* by Mary Shelley. The illustrations of some monographs, especially those on medusae by Haeckel, are renowned for their beauty. The modern music composer, Frank Zappa, wrote a song on a hydromedusa that has been named after him: *Phialella zappai*.

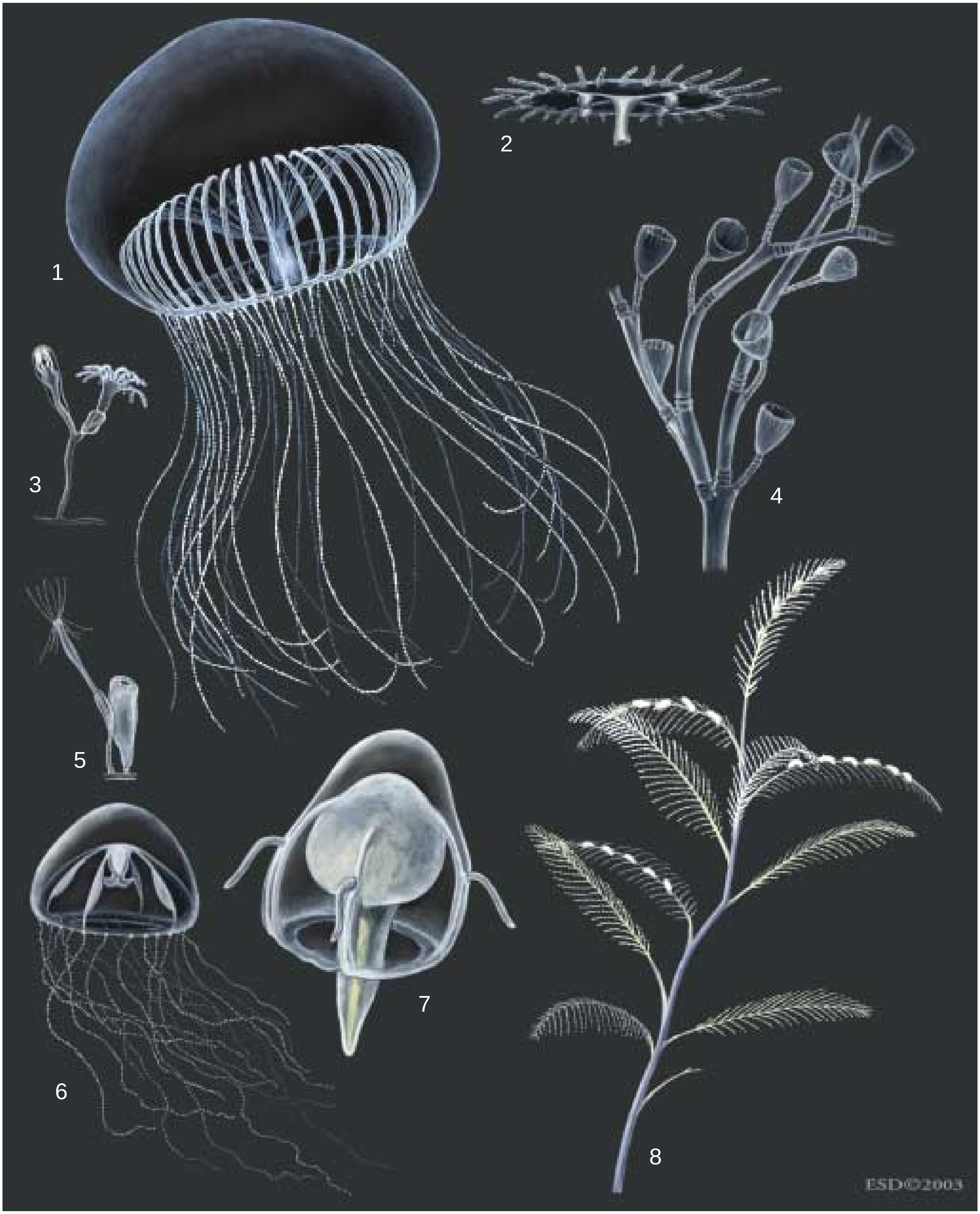
“White weeds” (the colonies of hydroids of the genera *Hydrallmania* and *Sertularia*) had been used as decoration before the sharp reduction of their populations. Some Hydrozoa are used as laboratory animals for experimental biology; *Hydra* is the most popular one, but others include *Aequorea victoria* (for the production of the labeling enzyme aequorein), *Hydractinia* spp., *Laomedea* spp., and *Tubularia* spp.

Hydroids are important members of fouling communities, inhibiting the functioning of power plants by clogging their pipes and reducing the velocity of ships by settling on their hulls. Some species have been reported as pests in aquaculture, feeding on the larvae of the reared species or on their food. *Polypodium hydriforme* is a threat to the production of caviar, being a parasite of sturgeon eggs.

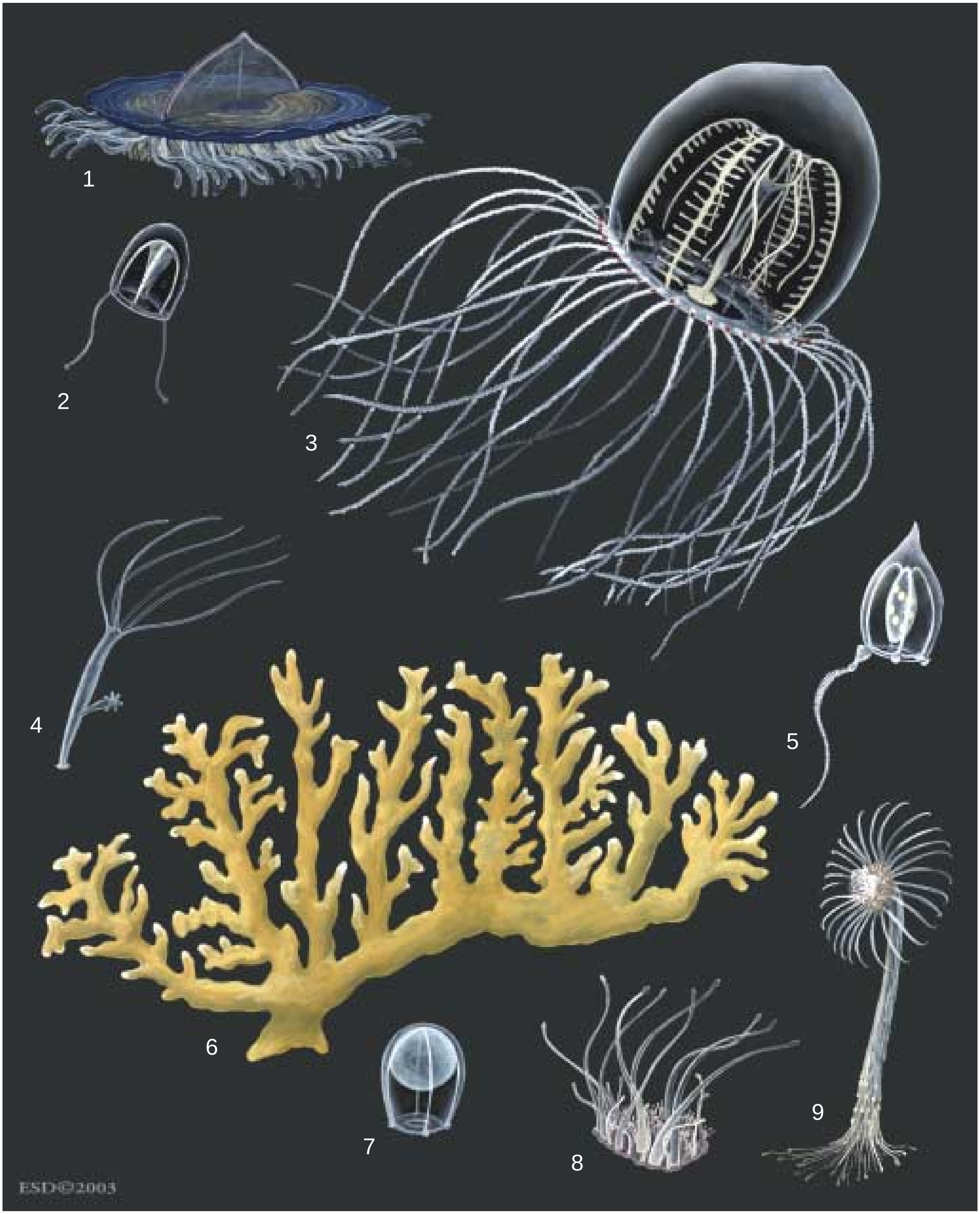
Some species of medusae (e.g., *Gonionemus*) can inflict severe stings on humans, as do some hydroid colonies such as the species of *Millepora* (fire corals) and some aglaopheniids. When present in swarms, even small medusae like those of *Clytia* can inflict slight stings on swimmers. The most important threat to human activities is the predation of some medusae (e.g., *Aequorea victoria*) and floating hydroids (e.g., *Clytia gracilis*) on the eggs and larvae of commercially exploited fish. This kind of predation can reduce the success of fish recruitment, reducing the yield of fisheries.



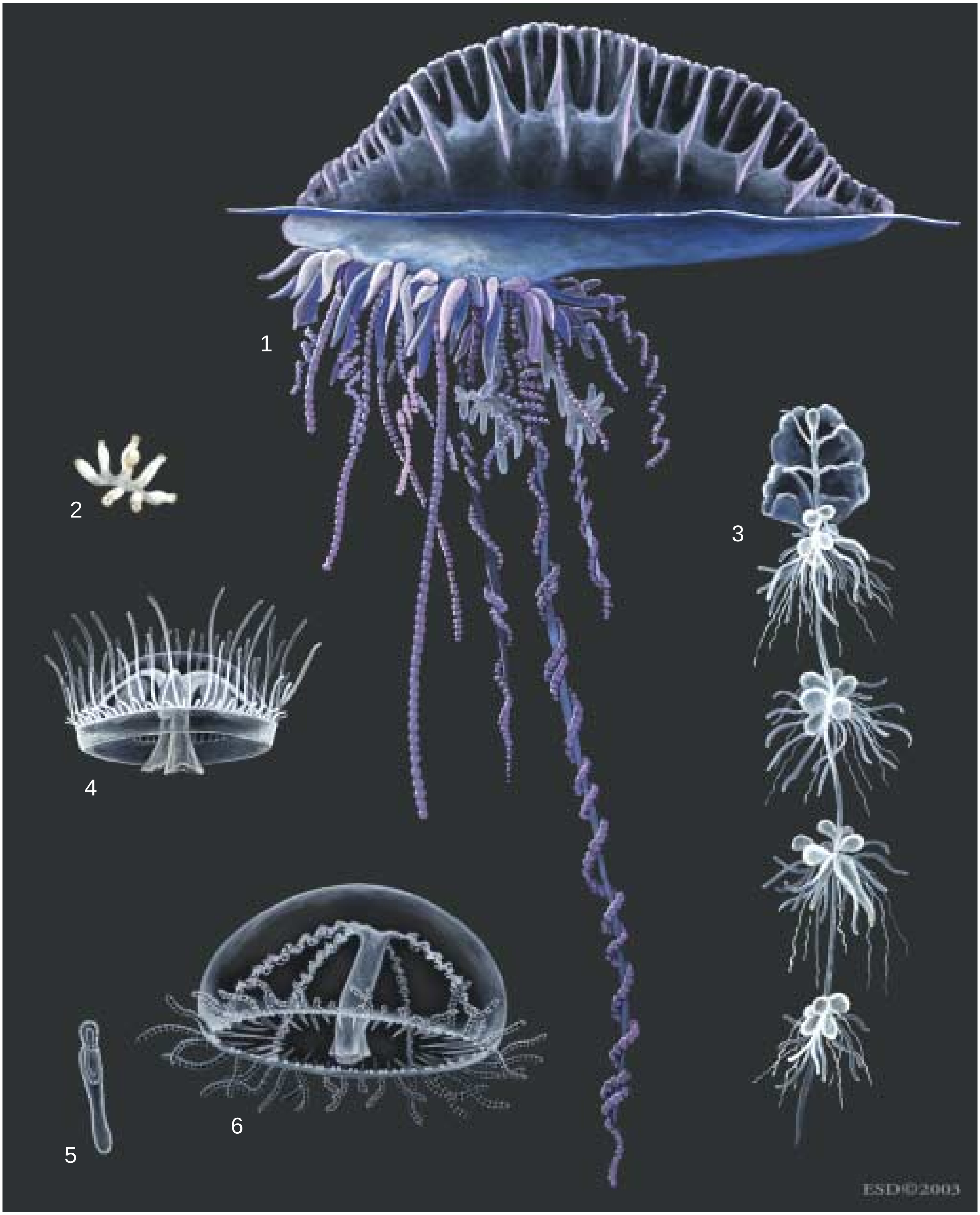
1. *Eudendrium glomeratum* polyp; 2. *E. glomeratum* medusa; 3. Immortal jellyfish (*Turritopsis nutricula*) polyp; 4. *T. nutricula* medusa; 5. *Hydrichthys mirus* medusa; 6. *Hydractinia echinata* polyp; 7. *Liriope tetraphylla* medusa; 8. *H. mirus* polyp; 9. *Distichopora violacea* polyp; 10. *Solmundella bitentaculata* medusa; 11. *Aglantha digitale*; 12. *Halammohydra schulzei* polyp. (Illustration by Emily Damstra)



1. *Aequorea victoria* medusa; 2. *Obelia dichotoma* medusa; 3. *A. victoria* polyp; 4. *O. dichotoma* polyp; 5. Zappa's jellyfish (*Phialella zappai*) polyp; 6. *P. zappai* medusa; 7. *Laingia jaumotti* medusa; 8. *Aglaophenia pluma* polyp. (Illustration by Emily Damstra)



1. By the wind sailor (*Velella velella*) polyp; 2. *V. velella* medusa; 3. *Polyorchis penicillatus* medusa; 4. *Hydra vulgaris* polyp; 5. *Corymorpha nutans* medusa; 6. Fire coral (*Millepora alcicornis*) polyp; 7. *M. alcicornis* medusa; 8. *Paracoryne huvei* polyp; 9. *C. nutans* polyp. (Illustration by Emily Damstra)



1. Portuguese man of war (*Physalia physalis*) polyp; 2. *Craspedacusta sowerbyi* polyp; 3. *Apolemia uvaria* polyp; 4. *C. sowerbyi* medusa; 5. *Olindias phosphorica* polyp; 6. *O. phosphorica* medusa. (Illustration by Emily Damstra)

Species accounts

No common name

Halammohydra schulzei

ORDER
Actinulida

FAMILY
Halammohydridae

TAXONOMY
Halammohydra schulzei Remane, 1927, North Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body as a long gastric tube (manubrium) with a terminal mouth, with a small aboral cone, separated from manubrium by a neck, bearing an adhesive organ; aboral nerve ring; one aboral whorl of 28 (sometimes up to 32) amphicoronate solid tentacles with a large basal thickening, alternating with 12 ecto-endodermic statocysts; gonochoric; generally two opposite gonads; without brood pouch. Body 0.027–0.031 in (0.7–0. 8 mm) high.

DISTRIBUTION
Cosmopolitan. (Specific distribution map not available.)

HABITAT
Interstices of marine sand.

BEHAVIOR
Eretant in the marine sand.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Dioecious, sex cells released in the sea, reproduction through a special actinulid larvae or halhydrula.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Corymorpha nutans

ORDER
Capitata

FAMILY
Corymorphidae

TAXONOMY
Corymorpha nutans M. Sars, 1835, Norway.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hydroid: large, solitary, hydrocaulus subcylindrical, with short sensory papillae at base and numerous long, anchoring filaments; hydrocaulus with parenchymatic endoderm with numerous longitudinal anastomizing peripheral canals; hydrocaulus protected by a transparent membranous tube; hydranth flask-shaped to vasiform with about 20–80 oral filiform tentacles in several irregular whorls, and 20–32 aboral considerably longer filiform tentacles; hydranth and distal part of hydrocaulus bend downward; medusa buds in dense clusters on about 15–20 branching peduncles just above aboral tentacles.

Medusa: umbrella up to 0.23 in (6 mm) high (including apical process), cylindrical, with a high, pointed apical process and a long, narrow umbilical canal; mesoglea thick; velum wide; manubrium large, cylindrical, on short gastric peduncle, about two-thirds of the length of subumbrella, in full extension reaching slightly beyond exumbrellar margin; mouth simple, tube like, armed with cnidocysts; four radial canals and circular canal fairly broad; gonads completely surrounding manubrium, but living peduncle and mouth free; one single, long, marginal tentacle, moniliform; three perradial non-tentacular bulbs smaller than the tentacular one.

DISTRIBUTION
Atlantic, the Mediterranean, and Black Sea. (Specific distribution map not available.)

HABITAT
The hydroid lives at moderate depth with its basal part embedded in soft bottoms. The medusae are planktonic in coastal waters.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
The hydroid, with its typical posture, is oriented with the mouth near to the bottom and it probably captures epibenthic vagile animals. The medusae feed on planktonic animals.

REPRODUCTIVE BIOLOGY
Both hydroids and medusae are sharply seasonal, occurring in correspondence with spring plankton blooms. Hydroids are not produced immediately, fertilization and the sexual reproduction originate an encysted embryo that spends the unfavorable season in the sediments, to become a polyp at the onset of the following favorable season.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Fire coral

Millepora alcicornis

ORDER

Capitata

FAMILY

Milleporidae

TAXONOMY

Millepora alcicornis Linnaeus, 1758, West Indies.

OTHER COMMON NAMES

English: Sea ginger; French: Corail de feu; German: Feuerkorallen.

PHYSICAL CHARACTERISTICS

Hydroid: colony forms massive, calcareous exoskeletons (coenosteum), forming horn-shaped, upright branches or plates; coenosteum with an internal complex network of coenosarcal tubes, covered externally by a thin ectodermal layer, coenosteal surface perforated by pores; margins of pores not protruding from surface of coenosteum; large gastropores surrounded by smaller dactylopores, forming indistinct cyclosystems; no gastrostyles or dactylostyles; polyps polymorphic; gastrozooids relatively short and stout, with an oral whorl of 4–6 short capitate tentacles, arising from gastropores; dactylozooids long, slender, mouth less, with scattered capitate tentacles, arising from dactylopores; cnidome with macrobasic mastigophores; gonophores arising from coenosarc within ampullae embedded in the coenosteum. Color variable, usually yellow-brown because of algal symbionts.

Medusa: short-lived, free-swimming eumedusoids with exumbrellar cnidocyst patches, narrow velum, four radial and circular canals, gonads occupying the place of an indistinct manubrium; without tentacles, without sense organs (this description applies to the eumedusoid of *M. complanata*, the only *Millepora* eumedusoid known in detail).

DISTRIBUTION

Tropical Pacific, Indian Ocean, Red Sea, and Caribbean. (Specific distribution map not available.)

HABITAT

Common to abundant in shallow waters, or in inner ledges and outer reefs, usually not exceeding 98.4 ft (30 m), correlated with dependence of the colonies on their symbiotic unicellular algae or zooxanthellae that need light for their processes of assimilation.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Feed upon planktonic animals, mostly crustaceans.

REPRODUCTIVE BIOLOGY

Sexual reproduction by free-swimming eumedusoids, usually ripe from April–July.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

Millepora are severe stingers and can cause violent, uncomfortable burning, even in dried state. ◆

No common name

Paracoryne huvei

ORDER

Capitata

FAMILY

Paracorynidae

TAXONOMY

Paracoryne huvei Picard, 1957, Mediterranean coast of France.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Stolonal colonies with encrusting hydrorhizae composed of naked coenosarc, with gastrozooids, dactylozooids, and gonozooids; gastrozooids with 12–26 tentacles irregularly distributed in four verticils at distal half; dactylozooids large, without tentacles or mouth; gonozooids without tentacles or mouth; gonophores as fixed sporosacs (cryptomedusoids), male and female in different colonies; male gonophores in number of 2–10 per gonozooid, ovoids, with a characteristic apical prolongation; female gonophores 2–4 per gonozooid, bigger and more spherical than males; young gonophores with an apical prolongation (as in the males), which is absent and replaced by an orifice at maturity.

DISTRIBUTION

Western Mediterranean. (Specific distribution map not available.)

HABITAT

The colonies live on rocks and mussels, from the intertidal to the very shallow subtidal. They form very evident pink patches on bare rocks.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Nothing is known.

REPRODUCTIVE BIOLOGY

The dioecious colonies are present in the winter and disappear in the summer. After sexual reproduction, the planulae encyst and remain dormant until the onset of the following favorable season.

CONSERVATION STATUS

In spite of the great tradition of biodiversity exploration in the Mediterranean, this very distinctive species has been discovered in relatively recent times. It became very frequent and abundant in the 1970s and 1980s, but is now extremely rare again. The resting stages surely play an important part in these patterns of abundance.

SIGNIFICANCE TO HUMANS

None known. ◆

No common name

Polyorchis penicillatus

ORDER

Capitata

FAMILY

Polyorchidae

TAXONOMY

Melicertum penicillatum Eschscholtz, 1829, California, United States.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: unknown.

Medusa: bell up to 2.3 in (60 mm) high, with a gastric peduncle, up to 160 marginal hollow tentacles in a simple row along exumbrellar margin; tentacular bulbs tubular, adnate, with bright red ocellus on short spur; four radial canals with numerous, short, blind lateral diverticula; ring canal with centripetal diverticula; manubrium prismatic, pendulous, sausage shaped; four crenulated oral lips with distinct cnidocyst row; gonads pendulous and long, hanging from peduncular manubrium pouches.

DISTRIBUTION

Pacific Ocean, from the coasts of the North American continent to Hawaii. (Specific distribution map not available.)

HABITAT

Bays and gulfs.

BEHAVIOR

It is a benthic medusa, but it can periodically come to the surface and sink back to the bottom.

FEEDING ECOLOGY AND DIET

Foraging takes place mostly on the bottom of bays, where the medusae feed on crustaceans, mainly copepods.

REPRODUCTIVE BIOLOGY

The medusae are present all year round and are mostly ripe. In spite of this widespread occurrence of the medusae, the polyp stage remains unknown.

CONSERVATION STATUS

Concern has been expressed about the impact of coastal development on this animal. Because of its preference for bays, it is very sensitive to coastal pollution.

SIGNIFICANCE TO HUMANS

It is used in aquarium displays for educational purposes. ◆

By the wind sailor

Velella velella

ORDER

Capitata

FAMILY

Porpitidae

TAXONOMY

Medusa velella Linnaeus, 1758, Mediterranean Sea.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: the colony is a flattened oval to slightly S-shaped float, with a triangular sail and concentric air chambers; up to 1.5 in (40 mm) long and 0.78 in (20 mm) wide, higher in the center than at the edges. Float and sail are supported by chitin covered by mantle tissue; margin of float is soft and flexible. The center of colony underside is a single large gastrozooid encircled by a ring of medusa-producing gastro-gonozooids and a peripheral band of dactylozooids. Central-feeding zooid oval, with an elongated hypostome, without tentacles or medusa buds. Gastro-gonozooids are spindle shaped, with a swollen mouth region, lacking tentacles, but with warts of cnidocyst clusters concentrated in distal half; on proximal half of hydranth, numerous medusa buds growing in groups from short blastostyles. Dactylozooids are mouth less, long, and tapering, oval in cross section, with cnidocysts concentrated in two lateral bands on the narrow sides. The float is deeply blue when alive, medusa buds yellow-olive from symbiotic algae.

Medusa: with four exumbrellar cnidocyst rows, four radial canals; two pairs of opposite, perradial tentacles, a short adaxial one and a long abaxial one, each with a large terminal cnidocyst cluster; two perradial marginal bulbs without tentacles; manubrium conical with quadrate base; mouth tubular; gonads irregularly arranged perradially and interradially.

DISTRIBUTION

Atlantic and Indo-Pacific. (Specific distribution map not available.)

HABITAT

The hydroid floats, with the sail out of the water and the zooids hanging down in the hyponeuston. The medusae are planktonic, in shallow water and possibly in deep water as well, where the young colonies have been recorded, before climbing to the surface.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

The hydroid colony feeds on surface plankton, from crustaceans to appendicularians, and especially on fish eggs.

REPRODUCTIVE BIOLOGY

Floating hydroids can occur in immense offshore swarms, sometimes stranding along shorelines. The colonies liberate rarely observed young medusae that sink toward the bottom. Development of new colonies occurs in deep waters.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The massive strandings can entrap sand and protect the shore from erosion. Feeding on fish eggs makes *Velella* a potential competitor for man in the use of fish resources. ◆

No common name

Aequorea victoria

ORDER
Conica

FAMILY
Aequoreidae

TAXONOMY
Mesonema victoria Murbach and Shearer, 1902, British Columbia, Canada.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hydroid: small colonies, unbranched, with creeping hydrorhiza; pedicels twice as long as hydrotheca. Hydrotheca thin, with an operculum made by many flaps not articulated to hydrothecal rim that converge and close the theca when the hydranth is contracted. Hydranth has 20 tentacles, with an intertentacular membrane at base; gonotheca of thin perisarc, originating right below the theca; a single medusa bud.

Medusae are small at liberation, with two tentacles and four radial canals. They can grow up to 4.7 in (120 mm) wide and 1.5 in (40 mm) high. Umbrella saucer shaped to hemispherical, a thick hemispherical projection of mesoglea protrudes into the manubrium; lips of manubrium are fringed and can close the manubrium completely on the sides of the mesogleal projection. Tentacles can be up to 150, lip lobes are usually half the number of tentacles. Each tentacular bulb has an abaxial pore connecting the circular canal to the outside.

DISTRIBUTION
Northeastern Pacific. (Specific distribution map not available.)

HABITAT
The hydroid grows on mussel shells. The medusae are planktonic, in coastal and open waters.

BEHAVIOR
The function of the hemisphercal mesogleal projection into the manubrium is to allow the closed mouth to rotate around it, thus pushing the contents of the stomach into the radial canals. The pores in the circular canal are used to eject undigested materials and are more anal pores than excretory pores (as they are commonly called).

FEEDING ECOLOGY AND DIET
Unknown for the hydroid, whereas the medusae have been reported to feed on fish larvae and on gelatinous plankton.

REPRODUCTIVE BIOLOGY
The hydroid is tiny and rarely observed, as are the newly released medusae. Medusa production, however, is very intense, since the species can be present in swarms. The swarms produce great quantities of planulae to support future blooms through the hydroid generation.

CONSERVATION STATUS
The massive use of this species to extract the bioluminescent enzyme aequorein might have some influence on population viability.

SIGNIFICANCE TO HUMANS
By feeding on larvae, it might have a negative impact on fish recruitment; but it has a great role in experimental biology because of its bioluminescent enzyme. ◆

No common name

Aglaophenia pluma

ORDER
Conica

FAMILY
Aglaopheniidae

TAXONOMY
Sertularia pluma Linnaeus, 1758, North Sea, United Kingdom.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The colonies resemble a feather, with a straight stem (hydrocaulus) and two series of alternate branches (hydrocladia). Hydrocaulus monosiphonic up to 5.9 in (150 mm), brown, unbranched or dichotomously branched; basal part athecate, followed by one or two prosegments; remainder internodes, each with three nematothecae and a pseudonematotheca; nodes oblique; hydrocladia alternate, with whitish cormidia separated by transverse nodes. Hydrotheca deep, rim with nine cusps of varied length; intrathecal adcauline septum usually well developed, median nematothecae two-thirds adnate, not reaching the margin of the hydrothecae; lateral nematothecae reaching the rim of the hydrothecae; aperture of nematothecae gutter shaped. Male and female corbulae white, with free costa; male close, with slit-like openings between the costae, female with fused costae and smaller slits. Hydranth small, transparent, cylindrical; hypostome held at level of hydrothecal rim, rounded and low; 10 tentacles emerging at hydrothecal rim.

DISTRIBUTION
Usually considered cosmopolitan, but many other species of the same genus have probably been identified as this nominal species. (Specific distribution map not available.)

HABITAT
It grows on algae, in shallow rocky bottoms.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
The shape of the colonies is suited to intercept food particles suspended in the water column. The feeding hydranths are small and in great number; they have been observed to beat their tentacles to create a current towards the mouth. This might be an adaptation for active filter feeding of small food items such as phytoplankton.

REPRODUCTIVE BIOLOGY
Colonies dioecious, almost continuously fertile.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Zappa's jellyfish

Phialella zappai

ORDER

Conica

FAMILY

Phialellidae

TAXONOMY

Phialella zappai Boero, 1987, Bodega Bay, California, United States.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: colony simple, unbranched; hydranth very extensile, with about 14 tentacles, alternately held upward and downward. Oral part of the hydranth is globular, separated from the rest of the body. Hydrotheca cylindrical, elongated, with an operculum of about seven cusps separated from the hydrothecal wall by a thin line, not always evident. Diaphragm present. Pedicel is as long as the hydrotheca or a little shorter, annulated throughout. Gonothecae on the stolon, arising from short, annulated pedicels, with wavy or smooth walls, tapering below and truncate above, with one or two medusa buds.

Medusa: newly released medusae sub-spherical, about 0.002 in (0.6 mm) in diameter, with four tentacles, four interradial tentacular bulbs deprived of tentacles, and four radial canals with medial darker areas. Eight statocysts, with 1–3 statoliths, are on the inner edge of the ring canal, supported by a cushion of cells. Manubrium is short (one third of the bell cavity), with four short lips. Tentacular nematocysts are in clusters, giving a moniliform appearance to the tentacles. Perradial tentacular bulbs are almost round or triangular, interradial tentacular bulbs much smaller, but evident. The medusae grow rapidly, reaching 0.11 in (3 mm) in diameter in 10 days, dome shaped with four well-developed inter-radial tentacles, and eight developing adradial tentacles. At this age, the eggs are clearly visible. Manubrium cruciform, lips more evident and starting to bend upward. Tentacular bulbs still round, tending to elongate. Tentacles moniliform. Development continues with an increase in size and number of tentacles (36 the highest number observed). Adult specimens dome shaped, with gonads almost in the middle of the radial canals. Manubrium cruciform, with folded lips bending upward, with four gastric pouches; four black spots may be present at its base. Tentacular bulbs triangular, but still rounded. Tentacles evidently moniliform.

DISTRIBUTION

Endemic to the west coast of the United States (California). (Specific distribution map not available.)

HABITAT

The hydroid grows on mussel shells. The medusa is in coastal plankton.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Under laboratory conditions, both polyps and medusae feed on *Artemia nauplii*; in the wild they probably feed on small crustaceans.

REPRODUCTIVE BIOLOGY

Each gonotheca produces one or two medusae that, under laboratory conditions, continue to develop also after reaching sexual maturity. Some specimens become mature 10 days after liberation. They can develop a new gonad after the first spawning.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

This species was named after the modern music composer Frank Zappa (1940–1993), who, in exchange, wrote a song about it ("Lonesome Cowboy Nando"). ◆

Portuguese man of war

Physalia physalis

ORDER

Cystonectae

FAMILY

Physaliidae

TAXONOMY

Holothuria physalis Linné, 1758, Atlantic Ocean.

OTHER COMMON NAMES

English: Blue bottle; French: Galère, frégate, vaisseau de guerre hollandais, vaisseau de guerre portugais.

PHYSICAL CHARACTERISTICS

The only pleustonic siphonophore. Colonies consist of a large, purplish blue horizontal pneumatophore that floats on the sea surface, reaching 11.8 in (30 cm) in length in the largest specimens; pneumatophore carries the polyps, which form cormidia at the oral end; at its top, an erectile, longitudinal crest or sail that may be left- or right-handed, all drifting at the mercy of the winds. Pneumatophore asymmetrical; two forms, each the mirror image of the other. Each cormidium consisting of a gastrozooid associated with a tentacle and a gonodendron; however, unlike other siphonophores, tentacle separating from the basigaster during the later stages of development. The tentacles may attain several meters in length; a continuous formation of new cormidia. As the cormidia mature, new gastrozooids gradually lose their tentacles and becoming palpons. Small medusoid gonophores develop at the bases of the terminal palpons. Functional gonophores of a given colony are of a single sex only.

DISTRIBUTION

Widely distributed in tropical and subtropical regions in the three great oceans and in the Mediterranean. (Specific distribution map not available.)

HABITAT

Only pleustonic siphonophore can occur in great numbers (navies); frequently blown ashore by strong winds.

BEHAVIOR

The effect of the wind on the sail is to move the left-handed specimens to the right of the wind direction and vice versa for the right-handed ones.
feeding ecology and diet
Feed on small planktonic organisms or small fishes.

REPRODUCTIVE BIOLOGY

Dioecious, release their sexual cells in the sea, development through siphonula larvae.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The tentacles can stretch out to many feet (meters) below the float and can inflict powerful and very painful stings on swimmers who become entangled in their tentacles. ◆

Immortal jellyfish

Turritopsis nutricula

ORDER

Filifera

FAMILY

Clavidae

TAXONOMY

Turritopsis nutricula McCrady, 1859, South Carolina, United States.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: small colonies stolonal, monosiphonic (simple stem), larger ones erect, irregularly branched and increasing in diameter from base to apex, polysiphonic (compound stem); branches basally adnate to hydrocaulus or other branches, then curving away at an acute angle and becoming free; hydrocaulus and hydrocladia covered by a firm bi-layered perisarc, mostly encrusted with detritus and algae, terminating below hydranth base; hydranths terminal, naked, elongated, fusiform, with 12–38 filiform tentacles scattered over distal three quarters of column, proximal ones shorter than distal; hypostome elongated conical; medusa buds arising mostly one by one from short pedicels below hydranths, pear shaped, enclosed in perisarc.

Medusa: umbrella 0.15–0.43 in (4–11 mm) high, bell shaped to piriform, higher than wide, mesoglea thicker at apex; manubrium large, cross-shaped in transverse section, red; four radial canals passing through the four compact vacuolated endodermal masses situated above digestive part of manubrium; four-lipped mouth with a continuous row of sessile cnidocyst clusters along margin; 80–120 closely spaced marginal tentacles; gonads interradial, mature females often with developing embryos and planulae; with adaxial ocelli.

DISTRIBUTION

Atlantic, Indo-Pacific, and the Mediterranean. (Specific distribution map not available.)

HABITAT

The hydroids live in shallow, highly oxygenated water, often under overhangs. The medusae are members of the coastal plankton.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

In the laboratory, both hydroid and medusae can survive with a diet of *Artemia nauplii*; the diet in the wild is unknown.

REPRODUCTIVE BIOLOGY

Medusae are produced by the hydroid in summer months and can survive in the laboratory for one month. A peculiarity of this species is the possibility of ontogeny reversal under laboratory conditions: the medusae, in fact, can rearrange their tissues and go back to the polyp stage if subjected to sub-lethal stress and also at the end of their lifespan, after spawning. For this reason, this medusa has been called “the immortal jellyfish” by the media.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The possibility for this species to perform ontogeny reversal in the laboratory offers a unique opportunity to study the genetic control of aging and the mechanisms of rejuvenation. ◆

No common name

Eudendrium glomeratum

ORDER

Filifera

FAMILY

Eudendriidae

TAXONOMY

Eudendrium glomeratum Picard, 1951, Banjuls-sur-Mer, Mediterranean Sea.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Colonies up to 11.8 in (30 cm) high, composed of compound and branched hydrocauli; older perisarc brown and thick; thin and yellowish to transparent in younger regions. Polyp is urn shaped, hypostome peduncled, tentacles filiform, 24–28 in one whorl. Gonophores are fixed. Female mature gonophore with unbranched spadix; male gonophore provided with one or two chambers; mature balstostyle with either a normal number of tentacles or a reduced number of partly atrophied tentacles. Diagnostic feature is holotrichous macrobasic euryteles (24 × 10–28 × 11µm), concentrated in several groups characteristically conspicuous at the basal half of the polyp, with long butt (four times length of capsule), spirally coiled around the main axis of the cnidocyst.

DISTRIBUTION

Atlantic, Indo-Pacific; mostly in temperate waters. (Specific distribution map not available.)

HABITAT

Rocky cliffs, from the surface to 328 ft (100 m) and below. It can be very abundant under favorable conditions, forming a facies.

BEHAVIOR

The hydranths use the peduncled hypostome as a sphincter dividing the coelenteron from the outside. They stretch their tentacles in the water to catch their prey.

FEEDING ECOLOGY AND DIET

Some species of the genus *Eudendrium* have been reported to feed on the plankton surrounding their colonies. They can also ingest the mucus that they produce and possibly digest organic particles and organisms trapped into it, acting as mucous filter feeders.

REPRODUCTIVE BIOLOGY

Fertilization occurs while eggs are still on the gonophores; the planulae can remain attached to the mother colony by mucous threads to be able to settle in its vicinities. Planulae can aggregate and form chimerical hydroid colonies.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

No common name

Hydractinia echinata

ORDER

Filifera

FAMILY

Hydractiniidae

TAXONOMY

Alcyonium echinatum Fleming, 1828, (Scotland, United Kingdom).

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydrorhiza about 0.11 in (3 mm) thick, with numerous blunt conical chitinous spines with jagged edges, encrusting on gastropod shells but also other solid substrata; white to pale pink, giving rise to different kinds of polyps: gastrozooids slender, widening upwards, about eight tentacles in one whorl, hypostome conical; gonozooids shorter than gastrozooids, with few tentacles and a ring of gonophores; dactylozooids long, slender.

Medusae reduced to fixed gonophores, sexes generally on different gonozooids; male gonophore yellow to white, ovoid; female gonophore pink and spherical.

DISTRIBUTION

Atlantic, Arctic, and the Mediterranean. (Specific distribution map not available.)

HABITAT

Hydroids grow on gastropod shells inhabited by hermit crabs, on soft bottoms.

BEHAVIOR

Under laboratory conditions, the colonies can be aggressive with the formation of hyperplasic stolons that sting other organisms while competing for the substrate.

FEEDING ECOLOGY AND DIET

Gastrozooids feed on benthic organisms (nematodes, crustaceans, etc.) while being transported by the hermit crab. They also can feed on the larvae of the crab.

REPRODUCTIVE BIOLOGY

Eggs and sperms are released in the water, where fertilization occurs and planulae are formed. Gamete production is almost continuous, but at a slower pace in winter time.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

This species, and in general many Hydractiniids, is easy to rear under laboratory conditions and is widely used for experimental biology as a laboratory animal. ◆

No common name

Hydrichthys mirus

ORDER

Filifera

FAMILY

Pandeidae

TAXONOMY

Hydrichthys mirus Fewkes, 1887, New England.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: hydrorhiza as a thin encrusting plate on the skin of fish host. Polyps of two types: gastrozooids are elongate, tubular, with distal mouth, and no tentacles; nearly all with a small bud at base; mouth with an armature of some microbasic euryteles and desmonemes; no nematocysts in other regions of colony, apart from medusa buds; gonozooids very contractile, with up to three lateral branches bearing clusters of medusa buds at different stages of development; no sign of perisarc. Medusa buds on gonozooids, hydrorhiza, and possibly also on hydranths; exumbrellar nematocysts present; well-developed buds stiff, with two big tentacular bulbs and no apparent sign of tentacles.

Medusa: umbrella height 0.15 in (4 mm), dome shaped, with apical projection; jelly soft. Manubrium with well-developed folds in stomach wall, bearing the gametes; manubrial folds nearest to mouth much developed, almost covering lips. Above these main folds, two or three additional folds sometimes developed. Gametes almost completely covering interradial portions of stomach.

DISTRIBUTION

Indo-Pacific; very rare. (Specific distribution map not available.)

HABITAT

The hydroid lives symbiotically with fish; the medusa is planktonic, possibly with a tendency to forage near the bottom.

BEHAVIOR

The gastrozooids can bend to touch the surface of the fish. They have a distal annular contractile ring resembling a sucker, but feeding on fish was not observed. Under laboratory conditions, the hydroid do not take *Artemia nauplii*. After the death of the fish, colonies can detach and become free living. It is therefore possible that they can survive in the plankton if the host dies. In the laboratory, the medusae tend to stay on the bottom of rearing jars, with their long tentacles completely extended, attached to the bottom of the finger bowl, stretching them for a long distance while swimming parallel with the bottom. Tentacles are then contracted and the bell is drawn quickly backwards. Prey is captured in lips during this fast backward movement. Medusae possibly have a benthic feeding habit. After feeding, they swim vigorously for some hours.

FEEDING ECOLOGY AND DIET
The hydroid most probably feeds on the supporting fish, using the mouth as a sucker. The medusa feeds on crustaceans.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Distichopora violacea

ORDER
Filifera

FAMILY
Stylasteridae

TAXONOMY
Millepora violacea Pallas, 1766, Pacific Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hydroid: colony violet-blue, small, and flabellate; branches compressed and granular, with low longitudinal ridges, ending with two flattened lobes, usually whitish, growing in opposite directions; gastro- and dactylopores very long, extending for a great distance down the center of the lobes; pore rows on lateral edges of lobes and main stem; dactylopores in equal number on both sides of pore rows; gastrostyles ridges bearing tall, slender, often fused, spines; no ring palisade; ampullae in groups, opening to surface by irregularly shaped pores.

