1515
SCIENTIFIC AMERICAN OFFPRINTS

41

The Giant Squid

by Clyde F. E. Roper and Kenneth J. Boss

SCIENTIFIC AMERICAN
APRIL 1982
VOL. 246, NO. 4 PP. 96–105

PUBLISHED BY **W. H. FREEMAN AND COMPANY** 660 MARKET STREET, SAN FRANCISCO, CALIFORNIA 94104

The Giant Squid

This deep-sea cephalopod is so seldom seen, dead or alive, that it seems mythical. Numerous specimens have, however, been studied, and they have begun to reveal the animal's anatomy and its ecology

by Clyde F. E. Roper and Kenneth J. Boss

In *Moby-Dick* Herman Melville describes a sea creature of "vast pulpy mass, furlongs in length..., long arms radiating from its center and curling and twisting like a nest of anacondas." He apparently had in mind the giant squid; his description reflects the meager information that was available about the animal in his time. Indeed, until the crew of a French warship sighted one in 1861 and managed to haul in part of it the animal was quasi-mythical. Even now, when a considerable number of specimens have been reported, the giant squid (weighing up to 1,000 pounds and having an overall length of some 18 meters, or nearly 60 feet, if the tentacles are extended) remains largely mysterious. No living specimen has ever been maintained in a research institution or an aquarium. Most of what is known comes from strandings, when the squid is dead or dying; from capture by fishermen of animals that soon died, and from specimens removed from the stomach of toothed (fish- or squid-eating) whales. On the basis of this information one can state what a mature giant squid looks like and can say quite a bit about its internal anatomy. On other matters, such as its habitat and method of reproduction, one can offer only educated guesses based on what is known of related oceanic squids.

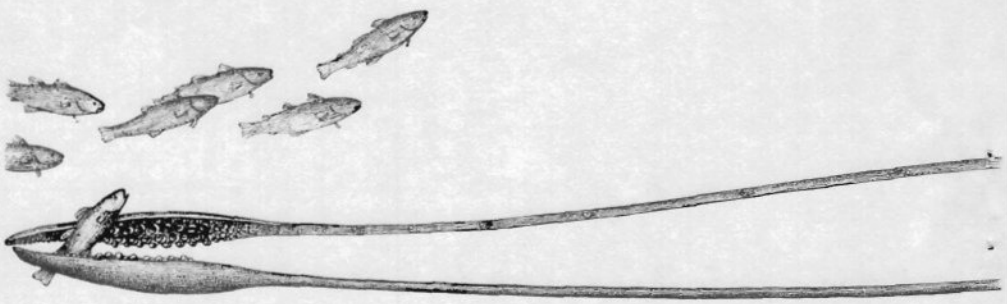
Teuthologists, the specialists who study cephalopods (the group of marine animals that includes the squid, the cuttlefish and the octopus), have placed the giant squid by itself in the genus *Architeuthis* of the family Architeuthidae. Nineteen nominal "species" have been described, some solely on the basis of individual parts of the animals. Until recently the tendency was to classify nearly every find as a new species. Although authorities differ, it has been suggested that the 19 nominal species can in fact be encompassed by only three: *Architeuthis sanctipauli* in the Southern Hemisphere, *A. japonica* in the northern Pacific and *A. dux* in the northern Atlantic. Some evidence, based mainly on the relative size of the head and the outline of the caudal fin, has been marshaled to indicate that as many as five species live in the Atlantic, two in the northern Pacific and several more in the southern Pacific.

In 1980 a specimen of medium size—about 10 meters in total length—was stranded on Plum Island in Massachusetts. The animal was preserved and was displayed for several months at the New England Aquarium in Boston. It is now in Washington at the Smithsonian Institution's National Museum of Natural History, where it is being studied in detail. The study provides much of the data for the following description, in which we adhere to the standard method for avoiding ambiguity about anatomical positions by relying on the terms dorsal for back or top, ventral for front or bottom, caudal for at or near the tail, anterior for forward, posterior for rearward, proximal for near a reference point and distal for far. The normal swimming position of the giant squid is horizontal, so that the animal's dorsal side is at the top and its ventral side is at the bottom.

The giant squid's cylindrical head may reach nearly a meter in length; it is connected to the body proper by a "neck" bearing a circumferential collar or sheath with a dorsal locking cartilage. A crown of eight thick, muscular arms and two very long and thin but muscular tentacles surrounds the buccal (mouth) apparatus and extends from the anterior end of the head. (Cephalopod means head-foot.)

Although the arms are proportionately long in young individuals, they are relatively much shorter than the tentacles in adults. An arm may attain a circumference of 50 centimeters at the base and a length of three meters. Each arm bears on its inner surface low, weak and sometimes scalloped protective membranes that border two rows of suckers. The suckers gradually decrease in size distally until at the tip of the arm they are merely tiny knobs.

The two ventral arms in males are hectocotylized, that is, specialized to facilitate the fertilization of the female's eggs. With them the male transfers spermatophores to the female in mating.



ADULT GIANT SQUID can be as much as 18 meters (60 feet) long and can weigh as much as 450 kilograms (1,000 pounds). This drawing is based on numerous specimens or parts of them that have been drawn, photographed or preserved over the past century. The squid in the draw-

These arms differ among species in their length and diameter and in the extent of their modification for the mating function. Distally the arms bear, as continuations of the two rows of suckers, two rows of rectangular pads separated by a deep furrow.

