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CAMERAL DEPOSITS IN CEPHALOPOD SHELLS

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ABSTRACT

A review of the history of investigation of cameral deposits in cephalopod shells leads to the conclusion that their organic origin must now be considered an established fact. It seems equally certain that these deposits were formed after formation of the camerae in which they are found had been completed. New observations on cameral deposits found in orthoconic shells preserved in the Pennsylvanian Buckhorn asphalt of southern Oklahoma support these conclusions in every respect. The morphology of the cameral deposits is described for *Pseudorthoceras knoxense*, "*Orthoceras*" *unicamera*, and other forms. Possible physiologic mechanisms which might have been operative in forming the deposits are discussed. FISCHER favors the hypothesis that in the Buckhorn cephalopods they were formed from intracameral ("extrapallial") fluids secreted by the siphuncle into the camerae, and he wants to see this hypothesis applied also to many other fossil groups in which cameral deposits occur. However, he acknowledges that cameral deposits must have been secreted by tissues in such forms as *Leurocycloceras*. TEICHERT prefers to apply the secretion-by-tissue hypothesis to the formation of all cameral deposits, although he acknowledges FISCHER's fluid precipitation hypothesis as a valid alternative.

INTRODUCTION AND ACKNOWLEDGMENTS

The origin of cameral deposits in the chambers of cephalopod shells has long fueled paleontological debates and controversies. The history of thought was summarized, in very condensed form, by TEICHERT (1964), but since then new knowledge concerning the chamber contents of *Nautilus* shells has given rise to new hypotheses, and has modified our own views somewhat. It seemed appropriate, therefore, to review the entire problem in the first part of this paper, before undertaking a detailed study of cameral deposits in some unusually well-preserved material, orthoconic nautiloids of the Pennsylvanian Buckhorn asphalt of Oklahoma.

Many colleagues have, over the years, contributed to this study by personal discussion and argument. We can single out only a few for special acknowledgment. Dr. HEINZ LOWENSTAM, whose chemical investigations we had hoped to include on a coauthor basis, helped to plan the paper; we are grateful to him for permission to proceed, when his own studies were delayed. Dr. CHARLES GRÉGOIRE contributed not only through his published electron micrographs of Buckhorn nautiloids, but also through personal discussions with both of us. He and Dr. HARRY MUTVEI are specifically responsible for the suggestion of epitaxial control as a source of symmetry in cameral

deposits. Dr. MUTVEI has throughout played the role of devil's advocate; his vigorous skepticism about the organic nature of cameral deposits initially goaded us into writing this paper. Dr. A. SELACHER brought MUTVEI, GRÉGOIRE and FISCHER together at a cephalopod symposium held in Tübingen in 1966, and participated vigorously in our discussions. Dr. R. H. FLOWER has ever

been ready to help and advise. Mr. G. TAPPAN and Dr. R. B. FINLEY participated in the early phases of the Buckhorn study, and Dr. ROBERT FAY prepared most of the photographs.

FISCHER's portion of this work—the study of the Buckhorn cephalopods—was supported in part by the National Science Foundation (GB-3766).

HISTORY OF INVESTIGATIONS

The camerae (or chambers) of the phragmocones of many fossil cephalopods are wholly or partly filled with deposits of calcium carbonate which line walls and septa, and in some shells even the siphuncle. While some of these deposits undoubtedly resulted from infiltration of CaCO_3 -bearing water into the empty camerae after burial of the shells by sediment, the disposition and geometrical shape of others has long been regarded as suggestive of organic origin, resulting from metabolic processes of the animal that built and inhabited the shell.

Discovery of organically constructed deposits, called *dépôts organiques*, in the camerae of fossil cephalopods was first announced by that ingenious observer, JOACHIM BARRANDE, at a meeting of the Société géologique de France held on 20 June, 1859. Presentation of his paper seems to have been followed by lively discussion in which D'ARCHIAC, DELESSE, HÉBERT, and MICHELIN participated.

BARRANDE (1859) developed the following criteria for recognition of organically constructed deposits in cephalopod camerae: 1) They were formed before mud could penetrate into the camerae. 2) In Bohemian Paleozoic specimens they commonly are the same in color as endosiphuncular deposits of demonstrably organic origin. 3) They have a slightly irregular to mammillate surface and may be absent from the convex side of the septa. 4) They are generally unevenly distributed within camerae, being more heavily deposited in one half of a camera than the other. 5) They are never found on the surface of connecting rings. 6) They show regular increase or decrease in thickness and bulk longitudinally in the shell from one camera to the next. 7) They are more common in forms with eccentric siphuncles than in those with central ones and their

bulk is generally heaviest on the side opposite the siphuncle.

BARRANDE stated that he had observed organic deposits in the chambers of straight, longiconic forms only, not in breviconic, curved, or coiled shells. From this he concluded that the deposits were formed by the mantle in the same way as the septa and that each septum and its deposits were completed before the animal moved on in its shell.

The age of species discussed by BARRANDE as examples was not reported except to state that they were Paleozoic. In fact, his material came from several beds of Late Ordovician to Middle Devonian age.

Next mention of organic deposits in camerae was by MEEK & WORTHEN (1868, p. 298) who described them in an Ordovician (Trenton) cephalopod identified as "*Orthoceras (Ormoceras) Backii*, STOKES?". This was the first mention of these structures in North American paleontological literature.

MOJSISOVICS (1873) reported *organisches Depot* in several species of nautiloids and ammonoids. In the former the deposit is spread rather evenly over the septa and in the latter on saddles of the sutures, but its distribution across the septa is not known. MOJSISOVICS described the *Depot* as a brown substance, evidently different in composition from the septa.

BARRANDE returned to the subject of the *dépôts organiques* in greater detail in his *Système Silurien* (BARRANDE, 1877, p. 264-290) where he discussed them with references to many illustrations published between 1866 and 1870 (BARRANDE, 1866, 1868, 1870). He reported occurrence of these deposits in 48 Bohemian species, mostly orthocerids, and called attention to their presence

in six species found outside of Bohemia, all actinocerids. In addition to observations made in 1859, BARRANDE noted that the bulk of deposits in each camera in most shells diminishes in a regular manner from the apical toward the oral part of the shell and he regarded this observation as one of the strongest proofs for their organic origin.

In 1859 BARRANDE had stated that he believed camerall deposits to be secretions of the mantle. In 1877 he elaborated his views and suggested that the processes of deposit-secretion might have been as follows (BARRANDE, 1877, p. 277-278): After completion of construction of a septum the mantle remained in position and continued to secrete calcium carbonate, although on a reduced scale, mainly in the ventral part of the shell. After some time the animal moved forward in the body chamber and the mantle became detached from the last-formed septum and overlying deposit, but continued to secrete calcareous substance. When the base of the mantle had reached the position where the new septum was to be built, a certain amount of *dépôt organique* had accumulated and on this the new septum was secreted. The deposit formed during the forward movement of the animal in the shell is that seen on the convex side of the septa.

In 1879, HALL described what he called an organic deposit in specimens from the Schoharie grit, identified by him as *Orthoceras luxum*, but later separated from this species under the name *Ormoceras schohariense* by FLOWER (1940). Subsequently in this country, interest in these camerall structures lapsed. RUEDEMANN (1906, p. 414-417) discussed them in connection with deposits, certainly not organic, in an endocerid, but they were largely ignored by such outstanding students of cephalopods as HYATT, FOERSTE, and A. K. MILLER, to mention only some.

In Europe camerall deposits received sporadic attention by some students of cephalopods, while they were ignored by others. NOETLING (1882) and other early German authors called them *Horizontallamellen*. GRABAU (1922), KOBAYASHI (1936), and other Asian paleontologists referred to them as "stereoplasm," and they are the "*primäre Intrakamerallagerungen*," or "primary intracamerall deposits," of TEICHERT (1933, 1935). More simply, following FLOWER (1939, 1955), they are now generally known as "camerall deposits."

No exhaustive historical treatment of the subject is contemplated. The most important developments were discussed by HOLM (1885), FLOWER (1955), and, more summarily, TEICHERT (1964). A few highlights not touched upon by these writers, as well as more recent developments, are added below.

Among earlier descriptions of camerall deposits, those by GIRTY (1915, p. 230-231) of *Pseudorthoceras* have been generally overlooked. He described them accurately and in some detail and believed that the mural deposits joined together provided a kind of inner shell that served as a protective cover when the outer shell was "dissolved away," a process which he believed to have affected many cephalopod shells. GIRTY stated that camerall deposits were secreted in the body chamber and that secretion ceased when the mantle moved forward in the shell with the animal to construct the next septum.

MISCH (1930) was the first to announce occurrence of *Pseudorthoceras* in Europe. He called the camerall deposit "*sekundäre Kalkabscheidungen*" and reported that they have a lamellar structure showing alternating light and dark laminae, but he offered no opinion on their mode of formation.

GRABAU (1922, p. 74) regarded it as evident that camerall deposits were built at the "floor of the living-chamber, i.e. that each deposit was formed before the next covering septum was built . . . for there is absolutely no indication that the camerae were in subsequent communication with the animal, the small tubuli of the siphuncle notwithstanding." Later TEICHERT (1933) called the "tubuli" radial canals and suggested that they might play a part in bringing body fluids to the camerae. GRABAU also believed in the reality of the "pseudoseptum" and described the entire process as follows (p. 74):

Thus, after the formation of each septum deposition of lime continued upon it for a time, after which, during a resting stage, a pseudoseptum in close contact with the crystalline lime was formed. This was followed by a forward movement of the animal in the shell, and the formation of a new septum, which thus was distant for a certain space (generally less than half the height of the camera) from the pseudoseptum and crystalline deposit. After that the deposition of crystalline lime recommenced upon the surface of the new septum.

The case of *Rayonnoceras* is interesting. When CRONEIS (1926) named and described this genus, he expressed no doubt about the organic nature of its cameral deposits which he referred to as "stereoplasm, or calcareous, organic material." FOERSTE & TEICHERT (1930) described additional species of the genus from North America and stated that there was no reason to believe that deposits in the camerae were formed during the animal's life. However, this statement, although quoted by MILLER, DUNBAR & CONDRA (1933), reflected the views of FOERSTE, rather than of TEICHERT, who at that time was engaged in a morphological study of cameral deposits, including those of *Rayonnoceras* (TEICHERT, 1933, p. 167, 177-178, 185-186, 197).

Rayonnoceras was again studied by TURNER (1951), who in the matter of the cameral deposits quoted FOERSTE & TEICHERT (1930), but not TEICHERT (1933). He seems to have believed that only some of the deposits, which he called "septal linings," are organic in origin. SCHMIDT (1956) described Carboniferous cephalopods from Germany, some of which had cameral deposits, including *Rayonnoceras*. He did not doubt their organic origin, but did not speculate on their mode and time of formation.