DISTRIBUTION
Indo-Pacific. (Specific distribution map not available.)

HABITAT
Coral formations in shallow water.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Like almost all stylasterids, it is protected by international treaties.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Laingia jaumotti

ORDER
Laingiomedusae

FAMILY
Laingiidae

TAXONOMY
Laingia jaumotti Bouillon, 1978, Laing Island, Bismarck Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hydroid: unknown.

Medusa: umbrella lobed, divided by peronial grooves or similar structures, with no exumbrellar cnidocyst tracks; four radial canals; no typical circular canal, but a solid core of endodermal cells around umbrellar margin; tentacles solid, bent shortly after their point of origin, inserted on the exumbrellar surface above bell margin; marginal bulbs largely displaced towards exumbrella, forming peronial-like structures; manubrium simple, quadrangular, tubular, or conical; mouth opening quadrangular to circular; gonads on manubrium in four interradial pouches; no sense organs.

DISTRIBUTION
Bismarck Sea, Papua New Guinea. (Specific distribution map not available.)

HABITAT
Superficial layers of the sea.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Craspedacusta sowerbyi

ORDER
Limnomedusa

FAMILY
Olindiidae

TAXONOMY
Craspedacusta sowerbyi Lankester, 1880, found on a water-lily in a tank at Regent's Park, London.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS

Hydroid: freshwater, solitary or forming small colonies of 2–4, rarely 7 polyps; hydranths without tentacles, cylindrical, with apical mouth (hypostome) surrounded by cnidocysts forming a spherical capitulum under which the polyp is slightly tapering, forming a distinct neck; basal portion of hydranths with periderm covering, attaching colony to substrate; medusa buds lateral, on the middle or lower part of body column, often becoming terminal by hydranth reduction; asexual reproduction by frustules, transversal division and resting stages (cysts).

Medusa: umbrella 0.39–0.78 in (10–20 mm) wide, slightly flatter than a hemisphere; mesoglea fairly thick; with well-developed, marginal cnidocyst ring; velum broad and well developed; manubrium large, upper portion conical with broad square base, tapering downwards to cross shaped distal region; mouth with four simple or slightly folded lips, extending beyond umbrella margin; four straight radial canals and circular canal broad and massive; four large, smooth, triangular pouch-like gonads, with rounded comers, hanging down into subumbrellar cavity from points of junction of radial canals with manubrium; with 200–400 or more hollow marginal tentacles, in several series situated at different levels on umbrella margin; oldest four perradial marginal tentacles being largest and highest; bases of marginal tentacles adherent to exumbrella; surface of marginal tentacles covered with evenly distributed papillae, each with 3–10 cnidocysts; 100–200 or more statocysts, usually about half number of marginal tentacles; statocysts situated in velum, forming centripetal tubes with basal enlargements near umbrella margin.

Numerous species of *Craspedacusta* have been described, mainly from China; it is not excluded that they represent anything more than variations of a single species.

DISTRIBUTION

Cosmopolitan in freshwaters and sometimes in brackish waters of temperate and tropical areas. (Specific distribution map not available.)

HABITAT

Freshwater surfaces and calm rivers, often found in tanks and aquaria.

BEHAVIOR

Hydroids live on water plants; the medusae are active swimmers, living usually near surface.

FEEDING ECOLOGY AND DIET

Feed on small freshwater planktonic organisms, mainly protozoa, rotifers, crustaceans, worms, and fish larvae.

REPRODUCTIVE BIOLOGY

Dioecious, sex cells released in freshwater; the planula gives rise to polyp colonies.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The medusae may damage and injure fishes in fish farms. ◆

No common name

Olindias phosphorica

ORDER

Limnomedusa

FAMILY

Olindiidae

TAXONOMY

Oceania phosphorica Delle Chiaje, 1841, Mediterranean Sea.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Hydroid: the polyps have not been yet found in field. Weill (1936) described from laboratory observations a small solitary hydranth without tentacles enclosed in a cylindrical or irregularly curved hydrothecae covering more than half its length, and much longer than the polyp itself; mouth distal surrounded by large cnidocysts.

Medusa: umbrella 0.78–1.5 in (40–60 mm) wide, almost hemispherical, mesoglea fairly thick; 11–19 centripetal canals per quadrant; 30–60 primary tentacles; usually two ecto-endodermal statocysts at base of each primary tentacle; 100–120 secondary tentacles; 100–170 marginal clubs.

DISTRIBUTION

Atlantic and the Mediterranean. (Specific distribution map not available.)

HABITAT

Lives near the bottom or at the surface near shores.

BEHAVIOR

Lives usually fixed to algae or *Posidonia*.

FEEDING ECOLOGY AND DIET

Feeds on small planktonic organisms.

REPRODUCTIVE BIOLOGY

Dioecious, the sex cells are released in the sea; the planula gives rise to a reduced polyp stage.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The sting of the medusae may cause skin irritations. ◆

No common name

Hydra vulgaris

ORDER

Moerisiida

FAMILY

Hydridae

TAXONOMY

Hydra vulgaris Pallas, 1766, European freshwaters.

OTHER COMMON NAMES

French: Hydre d'eau douce.

PHYSICAL CHARACTERISTICS
Solitary freshwater hydroids; 0.47 in (12 mm) in height; with 7–12 hollow filiform tentacles, but often moniliform distally, in one whorl under hypostome; hermaphrodic species, eggs and sperm developed directly in ectoderm of polyps in wart-like protuberances, "testis" developing on upper part of hydranth, "ovaries" on lower part, with up to eight eggs enveloped; in a chitinous embryotheca when fecundated, embryotheca with long, thin spines; asexual reproduction by lateral buds, leading only to temporary colonies; lower part of hydranth with simple pedal disc and with central pore, no perisarc except on encysted embryos.

DISTRIBUTION
Cosmopolitan. (Specific distribution map not available.)

HABITAT
Freshwater surfaces, rivers, and ponds.

BEHAVIOR
Fixed on freshwater plants, stones, empty freshwater shells, and worm larval tubes (*Trichoptera*); able to move with the help of the tentacles.

FEEDING ECOLOGY AND DIET
Feed on small freshwater planktonic organisms: primarily protozoa, rotifers, crustaceans, and worms.

REPRODUCTIVE BIOLOGY
Protanderic hermaphoditic; female sex cells fertilized when fixed on mother and enveloped in a chitinous spiny embryotheca.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Hydra is one of the most popular laboratory animals and has greatly contributed to the development of experimental biology. ◆

No common name
Solmundella bitentaculata

ORDER
Narcomedusa

FAMILY
Aeginidae

TAXONOMY
Charybdea bitentaculata Quoy and Gaimard, 1833.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Umbrella up to 0.4 in (12 mm) wide, usually much smaller, rounded apex, keel-shaped along the axis leading to tentacles, apical mesoglea very thick, lateral walls thin; velum well developed; manubrium short, lenticular, with eight rectangular manubrial pouches with rounded edges; mouth circular, simple; two long, tapering, opposite tentacles issuing from umbrella above manubrium, near apex; gonads in subumbrellar wall, under manubrial pouches; four peronia in deep grooves; no peripheral system or otoporpae; 8–32 statocysts. Monotypic genus.

DISTRIBUTION
Widely distributed in all oceans and in the Mediterranean. (Specific distribution map not available.)

HABITAT
From surface to bathypelagic zone.

BEHAVIOR
Often parasitized by larvae of another Narcomedusae, *Cunina peregrine*.

FEEDING ECOLOGY AND DIET
Small planktonic animals.

REPRODUCTIVE BIOLOGY
Dioecious, sex cells released in sea water, direct development.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Obelia dichotoma

ORDER
Proboscoida

FAMILY
Campanulariidae

TAXONOMY
Sertularia dichotoma Linnaeus, 1759, coast of southwest England.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Hydroid: colonies extremely varied in size and shape. Stems erect, up to 13.7 in (35 cm) high, monosiphonic and branched, flexuous to straight, thickened in old colonies. Internodes have several annuli at their base. Hydrothecae alternate, lateral, borne on completely annulated pedicels at the upper part of the internodes. Hydrotheca bell shaped, usually not very deep, thin walled; rim to crenate, slightly flared; diaphragm transverse to oblique. Gonothecae usually inverted, conical on annulated pedicels, truncated at the distal end, with a short distal neck when mature, where the aperture is.

Medusa: umbrella 0.09–0.23 in (2.5–6 mm) wide, circular, flat; mesoglea very thin; without gastric peduncle; mouth with four simple lips; four radial canals; gonads sac like, hanging from middle to end of the radial canals; numerous short, stiff, solid, not extensile marginal tentacles; tentacles with short endodermal roots extending into bell mesoglea; eight statocysts situated on underside of basal bulbs of some marginal tentacles. The velum is absent.

DISTRIBUTION
Almost cosmopolitan, even though the identity of the many nominal species of *Obelia* is still matter of debate, as is their distribution. (Specific distribution map not available.)

HABITAT
The hydroid is very common on rocks and algae on shallow hard bottoms; the medusa is very common in coastal waters.

BEHAVIOR
Both polyps and medusae can move their tentacles in a rhythmic way to create currents that bring food particles toward the mouth.

FEEDING ECOLOGY AND DIET
Both hydroids and medusae feed on plankton, usually crustaceans, but also possibly phytoplankton.

REPRODUCTIVE BIOLOGY
Both medusae and polyps are quite constant in presence in their respective environments and reproduction occurs continuously.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Obelia is traditionally depicted in all zoology textbooks as a paradigmatic hydrozoan, so that many generations of students have learned its name. Unfortunately, the medusae of *Obelia*, being deprived of velum, are far from being the archetype of the medusae of the Hydrozoa. Furthermore, the figures of *Obelia* medusae present in many textbooks depict a campanulate medusa, and not a flat one, as is the medusa of this genus. ◆

No common name

Apolemia uvaria

ORDER
Physonectae

FAMILY
Apolemiidae

TAXONOMY
Stephanomia uviformis Lesueur, 1811, Nice (France).

OTHER COMMON NAMES
French: Stéphanomie pamproide, stèphanomie à, grains de raisins.

PHYSICAL CHARACTERISTICS
Pneumatophore bulb shaped, widening near the apex. Extended colonies are up to 32.8–98.4 ft (10–30 m). Nectosome with up to 12 nectophores in two parallel rows on the stem; largest is 0.14 in (3.7 mm) high by 0.13 in (3.4 mm) wide by 0.16 in (4.2 mm) deep. Nectophore consisting of two wings looking like those of a butterfly, with a deep ventral furrow. Nectosac large. Lateral radial canals form S-shaped bends with short branches on the upper bend. Groups of five or six nectosomal tentacles issuing from the base of the nectophores near the pedicular canal, at the base of the muscular lamellae. Siphosome measuring up to several feet (meters) in length, composed of several cormidia. Each cormidium consists of a gastrozooid and about 50 palpons, both with thin filiform tentacles of a single type issuing from their bases. Palpons are very long and delicate. Opaque spots bearing cnidocysts on the outer surface cover bracts, like the nectophores. Only physonect siphonophore whose nectophores are separated from each other by a cluster of 5–6 nectosomal tentacles.

DISTRIBUTION
The Mediterranean and Atlantic Ocean. (Specific distribution map not available.)

HABITAT
Occurs in the top 328 ft (100 m) of water.

BEHAVIOR
Epiplanktonic.

FEEDING ECOLOGY AND DIET
Feeds on other planktonic organisms such as crustaceans, polychaetes, mollusks, tunicates, and even small fishes.

REPRODUCTIVE BIOLOGY
Dioecious, release their sexual cells in the sea, development through siphonula larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Polypodium hydriforme

ORDER
Polypodiozoa

FAMILY
Polypodiidae

TAXONOMY
Polypodium hydriforme Ussov, 1885, Black Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Polypodium lifecycle as a succession of a free-living stage and of a stage parasitizing the eggs of some Acipenseridae and Polyodontidae fishes. The earliest known stage is a binucleate cell, parasitizing previtellogenetic fish oocytes. Further development may last several years, leading to a convoluted didermic stolonal structure, with inverted germ layers, forming numerous inverted buds. Before fish spawning, eversion takes place and the germ layers take their normal position (ectoderm outside, endoderm inside). The stolon exits the egg and becomes fragmented into individual buds, each giving rise to a free-creeping globular stage that multiplies by longitudinal fission. Globular stages can move and feed, having an oral mouth-cone and either 24, 12, or six tentacles, according to season. Germ cells are endodermal. So-called females have two kinds of gonads, each with a gonoduct opening in the gastral cavity; so-called males deprived of gonoducts, their gonads forming gametophores carrying cnidocysts. It is not known how the parasites get into young previtellogenic fish oocytes. The free-living stages are presumably homologous to sexual medusae, the parasitic stages being considered as polypoid. By their stolonal parasitic budding stage and their cnidome, the Polypodiozoa seem to present some affinities with the Narcomedusae, to which they were previously associated. *P. hydriforme* was, until recently, the only known metazoan adapted to an intracellular parasitic life.

DISTRIBUTION
Freshwater basins of Russia, Romania, Iran, and North America. (Specific distribution map not available.)

HABITAT
Fish gonads.

BEHAVIOR
Parasitic.

FEEDING ECOLOGY AND DIET
Parasitic.

REPRODUCTIVE BIOLOGY
Early developmental stages intracellular parasites of the eggs of Acipenseridae and Polyodontidae fishes; free-living stages a small medusae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Polypodium parasitize and destroy the eggs of the fishes producing caviar and, consequently, has a great economical impact. ◆

No common name

Liriope tetraphylla

ORDER
Trachymedusa

FAMILY
Geryoniidae

TAXONOMY
Geryonia teraphylla Chamisso and Eysenhardt, 1821, Indian Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Umbrella 0.39–1.1 in (10–30 mm) wide, hemispherical, apex somewhat flattened; mesoglea thick, rigid; velum broad; manubrium small, on long, cylindrical gastric peduncle, longer than umbrellar diameter; mouth with four simple lips lined with cnidocysts; with normally four radial canals (sometimes more); 1–7 centripetal canals in each quadrant; with marginal cnidocyst ring; typically four long hollow perradial tentacles with cnidocyst rings and four small solid interradial tentacles with adaxial cnidocyst clusters; with gonads variable in shape and size, generally heart shaped, on either side of the middle of radial canals; eight statocysts. Extremely variable species.

DISTRIBUTION
Worldwide distribution, common in temperate regions of all oceans and the Mediterranean. (Specific distribution map not available.)

HABITAT
Chiefly near surface, sometimes in great shoals.

BEHAVIOR
Bold and rapid medusa.

FEEDING ECOLOGY AND DIET
Very rapacious, feeds on other small planktonic animals and fishes sometimes three times its size.

REPRODUCTIVE BIOLOGY
Dioecious, sex cells released in sea water, direct development.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Aglantha digitale

ORDER
Trachymedusa

FAMILY
Rhopalonematidae

TAXONOMY
Medusa digitale O. F. Müller, 1776, North Atlantic.

OTHER COMMON NAMES
French: Méduse doigtier.

PHYSICAL CHARACTERISTICS
Umbrella cylindrical, 0.39–1.5 in (10–40 mm) high, about twice high than wide, with a small conical projection; lateral mesogleal walls thin, subumbrellar muscles strong; peduncle slender, long, conical, almost as long as subumbrellar cavity; manubrium small; mouth with four simple lips; eight long, sausage-shaped gonads, arising from the radial canals near the apex of the subumbrella and hanging freely in subumbrellar cavity; 80 or more solid marginal tentacles with a core of single endodermal chordal cells; eight free statocysts.

DISTRIBUTION
Worldwide distribution in all oceans and entering the Mediterranean. (Specific distribution map not available.)

HABITAT
From surface down to considerable depths, 1,970 ft (600 m).

BEHAVIOR
Prolate medusae using the entire bell for jet propulsion; extremely active medusae.

FEEDING ECOLOGY AND DIET
Other small planktonic animals.

REPRODUCTIVE BIOLOGY
Dioecious, sex cells released in sea water, direct development.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

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Ferdinando Boero
Jean Bouillon

Cubozoa

(Box jellies)

Phylum Cnidaria
Class Cubozoa
Number of families 2

Thumbnail description
Gelatinous animals that possess image-forming eyes and complex behavior, including internal fertilization in at least one species; often known as "killer box jellies," although only one of the seven genera (*Chironex,* in the family Chirodropidae) is potentially lethal to humans

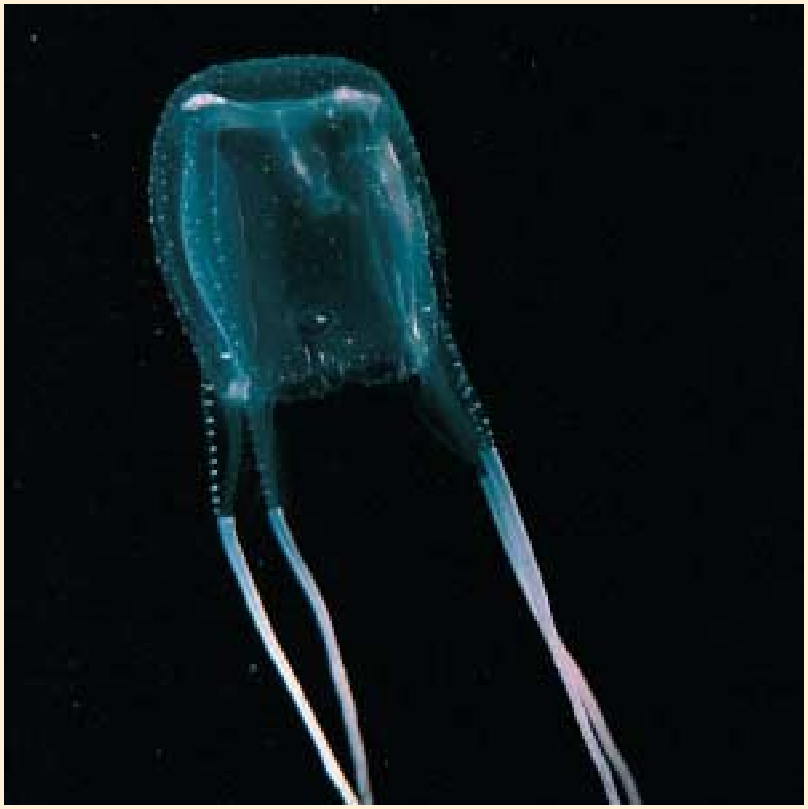


Photo: The southern sea wasp (*Carybdea rastoni*) can give painful stings with its tentacles. (Photo by Animals Animals ©Gowlett-Holmes, OSF. Reproduced by permission.)

Evolution and systematics

At one time cubozoans were placed within the class Scyphozoa (true jellyfishes), but recent research supports the Cubozoa at the class level. There is one order, Cubomedusae, with two families, Chirodropidae and Carybdeidae, and 19 described species. There is only one recognized fossil species, *Anthracomedusa turnbulli*, which was found near Chicago, Illinois, United States. This fossil dates from the Pennsylvanian age (323–290 million years ago), and with its square shape and clusters of tentacles, was likely within the family Chirodropidae.

Physical characteristics

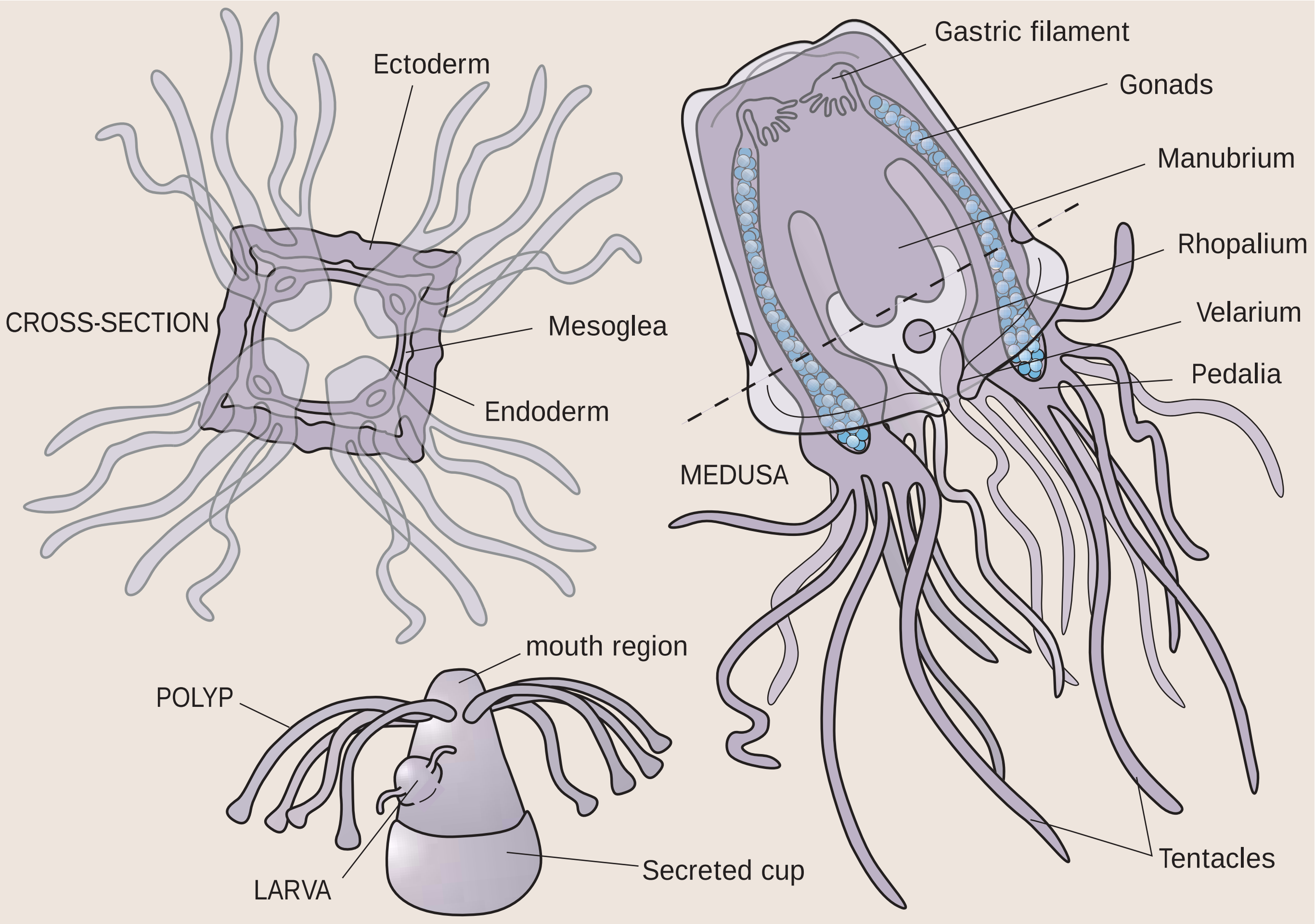
The most obvious characteristic of cubozoans is the box-like shape of their bell. The manubrium and mouth are located inside the bell, and the velarium is along the edge of the bell. Pedalia are muscular extensions of the bell and the tentacles are attached to the pedalium. Chirodropids have multiple tentacles attached to each pedalium; carybdeids have only have one tentacle per pedalium. Between the pedalia are the unique sensory structures known as rhopalia. Each rhopalia has a statocyst and six eyes, four simple eyes, and two relatively complex eyes composed of an epidermal cornea, spheroidal cellular lens, and an upright retina. Antisera testing has revealed that cubozoans possess blue-, green-, and ultraviolet-sensing opsins in the both the small and large complex eyes. The cubomedusan nervous system is complex compared to that of other cnidarians. A diffuse synaptic nerve net throughout the bell region is connected to a subumbrellar nerve ring, and nerve processes extend from this ring into the rhopaliar stalks. The processing of visual images probably occurs on this nerve ring.

Distribution

Cubozoans can be found in most tropical and subtropical waters *Carybdea marsupialis* and *Carybdea rastoni* have been found in temperate waters as well. It is likely that the distribution records are incomplete as the transparent nature of these medusae make them very difficult to locate despite their shallow and coastal distribution.

Habitat

The preferred habitat of cubozoans appears to be over sandy substrate, with box jellies located just above the bottom during the day and moving up toward the surface at night. Field observation is extremely difficult, as the jellies react to the presence of divers by rapidly moving away. *Carybdea*



Box jelly anatomy. (Illustration by Christina St. Clair)

sivickisi possesses adhesive pads on the exumbrellar surface which enables it to attach to various substrates in the field.

Behavior

Cubozoans have the most complex behavior of any cnidarian. They are active swimmers capable of moving 9.8–19.7 ft (3–6 m) per minute. They are positively phototactic (move toward light) and are active during the day and night, although they may feed only during the night or predawn hours. Vision clearly plays a role in both feeding and reproduction. One characteristic that makes them interesting, their image forming eyes, also makes them difficult to study in the field or the laboratory because they react to the presence of their human observers by swimming away.

Feeding ecology and diet

Cubozoans are important predators in the nearshore ecosystem, feeding mainly on fishes and crustaceans. Additional prey items include polychaetes, crab megalopae (postlarvae), isopods, amphipods, stomatopod ("mantis shrimps") larvae, and chaetognaths (arrow worms). As active predators, cubozoans chase, catch, and eat fishes and other organisms. Feeding behavior varies slightly between species. The prey are caught on the tentacles and brought up towards the pedalia by the tentacle contracting. The medusa then either remains upright in the water or turns upside down. The pedalium with the prey item than bends inward toward the manubrium, and the prey are then engulfed.

Reproductive biology

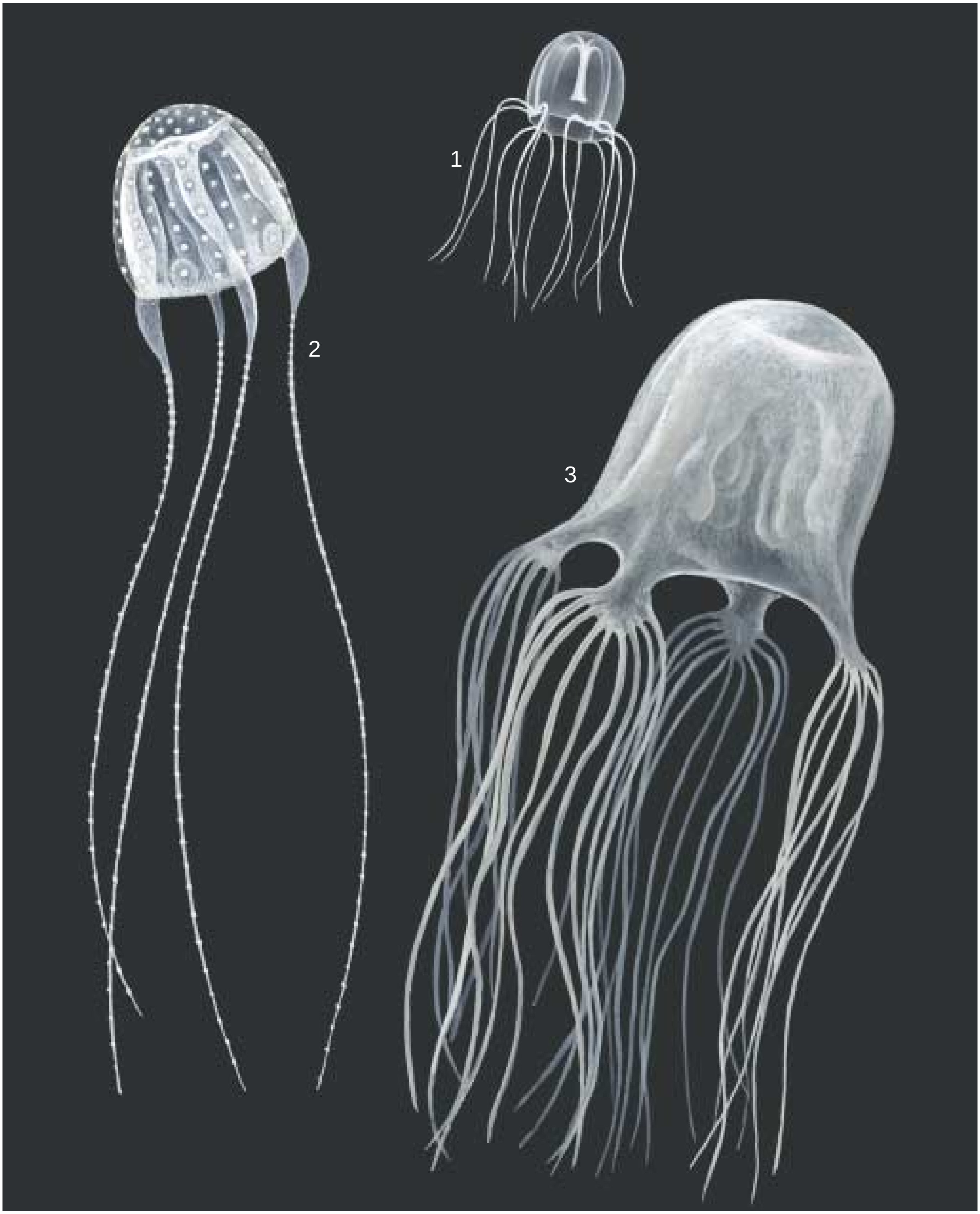
Little is known about the reproductive biology of cubozoans. The life history includes a benthic stage, the polyp, which can reproduce asexually by budding, and a pelagic stage, the medusa. Eggs and sperm combine to form a ciliated larva (planula), which settles on the bottom and becomes a polyp. Unlike scyphozoans, cubozoan polyps do not undergo strobilation (asexual reproduction by division into body segments); rather, the entire polyp becomes the juvenile medusa. *C. sivickisi* uses spermatophores that can be stored by the female, and it has been hypothesized that female *C. rastoni* may collect sperm strands produced by the males. Other cubozoans may have internal fertilization as well, but most broadcast their gametes.

Conservation status

No species of cubozoans is listed by the IUCN.

Significance to humans

The presence of "stinger-resistant enclosures" on beaches in northern Queensland, Australia, is indicative of the impact that cubozoans can have on humans. Although deaths are reported almost every year from encounters with *C. fleckeri*, the overall impact of cubozoans is much greater as stings are not always reported. *Carukia barnesi* is now recognized as the cause of "Irukandji syndrome," which results in severe backache, muscle pains, chest and abdominal pains, headache, localized sweating, and piloerection, as well as nausea and reduced urine output. There is a box jelly antivenom that binds to both *C. fleckeri* and *C. barnesi*, and vinegar can inhibit unfired nematocysts from firing (although it stimulates nematocyst firing with other cnidarians).



1. Irukandji (*Carukia barnesi*); 2. *Tripedalia cystophora*; 3. Sea wasp (*Chironex fleckeri*). (Illustration by John Megahan)

Species accounts

Irukandji

Carukia barnesi

FAMILY

Carybdeidae

TAXONOMY

Carukia barnesi Southcutt, 1967, Cairns, Australia.

OTHER COMMON NAMES

English: Box jelly.

PHYSICAL CHARACTERISTICS

The bell is transparent, reaching to 0.8 in (20 mm) in diameter and 1 in (25 mm) in depth; each of the four tentacles may extend to 25.6 in (650 mm).

DISTRIBUTION

Tropical Australian waters from central Queensland (Agnes Water) to Broome, Western Australia.

HABITAT

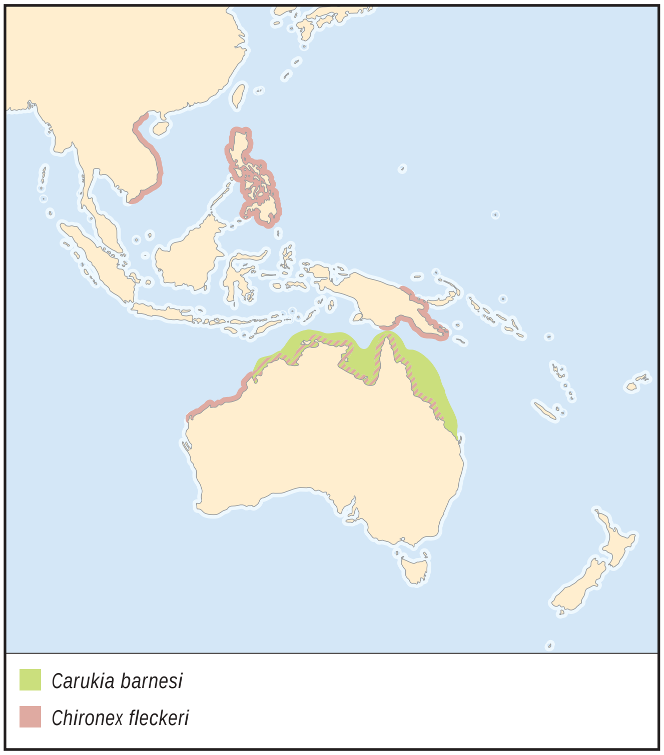
Occurs in deeper waters of the reef, although often swept inshore by currents.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Nothing is known.



REPRODUCTIVE BIOLOGY

Nothing is known about the life cycle. The only time juveniles were collected was in 1997, when four small jellies were collected 3.1 mi (5 km) north of Mackay Harbor in Queensland. This led researchers to postulate that the early part of the life cycle may be in creeks or rivers as in *C. fleckeri.*

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

Stingings were named the Irukandji syndrome (after a local aboriginal tribe) as early as 1943, but the species was not collected and identified until 1964 to 1966. The venom is extremely potent, and may be responsible for some fatalities. Research in 2002 focused on the use of magnesium infusions to counter the toxic sting. ◆

Sea wasp

Chironex fleckeri

FAMILY

Chirodropidae

TAXONOMY

Chironex fleckeri Southcutt, 1956, Australia.

OTHER COMMON NAMES

English: Box jelly.

PHYSICAL CHARACTERISTICS

Reaches up to 11.8 in (30 cm) in diameter, but is difficult to see despite its large size. The as many as 15 tentacles in each corner can reach up to 98.4 ft (30 m) distance from the bell.

DISTRIBUTION

Tropical waters around Australia, from Exmouth, Western Australia, to Bustard Heads, Queensland, as well as around the Indo-west Pacific Ocean near Papua New Guinea, the Philippines, and Vietnam. Full extent of the distribution has not yet been determined.

HABITAT

Usually shallow waters around creek or mangrove outlets; often reported swimming around pier pilings in search of food.

BEHAVIOR

Swims around pier pilings.

FEEDING ECOLOGY AND DIET

Primary diet items are fishes and prawns.

REPRODUCTIVE BIOLOGY

The search for the polyp of *Chironex fleckeri* took years before polyps were found attached under some rocks in a northern Australian estuary. Polyps have been found in mangrove swamps and river outlets, but not much is known about how the planulae find their way to these locations. Polyps start to metamorphose into medusae in the Australian spring (September) and continue until the first large summer rains (January), when they are flushed out into the ocean.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
The venom is neurotoxic, cardiotoxic, and dermonecrotic (causes skin tissue to be damaged). Death can occur extremely rapidly while the victim is still in the water or on the beach. Antivenom is available but must be administered quickly. Vinegar can be used to remove undischarged nematocysts. ◆

No common name

Tripedalia cystophora

FAMILY
Carybdeidae

TAXONOMY
Tripedalia cystophora Conant, 1898, Kingston Harbor, Puerto Rico.

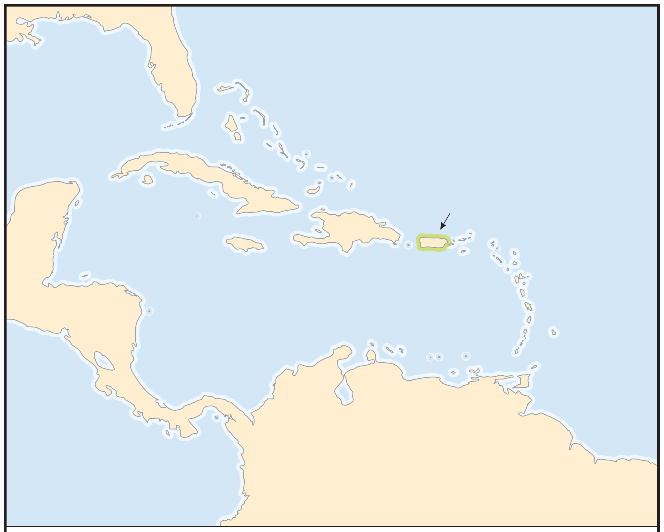
OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Small, mature jellies 0.02–0.4 in (0.5 mm–1.0 cm) in diameter. Bell slightly yellow brown, blends well with the mangrove habitat.

DISTRIBUTION
Puerto Rico and the Caribbean.

HABITAT
Shallow waters among mangrove roots.

BEHAVIOR
As *D. oculata* aggregate in vertical lift shafts generated by the sun shining through the mangrove roots, *T. cystophora* change their swimming speed and turning rate in the light shafts, resulting in the jellies spending more time in the light shafts where they can feed on the copepods.


🟩 *Tripedalia cystophora*

FEEDING ECOLOGY AND DIET
Preys on dense swarms of the copepod *Dioithona oculata* in the mangrove prop-root habitat of Puerto Rico, where it has been intensely studied.

REPRODUCTIVE BIOLOGY
Unique in cubozoans, broods fertilize eggs until they develop into planulae within gastral pockets. Planulae are released upon maturity. Show a preference for settling on substrates in the dark where they develop directly into a medusa.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Not harmful to humans, but plays an important role in marine education as it is exhibited in many aquaria. ◆

Resources

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George I. Matsumoto, PhD

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Scyphozoa

(Jellyfish)

Phylum Cnidaria

Class Scyphozoa

Number of families 20

Thumbnail description
Large, soft-bodied, gelatinous marine invertebrates that swim by contracting their umbrella-shaped swimming bell and catch small prey by means of stinging tentacles

Photo: *Chrysaora dactylometre.* (Photo by William H. Amos. Bruce Coleman, Inc. Reproduced by permission.)

Evolution and systematics

The class Scyphozoa includes four orders, 20 families, 66 genera, and about 200 species. The four orders are Stauromedusae, the stalked jellyfish; Coronatae, the crown or grooved jellyfish; Semaeostomeae; and Rhizostomeae.

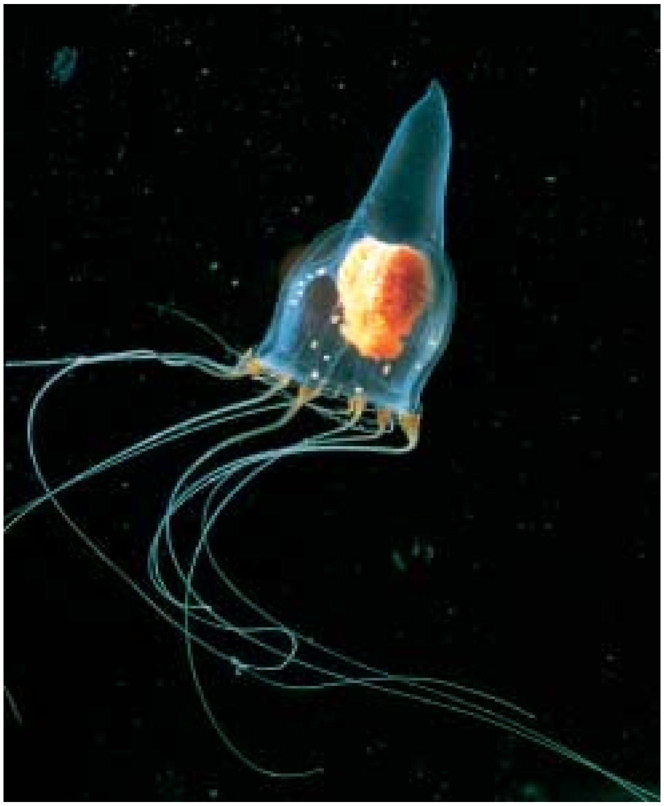
Animals in the phylum Cnidaria may have one or both of two body forms, the benthic polyp and the pelagic medusa. The four orders within the class Scyphozoa emphasize these two forms to different degrees. Specifically, in the order Stauromedusae, there is only a benthic stage, which is considered the medusa. In the orders Coronatae, Semaeostomeae, and Rhizostomeae both stages occur in most species, with the medusa stage being the largest and most conspicuous.

The phylum Cnidaria is considered to be of early evolutionary origin, but the position of the Scyphozoa relative to other cnidarian classes (Anthozoa [corals and anemones], Cubozoa [box jellyfish], and Hydrozoa [hydroids, hydromedusae, fire corals, and siphonophores]) is uncertain. It is debated whether the polyp or the medusa form is most primitive. The scyphozoans are related most closely to cubozoans, which were placed in the same class until recently. They have similar body forms and life cycles. The scyphozoans are related least to the Anthozoa. Molecular evidence suggests that Anthozoa represents the most primitive class in the phylum Cnidaria.

