UMBILICAL SHOULDER. Strongly bent portion of whorl between flank and umbilical slope or wall.

UMBILICAL SLOPE. Inner part of umbilical area, tilted more or less toward umbilicus and separating umbilical seam from umbilical shoulder.

umbilical suture. *See* umbilical seam.

UMBILICAL WALL. Inner part of umbilical area sloping toward umbilical seam from umbilical shoulder.

UMBILICUS. External depression around axis of coiling near center of whorls of coiled conchs.

upper annular ridge(*). Ridgelike thickening of posterior edge of "annular elevation" (fossil nautiloids only).

vacuosiphonate. Sometimes used to describe empty siphuncles, without deposits.

VENTER. Underside of organism and of conch, distinguished generally by hyponomic sinus and often by conchal furrow.

VENTRAL LOBE. Main adapical inflection of suture on venter, in coiled conchs also called external lobe.

ventral sinus. Furrow in the cameral deposits along ventral side.

VENTROLATERAL ANGLE. Angle between venter and flank of coiled conch.

ventrolateral masses. Cameral deposits on both sides of ventral sinus.

VENTROLATERAL SHOULDER. Same as ventrolateral angle but blunt.

VENTROMYARIAN. Descriptive term applied to nautiloid cephalopods in which shell or retractor muscles of head-foot are attached along areas of interior of body chamber adjacent to, or coincident with, its ventral mid-line.

VINCULUM. Calcitic portion of thick discosorid connecting rings attached to posterior side of septum.

volution. *See* whorl.

WHORL. Complete turn of coiled conch (*syn.*, volution).

WHORL SECTION. Transverse section of whorl.

whorlsides. *See* flanks.

LIVING NAUTILUS

By H. B. Stenzel

[Shell Development Company, Houston, Texas]

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INTRODUCTION

The fleshy parts of Tetrabranchiata are known only from the sole surviving genus *Nautilus* and traces or imprints of soft parts found in a few Ammonoidea and some of the extinct nautiloid orders. The anatomy of *Nautilus* is described by Griffin (11), Mugglin (17), and Willey (28). Observations on the general biology of living animals were made by Dean (8) and Willey (28). In 1960-61 *Nautilus* was studied at New Caledonia, the Loyalty Islands, and New Guinea by Dr. Anna Bidder (2a,2b), who reviewed this chapter.

The fleshy parts of *Nautilus* occupy the interior of the planispirally coiled shell, and the body occupies and conforms exactly to the shape of the body chamber, which is the last or outermost of the chambers and is open at the shell aperture (Figs. 43, 68). In natural position, the plane of bilateral symmetry stands vertical and the shell coil is above or dorsal to the body chamber. The body is nearly horizontal. The head, surrounded by tentacles (together constituting the head-foot), protrudes at the shell aperture, pointing forward.

Morphological orientation of the animal is complicated by planispiral coiling. Hence, to some extent its terminology is arbitrary: the head-foot is anterior, the longitudinal horizontal direction toward the shell away

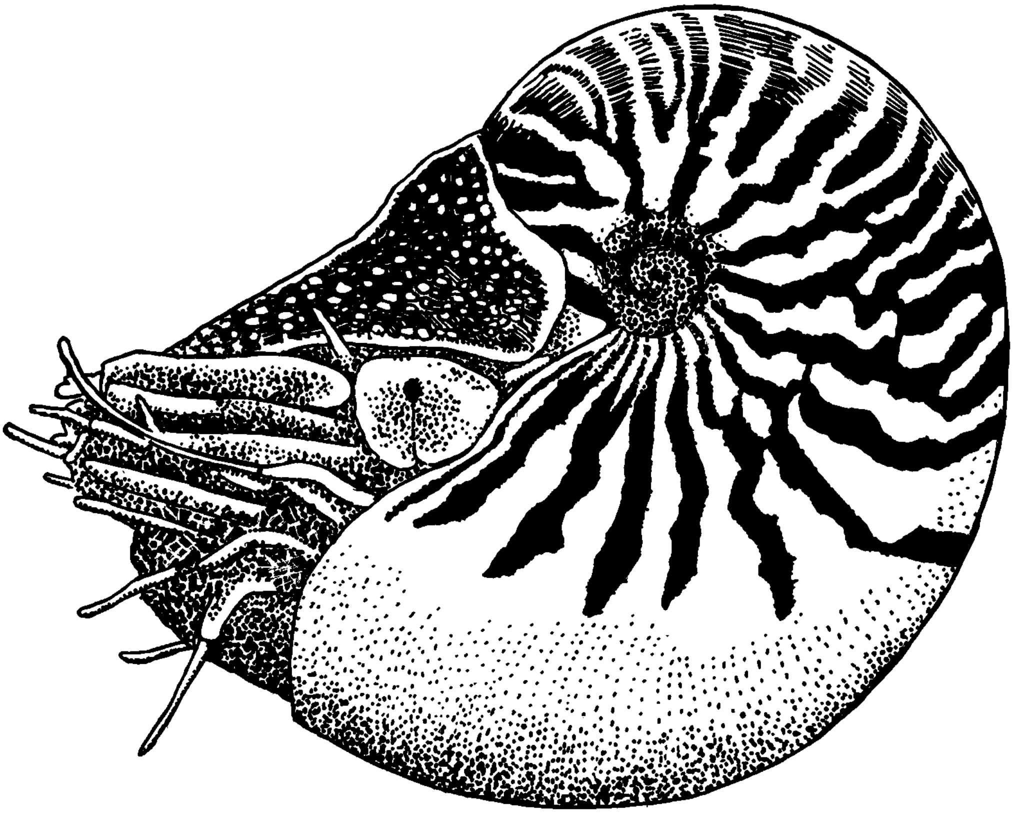

FIG. 43. *Nautilus macromphalus* G. B. SOWERBY (1849), drawn by H. B. STENZEL from photograph of live individual in the aquarium of Dr. RENÉ CATALA in Nouméa, New Caledonia, ×0.7 (from a photograph in *The Lower Animals* by Ralph Buchsbaum & L. J. Milne).

from the head-foot is called posterior, the shell coil is dorsal, and the convex outside curve of the body is called ventral. However, if only a piece of the shell coil is described, very arbitrarily its convex outside is called ventral and its concave side is called dorsal, irrespective of the particular position this piece may have occupied on the living animal.

ANATOMY OF SOFT PARTS OF NAUTILUS

The soft parts of the animal consist of the following regions: (1) **head-foot** or capitopedal region [*cephalopodium, Kopffuss*], including mouth, buccal mass, eyes, hood, tentacles, and locomotor organ (hyponome); (2) **body,** from the posterior edge of the head-foot to the septum that closes off the rear end of the body chamber, including the visceral sac, which contains the viscera, and the mantle with mantle cavity, which encloses the hyponome with its crura and the four gills and into which empty the reproductive, excretory, and digestive systems; and (3) **siphuncular cord,** the fleshy portion of the siphuncle, which is a long, slender, fleshy tube [*siphon* of some authors], extending through all air chambers to the apex of the shell and coiled like the shell.

The head-foot is not as well separated from the body as in the Coleoidea. Body and head-foot together are 15 to 18 cm. long in adult *Nautilus pompilius* LINNÉ.

HEAD-FOOT

CEPHALIC CARTILAGE AND BUCCAL MASS

The head is built on a large strong H-shaped cephalic cartilage, which is 4.75 cm.

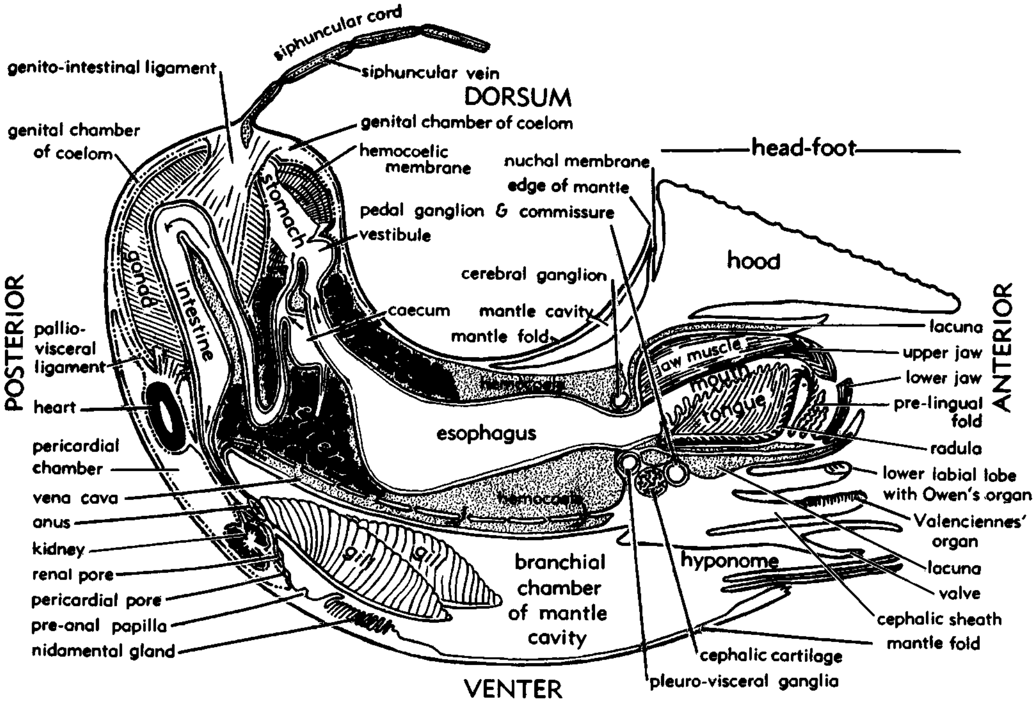

FIG. 44. Diagrammatic median section through the fleshy parts of *Nautilus*; venous blood indicated by stippling and outline of the coelom shown by dash-dot line, ×0.6 (modified from 11, 12, 30).

long and 3 cm. wide in an average adult (Fig. 44). The cartilage anchors the hyponome and major muscles, supports the nerve centers and balance organs (statocysts) and protects but does not enclose them as in the Dibranchiata.

Adjacent to and connected with the cartilage by muscles is the large and bluntly conical buccal mass, surrounding the mouth; it is built around a large, horny two-jawed beak, like that of a parrot, which is activated by strong muscles anchored on the cartilage. The upper jaw fits snugly into the projecting lower jaw; both are massive and made of conchiolin reinforced by hard calcareous material. The lower jaw is 30 mm. long and 28 mm. wide; the upper is 32 mm. long and 17 mm. wide (Fig. 44A). Both jaws are hooked, the upper less so than the lower one. The upper jaw is more pointed, with calcification concentrated in front to form a strong, sharp beak. The calcified portion has the shape of a low pyramid which is roughly four-sided and bilaterally symmetrical, with two rounded and two sharp edges converging into a tip; the tip curves downward to form the point of the beak and the sharp edges form its sides to left and right. Its black, tough, conchiolinous portion extends backward into the buccal mass and forms two flanges; the upper flange is much shorter than the lower one, which occupies the roof and sides of the mouth. Calcification of the lower jaw, distributed on both sides of the black conchiolin layer, is less concentrated. The conchiolinous portion of the lower jaw extends backward to form two flanges, the inner much shorter than the outer one, which covers much of the outside of the buccal mass. The upper jaw is rigid, whereas the lower jaw is somewhat flexible because calcification of the beak is less strong and less concentrated. The lower jaw can yield slightly when the jaws bite through bones or the hard coverings of prey, thereby protecting the beaks from accidental fracture. Because of their calcification, the beaks in the jaws may be fossilized; such fossils (rhyncholites) are known, although they are much less common than shells or internal molds of shells.

On the floor of the mouth is the large tongue (subradular organ), which bears a long-toothed radula reaching into

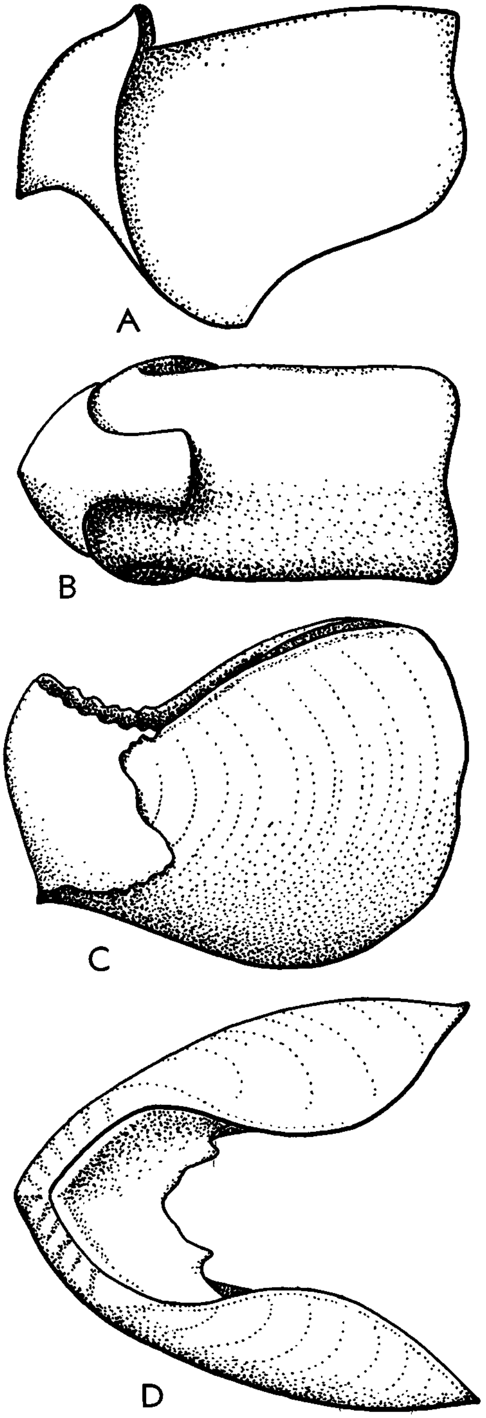

FIG. 44A. Beaks of *Nautilus pompilius* LINNÉ, ×2.4. *A*, upper beak, side view; *B*, upper beak, occludent view; *C*, lower beak, side view; *D*, lower beak, occludent view (Stenzel, n).

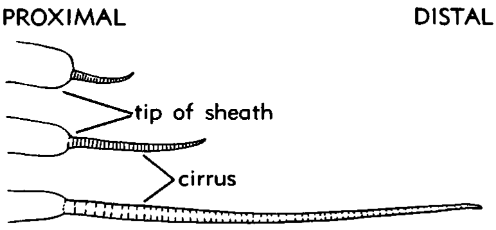

FIG. 45. Digital tentacle of *Nautilus* in 3 stages of protrusion of cirrus from its sheath, ×0.6 (from 8).

the cavity between the beaks of the jaws. Two prelingual folds rise in front of the radula, near a pair of salivary glands, one at each side of the tongue.

TENTACLES AND HOOD

The tentacles are arranged in three separate groups, called ocular, digital, and labial. Ideally, each tentacle, whether ocular, digital, or labial, has a proximal sheath and a distal finger-like cirrus, which can retract into its sheath; but only the ocular and digital cirri can do this completely (Fig. 45). However, there are several modifications of the basic pattern.

The two short ocular tentacles spring from near the base of each eyestalk, one in front and the other behind the eye. They are highly sensitive to touch and smell.

Surrounding the buccal mass are two more or less complete rings of tentacles: an inner ring of labial tentacles and an outer one of digital tentacles. The outer ring and the cephalic sheath, formed by the partial fusion of the individual sheaths of the digital tentacles, are alike in both sexes, but the labial tentacles differ greatly. Those of the female are less specialized than those of the male (Figs. 46, 47).

The digital tentacles and cephalic sheath enclose the labial tentacles and buccal mass. Although the number of digital tentacles is 38, they are strikingly constant in number and position in both sexes and in three of the five living species so far studied. However, different groups among them are highly specialized as to function. Some are primarily olfactory, others respond mainly to touch, but most are prehensile.

At its ventral mid-line, the cephalic sheath has a longitudinal groove ending in a notch, into which the free front of the hyponome fits snugly from below. On the opposite side,

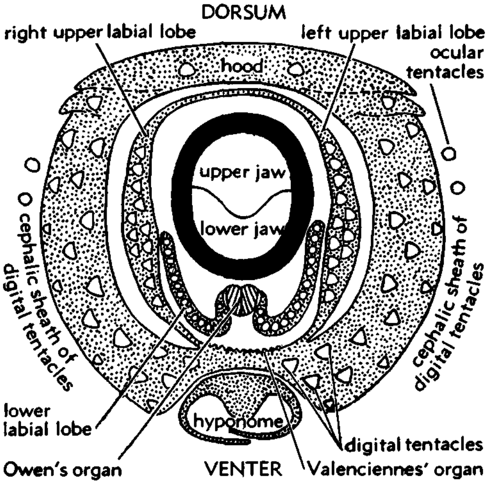

FIG. 46. Arrangement of tentacles in a female *Nautilus,* seen from the front; cirri of tentacles indicated by round or triangular white areas (modified from 11, 30).

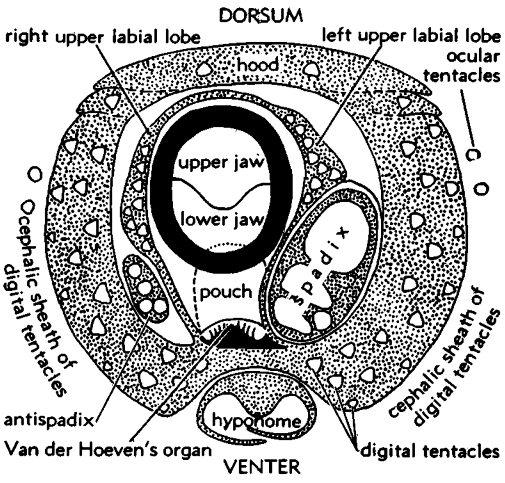

FIG. 47. Arrangement of tentacles in a male *Nautilus,* seen from the front; cirri of tentacles indicated by round or triangular white areas (modified from 11, 30).

at the dorsum, the sheaths of two digital tentacles are much enlarged and fused to form the hood.

The hood *(capuchon céphalique, Kopfkappe)* conforms closely in size and outline to the shell aperture (Fig. 48). The outer surface of the hood in *Nautilus pompilius* carries two ridges and has an irregular, somewhat warty brown surface, which has white spots. The warty prominences on the hood of *N. scrobiculatus* SOLANDER are larger and form flat-topped areas having angular outlines, separated by deep grooves. The hood is thickest in the middle-posterior part and slopes from there to a thin outer edge, the front part of which is straight. The rear presses closely against the surface of the dorsal shell coil, and following the shape of the coil, is deeply concave. Laterally and posteriorly, the hood extends on each side into an auricle, which fits into the shell aperture at the umbilicus, but leaves a small gap there that serves as the inhalant passage for the water stream which enters the mantle cavity.

At the tip of the hood, two small orifices lead into deep cavities, in each of which sits a cirrus, similar to that of other tentacles. Some individuals have a cleft of varying penetration in the middle of the tip of the hood. This cleft is caused by incomplete fusion of the two greatly enlarged tentacular sheaths from which the hood originated.

The digital tentacle that lies next to the hood on each side has a broad flattened sheath, which is fused along nearly its entire length to the ventral side of the hood, is overlapped greatly by the margin of the hood, and in turn overlaps the next lower tentacle sheath. Its upper surface resembles that of the hood.

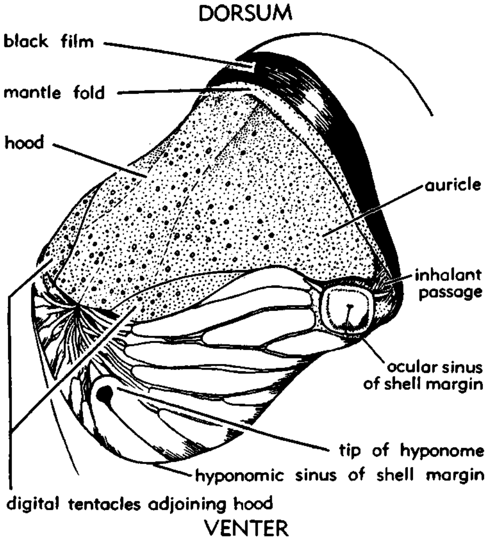

FIG. 48. Oblique frontal view of *Nautilus* in resting position, partially retracted into its shell, ×0.45 (from 8).

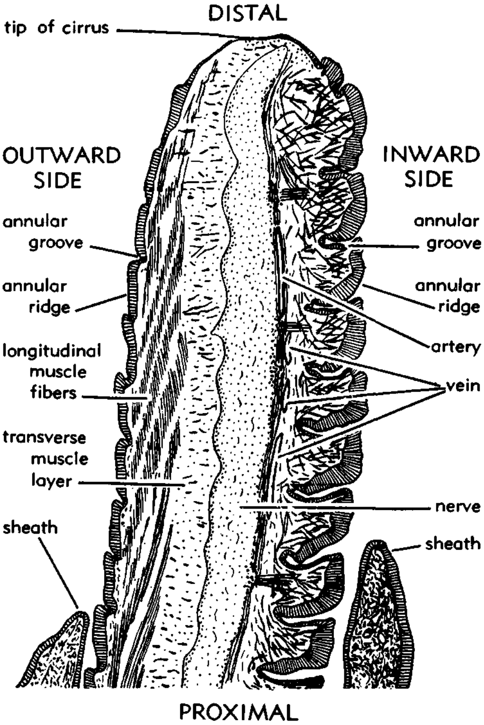

FIG. 49. Longitudinal section through the tip of a digital tentacle of *Nautilus*, ×17 (from 11). The same annular ridge and groove is labeled on both sides.

The hood and one adjoining tentacular sheath on each side compose the cover that closes over the head-foot, shutting the shell aperture like a countersunk lid and protecting the soft parts when the animal withdraws into its shell. Thick elastic tissue beneath the surface skin makes the hood very tough and difficult to penetrate, but leaves it flexible to some extent.

Next follow 17 digital tentacles upon each side. The sheaths of these tentacles are fused to each other to about 1 or 2 cm. from the distal end of the sheaths. The fusion forms the cephalic sheath, which is ridged on the outside but perfectly smooth on the inside, except that in the female one of the lamellated accessory sexual organs (Valenciennes' organ) is on the inside of the cephalic sheath just behind the ventral notch. This organ receives the spermatophore from the male. Four of the digital tentacles, located on the outside of the cephalic sheath on each side, are so much smaller that they do not reach the distal end of the sheath; the others are arranged roughly in two rows.

The cirri of the larger digital tentacles are 10 cm. long and 0.4 cm. in diameter. They are muscular, supple, and slender, tapering slightly to a bluntly rounded point. They are three-sided, the broadest with flattest side facing inward toward the mouth. Each cirrus is both adhesive and prehensile and carries many annular grooves and ridges (Fig. 49). The latter are more prominent on the inward face, and this projecting part of each ridge serves as an adhesive organ that functions like a sucking cup. True suckers, like those of the dibranchiate cephalopods, are not present, however. Although the sheaths of the tentacles are shorter than the extended cirri, their cavities are long enough to accommodate the retracted cirri. The sheaths are tough, slightly muscular, and have but little movement of their own.

In the female, the inner ring of labial tentacles is divided into three lobes, the unpaired lower lobe and the right and left upper lobes (Fig. 46). The ventral or lower labial lobe, below the buccal cone, is 2.5 cm. long and 0.8 cm. thick; distally the lobe splits, and each half widens like a fan and bears a single row of 14 labial tentacles at its edge. At the junction of the two fans is a lamellated accessory sexual organ (Owen's organ), probably olfactory in function. The right and left upper labial lobes of the female are each about 3 cm. broad and 2 cm. high; a low ridge unites them dorsally, but ventrally the two lobes end above the hyponome. Each lobe carries 12 tentacles disposed in two unequal rows.

In the male, the lower labial lobe and its tentacles are highly modified as an accessory sexual organ (Van der Hoeven's organ), 2.5 cm. long, which lies in a pouch below the buccal mass (Fig. 47). It is secretory and sensory, but its exact functions are unknown. The right and left upper labial lobes of the male are similar to those of the female but each lobe has only eight tentacles instead of 12. The other four tentacles of each upper labial lobe are permanently and highly modified as copulatory organs, the larger spadix and the smaller antispadix. These two homologous organs are symmetrically placed between the labial lobes and the cephalic sheath. The spadix is on the left and the antispadix is on the right side in three out of four males; in others, positions are reversed. The spadix transfers the spermatophore from the male to the Valenciennes' organ of the female. Spadix and antispadix are identical and quite small in less than half-grown males; modification into the two and rapid growth come late in the life of *Nautilus.* At maturity, the spadix forms a large, very solid, protrusible organ, 5 to 7 cm. long, 2 to 3 cm. high, and 0.5 cm. thick. Because of its large size, it distorts the arrangement of the surrounding parts of the head-foot and influences even the configuration of the shell cross section (Fig. 50).

All tentacles of *Nautilus,* ocular, digital, and labial ones, are innervated from the pedal ganglia. Hence, they probably evolved from the foot of the molluscan ancestor, and the head-foot arose through fusion of head with foot. Which portion of the foot of the ancestor developed into the tentacles of *Nautilus* has been discussed at length (30, p. 800-804; 16; 23). However, reported homologies are open to question.

Even the derivation of the tentacles of the Cephalopoda from a part of the foot of the molluscan ancestor, at one time widely accepted, is now vigorously denied by Kerr (16). The tentacles are said to have developed independently from parts of the head. The fact that in the embryo of dibranchiate cephalopods the tentacles develop from the same region as the hyponome, a region that in other mollusks gives rise to the foot of the adult, is explained by Kerr as caused by distortion of the embryonic blastoderm through the large yolk, which is characteristic of the cephalopod egg.

The outer ring of 38 digital tentacles of *Nautilus,* taken as a whole, is homologous to the ring of arms (ten or eight) of the dibranchiate cephalopods, but individual tentacles cannot be homologized. The inner ring of labial tentacles of *Nautilus* may be homologous to the buccal membrane of the dibranchiates—a conical membrane surrounding the mouth present only in the decapodous Coleoidea—which in some species of squid even bears seven to ten rudimentary tentacles carrying suckers.

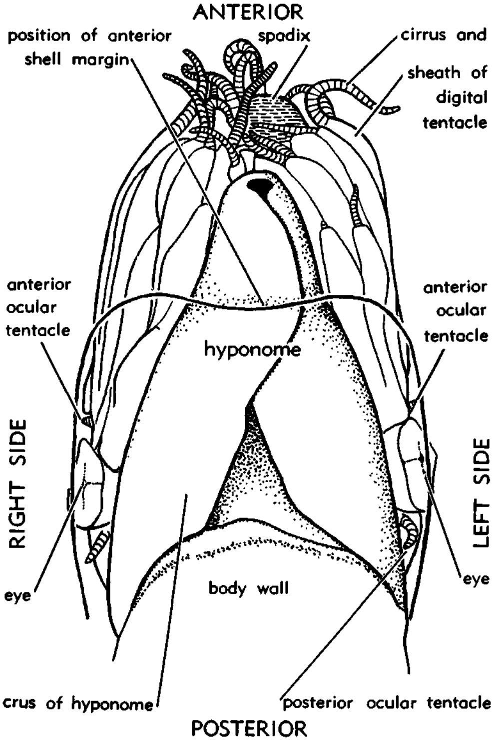

Fig. 50. Male *Nautilus pompilius* Linné, seen from below, ×0.6 (drawn by Stenzel, based on 11). Shell and mantle fold are represented as transparent, allowing the organs within to be seen in their natural positions.

HYPONOME

The long funnel of the hyponome (*siphonopodium* of Willey, or funnel, *entonnoir, Trichterrohr*) is part of the head-foot (Fig. 50). It is about 8 cm. long and 4 cm. wide, presses against the ventral side of the head, and is anchored onto the cartilage of the head. Two ridges outlining the prongs of the cartilage are visible under the roof of the hyponome in live individuals of *Nautilus.* Its wider posterior part extends well into the mantle cavity, its narrower anterior part rests in the ventral groove of the cephalic sheath, and its blunt tip reaches a little beyond the ventral notch of that sheath. Beneath the roof of the hyponome, near its tip, is a thin, tongue-shaped valve capable of blocking water from entering the hyponome from the outside. The ventral edges of the hyponome are not fused, as in the Dibranchiata, but merely overlap one another tightly; hence, they possibly represent a more primitive stage in specialization of the hyponome and recall its primitive condition as a flat surface. At the rear of the hyponome, its edges diverge and pass upward over the sides of the body forming the crura (plural; crus, singular; alae of WILLEY). The tips of the crura merge into the nuchal membrane, a crescentic skin fold at the dorsum behind the hood. Only the strongly muscular and contractile posterior three-eighths of the hyponome is attached to the head; the free and less muscular anterior portion is able to move and bend in any direction. The crura of the hyponome produce by their rhythmic movements a current of water that enters the inhalant passages behind the auricles of the hood so as to bring oxygen to the gills in the mantle cavity; the hyponome functions secondarily as a powerful locomotor organ.

The hyponome is innervated from the pedal ganglia and is generally considered to have evolved from a portion of the foot of the molluscan ancestor.

SENSE ORGANS

The eyes are in the corner between the hood, the roots of the cephalic sheath, and the hyponome with its crura. The eye is large, 2.2 cm. long and 1.5 cm. high, short-stalked, and rounded-triangular in outline. A retina lines the cup of the eye, and a stout cover with a small pupil closes it. It lacks a lens and lets sea water in. A groove leads down from the pupil to the ventral edge. The lack of movement and accommodation of the eye indicates its great limitation as a visual organ.

The two ocular tentacles are tactile and olfactory. The tips of some of the digital tentacles also have tactile functions.

Between the eye and the posterior projecting edge of the cephalic sheath and largely hidden by the eye is the rhinophore, a sense organ of unknown function, possibly olfactory. The rhinophore is a small pyramid only 8 to 10 mm. high. A pair of statocysts lie upon the anterior side of the cephalic cartilage immediately behind the pedal ganglia. They are thin-walled sacs, 3.5 mm. long, filled with a highly fluid milky substance laden with many tiny crystals of calcite (otocones); they are stability sense organs.

The abundant supply of olfactory tentacles in *Nautilus* confirms the observations of WILLEY (30, p. 774) that *Nautilus* finds its food chiefly by smell and that its eye is ill fitted to discern objects.

NERVOUS SYSTEM

The central nervous system is concentrated in the head in three half-circle bands around the esophagus. One band passes dorsally over the esophagus and contains the cerebral ganglia; the anteroventral band is composed of the two pedal ganglia and their commissure; the pleurovisceral ganglia and their commissure are posteroventral. The three bands are joined to either side of the esophagus. The cerebral band sends off a thick nerve to each eye, indicating great importance of the eye to the animal in spite of the primitive equipment of the eye; other nerves are sent off to the buccal mass and statocysts. The pedal ganglia innervate the hyponome and all the tentacles with their accessory sexual organs. The pleurovisceral ganglia send nerves to the gills, excretory renal organs, reproductive system, shell muscles, body wall, digestive system, and mantle. The posterior part of the hood receives nerves from the pleurovisceral ganglia as well as from the cerebral and pedal ganglia, but the anterior part is served from the pedal ganglia alone. In comparison with the Coleoidea, the central nervous system of *Nautilus* is much less concentrated, and hence more primitive.