A major step toward knowledge of cameral deposits was taken by FLOWER (1939) when he made a systematic study of their morphology in Pseudorthoceratidae. In 1941, FLOWER studied cameral deposits in *Leurocycloceras* and discovered impressions of vascular strands or tubes on both surfaces of the septa. More recent papers by FLOWER (1955, 1964) are also important. The most recent has an up-to-date summary of the subject, but did not yet take into account investigations on ultrastructure of the cameral deposits on which GRÉGOIRE had published the first study in 1962.

TEICHERT (1961) described the highly unusual cameral deposits of the Lamellorthoceratidae which are arranged as radially oriented lamellae, and rejected as unrealistic the thesis of MUTVEI (1956) that such geometrically complex structures could be the result of inorganic precipitation of calcium carbonate.

An important recent contribution to knowledge of the morphology of cephalopod cameral deposits is one by HOLLAND (1965) who studied them in Silurian *Leurocycloceras* from England.

He confirmed the presence of vascular impressions on the septal surfaces which FLOWER (1941) had described from American material of the same genus. In the English specimens the vascular marks are arranged in radial symmetry with regard to the siphuncle and many of them are dichotomous or even weakly fasciculate toward the periphery of the septum.

The earliest recorded geological occurrence of cameral deposits in Cephalopoda is in a species of the ellesmerocerid genus *Protocycloceras* of late Canadian age described by FLOWER (1964, p. 54-55).

Of great importance were the electron microscopic studies of GRÉGOIRE (1962; in TEICHERT, 1964; in GRÉGOIRE & TEICHERT, 1965) who proved presence of conchiolin in cameral deposits of *Pseudorthoceras*. The conchiolin occurs as reticulate sheets, alternating with aragonite, and similar to those found in the nacreous layer of the shell.

LOWENSTAM (1963) reported discovery by E. HARE of eight amino acids in cameral deposits of *Pseudorthoceras*, but no further details have been published to date.

More recently, RABITZ (1966) has described *Pseudorthoceras knoxense* from a marine band in the Ruhr coal measures of Westphalian age. He discussed the cameral deposits in some detail, concluding that they began to grow in the ventral parts of camerae, whence they spread into dorsal parts in more mature stages.

The relationship of cameral deposits to endosiphuncular deposits shows notable variations. FLOWER (1939, p. 55) found continuity between cameral deposits and adjacent endosiphuncular deposits in some cephalopods, such as *Geisonoceras*, and concluded that in these "there is a single active secreting surface in the phragmocone which is continuous from one camera to the next." SWEET (1958, p. 121) illustrated and described a specimen of *Rhynchorthoceras helgoeyense* which in one camera shows continuity between cameral and endosiphuncular deposits. Here the connecting ring is ruptured or resorbed, and the endosiphuncular lining merges with both episeptal and hyposeptal deposits. Somewhat similar relationships have also been observed by us in a thin section of *Pseudorthoceras knoxense* (Fig. 7; Pl. 2, fig. 4), but in this case the connecting rings are intact.

Cameral deposits are also present in the

chambers of many belemnites. They were discovered, though not fully understood by CHRISTENSEN (1925) in Jurassic belemnites; illustrated (though not recognized) by FISCHER (1947) in a Permian aulacoceratid; found in Mississippian *Eobelemites* by FLOWER (1945) and they are present in Mississippian *Hematites* (types examined by FISCHER). JELETZKY (1966, p. 130-137) has shown that belemnites may possess episeptal, mural, and hyposeptal deposits, similar to those in orthoconic ectocochlean shells, and thinly

laminated when well preserved. They are found in all representatives of the Belemnitidae and Hastitidae, but are absent in almost all other belemnitid families. Their occurrence is thus largely restricted to belemnites with short, conirostrid, juvenile guards. The loss of cameral deposits in belemnites endowed with long, clavirostrid guards, and thereby with efficient counterweights to the buoyant phragmocone, lends further support to the view that the function of cameral deposits was to balance the phragmocone.

VIEWS ON ORIGIN

HYPOTHESES OF INORGANIC ORIGIN

DIAGENETIC PRECIPITATION

Inorganic origin of cameral deposits was postulated by G. & F. SANDBERGER (1852, p. 160, 163) in their descriptions of *Orthoceras planiseptatum* and *O. undatolineatum*, two species now placed in the genus *Arthrophyllum* BEYRICH (TEICHERT, 1961), which is characterized by complex cameral deposits having configurations reminiscent of coral septa. The SANDBERGERS suggested that these deposits represented calcium carbonate precipitations from infiltrating waters, formed after death of the animal. This hypothesis was soon superseded by BARRANDE'S (1859) hypothesis of organic origin and was, in its original form, not seriously entertained by most paleontologists.

However, MUTVEI (1956, p. 188) summarily rejected the organic hypothesis, holding that it had arisen "owing to the imperfect knowledge of the above-mentioned writers of the anatomy of Cephalopods and of Molluscs in general." He reasoned from analogy with *Nautilus* and *Spirula*, which have no cameral deposits. But as FLOWER (1964, p. 45) has aptly remarked, "one wonders where similar reasoning would lead if it were applied to other groups"—possibly to the conclusion that "carpoids as a group are fossil hallucinations."

In 1964, MUTVEI repeated that cameral deposits "must be of inorganic origin" but conceded that in certain forms they could be "due to a special chemical reaction between the liquid secreted by the epithelium of the siphonal cord into the

shell chambers and sea water penetrating post-mortally into the shell chambers" (MUTVEI, 1964, p. 89).

FLOWER (1964, p. 45) has compiled a list of ten morphological criteria of cameral deposits which need to be explained away before their inorganic origin can be considered. To his list must be added the ultrastructure and organic chemistry of cameral deposits (GRÉGOIRE & TEICHERT, 1965).

DIAGENETIC INFILLING OF SPACES BETWEEN SEPTA AND MEMBRANES

It was first suggested by WOODWARD (1851, 1856) that the camerae of some fossil nautiloids were lined by membranes and that, if these became detached from the septa, the space between them and the latter was infiltrated by secondary calcite.

This hypothesis was modified by DEWITZ (1878) during a study of *Ancistroceras* and other genera. He found that the membrane observed by WOODWARD occupied about the same position in each camera at the plane of contact of what are now known as episeptal and hyposeptal deposits. In cross section this contact plane appears as a line running from the anterior outer corner of the camera obliquely backward toward the siphuncle and usually ending in an open space of subtriangular cross section where it seems to bifurcate (see Pl. 4, fig. 5b). DEWITZ called the membrane he believed to have recognized in this place a *Hilfskammerwand* ("auxiliary septum"). He believed that it was secreted by the mantle during an intermediate resting stage of the animal when it proceeded forward in the shell for the

purpose of constructing another true septum. Such an animal was supposed by DEWITZ to build alternately normal, calcareous septa and intermediate, membranous ("chitinous") auxiliary septa.

DEWITZ's hypothesis was again modified by HOLM (1885) who returned to a version closer to that proposed by WOODWARD. He did not believe that the so-called auxiliary septum was built in the place where it is now found and he named this structure "pseudoseptum." The term has been widely, though often loosely, used in the literature. HOLM gave a very complex explanation of the mode of formation of "pseudosepta" which need not be recorded here. However, it seemed plausible to APPELLÖF (1892, p. 98-99), who considered it in discussion of his theory of the formation of *Nautilus* septa. It also found a follower in HYATT (1900).

Neither DEWITZ nor HOLM concerned themselves with the calcitic matter that filled the space between septa and membranes ("auxiliary septa," "pseudosepta"), but it is implicit in their writings that they did not regard it as being of organic origin.

HYPOTHESES OF ORGANIC ORIGIN

Numerous students of cephalopods while recognizing the organic nature of cameral deposits, have not speculated on the time and mode of their formation. The following brief review deals only with authors who have offered such speculations.

DEPOSITION IN STAGES DURING GROWTH OF SHELL

Already described is how BARRANDE (1859, 1877) explained cameral deposits as products of continuous secretion in stages immediately preceding and following formation of the septa.

A similar, though more complex, mode of origin was postulated by SCHRÖDER (1888) who attempted to arrive at a unified interpretation of all cameral structures. He accepted DEWITZ's concept of the auxiliary septum for which he retained HOLM's term "pseudoseptum." He complicated matters by assuming the existence of basically two pseudosepta. The calcitic matter between pseudosepta and septa he called *Pseudoseptallamelle* and believed that all three structures (septa, pseudo-

septa, and pseudoseptal lamellae) had been secreted by the mantle either during resting stages or during periods of slow growth.

POMPECKJ (1912) and GRABAU (1922) developed similar ideas, but were less specific about the processes involved.

In their discussion of *Pseudorthoceras*, MILLER, DUNBAR & CONDRA (1933, p. 79), concluded that cameral deposits were formed "at the adapical end of the living chamber and lined the walls of at least the adapical portion of it." While this hypothesis might be invoked to explain presence of episeptal deposits, it fails to explain the existence of hyposeptal deposits. Logically, MILLER, DUNBAR & CONDRA stated that to substantiate their hypothesis, it would be necessary to search for deposits in actual body chambers, but their material did not allow them to do this. It seems to be a fact that cameral deposits have never been observed in the body chamber of any cephalopod.

DEPOSITION AFTER CAMERAE WERE COMPLETED

Deposition within chambers can be imagined in two distinct ways: Either from living tissues existing within the chambers, or from fluids filling the chambers, into which mineral salts and organic matter were secreted from the siphuncle.

DEPOSITION FROM TISSUES WITHIN CHAMBERS

In contrast to the complex processes suggested by HOLM and SCHRÖDER, TEICHERT (1933, 1934, 1935) postulated that cameral deposits were formed in the camerae at some time after these had been completed. He suggested that they were secretions of "membranes" or "tissues" fed with body fluids pumped through the connecting ring from the endosiphuncle. TEICHERT believed that the shape and disposition of cameral deposits were decisive proof of their continuous formation during life of the animal, for in most shells where they are present, they decrease in bulk and thickness from the apical to the oral end of the phragmocone in a more or less regular manner. TEICHERT also listed criteria for distinguishing between what he called primary (organic) and secondary (inorganic) deposits; he coined the terms episeptal and hyposeptal which are now in general use, and he gave detailed descriptions of the geometry of many types of cameral deposits, especially in actinocerids.

