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SIZE OF ENDOCEROID CEPHALOPODS[1]

BY CURT TEICHERT[2] AND BERNHARD KUMMEL[3]

The maximum size of fossil animal groups, whether mammals, reptiles, or invertebrates has always been a fascinating subject of inquiry, because phyletic size increase is one of the important trends that dominate the evolution of living things. In the case of large animals, the evidence is often hard to assemble because their remains are difficult to obtain, to transport, and to store. Squids are the largest living invertebrates and a tradition has been handed down in paleontological literature that the largest fossil invertebrates likewise are to be found among the cephalopods, but few accurate data are to be found in published sources which are now readily available.

Among the nautiloid cephalopods, it has long been suspected that the Endoceratida furnished the real giants, but no accurate measurements in support of this statement are available.

Clarke (1897) stated that entire shells of *Cameroceras proteiforme*, 10 to 15 feet long (3 to 5 meters), had been found in the Middle Ordovician of Minnesota. In the same publication, Clarke figured an internal cast of part of a siphuncle, from the base of the body chamber to the adapical end of the spiess, which was 3 feet and 3 inches long. Miller and Kummel (1944) described and illustrated additional species of these Middle Ordovician endoceroids from Minnesota, which are deposited in the Carnegie Museum. One of their paratypes of *Endoceras clarkei* measured 750 mm long, is septate throughout and is not complete, adapically or adorally. The holotype of *Endoceras gracillimum* Miller and Kummel (1944) measured 670 mm in

[1] Publication authorized by the Director, U. S. Geological Survey.

[2] U. S. Geological Survey, Denver, Colo.

[3] Museum of Comparative Zoology.

length, again an incomplete specimen consisting only of phragmocone. These same authors described a new species, *Endoceras decorahense,* on two portions of the internal mold of the phragmocone from the Decorah formation, Winneskiek County, Iowa. The larger portion is about 625 mm long and the length of the smaller measures about 320 mm. They estimated the interval between the two pieces as about 115 mm, so the total length of this phragmocone was about 1,060 mm. These authors also mentioned that there is on display in the Chicago Natural History Museum a larger endoceroid that measures 6 feet in length.

Teichert (1927) noted the occurrence, in Middle Ordovician limestones of Estonia, of endoceroids as much as 5 meters long, but gave no further details. Flower (1955) stated that specimens 12 feet in length had been collected and added that he was "not wholly inclined to discredit a report of an endoceroid found in a quarry near Watertown, New York, which was measured before it was broken up and found to attain a length of 30 feet." As far as we have been able to ascertain, these somewhat vague statements are all that is presently available in the published record on the subject of the maximum size of endoceroid cephalopods.

It does not seem to be generally known that the Museum of Comparative Zoology at Harvard University possesses what appears to be the largest fragment of an endoceroid cephalopod on display anywhere in the world. As Flower (1955) has stated, "the removal of even reasonably complete specimens involves something very close to quarrying operations, storing them is another problem." The specimen in the collections of the Museum of Comparative Zoology is, therefore, probably unique in museums of the world.

The specimen measures 3,000 mm in length but is not complete, adorally or adapically. In general the preservation is fair, but as a result of weathering and crushing the full diameter of the conch is preserved only in one plane, and in the other plane the outer shell is removed exposing traces of septa and in places the siphuncle. The first recognizable septa are 500 mm from the adoral end but the whole specimen could well be phragmocone as this adoral 500 mm is slightly crushed and weathered and one cannot tell whether septa are present or absent. The adoral diameter of the specimen is 280 mm. The conch tapers at a uniform rate and the adapical diameter measures 120 mm.