The two tentacles, with which the squid seizes its prey in a motion rather like the thrusting and closing of a pair of pliers, are about 25 centimeters in circumference at the base and can reach a length of more than 10 meters. The stalk of a tentacle is bare along the base; alternating small suckers and adhesive knobs may appear farther along its length. The suckers and knobs increase in size and frequency toward the club: the slightly expanded distal end of the tentacle. The manus, or palm, of the club has four rows of finely toothed suckers. The larger medial ones (in two rows) are about two and a half times the diameter of the smaller ones in the marginal rows. The diameter of a tentacular sucker may reach 5.2 centimeters. The distal end of the club, the dactylus (finger), is pointed and attenuated but is covered with hundreds of small suckers.

All the suckers of a giant squid are shaped like a suction cup. Each sucker is set on a muscular pedicle, or short stalk, that can be moved by the animal. The perimeter of a sucker is rimmed by a sharply toothed ring of chitin (the hard material that forms the outer covering of many crustaceans and insects) that adheres to the surface of the prey when the sucker is applied. No specialized hooks appear in place of suckers, as they do in certain other oceanic squids.

Imprints or scars from squid suckers have been found on the skin of sperm whales and even in their stomach. The diameter of these scars has been variously exaggerated, sometimes to as much as 20 centimeters (eight inches). Such reports have led by extrapolation to a distorted estimate of the maximum length of giant squids. The most reliable evidence suggests that the average diameter of the suckers on the arms is about 2.5 centimeters and that the maximum diameter is 5.2 centimeters, the size sometimes found on a tentacular club.

The mantle, or body, of the giant squid is more or less narrowly cone-shaped. It tapers to a bluntly pointed tail. In adults a short, stout, taillike projection extends beyond the fins; juveniles do not have it. The fins are flexible but not strongly muscular, suggesting that they serve as stabilizing vanes.

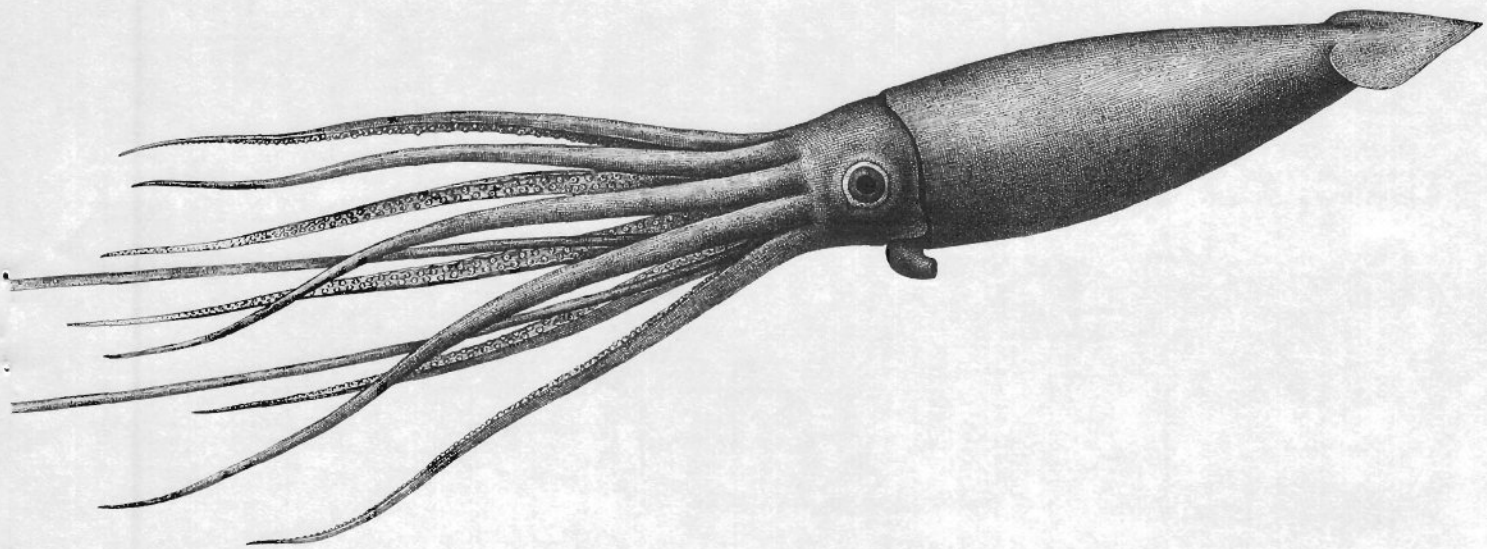
As a modification of the molluscan foot a large, muscular funnel rises ventrally behind the head at the anterior end of the mantle. With it the squid propels itself by squirting water out of its mantle cavity. The funnel is highly mobile, so that the squid can dart forward, backward, up, down or to the side. Inside the funnel is a flaplike valve that prevents the backflow of water between squirts. Ventrally at the base of the funnel on each side is a groove of cartilage that interlocks with corresponding cartilaginous ridges on the inner surface of the mantle when the squid is expelling water. This funnel-locking mechanism prevents water from escaping around the neck, forcing all the water to go through the funnel.

The giant squid also has a translucent internal supportive structure variously called the gladius or the pen. It is the remnant of an archaic internal calcareous shell that is still found in more primitive cephalopods such as the cuttlefish. The gladius lies in a sac in the musculature of the mantle, extending posteriorly from the anterior edge of the mantle to the taillike posterior extremity. It functions as a skeletal rod for the attachment of muscles and as a supporting staff for the elongated body.