The fossil record of Scyphozoa is poor. Radially symmetrical impressions have been interpreted to be casts of primitive scyphomedusae. Recently, a large number of scyphomedusae that apparently were stranded and buried on a beach was discovered in central Wisconsin in the United States. Other fossil groups that may be ancient scyphozoan polyps are the conulariids, which were similar to modern coronate polyps and were present from the Ordovician to the late Triassic, and *Bryonia* from the Upper Cambrian and Ordovician, which is from the extinct order Bryoniida of the Scyphozoa.

Physical characteristics

Most species in the class Scyphozoa, excluding the order Stauromedusae, have two life stages, the predominant medusa stage (up to 80 in, or 2 m, in diameter) and the small, inconspicuous polyp stage (less than 0.13 in, or 4 mm, long). The medusa, or jellyfish, stage has a saucer- to umbrella-shaped body with two epithelial layers (epidermis and gastrodermis) separated by a thick layer of mesenchyme, a gelatinous connective tissue containing cells. Near the edge of the bell in the orders Coronatae and Semaeostomeae are tentacles used in



The medusa of *Leuckatiara octona* has a jelly filled projection at the tip of the bell-like body which is a distinguishing feature of this genus. (Photo by ©Sinclair Stammers/Science Photo Library/ Photo Researchers, Inc. Reproduced by permission.)

feeding. The tentacles have millions of microscopic intracellular organelles called nematocysts that evert a hollow thread from a capsule and may inject toxin into or entangle their small prey (zooplankton, fish eggs and larvae, or other gelatinous species). In the Semaeostomeae and Rhizostomeae, there are four oral or mouth arms on the underside (concave) of the bell, which also have stinging nematocysts for feeding. The polyps, called scyphistomae, can form colonies of individuals by budding or, in the case of coronate polyps, true colonies that have a chitinous sheath. Polyps are cup-shaped, attached to the substrate by a "foot," and with the central mouth surrounded by a single ring of tentacles with nematocysts.

Stalked jellyfish in the order Stauromedusae attach to seaweed or sea grasses by an aboral stalk. The main body (calyx) is funnel- or goblet-shaped and grows to 1.2 in (3 cm) wide, with eight arms, each bearing a cluster of as many as 100 short, clubbed tentacles. In the common genus *Haliclystus*, between each arm there is an adhesive disk, by which the animal can attach to move about. The gonads extend down the arms. The mouth is located at the inside center of the funnel-shaped body. Coloration varies; it may be shades of green, brown, yellow, or maroon and often matches the color of the substrate, making these jellyfish difficult to see. This form is considered the medusa stage, and there is no polyp or swimming stage.

Jellyfish in the order Coronatae have a deep groove around the aboral surface that separates the swimming bell into a central disk and a peripheral zone, which has lappets. One thick tentacle emerges between lappets on the upper surface of the bell; depending on the species, there are between eight and 36 tentacles. The mouth opens into a large, pouchlike stomach on the underside of the bell. Most of the species are deep living, and thus the central disk is colored dark red to maroon, making it invisible at depths and presumably concealing the bioluminescence emanating from consumed prey. Most of the medusae are small, less than 2 in (5 cm) in diameter or bell height, but some species may attain 6 in (15 cm) in diameter. The known polyps are colonial and covered with a chitinous sheath.

Adult jellyfish in the order Semaeostomeae generally are large, up to 80 in (2 m) in diameter, but usually less than 12 in (30 cm). The swimming bell is flat to hemispherical in shape. The bell edge may have lappets, or it may be smooth. From eight to hundreds of tentacles are present at the bell margin or beneath the bell. In the center of the concave side of the bell are four diaphanous or frilled oral arms that lead to the central mouth. The bell ranges from translucent to opaque and from white to dark orange in color, and it may have radiating stripes in some species. The polyp stage is small and may form groups of individuals by budding.

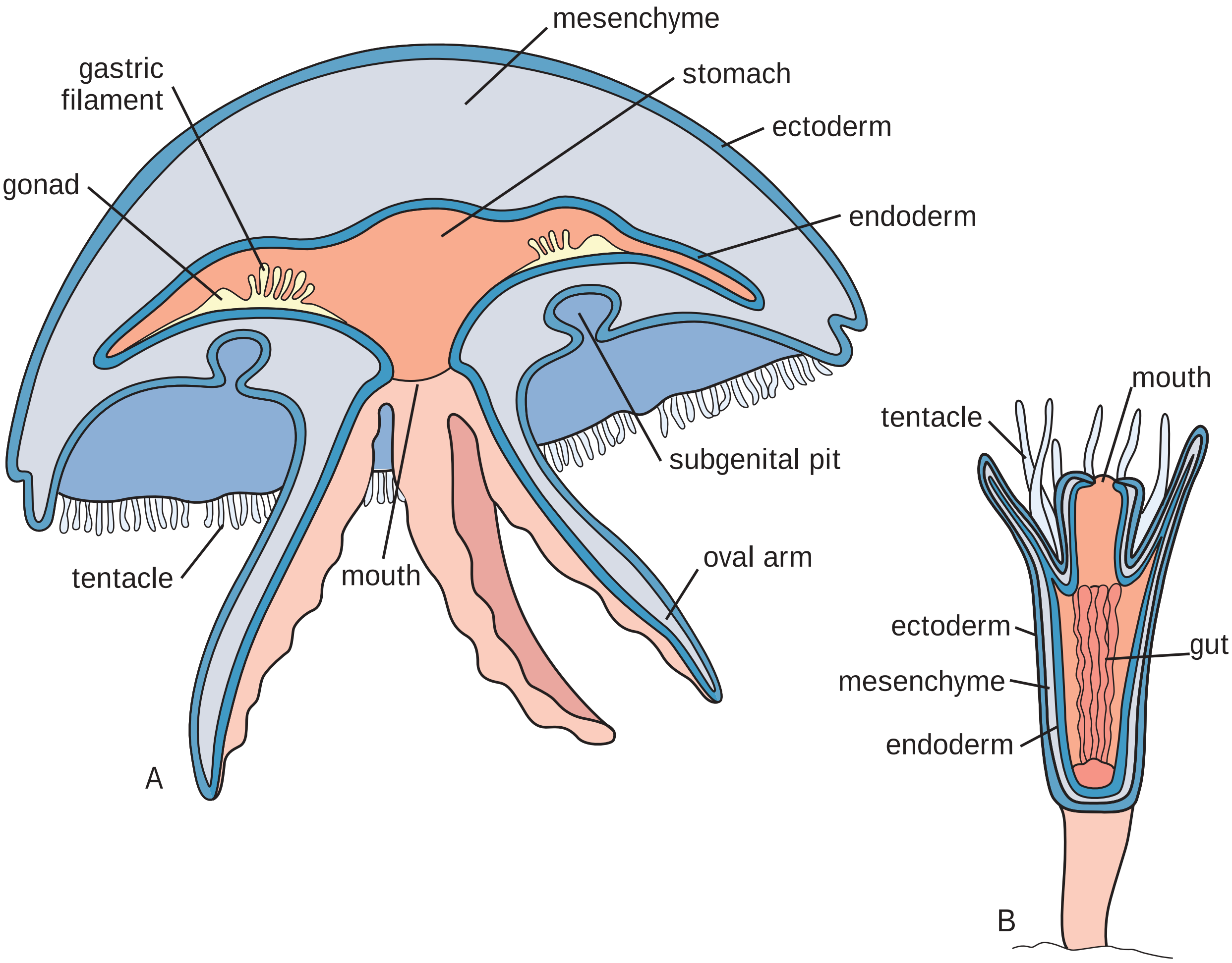
The rhizostome medusae also are large, up to 80 in (2 m) in diameter. The swimming bell is hemispherical and very firm in texture and lacks tentacles at the edge. The bell margin has eight or 16 lappets. The four oral arms of rhizostome medusae are fused and usually very elaborate, with many tiny tentacles and small mouths for feeding. There may be clublike projections from the oral arms. The medusae are translucent to opaque, with colors ranging from white to dark red; some have patterns that include stripes and spots. The polyp stage is small and may form clusters of individuals by budding.

Distribution

Scyphozoans are found in all marine waters. Most Stauromedusae are found in cool waters along temperate to subpolar shorelines spring through autumn. Coronate medusae generally occur at great depths, where temperatures are a cool 40–46°F (5–8°C), but a few species occur in subtropical to tropical waters. Semaeostome species are the predominant large medusae in polar to temperate oceans, and they also inhabit subtropical and tropical waters. The scyphistomae of those species are active only in warm months; however, they can become dormant and survive through winter months. Rhizostome species live mostly in tropical waters, with only a few species found in subtropical or temperate regions. The medusae of shallow-living scyphozoans are seen during late spring to early autumn in surface waters of temperate to polar seas. In tropical waters and among deep-dwelling species, medusae may be present all year.

Habitat

Scyphozoan medusae are found from surface waters to abyssal depths, and the polyps are attached to hard surfaces, such as pilings, shells, and rocks, at various depths, depending on the species. Most Stauromedusae are seen at intertidal



Jellyfish anatomy. A. Medusa; B. Polyp. (Illustration by Patricia Ferrer)

down to shallow subtidal depths, usually attached to benthic plants (algae or sea grasses). One species is known from deep hydrothermal vent communities. Coronate medusae typically are found at mesopelagic depths (1,625–4,875 ft, or 500–1,500 m), but a few species occur near the surface. Deep-living species may have polyps at abyssal depths, but the polyps of shallow-living species are on shallow substrates. Semaeostome and rhizostome medusae occur most abundantly near shore in surface waters above 165 ft (150 m), where food supplies are greatest. Their polyps also are found at shallow depths, often on the underside of structures away from direct light. Some semaeostome species are deep living, and their polyps generally are not known. There are no known deep-dwelling rhizostome species.

Behavior

Jellyfish behavior generally is simple, owing to their simple nervous system. Stauromedusae move around on the substrate by somersaulting, which they accomplish by alternating adhesion of the basal disc with that of tentacles or adhesive pads located between the tentacles of some genera. The most noticeable behavior of jellyfish is the rhythmic pulsation of the swimming bell, which moves them through the water for feeding and respiration. The swimming pulsations are coordinated by nerve centers around the edge of the bell. At the bell margin there also are sensory clubs (rhopalia), each consisting of a light-sensing organ (ocellus) and a gravity-sensing organ (statocyst); thus, medusae can sense light and dark and can determine their orientation in the water column. Semaeostome and rhizostome jellyfish swim continuously. This is important for oxygen exchange, which occurs over the entire body surface, and for feeding. The swimming of several species is known to be against flow in the water column; the result is that they all swim in the same direction and may become concentrated in convergences, like bales of hay stacked up to dry. Some species move up in the water column at night and down in the day ("diel vertical migration"). The scyphistomae (polyps) are able to move by the so-called foot and its extensions. They feed when prey makes contact with their tentacles, which have nematocysts; the jellyfish contract the tentacles and bring the prey to their mouths.

Feeding ecology and diet

All scyphozoans feed with tentacles or tentacle-like projections that have millions of microscopic intracellular organelles called "nematocysts." Some nematocysts act to

Moon jellies (*Aurelia aurita).* ©Shedd Aquarium. Photo by Edward G. Lines, Jr. Reproduced by permission.)

paralyze or kill the prey, whereas others entangle them. Stauromedusae catch prey by the tentacles and fold the arm inward to bring the prey to the mouth. Many coronate medusae do not swim actively while feeding but instead remain nearly motionless with their tentacles extended above the bell. For semaeostome and rhizostome medusae, the pulsations of the swimming bell force water through the tentacles and create vortices that may bring prey into contact with the tentacles and oral arms. For semaeostome medusae, when a prey item is immobilized on a tentacle, the tentacle contracts and transfers the prey to an oral arm. The prey is moved by cilia up the inside of the folded oral arm to the mouth and into one of the four gastric (stomach) pouches, where short, fingerlike projections wrap around the prey and secrete digestive enzymes. For rhizostome medusae, prey capture is by the small tentacles on the oral arms, which transfer the prey to one of the many small mouths nearby.

Most species feed on small crustaceans that predominate in most habitats. Stauromedusae consume epibenthic crustaceans, including gammarid amphipods and harpacticoid copepods. Medusae in the other orders primarily eat abundant calanoid copepods but also eat other small zooplankton, such as cladocerans, larvaceans (= appendicularians), and chaetognaths. Many semaeostome species also feed on other gelatinous species, including scyphomedusae, hydromedusae, siphonophores, and ctenophores. It is of particular interest that several species are known to consume the eggs and larvae of fish. Thus, scyphomedusae may be detrimental to fish populations, both by consuming the zooplankton foods needed by fish larvae and zooplanktivorous fish species, like herring, and by feeding on the young fish directly.

Reproductive biology

Scyphozoans generally reproduce both asexually and sexually. The benthic forms, Stauromedusae and scyphistomae (polyps) of the other orders, reproduce asexually by budding new polyps or cysts from the body or foot. Scyphistomae, which are present in most species of all orders except Stauromedusae, also produce the medusa stage by an asexual budding process called strobilation. Strobilation typically takes place at a certain time of year and is triggered by environmental factors, which differ by species; these factors include rising (spring) or falling (autumn) temperatures or changes in light levels. During strobilation, the polyp undergoes transverse segmentation, forming one to several small medusae, called "ephyrae." The process requires days to weeks, depending on temperature.

The fully formed ephyrae break free by swimming pulsations. The ephyrae grow into sexually mature medusae over the course of a month or longer. The medusae of most species have separate sexes, but a few species are sequential hermaphrodites. The males and females are indistinguishable except by examination of the gonads. No mating occurs. Sperm strands are released into the water by males and are taken up by the females during feeding. The gonads surround the gastrovascular cavity, and eggs may be fertilized in the ovary or after they are released into the gastrovascular cavity. In most species the fertilized eggs develop into small ciliated larvae (planulae) that swim to a suitable substrate, attach, and develop into polyps. In some species, the planulae are retained (brooded) by the female before settlement. Some species lack a polyp stage.

Conservation status

No species of Scyphozoa is listed by the IUCN.

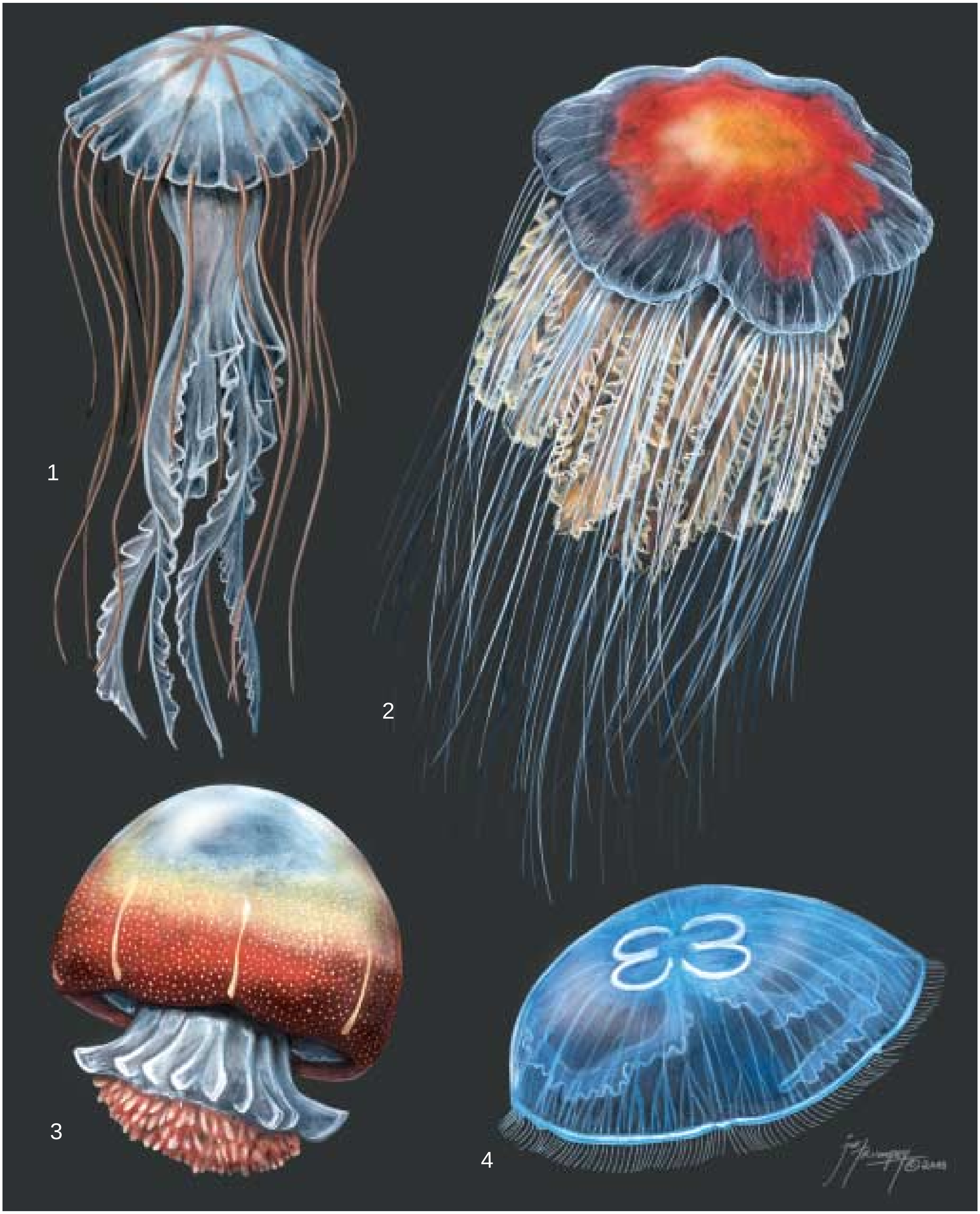
Significance to humans

Scyphozoan jellyfish have direct and indirect effects on humans, many of which are negative. Swimmers fear them for their painful stings. All jellyfish sting, but the stings of small specimens and those with short tentacles often are not painful to humans. The genera *Chrysaora* and *Cyanea* are known for painful stings. Scyphozoan stings are painful but not deadly. More painful and dangerous stingers are in the class Cubozoa (box jellyfish) and the class Hydrozoa (specifically, the Portuguese man of war, *Physalia physalis*).

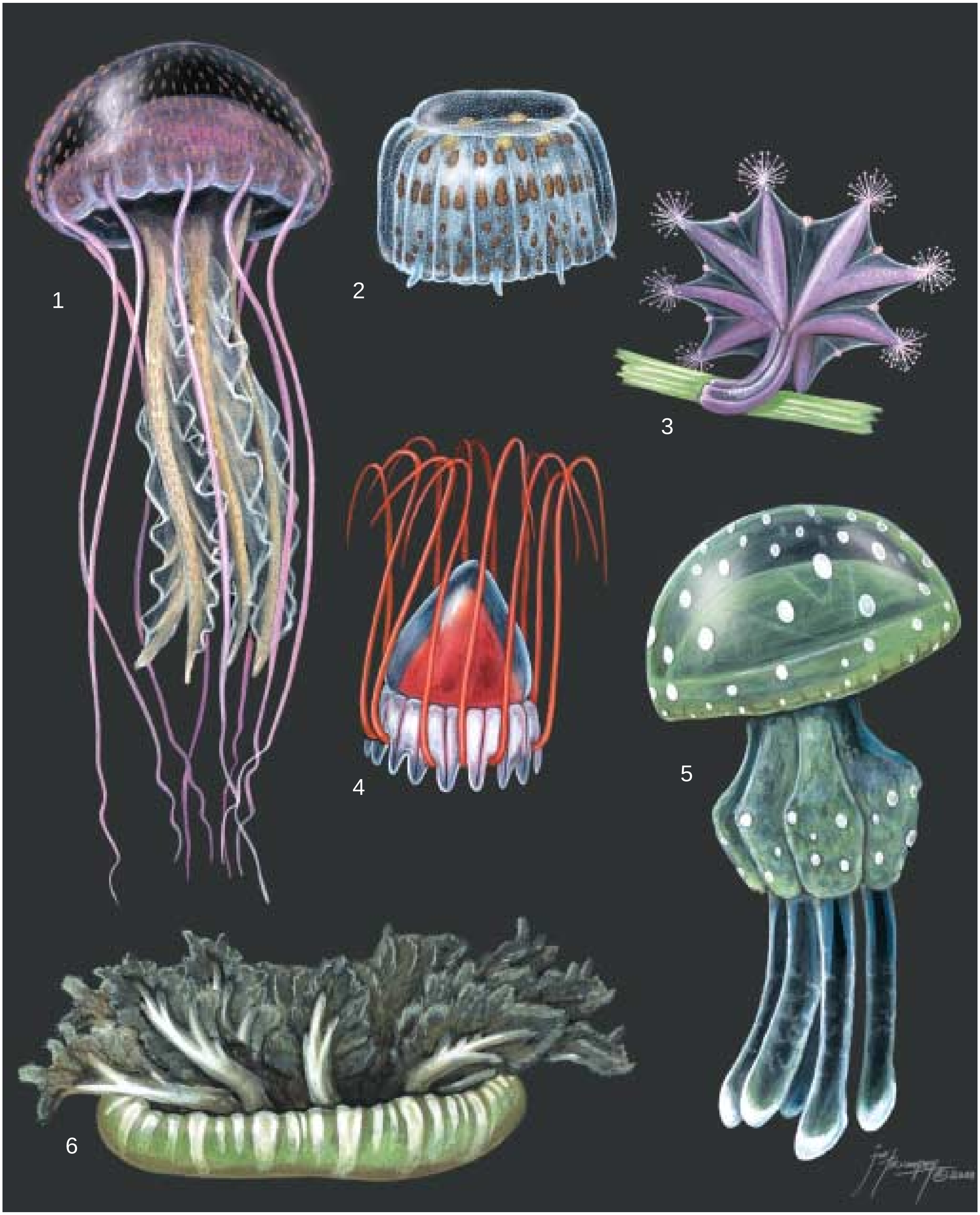
Fish populations and commercial fisheries may be affected detrimentally by jellyfish. Jellyfish may occur in great abundance, and, if they are caught in fishing nets, their great weight may cause the nets to rip or the fish catch to be damaged. Jellyfish eat the pelagic eggs and larvae of fish as well as the small zooplankton prey of fish larvae and zooplanktivorous fish species. Therefore, jellyfish both eat fish and compete with them for food. Jellyfish also appear to be intermediate hosts for some parasites of fish. Jellyfish have been a nuisance to fish farms, where they break up on the fish impoundments and sting and kill the fish, and to power plants, where they may clog the cooling water intake screens, sometimes causing the plants to suspend operations. On the positive side for fish and fisheries, the juveniles of at least 80 species of fish, many of which are commercially important, associate with large jellyfish. While the relative advantages of such associations are not known, they are thought to benefit the fish partners most.

Jellyfish also have a place of value in human enterprise. In Japan and China jellyfish are an important food and have been exploited for more than 1,700 years. In China they are considered a culinary delicacy and are thought to have medicinal value. A multimillion-dollar commercial fishery exists for at least 10 species of rhizostome medusae throughout Southeast Asia, and a fishery for *Stomolophus meleagris* has been started in the Gulf of Mexico. The swimming bell of the jellyfish is processed in a mixture of salt and alum and packaged for distribution. The semidried jellyfish is rehydrated, desalted, blanched, and served in a variety of dishes. The prepared jellyfish has a special crunchy texture.

Owing to their great beauty and the relaxing effect of their swimming pulsations, jellyfish have been a great success as specimens in public aquariums and even as household pets. Over the past decade, considerable advances have been made in jellyfish husbandry, and several species are on display at aquariums worldwide. In Japan jellyfish are kept as pets in special aquariums.



1. Sea nettle (*Chrysaora quinquecirrha*); 2. Lion's mane jellyfish (*Cyanea capillata*); 3. Cannonball jellyfish (*Stomolophus meleagris*); 4. Moon jelly (*Aurelia aurita*). (Illustration by Joseph E. Trumpey)



1. Nightlight jellyfish (*Pelagia noctiluca*); 2. Thimble jelly (*Linuche unguiculata*); 3. Stalked jellyfish (*Haliclystus auricula*); 4. Crown jellyfish (*Periphylla periphylla*); 5. Golden jellyfish (*Mastigias papua*); 6. Upside-down jellyfish (*Cassiopea xamachana*). (Illustration by Joseph E. Trumpey)

Species accounts

Thimble jelly

Linuche unguiculata

ORDER

Coronatae

FAMILY

Linuchidae

TAXONOMY

Linuche unguiculata Schwartz, 1788, American Tropical Atlantic.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

The medusae grow only to 1 in (2.5 cm) in height. As the name implies, they are thimble-shaped, with a shallow groove near the top of the bell. They have eight very short tentacles and eight rhopalia alternating between the 16 lappets at the bell margin. The outside of the bell is transparent, with numerous warts of stinging cells. The inner part of the bell is white with greenish brown spots. The polyps form colonies and are covered by a thin, chitinous sheath.

DISTRIBUTION

This species lives in tropical and subtropical waters worldwide.

HABITAT

The medusae occur near the surface in near shore waters in spring and summer, which is unusual for coronate species. Polyps occur on coral rubble.

BEHAVIOR

The thimble jelly usually is found in large groups, up to 0.6 mi^2 (1 km^2) in area, just beneath the surface. They are very active swimmers, moving horizontally in circles. Surface convection cells cause them to become concentrated, and their swimming behavior helps them remain in an aggregation.

FEEDING ECOLOGY AND DIET

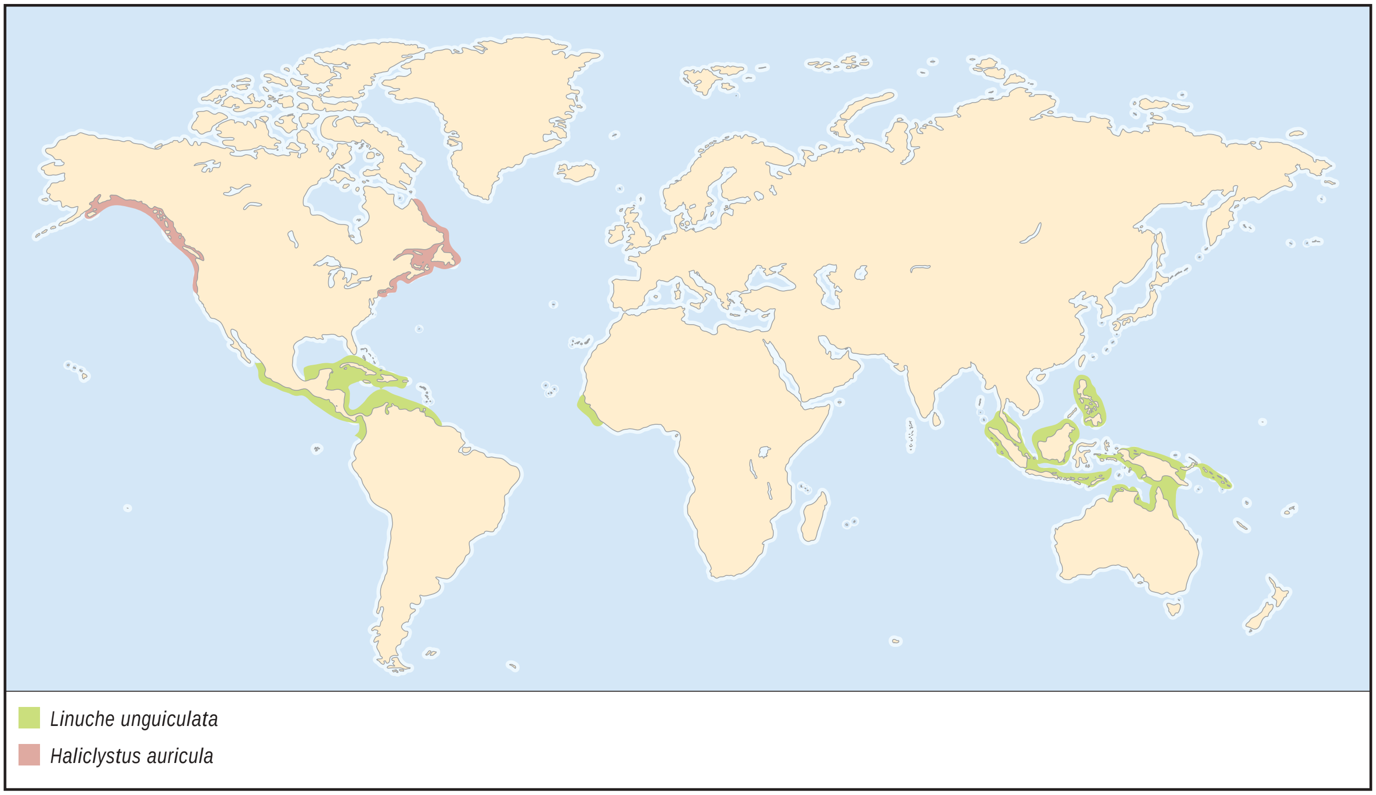
The medusae catch a variety of zooplankton prey on the lappets. The colored spots in the bell are filled with intracellular algae (zooxanthellae) that transfer some of their photosynthesized carbon to the medusa, contributing to the animal's nutrition.

REPRODUCTIVE BIOLOGY

The fertilized eggs of the thimble jelly form large larvae that remain planktonic for three to four weeks. They settle and form an unbranched colony of polyps. Each polyp can produce an unusually large number (up to 40) of ephyrae that grow into sexually mature medusae.

CONSERVATION STATUS

Not listed by the IUCN.



SIGNIFICANCE TO HUMANS
Stings from the planktonic larvae or medusae of the thimble jelly cause the syndrome called "seabathers' eruption." The problem is aggravated when they become trapped underneath a swimsuit. This syndrome, characterized by a prickling sensation and red bumps persisting for 7–12 days, is an irritating but not a dangerous condition. ◆

Crown jellyfish

Periphylla periphylla

ORDER
Coronatae

FAMILY
Periphyllidae

TAXONOMY
Periphylla periphylla Peron and Lesueur, 1809, equatorial Atlantic Ocean.

OTHER COMMON NAMES
None known.

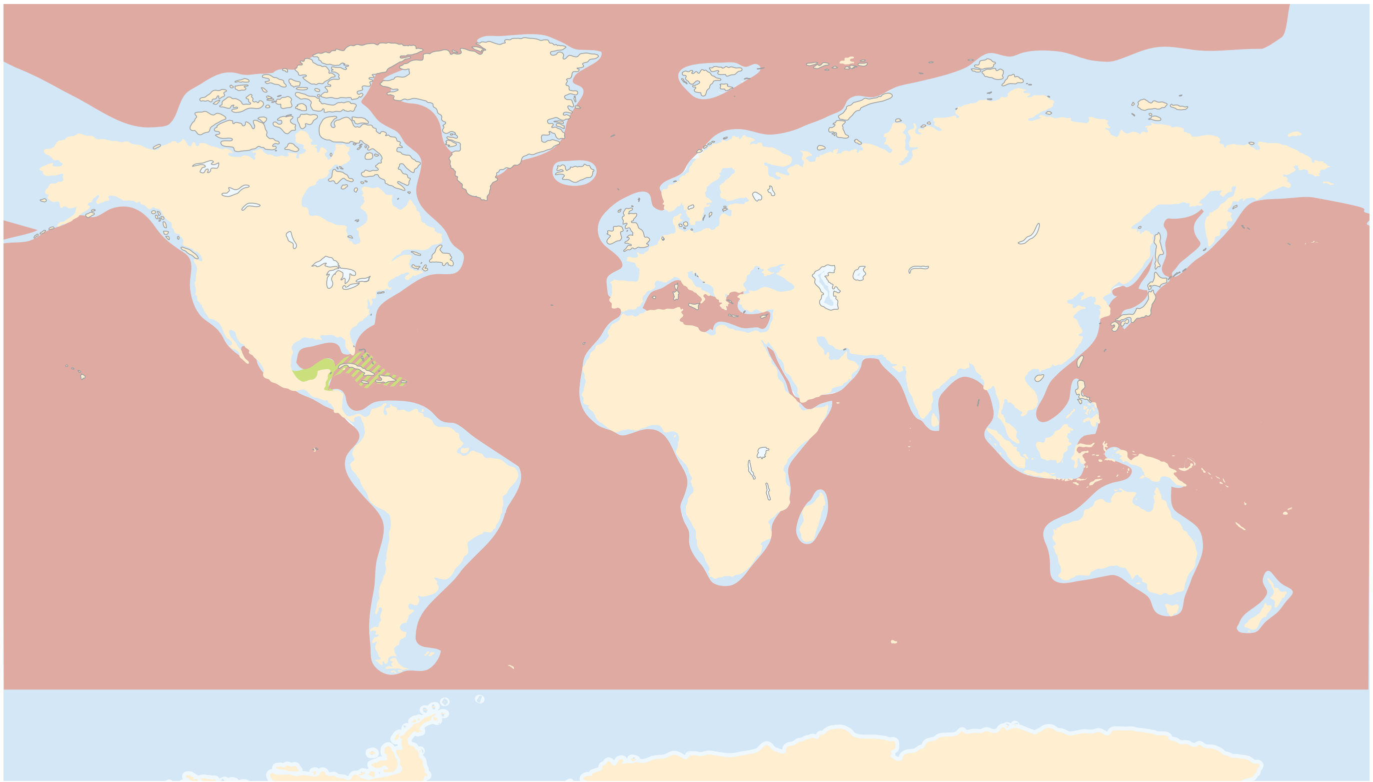
PHYSICAL CHARACTERISTICS
These medusae have a conical swimming bell that is up to 8 in (20 cm) tall and 6.5 in (17 cm) in diameter, but specimens from oceanic waters usually are less than 2 in (5 cm) in size. The bell of small specimens is transparent and reveals the reddish brown stomach. In large specimens, the bell is opaque and maroon in color. The bell has a pronounced groove with 16 deeply notched lappets beneath it. Twelve thick tentacles emerge from the bell surface above the clefts, in a repeating pattern of three tentacles and one rhopalium. The stomach is baglike. Oral arms and the polyp stage are lacking.

DISTRIBUTION
This species is found at mesopelagic depths in all oceans worldwide. Populations that are several orders of magnitude greater than they are in the open ocean have been found in Norwegian fjords, especially Lurefjorden.

HABITAT
The crown jellyfish generally is found at depths below 3,000 ft (900 m), where water temperatures remain a cool 45°F (7°C) or less all year. At high latitudes they inhabit shallower depths, 650–1,300 ft (200–400 m) in the daytime and from the surface to 650 ft (200 m) at night.

BEHAVIOR
These medusae undergo vertical migration from deepwater in the daytime to shallower depths at night, presumably following their prey. Exposure to white light causes rapid downward swimming. As with other deep-dwelling coronate medusae, when they are disturbed, the bell and ovaries are brilliantly bioluminescent. They also produce copious amounts of luminescent mucus that contains stinging cells.

FEEDING ECOLOGY AND DIET
The natural behavior of medusae was observed with red light and video cameras on a Remotely Operated Vehicle (ROV) in Lurefjorden, Norway. The medusae hold their tentacles up alongside the bell or at right angles to the bell. They swim downward for about 30 ft (10 m) and then drift upward. The tentacles sometimes quickly arch toward the mouth, coil, and enter the stomach. Few prey (copepods, ostracods, and chaetognaths) were found in ROV-collected specimens. These



FEEDING ECOLOGY AND DIET

Prefers small copepods.

REPRODUCTIVE BIOLOGY

Two mature individuals with full seminal vesicles maneuver close to each other to mate. One will deposit a sperm package or spermatophore on the dorsal neck region of the other individual. Then the sperm moves toward the genital opening and is stored until eggs are mature. The eggs are fertilized internally and then released into the water.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

Bone, Q., H. Kapp, and A. C. Pierrot-Bults, eds. *The Biology of Chaetognaths*. Oxford, New York, Tokyo: Oxford University Press, 1991.

Conway Morris, S. *Fossil Priapulid Worms*. London: Palaeontological Association, 1977; distributed by B.H. Blackwell.

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Schram, F. R. “Pseudocoelomates and a nemertine from the Illinois Pennsylvanian.” *Journal of Palaeontology* 47 (1973): 985–989.

Annelies C. Pierrot-Bults, PhD

Hemichordata

(Hemichordates)

Phylum Hemichordata

Number of families 8

Thumbnail description
Small wormlike marine animals that live individually or in colonies, depending on the species

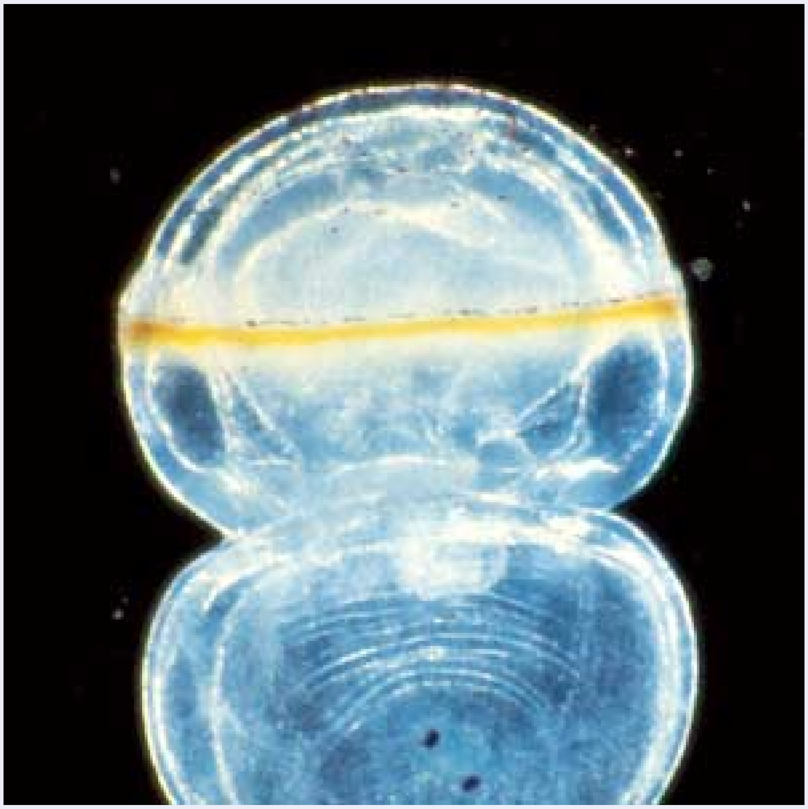


Photo: Tornaria larva of an *Enteropneusta* worm. (Photo by Animals Animals ©Peter Parks, OSF. Reproduced by permission.)

Evolution and systematics

The extant members of the phylum Hemichordata (formerly called Stomochordata) number about 92 and are typically divided into three classes:

- Enteropneusta or acorn worms: four families;
- Pterobranchia or pterobranchs: three families; and
- Planctosphaeroidea: one family.

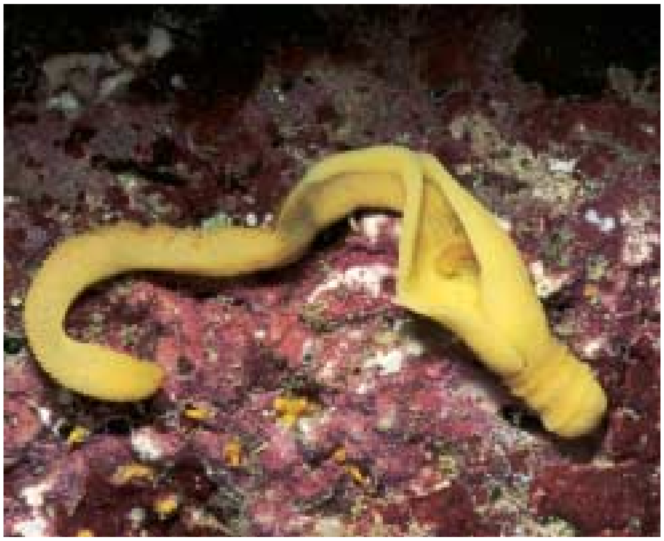
Hemichordates are closely related to the chordates, sharing many chordate or chordate-like features. In the enteropneusts, these features include lateral openings, which are pharyngeal gill pores that connect the pharynx or airway to the exterior; and a stomochord that is somewhat analogous to the chordate notochord, although it has been described as "no more than an anterior extension of the buccal cavity." Despite these similarities, genetic studies, morphological comparisons of the larvae and anatomy of the nervous system, and biochemical evidence have recently indicated that hemichordates may be more closely related to echinoderms (starfishes and sea urchins) than to chordates.

In addition, recent genetic analyses of the extant hemichordates suggest that the pterobranchs are not plesiomorphic (similar in form) as previously thought, but have actually evolved from a forerunner to the enteropneusts. Under this arrangement, the lineage of the Ptychoderidae family within the enteropneusts split off first in the course of evolution, followed by a later separation of the Harrimaniidae family of the enteropneusts and the pterobranchs.