TEICHERT's hypothesis of continuous deposit formation was embraced and supported by FLOWER (1939) who introduced the concept of the "cameral mantle" as the organ responsible for secretion of organic calcareous deposit in the camerae. Later, FLOWER (1941, 1943) described vascular markings on the surface of cameral deposits. Somewhat similar structures had been observed earlier by NOETLING (1882), SCHRÖDER (1888), REMELÉ (1890), and others (see also TEICHERT, 1964, p. K33-34).

The hypothesis was again discussed by HOLLAND (1965) who concluded that "the vascular markings of *Leurocyloceras* [and, by implication, the cameral deposits] were actually formed within the completed chambers as envisaged by Flower." He also thought that "both Teichert (1934) and Flower (1943) have provided evidence for the former existence of the cameral mantle. . . ."

Finally, SCHINDEWOLF (1967), when announcing discovery of conchiolin membranes in the chambers of a Jurassic ammonite (*Craspe-*

dites), discussed cameral deposits and concluded that the evidence favored their formation from cameral tissues.

Subsequent to 1950 at least, the presence of organic deposits in the camerae of cephalopod shells has been accepted in practically all paleontological textbooks and their morphology described in greater or lesser detail. Authors who have discussed their mode of origin at all accepted the hypothesis of a cameral mantle or similar organ (FISCHER, 1952; SHROCK & TWENHOFEL, 1953). The hypothesis is discussed further in the concluding chapter of this paper.

DEPOSITION FROM CAMERAL FLUIDS

The possibility that cameral deposits may have been precipitated from fluids in chambers was first expressed by JOYSEY (1961) and rests in part on the discovery by BIDDER (1962) that some of the chambers of *Nautilus* are partly filled with water, an observation later confirmed by DENTON & GILPIN-BROWN (1966). This possibility is explored in greater detail below.

CAMERAL DEPOSITS IN NAUTILOIDS OF BUCKHORN ASPHALT

Deeper insights in paleontology commonly depend on the study of exceptionally well-preserved material, hence localities with such fossils have played a large role in paleontological progress. The Buckhorn asphalt is of great significance, for it is one of a very few known Paleozoic deposits in which aragonitic shells are preserved in unaltered or only slightly altered form (FISCHER & FINLEY, 1949; STEHLI, 1956; GRÉGOIRE & TEICHERT, 1965).

This deposit occurs in a set of outcrops, formerly quarried for road material, in the Arbuckle Mountains, near Sulfur, Oklahoma (GRÉGOIRE & TEICHERT, 1965). Its stratigraphic position is within the Boggy Formation of the Pennsylvanian (Desmoinesian) Krebs Group (UNKLESBAY, 1962). The specimens are excellently preserved mineralogically, but physically they leave much to be desired, being mostly fragments consisting of only a few chambers. The bulk of the material here studied was found in fossil collections of the University of Kansas made years ago by R. C. MOORE; additional material has been collected by FISCHER. All of it belongs to the Museum of

Invertebrate Paleontology, University of Kansas. This depository is indicated by the symbol KUI, followed by museum number.

TAXONOMIC VARIETY

The orthoconic nautiloid shells of the Buckhorn asphalt for the most part are preserved as small fragments, consisting of a few to a dozen chambers, mainly from the early parts of shells. Each such fragment presents only a fraction of the ontogeny of the phragmocone, only a fraction of the ontogeny of cameral deposits, and a fraction of the ontogeny of endosiphuncular deposits. Whereas these three fractions of the ontogeny are spatially associated, they were not formed at the same time: the cameral deposits filling a given chamber of the phragmocone belong to a later stage of the animal's life history than do the walls and septa of that chamber, and the filling of the siphuncle belongs possibly to a still later stage.

Classification of such fragmentary remains is difficult. The characters which serve as the basis for classification of orthoconic nautiloids, e.g., nature of siphuncle, ornamentation of the shell,

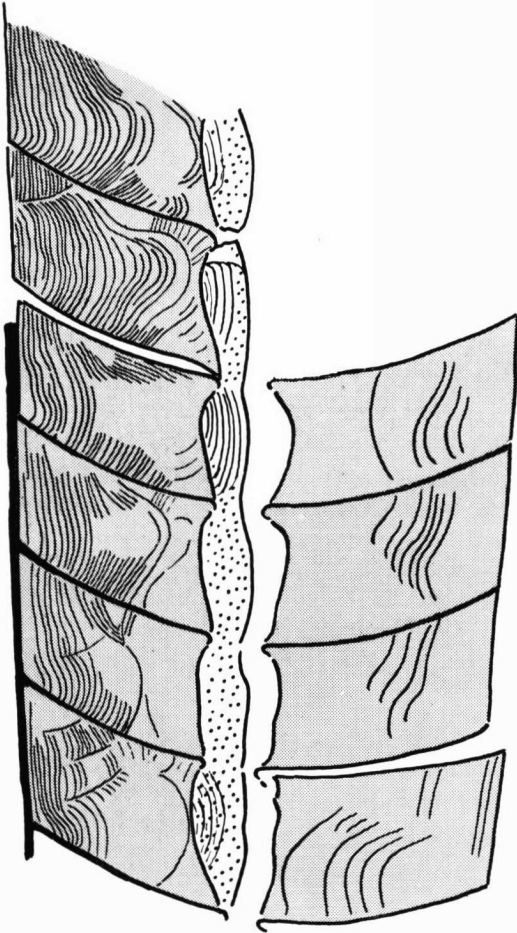


FIG. 1. *Pseudorthoceras knoxense* (McCHESNEY), dorso-ventral longitudinal section, $\times 18$. Cameral deposits are mainly mural, grading into latero-episepal. In this section the plano-mural and latero-mural deposits are not distinguishable, but the deposits of the ventral side are mainly of the latter sort, as may be seen by reference to cross sections (Fig. 2). Note that the endosiphuncular deposit shows some growth lines, which are not of the normal annulosiphonate type, in that they do not show an origin of growth at the septal necks, but are continuous with adjacent cameral deposits. KUI 500,537.

chamber proportions, and character of cameral and endosiphonal deposits, change with ontogeny. Most descriptions of nautiloids have been based chiefly on the larger, mature parts of the conch, including adult living chambers, which are rare in the Buckhorn asphalt. The segregation of various taxa, therefore, is a jigsaw puzzle which is not as yet satisfactorily assembled. A study of Buckhorn cephalopods by SMITH (1938) was

handicapped not only by these limitations, but by an inadequate collection and by having been written before many of the general problems of nautiloid classification had become as plain as they are now. UNKLESBAY (1962) recognized three orthoconic species from the Buckhorn asphalt but did not study their cameral deposits. A taxonomic study involving mainly the protoconchs and early stages of the conch is being carried out by FISCHER and RISTEDT, but as yet most of the Buckhorn nautiloids remain unassigned on the generic level, and even some family assignments remain in doubt.

We have recognized more than a dozen species, of which the majority belong to the Pseudorthoceratinae (subfamily Pseudorthoceratinae); the genera *Pseudorthoceras* and *Pseudocyrtoceras* are represented, and much of the present paper deals with the commonest species, referred to *Pseudorthoceras knoxense* (McCHESNEY) by SMITH (1938) and by UNKLESBAY (1962), a usage which we follow provisionally but which eventually will have to be tested by detailed investigations of type material of the species. There are also other unassigned pseudorthoceratid species.

Alongside such undoubted members of the Pseudorthoceratinae are other nautiloids which resemble the Orthoceratidae of the early and middle Paleozoic in their suborthochoanitic to orthochoanitic siphuncles, their long chambers, and deeply cupped septa, but which differ drastically from most of the Orthoceratidae and most of the Pseudorthoceratinae in having extremely flat protoconchs, resembling that of *Nautilus*. These forms appear in a variety of species distinguished by ornamentation. Their generic and family relationships are wholly obscure at present. In this paper we deal at some length with the commonest of these forms, which we refer to here as "*Orthoceras*" *unicamera* SMITH (1938); its specific characteristic is ornamentation by transverse lirae or annulations in intermediate and presumably in adult stages. A relative, distinguished by a *Kionoceras*-like cancellate ornamentation, is here simply indicated as cancellate "*Orthoceras*." A third member of the group, characterized by imbricate annulations, is termed imbricate "*Orthoceras*." These species appear to be inseparable in early stages of ontogeny. Other genera of orthocones are present but are not dealt with here.

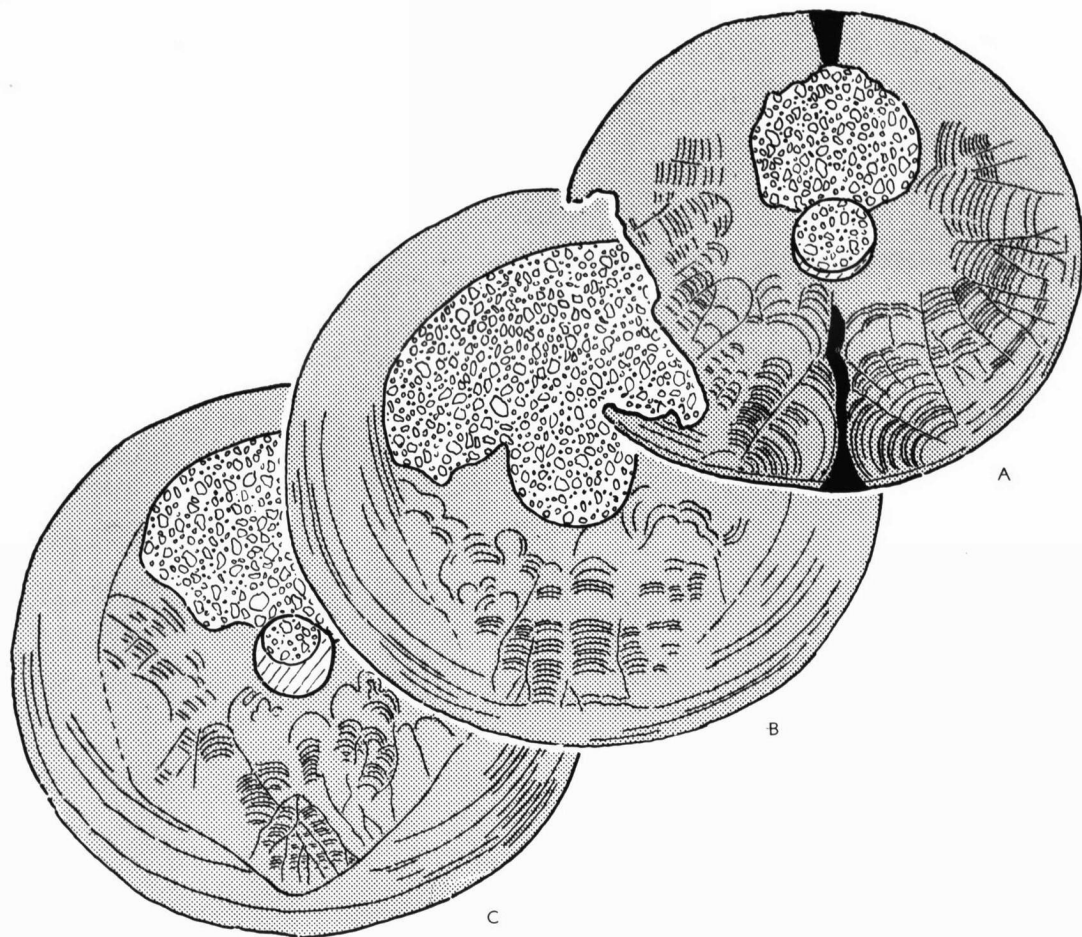


FIG. 2. *Pseudorthoceras knoxense* (McCHESNEY), cross sections through successive chambers of large part of conch, incompletely filled with cameral deposits, $\times 12$. KUI 500,539.