The multilayered integument that envelops the body, the head and the arms is a dark purplish red to maroon dorsally and slightly lighter ventrally. The color of the dorsal and ventral surfaces of the arms is less intense than that of the lateral ones. The color arises not only from a background pigmentation but also from a layer of chromatophores: pigment-bearing cells that can change the coloration of the integument by expanding or contracting. In the squid the chromatophores probably serve to modify the color of the integument according to behavioral requirements or changes in the amount of light in the water. The internal surface of the mantle and some of the viscera also have dark reddish pigmentation, an uncommon feature in oceanic squids. Photophores, or bioluminescent organs, are not known in *Architeuthis.*

The giant squid's eyes are enormous, larger than the headlights of an automobile. With a diameter approaching 25 centimeters (10 inches), they are the largest eyes in the animal kingdom. They are positioned laterally on the head and are circular in outline. Each eye has an adjustable lens and a dark iris but no cornea.

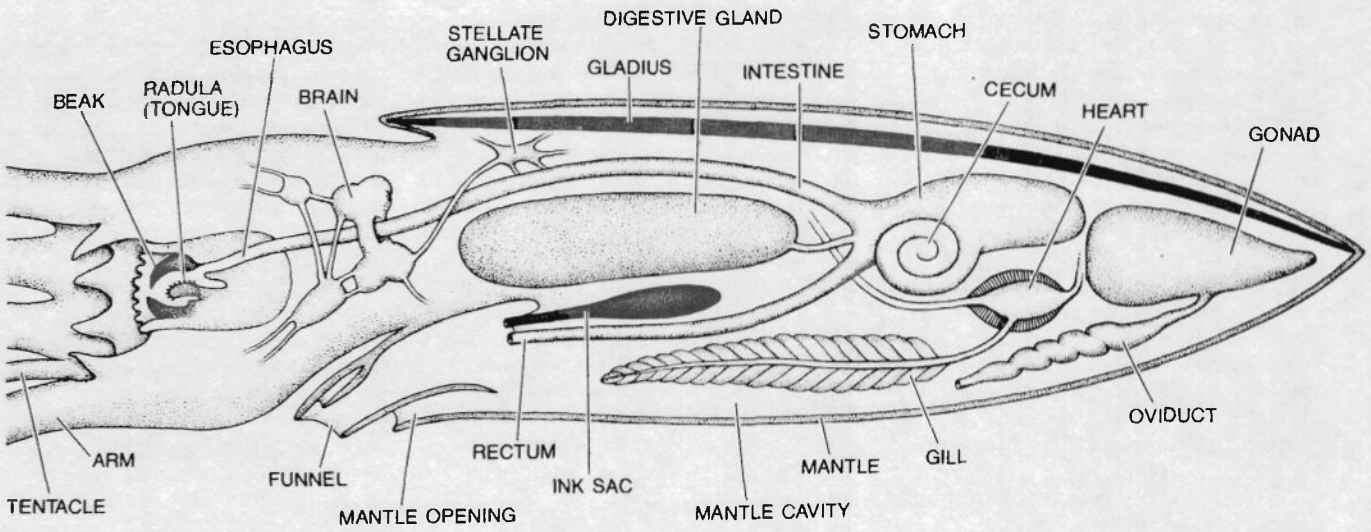
The mouth is at the center of the circular crown of arms. Powerful chitinous jaws, encased in a muscular mass and capable of rotation and protrusion, are utilized to bite prey into chunks of a size suitable for swallowing. These parrotlike beaks, which can be more than 15 centimeters in length, consist of upper and lower mandibles. The strong upper mandible bears a pointed and acute-angled rostrum that forms a cutting edge with the lower mandible, which characteristically has a short, blunt rostrum and rounded winglike extensions. By



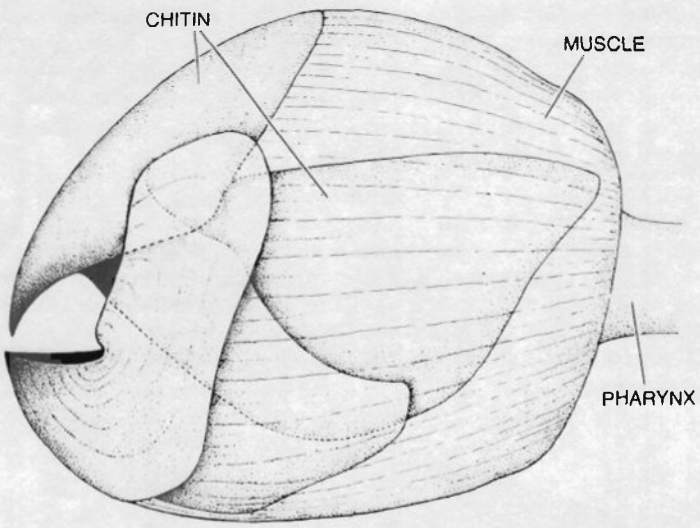
ing is depicted seizing a fish by thrusting out its long tentacles as it attacks, propelling itself forward by squirting water through the back-turned funnel that is visible below the eye. By appropriately turning the funnel the squid is able to move in any direction. In the class of cephalopods the giant squid is placed in the genus *Architeuthis;* the number of species in the genus has yet to be firmly established.

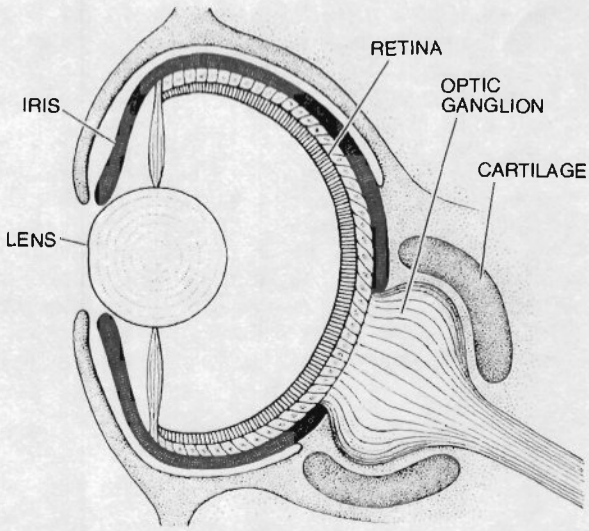
careful examination the isolated jaws of individual squid species can be distinguished from those of other species. Hence it is possible to identify the otherwise unrecognizable digested contents of whale stomachs and the inclusions in ambergris, the waxy substance made by the sperm whale to enable it to purge itself of indigestible squid beaks.