In addition to these three extant classes of Hemichordata, there is an extinct class, Graptolithina, known from fossils found in rocks dating from the Ordovician and Silurian periods (505–410 million years ago).

Physical characteristics

Hemichordates have two major body plans. One of the most notable characteristics of the enteropneustan hemichordates is their three-part body plan, which includes a protosome, or anterior proboscis (sometimes called a pre-oral lobe); followed by a mesosome or collar; and finally a metasome, or trunk. Cilia, which are present over all body areas, play roles in locomotion and in distributing the proteinaceous mucus secreted by the acorn worms. The largest species is the enteropneust *Balanoglossus gigas* of Brazil, an acorn worm that reaches 4.9 ft (1.5 m) in length and lives in long burrows stretching over more than 9.8 ft (3 m).



A Hawaiian acorn worm (*Ptychodera flava*) near the Lizard Islands, northern Great Barrier Reef. (Photo by © A. Flowers & L. Newman/Photo Researchers, Inc. Reproduced by permission.)

Pterobranchs have a three-part body plan like the enteropneusts, but with a shorter, shield-shaped proboscis and a more complex collar. In some species, the collar has tentacled arms. Pterobranchs form colonies, often with individuals attached by so-called stolons or stems. The individual animals are called zooids and are quite small, typically less than 0.04 in (1 mm) long. Groups form and live within a coenecium, which is a network of proteinaceous tubes built with secretions from each animal's proboscis.

The class Planctosphaeroidea has only one species, *Planctosphaera pelagica*, and it is known only from its larvae. Although several times larger at 0.3–1 in (8–25 mm) long, the almost-spherical, transparent *P. pelagica* larva is otherwise quite similar to enteropneust tornaria, having a gelatinous body covered with cilia. Unlike tornaria, however, the epidermis of *P. pelagica* has two deep invaginations (pouchlike formations) as well as numerous glands that secrete mucus.

Distribution

Enteropneusts, pterobranchs, and planctosphaeroids occur in oceans throughout the world. In general, the acorn worms live in shallower areas and the pterobranchs in deeper waters. The single species known from the class Planctosphaeroidea is found in both the Atlantic and Pacific Oceans at depths between 246 ft (75 m) and about 3,280 ft (1,000 m).

Habitat

Habitat varies by class. Adult acorn worms are typically found in either intertidal or shallow marine areas, although they are occasionally found in deeper water. They generally inhabit burrows in the sea bottom but also live sometimes in the sand inside shells, under rocks, in thick seaweed, or between root tangles. Adult pterobranchs are colonial forms that live in secreted tubular coenecia, and the planctosphaerids are planktonic.

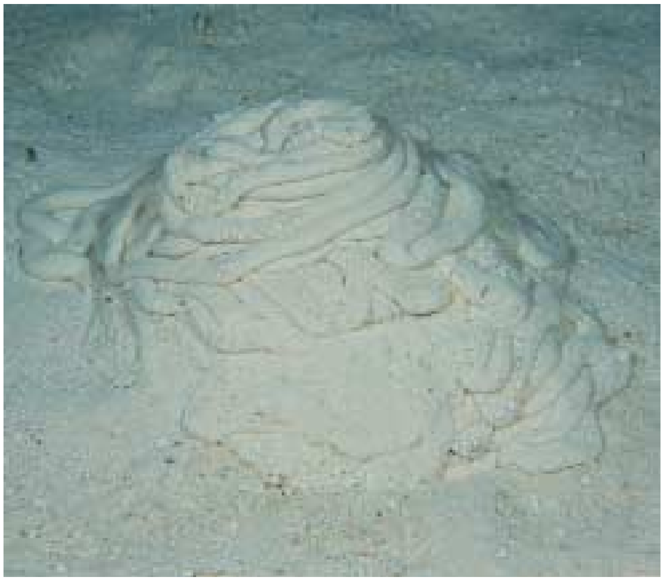
Behavior

The acorn worms are solitary animals that are generally found sheltered in burrows, under rocks, or in thick vegetation. The burrowing species, like *Balanoglossus clavigerus*, use their proboscis primarily to fashion U-shaped burrows. They line the burrow walls with epidermal secretions that provide added strength. Each end of the burrow lies at the surface of the sea bottom and the remainder of the "U" is underground. One end is a cone-shaped depression in the sand bottom, and the other can be identified by a several-inch-tall pile of worm castings a short distance away. Besides this main burrow, *Balanoglossus* also employs a few side tunnels. Frequently, acorn worms will stretch their proboscis and collar out of the tunnel, but they spend the bulk of their time underground. When threatened, acorn worms respond by expanding the proboscis, effectively anchoring the animal in its burrow or tangle of vegetation while withdrawing the rest of the body. Studies of phototaxis (movement toward or away from a light source) reveal that illumination stimulates some species, like *Saccoglossus ruber*, to burrow deeper.

Because of the burrowing nature of most hemichordates, little is known about the reproductive and other behaviors of many species.

Feeding ecology and diet

Hemichordates may be either suspension- or sediment-feeders. The latter, like *Balanoglossus clavigerus*, take in sediment and obtain nutrients from the organic matter contained



Acorn worms, such as *Balanoglossus australiensis* are named for their acorn shaped head. They dig a U-shaped burrow, and live there with only the head sticking out of one opening, eating bacteria, micro-algae, and detritus. (Photo by Animals Animals ©Joyce & Frank Burek. Reproduced by permission.)

in it. The suspension-feeding adult hemichordates, as well as the filter-feeding tornaria larvae, gather their meals by generating currents with the cilia located on their bodies and drawing in organic matter. There is some uncertainty about the role their mucus plays in prey capture. Some scientists believe food sticks to the mucus-covered proboscis, and the cilia then beat in a pattern that draws the mucus and the food together to the mouth at the bottom of the proboscis. Researchers studying such species as *Rhabdopleura normani*, on the other hand, have found that normal feeding does not involve mucus; instead, the organism relies on the cilia to change direction in movements called local reversals and thereby directs food particles to its mouth.

Indirect-developing species have free-swimming tornaria larvae that live on plankton for weeks to months. Some species, like *Saccoglossus horsti*, have free-swimming larvae that obtain all their nutrition from their yolk, and within a few days take up the sessile (permanently attached) lifestyle. Studies of *P. pelagica* larvae indicate that their mucus may facilitate feeding, although the details are unclear and several alternative hypotheses have been suggested for the mucus.

Reproductive biology

Enteropneusts normally reproduce sexually via external fertilization, and develop either directly or via tornaria larvae. The indirect developers, including *Balanoglossus* and *Ptychodera* species, are in the majority. These species develop from egg to planktonic tornaria larva to adult form. The tornaria larvae eventually become sessile, with the burrow-dwellers developing tails behind the anus that they use to anchor themselves in their mucus-lined tunnels. Direct developers, on the other hand, hatch into adult animals, bypassing the planktonic phase. An example is *Saccoglossus kowalevskii*. Enteropneusts are also known to reproduce asexually by fragmentation of the adult's body, but this mode of reproduction is uncommon. Typically, the females lay up to 3,000 eggs at a time, and the males release sperm that appear to find the eggs by following chemical cues. Reproduction in many species is cyclical. *Saccoglossus horsti*, for example, breeds in late spring to midsummer. Water temperature and tides appear to affect reproductive timing in hemichordates.

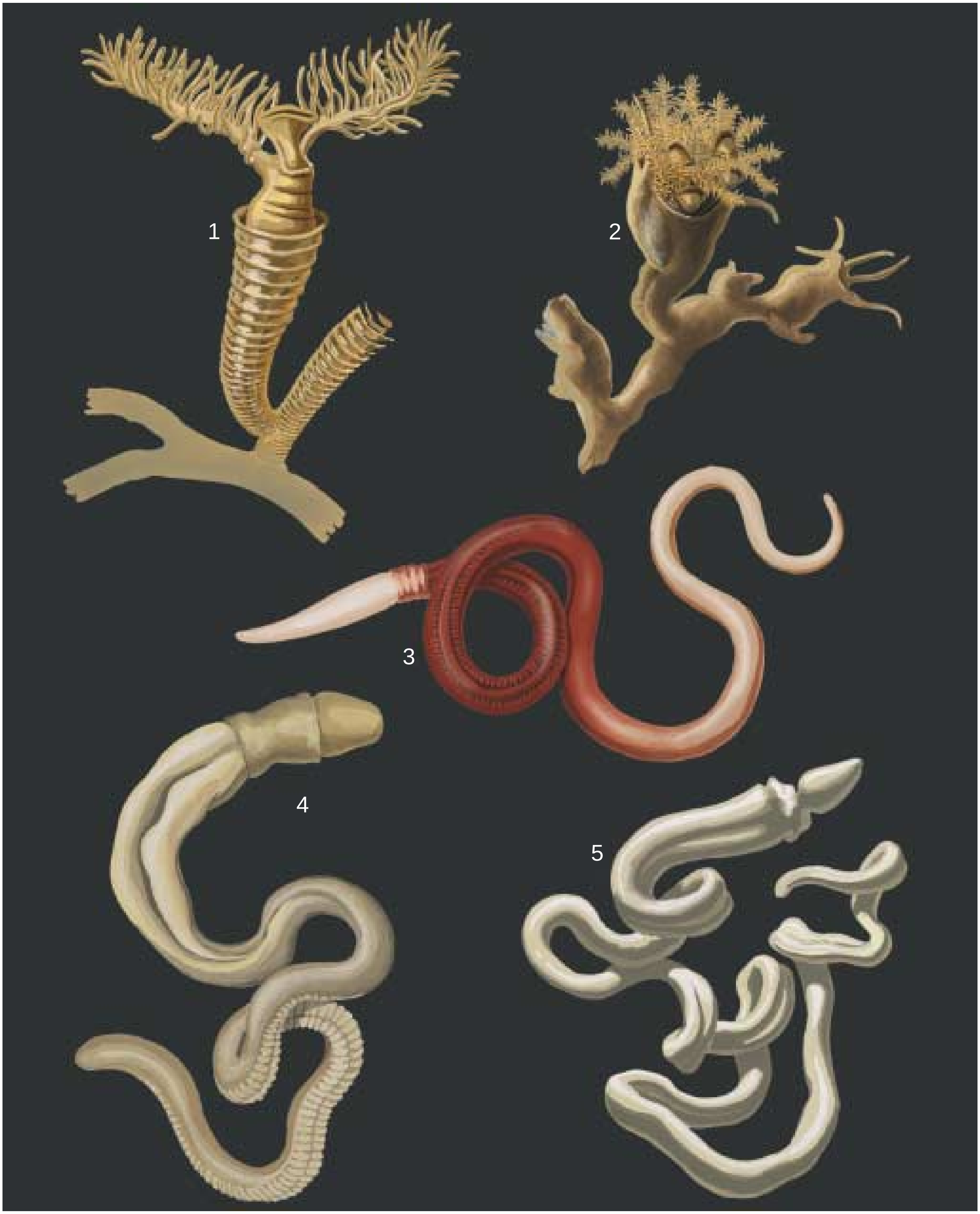
The pterobranchs reproduce via short-lived larvae in a fashion similar to the enteropneusts, but more often resort to reproduction by asexual budding. Many, perhaps all, of the hemichordates are able to regenerate portions of their trunks.

Conservation status

No hemichordates are listed as threatened by the IUCN.

Significance to humans

The hemichordates are perhaps most important to humans for the information they can provide about the origin of chordates, deuterostomes, and bilateral animals.



1. *Rhabdopleura normani*; 2. *Cephalodiscus gracilis*; 3. *Saccoglossus kowalevskii*; 4. Hawaiian acorn worm (*Ptychodera flava*); 5. Spaghetti worm (*Saxipendium coronatum*). (Illustration by John Megahan)

Species accounts

No common name

Cephalodiscus gracilis

ORDER

Cephalodiscida

FAMILY

Cephalodiscidae

TAXONOMY

Cephalodiscus gracilis M'Intosh, 1882, Straits of Magellan.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Cephalodiscus gracilis is a three-part animal with a cephalic shield, complex collar, and trunk. The collar has two rows of up to five arms each. The arms have ciliated tentacles that reach 0.2–0.3 in (5–7 mm) in length.

DISTRIBUTION

Originally found at the southern tip of South America, they have since been found in Atlantic and Indo-Pacific waters.

HABITAT

These marine hemichordates live in hollow coenecia, but are able to travel freely inside each coenicium and on its tubes. They are typically found in waters less than 65.6 ft (20 m) deep.

BEHAVIOR

Little is known about the behavior of this species.

FEEDING ECOLOGY AND DIET

These organisms are filter feeders, using their cilia to create currents to direct the food. Their tentacles also flick food into the food canal. Their diet consists of organic food particles.

REPRODUCTIVE BIOLOGY

Embryos are brooded in the coenecium tubes. *Cephalodiscus* has a free-swimming larval stage followed by a enteropneust-like adult form. Adults eventually take on the characteristic U-shape.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

No common name

Saccoglossus kowalevskii

ORDER

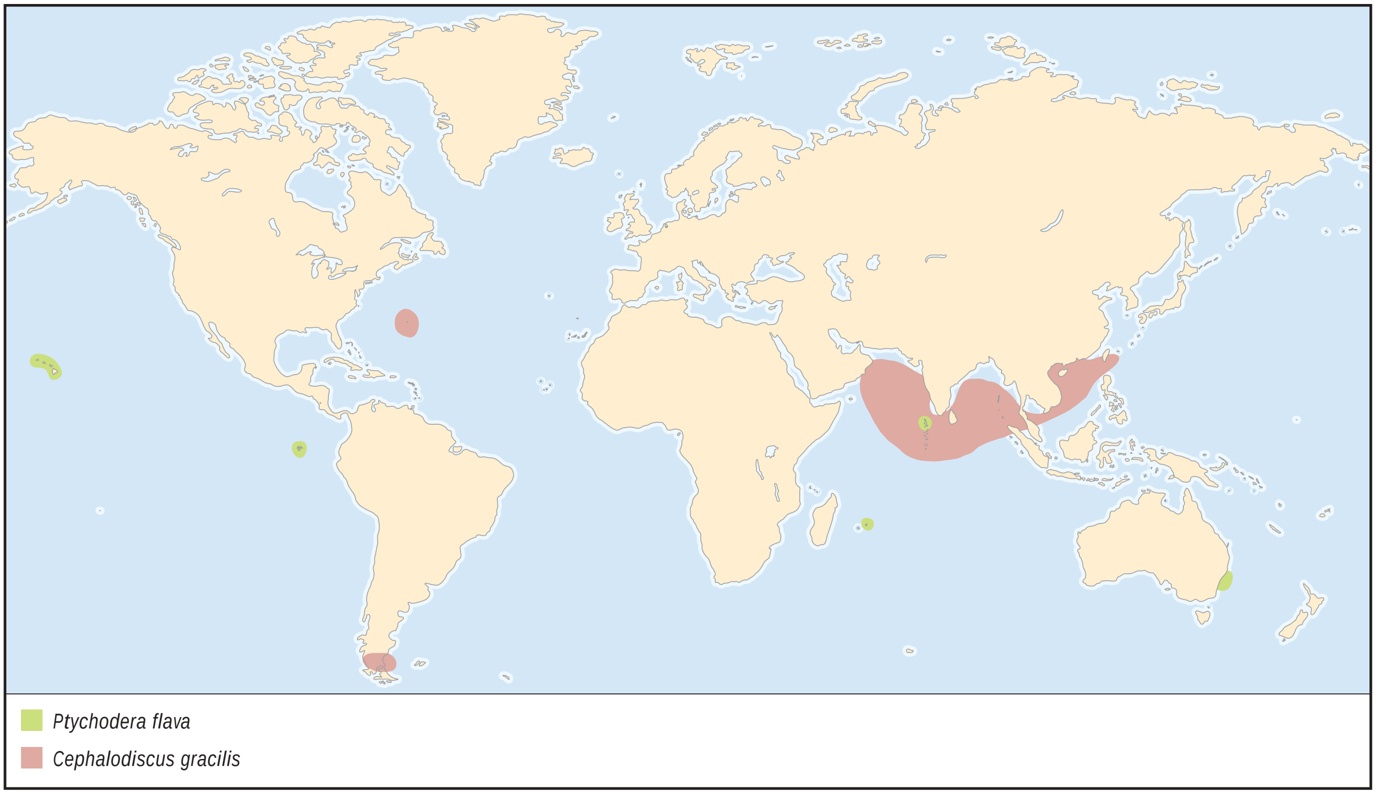
No order designation

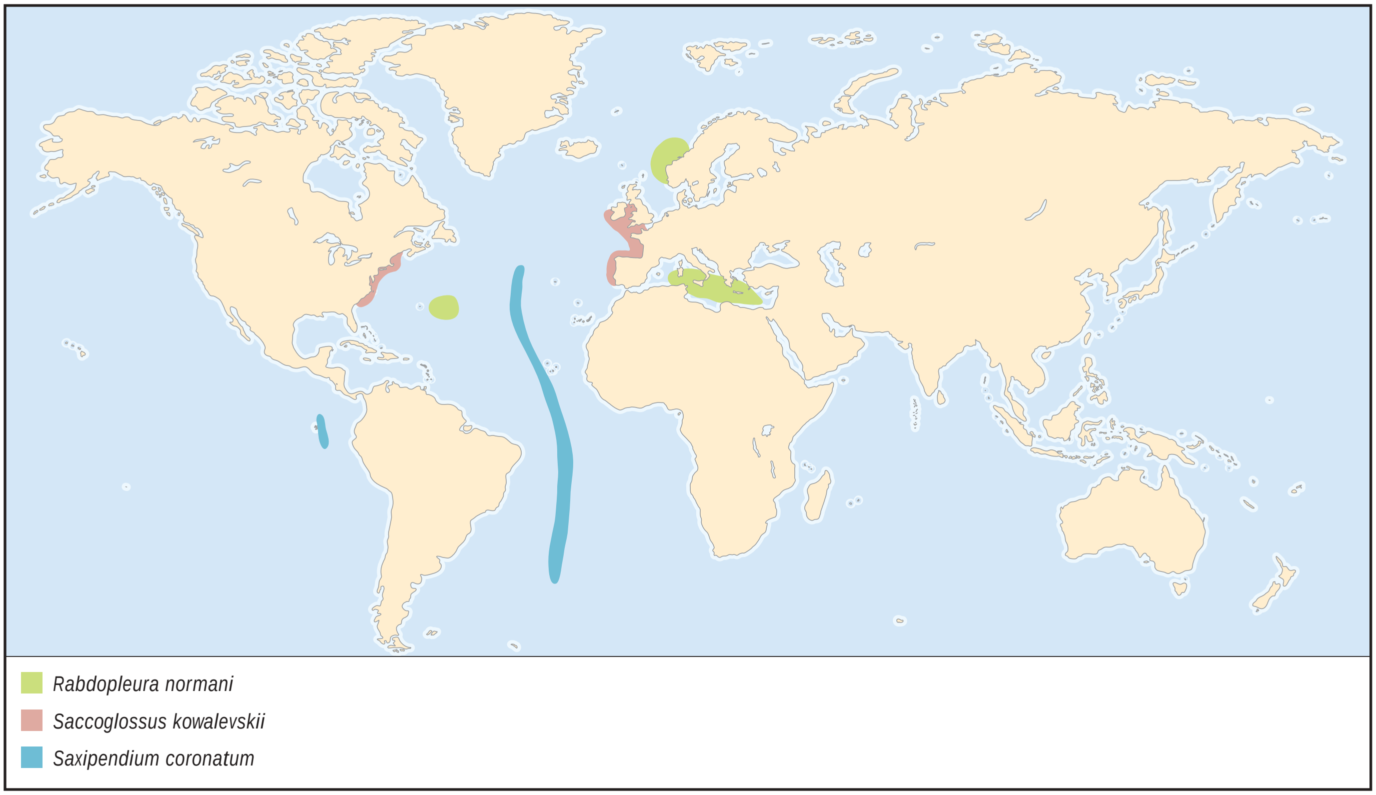
FAMILY

Harrimaniidae

TAXONOMY

Saccoglossus kowalevskii Agassiz 1873.





OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Adults are wormlike animals with a pointed proboscis, followed by a short collar and a long trunk. They range 4.0–5.9 in (10–15 cm) long. The proboscis is generally whitish yellow or light pink, the collar is orange, and the trunk can be pink to orange-brown.

DISTRIBUTION

North Atlantic, off the coast of Europe and the United States from Massachusetts to South Carolina.

HABITAT

Intertidal zones, typically sandy or silty areas.

BEHAVIOR

When threatened, an individual of this and other species of the genus *Saccoglossus* will swell its proboscis to serve as a holdfast in its burrow while drawing in the rest of its body. A mostly subterranean animal, *Saccoglossus* is most often seen with its proboscis poking out from its sea-bottom burrow. Its reproductive activity appears to be affected by seawater temperature, with spawning stimulated when temperatures shift from 80.6 to 71.6°F (27 to 22°C).

FEEDING ECOLOGY AND DIET

Saccoglossus kowalevskii gathers food from the uppermost layer of sediment in its immediate surroundings. Food items may include bacteria, microalgae and diatoms that live in the sediment, and dissolved or particulate organic material in the water. Each day, individuals of this species may take in as much as 300 times their body weight in sediment. Research indicates that this acorn worm is induced to feed by the presence of microalgae and diatom populations as well as other food sources that are high in chlorophyll.

REPRODUCTIVE BIOLOGY

Fertilization is external. Females release mucus-bound eggs into the water, males respond by releasing sperm, and fertilization occurs in the sea water. The eggs, which average about 0.02 in (0.4 mm) in diameter, hatch in seven days into wormlike young that begin a sessile lifestyle immediately. *Saccoglossus kowalevskii* is a direct-developing species that hatches from eggs into the adult form without the planktonic larval stage common to many other hemichordates.

CONSERVATION STATUS

Not listed by IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Hawaiian acorn worm

Ptychodera flava

ORDER

No order designation

FAMILY

Ptychoderidae

TAXONOMY

Ptychodera flava Eschscholtz, 1825.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The adult is a yellowish brown animal with a small cone-shaped proboscis, short collar, and long trunk.

DISTRIBUTION
Pacific Ocean, particularly near Hawaii and Japan.

HABITAT
Coastal marine waters.

BEHAVIOR
Spawning times are related to sea water temperatures. In Hawaii, these acorn worms spawn in late November to early December, usually around 6 P.M. or dusk.

FEEDING ECOLOGY AND DIET
The diet of *Ptychodera flava* consists of organic food particles.

REPRODUCTIVE BIOLOGY
Fertilization, which is external, occurs when females release mucus-bound eggs into the water, and the males respond by releasing sperm. Fertilization occurs in the sea water. The eggs, which measure about 0.00433–0.00472 in (110–20 µm) in diameter, hatch into tornaria larvae in about two days. Tornaria larvae have a keyhole shape with a sphere above a broadened bell-shaped bottom. Two eyespots are present on the dorsal (upper) surface.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Rhabdopleurida normani

ORDER
Rhalodopleurida

FAMILY
Rhabdopleuridae

TAXONOMY
Rhabdopleura normani Allman, 1869, Norway.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Adults have a cephalic shield, complex collar, and trunk. They can reach 0.1 in (3 mm) long, but typically are about 0.04 (1 mm) in length. There are two tentacled arms rising from the collar. The tentacles may reach 0.06 in (1.5 mm) in length.

DISTRIBUTION
Atlantic and Arctic Oceans, Mediterranean Sea.

HABITAT
These marine hemichordates are sessile colonial organisms found in shallow water up to 33 ft (10 m) deep, clinging to the bottoms or other protected nooks and crannies of rocks, corals, and other hard underwater surfaces. They live in and are confined to a coenecium because of their attachment to a continuous organic stem or stolon.

BEHAVIOR
Adult individuals are known as zooids. They live in separate, translucent tubes within a coenecium built out of secretions from their cephalic shields. The zooids are attached to a stolon and are unable to leave the coenecium. The larvae, on the other hand, use their cilia for swimming.

FEEDING ECOLOGY AND DIET
Individual adult *R. normani* worms feed by poking their proboscis, or cephalic shields, out of the coenecium and extending their two ciliated "arms" into the water. Although it has been suggested that other hemichordates use the mucus they secrete to transport food items, recent research indicates that individuals of this suspension-feeding species beat their cilia to draw food particles toward the mouth and do not rely on mucus to trap their food.

REPRODUCTIVE BIOLOGY
R. normani engages in sexual and asexual reproduction. Asexual budding occurs at the stolon, which runs along the bottoms of the tubes and forms connections among the zooids. Sexual reproduction occurs throughout the year. Females secrete tubes that are coiled at the base. The coils serve as brood chambers for one to seven eggs, which are deposited at different times, and therefore are at different developmental stages. The eggs are yolky, a creamy yellow in color, and about 0.0078 in (200 µm) in diameter. Each larva hatches and grows to a size of 0.016–0.018 in (400–450 µm). At that point, it swims past the other eggs and exits the tube. The larva continues swimming in search of its own place to settle on the bottom.

CONSERVATION STATUS
Not listed by IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Spaghetti worm
Saxipendium coronatum

ORDER
No order designation

FAMILY
Saxipendiidae

TAXONOMY
Saxipendium coronatum Woodwick & Sensenbaugh, 1985, near "Rose Garden" geothermal vent, Galápagos Rift, at a depth of 8130 ft (2478 m).

OTHER COMMON NAMES
Italian: Verme tentacolato.

PHYSICAL CHARACTERISTICS
A long thin yellowish-white hemichordate, this species can reach 6.6–9.8 ft (2–3 m) in length. The proboscis is tapered to a soft point toward its front, and the collar is short.

DISTRIBUTION
Near the Galápagos Islands.

HABITAT

Found near hydrothermal vents in the deep sea, loosely attached to rocks.

BEHAVIOR

Little is known about the behavior of this species, but individuals are typically seen in "tortuous coils, wrapped upon themselves and welded in mucus."

FEEDING ECOLOGY AND DIET

Little is known about the diet of *S. coronatum*.

REPRODUCTIVE BIOLOGY

Fertilization is external; otherwise, little is known about this species' mode of reproduction.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

Books

Barrington, E. J. W. *The Biology of Hemichordata and Protochordata.* San Francisco: W. H. Freeman and Co., 1965.

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Halanych, K. M. "Suspension Feeding by the Lophophore-Like Apparatus of the Pterobranch Hemichordata *Rhabdopleura normani*." *Biology Bulletin* 185 (December 1993): 417–427.

Hart, M. W., R. L. Miller, and L. P. Madin. "Form and Feeding of a Living *Planctosphaera pelagica* (Phylum Hemichordata)." *Marine Biology* 120 (1994): 521–533.

Lester, S. M. "Ultrastructure of Adult Gonads and Development and Structure of the Larva of *Rhabdopleura normani* (Hemichordata: Pterobranchia)." *Acta Zoologica (Stockholm)* 69, no. 2 (1988): 95–109.

Organizations

British & Irish Graptolite Group. c/o Dr. A. W. A. Rushton, The Natural History Museum, Cromwell Rd., South Kensington, London, SW7 5BD United Kingdom. Web site: <http://www.graptolites.co.uk/>

The Graptolite Working Group of the International Palaeontological Association. c/o Dr. Charles E. Mitchell, Department of Geology, State University of New York at Buffalo, Buffalo, NY 14260-3050 United States. E-mail: cem@acsu.buffalo.edu Web site: <http://www.geology.buffalo.edu/gwg/index.htm>

Other

"Chris Cameron's Homepage." (15 July 2003). <http://cluster3.biosci.utexas.edu/faculty/cameronc/CBC.htm>.

"Hemichordate Phylogeny." University of Washington Faculty Web Server. (15 July 2003). <http://faculty.washington.edu/bjswalla/Hemichordata/hemichordata.html>.

Leslie Ann Mertz, PhD

◆

Ascidiacea

(Sea squirts)

Phylum Chordata

Class Ascidiacea

Number of families 24

Thumbnail description
Benthic, solitary, and colonial species whose adults are sessile, almost exclusively fixed, firmly attached, or lying free on the sea floor; they usually filter feed; larvae are free swimming

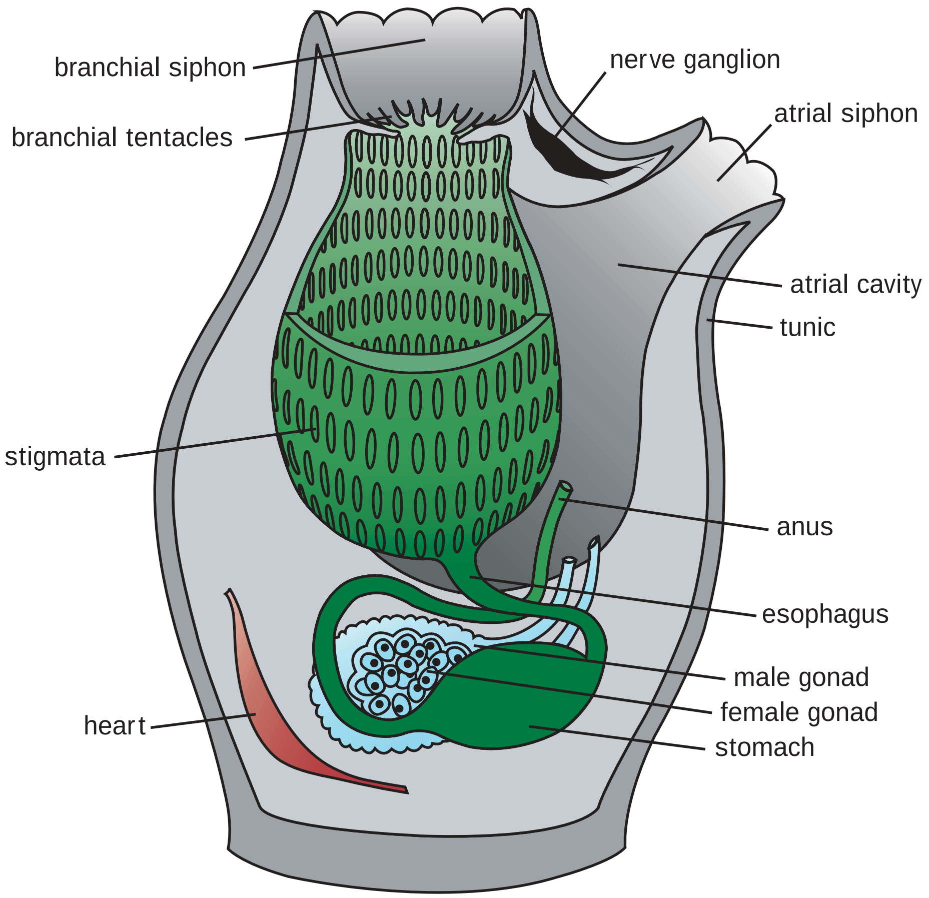
Photo: These tunicates (*Phallusia julinea*) have a larval stage with notochord, forerunner of the vertebrate spine. (Photo by ©David Hall/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

There are very few fossil organisms that can be interpreted as ascidians: ascidians have no hard skeleton elements or calcareous shells, making it unlikely that their soft bodies can be fossilized. The single known fossil species (from the Pliocene), *Cystodytes incrassatus*, belongs to the widely distributed recent genus *Cystodytes*, characterized by the presence of relatively large (up to 0.04 in, or 1 mm, in diameter) spicules of discoid form, allowing easy identification. Another, much more ancient (about 300 million years old) form, *Jaekelocarpus oklahomensis*, has been interpreted as a tunicate, but recent ascidian taxonomists do not support this view. Thus, in the absence of paleontological data, phylogenetic relationships of ascidians can be understood mainly on the basis of the morphological characteristics of the recent forms.

The nature and relationships of ascidians were not understood for a long time, although these common marine animals were known even to Aristotle, more than 2,300 years ago. Earlier authors, including Carl Linnaeus, placed colonial ascidians in Zoophytes, a compound group that contained many different unrelated taxa, while the solitary ascidians were regarded as members of the phylum Mollusca. This view was based mostly on a wrong opinion, that the tunic, or the test, covering the body of adult ascidians is a modification of the calcareous shell of mollusks; furthermore, solitary ascidians and bivalve mollusks both are filter feeders and have two siphons, intruding and extruding. In 1816 J. C. Savigny first recognized the common nature of the solitary and colonial ascidians, as well as some pelagic forms, and in the same year J. B. Lamarck created the group Tunicata. He believed that it was a distinct class between Alcyonaria and Vermes, although other authors still treated this group as a class Molluscoides of Mollusca. From 1867 to 1872 the Russian embryologist A. Kowalevsky published several works on larval development and morphological characteristics of ascidians and was the first to recognize the close relationship between ascidians and chordates. Kowalevsky showed that the development of ascidians was similar to that of lancelets, a small group of primitive chordate animals now placed in the subphylum Cephaolchrodata of the phylum Chordata.

There are three important features linking ascidians and other tunicates with the chordate animals. First there is the presence of a notochord, a rod of specialized cells in the tail of ascidian larvae. The notochord disappears during the metamorphosis from free-swimming larva to sessile adult ascidian. In lancelets it is well developed in adults. In adult vertebrates the chorda dorsalis is wholly retained only in some fishes or is represented by remnants between the vertebrae. Second, a dorsal hollow nerve chord also is present only in ascidian larvae and disappears in adults. It lies dorsal to the notochord,



Tunicate anatomy. Tunicates are invertebrate chordates. (Illustration by Laura Pabst)

as in chordates, whereas it is always ventral in other phyla of invertebrate animals. Third, pharynx perforations, or gill slits, known in Ascidiacea as "stigmata," are present in all chordates, at least during embryonic development, but such structures are never present in invertebrate animals.

Class Ascidiacea belongs to the subphylum Tunicata and is divided into two orders: Enterogona (with two suborders, Aplousobranchia and Phlebobranchia) and Pleurogona (with one suborder, Stolidobranchia). The definition of the orders is based entirely on embryonic characters and reflects the origin of the atrial cavity—from a single or paired dorsal invaginations. For practical purposes, taxonomists use mostly suborders, saying that the ascidians are divided into three main groups, Aplousobranchia, Phlebobranchia, and Stolidobranchia. This subdivision is based mostly on the morphological features of adults, in particular, the structure of the branchial sac, the position of the gut, and some other features. This subdivision does not reflect colonial organization: Stolidobranchia and Phlebobranchia contain mostly solitary species but also include colonial species, and most Aplousobranchia are colonial, but some species are solitary.

There are 24 families, and, at present, about 185 (from about 240 described) genera are treated as valid. The number of valid species is more difficult to count; the estimated number is 2,500–2,800. The interesting peculiarity of the ascidian classification is the relatively small number of genera in relation to the number of species. More than half of all known species belong to 10 very large genera listed here in decreasing order of number of species: *Aplidium*, *Didemnum*, *Molgula*, *Polycarpa*, *Ascidia*, *Styela*, *Eudistoma*, *Pyura*, *Cnemidocarpa*, and *Synoicum*. Most genera are well separated and can be identified easily, but species identification is often much more difficult. In general, the current ascidian classification seems to be close to the ideal, or "natural," system; that is, it appears to reflect the real phylogenetic relationships between taxa.

Physical characteristics

Usually, ascidians are described as sessile organisms with sac-like bodies firmly attached by the posterior end to the substratum. In reality, the shape of different ascidian species may be very diverse, and sometimes it is even difficult to recognize them as belonging to Ascidiacea. Although they grow side by side, is hard to imagine that the large, upright, cylindrical, solitary *Ciona* species belong to the same order as the *Didemnum*, which look like thin, encrusting stones and resemble a sponge colony.

Painted tunicates (*Clavelina picta*) in Saba, Dutch Antilles. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

The body is always covered with the test, a protective layer of cellulose-like material secreted by the epithelium. The test may be clear and often brightly colored, as in the spectacular Pacific species *Halocynthia aurantium*, or it may be covered by various kinds of spines, as in the northern *Boltenia echinata*; it even may contain calcareous spicules, as in snow-white *Bathypera ovoida*. Among species living on a sandy or muddy bottom, the test often has long, thin outgrows, or test hairs, and sometimes is covered by a dense layer of sand grains, making the specimen cryptic, like many species of the family Molgulidae.

The body muscles typically are arranged in transverse and longitudinal bands. Sometimes they are numerous, thick, and strong, forming a solid muscular wall; in many species, however, the muscles are represented by only a few thin fibers. There are two openings on the body: an oral or branchial opening and an atrial opening. These openings may be sessile or set on the ends of siphons of various lengths, the atrial siphon always dorsal to the branchial siphon. The oral siphon leads to the voluminous pharynx, called in ascidians the "branchial sac," The branchial sac occupies most the space in the body of solitary ascidians. The space inside the branchial sac is the branchial cavity, and the space between the branchial sac and the body wall is the atrial cavity. The atrial cavity opens to the exterior through the atrial siphon, and the branchial and atrial cavities are filled with seawater. The seawater, with food particles and oxygen, is drawn into the branchial sac through the branchial siphon and a circle of oral tentacles and passes from the branchial to the atrial cavity through numerous perforations in the wall of the branchial sac, where food items are sieved; then filtered water moves out from the body through the atrial siphon.

Perforations of the wall of the branchial sac generally are small and have ciliated margins called stigmata, The shape of the stigmata is an important taxonomic character: they may be straight and arranged in transverse or sometimes longitudinal rows, or they may be spiral figures, sometimes forming high funnels protruding into the branchial cavity. The wall of the branchial sac has transverse and longitudinal branchial vessels crossing each other and forming rectangular meshes. In some deepwater ascidians true stigmata are absent, the wall of the branchial sac is reduced, and the branchial sac is represented only by wide rectangular meshes formed by crossing longitudinal and transverse branchial vessels. The branchial sac is bilaterally symmetrical, with its mid-dorsal line marked by a fold termed the "dorsal lamina." The mid-ventral line has an endostyle, a groove lined with ciliated glandular epithelium secreting mucus. The mucus constantly moves from the endostyle to the dorsal lamina and then, with the filtered food particles, to the esophagus, to which the bottom of the branchial sac opens. The esophagus typically is short and always is much narrower than the branchial sac. It leads to the stomach and then to the intestine. The intestine makes a loop and opens into the atrial cavity.

The position of the gut loop in relation to the branchial sac is an important taxonomic character of the suborder and family levels: the gut loop may be on the left or, in one family, on the right side of the branchial sac; between the branchial sac and the body wall; or, mostly in colonial ascidians, under the branchial sac. Gonads are hermaphroditic and situated in the gut loop, under the gut, or on the body wall on the sides of the branchial sac. Gonoducts always open into the atrial cavity, and only in one highly specialized genus do they penetrate the test and open directly to the exterior. The nervous system, as in all sessile animals, is simple and represented by an elongated ganglion situated on the dorsal side between the siphons and a few nerves running from it. The heart is a thin-walled tubular organ on the ventral side of the body or, in colonial ascidians, in the bottom of elongated zooids.

In the case of colonial ascidians, the test forms the so-called common test, a mass in which individuals, called "zooids," are completely or partly embedded. The general plan of the structure of the zooids is the same as in solitary ascidians, but details may differ significantly. The body may be undivided or divided into two (thorax and abdomen) or three (thorax, abdomen, and post-abdomen) regions. The thorax contains the branchial sac, the gut loop is in the abdomen, and the gonads are either in the abdomen or the post-abdomen. Branchial siphons of all zooids in a colony open directly to the exterior, but atrial apertures in many species open into the cloacal cavity within the common test. The colony may contain single or several isolated cloacal cavities, each exposed to the exterior through one or several openings. Zooids connected with one cloacal cavity form a system. The shape of the systems varies; zooids may be arranged in circular systems around the single cloacal opening in the center, or they may form long double rows along cloacal canals. The form of the systems usually can be recognized easily on living colonies; the systems make a characteristic pattern on the surface of the colony, which, in certain cases, helps to identify the species.

The size of most ascidians varies from 0.04 to 0.4 in (1–10 mm), rarely 0.6 in (15 cm). Certain species, however, are much larger; in favorable conditions some solitary species may reach

Sea pig (*Halocynthia pyriformis*) nestled into the rocks in the Gulf of Maine. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

19.7 in (50 cm) in height, and thin, encrusting colonies of certain species of didemnids grow to 9.8 sq ft (3 sq m). The largest species is the colonial Antarctic *Distaplia cylindrica*; its long, sausage-shaped colonies may be up to 23 ft (7 m) in length and 3 in (8 cm) in diameter. The smallest species is the deepwater *Minipera pedunculata*, whose diameter is only 0.02 in (0.5 mm).

Many ascidians are brightly colored, usually red, brown, and yellow or, rarely, blue. The coloring of colonial ascidians is especially diverse: that of the zooids and the common test may be different, resulting in complex, often very beautiful patterns on the colony surface. Some species, such as *Clavelina*, have a transparent body, often marked with variously colored spots and lines.