- A. Section through adapical part of a chamber, intersecting the mural delta (filled by latero-mural deposits, except for the remaining ventral cleft shown in black).
 B. Section through mid-part of a chamber (note large diameter of siphuncle), adorally of mural delta, showing

overlap of mammillary latero-mural deposits over plano-mural layers.

- C. Section through adoral part of a chamber, showing sharply defined "unconformity" between plano-mural and latero-mural deposits. [For a diagrammatic view of partial fillings in three dimensions, see Fig. 8.]

In summary, species dealt with in this paper are the following:

1) *Pseudorthoceras knoxense* (McCHESNEY) (order Orthocerida, family Pseudorthoceratidae) (Fig. 1, 2; Pl. 2, fig. 4; Pl. 3, fig. 1, 2, 4; Pl. 4, fig. 1, 3, 4).

Protoconch essentially conical, with spheroidal siphonal caecum; septa gently concave, chambers short; siphuncle suborthochoanitic in early chambers, cyrtochoanitic in later ontogeny. Conch essentially smooth, lacking surface ornament.

Hyposeptal deposits (of lateral type) in first four chambers only; mural deposits and episeptal deposits dominant throughout. In earlier chambers mural deposits fail at first to cover a triangular area on the ventral side of the chamber—the mural delta, which is later closed by overgrowth from the sides. In one of our specimens the endosiphuncular deposits are continuous with the cameral deposits, the latter having grown right through the connecting rings without breaking them.

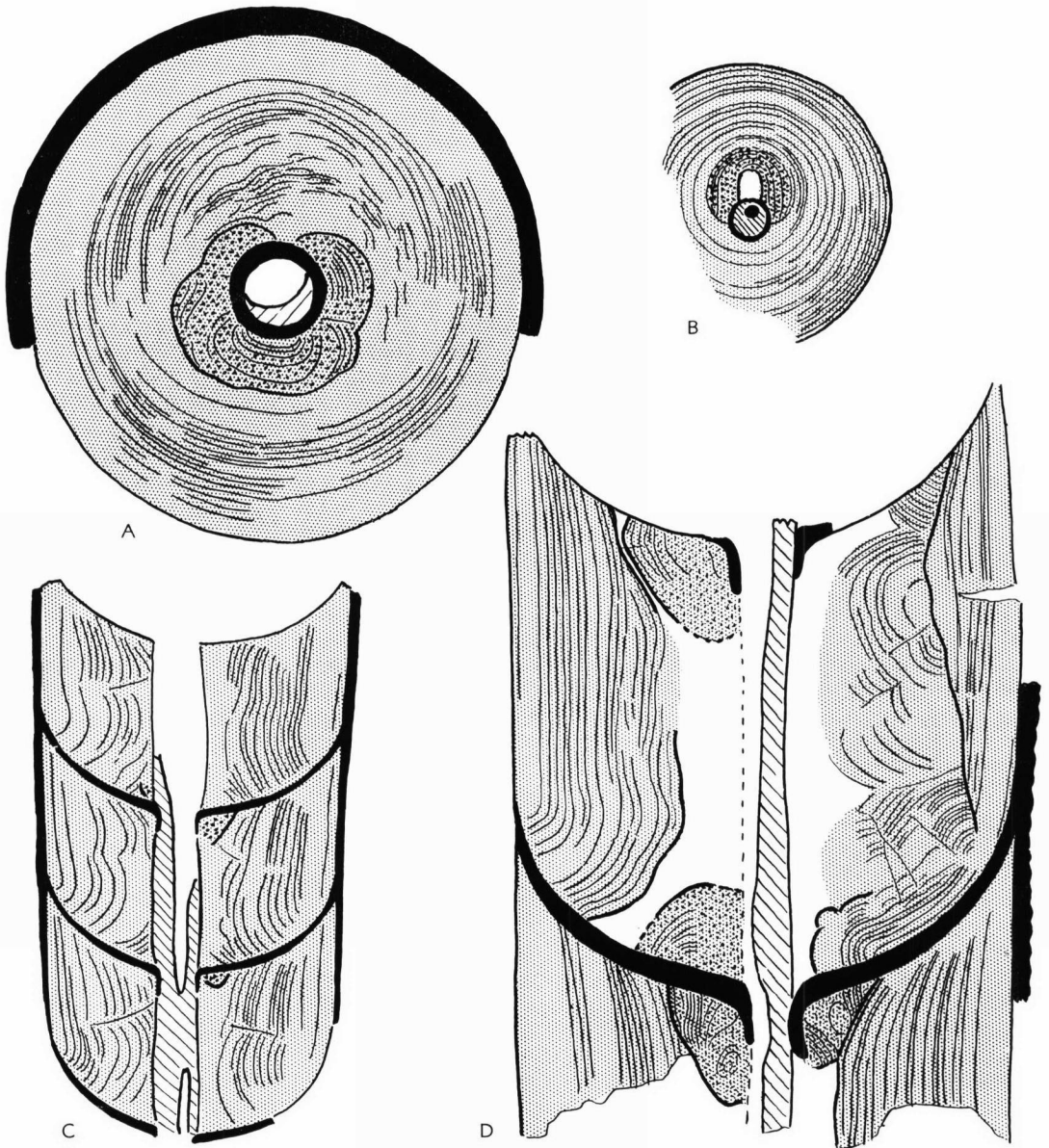


FIG. 3. "*Orthoceras*" *unicamera* SMITH in various sections, $\times 10$; circulus stippled, endosiphonal deposits hachured.

- A. Cross section of fairly mature chamber, cut through septal neck and hyoseptal circulus embracing siphuncle from ventral side. Note divergence in symmetry between cameral and endosiphonal deposits. (See also Pl. 2, fig. 2.) KUI 500,534.
- B. Cross section through a much smaller chamber, cut behind septal neck. Note circulus on dorsal side, and divergence of symmetry between cameral and endosiphonal deposits. KUI 500,551.
- C. Longitudinal section of juvenile part of conch (shell smooth). Section is not dorso-ventral, as seen by double intersection of the lunate endosiphonal deposit. Cameral

deposits show a combination of plano-mural and slightly differentiated latero-episeptal types. KUI 500,550.

- D. More mature stage of conch, ornamented with transverse lirae. Section essentially dorso-ventral, showing endosiphonal deposits on venter. Cameral deposits mainly plano-mural, overlapping against septal surfaces; on ventral side, however, a chamber shows, for this growth stage, exceptional plano-episeptal and latero-episeptal deposits, followed by a marked "uncomformity" succeeded by irregular mammillary growth. (See also Pl. 2, fig. 3.) KUI 500,535.

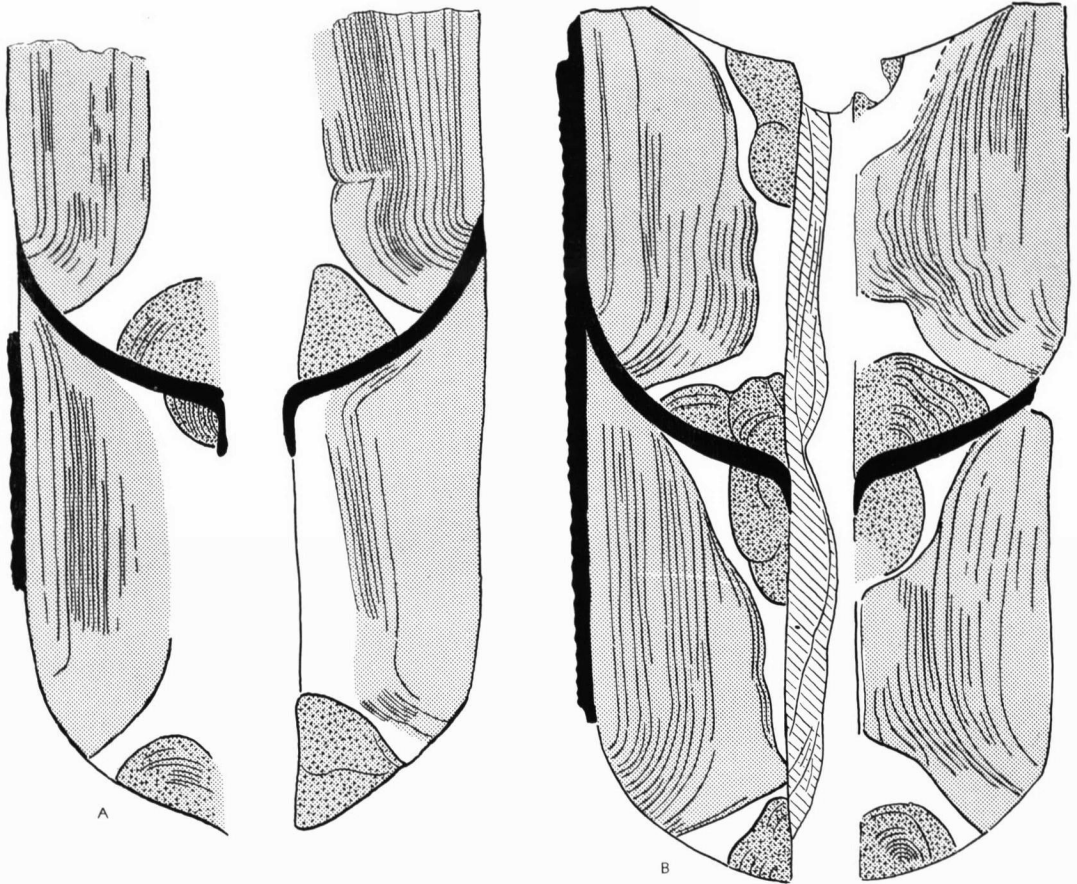


FIG. 4. "*Orthoceras*" *unicamera* SMITH, longitudinal sections of fairly mature chambers, $\times 10$; circuli stippled, endosiphonal deposits hachured.