BODY

MANTLE

The body is fully enclosed by the mantle (pallium), which therefore lines the inside of the body chamber. In the posterior or visceral region, the mantle forms merely the surface membrane of the visceral sac and is so thin that the viscera can be seen through it easily, but in the anterior or pallial region, the mantle forms a fold (pallial fold or duplicature). Between body and mantle fold is the mantle cavity (pallial cavity), which encircles the body. In the dorsum, the cavity is 4 cm. deep; where the umbilical shoulder of the shell is located, it is only 1 cm. deep; but at the venter, it is 10 cm. deep and capacious, containing the hyponome, gills (branchiae), and orifices of the digestive, excretory, and reproductive systems. This ventral portion of the mantle cavity is known as the branchial chamber. The mantle fold lines the inside of the body chamber and is very thin and only slightly

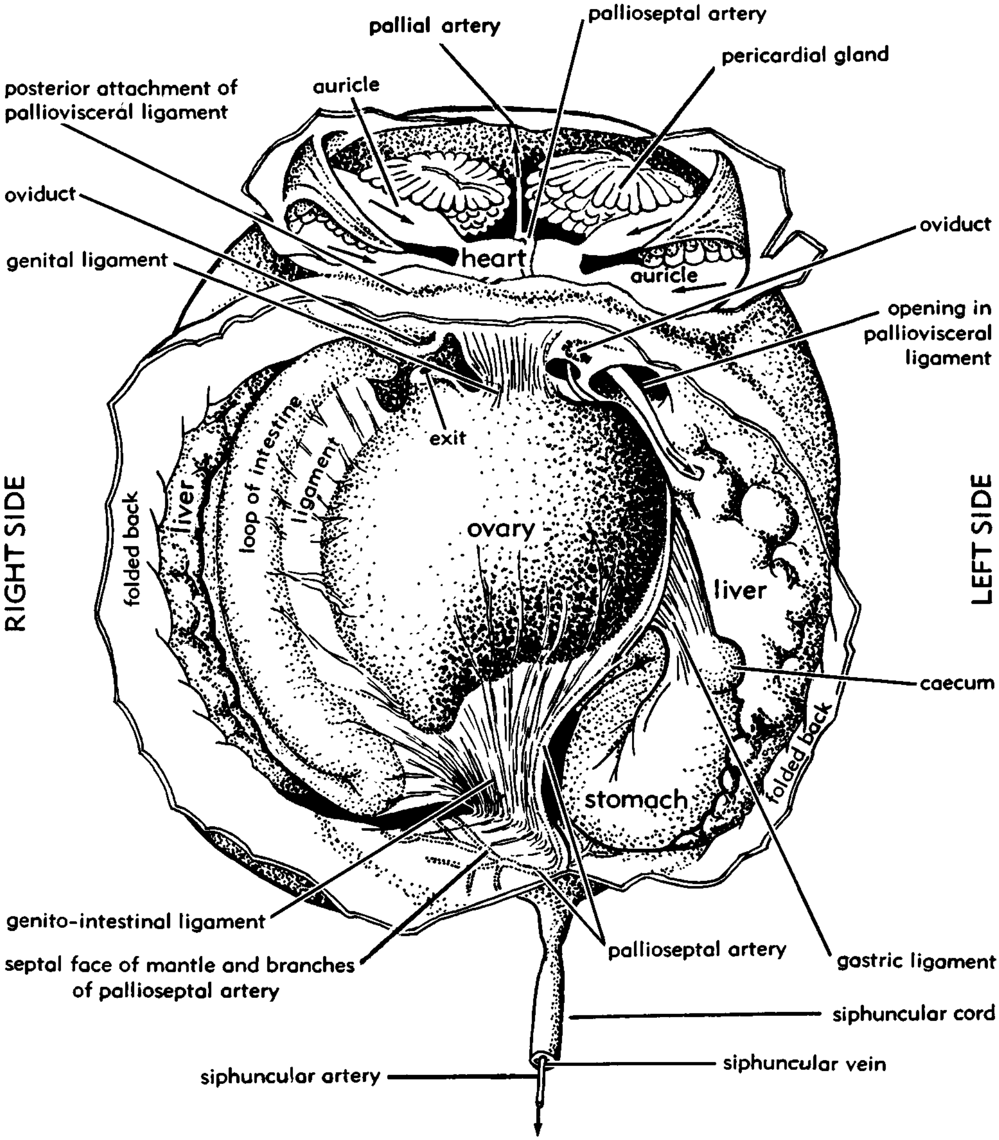

Fig. 51. The visceral sac of an immature female *Nautilus* seen obliquely from the posteroventral side; the genital and pericardial chambers of the coelom are cut open to show the organs contained in them, ×1 (modified after 12).

muscular for the most part. At the ventral and lateral margins of the shell aperture, it is firmly attached to the body chamber along a band 1 to 1.5 cm. wide. This band of the mantle fold is slightly thicker and its anterior edge has two parallel grooves, separated by a sharp ridge (Fig. 44).

GILLS AND EXCRETORY SYSTEM

The four gills are about 5 cm. long, 1.5 to 1.8 cm. wide, and 1 cm. thick. Only their bases are attached to the mantle near the rear of the pallial cavity. Two gills lie on each side, one slightly in front of the other. The gills are not ciliated.

Near the base of each of the four gills is a renal pore, the exit of a kidney. The principal excretion of the kidneys is said to be calcium phosphate (in the form of small, solid, oölitic concretions) and guanine ($C_5H_5ON_5$).

DIGESTIVE SYSTEM

The esophagus opens immediately behind the tongue. It is long and distensible, and when full, it forms a capacious crop. The esophagus passes straight through the body into the vestibule of the muscular stomach. The intestine passes from the right side of the stomach, makes two sharp turns, and runs into the posterior part of the pallial cavity. At one point it connects with the caecum, into which the duct of the large-lobed liver empties. The last loop of the intestine is used for storage of feces. The shortness of the digestive system is consistent with the animal's carnivorous nature.

REPRODUCTIVE SYSTEM

Although sexes are separate in *Nautilus,* as in all Cephalopoda, the gonad—testis of the male or ovary of the female—occupies the same position in the body, that is, the posterior extremity, directly ventral from the root of the siphuncle, cradled on the last shell septum so that the smooth posterior face of the gonad fits the concavity of the septum, lying between the septal foramen and the ventral part of the septal suture (Fig. 51). The gonad is enveloped and suspended in the body cavity by ligaments, two of which are attached to the rear wall of the stomach (gastric ligament) and second loop of the intestine and one of which is attached to the rear wall of the visceral sac (genito-intestinal ligament). The posterior insertion of the genito-intestinal ligament is 2 cm. long and runs in a dorsoventral direction. Near the middle of this insertion is the root of the siphuncle.

The testis is slightly larger than the ovary, and the male system ends in a penis, which lies in the branchial chamber of the pallial cavity in the mid-line of the ventral body surface. The female system empties through two pores (pore of oviduct) into the branchial chamber near the base of the posterior gills; only the right pore is functional, since the left one is atrophied.

CIRCULATORY SYSTEM

The heart is ventral in the body cavity, between the gonad and the rear end of the pallial cavity (Figs. 44, 51). It is transversely oblong, and each of its four auricles receives a branchial vein, bringing oxygenated blood from a gill to the heart. Five aortas and arteries lead the oxygenated blood from the heart to various organs and muscles. Notable is the lesser aorta, because one of its two branches is the pallioseptal artery. The two distal branches of the latter supply the part of the mantle which rests on the last septum of the shell. The siphuncular artery, a branch of one of the two branches of the pallioseptal artery, enters the siphuncle, runs nearly to its posterior tip, and ends there openly. The branchial hearts, so well developed in the Coleoidea are not found in *Nautilus.*

Returning venous blood does not run in closed vessels, as does the arterial blood, but collects in many irregular, intercommunicating blood-filled spaces (lacunae or sinuses) located in and between the organs and muscles. Blood from these lacunae collects in the anterior part of the body in the blood-filled hemocoele, the main portion of which forms a space around esophagus and liver. From the hemocoele, venous blood enters the vena cava through 20 to 75 holes in its dorsal wall. This vein begins near the cephalic cartilage, runs along the ventral body wall, and splits at its posterior into four branches. Each branch takes venous blood to a gill, where it is oxygenated and returned to the heart. Venous blood is blue and of syrupy consistency; it contains dissolved hemocyanin, which becomes colorless on oxygenation.

COELOM

The anterior, blood-filled hemocoele and the posteroventral coelom, filled with a watery liquid, are the two distinctly separate portions of the extensive body cavity of *Nautilus,* which is the cavity between the viscera and the body wall. A thin membrane (hemocoelic membrane) separates hemocoele from coelom, and envelops the posterior parts of the liver, stomach, and second loop of the intestine. Pouches of the membrane containing these three organs

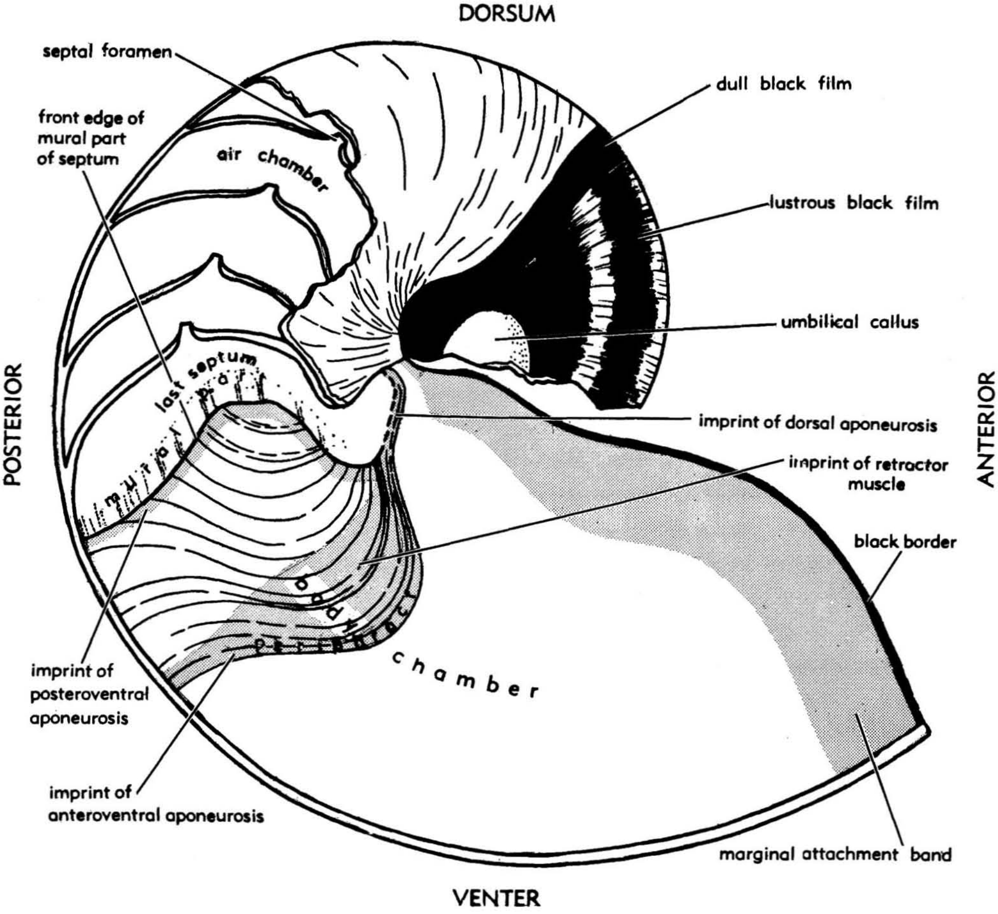

FIG. 52. Shell of mature *Nautilus pompilius* LINNÉ, partly cut open along plane of bilateral symmetry, seen from the right side, ×0.7 (Stenzel, n).

project backward into the coelom. This thin hemocoelic membrane is attached to the body wall dorsally by a tendon in the form of a fibrous sheet (dorsal aponeurosis); at the sides of the body it is fastened to the inner surfaces of the retractor muscles, passing downward and slightly backward. The ventral margin of the hemocoelic membrane joins the ventral body wall where the body wall and the inner wall of the mantle fold are joined. Placement of these attachments where firm suspension can be provided offers considerable mechanical advantage. The membrane supports the organs which it envelops against hydrostatic pressure of the sea water (Fig. 44).

In the coelom are the gonad, heart, and renal organs. The pallioviscera ligament crosses the coelom from back to front and divides it into two communicating chambers. On the dorsal side is the large genital chamber (gonocoele), which encloses the gonad and into which the stomach and second loop of the intestine project; on the ventral side is the small pericardial chamber, which encloses the renal organs and into which the heart projects from the ligament that suspends it. The pallioviscera ligament is attached by its posterior end to the body wall about halfway between the two ventral aponeuroses. From there it extends forward in a nearly horizontal plane; its anterior attachment is on the mantle fold.

MUSCLES AND SHELL ATTACHMENTS

Two powerful retractor muscles, about 5 cm. long, connect with the cartilage in the

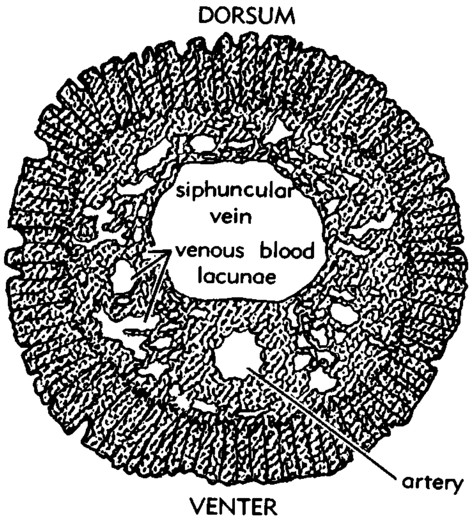

FIG. 53. Cross section of the siphuncular cord showing its blood supply, ×30 (from data given by 12, 30).

head, where each muscle is inserted on a short prong of the cartilage. From the cartilage, they diverge backward in the shape of a V, forming the sides and part of the ventral wall of the body within the mantle cavity. Each muscle is firmly attached at its origin to the inside of the shell in front of the edge of the last septum. Each area of attachment is 2 by 4 cm. in size and rounded-triangular, because each muscle is convex toward the outside and concave toward the inside of the body and the cross section of each muscle is about the same as the outline of its attachment. A thin, transparent, conchiolin film, secreted by epithelium at the origin of the muscle, covers the attachment area and separates the muscle from the calcareous shell wall. Hence, the imprint made by the muscle on the shell wall is shallow, and the muscle can be pulled off without tearing. When the retractor muscles contract, they withdraw the head-foot of the animal into the shell and the hood closes the shell aperture automatically.

Shell and fleshy parts are firmly joined together in several places (Fig. 52). (1) The anterior edge of the mantle fold is attached to the inside of the shell along the lateral and ventral parts of the aperture. The width of this attachment band is 1 to 1.5 cm. At the shell aperture of adults, this band leaves a black border, in most individuals 1 to 4 mm. wide but in a few up to 23 mm. wide. The border is continuous with the black film of the dorsal shell coil. (2) The mantle cover of the visceral sac is attached by the periphract, which leaves a continuous imprint band 3 mm. wide, consisting of the imprints of the dorsal aponeurosis, retractor muscles and anteroventral aponeurosis.[1] As at the retractor muscle attachments a conchiolin film separates shell wall from body wall along the rest of the periphract imprint. (3) The mantle cover of the visceral sac is attached along the septal contour, which is a continuous, slightly thickened, whitish band of the mantle, about 1 mm. wide, developed along the posterior margins of the dorsal and posteroventral aponeuroses. The narrow band of the septal contour lies at the anterior edge of the mural part of the last septum. Hence, the curves of the septal contour follow closely the curves of the edge of the septum and vice versa. The anteroventral aponeurosis imprint connects the two retractor muscle imprints and is anterior to the edge of the mural part of the septum.

SIPHUNCULAR CORD

The siphuncle consists of fleshy, conchiolinous, and shelly parts. The conchiolinous and shelly portion (ectosiphuncle) encloses the fleshy portion, the siphuncular cord (siphon of some authors).

The long, slender, fleshy cord passes through every septum to the shell apex. Arterial blood is supplied to it by the siphuncular artery, which branches off from one of the two distal branches of the pallioseptal artery, enters the root of the cord, lies in its ventral wall, and extends through the cord nearly to its beginning at the shell apex (Figs. 51, 53). The venous blood is collected in countless peripheral interconnecting blood lacunae, from which it enters the central cavity of the cord. This large central tubulous cavity is, in effect, a vein that leads the blood back through the whole length of the cord to its root. At the root, the siphuncular vein enters the genito-intestinal ligament, crosses the coelom by way of this ligament, and empties into the hemo-

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[1] An aponeurosis differs from a tendon in that the former is a band or sheet and its attachment is linear, whereas the latter is stringlike and its attachment is a small round area; both are fibrous tissues providing means of attachment to muscles or other organs.

coele. Although the siphuncle is narrowed where it passes through a septum, its blood vessels are not blocked off at these places.

None of the blood vessels extend from the siphuncle into the air chambers. This fact confirms the observation that no live epithelium or other live tissue lines the air chambers. If such tissues were present, they would have to have a blood supply.

Contrary to statements made by OWEN (22) and GRIFFIN (11), the coelom has no access to the siphuncular cord, as has been demonstrated by WILLEY (30). Hence, the cord is not a part of the visceral sac, but only an extension of the mantle covering the visceral sac.

The cord is encased in a tube of conchiolin, secreted by the epithelium of the cord. Since the cord is an attenuated extension of the mantle, the deposits secreted by both, that is, ectosiphuncle and septum, are continuous and to some extent similar. At its apical end, the siphuncle is closed, forming the siphuncular caecum, which rests against the concavity of the shell apex. In the first and second air chambers, the siphuncle has a somewhat greater diameter but narrows in the third chamber.

SHELL

The planispiral, bilaterally symmetrical, external shell (or conch) of *Nautilus* is divided into chambers (*loculi* or camerae, *loges, Kammern*) by cross walls or septa *(cloisons, Scheidewände),* which are concave toward the aperture (procoelous) (Figs. 54, 55). If the shell were unrolled, it would be a long, tapering, chambered cone consisting of shell wall and numerous septa. Each complete 360°-turn of the shell spiral is a whorl or volution *(tour, Windung).* Adult *Nautilus* has about three whorls. Because the venter of the animal is at the convex exterior of the body chamber, the shell is called exogastric.

CHEMICAL COMPOSITION

The shell contains about 2.03 percent of organic matter; of the remaining percentage, comprising the inorganic constituents, 99.50 percent is $CaCO_3$, 0.16 percent $MgCO_3$, 0.15 percent $(Al, Fe)_2O_3$, 0.19 percent SiO_2. A trace of calcium phosphate is found, and Sr(atoms)/Ca(atoms) are 3.8-4.8/1000.

The calcium carbonate is aragonite (orthorhombic). Organic matter is chiefly conchiolin—a horny-appearing substance characteristic of the Mollusca, which composes the ligament of Bivalvia, the periostracum of Bivalvia and Gastropoda, and the bonding matrix of the calcium-carbonate crystals in all Mollusca. Conchiolin is a complicated organic substance composed of polysaccharides, polypeptides, and scleroprotein fractions. The amino acids of conchiolin in the nacreous layer of *Nautilus macromphalus* are mainly glycine, alanine, and arginine.

COLORATION

The shell is brilliantly clean in life, and its ground color is white. A black film covers the shell coil at the dorsal side of the aperture in all species and also the two umbilici in *Nautilus pompilius.* In normal life attitude, the black film is covered by the dorsal fold of the mantle and the rear of the hood, but becomes exposed when the animal withdraws into its shell.

All other color markings are brown, and although they differ in shade and extent from species to species, the living species of *Nautilus* have much in common (Fig. 56). The value and chroma of the brown change rapidly after death of the animal. A variable patch of brown covers the umbilicus and umbilical slopes. Irregular, confluent, transverse bands cover the dorsal shell coil of the adult animal but fade out toward the venter. In some species, the bands run into the umbilical patch, in others they leave a white circumumbilical area. This white area is largest in *N. repertus* IREDALE.

Colorations of shell and exposed fleshy parts harmonize, and in adults at least, the top is brown or striped with brown and the bottom is white. This type of coloration is protective. The brown bands disrupt the contour of the animal, like the bands on zebras and warships; *Nautilus* is extremely difficult to see even in clear shallow water, because the color markings resemble shadows cast by sea fans and seaweeds and simulate the effect of the play of sunlight on surface ripples of the sea.

BLACK LAYERS

The animal deposits a lusterless, black, organic film at the shell aperture over dorsal shell coil and umbilicus. In adults the black film continues as a border at the inside of the shell margin all around the aperture but the border is only 1 to 4 mm. wide.[1]

Glands in the dorsal portion of the man-

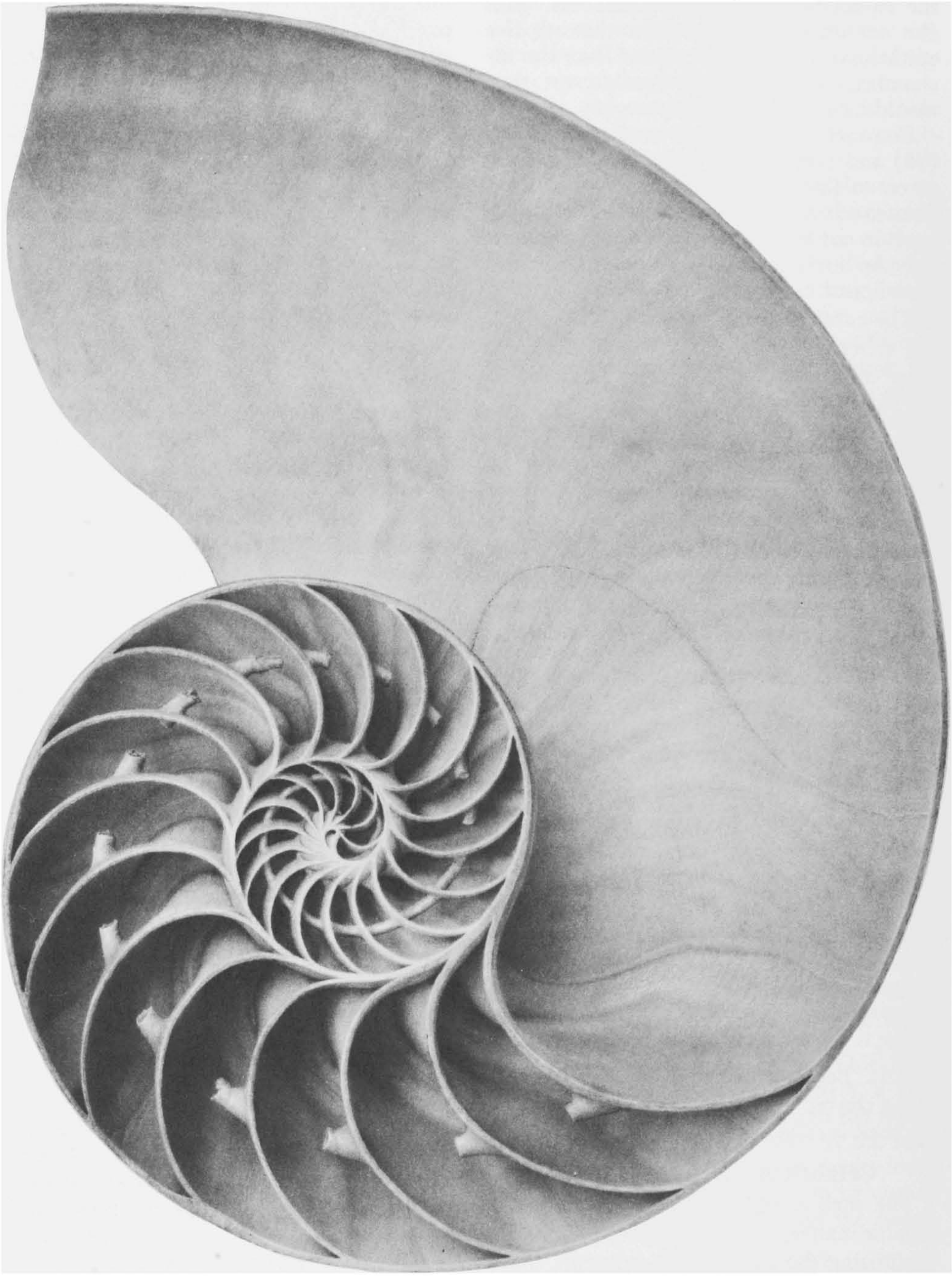

FIG. 54. Shell of *Nautilus pompilius* LINNÉ cut longitudinally slightly to right of the median plane, ×1 (from 124).

tle fold deposit the film (15). However, GRIFFIN (11, p. 138) suggested that the posterior concave surface of the hood deposits the film. There, the epithelium of the hood is glandular and pigmented. In view of the fact that at least in adults the black deposits extend all around the shell aperture, it seems

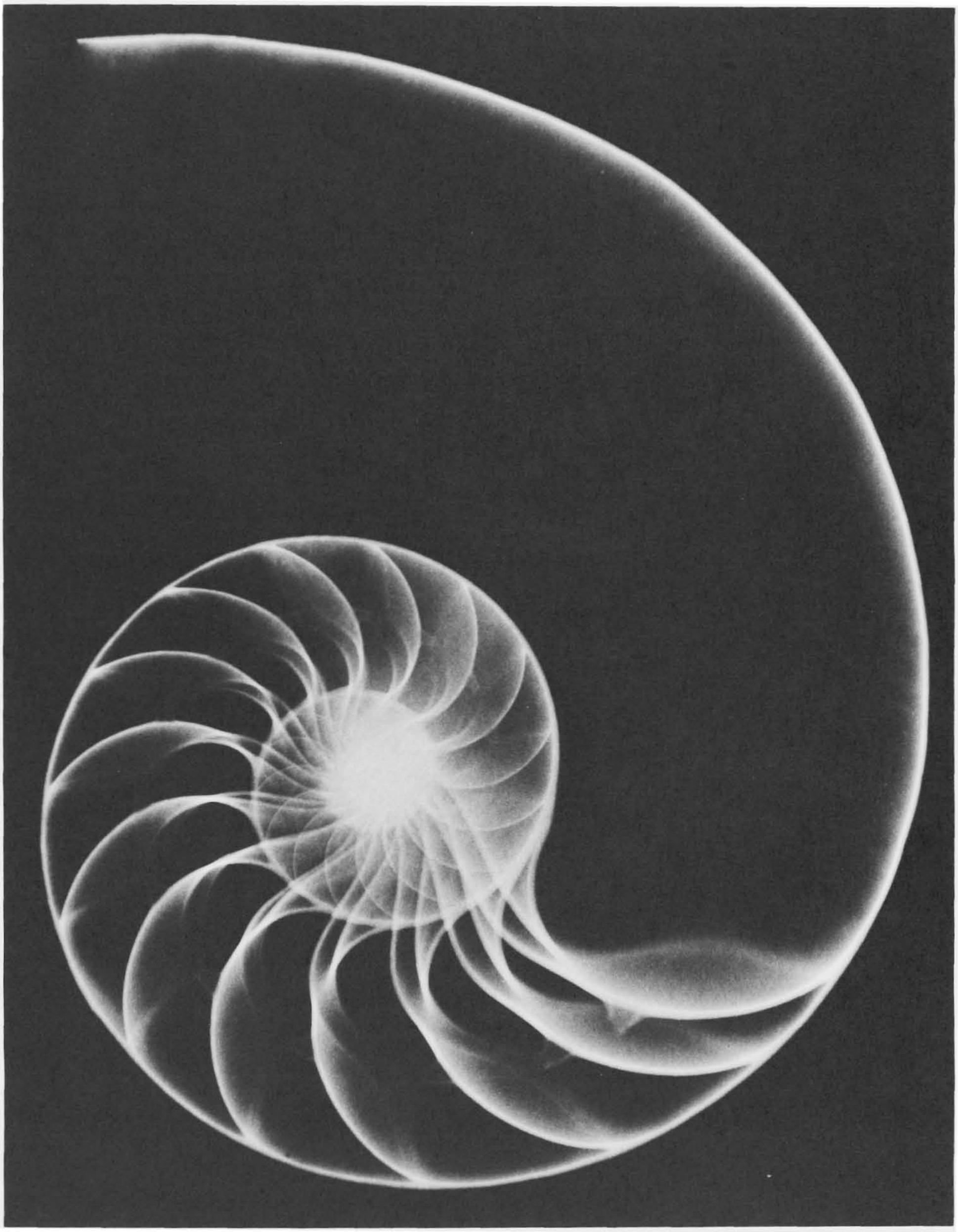

FIG. 55. X-ray photograph of longitudinally sectioned shell of *Nautilus pompilius* showing form of septa both in the axial part of the conch and their lateral extensions toward the umbilicus, ×0.8 (from *Medical Radiography and Photography*, courtesy Charles F. Bridgman).

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[1] Correct observations of border and black film can be made only on shells that have neither been ground off at the apertural margins nor cleaned with acid. Most commercially sold shells have been disfigured in this manner.

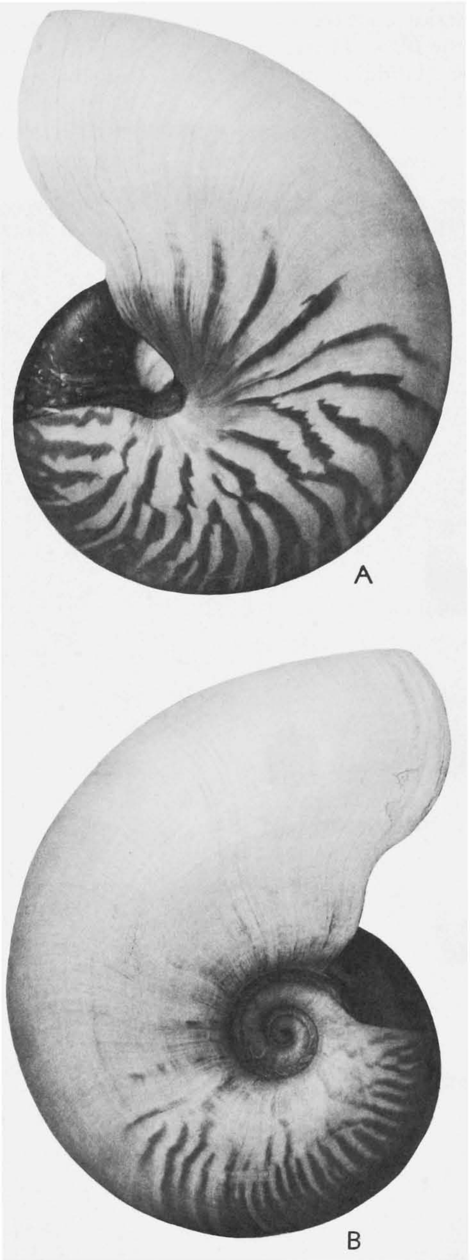

FIG. 56. Exterior of shells of *Nautilus pompilius* LINNÉ *(A)* and *N. scrobiculatus* (SOLANDER) *(B)*, ×0.5 (from 124).

more likely that the mantle fold is responsible (24).

The black film is soon covered by an exceedingly thin nacreous shell layer which is translucent and colorless. The layer makes the originally dull black film lustrous, so that only the outermost, not yet covered, part remains devoid of luster. At the dorsal mid-line of the aperture, the lusterless part sometimes is only 8 mm. in extent; at other times the deposition of the thin shell layer lags behind, so that the lusterless part extends for as much as 60 mm. at the expense of the lustrous part (Fig. 52).

Farther back in the interior of the living chamber, and also at the umbilicus of those species which have an umbilical callus, nacreous shell films gradually pile up over the black film, finally covering it completely. The black film can be seen as a thin black line separating the volutions when the shell is cut in two (see FIG. 66, on right).

The organic material composing the black deposits is regarded by PRUVOT-FOL (24) essentially as an excretion of metabolic waste analogous to the black excretion in the ink sac of the Coleoidea. The cephalopod ink and probably the black deposits of *Nautilus* contain melanins, a group of black, brown, or reddish organic compounds derived from tyrosine (6).

SEXUAL DIMORPHISM

Males are larger than females and their shells are accordingly different in size. Antispadix and spadix, the bulky secondary sexual organs of the mature male, are situated beside the mouth and hence increase the size of the entire crown of tentacles. As the tentacles have to be protected and concealed under the hood when the animal retracts, the hood of the male must be broader than that of the female. Shape and size of the hood, in turn, determine those of the aperture. Therefore, shells of mature males have a broader and more evenly rounded aperture than those of mature females, but the differences are rarely sufficient to distinguish sexes by shell shape alone (Fig. 57).

