PART K

MOLLUSCA 3

CEPHALOPODA—GENERAL FEATURES
ENDOCERATOIDEA—ACTINOCERATOIDEA
NAUTILOIDEA—BACTRITOIDEA

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INTRODUCTION

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The cephalopods described in this volume are divided into the orders Ellesmerocerida, Endocerida, Intejocerida, Actinocerida, Orthocerida, Ascocerida, Discosorida, Oncocerida, Tarphycerida, Barrandeocerida, and Nautilida. Descriptions of them are followed by that of the Bactritida, the taxonomic status and affinities of which are unsettled. The named orders include all the cephalopods which from the middle of the 19th century until comparatively recently were assigned to a single taxon "Nautiloidea," first recognized and named by de Blainville in 1825 and generally regarded as a suprafamilial category, being classified by different authors as suborder, order, superorder, or subclass. This taxon was long contrasted with the Ammonoidea (*Treatise,* Part L), and considered to be equal in rank with this assemblage.

In general, and as compared with other molluscan groups, including ammonoids, "nautiloid" cephalopods are rare fossils. Most fossiliferous formations contain no, or only a few, nautiloid conchs. Mass occurrences such as are abundantly known among ammonoids, gastropods, and pelecypods, are very rare. Among the few recorded mass occurrences of fossil "nautiloids" the following deserve mention: the widespread mass accumulations of large endocerids in the Middle Ordovician (Vaginatum Limestone and equivalents) of Norway, Sweden, and Estonia (2), the so-called Maquoketa coquina of Late Ordovician age in Iowa, consisting of large concentrations of conchs of *Dolorthoceras sociale* (3), mass occurrences of *Pseudorthoceras* in the Lower Permian of north-central Texas (Clifton, 1944).

Miller & Youngquist (3), Flower (1), and Reyment (4) have cited and discussed a few additional examples, but such occurrences are uncommon. A considerable number of nautiloid genera recognized and described in the present volume are known from only a few specimens, and some from only one specimen. Stenzel (6) reports that in rocks of Tertiary age the proportion of nautilids to other mollusk specimens may be of the order of 1:1,000 to as much as 1:10,000. The fossil record suggests that, in spite of their considerable morphological diversification and their long geological record, nautiloid cephalopods were at all times and in most places subordinate constituents of contemporaneous faunas.

Systematic and structural studies during the last three decades have shown that the "Nautiloidea" include several specialized taxa that, although doubtless stemming from the common ancestral stock of the Ellesmerocerida, had diverged strongly in morphological and structural characters. In fact, some of the taxa are less similar to each other than some of them are to the ammonoids. Although it is difficult to distinguish various early ammonoids from their "nautiloid" ancestors, no difficulties exist, as a rule, in distinguishing between representatives of different taxa within the so-called "Nautiloidea." Thus, no longer does any sound biologic foundation seem to exist for uniting the many diverse "nautiloid" taxa into one taxonomic unit.

Subsequent to a decision by Teichert and others concerned with preparation of *Treatise* Part K that the recognized main assemblages of nautiloid cephalopods should be described independently under the informal heading of "Nautiloid Orders," Shimanskiy & Zhuravleva in 1961 (5) published a penetrating discussion of these groups: this was intended to provide a classification suitable for adoption in the Soviet paleontological treatise (Osnovy Paleontologii). Following Schwarz (1894) they divided the class Cephalopoda into two subclasses, the first (named Ectocochlia) containing all forms characterized by the presence of an external shell and the second (named Endocochlia) consisting of the internal-shell and shell-less forms. The Ectocochlia were defined to include five main groups designated as superorders, namely, Nautiloidea, Actinoceratoidea, Endoceratoidea, Bactritoidea, and Ammonoidea. This arrangement seems superior to classification of external-shell cephalopods in a dozen or more orders, all of equal rank, one of which embraces the host of highly varied ammonoids. Accordingly, the systematic framework proposed by Shimanskiy & Zhuravleva is accepted by us, except for classifying their so-called superorders as subclasses and adopting the name Coleoidea in place of Endocochlia. The Ammonoidea (already published in *Treatise* Part L) are then to be defined as a subclass in a projected future revision, and the suborders given in Part L will be raised to the rank of orders. *Treatise* Part M will describe and illustrate representatives of the subclass Coleoidea.

The originally determined sequence of "nautiloid orders" in Part K is retained, in spite of the seemingly anomalous separation of Ellesmerocerida from the remaining orders of the subclass Nautiloidea. Reasons for such retention are (1) the avoidance of otherwise necessary extensive resetting of type, accompanied by rearrangement of figures with already assigned numbers, and (2) the maintained judgment that ellesmerocerids comprise the rootstalk from which other main groups of nautiloids were evolved.

Because of the generally clear morphological differentiation of nautiloid orders, individual authors' assignments were well defined as a rule and authorship of individual contributions is indicated in the table of contents.

The preparation of this volume of the *Treatise* has encountered sundry difficulties and special problems. The chief of these have arisen from the need to revise authorship assignments drastically and from what now is seen as a premature start on publication. Firmly assured completion dates given by some authors could not be met, and since the sequence of the several nautiloid orders in the section on systematic descriptions had been agreed upon previously, various unfinished units had to be skipped if typesetting work on others was to go forward. Therefore, this volume has been built like a wall with gaping holes into which properly shaped stones later had to be fitted with minimum visible signs of patchwork. Teichert was charged with assembling and co-ordinating the individual typescripts, and he reviewed the contributions of all other authors up to the time of his departure for an extended stay in Pakistan; this was in October, 1961. Subsequently, a half-dozen chapters and co-ordination of the whole volume have been handled editorially by Moore. The chapter describing general features of cephalopods was prepared last of all by Sweet, substituting on short notice for originally designated authors who failed to write it.

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CEPHALOPODA—GENERAL FEATURES[1]

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CEPHALOPODA Cuvier, 1797

[*nom. correct.* Duméril, 1806 (*pro* Les Céphalopodes Cuvier, 1797)] [Naef (1923) attributed authorship of the name Cephalopoda to Schneider, 1784, who actually only grouped all living cephalopods into two "classes" of a category he termed "Octopodia." Thus we cannot ascribe the name to Schneider, since he seems not to have used it.]

BIOLOGY OF CEPHALOPODA

Mollusks of the class Cephalopoda are agile, bilaterally symmetrical, predacious carnivores that have achieved a structural complexity and metabolic efficiency without peer among unsegmented invertebrates. The class is represented in the modern marine fauna by some 650 species of octopuses, squids, cuttlefishes, argonauts (Lane, 1957, *Kingdom of the Octopus*), and *Nautilus,* the only living form with an external shell. The class also includes more than 10,000 fossil species informally termed nautiloids and bactritids (the subjects of this volume), ammonoids (described in *Treatise* Part L, 1957), and coleoids (to be discussed in *Treatise* Part M).

The oldest undisputed cephalopods are from strata of Late Cambrian age, and a very considerable fossil record indicates that they were most abundant in the Paleozoic and Mesozoic. Except for such now-flourishing coleoid orders as Teuthidida, Sepiida, and Octopodida, the class has declined in both numbers and diversity since the Triassic and especially since the Cretaceous. Invertebrates associated with fossil cephalopods indicate that the class has always been exclusively marine in habitat, as is true of all living representatives. Although some of the latter are adapted to intermediate and abyssal depths of the oceans, the majority are most abundant in shallow seas. The ecology of fossil species is more difficult to reconstruct, for, after the animal's death, the gas-filled shells of *Nautilus* drift widely in modern oceans and those of many fossil species are assumed to have done so in the past. However, both the rocks and the remains of other invertebrate groups commonly associated with fossil cephalopods suggest that the group has always been most abundant in shallow seas on continental shelves.

Both embryology and comparative anatomy indicate that cephalopods arose from an "ancestral mollusk" similar in form to certain primitive gastropods. The steps by which this may have taken place are ably outlined by Yonge (6) and need only be summarized here. The initial stage probably involved isolation of segments in the

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[1] A short chapter by A. K. Miller & W. M. Furnish, entitled "Introduction to Cephalopoda," was included in the Editorial Preface to *Treatise* Part L, published in 1957. Revision of the introductory chapter was undertaken at a very late date by the present author, who has retained large parts of the original and has expanded or partially rewritten others. He acknowledges his debt to Miller & Furnish, but assumes full responsibility for the present summary, which also incorporates suggestions by Curt Teichert, J. A. Jeletzky, and R. C. Moore.

apex of the domelike shell of the ancestral mollusk by a succession of transverse partitions (septa) traversed by a fleshy tube, the siphuncle. Associated with this was undoubtedly a pronounced ventral flexure of the animal such that the head and the opening to the pallial cavity, separated only by a much modified foot, came to face ventrally. The primitive molluscan foot developed into the muscular hyponome, or swimming funnel of the cephalopods, and the chambered, gas-filled shell came gradually to serve as a functional hydrostatic device.

Because of the developmental pattern suggested by YONGE, logical objections have been voiced to the application to cephalopods of such terms as anterior, posterior, dorsal, and ventral, with what appears to be their customary meaning. That is, if shells of fossil cephalopods, or the bodies of living forms, are oriented for descriptive purposes in a manner anatomically comparable with that employed in describing pelecypods and gastropods, the adapical portion of the body is dorsal, the head and arms ventral, the hyponomic side posterior, and the opposed side anterior. However, it is doubtful if more than a few groups of early cephalopods (and some specialized later derivatives) lived in any such position. Consequently, the more familiar terminology is applied to animals oriented in a living position (insofar as this can be determined) and the few anatomical terms commonly used by paleontologists are employed in a functional sense. The head, bearing eyes, tentacles or arms, and the mouth, is anterior; the opposite end of the visceral complex is posterior; the hyponomic side of the body is ventral; and the opposed side dorsal. After more than a century of error, it is doubtful that the revised orientation urged by MUTVEI (1957) will come to be widely adopted (*see* p. *K*15).

Cephalopods are the most highly organized mollusks and among them are the most accomplished swimmers other than the fishes. Some are minute, but the class also includes the giant squid, *Architeuthis,* which, with a body (including tentacles) as much as 16 m. (52 feet) long, is not only the largest living mollusk, but also the largest living invertebrate. The shells of some Ordovician nautiloids (e.g., *Cameroceras*) attained a length of nearly 10 m., and those of immense Cretaceous ammonoids (e.g., *Pachydiscus*) have a diameter of some 2.5 m.

The principal anatomic features of two living cephalopods are shown in Figure A. It can be seen that the body is elongate, with a distinct anterior **head** that bears large **eyes** and a **mouth** that is surrounded by a crown of mobile, prehensile arms or **tentacles.** Behind the head is the saclike **visceral mass,** and ventrally is the **hyponome** and a capacious **branchial cavity.** The latter is completely enveloped by the **mantle,** which is undivided and also encloses the remainder of the body. In ten-armed coleoids lateral fins are developed from the mantle, and in *Nautilus,* the mantle is prolonged posteriorly as the **siphuncular cord.**

The head is built around an internal cartilaginous skeleton that supports or encloses the central nervous system and balance organs, and provides attachment for the hyponome and many of the principal muscles. At its anterior end is the mouth, surrounded by one or several series of arms or tentacles and equipped with a buccal mass that includes a parrot-like beak with upper and lower jaws or mandibles (see p. *K*62, *K*470).

The cephalic processes that surround the mouth vary considerably in number, structure, and size in living cephalopods. Most authors hold that they are elaborations of the anterior part of the primitive molluscan foot, but that interpretation is rejected by others. In *Nautilus,* 94 sheathed cirrate tentacles are arranged on ocular, labial, and digital lobes (Fig. A,*1*); in other living cephalopods the number of arms is less. Many living ten-armed coleoids (e.g., squids) have the arms arranged in five pairs (Fig. A,*2*). Four pairs are short, stout, and bear suckers on their inner sides, whereas tentacles of the fifth pair are long, retractile, and have suckers only at their somewhat expanded distal ends. Suckers of many ten-armed coleoids have horny or toothed rims; denticles of some of these develop into large formidable hooks. Octopods, as the name suggests, have eight circumoral arms provided with suckers; in some (Vitreledonellidae) the arms are joined by a web and are used for swimming.

Eyes, which are particularly well developed in various coleoids but are primitive "pin-hole" structures in *Nautilus,* are borne laterally on the head. In *Nautilus,* they are open water-filled pits at the ends of short stalks, and have a retina but lack iris, cornea, lens, or eyelid. In other cephalopods, however, they are complex organs of ectodermal origin capable of forming an image and similar in both structure and development to those of vertebrates.

The dorsal surface of the head is protected by a thick, commonly warty, hood in *Nautilus* (Fig. A,*1*), which serves to close the aperture of the external shell when the animal is retracted into it. No comparable feature is found in other living cephalopods, which lack an external shell.

The foot of the ancestral mollusk is represented in cephalopods by the muscular hyponome, through which water is ejected from the mantle cavity. The tip of this structure is highly mobile; it arises as a pair of flaps, the margins of which overlap in *Nautilus,* but are fused together in other living cephalopods. In many forms a small supplementary flap in the hyponome acts as a check valve, permitting water to flow only in an outward direction. A hyponome is peculiar to the class, and rapid swimming results when water is forcefully ejected from it either by pulsations of the muscular hyponome (in *Nautilus*) or by powerful contraction of the muscular mantle (in all other living cephalopods).

The more or less elongate visceral mass is enveloped by the mantle, which is only weakly muscular in *Nautilus,* but contains thick layers of both circular and longitudinal muscle in other living forms. Besides commonly secreting a shell, the mantle has a forward-projecting undivided fold that forms the outer wall of a ventral pallial or branchial cavity, within the posterior portion of which the gills are suspended. Except in the Vitreledonellidae in which they are vestigial, the gills are paired plumelike structures, of which two (a pair) occur in all living forms but *Nautilus,* which has four (two pairs). In *Nautilus,* gills are attached only at the base, but in other living forms they are attached also along the afferent sides of the axis. Ctenidial filaments are alternately arranged on either side of a central axis, and their respiratory surface is greatly increased by lateral and secondary folding. Some living ten-armed coleoids have 40 filaments on either side of the axis; in octopods, however, the number is smaller and in some abyssal forms gill filaments are further reduced in number and length. Supporting rods occur on the afferent sides of gill filaments; these arise in a membrane that extends from the afferent surface of the filaments to the afferent membrane. These apparently serve as ties between the margins of filaments and the afferent membrane (5). Unlike those of other mollusks, the ctenidia of cephalopods are not ciliated, probably because they are constantly bathed and cleansed by sea water forced into and out of the mantle cavity either by pulsations of the hyponome or by muscular contractions of its walls.

Contraction of the longitudinal mantle muscles causes the mantle cavity of coleoids to be enlarged and sea water is drawn into it laterally and ventrally between the anterior margin of the mantle and the head. Subsequent contraction of the powerful circular muscles (and relaxation of the longitudinal ones) reduces the capacity of the cavity and locks the mantle firmly around the head so that water is forced out of the hyponome under great pressure. Consequently, the inhalant current is ventral to the exhalant one. The mantle of *Nautilus* is only slightly muscular; hence, water both enters and leaves the pallial cavity by way of the hyponome and inhalant and exhalant currents are correspondingly weaker than in coleoids. In *Nautilus* the mantle cavity also contains an **osphradium,** situated below the gills and directly in the path of the respiratory current. Such organs have commonly been interpreted as chemoreceptors concerned with testing the water that enters the mantle cavity or with detecting food. YONGE (5), however, has interpreted the osphradium as a tactile organ, the principal function of which is estimation of the amount of sediment entering the pallial cavity. This interpretation would explain the presence of an osphradium in *Nautilus* and its absence in coleoids, for sediment would be more likely to accumulate in the mantle cavity of bottom-living *Nautilus* (which has a relatively feeble respiratory

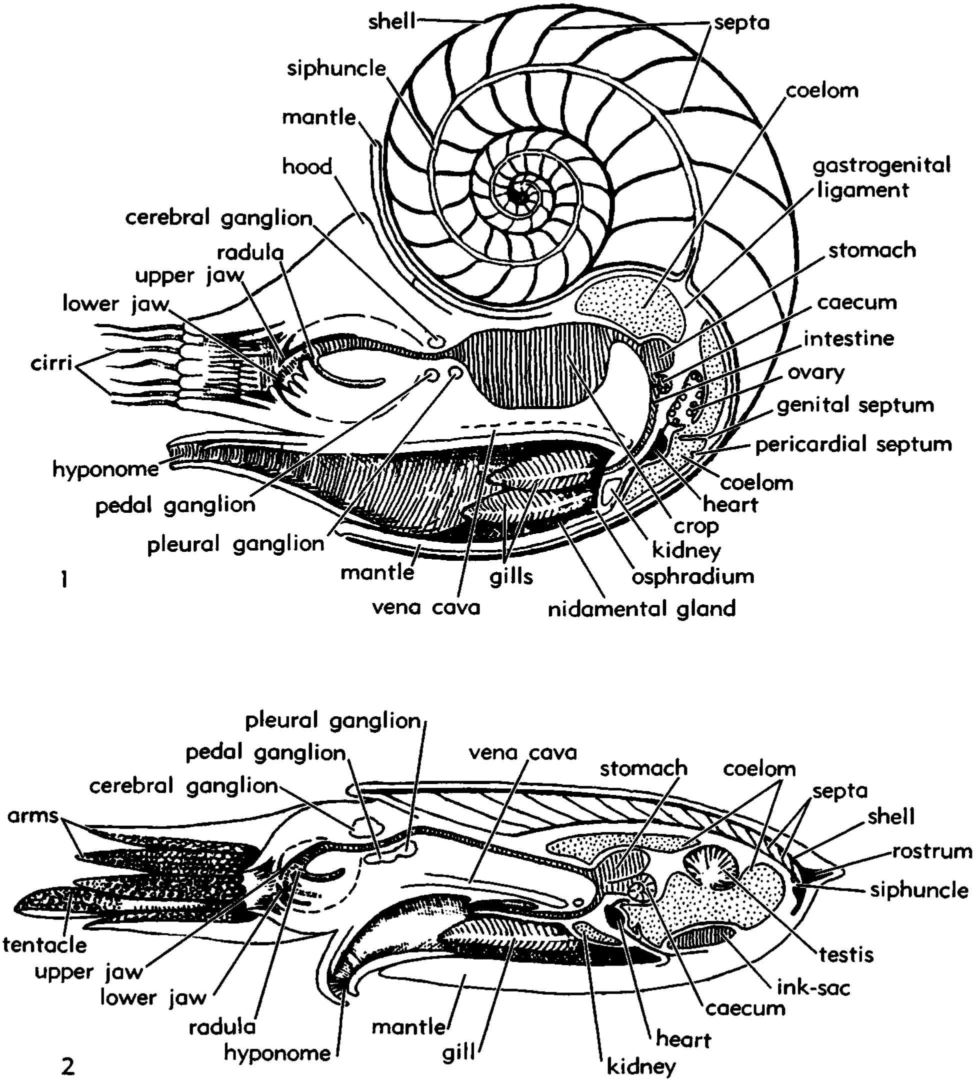

Fig. A.—Median longitudinal sections of *(1) Nautilus* and *(2) Sepia,* showing anatomy of typical representatives of the two major groups of living cephalopods (from Naef, 1928, p. 83).

current) than in that of the living ten-armed coleoids and octopods, from which water is violently expelled.

The mantle of coleoids (but not of *Nautilus,* in which it is largely covered by shell) is liberally supplied with chromatophores that, in various species, contain black, pink, brown, blue, or purple pigment. Contraction of muscle fibers attached to these structures flattens or draws them out and cephalopods so equipped can simulate the color of their surroundings with astonishing rapidity. The change is so obvious in *Octopus* that the animal literally blushes when frightened. In some living ten-armed coleoids and in one octopod species, which live at great depths, special phosphorescent organs are developed in various parts of the mantle, arms, and head.

The **alimentary canal** does not extend from pole to pole but forms a loop so that the mouth as well as the anus is more or less anterior in position. The buccal cavity, which contains a toothed radula or its degenerate equivalent, and into which two pairs of salivary glands discharge, gives way posteriorly to a muscular esophagus, which expands to form a crop in *Nautilus* and *Octopus,* but not in other cephalopods. Peristaltic contraction of the esophagus passes food back to the muscular stomach, to which is attached a large caecum that is straight in squids, but spirally constructed in *Sepia, Octopus,* and *Nautilus.*

A process of **digestion,** entirely extracellular, is accomplished by enzymes discharged into the caecum by the small "pancreas" and the large "liver." When food reaches the stomach, digestive enzymes stored in the caecum pour into it and digestion begins. The process is completed in the caecum itself and absorption takes place largely through its walls. Indigestible refuse is returned to the second portion of the stomach, from which it passes to the straight or coiled intestine and is ultimately discharged through the anus, which opens into the pallial cavity near the posterior end of the hyponome.

Squids and *Octopus* have two compact, saclike **nephridia** which enclose the renopericardial canal, but the four nephridia of *Nautilus* have no connection with the pericardial cavity. Waste is excreted through renal pores which open into the mantle cavity near the anus.

An **ink sac,** containing ink gland and reservoir, opens into the rectum of all cephalopods but *Nautilus* through a duct situated just behind the anus. The black or brown alkaloid ink is rich in melaniniferous pigment, which, when discharged, forms a murky cloud that apparently anesthetizes the chemoreceptors of some predators and provides a screen behind which the cephalopod can escape.

The **circulatory system** of cephalopods is fundamentally molluscan, but is modified in several noteworthy respects. The heart, enclosed in a pericardium, has a median ventricle and as many auricles as there are gills. Ventricles pump blood to the body through anterior and posterior aortas which branch to form several arterial systems. In *Nautilus,* returning blood trickles back to the haemocoel through interconnected sinuses, then passes by way of the vena cava to the gills. In coleoids, however, the system is entirely closed and veins replace the sinuses of *Nautilus.* In these forms, blood returns from the head via the vena cava, which divides into right and left branches. The right branch receives blood from veins that drain the ink sac and gonad, and each branch passes through a nephridial sac and a muscular branchial heart before entering the ctenidia. Anterior and posterior vein pairs return blood from the mantle and visceral mass. Supplementary branchial hearts provide coleoid cephalopods with the additional pressure necessary to impel blood through the gill capillaries, from which it is sucked into the auricles of the heart and eventually passed to the median ventricle.

The **nervous system** of cephalopods is complex in that the typical molluscan ganglia blend to form a massive circumesophageal "brain." Above the esophagus of living coleoids are the large cerebral ganglia, which give rise not only to large optic nerves but also to a pair of buccal nerves extending anteriorly to an upper pair of buccal ganglia and then, by way of a commissure around the esophagus, to a lower pair of buccal ganglia. The pedal ganglia supply nerves to the hyponome and forward divisions send nerves to each arm, which suggests to some that both hyponome and arms were derived from the primitive molluscan foot. Visceral ganglia give rise to three pairs of posteriorly directed nerves: one pair innervates various internal organs and the gills; another pair joins in a gastric ganglion between stomach and caecum, which it innervates; and the third pair, which contains giant motor neurons, innervates the mantle and its respiratory muscles. The nervous system of *Nautilus* is described in detail by STENZEL in another part of this volume. It is sufficient to point out here that it is similar to that of living coleoids, but the brain is much less concentrated and forms a heavy collar around the esophagus. For these and other reasons it is regarded as the more primitive structure.

The **sexes** are separate, the animals are oviparous, and in some (e.g., the octopod *Argonauta*) sexual dimorphism is conspicuous. A single saclike gonad in the large genital coelom discharges by one or two genital ducts into the mantle cavity. A capped, club-shaped spermatophore, which contains a springlike ejaculatory organ and masses of sperm and cement, is formed in the male seminal vesicle. Spermatophores are transferred to the mantle cavity or to suboral seminal receptacles of females by special copulatory structures quite separate from the genital ducts. In adult males of *Nautilus,* four modified arms form a permanent erectile intromittent organ (the spadix), but in other living cephalopods the male copulatory structure is a seasonally modified arm, the hectocotylus. Eggs are commonly protected by individual capsules secreted by the oviductal glands and may be aggregated in masses that are embedded in a gelatinous material secreted by the nidamental glands.

Cephalopod **eggs** are large and contain greater quantities of yolk than do those of other mollusks. Nothing is known about the early stages of development in *Nautilus,* but in other living forms cleavage is meroblastic and results in formation of a germinal cap of cells at the animal pole. The margins of this grow downward and envelop the yolk to form a yolk sac, which is gradually absorbed during later development. Development is direct and differs from that of other mollusks in that the embryo proceeds to the adult form without any intervening trochophore or veliger larval stage.

All cephalopods have **hard parts;** in many, however, they are inconspicuous and only the shells are commonly preserved as fossils. The univalved shell is external in *Nautilus* and presumably was borne in a similar manner in the many fossil nautiloids, bactritids, and ammonoids. In the modern coleoids and their fossil kin, the shell is overgrown by the muscular mantle and is at least largely internal. The well-developed shell of the extinct belemnoids and phragmoteuthidids is typical of the subclass; its chambered part, the phragmocone, does not differ materially from that of ammonoids and nautiloids, including the apparently ancestral bactritids. It is enveloped, however, in the more or less massive, calcitic sheath, the guard, which does not seem to have any equivalents in ammonoids and nautiloids. Furthermore, the shelly wall of the ammonoid and nautiloid body chamber is reduced in belemnoids and phragmoteuthidids to a dorsal, blade- or fan-shaped rudiment, the proostracum, which is perhaps the most diagnostic feature of coleoid shells. This typical coleoid shell is considerably reduced or modified in teuthidoids and sepioids. Only the proostracum is well developed in teuthidoids, the majority of which lack any trace of the phragmocone and guard of their presumably *Phragmoteuthis*-like ancestors. In most sepiids, just the greatly modified, dorsal part of the phragmocone remains; its ventral and lateral parts, as well as the siphuncle, are represented by small, nearly unrecognizable vestiges. The shell of the sepiid *Spirula,* a bathypelagic drifter, is a coiled normally chambered phragmocone that includes a siphuncle. In octopods the shell is reduced to paired or unpaired cartilaginous stylets.

Most living cephalopods are denser than the sea water in which they live and support themselves by active swimming. *Sepia, Spirula,* and *Nautilus,* however, have a density near that of sea water because of the presence of gas in the chambers of their rigid shells. *Sepia* can adjust its buoyancy in submarine-like fashion by pumping liquid into and out of shell chambers (1). This liquid has a salt content lower than the body fluid; hence osmotic pressure aids in counteracting hydrostatic pressure, at least at moderate depth. BIDDER (in 1) has noted the presence of liquid in the chambers of *Nautilus,* which is also known to accommodate itself effectively to greatly different depths during its lifetime. Presumably gas pressure can also be increased to prevent liquid from flowing into chambers and to prevent implosion of the shell. However, BIDDER has also noted that gas in the chambers of a *Nautilus* hauled up from 200 m. was not under noticeable pressure.