A. Section showing plano-mural deposits lapping onto septal surfaces, and episepal and hyoseptal circuli. Siphuncle and some of interior cameral deposits broken out. KUI 500,552.

B. Section showing similar features, and more completely preserved circuli, as well as multiple endosiphonal deposits. KUI 500,553.

2) *Pseudorthoceras* spp. Some specimens illustrated (Pl. 1, fig. 2; Pl. 3, fig. 5) may or may not belong to *P. knoxense*. Another (Pl. 3, fig. 6) shows a more attenuated mural delta and is likely to represent a distinct species.

3) "*Orthoceras*" *unicamera* SMITH, 1938 [= *Michelinoceras directum* UNKLESBAY, 1962] (order Orthocerida, family uncertain) (Fig. 3-5; Pl. 1, fig. 1; Pl. 2, fig. 2, 3; Pl. 3, fig. 3). Protoconch a flat cap like that of *Nautilus* with adnate siphuncular caecum. Phragmocone slender, with long chambers and deeply cupped septa. Siphuncle suborthochoanitic in earliest chambers, orthochoanitic in later ontogeny.

Ornamentation on earliest few chambers a faint cancellate pattern, followed by a smooth stage; more mature stages of conch ornamented by transverse lirae of rounded cross section, confined to the outer shell layer.

Plano-hyoseptal deposits occur in first four chambers only. Normal mural and episepal deposits predominate throughout, but in the more mature chambers episepal and hyoseptal circuli partly surround the siphuncle. Endosiphuncular deposits normally present.

4) Imbricate "*Orthoceras*" (order Orthocerida, family uncertain) (Fig. 6). Differs from "*O.*" *unicamera* in having distinctly asymmetrical

annulations, which appear as imbricate rings of the outer shell layer, truncated at the adoral end and sloping gently to the rear; also in its cameral deposits, which show well-developed hyposeptal deposits through much of the ontogeny, and lack circuli.

5) Cancellate "*Orthoceras*" (order Orthocerida, family unknown) (Pl. 1, fig. 3; Pl. 2, fig. 1). Much like "*O. unicamera*", but differs in having the more advanced stages of phragmocone ornamented both with transverse and longitudinal lirae, thus producing a cancellate pattern. Episeptal cameral deposits crenulate in radial patterns. Circuli appear to be absent.

6) "*Orthoceras*" spp. (Pl. 4, fig. 2, 5). We have not been able to separate apical tips belonging to the three above-mentioned species of "*Orthoceras*," and must therefore leave unassigned the tips here illustrated.

GENERAL STRUCTURE AND PRESERVATION

The shell wall is normally preserved as aragonite. In general it resembles that of *Nautilus* (Pl. 1, fig. 1). There is an outer layer of porcelaneous appearance and fibrous structure, as shown in thin sections. This layer carries the ornamentation. In most specimens, unlike *Nautilus*, it is divisible into two laminae on the basis of pigmentation; in most species the inner lamina is pigmented, the outer lamina clear.

The middle layer of the shell wall consists of nacreous material, interlayered sheets of aragonite and organic matter, which is golden yellow or brown in transmitted light. The organic laminae are exceedingly delicate films, which may be freed by digestion in acid. GRÉGOIRE (1959b) has shown that the organic films have the characteristic conchiolin textures found in the nacreous layer of living *Nautilus*.

The innermost layer of the wall is clear and fibrous, commonly very thin, and more subject to recrystallization than the other two. This is presumably the annulus layer, recognized in *Nautilus* by APPELLÖF.

The septa are nacreous, and are largely identical in structure to the material of the nacreous wall layer, though in some specimens they show a three-layer structure. The septal necks are enriched in organic content, especially toward their tips.

The connecting rings are delicate segments of dark brown organic matter showing no sign of calcification or visible signs of regular resorption or perforation.

Cameral deposits are discussed in the next section.

Endosiphuncular deposits are present in most specimens, and, where not recrystallized to calcite, show fine fibrous structure and delicate growth banding. Unlike the cameral deposits, they appear to lack appreciable organic admixture. While most of our sections show no direct connection between endosiphuncular deposits and cameral

EXPLANATION OF PLATE 1

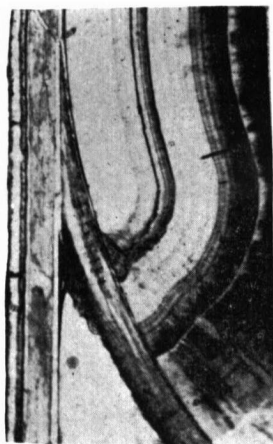
THIN SECTIONS OF BUCKHORN NAUTILOIDS

FIGURE

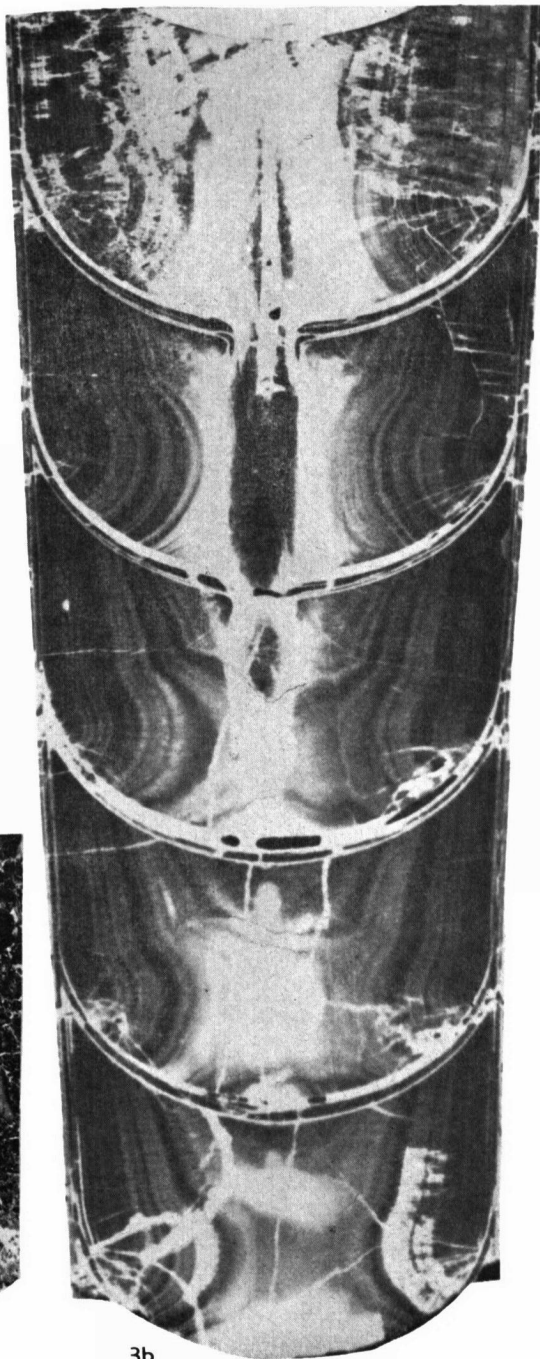
1. "*Orthoceras*" *unicamera* SMITH, junction of septum with shell wall, $\times 85$. Shell wall shows outer fibrous layer, divided into a clear external and a darkly pigmented internal region, a thick middle layer of nacreous structure, and the very thin, clear annulus layer. Septum shows nacreous structure. Cameral deposits of plano-mural type grading into plano-episeptal deposits on edge of septum, which then become latero-episeptal. KUI 500,536.
2. *Pseudorthoceras* sp., longitudinal section of a large specimen, $\times 3.6$. Chambers only partly filled with cameral deposits which decrease regularly toward oral end. Deposits are confluent plano-mural, plano-episeptal, latero-episeptal. Where not supported by cameral deposits the delicate septa have been broken,

and the matrix of asphalt and shell debris has invaded the chambers and is packed around the antecedent cameral deposits. KUI 500, 549.

3. Cancellate "*Orthoceras*" in longitudinal section oriented right-left rather than dorsoventrally.—3a,b. Entire specimen, $\times 6$; negative print of first five chambers, $\times 26$. Due to slight curvature of specimen the siphuncle is intersected twice. Cameral deposits mainly plano-mural, with some development of latero-episeptal deposits in earlier chambers. Earlier chambers filled completely with mural deposits abutting against siphuncle; in adoral direction, chambers show progressively less filling, the remaining void being occupied by asphaltic matrix. The symmetry of the cameral deposits is brought out particularly well in this section, because of its orientation at right angles to the dorsoventral plane of symmetry. KUI 500,532.