GROWTH LINES

The shell grows in size along the apertural margin by deposition of shell matter from the slightly thickened and attached mantle edge (Fig. 52). As the rate of deposition is not uniform, slight wrinkles parallel to the apertural margin result. These growth lines outline former positions of the shell margin. Irregularities indicate injuries of shell or mantle margin.

The apertural margins and also the growth lines have three sinuses concave toward the aperture, a large one in mid-venter, marking location of the hyponome, called the hyponomic sinus, and a pair of small and shallow ones on the sides, in the position of the eyes, the ocular sinuses. The hyponomic sinus permits free motion of the hyponome and is indicative of the animal's swimming habit. The ocular sinuses allow the eyes to peer out between the hood and shell margin, when the animal is partially withdrawn into its shell (see Fig. 68B).

CHAMBERS AND SEPTA

The body occupies and conforms exactly to the shape of the body chamber *(chambre d'habitation, Wohnkammer),* which is the last or outermost of the chambers and is open at the shell aperture. The body chamber occupies 14/36 to 15/36 of the last volution. All other chambers are air-filled in life; they are air chambers *(Luftkammern).*

The number of septa in mature adults is variable within limits; *Nautilus pompilius* has 33 to 38; *N. macromphalus,* 27 to 28; and *N. scrobiculatus,* 32.

Each septum has a septal foramen near its center; this is a slightly oval to circular hole for the siphuncle, around which the septum is turned toward the shell apex, forming a septal neck *(goulot siphonal, Siphonaldüte).* The hole is 4 by 3 mm. in size, and its neck is 4 mm. long in the last septum of mature shells.

The concave face of the septum has shallow, branching grooves symmetrically arranged. These are imprints of the two branches of the pallioseptal artery that supply blood to the septal face of the mantle.

The septum joins the shell at a very acute angle and there the margin, or mural part, of the septum is attached to the wall. Hence, the joint is really a band made by the mural part of the septum, but it is commonly represented in illustrations as a line, the suture or suture line *(suture* or *ligne sutural, Sutur* or *Suturlinie),* which is the line of juncture between shell wall and the free unattached part of the septum. The suture has several bends; those convex to the shell apex are called lobes *(lobes, Loben)* and those concave are termed saddles *(selles, Sättel).* At the dorsum of the third to 25th septum, approximately, there is a median dorsal lobe (annular lobe), which gradually disappears in later septa and is best developed at the 20th septum approximately (Fig. 58). The edge of the mural part of the septum, in front of the annular lobe, has a V-shaped notch, pointing to the apex and in some shells extending into a furrow, which persists to the last septum made. A similar median dorsal septal furrow *(Normallinie),* V-shaped, linear, or tear-shaped, in which the mural part of the septum is thin or lacking, is present in other nautiloids.

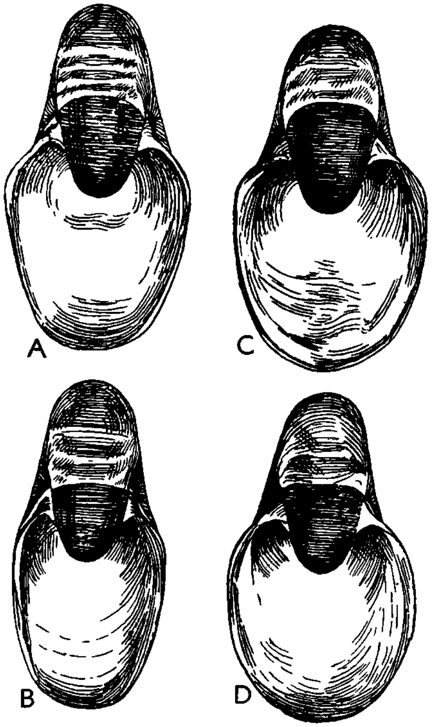

FIG. 57. Sexual dimorphism of the shell in *Nautilus pompilius* LINNÉ, *(A,B)* females, *(C,D)* males, ×0.25 (after 30). Minimum difference is shown in the upper figures *(A,C)* and maximum in the lower ones *(B,D).*

ECTOSIPHUNCLE

The conchiolinous and aragonitic cover (siphuncle of some authors) of the siphun-

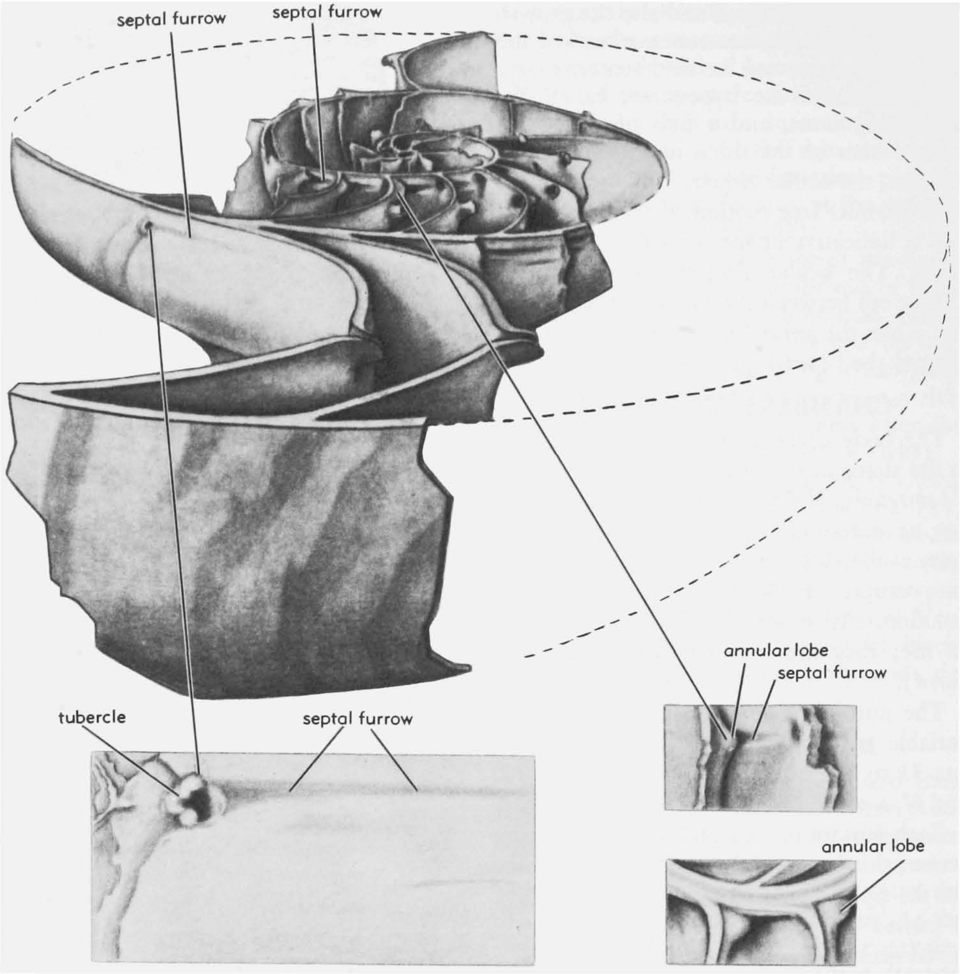

FIG. 58. Shell of *Nautilus pompilius* LINNÉ, cut open parallel to and slightly to the left of the plane of bilateral symmetry to show the annular lobe and septal furrow, enlarged (19).

cular cord consists of a series of tubes, each extending from septum to septum, increasing in diameter with the growth of the shell (Fig. 59). A tube (connecting ring) traversing an air chamber has two layers: (1) an outer layer of tiny calcareous spicules, irregularly arranged and held in place by a porous conchiolin matrix, and (2) an inner thin lining of conchiolin. The spicule-bearing layer continues directly into the conchiolin base layer of that septum of which the tube is the apical extension; it embraces the neck of this septum and extends apically to the septal foramen of the preceding septum, where it is inserted. At the place of insertion the apical end of the spicule-bearing layer becomes quite dense through abundance and coalescence of spicules. The inner conchiolin lining arises from the apical edge of the nacreous shell layer of the septal neck and extends apically to the next preceding neck, where it is inserted.

Sections of a septal neck (Fig. 59) reveal five layers: (1) an outer spicule-bearing layer formed by the apertural embracing part of the spicule-bearing outer tube (connecting ring), (2) a dark, dense layer restricted to the neck, (3) the nacreous layer of the septal neck, which is a continuation of the nacreous layer of the septum, (4) the apical

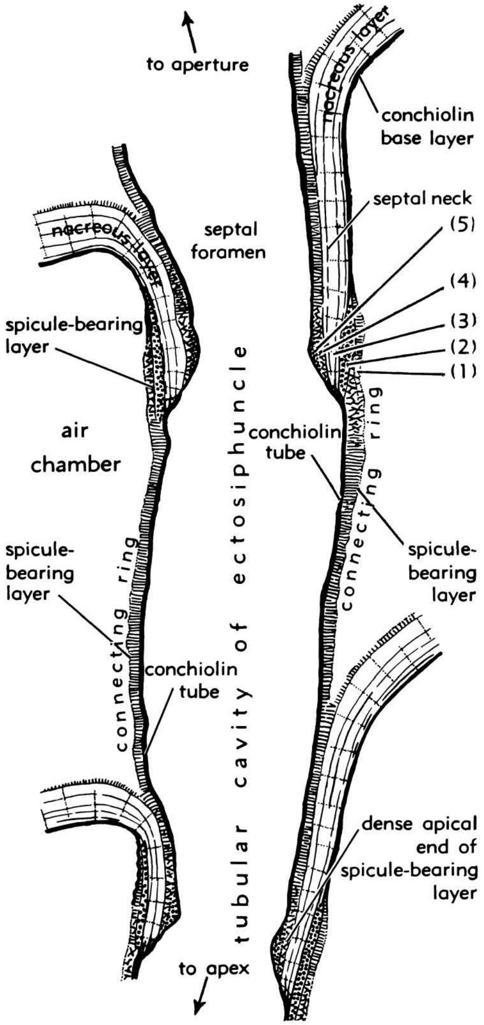

Fig. 59. Longitudinal and vertical section through the ectosiphuncle in *Nautilus,* ×12 (modified from 2, 5). Conchiolin is shown in solid black, aragonite spicules by crowded cross lines, coalescent spicules by short branching cross lines, dense aragonitic portions by heavy black dots, and nacre by widely spaced parallel lines crossed with dotted orthogonal lines. Numbers in parentheses at upper right refer to the 5 layers described in the text.

and dense end of the succeeding siphuncular cover (connecting ring), and (5) a short, dense layer (auxiliary deposit) in the form of a ring, constricting the foramen. The last two layers are not present in the neck of the body-chamber septum; hence they were the last deposits to form in the preceding septal necks (2, 5).

SHELL STRUCTURE

As the animal grows, it builds onto the shell margin at the aperture and thereby lengthens and enlarges its body chamber. The newly deposited marginal shell material is a continuation of the thin outer shell layer, the porcelaneous ostracum, and is deposited by the apertural edge of the mantle fold alone.

The porcelaneous ostracum (Fig. 60) is composed of microscopic aragonite grains held together by a dark conchiolin matrix; toward the inside of the porcelaneous layer the grains are replaced by microscopic closely packed vertical prisms of aragonite (*Verkalkungstreifen* of Appellöf).

The porcelaneous ostracum is later strengthened by the nacreous layer of the ostracum formed from films deposited one over the other inside the body chamber by the whole surface of the mantle. Each film is composed of closely packed, flat-lying, tabular, hexagonal crystals of aragonite (tabular parallel to their crystallographic bases), united into thin lamellae (0.2 microns) and held together by conchiolin. Within a lamella and in successive lamellae the aragonite crystals lie one upon the other like stacks of coins, with the stacks closely crowded. Hence the conchiolin matrix binding the stacks together shows under the microscope as thin vertical slightly irregular dark lines. Some of the lamellae have more

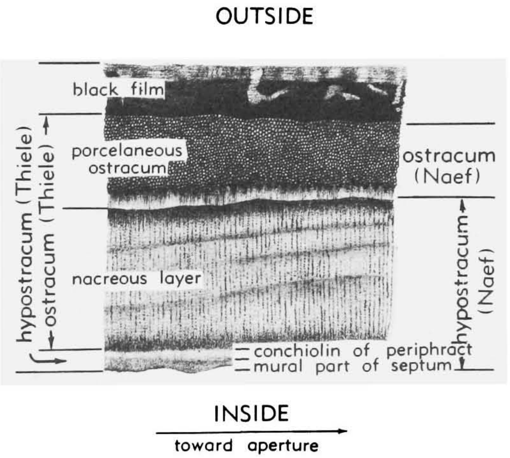

Fig. 60. Section through the shell wall of *Nautilus,* ×30 (after 2).

conchiolin matrix than others; these show as darker parallel bands slightly inclined to the base of the nacreous layer and converging with the base toward the shell aperture. Over the nacreous layer a conchiolin film is deposited by the periphract, that is, the retractor muscles and dorsal and anteroventral aponeuroses.

The conchiolin matrix of the nacreous layer forms extremely thin parallel films, which alternate with the aragonite layers. The films are connected by transverse conchiolin bridges between the individual tabular crystals of the aragonite layers. The whole arrangement resembles mortar in a brick wall.

THIELE (27) regarded the ostracum as composed of two layers, the porcelaneous layer and an adjoining nacreous layer; the conchiolin film deposited by the periphract and the mainly nacreous septa, deposited upon this film, he called the hypostracum. NAEF (20) restricted the ostracum to the porcelaneous outer layer and united as the hypostracum the two nacreous deposits with the conchiolin film between them. The extent of the hypostracum and ostracum involve exact comparison with these layers as developed in the other mollusks. Such exact homologies have not yet been demonstrated. Provisionally, the following terminology is recommended: **outer ostracum,** composed of the porcelaneous and nacreous layers, **hypostracum,** composed of the conchiolin of the periphract and the thin layer of columnar crystals lying between the conchiolin film and the nacreous wall layer, and **inner ostracum,** composed of the septa including their mural parts.

The septum is secreted by the septal face of the mantle; therefore, its shape exactly conforms to this face. Not only is it concave toward the aperture, but on its concave face it has faint branching imprints of the ramifying pallioseptal arteries, which supply that part of the mantle, and it even has slightly wrinkled folds spreading from the anterior edge of the mural part of the septum, marking places where the visceral sac had been suspended from the shell wall by attachment along the septal contour.

The septum has a conchiolin base layer, on which is deposited the nacreous layer of the septum. A layer of aragonite spicules is on top of the nacreous layer (Fig. 59).

SUBMICROSCOPIC SHELL STRUCTURE

The shell structure under the electron microscope (9, 10, 10a) confirms and extends observations on features seen under ordinary and polarizing microscopes (1, 2, 3).

The main part of the porcelaneous layer has irregularly disposed crystal aggregates, about 6 microns in size. The aggregates are radially divergent or parallel imbricate. In any case, the various aggregates differ greatly in the arrangements of their crystals so that the whole appears disordered (Fig. 60A,*1*).

Along the boundary with the nacreous layer, the porcelaneous layer develops aggregates of long, parallel sharp-edged bars, rods, or blades of aragonite arranged at right angles to the boundary plane, forming the *Verkalkungstreifen* of APPELLÖF. This special part of the porcelaneous layer has wedge-shaped protuberances that penetrate short distances into the adjoining nacreous layer in a few places, but the boundary is smooth for much of its course (Fig. 60B,*1*).

Cross sections through the nacreous layer of the outer ostracum show thicker (0.9 to 1.4 microns) and thinner (0.4 to 0.6 microns) tabular aragonite crystals. A single layer of the former alternates with a group of 6 to 7 layers of the latter, exhibiting vertical stacking (Fig. 60B,*2*). Along the boundary with the porcelaneous layer, stacking does not show and the arrangement is irregular, because the crystals are lenticular rather than tabular (Fig. 60B,*1*). Here the thinner layers are 0.01 to 0.023 microns and

EXPLANATION OF FIGURE 60A,*1*,*2*

1. View of polished and etched transverse section through porcelaneous layer of outer ostracum; crystal units are arranged in many different directions and compose aggregates of radially divergent or parallel imbricating bundles; ×19,000.——*2*. View of slightly etched surface at concave, adapertural side of penultimate septum; thin hexagonal tabular crystals of aragonite, stacked one over the other, leave wide interspaces unfilled between them, ×4,000 (10a).

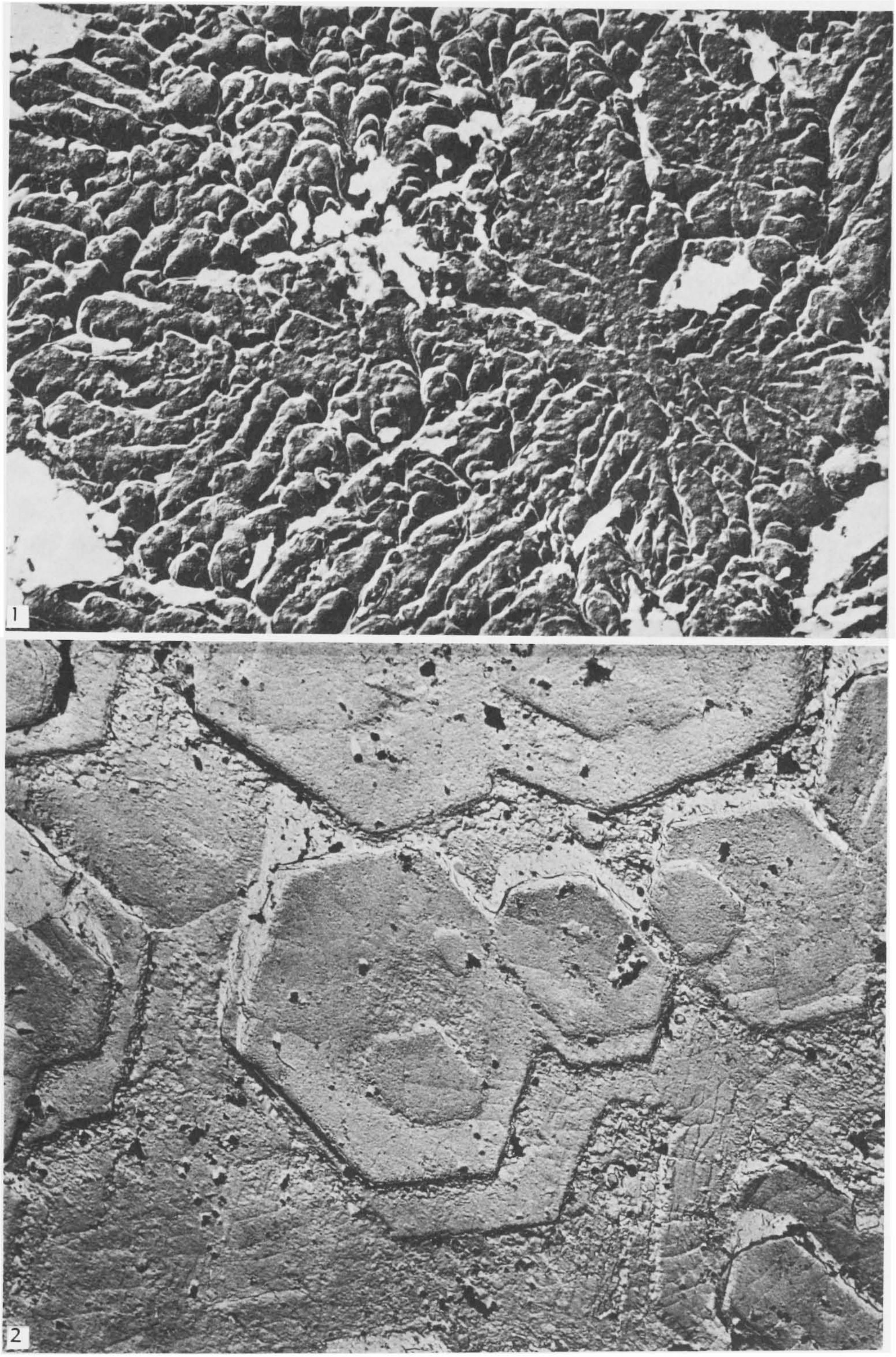

FIG. 60A. *1,2*. Electron micrographs showing submicroscopic shell structures of *Nautilus pompilius* LINNÉ, Rec. (explanation on facing page).

the thicker layers are 0.45 to 1.1 microns thick.

Similar features are visible on the surface of the nacreous layer on the concave adapertural face of some septa and on that of the nacreous layer lining the body chamber between aperture and retractor muscle, that is, the growing inner surface of the outer ostracum. These surfaces are partly covered with a pavement of countless flat tabular hexagonal crystals of aragonite, which are very thin and have parallel outlines, although they are separated by wide interspaces as yet unfilled. The crystals are stacked, and as many as 5 superposed crystals can be discerned in some of the stacks. These observations indicate that the last 5 crystals of the stacks were still growing at their peripheries to fill up the empty interspaces until only a narrow crack, filled with conchiolin, separates adjoining stacks (Fig. 60A,*2*).

The inner surface of the hypostracum, directly beneath the transparent conchiolin film that separates shell from muscle, shows sturdy bundles of columnar girder-like blunt-pointed aragonite crystals forming short, warty protuberances pointing in various directions (Fig. 60B,*3*). The arrangement of the bundles helps to produce a firm bond between shell and muscle and is probably caused by the tension exerted by the muscle during the growth of the crystals.

The corner spaces between the septa and the outer ostracum and the joint between the outer ostracum and the mural parts of the septa are filled with several layers which are partly conchiolinic and partly aragonitic. Their structure is variable and complicated (2). This complicated and somewhat obscure submicroscopic structure has been described from 17 regions of the shell (10a).

The conchiolin base layer of some of the septa consists of a felting of microfibrils, which are 4 to 8 millimicrons thick and solitary or associated in bundles, but appear to have no definite orientation. This microfibrillar structure of the base layer presumably results in high tensile strength of this layer. The nacreous layer of the septa has a structure very similar to that of the nacreous layer of the outer ostracum. The thin conchiolin layers between the individual crystals of a stack in these nacreous layers are very characteristic lacelike reticulate films.

The submicroscopic structure, as examined under the electron microscope (Figs. 61, 62), shows pattern differences on the species level and on higher taxonomic levels. For instance, the conchiolin films are 4 to 12 millimicrons thick in *Nautilus,* 8 to 12 in gastropods, and 2 to 9 in bivalves (9, 10).

ONTOGENY

The ontogeny of *Nautilus* is nearly unknown. The only observations available are those made by Willey (29, 30).

EGGS

Eggs of *Nautilus macromphalus* are laid singly and attached by a spongelike base. The egg is 45 mm. in diameter. As in all cephalopod eggs, there is much yolk.

EMBRYO

Nothing is known of the embryonic development, but the large yolk makes it certain that when the young emerges from the egg, it already possesses the main features of the adult, bearing a sizable shell, probably provided with several septa, but possibly with yolk sac still attached. Like the embryo of other cephalopods and, unlike that of other mollusks, it probably does not go through such stages as the planktonic veliger larva, either within the eggs or after hatching.

Explanation of Figure 60B,*1-3*

1. View of polished and etched transverse section through shell wall of body chamber, showing *Verkalkungstreifen* of the porcelaneous layer (band 20μ wide, at the top) and the nacreous layer. The latter has a thick aragonite crystal (at bottom) and several thinner crystals, all somewhat lenticular. The boundary between the two layers is uneven and has protuberances, ×22,000.——*2.* View of polished and etched transverse section through shell wall of body chamber, showing the nacreous layer. A few thicker and many thinner tabular aragonite crystals form a structure like a brick wall and show good vertical stacking. Many conchiolin films between the crystal layers are torn and flapped aside, resting on the crystals and showing their lacelike construction, ×14,400.——*3.* View of inner surface of hypostracum beneath the conchiolin pad that separates the shell wall from the muscle in the body chamber, ×9,000 (*1,3,* from *N. pompilius* Linné, *2,* from *N. macromphalus* G. B. Sowerby) (10a).

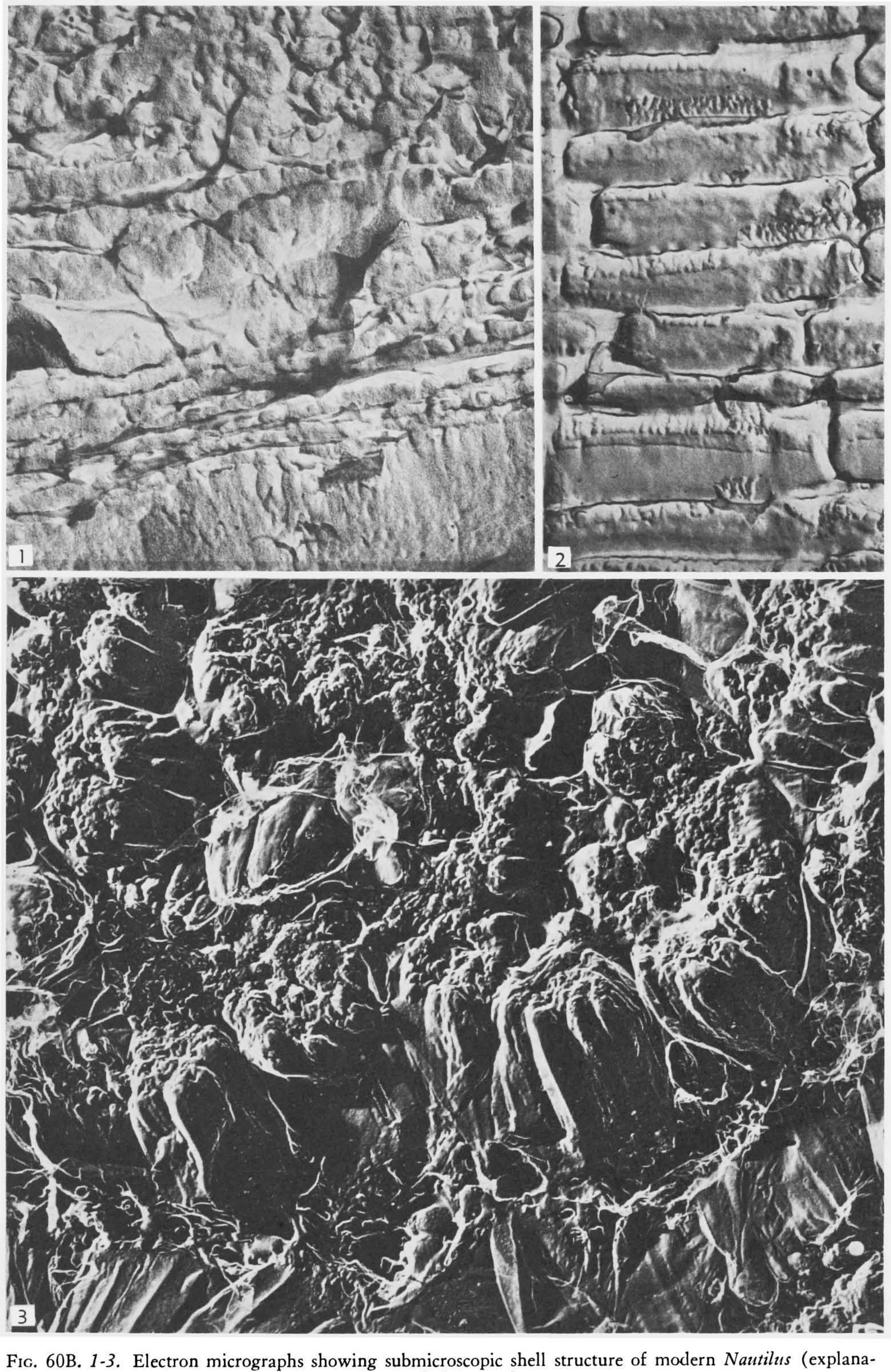

FIG. 60B. *1-3.* Electron micrographs showing submicroscopic shell structure of modern *Nautilus* (explanation on facing page).

PROTOCONCH AND EARLY SHELL

By chipping away the rest of the shell, one can free the first chamber of *Nautilus* (Fig. 63). It is slightly curved and thimble-shaped. Its apex has a slightly raised, elongate boss with a shallow, linear central depression. This feature was discovered and interpreted as a scar (cicatrix) by HYATT (13). According to HYATT, the first embryonic shell, the protoconch, of *Nautilus* is composed of conchiolin only, and does not calcify; therefore, it is destroyed or becomes detached at a later stage, and the cicatrix is either the original attachment area of the conchiolin protoconch or a connecting passage that was closed after the protoconch was shed. If this interpretation is correct, the first calcareous chamber of *Nautilus* is really its second chamber. However, SPATH (25, p. 421) pointed out that HYATT's interpretation of the so-called cicatrix is merely an assumption. SPATH has maintained that *Nautilus* has a calcareous protoconch, which is preserved in the apical portion of the shell. Similarly, NAEF (20) believed that the cicatrix marks the beginning of the shell and that the first air chamber is a modified protoconch. This interpretation is followed here because it is highly unlikely that a conchiolin protoconch can be reabsorbed or detached within the egg. Whether one or the other interpretation is correct can be decided only when the embryology and ontogeny of living *Nautilus* become known. A discussion of this same problem in fossil nautiloids is given in a preceding section on "Morphology."

The shape and size of the embryonic shell, as it was when the young animal emerged from its egg, can be seen on nepionic shells (Figs. 64, 65). These have a line of discontinuous growth, marked by a shallow and narrow groove, particularly well displayed on the flanks and at the umbilical shoulders. This constriction, signifying the end of the embryonic stage, is at a constant position in all individuals seen, about 1.25 volutions from the apex, and at that stage of growth the shell is 25 to 27 mm. in diameter and 16 mm. wide in *Nautilus pompilius*. From the apex to this terminal embryonic constriction, the shell of this species has (1) glossy luster, (2) light brown color, (3) cancellate sculpture, consisting of very fine, smooth lirae, among which the radial ones are broader than the spiral lirae, (4) no ocular sinuses on the growth lines, (5) a shallow hyponomic sinus on the growth lines, (6) a deep and narrow umbilicus without a callus, and (7) smooth, continuous growth lines without a trace of traumatic breakage of the shell. Beyond this constriction, the nepionic shell of *N. pompilius* has (1) much less glossy luster, (2) darker color of somewhat reddish-brown interrupted by sharply defined white gaps, which become broader as growth continues, (3) either no or only obsolescent cancellate sculpture gradually fading away during growth of the shell, (4) shallow ocular sinuses, which become deeper only as maturity is reached, (5) a deeper hyponomic sinus on the growth lines following the constriction, (6) a wider umbilicus that becomes filled by callus at a late stage of growth, and (7) many broken growth lines and injured former apertural margins. The last of the seven enumerated symptoms is particularly significant, because it proves that the embryonic stage ended at the time the con-

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EXPLANATION OF FIGURE 61

Conchiolin from decalcified mother-of-pearl (inner layer of the shell wall, body chamber). The soft iridescent membranes, freed by decalcification of mother-of-pearl, were cleaved and broken into thin fragments by ultrasonic waves. Drops of aqueous suspensions of the disintegrated materials were deposited on screens coated with supporting films, to which they collapsed by desiccation. The preparation here shown was first coated with a film of carbon (10), then shadow-cast with palladium. The membranes appear in the electron microscope as fragments of lacelike reticulated sheets, with sturdy trabeculae separating rounded or elongated openings of irregular outlines. The trabeculae are sprinkled with hemispheric tuberosities of various sizes. This type of texture is one of the three "patterns" of conchiolin provisionally described at the electron microscope level in the nacreous shells of mollusks (Grégoire, Duchâteau & Florkin, 1950, 1955; Grégoire, 9, 10). In *Nautilus pompilius* (Grégoire, unpublished), the structure of the reticulated sheets closely resembles that previously observed in *Nautilus macromphalus,* with possible differences in size and arrangement of the tuberosities on the trabeculae (×42,000). (Micrograph, Grégoire, n).