External shells, which form the bulk of the fossil record of cephalopods, can be visualized as more or less modified hollow cones that are straight, curved, or coiled (generally in a single plane). These are divided by septa into camerae pierced by the siphuncle. The septa and siphuncle readily distinguish the external shells of cephalopods from those of gastropods and scaphopods; furthermore, in only a few gastropods is coiling of the shell planispiral.

Both the external and internal shells of ancient cephalopods are among the best of stratigraphic indexes, for the animals evolved rapidly and along many different lines and this development is traceable in their hard parts. Furthermore, fossil cephalopods are abundant in rocks of many ages and they are easily identified even though incomplete and when preserved only as internal molds. Because many cephalopod shells were gas-filled and relatively light in weight, it was possible for the animals that bore them to range widely in shallow seas and some of them may have had the cosmopolitan distribution of many modern species. Many genera and possibly some extinct species are common to the eastern and western hemispheres.

MAJOR DIVISIONS OF CEPHALOPODA

The problem of defining main divisions of cephalopods, with designation of their names and authorship, offers sundry difficulties. First to be determined are the most acceptable criteria for classification, taking account of both living and fossil forms. Then, arrangement of assemblages of widely different comprehensiveness and magnitude in appropriate categories of taxonomic rank must be undertaken. Finally, questions of nomenclature must be settled and decisions reached about authorship of names and their dates.

It is clear from our summary discussion of their anatomy that living cephalopods can be divided readily into two major groups. The first, represented only by *Nautilus,* has an external shell, a bilobed hyponome, 94 tentacles, a mantle that is weakly muscular, two pairs of gills, and a primitive circulatory system. The second includes all other living cephalopods, which have 8 to 10 arms, a highly muscular mantle, a fused hyponome, a circulatory system that includes well-developed capillaries and supplementary branchial hearts, a single pair of ctenidia, and a shell that is internal or so reduced as to be vestigial.

Several (but not all) of these facts were noted by OWEN (4) in 1832, and he divided the Cephalopoda into two divisions, which he named Tetrabranchiata and Dibranchiata in accordance with the number of gills present in living representatives. Other authors have recognized the same two divisions, but have named them from other anatomic or developmental features. For example, Tentaculifera of D'ORBIGNY, 1852, and Acetabulifera of OWEN, 1836 [=Acetabulifères FÉRUSSAC & D'ORBIGNY, 1835] refer to the nature of the circumoral appendages; and Schizosiphona and Holosiphona of LANKESTER, 1883, as well as Tomochonia (or Funnaperta) and Gamochonia (or Funnoclausa) of HAECKEL, 1896, recognize differences in the structure of the hyponome. Ectocochlia and Endocochlia of SCHWARZ, 1894, give major prominence to the external or internal situation of the shell. Protocephalopoda and Metacephalopoda were proposed without explanation by GRIMPE (1922) as replacements for Tetrabranchiata and Dibranchiata, respectively, apparently to underscore the prevalent view (emphasized repeatedly by NAEF) that the characters of *Nautilus,* and thus supposedly of all fossil nautiloids and ammonoids, are primitive and represent those of the ancient stock from which all other cephalopods were derived.

Of all the many names available for major cephalopod divisions, only Tetrabranchiata and Dibranchiata (sometimes used in the shortened forms Tetrabranchia and Dibranchia) have been generally adopted. Even though this classification is eminently sound for living forms and has become firmly entrenched in most leading texts on invertebrate zoology, the legitimacy of applying it to other than living forms can be seriously questioned. That is, no fossil cephalopods are known in which the number of gills or arms (or the nature of the hyponome) can be observed and correlation of gill or arm number (or hyponome structure) with other anatomical features must always be at least partly conjectural. Furthermore, it is probable that the structures that distinguish the two modern groups of cephalopods are somewhat different answers to a common problem in cephalopod development, that of increasing respiratory and metabolic efficiency in connection with increased size and mobility (5). If this is so, both living groups are derived; neither is ancestral to, or more "primitive" than, the other.

From the start, however, OWEN (4) grouped in the Tetrabranchiata not only present-day *Nautilus* but also fossil nautiloids and extinct ammonites, as these groups were then understood. Later he included the extinct belemnites in the Dibranchiata. Although OWEN's classification has been followed by nearly all subsequent students of cephalopods, it is here rejected in large part, as are the denominations Tetrabranchiata and Dibranchiata (and their many equivalents).

Reasons are certainly in order for what may appear to be such summary rejection of a venerable and widely accepted scheme of cephalopod classification. Although not supported by concrete evidence, there are sound reasons for assuming that the earliest cephalopods had a single pair of gills (6, p. 32). This is a logical attribute of the "ancestral mollusk" and is the pattern displayed by primitive gastropods that have diverged from the ancient pattern far less than living cephalopods. Furthermore, a limited number of observations (summarized on page *K*111) supports the view that some Ordovician and Silurian nautiloids (Orthocerida and possibly Actinocerida, and thus supposedly tetrabranchiate) had some coleoid characters; that is, they possessed an ink sac and had few arms. Orthocerids were derived from the even more primitive ellesmerocerids (which include the oldest known cephalopods) (Fig. 70), and they undoubtedly gave rise to the bactritids, from which the belemnoids and most modern coleoids probably are descended. Although such speculation is probably idle, it is nevertheless tempting to attribute some dibranchiate characters not only to orthocerids and bactritids but to ellesmerocerids, as well. Beyond this, however, there is no information whatsoever as to the number of arms or gills in such important groups of nautiloids as the Endocerida, Actinocerida, Discosorida, Barrandeocerida, or Tarphycerida.

It is probably sound to assume that the entire order Nautilida, like its sole survivor *Nautilus,* was tetrabranchiate. This might also have been the condition of the Oncocerida (the supposed progenitors of the nautilids). However, it is the possibly dibranchiate Orthocerida, not the nautilids, that are usually singled out as ancestors of the bactritids, from which the Ammonoidea are thought to have evolved (Fig. 70). Although it is probable that ammonoids had essentially the same mode of life as nautilids and thus may have solved the problem of increasing respiratory needs by adopting the tetrabranchiate option, they must have done so independently of the stock that ultimately gave rise to *Nautilus.* Thus, the Tetrabranchiata, in which OWEN and others have consistently included both Nautiloidea and Ammonoidea, is polyphyletic in this inclusive sense and should either be abandoned or revised to include only the Nautilida (and possibly the Oncocerida). This possibility is rejected because it requires drastic revision in content of a well-known taxon and is based on assumptions too tenuous to be acceptable.

Finally, it is by no means certain that all living Dibranchiata have common ancestors in the Belemnoidea. Even if they do, however, they are clearly separated from the possibly dibranchiate ellesmerocerids, orthocerids, and bactritids by the profound structural and anatomical differences already noted. A major cephalopod division conceived to embrace them all would merely be meaningless; in any event, it would not serve the more pragmatic ends of paleontological taxonomy. The possibility of revising the Dibranchiata to include orthocerids, ellesmerocerids, and possibly actinocerids is rejected on that basis.

As an alternative, several authors prefer a threefold division of the Cephalopoda on a different basis. Major divisions, variously termed classes, subclasses, superorders, or orders, are recognized in these schemes as Nautiloidea, Ammonoidea, and Coleoidea; or as Nautiloidea, Ammonoidea, and Dibranchiata (e.g., BASSE, 1952). Rankings in all these schemes suggest that nautiloids, ammonoids, and dibranchiates (or coleoids) are of equivalent taxonomic rank, although it has been clear for more than a century that fossil representatives of the Nautiloidea *(sensu lato)* are characterized by a diversity of fundamental structural plans quite without parallel in either the ammonoids or dibranchiates. RUZHENTSEV's scheme of 1960, in which cephalopods are divided into subclasses Ectocochlia and Endocochlia (with the former subdivided into superorders Nautiloidea, Ammonoidea, and Bactritoidea) fails, also, to recognize this diversity among nautiloids and tends to perpetuate the unrealistic dichotomy suggested by study of living forms alone.

The arrangement of nautiloid orders in groups of higher taxonomic rank as proposed by SHIMANSKIY & ZHURAVLEVA (1961) is judged by contributors to the present volume to be the most suitable yet formulated in that (1) it provides indication that some orders are more closely related among themselves than to others and in that (2) it supplies an improved expression of classificatory rank correlated with the main non-nautiloid divisions of the Cephalopoda (e.g., Ammonoidea and Coleoidea). However, instead of the category superorder, used by SHIMANSKIY & ZHURAVLEVA, it is preferred to adopt subclass for rank designation of main divisions of the class Cephalopoda; furthermore, the name Coleoidea is preferred to Endocochlia. Elevation of cephalopods to the rank of a subphylum, as suggested by FLOWER & KUMMEL (1950), lacks merit in the view of the *Treatise* editor and authors working on the present volume.

An outline of the general classification adopted for organization of the present *Treatise* volume is given at the end of this chapter. Because this classification proposes revisions in rank of major taxa previously published in *Treatise* Part L on Ammonoidea, and includes names, authors, and dates that may appear novel, a statement of the principles followed in compiling it seems in order.

Guidance in naming species, genera, and family-group taxa is furnished by the Zoological Code (1961), but suprafamilial groups are expressly omitted from mention in it. Consequently, students of cephalopods, like workers on any large division of the animal kingdom, are faced with the task of rejecting various published suprafamilial names, accepting others, and possibly of coining entirely new names. Seemingly, choice must depend entirely on judgment, influenced but not controlled by usage. These matters are discussed in the Editorial Preface, accompanied by statement of a few informal rules that pertain especially to the *Treatise*.

Major Classification

- Class Cephalopoda Cuvier, 1797
  - Subclass Nautiloidea Agassiz, 1847
    - Order Ellesmerocerida Flower in Flower & Kummel, 1950
    - Order Orthocerida Kuhn, 1940
    - Order Ascocerida Kuhn, 1949
    - Order Oncocerida Flower in Flower & Kummel, 1950
    - Order Discosorida Flower in Flower & Kummel, 1950
    - Order Tarphycerida Flower in Flower & Kummel, 1950
    - Order Barrandeocerida Flower in Flower & Kummel, 1950
    - Order Nautilida Agassiz, 1847
  - Subclass Endoceratoidea Teichert, 1933
    - Order Endocerida Teichert, 1933
    - Order Intejocerida Balashov, 1960
  - Subclass Actinoceratoidea Teichert, 1933
    - Order Actinocerida Teichert, 1933
  - Subclass Bactritoidea Shimanskiy, 1951
    - Order Bactritida Shimanskiy, 1951
  - Subclass Ammonoidea Zittel, 1884
    - Order Anarcestida Miller & Furnish, 1954
    - Order Clymeniida Hyatt, 1884
    - Order Goniatitida Hyatt, 1884
    - Order Prolecanitida Miller & Furnish, 1954
    - Order Ceratitida Hyatt, 1884
    - Order Phylloceratida Arkell, 1950
    - Order Lytoceratida Hyatt, 1889
    - Order Ammonitida Zittel, 1884 [*non* Hyatt, 1889]
  - Subclass Coleoidea Bather, 1888 [includes Decapoda Leach, 1818 (*non* Latreille, 1802, Crustacea)]
    - Order Belemnitida Naef, 1912
    - Order Phragmoteuthidida Jeletzky, new
    - Order Teuthidida Naef, 1916
    - Order Sepiida Naef, 1916
    - Order Octopodida Leach, 1818

REFERENCES

Accounts of the anatomy and biology of cephalopods are to be found in nearly every good text on invertebrate zoology. No list of these is attempted here. The following contain supplementary information especially pertinent to matters discussed in this chapter.

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Yonge, C. M.

(5) 1947, *The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca:* Phil. Trans. Roy. Soc. London, ser. B, v. 232, p. 443-518, pl. 18.

(6) 1960, *General characters of Mollusca:* in Mollusca 1, Treatise on Invertebrate Paleontology, Moore, R. C., ed., Pt. I, p. 3-36.

ENDOCERATOIDEA—ACTINOCERATOIDEA—NAUTILOIDEA

By Curt Teichert and others

MORPHOLOGY OF HARD PARTS

By Curt Teichert

[United States Geological Survey]

In this chapter only those morphological features will be discussed that are common to two or more orders of the subclasses Nautiloidea[1], Endoceratoidea[1], Actinoceratoidea[1], and Bactritoidea. These cephalopod groups are highly diversified in regard to external shape and internal structure, and discussion of specialized structures within particular orders, and their terminology, is relegated to the introductory chapters under the orders concerned.

GENERAL FEATURES

All hard parts secreted by the animal, with exception of the jaws (*see* Rhyncholites), constitute the **conch** or shell, also (more rarely) called **conotheca** (Fig. 1). The conch consists of a posterior part, customarily called the **phragmocone** (although only partly homologous to the phragmocone of the Belemnoidea), which is divided into **chambers** (or **camerae**) by **septa,** and of an anterior, undivided and open part, the **body chamber,** which contains most of the soft tissues of the live animal. The septa are perforated by **septal foramina** through which passes the siphuncular cord, a fleshy extension from the body of the animal, called the **sipho.** The siphuncular cord is enclosed by **septal necks,** which are backward inflections of the septa extending from the periphery of the septal foramina, and by a series of distinct walls or sheaths, extending between successive septal necks, called **connecting rings.** Septal necks and connecting rings are jointly known as **ectosiphuncle;** the ectosiphuncle and the siphuncular cord compose the **siphuncle.**

CONCH

The conch can be visualized as a primarily conical wall of conchiolin and calcium carbonate (probably aragonite commonly), in the apical part of which septa are inserted with their concave faces directed toward the broad end of the cone. The outer wall of the conch is known as the **shell wall** or **wall of the conch,** sometimes erroneously referred to as the **test.** Little is known about the structure of the shell wall in fossil nautiloids.

The two principal layers that give rigidity to the shell of modern *Nautilus* and that are supposedly preserved in fossils are the porcelaneous ostracum and the inner, nacreous layer (*see* chapter on "Living Nautilus"). The ostracum consists of microscopic aragonite grains cemented by conchiolin, the nacreous layer of interlayered very thin lamellae of aragonite and conchiolin (Fig. 2,6). Shell walls of *Cimomia* and *Aturia* and of *Eutrephoceras* have been shown to consist wholly or in part of aragonite and thus may be supposed to have

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[1] Referred to in this chapter, prepared before final classification was adopted, as "nautiloids" or "nautiloid orders."

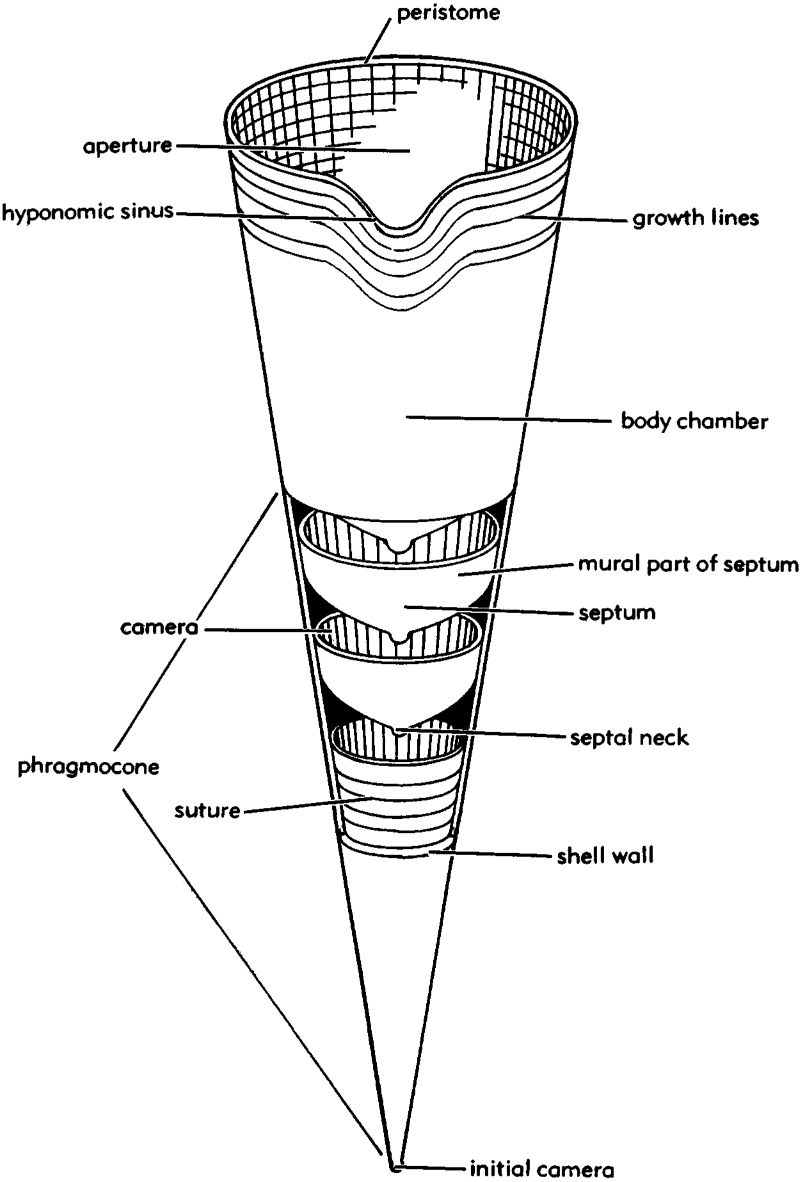

FIG. 1. Diagrammatic sketch of orthoconic conch. In the anterior part of the phragmocone septa are shown widely spaced to demonstrate their true shape (Teichert, n).

had a structure similar to that of *Nautilus* (3,36a). In Paleozoic *Dawsonoceras, Discoceras,* and *?Ptenoceras,* however, BØGGILD found an outer layer of regularly prismatic calcite and an inner layer of irregularly granular calcite. The outer layer is probably primary calcite while the inner layer is recrystallized, possibly from a primary aragonitic nacreous layer. An outer calcite and an inner aragonite layer is also present in many living bivalves and gastropods.

Excellently preserved shells of Pennsylvanian *Pseudorthoceras,* embedded in asphaltic substance, consist of aragonite (31).

In shells of Cretaceous nautilids, chiefly *Eutrephoceras,* TUREKIAN & ARMSTRONG (36a) found a relatively high concentration of some trace elements: Mg 375-1,615 ppm, Sr 1,650-10,000 ppm, Ba 95-1,000 ppm. These amounts are much higher than those in the shell of Recent *Nautilus* and are probably due to secondary enrichment during diagenesis.

When studied with the electron microscope, the conchiolin of the nacreous layer of fossil nautiloids (e.g., *Dolorthoceras, Pseudorthoceras, Eutrephoceras, Aturia*) exhibits the same characteristic reticulate texture as that of modern *Nautilus* (13, 14) (compare Fig. 2,*1-4* and Fig. 61).

Artifically or naturally etched surfaces of the nacreous layer, possibly also those of individual laminae within this layer, are characteristically sculptured by very fine, winding and contorted, or more rarely straight, raised lines. These are the **"wrinkled layers,"** well seen on internal molds or where shell layers are exfoliated (=*épidermides* of BARRANDE, *Runzelschicht* of German authors) (Fig. 3).

In most fossil nautiloids the original material of the shell wall has been converted to granular calcite, as demonstrated by BØGGILD (3) and by REYMENT & EKSTRAND (23).

Diagenetic recrystallization of shell layers of the type that results in formation of minute calcite pyramids, called **conellae,** well known from Mesozoic ammonoids (*Treatise,* p. *L*83) appears to occur extremely rarely in nautiloid shells. The only record of conellae in nautiloids is in a specimen of *Permonautilus* from the Permian of Kazan (USSR) (14a).

Formation of pearls in or upon the nacreous layer is rare in living *Nautilus.* One case of fossil-pearl formation has been reported in Triassic *Pleuronautilus* (18).

ORIENTATION OF CONCHS

As long as chambered cephalopods have been studied, at least since the early 19th century, orientation of the conch has been expressed in the following terms (Fig. 4): **anterior,** area of the aperture; **posterior,** apex of conch; **ventral,** side on which the hyponome and hyponomic sinus are situated; **dorsal,** side opposite the ventral side as defined above; **lateral,** areas between ventral and dorsal sides.

This terminology is based on comparison with the living *Nautilus,* in which the head-foot is anterior and the hyponome is the ventral part of the head-foot (compare chapter on "Living Nautilus").

As pointed out by FLOWER (8) and others, this conventional orientation of cephalopod shells perhaps is not in harmony with the biologic orientation as referred to the so-called hypothetical "primitive cephalopod." If, as is assumed by some authors, the *Nautilus* hyponome is a modified molluscan foot, its position is ventral, not anteroventral as in the conventional orientation. The "hypothetical" and "conventional" orientations are compared in Figure 4.

In view of the fact that the conventional orientation of cephalopods has been employed for more than a century and a half, being used in thousands of papers, and has been applied to descriptions of tens of thousands of specimens belonging both to nautiloid and ammonoid orders, any attempt to replace the conventional terminology with one based on hypothetical considerations would result in much confusion and would render difficult the use of all previously published literature dealing with chambered cephalopods. In this volume, as in the ammonoid volume of the *Treatise,* the conventional orientation is accepted, therefore.

For purposes of illustration the generally adopted orientation of figures on a page differs from both the conventional and the hypothetical orientation. Customarily, illustrations of orthoconic and cyrtoconic conchs are arranged with the apical end pointing to the lower edge of the page. Gyroconic and more tightly coiled conchs are shown with the aperture or, in case of fragmentary preservation, with the open end of the last preserved whorl pointing either to the upper left or to the upper right. This orientation of illustrations can be traced back to early monographs by SANDBERGER, QUENSTEDT, EICHWALD and others, and was more firmly established through publication by BARRANDE of the many volumes of plates illustrating Bohemian Paleozoic cephalopods. Over the years there have been comparatively few deviations from this pattern.

The following features of shell morphology may be used as evidence for the (conventional) orientation of fossil conchs.

Criteria Used for Orientation of Cephalopod Conchs

Morphological Feature	Special Characteristics	Position
Hyponomic sinus	Position ascertained from growth lines if aperture not preserved	Ventral
Conchal furrow	Continuous along inside of test (ridge on steinkern)	Ventral
Dorsal furrow	Discontinuous along mural part of septa (discontinuous ridges on steinkern)	Dorsal
Color markings	Rare and not unfailing	Dorsal and lateral
Marginal siphuncle position	Valid for eurysiphonate forms only	Ventral
Endosiphuncular canal closer to one side of siphuncle than to other	Valid for endocerids, actinocerids, some discosorids	Dorsal
Cameral deposits more strongly developed in one half of camerae than in other		Ventral

CONCH SHAPE

The shape of conchs of fossil nautiloid cephalopods ranges from conical, with straight central axis, through all degrees of curvature and coiling to tightly involute forms such as modern *Nautilus* (Fig. 5). Straight conchs are called **orthocones;** conchs curved in varying degrees, though completing less than one full circle, are called **cyrtocones.** Both may be either **longiconic** (long, slender, tapering gradually), or **breviconic** (short, stout, tapering rapidly). Conchs curved through 360 degrees have completed one **whorl** or **volution.** Each ad-

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Explanation of Figure 2,*1-4*

The micrographs show lacelike reticulated sheets of conchiolin from nacreous fragments of shell walls or of septa of various fossil nautiloids. The organic remnants, obtained by decalcification, were thinned by shaking or ultrasonic treatment into sheets permeable to electrons. Drops of aqueous suspensions of this material were deposited on screens previously coated with support films of formvar or carbon. Figures *1-4* illustrate exceptionally well-preserved organic residues from Pennsylvanian nautiloids collected in the Buckhorn asphaltic formations at Sulphur, Oklahoma. The chief features of the nautiloid "pattern"—sturdy trabeculae, sprinkled with hemispheric tuberosities, elongated or rounded openings (see chapter on "Modern *Nautilus*")—are recognizable. (Grégoire, 1958, Arch. internat. Physiol. Biochem., v. 66, p. 674; 1959, Bull. Inst. royal Science Nat. Belg., v. 35, p. 1; 1959, Nature, v. 184, p. 1157; and 1962, Bull. Inst. royal Sci. Nat., Belgique, v. 38, no. 49.)

1.—Unidentified orthoconic nautiloid, supplied by C. C. Branson. Iridescent blue-violet loose flakes of the shell wall. Decalcification left substantial, biuret-positive, brown organic particles. In this fragment of sheet, preserved small tuberosities scattered on the trabeculae, are still visible (×42,000).

2.—*Pseudorthoceras knoxense* McChesney, supplied by G. A. Cooper and U.S. National Museum. Biuret-positive residues. Flattening of trabeculae and disappearance of tuberosities are shown (×42,000).

3.—Splinter of fracture of curved, dark brown, iridescent flake from shell wall of an unidentified specimen, supplied by W. M. Furnish. This splinter was part of a fragment of a coiled shell, either an unidentified nautiloid, or possibly an ammonoid, identified by Furnish as *Eoasianites?* sp. The brown organic residues of the splinter were biuret-positive. The edges of three crystals belonging to the lamella, originally resting on this reticulated sheet and dissolved by the decalcifier, appear as white ridges rising slightly above the sheet (×42,000).

4.—Dark brown, curved, loose flake from an unidentified specimen supplied by N. D. Newell. Substantial biuret-positive organic residues. In other fragments of this sample, reticulated sheets closely resembled those represented in Fig. *1-3* (×42,000).