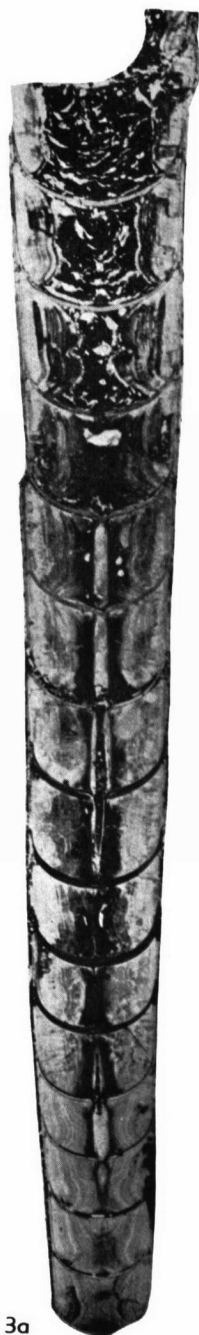
1



3b

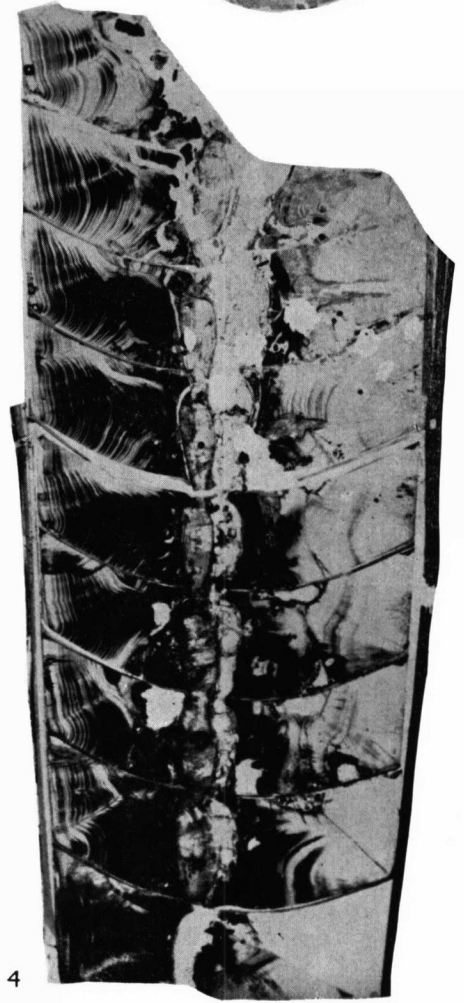
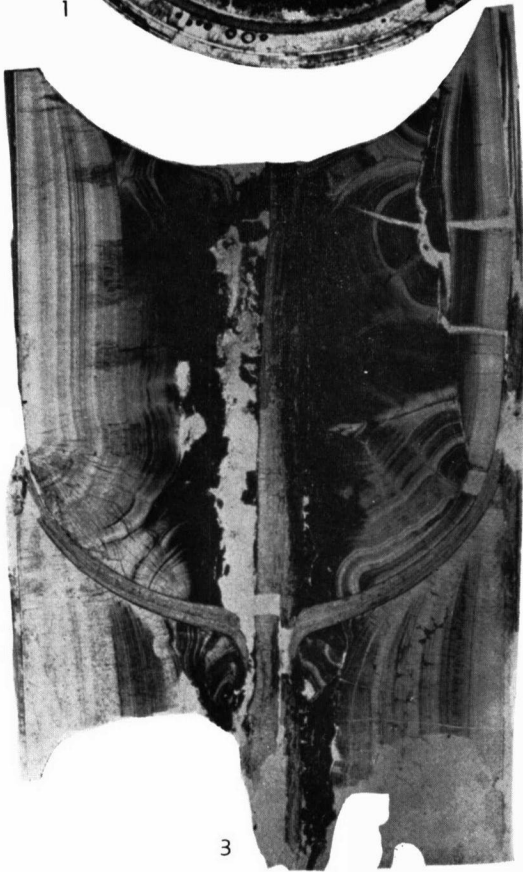
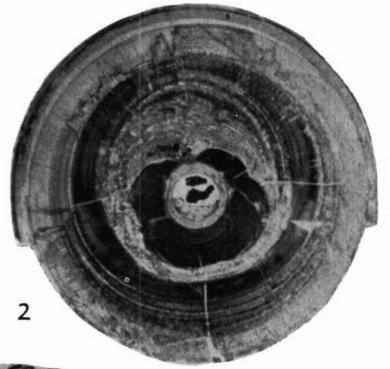
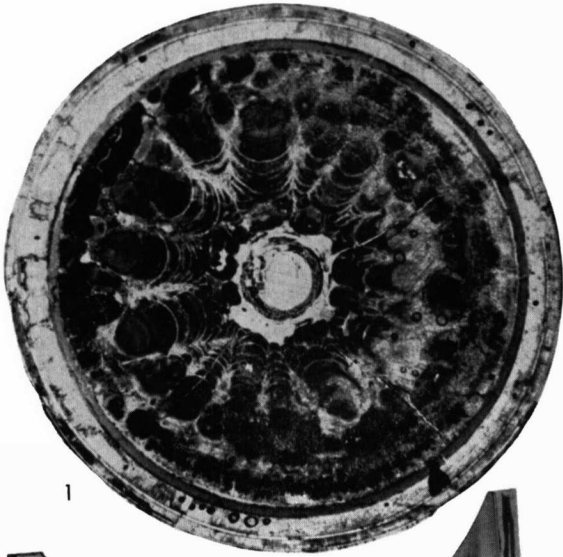


2



3a

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Paper 37, Plate 2 Fischer & Teichert--Cameral Deposits in Cephalopod Shells



deposits, one section of *Pseudorthoceras knoxense* (Fig. 1; Pl. 2, fig. 4) shows endosiphuncular deposits which are simply extensions of cameral deposits into the siphuncle through the connecting rings. This phenomenon, which has also been noted by FLOWER (1939) and SWEET (1958) is further discussed below.

Some fragmentary specimens consist almost entirely of aragonite and organic matter. In a few, all of the aragonite has changed to calcite, with a corresponding loss of microstructure. But in the majority of specimens sectioned a partial conversion to calcite has occurred selectively.

The endosiphuncular deposits were most susceptible to calcitization and have been altered in the majority of specimens (Pl. 4, fig. 1).

The cameral deposits are next in stability. Coarse fibers or large anhedral patches of coarsely crystalline calcite have developed in many chambers, especially in dorsal parts of the cameral deposit, in and adjacent to the structure which is here described as the dorsal cleft (Pl. 4, fig. 3, 4).

Rarely, parts of the septa and shell wall have also been calcitized. In these cases the calcitization has blurred, but generally not completely obliterated, the original microstructure. It is thus quite clear that calcitization is a secondary, diagenetic effect, which attacked primary structures of relatively pure aragonite, avoiding areas of much organic admixture.

CAMERAL DEPOSITS

COMPOSITION AND GENERAL STRUCTURE

The cameral deposits are composed mainly of fibrous aragonite, which has locally been altered to calcite with corresponding loss of microstructure. The aragonite fibers are oriented normal to the surface of deposition, forming a radial-fibrous fabric, with a tendency to become mammillary. A distinct growth banding (Pl. 1, fig. 1) within much of the cameral deposits results from variable admixture of organic matter, giving a yellow or brown color to the more organic-rich laminae. In a very general way one can recognize two tendencies in organic content. On the one hand, a given growth lamina tends to contain more organic matter on the ventral side of the chamber than on the dorsal; on the other hand, the amount of organic admixture tends to increase as the chamber becomes filled, so that in general the deposits darken from the walls toward the middle of the camerae (Pl. 2, fig. 3, 4; Pl. 3, fig. 1, 6). In all but early chambers, organic matter becomes dominant over aragonite in the final stages, producing dark brown, crumbly deposits in the region of the siphuncle. GRÉGOIRE (1962; in TEICHERT, 1964; GRÉGOIRE & TEICHERT, 1965) showed by electron microscopy that some of this organic matter consists of reticulate conchiolin sheets similar to that in mother-of-pearl.

EXPLANATION OF PLATE 2

THIN SECTIONS OF BUCKHORN NAUTILOIDS

FIGURE

1. Cancellate "*Orthoceras*" in cross section, $\times 20$. Cut just behind a suture, so as to intersect a septum and the episeptal cameral deposits, which are distinctively aligned in radial ridges. KUI 500,533.
2. "*Orthoceras*" *unicamera* SMITH, cross section through chamber and septal neck, $\times 8.5$. Cameral deposits of plano-mural type, with a dark three-lobed hyposeptal circulus surrounding the septal neck. The larger of the lobes of this circulus is in ventral position. Siphuncle partly filled with an endosiphuncular deposit of crescentic cross section. Planes of symmetry of cameral deposits and of endosiphuncular deposit deviate by about 17° , suggesting that considerable time elapsed and torsion of animal to conch occurred during the interim. (See also Pl. 2, fig. 4.) KUI 500,534.
3. "*Orthoceras*" *unicamera* SMITH, longitudinal section, $\times 8.5$. V on ventral side. Chambers filled with cameral deposits, and siphuncle filled on ventral side by endosiphuncular deposit. Cameral deposits mainly of plano-

mural type, with well-developed hyposeptal circulus surrounding septal necks. On ventral side the plano-mural deposits grade into plano-episeptal ones which reach across two-thirds of the septal surface before becoming latero-episeptal. On dorsal side the episeptal surface is laterally overgrown, both from the direction of the suture, and from the septal foramen. In the adoral one of the two chambers, normal plano-mural deposition was interrupted on the ventral side in early stages, and was succeeded by "wild" mammillary growth, including a latero-hyposeptal wedge. (See also Pl. 2, fig. 4.) KUI 500,535.

4. *Pseudorthoceras knoxense* (MCCHESENEY), longitudinal section, $\times 19$. Endosiphuncular deposits fill ventral side of cyrtocoanitic siphuncle. Cameral deposits show a combination of plano-mural and sharply defined latero-episeptal deposits in the first three chambers, and simple mural deposits in the succeeding ones. These may in part be latero-mural deposits intersected parallel to their direction of overlap. (See also Fig. 1.) KUI 500,537.

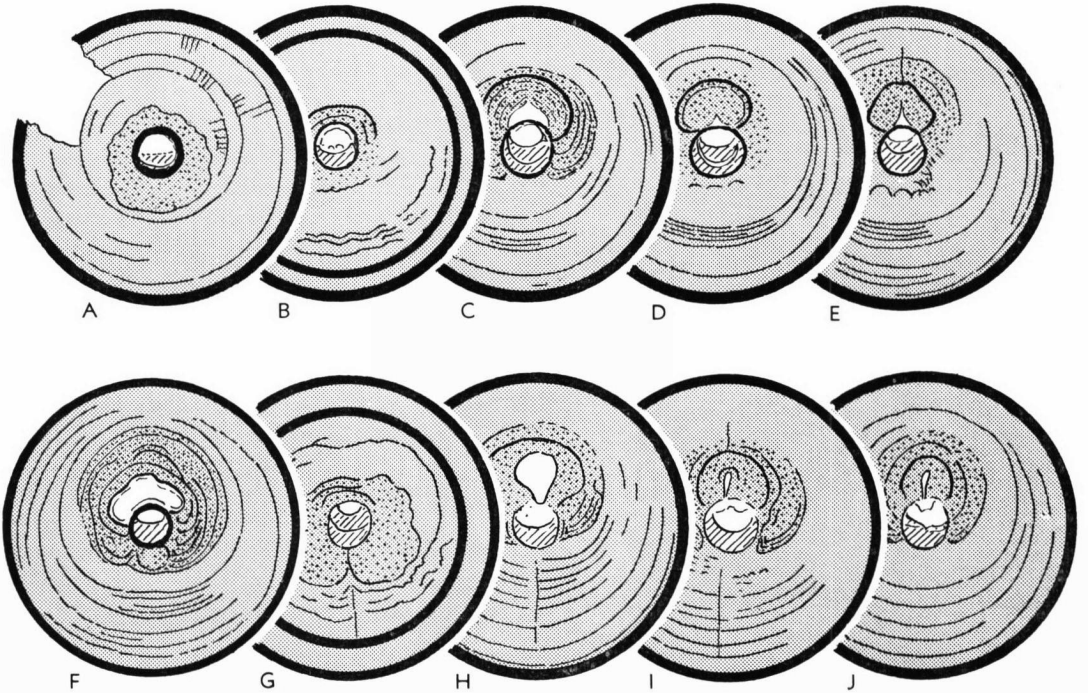


FIG. 5. "*Orthoceras*" *unicamera* SMITH, serial peels through three chambers at 1-mm. intervals, in adoral direction, $\times 6$. KUI 500,554.