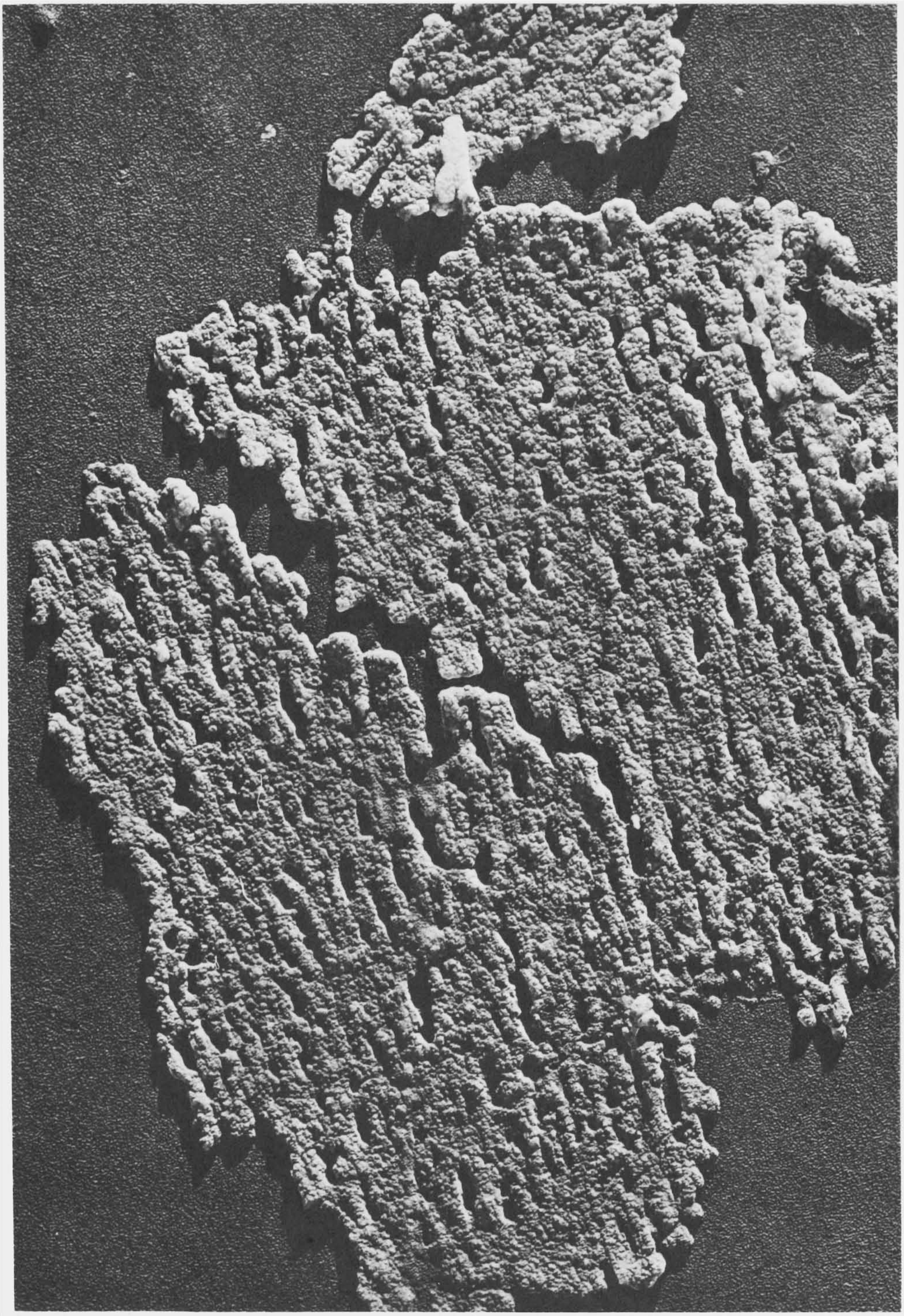

FIG. 61. Electron micrograph of mother-of-pearl from *Nautilus pompilius* (explanation on facing page) (compare Fig. 2).

striction originated, since from the apex to the constriction, shell growth was continuous and no traumatically broken growth lines or repaired former apertural margins are found, whereas immediately beyond the constriction many such breaks are visible and they are more numerous than at later stages of growth. These hitherto unnoticed facts show that growth from the apex to the constriction of the shell was protected from breakage, that is, within the egg.

The white gaps in the color pattern begin to show up first on the flanks and later on the venter. Both kinds appear on the embryonic shell, the first approximately 130 degrees of a volution adapically from the constriction and the second kind approximately 60 degrees of a volution adapically from the constriction. On the embryonic shell, the white gaps are narrow and their margins ill defined, so that the pattern appears out of focus, so to say. The ocular sinuses begin to show as very shallow features shortly before the constriction is developed. The umbilical callus begins to be deposited when the postembryonic shells reach a diameter of about 5 cm. or a little more; one shell observed by me lacked a completely covered umbilicus at a diameter of 7.7 cm. The umbilicus changes rapidly during the earliest postembryonic stage in that the umbilical seam rapidly changes from one spiral ratio to another and in doing so widens the umbilicus (Fig. 64).

WILLEY (28, p. 225) appears to have been the first to notice the terminal embryonic constriction or line of discontinuous growth and to interpret it as the end of the embryonic stage. According to BÖHMERS (4), it is the position of the aperture when the first septum is built; this interpretation is unlikely, as shown by the observations made by NAEF (20).

On comparing *Nautilus* with *Sepia,* the common cuttlefish, NAEF (20) conjectured that *Nautilus* emerges from the egg having a shell with seven air chambers already formed, because septa 3 to 7 are the most widely spaced and septum 8 is fairly close to its predecessor. However, there is some individual variation in these spacings. One shell seen by me shows the first four septa

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EXPLANATION OF FIGURE 62, *1-4*

1. Positive carbon replica, shadow-cast with palladium, of a fracture surface in the nacreous layer of an adoral septum of *Nautilus pompilius,* showing 18 superimposed broken lamellae in transverse section. Interlamellar reticulated sheets of conchiolin (horizontal white strings in picture) alternate with the aragonite lamellae. The white rectangular structures (on right side of figure) are fragments of aragonite crystals removed with the negative replica and transferred to the positive replica. On the tenth lamella down from the top, a conchiolin bridge (separating two crystals of aragonite in this lamella) forms a right angle with the adjacent interlamellar sheets above and below. The lace-like texture of the interlamellar reticulated sheets of conchiolin are visible as lattice-works protruding from the background and projecting shadows over the second, third, and ninth aragonite lamellae, respectively (×19,000) (micrograph, Grégoire, n).

2. Positive carbon replica, shadow-cast with palladium, of a nacreous surface (shell wall) of *Nautilus macromphalus* polished obliquely to the plane of the stratified aragonite lamellae. Etching freed seven imbricated interlamellar reticulated sheets of conchiolin. The structural features of the nautiloid pattern (sturdy trabeculae, sprinkled with tuberosities, elongated or rounded, irregular openings) are visible. Except for scattered areas with a finely granular surface, the aragonite lamellae alternating with these sheets are either hidden by the superimposed organic structures or were partly dissolved by the corrosion process, leaving the organic sheets piled upon each other (×27,000). (Grégoire, 1957, *Biophysical and Biochemical Cytology,* fig. 5, with permission of the Editors.)

3,4. Membrane coating the adapical convex side of the septum (Edwards, 1849; Barrande, 1857, 1877; Appellöf, 1893) from a living specimen of *Nautilus pompilius* immersed in alcohol immediately after capture and preserved in the U.S. National Museum; material supplied by CURT TEICHERT. The membrane was gently thinned by teasing *(3)* or treated by ultrasonic waves *(4).* The chief components of this septal membrane appear to be fibrils and nodules. In the original state of the membrane, the fibrils, either isolated or arranged in bundles, formed a dense felting. The nodules, faintly visible in *3,* are thick, irregularly rounded bodies scattered between the fibrils and adhering to them. The fibrils are frequently anchored on the nodules in a beamlike fashion. In *4,* the relation between fibrils and nodules is shown after loosening and moderate disintegration of the felting by ultrasonic waves (×42,000). (Grégoire, n, unpublished observation, 1961.)

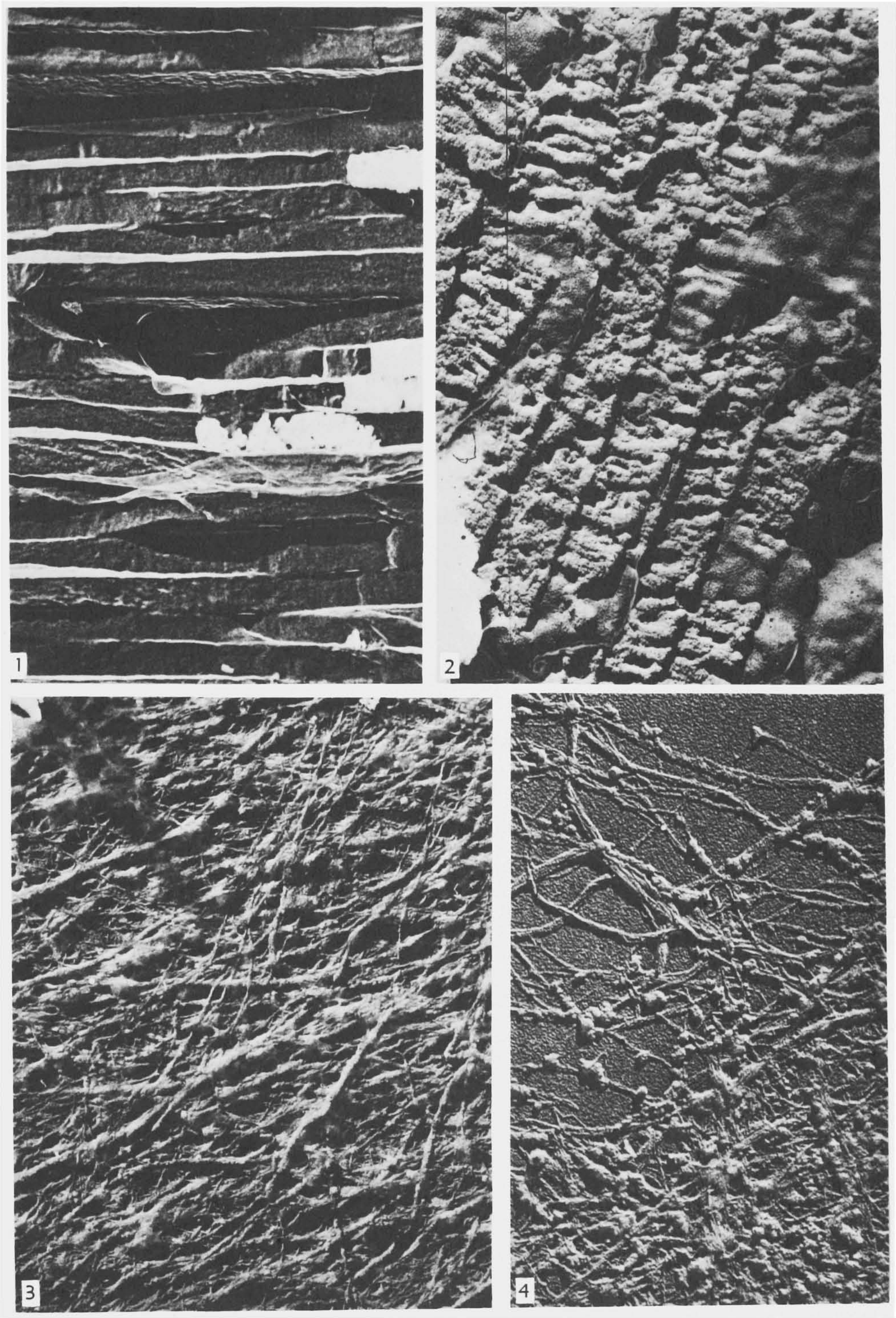

FIG. 62. Electron micrographs of mother-of-pearl from modern *Nautilus* (explanation on facing page) (compare Fig. 2).

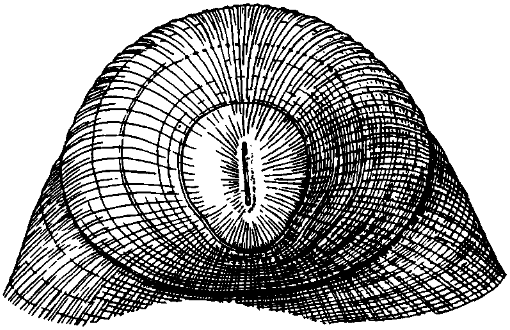

FIG. 63. Apex of the shell of *Nautilus pompilius* LINNÉ, showing the cicatrix of HYATT, ×10 (from 13).

widely spaced, septa 4 and 5 close together, and septa 5 and 6 spaced wider apart, although not as much as the first three or four septa. Therefore, it is possible that this individual had only four septa at the time when it emerged from the egg.

The apical portion of the shell has reticulate sculpture of fine, raised, intersecting longitudinal and transverse lines (Fig. 63). These become obsolete in later growth stages of all living species except one, *Nautilus scrobiculatus*.

The curvature of the shell is only slight in the first three chambers, but at the third septum it increases abruptly and from then on it continues in a regular spiral (Fig. 66). These changes in curvature produce a small umbilical perforation between the dorsum of the first three chambers and that of the succeeding chambers in the first volution in *Nautilus pompilius,* but in *N. macromphalus* there is no perforation, only a pit on each side.

The beginning of the siphuncle is a closed and saclike structure, the siphuncular caecum, which rests against the inner surface of the shell apex in a shallow depression located over the cicatrix, or a little to one side or the other of it. In the first and second chambers, the siphuncle has a somewhat greater diameter than in the third and succeeding chambers.

GROWTH OF SEPTA

The shell muscles grow with the animal and gradually move forward, together with the whole periphract, leaving a series of faint concentric growth lines impressed on the conchiolin film, which they have deposited. Thereby the body gradually slips forward in its chamber; the siphuncular cord grows correspondingly in length. In this way, a space is vacated between the last septum and visceral sac, which with its gradual growth simultaneously fills with air, probably liberated from the pallioseptal arteries that ramify in the mantle covering the rear of the visceral sac. The air space increases until a certain volume is attained. Then the mantle, which covers the visceral sac and as an attenuated extension forms the siphuncular cord, secretes a very thin, somewhat flexible, easily torn membrane of conchiolin. The membrane conforms to the shape of the cord and to that of the rear end of the visceral sac and is firmly attached to the shell wall at the septal contour—the whitish, slightly thickened line in the mantle that encircles the rear end of the visceral sac. Upon this conchiolin membrane successive films of nacre are secreted by the septal face of the mantle, commencing from the suture and gradually spreading to the septal neck, so that a septum, at first thin and fragile, is built up through successive films. The whole process must be rapid, because very few individuals have been caught while growing a septum.

During the making of a new air chamber, particularly during the time the air space between last septum and visceral sac is gradually enlarged, the cord of the siphuncle is kept in position by its insertion in the last septal foramen on one end and on the other end by the genito-intestinal ligament, which rises from the root of the tube and connects with stomach, intestine, and gonad.

The septa are regularly spaced, but distances between them change in an orderly fashion during growth; the first three are close together, septa 3 to 7 are the most widely spaced, from septum 7 on they are fairly close together again. At the end of growth of the individual, the interval between the septa decreases, so that the last two or three septa are more crowded together than their predecessors. It is then that the animal reaches sexual maturity and propagation takes place (Fig. 54, 55).

Each septum is larger and thicker than its predecessor. The increase is gradual and regular, except for the last septum of the

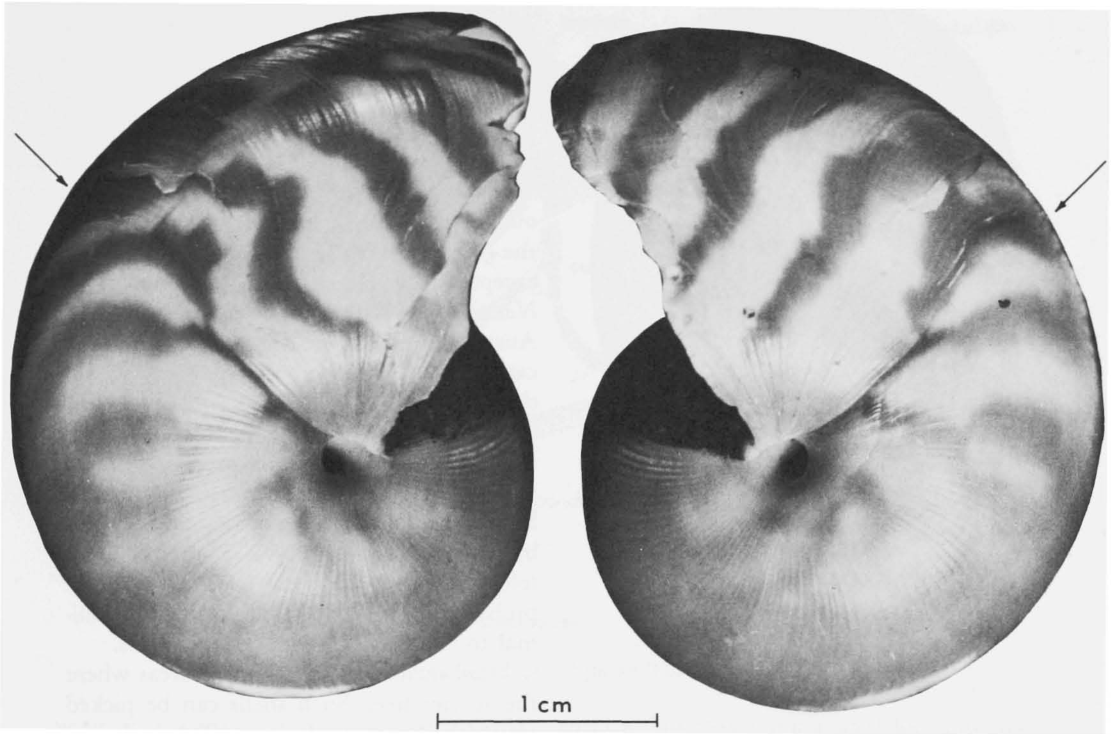

FIG. 64. Side views of a juvenile *Nautilus pompilius* from Cuyo Island, Palawan Province, Philippine Islands (Acad. Nat. Sci. Philadelphia, No. 223519, collected in 1958), showing (arrows) part of terminal embryonic constriction that is particularly well displayed on flanks and umbilical shoulders (Stenzel, n).

mature animal. This septum is not only closer to its predecessor but also noticeably thicker, up to 1.5 mm. in thickness.

MATURITY

Propagation takes place only after the final septum has been formed (30, p. 746). Maturity is indicated in the shell by (1) thickening of the apertural shell margin, which is thin and fragile as long as the animal is immature, (2) decrease in the volume of the last air chambers formed, as shown by a crowding together of the last two or three septa, and (3) greater thickness of the last septum, which is noticeably thicker than its predecessor, and (4) widening of the black border on the inside of the shell aperture. The ocular sinuses become more prominent at maturity as age of the animal advances.

Formation of septa and their regular spacing in the shell have nothing to do with reproductive cycles of the animal.

GENERAL BIOLOGY

SPECIES

Five species and an unknown number of geographic subspecies of *Nautilus* are living representatives of the genus. The species differ in smoothness or reticulate (scrobiculate) sculpture of the shell, presence or absence of an umbilical callus and perforation, degree of involution, surface features of hood, adult size, number of septa, and coloration of the shell. Coloration, particularly its value and chroma, is variable and cannot be used to the extent that IREDALE thought possible, although subspecies might be defined by it in the future. One of the species, *N. scrobiculatus,* differs in so many features from the others that it is logical to place it in a separate subgenus.

The following species of *Nautilus* are recognized: (1) *N. pompilius* LINNÉ, 1758, type-species of the genus (Figs. 54,55,56,*A*); (2) *N. repertus* IREDALE, 1944 (14) [=*N.*

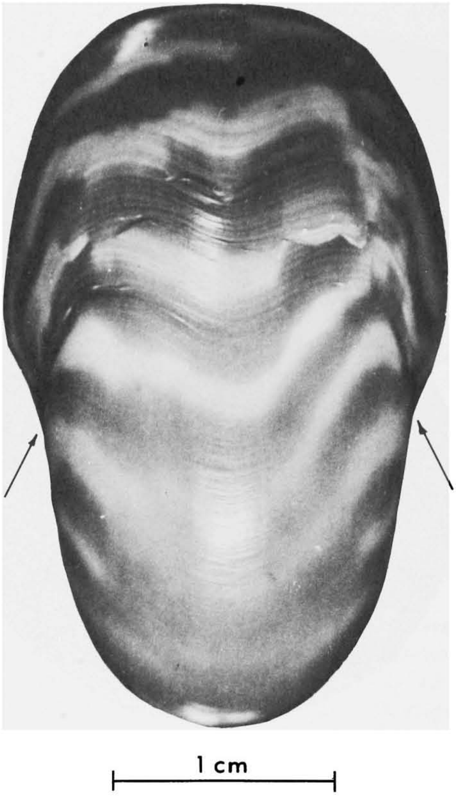

FIG. 65. Ventral side of specimen illustrated in Figure 64 (Stenzel, n).

ambiguus G. B. SOWERBY, 1849 (*non* FICHTEL & MOLL, 1798)]; (3) *N. stenomphalus* G. B. SOWERBY, 1849; (4) *N. macromphalus* G. B. SOWERBY, 1849, and (5) *N. scrobiculatus* SOLANDER, 1786 (Fig. 56,*B*) [=*N. umbilicatus* LAMARCK, 1822 (*non* LINNÉ, 1758, which is a foraminifer)].

The first two species listed have an umbilical callus, the next two do not; the last is the only one that has scrobiculate sculpture in the adult. *Nautilus alumnus* IREDALE, 1944 (14), is a *nomen nudum,* since neither a description nor a figure nor adequate literature reference was given to validate the name.

DISTRIBUTION

The genus *Nautilus* is restricted to the southwestern Pacific Ocean, where it ranges from northwestern Australia and tropical Queensland to the south coast of Luzon Island in the Philippines and from Macassar Strait to the Fiji Islands (26). Hence the geographic range is very large, embracing 60° of longitude and 35° of latitude (Fig. 67). Nevertheless, it is a relict in the sense that its present range is only a small fraction of the combined geographic ranges of various Tertiary Nautilida.

Some of the species live side by side without interbreeding. The geographic area of the genus apparently is continuous, with the exception of the isolated populations of *Nautilus repertus* off the coast of southern Australia, one of which is now authenticated by the finding of two stranded individuals (7).

Except for these isolated populations, *Nautilus* is restricted to warm tropical marine waters. It is recorded from 315 fathoms, but most catches are made in shallow water by native fishermen. Evidently, it has great tolerance for depth changes. The siphuncle probably plays a role in adapting the animal to changes of hydrostatic pressure.

Dead shells float far from the areas where the species live. Such shells can be picked up on the beach not far from Tokyo, Japan, at least 1,800 miles from the habitat of living species. Other drifted shells have been recorded from the Ryukyu Islands, Taipei, Nicobar Islands, Cocos Keeling Islands, New South Wales, New Zealand, Sunday Island of the Kermadec Islands (26), the east coast of Madagascar,[1] and other places.

FOOD

The tentacles of *Nautilus* are highly specialized as to functions, and in seizing prey the various groups of tentacles act in a regular sequence. When resting or quietly swimming, all the cirri remain withdrawn in their sheaths, but sometimes their tips are visible. When alerted, the animal extends the ocular tentacles and the four small outer-most digital tentacles on each side. When it notices food, the animal brings out the outer row and part of the median row of digital tentacles and spreads them to form a cone of search. This cone is kept al-

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[1] Reported by DAVYDOV, K. N., 1906, Poostrovam Indo-Avstraliyskago Arkhipelaga. Vpechatlyeniya i nablyuďeniya naturalista. Pt. 3. Na ostrovakh Aru: Acad. Impér. Sci. St. Pétersbourg, Bull., ser. 5, v. 25, no. 5, p. 245-351.

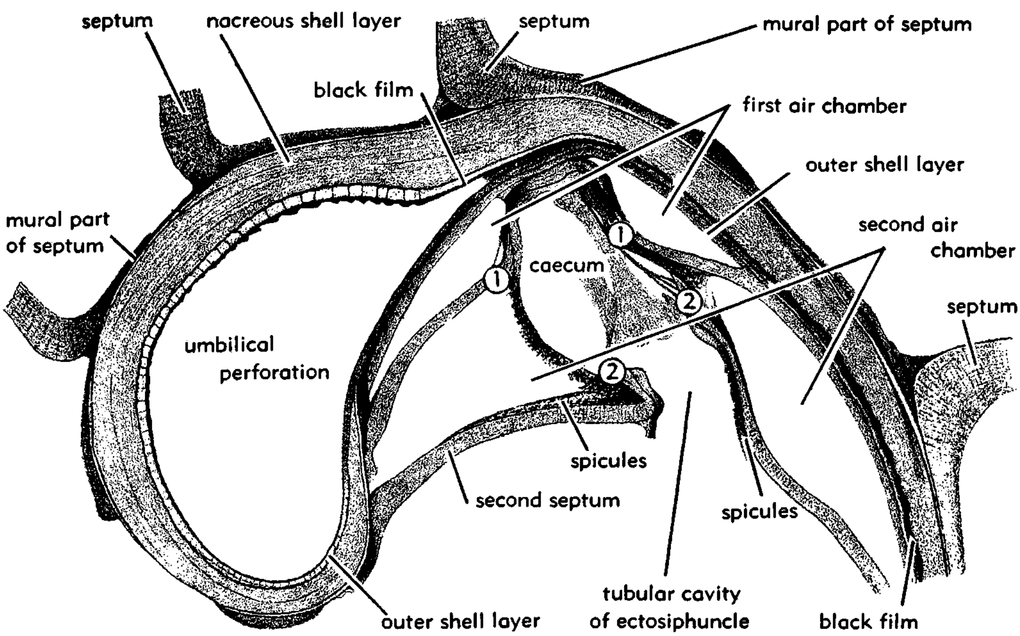

FIG. 66. Vertical section through the apex of the shell of *Nautilus*, ×15 (after 2).

ways at a constant angle of spread, while the animal backs up or moves forward or circles around, until the food is found. The cone of search is thrust out also when the animal is hungry or explores new territory or swims in search of food. As soon as it touches the food, the animal thrusts out the inner ring of digital tentacles to grasp the food and to draw it under the hood, while the cone-of-search tentacles let go (2b).

Because the suction exerted by the annular ridges of the tentacles is very strong, their hold is tenacious. Laboratory observations show that a tentacle attached to an object can be torn in two by a sudden jerk (30).

The sharp jaws are powerful nippers, capable of shearing through chicken bones. Much of the food, cut into pieces, is first lodged in the extensible esophagus, which serves as a crop; then the muscular stomach takes over the diminution of food. Chief food consists of fish, crabs, and lobsters. The animal is a carnivore and scavenger, probably feeding on or near the sea bottom.

LOCOMOTION

The tentacles serve to anchor the animal temporarily by adhesion to some suitable surface, but they are not used for crawling, and the animal does not crawl about on the bottom. Older accounts of crawling *Nautilus* have been disproved definitely and repeatedly.

Swimming is the sole means of moving. *Nautilus* is a rapid swimmer and moves by jet propulsion. Water is ejected forcibly through the hyponome and directed by it, and the tip of the hyponome is very active and flexible. The jet propels the animal backward, as well as in many other directions, depending on the attitude of the hyponome.

The water of the jet comes from the branchial chamber of the pallial cavity. It is forced out rhythmically by the crura and the posterior three-eighths of the hyponome. These strongly muscular and contractile parts lie inside the branchial cavity. The mantle itself does not take part in these contractions, being only slightly muscular and attached to the shell at the apertural margin. Herein the Tetrabranchiata differ from the Coleoidea, which are more powerful and faster swimmers, because their mantle is very muscular and produces the jet. In a swimming animal, the crura of the hyponome have been seen to rise and

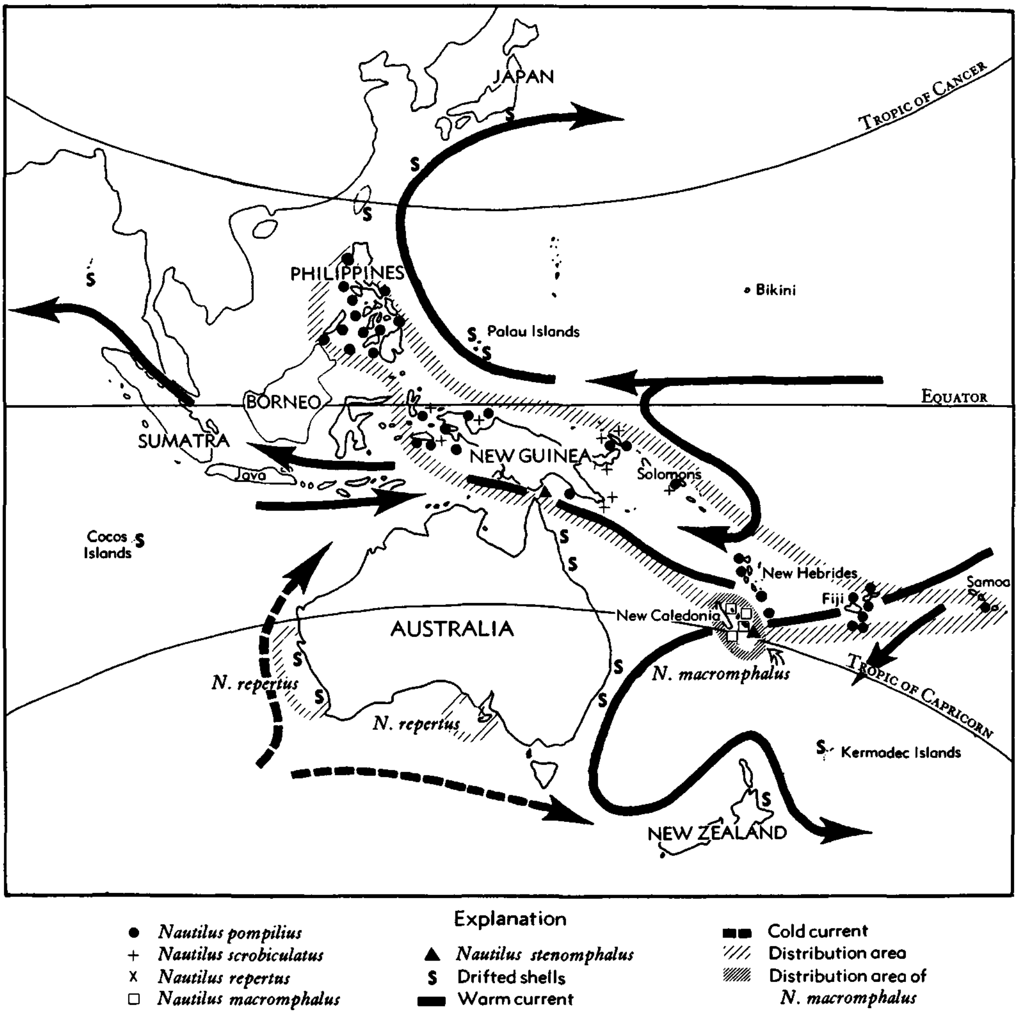

Fig. 67. Geographic distribution of living *Nautilus* (Stenzel, n).

fall with a regular pulsating motion, which also renews rhythmically the water in the branchial chamber, where the four gills lie, allowing the animal to breathe. The inhalant current enters at the inhalant passage, and the exhalant current escapes through the hyponome.

The whole animal, shell and all, is excellently streamlined in the form of a laterally compressed ellipsoid. No ribs or spines break the streamlining of the smooth, clean shell in *Nautilus pompilius.* Some other species of *Nautilus* have low, smooth, falcate ribs that are undulations of the shell wall, parallel to the growth lines on the flanks between the ocular and hyponomic sinuses. However, these ribs are so low that they offer no serious hindrance to swimming.

FUNCTION OF SHELL

Primary function of the shell is to protect the soft parts of the animal, particularly the visceral sac, in which are organs (such as heart and gonad) indispensable to survival of the individual and the species. Herein its function is the same as that of a gastropod shell.