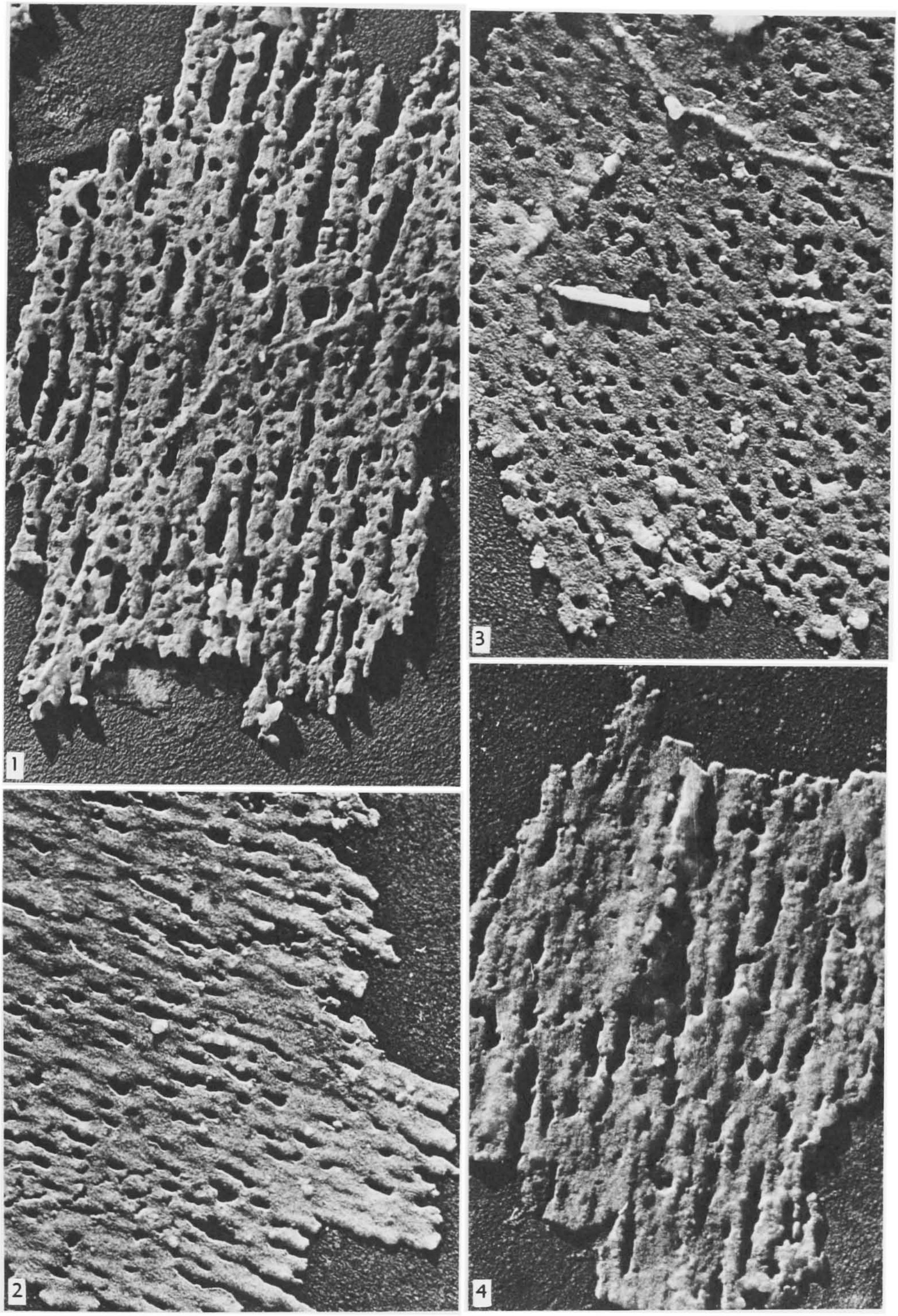

Fig. 2,*1-4*. Electron micrographs of mother-of-pearl from fossil nautiloids (explanation on facing page) (compare Fig. 61, 62) (courtesy of Charles Grégoire).

ditional coiling through 360 degrees constitutes another whorl. Openly coiled conchs in which successive whorls are not in contact with each other are called **gyrocones.** In closely coiled conchs, successive whorls are in contact with each other, and a number of terms are commonly applied to them to express degree of coiling and general shape: **serpenticone, tarphycone, ellipticone, sphaerocone, nautilicone, oxycone, platycone** (see glossary). Conchs that are closely coiled in early ontogeny but straight at maturity are known as **lituicones.** Conchs that are not coiled in a plane spiral, but in a three-dimensional spiral, like most gastropods, are **torticones** (often called **trochoceroid,** especially in older literature).

Coiled and curved conchs that have the venter on the outer, or convex, side are called **exogastric;** those that have it on the inner, or concave, side are **endogastric** (Fig. 6). In many forms in which the ventral side cannot be determined through observation of the hyponomic sinus, the position of the siphuncle is conventionally taken to be near the ventral side and endogastric or exogastric nature of the curvature is determined by siphuncle position.

Cross sections of orthocones or cyrtocones are generally circular, elliptical, or ovoid in shape. If the dorsoventral diameter exceeds the lateral one, the cross section is called **compressed;** if the lateral diameter is greater, the cross section is said to be **depressed** (Fig. 7). In coiled conchs, **whorl sections** may be modified in many ways.

A coiled conch in which all successive whorls are exposed in lateral view is called **evolute;** when successive whorls partly overlap and envelop preceding ones the conch is **convolute;** and if the last whorl envelops and covers all preceding ones the conch is **involute,** as in *Nautilus pompilius.*

In convolute and involute conchs, the concave, dorsal part of a whorl in contact with the convex, ventral part of the preceding whorl is called the **impressed zone** or **impressed area** (Fig. 8). The sides of the whorls are generally called **flanks** but are also known as **whorl sides** or **lateral areas.** As in straight or cyrtoconic forms, the cross section, or whorl section, of coiled conchs may be compressed or depressed, or more rarely, circular, or its shape may be modified in various ways, being subquadratic (with angular shoulders), **oxyconic** (with sharp external keel), or having other shapes.

The center of a coiled shell is the **umbilicus,** which may be **closed,** or **open (perforated),** according to whether the first whorl is tightly coiled around itself or not. The line of contact between the flanks of

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EXPLANATION OF FIGURE 2,*5-8*

The preparation of specimens is the same as stated for Figures *1-4.* The nacreous patterns of conchiolin are less well preserved in Figures *5, 7,* and *8.*

5.—Debris of a reticulated sheet from *"Nautilus"* sp., Eocene (Bartonian, Sables de Wemmel) from Brabant, Belgium, supplied by M. GLIBERT and Institut Royal des Sciences Naturelles de Belgique. The nautiloid pattern is still recognizable (×36,000). (Grégoire, 1959, Bull. Inst. royal Science Nat. Belg., v. 35, fig. 13, with permission of the Editor.)

6.—Positive carbon replica, shadow-cast with palladium, of a polished and heavily etched shell wall of *Nautilus* sp., Eocene (Bartonian), from the Wemmel, Brabant, Belgium. Plane of polishing transverse to the surface of mother-of-pearl and sectioning about 14 consecutive nacreous lamellae. A substantial system of interlamellar and intercrystalline organic reticulated sheets was freed by the decalcification process (×23,000). (Grégoire, 1959, Bull. Inst. royal Science Nat. Belg., v. 35, fig. 12, with permission of the Editor.)

7.—Iridescent silvery material from nacreous layers of shell wall or septum of *Aturia* sp., Oligocene (U. Rupellian), from Boom, Belgium, supplied by M. GLIBERT and Institut Royal des Sciences Naturelles de Belgique. Pebble-like alterations of the trabeculae are shown. All transition stages were found between a relatively well-preserved nautiloid pattern (*see* Grégoire, 1959, Bull. Inst. royal Science Nat. Belg., v. 35, fig. 14) and this structure (×42,000) (Grégoire, n).

8.—Remnants of brownish-gray fragments of shell wall of *Domatoceras* or *Stenoceras,* from Permian (San Andres Ls.), New Mexico, supplied by R. H. FLOWER. Pebble-like alteration and shrinkage in decalcified, organic, slightly biuret-positive material (×42,000) (Grégoire, n). [Some inorganic salts resistant to decalcifiers may assume, when agglutinated, shapes resembling those here shown. It is then necessary to use special procedures allowing these salts to dissolve while the organic matter remains unaffected.]

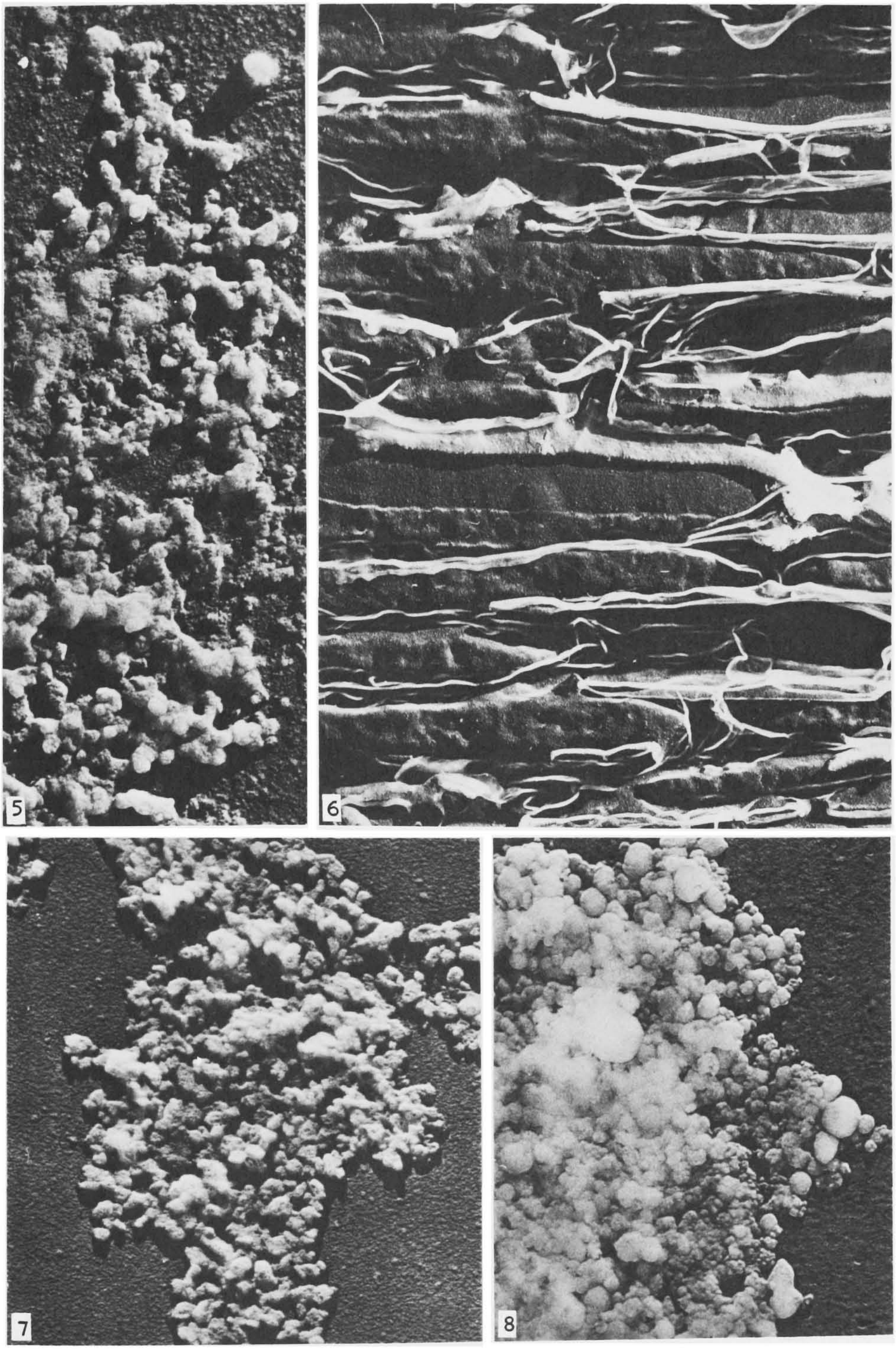


FIG. 2,*5-8*. Electron micrographs of conchiolin and mother-of-pearl from fossil nautiloids (explanation on facing page) (compare Fig. 61, 62) (courtesy of Charles Grégoire).

FIG. 3. Wrinkled layer in *Leurocycloceras subannulare* (MÜNSTER), Sil., Czech., ×8 (2).

successive whorls is called the **umbilical seam** (or **suture**). The flanks may at some point be bent strongly toward the umbilical seam and this portion is called the **umbilical angle** (or **umbilical shoulder**). The inner area of the whorl side tilted toward the umbilicus is called **umbilical slope,** or if sloping very steeply, **umbilical wall.**

SURFACE OF CONCH

The most delicate type of external ornamentation is represented by **growth lines,** which are lines on the surface of the conch marking its gradual increase in size. Their course is roughly transverse to the longitudinal axis of the conch, but generally they are sinuous. Most marked is the **ventral sinus,** a backward-bent indentation of the growth lines. Since every growth line marks a former aperture, the position of the ventral sinus indicates position of the hyponomic sinus of the body chamber and thus serves to orient conch fragments with imperfectly preserved or missing body chambers. Conchs in which growth lines form the only kind of external sculpturing present are generally called smooth.

The conch wall of many nautiloids is more or less elaborately sculptured. Simple parallel, small to minute grooves are called **striae,** and corresponding small ridges or raised lines, **lirae.** Both striae and lirae may run parallel or transverse to the longitudinal axis of the conch. **Costae** or ridges are larger elevations that in straight or cyrtoconic nautiloids generally run subparallel (longitudinally) to the long axis of the conch. In coiled conchs costae may be arranged parallel to the umbilical seam (revolving costae, striae, lirae) or they may be a feature of the flanks, arranged more or less radially with respect to the umbilicus.

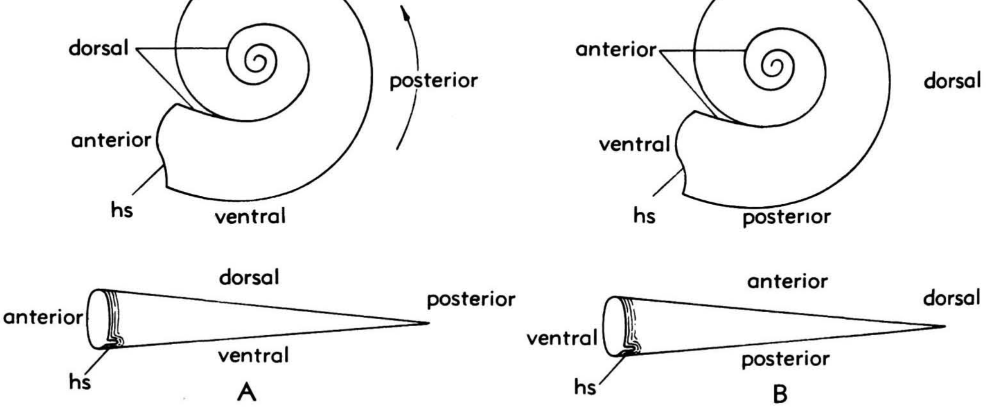


FIG. 4. Comparison of *(A)* "conventional" and *(B)* "hypothetical" orientation of coiled and straight cephalopod shells (*hs,* hyponomic sinus) (Teichert, n).

Transverse elevations that surround the entire conch in orthocones and cyrtocones are called **annulations;** shells with annulations are **annulate (annulated).** Annulations may be thickenings of the walls of the conch, in which case the internal mold of the conch is smooth. More commonly annulations are due to undulations of the conch wall and then the internal mold is annulate as well.

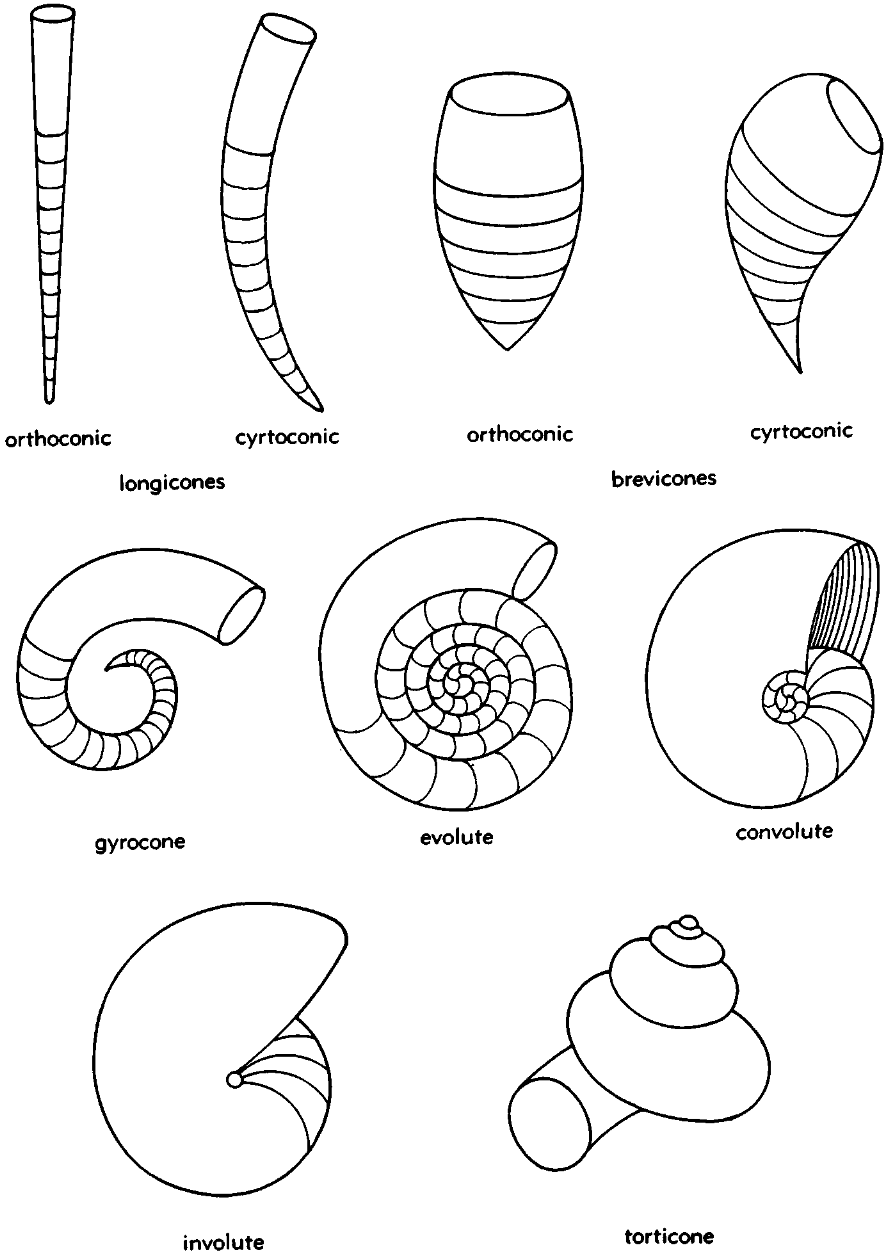


FIG. 5. Some common types of nautiloid conchs (Teichert, n).

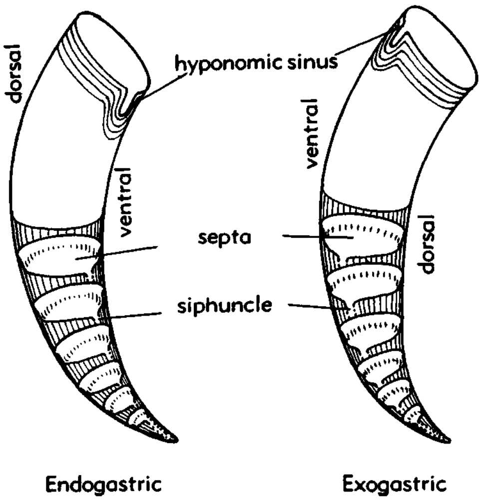


FIG. 6. Diagram explaining difference between endogastric and exogastric conchs. Body chamber shown in external view, phragmocone cut in half (Teichert, n).

In different genera many combinations of transverse and longitudinal striae, lirae, and costae occur, with or without presence of annulations, especially among the Orthocerida.

The surface of many nautiloids, especially curved and coiled ones, is ornamented with nodes, more rarely with spines or ribs. A special type of ornamentation consists of **apertural flanges,** more or less regularly spaced, giving some shells a frilled exterior (*Zittelloceras,* some Rutoceratidae). Apertural flanges are known in nautiloids of all ages excepting the Cenozoic ones, beginning in those of the Lower Ordovician *(Diastoloceras, Aethoceras).*

To describe the ornamental features of coiled conchs, essentially the same terminology applies as that used for ammonoids, although in a somewhat simplified form, because nautiloid conchs, in general, never attain the elaborate surface sculpturing that is characteristic of many ammonoids, es-

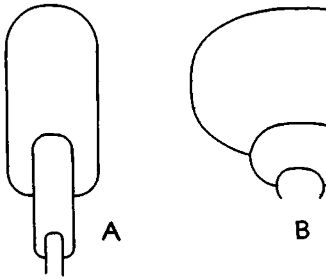


FIG. 7. Compressed *(A)* and depressed *(B)* whorl section in coiled conchs (Teichert, n).

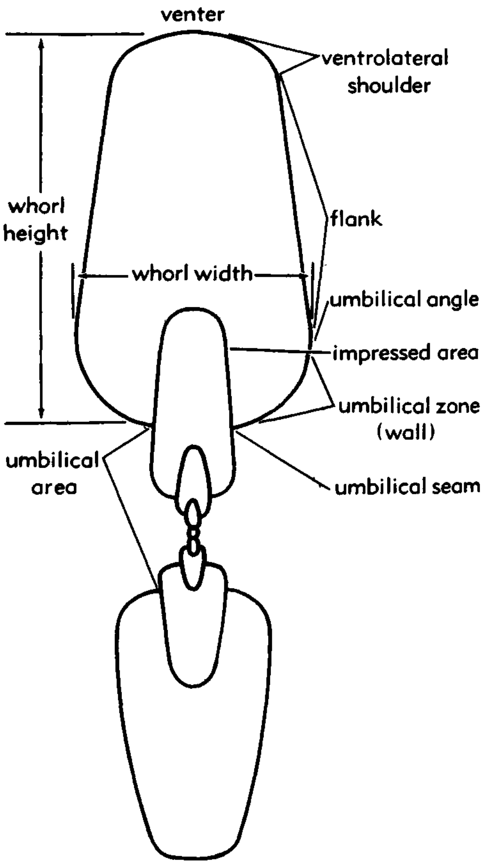
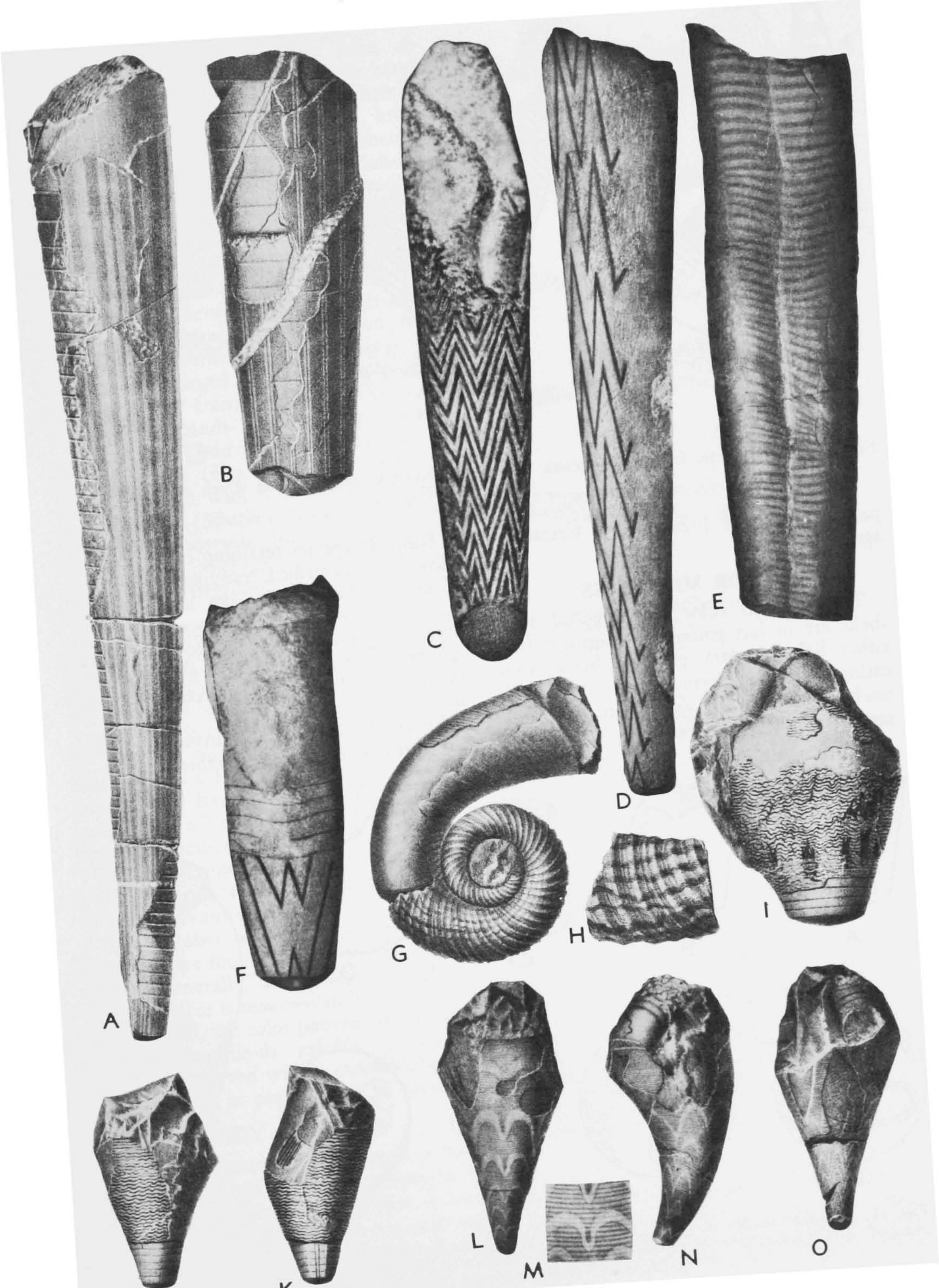


FIG. 8. Diagrammatic cross section of coiled conch (Teichert, n).