Many ascidians have a peculiar feature: they are able to accumulate vanadium. More primitive species tend to have higher levels of vanadium in their tissues.

Distribution

Ascidians are distributed widely in all oceans and seas, from the intertidal zone to the abyssal depths. In exceptional cases, species can survive in brackish or freshwater. Several species have expanded outside their original range and propagated all over the world. For example, *Molgula manhattensis*, naturally distributed on the Atlantic coast of North America from Maine to Louisiana, was found in large numbers on the Pacific coast in San Francisco Bay in the 1950s, and later it was introduced into Japan on ships' hulls. In 1975 it was recorded in Australia, and in 2000 it was recorded in large numbers on the Russian coast of the Sea of Japan.

Habitat

Ascidians cover a wide range of benthic habitats. Most species require a hard substratum and firmly attach themselves to rocks, stones, shells, algae, and so on. Other species are adapted for living on soft, muddy or sandy bottoms; such species are not firmly attached but often have thin hairlike outgrows on the test, anchoring them in the mud. There is a group of several interesting interstitial species: these rarely recorded minute species live between gravel grains; some of them are not fixed and can move. Ascidians occur from the intertidal zone to abyssal depths and have been recorded in all deepwater trenches; the maximal recorded depth is 27,560 ft (8,400 m). Most species inhabit shallow waters, some of them, such as the thin calcified colonies of certain didemnids, can survive on the open shores under strong wave actions.

Behavior

Ascidians are sessile, usually firmly fixed to the substratum. In response to an external stimulus, they can only slowly contract the body and close the siphons. Some of the very few interstitial species can actively move between gravel particles. Very slow movement of the colony also has been recorded in one or two tropical colonial species. Abyssal *Situla* and *Megalodicopia* species can quickly close their enormously large, bilobed branchial siphons in attempt to catch small swimming invertebrates, such as copepods.

Feeding ecology and diet

Almost all ascidians are filter feeders. The cilia lining the stigmata on the pharyngeal wall constantly pump water with suspended organic particles through the branchial sac. This feeding method is called active filtration: an ascidian expends energy to create a steady flow of water through the branchial sac. With the filtration membrane, a constantly moving mucous sheet on the inner surface of the branchial sac, ascidians are able to capture very fine organic particles including bacteria and phytoplankton. The species living in water with higher concentrations of suspended particles usually have more complex and dense branchial sacs; the stigmata in these species typically are small and numerous, and high branchial folds increase the branchial surface.

At great depths, water contains very little organic matter. Ascidians having the usual type of branchial sac, with ciliated stigmata, are very small in size there. Some deepwater species, such as *Culeolus*, have lost true ciliated stigmata; the branchial sac in such species resembles a loose net made by the crossing vessels, without tissue between them. These branchial sacs have less resistance to water flow than do the dense filters of shallow-water ascidians. These species typically have very large, widely opened branchial siphons oriented to the water current, allowing so-called passive filtration: water passes through the branchial sac without any muscular action or beating of the cilia, thus saving energy. Such highly adapted abyssal species often are large. Ascidians of the family Octacnemidae have a mixed diet. Some of them apparently can catch small swimming invertebrates with their large, bilobed branchial siphons.

Reproductive biology

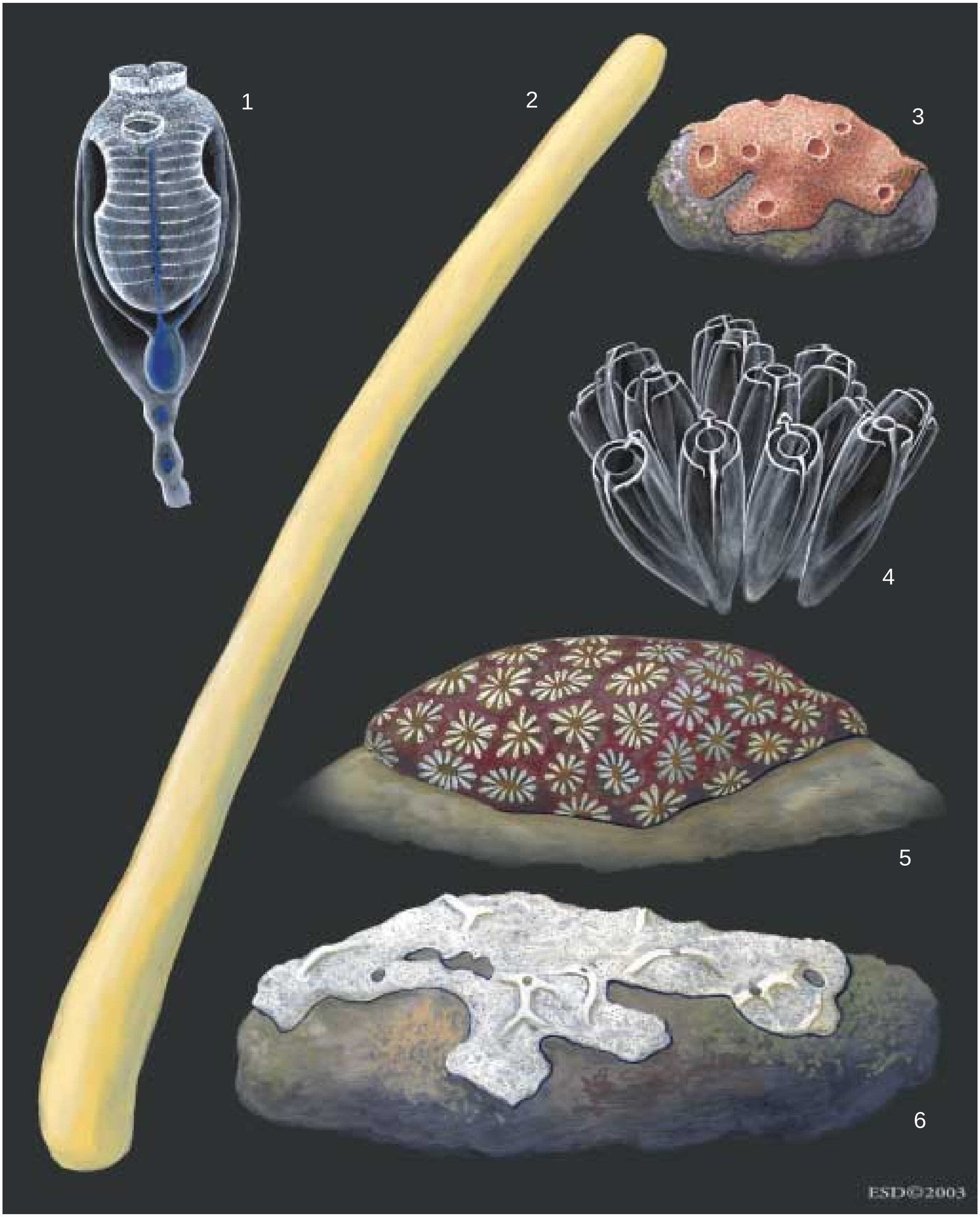
All ascidians are hermaphroditic. All colonial species of the suborder Aplousobranchia are viviparous; in these species ova are fertilized internally and developed within the parent colony, in the atrial cavity of zooids or in special outgrowths of the zooid body wall, termed brood pooches, or in the common test of the colony. Viviparous species release swimming larvae. Solitary species are either viviparous or oviparous, releasing ova. In viviparous solitary species, larvae are incubated in the atrial cavity. Ascidian larvae are called tadpole larvae. Larvae have an oval trunk, usually less than 0.04 in (1 mm) long, and a tail that is longer than the trunk. The larval trunk contains the larval organs, including the cerebral vesicle with a light receptor and statocyte and adhesive papillae on the anterior end, and a rudiment of the future adult. In many colonial species this rudimentary ascidian within the larval trunk is rather well developed and resembles a zooid of the adult ascidian. Sometimes, as in colonial *Diplosoma*, the larval trunk may contain two or more future zooids. Ascidian larvae never feed; they swim for a short time and then attach to the substratum and start metamorphosis. During metamorphosis all larval organs degenerate, and an ascidian develops from the rudiment located in the larval trunk. In the case of solitary ascidians only one specimen develops from each larva, whereas in colonial ascidians individuals (zooids) replicate themselves by asexual reproduction (budding) and form a colony.

Conservation status

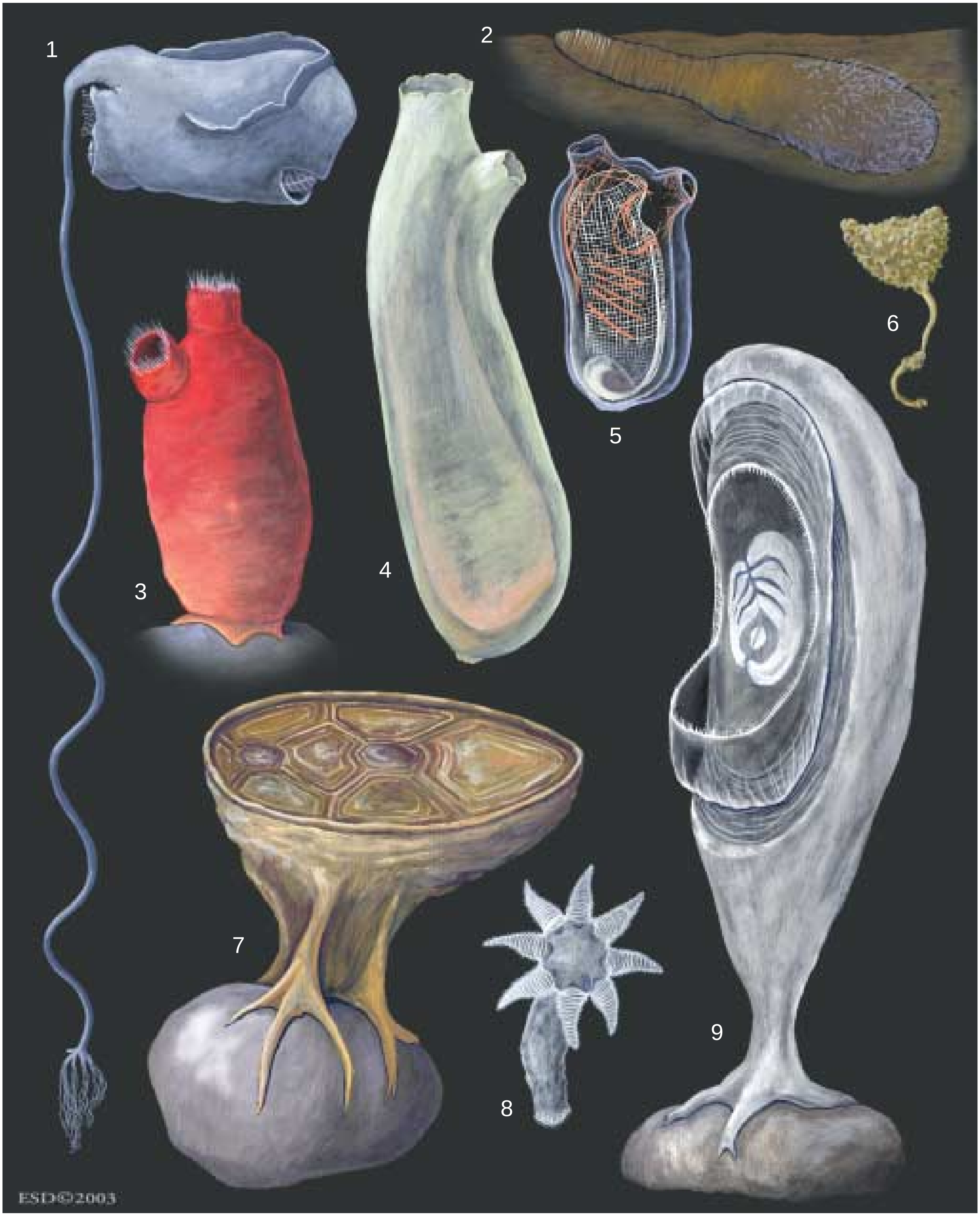
No species of Ascidiacea are listed by the IUCN.

Significance to humans

Ascidians have no direct and important significance to humans. Like many other marine organisms, they are a potential source for bioactive chemicals that may be used in pharmacology. Also, several species are consumed as food in some countries, for example, Japan. Some species may cause problems in fish farming operations, growing on the bottoms of ships and negatively affecting operations such as mussel and oyster cultivation.



1. *Clavelina dellavallei*; 2. *Distaplia cylindrica*; 3. *Didemnum commune*; 4. *Clavelina lepadiformis*; 5. *Botryllus schlosseri*; 6. *Didemnum studeri*. (Illustration by Emily Damstra)



1. *Culeolus likae*; 2. *Pelonaia corrugata*; 3. Sea pig (*Halocynthia pyriformis*); 4. *Ciona intestinalis;* 5. *Corella parallelogramma*; 6. *Hartmeyeria triangularis*; 7. *Chelyosoma orientale*; 8. *Octacnemus kottae*; 9. *Situla pelliculosa*. (Illustration by Emily Damstra)

Species accounts

No common name
Ciona intestinalis

ORDER
Enterogona

FAMILY
Cionidae

TAXONOMY
Ascidia intestinalis Linnaeus, 1767, Europe.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Cylindrical body up to 5.9 in (15 cm) in length, attached by posterior end. Test soft and translucent, colorless. Siphons are prominent and terminal, the branchial siphon marked by eight and the atrial siphon by six red pigment spots on the margin.

DISTRIBUTION
One of the most widely distributed, almost cosmopolitan ascidian species, especially abundant along the coasts of northern Europe. Recorded also in the Mediterranean Sea, along the Atlantic coast of North America and parts of the Atlantic and Pacific coasts of South America, California, Hawaii, South Africa, Australia, New Zealand, and Japan.

HABITAT
Occurs on rocks, stones, shells, and algae at depths from 0 to about 1,640 ft (0–500 m).

BEHAVIOR
Solitary species, often forming large populations of many crowded specimens. Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Ova released directly into seawater through the atrial siphon. Larvae are not incubated in the atrial cavity.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
Often used as a laboratory specimen for various general types of biological research, in particular, cell biology and embryology.

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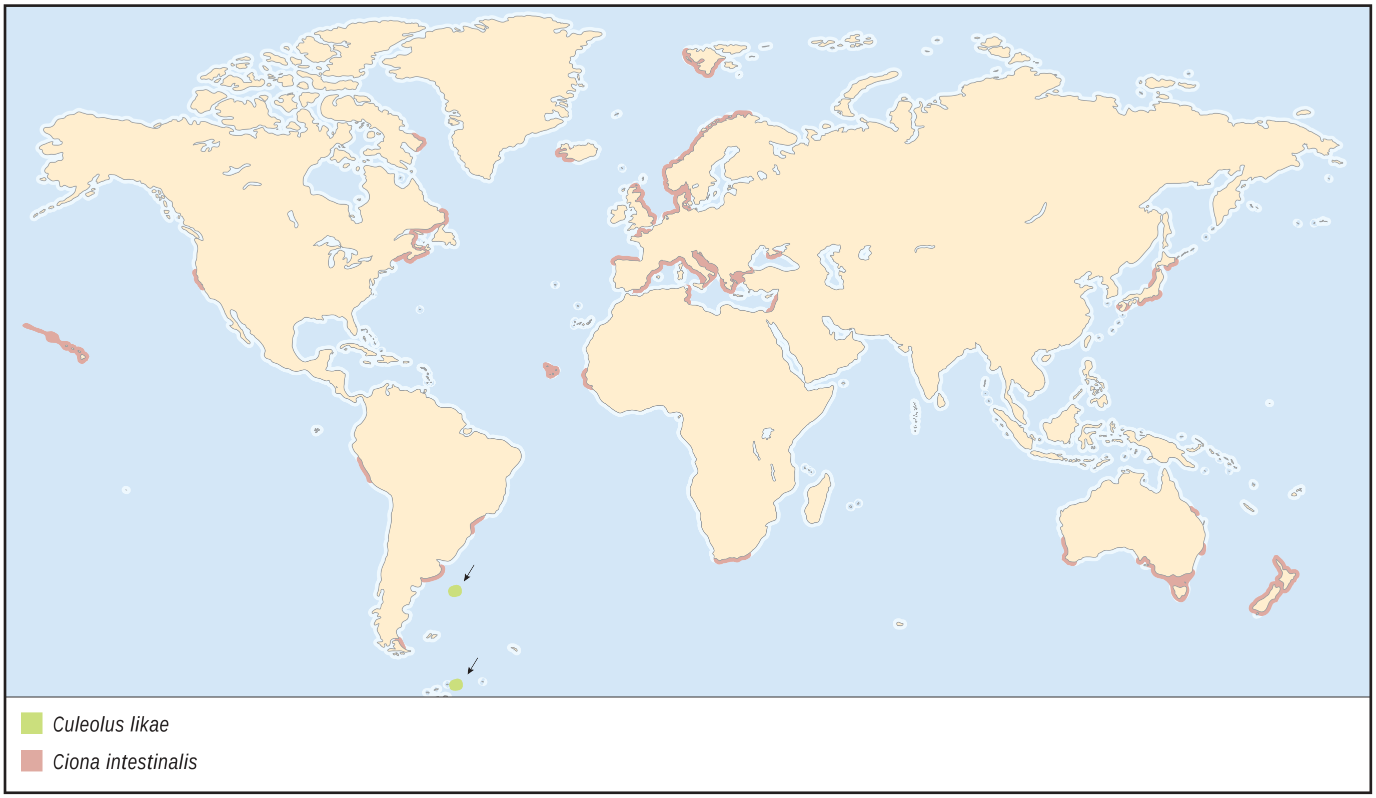
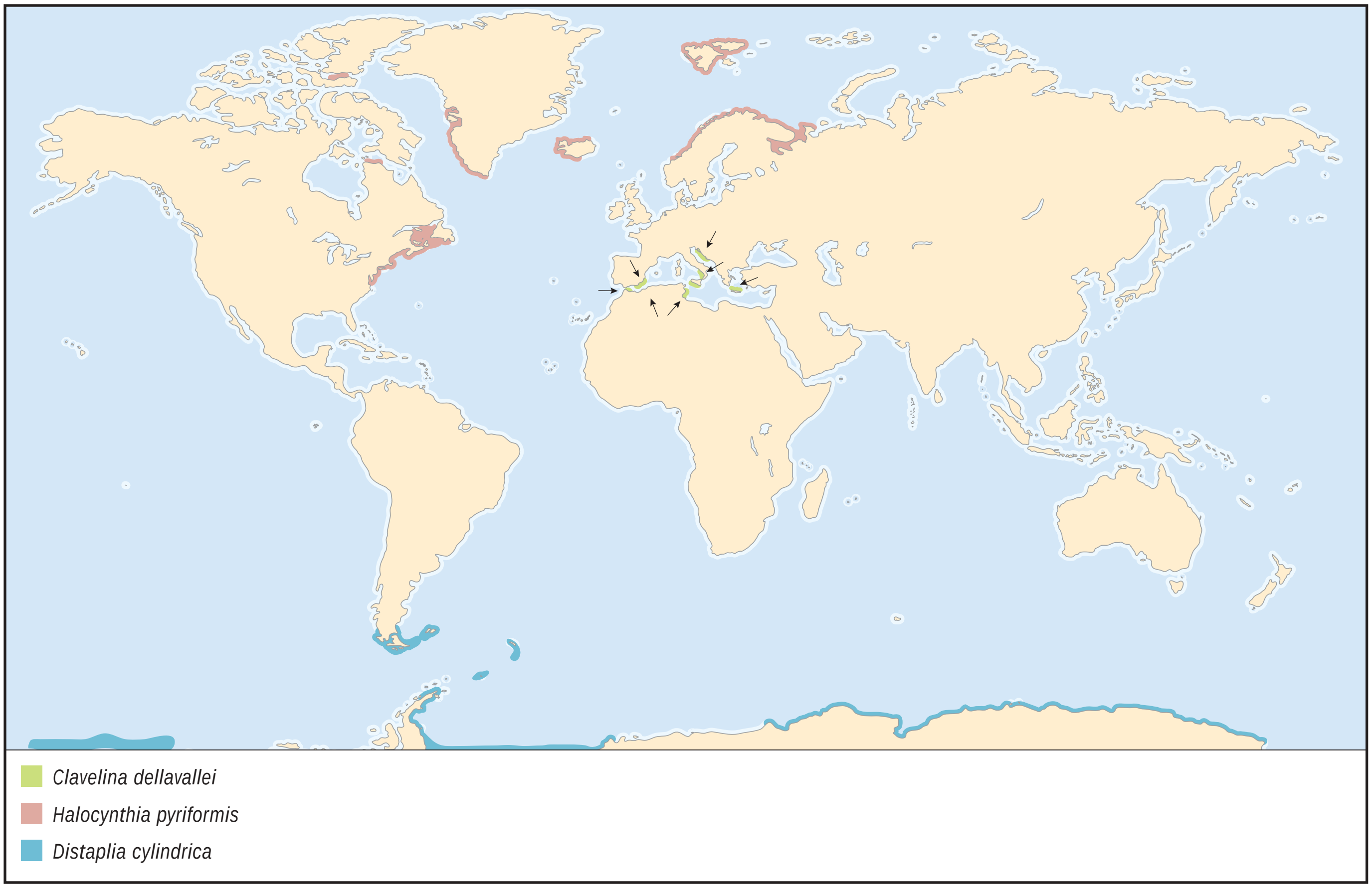


🟩 *Culeolus likae*

🟥 *Ciona intestinalis*



No common name

Clavelina dellavallei

ORDER

Enterogona

FAMILY

Clavelinidae

TAXONOMY

Bradiclavella dellavallei Zirpolo, 1925, Naples Gulf, Italy.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Colonial species. Colony consists of a few, sometimes only one, upright zooids connected by basal stolons. Zooids are club-shaped, up to 2.4 in (6 cm) in length, and taper basally to a thin stalk. There are two large, plain-edged terminal siphons. Test is completely transparent, and all internal organs are clearly visible through it. The only opaque organ is the small gut loop; it is situated under the branchial sac and has deep blue coloring. Two vertical blue lines are seen inside the branchial sac, corresponding to the dorsal lamina and the endostyle.

DISTRIBUTION

This species is known only from the Mediterranean Sea.

HABITAT

Rocky bottoms at depths from 33 to 295 ft (10–90 m).

BEHAVIOR

Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET

Filter feeder.

REPRODUCTIVE BIOLOGY

Embryos are incubated in the atrial cavity on the right side of the branchial sac; they are very numerous, up to 50 in each zooid.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

No common name

Clavelina lepadiformis

ORDER

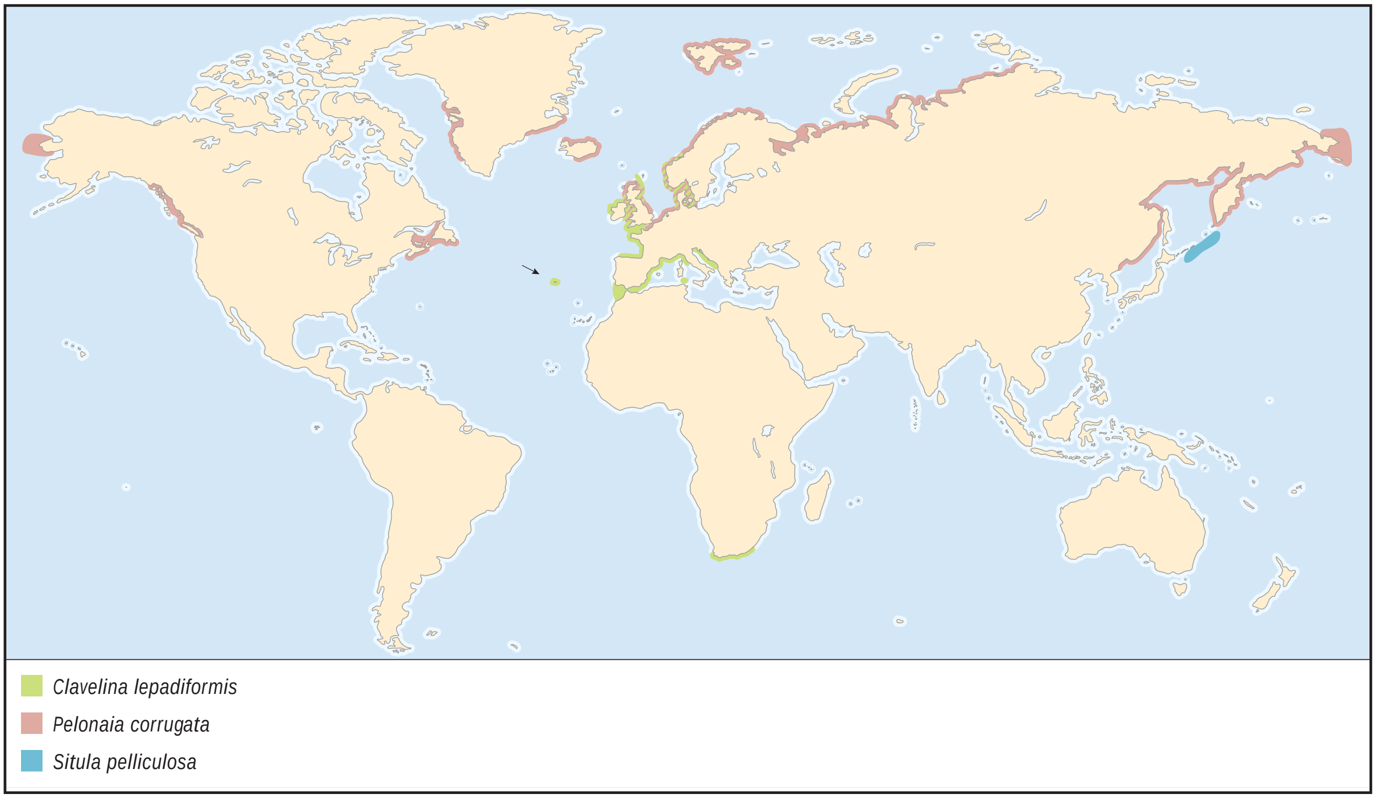
Enterogona

FAMILY

Clavelinidae

TAXONOMY

Ascidia lepadiformis Mueller, 1776, Norwegian fjords.



OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial species. Colony consists of numerous upright (up to 1.2 in, or 3 cm, in height) zooids united only by their bases. The species can be recognized easily by its color pattern: completely transparent zooids have longitudinal white lines along the endostyle and dorsal lamina, white rings on the siphons and on the upper edge of the branchial sac, and a short white strip between the siphons.

DISTRIBUTION
Europe from western Norway to Spain and the Mediterranean Sea. Local populations are found in Morocco, Madeira, and the Azores. Introduced to South Africa, probably via the bottoms of ships.

HABITAT
Rocky bottom at depths from 0 to 164 ft (0–50 m).

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Larvae incubated in the atrial cavity.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Chelyosoma orientale

ORDER
Enterogona

FAMILY
Corellidae

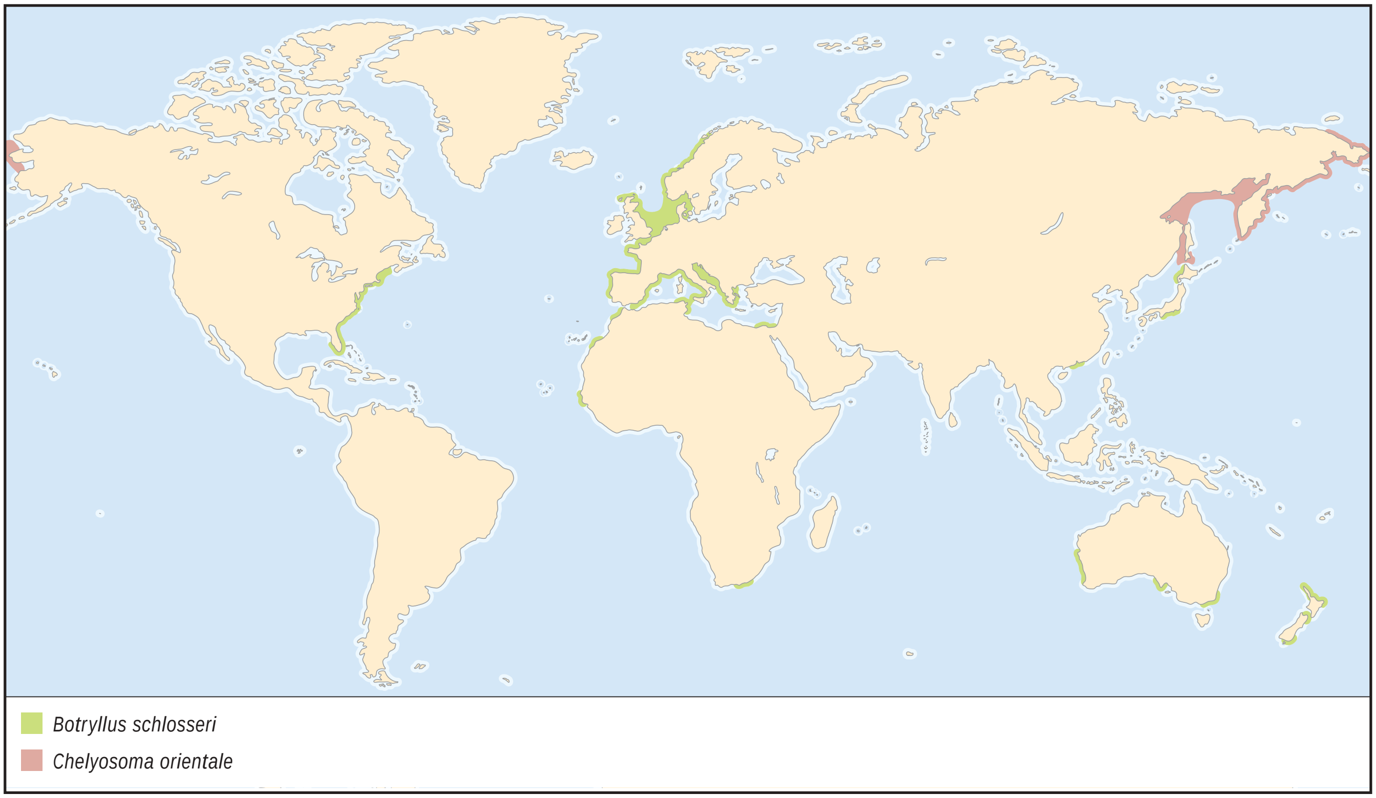
TAXONOMY
Chelyosoma orientale Redikorzev, 1911, Tatarsky Strait, Sea of Japan.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. The external appearance very characteristic: the low, wide body forms a flat disk, up to 3.9 in (10 cm) in diameter, covered by horny plates that have concentric lines of growth. Tunic is very hard, brown. Two sessile siphons on the disk, each siphon surrounded by six triangular plates. When growing on the sandy bottom, the species forms long, thick, root-shaped outgrows firmly anchoring the specimen to the substratum, but these outgrows are not present in specimens attached to stones.

DISTRIBUTION
Northwestern Pacific from the north part of the Sea of Japan to the Bering Strait and Chukchi Sea.

HABITAT
Occurs at depths from 66 to more than 984 ft (20–300 m) on stony, sandy, or muddy bottoms.



BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Nothing is known, except that this species does not incubate larvae.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Corella parallelogramma

ORDER
Enterogona

FAMILY
Corellidae

TAXONOMY
Ascidia parallelogramma Mueller, 1776, Oslo Fjord, Norway.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. Body reaches 2 in (5 cm) in height and is nearly rectangular in outline and attached by the posterior end. Test transparent and colorless; internal organs clearly seen through it. Red lines, making a characteristic pattern on living specimens, are body muscles; they are better developed on the left side of the body.

DISTRIBUTION
Norway, Sweden, North Sea, United Kingdom, and Mediterranean Sea.

HABITAT
On hard substratum (shells, stones, and algae) at depths from 0 to about 656 ft (0–200 m).

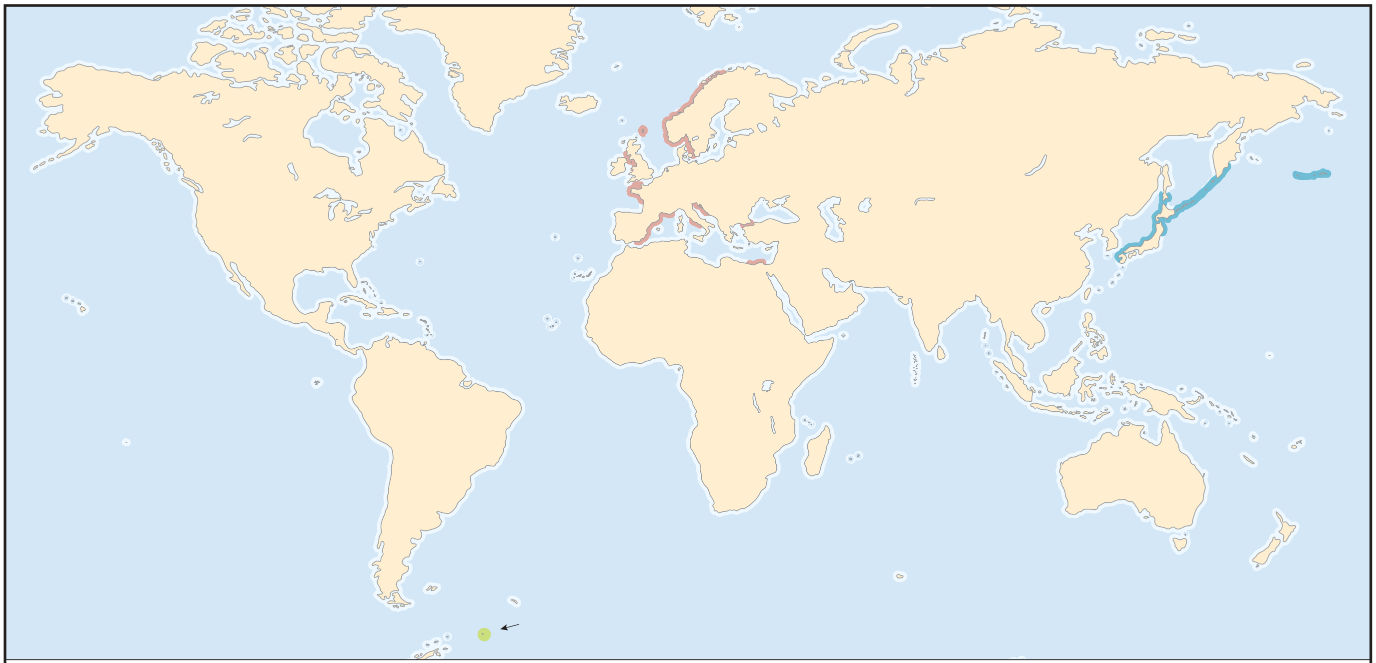
BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Larvae are not incubated in atrial cavity.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆



🟩 *Octacnemus kottae*
🟥 *Corella parallelogramma*
🟦 *Hartmeyeria triangularis*

No common name

Didemnum commune

ORDER
Enterogona

FAMILY
Didemnidae

TAXONOMY
Leptoclinum commune Della Valle, 1877, Naples Gulf, Italy.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial species with small (up to 1.2 in, or 3 cm, in diameter), red, encrusting colonies. Colony contains numerous minute calcareous spicules and feels hard to the touch. Very small zooids are completely embedded in the common test; numerous small openings of branchial siphons and several larger cloacal openings are seen on the colony surface.

DISTRIBUTION
European coasts of the Mediterranean Sea.

HABITAT
Rocky bottoms at depths from 0 to 230 ft (0–70 m). Common below intertidal zone, crevices, and caves exposed to strong wave actions.

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Larvae found in the colony from April to October.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Didemnum studeri

ORDER
Enterogona

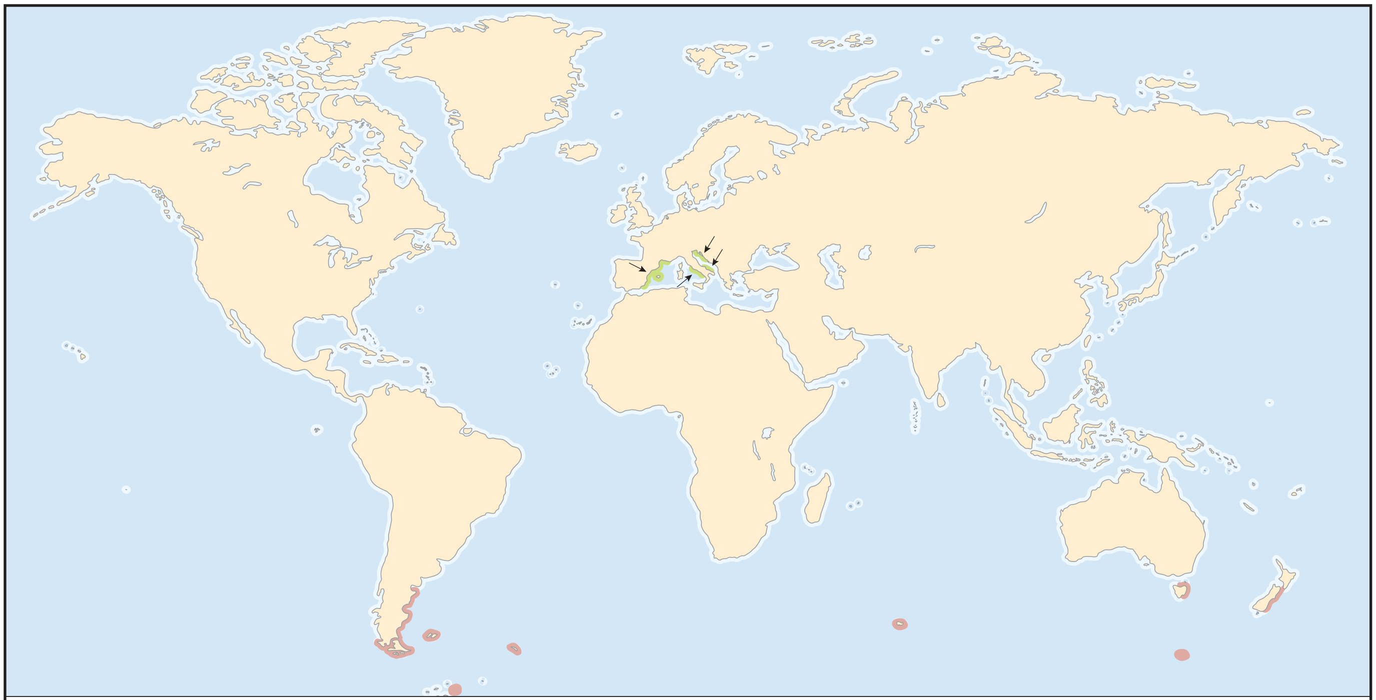
FAMILY
Didemnidae

TAXONOMY
Didemnum studeri Hartmeyer, 1911, Kerguelen Islands.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial species forming thin stone colonies on rocks, which may reach 0.4 ft (1 m) or more in diameter, while the thickness is always less than 3.3 in (5 mm). Colony contains minute calcareous spicules and is white.

DISTRIBUTION
Circumpolar in the subantarctic. Especially common in the Strait of Magellan and surrounding islands.



🟩 *Didemnum commune*

🟥 *Didemnum studeri*

HABITAT
Grows on stones and rocks and often found on roots or stems of algae. Occurs at depths from 16 to 5,554 ft (5–1,693 m) but chiefly in shallow waters.

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Larvae incubate in colony in September.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Distaplia cylindrica

ORDER
Enterogona

FAMILY
Holozoidae

TAXONOMY
Holozoa cylindrica Lesson, 1830, Magellan Strait.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial species with very long, sausage-shaped colonies. This species is the largest known ascidian; the colonies may reach 23 ft (7 m) in length and 3 in (8 cm) in diameter. Colony is white or yellowish and soft to the touch; it is attached by one end to rocks and grows vertically. As for most ascidians, individual zooids are small and located only in the superficial layer of the colony, where they form numerous small, oval systems.

DISTRIBUTION
Completely circumpolar in the Antarctic.

HABITAT
Rocky bottoms at depths from 66 to 1,444 ft (20–440 m). Sometimes colonies are found floating on the surface, but such detached colonies always have degenerated zooids.

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Hermaphrodite, but zooids in distinct parts of the colony may have different sexual status: some zooids have better developed male gonads, whereas others have better developed female gonads. Zooids with well-developed gonads are found in colonies in December and January; fully developed tailed larvae appear from January to April. Larvae are incubated in brood pooches within parent colony.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Octacnemus kottae

ORDER
Enterogona

FAMILY
Octacnemidae

TAXONOMY
Octacnemus kottae Sanamyan and Sanamyan, 2002, west of South Sandwich Trench, Atlantic.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. This transparent abyssal species resembles enlarged zooids of Octocorallia, rather than ascidians. It has a distinct cylindrical peduncle about 1.2 in (3 cm) long and a flattened oral disk with a crown of eight triangular lobes that have well-developed musculature and numerous lateral pinnules.