In addition, it functions as a hydrostatic apparatus. The air in the air chambers counteracts the weight of the animal's shell and fleshy parts so that the whole animal's buoyancy is in balance. To preserve this balance, new air chambers have to be built as long as the animal grows and adds weight to the whole. Hence, the shell aids the animal in swimming, and muscular energies are expended for locomotion only, but need not be used to keep it from sinking.

The air in chambers is approximately at a pressure of 1 atmosphere, both in an animal which had been in an aquarium for some time and in an animal brought up from 100 fathoms (180 meters) 6 to 8 minutes before testing. Two samples of the gas scanned by mass-spectrograph showed that the proportion of argon to nitrogen was three times that of atmospheric air scanned simultaneously. The proportion of oxygen to carbon dioxide was variable (2b).

In addition to air, several of the chambers contain fluid while the animal is alive. The fluid contains organic materials and dissolved salts. The small quantity of fluid found in the older chambers is viscous. The various chambers contain different amounts of fluid.

The fluids in the various air chambers are distributed in such a way as to keep the animal well balanced and in stable equilibrium in the sea water. When tilted or rotated from its normal vertical position, the animal, including its shell, returns automatically to normal. Much greater volumes of fluid are in the last-formed chambers than in the older ones, and counterbalancing the former are the chambers overhanging the back of the hood, which also carry small amounts of fluid. However, the chambers that are in the uppermost dorsal position in life contain little or no fluid, as has been demonstrated by X-ray shadow graphs (2b).

Because the siphuncle fills the hole completely, air chambers are fully sealed from each other, and such gas exchange as may take place between them must go by way of diffusion through the siphuncle and its blood vessels.

The siphuncle is certainly a functional organ and is by no means vestigial, for it is well supplied with arterial blood and is little variable in size, shape, or position in different individuals. Vestigial organs that have lost their function commonly are highly variable and ill supplied with arterial blood. The exact function of the siphuncle, however, is not known and has been the subject of conjecture. WILLEY's crude experiments showed that it can be cut without seeming to affect the ability of the animal to swim, at least until loss of blood has made itself felt. Because the air chambers are cut off completely by the septa, the siphuncle is the only avenue by which air can be exchanged and gas pressure equalized between the chambers. Possibly the blood in the siphuncle gradually equalizes and adjusts the gas pressure in the air chambers to conform with the hydrostatic pressure of the

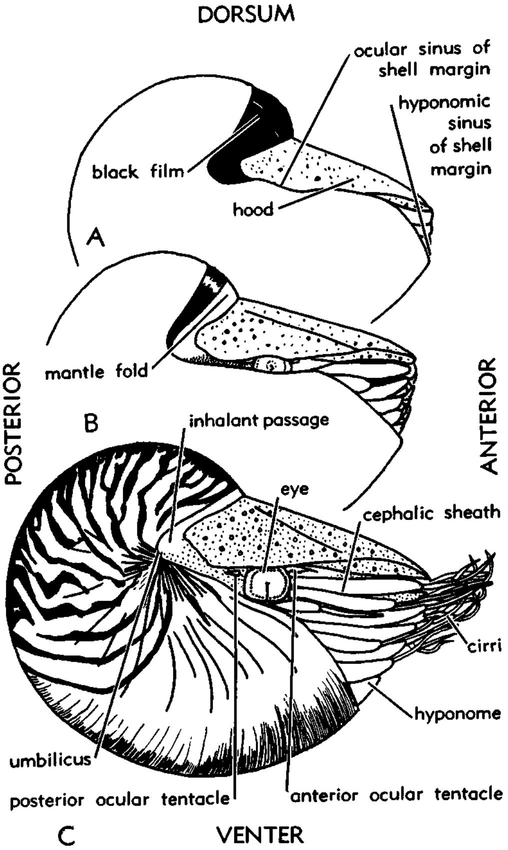

FIG. 68. Living *Nautilus pompilius* LINNÉ, seen from right side in position of rest. *(A)* Animal completely withdrawn into shell; *(B)* partially withdrawn; *(C)* normal attitude of rest; ×0.25 (modified from 8).

water surrounding the animal. When interior and exterior pressures are equal, no undue stress is exerted on the shell; hence, the shell cannot be crushed by the hydrostatic pressure of the surrounding water.

To aid in swimming—or rather, not to be a hindrance—the shell must be symmetrical and as compact as possible. Planispiral coiling and effective streamlining of the shell take care of this need, combining economy of space with added strength of construction.

Strength of construction permits the hydrostatic apparatus to be built with least weight and adds to the primary function as protective cover. Strength of construction is such that the shell can withstand hydrostatic pressure changes very well. Use of enclosed air as hydrostatic apparatus is not unique; a well-known example is the air bladder of fish. For reasons of stability, the air chambers have to be above the dead weight, which comprises the fleshy parts in the body chamber. This is the reason for the exogastric coiling. Only such coiling can bring the air chambers above the dead weight of the animal. *Nautilus* can no more turn over in water than a balloon can float with the gondola on top.

The shell is usually free of encrusting organisms as long as the *Nautilus* lives, because the animal is active and a rapid swimmer. However, a few live individuals of species lacking an umbilical callus bear groups of small tubicolous annelids or small stalked cirripeds attached at each umbilicus. These are too small to add much weight to the shell.

ACTIVITY AND REST

During the day the animal rests with the shell touching or nearly touching the sea bottom and the hood almost shut, so that the eyes are hardly showing. About a half hour before sunset the animal becomes active.

When the animal swims and breathes, the hood is raised above the shell aperture so as to expose eyes, tentacles, and the hyponome tip, and to allow free communication between the mantle cavity and surrounding water. In this position, the lower edge of the hood is horizontal, its concave posterior edge concealing the black film entirely, and the tip of the hyponome projects beyond the shell margin at the hyponomic sinus (Fig. 43). The eye, in the corner between hood and shell margin, can protrude slightly beyond the plane of the shell surface.

When disturbed, the animal at first withdraws only partially into its protective shell (Fig. 68). Then the hood exposes part of the black film, and the eye is still able to peer out because of its position at the ocular sinus of the shell margin. The tentacles are largely retracted and arranged in a close fit. If necessary, the animal can retract quickly and completely, shutting the shell aperture with its hood.

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CLASSIFICATION AND STRATIGRAPHIC DISTRIBUTION

By Curt Teichert[1] and R. C. Moore[2]

[[1]United States Geological Survey; [2]University of Kansas]

DEVELOPMENT OF CLASSIFICATION

The earliest attempts to classify the bewildering variety of shell forms represented by the nautiloid and related orders were handicapped by lack of understanding of their morphology and habitat. Also, recognition of many elementary taxonomic relationships was retarded until well into the 20th century, because of failure to investigate the internal structures of many shells.

Nautilus was known to Aristotle and probably named by him. It became available as a generic name in systematic zoology through being listed in the 10th edition (1758) of Linné's *"Systema Naturae."* It is of historical interest that of 17 species originally included in *Nautilus* by Linné, 14 were Foraminifera. The three remaining species, *N. pompilius, N. spirula,* and *N. orthocera,* were an odd assortment of not very closely related living and fossil cephalopods.

Until about the year 1800, few authors distinguished between chambered cephalopods and Foraminifera, and many of the latter were described under names such as *Nautilus, Orthocera,* and *Orthoceratites.*

Early in the 19th century the distinctiveness of Foraminifera and cephalopods was recognized and the latter were described and grouped according to their external shell form.

The generic name *Nautilus* was formally restricted to cephalopods in 1808 by de Montfort (7), who listed *Nautilus pompilius* as the only formally named (Linnean) species in a long list of synonyms of the "espèce servant de type au genre."

F. A. Quenstedt's (8) doctor's dissertation *"De notis Nautilearum primariis"* (1836) was a milestone in nautiloid classification. Like the pre-Linnean author Breynius (1732) before him, Quenstedt grouped all fossil "nautiloids" into three "genera": *Orthoceras,* consisting of straight shells, *Nautilus* of coiled shells, and *Lituites* comprising all curved, and loosely or imperfectly coiled shells. Within each "genus" he established informal groups of shells sharing certain external, or even internal, characteristics. Thus, within *Orthoceras* he distinguished assemblages termed "Vaginati" (=order Endocerida), "Cochleati" (=families Actinoceratidae+Armenoceratidae), "Gigantei" (=genus *Huronia*), "Regulares" (essentially=order Orthocerida), and others. The other two genera included similarly heterogeneous mixtures of what we now know are unrelated groups.

Monographic work by many paleontologists during the second and third quarter of the 19th century brought to light the existence, especially in early Paleozoic rocks, of very unorthodox types of chambered cephalopods that differed greatly from any of the three simple prototypes separated by Breynius and Quenstedt. Consequently, by the middle of the 19th century a sizable number of new genera had been described by Stokes, Hall, Sowerby, Bronn, M'Coy, and other noted paleontologists. Of these early genera some (e.g., *Actinoceras, Ormoceras, Huronia, Gonioceras, Endoceras, Phragmoceras*) are still in good standing, whereas others (e.g., *Gomphoceras, Cyrtoceras*) are no longer recognized as valid genera.

Far ahead of other workers on nautiloids, Saemann (10), in 1852, emphasized the importance of endosiphuncular structures and proposed to divide the "Nautilidae" into two major groups, namely, Actinosiphitae, with expanded siphuncle segments and an internal radial apparatus, and Coelosiphitae, with empty siphuncle. Saemann's Actinosiphitae included what are now the Actinoceratoidea, as well as some Oncocerida with actinosiphonate structure. Saemann's ideas had little influence on contemporary trends in nautiloid classification.

Barrande's description of the cephalopods in his classic *"Systême silurien du centre de la Bohême"* (1865-77 marks the culmination and end of the period of nautiloid classification based on external shell morphology. BARRANDE accommodated almost 1,000 species of European (mostly Bohemian) and North American cephalopods in the two "genera" *Orthoceras* and *Cyrtoceras.* Next in order of number of species were the "genera" *Gomphoceras,* with about 80 species, and *Phragmoceras* and *Trochoceras,* with about 50 species each. But BARRANDE was increasingly troubled by the necessity to erect genera for one or only a few species that differed so distinctively from all other chambered cephalopods that it was impossible to place them in any of the catch-all genera. Among these oddities were such genera as *Bathmoceras, Nothoceras, Adelphoceras, Hercoceras, Mesoceras, Ascoceras,* and *Glossoceras,* all of which are recognized today, though their true affinities and relationships are now generally better understood than in BARRANDE's time.

Study of nautiloids during the last quarter of the 19th century was dominated by HYATT, who advanced nautiloid classification by discarding shell shape as the basic criterion. HYATT (2) based his new (1883) classification of the order "Nautiloidea," which he adapted from Agassiz (1847), on the structure of the septal neck and proposed to distinguish two "genetic groups": (1) the Holochoanoida, with septal necks extending from one septum to the next, either forward (Prochoanites, including *Bathmoceras* and *Nothoceras*) or backward (Metachoanites=Endoceratidae), (2) the Ellipochoanoida, "with short funnels and the siphon completed by an intervening connective wall of distinct structure from the septal funnels." Within the Ellipochoanoida, HYATT distinguished the Bactritidae as "Macrochoanites," separating them from the "Microchoanites," which included the majority of all nautiloids.

A further refinement of this classification was offered by HYATT (3) in 1898, when he divided the "Nautiloidea" into the following suborders: (1) Holochoanites, with septal necks reaching backward from one septum to the preceding one; (2) Mixochoanites (equivalent to Ascocerida of present usage); (3) Schiztochoanites *(sic)* [*recte* Schistochoanites], with "funnels imperfect, or split on the outer side" (including *Bathmoceras,* but ill-defined by present standards); (4) Orthochoanites, with straight and short septal necks; (5) Cyrtochoanites, with septal necks short and bent outward, divided into "subgroups" termed Annulosiphonata (equivalent to present order Actinocerida) and Actinosiphonata (now known to be an artificial grouping of genera within the order Oncocerida).

With minor modifications the same classification was used by HYATT in Part II of the English edition of ZITTEL's *Text-book of Palaeontology,* vol. 1 (1900) (14).

Although HYATT's classification constituted a considerable advance towards disentanglement of the bewildering variety of nautiloid forms which became ever more apparent as new genera continued to be described, it was slow to gain ground outside of North America. In his revision of the last German edition of ZITTEL's *Grundzüge der Paläontologie,* BROILI (1924) retained the Nautiloidea as a suborder, dividing it into five families.

No significant contributions to nautiloid classification were made during the first third of the 20th century, although NAEF (1922) pointed out that such diverse morphological types of *Endoceras, Actinoceras, Orthoceras, Phragmoceras, Nautilus,* and the ammonoids could not possibly be regarded as very closely related to each other. In 1933, TEICHERT (13) emphasized the importance of endosiphuncular structures. He proposed subdivision of the Cephalopoda into the following orders: (1) Nautiloidea, with empty, narrow, cylindrical siphuncles; (2) Endoceroidea, with endocones; (3) Actinoceroidea, with an endosiphuncular vascular system; (4) Cyrtoceroidea, with actinosiphonate siphuncular structures; and (5) Gomphoceroidea, with relatively large empty siphuncles, not regarded as a natural unit at the time. These five orders were considered to be equivalent in taxonomic rank to the Ammonoidea and Belemnoidea. Although this proposed scheme suffered from many defects, it was adopted by SCHINDEWOLF (11), who, however, preferred to reduce the rank of all above-mentioned groups to suborders.

Essentially the same classification was presented by KUHN (5), who separated the straight, orthochoanitic nautiloids as a new "suborder" termed Orthoceracea. In 1949, the same author adopted the taxonomic procedure suggested by TEICHERT, elevating all groups to the rank of orders within the superorder Nautiloidea. At the same time KUHN (6) established a new order termed Ascoceracea for a group of specialized forms previously included in the "Orthoceracea."

Further refinement was offered in 1950 by FLOWER & KUMMEL (1) by combining the criteria of shell form, structure of septal necks and connecting rings, and endosiphuncular structures into an integrated system of classification of the so-called class Nautiloidea. This afforded basis for distinction of 14 orders, named Ellesmeroceratida, Endoceratida, Actinoceratida, Michelinoceratida, Ascoceratida, Bassleroceratida, Oncoceratida, Discosoroidea, Tarphyceratida, Barrandeoceratida, Rutoceratida, Centroceratida, Solenochilida, and Nautilida.

In its major outlines, this classification has stood the test of subsequent investigations, although the number of orders has now been slightly reduced. The very small order, Bassleroceratida, has been divided between the Oncoceratida (Oncocerida) and the Tarphyceratida (Tarphycerida); and the Rutoceratida, Centroceratida, and Solenochilida (=Aipocerataceae of this volume) have been merged as superfamilies within the order Nautilida.

Attempts have been made to arrange these orders (or suborders, according to some authors) into larger taxonomic units, but no entirely natural grouping has as yet been proposed. TEICHERT (13) proposed the Stenosiphonata and the Eurysiphonata, both of unspecified rank, the former to include all conch-bearing cephalopods with narrow siphuncles (including the Ammonoidea), the latter to receive all other nautiloid orders (most of which were as yet ill-defined at the time). This scheme won temporary support from FLOWER and is still being used by DAVITASHVILI. However, since it now appears that the stenosiphonate Nautilida developed from eurysiphonate oncocerids, whereas other stenosiphonate stocks developed directly from the ellesmerocerids, grouping of the nautiloid orders according to size of siphuncle would be highly artificial.

KOBAYASHI (4) suggested two major divisions of nautiloids according to the primary position of the siphuncle: Ventrosiphonata for forms with a primarily ventral siphuncle (ellesmerocerids, endocerids), and Centrosiphonata for forms with a primarily central or subcentral siphuncle. As examples of the latter he cited the orthocerids and the actinocerids. Some endocerids have a subcentral siphuncle, however, and many actinocerids show the siphuncle in a ventral position. We may agree with SCHINDEWOLF (1943) that positions of the siphuncle in nautiloids are too variable to serve as reliable guides to classification.

A comprehensive review of the history of classification of the Cephalopoda, with special emphasis on treatment of the nautiloid orders since the time of HYATT, has been given by SHIMANSKIY & ZHURAVLEVA (12).

CLASSIFICATION ADOPTED IN TREATISE

We accept, with minor changes, grouping of nautiloid orders by SHIMANSKIY & ZHURAVLEVA which leads to a threefold arrangement: (1) subclass Endoceratoidea, comprising the orders Endocerida and Intejocerida; (2) subclass Actinoceratoidea, containing the single order Actinocerida; and (3) subclass Nautiloidea, composed of the remaining orders, Ellesmerocerida, Orthocerida, Ascocerida, Oncocerida, Discosorida, Tarphycerida, Barrandeocerida, and Nautilida. These divisions may be characterized briefly as follows, with accompanying graphic representation of their stratigraphic distribution and approximate abundance of contained genera in successive geologic series and systems (Fig. 69).

An additional subclass, Bactritoidea, is recognized and this assemblage is treated in a chapter at the end of the present volume.

ENDOCERATOIDEA

This group consists mostly of medium-sized but also some very large forms, mostly with orthoconic, more rarely with cyrtoconic conchs. The siphuncles are large, generally marginal; septal necks short in early forms, long in later (Middle Ordovician) representatives. The endoceratoids invariably have deposits within the siphuncle, generally in the form of conical sheaths. They are most abundant in Lower and

Middle Ordovician deposits but range well into the Silurian. The subclass is judged to have been derived from the order Ellesmerocerida of the subclass Nautiloidea. It is divided into two orders named Endocerida and Intejocerida.

ENDOCERIDA

The endocerids are distinguished primarily by the nature of their endosiphuncular deposits, which consist of calcareous, conical sheaths. They are found chiefly in Ordovician formations, one genus being recorded doubtfully from the Middle Silurian.

INTEJOCERIDA

The intejocerids have generally straight conchs with short chambers, straight sutures, and unusually large siphuncles, which are filled by radially disposed, rather tightly packed, longitudinal lamellae. Four described genera occur in Lower and Middle Ordovician rocks of Siberia.

ACTINOCERATOIDEA

The assemblage of actinoceratoids have generally orthoconic conchs with short, bent septal necks and generally broad siphuncle segments which contain many peculiar and specialized structures, such as radial canals and perispatia. Cameral deposits are a characteristic feature of this group that ranges from the Middle Ordovician into the Upper Carboniferous. The subclass contains a single order, named Actinocerida. Genera are most numerous in the Middle and Upper Ordovician.

NAUTILOIDEA

All cephalopod groups which formerly were assigned to the order (or suborder) Nautiloidea, excepting the endoceratoids and actinoceratoids, now are included in the subclass Nautiloidea. Even after removal of the two mentioned groups as independent subclasses, the diversity of the Nautiloidea in a restricted sense is so great that no simple diagnosis is possible. Every variety of shell form, from straight to tightly coiled, is represented. The siphuncle is variable in position within the conch, slender to moderately large in diameter (none very large), with septal necks orthochoanitic or cyrtochoanitic (never holo- or macrochoanitic), and connecting rings which are thick in some earlier forms but invariably thin in later and more advanced genera. Endosiphuncular and cameral deposits may be present or absent. Representatives of the subclass, which are divided among the following eight orders, range from Upper Cambrian to Recent.

ELLESMEROCERIDA

This group, because of its antiquity and various primitive morphological characters, probably comprises the rootstock from which the endoceratoids, actinoceratoids, and all nautiloid groups were derived, directly or indirectly (Fig. 69, 70). Most genera have straight to weakly cyrtoconic shells with marginal, empty siphuncles of small to medium size. Earliest representatives of the order are very small forms found in Upper Cambrian; these were followed by genera with larger conchs, yet still moderate in size (perhaps 1 foot in length) in the Lower Ordovician. Three Upper Cambrian genera are known, whereas 60 are recorded from the Lower Ordovician; five genera occur in the Middle Ordovician and only two in the Upper Ordovician. A single genus is doubtfully reported from Silurian rocks.

ORTHOCERIDA

The orthocerids are characterized by orthoconic or weakly cyrtoconic, generally slender, shells, formerly collectively referred to the genus *Orthoceras.* They have narrow siphuncles, with cylindrical, or only weakly inflated siphuncle segments, and both endosiphuncular and cameral deposits. They are divided into the essentially orthochoanitic Orthocerataceae and the cyrtochoanitic Pseudorthocerataceae. In the former, endosiphuncular deposits are usually restricted to ring-shaped structures constricting the septal foramina; the latter have more strongly developed and elaborately fashioned parietal deposits. Cameral deposits are present in both superfamilies. In the Pseudorthocerataceae they are commonly characterized by lamellar structure and by heavy emphasis on mural deposits. The Orthocerida range from the Lower Ordovician into the Triassic. Genera are most numerous in Middle and Upper Ordovician and Silurian formations (Fig. 69).

ASCOCERIDA

Genera of the ascocerid group possess conchs consisting of two rather distinct growth forms. An early stage is slender cyrtoconic, with orthochoanitic septal necks and narrow siphuncle. This is suddenly followed by a bulbous, breviconic stage with large siphuncle and cyrtochoanitic septal necks. The early, slender part of the conch is either thrown off in the adult stage, or it breaks off after death of the animal. The ascocerids are relatively rare fossils, classified in a small number of genera (total, 13). They range from the Middle Ordovician through the Silurian.

ONCOCERIDA

This assemblage includes forms with conchs consisting predominantly of brevicones, either straight or curved, but also more slender cyrtocones and even orthocones (Jovellaniidae) and coiled forms (Nothoceratidae). The conchs are characterized by thin septa, recumbent septal necks, thin connecting rings, and usually broadly expanded siphuncle segments. Endosiphuncular structures occur either in the form of bullettes, or as actinosiphonate deposits, or both. Cameral deposits, if present at all, are thin. The order ranges from Middle Ordovician through Lower Carboniferous (Mississippian). Largest numbers of genera are found in the Middle and Upper Ordovician, Silurian, and Middle Devonian (Fig. 69).

DISCOSORIDA

The discosorids have mostly breviconic and stoutly cyrtoconic conchs, generally with thick, complex connecting rings and differentiated endosiphuncular deposits that consist of parietal deposits, with or without accompanying endocones. Cameral deposits are relatively rare. Advanced forms exhibit a tendency toward contracted and elaborately modified apertures, such as occur in the Phragmoceratidae. The order ranges from the Middle Ordovician well into the Devonian, with chief development in the Ordovician and Silurian (Fig. 69).

TARPHYCERIDA

This group of early Paleozoic nautiloids is characterized by genera with mostly coiled conchs in which the siphuncles bear thick connecting rings. Widely umbilicate shells with slowly expanding whorl diameters prevail, but they include some gyrocones and torticones, as well as conchs which are straight at maturity (Lituitidae). The range of the Tarphycerida is Lower Ordovician to Upper Silurian.

BARRANDEOCERIDA

In general morphological character, the barrandeocerids resemble the tarphycerids but are distinguished by their thin connecting rings. The stratigraphic range of the group is relatively large (Middle or possibly Lower Ordovician to Middle Devonian), but the number of known genera in any series or system in which they occur is small (Fig. 69).

NAUTILIDA

Cephalopods of the order Nautilida include a rich variety of closely coiled, widely umbilicate to convolute and involute conchs, ranging from Lower Devonian to Recent (Fig. 69). In nautilids, with rare exception, the siphuncle is narrow and cylindrical; it has thin connecting rings and is subcentral in position. In a few specialized groups, however, the siphuncle position is at the margin, either ventral or dorsal. The nautilids include forms with the most elaborate suture patterns known among the nautiloid orders. The sutures of some specialized forms, such as the Triassic *Siberionautilus* or the Paleogene *Aturia,* are considerably more complex than those of primitive ammonoids.

Most Nautilida were of moderate size, the great majority being smaller than the contemporary *Nautilus pompilius.* The order, however, includes the largest known coiled nautiloids, represented by *Titanoceras* (more than 3 feet in diameter) from the Upper Pennsylvanian (Chaffin Ls., Cisco Gr.) of Texas.

DISTRIBUTION OF SUPRAGENERIC NAUTILOID TAXA

The following tabulations record numbers of genera in suprageneric divisions of the Endoceratoidea, Actinoceratoidea, and Nautiloidea recognized in the *Treatise,* accompanied by statements of stratigraphic ranges. Family-group taxa or other assemblages which contain subgenera are accompanied by two figures, the number of included genera being indicated by the first and subgenera additional to nominotypical subgenera by the second. For example, the figures 16;1 indicate 16 genera and 1 subgenus in addition to the nominotypical one, which is not counted.

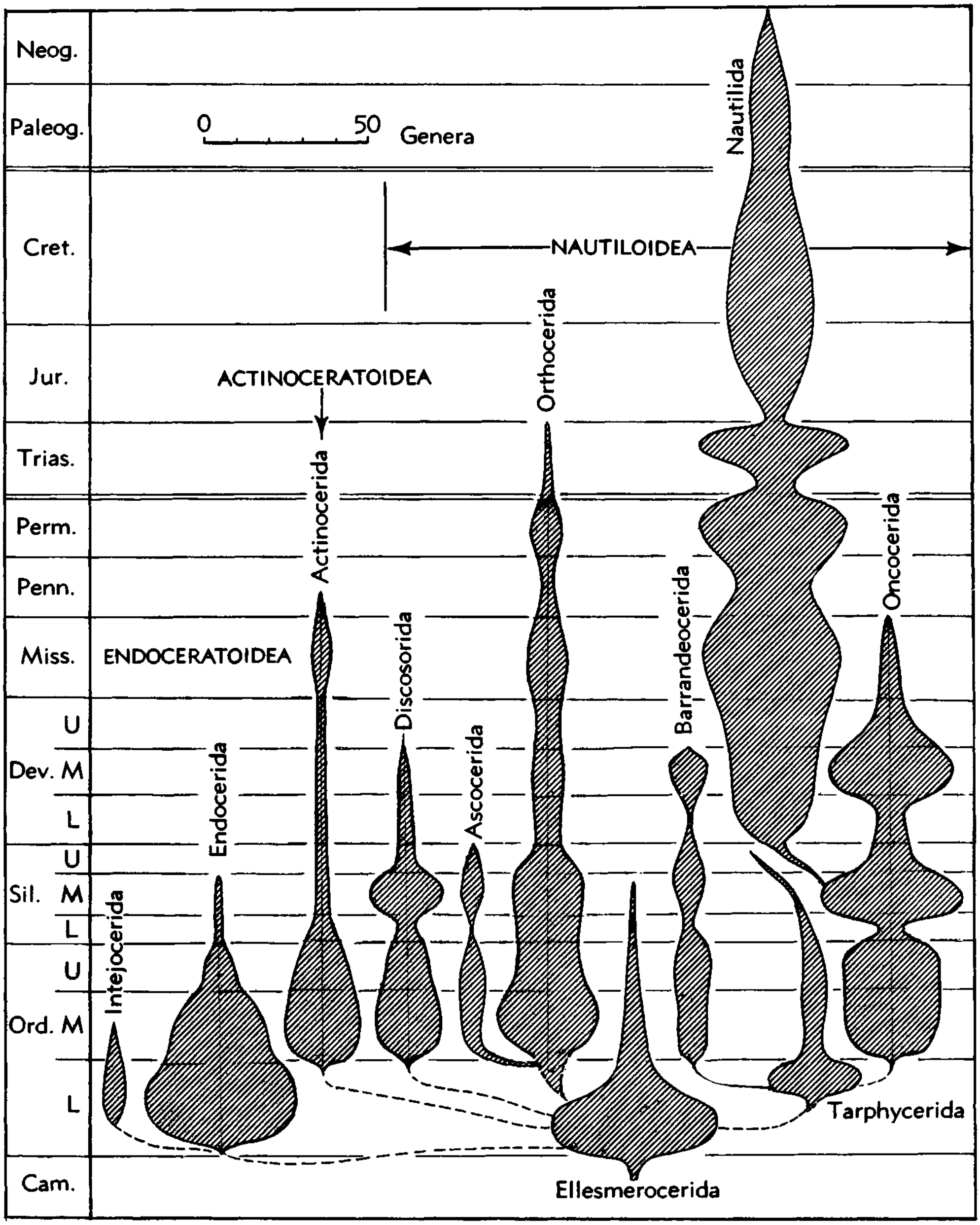

FIG. 69. Stratigraphic distribution, relative numbers of genera, and inferred origins of nautiloid orders (Teichert & Moore, n).