FIG. 9. *(Facing page.)* Principal pigmentation patterns of nautiloid conchs.——*A,B. Ormoceras? pellucidum* (BARRANDE), Sil., Czech., ×0.7.——*C. Michelinoceras? anguliferum alpenense* FOERSTE, Dev., USA (Mich.), ×1.1.——*D. M.? anguliferum* (D'ARCHAIC & DE VERNEUIL), Dev., Ger., ×1.3.——*E. M.? dunbari* FOERSTE, Penn., USA(Okla.), ×1.——*F. Hedstroemoceras haelluddenense* FOERSTE, Ord., Sweden, ×1.——*G, H. Trochoceras pulchrum* BARRANDE, Sil., Czech., ×0.7, ×1.——*I. Rizosceras? zebra* (BARRANDE), Sil., Czech., ×0.7.——*J,K. R.? cyathus* (BARRANDE), Sil., Czech., ×0.7.——*L-O. R.? parvulum* (BARRANDE), Sil., Czech., ×0.7 (2; 12).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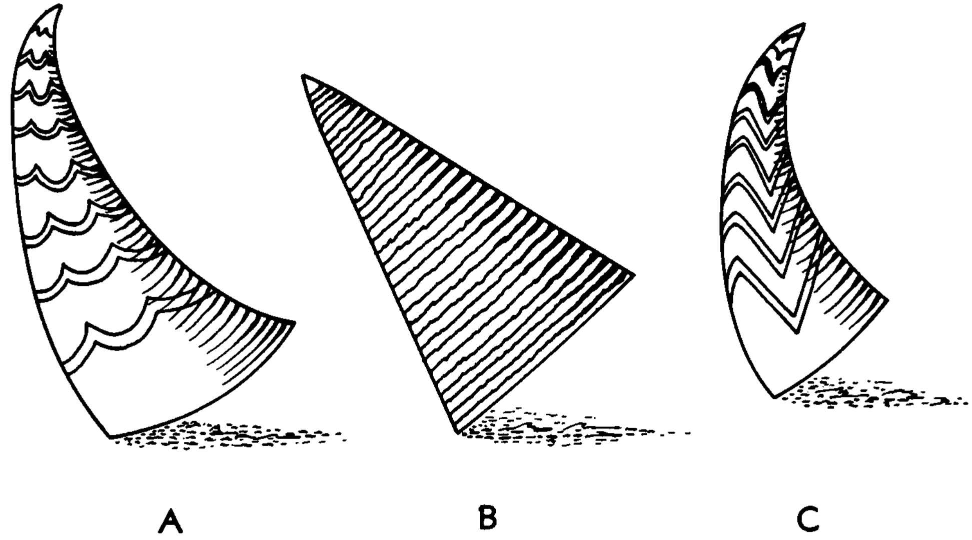

FIG. 10. Color patterns in some cyrtoconic brevicones, shown in shell position which probably occurred during life (25).

pecially those of Jurassic and Cretaceous age.

COLOR MARKINGS

The so-called color markings of fossil shells are in fact patterns of pigmentation, either light or dark gray, or black, indicating presence of former color patterns. No unchanged, original colors are ever preserved in fossil cephalopods.

Some 40 species retaining color markings have been described, ranging from Ordovician to Tertiary in age and including representatives of the Orthocerida, Actinocerida, Discosorida, Barrandeocerida, Oncocerida, and Nautilida. Most of the relevant observations have been collected and summarized by FOERSTE (12).

In straight and weakly curved longicones and brevicones a considerable variety of

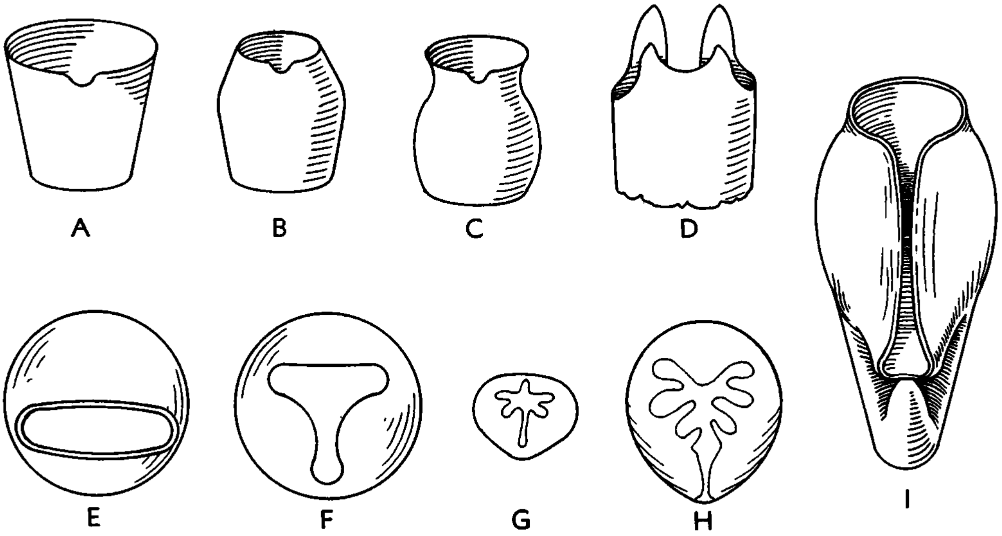

FIG. 11. Different shapes of body chambers in nautiloids: *A*, open; *B*, contracted; *C*, constricted; *D*, pronged; *E-H*, various types of contracted apertures (*Mesoceras, Mandaloceras, Pentameroceras, Octamerella*); *I*, visored (*Phragmoceras*) (Teichert, n).

patterns of color banding has been observed: (1) transverse, wavy, narrow bands (Silurian *Rizosceras?* from Bohemia) (Figs. 9,*J*,*K*; 10,*B*); (2) transverse, broad bands (Silurian *Rizosceras?* from Bohemia, Carboniferous orthocerids from Oklahoma and Belgium) (Fig. 9,*E*); (3) longitudinal bands and lines (orthocerids from Silurian of Bohemia, Ordovician and Silurian of North America) (Fig. 9,*A*,*B*); (4) combination of longitudinal and transverse lines (Silurian *Hexameroceras*); (5) longitudinal series of short transversely oriented lines (Silurian *Rizosceras?* from Bohemia); (6) irregularly arranged black blotches (Silurian *Rizosceras?* from Bohemia) (Fig. 9,*I*); (7) oblique bands with zigzag pattern across venter (Ordovician *Hedstroemoceras* from Sweden) (Fig. 9,*F*); (8) bands in chevron pattern with 6 to 8 chevrons per circumference (Silurian *Rizosceras?* from Bohemia, orthocerids from Devonian of Germany and Michigan, and Lower Carboniferous of Belgium) (Fig. 9,*C*,*D*, *L-O*; 10,*A*,*C*).

In coiled forms color markings have been described from Devonian *Trochoceras,* where they appear as longitudinal, revolving bands (Fig. 9,*G*,*H*). A *Vestinautilus* from the Carboniferous of Ireland is colored by irregular spots and bands. A *Stenopoceras* from the Permian of Texas has been described as having a colored growth-line pattern and a Tertiary *Aturia* was found to have semicircular, transverse zones or bands.

No fossil coiled conch has been found with a color pattern closely similar to that of modern *Nautilus.*

In a number of orthoconic forms, color markings are found on only one side of the conch. Generally, this is demonstrably the dorsal side, or is assumed to be so.

In general, the color patterns of the shells of fossil nautiloids exhibit considerable diversity and even within individual orders no uniformity in patterns can be discerned.

BODY CHAMBER

In stenosiphonate conchs, just as in living *Nautilus,* the body chamber contained the animal's entire visceral mass, but in eurysiphonate form, part of the visceral mass was probably lodged in the anterior division of the siphuncle.

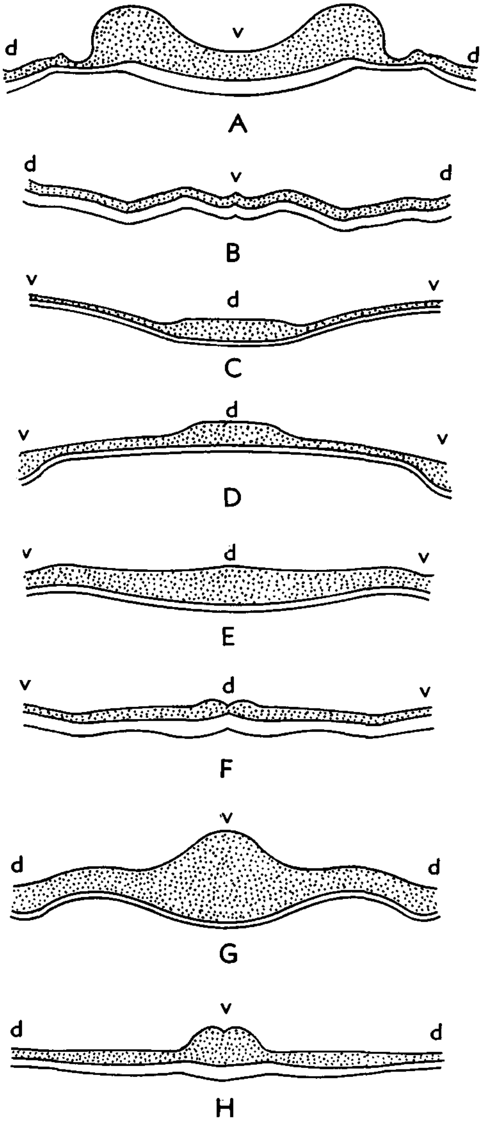

FIG. 12. The periphract (stippled) in some nautiloid orders (*v*, ventral and *d*, dorsal side of body chamber).——*A*. Nautilida (*Eutrephoceras*) (21).——*B*. Orthocerida (*Clinoceras*) (Mascke, 1876).——*C*. Ellesmerocerida (*Cochlioceras*) (21).——*D*. Orthocerida (*Lyecoceras*) (21).——*E*. Endocerida (*Cameroceras?*) (Schröder, 1882).——*F*. Tarphycerida (*Lituites*) (22).——*G*. Tarphycerida (*Estonioceras*) (21).——*H*. Barrandeocerida ("*Uranoceras?*") (21).

The body chambers of some nautiloid orders exhibit an extraordinary variety of form (Fig. 11). The body chamber is open at the anterior end, where head and tentacles of the animal protrude. This is the **aperture;** the edge of the conch surround-

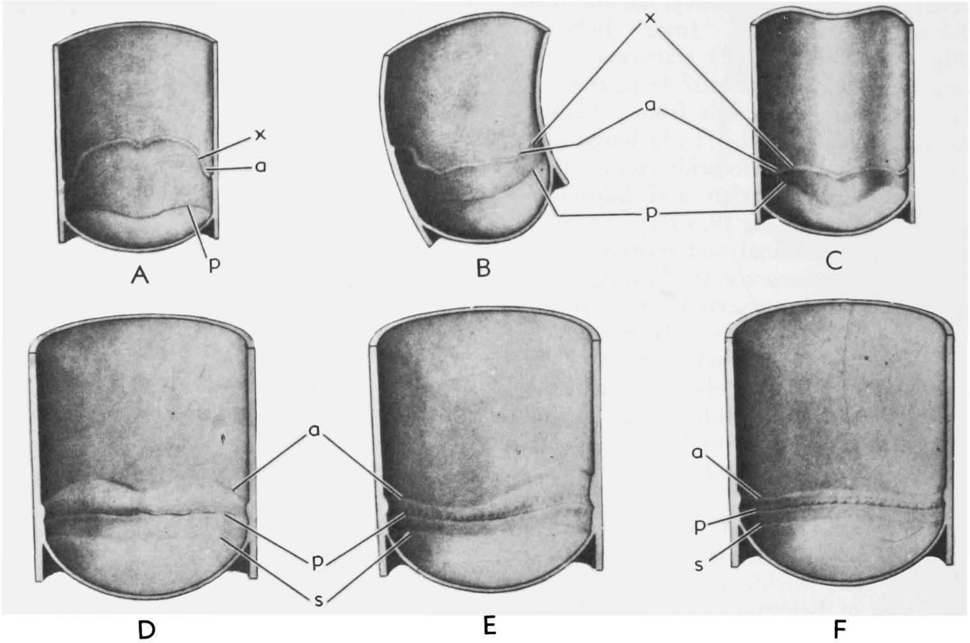

FIG. 13. Reconstructions of body chambers showing periphracts (*a*, anterior and *p*, posterior margins of annular elevation, *x*, anterior annular ridge; *s*, edge of free part of septum).——*A-C. Discoceras* sp., Ord., Est.; vent., lat., dors. interiors (ventromyarian), ×1.25 (21).——*D-F. Lyecoceras?* sp., Sil., Swed.; dors., lat., vent. interiors (dorsomyarian), ×2 (21).

ing the aperture is called the **peristome.** The peristome has a ventral indentation, termed the **hyponomic sinus.** Apart from this, the peristome may be smooth, or it may have additional indentations. Rarely, the peristome may be produced into pointed salients and broadly rounded recesses, as in *Lituites*.

The simplest form of body chamber expands from the base to the aperture at the same rate as the anterior portion of the phragmocone and has an unmodified, **open** and **entire aperture** with outline larger than, but congruent to any chosen cross section of the conch. Such simple geometrical relationships are present in the Ellesmerocerida, Orthocerida, Endocerida, and in most coiled forms.

In the orders Ascocerida, Actinocerida, Discosorida, and Oncocerida, many modifications in the shape of the body chamber, and especially of its aperture, occur. A body chamber may first expand from its base, then gradually diminish toward the aperture. Such apertures are said to be **contracted.** Body chambers with their smallest diameters a short distance behind the aperture are called **constricted,** and the constricted part is sometimes called the **neck.** In front of the neck, the body chamber of such forms expands into a **flared aperture.**

In some body chambers an internal thickening occurs behind the aperture. In such chambers only the interior (and the internal mold) may appear to be constricted.

Contracted apertures may be either simple and congruent to the general cross section of the conch, or they may be greatly modified by being compressed or incised in various manners (Fig. 11, *E-H*). The most elaborately shaped apertures are found among the Oncocerida.

In a few Orthocerida the body chamber has two or more external grooves or furrows (*Orthoceras, Bifoveoceras, Ctenoceras*).

A **conchal furrow** may also be present on the inside of the body chamber, though generally only along the posterior part of its ventral side (*see* under phragmocone).

The problem of attachment of the body to the body chamber is of a different magni-

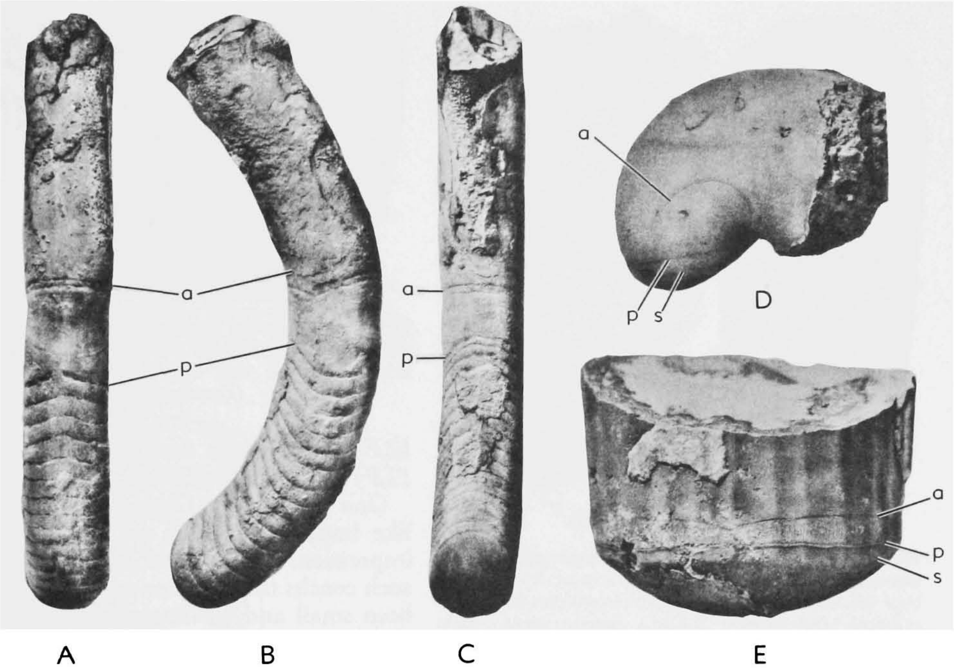

FIG. 14. Types of periphracts shown as impressions on internal molds (*a*, anterior and *p*, posterior edges of periphract; *s*, edge of free part of septum).——*A-C. Tragoceras falcatum* (VON SCHLOTHEIM), Ord., Est.; vent., lat., dors. (ventromyarian), ×0.7.——*D. Eutrephoceras bellerophon* (LUNDGREN), Swed.; lat. (pleuromyarian), ×0.7.——*E. Kionoceras angulatum* (WAHLENBERG), Sil., Swed.; dors. (dorsomyarian), ×0.7 (21).

tude in conchs with contracted and with open apertures.

In body chambers with open apertures the body must be firmly anchored to the wall as in *Nautilus* (see below), where the attachment areas of the retractor muscles and sheetlike tendons (aponeuroses) form a continuous ring, the periphractic imprint. This condition is found in all groups that have body chambers with open apertures, but several modifications from the nautilid pattern are observed (Fig. 12). The anterior and posterior borders of the periphract imprint may be slightly raised and are then called the **anterior** and **posterior annular ridges** (Fig. 13,*D-F*).

In living *Nautilus* it is possible, within the ring of attachments, which are flush with the shell wall, to discern the attachment areas of various muscles and ligaments. In fossil nautiloids these areas cannot be discerned, but the place or places where the ring of attachments is wide indicates the area, or areas, of attachment of the powerful retractor muscles. In addition, the attachment areas are often buttressed or elevated (annular elevation of MUTVEI) in these fossils. In *Nautilus* (see chapter on "Living Nautilus") the retractor muscles are attached to the opposite flanks of the body chamber, a condition known as **pleuromyarian.** This disposition of the retractor muscles is typical, as far as is known, for all members of the order Nautilida (Figs. 12,*A*, 14,*D*), and has been traced back to Early Carboniferous forms.

Present investigations suggest that the pleuromyarian disposition of the retractor muscles is a comparatively late feature in evolution of the nautiloids and that the retractor muscles of earlier nautiloids were closely paired either on the ventral or dorsal side of the body chamber. The former condition is called **ventromyarian,** the latter **dorsomyarian.** In view of the extreme scantiness of information on the periphract and its retractor muscle impressions in fossil nautiloids, it is difficult to give generally valid characterizations of the various orders in regard to these features, but some interesting facts have emerged.

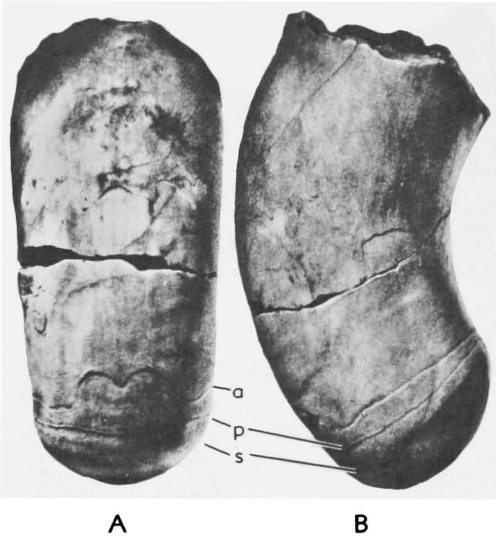

FIG. 15. Types of periphracts shown as impressions on internal molds (explanation of letter symbols as for Fig. 14).——*A,B. Uranoceras? longitudinale* (ANGELIN), U.Ord., Swed.; vent., lat. (ventromyarian), ×0.5 (21).

The dorsomyarian condition is possibly the most primitive one. It appears in *Cochlioceras* (Fig. 12,*C*), the only ellesmerocerid in which presence of this feature has as yet been demonstrated. It has been found in various orthocerids *(Orthoceras, Geisonoceras, Kionoceras, Lyecoceras)* (Figs. 12,*D*; 13,*D-F*, 14,*E*), in the Endocerida (Fig. 12,*E*), and in the family Lituitidae (Fig. 12,*F*) of the Tarphycerida.

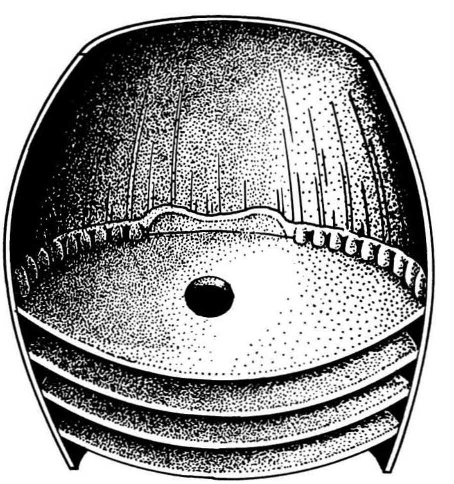

FIG. 16. Body chamber of typical oncocerid, showing periphract with buttresses of the "basal zone" and ventromyarian muscle impressions (Teichert, n).

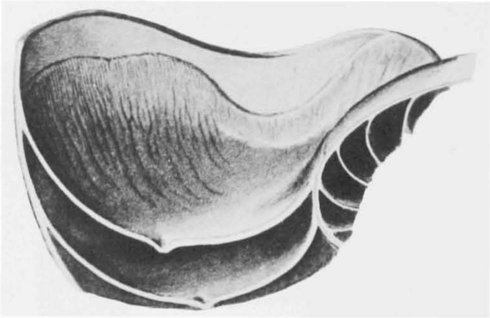

FIG. 16A. Sectioned specimen of *Nautilus pompilius* showing impressions of vascular system on adoral side of septum that adjoins body chamber, ×1 (Deecke, 1913).

One orthocerid *(Clinoceras)* has a ring-like imprint in which no retractor muscle impressions are discernible (Fig. 12,*B*). In such conchs the retractor muscles must have been small and weak, perhaps indicating a sluggish, inactive mode of life of the animal concerned.

The ventromyarian condition is known to occur in openly or closely coiled Tarphycerida (Figs. 12,*G*; 13,*A-C*; 14,*A-C*) and in the Ascocerida and Barrandeocerida (Figs. 12,*H*; 15,*A,B*). It is illustrative of the unsatisfactory state of our knowledge that for the two last-mentioned orders only one specimen of Ascocerida and very few of the Barrandeocerida are known that show the imprints. In slender, open chambers, such as that of *Tragoceras* (Fig. 14,*A-C*), the annular elevation may be exceptionally wide, providing a greater muscle attachment area.

The Oncocerida and Discosorida are also ventromyarian, but the tendon and muscle imprints are modified by the appearance of short longitudinal ridges or buttresses (Fig. 16). This ridged area was formerly described as the "basal zone," a designation that is now obsolete. The purpose of the ridges is not immediately evident. They enlarge the surface of the muscle attachments, but most forms that have them also have contracted apertures and were, therefore, not in great need of an increased muscle-attachment area.

No actinocerid in which impressions of the muscles are preserved has as yet been described.

Very rarely, impressions of a vascular system have been observed on the concave side of the last septum in modern *Nautilus* (37; DEECKE, 1913, fig. 5). DEECKE observed its presence also in fossil conchs identified as *Eutrephoceras*. I have been able to confirm these observations by examination of DEECKE's specimens (Fig. 16A).

PHRAGMOCONE

The phragmocone is the chambered part of the conch. It extends from the apex to the last septum which forms the base of the body chamber. The following description is concerned with features of the mature phragmocone. Special conditions in the extreme apical part will be described in the chapter on early ontogeny.

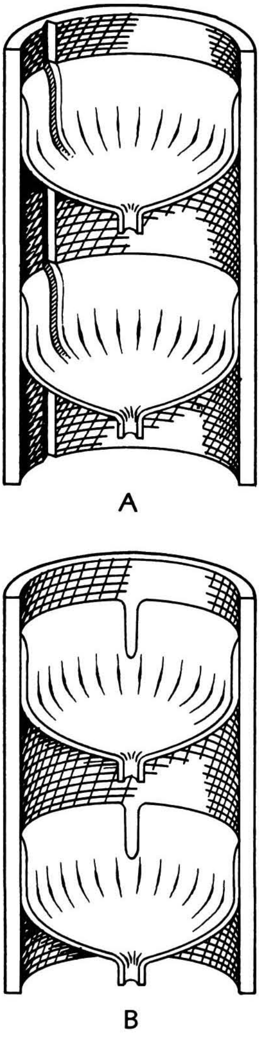

FIG. 17. Diagram to explain difference between conchal furrow *(A)* and dorsal furrow *(B)* (Teichert, n).

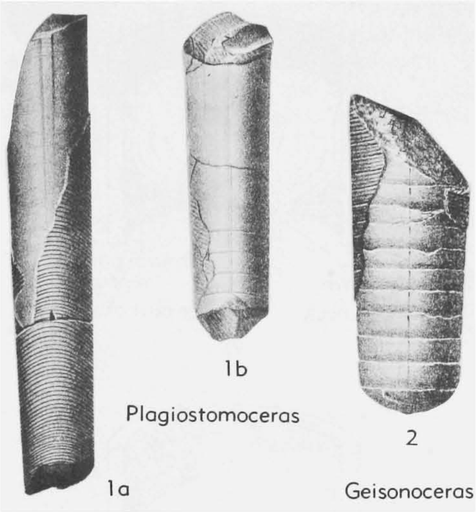

FIG. 18. Appearance of conchal and dorsal furrows on internal molds.——*1a,b.* Body chambers of *Plagiostomoceras* with double and single conchal furrows; Sil., Czech., ×0.7 (Barrande, pl. 297, 1870).——*2.* Steinkern of phragmocone of *Geisonoceras bipellis* (BARRANDE), showing impression of dorsal furrow; Sil., Czech., ×0.7 (Barrande, pl. 308, 1870).

The inside of the wall of the phragmocone is generally smooth, except for a sharply incised mid-ventral furrow that is present in many nautiloids and which is called the **conchal furrow** (Fig. 17,18). On internal molds it appears as a fine mid-ventral line or ridge. It occurs frequently in the Orthocerida, the Nautilida, and also in the Bactritida. In some genera (e.g., *Plagiostomoceras*) there may be two parallel conchal furrows; in others (e.g., *Striacoceras*) the main conchal furrow is paralleled by weaker furrows, the **ventrolateral furrows,** one on each side.

The septa that subdivide the phragmocone into camerae are saucer- or cup-shaped partitions that fit tightly into the inside of the conch wall (Fig. 19). Degree of concavity of the septa and their spacing in relation to the conch diameter are important criteria for differentiation of species. Occasionally, odd septa may be found missing

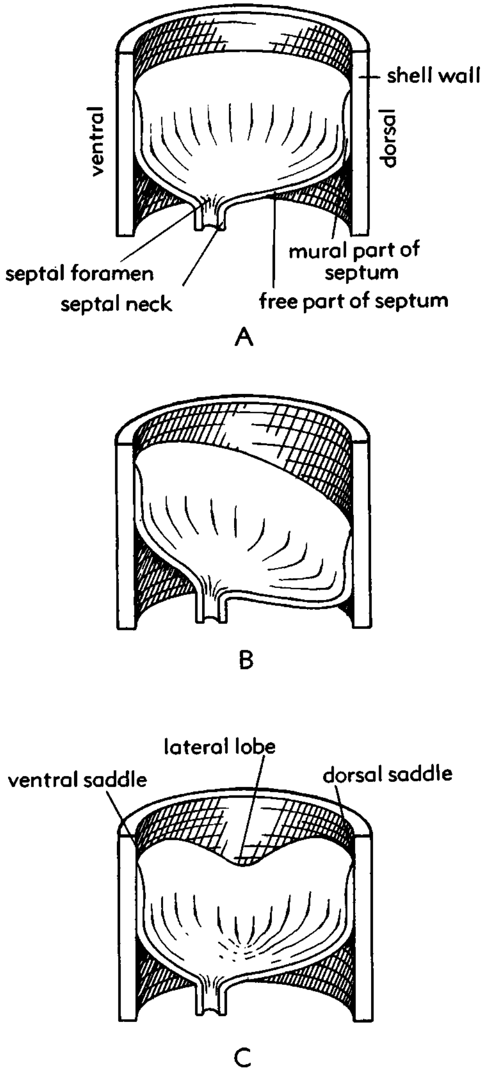

FIG. 19. Relationship of septum to shell: *A,* septum with straight, transverse suture; *B,* with straight, oblique suture; *C,* with suture having dorsal and ventral saddles and lateral lobes (Teichert, n).

or only incompletely developed, but such cases are rare (17) (Fig. 20).