- A. Section through anterior part of a chamber and a septal neck.
 B. Section through the succeeding septum.
 C-E. Sections through midparts of succeeding chamber.
 F. Section through anterior portion thereof, and a septal neck.
 G. Section through septum.
 H-J. Sections through midregion of succeeding chamber.

Intraseptal deposits hachured, circuli stippled. Circuli are especially strongly developed in this rather mature specimen, completely embracing the siphuncle on either side of the septal foramen, and extending the length of the chamber along the dorsal side of the connecting ring. Note that hyoseptal deposits embrace siphuncle from the venter, episeptal deposits from the dorsum.

TYPES OF CAMERAL DEPOSITS AND THEIR TERMINOLOGY

Our terminology is based on the standard system of TEICHERT, in which three basic types are distinguished, according to the surface on which cameral deposits have grown. Deposits which coat the outer walls of the chamber are termed **mural**; those laid down on the concave adoral side of a septum are termed **episeptal**; and those formed on the convex, adapical face of septa, are termed **hyoseptal**. Commonly the episeptal deposits are continuous with mural ones, and division becomes arbitrary.

For purposes of this paper the classification needs to be refined. Where growth laminations within the cameral deposits have been preserved, as in the Buckhorn specimens, two types of

growth in each category are distinguished and illustrated diagrammatically (Fig. 7). In one type, designated as **planar** or **plano-**, the deposit is formed by a uniform overgrowth of a surface in layers parallel to that surface. On the other hand, cameral deposits of the type designated as **lateral** or with prefix **latero-** result from a lateral encroachment of cameral deposits over a given surface. In the planar deposits, growth lines are parallel to the overgrown surface, whereas aragonite fibers stand normal to it; in the lateral deposits, growth lines meet the overgrown surface at angles approaching 90 degrees, and fibers lie parallel or nearly parallel to it. Lateral deposits show a particularly strong tendency to become mammillary. Transition from plano-mural to latero-episeptal deposits is observed (Fig. 1, 4, 6; Pl. 1, 2, 4).

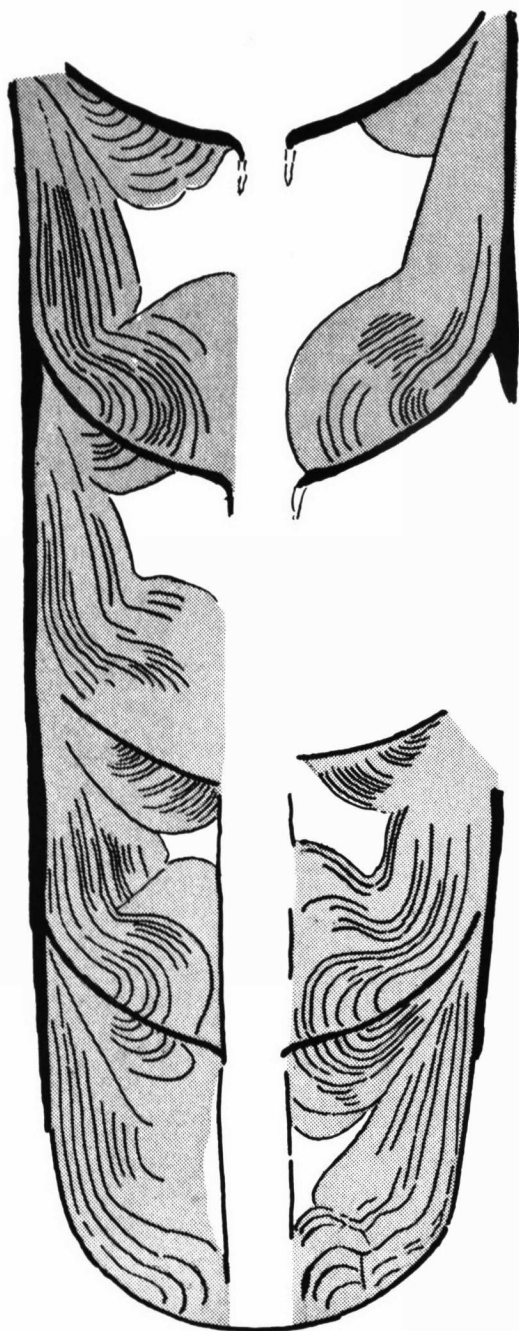


FIG. 6. "Orthoceras" with imbricate ornamentation, in longitudinal section. Intermediate ontogenetic stage of conch. Cameral deposits of plano-mural type grade into partial plano-episeptals, and these overlap toward siphuncle by lateral growth. Hyposeptal surfaces similarly covered by plano-hyposeptals in outer parts, and by latero-hyposeptals toward siphuncle; $\times 18$. KUI 500,549.

PLANO-MURAL DEPOSITS

Plano-mural deposits are invariably present in cameral deposits, and play a dominant role.

LATERO-MURAL DEPOSITS

Latero-mural deposits have been recognized by us only in *Pseudorthoceras*, and not in all specimens referred to this genus. In small and intermediate-size chambers of *P. knoxense*, a large triangular patch on the ventral side of each chamber was left bare by the initial plano-mural deposits. This patch, tapering adorally from a broad base at the suture, is here designated as the **mural delta**. It was subsequently gradually overlapped by latero-mural deposits growing from its sides toward the middle (Fig. 2, 7,B, 8; Pl. 3, fig. 1c, 2b, 4a, 6a). These latero-mural deposits are comparatively rich in organic matter, notably mammillary in form, and they grew more rapidly than plano-mural deposits to form what FLOWER (1939, 1964) termed the ventrolateral masses. They encroached not only over the delta, but also, in adoral direction, over the plano-mural deposits, along a sharp discontinuity which, in cross section, truncates the plano-mural laminations (Fig. 2; Pl. 3, fig. 1a-c). They also overlapped onto the episeptal surface. The absence of a mural delta and latero-mural deposits in some specimens of *Pseudorthoceras* (Pl. 2, fig. 5a,b) may be related to growth stage rather than species differences. All small-diameter specimens examined show at least traces of the delta, whereas large-diameter conchs do not.

PLANO-EPISEPTAL DEPOSITS

Plano-episeptal deposits (Fig. 7,C,D) may cover all or part of the episeptal surface. They are generally confluent with plano-mural deposits, and are most extensively developed in the earliest chambers (Pl. 4, fig. 1-5) generally giving way in later chambers to a predominance of latero-episeptal layers (see, however, Fig. 3,D).

LATERO-EPISEPTAL DEPOSITS

Latero-episeptal deposits (Fig. 7,D,E) rival the plano-mural deposits for dominance. They may be confluent with the mural layers or with plano-episeptal deposits (Fig. 3, 6, 7,D; Pl. 1, fig. 1-3; Pl. 2, fig. 3; Pl. 4, fig. 2, 5), or may come to be sharply divided from the plano-mural deposits (Fig. 3,C, 7,E; Pl. 2, fig. 4; Pl. 4, fig. 1, 4,

5). Whereas deposition normally encroached over the episeptal face in centripetal direction, toward the siphuncle, a special kind of episeptal deposit dealt with below, under **circuli**, grows outward from the siphuncle. The cancellate "*Orthoceras*" (Pl. 2, fig. 1) shows latero-episeptal deposits of a very special kind, growing in radially arranged mammillary rows.

HYPOSEPTAL DEPOSITS

Hyposeptal deposits in most of our species are confined to the earliest chambers. **Plano-hyposeptal deposits** (Fig. 7,G) are found in the first four chambers of "*Orthoceras*" spp. (Pl. 4, fig. 2, 5), while **latero-hyposeptal deposits** are found in the first three chambers of *Pseudorthoceras knoxense* (Pl. 4, fig. 1, 4). In the imbricate "*Orthoceras*" (Fig. 6) hyposeptal deposits persist through much more of the ontogeny, and show a combination of planar and lateral growth. Hyposeptal circuli are discussed in the next paragraph.

CIRCULI

Circuli are rings of cameral deposit growing outward from the siphuncle (Fig. 7,A). They are generally high in organic content and irregularly calcified. The term *circulus* was proposed by FLOWER (1939) to supplant TEICHERT's somewhat unwieldy "supporting ring" (TEICHERT, 1935), an adaptation from the shorter German *Stützring* (TEICHERT, 1933). This was a name originally coined for cameral deposits on the outer, concave, side of cyrtochaontic septal necks, especially in actinocerid cephalopods. It is here used in a somewhat broader sense to include all cameral deposits just outside the siphuncle, both on episeptal and hyposeptal surfaces.

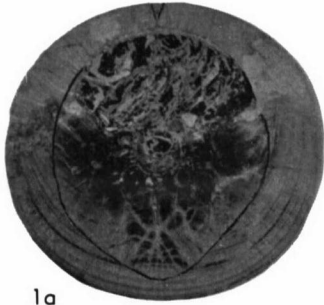
In our material circuli are limited to intermediate and mature chambers of "*Orthoceras unicamera*" (Fig. 3-5; Pl. 2, fig. 2, 3). The **episeptal circulus** embraces the siphuncle from the dorsal side, and may extend along the dorsal side for the length of the chamber (Fig. 5). It may sur-