Main Divisions of Nautiloid Subclasses and Orders

- Endoceratoidea *(subclass)* (63). *Ord., ?M.Sil.*
  - Endocerida *(order)* (59). *Ord., ?M.Sil.*
    - Thylacoceratidae (2). *L.Ord.*
    - Proterocameroceratidae (22). *L.Ord.-M.Ord.*
    - Piloceratidae (5). *L.Ord.*
    - Endoceratidae (17). *L.Ord.-U.Ord., ?M.Sil.*
    - Chihlioceratidae (1). *L.Ord.*
    - Manchuroceratidae (2). *L.Ord.*
    - Cyrtendoceratidae (4). *L.Ord.-M.Ord., ?U.Ord.*
    - Emmonsoceratidae (2). *Low.M.Ord.*
    - Narthecoceratidae (1). *M.Ord., ?U.Ord.*
    - Allotrioceratidae (2). *M.Ord.*
    - ?Humeoceratidae (1). *M.Sil.*
  - Intejocerida *(order)* (4). *L.Ord.-M.Ord.*
    - Intejoceratidae (2). *L.Ord., ?M.Ord.*
    - Padunoceratidae (1). *M.Ord.*
    - ?Bajkaloceratidae (1). *L.Ord.*
- [Excludes 17 endoceratoids of unknown affinities and unrecognizable genera]
- Actinoceratoidea *(subclass)* (35). *M.Ord.-U.Carb.*
  - Actinocerida *(order)* (35). *M.Ord.-U.Carb.*
    - Polydesmiidae (2). *L.Ord.-M.Ord.*
    - Actinoceratidae (8). *M.Ord.-L.Sil.*
    - Armenoceratidae (8). *M.Ord.-Sil.*
    - Gonioceratidae (2). *M.Ord.-U.Ord.*
    - Huroniidae (3). *M.Ord.-Sil.*
    - Ormoceratidae (8). *M.Ord.-Dev., ?M.Dev., L.Carb.*
    - Carbactinoceratidae (3). *L.Carb.-U.Carb.*
    - Family Uncertain (1)
- [Excludes 2 unrecognizable genera]
- Nautiloidea *(subclass)* (646;6). *U.Cam.-Rec.*
  - Ellesmerocerida *(order)* (64). *U.Cam.-U.Ord., ?M.Sil.*
    - Ellesmeroceratidae (30). *L.Ord., ?M.Ord.*
    - Plectronoceratidae (6). *U.Cam.-L.Ord.*
    - Bassleroceratidae (8). *L.Ord.*
    - Protocycloceratidae (11). *L.Ord.*
    - Baltoceratidae (5). *L.Ord.-M.Ord.*
    - Bathmoceratidae (2). *L.Ord.-M.Ord., ?M.Sil.*
    - Cyrtocerinidae (1). *M.Ord.-U.Ord.*
    - Shideleroceratidae (1). *U.Ord.*
  - Orthocerida *(order)* (125). *L.Ord.-U.Trias.*
    - Orthocerataceae *(superfamily)* (57). *L.Ord.-U.Trias.*
      - Orthoceratidae (22). *L.Ord.-U.Trias.*
        - Orthoceratinae (3). *M.Ord.*
        - Michelinoceratinae (10). *L.Ord.-U.Trias.*
        - Kionoceratinae (5). *M.Ord.-L.Perm.*
        - Leurocycloceratinae (4). *M.Ord.-Sil.*
      - Sphooceratidae (1). *M.Sil.*
      - Brachycycloceratidae (1). *U.Miss.-U.Penn., ?L.Perm.*
      - Sactorthoceratidae (3). *M.Ord.*
      - Lamellorthoceratidae (3). *L.Dev.-M.Dev., ?L.Carb.*
      - Troedssonellidae (5). *L.Ord.-M.Ord.*
      - Geisonoceratidae (11). *M.Ord.-M.Dev.*
      - Dawsonoceratidae (2). *?U.Ord., L.Sil.-U.Sil., ?M.Dev.*
      - Clinoceratidae (3). *M.Ord.-U.Ord.*
      - Paraphragmitidae (5). *M.Sil.*
      - Offleyoceratidae (1). *M.Sil., ?L.Dev., ?M.Dev.*
    - Pseudorthocerataceae *(superfamily)* (54). *M.Ord.-Perm.*
      - Pseudorthoceratidae (43). *L.Sil.-L.Perm.*
        - Pseudorthoceratinae (7). *M.Dev.-L.Perm.*
        - Spyroceratinae (23). *?L.Sil., M.Sil.-Perm.*
        - Cayutoceratinae (7). *L.Sil.-Dev.*
        - Pseudactinoceratinae (6). *U.Dev.-L.Carb.*
        - Mysterioceratidae (1). *M.Ord., ?U.Ord.*
      - Stereoplasmoceratidae (1). *M.Ord.*
      - Proteoceratidae (9). *M.Ord.-M.Sil.*
    - Superfamily and family uncertain (14).
  - Ascocerida *(order)* (13). *M.Ord.-U.Sil.*
    - Ascoceratidae (9). *M.Ord.-U.Sil.*
      - Ascoceratinae (7). *M.Ord.-U.Sil.*
      - Probillingsitinae (2). *M.Ord.-U.Ord.*
    - Choanoceratidae (1). *M.Sil.*
    - Hebetoceratidae (3). *M.Ord.-?U.Ord.*
  - Oncocerida *(order)* (143). *M.Ord.-L.Carb.*
    - Graciloceratidae (4). *M.Ord.-U.Ord.*
    - Oncoceratidae (24). *M.Ord.-U.Sil.*
    - Tripteroceratidae (5). *M.Ord.-U.Ord.*
    - Valcouroceratidae (8). *M.Ord.-U.Ord.*
    - Diestoceratidae (5). *M.Ord.-U.Ord.*
    - Hemiphragmoceratidae (5). *M.Sil.-U.Sil., ?M.Dev.*
    - Trimeroceratidae (6). *M.Sil.*
    - Brevicoceratidae (17). *M.Sil.-U.Dev.*
    - Jovellaniidae (5). *?U.Ord., M.Sil.-L.Dev.*
    - Tripleuroceratidae (2). *?L.Dev., M.Dev.-L.Carb.*
    - Nothoceratidae (10). *Sil.-U.Dev.*
    - Acleistoceratidae (22). *M.Sil.-M.Dev.*
    - Archiacoceratidae (3). *Dev.*
    - Karoceratidae (3). *L.Sil.-M.Sil., ?L.Dev.*
    - Poterioceratidae (7). *L.Dev.-L.Carb.*
    - Polyelasmoceratidae (13). *M.Sil.-U.Dev.*
    - Family Uncertain (4).
- [Excludes 8 genera dubia]
  - Discosorida *(order)* (46). *M.Ord.-M.Dev., ?U.Dev.*
    - Ruedemannoceratidae (3). *M.Ord.*
    - Cyrtogomphoceratidae (7). *M.Ord.-L.Sil.*
    - Westonoceratidae (13). *M.Ord.-L.Sil.*
    - Lowoceratidae (2). *M.Sil.*
    - Discosoridae (5). *M.Sil.-M.Dev., ?U.Dev.*
    - Phragmoceratidae (7). *M.Sil.-L.Dev.*
    - Mandaloceratidae (7). *M.Sil., ?U.Sil.*
    - ?Mesoceratidae (1). *M.Sil.*
    - ?Greenlandoceratidae (1). *M.Ord., ?U.Ord.-?Sil.*
  - Tarphycerida *(order)* (38). *L.Ord.-U.Sil.*
    - Tarphyceratidae (9). *L.Ord.*
    - Estonioceratidae (9). *L.Ord.*
    - Trocholitidae (11). *L.Ord.-M.Sil.*
    - Lituitidae (8). *L.Ord.-U.Ord.*
    - Ophidioceratidae (1). *U.Sil.*
  - Barrandeocerida *(order)* (37). *M.Ord.-M.Dev.*
    - Barrandeoceratidae (10). *M.Ord.-M.Dev.*

Plectoceratidae (1). *M.Ord.-U.Ord.*
Uranoceratidae (4). *?U.Ord., M.Sil.*
Lechritrochoceratidae (6). *M.Sil.-U.Sil.*
Nephriticeratidae (9). *L.Dev.-M.Dev.*
Apsidoceratidae (7). *M.Ord.-U.Ord.*

Nautilida *(order)* (165). *L.Dev.-Rec.*
Tainocerataceae *(superfamily)* (64). *L.Dev.-Trias.*
Tainoceratidae (23). *L.Carb.(Miss.)-Trias.*
Rutoceratidae (23). *Dev.-L.Carb.*

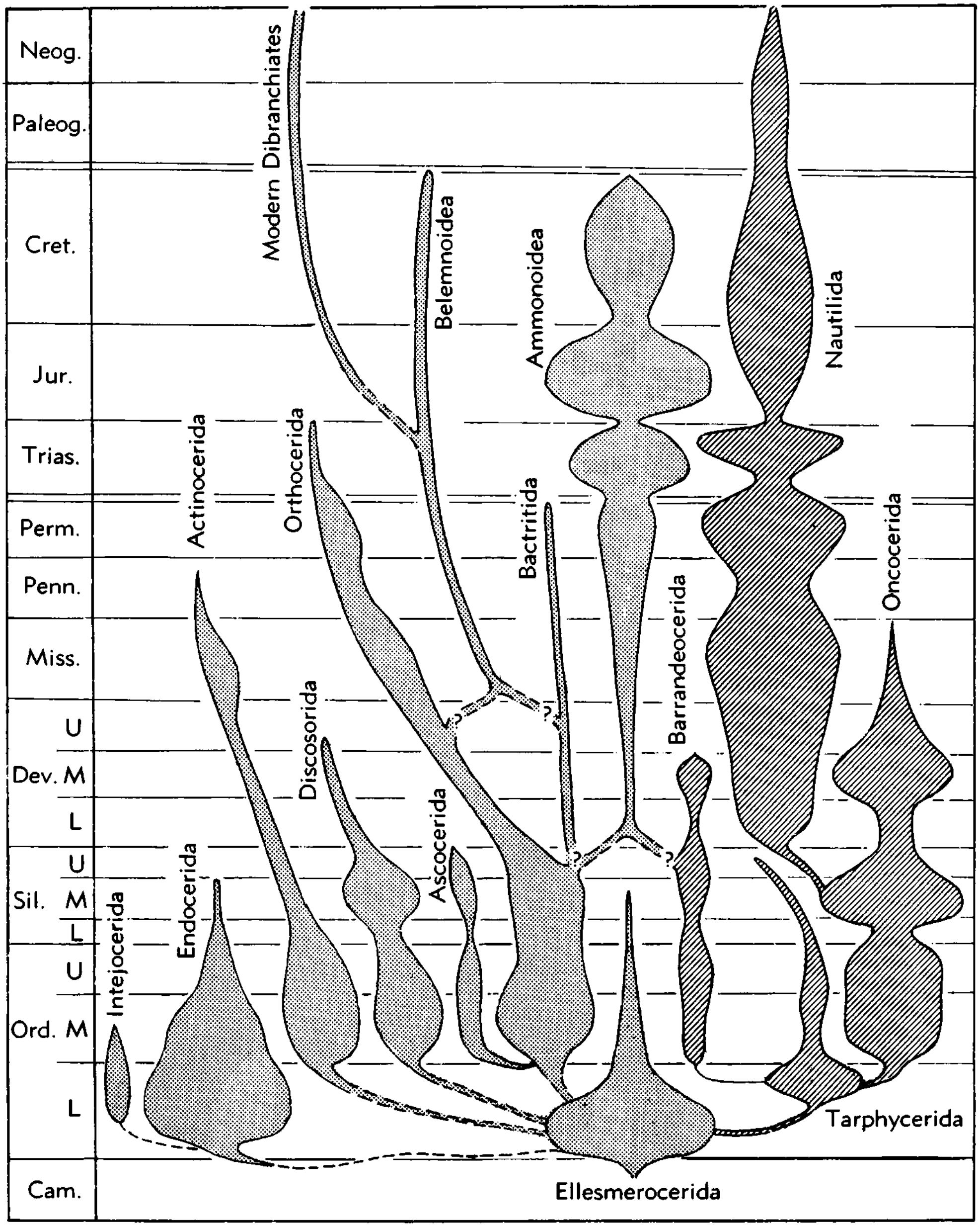

FIG. 70. Inferred phylogeny of nautiloid orders and suggested relationships to other cephalopod groups (Tarphycerida and derivative orders oblique-ruled). Approximate abundance in various periods is indicated by width of pattern, except that divisions other than the nautiloid orders are not drawn at the same scale (Sweet & Moore, n).

- Tetragonoceratidae (3). *M.Dev.*
- Rhiphaeoceratidae (4). *L.Perm.*
- Koninckioceratidae (11). *L.Carb.(Miss.)-Perm.*
- Trigonocerataceae *(superfamily)* (42). *Dev.-Trias.*
  - Trigonoceratidae (17). *L.Carb.(Miss.)-L.Perm.*
  - Centroceratidae (6). *M.Dev.-L.Perm.*
  - Grypoceratidae (13). *L.Carb.-Trias.*
  - Permoceratidae (1). *L.Perm.*
  - Syringonautilidae (5). *M.Trias.-U.Trias.*
- Aipocerataceae *(superfamily)* (9). *L.Carb.(Miss.)-L.Perm.*
  - Aipoceratidae (3). *L.Carb.(Miss.)-U.Carb.*
  - Solenochilidae (2). *L.Carb.(U.Miss.)-L.Perm.*
  - Scyphoceratidae (4). *L.Perm.*
- Clydonautilaceae *(superfamily)* (21). *?U.Dev., L.Carb.-Trias.*
  - Clydonautilidae (5). *M.Trias.-U.Trias.*
  - Liroceratidae (12). *?U.Dev., L.Carb.(Miss.)-Trias.*
  - Ephippioceratidae (2). *L.Carb.(Miss.)-L.Perm.*
  - Gonionautilidae (1). *U.Trias.*
  - Siberionautilidae (1). *U.Trias.*
- Nautilaceae *(superfamily)* (29). *U.Trias.-Rec.*
  - Nautilidae (7). *U.Trias.-Rec.*
  - Pseudonautilidae (3). *Jur.-L.Cret.*
  - Paracenoceratidae (4). *M.Jur.-L.Cret.*
  - Cymatoceratidae (10). *M.Jur.-Oligo.*
  - Hercoglossidae (4). *U.Jur.-Oligo.*
  - Aturiidae (1). *Paleoc.-Mio.*
- Order Uncertain
  - Neptunoceratidae (2). *U.Carb.*
- Order and Family Uncertain (13;6).
  - Conchs (2).
  - Rhyncholites (11;6).

- Bactritoidea *(subclass)* (16;1). *Ord.-Perm.*
  - Bactritida *(order)* (16;1). *Ord.-Perm.*
    - Bactritidae (8;1). *Ord.-Perm.*
    - Parabactritidae (5). *?Carb., Perm.*
    - Doubtful genera (3). *M.Dev.*

Total genera, 760, and 7 subgenera in addition to nominotypical subgenera.

COMPARISON OF TREATISE AND OSNOVY CLASSIFICATION

The systematic treatment of the "nautiloids" in the Russian treatise *Osnovy* (Ruzhentsev *et al.*, 1962) (9) follows essentially that proposed by Shimanskiy and Zhuravleva (1961) (12). The taxonomic units recognized in the *Osnovy* down to subfamily level are the following (numbers of genera indicated in parentheses):

Classification of Nautiloid Cephalopods in Osnovy Paleontologii *(1962)*

- Endoceratoidea *(superorder)* (76). *L.Ord.-U.Ord.*
  - Endoceratida *(order)* (73). *L.Ord.-U.Ord.*
    - Proterocameroceratina *(suborder)* (37). *Ord.*
      - Proterocameroceratidae (25). *L.Ord.-M.Ord.*
      - Manchuroceratidae (6). *L.Ord.-M.Ord.*
      - Chihlioceratidae (1). *L.Ord.*
      - Allotrioceratidae (2). *M.Ord.*
      - Cyrtovaginoceratidae (2). *M.Ord.*
      - Narthecoceratidae (1). *M.Ord.-U.Ord.*
    - Endoceratina *(suborder)* (36). *Ord.*
      - Piloceratidae (4). *L.Ord.*
      - Cyrtendoceratidae (2). *L.Ord.-M.Ord.*
      - Emmonsoceratidae (2). *L.Ord.-M.Ord.*
      - Endoceratidae (28). *Ord.*
  - Intejoceratida *(order)* (3). *L.Ord.-M.Ord.*
    - Intejoceratidae (2). *L.Ord.*
    - Padunoceratidae (1). *L.Ord.-M.Ord.*
- Actinoceratoidea *(superorder)* (52). *L.Ord.-Carb.*
  - Actinoceratida *(order)* (57). *Ord.-Carb.*
    - Actinocerataceae *(superfamily)* (51). *Ord.-Carb.*
      - Polydesmiidae (2). *L.Ord.*
      - Deiroceratidae (3). *Ord., ?Dev.*
      - Ormoceratidae (2). *Ord.-Dev.*
      - Actinoceratidae (11). *Ord.-L.Carb.*
      - Armenoceratidae (9). *Ord.-Sil.*
      - Gonioceratidae (4). *M.Ord.-U.Ord.*
      - Huroniidae (3). *Ord.-Sil.*
      - Pseudactinoceratidae (5). *Ord.-Carb.*
      - Sactoceratidae (9). *Ord.-Dev.*
      - Loxoceratidae (3). *L.Carb.*
    - Ellinocerataceae *(superfam.)* (1). *M.Ord.*
      - Ellinoceratidae (1). *M.Ord.*
- Nautiloidea *(superorder)* (672).
  - Ellesmeroceratida *(order)* (84). *U.Cam.-U.Ord.*
    - Bathmocerataceae *(superfam.)* (67). *U.Cam.-M.Ord.*
      - Plectronoceratidae (5). *U.Cam.-L.Ord.*
      - Ellesmeroceratidae (28). *Cam.-Ord.*
      - Cyclostomiceratidae (3). *L.Ord.*
      - Protocycloceratidae (10). *L.Ord.*
      - Baltoceratidae (9). *Ord.*
      - Buttsoceratidae (1). *L.Ord.*
      - Eothinoceratidae (3). *Ord.*
      - Bathmoceratidae (1). *L.Ord.*
      - Apocrinoceratidae (3). *L.Ord.*
      - Thylacoceratidae (4). *L.Ord.-M.Ord.*
    - Basslerocerataceae *(superfam.)* (17). *L.Ord.-U.Ord.*
      - Bassleroceratidae (11). *L.Ord.-M.Ord.*
      - Graciloceratidae (5). *Ord.*
      - Shideleroceratidae (1). *U.Ord.*
  - Orthoceratida *(order)* (103). *Ord.-Trias.*
    - Orthoceratidae (31). *Ord.-Trias.*
      - Orthoceratinae (13). *Ord.-Trias.*
      - Kionoceratinae (6). *Ord.-Perm.*
      - Cycloceratinae (12). *Ord.-Perm.*
    - Sactorthoceratidae (3). *Ord.*
    - Geisonoceratidae (6). *Ord.-Dev.*
    - Pseudorthoceratidae (48). *Ord.-Perm.*
    - Lamellorthoceratidae (4). *Dev.*
    - Eskimoceratidae (2). *Ord.*
    - Clinoceratidae (3). *Ord.*
    - Paraphragmitidae (4). *Sil.*

Greenlandoceratidae (2). *M.Ord.* or *U.Ord.*
Ascoceratida *(order)* (15). *Ord.-Sil.*
Hebetoceratidae (6). *Ord.*
Choanoceratidae (1). *Sil.*
Ascoceratidae (8). *Ord.-Sil.*
Oncoceratida *(order)* (153). *Ord.-L.Carb., ?Perm.*
Cyrtocerataceae *(superfam.)* (141). *Ord.-L.Carb., ?Perm.*
Maelonoceratidae (45). *Ord.-Dev.*
Ooceratidae (2). *Ord.-Sil.*
Allumettoceratidae (6). *Ord.*
Gomphoceratidae (1). *Sil.-Dev.*
Hemiphragmoceratidae (5). *Sil.-Dev.*
Bolloceratidae (3). *Dev.*
Trimeroceratidae (9). *?Ord., Sil.*
Oocerinidae (13). *Ord.-Dev.*
Diestoceratidae (3). *Ord.*
Brevicoceratidae (17). *Dev.*
Archiacoceratidae (6). *?Sil., Dev.*
Polyelasmoceratidae (11). *Sil.-Dev.*
Cyrtoceratidae (5). *Sil.-Dev.*
Karoceratidae (1). *U.Sil.* or *L.Dev.*
Jovellaniidae (5). *Sil.-Dev.*
Tripleuroceratidae (2). *Dev.-L.Carb.*
Antonoceratidae (2). *L.Carb., ?Perm.*
Poterioceratidae (5). *L.Carb.*
Ptenocerataceae *(superfam.)* (12). *Sil.-Dev.*
Nothoceratidae (2). *?Sil., Dev.*
Naedyceratidae (7). *Sil.-Dev.*
Naedyceratinae (5). *Sil.-Dev.*
Mitroceratinae (2). *Dev.*
Ptenoceratidae (3). *Dev.*
Discosorida *(order)* (45). *Ord.-Dev.*
Ruedemannoceratidae (3). *Ord.*
Cyrtogomphoceratidae (12). *Ord.-Sil.*
Westonoceratidae (8). *Ord.-Dev.*
Lowoceratidae (2). *Sil.*
Discosoridae (5). *Sil.-Dev.*
Phragmoceratidae (7). *Sil.*
Mandaloceratidae (7). *Sil.*
Mesoceratidae (1). *U.Sil.*
Tarphyceratida *(order)* (88). *Ord.-Dev.*
Tarphyceratina *(suborder)* (37). *Ord.-Sil.*
Tarphyceratidae (25). *L.Ord.-M.Ord.*
Trocholitidae (11). *Ord.-Sil.*
Beekmanoceratidae (1). *L.Ord.*
Barrandeoceratina *(suborder)* (51). *Ord.-Dev.*
Barrandeoceratidae (6). *Ord.-Sil.*
Bickmoritidae (8). *U.Ord.-Sil.*
Uranoceratidae (2). *Sil.*
Plectoceratidae (2). *M.Ord.-U.Ord.*
Lechritrochoceratidae (6). *Sil.*
Apsidoceratidae (6). *Ord.*
Lituitidae (11). *Ord.*
Rhadinoceratidae (10). *Dev.*
Nautilida *(order)* (184). *?U.Sil., Dev.-Rec.*
Rutoceratina *(suborder)* (32). *?U.Sil., Dev.-Carb.*
Rutocerataceae *(superfam.)* (19). *?U.Sil., Dev.-Carb.*
Rutoceratidae (16). *?U.Sil., Dev.-Carb.*
Neptunoceratidae (3). *Carb.*
Aipocerataceae *(superfam.)* (13). *Dev.-Carb.*
Litogyroceratidae (4). *Dev.-Carb.*
Scyphoceratidae (3). *Carb.-Perm.*
Dentoceratidae (1). *L.Perm.*
Aipoceratidae (5). *Carb.-Perm.*
Tainoceratina *(suborder)* (47). *Dev.-Trias.*
Tainocerataceae *(superfam.)* (30). *Dev.-Trias.*
Tetragonoceratidae (4).*Dev.*
Tainoceratidae (23). *Carb.-Trias.*
Tainoceratinae (14). *Carb.-Perm., ?Trias.*
Pleuronautilinae (9). *Perm.-Trias.*
Mosquoceratidae (3). *Carb.-Perm.*
Encoilocerataceae *(superfam.)* (1). *U.Trias.*
Encoiloceratidae (1). *U.Trias.*
Temnocheilaceae *(superfam.)* (9). *?Dev., Carb.-Perm.*
Temnocheilidae (3). *?Dev., Carb.-Perm.*
Gzheloceratidae (6). *Carb.-Perm.*
Rhiphaeocerataceae *(superfam.)*. *Perm.*
Rhiphaeoceratidae (5). *Perm.*
Actubonautilidae (2). *Perm.*
Centroceratina *(suborder)* (44). *Dev.-Trias.*
Trigonocerataceae *(superfam.)* (19). *Carb.-Perm.*
Trigonoceratidae (16). *Carb.-Perm.*
Trigonoceratinae (8). *Carb.-Perm.*
Aphelaeceratinae (2). *L.Carb.*
Thrinococeratinae (4). *Carb.*
Knightoceratidae (2). *Carb.-Perm.*
Subclymeniidae (1). *L.Carb.*
Phacoceratidae (2). *L.Carb.*
Centrocerataceae *(superfam.)* (25). *Dev.-Trias.*
Centroceratidae (4). *Dev.*
Grypoceratidae (19). *Carb.-Trias.*
Domatoceratinae (12). *Carb.-L.Trias.*
Grypoceratinae (2). *Trias.*
Syringonautilinae (4). *Trias.*
Clymenonautilinae (1). *U.Trias.*
Neothrincoceratidae (1). *L.Perm.*
Permoceratidae (1). *L.Perm.*
Liroceratina *(suborder)* (28). *?U.Dev., Carb.-L.Cret.*
Lirocerataceae *(superfam.)* (18). *?Dev., Carb.-Perm.*
Liroceratidae (9). *?Dev., Carb.-Perm.*
Ephippioceratidae (2). *Carb.-Perm.*
Koninckioceratidae (3). *Carb.-Perm.*
Paranautilidae (4). *?U.Perm., Trias.*
Clydonautilaceae *(superfam.)* (10). *Trias.-L.Cret.*
Clydonautilidae (5). *Trias.*
Gonionautilidae (1). *U.Trias.*
Siberionautilidae (1). *U.Trias.*
Pseudonautilidae (3). *U.Jur.-L.Cret.*
Nautilina *(suborder)* (32). *U.Trias.-Rec.*
Nautilaceae *(superfam.)* (31). *U.Trias.-Rec.*
Nautilidae (15). *U.Trias.-Rec.*

Nautilinae (12). *U.Trias.-Rec.*
Pseudaganidinae (2). *Jur.*
Cymatoceratidae (11). *Jur.-Paleog.*
Cymatoceratinae (9). *Jur.-Paleog.*
Heminautilinae (2). *Cret.*
Hercoglossidae (5). *U.Jur.-Paleog.*
Aturiaceae *(superfam.)* (2). *?U.Cret., Paleoc.-Mio.*
Aturiidae (2). *?U.Cret., Paleoc.-Mio.*

In the present volume (Part K) of the *Treatise* a total of 744 valid genera (exclusive of Bactritoidea) are recognized, whereas in the *Osnovy* the total of genera described or listed as valid is 799. The number of family taxa used is 108 in the *Treatise* and 122 in the *Osnovy*. A breakdown of these numbers according to subclasses and orders gives some insight into the main areas of discrepancy.

Numbers of Genera and Families Recognized in the Treatise *and* Osnovy

	No. of genera		No. of families	
	Treatise	*Osnovy*	*Treatise*	*Osnovy*
Endoceratoidea	63	76	13	12
Actinoceratoidea	35	51	7	11
Nautiloidea	646	672		
Ellesmerocerida	64	84	9	13
Orthocerida	125	103	11	9
Ascocerida	13	15	3	3
Oncocerida	143	153	16	21
Discosorida	46	45	9	8
Tarphycerida	38	37	3	3
Barrandeocerida	37	51	6	8
Nautilida	165	184	24	34
Order Uncertain	15			
Totals	744	799	101	122

In addition, the names of 33 invalid genera are listed in the *Osnovy,* whereas the present volume contains bibliographic information on 101 taxa of generic rank which are classified as unrecognizable, invalid, or rejected.

It will be seen that the number of genera by which the *Osnovy* exceeds those of the *Treatise* is almost entirely concentrated in the subclasses Endoceratoidea and Actinoceratoidea and in the order Nautilida. The reasons for this are of two kinds. For the subclass Endoceratoidea the *Treatise* lists 17 genera of unknown affinities, raising the total for the subclass to 80. Of these 17 genera, one is described and 10 are listed in the *Osnovy* as valid, and the names of six have been omitted. These data suggest a certain divergence of opinion regarding the recognizability of many of the proposed generic taxa. Apart from that, treatment of the subclass is reasonably uniform in both volumes.

The case of the Actinoceratoidea and Nautilida is different, because *Treatise* authors of these two taxa have been unable to recognize a number of more recently established genera, placing them in synonymy of earlier names. In the *Treatise* chapter on Actinoceratoidea 31 generic names are listed as junior synonyms, in the chapter on Nautilida 80. Both figures, however, include a number of *nomina nulla,* a name category which is ignored in the *Osnovy.* In the corresponding *Osnovy* chapters 5 synonyms are cited for the Actinoceratoidea and 32 for the Nautilida. These discrepancies reflect difficulties inherent in the study and systematic treatment of these two groups. In the Actinoceratoidea they lie in insufficient knowledge of many endosiphuncular structures or their inadequate preservation. In the Nautilida, as in the ammonoids, it is difficult to establish, and to agree on, standardized procedures in the taxonomic evaluation of minor variations in shell form and ornamentation.

Similarly, in the *Osnovy* 84 valid genera of Ellesmerocerida are recognized, whereas the *Treatise* recognizes only 64. In addition, however, the *Treatise* lists 23 generic names in synonymies, as against 2 in the *Osnovy.* Total number of ellesmerocerid generic names listed in the *Treatise* is thus 87 (including some *nomina nulla*), in the *Osnovy* 86 (without *nomina nulla*). The *Treatise* authors' reluctance to recognize numerous established genera of Ellesmerocerida was due to the conviction that morphological features of many genera are inadequately known and that in many cases safe criteria for the separation of generic categories are lacking. In many cases this uncertainty is due to the poor state of preservation of the type-specimens.

Difficulties attending the systematic treatment of the Orthocerida and the Oncocerida are of a somewhat different nature. The numbers of genera recognized in these two orders in the two volumes are satisfactorily close to each other, but considerable discrepancies are apparent on the suprageneric level. Only seven out of 13 families of Orthocerida, used in the present volume, are also found in the *Osnovy,* and the two works have only 11 families of Oncocerida in common (out of 16 in the *Treatise,* and 21 in the *Osnovy*). Obviously, in these two orders the difficulties do not lie so much in differentiation at the generic level, but in arriving at a satisfactory recognition of relationships at the suprageneric level.

The equality of treatment of the Tarphycerida is more apparent than real, because in the *Osnovy* 11 genera of Lituitidae are included in the Barrandeoceratida, whereas in the *Treatise*, based on SWEET's researches, they are treated with the Tarphycerida. With the removal of the Lituitidae from Barrandeocerida the systematic treatment of this order in the two volumes shows good agreement.

The general agreement in treatment of the Discosorida and Ascocerida in the two volumes is explained by the fact that systematic arrangements of these groups in both works are based on standard monographs by North American and European paleontologists, and that no significant recent, "post-monographic" additions to the knowledge of these groups have been made elsewhere.

In the *Osnovy* the rhyncholites are treated somewhat summarily on slightly less than two pages. A total of nine genera and nine subgenera are recognized and seven genera are diagnosed and illustrated. The oldest rhyncholite genus is listed as *"Rhyncolites* Faure-Biguet, 1819," with *Rhombocheilus* SHIMANSKIY, 1947, in synonymy. *Hadrocheilus* TILL, 1907, is listed as a synonym of *Rhynchoteuthis* D'ORBIGNY, 1847. By comparison the *Treatise* describes 11 genera and 6 subgenera and cites 11 generic names in synonymies.

All in all, *Osnovy* authors have shown greater inclination to split genera and families than *Treatise* authors. As compared with the *Treatise,* the *Osnovy* recognizes as valid 10 per cent more genera and 20 per cent more families.

A tabulation of total number of generic names listed in both volumes (exclusive of Bactritoidea) brings to light some additional interesting differences.

Summary of Generic Taxa in Treatise *and* Osnovy

	Treatise	*Osnovy*
Valid genera	744	800
Doubtful, invalid, and rejected generic taxa	67	32
Synonyms	286	62
Total number of names listed	1097	894

A more detailed analysis of the differences in taxonomic treatment of individual orders in the two volumes would, no doubt, lead to a clearer understanding of the causes of these differences and might well suggest future avenues of fruitful research to achieve a better understanding of all these groups and their interrelationships.

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PHYLOGENY AND EVOLUTION

By WALTER C. SWEET,[1] CURT TEICHERT,[2] and BERNHARD KUMMEL[3]

[[1] Ohio State University; [2] United States Geological Survey; [3] Harvard University]

INTRODUCTION

As with nearly every other group of organisms, there is no objective record of the earliest stages in the history of cephalopods. Presumably, however, cephalopods developed from the primitive mollusk in the fashion outlined by YONGE (7) in an earlier volume (Part I) of this *Treatise*. That is, accelerated secretion of shell material by peripheral zones of the mantle altered the primitively domelike shell to a progressively more highly conical one that grew more rapidly than the enclosed visceral mass. In association with this, the body migrated toward the shell opening, and apical parts of the conical shell were isolated by first one, then by a succession of transverse septa, so as to form a series of chambers, progressively evacuated by the animal, but connected with it by the fleshy siphuncle. At the same time, a pronounced ventral flexure of the body developed so that the head and the opening to the mantle cavity, separated only by a much reduced foot, came to be directed ventrally. Ultimately, the foot developed into the hyponome, or swimming funnel.

For several reasons, more fully explored in later parts of this chapter, we agree with YONGE that the earliest cephalopods probably retained the single pair of ctenidia thought to have characterized the ancestral mollusk, and that the two pairs of gills found in modern *Nautilus* appeared later in the history of cephalopods in association with increased activity and necessarily heightened metabolism. Thus, it seems to us that the dibranchiate plan, perfected in modern Coleoidea, is more fundamental among cephalopods than the tetrabranchiate plan exhibited by *Nautilus,* which probably developed progressively and was finally perfected in the tarphycerid-oncocerid-nautilid line. For several of the same reasons, it is also more attractive to assume that early cephalopods had the small number of arms (8 to 10) characteristic of modern coleoids and their Mesozoic forebears, rather than the large number (40) of modern *Nautilus,* and probably characteristic of the stock of which it is the sole survivor.

OLDEST CEPHALOPODS

The oldest certain cephalopods are the ellesmerocerids *Palaeoceras, Plectronoceras, Ruthenoceras,* and *Shantungendoceras,* from Upper Cambrian rocks in the United States, China, Manchuria, and the USSR. The shell morphology of these genera, together with the developmental trends indicated by the several post-Cambrian nautiloid orders traced back to them, indicates that the earliest shelled cephalopods were less than an inch long and secreted compressed, straight to endogastrically curved, closely septate shells with large subventral siphuncles composed of relatively short septal necks and, if present at all, generally thick, complex connecting rings. The closely spaced septa of the earliest cephalopods known suggest that, even if gas were present in their camerae, phragmocones were probably not very buoyant and were borne horizontally in life.

It should be noted here that tiny, conical, septate shells, referred to *Volborthella, Vologdinella,* and *Salterella,* have been reported from both Lower and Middle Cambrian strata, and many have regarded them as remains of the most primitive cephalopods. They are described and discussed by TEICHERT in a later section on "Doubtful Taxa." Although the question of their zoologic affinities has not been settled, these shells are not now generally regarded as belonging to the cephalopods. Shells of these genera are circular to somewhat elliptical in section and the axial tube, regarded by some as a siphuncle, is small and central in position (rather than large and marginal). Furthermore, the shell of *Volborthella* may have been arenaceous (rather than calcareous), and that of *Salterella,* although originally calcareous, seems to have been composed of thick adapically invaginated laminae, which are not separated by spaces that could be considered camerae. None of these characters is consistent with the model of early cephalopods deduced from studies of the morphology and development of Upper Cambrian and later forms (2). If these Lower and Middle Cambrian shells are those of primitive cephalopods, which seems unlikely, they must represent a group that became extinct in the Cambrian and that was not in the main line of cephalopod evolution.