Normally the septa are equidistantly spaced except for the last two or three septa which at maturity are more closely spaced than the others. Spacing of the septa just behind the body chamber is thus a diagnostic feature for separation of mature conchs from those that have not yet reached maturity.

Abnormal crowding of septa in other parts of the phragmocone indicates almost certainly a pathologic condition (Fig. 21).

Each septum consists of an anterior, cylindrical part firmly attached to the inside of the shell wall and called the **mural part** of the septum, and of an evenly concave part which crosses the conch transversely and is called the **free part** of the septum (Fig. 19). The free part is perforated by a circular to oval opening, the **septal foramen,** around which the septum extends backward to form the **septal neck** either resembling an open cylinder or various modifications of a cylindrical form. The septal necks are generally regarded as part of the siphuncular structure of the conch, and they will be discussed in more detail in the subsequent description of the siphuncle.

The length of the mural part of the septum differs greatly in different groups. In the Actinocerida it extends the full length of one camera—that is, the inside of the shell wall is entirely lined by the mural parts of all septa. In *Nautilus* the mural parts of the septa are very short. In other groups they are of intermediate length.

In many genera, erratically distributed in various orders (Orthocerida, Actinocerida, Nautilida), the mural parts of septa are not developed along a narrow mid-dorsal line. This is the **septal furrow,** also called **dorsal furrow,** because it is present only on the dorsal side of the conch (see Fig. 64). It is the *"ligne normale"* of BARRANDE, and the *"Normallinie"* of earlier German authors (DEWITZ, SCHRÖDER, and others). Where present, it is generally discontinuous, because in many nautiloids the mural part of the septum extends only part of the way between one septum and the next (Figs. 17, 18).

The free part of a septum in its simplest form is concave forward, the concavity varying greatly in different forms. This simple condition is found in the majority of nautiloids, straight, curved, or coiled. In some advanced Nautilida, however, the free part of the septum may be undulating.

On an internal mold (steinkern) of a conch, the outer edge of the free part of the septum is visible as a transverse line, which is called the **suture.** In its simplest form the suture is circular or elliptical, and

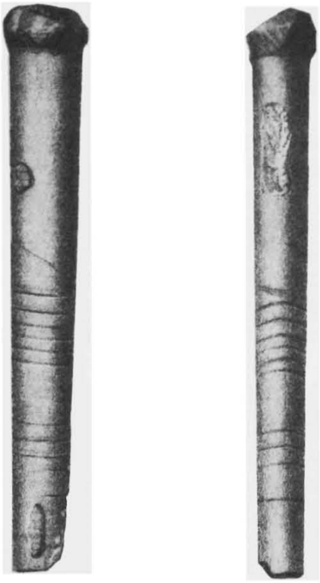

FIG. 20. Portions of phragmocones of *Plagiostomoceras panderi* (BARRANDE) with missing septa. Sil., Czech., ×1 (Barrande, pl. 225, 1866).

transverse, with the diameters of the circle or ellipse oriented perpendicularly to the long axis of the conch. Such a suture is called straight, because sutures are best illustrated as if they were unrolled on a flat plane.

If the peripheral area of the free part of the septum is wavy, the suture is sinuous. The major parts of a suture directed alternately forward and backward are called **sutural elements.** The forward bulging parts of a suture are called **saddles,** and the backward bulging parts **lobes.** The simplest and most common type of sinuous suture has one saddle on the ventral side, and another on the dorsal side, and one lobe on each of the flanks of the conch (Fig. 19,*C*).

In coiled conchs the part of a suture exposed on the outside of a whorl, between the umbilical seams, is called the **external suture,** and the part situated on the dorsum, hidden from view in an undamaged shell, is the **internal suture.** Many coiled conchs possess a small, acute dorsal lobe occupying the center of the main internal lobe. This is called the **annular lobe** (*see* Fig. 58).

Only among the Nautilida do somewhat more elaborate sutures develop, especially in certain Triassic and early Tertiary groups (Syringonautilidae, Siberionautilidae, Hercoglossidae, Aturiidae, and some others). The most complex suture yet found among nautiloids is that of *Siberionautilus,* in which the suture across the ventral region is subdivided into numerous small saddles and lobes.

CAMERAL DEPOSITS

In many nautiloids the camerae are wholly or partly filled by linings of calcium carbonate deposits, which, as suggested by various lines of evidence, were secreted by the animal while it was alive. These are called **cameral deposits.**

Most cephalopod shells when entombed in sediment have empty camerae except for water that may enter them. Later, during diagenesis, calcite from circulating solutions gradually is deposited in the camerae.

Distinction between deposits due to diagenetic infiltration ("secondary deposits") and deposits made by the living animal ("primary deposits") is generally easy to establish. Secondary (diagenetic) deposits surround more or less uniformly all walls of camerae (including septa), inside the

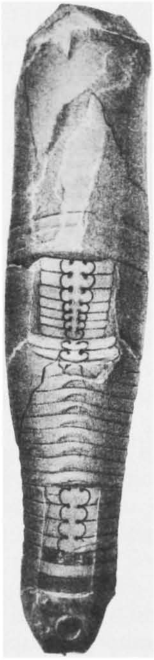

FIG. 21. Conch of *"Cyrtoceras" repletulum* BARRANDE with retarded growth stages of camerae and siphuncle, probably due to disease. Sil., Czech., ×0.7 (Barrande, pl. 499, 1877).

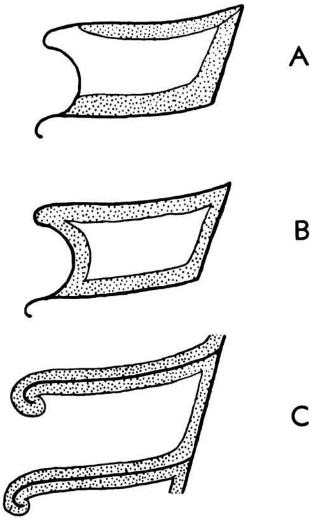

FIG. 22. Primary and secondary deposits in camerae: *A,* primary (no deposits along connecting ring); *B,* secondary (connecting ring preserved); *C,* secondary (connecting ring destroyed) (35).

shell wall, and ectosiphuncle (Fig. 22). Primary (organically precipitated) deposits cover only the anterior and posterior parts of the septa and their mural parts (Fig. 23). Furthermore, primary deposits decrease in bulk from the apical toward the oral end of the phragmocone, in some genera with great regularity (Fig. 24). They may be absent in the anterior portion of the phragmocone and they are never present at the bottom of the body chamber.

Cameral deposits are of the following basic types (Fig. 25): (1) **episeptal,** deposited on the anterior, or concave, surface of a septum; (2) **hyposeptal,** deposited on the posterior, or convex, surface of a septum. Episeptal deposits covering the mural parts of septa are often referred to as **mural deposits.**

Episeptal (and mural) deposits may be present either alone or in combination with hyposeptal deposits. The latter rarely occur alone, except in adoral portions of phragmocones, where their formation may precede that of episeptal deposits.

As episeptal and hyposeptal deposits grow, they may meet somewhere approximately at mid-height of the camerae. In transverse section their contact plane appears as a thin line running from the anterior outer corner of a camera down the middle of the camera to the vicinity of the siphuncle, generally ending in a small, open space of subtriangular cross section not occupied by deposits.

This contact plane has been called the "pseudoseptum" by several earlier students of cephalopods (HOLM, SCHRÖDER, and others), because a brown amorphous substance is often seen between the epi- and hyposeptal deposits. Most probably this substance stems from an organic membrane that originally covered the deposits and was functionally connected with their formation.

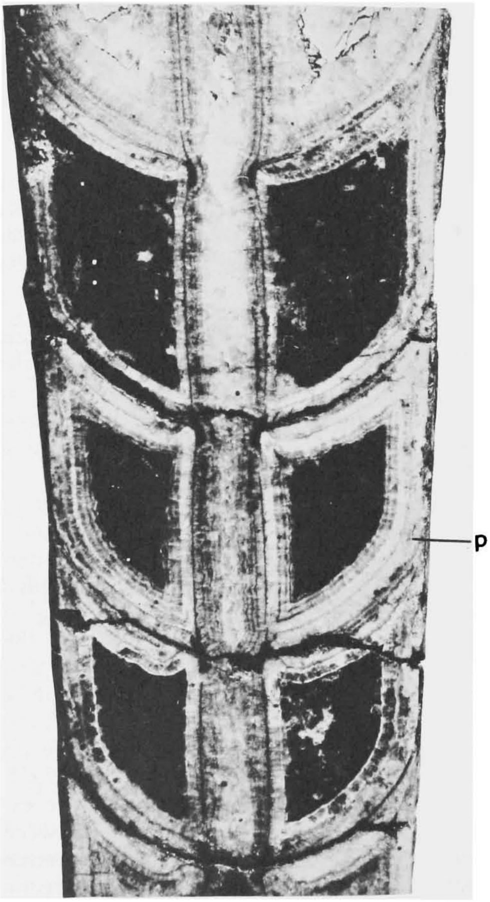

FIG. 23. Portion of phragmocone of *Geisonoceras teicherti* FLOWER, camerae lined with primary and secondary deposits. Outermost layer *(p)* extends along anterior, posterior, and mural parts of septa, but not along outside of connecting ring. This is a primary cameral deposit; all other layers in the camerae and in the siphuncle are inorganically deposited during diagenesis. M.Dev., USA(N.Y.) (35).

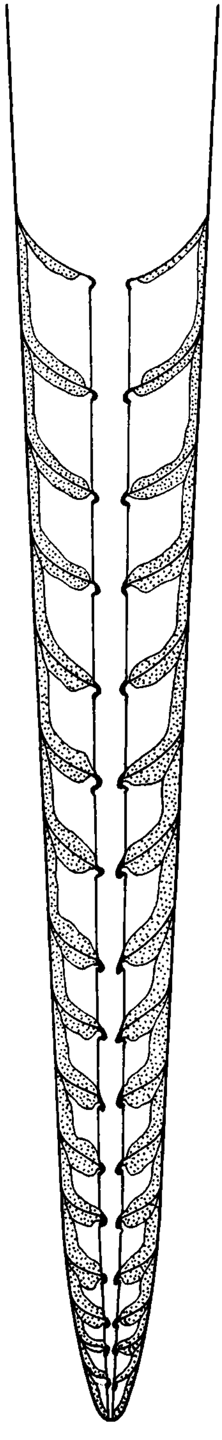

FIG. 24. Reconstructed longitudinal section of *Geisonoceras teicherti* FLOWER, showing regular disposition of cameral deposits in phragmocone (35).

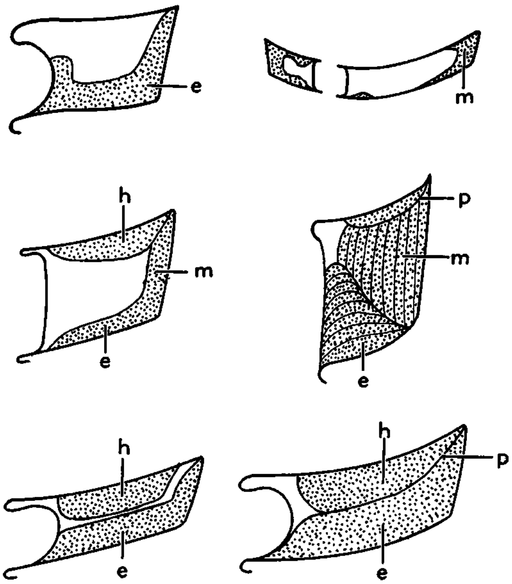

FIG. 25. Various types of cameral deposits: *e*, episeptal; *h*, hyposeptal; *m*, mural; *p*, "pseudoseptum" (35, and Teichert, n).

This suggestion is supported by the observation of vascular tubes on the surface of cameral deposits. These were seen, described, and correctly interpreted in Ordovician and Silurian orthocerids and lituitids by such early observers as DEWITZ, NOETLING, SCHRÖDER, HOLM, and REMELÉ (Fig. 26,*A*). They were largely ignored by later workers. More recently FLOWER (1941) has called attention to the presence of "circumferential tubes" on the surface of cameral deposits in *Leurocycloceras* and other forms (Fig. 26,*B*).

It seems that the inner surface of cameral deposits which can sometimes be studied on internal molds may be mammillate or pitted (Fig. 26,*C-G*).

While in most conchs cameral deposits form laterally continuous layers covering the septa, modifications may occur such as in the Lamellorthoceratidae (order Orthocerida), where cameral deposits are secreted as longitudinal radial lamellae (TEICHERT, 1961).

The disposition of the deposits within individual camerae is, as a rule, asymmetrical, the deposits being more strongly developed in the ventral than dorsal half of the camerae (Fig. 27). This demonstrates that it was the function of the cameral deposits to

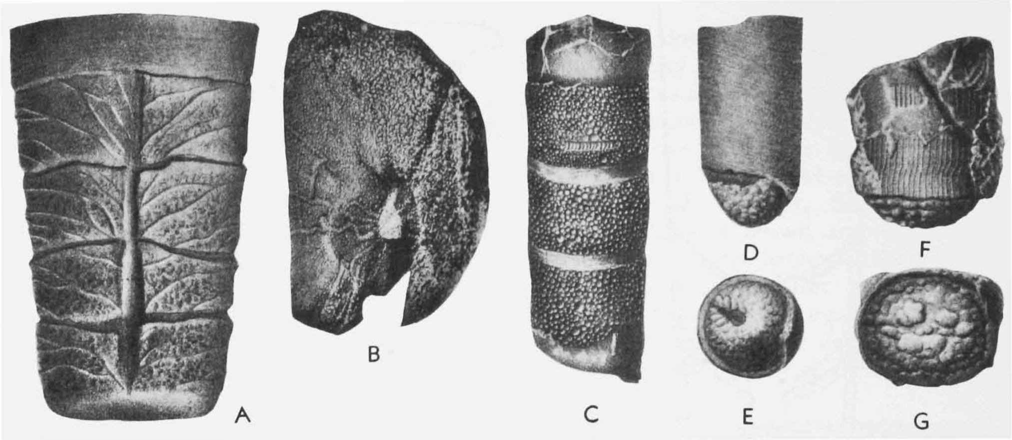

FIG. 26. Features of the inner surface of cameral deposits.——*A*. Steinkern of orthocerid with impressions suggesting vascular tissues on the surface of the mural deposits or of the mural part of the septa; Sil. (Pleist. drift), Ger., ×1.3 (29).——*B*. Dolomitized camera filling of *Leurocycloceras* sp., cf. *L. niagarense*, preserving replica of surface of cameral deposits with vascular tubes, Sil., USA (Wis.), ×1.3 (Flower, 1941).——*C*. Steinkern of orthocerid phragmocone showing replica of mammillate surface of mural cameral deposits, Sil., Czech., ×0.7 (Barrande, pl. 227, 1868).——*D-G*. Replicas of cameral deposit surfaces in orthocerids, showing especially regular pattern in *F*; *D,E*, Dev., *F,G*, Sil., Czech., ×0.7 (Barrande, pl. 228, 1868).

help stabilize the conch in a position with the ventral side downward during the life of the animal.

Some forms, especially Pseudorthocerataceae, have a furrow in the cameral deposits along the ventral side. Heavy accumulations on both sides of this ventral furrow have been called **ventrolateral masses.**

In view of their stabilizing role, it is obvious that cameral deposits are most important in straight or nearly straight forms. They reach their greatest development in the Orthocerida and Actinocerida, but thin and slender shells may be without them. Cameral deposits are erratically developed in the Discosorida, and in the Oncocerida they are, when present, very thin. In the Ellesmerocerida they are found only in the advanced families Baltoceratidae and Protocycloceratidae. Cameral deposits do not occur in the Endocerida, where the stabilizing function is exercised by heavy endosiphuncular deposits. True cameral deposits are also unknown in the Barrandeocerida and reports of their presence in Nautilida are few (Fig. 28). Among Tarphycerida cameral deposits occur only in the family Lituitidae which has conchs that are straight at maturity. Coiled shells generally had no need for stabilizers of this type.

The mode of origin of cameral deposits and the time of their formation have been much discussed. Some authors have rejected even the postulate of their organic origin. Criteria which may be applied to differentiate between organic (primary) and inorganic (secondary) deposits of calcium carbonate in the camerae have already been discussed. As may be expected, cameral deposits in fossil conchs generally consist of calcite. However, FISCHER, LOWENSTAM, & TEICHERT observed that cameral deposits occurring in exceptionally well-preserved specimens of *Pseudorthoceras* found in asphalt consist of aragonite. These deposits consist of thin lamellae composed of fine aragonite needles separated by thin, dark membranes. According to GRÉGOIRE (written communication and Fig. 29) these membranes consist of minute mineral prisms in parallel orientation, separated by shreds of organic matter. Presence of aragonite and of organic substance in the cameral deposits of *Pseudorthoceras* is incontrovertible proof of the organic origin of these deposits. As may be expected, preservation of these delicate cameral structures is extremely rare, but all primary cameral deposits are sufficiently similar in gross features of morphology to allow of only one unified interpretation.

Two hypotheses have been offered to explain the formation of organic cameral deposits: (1) They were formed simultaneous-

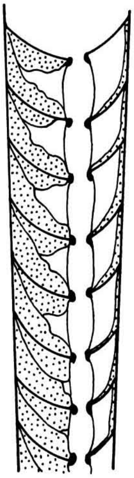

FIG. 27. Strongly asymmetrical distribution of cameral deposits in an orthocerid; Sil., Czech., ×0.7 (Barrande, pl. 285, 1868).

ly with the septa with which they belong and are thus excretions of the mantle; (2) They were formed later than the septa and after the camerae had been closed by the siphuncle.

The principal proponent of the first hypothesis was BARRANDE. Others were DEWITZ, HOLM, and GRABAU, to mention only a few. Considerable difference in interpretation of structural details and of the exact sequence of events leading to the formation of the deposits is indicated, however. Some authors regarded the "pseudosepta" as purely mechanical contact planes of epi- and hyposeptal deposits. Others believed that they represent organic membranes secreted by the mantle in intermediate positions between the septa and indicating positions of rest in the process of almost continuous secretion of calcium carbonate either as septa or as cameral deposits.

The postulate in either form is here regarded as unlikely, first, because the anterior portion of the phragmocone, and especially the last few septa, are generally entirely free from cameral deposits; second, because in almost all cases cameral deposits increase gradually and regularly in bulk and thickness from chamber to chamber in an apical direction. This condition is suggestive of progressive growth of the deposits during life of the animal, because it is quite unlikely that young shells should have been almost or entirely filled with calcareous deposits.

The hypothesis of continuing formation of cameral deposits within the camerae during life of the animal and after the camerae had been completed was first proposed by TEICHERT (35), who envisaged the possibility that the camerae might have contained some kind of organic tissue that formed the cameral deposits. This concept was explored by FLOWER (8), who succeeded in putting it on a biologically sound basis. FLOWER suggested that the camerae were lined with tissue which he proposed to call **cameral mantle.** This was presumed to develop from the mantle enveloping the posterior part of the visceral mass, when the animal was moving into position to build the next following septum. According to reasonable interpretation, part of the old mantle remained adherent to the old septum, and the new septum was secreted by a newly formed posterior mantle. The mantle remaining in the camera continued to be supplied with blood through the newly formed connecting ring. It continued to grow over the posterior side of the newly formed septum, and in due course excess supply of mineral matter to the cameral mantle led to secretion and continued growth of cameral deposits.

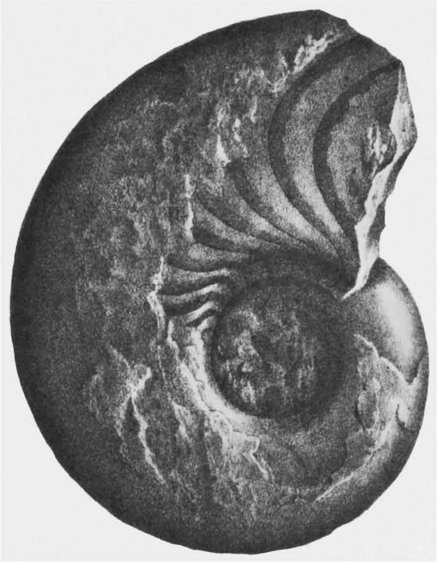

FIG. 28. Cameral deposits in a nautilid, *Grypoceras obtusum* (MOJSISOVICS); Trias., Alps, ×0.7 (Mojsisovics, 1873).

Contrary to FLOWER's opinion, the cameral mantle probably did not envelop the connecting ring, because no cameral deposits are ever found on its outer surface.

The "pseudoseptum" was the plane along which the hyposeptal and the episeptal portions of the cameral mantle were brought into contact through growth of the deposits secreted by them. Earlier authors, especially HOLM, APPELLÖF, NOETLING, and SCHRÖDER, have described the "pseudoseptum" as a distinct membrane on which, in rare cases, impression of vascular systems have been observed. HOLM (15) believed that the "pseudoseptum" represents a membranous soft "double sack" which surrounded the posterior end of the mantle and became detached from it as the animal moved on in the conch to build a new septum.

The cameral mantle, as here described, is a hypothetical organ which was developed in some extinct nautiloids and which was lost in evolution of the nautiloid lineage.

It should be remembered, however, that small secretions of aragonite are also known in the camerae of living *Nautilus*. APPELLÖF has shown that the anterior corner of the camerae of *Nautilus pompilius* contains a filling of conchiolin in which small bodies of aragonite are embedded. The formation of this filling (*"Ausfüllungsmasse"* of APPELLÖF) must have followed that of the septum behind which it occurs. GRÉGOIRE (1962) found that this filling consists of several substances of aragonitic and organic composition. The electron microscopic structure of some of the substances is strikingly similar to that of cameral deposits of *Pseudorthoceras*.

Some specialized features of cameral deposits of Actinocerida and Orthocerida are discussed in descriptions of these orders.

SIPHUNCLE

In fossil cephalopods the term *siphuncle* is applied to all fossilizable structures connected with the siphuncle of the living animal. Conchs with relatively wide siphuncles are called **eurysiphonate** and those with narrow siphuncles **stenosiphonate.** Use of these terms is generally restricted to very large (e.g., Endocerida) and very narrow (e.g., Orthocerida) siphuncles, respectively. No special terms for intermediate siphuncle sizes exist.

In eurysiphonate cephalopods, such as the Endocerida and Actinocerida, but also in some Discosorida, Ellesmerocerida, and even in some Oncocerida, part of the endosiphuncle not occupied by deposits is so large in relation to volume of the body chamber that it must have contained important organs of the body. Whereas in forms like modern *Nautilus*, the siphuncle no longer contains more than an extension of the mantle, the siphuncle of eurysiphonate forms must have included

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EXPLANATION OF FIGURE 29,*1-3*

Representative aspects of the structure of cameral deposits, with increasing amounts of organic substance from *1* to *3*, are shown by positive carbon replicas (shadow-cast with palladium) of polished surfaces of shell sections.

1.—Sagittal section of region having marble-like hardness, parallel crystals without visible interposition of organic substance, probably revealing local recrystallization of calcium carbonate (reversed print), ×9,000.

2.—Transverse section of shell showing partially calcified portion of cameral deposits. The basic mineral unit consists of elongated, sharp-edged tablets, blades, or bars, appearing as needles or spindles viewed on edge, the parallel spindle-shaped crystals being grouped in variously oriented bundles with components disposed at different angles to crystals of neighboring bundles. Shreds of organic substance are visible (white) and incidental twinnings appear in right-hand part of figure (reversed print), ×22,000.

3.—Polished sagittal section of thinly stratified dark brown area of cameral deposits, etched by chelation (Titriplex III for 2 minutes). Parallel elongated mineral elements seen on edge are arranged in palisade alternating with shreds of organic substance (white ribbons), decalcification of this area having left substantial organic residues (reversed print), ×22,000.

[Other regions of poorly calcified cameral deposits (not illustrated) mostly in central parts of camerae near the siphonal complex, consist of soft, dark brown, crumbly organic material, in part biuret-positive. Polished surfaces could not be prepared from these regions. Thoroughly decalcified and thinned mechanically for examination with phase-contrast and electron microscopes, the soft material appears as fragments of sheets in which traces of structural organization are visible but not so far identifiable.]