DISTRIBUTION
Although it is recorded only from the southern Atlantic, near the South Sandwich Islands, the species probably has a wider distribution, because several other records of *Octacnemus* may belong to this species.

HABITAT
Soft, muddy bottoms at depths of 12,140–12,830 ft (3,700–3,910 m).

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Nothing is known about how this and other species of *Octacnemus* feed. Unlike many other ascidians, this species probably is not a filter feeder. In the gut of other *Octacnemus* species, fragments of copepods, polychaetes, and diatoms have been found.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Situla pelliculosa

ORDER
Enterogona

FAMILY
Octacnemidae

TAXONOMY
Situla pelliculosa Vinogradova, 1969, Kurile-Kamchatka Trench, northwestern Pacific.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
This species is one of the most unusual ascidians. Large, up to 13.4 in (34 cm) in height. Upright, very soft body attached to small stones by a short, thick stem. Branchial orifice is enormously large and opens wide, exposing all internal organs. Atrial orifice is small and inconspicuous. Branchial sac is modified to thin, flat membrane; all organs are in small nucleus in the center of this branchial membrane.

DISTRIBUTION
Kurile-Kamchatka Trench, northwestern Pacific.

HABITAT
Abyssal species recorded at depths from 16,400 to 27,560 ft (5,000–8,400 m).

BEHAVIOR
Sessile species.

FEEDING ECOLOGY AND DIET
The species probably has a mixed diet that includes small plankton invertebrates, such as copepods, and fine organic particles obtained by passive filtration.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Culeolus likae

ORDER
Pleurogona

FAMILY
Pyuridae

TAXONOMY
Culeolus likae Sanamyan and Sanamyan, 2002, Scotia Sea between South Georgia and Falkland Islands.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. Barrel-shaped body, 3.1 in (8 cm) in length, is supported on thin and very long, up to 33.5 in (85 cm), peduncle. Peduncle breaks basally into small tufts of delicate rhizoids anchoring the specimen in the mud. Peduncle inserted into anterior end of the body, on ventral side of large and widely opened branchial siphon. Atrial siphon is smaller and situated on the opposite end of the body. Soft and transparent body has characteristic posteroventral crest consisting of three high lamellae.

DISTRIBUTION
Southern Atlantic: recorded between South Georgia and South Falkland Islands and in the Argentine basin.

HABITAT
Abyssal species recorded at 15,301–18,474 ft (4,664–5,631 m).

BEHAVIOR
Immobile species fixed on a stalk.

FEEDING ECOLOGY AND DIET
Passive filter feeder. Large branchial siphon with peduncle inserted near it, oriented in such a way that the bottom current passes through the branchial sac.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Sea pig
Halocynthia pyriformis

ORDER
Pleurogona

FAMILY
Pyuridae

TAXONOMY
Ascidia pyriformis Rathke, 1806, Bergen, Norway.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. Red or purple barrel-shaped body, up to 3.9 in (10 cm) in height, attached by the posterior end to hard substratum. Two well-developed siphons are positioned on the anterior end of body and covered by thin spines. Similar, but smaller spines cover the whole test.

DISTRIBUTION
Arctic North America and north Atlantic coasts of North America; Greenland; Iceland; Spitsbergen, Norway; White Sea; Barents Sea.

HABITAT
Rocky or stony bottoms at depths from 0 to about 656 ft (0–200 m).

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Larvae are not incubated in the atrial cavity.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Hartmeyeria triangularis

ORDER
Pleurogona

FAMILY
Pyuridae

TAXONOMY
Hartmeyeria triangularis Ritter, 1913, Kyska Harbor, Aleutian Islands, Alaska, United States.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species. Small, not exceeding 0.4 in (1 cm) in diameter; triangular and slightly flattened laterally, with body covered by thick layer of sand grains. Two small red siphons are set on opposite ends of upper body and covered by minute spines. Thin and relatively long peduncle anchors the specimen in the sand.

DISTRIBUTION
North Pacific from Alaska and Aleutian Islands to Kamchatka and further south the middle of Japan.

HABITAT
Lives on sandy bottoms at depths from 23 to 98 ft (7–30 m). Apparently cannot survive if the sand contains large amounts of mud.

BEHAVIOR
Immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Botryllus schlosseri

ORDER
Pleurogona

FAMILY
Styelidae

TAXONOMY
Alcyonium schlosseri Pallas, 1766, Falmouth, English Channel.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Colonial species. Colonies usually are flat, encrusting stones or algae, or sometimes lobed. Typically not exceeding 3.9 in (10 cm) in diameter. Zooids completely embedded in common test and arranged in circular systems. Each system has single central, common cloacal opening surrounded by a circle of branchial openings for each zooid. The test is soft and slimy, generally dark brown. Each zooid has a white or yellow strip on the dorsal side between the orifices; whole colony has a beautiful stellate color pattern. The color pattern, however, may vary significantly.

DISTRIBUTION
Common on northern European coasts and the Mediterranean Sea. Recorded on Atlantic coasts of North America, South Africa, Australia, New Zealand, and Japan. There is an opinion, however, that Pacific records belong to another similar, but distinct species.

HABITAT
Shallow-water species may grow on all kinds of hard substratum: stones, shells, and algae.

BEHAVIOR
Sessile, attached, immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Egg fertilization and larvae development occur within parent colony.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Pelonaia corrugata

ORDER
Pleurogona

FAMILY
Styelidae

TAXONOMY
Pelonaia corrugata Forbes and Goodsir, 1841, Firth of Clyde, Scotland.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary species with elongated (up to 3.9 in, or 10 cm long) vermiform body resembling a sipunculid rather than an ascidian. Test is brown and leathery, covered by short, thin hairs. Branchial and atrial apertures are on small sessile siphons close to each other on the anterior, narrower end of the body.

DISTRIBUTION
Widely distributed in cold and temperate waters of Northern Hemisphere, in the North Atlantic and North Pacific, probably circumpolar in the Arctic.

HABITAT
Lives unattached in soft mud or sand at depths from 6.6 to 656 ft (2 to 200 m).

BEHAVIOR
Immobile species.

FEEDING ECOLOGY AND DIET
Filter feeder.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Periodicals

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Karen Sanamyan, PhD

◆

Thaliacea

(Salps)

Phylum Chordata
Class Thaliacea
Number of families 5

Thumbnail description
Marine, holoplanktonic organisms with cylindrical bodies that have openings on both ends

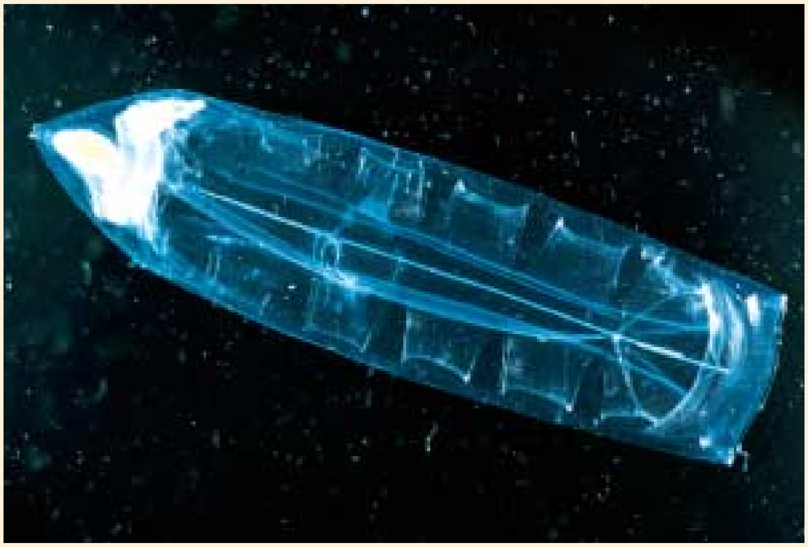


Photo: An open water solitary salp (*Lasis* sp.), seen only in the deep sea. (Photo by ©OSF/Animals Animals. Reproduced by permission.)

Evolution and systematics

The class Thaliacea is made up of three orders, five families, and 73 species. The three orders are Pyrosomatida, with one family and 10 species; Doliolida, with three families and 23 species; and Salpida, with one family and 40 species. Recent work indicates the thaliaceans are an artificial group because each of the orders evidently arose from a different group of benthic tunicates (class Ascidiacea). Evidence for this polyphyly is in comparative embryology and anatomy, where each of the orders show their ascidiacean ancestry to greater or lesser degrees. Their similar body forms are an example of convergent evolution in which animals look alike despite their differing phylogeny. Molecular work being done on thaliaceans should help determine relationships more precisely; consequently, this group may be dismantled and reorganized into separate groups in the future. Salps are related to the benthic tunicate class Ascidiacea.

Physical characteristics

Salps have a cylindrical body, called the test, that is mostly clear with openings called siphons on both ends. One opening is the oral and the other the cloacal siphon. Their body walls appear jelly-like and are therefore grouped as gelatinous zooplankton. Varying numbers of muscle bands are embedded within the gelatinous wall of the test. They range in size from 0.2–7.8 in (5 mm–20 cm), with some colonial forms many feet (meters) in length

Distribution

Thaliaceans are found in tropical and temperate seas. They tend to be found in the epipelagic zone from the surface to 656 ft (200 m), but some have been found in the mesopelagic zone from 656 to 3,280 ft (200 to 1,000 m).

Habitat

Thaliaceans tend to be more abundant in phytoplankton-rich surface waters of tropical and temperate seas. They are free swimming and holoplanktonic (at the mercy of ocean currents during their whole lives). Thaliaceans are often found with hyperiid amphipods living on the outside or even on the inside of their bodies in a symbiotic relationship.

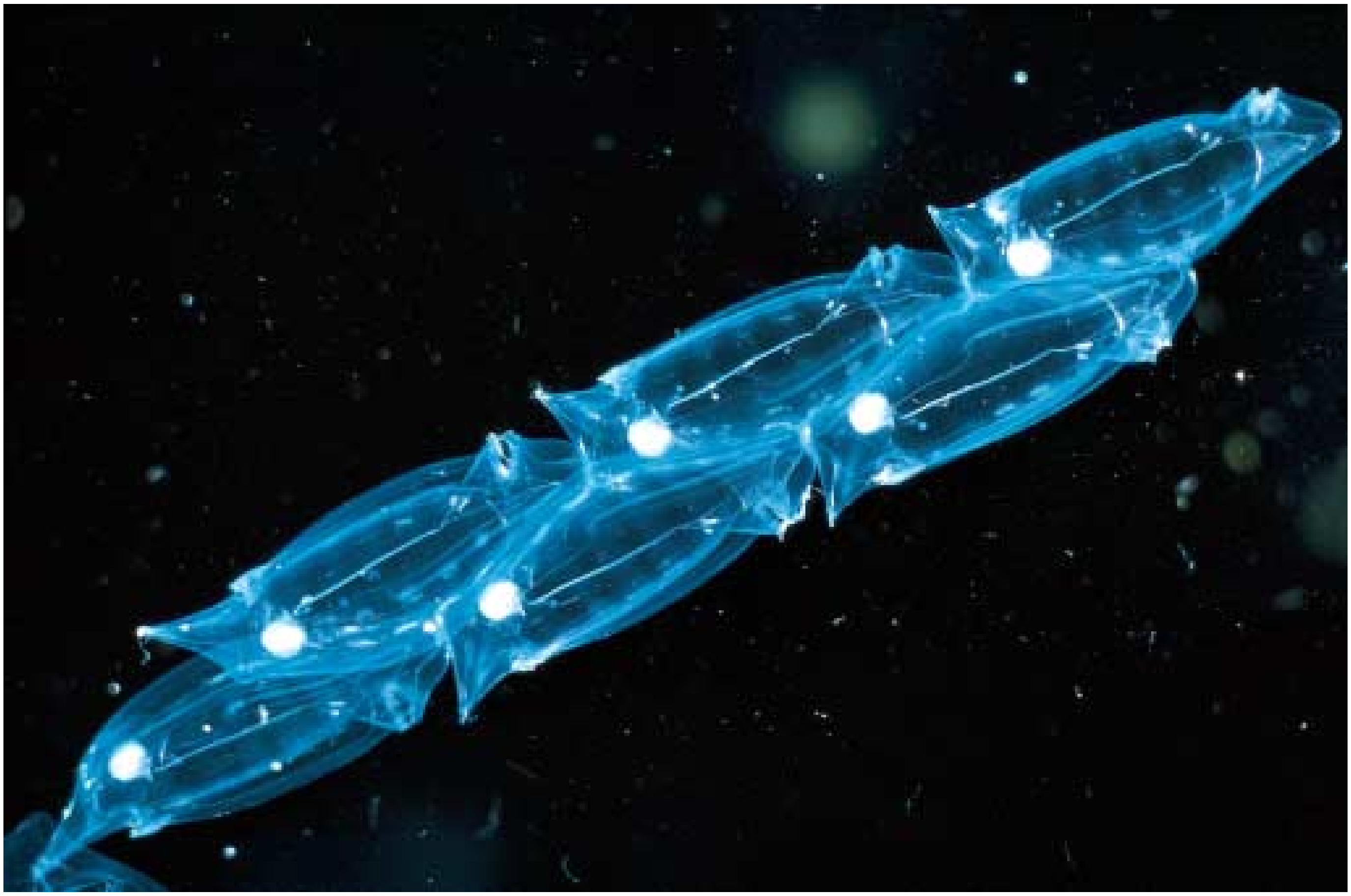
Behavior

They move through the water by either ciliary action, as in the pyrosomatids, or by contraction of muscles embedded in the tunic, as in the doliolids and salps moving water into the oral siphon and out the cloacal siphon.

At times, because of their fast generation time, large numbers of thaliaceans can make up the largest proportion of gelatinous zooplankton.

Feeding ecology and diet

Thaliaceans are all filter feeders upon phytoplankton. Water flows into the oral siphon through a mucous sheet covering a basket and out the cloacal siphon. Phytoplankton and other small organisms are caught on the mucus. The mucus is then moved to the mouth and eaten. Because of their large numbers at certain times of the year, thaliaceans are important consumers of phytoplankton and make a large impact on the flux of carbon because of their production of massive amounts of fecal material.



Chain salps (*Urochordata iasis atlantic*) are abundant in the Atlantic and Indian Oceans. (Photo by ©OSF/Animals Animals. Reproduced by permission.)

Reproductive biology

Alternation of generations enables thaliaceans to colonize seas quickly, taking advantage of phytoplankton blooms resulting in large swarms. One of the generations is asexual with vegetative growth resulting in the sexual stage. The other generation is sexual, which produces the egg and sperm that fuse to make the asexual stage.

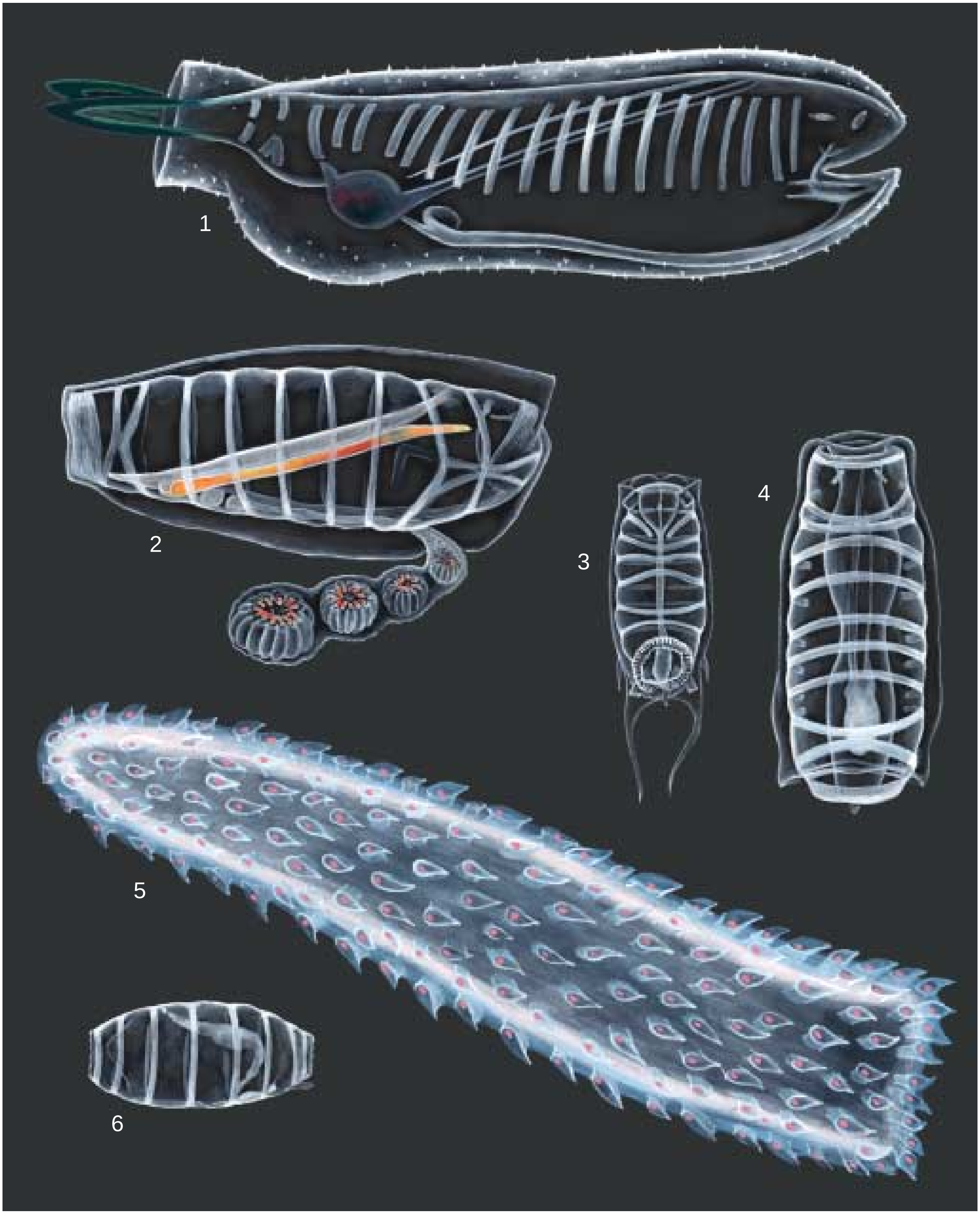
Thaliaceans show different strategies to ensure successful reproduction. Pyrosomatids develop eggs that, when fertilized, develop to hatching inside the zooid. Doliolids retain the tadpole larval stage of their benthic tunicate ancestors during development. Salpids retain both asexual and sexual stages and true embryonic connection (via a placenta) to the parent during development.

Conservation status

Although there is much more to be learned about the ecology of thaliaceans, none of them is known to be in danger of extinction. No species is listed by the IUCN.

Significance to humans

At times, some thaliaceans can become so abundant that they can outcompete other herbivores at the base of the oceanic food web, such as copepods. Copepods are important in the diet of young fish species that humans rely on for food. In this way, the thaliaceans have a negative impact on human fishing activities.



1. Salp (*Thetys vagina*); 2. Salp (*Cyclosalpa affinis*); 3. Salp (*Salpa fusiformis*); 4. Salp (*Thalia democratica*); 5. Pyrosome (*Pyrosoma atlanticum*); 6. Doliolid (*Dolioletta gegenbauri*). (Illustration by Emily Damstra)

Species accounts

Doliolid

Dolioletta gegenbauri

ORDER

Doliolida

FAMILY

Doliolidae

TAXONOMY

Dolioletta gegenbauri (Uljanin, 1884).

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Barrel-shaped, clear, gelatinous body about 0.35 in (9 mm) in length with eight prominent muscle bands in the asexual stage and the 0.47-in (12-mm) sexual stage has nine muscle bands.

DISTRIBUTION

Semi-cosmopolitan in cool waters of both hemispheres. (Specific distribution map not available.)

HABITAT

Little is known about vertical distribution, but commonly found in oceanic surface waters.

BEHAVIOR

Known for their jumpy swimming pattern when disturbed. Swims by contracting muscle bands present in the gelatinous body.

FEEDING ECOLOGY AND DIET

Can feed on a wide variety of food particle sizes ranging from bacteria 0.0002 in (5 µm) to large diatoms >0.00394 in (>100 µm). Can be very important herbivores, completely clearing the waters they inhabit in about two days.

REPRODUCTIVE BIOLOGY

The complicated lifecycle includes an asexual stage (sometimes called a nurse) during which a tail will grow. Many feeding stages bud on the tail, when released they grow a tail on which the sexual stage grows. The hermaphroditic sexual stage releases fertilized eggs that develop into tadpole larvae lacking the characteristic ascidiacean tail; the larvae quickly grows into the asexual nurse stage. Although complicated, the lifecycle helps doliolids respond to blooms of phytoplankton, resulting in blooms of their own, reported to be hundreds of square miles (kilometers) in the open ocean.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆

Pyrosome

Pyrosoma atlanticum

ORDER

Pyrosomatida

FAMILY

Pyrosomatidae

TAXONOMY

Pyrosoma atlanticum (Peron, 1804), Mediterranean Sea.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Individuals called zooids are about 0.33 in (8.5 mm) and embedded in a thick, clear tubular test that can reach 23.6 in (60 cm) in length. Colonies are pink or yellowish pink. The oral siphons of the zooids are on the outer surface of the tube and the cloacal siphon point to the inside. Water comes in the oral siphon and empties into the common opening inside of the tube. One end is closed and the water exits out a common opening at the other end of the colony, propelling it through the water. Each of the zooids is brilliantly bioluminescent and this is the reason for the scientific name of pyrosoma, “fire body.”

DISTRIBUTION

Semi-cosmopolitan in temperate to tropical waters, it is the most common pyrosome. (Specific distribution map not available.)

HABITAT

Commonly seen in surface waters, but daily vertically migrates more than 2,460 ft (750 m).

BEHAVIOR

Known for the brilliant luminescence of each zooid, communication among zooids results in waves of light along the entire colony.

FEEDING ECOLOGY AND DIET

Water passes into each zooid through the oral siphon, into a mucous filter where phytoplankton is filtered out for food. Pyrosomes can form huge swarms that can result in significant quantities of fecal pellets. The sinking pellets can be very important in carbon input into the depths.

REPRODUCTIVE BIOLOGY

Zooids are hermaphrodites, possessing both testis and ovary. In each zooid of the colony a single egg is fertilized, which grows to a four-zooid stage that leaves the parent to start a new colony asexually by budding. This form of reproduction can result in huge swarms of pyrosome colonies that are dependent upon abundant phytoplankton for food.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

The brilliant light displays given off from colonies of pyrosomes have bewildered and fascinated sailors for generations.◆

Salp
Cyclosalpa affinis

ORDER
Salpida

FAMILY
Salpidae

TAXONOMY
Cyclosalpa affinis (Chamisso, 1819).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Both stages possess a clear, barrel-shaped, gelatinous body with circular muscle bands embedded in the body wall. Solitary (asexual) stage 2.9 in (74 mm) in length with seven muscle bands and a thick test. Aggregate form (sexual) is irregularly shaped, about 1.7 in (4.5 cm) long with four muscle bands. The aggregates are connected to form a chain of linked circles.

DISTRIBUTION
Temperate and tropical oceanic waters. (Specific distribution map not available.)

HABITAT
Most commonly found in surface of offshore waters.

BEHAVIOR
The only salp to form chains of linked circles.

FEEDING ECOLOGY AND DIET
Known for the ability to filter small food particles like phytoplankton with 100% efficiency.

REPRODUCTIVE BIOLOGY
The fertilized egg grows into the asexual stage inside the sexual stage, connected to the parent by a placenta used for norishment. Once released the sexual stage grows a tail where the sexual stage buds in chains of linked circles. Each sexual stage contains testis and ovary, which produce sperm and egg to produce the next generation of the asexual stage. They lack the tadpole larval stage.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Salp
Salpa fusiformis

ORDER
Salpida

FAMILY
Salpidae

TAXONOMY
Salpa fusiformis (Cuvier, 1804).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Both stages possess a clear, barrel-shaped, gelatinous body with circular muscle bands embedded in the body wall. Solitary (asexual) stage 0.39–1.9 in (1–5 cm) in length with nine muscle bands. Aggregate form (sexual) 0.39–1.5 in (1–4 cm) long with six muscle bands and can be found solitary after breaking off long chain. The body shape of the solitary (asexual) stage is symmetrical; it is asymmetrical for the aggregate (sexual) stage, with short outerior and posterior projections. Gut is the only prominently colored part of the body.

DISTRIBUTION
Semi-cosmopolitan in temperate to tropical waters, mostly oceanic with occasional near-shore swarms. (Specific distribution map not available.)

HABITAT
Most commonly found in surface waters at night. Can make daily vertical migrations of up to 1,640 ft (500 m).

BEHAVIOR
Long chains of aggregrate forms can move through the water surprisingly quickly, up to 1.85 in (4.7 cm) per second.

FEEDING ECOLOGY AND DIET
Important filter feeders on phytoplankton. Known for fast growth rates.

REPRODUCTIVE BIOLOGY
Asexual stage produces a tail onto which bud two rows of the sexual stage that stay connected together, forming long chains several feet (meters) in length. The sexual stage can break away from the chain and swim along independently. The sexual stage bears fertilized eggs that are connected to a kind of placenta.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Salp
Thalia democratica

ORDER
Salpida

FAMILY
Salpidae

TAXONOMY
Thalia democratica (Forskal, 1775).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
The asexual stage is about 0.47 in (12 mm) long with a pair of lateral posterior projections. The sexual stage is about 0.23 in (6 mm). The test is thick and has five prominent muscle bands.

DISTRIBUTION
Semi-cosmopolitan in temperate to tropical waters. (Specific distribution map not available.)

HABITAT
Usually found in surface waters.

BEHAVIOR
Swim actively through the water by contraction of the muscles in the test.

FEEDING ECOLOGY AND DIET
Important filter feeders on phytoplankton. Recorded growth rates among the fastest of any multicellular organism (up to 70% length increase per hour).

REPRODUCTIVE BIOLOGY
Asexual stage produces a tail onto which bud rows of the sexual stage that stay connected together, forming long chains several feet (meters) in length. They lack the tadpole larval stage, the egg develops directly into the asexual stage. Generation times can be as fast as a few days, resulting in huge swarms covering hundreds of square miles (kilometers) of open ocean.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Salp
Thetys vagina

ORDER
Salpida

FAMILY
Salpidae

TAXONOMY
Thetys vagina (Tilesius, 1802).

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Solitary stage has a very thick test, 20 weakly developed muscle bands, two prominent posterior green lateral projections, and can reach up to 13 in (33 cm) in length, making it the largest of all salps. Aggregate stage up to 10 in (25 cm) and five muscle bands. Prominent gut mass is often red-pigmented in both stages.

DISTRIBUTION
Semi-cosmopolitan in temperate to tropical waters. (Specific distribution map not available.)

HABITAT
Commonly found in oceanic surface waters down to 490 ft (150 m).

BEHAVIOR
Can be very prominent member of oceanic and near-shore surface waters. The large aggregate stage stays connected, forming very long chains many feet in length.

FEEDING ECOLOGY AND DIET
Feed on phytoplankton.

REPRODUCTIVE BIOLOGY
The fertilized egg is connected to the inside of the sexual stage by a placenta; it swims out only when it has developed. It grows into the asexual stage, which grows a tail where the sexual stages bud in two rows. Each sexual stage contains testis and ovary, which produce sperm and egg to produce the next generation of asexual stage.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

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Michael S. Schaadt, MS

◆

Appendicularia

(Larvaceans)

Phylum Chordata
Class Appendicularia
Number of families 3

Thumbnail description
Transparent, generally small organisms that produce a complex external mucous net (the house) to collect tiny planktonic food and that retain the larval tadpole stage as sexually mature adults

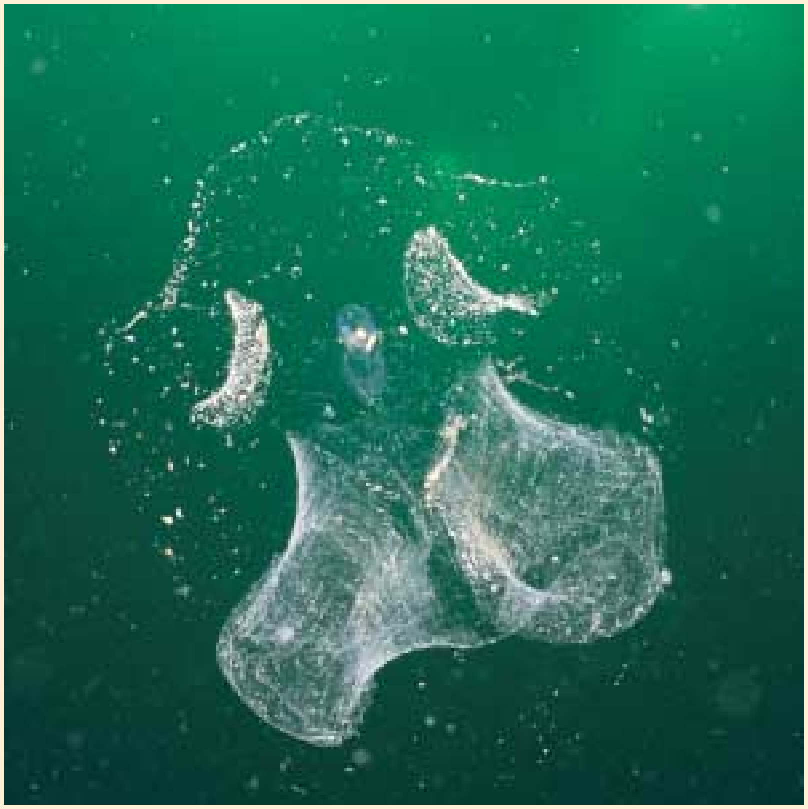


Photo: An appendicularian (*Oikopleura labradoriensis)* seen in the Gulf of Maine, USA. (Photo by ©Andrew J. Martinez/Photo Researchers, Inc. Reproduced by permission.)

Evolution and systematics

The class Appendicularia is made up of one order, three families, and 64 species. Appendicularians are related to benthic tunicates and are commonly called larvaceans because they retain the larval tadpole stage as sexually mature adults. These animals are transparent and lack the outside covering, or tunic, of their benthic relatives. The body is composed of a trunk containing most of the internal organs and of a tail with a notochord running down the middle. The trunk secretes a mucous house, which may enclose the animal, as in *Oikopleura* and *Bathochordaeus* species, or enclose only the tail, as in *Fritillaria* species. The body and house appear jelly-like and are therefore grouped as gelatinous zooplankton. Larvaceans are small, ranging from a 0.04 in (1-mm) body length with a 0.2 in (4 mm) house to *Oikopleura* to 1 in (25 mm) body length with a house more than 6.6 ft (2 m) in diameter for the giant larvacean *Bathochordaeus.*

Physical characteristics

Body length ranges from 0.04 in (1 mm) for *Oikopleura dioica* to 1 in (25 mm) for *Bathochordaeus charon.*

Distribution

Cosmopolitan in ocean currents.

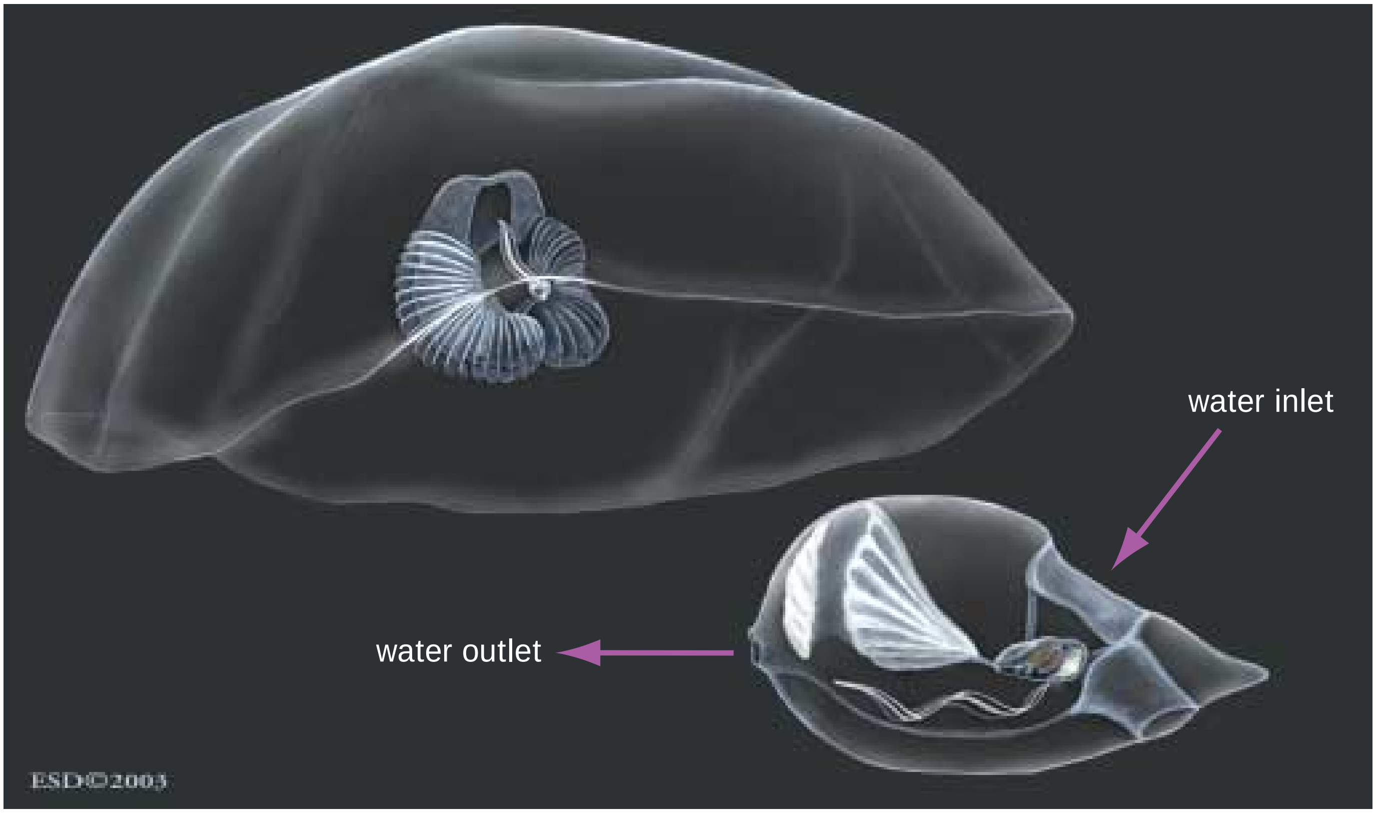
Habitat

Appendicularians are pelagic and live in oceanic and nearshore waters.

Behavior

Appendicularians move their tails rhythmically inside the house to produce a current that filters tiny food particles and to move the house through the water. If the filters become clogged or something bumps the house, the appendicularian abandons the house through a mucous trap door in the posterior of the house. The beginnings of a new house lie on the trunk of the body, and the animal inflates the new house and flips inside.

Some appendicularians have bioluminescent granules embedded in the house wall. It is thought that predators of the animal may eat an empty house that is flashing light while the



Giant appendicularian with feeding filters and mucous sheet (top). Mucous house of *Oikopleura* (bottom). (Illustration by Emily Damstra)

original house builder swims away to make another house. Surface waters of some coastal bays and harbors can look brilliantly bioluminescent from large aggregations of appendicularians.

Feeding ecology and diet

All appendicularians are filter feeders with an amazing filtration apparatus. The mucous house has two prefilters embedded in the wall and an inner filter connected to the animal's mouth. The filters are made of strands of mucus that allow only the smallest food particles <0.0004 in (<1 µm) into the tube leading to the mouth.

Appendicularians can be important prey for many animals, including larval and adult fish. At least one fish important to humans, the anchovy, relies heavily on appendicularians for food.

Reproductive biology

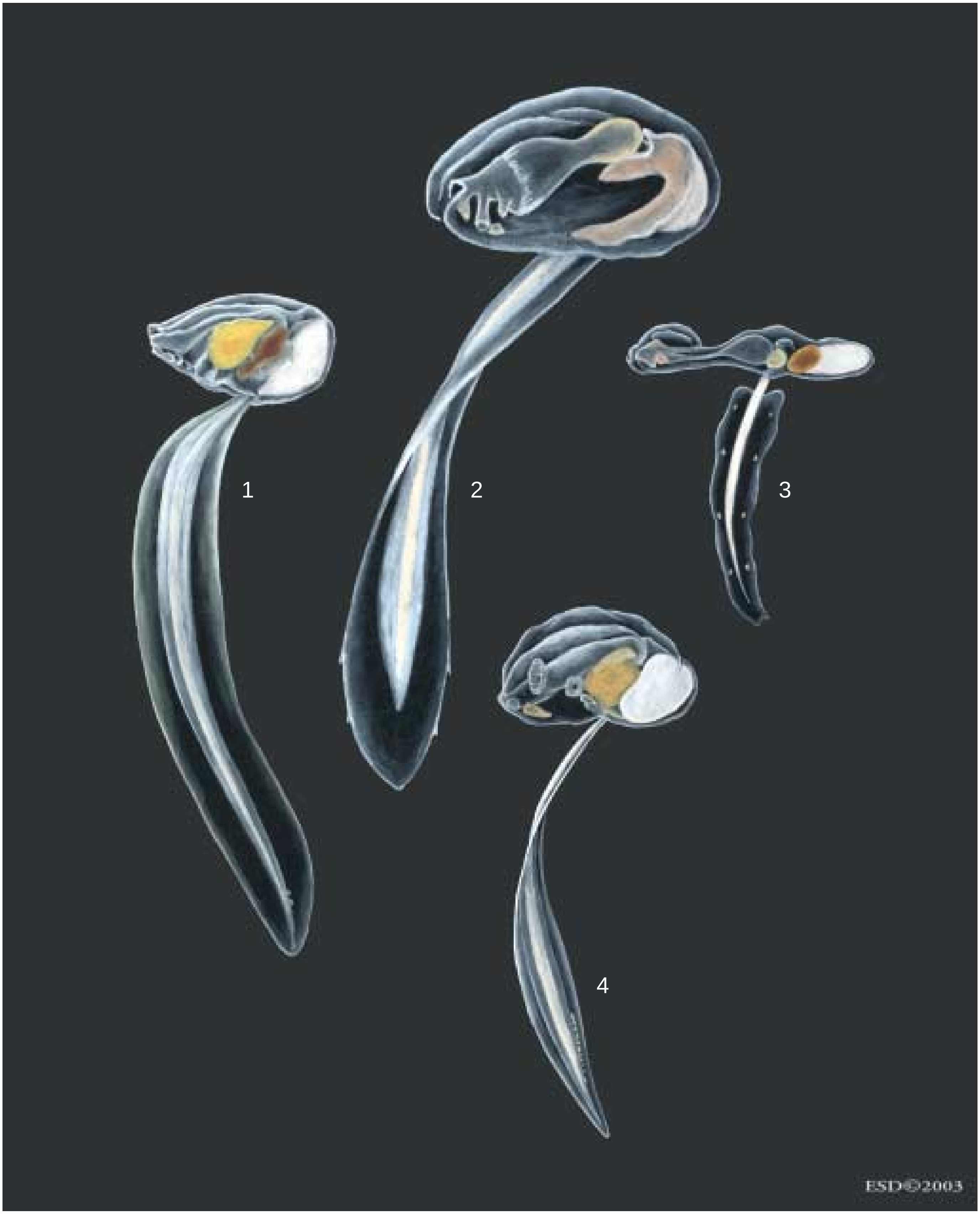
Only sexual reproduction occurs in appendicularians. All except *Oikopleura dioica* are hermaphrodites. Gametes are shed directly into the surrounding water. Hermaphrodites release sperm, and the eggs burst out of the body wall, a process that results in the death of the animal. If phytoplankton numbers are high, production of a large number of eggs and a fast generation time result in rapid development of blooms of appendicularians, sometimes in a matter of a few days.

Conservation status

Although there is much to be learned about the ecology of appendicularians, none of these species is known to be in danger of extinction. No species is listed by the IUCN.

Significance to humans

Because of potentially high population numbers, fast generation times, and ability to clear waters of phytoplankton, appendicularians can have considerable effect on the food web of the pelagic environment and thus on the numbers of fish important to humans.



1. *Oikopleura dioica*; 2. Giant larvacean (*Bathochordaeus charon*); 3. *Fritillaria borealis*; 4. *Oikopleura labradoriensis*. (Illustration by Emily Damstra)

Species accounts

No common name

Fritillaria borealis

ORDER
Copelata

FAMILY
Fritillaridae

TAXONOMY
Fritillaria borealis (Lohmann, 1896), Irminger Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body length to 0.2 in (4.5 mm) (trunk, 0.06 in [1.5 mm]; tail, 0.1 in [3 mm]). Distinguished from other appendicularians by connection of the tail at the midpoint of the trunk. The tail is the only part that is entirely inside the very small house.