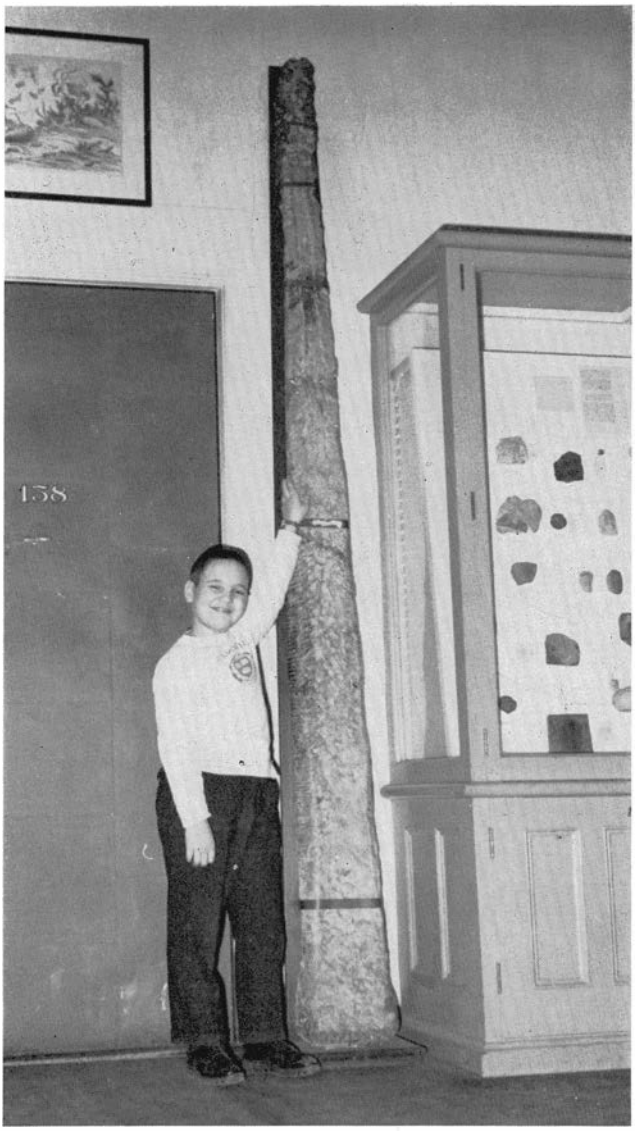

Figure 1 — Large endoceroid on exhibit in the Museum of Comparative Zoology.

The septa slope adapically at an angle of about 45° and in the mid-part of the specimen are spaced 17 to 20 mm apart. The siphuncle is visible only on the adapical half of the specimen. About 1,000 mm from the adoral end of the shell the siphuncle has a diameter of about 95 mm; at 1,750 mm from the adoral end of the shell the siphuncle has a diameter of 75 mm. The first endocones appear 2,000 mm behind the adoral end of the shell. The spiess measures 510 mm in length. The surface of the shell bears faint annulations that are spaced approximately 10 to 12 mm apart.

SUMMARY OF MEASUREMENTS

Length	3,000 mm
Adoral diameter	280 mm
Diameter 1,000 mm from adoral end	220 mm
Diameter 1,750 mm from adoral end	170 mm
Adapical diameter	120 mm
Diameter of siphuncle 1,000 mm from adoral end	95 mm
Diameter of siphuncle 1,750 mm from adoral end	75 mm
Spiess length	510 mm

A graphical reconstruction of the shell on the basis of these measurements shows that the entire fossil from its presently preserved adoral end to the apex may have measured about 5,800 mm.

The total length of the body chamber is a matter of guesswork. There are few published and illustrated records of any straight fossil cephalopod shells, complete from apex to aperture, which are more than a foot or so long. In short shells the ratio of body chamber to phragmocone may be high, even larger than 1:1. With increasing total length of conch, however, ratio of body chamber to phragmocone is likely to decrease, although no definite figures can be stated. In a specimen of *Actinoceras beloitense* (Foerste and Teichert, 1930, pl. 28), which was 450 mm long, the ratio of body chamber to phragmocone was about 1:2. Leith (1942) described a specimen of *Lambeoceras lambii* (Whiteaves) which was 45.5 in. (1,155 mm) long. He estimated the total length of the shell at 1,405 mm. The body chamber was almost wholly preserved and not more than 250 mm long. Ratio of body chamber to phragmocone was thus 1:4.6 in this specimen.

It should be noted, however, that both *Actinoceras beloitense* and *Lambeoceras lambii* have body chambers with constricted

apertures, whereas no endoceroids with constricted apertures are known. It seems physiologically plausible that in large straight cephalopod shells the animal should have a better "grip" on a body chamber with constricted aperture than on one with an unconstricted aperture; therefore, in shells which expanded uniformly from the apex to the aperture, like the endoceroids, the animal itself, and thus its body chamber, should have been relatively larger.