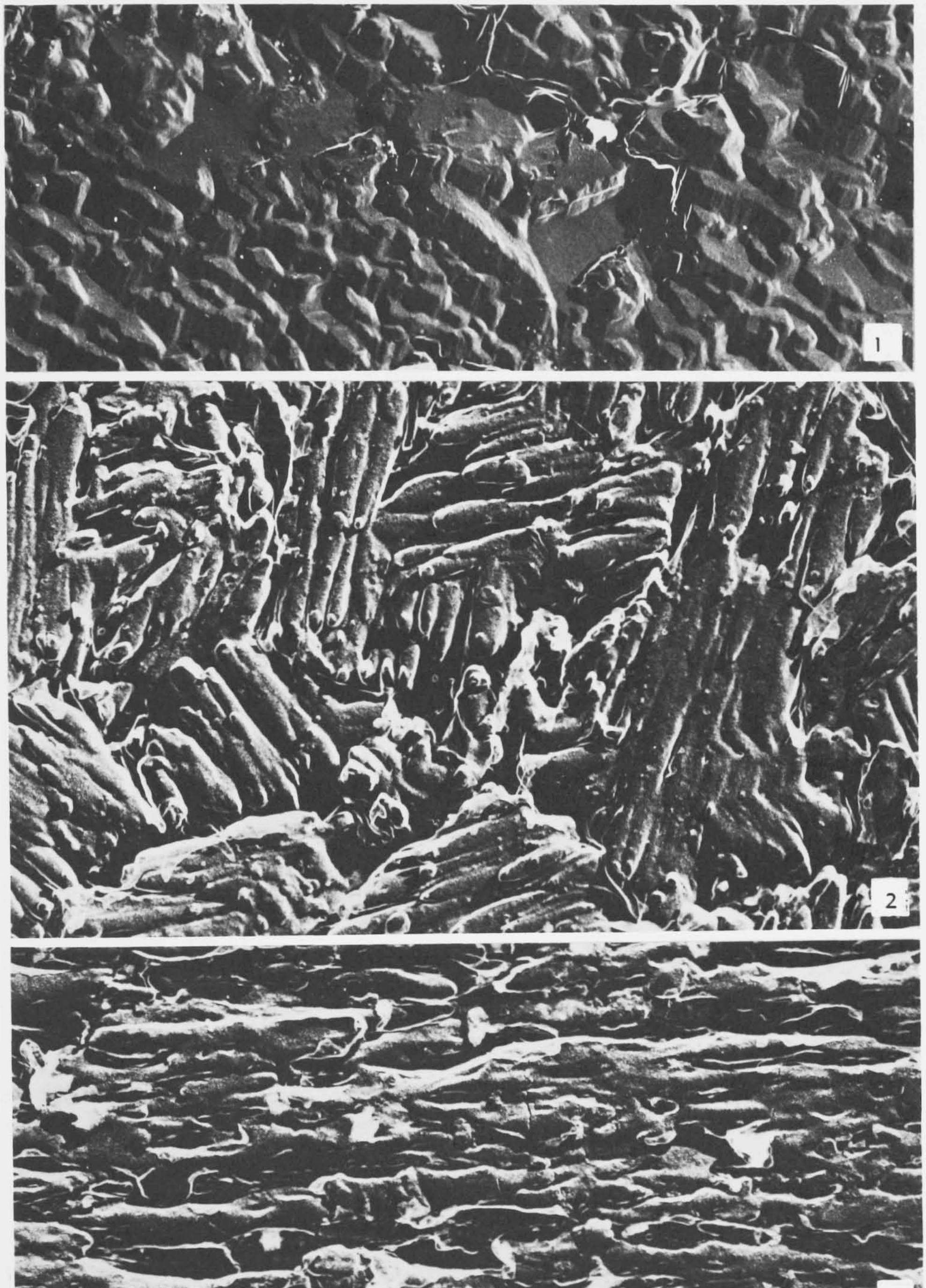

FIG. 29,*1-3*. Electron micrographs of cameral deposits of *Pseudorthoceras knoxense* (MCCHESNEY) from lower Middle Pennsylvanian deposits (Buckhorn asphalt) near Sulphur, Oklahoma (Grégoire, n; specimens supplied by A. G. Fischer) (explanation on facing page).

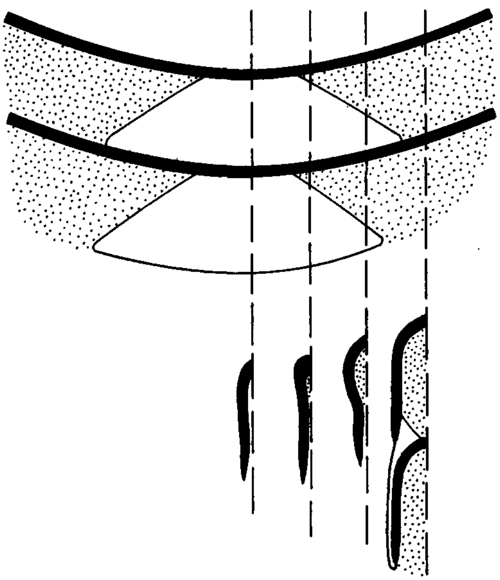

FIG. 30. Ectosiphuncular suture diagrammatically showing ventral surface of two camerae (shell removed) and four longitudinal sections of the ectosiphuncle (septa represented by thick black lines and unshaded areas adjacent to septa indicating regions where septal necks are flattened against the inner shell wall). An ectosiphuncular suture occurs on either side of the mid-ventral line in each camera. They are lines along which the gap between the septal necks and the inner shell wall becomes sufficiently wide for introduction of matrix (dotted) between these two components of the conch (Teichert & Glenister, n).

some of the visceral mass. It has been suggested that it might have housed the liver and the gonads—in analogy to the gastropods, where these organs are found in the dorsal (or posterior) part of the body.

The outer sheath, inside which the fleshy sipho or siphuncular cord was situated, is the **ectosiphuncle,** also called the siphonal tube. The space inside it is the **endosiphuncle** and fossilized structures of any kind in this space are known as **endosiphuncular structures.**

This terminology, though convenient for purposes of morphological description, is somewhat artificial, because all structures concerned were probably secreted by the same mantle surface.

The early ontogeny of the siphuncle will be treated in the general chapter on early ontogeny of the nautiloid conch.

The position of the siphuncle within the phragmocone may be anywhere from marginal to central. Most eurysiphonate forms have marginal to submarginal siphuncles, whereas these positions are rare in stenosiphonate conchs. Wide, marginal siphuncles may be in broad contact with walls of the conch (*Cameroceras, Kochoceras*). In groups with broadly expanded siphuncle segments (actinocerids, oncocerids, some discosorids), the contact area between segments and conch wall is well seen on the surface of internal molds, where it is set off from the camerae by the **ectosiphuncular suture** (Fig. 30).

ECTOSIPHUNCLE

The ectosiphuncle consists basically of **septal necks** and **connecting rings.**

The septal necks may not be developed or they may be rudimentary, indicated by a

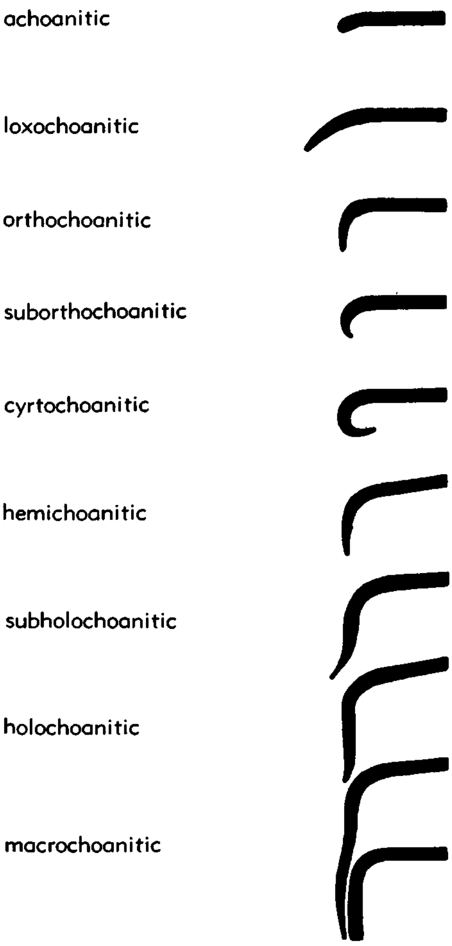

FIG. 31. Diagram explaining septal neck terminology (Teichert & Glenister, 1954).

slight inflection of septa around the septal foramen. This condition is known as **achoanitic** (Fig. 31). Septal necks of nautiloid cephalopods are invariably **retrochoanitic,** that is, pointed backward toward the apex of the conch. The principal terms for different types of septal necks which have long been recognized are **orthochoanitic,** for short cylindrical necks; **cyrtochoanitic,** for necks that are bent outwardly in cross section; and **holochoanitic,** for long, cylindrical necks reaching from one septum to the preceding one. More recently, it has become necessary to establish a more elaborate terminology for intermediate or deviating types of necks (Fig. 31, and glossary).

The distribution of these various types of septal necks among the different orders is approximately as follows: (1) **Achoanitic necks** are rare; restricted to the Ellesmerocerida. (2) **Orthochoanitic necks** are found in many Ellesmerocerida, in the superfamily Orthocerataceae of the order Orthocerida, and in most coiled forms (Tarphycerida, Barrandeocerida, Nautilida). (3) **Hemichoanitic necks** are most common in the Proterocameroceratidae (order Endocerida), occurring also, though rarely, in the Orthocerida. (4) **Loxochoanitic** and **subholochoanitic necks** are almost restricted to Ellesmerocerida and early Endocerida, and are found in a few Orthocerida. (5) **Cyrtochoanitic necks** characterize the Actinocerida, Oncocerida, and Discosorida, and the superfamily Pseudorthocerataceae of the Orthocerida. (6) **Holochoanitic necks** are most typical of the Endocerida, but occur in some genera (e.g., *Aturia*) of the Nautilida. (7) **Macrochoanitic necks** are found only in the Endocerida.

Orthochoanitic and cyrtochoanitic necks were formerly collectively called **ellipochoanitic** and contrasted with the long, holochoanitic necks. This term, though still useful on occasion, is no longer part of formal terminology, because of the discovery that many septal necks are intermediate between the ellipochoanitic and holochoanitic conditions.

The connecting ring is a cylindrical or ring-shaped sheath, which extends between two succeeding septa or septal necks. The connecting ring of living *Nautilus* is very thin; it consists of an inner layer of conchiolin and an outer layer of aragonite spicules and granules, cemented by conchiolin. This outer layer is porous. All members of the order Nautilida have similarly thin connecting rings and it is reasonable to suppose that all had a similar composition. The same may be true for the thin connecting rings of extinct orders such as the Barrandeocerida, Oncocerida, Actinocerida, and Orthocerida. They are known to have consisted of a rigid, yet flexible material (Fig. 32).

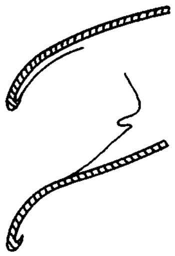

FIG. 32. Torn and folded connecting ring in a specimen of *Actinoceras* (35).

In the Ellesmerocerida, Endocerida, Discosorida, and Tarphycerida, the connecting rings are thick and commonly of complex structure and elaborate shape. In many genera the connecting ring is clearly composed of two or even three layers of different structure, color, and transparency, but little is known about the nature of the original material of which these complex connections consisted. The connecting ring of *Cochlioceras* is said to consist of calcium carbonate with an admixture of phosphorite (27).

Thin connecting rings are as a rule attached anteriorly to the thin edge or to the area just outside the edge of the proximal septal neck, posteriorly to the inside of the distal septal neck in which they form a continuous lining (Fig. 33,*A,B*). Thick rings are attached to the entire outside of the septal necks and to the posterior and anterior surfaces of the septa in a narrow area surrounding septal neck and septal foramen (Fig. 33,*C-E*).

The simplest form of connecting ring is cylindrical, as usual in orthochoanitic siphuncles. In conchs with suborthochoanitic to cyrtochoanitic septal necks, the connecting ring bulges outward and may be barrel-

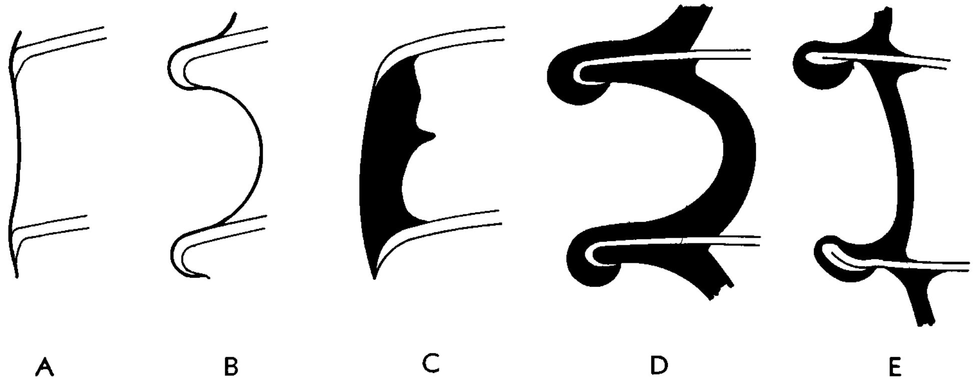

FIG. 33. Various kinds of thin *(A,B)* and thick *(C-E)* connecting rings and their mode of attachment to septa and septal necks (Teichert, n).

shaped, globular, or even very broadly expanded. Siphuncles with globular to broadly expanded segments are often called **nummuloidal.** The area of attachment of expanded segments to the anterior, more rarely the posterior surface of septa, is called **adnation area.**

The comparatively rare condition in which the connecting rings are convex inward is called **concavosiphonate.** It is almost entirely restricted to the Oncocerida.

Further specializations of shape and structure of the connecting rings occur in the Ellesmerocerida, Endocerida, and Discosorida, and will be described in the introductions to the systematic treatment of these orders.

ENDOSIPHUNCLE

For descriptive purposes, the endosiphuncle includes the space inside the ectosiphuncle and all contained fossilizable structures built by organic activity during the life of the animal. Like cameral deposits, many of these are difficult to interpret, because they lack analogies in modern cephalopods. All calcareous, primary structures in the endosiphuncle are collectively referred to as **endosiphuncular deposits.**

Noncalcareous inward expansions or outgrowths of the connecting rings, as seen in some Ellesmerocerida *(Eothinoceras, Cyrtocerina, Bathmoceras),* are analogous, not homologous to endosiphuncular deposits and are not grouped with them. They have been little studied as yet.

Endosiphuncular deposits exhibit considerable variety in regard to morphology and structure. Some features are characteristic of certain orders; others occur in different combinations in different orders.

Endosiphuncular deposits are known to occur in the following orders: Ellesmerocerida (diaphragms only), Endocerida, Actinocerida, Discosorida, Orthocerida, and Oncocerida. They are virtually absent in the Ascocerida and such stenosiphonate groups as the Tarphycerida, Barrandeocerida, and Nautilida.

In most orders in which endosiphuncular structures occur, the latter may attain a considerable degree of complexity and many specialized features have developed, which will be discussed separately for each order. This introductory chapter can serve only as a review of and an introduction to the general field of endosiphuncular structures.

Endosiphuncular deposits are of the following six basic types (Fig. 34): (1) Transverse diaphragms. (2) Longitudinal lamellae in radial orientation, converging from the ectosiphuncle toward a longitudinal axis in the siphuncle; this structure is called **actinosiphonate.** (3) Superimposed cone-shaped layers, with the axes of the cones in, or parallel to, the central axis of the siphuncle and with their apices pointing backward toward the apex of the conch. (4) Cylindrical tubes running along or close to the longitudinal axis of the siphuncle. (5) Internal linings of the ectosiphuncle. (6) Deposits first developing on the inside of the septal necks, then growing and expanding inward to fill almost the entire endosiphuncle, but not coming into contact with the connecting rings; these are the

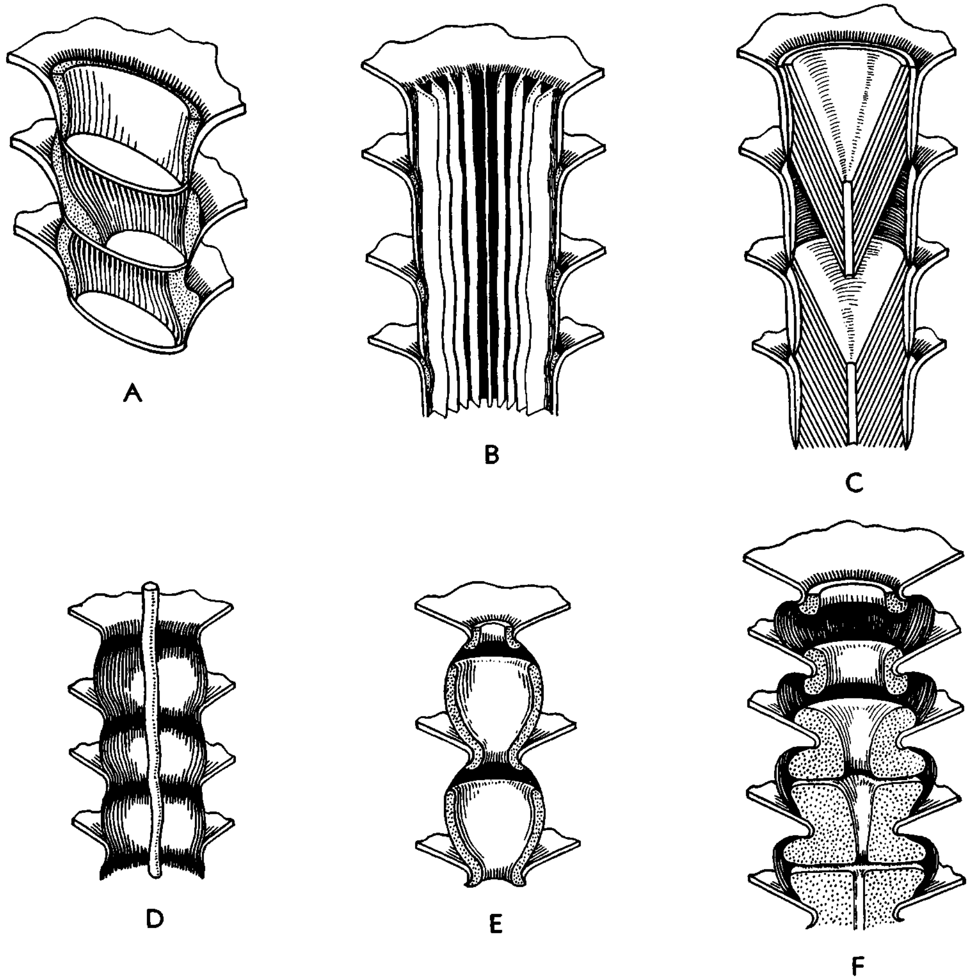

Fig. 34. Types of endosiphuncular structures; *A*, diaphragms; *B*, longitudinal lamellae; *C*, endocones; *D*, central cylindrical tube; *E*, parietal deposits; *F*, "annulosiphonate" deposits (not to scale). In *A* and *B* connecting rings are stippled; in *E* and *D* endosiphuncular deposits are stippled (Teichert, n).

annulosiphonate deposits of Hyatt and other authors, but the term is now rarely used, because in the mature stage these deposits fill the entire siphuncle with the exception of a usually complex system of **endosiphuncular canals.**

These six basic types will now be briefly discussed, leaving specializations to later treatment. They may occur alone or in combination. Thus, diaphragms are found in some Ellesmerocerida. Radial, longitudinal lamellae occur in the Intejocerida and Oncocerida. Cone-shaped deposits are common in the Endocerida, but are also found in many Discosorida, and very rarely in the Orthocerida. Cylindrical tubes are known rarely from Orthocerida, Discosorida, and Oncocerida. Interior linings of the ectosiphuncle are characteristic of the Discosorida and of a large group of Orthocerida, the Pseudorthocerataceae. Deposits growing out from the inside of the septal neck are the most characteristic feature of the Actinocerida, but are also very typical of some Oncocerida and Orthocerida.

Type 1. Transverse diaphragms are of rare occurrence. They are known in some genera of the Ellesmerocerida, where, with few exceptions, they have not been studied in great detail. Some diaphragms have been

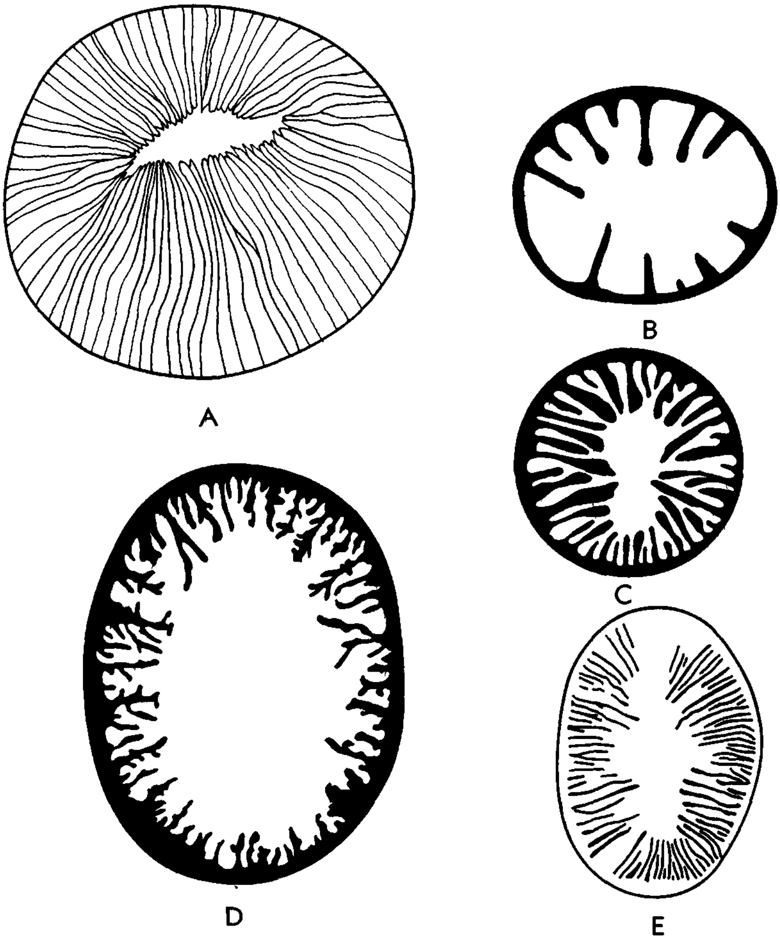

FIG. 35. Several types of actinosiphonate structures.——*A*, Endocerida (*Padunoceras*, ×2).——*B-E*, Oncocerida (*B, Conostichoceras*, ×4; *C, Jovellania*, ×5.5; *D, Pectinoceras*, ×7; *E, Polyelasmoceras*, ×2.7) (Adapted from Balashov, 1960; Teichert, 1939; Lemaitre, 1940; Teichert, 1940; Teichert & Glenister, 1952).

described to have a structure similar to that of the connecting rings, from which, however, they are always distinct. Endosiphuncular diaphragms are homologous to the transverse partitions found in the endosiphuncular central canals of certain endocerids (Fig. 34,*A*).

Type 2. Structures of this type are in need of much more detailed study. They probably fall into several different groups some of which may be characterized as follows: (a) Closely spaced lamellae converging from the ectosiphuncle on the center or an off-center axis of the siphuncle; known in the orders Intejocerida and Endocerida, and almost certainly of calcium carbonate (Fig. 35,*A*). (b) Closely or widely spaced, short to medium long lamellae which are of the same material as the connecting ring and may be club-shaped in cross section; they are inward folds or extensions of the connecting ring (e.g., *Conostichoceras, Jovellania, Archiacoceras*) (Fig. 35,*B,C*). (c) Closely spaced, thin lamellae, irregularly alternating long and short, slightly irregular or wavy in cross section, rarely dichotomous (e.g., *Polyelasmoceras*) (Fig. 35,*E*). (d) Closely spaced lamellae, irregularly alternating long and short, all (except shortest) developing lateral projec-

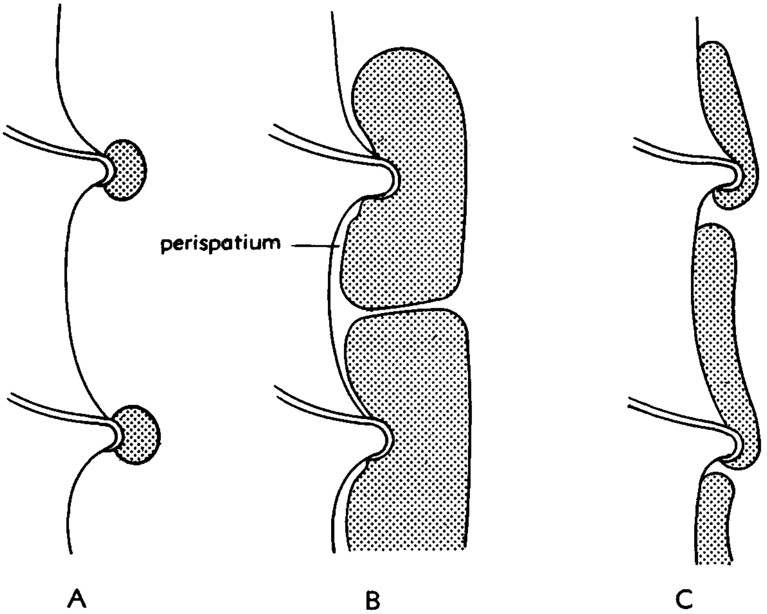

FIG. 36. Parietal and annulosiphonate deposits: *A*, incipient rings; *B*, annulosiphonate deposits, fully developed, with perispatium; *C*, parietal deposits, not yet quite fused to form continuous lining (adapted from 9).

tions, longer lamellae being bipectinate in cross section; primarily probably excrescences of the connecting ring, but secondarily covered with film of calcium carbonate (e.g., *Pectinoceras, Actinomorpha*) (Fig. 35,*D*).

Structures of groups (b) to (d) are known from various families of the Oncocerida and probably persist in their derivatives, the earliest Rutoceratidae. The lamellae may be continuous throughout a considerable part of the siphuncle or through several segments only, or they may occur in discontinuous clusters around successive septal necks. Some evidence suggests that lamellae generally may first form inside the septal necks and that they may coalesce into longitudinally continuous structures through gradual growth.

Type 3. The basic type consists of conical layers, called **endocones,** consisting of calcium carbonate, not more than a few millimeters thick, with a perforated, backward-directed apex. The apical foramina line up into a straight (or in cyrtoconic forms, curved) cylindrical tube, the **endosiphuncular canal.** In some forms this canal is traversed by transverse diaphragms. Many modifications of this simple pattern are observed. The endocones may be greatly modified in cross section, being elliptical, subtriangular, or crescent-shaped (e.g., *Meniscoceras, Tasmanoceras*). Two or more systems of endocones may be present (Chihlioceratidae, Allotrioceratidae). The endosiphuncular canal may be flattened or crescent-shaped (e.g., *Emmonsoceras*), and if a multiple endocone system is present, there is one canal for each set of endocones. Additional specialized features associated with this type of endosiphuncular structure are restricted to the Endocerida and will be discussed under that order (Fig. 34,*C*).