The radula, or rasping tongue, is a characteristic feature of mollusks and usually consists of a long cuticular ribbon bearing transverse rows of chitinized teeth with cusps of various shapes. In *Architeuthis* the radula is small for an animal of such huge proportions. It is nonetheless impressive compared with the radulas of other mollusks, being about 100 millimeters long and a little more than 10 millimeters wide. Each row has a three-cusp central tooth and three smaller teeth on each side. Food bitten into chunks by the jaws is forced into the buccal cavity by the bolting

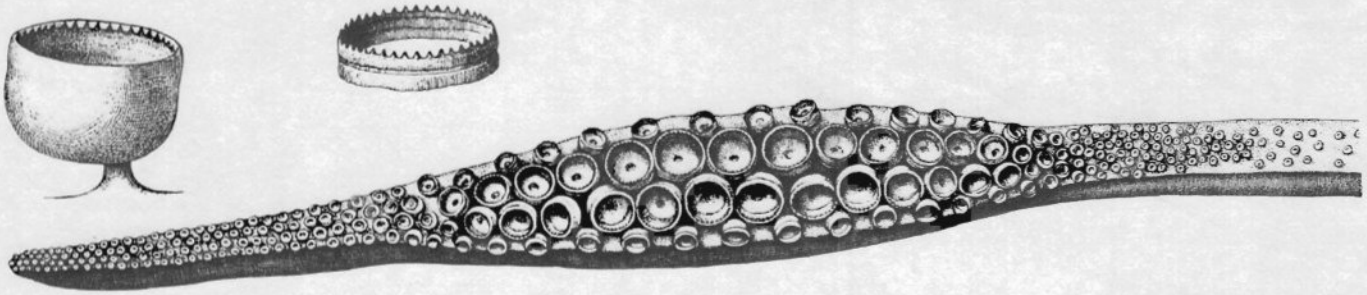


INTERNAL ANATOMY of a female giant squid is indicated on the basis of present knowledge. The gladius, which is also known as the pen, is a fairly stiff structure that serves as a supporting rod for the animal's long body and also as a point of attachment for muscles.





MOUTH AND EYE of the giant squid are among the animal's noteworthy features. The powerful beak consists of chitin, the hard material that forms the external covering of many crustaceans and insects. With its beak the squid cuts its prey into pieces it can swallow. The eyes of the giant squid are the largest in the animal kingdom, each one being approximately 25 centimeters (10 inches) in diameter.



CLUB END OF A TENTACLE of the giant squid is distinguished by a manus, or palm, where the tentacle becomes slightly wider. The manus has four rows of finely toothed suckers, the larger ones being about five centimeters in diameter and the smaller ones about two centimeters. Each sucker can be moved. One sucker and its toothed chitinous ring are shown above the end of the tentacle at the left.

movement of the radula. In addition many minute backward-sloping denticulations (the pharyngeal teeth) in the cuticle lining the pharynx facilitate swallowing and ensure that food moves inward to the alimentary canal.

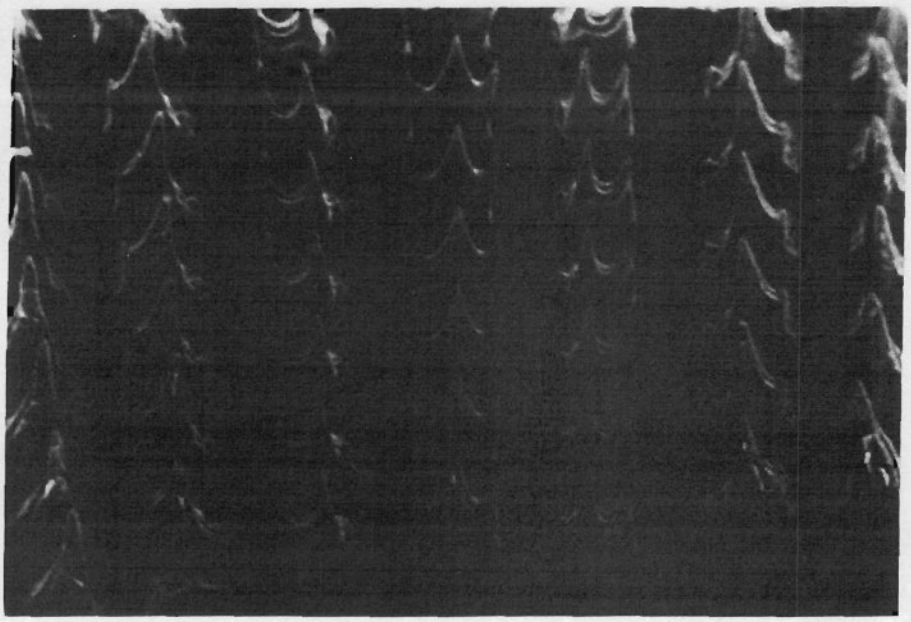
The alimentary canal continues into a muscular esophagus that forces food by peristaltic contractions into the thick-walled stomach and the associated cecum. Digestive enzymes are secreted by the massive salivary glands and by the single medial "liver," or digestive gland, and the anterior pancreas. Assimilation is further advanced in the cecum. Wastes pass through the short intestine and out through a flapped rectum, which discharges near the internal opening of the funnel. The wastes are flushed out through the funnel with the water expelled for propulsion.