DISTRIBUTION
Cosmopolitan in epipelagic zone (less than 656 ft [200 m]). (Specific distribution map not available.)

HABITAT
One of the most common appendicularians worldwide.

BEHAVIOR
The house is small and encloses only the tail and part of the trunk. When the tail stops moving, the house collapses on the body. Once the animal floats away, the tail starts moving again, inflating the house. Filter feeding continues in a new area.

FEEDING ECOLOGY AND DIET
Filters only the smallest particles out of the water (less than 0.0004 in [1 µm]).

REPRODUCTIVE BIOLOGY
These hermaphrodites release sperm first then release eggs by rupturing their body wall, a process that results in the death of the animal.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Giant larvacean

Bathochordaeus charon

ORDER
Copelata

FAMILY
Oikopleuridae

TAXONOMY
Bathochordaeus charon (Chun, 1900), Cape of Good Hope.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Largest of all appendicularians, reaching a length of 1 in (25 mm). Short, broad tail with clearly visible notochord embedded. The gut and gonads are easily seen in the large conspicuous trunk. The house is a series of elaborate tubes and filters used for feeding. A roughly ovoid sheet of mucus that can reach 6.6 ft (2 m) in diameter is continuously secreted above the house for protection and for catching sinking food particles.

DISTRIBUTION
Cosmopolitan in mesopelagic zone (328–1,640 ft [100–500 m]) (Specific distribution map not available.)

HABITAT
Pelagic in deeper waters (328–1,640 ft [100–500 m]).

BEHAVIOR
The tail beats slowly inside the house producing a current that moves water and food particles into the filters. The giant larvacean discards its mucous sheet and house when disturbed or when food particles clog the filters. Because abandoned mucous sheets and houses are laden with food, detritus-feeding zooplankton, and smaller microbes, they become important contributors of organic materials to the deep ocean as they sink to the botoom.

FEEDING ECOLOGY AND DIET
The large mucous sheet secreted above the house catches sinking particles, which are strained and directed to the inner filter of the house. The house filters further strain food particles of the proper size onto a mucous sheet, which is eaten.

REPRODUCTIVE BIOLOGY
Little is known except that these animals are hermaphrodites.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name

Oikopleura dioica

ORDER
Copelata

FAMILY
Oikopleuridae

TAXONOMY
Oikopleura dioica (Fol, 1872), Mediterranean Sea.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Smallest of all appendicularians with a body length to 0.1 in (3 mm) (trunk, 0.04 in [1 mm]; tail, 0.08 in [2 mm]). House approximately 0.2 in (4 mm) long.

DISTRIBUTION
Cosmopolitan in tropical and temperate waters in epipelagic zone (less than 656 ft [200 m]). (Specific distribution map not available.)

HABITAT
Can be abundant in coastal surface waters and is one of the most common appendicularians worldwide.

BEHAVIOR
When the filters become clogged, the house is abandoned, and a new house is inflated. Studies have shown that on average a new house can be made every 4 hours.

FEEDING ECOLOGY AND DIET
Filters only the smallest particles out of the water (less than 0.0004 in [1 µm]). Some fish, such as the blacksmith *Chromis bipunctata* in California kelp forests, are known for feeding almost exclusively on *Oikopleura dioica*.

REPRODUCTIVE BIOLOGY
Separate male and female forms release their sperm and eggs into the surrounding water.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

No common name
Oikopleura labradoriensis

ORDER
Copelata

FAMILY
Oikopleuridae

TAXONOMY
Oikopleura labradoriensis (Lohmann, 1892), Labrador Current.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Body length to 0.24 in (6 mm) (trunk, 0.08 in [2 mm]; tail, 0.16 [4 mm]). House is approximately 0.4 in (9 mm).

DISTRIBUTION
Cosmopolitan in temperate to cold waters, in epipelagic zone (less than 656 ft [200 m]).

HABITAT
Can be abundant in cooler offshore and coastal surface waters.

BEHAVIOR
These animals have bioluminescent granules embedded in the walls of the house that may help confuse predators, who eat abandoned houses rather than animals that have abandoned the houses.

FEEDING ECOLOGY AND DIET
Filters only the smallest particles out of the water (less than 0.0004 in [1 µm]).

REPRODUCTIVE BIOLOGY
These hermaphrodites release sperm first then release eggs by rupturing the body wall, a process that results in the death of the animal.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

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◆

Sorberacea

(Sorberaceans)

Phylum Chordata

Class Sorberacea

Number of families 1

Thumbnail description
Small group of exclusively deep-water Tunicata comprising solitary benthic species with a strongly reduced branchial sac

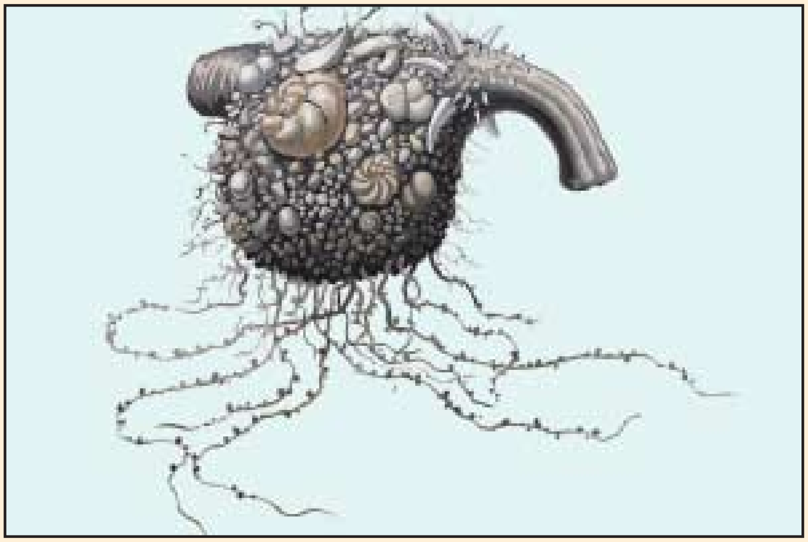


Illustration: *Oligotrema sandersi.* (Illustration by John Megahan)

Evolution and systematics

The class Sorberacea was erected in 1975 by the French ascidiologists Claude and Françoise Monniot and Françoise Gail for several highly adapted deepwater species belonging to four genera (*Oligotrema*, *Hexacrobylus*, *Gasterascidia*, and *Sorbera*) united in the family Hexacrobylidae. The characters used to distinguish the Sorberacea from class Ascidiacea were the absence of the branchial sac, the presence of dorsal nervous cord, a very superficial position of the nervous ganglion, the histology of the digestive tract, and some other features.

The taxonomic position of Hexacrobylidae was not certain, but the family was most often considered as related to the ascidian family Molgulidae, or placed into a separate order, Aspiraculata, within the Ascidiacea. However, other taxonomists, including the Australian ascidiologist Patricia Kott, doubted whether the Hexacrobylidae should be removed from the class Ascidiacea. Kott considered that the characters used to distinguish Sorberacea and Ascidiacea could not be confirmed as true differences between Hexacrobylidae and the rest of the Ascidiacea. In particular, although the branchial sac is strongly reduced in Hexacrobylidae, it is not absent, and the neural complex in Hexacrobylidae is in the same position beneath the epidermis as in other ascidians. In addition, the structure and histology of the digestive tract varies in other ascidiaceans.

There are also problems in defining genera and species in the group. Of the four nominal genera mentioned above, *Gasterascidia*, *Sorbera*, and *Hexacrobylus* are now treated as synonyms of *Oligotrema*, and all species assigned previously to *Hexacrobylus* (apart from the type species of this genus) now belong to *Asajirus.* Thus the family Hexacrobylidae contains only two valid genera: *Oligotrema* and *Asajirus. Oligotrema* contains five species, and *Asajirus* (formerly known as *Hexacrobylus*), contains 12 nominal species, six of which are most probably synonyms of widely distributed *Asajirus indicus.*

Physical characteristics

All species of sorberaceans are solitary. Body shape is rather constant, *Asajirus* species almost always have an oval or egg-shaped body, and *Oligotrema* species are usually slightly more elongated and the siphons are situated on opposite ends of the body and directed away from each other. The test, a protective layer secreted by epithelium, is covered by short hair-like processes with adhering sand, mud particles, or, more often, tests of foraminiferans. The cloacal siphon is always small and inconspicuous. The branchial siphon is large, situated on the anterior end or on a side of the body, and surrounded by six large lobes. The opening of the branchial siphon leads to the buccal cavity lined with the test; the buccal cavity is homologous to the branchial siphon of other ascidians. As in all tunicates, The pharynx is perforated, but unlike in other ascidians, is small and has only a few openings leading to a system of thin-walled chambers that open into the atrial cavity by ciliated stigmata. Some species have a very large globular stomach, which occupies most of the internal space of the animal. All species have a kidney, a large thin-walled excretory organ, similar to the kidney of ascidians in the family Molgulidae (suggesting a possible relationship with this family).

All Hexacrobylidae are relatively small, from less than 1 in (3 mm) up to 2.4 in (6 cm), but usually they are usually no more than 1.4 in (1 cm) in greatest dimension.

Distribution

Sorberaceans are widely distributed in bathyal and abyssal depths in all oceans, but records are not numerous. They have not been recorded in the high Arctic and North Pacific Oceans, but deepwater tunicates in these regions have been less intensively sampled.

Habitat

Most specimens of sorberaceans were collected in deep waters at 3,280–16,400 ft (1,000–5,000 m). However, in 1903 a single specimen of *Oligotrema psammites* was recorded at 308 ft (94 m), and in 1990 another specimen of the same species was recorded at 886 ft (270 m). The deepest record is of a single specimen of *Asajirus indicus* at 25,853 ft (7,880 m); only four other tunicates have been recorded at such great depths. The bottom at abyssal depths is almost always soft and covered by thick layer of mud, sorberaceans live unattached on the mud.

Behavior

Sorberaceans do not survive capture, and no one has directly observed their behavior. Although they are not firmly attached to the substratum, it is unlikely that they are mobile, as their body covered by hairs with attached sediments suggests that they are anchored in the mud and cannot actively move. Their muscular branchial siphon has fingerlike lobes on the end, suggesting that it can operate as a hand to capture small invertebrates.

Feeding ecology and diet

Unlike most other benthic tunicates sorberaceans are carnivorous and not filter feeders. The specimens examined had an almost-empty digestive tract, so they are certainly not detritus-feeders, otherwise the digestive tract would be full of sediments. Possibly they can actively search and capture small moving invertebrates using their muscular (and sometimes eversible) branchial siphon. The large globular stomachs of some species suggest that the prey may be relatively large, and small copepods, isopods, ostracods, nematodes, and polychaetes were found in the stomachs of some specimens.

Reproductive biology

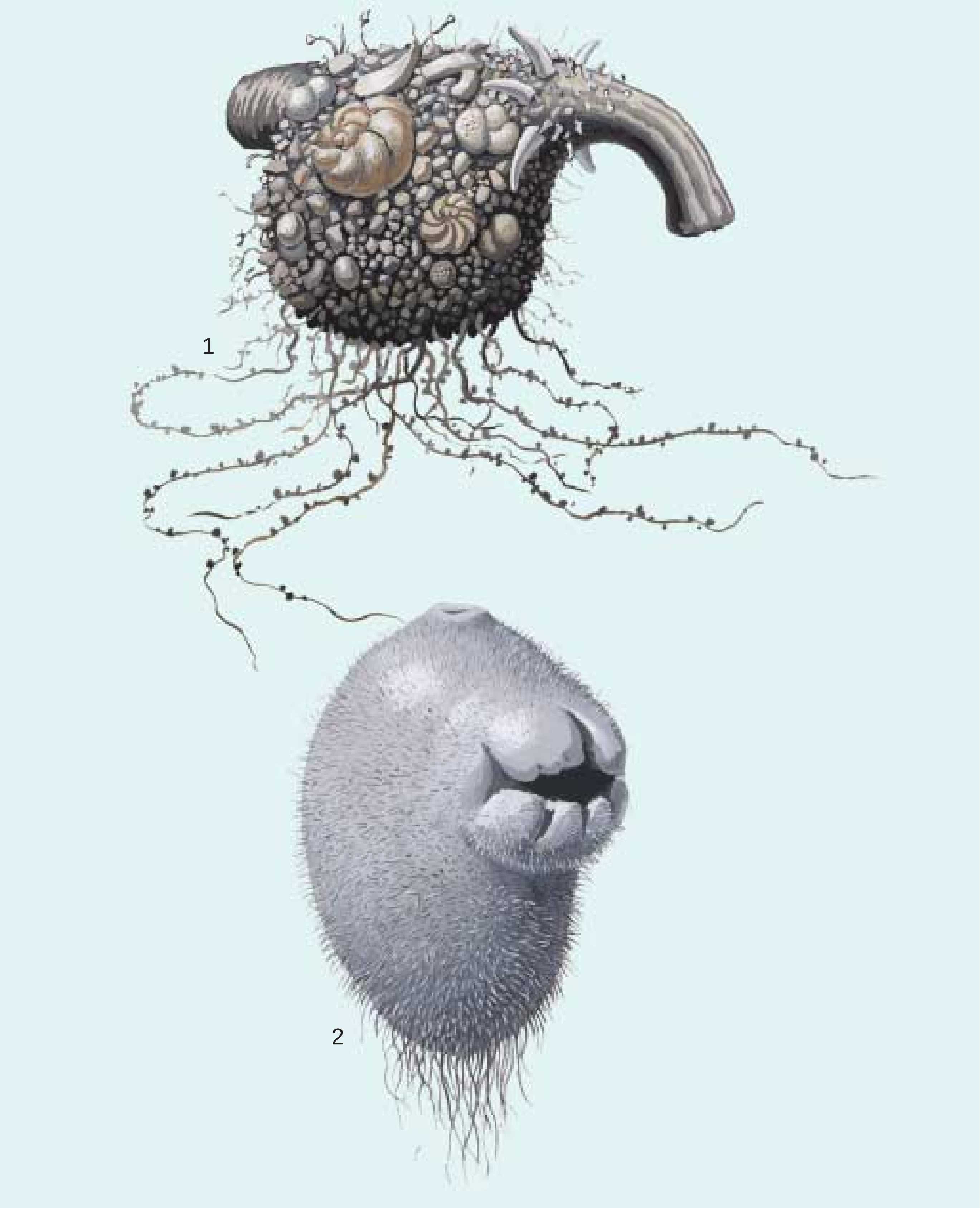
Almost nothing is known about sorberacean reproduction. As with all other benthic tunicates, they are hermaphrodites. All species are apparently oviparous, and larvae are not known. The youngest recorded specimens, 0.02 in (0.5 mm) in diameter, already resembled adult forms.

Conservation status

No species of Sorberacea are listed by the IUCN.

Significance to humans

None known.



1. *Oligotrema sandersi*; 2. *Asajirus indicus*. (Illustration by John Megahan)

Species accounts

No common name

Asajirus indicus

FAMILY

Hexacrobylidae

TAXONOMY

Hexacrobylus indicus Oka, 1913, Sri Lanka, Indian Ocean.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

Body oval, not usually exceeding 0.8 in (2 cm) high. Atrial siphon relatively long, but it is internal, and thus can be seen only on dissected specimens after test is removed. On surface of test, only small inconspicuous atrial opening is present on top of body. Branchial siphon is large and muscular. On preserved specimens, siphon is internal, lying wholly within the body, but it is not known whether this is normal in living specimens. Branchial siphon opens on anterior part of the body by wide slit surrounded by six wide lobes. Body coated by fine short hairs that are significantly longer on the posterior end of body, suggesting specimens sit vertically at the bottom.

DISTRIBUTION

All oceans except central Arctic and North and East Pacific Oceans.

HABITAT

Lives unattached on soft muddy bottom of continental slopes and abyssal plains and trenches; recorded from 1,970 to 24,540 ft (600 to 7,480 m) deep.

BEHAVIOR

Nothing is known.

FEEDING ECOLOGY AND DIET

Carnivorous, including small invertebrates.

REPRODUCTIVE BIOLOGY

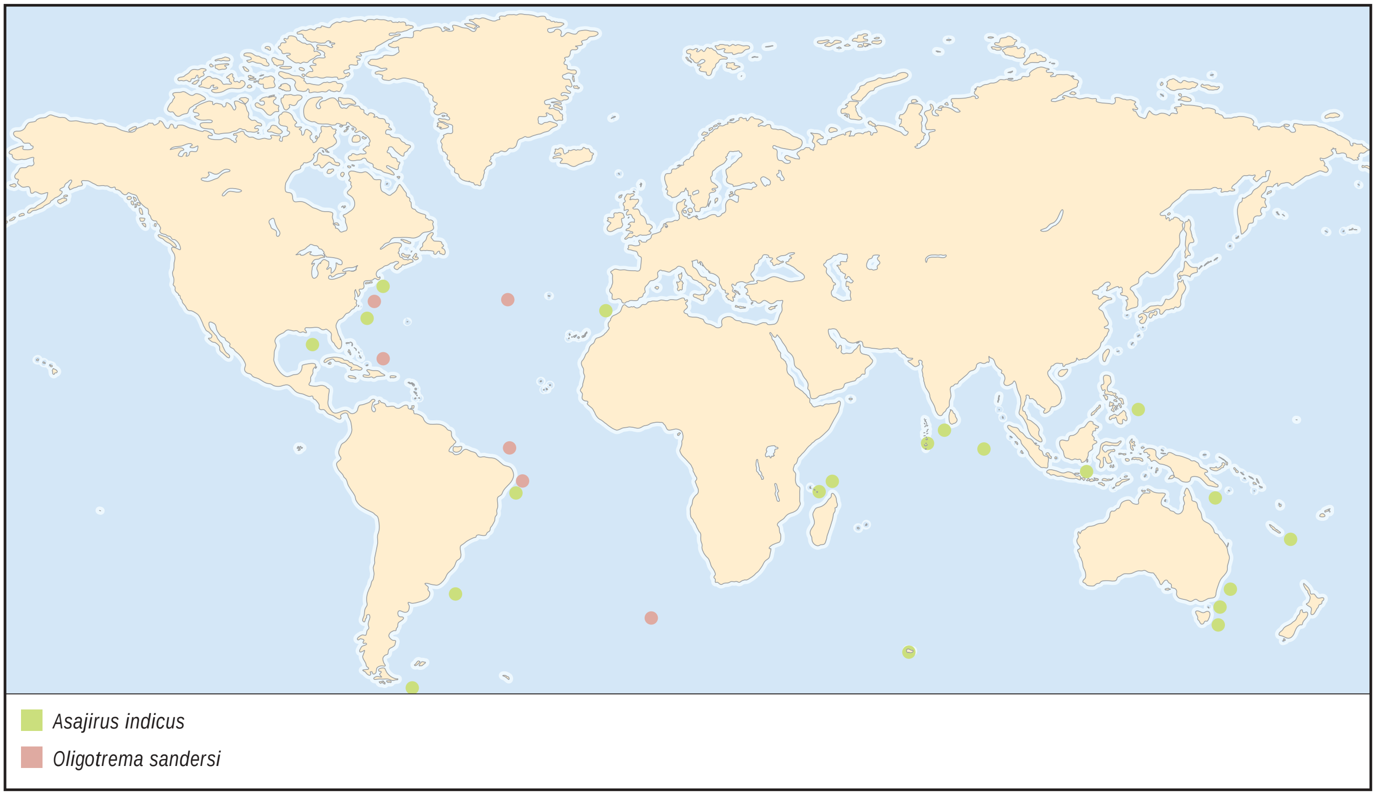
Nothing is known.

CONSERVATION STATUS

Not listed by the IUCN.

SIGNIFICANCE TO HUMANS

None known. ◆



No common name

Oligotrema sandersi

FAMILY
Hexacrobylidae

TAXONOMY
Gasterascidia sandersi Monniot and Monniot, 1968, northwest Atlantic Ocean.

OTHER COMMON NAMES
None known.

PHYSICAL CHARACTERISTICS
Small, not exceeding 0.2 in (5 mm). Oval body covered by sparse hairs with attached mud particles and foraminiferan tests. Two prominent siphons on opposite sides of body. Highly muscular, completely eversible branchial siphon longer than atrial siphon, has six fingerlike lobes. Stomach very large, occupies most of body.

DISTRIBUTION
Widely distributed in Atlantic Ocean, not recorded in other oceans.

HABITAT
Abyssal; recorded at about 4,920–16,400 ft (1,500–5,000 m) deep.

BEHAVIOR
Nothing is known.

FEEDING ECOLOGY AND DIET
Carnivorous, including small invertebrates.

REPRODUCTIVE BIOLOGY
Nothing is known.

CONSERVATION STATUS
Not listed by the IUCN.

SIGNIFICANCE TO HUMANS
None known. ◆

Resources

Periodicals

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◆

Cephalochordata

(Lancelets)

Phylum Chordata
Class Cephalochordata
Number of families 1

Thumbnail description
Exclusively marine species with slender, fish-like shape, tapered at both ends; easily recognized by the externally visible v-shaped lines that separate the iterated muscle blocks and by the oral cirri that guard the mouth opening against unwarranted particles

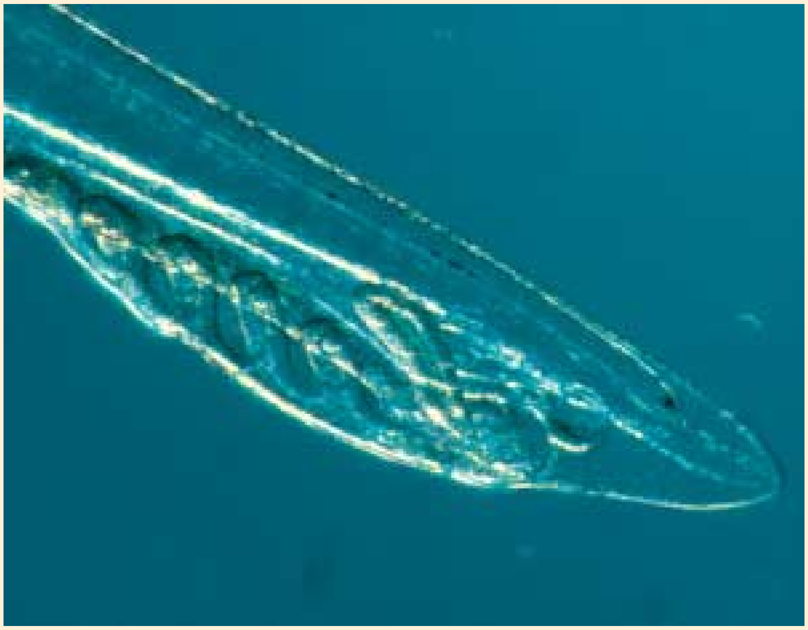


Photo: Lancelet (*Amphioxus lanceolatus*) larva head. Lancelets have no heart but do have gills. (Photo by Animals Animals ©P. Parks, OSF. Reproduced by permission.)

Evolution and systematics

Cephalochordates (also called acraniates or lancelets) possess key features that characterize them as chordates. Those characters include the notochord, dorsal nerve cord, branchial basket, and a post anal tail with fins. It is generally believed that cephalochordates are the closest living relatives to the vertebrates. The two groups share unique traits such as the organization of the main body musculature into separate segments and the organization of the circulatory system. Another feature, which unites cephalochordates and vertebrates, is a caecum that is probably homologous to the vertebrate liver. Thus, the morphological evidence is strong. In fact it is so strong that it was used as evidence against phylogenetic conclusions, which were drawn solely from DNA sequences when a molecular study placed the cephalochordates as relatives of echinoderms, not even within the chordates.

The potential for fossilization of cephalochordates is limited because the animals are soft bodied. Even their main skeletal element, the notochord, consists of specialized muscle tissue. Nevertheless several fossils have been described that could have affinities to cephalochordates.

Pikaia gracilens from the Canadian Burgess Shale (Cambrian, ca. 530 million years old) is a promising candidate for consideration as a cephalochordate fossil. It has the typical tapered body form at both ends, and it has been argued that it possessed a notochord. However, *Pikaia* also shows characters not found in extant cephalochordates. In some fossils the lines, interpreted as myocommata, are w-shaped rather reminiscent of vertebrates than of the simpler v-shape of cephalochordates. Also, the anterior end of some fossil remnants displays tentacles, a feature not found in living cephalochordates, but known, for example, from hagfishes.

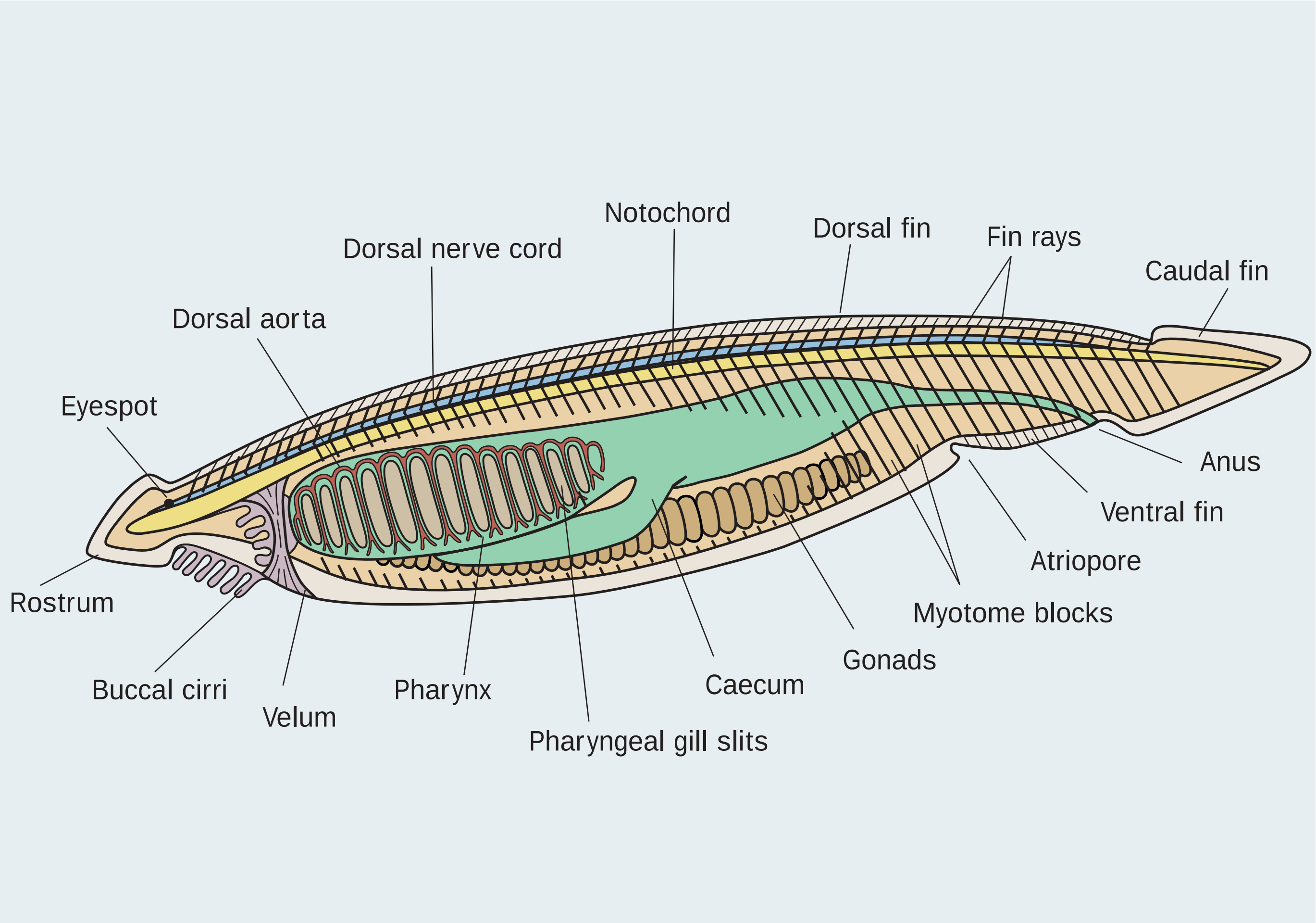
The nature of several other fossils (e.g., *Cathaymyrus diadexus* [Cambrian], *Lagenocystis pyramidalis* [Ordovician], *Palaeobranchiostoma hamatotergum* [Permian]) remains more equivocal. An instructive example is the fossil *Yunnannozoon lividum* (Cambrian). Originally reconstructed as a cephalochordate, it was re-described as a worm-like hemichordate only to be interpreted as a sea pen (phylum Cnidaria) shortly thereafter.

Evolutionary relationships among cephalochordate species are unclear. However, it is thought that the genus *Epigonichthys* is more derived compared to *Branchiostoma*.

The class Cephalochordata (some experts now categorize it as a subphylum) contains one order, Amphioxiformes, and one family, Branchiostomatidae.

Physical characteristics

As the closest living relatives of vertebrates, cephalochordates occupy an eminent phylogenetic position. They are invaluable in reconstructing the evolutionary step from invertebrate to vertebrate along the lineage that leads to mammals and humans. Therefore, cephalochordates are of great interest to numerous researchers and consequently their anatomy is well known.



Lancelet anatomy. (Illustration by Christina St. Clair)

A median fin is present along the entire dorsal length of the animals, extending at the anterior end into a short rostral fin and at the posterior end a tail fin. The ventral fin runs between anus and atriopore. In front of the atriopore paired fin-like folds, the metapleural folds, extend to the anterior region of the pharynx. The dorsal and ventral fins contain so-called fin chambers enclosing coelomic cavities and fin rays that consist of a substance that could serve as an energy store.

The epidermis consists of a single-celled layer, a primitive feature compared to the multi-cellular epidermis in vertebrates. It contains gland cells that secrete a thin sheet of mucus covering the surface of the animal. Different types of sensory cells are distributed in the epidermis, especially in the rostral region.

The dorsal nerve cord of cephalochordates has a central canal that is enlarged at the anterior end of the cord. This enlarged region is known as the cerebral vesicle and is homologous to parts of the vertebrate brain as indicated by morphological similarities (infundibular cells, Reissner's fiber) and similarities in the expression patterns of developmental genes. A peculiarity of the cephalochordate neural cord is the presence of numerous pigmented ocelli, the so-called pigment-cup ocelli. In addition, several more structures in the neural cord are probably light sensitive, e.g., the Joseph cell receptors and the lamellar body in the cerebral vesicle. A photoreceptor in the anterior cerebral vesicle of larvae shows significant similarities to the paired eyes of vertebrates and could be homologous to them. Outside the central nervous system one finds receptors (e.g., corpuscules de Quatrefage), especially in the epidermis of the buccal cirri, velar tentacles, the atrium, and along the metapleural folds.

The notochord extends from the anterior to the posterior end. It is a skeletal element that is the antagonist of the lateral muscle cells that attach to it. Curiously, it is itself an active tissue. It consists of specialized muscle cells and is innervated from the nerve cord. Vacuoles within and between the cells act as a hydroskeleton and help in adjusting the rigidity of the notochord. The notochord is the main skeletal element. Aside from it, in the pharynx, between the gill slits, the branchial bars contain skeletal, cartilaginous rods. In addition, similar rods support the anterior cirri.

A pattern of repeated V-shaped lines is visible on the side of a cephalochordate. It is similar to the pattern seen in a fish fillet, though simpler, and of course, minute. This pattern is caused by the connective tissue that separates individual muscle segments. The innervation of the muscle cells is quite different from the vertebrates. There are no ventral spinal nerves that innervate the cells as in vertebrates. Instead the muscle cells themselves form long thin extensions that approach the nerve cord and are innervated directly there.

It has long been believed that cephalochordates possessed excretory cells very similar to polychaetes. Electron microscopy showed that the similarity is superficial. The excretory cells of cephalochordates are unique in the animal kingdom though in evolutionary terms they are probably derived from the so-called podocytes that are found in other deuterostomes. Excretory organs (nephridia; sing. nephridium) are found serially along the dorsal part of the pharynx. They are associated with blood vessels and function in a similar way as the vertebrate kidney. In addition to these nephridia a nephridium is situated just in front of the mouth (Hatschek's nephridium).

The general arrangement of blood vessels is similar to vertebrates, but the vessels are not lined by cells as in vertebrates. The region where a heart would be expected is contractile. In notable similarity with vertebrates a portal vein connects a capillary system around the posterior intestine with a capillary system around the hepatic caecum.

A pharynx with gill slits is common to all chordates: tunicates, cephalochordates, and the more primitive members of the vertebrates. In cephalochordates a vestibule lies in front of the pharynx that is guarded by the cirri. The vestibule contains ciliated tracts (wheel organ), an excretory organ (Hatschek's nephridium), and a shallow groove (Hatschek's pit) that is probably homologous to the adenohypophysis in vertebrates. The pharynx proper begins with the mouth opening that is surrounded by velar tentacles. The pharynx is perforated by up to 200 gill slits. Along its ventral midline runs a groove, the endostyle that produces mucus and thyroxine, indicating homology to the thyroid in vertebrates. The gill slits do not open into the open water, but the whole pharynx is covered by the outer body wall. In this way a space around the pharynx is created, which is called the atrium. The atrium opens in the ventral midline through the atriopore anterior to the anus.

The pharynx leads into the short esophagus and from there the gut extends straight posteriorly and opens through the anus. Ventrally, at about the junction of the pharynx and esophagus a blind ending caecum projects anterior. It is called the hepatic caecum and is probably homologous to the vertebrate liver.

Depending on species, adult animals range in size 0.4–3.2 in (1–8 cm) in total length. The color of all species is whitish to a creamy yellow, sometimes with a tint of pink. The mucus covering the epidermis can reflect iridescently.

For identification and taxonomic purposes the so-called myotome (muscle block) formula is used. Three numbers signify the number of myotomes anterior to the atriopore, between atriopore and anus, and posterior to the anus. In addition, the number of fin chambers in the dorsal fin serves as a diagnostic character. *Epigonichthys* differs from *Branchiostoma* in that it possesses only one series of gonads on the right side of the body, whereas the gonads are paired in *Branchiostoma*.

A lancelet (*Amphioxus*) is seldom more than 3 inches (8 cm) long; it resembles a slender fish without head definition or eyes. (Photo by Animals Animals ©E. R. Degginger. Reproduced by permission.)

Distribution

Cephalochordates are known from continental shelves of the tropic and temperate regions worldwide.

Habitat

Cephalochordates are semi-sessile filter feeders. They can swim vigorously, forward and backward, yet they live most of their life buried halfway in the substrate. Cephalochordates are found in shallow coastal areas, where they inhabit sandy bottoms. They prefer stable, well-reutilated, and smooth-textured grains. Larvae are planktonic and may drift over long distances before colonizing a suitable habitat.

Behavior

Cephalochordates can be found in high densities of over 9,000 animals per square meter. Sexes in cephalochordates are separate, and males and females are equally abundant within a population. Recruitment of larval stages influences the age structure in a population, which in turn depends on the currents.

Depending on the coarseness of the habitat, cephalochordates assume different feeding positions. In coarse sediment they bury their body entirely within the substrate. The preferred position is with their anterior end exposed to the open water. In fine sediment they lie on the substrate.

Feeding ecology and diet

Cephalochordates feed on plankton with plant cells, diatoms being the most important. The entire branchial basket is an adaptation for feeding with the endostyle continuously producing a mucus-net that is transported over the gill slits by cilia and capturing particles out of the water. The food particles together with the mucus net are rolled into a mass and passed on into the esophagus and the posterior intestine where they are digested.

Reproductive biology

Eggs are about 0.00394 in (100 µm) in diameter and contain numerous yolk droplets. Spermatozoa are simple and typical for marine invertebrate species with external fertilization.

Eggs and sperm are released into the water. How spawning is synchronized is not known. In subtropical populations the reproductive period stretches over several months and individuals spawn repeatedly. In temperate areas the reproductive period is shorter.

Total, radial cleavage is followed by the formation of a blastula, then gastrulation and neurulation ensue, and a peculiarly asymmetric larva is formed. The large mouth is situated on the left side. A single row of gill slits forms and the larvae start feeding immediately. More gill slits are added and later an additional row of gill slits forms on the right side. When about 12–15 pairs of gill slits are formed the larvae sink to the bottom and metamorphose into juveniles. This metamorphosis mainly involves the formation of the atrium by an outgrowth of the epidermis that surrounds the pharynx. Simultaneously the gill slits are divided and new gill slits are added. From now on the animals only grow in size, adding additional gill slits and segments while developing the gonads to full maturity. The larval period in the plankton lasts from several weeks up to a few months. In the following year the animals become sexually mature. Offshore plankton samples yielded relatively large cephalochordates that resembled larval stages but had developed rudimentary gonads. These were described under the genus name *Amphioxides*. However, it is more likely that these forms are merely larval forms of typically benthic species that did not encounter a suitable substrate rather than representing a genus with a different life history.

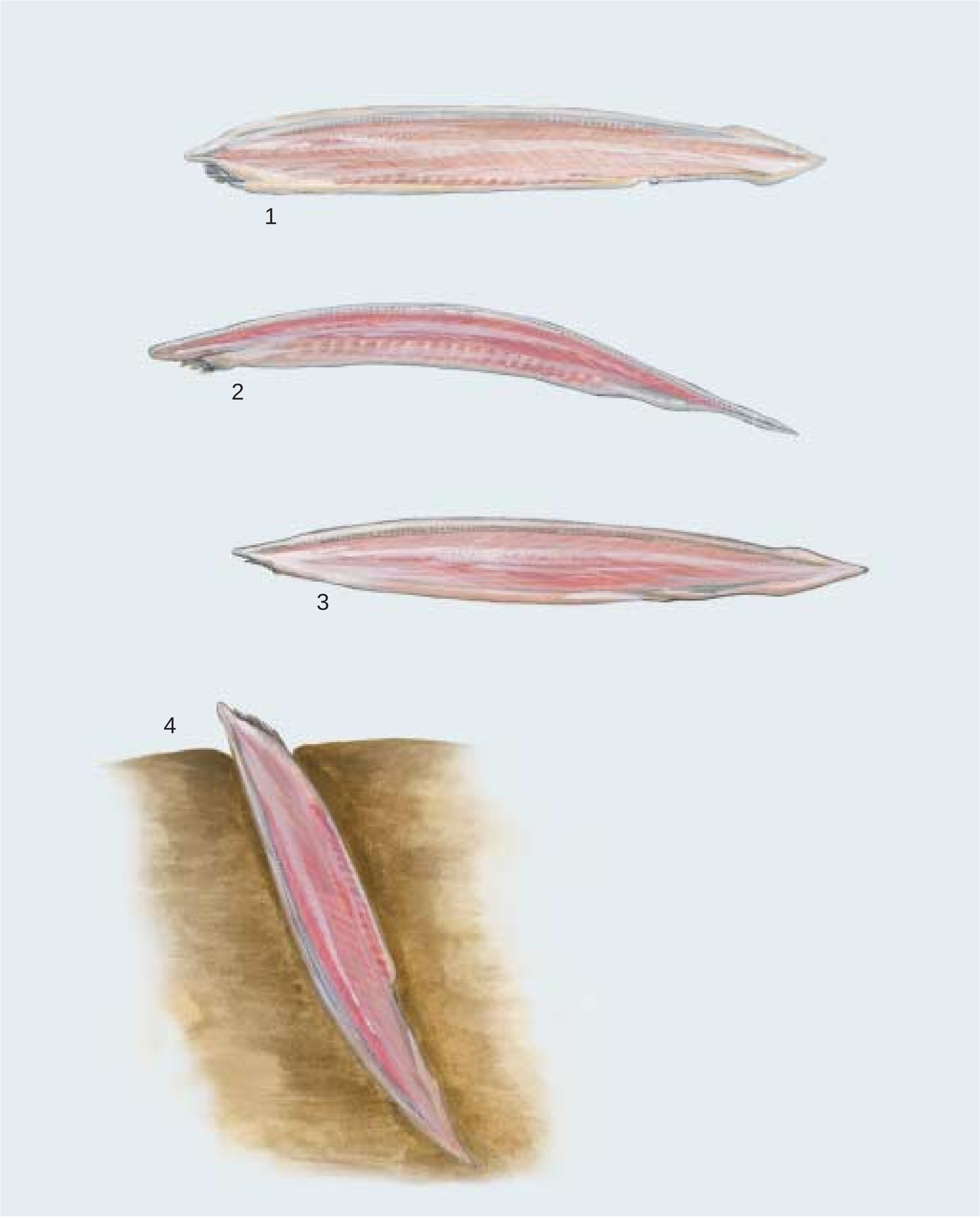
Conservation status

No cephalochordate species is regarded as threatened.