In connection with our discussion of the nature and development of the earliest cephalopods, it should also be mentioned that HUTCHINSON (5) has recently suggested that preservable shells appeared in several animal groups in connection with the rise of predation in the Lower Cambrian. However, since no indication of powerful predators among known Lower Cambrian fossils is found, he assumes that the predators did not secrete fossilizable skeletons. This chain of reasoning leads him to suppose the existence of Early Cambrian "protonautiloids" with thin, conchiolinous shells, but with powerful horny jaws ". . . cruising about just over the bottom." If we grant the plausibility of HUTCHINSON's hypothesis, it seems necessary to assume that the unfossilized predatory "protonautiloids" of the Early Cambrian were much larger than the tiny Late Cambrian forms that provide our oldest objective record of cephalopods. Possibly, then, there were several stocks of primitive cephalopods in Early and Middle Cambrian seas, of which only the progenitors of the tiny Late Cambrian ellesmerocerids survived. Without doubt the Ordovician and later cephalopods developed from these Upper Cambrian ellesmerocerids.

EARLY CANADIAN ELLESMEROCERID RADIATION

Cephalopods developed explosively and radiated widely in early Canadian time (earliest Early Ordovician). Late Cambrian cephalopods are represented by mostly tiny shells, referred to eight species of four ellesmerocerid genera, whereas early Canadian forms are larger, include at least 165 species distributed among more than 20 genera, and represent three ellesmerocerid families (Ellesmeroceratidae, Plectronoceratidae, and Protocycloceratidae). For the most part, early Canadian ellesmerocerids are larger than their Late Cambrian predecessors, and average between one and two inches in over-all length. However, Late Cambrian *Palaeoceras* is estimated by FLOWER (2) to have been about three inches long, and some early Canadian forms (e.g., *Pachendoceras*) were veritable "giants," attaining an over-all length of seven to nine inches. Nearly all early Canadian ellesmerocerids are similar, however, in being laterally compressed, faintly or considerably curved endogastrically, and in having short chambers, long body chambers, and relatively large ventral or subventral siphuncles. In most early Canadian ellesmerocerids, the latter structures are empty, but diaphragms or dissepiments transverse to the siphuncular axis have been reported in some species (Fig. 70).

MIDDLE AND LATE CANADIAN DEVELOPMENT

As indicated by Figure 70, the explosive early Canadian development and radiation of primitive ellesmerocerids was followed in the middle and late Canadian (later Early Ordovician) by considerable and fairly rapid morphological diversification among the Ellesmerocerida and by the introduction and principal development of both the Endocerida and Tarphycerida. Each of these groups merits separate discussion.

ELLESMEROCERIDA

By middle Canadian time, all of the archaic Plectronoceratidae and most of the primitive Ellesmeroceratidae had disappeared. Middle and late Canadian representatives of the latter family retain the primitive features of, but are generally larger and less compressed than, their early Canadian forebears; some retained strong endogastric curvature, but others developed long orthoconic conchs. By the end of the Early Ordovician, the Ellesmeroceratidae were gone entirely.

The Protocycloceratidae, similar in general to their ellesmeroceratid ancestors, developed long, straight (or only faintly curved), annulated shells in the middle and late Canadian, whereas the Baltoceratidae secreted long, straight, smooth conchs with broad, empty siphuncles. Other variations among middle and late Canadian Ellesmerocerida gave rise to the Cyclostomiceratidae (with thick-walled marginal siphuncles and uncompressed, straight to faintly curved or breviconic shells), and to the early Paleozoic Bathmoceratidae, endogastrically curved and straight shells characterized by greatly thickened connecting rings. The latter families, as well as the Baltoceratidae, survived into the Middle and Late Ordovician (Fig. 70).

The Bassleroceratidae are like other ellesmerocerids in being closely septate, laterally compressed, and in retaining a marginal siphuncle with thick, complex connecting rings. They differ in being a first group of cephalopods to develop an exogastrically curved shell, which may be considered to be another answer to the common problem of efficient mobility associated with increased shell buoyancy. In these forms the shell lost its primitively horizontal position and its apex came to point upward and the aperture to face obliquely downward and forward.

ENDOCERATOIDEA

The Endoceratoidea, which first appeared in the middle Canadian, stem from early Canadian Ellesmeroceratidae, from which they are distinguished primarily by the presence of endocones in the siphuncle. Some endocerids retained the short, primitive septal necks of the Ellesmerocerida; others, however, developed progressively longer, hemichoanitic to subholochoanitic necks, but, for the most part, retained the complex connecting rings of the ellesmerocerids. In the Endoceratidae and Piloceratidae, as well as in some Manchuroceratidae, septal necks became holochoanitic, even macrochoanitic, and virtually all of the Endocerida exhibited a tendency toward great size and considerable elaboration of structures within the endocones.

Although the Endoceratoidea were most numerous and varied in the Early Ordovician, the Endoceratidae underwent a great expansion in the Middle Ordovician, during which time they produced shells as much as 30 feet long—the largest invertebrate fossils of the Paleozoic. Other short-lived, minor families of endocerids also appeared in the Middle Ordovician, but did not survive into the Late Ordovician. The Endoceratidae are represented in the Late Ordovician and may have survived in limited numbers into the Silurian; however, endoceratoids are not well represented in Silurian strata and the order as a whole was clearly extinct well before the end of that period.

The Endoceratoidea appear to represent one of several answers among early Paleozoic cephalopods to the problem of increased shell buoyancy that came with longer chambers and phragmocones of greater size. It seems fairly clear that the elaborate endocones of the Endocerida were secreted as counterweights and thus served a hydrostatic function in maintaining a near-horizontal position of the shell. The tightly packed longitudinal radial lamellae in the siphuncle of Intejocerida served the same purpose. A similar problem was answered by exogastric coiling in other nautiloids, or through formation of cameral deposits or various other types of siphuncular deposits in additional groups.

No evidence indicates that endoceratoids were ancestral to any other group of cephalopods. They seem to have disappeared without issue in the Silurian (Fig. 70).

TARPHYCERIDA

The middle and late Canadian also include the early history of the Tarphycerida, a relatively small nautiloid order (five families, 38 genera, about 170 species).

From the Bassleroceratidae developed the loosely to more tightly coiled Tarphyceratidae and Trocholitidae, and, from one of the latter families, developed the partially to completely uncoiled Lituitidae. Both the Trocholitidae and Lituitidae continued into the Late Ordovician; the Ophidioceratidae are Middle and Upper Silurian. Even though coiled (or secondarily uncoiled), typical tarphycerids retain evidence of their ellesmerocerid ancestry in the thick connecting rings of the siphuncle.

Although the exogastrically curved (and ultimately coiled) Tarphycerida solved the problem of increased shell buoyancy by bringing the gas-filled phragmocone to a position above the body mass, it is interesting and perhaps significant to note that some species of the Lituitidae, which became secondarily uncoiled—even orthoconic—secreted heavy organic deposits in chambers of the phragmocone to counterweight the visceral mass and keep the longiconic shell in a nearly horizontal position. Retention by tarphycerids of the capacity to do this suggests, of course, the existence of a fundamentally similar plan of organization in the adapical parts of the mantle and siphuncular tissues in all groups of early cephalopods.

MIDDLE ORDOVICIAN AND LATER RADIATIONS

The interval between the beginning of the Middle Ordovician and the end of the Middle Silurian may be regarded as the "heyday" of the nautiloid cephalopods, for at no other time in their history had they been either as numerous or as diversely and highly specialized as then. Furthermore, it was during this interval in their history that the lineages of the two major modern groups of cephalopods (dibranchiates and tetrabranchiates) first became clearly distinguished.

Six new "nautiloid" orders (Actinocerida, Discosorida, Orthocerida, Ascocerida, Barrandeocerida, and Oncocerida) appeared in the early Middle Ordovician. As shown in Figure 70, four of these (Actinocerida, Discosorida, Ascocerida, and Barrandeocerida) were successful, varied, and widespread in their distribution in the remaining early Paleozoic, but declined to extinction well before the end of that era. With exception of the Barrandeocerida, which may be ancestral to the Ammonoidea, representatives of these four nautiloid orders seem to have been specialized groups, off the "main line" of cephalopod evolution; there is no evidence that they gave rise to any more advanced group of cephalopods. The remaining two nautiloid orders that appeared for the first time in the earliest Middle Ordovician—Orthocerida and Oncocerida—are of paramount importance in the later history of the Cephalopoda, for not only were they numerous, varied, and important contributors to the Paleozoic fossil record, but they are ancestral to the two surviving groups of modern cephalopods, and one of them (Orthocerida) is ancestral to the Dibranchiata and may well have given rise to the Ammonoidea (Fig. 70).

ACTINOCERATOIDEA

For the most part, actinocerids are represented in the fossil record by long, straight conchs wtih heavy cameral deposits and a large siphuncle of broadly expanded segments that contains complex annulosiphonate deposits that are separated from the connecting rings by a perispatium and traversed by a network of complex radial canals. The origin of the subclass is unknown, for no transitional forms are known that link it with contemporaneous or earlier ellesmerocerids. It has been suggested several times by FLOWER that the late Canadian and early Middle Ordovician *Bathmoceras* is ancestral to the Actinocerida, but that hypothesis is here rejected. That is, the elaborately produced endosiphuncular structures of *Bathmoceras* are clearly outgrowths of greatly thickened connecting rings, whereas endosiphuncular deposits in the actinocerids are separated from connecting rings by a clearly defined perispatium.

Between their introduction in earliest Middle Ordovician time and their eventual extinction in the Pennsylvanian, the Actinoceratoidea exhibited three distinct evolutionary tendencies. As in the evolutionary history of many other groups of animals, actinocerids show the over-all tendency toward a considerable increase in size; conchs as much as 20 feet long were formed by some Carboniferous species. In addition, the actinoceratoids exhibit the tendencies toward progressive decrease in width of siphuncular segments and concomitant simplification of the siphuncular canal systems. The earliest actinoceratoids have siphuncular segments six times as wide as long, whereas in no post-Silurian form is this ratio any greater than two to one. Radial canals in the earliest actinoceratoids are surprisingly complex and form a system of simply curved main canals and a network of dendritic or anastomosing fine canals. Later development resulted in a much simpler pattern. Apparently, these several evolutionary tendencies characterized several co-existing families and were not confined to any single lineage.

DISCOSORIDA

The Discosorida are dominantly cyrtocones and brevicones. Their origin in the Ellesmerocerida is clearly indicated by the fact that primitive discosorids are endogastric, closely camerated cyrtocones with relatively large siphuncles and thick, complex connecting rings. Siphuncular segments, however, are broadly expanded in all of the earliest Discosorida, suggesting an origin in the most primitive ellesmerocerids (Plectronoceratidae) rather than in one of the more evolved, orthochoanitic families of that order. Discoscorids are distinguished from ellesmerocerids by thicker, inflated connecting rings that are clearly differentiated in early forms, at least, into distinct regions and layers. Later developments included the introduction of exogastric curvature in one branch of the order, and in both branches, the addition and elaboration of bullettes, parietal deposits, and endocones within the siphuncle, accompanied by progressive simplification in structure of the initially complex connecting rings.

BARRANDEOCERIDA

The earliest Barrandeocerida are closely similar in both shell form and external ornamentation to late Early and early Middle Ordovician Tarphycerida, from which they differ primarily in having thin, rather than thickened, connecting rings. Thus, one can hardly doubt that the Tarphycerida are ancestral to the Barrandeocerida. As in the Tarphycerida, tendencies in the later evolutionary history of the Barrandeocerida include a marked tendency to uncoil or even to form torticonic and breviconic conchs, probably in association with the development of a much elongated visceral mass and a very long body chamber. In some families the primitively conspicuous shell ornament was progressively reduced, whereas in others it was accentuated; furthermore, in at least one family a cyrtochoanitic siphuncle and somewhat expanded siphuncular segments developed. The group became extinct before the close of the Devonian and is generally believed to have given rise to no younger forms. SPATH (6) and others, however, have suggested that some species of the Barrandeocerida may have been ancestral to the Ammonoidea. SPATH's suggestion has never gained wide support, but it cannot be said to have been disproved.

ORTHOCERIDA AND ASCOCERIDA

One of the two most significant events in the early Middle Ordovician history of cephalopods was the development of the

Orthocerida. Orthocerids, which are largely slender, long-chambered orthocones, developed from orthochoanitic Ellesmerocerida (Baltoceratidae) through shrinkage in siphuncle size and reduction in thickness and complexity of connecting rings. Although the order exhibited its greatest diversity and evolutionary advancement in the interval from the Middle Ordovician through the Middle Silurian, orthocerids are common throughout the Paleozoic and did not become extinct until late in the Triassic.

Soon after their differentiation from ancestral ellesmerocerids, two distinct lineages appeared in the Orthocerida. In the most conservative line (Orthocerataceae), the primitive orthochoanitic to suborthochoanitic siphuncle was retained and evolutionary development was confined largely to ornamentation and to formation of a variety of complex cameral deposits and simple endosiphuncular annuli. Early and late Paleozoic branches from this line (Sphooceratidae, Brachycycloceratidae) developed the capacity to shed the early straight to slightly curved phragmocone and, later in its life history, to secrete a gibbous, breviconic conch with a suborthochoanitic to strongly cyrtochoanitic siphuncle and broadly expanded segments. In these capacities, this late Paleozoic derivative of the Orthocerataceae in a sense mimics the Ascocerida, a group derived from orthocerids early in their history, but extinct by the end of the Silurian.

In a more specialized orthocerid lineage (Pseudorthocerataceae), siphuncular segments became slightly to broadly expanded and cyrtochoanitic and, in addition to complex deposits in the camerae, thick annulosiphonate and parietal deposits developed in the siphuncle.

Ehrenberg (1) has made a convincing case for the presence of an ink-sac in a Middle Silurian *Michelinoceras*, a typical long-ranging genus of the conservative Orthocerataceae. In addition, Flower (3, 4) has suggested, from a reasonable interpretation of the trails and tentacular impressions of Late Ordovician orthoconic nautiloids (probably pseudorthoceraceans or actinocerids) that these forms had relatively few arms, as in the squids, rather than many short arms as in *Nautilus*. Furthermore, comparative morphology indicates fairly certainly that orthocerids were ancestral, in the Devonian or earlier, to the Bactritida, and, in the Mississippian or earlier to the Belemnoidea (either directly or via the Bactritida). Belemnoids are almost surely in the direct ancestry of modern dibranchiate cephalopods, which have both the ink-sac and small number of arms apparently possessed by at least some orthocerids.

The several features and presumed relationships just mentioned, together with the fact that only minor internal features separate the oldest orthocerids from the primitive ellesmerocerids, suggest that the dibranchiate (or coleoid) pattern (a single pair of ctenidia, ink-sac, few arms) is probably closer to the primitive cephalopod form than is that of *Nautilus* (two pairs of gills, no ink-sac, 40 arms), which is the only survivor of quite a different lineage, but which has traditionally been considered the most primitive living cephalopod.

Like orthocerids, ammonoids possibly had only a few arms, perhaps no more than eight, as suggested by Kolb (5a) from a study of drag marks made by the arms of a drifting, dead or dying ammonite found in the Solnhofen Limestone.

As Miller & Furnish have pointed out in their discussion of Paleozoic Ammonoidea (Treatise, p. *L*25), ammonoids evolved from nautiloids, but there are as yet no "preponderant supporting data to establish the identity of the ancestral form." Most recent students of cephalopods, however, follow Schindewolf (5b) in the belief that ammonoids evolved from straight orthocerid nautiloids, either directly, or more probably, by way of the Bactritida, a group that has been included at one time or another both in the Ammonoidea and among the nautiloid orders. Bactritids have many features in common with orthocerids, as do some of the earliest ammonoids, which differ primarily in being loosely to tightly coiled. Thus, it may well be that the Orthocerida are of further significance in cephalopod phylogeny in being directly or indirectly (via the Bactritida) ancestral to the Ammonoidea.

The Ascocerida are specialized offshoots of early Middle Ordovician Orthocerida, which, like the Sphooceratidae and Brachycycloceratidae (Orthocerataceae), developed the capacity to discard an early-formed orthoconic or cyrtoconic conch and retain a later-formed, generally inflated breviconic portion in adulthood. Presumably, as in the Brachycycloceratidae, natural truncation of the shell and late assumption of a much different conch form are to be associated with a change of living habits by the animal during its ontogeny. Primitive ascocerids are sparingly represented in Middle and Late Ordovician rocks; more specialized forms appear in the Silurian, at the end of which period the entire order abruptly became extinct (Fig. 70).

ONCOCERIDA AND NAUTILIDA

The Oncocerida, a large group of immensely variable Middle-Ordovician-through-Mississippian cephalopods, bear essentially the same relation to Early Ordovician Bassleroceratidae that the Orthocerida bear to Early Ordovician Baltoceratidae (both Ellesmerocerida). That is, like the Orthocerida, oncocerids developed from their Early Ordovician predecessors primarily through simplification in structure of the connecting rings. Very early in their history, however, oncocerids replaced the primitive orthochoanitic siphuncle by one composed of faintly to broadly expanded segments and cyrtochoanitic septal necks.

Although the earliest oncocerid conchs are elongate, compressed cyrtocones, essentially similar to those of their Early Ordovician ancestors, wide adaptive radiation in the Middle and Late Ordovician produced oncocerids with virtually straight or breviconic shells, some of them faintly curved endogastrically. A second adaptive surge from the primitive oncocerid stock, beginning in the Middle and Late Silurian, produced not only additional series of straight and breviconic species, but gyroconic, torticonic, serpenticonic, and nautiliconic forms, as well. Although the siphuncle of the more or less generalized stem group of the Oncocerida (Oncoceratidae) remained largely (but not entirely) free of organic deposits throughout its history, the siphuncles of most later, more specialized groups show a rather consistent pattern of variably developed actinosiphonate deposits.

The Nautilida, including the great bulk of the late Paleozoic, and all of the Mesozoic and Cenozoic coiled nautiloids, stem from cyrtoconic and breviconic nautiloids developed in the great oncocerid expansion of the Middle and Late Silurian. Although authors of earlier phylogenetic schemes (e.g., FLOWER & KUMMEL, 1950) reasonably concluded that the dominantly coiled Nautilida developed from coiled Barrandeocerida, later evidence has shown the siphuncle in some of the earliest Nautilida (Rutoceratidae) to be cyrtochoanitic and actinosiphonate. Consequently, it now seems clear that the highly ornamented and typically cyrtoconic and gyroconic Rutoceratidae, most of which have empty orthochoanitic siphuncles, but a few of which are cyrtochoanitic and actinosiphonate like ancestral oncocerids, are the most primitive Nautilida.

The later history of the Nautilida includes differentiation of four principal stocks in the Middle and Late Devonian and Early Mississippian. From the Rutoceratidae were developed the Tainocerataceae (characterized by straight to loosely coiled conchs, for the most part ornamented by wings, spines, nodes, ribs, or frills), the Trigonocerataceae (with mostly unornamented evolute to involute conchs), the Clydonautilaceae (which are smooth, involute to occluded shells with straight to highly sinuous sutures), and, in the Mississippian, the Aipocerataceae (coiled conchs with marginal, ventral siphuncles). These four stocks proliferated greatly and became widespread geographically during the late Paleozoic, and all but the Aipocerataceae extended into and through the Triassic. Near the end of the Triassic, the remaining three groups (Tainocerataceae, Trigonocerataceae, Clydonautilaceae) vanished abruptly, leaving behind only a single genus representing the first of the smooth, involute Nautilaceae. From the sole survivor of the Late Triassic nautilid reduction, a second nautilid radiation developed in the Jurassic and Cretaceous, confined to representatives of the Nautilaceae and never achieving the evolutionary tempo of the pre-Jurassic radiation (Fig. 292, 293).

Most Devonian nautilids belong to the Rutoceratidae, but four genera of the Centroceratidae and three of the Tetragonoceratidae also were present. None of these Devonian genera persisted into the Mississippian, but during that period, there appeared several distinct, long-ranging evolutionary lines derived from the Rutoceratidae and Centroceratidae. The Koninckioceratidae and Tainoceratidae, as well as the Liroceratidae and Aipocerataceae, stemmed from the Rutoceratidae, whereas the Grypoceratidae and Trigonoceratidae descended from the Centroceratidae.

Of the 35 nautilid genera known from the Mississippian, nearly half belong to the Trigonoceratidae, which is almost completely confined to the Mississippian (one genus ranges into the Permian and another is restricted to Lower Permian rocks of Russia). The only other nautilid family that shows a high rate of differentiation in the Mississippian is the Koninckioceratidae, in which 9 of the 11 genera known were introduced in the Mississippian. Remaining Mississippian genera belong to families that have long histories and low rates of evolution (e.g., Ephippioceratidae), or to long-ranging families such as the Tainoceratidae and Grypoceratidae.

We do not regard the reduction in number of nautilid genera in the Pennsylvanian as an indication of a significant decline in the over-all evolutionary development of the order, for if one discounts the Trigonoceratidae, the total number of Mississippian and Pennsylvanian genera is about the same and nearly a half of the remaining Mississippian genera continued into the Pennsylvanian (Fig. 292, 293).

Families that account for peak development of the Nautilida in the late Paleozoic and Triassic are the Tainoceratidae, Grypoceratidae, and Liroceratidae. Except for a liroceratid doubtfully recorded from the Devonian, all these families began in the Mississippian. Whereas the number of genera gradually increased with time in each of these evolutionary lines, rates of evolution were not such as to produce many new families. Thus, it seems that as early as the Mississippian the principal evolutionary lines of nautilids had become firmly established and these maintained their identity and character until the close of the Triassic. Only a few, minor radiations (families) appeared in this interval. This pattern is also reflected in the number of genera carried over from one period to the next. Eleven genera persisted from Mississippian to Pennsylvanian, and 20 from Pennsylvanian to Permian. Only four Triassic genera are also known from the Permian, but this number is deceptive, for in each of the three evolutionary lineages that extend from the Permian into the Triassic, the core Permian genus evolved directly into the core Triassic genus—*Metacoceras* (Penn.-Perm.) to *Mojsvaroceras* (Trias.), *Domatoceras* (Penn.-Perm.) to *Grypoceras* (Trias.), and *Liroceras* (Miss.-Perm.) to *Paranautilus* (M.Trias.-U.Trias.). Consequently, the large number of Triassic genera is the result of a broad evolutionary radiation in each of the principal evolutionary lineages during the Late Triassic. Triassic nautilid evolution, then, represents just the culmination of patterns and trends begun in the Mississippian.

Nautilids nearly became extinct after their peak development in the Late Triassic; only *Cenoceras* survived from the Triassic into the Early Jurassic. At this time, a new radiation began, resulting in a modest proliferation of new genera in the Late Jurassic. In the Cretaceous, the total number of genera was maintained, but the number of new genera began to decline. Decrease in the Cenozoic was very marked and the majority of Cenozoic nautilids are holdovers from the Cretaceous and Jurassic. Although *Nautilus* (Oligo.-Rec.) and the monotypic *Obinautilus* (Oligo.) appeared during this interval, the only successful, widespread new genus that evolved during the Cenozoic was *Aturia* (Oligo.-Mio.) (Fig. 70, 292, 293).

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PALEOECOLOGY

By W. M. Furnish & Brian F. Glenister

[State University of Iowa, Iowa City, Iowa]

INTRODUCTION

An almost unique series of difficulties is encountered in any attempt to interpret the mode of life and the habitat of fossil cephalopods. *Nautilus,* the single living externally shelled descendant of the abundant and varied nautiloid stocks of the Paleozoic, is restricted geographically and apparently should be regarded as a stenotopic form. However, published information on the ecology of *Nautilus* is far from complete, and danger of misinterpretation must inevitably accompany any attempt to draw general paleoecological inferences from a single extant representative. In fact, great diversity in the morphology of fossil nautiloids[1] suggests strongly that corresponding differences existed in their mode of life and ecology. Likewise important is the presumed susceptibility of most nautiloids to long-range post-mortem transportation after buoyancy was increased by decay of tissues and possible fragmentation of the body chamber.

Published discussions of nautiloid paleoecology are of necessity highly speculative, even though some are based on careful evaluation of such relevant factors as the ecology of living *Nautilus,* hydrostatic equilibrium of fossil forms, color markings, configuration of the aperture, localization of abrasion, hydrodynamic form, post-mortem distribution, and facies relationships. Summary accounts of previous contributions to understanding of the paleoecology of Paleozoic nautiloids have been given by Miller & Furnish (9) and Flower (3). Annotated bibliographies are available for Cenozoic nautiloids (15) and modern *Nautilus* (14), but no adequate general treatment of the paleoecology of Mesozoic nautiloids exists.

ECOLOGY OF MODERN NAUTILUS

Because of morphological resemblances to many fossil cephalopods, *Nautilus* is of

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[1] The term "nautiloids" here is used broadly to include the subclasses Endoceratoidea and Actinoceratoidea, as well as the Nautiloidea.—Editor.

unique significance. However, extreme caution needs to be exercised in applying generalizations derived from study of this living form to the ancestral nautiloids of the Mesozoic and Paleozoic.

Modern *Nautilus* is confined almost entirely to the southwestern Pacific Ocean. The genus is fairly abundant only in a relatively small area extending northwestward from New Caledonia and the Loyalty Islands to New Guinea and the Bismarck Archipelago. Authenticated extreme ranges for distribution of live specimens are bounded by the Fiji Islands to the east, the Philippines to the north, Makassar Strait and northwestern Australia to the west, and South Australia to the south. All of these localities lie within the tropics, except for South Australia, which has yielded only a single live specimen. Information is insufficient to allow generalizations as to the salinity and temperature of the biotope of *Nautilus.* Dead shells occur in moderate abundance in some areas well beyond the recorded limits of live specimens. Small numbers of shells have been collected from as far south as extreme southwestern Australia and the North Island of New Zealand, as far north as Japan, and from Madagascar to the west. In most instances it is doubtful to what extent these latter occurrences are a function of post-mortem distribution.

Live representatives of *Nautilus* have been secured in moderate abundance from traps set at depths even greater than 300 fathoms. However, they apparently migrate nocturnally, in shoals, to shallow water close to shore. Specimens may be taken in fish traps set as shallow as three fathoms, but all representatives found floating at the surface are in moribund condition. Some degree of success has been achieved in maintaining live *Nautilus* under shallow-water aquarium conditions.

Small decapod crustaceans are a main source of food for modern *Nautilus.* However, the animals are both carnivores and scavengers. They are attracted to traps baited with a great variety of fresh or decomposing marine invertebrates and vertebrates or the remains of domestic animals.

The numerous tentacles of *Nautilus* may be used to anchor the animal to the substratum for short periods. Reports that the organism crawls by manipulation of the tentacles are incorrect. *Nautilus* is a facile swimmer, and this is virtually the sole means of locomotion. It is an active member of the nektobenthos. Movement is by jet propulsion and results from rhythmic, forcible ejection of water from the branchial chamber of the pallial cavity. The water leaves the pallial cavity through the infundibular hyponome; movement is backward, and direction is controlled by the attitude of the muscular hyponome. The weight of the animal is delicately balanced by gas in the camerae, so that the mean density of the entire animal is the same as that of sea water. A high degree of stability is achieved by location of the buoyant phragmocone above the heavy body chamber.

A common general pattern of protective coloration characterizes both the soft part and the shell of all postembryonic ontogenetic stages of living *Nautilus,* although interspecific differences are apparent. The effectiveness of the protective pattern is such that *Nautilus* is extremely difficult to distinguish, even in clear shallow water. Upper portions of the shell are characterized by irregular brown transverse bands, whereas the mature lower shell surface is white.

INFERENCES FROM CONCH MORPHOLOGY

Consideration of the details of conch morphology is generally regarded as the most fruitful approach to interpretation of the life habits of fossil nautiloids. Many uncertainties are involved, but several independent lines of reasoning result in fairly compatible conclusions.

SHELL EQUILIBRIUM

In order to facilitate level backward propulsion, all active nektonic nautiloids must have maintained the terminal portion of the body chamber and the hyponome in approximately horizontal alignment. Any major variation from this horizontal orientation would have restricted the animal to either a sluggish benthonic mode of life or hyponomic propulsion in a more nearly vertical direction. Whereas the former alternative is a distinct possibility, the latter seems highly improbable from both biologic and hydrostatic considerations. Several lines of evidence, particularly the development of primary cameral deposits, indicate that the great majority of fossil nautiloids resembled living *Nautilus* in the presence of gas in the camerae. However, it is possible that septation in the ancestral nautiloid shell developed for mechanical and physiologic functions (12), so that some ancestral ellesmerocerids and perhaps a few of their breviconic descendants may have lacked cameral gas. Even if gas were present in the camerae of all nautiloids, the extremely close spacing of the septa in some ellesmerocerids and a few other brevicones would have precluded the presence of a sufficient volume of gas to balance the weight of the animal. Consequently, it appears that crawling by use of the tentacles may have been the main means of locomotion for at least some nautiloids, and that these forms should be considered as motile members of the epifauna.

With the exception of some ancestral ellesmerocerids and a few breviconic descendants, all nautiloids probably shared the common equilibrium problem of counterbalance of gas in the camerae. The basic requirement for mobile stability in these forms was that the center of buoyancy should lie proximal to the center of gravity. It seems a plausible assumption that almost all nautiloids achieved this condition with the terminal part of the body chamber in approximately horizontal position and that, therefore, most fossil nautiloids resembled living *Nautilus* in swimming prowess. Four fundamentally different solutions to the general problem of shell equilibrium were achieved: coiling of the entire conch or a major part of it, secretion of heavy mineralized cameral and siphuncular deposits, ontogenetic shell truncation, and formation of a breviconic conch.

The recent discovery of aqueous fluid in some of the camerae of living *Nautilus* (Bidder, 1962) indicates an additional means of maintaining shell equilibrium, although the importance of this mechanism for fossil cephalopods cannot be evaluated in particular cases. Examination of the liquid was inconclusive, although it contains organic material and dissolved salts and is viscous in the apical chambers. Bidder indicated that the largest volumes of liquid occur in the camerae adjacent to the body chamber; little or no fluid is present in chambers situated uppermost when the animal is in living position, whereas liquid is present in apical camerae. Variation of the quantity of fluid present in the various ontogenetic stages suggests that fluids within the camerae can be controlled through the siphuncle. Change from positive to negative buoyancy, or vice versa, may occur within a few hours under aquarium conditions.

Cameral liquids may have been of primary importance in mantaining equilibrium in some orthoconic forms, such as the Bactritida. Representatives of that order commonly retain all ontogenetic stages and are devoid of siphuncular and cameral deposits.

Coiling alone was sufficient to locate the center of buoyancy close to the center of gravity with the hyponome in horizontal position (Fig. 43, 44, 52; see also *Treatise* Part L, Fig. 124, 157). This solution to the problem of equilibrium was adopted by the Nautilida, Tarphycerida, and Barrandeocerida. It is significant that primary cameral and siphuncular deposits are practically unknown in these three orders. No such deposits were needed for mobile stability. The only group of coiled nautiloids in which voluminous cameral deposits occur is the tarphycerid family Lituitidae. This group is characterized by association of an adoral orthocone with the adapical spiral (Fig. 268,*1a,b*), so that general coiling of the shell is quite different from that of other members of the three orders.

The center of gravity would have been located adorally from the center of buoyancy in orthoconic longicones if all camerae were retained during ontogeny and the chambers themselves were devoid of mineralized deposits or liquid. Stability was achieved under these conditions only if the shell were held in a vertical position, and effective horizontal hyponomic propulsion would have been precluded by this orientation. It is not surprising, therefore, to find that most longiconic orthocones either developed mineralized primary deposits in the phragmocone or, probably less commonly, underwent periodic truncation of the apical camerae. The result of either procedure was to move the center of buoyancy forward, coincident with anterior migration of the center of gravity as growth proceeded. Superposition of the centers of buoyancy and gravity with the shell in horizontal position thus allowed effective backward movement by use of the hyponome.