The squid obtains oxygen through a pair of long gills, which have many (sometimes more than 100) of the lamellae, or leaflets, that are the basic structures for the exchange of oxygen and carbon dioxide. Another feature is the ink sac characteristic of most squids. In the giant squid the sac is large and elongated, with a long duct that empties into the rectum. The black, mucous ink is thought to serve the giant squid as the ink of other squids does when it is extruded through the funnel in an escape reaction, that is, it maintains a cohesive shape resembling that of the squid, presumably confusing a predator as the squid jets away.

A female squid produces enormous numbers of whitish eggs. The eggs are relatively small, being from .5 millimeter to 1.4 millimeters long and .3 to .7 millimeter across. One specimen carried more than 5,000 grams (11 pounds), or perhaps a million eggs.

The female reproductive apparatus consists of (1) a single median ovary, lying posteriorly in the visceral mass; (2) paired, convoluted oviducts through which the mature eggs pass out into the mantle cavity, and (3) large nidamental glands, which manufacture a gelatinous mass that envelops the eggs in the mantle cavity. The site and method of fertilization are not known, but presumably it takes place as the mature eggs leave the oviducts. Whether the eggs float in the ocean or are attached to the ocean bottom is also not known, but it seems likely that they float in huge gelatinous masses because this mode is characteristic of all other known oceanic squids. The females of many shallow-water squid species have a receptacle for spermatophores below the mouth, but no such structure is found in *Architeuthis* females. Moreover, no spermatophores have been found implanted in female giant squids, although such implantation (in the mantle cavity or at the opening of the mantle near the neck) is common in other oceanic squids.

SPECIALIZED ARM of the male squid serves for transferring spermatophores to the female. Two of the male giant squid's eight arms are specialized in this way; they are called hectocotylized arms. They are distinguished by two rows of rectangular pads (in place of suckers).



RADULA, or tongue, of the giant squid is shown at an enlargement of 22 diameters in this scanning electron micrograph. The teeth slope toward the back of the squid's mouth and assist the movement of food into the esophagus. The entire radula is about 10 centimeters long.

SUCKER SCARS of a giant squid appear on the skin of a sperm whale, the chief predator of *Architeuthis*. Such scars, made when a squid fought to escape from the whale, have often been cited as evidence for squids of monstrous size. Since a scar grows as the whale grows, however, scars are unreliable evidence for the size of the squid unless they are known to be recent.

The males are externally differentiated from the females by their two hectocotylized arms. The testis consists of a white filamentous mass embedded posteriorly in the visceral mass. The spermatophores, long tubes filled with sperm, are manufactured in the complex spermatophoral apparatus, which is on the left side anterior to the testis.

The long, thin-walled spermatophoral sac (often called Needham's sac because it was first discovered and described by John Turberville Needham) with its basal seminal vesicle is attached to the visceral mass along the left side of the intestine in the mantle cavity. As such structures go it is enormous, reaching a length of a meter and serving as a storage chamber for hundreds (perhaps thousands) of spermatophores packed parallel to one another.

The distal extension of Needham's sac is often termed the penis, but that is probably a misnomer because the structure seems not to be an intromittent organ. Even in a small mature male it may be some 80 centimeters long and may protrude as much as 5.5 centimeters beyond the free edge of the mantle. The tip of the "penis" is mushroom-shaped and has in it a ventral slit about 15 millimeters long.