Significance to humans

It is believed that the "crocodile fish" that occurs in southern Chinese mythology is the cephalochordate species *Branchiostoma belcheri*. The mythical hero Han Yü killed many crocodiles, some of which escaped mortally wounded to the Xiamen region before they died. The maggots that emerged from the crocodile carcasses gradually changed into cephalochordates. This myth originated in the Tan Dynasty (A.D. 616–905).

In southern China local fishermen, deploying traditional techniques, fish for *Branchiostoma belcheri.* The catch is used for human consumption. *Branchiostoma lanceolatum* occurs as an appetizer on a gala dinner menu in honor of the influential German zoologist Ernst Haeckel. The greatest importance of cephalochordates to humans, however, is cultural: they occupy a prominent place as a linchpin for the theory of evolution.



1. *Epigonichthys cultellus*; 2. Bahama lancelet (*Epigonichthys lucayanus*) 3. Smalltail lancelet (*Branchiostoma belcheri*); 4. European lancelet (*Branchiostoma lanceolatum*). (Illustration by Michelle Meneghini)

Species accounts

Smalltail lancelet

Branchiostoma belcheri

ORDER
Amphioxiformes

FAMILY
Branchiostomatidae

TAXONOMY
Branchiostoma belcheri Gray, 1847, Borneo. Possibly three subspecies: *B. belcheri belcheri*, *B. belcheri japonicus*, *B. belcheri tsingtauense*.

OTHER COMMON NAMES
(Listed names were originally coined for the European species *Branchiostoma lanceolatum.* Because of the morphological uniformity of cephalochordates they are usually used for all species.) English: Amphioxus, lancelet; French: Amphioxus, lancelet; German: Amphioxus, Lanzettfischchen; Spanish: Anfioxo, pez lanceta, lanceta.

PHYSICAL CHARACTERISTICS
Sixty-five (61–69) myotomes: 38 (34–43) preatriopore, 17 (14–21) atriopore to anus, 10 (8–12) postanal. Two hundred ninety (222–360) dorsal fin chambers. Reaches up to 2.8 in (70 mm) in total length.

DISTRIBUTION
A widespread species found from southern Japan, along the Chinese coast, the Philippines, the northern Australian coast, to Madagascar, and southeastern Africa.

HABITAT
Sandy bottoms from 3.28–82.02 ft (1–25 m) in depth.

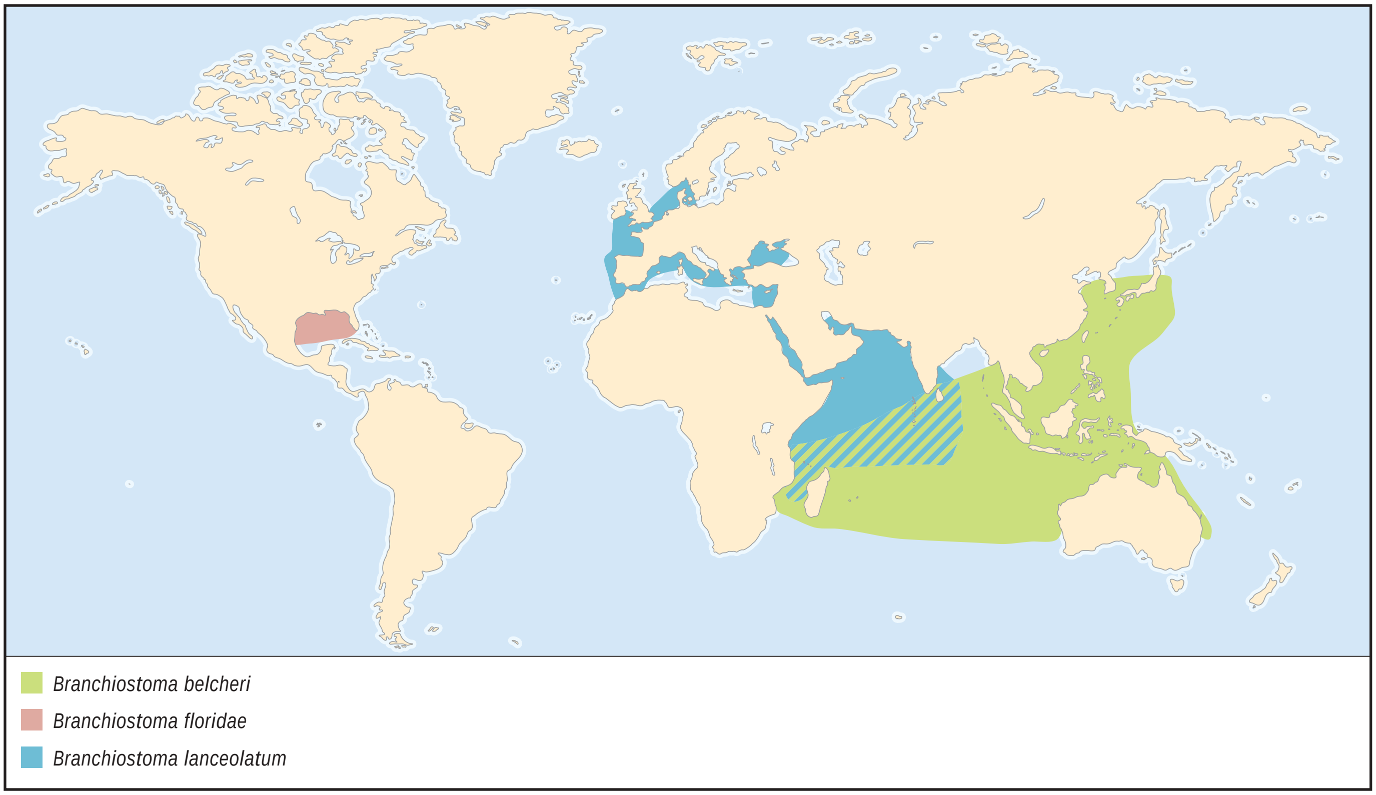
BEHAVIOR
Seems to avoid mud.

FEEDING ECOLOGY AND DIET
Consumes microscopic plankton, mainly diatoms.

REPRODUCTIVE BIOLOGY
Reproductive season in Amoy (China) lasts from May to July. Second reproductive period seems to occur in December.

CONSERVATION STATUS
Not threatened. For cultural reasons, *Branchiostoma belcheri* is protected in the “Xiamen Rare Marine Creatures Conservation Area.”

SIGNIFICANCE TO HUMANS
In some villages at the southern coast of China the majority of fishermen were fishing for *Branchiostoma belcheri.* Although the importance of this specialized and traditional fishery has declined, it is still viable in the area around Xiamen. The animals


🟩 *Branchiostoma belcheri*
🟥 *Branchiostoma floridae*
🟦 *Branchiostoma lanceolatum*

are intended for human consumption. Some animals also are fished for academic purposes and support active research programs around the world. ◆

Florida lancelet

Branchiostoma floridae

ORDER
Amphioxiformes

FAMILY
Branchiostomatidae

TAXONOMY
Branchiostoma floridae Hubbs, 1922, Tampa Bay, Florida.

OTHER COMMON NAMES
(Listed names were originally coined for the European species *Branchiostoma lanceolatum.* Because of the morphological uniformity of cephalochordates they are usually used for all species.) English: Amphioxus, lancelet; French: Amphioxus, lancelet; German: Amphioxus, Lanzettfischchen; Spanish: Anfioxo, pez lanceta, lanceta.

PHYSICAL CHARACTERISTICS
Sixty (56–64) myotomes: 36 (33–40) preatriopore, 16 (14–17) atriopore to anus, 8 (6–11) postanal. Two hundred eighty-six (206–349) dorsal fin chambers. Reaches up to 2.3 in (59 mm) in total length.

DISTRIBUTION
Gulf of Mexico from southwestern Florida westward to Texas. Maybe also along Central American coasts from Mexico to Venezuela.

HABITAT
Sandy bottoms from 1.64–98.42 ft (0.5–30 m) in depth.

BEHAVIOR
Probably same as for family.

FEEDING ECOLOGY AND DIET
Probably same as for family.

REPRODUCTIVE BIOLOGY
Reproductive period occurs in Tampa Bay, Florida, from late spring to late summer. Individuals can spawn, ripen, and spawn again in the same breeding season.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Branchiostoma floridae occurs in very shallow water where it is accessible without boats. A population in Tampa Bay, Florida, has recently become a major source especially for molecular studies of embryonic development. ◆

European lancelet

Branchiostoma lanceolatum

ORDER
Amphioxiformes

FAMILY
Branchiostomatidae

TAXONOMY
Branchiostoma lanceolatum Pallas, 1774, Cornwall, England.

OTHER COMMON NAMES
English: Amphioxus, lancelet; French: Amphioxus, lancelet; German: Amphioxus, Lanzettfischchen; Spanish: Anfioxo, pez lanceta, lanceta.

PHYSICAL CHARACTERISTICS
Sixty-one (59–65) myotomes: 36 (34–38) preatriopore, 14 (11–17) atriopore to anus, 11 (10–14) postanal. Two hundred twelve (183–288) dorsal fin chambers. Reaches up to 2.4 in (60 mm) in total length.

DISTRIBUTION
Most widespread species in the genus. Reported from the North Sea to the Mediterranean and the Black Sea. Also found in the Suez Canal, off the East Africa coast, Oman, India, and Sri Lanka. Specimens from the Solomon Islands also may belong to this species.

HABITAT
Sandy bottoms from 3.28–196.85 ft (1–60 m) in depth.

BEHAVIOR
Probably same as for family.

FEEDING ECOLOGY AND DIET
Semi-sessile filter feeders. Feed on plankton organisms, especially diatoms, but foraminiferans, radiolarians, and cladocerans were also found in content analyses of the gut.

REPRODUCTIVE BIOLOGY
Reproductive period starts in April in the Mediterranean, and in June/July in the North Sea. Spawning seems to occur in the evening; spermatozoa are shed before the eggs.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
Several European marine biological stations supply this species to educational and research institutions. ◆

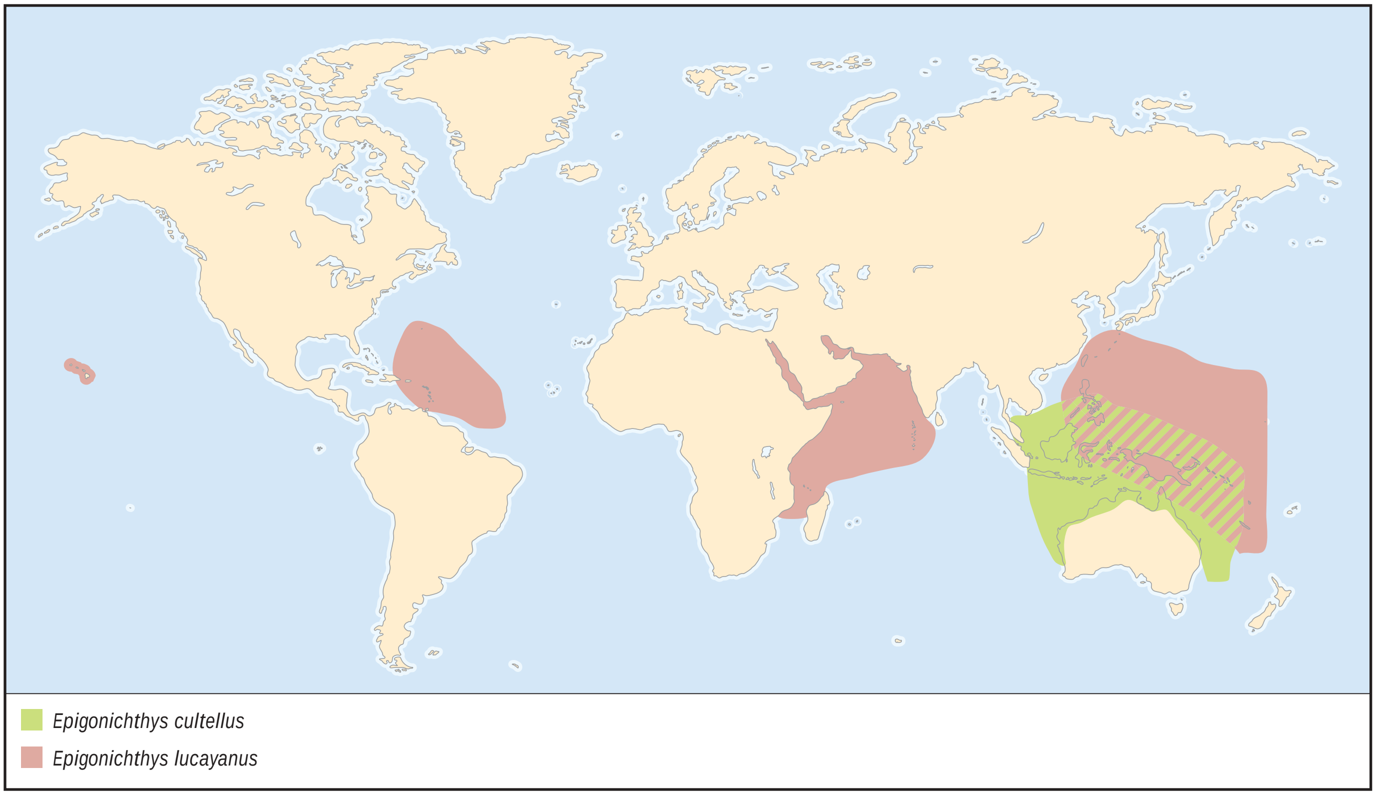
No common name

Epigonichthys cultellus

ORDER
Amphioxiformes

FAMILY
Branchiostomatidae

TAXONOMY
Epigonichthys cultellus Peters, 1877, Moreton Bay, Australia.



OTHER COMMON NAMES
(Listed names were originally coined for the European species *Branchiostoma lanceolatum.* Because of the morphological uniformity of cephalochordates they are usually used for all species.) English: Amphioxus, lancelet; French: Amphioxus, lancelet; German: Amphioxus, Lanzettfischchen; Spanish: Anfioxo, pez lanceta, lanceta.

PHYSICAL CHARACTERISTICS
Gonads on right side of body only. Fifty-one (48–52) myotomes: 31 (29–36) preatriopore, 15 (13–18) atriopore to anus, 9 (9–13) postanal. Two hundred twenty (180–254) dorsal fin chambers. Reaches up to 1.6 in (40 mm) in total length.

DISTRIBUTION
Solomon Islands, Queensland, Indonesia, Philippines, western Australia, Thailand, Sri Lanka, and Tanzania.

HABITAT
Sand and mud from about 13.12–65.6 ft (4–20 m).

BEHAVIOR
Probably same as for family.

FEEDING ECOLOGY AND DIET
Probably same as for family.

REPRODUCTIVE BIOLOGY
Probably same as for family.

CONSERVATION STATUS
Not threatened.

SIGNIFICANCE TO HUMANS
None known. ◆

Bahama lancelet

Epigonichthys lucayanus

ORDER
Amphioxiformes

FAMILY
Branchiostomatidae

TAXONOMY
Epigonichthys lucayanus Andrews, 1893, Alice Town, North Bimini, Bahamas.

OTHER COMMON NAMES
(Listed names were originally coined for the European species *Branchiostoma lanceolatum.* Because of the morphological uniformity of cephalochordates they are usually used for all species.) English: Amphioxus, lancelet; French: Amphioxus, lancelet; German: Amphioxus, Lanzettfischchen; Spanish: Anfioxo, pez lanceta, lanceta.

PHYSICAL CHARACTERISTICS
Gonads on right side of body only. Sixty (55–62) myotomes: 37 (35–52) preatriopore, 16 (13–18) atriopore to anus, 8 (6–9) postanal. Three hundred seven (167–484) dorsal fin chambers. Reaches up to 0.83 in (21 mm) in total length.

DISTRIBUTION
Tropical and subtropical regions of Atlantic, Pacific, and Indian Oceans.

HABITAT
Coral sands to mud flats, from 0–65.61 ft (0–20 m) in depth (up to 3,001.97 ft [915 m] for larvae).

BEHAVIOR

Probably same as for family.

FEEDING ECOLOGY AND DIET

Semi-sessile filter feeder. Feeds on plankton organisms, especially diatoms and coccolithophorids.

REPRODUCTIVE BIOLOGY

Probably same as for family.

CONSERVATION STATUS

Not considered threatened.

SIGNIFICANCE TO HUMANS

None known. ◆

Resources

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Thomas Günther Stach, PhD

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For further reading

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Organizations

Agricultural Research Service
<http://www.ars.usda.gov/is/AR/archive/may01/worms0501.htm>

American Society of Parasitologists
<http://asp.unl.edu>

American Zoo and Aquarium Association
8403 Colesville Road, Suite 710
Silver Spring, MD 20910 USA
<http://www.aza.org>

Australian Regional Association of Zoological Parks and Aquaria
PO Box 20
Mosman, NSW 2088
Australia
Phone: 61 (2) 9978-4797
Fax: 61 (2) 9978-4761
<http://www.arazpa.org>

British and Irish Graptolite Group
c/o Dr. A. W. A. Rushton
The Natural History Museum, Cromwell Rd.
London SW7 5BD United Kingdom
<http://www.graptolites.co.uk/>

European Association of Zoos and Aquaria
PO Box 20164
1000 HD Amsterdam
The Netherlands
<http://www.eaza.net>

Helminthological Society of Washington
Allen Richards, Ricksettsial Disease Department
Naval Medical Research Center
503 Robert Grant Ave.
Silver Spring, MD 20910-7500 USA

Hydrozoan Society: Dedicated to the Study of Hydrozoan Biology
<http://www.ucmp.berkeley.edu/agc/HS/>

International Society of Endocytobiology
<http://www.endocytobiology.org/>

International Symbiosis Society
<http://www.ma.psu.edu/lkh1/iss/>

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Glossary

4d cell—Mesentoblast; a blastomere cell that results from zygotes that have spiral cleavage divisions, and contains an unidentified cytoplasmic factor that causes the cell and its progeny to form mesoderm.

Abdomen—The posterior of the main body divisions.

Abyssal—Of, or relating to, the deepest regions of the ocean.

Acanthor—First larval stage of acanthocephalans.

Aciculum—Small needlelike structure resembling a rod that supports the divisions of the parapodium.

Acoelomate—An organism, particularly an invertebrate, lacking a coelom that is characterized by bilateral symmetry.

Actinotrocha—Tentacle-like ciliated larva of phoronids.

Aestivation—A period of dormancy that is entered into when conditions are not favorable, particularly during very warm or very dry seasons.

Aflagellate—An organism that lacks a flagella.

Agamete—Nucleus within the plasmodium that divides mitotically and gives rise to a sexual adult.

Ametabolous—Development in which little or no external metamorphic changes are noticeable in the larval to adult transition.

Amphiblastula—Free-swimming larval stage of sponges.

Anal—Relating to or being close to the anus.

Anamorphic—Development in which only part of the adult segments are present in recently hatched young.

Ancestrula—Zooid that develops from an egg.

Antibiosis—A provocative association between organisms that is detrimental, inhibitive, and preventative to one or more of them but produces a metabolic product in another.

Aphotic zone—Region of the ocean where no sun light reaches and exists in complete darkness.

Apical field—An area inside the circumapical band of rotifers that is devoid of cilia.

Arboreal—An organism that lives in, on, or among trees.

Ascidiologists—Scientists who study the Ascidiacea.

Auricularia—Primary larval stage in holothuroid development.

Autapomorphy—A derived trait unique to a taxonomic group.

Benthic—An organism that lives on the bottom of the ocean floor.

Bipinnaria—Free-swimming larval stage of asteroids.

Bivoltine—The production of two broods or generations in a season or year.

Blastomere—Zygote cleavage divisions that result in a cell.

Blastopore—The first opening of the early digestive tract.

Blastula—Sphere of blastomeres.

Brachiolaria—Second stage of asteroid larva.

Brood—When the care of eggs takes place outside or inside of the mother's body for at least the early part of development.

Buccal cavity—A cavity that is present within the mouth.

Bud—The development of new progeny cells or new outgrowth.

Caudal—Referring or pertaining to the posterior end of the body.

Cephalic—Referring or pertaining to the anterior end of the body.

Cephalothorax—The body region that consists of the head and thoracic segments.

Chelicera—Pair of appendages present in the anterior body of arachnids.

Chorion—The shell or covering of an egg.

Cilia—Outgrowth present on the cell surface that is short and produces a lashing movement capable of creating locomotion.

Cleavage—The process of cellular divisions in a fertilized egg that changes it from a single-celled zygote into a multicellular embryo.

Cloaca—Chamber into which the intestinal and urogenital tracts discharge.

Cnidocytes—Prey-capture and defensive cells unique to cnidarians.

Coelom—The epithelium-lined space between the body wall and the digestive tract.

Colony—Body composed of zooids that share resources.

Commensalism—Symbiotic relationship between two or more species in which no group is injured, and at least one group benefits.

Commercial fishery—The industry of catching a certain species for sale.

Communal—Cooperation between females of one species in production and building, but not in caring for the brood.

Conspecific—Belonging to the same species.

Coracidium—Ciliated free-swimming stage of cestode.

Cosmopolitan—Occurring throughout most of the world.

Cuticle—The noncellular outer layers of the body.

Cydippid—Free-swimming ctenophore larva.

Cyphonarutes—Planktonic larva of some nonbrooding gymnolaemate bryozoans.

Definitive host—See Primary host.

Demersal—Aquatic animals that live near, are deposited on, or sink to the bottom of the sea.

Dentate—Having teeth, or structures that function as teeth.

Denticles—Teeth, or structures that function as, or are derived from, teeth.

Deposit feeders—Animals that feed upon matter that has settled on the substrate.

Desmosomes—Structures involved in cellular adhesion.

Detritus—Fragments of plant, animal, or waste remnants.

Deuterostome—Division of the animal kingdom that includes animals that are bilaterally symmetrical, have indeterminate cleavage and a mouth that does not arise from the blastopore.

Diapause—A period of time in which development is suspended or arrested and the body is dormant.

Dioecious—Organisms that have male reproductive organs in one individual and female in another.

Diverticulum—A pouch or sac on a hollow structure or organ.

Doliolaria—Barrel-shaped larval stage.

Ecdysis—Molting or shedding of the exoskeleton.

Ectoparasite—A parasite that lives on the outside of a host.

Endemic—Belonging to or from a particular geographical region.

Endocuticle—The innermost layer of the cuticle.

Endoparasite—A parasite that lives inside the body of its host.

Endosymbiont—Symbiotic relationship in which a symbiont dwells within the body of its symbiotic partner.

Epicuticle—The surface layers of the cuticle.

Epiphragm—Temporary mucus door over the aperture (opening) that hardens to seal the snail inside.

Epithelium—Membranous tissue that covers the body or lines a body cavity or tube.

Epizoic—An animal or plant that lives on another animal or plant.

Estuary—A semi-enclosed body of water that is diluted by freshwater input and has an open connection to the sea. Typically, there is a mixing of sea and fresh water, and the influx of nutrients from both sources results in high productivity.

Eukaryote—A cell with a nucleus that contains DNA; or an organism made up of such cells.

Eurybathic—An animal that occurs in a wide range of depths.

Euryhaline—An animal that occurs in a wide variety of salinities.

Eurythermic—An animal that occurs in a wide range of temperatures.

Eversible—Capable of being turned inside out.

Exocuticle—Hard and darkened layer of the cuticle lying between the endocuticle and epicuticle.

Exoskeleton—The external plates of the body wall.

Fibrillae—Small filaments, hairs, or fibers.

Fishery—The industry of catching fish, crustaceans, mollusks or other aquatic animals for commercial, recreational, subsistence or aesthetic purposes.

Fusiform—Having a shape that tapers toward each end.

Gametogenesis—Production of gametes (sex cells).

Ganglion—A nerve tissue mass containing cell bodies of neurons external to the brain or spinal cord.

Girdle—Outer mantle of the polyplacophoran that is thick and stiff, extending out from the shell plate.

Glycocalyx—Protein and carbohydrate surface coat in cells.

Gonochoric—An animal with separate sexes.

Gonopore—Reproductive aperture or pore present in the genital area.

Gonozooid—A reproductive zooid of a hydroid.

Gynandromorph—An individual that exhibits both male and female characteristics.

Hematophagous—A group that feeds or subsides on blood.

Hemitransparent—Half or partially transparent.

Hermaphrodite—An organism that has both male and female sexual organs.

Heterothermic springs—Springs (of water) that may freeze in the winter.

Heterotroph—An organism that is unable to produce its own food, but must obtain its nutrition by feeding on other organisms.

Higgins larva—Loriciferan larval stage.

Holoplankton—An animal that lives in plankton all of its life.

Homothermic springs—Those with a constant temperature throughout the year.

Host—The organism in or on which a parasite lives.

Hyaline—Transparent, clear, and colorless.

Hydromedusa—Medusa of the hydrozoans.

Hyperparasite—A parasitic organism whose host is another parasite.

Infauna—An animal that lives among sediment.

Inquiline—Animal that lives in the nests or abode of another species.

Integument—A layer of skin, membrane, or cuticle that envelops an organism or one of its parts.

Intermediate host—Host for the larval stage of a parasitic organism.

Intracytoplasmic—Located within or taking place within a cell's cytoplasm.

Kinesis—A movement that lacks directional orientation and depends upon the intensity of stimulation.

Lamina—Thin, parallel plates of soft vascular sensitive tissue.

Larva—An immature development stage.

Larviparous—Eggs brooded within the female that are later released as larvae.

Lecithotrophic—Larvae that do not feed, but rather derive nutrition from yolk.

Lorica—Specialized girdle-like structure made of a set of hardened parts that protect the body, named for the segmented corselet of armor worn by Roman soldiers.

Lumen—Cavity of a tubular organ.

Mandible—The jaw.

Manubria—Tube that bears the mouth and hangs down from the subumbrella or medusae.

Maxilla—One of two components of the mouth immediately behind the mandibles.

Medusae—Well-developed cnidarian that is gelatinous and free-swimming.

Meiosis—Cellular process that results in the number of chromosomes in gamete-producing cells (usually sex cells) being reduced to one half.

Mesoderm —Tissue derived from the three primary embryonic germ layers, and the source of many bodily tissues and structures.

Metachronous—Using coordinated waves, as in bands of cilia beating metachronously.

Metamorphosis—A change in physical form or substance.

Miracidium—Free-swimming first larva of trematodes that is ciliated.

Mitosis—A process that takes place in the nucleus of a dividing cell that results in the formation of two new nuclei having the same number of chromosomes as the parent nucleus.

Moult—The shedding of the exoskeleton.

Mutualism—Symbiotic relationship in which both members of the relationship benefit.

Myoepithelial—Cells of the epithelium.

Nematocyst—Stingers of cnidarians.

Neoblasts—Undifferentiated cells that form the blastema, which precedes regeneration in planarians.

Neritic—An organism that inhabits the region of shallow water adjoining the seacoast.

Nocturnal—An organism that is active mostly at night.

Obligate ectoparasites—External parasites that cannot complete their cycle when removed from their host.

Oocyte—The egg before it has reached maturation.

Ootheca—The cover or case that surrounds a mass of eggs.

Oozoid—The zooid that develops from the fertilized egg of urochordates.

Ophiopleuteus—Planktonic larva of echinoids (urchins).

Oral lamella—Oral membrane or layer.

Oviparous—An organism that lays eggs.

Ovipositor—The apparatus through which the female lays eggs.

Ovoviviparous—An organism that produces young that hatch out of their egg while still within their mother.

Paedomorphosis—Retention of juvenile characteristics by adults.

Paraphyletic—A group that contains some of the descendants of a common ancestor.

Parapodium—Appendage present on annelids that resembles a paddle.

Parasite—An organism that lives in or on the body of another living organism, feeding off of its host.

Parenchymula—Larval sponge.

Parthenogenetic—Development of an egg without fertilization.

Pelagic—Organisms that live in the open sea, above the ocean floor.

Pelagosphera—Second planktotrophic larva of sipunculans.

Pentaradial symmetry—Five-part radial symmetry, as seen in echinoderms.

Petancula—Stage of metamorphosis for holothuroids.

Phoresy—Nonparasitic relationship between two organisms in which one uses the other as a means of transportation.

Photokinesis—Activity induced by the presence of light.

Photophore—Cell or group of cells that produce light.

Phytophagous—An organism that solely feeds upon plants.

Pilidium—Free-swimming, planktotrophic larva of heteronemerteans.

Pinnules—Small branches.

Planktotrophic larvae—Larvae that feed during their planktonic phase.

Planulae—Larval cnidarians.

Plasmodium—A life cycle stage in which several young organisms join to form a mass of protoplasm.

Plerocercoid—Last larval lifestage of tapeworms.

Polyembryony—The production of several embryos from a single egg.

Polyp—Cnidarian form that is sessile.

Polyphagous—An organism that consumes a variety of foods.

Polyphyletic—A group that does not contain the most recent ancestor of the organisms.

Positively phototactic—Movement toward light.

Predaceous—An organism that preys on other organisms.

Predator—An animal that attacks and feeds on other animals.

Primary host—An organism that acts as the host for an adult stage of a parasite. Also called definitive host.

Protandric hermaphrodites—Animals hatch as males and later develop into females.

Protonephridia—Ciliated excretory tube that is specialized for filtration.

Protonymph—The second instar of a mite.

Protostome—Bilateral metazoans characterized by determinate and spiral cleavage, the formation of a mouth and anus directly from the blastopore, and the formation of the coelom by the embryonic mesoderm having split.

Pseudovipositor—Terminal abdominal segment of females from which eggs are layed.

Radial symmetry—The exact arrangement of parts or organs around a central axis.

Ramate—An animal or organism with branches.

Raptorial—An organism that has specially adapted the ability to seize and grasp prey.

Rhagon—Stage of development in demosponge larva.

Rostrum— The beak, snout, spine, proboscis, or anterior median prolongation of the carapace or head of an organism.

Saprophytic—An organism that lives on dead or decaying organic matter.

Scalids—Sets of complex spines that allow the organism to move, capture food, or sense changes in its environment.

Scyphistoma—Scyphozoan polyp.

Sclerites—Thick layer of the exoskeleton.

Segment—A rings or subdivisions of the body.

Sensu stricto—In the "strict sense."

Seta—A bristle.

Spermatophore—Packet of sperm that is usually transferred from one individual to another during mating.

Spicule—A slender, pointed structure.

Spiral cleavage—Cleavage pattern in which spindles or places are oblique to the axis of the egg.

Spiralians—Animal groups that show spiral cleavage patterns.

Spirocyst—Adhesive threads present on Cnidarians that capture prey and attach to immobile objects.

Stereom—A unique skeletal microstructure (a network of interconnected holes) in echinoderms.

Stock—A biologically distinct and interbreeding population within a species of aquatic animals.

Stoloniferous—An organism that bears or develops a branch from its base to produce new plants from buds, or an extension of the body wall that develops buds giving rise to new zooids.

Stomochord—A hollow pouch of the gut found in the proboscis of hemichordates.

Strobilation—Asexual reproduction by division into body segments.

Subsistence fishery—A fishery in which the harvested resource is used directly by the fisher.

Symbiont—An organism living in a close relationship with another organism.

Symbiosis—An intimate association, union, or living arragement between two dissimilar organisms in which at least one of the organisms is dependent upon the other.

Synanthropic—Associated with human habitation.

Synapomorphy—A derived trait shared by two or more taxonomic groups.

Syncytial—Multinucleate mass of cytoplasm resulting from the fusion of cells.

Taxis—Reflex movement by an organism in relation to a source of stimulation.

Tegument—Outer, nonciliated layer of the body wall of platyhelminth parasites.

Test—Shell-like encasement or skeleton.

Totipotency—The ability of a cell to differentiate into any type of body cell.

Triploblastic—Embryos with three germ layers.

Triradial symmetry—Three-part radial symmetry, as seen in the life stages of some echinoderms.

Trochophore—Larva that has a girdle ring of cilia.

Troglophilous—An organism that lives in caves.

Unci—Hooked anatomical structure.

Uncinus—Miniature hooked anatomical structure.

Univoltine—A group that produces only one generation per year.

Velum—Shelf present under the umbrella of most hydromedusae, or a ciliated growth with which larva swim.

Vermiform larva—A legless, worm-like larva without a well-developed head.

Vibrissae—A pair of large bristles that is present just above the mouth in some organisms.

Vitellarium—Part of the ovary that produces yolk-filled nurse cells.

Viviparous—An organism that produces live young.

Zoea—Second to last larval stage of many crustaceans.

Zooid—Individual invertebrate that reproduces nonsexually by budding or splitting, especially one that lives in a colony in which each member is joined to others by living material, for example, a coral.

Zooplankton—Free-swimming, microscopic planktonic animals present in lakes and oceans.

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Lower metazoans and lesser deuterostomes order list

Porifera [Phylum]
  Calcarea [Class]
    Baeriida [Order]
    Clathrinida
    Leucosoleniida
    Lithonida
    Murrayonida

  Hexactinellida [Class]
    Amphidiscosida [Order]
    Aulocalycoida
    Hexactinosida
    Lychniscosida
    Lyssacinosida

  Demospongiae [Class]
    Agelasida [Order]
    Astrophorida
    Chondrosida
    Dendroceratida
    Dictyoceratida
    Hadromerida
    Halichondrida
    Halisarcida
    Haplosclerida
    Homosclerophorida
    Poecilosclerida
    Spirophorida
    Verongida
    Verticillitida

Placozoa [Phylum]
    No order designations

Monoblastozoa [Phylum]
    No order designations

Rhombozoa [Phylum]
    Dicyemida [Order]
    Heterocyemida

Orthonectida [Phylum]
    Orthonectida [Order]

Cnidaria [Phylum]
  Anthozoa [Class]
    Actiniaria [Order]
    Alcyonacea
    Antipatharia
    Ceriantharia
    Corallimorpharia
    Helioporacea
    Pennatulacea
    Scleractinia
    Zoanthidea

  Hydrozoa [Class]
    Actinulida [Order]
    Capitata
    Conica
    Cystonectae
    Filifera
    Laingiomedusae
    Limnomedusae
    Moerisiida
    Narcomedusa
    Proboscoida
    Physonectae
    Polypodiozoa
    Trachymedusa

  Cubozoa [Class]
    Cubomedusae [Order]

  Scyphozoa [Class]
    Coronatae [Order]
    Rhizostomeae
    Semaeostomeae
    Stauromedusae

Ctenophora [Phylum]
    Beroida [Order]
    Cestida
    Cydippida
    Ganeshida
    Lobata
    Platyctenida
    Thalassocalycida

Platyhelminthes [Phylum]
  Acoela [Class]
    No order designations

  Turbellaria [Class]
    Catenulida [Order]
    Haplopharyngida
    Lecithoepitheliata
    Macrostomida
    Polycladida
    Prolecithophora
    Proplicastomata
    Proseriata
    Rhabdocoela
    Tricladida

  Trematoda [Class]
    Aspidogastrida [Order]
    Azygiida
    Echinostomida
    Opisthorchiida
    Plagiorchiida
    Strigeatida

  Monogenea [Class]
    Monopisthocotylea [Order]
    Polyopisthocotylea

  Cestoda [Class]
    Amphilinidea [Order]
    Caryophyllidea
    Cyclophyllidea
    Diphyllidea
    Gyrocotylidea
    Haplobothriidea
    Lecanicephalidea
    Litobothriidea
    Nippotaeniidea
    Proteocephalidea
    Pseudophyllidea
    Spathebothriidea
    Tetrabothriidea
    Tetraphyllidea
    Trypanorhyncha

Nemertea [Phylum]
  Anopla [Class]
    Heteronemertea [Order]
    Palaeonemertea

Enopla [Class]
Hoplonemertea [Order]

Rotifera [Phylum]
Bdelloida [Order]
Collothecacea
Flosculariacea
Ploimida
Seisonida

Gastrotricha [Phylum]
Chaetonotida [Order]
Macrodasyida

Kinorhyncha [Phylum]
Cyclorhagida [Order]
Homalorhagida

Nematoda [Phylum]
Adenophorea [Class]
Araeolaimida [Order]
Chromadorida
Desmodorida
Desmoscolecida
Dorylaimida
Enoplida
Isolaimida
Mermithida
Monhysterida
Mononchida
Muspiceida
Stichosomida
Trichocephalida

Secernentea [Class]
Aphelenchida [Order]
Ascaridida
Camallanida
Diplogasterida
Rhabditida
Spirurida
Strongylida
Tylenchida

Nematomorpha [Phylum]
Gordioidea [Order]
Nectonematoidea

Acanthocephala [Phylum]
Apororhynchida [Order]
Echinorhynchida
Gigantorhynchida
Gyracanthocephala
Moniliformida
Neoechinorhynchida
Oligacanthorhynchida
Polymorphida

Entoprocta [Phylum]
Coloniales [Order]
Solitaria

Micrognathozoa [Phylum]
Limnognathida [Order]

Gnathostomulida [Phylum]
Bursovaginoidea [Order]
Filospermoidea

Priapulida [Phylum]
Halicryptomorphida [Order]
Priapulimorphida
Seticoronarida

Loricifera [Phylum]
Nanaloricida [Order]

Cycliophora [Phylum]
Symbiida [Order]

Echinodermata [Phylum]
Crinoidea [Class]
Bourgueticrinida [Order]
Comatulida
Cyrtocrinida
Isocrinida
Millericrinida

Asteroidea [Class]
Brisingida [Order]
Forcipulatida
Notomyotida
Paxillosida
Spinulosida
Valvatida
Velatida

Concentricycloidea [Class]
Peripodida [Order]

Ophiuroidea [Class]
Euryalida [Order]
Oegophiurida
Ophiurida

Echinoidea [Class]
Arbacioida [Order]
Cassiduloida
Cidaroida
Clypeasteroida
Diadematoida
Echinoida
Echinothuroida
Holasteroida
Holectypoida
Pedinoida
Phymosomatoida
Salenoida
Spatangoida
Temnopleurida

Holothuroidea [Class]
Apodida [Order]
Aspidochirotida
Dactylochirotida
Dendrochirotida
Elasipodida
Molpadiida

Chaetognatha [Phylum]
Aphragmophora [Order]
Phragmophora

Hemichordata [Phylum]
Cephalodiscida [Order]
Rhabdopleurida

Chordata [Phylum]
Urochordata [Subphylum]
Ascidiacea [Class]
Enterogona [Order]
Pleurogona

Thaliacea [Class]
Doliolida [Order]
Pyrosomatida
Salpida

Appendicularia [Class]
Copelata [Order]

Sorberacea [Class]
Aspiraculatav [Order]

Cephalochordata [Subphylum]
Amphioxiformes [Order]

A brief geologic history of animal life

A note about geologic time scales: A cursory look will reveal that the timing of various geological periods differs among textbooks. Is one right and the others wrong? Not necessarily. Scientists use different methods to estimate geological time—methods with a precision sometimes measured in tens of millions of years. There is, however, a general agreement on the magnitude and relative timing associated with modern time scales. The closer in geological time one comes to the present, the more accurate science can be—and sometimes the more disagreement there seems to be. The following account was compiled using the more widely accepted boundaries from a diverse selection of reputable scientific resources.

Geologic time scale

Era	Period	Epoch	Dates	Life forms
Proterozoic			2,500-544 mya*	First single-celled organisms, simple plants, and invertebrates (such as algae, amoebas, and jellyfish)
Paleozoic	Cambrian		544-490 mya	First crustaceans, mollusks, sponges, nautiloids, and annelids (worms)
	Ordovician		490-438 mya	Trilobites dominant. Also first fungi, jawless vertebrates, starfishes, sea scorpions, and urchins
	Silurian		438-408 mya	First terrestrial plants, sharks, and bony fishes
	Devonian		408-360 mya	First insects, arachnids (scorpions), and tetrapods
	Carboniferous	Mississippian	360-325 mya	Amphibians abundant. Also first spiders, land snails
		Pennsylvanian	325-286 mya	First reptiles and synapsids
	Permian		286-248 mya	Reptiles abundant. Extinction of trilobytes. Most modern insect orders
Mesozoic	Triassic		248-205 mya	Diversification of reptiles: turtles, crocodiles, therapsids (mammal-like reptiles), first dinosaurs, first flies
	Jurassic		205-145 mya	Insects abundant, dinosaurs dominant in later stage. First mammals, lizards, frogs, and birds
	Cretaceous		145-65 mya	First snakes and modern fish. Extinction of dinosaurs and ammonites, rise and fall of toothed birds
Cenozoic	Tertiary	Paleocene	65-55.5 mya	Diversification of mammals
		Eocene	55.5-33.7 mya	First horses, whales, monkeys, and leafminer insects
		Oligocene	33.7-23.8 mya	Diversification of birds. First anthropoids (higher primates)
		Miocene	23.8-5.6 mya	First hominids
		Pliocene	5.6-1.8 mya	First australopithecines
	Quaternary	Pleistocene	1.8 mya-8,000 ya	Mammoths, mastodons, and Neanderthals
		Holocene	8,000 ya-present	First modern humans

*Millions of years ago (mya)