Type 4. Cylindrical tubes have been observed in many unrelated genera. They are either straight or slightly wavy, probably generally circular in cross section and situated close to the longitudinal axis of the siphuncle. Apparently, these tubes were embedded unsupported in the siphuncular tissues. When they are found in contact with the septal neck, it may be assumed that they came to rest on them, when the tissue decayed after death of the animal. They have

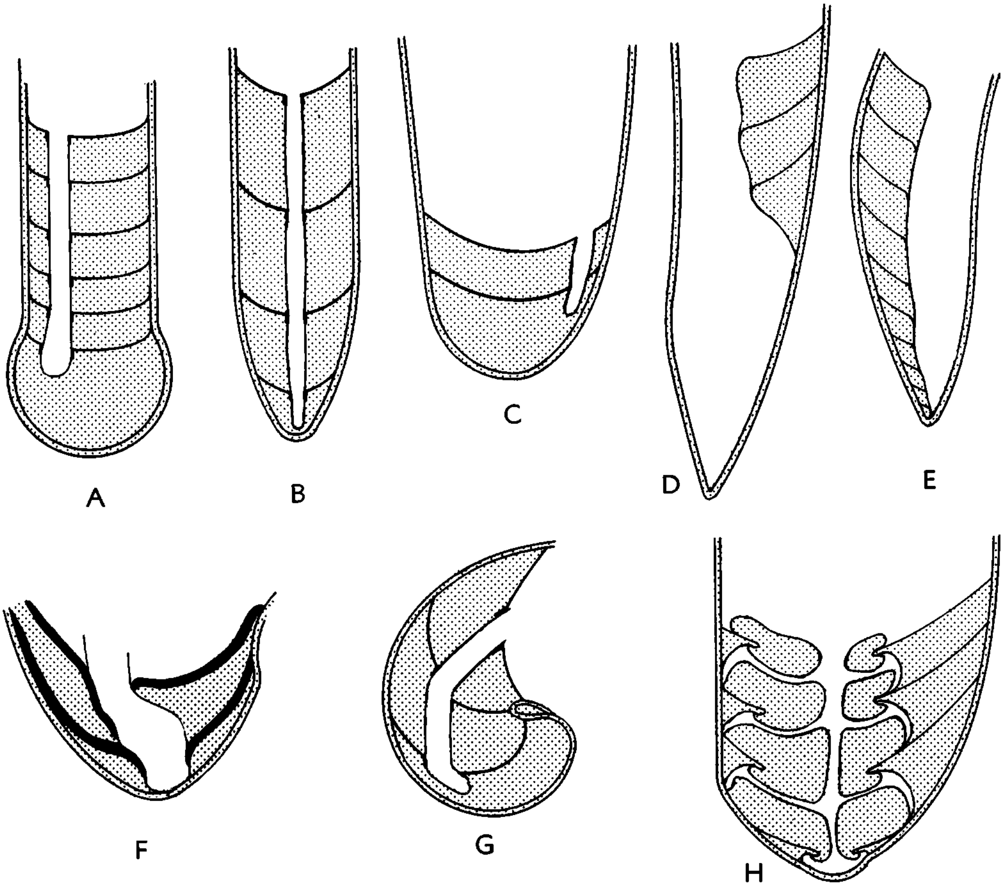

FIG. 37. Initial parts of conchs of several nautiloid orders (camerae stippled) (not to scale).——*A*, Orthocerida (*Orthoceras?*), Ord.——*B*. Orthocerida (*Trematoceras*), Trias.——*C*. Oncocerida (genus?), Sil.——*D*, Endocerida (*Suecoceras*), Ord.——*E*. Endocerida (*Nanno*), Ord.——*F*. Nautilida (*Nautilus*), Rec.——*G*, Tarphycerida (*Curtoceras*), Ord.——*H*, Actinocerida (*Armenoceras*), Ord. (adapted from Balashov, 1959; 19; 27; 38; Holm, 1884).

so far been found only in siphuncles of orthoconic or near-orthoconic forms (e.g., *Harrisoceras, Madiganella, Diestoceras*) (Fig. 34,*D*).

Type 5. Internal linings of the ectosiphuncle originate in the form of thin deposits along insides of septal necks (Fig. 34,*E*; 36,*A*) which, when small and of semicircular cross section, comprise a structure often called **annulus.**[1] They develop rapidly into ringlike structures of kidney-shaped cross section, called **bullettes.** These deposits extend generally predominantly in an anterior direction along the connecting rings. Less rapidly they also develop posteriorly into the preceding siphuncular segment (Fig. 36,*C*). They may then fuse and begin to form a continuous internal lining of the ectosiphuncle.

Considerable variation occurs in the morphology of these structures. The lining may be strongly developed along the ventral side of the siphuncle, being rudimentary or absent on the dorsal side. In other genera (e.g., *Buchanoceras, Bergoceras*) the bullettes grow strongly toward the center of the siphuncle, obstructing the septal foramen greatly. They then grow anteriorly and posteriorly until deposits issuing from successive septal neck regions approach each other very closely. In a dorsoventral section

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[1] It has not been possible in this volume to eliminate completely the inconvenience arising from use of the word *annulus* for a feature of the body chamber and also for an endosiphuncular structure. For recommended usage consult the glossary of morphological terms.

of the siphuncle this condition resembles closely that of certain actinocerids, but in siphuncles with parietal deposits, these deposits are in contact with the connecting rings, whereas Actinocerida invariably have a well-developed perispatium.

Quite commonly, especially in the Pseudorthocerataceae, parietal deposits occur in combination with cameral deposits. The physiologic conditions under which both types of deposits could be formed at the same time are not yet understood.

Parietal deposits may be accompanied by more complex endosiphuncular structures, including tubes in the Pseudorthocerataceae, and endocones in the Discosoridae.

Type 6. This type of endosiphuncular structure is found only in the Actinocerida and will be discussed in greater detail in the description of that order. It suffices to state here that, like parietal deposits, annulosiphonate deposits begin to form in the general area of the septal neck. Contrary to the parietal deposits, however, they do not grow along the inner side of the connecting ring (Fig. 36,*B*). Instead, they spread rapidly inward in the endosiphuncle, avoiding contact with the connecting ring. The space between them and the ring is called **perispatium.** When they have reached their maximum development, the endosiphuncular space not occupied by them forms an elaborate system of one or more central, longitudinal canals, connected with the perispatia by radiating lateral canals. (See Figs. 34,*F*; 36,*B*.)

EARLY ONTOGENY

Knowledge of the early ontogeny of fossil chambered cephalopods is based entirely on study of the most apical portions of the conch and of the siphuncle. These parts are well preserved in coiled conchs, though mostly difficult to expose or to extract from a fossil specimen. In orthocones and cyrtocones apical conch parts are rarely well preserved and knowledge of early ontogenetic stages of most such forms is very scanty.

An added handicap lies in the fact that many studies of early ontogenetic stages of orthoconic and cyrtoconic conchs are based on tiny, immature specimens, identification of which with species, or even genera, based on mature forms, is often in doubt.

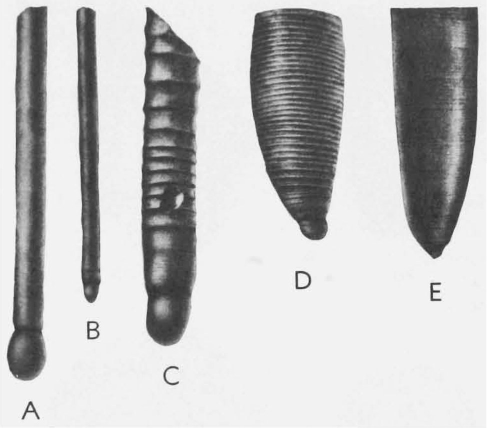

FIG. 38. Initial portions of nautiloid conchs: *A*, orthocerid, M.Dev., Ger.; *B*, orthocerid, U.Dev., Ger.; *C*, *Leurocycloceras?* sp., M.Dev., Ger.; *D*, *Geisonoceras? clavatum* (CORRENS), M.Dev., Ger.; *E*, *Trematoceras* sp., cf. *T. elegans* (MÜNSTER), U. Trias., Aus., ×6.6 (27).

The most apical part of the phragmocone is the space enclosed between the actual apex of the conch and the first septum. This is the **first** or **initial** or **apical camera.** Since it is the first shelly structure built by the animal it may also be called the **protoconch,** but this term has been controversial in nautiloid morphology and is now little used.

The initial camerae of nautiloid cephalopods have many different shapes (Fig. 37). They are better known from orthocerids, endocerids, and the orders that include coiled conchs (Tarphycerida, Barrandeocerida, Nautilida) than from actinocerids, ascocerids, and oncocerids.

In orthocerids the initial camera may be bulbous or bluntly cone-shaped. Bulbous initial camerae may have a larger or slightly smaller diameter than the next following camera (Fig. 38). Bluntly cone-shaped camerae may be slightly impressed near the apex (Fig. 37,*B*). Initial camerae of cyrtoconic conchs may themselves show a faint indication of curvature (Fig. 39,*2,3*).

In breviconic conchs the initial chambers are probably deeply cup-shaped (Fig. 37,*C*), but little is known about the early growth stages among the Oncocerida and the Discosorida, the two orders containing the bulk of breviconic shells.

In coiled conchs the initial camera is short and shallow. This is probably true for all

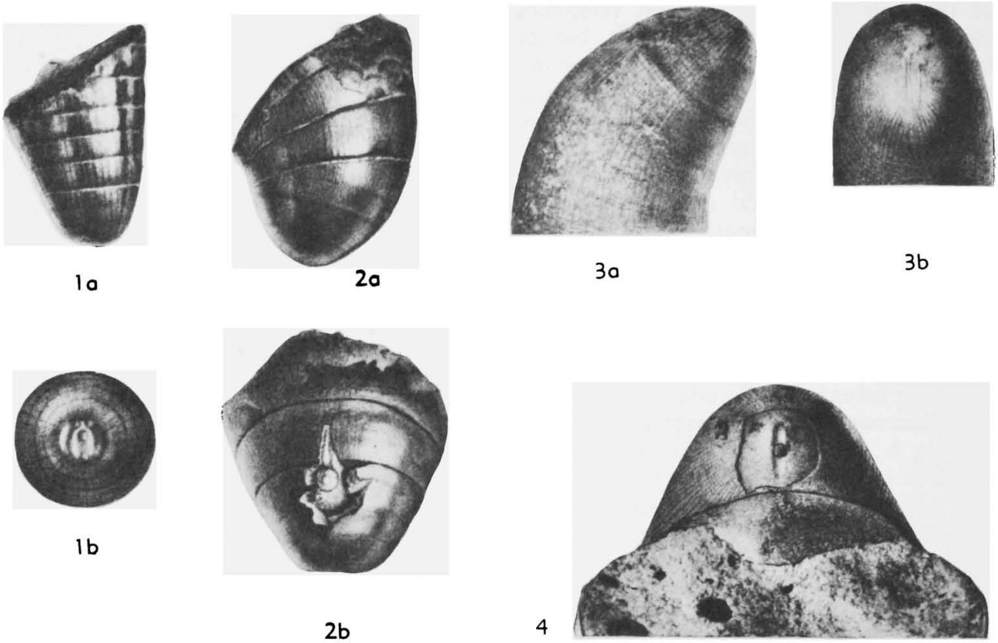

FIG. 39. Initial portions of nautiloid conchs with "cicatrix."——*1a,b, Kionoceras hyatti* (BARRANDE), U. Dev., Ger.——*2a,b,* Oncocerid, U.Dev., Ger.——*3a,b, Trochoceras* sp., Sil., Czech.——*4. ?Cymatoceras lineatum* (SOWERBY), M.Jur., Fr.; ×4 (27).

coiled nautiloids accommodated in the orders Tarphycerida, Barrandeocerida, and Nautilida (Fig. 37,*F,G*).

The only orthoconic group with short and shallow initial camerae is the Actinocerida, whose early ontogeny is very poorly known (Fig. 37,*H*), but a few genera (e.g., *Kochoceras, Selkirkoceras, Carbactinoceras*) seem to possess initial camerae that are broadly conical.

A somewhat different situation exists in the Endocerida (Fig. 37,*D,E*), but in order to understand the peculiar situation of this order it is necessary to discuss the early ontogeny of the siphuncle in the orders discussed above.

The initial segment of the siphuncle is called the **caecum.** It protrudes into the initial camera through the septal foramen of the first septum and is generally more or less bulbous. In some forms its diameter is slightly greater than that of the immediately following stages of the siphuncle. In living *Nautilus,* in many extinct nautilids, and probably in other coiled conchs, the caecum is attached to the bottom of the initial camera. In orthoconic forms, including breviconic oncocerids and in some early coiled shells of the Tarphycerida and Barrandeocerida, the caecum ends freely in the initial chamber (Fig. 37,*A-C,G*), as in most ammonoids, where it is attached to the apex by means of the prosiphon. Such a structure, however, has not yet been found in nautiloids.

Present evidence suggests that direct attachment of the caecum to the apical part of the initial chamber is a comparatively late development which occurred toward the end of Paleozoic times.

The early ontogeny of the Endocerida presents somewhat different problems. In this order the initial part of the conch is broadly conical. In many endocerids the initial camera is short (Fig. 37,*E*), but at variance with all forms discussed above, a considerable part—as much as half of it—is occupied by the initial siphuncle segment, which is in broad contact with one side of the initial camera.

In another group of endocerids, formation of the first septum is long delayed and the apical portion of the conch is, for a distance of up to 2 or 3 cm., solely occupied by the caecum, which takes up almost all the space of the initial camera (Fig. 37,*D*). Thus, the initial camerae of endocerids differ considerably from those of all other nautiloid orders, suggesting significant differences in organization of the animals during early ontogenetic stages.

On the exterior tip of the conch of living *Nautilus* there is a sharp, though shallow, slitlike furrow (Fig. 63, in chapter on "Living Nautilus"), generally called the **cicatrix.** Similar, or equivalent, features have been described from many fossil conchs (Fig. 39). The cicatrix is not always slitlike, as in *Nautilus,* but may be circular, ellipsoidal, cross-shaped, or quite irregular.

The cicatrix was regarded as a scar by HYATT and others—the place to which a nonpreservable "protoconch" had been attached, an original opening, later closed by a secondary deposit of calcium carbonate. However, nautiloids are known in which the apex is entirely smooth and it has been shown in *Nautilus* that the test is continuous across the cicatrix, with no indication of a secondary deposit. According to SCHINDEWOLF, the cicatrix was somehow connected with the caecum of the siphuncle. It is possible that traction exercised by the siphuncle on the inside of the test resulted in formation of a depression outside.

It is probable that at least in some nautiloids the initial camera, and two or three of the succeeding camerae developed inside the egg capsule. In living *Nautilus* the egg is known to be up to 45 mm. in diameter, thus comparable in size to the first whorl of the conch. It is, therefore, supposed that the conch is developed inside the egg at this stage (see chapter on "Living *Nautilus*"). Most probably, the early ontogeny of extinct members of the Nautilida followed a similar pattern.

In some orthocerids SHIMANSKIY (30) found that the first four or five camerae increase relatively rapidly in length and that a decrease in length occurs in the next following one or two chambers. SHIMANSKIY concluded that the change in camera length coincided with the moment of hatching. The same stage in bactritids is marked by a conspicuous constriction of the conch.

SHIMANSKIY (30) found that the number of septa in the first whorl of the conch is not constant within an investigated species in each of several members of Nautilida. At the same time SHIMANSKIY observed that the septal angle was greater in the first whorl than in the following volutions. In general, it seems to be difficult to determine at what stage any fossil nautiloid conchs may have hatched from the egg.

The early ontogeny of the soft parts of the Endocerida and Actinocerida cannot be reconstructed with any degree of confidence because of the profound differences of the morphology of their initial camerae and caecum.

SHELL TRUNCATION

In some orthoconic and cyrtoconic forms apical parts of phragmocones were severed during the lifetime of the animals from the rest of the conchs. This process is known as **truncation** or **decollation.** Truncation in such shells occurred once or several times. The truncated part of the phragmocone is called the **deciduous portion,** the body chamber and attached anterior part of phragmocone the **mature portion** of the conch.

Truncation and its effects were first described by BARRANDE (1855, 1877) on the basis of study of over 500 well-preserved specimens of *Orthoceras truncatum,* type-species of the genus *Sphooceras* FLOWER (1962). BARRANDE observed that the number of camerae in specimens of *O. truncatum* varied from four to eight. He calculated that the total length of an average shell without truncation would have been about 50 cm. and that a complete phragmocone would have had some 100 camerae. He, therefore, concluded that truncation had taken place about 24 times in these shells. However, since not all shells can be supposed to have grown to the same size, BARRANDE's figure for number of truncations is probably a maximum rather than an average.

The basal septum of the mature portion of the conch is called **septum of truncation.** At the transition from the deciduous to mature portion of the conch, a slight shift in position of the siphuncle is accomplished by the **siphuncular displacement canal** (see chapter on Ascocerida).

Only the mature portion of the conch of *Sphooceras truncatum* is known with certainty, but FURNISH, GLENISTER & HANS-

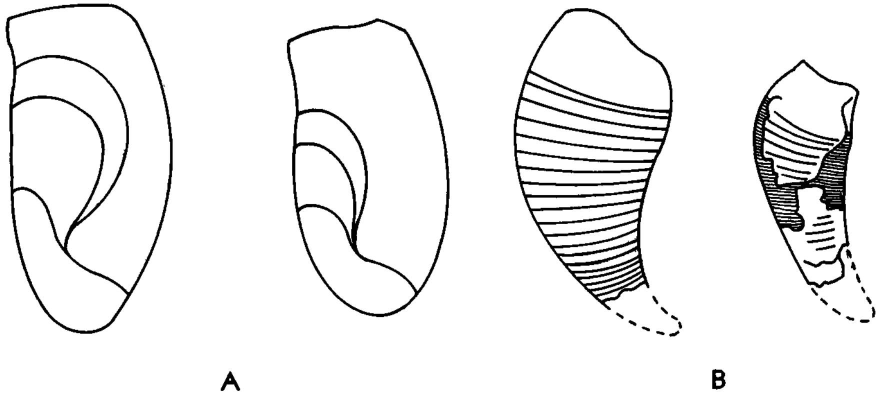

Fig. 40. Possible cases of sexual dimorphism in nautiloid orders (not to scale); *A*, Ascocerida *(Schuchertoceras)*, Ord., USA, ×0.7; *B*, Oncocerida *(Oncoceras)*, Ord., USA, ×0.7 (adapted from 9*a*,25).

man (1962) have listed several species of *"Orthoceras"* described by Barrande which could possibly represent deciduous portions of conchs of the same species. The same authors also called attention to the fact that *Plagiostomoceras pleurotomum* Barrande (family Orthoceratidae, subfamily Michelinoceratinae, p. *K*226) apparently shows a septum of truncation. This species occurs associated with *Sphooceras,* and both are of Silurian age.

Cases of truncation in another family of orthocerids, the Brachycycloceratidae of Carboniferous age, have only recently been demonstrated (12a). The genus *Brachycycloceras* (p. *K*232) was found to have been based on deciduous portions of conchs whose mature portions had been assigned to the genus *Poterioceras.* Furthermore, Furnish, Glenister & Hansman have suggested that representatives of the family Neptunoceratidae (Carboniferous of the Ural Mountains) could well be truncated shells and even be congeneric with *Brachycycloceras.*

While it is thus obvious that the habit of shell truncation developed independently and at different times in at least two, possibly more, families of the Orthocerida, the same feature is characteristic of all representatives of the order Ascocerida, of Late Ordovician to Silurian age. This order is abundantly represented only in the Silurian rocks of the Island of Gotland, and it is from this locality that individuals of several species have been found consisting of deciduous and mature portions before truncation occurred (19a). The morphology and ontogeny of the Ascocerida are discussed in detail in the systematic part of this volume (p. *K*263).

The biological processes that led to truncation are little understood. Barrande suggested that truncation was preceded by formation of a calcareous plug in the siphuncle at the septum of truncation. The posterior portion of the phragmocone was thus cut off from all metabolic processes, resulting in progressive solution and final destruction of the deciduous portion. On the other hand, Tasnádi-Kubacska (34a) believes that truncation may have been due to resorptive processes, activated by the siphuncle and the intracameral tissues (i.e., cameral mantle) and isolating the deciduous portion which finally broke off.

SEXUAL DIMORPHISM

The conchs of the two sexes in living *Nautilus* differ only slightly in size and contradictory statements have been made as to the interpretation of these small differences. Dean (1901) considered that the female conch was wider at the sides and the aperture more oval than that of the male conch, whereas Willey (1902) regarded the broader and more evenly rounded conch as that of a male and the narrower shape as a female conch. The latter view seems now, however, to have been confirmed (compare "Living Nautilus," p. *K*74).

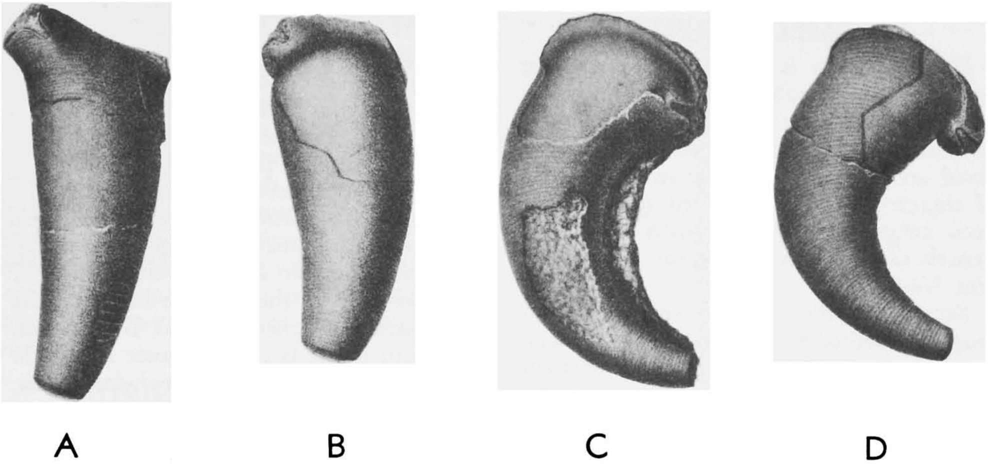

Fig. 41. Possible sexual dimorphism in Oncocerida *(Inversoceras),* M.Sil., Czech. The paired "species," *A, I. perversum* (Barrande) and *B, I. constrictum* Foerste, possibly are only sexual variants; the same may be true of *C, I. percurvatum* Foerste, and *D, I. barrandei* Foerste, ×1 (Barrande, pl. 53, 1865).

The possibility of recognizing sexual dimorphism in fossil nautiloids was first discussed by Ruedemann (24, 25) for Ordovician oncocerids. An assemblage of *Oncoceras* specimens studied by him fell into three morphological groups, two of which resembled each other in all respects except size and which Ruedemann considered to represent the two sexes of one and the same species. Following Dean, he suspected that the larger variety might be the female (Fig. 40,*B*).

Similarly, Teichert (36) interpreted size difference of closely associated specimens of *Wadeoceras* as possible manifestation of sexual dimorphism in this genus.

Flower (7) also called attention to possible cases of sexual dimorphism among the brevicoceratid genera *Ovoceras, Brevicoceras,* and *Verticoceras.*

Foerste (11) suggested that presence or absence of a marked constriction at the base of the dorsal collar in Silurian *Inversoceras* might indicate sexual differences, but this possibility cannot be evaluated until it is more definitely known whether these varieties occur in assorted pairs (Fig. 41).

While all the above-mentioned examples concern members of the order Oncocerida, Flower (1946) also has cited cases of pairs of "species" or "varieties" of ascocerids occurring in the same bed, and resembling each other closely except for differences in size. Examples are taken from the genera *Probillingsites* and *Schuchertoceras* (Fig. 40,*A*). Flower regarded the explanation of sexual dimorphism at least as an "interesting possibility."

In Actinocerida Kobayashi (19) called attention to the peculiar fact that in some species of *Armenoceras* and *Cyrtonybyoceras* the first, or first two, segments of the siphuncle are comparatively narrow and that a sudden increase in width takes place in the next following segment. He suggested that this sudden size increase of the siphuncle might indicate the onset of sexual maturity and might be especially characteristic of females. Doubt is thrown on this interpretation by the observation that in some genera (e.g., *Kochoceras, Selkirkoceras*) the first siphuncle segment is invariably larger than any of the following segments.

Few observations on possible sexual dimorphism have been recorded for fossil Nautilida. Stenzel (1940) observed that in *Aturia,* if present at all, such differences were extremely slight.

In summary, no conclusive evidence has as yet been offered to demonstrate beyond doubt the presence of sexual dimorphism in extinct nautiloids. Observations that point in this direction have been cited mostly from the Oncocerida, but also from Ascocerida and Nautilida, and still more vaguely, from the Discosorida and Actinocerida.

HOMEOMORPHY

Homeomorphy is widespread among the nautiloid orders, which is one reason why recognition of their relationships and their natural classification has been so long delayed and why, until rather recently, hosts of somewhat distantly related species have been assigned to a few, mostly ill-defined generic taxa such as *Orthoceras, Cyrtoceras,* and *Nautilus.*

Because of the basically simple conical shape of orthoconic or weakly cyrtoconic conchs, external homeomorphy is common among orders in which such types of conchs predominate. The conchs of many ellesmerocerids are indistinguishable externally from endocerids, on the one hand, and from some orthocerids, on the other. Among the oncocerids and the discosorids are a considerable number of externally homeomorphic, breviconic and short cyrtoconic forms. Considerable confusion prevailed in the classification of these two orders, until their siphuncle structures became better known.

Among coiled groups considerable external homeomorphy exists between the Tarphycerida and the Barrandeocerida, and also within the order Nautilida, examples of which are given in the introduction to that order.

Torticonic shells developed independently in the Tarphycerida *(Aethoceras),* the Barrandeocerida (*Mitroceras* and others), and even in the Oncocerida *(Nothoceras)* and in the Nautilida *(Trochoceras).*

A remarkable case of homeomorphy is the development of constricted ("visored") apertures of the *Phragmoceras*-type several times independently in entirely different lines of descent (Flower & Teichert, 1957): (1) In the Early Ordovician ellesmerocerid *Burenoceras,* (2) in Ordovician *Antiphragmoceras* (Discosorida), (3) in Middle Silurian *Phragmoceras* (Discosorida), and (4) in the Devonian oncocerid *Bolloceras.* In the Middle Silurian independent of the Phragmoceratidae, additional groups with visored apertures developed. These were the Hemiphragmoceratidae and the Mandaloceratidae.

Homeomorphic development of internal structures is likewise common. Thus, closely similar, evenly curved, cyrtochoanitic septal necks appear independently in the Actinocerida, Orthocerida (superfamily Pseudorthocerataceae and Paraphragmitidae of superfamily Orthocerataceae), Barrandeocerida (Nephriticeratidae), and in some Nautilida (Tainocerataceae). Abruptly recumbent, cyrtochoanitic necks develop in the Oncocerida, the Discosorida, as well as in some Actinocerida (Armenoceratidae).

Along with cyrtochoanitic septal necks goes the development of expanded, nummuloidal siphuncle segments which appear independently in the Pseudorthocerataceae, Actinocerida, Oncocerida, and Discosorida, and again much later in Triassic Nautilida (e.g., *Germanonautilus, Proclydonautilus, Pleuronautilus*).