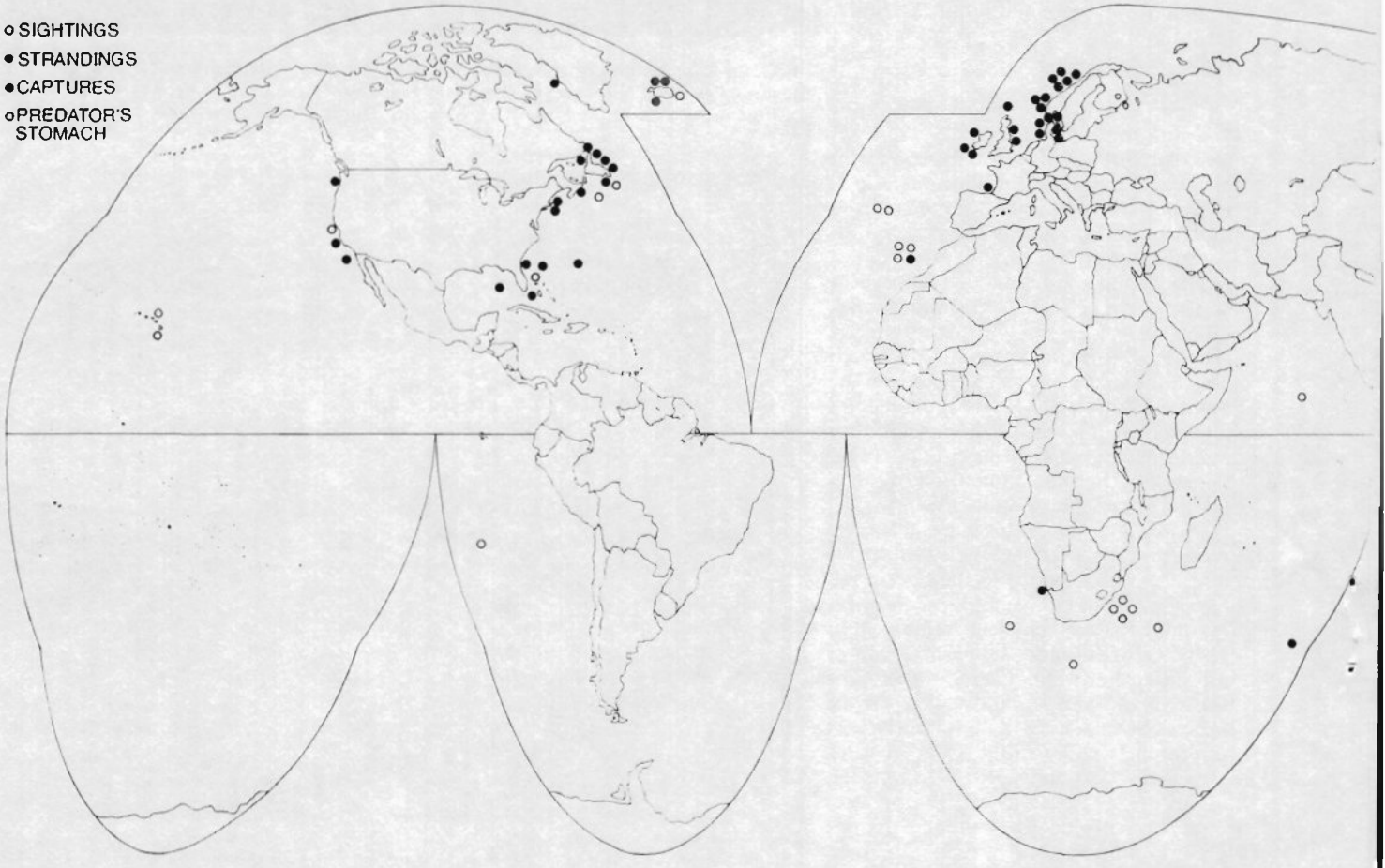
The spermatophores range between 10 and 20 centimeters in length, apparently varying in total length and in the size of the constituent parts depending on the species and the stage of development. As in other squids, the spermatophore of *Architeuthis* has a proximal thread and cap, a springlike ejaculatory cell, a cement body and a distal sperm mass enveloped by a tunic. An external coating of jelly that envelops the spermatophore is peculiar to *Architeuthis*.

It is likely that the giant squid, like other squids, has a mechanism whereby the cap and thread are pulled, much like the pin of a hand grenade, triggering the release of the tightly coiled ejaculatory apparatus and ejecting the sperm-containing capsule and the cement body. The cement body functions as an adhesive mechanism to attach the sperm mass in or near the mantle cavity of the female. Males apparently become sexually mature quite early; specimens with a mantle length of less than a meter have been found to have completely formed spermatophores.

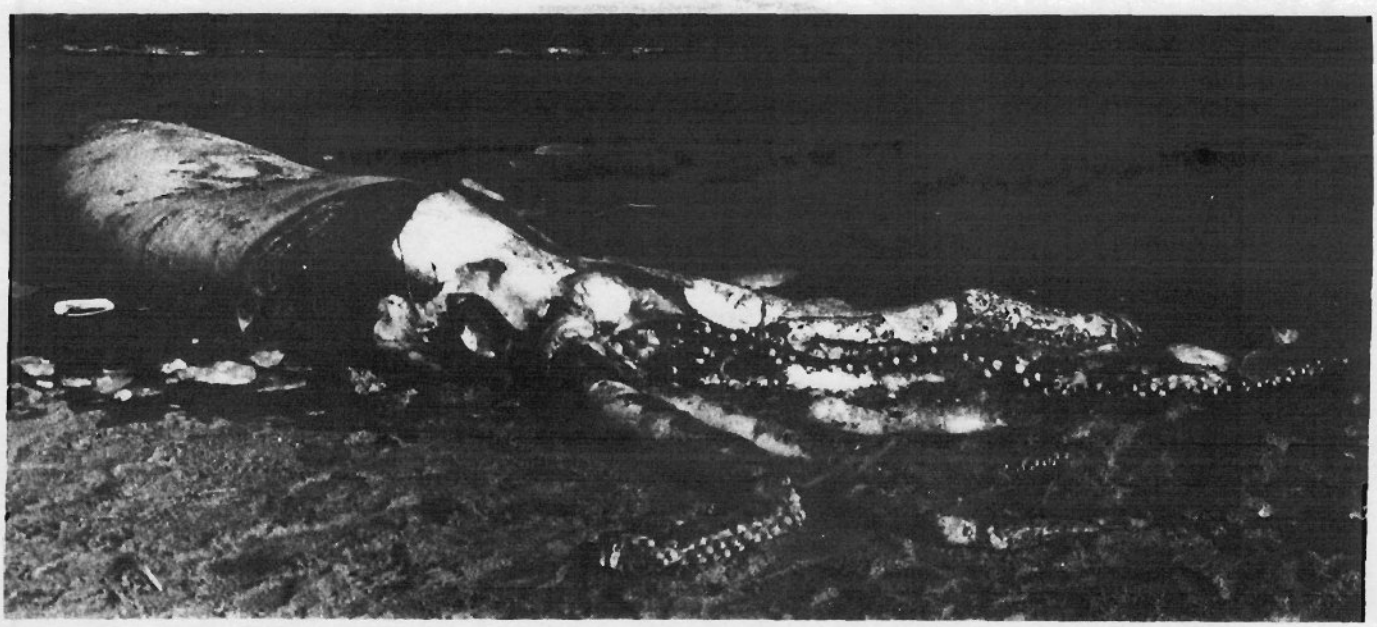
Even though a giant squid is notably large and heavy out of the water, it is quite buoyant in the water. The buoyancy is due to the relatively high concentration of ammonium ions (NH_4^+) in the muscles of the mantle, head and arms. The concentration of ammonium ions probably explains why dead or dying squids rise to the surface and are often washed ashore. Ammonium ions have a specific gravity of 1.01, which is lower than that of seawater (1.022 at a depth of 50 meters and a temperature of 28 degrees Celsius). Without the ammonium ions the tissues of the squid are heavier than seawater, their average specific gravity being 1.046, but with them the animal can maintain its level in the water without having to expend energy by constant swimming.