Most representatives of the orders Endocerida, Actinocerida, and Orthocerida are longiconic orthocones in which primary mineralized cameral deposits, siphuncular deposits, or both are found. Secretion of these deposits invariably was progressive, beginning near the apical end of the phragmocone and extending farther adorally at successively later ontogenetic stages (Fig. 23, 24, 33-37). Concentration of deposits adapically served the dual purpose of weighting the apical end and reducing its buoyancy by displacement of gas. In addition, these mineralized deposits undoubtedly strengthened the apical part of the phragmocone, which otherwise would have been vulnerable to damage during backward hyponomic propulsion. Presumably, a delicate balance was achieved at all growth stages so as to allow superposition of the centers of buoyancy and gravity when the conch was in horizontal position and thus permit effective horizontal propulsion by the hyponome. Also, it is reasonable to assume that all active nektonic nautiloids maintained hydrostatic equilibrium, the weight of the organism being balanced by the buoying effect of cameral gas. A noteworthy feature is that both cameral and siphuncular deposits commonly are concentrated in the ventral part of the phragmocone. This had the effect of producing a more stable form by lowering the center of gravity.

A second alternative for reducing the apical buoyancy of horizontally oriented orthoconic longicones was periodic decollation of the apical camerae, or ontogenetic shell truncation (Fig. 190). This means of maintaining mobile stability during horizontal propulsion was utilized by all Ascocerida and at least some Orthocerida (7). Most taxa of orthocones are known only from fragmentary specimens, so that the numerical importance of ontogenetic shell truncation is unknown. Accompanying the achievement of periodic decollation in almost all Ascocerida and at least some Orthocerida was an evolutionary trend towards concentration of the camerae dorsally, above the body chamber. Again, the effect of this trend was to decrease the vertical separation of the centers of gravity and buoyancy and thus to improve stability during horizontal movement of the animal. The ascocerid phragmocone was devoid of deposits, but cameral deposits are known in *Sphooceras truncatum,* a species for which periodic decollation has been documented thoroughly (1).

Whereas the mode of life of the coiled nautiloids and orthoconic longicones can be inferred with reasonable confidence, greater difficulties are encountered in paleoecological interpretations for the host of brevicones and cyrtocones included in the Oncocerida and Discosorida. Most straight brevicones, and in fact virtually all oncocerids lack cameral deposits. However, many of the cyrtoconic discosorids are characterized by voluminous cameral and siphuncular deposits. The relative volume of the phragmocone and the body chamber varies greatly in orthoconic brevicones. In many forms, the phragmocone was of such relatively small dimensions that buoyancy could not have compensated fully for the weight of the animal. A vagrant benthonic mode of life probably should be attributed to these forms. Other brevicones with proportionally larger phragmocones could have been fully buoyant, and can be considered as swimmers. However, equilibrium would have been achieved only if the axis of the conch were near-vertical in position, and rapid horizontal movement appears to be precluded by this orientation. By contrast, even moderate conch curvature, as in the cyrtocones, would have produced stable orientation of the shell with the hyponome in approximately horizontal position. A nektonic or nektobenthonic mode of life can thus be attributed to buoyant cyrtocones.

COLOR MARKINGS

Nautiloids which preserve color patterns occur sporadically throughout the geological column and are known from strata as old as the Ordovician (3, 6). They provide a basis for paleoecologic interpretation, as the distinctness of color markings of modern marine shells bears a direct relationship to light intensity. Thus, shells possess more varied colors and more distinct designs in shallow than in deep water, and only some 5 per cent of organisms inhabiting water deeper than 100 fathoms possess conspicuous color markings. In addition most marine organisms resemble living *Nautilus* in lacking color patterns entirely, or having them less conspicuously developed, on the lower surface of the shell.

Color markings in fossil nautiloids are known in a variety of patterns. Commonly they consist of fairly straight longitudinal bands or of chevron-like or sinuous transverse belts (Fig. 9, 10). Evidence is far from conclusive for longiconic orthocones but suggests that color bands were generally absent from one side of the conch, presumably the lower surface. This distribution lends support to the conclusion that the axis of most longicones was oriented horizontally. Color-banded orthoconic and cyrtoconic brevicones are more numerous than colored longicones, but are still rare. The majority of these brevicones exhibit equal development of banding on all sides, thus supporting the conclusion from studies of equilibrium that the axis of the conch was oriented at a high angle to the horizontal.

CONFIGURATION OF APERTURE

The nature of the aperture, particularly the form of the peristome adjacent to the hyponome, provides a basis for paleoecologic inference (Fig. 11). A basic assumption in evaluating this type of evidence is that the presence of a hyponomic sinus, or re-entrant in the peristome adjacent to the hyponome, permitted greater flexibility of that propulsive organ, and that nektonic prowess was thus proportional to the area of the sinus. This assumption may not be justified when applied to the group as a whole, as practically all orthoconic longicones lack a conspicuous hyponomic sinus, whereas most brevicones, cyrtocones, and coiled forms exhibit some modification of the peristome. Other possible features of the peristome, such as a dorsal salient and paired ocular sinuses (Fig. 196,*2a-e*), are considered to be of secondary importance in paleoecologic interpretations.

Several nautiloid groups exhibit striking ontogenetic changes in form of the aperture. For example, the whorls of the juvenile spire in the tarphycerid *Angelinoceras* (Fig. 267,*3*) possess a deep hyponomic sinus, whereas this feature is lost almost completely on the adoral parts of the associated orthocone. More commonly, the indentations of the peristome became more pronounced in later ontogenetic stages. Of great interest are the numerous Ascocerida (Fig. 196,*2a-e*), Oncocerida (Fig. 210, 211), Discosorida (Fig. 247), Tarphycerida (Fig. 268, 269), and Nautilida (Fig. 319) which developed spectacular modifications of the aperture only near full maturity. The implications of these modifications are not fully understood. It is tempting to postulate that drastic modification of the aperture was accompanied by a correspondingly pronounced alteration in habitat and mode of life. This is probably valid in most genera, but in at least some groups the juvenile conchs are associated directly with mature forms. For example, evidence from known occurrences suggests that the juvenile and mature ascocerids occupied the same habitat, as is the case with modern *Nautilus.*

Apertural modifications were apparently relatively rare in longiconic orthocones in comparison with the more nearly equidimensional brevicones. However, the paucity of evidence for such modifications is to some extent a function of the greater susceptibility of longicones to post-mortem fragmentation.

LOCALIZATION OF ABRASION

A few nautiloids are known to exhibit local abrasion of portions of the shell. These worn areas are interpreted as having resulted from repeated contact with the sea floor. The best-documented examples are referred to the nautilid genus *Cooperoceras* (10). Representatives of this genus show conspicuous beveling of the ventrolateral spines in the ultimate one-third of the fully mature whorl.

Abrasion of the lower shell surface of an active nektobenthonic nautiloid appears plausible when it is realized that nautiloids generally were incapable of adding to the outer shell after attainment of full maturity and coincident development of mature modifications. Whereas presently known examples of this type of abrasion are few, there is a good possibility that many other instances will be recognized once the paleoecologic significance of the phenomenon is generally understood. FLOWER (2) recorded numerous grouped trails and impressions which he attributed to the tentacles and shell of nautiloids (see "Nautiloid Trace Fossils," p. *K*487). These trails, if rightly interpreted, indicate repeated contact of nautiloids with the sea floor and imply the possibility of abrasion of the lower surface of the shell.

STREAMLINED FORM

The hydrodynamic form of the nautiloid provides an additional basis for paleoecologic inference. Quantitative data on relative streamlining of coiled cephalopod shells were presented by KUMMEL & LLOYD (8). They confirmed the previously held notions that involute and compressed shells are better streamlined than evolute and depressed whorls. No such quantitative data are available for most nautiloid groups, but it is certain that the orthocones presented less hydrodynamic resistance than cyrtocones and coiled forms. Spines and ribs would also have increased resistance drastically and thus have reduced the efficiency of jet propulsion.

POST-MORTEM DISTRIBUTION

Evidence already presented suggests that most, but not all, fossil nautiloids resembled living *Nautilus* in achieving a delicate balance between the total weight of the live animal and the buoyancy of gas in the phragmocone. The mean density of these live animals presumably was the same as that for the sea water in which they lived. As in the case of modern *Nautilus,* the mean density probably could have been changed slightly by physiological processes, thus enabling the animal to sink or rise.

The shell of those nautiloids which achieved equilibrium would have floated to the surface after death of the animal and consequent decay and loss of the content of the body chamber. Such floating shells were certainly susceptible to extensive post-mortem distribution by tides and ocean currents.

Many aspects of the phenomenon of post-mortem distribution of cephalopods were considered in detail by REYMENT (13). Experiments by that author confirmed that the orientation of a floating dead shell and the eventual mode of settling of a stranding conch are determined largely by the weight of the walls of the body chamber in relation to the buoyancy of the gas-filled phragmocone. Many coiled cephalopods with strongly depressed or highly compressed whorls were determined by REYMENT to be posthumous sinkers, whereas a great variety of other conch forms represented potential posthumous floaters, many of which would have been deposited near the strand line irrespective of original habitat. REYMENT also drew attention to the probability that damaged shells, unable to float at the surface, achieved additional dispersal at depth owing to presence there of denser bodies of more highly saline or colder water. (See chapter on Biostratonomy, p. *K*124.)

Distribution of rhyncholites commonly is different from that of the associated conch. This may be explained readily by assuming that the rhyncholites dropped from the rotting nautiloid bodies close to the habitat of the organisms, whereas the empty shells achieved more extensive post-mortem distribution.

INFERENCES FROM FACIES RELATIONSHIPS

Lithofacies and biofacies associations of fossil nautiloids are generally considered unreliable as a guide to habitat, and many apparently contradictory ecologic conclusions are based upon such associations. Errors in interpretation of habitat stem largely from extensive post-mortem distribution of most morphological types. However, practically all living cephalopods undergo seasonal and monthly migration, and it is reasonable to assume that similar changes of habitat were common in extinct groups. Because of these two factors, many of the sites of preservation of fossil faunas are undoubtedly far removed from areas in which the forms lived.

As indicated previously, heavy-shelled brevicones and cyrtocones with a proportionally large body chamber probably did not possess a sufficient volume of gas in the camerae to compensate completely for the weight of the animal. Consequently, these forms are best considered as elements of the motile benthos. Upon death, putrefaction of the body probably would not have resulted in sufficient loss of weight to allow the empty shell to float. Thus, accumulations of such shells can be considered as biocoenoses. In contrast, most longicones and coiled shells were probably in a state of equilibrium during life, and loss of the soft parts would have allowed the shells to float. Accumulations of these shells consequently should be considered as thanatocoenoses. Distribution of modern *Nautilus* suggests that dead shells may float the 1,000 miles from New Caledonia or eastern Australia to New Zealand, or even the 4,500 miles from northwestern Australia or Indonesia to Madagascar. Similar dispersal can be assumed for some fossil forms.

Two classic examples may be selected to support the assumed correlation between morphology and distribution of fossil nautiloids. Elements of the "Arctic Ordovician" fauna have been described in a series of publications by Foerste, Miller, and others. This fauna is widely distributed from the Canadian Arctic islands to the Mexican border. Both lithofacies and biofacies associations of the nautiloids indicate strand line or shallow water deposition. Large longicones dominate the faunas, and many of these nautiloids are in a highly fragmented state. Elsewhere, it is demonstrated that these longicones are best considered as posthumous floaters. The wide areal distribution of this "Arctic Ordovician" nautiloid fauna is compatible with its facies associations if the cephalopods are regarded as having floated into shallower water after putrefaction of the body.

The Silurian nautiloids of the Upper Mississippi Valley (5) represent a contrasting situation. Most of the 75 species described by Foerste were secured from the flanks of a single bioherm. Nautiloids occur sporadically but in moderate abundance in direct association with these bioherms, but they are exceedingly rare in the interreef facies. Possibly a majority of the species are brevicones with such proportionally small phragmocones that the live animals could not have been fully buoyant. Death must have resulted in immediate settling of the shells in a biocoenose. The sporadic and localized distribution of these Silurian nautiloids is thus completely compatible with previous conclusions on mode of life of the brevicones.

PALEOECOLOGY OF MAJOR TAXA

Morphological variation within individual nautiloid orders indicates differences in mode of life and habitat. However, the following broad generalizations for each of the groups can be devised by evaluation of the factors considered previously in this chapter.

ENDOCERIDA

Most endocerids were longiconic orthocones with a proportionally large submarginal siphuncle; the same is true of the much smaller group included in the Intejocerida. Endocones or longitudinal lamellae were developed progressively from the apical end of the siphuncle, but cameral deposits are unknown. These longicones are judged to have maintained equilibrium between the total weight of the animal and the buoyant effect of cameral gas, and to have carried the axis of the conch in horizontal position. Color bands are exceptionally rare, but apparently were confined to the dorsum. The endocerids can be considered as nektobenthos and most were posthumous floaters. It is difficult to envisage a connection between the siphuncle and the apical camerae of forms with macrochoanitic septal necks and endocones in the adjacent siphuncle.

Adequately known representatives of the breviconic Piloceratidae and Manchuroceratidae are characterized by a proportionally small phragmocone which probably could not have contained enough gas to have compensated fully for the weight of the entire animal. They are best considered as vagrant benthos and posthumous sinkers.

INTEJOCERIDA

Although the intejocerids are poorly known, it may be assumed that the calcareous lamellar deposits which fill the siphuncle solidly in most growth stages served the same purpose of maintaining hydrostatic equilibrium of the shell as endocones in the Endocerida.

ACTINOCERIDA

Practically all actinocerids are orthoconic longicones which developed voluminous cameral and siphuncular deposits. Secretion of these structures was progressive, from the apical end, so that equilibrium would have been maintained with horizontal orientation of the conch. With few exceptions, the actinocerids are inferred to have been active swimmers and posthumous floaters. Probable exceptions to these generalizations include strongly depressed forms, such as *Gonioceras* and *Lambeoceras*. These depressed conchs probably possessed such a relatively small volume of gas in the camerae that they were not fully buoyant either in life or after death.

ELLESMEROCERIDA

Included within this order are forms with such diverse morphology that no single morphologic peculiarity can be considered as characteristic of the entire group. However, septa are generally more closely spaced than in other nautiloids and both cameral and volumetrically significant siphuncular deposits are absent. There is no clear indication that cameral gas was present in these ancestral nautiloids. Even if gas filled all camerae, it is doubtful whether such closely septate forms could have been fully buoyant; breviconic representatives certainly were not.

Environmental associations of the Ellesmerocerida are generally with the shallow-water shelly facies. Gastropods, trilobites, and stromatolites commonly occur with them, and a degree of fragmentation of the conchs is almost invariable.

Although each line of evidence for ellesmerocerid paleoecology is inconclusive, it is most reasonable to assume that, in general, the group was benthonic. Breviconic representatives were probably crawlers. However, the septa of the longicones may have served the same balancing function as siphuncular and cameral deposits in other nautiloids, and this group may well have been characterized by a nektobenthonic mode of life. The axis of the conch would have been horizontal for active swimmers but more nearly vertical for benthonic forms.

ORTHOCERIDA

Almost all representatives of this order are orthoconic longicones with a proportionally small siphuncle. Voluminous cameral and siphuncular deposits are almost invariably present, at least in the apical portion of mature specimens, and concentration of these laminated structures is commonly in ventral position. Color bands are generally restricted to one surface, presumably the dorsum.

Progressive development of the deposits of the phragmocone, adorally from the apex, suggests that the orthocerids were in hydrostatic equilibrium and that the conch was maintained in horizontal position. This orientation is confirmed by available examples of color banding. Ventral concentration of cameral deposits resulted in lowering the center of gravity to achieve greater stability. Some Orthocerida underwent ontogenetic shell truncation. However, the numerical importance of this equilibrium device is not known. In view of these factors, it can be concluded that the orthocerids were active swimmers and posthumous floaters. The cephalopod coquina found locally in the Maquoketa Formation of Iowa (11) is one of the many prolific accumulations of orthocerids which clearly represent thanatocoenoses deposited in a turbid shallow-water environment.

ASCOCERIDA

Representatives of this order are characterized by ontogenetic shell truncation of the orthoconic to cyrtoconic adapical deciduous section and development of a highly modified inflated breviconic mature ascoceroid portion (Fig. 190). Structural components of the conch were unusually thin, and cameral and siphuncular deposits are unknown. Perhaps the most notable feature of the ascoceroid portion of the conch was the concentration of the camerae, in dorsal position, above the body chamber. Three to 12 septa are present in the ascoceroid portion.

Juvenile ascocerids, which invariably are associated with mature specimens, are best considered as nektobenthos. Through periodic truncation of the apical camerae they could have maintained equilibrium with the shell in an inclined position. Mature Silurian ascocerids were almost perfectly adapted to an active nektonic mode of life. The compressed attenuate fusiform contours offered minimum hydrodynamic resistance, and dorsal concentration of the camerae provided maximum mobile stability. Extreme maneuverability was facilitated by formation of a deep hyponomic sinus.

Presumably the ascocerids were posthumous floaters, and small numbers of specimens are known from widely scattered localities in North America and Europe. Rarity of these nautiloids may be largely attributable to fragile construction of the conch. Specimens have been secured in moderate abundance only from the Baltic Island of Gotland, the same area which has yielded all of the undoubted deciduous conchs. Consequently, it seems probable that these occurrences represent the only known biocoenoses.

ONCOCERIDA

Within this order are grouped the bulk of the brevicones and cyrtocones, although derivatives include some longiconic orthocones, gyrocones, torticones, serpenticones, and nautilicones. Spectacular modifications of the fully mature aperture are recorded for many forms. Both the camerae and the siphuncle are devoid of volumetrically significant mineralized deposits.

The relative sizes of the phragmocone and body chamber vary within wide limits in the breviconic orthocones and cyrtocones. However, the majority of such forms probably were not fully buoyant, owing to possession of a relatively small phragmocone, close septal spacing, and thick shell. They should be considered as benthos and posthumous sinkers. However, the persistent presence of a hyponomic sinus probably indicates that the hyponome functioned as a propulsive organ, so that a nektobenthonic mode of life is therefore plausible.

Color markings of the brevicones are invariably developed on all sides. This confirms the conclusion from studies of equilibrium, namely, that the axis of the shell was carried in inclined or vertical position. The development of even moderate curvature of the conch would have permitted horizontal disposition of the hyponome. Consequently, cyrtocones with a proportionally large phragmocone may be considered as swimmers, although the conch did not constitute an efficient hydrodynamic form.

Particular problems are posed by the many oncocerids with strongly contracted apertures. Possession of a proportionally small phragmocone in most such forms marks them as benthos, although the presence of a hyponomic sinus probably indicates ability for limited propulsion as well as for respiration. Detailed buoyancy studies of some few breviconic oncocerids with exceptionally large phragmocones and restricted apertures may well indicate that these forms were floaters which lived passively as members of the plankton.

DISCOSORIDA

Curved brevicones are characteristic of this order; both endogastric and exogastric forms may appear in the one lineage. Constricted apertures are common, and many such forms retain the prominent hyponomic sinus. Cameral and siphuncular deposits are present in some groups.

In gross conch form, the discosorids are homeomorphs of the oncocerids, and similar mode of life and habitat are likely for both (4). Most discosorids are best considered as sluggish nektobenthos, especially in view of the almost invariable benthonic associations. However, groups with a narrow siphuncle and proportionally large phragmocone, such as the Westonoceratidae, were probably in equilibrium with the sea water. They can be interpreted as active swimmers and posthumous floaters.

TARPHYCERIDA

Included here are evolute coiled nautiloids in which cameral and siphuncular deposits are virtually absent. The Lituitidae differ in morphology from other tarphycerids and will be considered separately. Most tarphycerids exhibit some degree of divergence of the adoral portion of the mature body chamber. The peristome is characterized by a prominent hyponomic sinus at all growth stages, and the fully mature aperture commonly exhibits some degree of modification.

Qualitative comparison of the phragmocone and body chamber suggests a fairly constant proportion between the volumes of these two parts of the conch. For example, the shell of most tarphycerids expands rapidly and possesses three to four whorls, including one-half of a volution of body chamber. However, more gradually expanded forms, such as *Hardmanoceras* and *Ophioceras* may possess six whorls, including slightly more than one volution of body chamber. Consequently, it appears that most tarphycerids lived in hydrostatic equilibrium, and were thus posthumous floaters. Presence of a deep hyponomic sinus tends to confirm interpretation of the group as active swimmers. The divergent adoral portion of the body chamber would have been oriented in horizontal position. We disagree with TEICHERT (chapter on Biostratonomy) in thinking that empty tarphycerid and barrandeocerid shells would not have floated readily.

Representatives of the tarphycerid family Lituitidae commonly have conchs with a relatively small adapical spiral and a larger straight to slightly sigmoid adoral longicone. Growth lines generally define a conspicuous hyponomic sinus. Modification of the peristome at full maturity commonly included deepening of the ocular and hyponomic sinuses and development of lappets. Apical buoyancy of the lituitids was balanced in at least some forms by secretion of dorsally discontinuous cameral deposits. Presumably those forms were active swimmers and posthumous floaters, not differing greatly in hydrostatic form from the orthocerids.

BARRANDEOCERIDA

Early representatives of this order are evolute forms closely resembling the ancestral Tarphycerida. Derivatives include a variety of conch types similar to those encountered in the Lituitidae. Both cameral and siphuncular deposits are absent. Modification of the mature peristome has been recorded for only one genus. A conspicuous hyponomic sinus is commonly present.

The resemblance in gross form between the Barrandeocerida and the Tarphycerida is such that similar mode of life and habitat can be assumed. Presumably most representatives were active elements of the nektobenthos and posthumous floaters. However, crawling must have been the dominant means of locomotion for some derivatives, such as the torticones. As noted in the preceding discussion of Tarphycerida, our interpretation of that group and of barrandeocerids differs from TEICHERT's.

NAUTILIDA

Most of the coiled nautiloids from Devonian and younger strata are more nearly involute than the serpenticones of the older Paleozoic, and they are referred to the Nautilida. Differences in rate of expansion, whorl section, and ornament are apparent, but basic similarity to modern *Nautilus* is such that comparable habitat and mode of life can be presumed. Coiling alone was sufficient to place the center of buoyancy near the center of gravity, with the hyponome in horizontal position, so that both cameral and siphuncular deposits are absent.

All Nautilida are judged to represent nektobenthos, although effectiveness of hyponomic propulsion probably varied widely. Qualitative evaluations of buoyancy suggest that most representatives were posthumous floaters. This conclusion is supported by the widespread occurrence of many taxa. However, the body chamber of some forms, such as *Aipoceras* (Fig. 317,*1a-d*), clearly was of such large size in relation to the phragmocone that the animal could not have been fully buoyant. Fossil occurrences of such forms thus approximate life sites.

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BIOSTRATONOMY

By Curt Teichert

Biostratonomy is concerned with the study of all factors and processes that influence and act upon organic remains from the time of death of animals and until they come to a final resting place in a sedimentary deposit. The biostratonomy of nautiloid cephalopods[1], like that of bactritids and ammonoids, is a complex and difficult subject, because the vast majority of their conchs has no modern counterpart. There has been much speculation on the possibility of widespread transportation of empty conchs of nautiloids and other chambered cephalopods (for a summary see Reyment, 12), but little concrete information on which to base speculations is available.

Geisler (2) immersed an undamaged and a slightly damaged shell of Recent *Nautilus* in water. Both shells floated with the body chamber downward. The damaged shell sank after 28 days, the undamaged shell 24 hours later, when enough water had penetrated the camerae.

Model experiments by Reyment (12) have shown that the length of the body chamber has great importance for the buoyancy of conchs. An empty endocerid model conch floated if the body chamber did not exceed a quarter of the length of the phragmocone. An orthocerid type model conch floated if the body chamber was less than half the length of the phragmocone. A conch of *Nautilus pompilius* floated freely in an upright position with the body chamber downward. After 32 days it was found to have sunk only slightly in the water. However, when the body chamber was artificially enlarged to equal two-thirds of one volution, the conch sank.

The following additional results of Reyment's experiments are of interest. (1) Evolute coiled conchs are less likely to float than highly involute ones. (2) Strongly compressed as well as strongly depressed coiled conchs tend to sink. (3) Strongly ornamented, tuberculated conchs will not

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[1] See footnote, p. K114.

float and even moderately strongly tuberculated conchs will sink, if the tubercles are solid. (4) Apertural modifications (such as presence of ears and lobate projections) adversely affect buoyancy.

Temperature fluctuations "tend to sink a floating shell, as warm water expels air and cold water replaces the lost air when the temperature sinks." Salinity is also important. A shell of *Nautilus pompilius* sinks in water of less than normal salinity. Its downward movement may be arrested, if it meets a water layer of normal salinity at greater depth. Such conditions exist at the entrance to inland seas such as the Baltic Sea of today. In the past, conditions might have existed locally under which bottom currents of normal salinity flowing into an inland sea could have carried empty cephalopod shells to areas with surface water of low salinity where the animals could not have lived.

Along the same line Kobayashi (6) believed that most finds of nautilids in Tertiary rocks of Japan are necroplanktonic drifted shells. Many of them occur in sedimentary rocks formed in coastal embayments and some occur associated with fossils indicative of water temperatures that would have been too cold for the living nautilids. Similarly, Stenzel (13) believed that *Aturia* was not indigenous in the Eocene of Texas, "but floated in as dead, empty shells from the deeper parts of the Gulf of Mexico." On the other hand, in other Tertiary formations in Texas, *Aturia* was apparently indigenous.

Reyment has demonstrated that conchs of longiconic orthocerids must have floated with the body chamber pointing downward. This may explain the common occurrence of phragmocones without body chambers, because the latter were more exposed to damage in the floating position. For certain breviconic conchs with cameral deposits *(Westonoceras)*, Teichert (14) earlier had concluded that they may have floated with the apex directed downward.

Although much remains to be learned about the conditions influencing transportation and settling of nautiloid conchs after death, some preliminary conclusions are possible. (1) Conchs of benthonic animals with heavy cameral deposits and thick siphuncles with siphuncular deposits (e.g., most Endocerida and Actinocerida) are likely to become entombed at or near their natural habitat. (2) Length of the body chamber and amount of cameral deposits determine whether longiconic, stenosiphonate conchs sink or float. The conchs of most Pseudorthocerataceae, of the Lamellorthoceratidae, and of similar forms can hardly have floated, whereas those of many Orthocerataceae may have done so. (3) The conchs of most early Paleozoic coiled forms (Tarphycerida, Barrandeocerida) were poor floaters and are most likely to be found not far from where they lived. (4) In evolution of the Nautilida a definite trend toward greater buoyancy of the empty conchs may be inferred, because Jurassic and later genera tend on the whole to be more involute and more globular than early Mesozoic and Paleozoic representatives of the order. (5) No experimental data and little information on the buoyancy of breviconic conchs are available from other sources. However, the distribution pattern of oncocerid and discosorid genera and families (which contain most of the brevicones) does not support the suggestion that these conchs might have floated during lengthy periods after death.

Nautilid shells infested with cementing organisms such as serpulids and certain clams have been described from Triassic rocks by Welter (15) and by Kieslinger (5). Irrespective of their normal buoyancy such shells cannot have floated appreciably after the animal died.

The orientation, especially of longiconic conchs, is another aspect of the biostratonomy of nautiloids. It may be used to determine the direction of ocean currents and shore-line trends at the time of the entombment of the fossils. Petránek & Komárková (10), from measurements of the orientation of nearly 1,000 orthocerid conchs in Silurian rocks of Czechoslovakia, found an overwhelming majority of them disposed in parallel position. They assumed that the apices pointed against the direction of the current. However, as pointed out by Quenstedt (11), orthoconic conchs with undamaged (hence, gas-filled) phragmocones must have been anchored by the heavy body chamber and the apices of such conchs would point in the direction of the current.

Kay (4) observed two orientation maxima for orthoconic cephalopod conchs in

Ordovician rocks of Ontario and Vermont, one for large specimens and the other for small conchs. The two were perpendicular to each other. KAY suggested that the large conchs were oriented normal to the contemporary shore line, whereas the small ones were parallel to it. Identical conditions were observed in Ordovician rocks of New York by CHENOWETH (1). Small orthocerids tended to be oriented parallel to ripple marks in the same beds, hence normal to the prevailing current. Large endocerid shells were found in orientation normal to the ripple marks, hence parallel to the current. CHENOWETH assumed that these shells pivoted around their apices, which would then point up-current. KRINSLEY (9) studied orthoconic conchs in Silurian rocks of Illinois and used their orientation to determine paleo-wind and -current directions. GOLDRING and FLOWER (1942) described beds containing abundant large orthoconic shells, arranged in prevailing parallel directions, from the Devonian of New York State. On the other hand, in reef flank deposits in a Silurian reef complex in Illinois, orthoconic cephalopods were found in haphazard orientation in a criss-cross pattern (3). The body chambers of conch-bearing cephalopods act as sediment traps, as first pointed out by QUENSTEDT (11) and later illustrated by means of experiments of REYMENT (12).

Experiments by KOLB (8) have shown that in the presence of a bottom current a dead *Nautilus* shell is oriented with the opening of the body chamber pointing in the direction of the current. A nautiloid shell, once in contact with sediment, is anchored down quickly and cannot be moved easily by bottom currents. Thus, most conchs of nektonic species or necroplanktonic conchs, once they sink to the bottom, are not likely to be transported any significant distances. This may not be true, however, for conchs having complex sutures (e.g., *Aturia*), which, because of greater internal rigidity provided by the folded septa, tend to have thinner shells than conchs with simple sutures (e.g., most Nautilidae). Shells of *Aturia* are almost always found without body chambers, for these are easily broken (7). It is possible that phragmocones without body chambers may be transported more widely than shells with the body chambers intact.

Undamaged nautiloid shells, when embedded in sediment, represent empty spaces which may be filled with calcite deposited from solutions infiltrating the camerae during diagenesis. However, many shells are filled with sedimentary material, forming internal molds or steinkerns. Just how this happens is not always fully understood. GEISLER (2) has shown experimentally that only very small amounts of a watery clay suspension penetrate into the last few chambers of a *Nautilus* shell through the septal foramina, even when all connecting rings had been removed. According to the same author, however, considerable quantities of fine mud can enter camerae from the outside through very fine cracks in the outer shell.

BARRANDE has described many examples of nautiloid shells, especially orthocerids, which are partly filled with rock matrix, partly with diagenetically deposited calcite, and TEICHERT (1930) described the same condition in siphuncles of *Endoceras*. Internal sediment, of course, accumulates in the lower part of shells and siphuncles, and such specimens may, therefore, be used to establish the original position of strata in tectonically disturbed areas.

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DESCRIPTIONS OF SUBCLASSES AND ORDERS

By Curt Teichert, Bernhard Kummel, W. C. Sweet, W. M. Furnish,
Brian F. Glenister, H. K. Erben, R. C. Moore, and D. E. Nodine Zeller

INTRODUCTORY DISCUSSION

By Curt Teichert and R. C. Moore

The purpose of this short chapter is to provide a general comparison of the large groups of nautiloid cephalopods included in the three subclasses Nautiloidea, Endoceratoidea, and Actinoceratoidea, accompanied by systematic diagnoses which may serve to complement all following chapters except the final one concerned with the Bactritoidea.[1] This last-mentioned group is considered to stand apart because of inferred (but not yet firmly assessed) relationships which suggest linkages between it and Nautiloidea, Ammonoidea, and Coleoidea (Fig. 70).

NAUTILOIDEA

Orders assigned to this subclass contain the preponderant majority of all described nautiloid genera. Among them are the oldest forms known (Upper Cambrian ellesmerocerids), if we exclude the families Volborthellidae and Vologdinellidae (Lower and Middle Cambrian) which are placed by Shimanskiy (1962, p. 60) and Balashov (1962, p. 72) in an order named Volborthellida and included in the Nautiloidea. In our view, these families (and likewise the Lower Cambrian Salterellidae) are doubtful taxa which may not even belong to the class Cephalopoda. The only known living nautiloids are species of *Nautilus,* included in the order Nautilida and subclass Nautiloidea.

In forms of the conch and in many internal morphological features the Nautiloidea exhibit utmost variation. Size also ranges from a shell length of less than 2 cm. to giants 9 m. in length and 30 cm. or more in diameter at the apertural end of

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[1] See footnote, p. K491.