In a juvenile specimen of a straight ammonoid, *Baculites ovatus,* Trueman (1941) determined the ratio of length of body chamber to phragmocone as 1:0.7, but in adult shells this ratio becomes much smaller. If we assume the ratio of length of body chamber to phragmocone in endoceroids to be more like that of *Actinoceras beloitense* we arrive at a length of the body chamber for the Harvard *Endoceras* of 2,650 mm and for the entire shell of 8,150 mm, or 28 feet. This is a conservative estimate, yet close to the possible maximum figure of 30 feet mentioned by Flower.

Add to this the length of the tenacles which must have extended a considerable distance in front of the aperture, certainly no less than half the length of the body chamber, and we have an invertebrate animal considerably longer than 30 feet — a truly imposing size. Today's giant squid, *Architeuthis,* rivals and slightly exceeds in length the largest extinct endoceroids. Spärck (1928) records specimens of *Architeuthis dux* from the North Atlantic, washed ashore on the Norwegian Coast, that have body lengths of up to 2 meters and tentacles as much as 10 meters long. The largest specimen to our knowledge is that of *Architeuthis harveyi?* recorded by Verrill (1879, p. 196) which measures 624 inches (17 meters). There is a model in the Museum of Comparative Zoology of a specimen of *Architeuthis princeps,* which was washed ashore in Newfoundland, which measures about 15 meters in length. More recently, Lane (1960, pp. 198-227) has critically reviewed a larger number of reports of finds of and encounters with giant squids. He is inclined to believe that individuals of *Architeuthis* or some other genus, as yet undescribed, may reach overall lengths of some 70 feet.

While the Harvard specimen represents by far the largest nautiloid cephalopod on which accurate data are now available, it is interesting to compare it with the largest ammonoid on record. This is *Pachydiscus seppenradense* Landois from the

Upper Cretaceous of western Germany (Landois, 1895, 1898). In 1895, Landois first described this fossil ammonoid whose shell was 1,800 mm in diameter and in which the last camera was 550 mm high. Landois' reconstruction provided the animal with a body chamber equivalent to only one-fourth of a complete whorl. From this he concluded that the total diameter of the complete specimen of his ammonoid had been about 2,550 mm. From later studies (Trueman, 1941) it is, however, likely that Landois' estimate of the length and bulk of living chamber was too low. If the body chamber of *Pachydiscus seppenradense* was equivalent, as is more likely, to three-fourths or one full volution of the shell, the diameter of the adult shell of this ammonite would have been of the order of 3,500 mm, or more than 10 feet. A very approximate graphic plot of a shell of this kind shows that the total length of the shell of *Pachydiscus seppenradense,* when unrolled, would have been of the order of 60 feet, or roughly twice as long as that of the largest endoceroid.

In another paper Landois (1898) attempted to estimate the weight of these giant cephalopods. On the basis of his estimated measurements he arrived at a total weight of the ammonite as 1,455 kg, or 750 kg for the weight of the animal itself, and 705 kg for the weight of the shell.

We shall abstain from any attempt to indicate exact weights of the large endoceroids. The order of magnitude was almost certainly the same as that inferred by Landois for the giant *Pachydiscus,* something of the order of 1 ton (about 1000 kg). It must be assumed that the weight of shell and siphuncle, which for a length of over 5,000 mm was entirely filled with calcareous deposits, balanced the buoyancy provided by the empty camerae and confined the animal to a strictly benthonic existence. Few, if any, fossil invertebrates ever surpassed them in bulk weight and size.

One other point deserves attention: Phyletic size increase is a trend that as a rule continues until the end, or very close to the end of the evolutionary life of a particular group of organisms, as, for example, in the ammonoids. The endoceratids, however, reached their maximum size long before the time of extinction, in fact relatively early in their evolution. In North America, as well as in northern Europe, endoceroid cephalopods survive to the end of the Ordovician period, but reach their maximal size during Middle Ordovician time (Teichert, 1930, pp. 235-236).

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