A side effect of this characteristic is that a freshly stranded giant squid is made unpalatable by the strong, bitter taste of ammonia. In fact, the first observation that *Architeuthis* concentrates ammonium ions in certain muscles was made by three teuthologists, including one of us (Roper), who cooked a piece of giant squid for a party celebrating the completion of a doctoral examination. Subsequent analysis of the tissue confirmed the observation.

Although certain scholars have described *Architeuthis* as a strong swimmer, that is probably not the case. It is true that some oceanic squids are spectacular swimmers, but compared with them *Architeuthis* has a poorly developed musculature. In addition its fins are relatively small and weak, and the locking apparatus of the funnel is con-



DATA ON THE GIANT SQUID have come mainly from strandings and from specimens found in the stomach of sperm whales. The sightings are less reliable, since at a distance an observer might mistake another kind of large squid for a giant squid. In addition to these



STRANDED GIANT SQUID was washed ashore on Plum Island in Massachusetts in 1980. It was an adult of medium size, about 10 meters in total length. Most of the skin was worn off by the sand, and the tentacles (along with the tips of some of the arms) were missing. An indication of the size of the animal is given by the human footprints in the foreground and the seashells on the smooth part of the beach.

siderably less complex and powerful than the one in the strong swimmers.

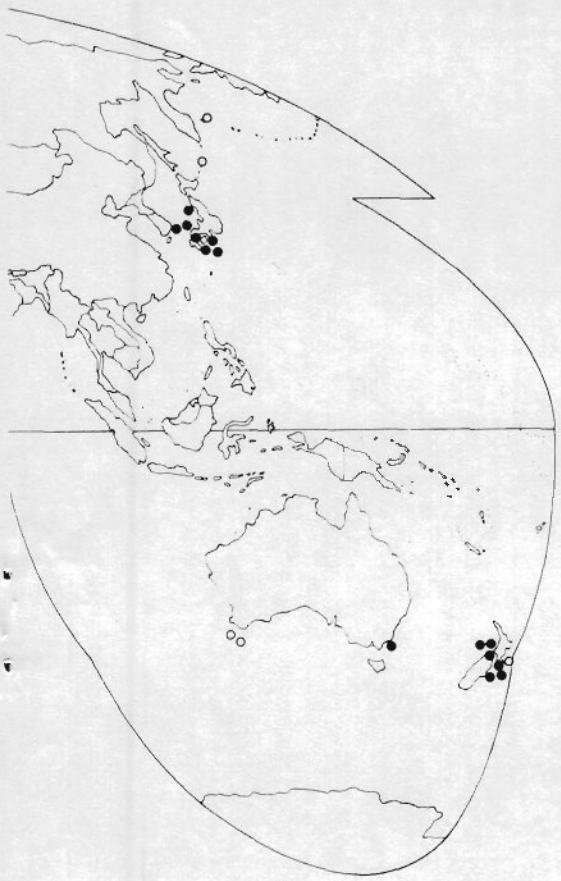
Little is known about what the giant squid eats. Most of the specimens collected have an empty stomach; if the squid were not sick and "off its feed," it would have been unlikely to come to the surface or to be stranded. Even when something is found in a squid's stomach, the chances of identifying it are slim because the beak and the radula reduce the prey to small pieces and the digestive enzymes work fast.

Nevertheless, various workers have guessed or apparently observed that *Architeuthis* feeds on small fish and large invertebrates such as other cephalopods. The few published accounts based on remnants of food found in the stomach of giant squids indicate that the animals do indeed feed on fish and other squids. Since *Architeuthis* appears to be a relatively poor swimmer, it presumably is a somewhat passive and sluggish predator, unable to chase and capture large, active prey.

As for the predators of the giant squid, the principal one is the sperm, or cachalot, whale, *Physeter catodon*. Immature giant squids are eaten by certain mid-water fishes. Notwithstanding the limitations of *Architeuthis* as a swimmer, it is formidable in size and dexterity and has arms that are heavy, suckered and highly motile. The large eyes, representing an efficient detection system, and the ink sac are among the giant squid's protective mechanisms.

In the literature of giant squids one occasionally finds an account of a battle between a giant squid and a sperm whale at the surface of the sea. We must surmise that such a struggle is an attempt by the squid to escape from the whale rather than an attack on the whale by the squid. The scars of giant-squid suckers on the skin around the mouth and head of sperm whales attest to the reality of these battles.

Sperm whales prey on numerous kinds of fish, crustaceans, octopuses and squids, but much of their diet consists of *Architeuthis*. Although only a few giant-squid beaks may be found in a sperm whale's stomach along with hundreds of beaks from other squid species, the sheer size of a single giant squid may take up a third of the volume of a whale's stomach. The fact that a sperm whale's gut is usually found to contain large numbers of other prey but only one *Architeuthis* suggests that giant squids may be solitary animals, except possibly during the mating period.



data there are 148 other records, mostly from near Japan and the southern tip of Africa.