The cameral deposits of many Orthocerataceae are quite similar to those of many Actinocerida, especially, where simple layers of episeptal and hyposeptal deposits are present.

Similar endosiphuncular structures develop homeomorphically in unrelated genera of diverse orders. For example, endosiphuncular central or subcentral tubes occur in the Orthocerida *(Harrisoceras)* Discosorida *(Madiganella),* Oncocerida *(Diestoceras)* and possibly in others. Actinosiphonate deposits are found in the Endoceratoidea (order Intejocerida) and in the Oncocerida, although the similarity of these structures in the two orders is probably more apparent than real. Endocones of very similar structure and appearance occur in the Endoceratoidea (order Endocerida), Discosorida (family Discosoridae and others), and Orthocerida (family Troedssonellidae).

Parietal deposits of closely similar shape and structure are characteristic of the Pseudorthocerataceae (order Orthocerida) and most members of the Discosorida. In certain late Paleozoic Pseudorthocerataceae (Pseudactinoceratinae) the parietal deposits develop to such an extent, filling almost the entire endosiphuncle, as to resemble closely the siphuncles of contemporaneous actinocerids (Carbactinoceratidae). Affinities of some genera are solely established on the basis of presence or absence of a perispatium.

Brachycycloceras represents a remarkable case of iterative evolution, resulting in homeomorphy of correlated morphological features with a genetically unrelated group of cephalopods of much earlier geologic age.

The shells of this genus consist of a deciduous, annulate, longiconic stage, and a rather plump, breviconic mature stage and body chamber, mimicking the Ordovician and Silurian Ascocerida with which the Pennsylvanian *Brachycycloceras* is not related through descent, although both stem from the Orthocerida. The genus shares with the Ascocerida such a specialized feature as the siphuncular displacement canal, which is a ventrally deflected portion of the siphuncle along the anterior face of the septum of truncation.

INJURIES AND DISEASE

Many conchs of living *Nautilus* show evidence of more or less severe damage to the apertural region of the body chamber at various growth stages, but the mantle possesses considerable healing power and the broken edges are soon repaired. Willey (1902) described a shell of *Nautilus pompilius* with a deep, almost mid-dorsally situated revolving furrow which must have been due to permanent injury suffered at an early age by the animal, or perhaps by its mantle alone. Loesch (20) has described a Jurassic nautilid shell with somewhat similar features in which, however, healing of the damaged or diseased mantle took place at full maturity.

Barrande (2) described a longiconic conch of *Plagiostomoceras* which is bent at an intermediate growth stage, but which straightened out again in later stages (Fig. 42). Since the test shows no sign of breakage the abnormal growth must have been caused by sickness or by internal injury.

In an assemblage of Cretaceous nautilids from Africa Sornay (30a) found several specimens which possessed a hollow hump on the ventral sides of their conchs, at growth stages well before maturity was reached. The origin of this feature is obscure, but may be supposed to be connected with some malfunctioning of the mantle tissue. Deformed nautilid shells have also been described from the Cretaceous of France and from the Eocene of North America (Maryland).

It has already been mentioned in the chapter on the phragmocone that abnormal spacing of septa, except of the last few, is a pathologic condition due to injury or disease (Fig. 21).

Fig. 42. Pathological growth disturbance in a conch of *Plagiostomoceras*, Sil., Czech., ×0.7 (Barrande, pl. 299, 1868).

More recently, Stumbur (33) has described a case of rather severe injury to a *Trocholites* conch at an intermediate growth stage. This injury seems to have affected the ventral sides of two chambers of the phragmocone, but the breakage was healed when the animal had completed an entire whorl and a new, distorted shell layer was formed over the injured part.

In rare cases, as has already been mentioned in the description of the phragmocone, septa were only incompletely developed or the body advanced in the body chamber for a distance equal to that between several septa before the animal constructed a new septum. Such conditions have been described by BARRANDE, KESSLER, and HÖLDER in straight and coiled Paleozoic and Mesozoic conchs. The origin of these malformations is not known. Presumably they were caused by malfunctioning of the mantle surface that secreted the septa (14b).

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GLOSSARY OF MORPHOLOGICAL TERMS USED FOR NAUTILOIDS

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ACHOANITIC. Descriptive of condition in which septal necks are vestigial or absent (*syn.*, aneuchoanitic).

ACTINOSIPHONATE. Descriptive of endosiphuncular deposits consisting of radially arranged longitudinal lamellae.

ADNATION AREA. Area along which connecting ring is in contact with adapertural surface of free part of septum.

air chamber. *See* camera.

AMORPHOUS BAND. Narrow bands surrounding conchiolinous zone in thick connecting rings of some specialized discosorids.

aneuchoanitic. *See* achoanitic.

annular elevation(*). Area on inside of posterior part of body chamber between anterior margin of anterior aponeurotic band and posterior margin of posterior aponeurotic band, and including retractor muscle attachment areas.

ANNULAR LOBE. Small, secondary dorsal lobe in center of main internal (dorsal) lobe of suture of some coiled forms.

ANNULATE. Marked by or bearing annulations.

ANNULATION. Ringlike expansion of conch, either transverse or slightly oblique to longitudinal axis of conch.

annulosiphonate. Descriptive of endosiphuncular deposits having shape of rings formed at septal foramen and attached to inside of septal neck.

ANNULUS. Thin, ring-shaped endosiphuncular deposit, semicircular in cross section, on inner side of septal neck.

annulus. *See* periphract.

apertural ridge (*). Ridgelike thickening inside apertural margin of body chamber.

APERTURE. Opening of shell through which head-foot protrudes.

APICAL CAMERA or CHAMBER. First camera of phragmocone. (*syn.*, initial camera or chamber).

APONEUROTIC BANDS. Areas of attachment of palliovisceral ligaments on inside of body chamber; anterior and posterior aponeurotic bands are recognized.

ASCOCEROID CONCH. Specialized brevicone, bounded at base by septum of truncation; consisting of inflated posterior portion with dorsal phragmocone, and anterior cylindrical neck.

ASCOCEROID SEPTUM. Specialized partition between chambers (septum) in late growth stages of Ascocerida, sigmoidal in section, and strongly bent forward on dorsum, with complex (sigmoid) suture.

BASAL SEPTUM. Wall (septum) with normal suture between septum of truncation and first ascoceroid septum (Ascocerida only).

basal zone. Adapical interior zone of body chamber in which shell wall is thickened, commonly with pitted or banded surface.

blade. *See* endosiphuncular blade.

BODY CHAMBER. Large undivided, anterior space in conch open at aperture, occupied by animal's body (*syn.*, living chamber).

BREVICONE. Short and rapidly expanding conch.

BRIM. Flared or recurved portion of cyrtochoanitic septal neck.

BULLETTE. Annulosiphonate deposits similar to annulus, but flatter and more elongated in cross section; name derived from knob- or bosslike appearance of deposit in cross section.

BUNDLED. Descriptive of ribs in coiled conchs, united in sheaves or bundles at or near umbilical shoulder.

CADICONE. Coiled conchs which are strongly depressed, and more or less evolute, with wide venter and deep umbilicus.

CAECUM. Sac-shaped apical end of siphuncle; also, cavity associated with digestive system (living *Nautilus*).

CAMERA. Space enclosed between two adjacent septa but not including siphuncle (adj., cameral) (*syn.*, chamber, gas chamber, air chamber).

CAMERAL DEPOSITS. Calcareous deposits secreted against original walls of camerae during life of animal (*syn.*, intracameral deposits).

CENTRAL CANAL. Longitudinal cavity (canal) in or near center of siphuncle of Actinocerida.

centrifugal deposits. *See* parietal deposits.

chamber. *See* camera.

chitinous zone. Referred to by authors who are unaware that mollusks do not secrete chitin; *see* conchiolinous zone.

CICATRIX. Small groove or scar on apex of some conchs.

CIRCULUS. Cameral deposit on concave surface of cyrtochoanitic septal neck (*syn.*, *Stützring*, supporting ring).

CIRCUMSIPHUNCULAR RIDGE. Ridgelike thickening of episeptal deposits in immediate neighborhood of connecting ring.

collum. *See* septal neck.

COMPRESSED. Descriptive of conch and dorsoventral diameter greater than lateral.

CONCAVOSIPHONATE. Descriptive of siphuncles concave in section between septa.

CONCH. All hard calcareous parts secreted by nautiloid animal including external shell, septa and siphuncle, but not cameral deposits and any structures within siphuncle (*syn.,* shell, test).

CONCHAL FURROW. Shallow groove on inside of conch wall, located mid-ventrally.

[**conchial** (*recte,* **conchal**) **zone I**(*). Anterior aponeurotic band.]

[**conchial** (*recte,* **conchal**) **zone II**(*). Posterior aponeurotic band.]

conchiolinous zone. Posterior half of free part of thick connecting ring in some discosorids.

CONNECTING RING. Partly calcareous, partly conchiolinous, tubular membrane, that connects septal neck of ellipochoanitic conchs with septum immediately behind it; vestiges of it are also found in holochoanitic forms.

conotheca. Part of conch comprising external shell (*syn.,* shell wall).

CONSTRICTED. Descriptive of body chamber having smallest diameter close behind aperture.

CONSTRICTION. Narrow transverse depression of conch.

CONTACT LAYER. Deposit formed between connecting ring and septum on area of adnation in some conchs (Actinocerida only).

CONTRACTED. Descriptive of aperture having diameter smaller than maximum diameter of body chamber.

CORONATE. Descriptive of whorl section (of coiled conchs) which is depressed and has divergent flanks.

costae. *See* ribs.

CYRTOCHOANITIC. Descriptive of comparatively short, retrochoanitic septal necks which are curved so as to be concave outward.

CYRTOCONE. Curved conch that completes less than one whorl.

DECIDUOUS CONCH. Apical juvenile phragmocone truncated during ontogeny (e.g., Ascocerida, some Orthocerida, and possibly other groups).

decollation. *See* truncation.

DEPRESSED. Descriptive of conch with lateral diameter greater than dorsoventral.

DIAPHRAGM. Imperforate partition crossing siphuncle.

distal deposits. *See* hyposeptal deposits.

distal division of siphonal funnel(*). Connecting ring.

domiciliary cavity(*). Body chamber.

domiciliary division(*). Body chamber.

DORSAL AREA. Part of whorl of coiled conch which is in contact with preceding whorl.

dorsal furrow. *See* septal furrow.

DORSAL HIATUS. Small area without deposits in mid-dorsal region of camerae which have cameral deposits.

DORSAL LOBE. Median primary lobe of suture on dorsum; in coiled forms, also called internal lobe.

DORSOLATERAL BANDS. Thin layers of cameral deposits on dorsolateral side of camerae.

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

DORSOVENTRAL SECTION. Longitudinal section through straight or symmetrically curved and coiled conchs, intersecting shell wall along mid-dorsal and mid-ventral lines, bisecting conch into two symmetrical parts.

DORSUM. Side of animal or conch opposite venter; in live *Nautilus* region occupied by shell coil above body chamber. [Among fossil nautiloids, if the position of the hyponomic sinus (and therefore venter) cannot be established, the term is somewhat loosely applied (1) in coiled forms to the concave side of a whorl, (2) in straight or curved conchs with eccentric siphuncle to the side farthest removed from the siphuncle.]

ectosiphon. *See* ectosiphuncle.

ECTOSIPHUNCLE. Wall of siphuncle consisting generally of septal necks and connecting rings (*syn.,* ectosiphon).

ECTOSIPHUNCULAR SUTURE. Line on inside of shell or on internal mold bounding area of contact of siphuncle and shell wall. [Ectosiphuncular sutures occur in each camera of nautiloids with marginal siphuncles, especially endocerids and actinocerids.]

ELLIPOCHOANITIC. Descriptive of relatively short retrochoanitic septal necks which do not reach as far as preceding septum (refers to all types of septal necks except holo-, subholo-, and macrochoanitic).

ELLIPTICONE. Coiled conch having elliptical coiling of last whorl or half-whorl, which breaks away from spiral.

ENDOCONE. One of series of calcareous cones formed in posterior or adapical portion of siphuncle mainly of endocerid and discosorid conchs.

ENDOGASTRIC. Descriptive of conchs curved or coiled in manner placing venter on or near inner or concave side.

endosiphoblade. *See* endosiphuncular blade.

ENDOSIPHOCOLEON. Flattened, ?conchiolinous tube or blade surrounding endosiphuncular tube in some endocerids.

ENDOSIPHOCONE. Conical space inside last-formed endocone in Endocerida and some Discosorida.

endosipholining. *See* endosiphuncular lining.

endosiphon. *See* endosiphuncle.

endosiphotube. *See* endosiphuncular tube.

endosiphowedge. *See* endosiphuncular wedge.

ENDOSIPHUNCLE. Space within ectosiphuncle including all organic tissues and calcareous structures.

ENDOSIPHUNCULAR BLADE. Longitudinal membranes or partitions traversing endocones in siphuncle of Endocerida.

ENDOSIPHUNCULAR LINING. Dark lining seen inside septal necks of some endocerids, probably formed by continuous connecting rings.

ENDOSIPHUNCULAR TUBE. (1) Circular tube formed by adapical thickening of lateral walls of endosiphocoleon in some Endocerida; (2) simple tubes connecting apices of endocones where no differentiation of coleon and tube is possible.

ENDOSIPHUNCULAR WEDGE. Wedge-shaped deposit in apical part of siphuncles of certain pilocerids.

EPISEPTAL DEPOSITS. Cameral deposits on concave (or adapertural) side of septum (*syn.*, proximal deposits).

episeptal tubercle(*). Dorsal or annular lobe as expressed on posterior side of septum.

EURYSIPHONATE. General term for forms with relatively large siphuncles.

EVOLUTE. Descriptive of coiled conchs in which whorls do not overlap considerably, hence having wide umbilicus.

EXOGASTRIC. Descriptive of conchs curved or coiled so that venter is on or near outer or convex side.

EXTERNAL LOBE. Often used for ventral lobe of suture in coiled conchs (*syn.*, ventral lobe; in ammonoids, siphonal lobe).

EXTERNAL SUTURE. Part of suture of coiled conchs exposed on outside of whorls between the umbilical seams.

EYELET. Specialized region in tip of connecting ring in many stenosiphonate cephalopods, characterized by dense fine-grained or amorphous material.

FALCATE. Sickle-shaped (ribs).

FALCOID. Somewhat sickle-shaped (ribs).

FALSE CONTACT. Condition in which connecting ring and septum are separated by contact layer (Actinocerida only).

FASCICULATE. Descriptive of ribbing in coiled conchs having bunched or bundled ribs at umbilical tubercles or near umbilical margin.

FIRST LATERAL LOBE. First primary adapical inflection of suture next to ventral (or external) lobe, usually situated on flank of coiled conchs.

FLANKS. Sides of conch between venter and dorsum (*syn.*, whorl sides, lateral areas).

FLARED. Descriptive of aperture of constricted body chamber having apertural diameter greater than diameter of inflated portion of body chamber.

foramen (pl., **foramina**). *See* septal foramen.

FREE PART OF CONNECTING RING. Part of connecting ring not in contact with septa.

FREE PART OF SEPTUM. Part of septum which separates camerae.

funnel. *See* septal funnel.

funnel emargination(*). Hyponomic sinus.

gas chamber. *See* camera.

GRANULAR ZONE. Anterior half of thick, specalized connecting rings in some discosorids.

GROWTH LINES. Markings on surface of conch that denote periodic increases in size and hence former positions of aperture.

GYROCONE. Loosely coiled conch in which successive whorls are not in contact with each other.

HEMICHOANITIC. Descriptive of retrochoanitic septal necks that extend one-half to three-fourths of distance to preceding septum.

HOLOCHOANITIC. Descriptive of retrochoanitic septal necks that extend backward through length of one camera.

HYPONOMIC SINUS. Large concave sinus in middle of aperture, marking location of hyponome, invariably ventral.

HYPOSEPTAL DEPOSITS. Cameral deposits on convex (adapical) side of septum (*syn.*, distal deposits).

hyposeptal fossa(*). Dorsal or annular lobe expressed on anterior side of septum.

IMPRESSED AREA. Concave dorsum in coiled conchs, in contact with venter of preceding whorl and tending to overlap it (*syn.*, impressed zone).

impressed zone. *See* impressed area.

INITIAL CHAMBER or CAMERA. First camera of phragmocone (*syn.*, apical camera or chamber).

intercostae. *See* interspaces.

intermediate area(*). Part of "annular elevation" which does not serve as muscle attachment area.

INTERNAL LOBE. Identical with dorsal lobe in coiled forms.

INTERNAL SUTURE. Part of suture in coiled conchs situated on dorsum and hidden from view unless conch is broken.

INTERSEPTAL LINING. Lining between mural parts of two successive septa, formed after earlier but before later septum.

INTERSPACES. Spaces between ribs in coiled conchs.

intracameral deposits. *See* cameral deposits.

INVOLUTE. Descriptive of coiled conchs with considerably overlapping whorls, hence with narrow umbilicus.

KEEL. Continuous sharp ridge along venter of conch, especially in coiled forms.

LACUNA (pl., **LACUNAE**). Axial septal discontinuity, within ascoceroid septum, bounded by line of contact with preceding septum.

LANCEOLATE. Descriptive of spear-shaped whorl sections with acute periphery.

LATERAL ANGLE. Angular bend in lateral part of ascocerid suture.

lateral areas. *See* flanks.

LATERAL LOBE. Any adapical inflection of suture between ventral and dorsal lobes. [In coiled conchs lateral lobes may be external or internal according to whether they are on flanks or dorsal area.]

LATERAL SADDLE. Any adapertural inflection of suture separating lateral lobes from each other or from external or internal lobes; distinction of external and internal lateral saddles same as for lateral lobes.

LATERAL SINUS. Re-entrant in lateral portion of apertural margin.

LINEATION. Pattern of fine linear markings, whether raised or incised, on surface of conch.

LIRAE. Parallel fine ridges or raised lines on surface of conch, transverse or longitudinal, separated by striae. [Restricted to features not easily discernible with the naked eye.]

LIRATE. Surface bearing lirae.

LITUICONE. Conch which completes few whorls in early stages and then becomes straight (*syn.*, lituiticone).

lituiticone. *See* lituicone.

living chamber. *See* body chamber.

LOBE. Adapically (or backward) convex undulation of suture (reverse of saddle).

lower annular ridge(*). Ridgelike thickening of anterior edge of "annular elevation."

LOXOCHOANITIC. Descriptive of retrochoanitic septal necks that are short, straight, pointing obliquely toward interior of siphuncle.

lunette. Sometimes used for annulosiphonate deposits which are large and massive, as in many Actinocerida.

MACROCHOANITIC. Descriptive of retrochoanitic septal necks that reach backward beyond preceding septum and are invaginated into preceding septal neck.

MARGINAL ATTACHMENT BAND. Attachment area of anterior mantle edge to inside of test along aperture.

MATURE PART OF CONCH. Body chamber and anterior portion of phragmocone after loss of deciduous portion of conch by truncation.

MURAL DEPOSITS. Cameral deposits along mural parts of septa.

MURAL PART OF SEPTUM. Part of the septum attached to wall of conch.

mural ridge(*). Ridgelike thickening of anterior margin of mural part of septum.

NAUTILICONE. Strongly involute coiled conch.

NECK. Constricted anterior part of body chamber in specialized brevicones between aperture and inflated portion (not to be confused with septal neck).

nepionic bulb. Term sometimes used for swollen apical part of siphon in some Endocerida.

nepionic flange. Short adapical extension of wall of first camera.

NEPIONIC LINE. Very distinct transverse line on test, slightly in front of first whorl of coiled conchs.

nummuli. Sometimes used for siphuncular segments that are strongly inflated between septa, mostly in Actinocerida.

ocular emargination(*). Ocular sinus (in *Nautilus*).

OCULAR SINUS. One of pair of small and shallow sinuses at sides of aperture in position of eyes in *Nautilus*.

ORTHOCHOANITIC. Descriptive of retrochoanitic septal necks which are straight, cylindrical, and extend only a short way to preceding septum.

ORTHOCONE. Straight conch.

OXYCONE. Laterally compressed coiled conch with acute periphery and usually narrow or occluded umbilicus.

PARIETAL DEPOSITS. Annulosiphonate deposits that grow close against connecting ring and do not normally project markedly into siphuncular cavity (*syn.*, centrifugal deposits).

PENDENT DEPOSITS. Annulosiphonate deposits in contact with wall of siphuncle only at their point of origin.

PERIPHRACT. Continuous band of muscles and aponeouroses that encircles body, consisting of dorsal aponeurosis, retractor muscles, and anteroventral aponeurosis (*syn.*, annulus). Term derived from Greek (*peri*, around; *phractos*, enclosed); adj., periphractic, multiply connected.

PERISPATIAL DEPOSITS. Primary lamellar deposits developed in perispatium of Actinocerida.

PERISPATIUM. Space between annulosiphonate deposits and free part of connecting ring in Actinocerida.

PERISTOME. Edge of aperture.

PHRAGMOCONE. Chambered portion of conch.

PLANULATE. Descriptive of coiled conchs which are moderately compressed and moderately evolute, with open umbilicus and bluntly rounded venter.

PLATYCONE. Coiled conch with flattened venter, without implications as to width of umbilicus or form of venter.

PLEUROMYARIAN. Descriptive term applied to nautiloid cephalopods in which shell or retractor muscles of head-foot are attached along lateral areas of interior of body chamber.

PLICATE. Surface covered with vague foldlike ribs.

PRE-BASAL SEGMENT. Segment of siphuncle lying between septum of truncation and basal septum (in Ascocerida).

PROTOCONCH. First portion of embryonic shell, its preservation in fossil and in living forms uncertain. [Some authors regard the first camera as the protoconch.]

proximal deposits. *See* episeptal deposits.

proximal division of siphonal funnel(*). Septal neck.

pseudoseptum. Plane of junction between hyposeptal deposits of one septum and episeptal deposits on preceding septum.

RADIAL CANALS. Tubes connecting central canal with perispatium in Actinocerida.

RECUMBENT BRIM. Brim of cyrtochoanitic septal necks, recurved so sharply that it lies in contact with adapical surface of free part of septum.

RETROCHOANITIC. Descriptive of septal necks which are directed backward (*syn.*, retrosiphonate).

retrosiphonate. *See* retrochoanitic.

RIBS. Raised radial ridges on coiled conch.

SADDLE. Adaperturally (or forward) convex undulation of suture (reverse of lobe).

SEGMENT OF SIPHUNCLE. Any part of siphuncle between two successive septal foramina.

septal elements. *See* sutural elements.

SEPTAL ANGLE. Angle between tangents drawn from apex of planispiral shell to two successive septa and measured on a section made along plane of symmetry.[1]

SEPTAL FORAMEN. Opening in septum allowing passage of siphuncular cord (*syn.*, siphuncular foramen).

septal funnel. Septal neck which extends at least as far as preceding septum and is more or less invaginated into next septal funnel.

SEPTAL FURROW. Narrow mid-dorsal region in which mural part of septum is lacking.

SEPTAL NECK. Portion of septum which is bent adapically (or backward) around septal foramen (*syn.*, collum).

septate division(*). Phragmocone.

SEPTUM. Partitions dividing phragmocone into camerae and attached to inside of wall of conch.

SEPTUM OF TRUNCATION. Transverse partition of conch comprising specialized thick septum which forms base of mature shell in groups which decollated juvenile phragmocone (e.g., Ascocerida, some Orthocerida).

septum proper(*). Free part of septum.

SERPENTICONE. Coiled many-whorled conch, very evolute, with whorls hardly overlapping.

shell. *See* conch.

SHELL WALL. Part of conch comprising external shell.

SIGMOID SUTURE. Prominent dorsal lobes, and more or less S-shaped suture in lateral aspect, as developed in late growth stages of Ascocerida.

SINUS. Any part of transverse feature (apertural margin, ribs, growth-lines) concave toward aperture.

siphon. See siphuncular cord (adj., siphonal).

siphonal caecum. *See* caecum.

siphonal funnel(*). Ectosiphuncle.

siphonal lobe. *See* external lobe.

siphonal tube(*). Ectosiphuncle.

SIPHUNCLE. Long slender or thick tube extending through all camerae to apex and consisting of soft and shelly parts, including septal necks, connecting rings, calcareous deposits, and siphuncular cord (adj., siphuncular).

SIPHUNCULAR CORD. Fleshy interior tissues of siphuncle.

SIPHUNCULAR DISPLACEMENT CANAL. Tube through which the siphuncle was deflected ventrally across anterior face of septum of truncation (e.g., some Ascocerida and Orthocerida).

SIPHUNCULAR SEGMENT. Portion of siphuncle between any two successive septal foramina.

SPHAEROCONE. Coiled conch, depressed, involute, globular, with round venter and umbilicus quite or nearly occluded.

STENOSIPHONATE. General term for forms with relatively narrow siphuncle.

STRIAE. Parallel, small to minute grooves or channels on surface of conch, either transverse or longitudinal, separated by lirae. [Restricted to features not easily discernible with the naked eye.]

Stützring. *See* circulus.

SUBHOLOCHOANITIC. Descriptive of retrochoanitic septal necks approximately equal in length to distance between two septa, but deflected inward at their tips, leaving appreciable gap between two successive septal necks.

SUBORTHOCHOANITIC. Descriptive of retrochoanitic septal necks that are short and straight, with slightly outwardly inclined tips but with no measurable brim.

supporting ring. *See* circulus.

SUTURAL ELEMENTS. Major parts of suture directed alternately forward (saddles) and backward (lobes) (*syn.*, septal elements).

SUTURE. Line of junction of free part of septum and inner side of phragmocone wall (*syn.*, systegnosis).

systegnosis(*). Suture.

tabulate. *See* platycone.

tarphophioceracone. Specialized lituicone.

tarphyceracone. *See* serpenticone.

test. *See* conch.

TORTICONE. Conch coiled in helicoidal spire, as in gastropods (*syn.*, trochoceroid).

trochoceroid. *See* torticone.

TRUNCATION. Natural loss, in life, of apical portion of shell (*syn.*, decollation).

UMBILICAL ANGLE. Same as umbilical shoulder, but angular.

UMBILICAL AREAS. Surface of inner whorl of coiled conchs exposed between umbilical seams.

UMBILICAL PERFORATION. Vacant space around axis of coiling and connecting umbilicus on opposite sides of shell.

UMBILICAL SEAM. Helical line of junction of adjacent whorls of coiled conchs (*syn.*, umbilical suture).

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[1] The whole complex of septal angles in an individual is a specific character according to SHIMANSKIY, V. N., 1948 (30) (p. K386).

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

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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