Much has been written about the maximum size attained by *Architeuthis*, with assertions of total lengths exceeding 75 meters. There is no firm evidence for such assertions. The usual basis for them is the size of sucker scars on whales, but since a scar grows as a whale grows, it is unreliable evidence for the size of a squid unless it is demonstrably recent.

The largest specimen recorded in the scientific literature measured approximately 20 meters in total length. (It was stranded on a beach in New Zealand in 1880.) A significant part of this length, probably from 10 to 12 meters, consisted of the tentacles, which in a dead squid are notably elastic and easily stretched. In all other squid species the length of tentacles is always regarded as an imprecise component of measurement. The largest giant-squid mantle lengths known to us are in the range from five to six meters, the largest head lengths about one meter.

Even with the fairly large number of records of *Architeuthis* now available, it is still impossible to identify the precise habitat of this elusive animal. Most of the records come from strandings and from the stomach contents of sperm

whales, neither of which give direct information about habitat. Sperm whales are known to feed in the depth range from 10 to 1,000 meters, and there is strong evidence that they go as deep as 2,000 meters. It is clear from their stomach contents that they feed partly along the bottom. Hence the *Architeuthis* individuals in sperm-whale stomachs could have been captured in mid-water or on the bottom. An educated guess, supported by the record of *Architeuthis* tissue recovered from the stomach of a deep-sea shark captured on the bottom at 1,246 meters near the Azores, is that as adults giant squids live near or on the bottom at a depth of about 1,000 meters. Even this evidence is indirect, however, because some species of bottom-living fishes and sharks often come off the bottom to feed.

It is remarkable that few giant squids have been caught in fishing nets. A few captures have been made in nets being trawled along the bottom at depths of from 200 to 375 meters. Since the specimens were reported to be alive at the time of capture, we must assume that they were in or near their natural habitat, probably on the bottom but possibly in mid-water when the net was being hauled in.

On the other hand, a fresh 12-foot section of a giant squid's tentacle was brought up 150 miles off the coast of California by a mid-water trawl at a depth of 600 meters over a bottom depth of 4,000 meters. Sightings of giant squids swimming at the surface have been reported from off Newfoundland near the Grand Banks, where the water is less than 100 meters deep, and from the central Pacific over depths exceeding 4,000 meters. In recent years specimens of *Architeuthis* have been found in the vicinity of the Hawaiian Islands, where there is virtually no continental shelf and the bottom drops off sharply to several thousand meters.

Then there are the strandings. Many of the specimens are washed ashore dead, but enough are so fresh (or even barely alive) as to indicate that they were alive not too long before or too far from where they came ashore. Still, large squids, like large whales, may be alive when they are stranded but may also be far from their normal habitat because they are sick.

The fact that so few giant squids are captured in nets is intriguing, particularly now that huge mid-water and bottom trawls are deployed by commercial fishermen and by research vessels. Do the squids detect the approach of a net and avoid capture, as so many other oceanic cephalopods do? Or do they live in habitats not normally entered by commercial fishermen or exploratory biologists because they are known to be unproductive, like the middle depths of the open ocean, or because they are too rocky and craggy and therefore dangerous to nets, like the deep canyons and edges of continental slopes? The fact that such questions still have to be asked about giant squids indicates how much remains to be learned about them.

The Authors

CLYDE F. E. ROPER and KENNETH J. BOSS are zoologists whose specialty is the anatomy and classification of marine animals. Roper is chairman of the department of invertebrate zoology at the National Museum of Natural History at the Smithsonian Institution. He was graduated from Transylvania University in 1959 with a B.A. and went on to get his master's and doctoral degrees from the University of Miami. In 1966 he joined the staff of the National Museum, becoming curator in 1972 and chairman of the department of invertebrate zoology in 1980. Boss is professor of biology at Harvard University and curator in malacology (the study of mollusks) at the Museum of Comparative Zoology at Harvard College. He received his B.A. in 1957 at Central Michigan College, his M.Sc. in 1959 at Michigan State University and his Ph.D. in 1963 from Harvard. After completing his doctoral degree he worked in a laboratory of the Bureau of Commercial Fisheries at the Smithsonian. He went to Harvard in 1966 as assistant curator in the Museum of Comparative Zoology; he was appointed professor of biology in 1970. Boss writes: "I am suffering from what I believe [Lawrence] Durrell called islomania, an uncommon passion for the escape and isolation offered by islands; to that end I have a book-filled old fisherman's house . . . on an island in the Gulf of Maine . . . It was there that Clyde and I became enthusiastic about the prospect of writing an article on *Architeuthis* [the giant squid]."

Bibliography

PIRATES OF THE DEEP—STORIES OF THE SQUID AND OCTOPUS. Paul Bartsch in *Smithsonian Institution Annual Report*, pages 347–375; 1917.

A REVIEW OF THE SYSTEMATICS AND ECOLOGY OF OCEANIC SQUIDS. M. R. Clarke in *Advances in Marine Biology*, Vol. 4, pages 93–300; 1966.

A SPECIMEN OF THE GIANT SQUID *ARCHITEUTHIS* FROM NEW ZEALAND. R. K. Dell in *Records of the Dominion Museum in Zoology*, Vol. 7, No. 4, pages 25–36; 1970.

FIRST RECORD OF JUVENILE GIANT SQUID, *ARCHITEUTHIS* (CEPHALOPODA, OEGOPSIDA). C. F. E. Roper and R. E. Young in *Proceedings of the Biological Society of Washington*, Vol. 85, No. 16, pages 205–222; 1972.

GIANT SQUIDS. K. N. Nesis in *Gidrobiologiia*, Vol. 6, No. 706, pages 55–60; 1974.