EXPLANATION OF PLATE 3

NAUTILOIDS FROM THE BUCKHORN ASPHALT

FIGURE

- Thin sections through three consecutive chambers of *Pseudorthoceras knoxense* (McCHESNEY), $\times 6.4$.—1a,b. Sections cut through the mid-part of the chamber; 1c, through rear portion, just ahead of suture. Cameral deposits fill all of chamber except a space above the siphuncle, which is filled with asphalt and calcitic veinlets. Siphuncle largely filled with endosiphuncular deposits of crescentic cross section, thickest on venter.—Fig. 1c intersects mural delta; whereas plano-mural deposits accumulated on dorsal and lateral walls of chamber, the ventral side remained free at first, but subsequently was overgrown from the sides, leaving at last only the prominent ventral cleft. Note mammillary nature of these latero-mural deposits, and their comparatively rapid growth. (See Fig. 7,7b,8.) Figs. 1a and 1b, which lie ahead of the mural delta, show a continuous lining of plano-mural deposits. However, the latero-mural deposits which closed the delta also grew forward, progressively overlapping the plano-mural deposits, and thus come to appear in the inner parts of sections 1a and 1b; they show an angular relationship to the plano-mural lining, along a sharp line of contact. Dorsal cleft is inked in 1a and 1c. KUI 500,538.
- Dorsal and ventral view of *Pseudorthoceras*, $\times 6.4$. Shell wall removed, to show sutures and surface of cameral deposits.—Fig. 2a shows dorsal cleft and 2b the ventral side with mural deltas closed by latero-mural deposits, leaving a ventral cleft. KUI 500,539.
- "*Orthoceras unicamera*" SMITH, dorsal view of single chamber with shell peeled away to show surface of cameral deposit, $\times 6.4$. Cameral deposit is plano-mural and the light mid-dorsal band, commencing at suture and wedging out in adoral direction, is surface expression of dorsal cleft. KUI 500,543.
- Pseudorthoceras knoxense* (McCHESNEY), with shell partly stripped, $\times 6.4$.—4a. Ventral view, showing gentle hyponomic sinus (growth lines in lower part of picture), and well defined mural deltas in cameral deposits, closed by latero-mural deposition.—4b. Dorsal view showing dorsal cleft. KUI 500,540.
- Pseudorthoceras* sp., a large specimen, $\times 6.4$. Shell stripped to expose sutures and cameral deposits.—5a. Ventral view, showing slight ventral saddle in suture, and absence of mural delta.—5b. Adapical end of chamber, showing spread-eagle pattern formed by overlap of dark latero-mural deposits over plano-mural deposits onto episeptal surface. Note ventral cleft in these latero-mural deposits. KUI 500,541.
- Pseudorthoceras* sp., a small specimen (definitely not the *P. knoxense* shown in fig. 2, 4), $\times 6.4$. Shell stripped to show surface of cameral deposits.—6a. Ventral view showing rotational displacement between chambers.—6b. View of adoral end of chamber (cameral deposits on hyposeptal surface), showing bilateral symmetry, concentration of organic matter on ventral side, and dorsal cleft.—6c. Adapical end (episeptal view), showing wing pattern and ventral cleft. KUI 500,542.



1a



2a



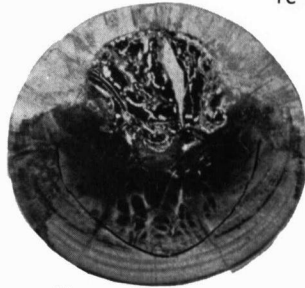
1c



4a



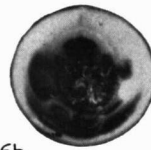
4b



1b



2b



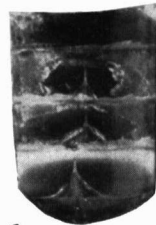
6b



3



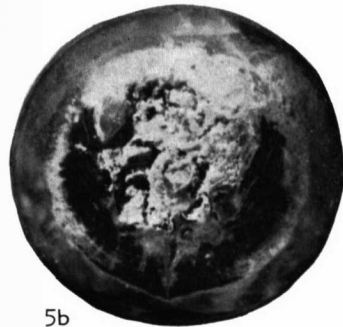
5a



6a

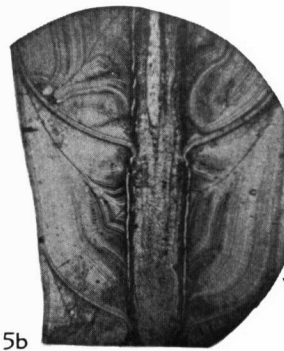
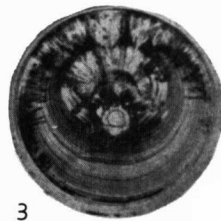
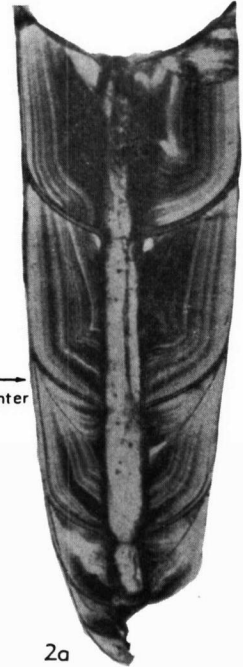
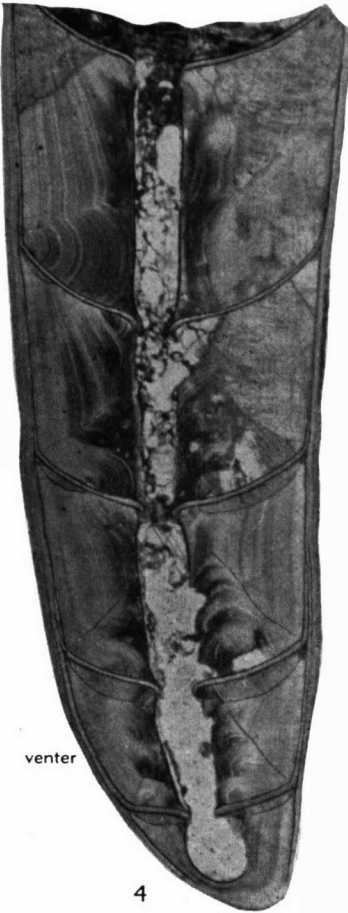
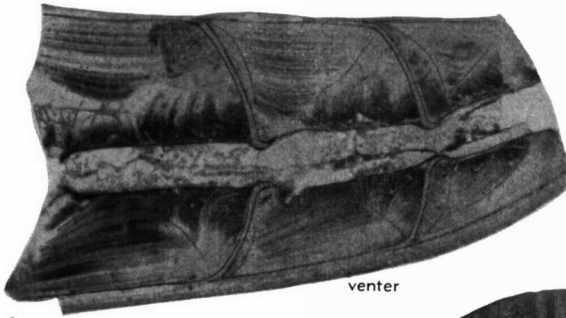


6c



5b

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round the entire siphuncle in the episeptal region, but fails to close around the ventral side of the connecting ring in the mid-region and oral end of the chamber. The **hyPOSEPTAL CIRCULUS** (=TEICHERT'S *Stützring*) grows around the septal neck, and comes to overlap onto the adjacent parts of the hyPOSEPTAL surface as well as onto the connecting ring. It appears to embrace the siphuncle from the ventral side (Fig. 5; Pl. 2, fig. 2).

DORSAL CLEFT

Several discontinuities occur regularly in the dorsoventral plane of cameral deposits. All of the species at hand show a structure here designated as the **dorsal cleft**, normally a wedge of clear calcite which extends into the cameral deposits from the mid-dorsal line (Fig. 2, 7,B, 8; Pl. 3, fig. 1-4). FLOWER (1939, 1955, 1964) recognized this interruption in the cameral deposits of the Pseudorthoceratidae and in some orthoceratids. In *Pseudorthoceras knoxense* it runs the full length of the chamber (Pl. 3, fig. 2a, 4b), whereas in "*Orthoceras*" it commences at the suture and wedges out in adoral direction (Pl. 3, fig. 3). The dorsal cleft

is related to a groove in the shell wall known as the septal furrow or "*Normallinie*" discussed by APPELLÖF (1892), FLOWER (1939, 1964) and MUTVEI (1957), and attributed by FLOWER to absence of the mural extension of the septum. We interpret the dorsal cleft as having resulted from lack of cameral deposition over this structure in the shell wall.

MURAL DELTA

In certain growth stages of the phragmocone of *Pseudorthoceras*, the cameral deposits are interrupted by another structure, the **mural delta**, already mentioned (Fig. 2, 7,B, 8; Pl. 3, fig. 1c, 2b, 4a, 6a). This is a triangular area on the ventral side of each chamber, on which no plano-episeptal deposits accumulated; in the early stages of chamber filling, this area thus must have formed a triangular pit on the ventral side of each chamber. As filling progressed, the pit became progressively closed, being overgrown from both sides by latero-mural deposits. FLOWER'S ventral sinus (FLOWER, 1939, 1955, 1964), described by him as an area of thinner cameral de-

EXPLANATION OF PLATE 4

THIN SECTIONS OF NAUULOID SHELL TIPS FROM BUCKHORN ASPHALT

[Some septal boundaries and shell wall retouched;
v=venter]

FIGURE

1. Shell tip of *Pseudorthoceras knoxense* (McCHESNEY), $\times 27$. Lacks protoconch, but retains traces of endosiphonal deposits, recrystallized to calcite. The cameral deposits are extremely similar to those of specimen KUI 500,544 (Pl. 4, fig. 4), with latero-hyPOSEPTAL deposits present in chambers 2 and 3, absent in 4. KUI 500,545.
2. "*Orthoceras*" sp.—2a. Projection enlargement, $\times 20$, showing part of protoconch and of chamber 2, and all of chambers 3-6.—2b. Photomicrograph of chambers 3-5, $\times 25$, in mirror image. HyPOSEPTAL deposits are of the planar type, and occur only in the first four chambers. Episeptal deposits are only incipiently divided from the mural deposits, and seem largely planar at first glance, but in detail they are seen to encroach laterally on the episeptal surface, and on the ventral side of chamber 6 they are distinctly latero-episeptal. The structureless patch in the upper right corner may be the dorsal cleft, or recrystallized cameral deposit adjacent thereto. The siphuncle is almost completely filled with unrecrystallized siphonal deposits, but in chamber 5 the section has intercepted the small remaining "endosiphontube", excentric toward the dorsum. KUI 500,546.
3. "*Orthoceras*" sp., cross section of a shell tip, $\times 25$. Mural deposits, well preserved on venter and recrystallized in dorsal region, concentric to a point dorsally from siphuncle. Siphuncle shows lining of siphonal deposit, thickest on venter. KUI 500,547.
4. Shell tip of *Pseudorthoceras knoxense* (McCHESNEY), $\times 27$. Siphuncle recrystallized or filled with inorganic calcite; chambers filled with cameral deposits, well preserved except on dorsal side of chambers 4 and 5, where the section may lie within the dorsal cleft, or, as commonly happens, the cameral deposits alongside the dorsal cleft have become crystallized to calcite. Protoconch shows bulbous siphonal caecum, and planomural as well as very narrow latero-hyPOSEPTAL deposits. Succeeding chambers contain plano-mural and sharply defined episeptal deposits showing a combination of plano-episeptal and latero-episeptal growth. HyPOSEPTAL deposits persist only through chamber 3. KUI 500,544.
5. "*Orthoceras*" sp.—5a. Projection, $\times 19$, showing chambers 3-6.—5b. Photomicrograph, $\times 19$, of chambers 4-5, in mirror image. Note the great similarity of chamber 4 in this and in specimen 500,546 (Pl. 4, fig. 2), and the notable differences in chamber 5, which in this case shows latero-episeptal deposits. KUI 500,548.

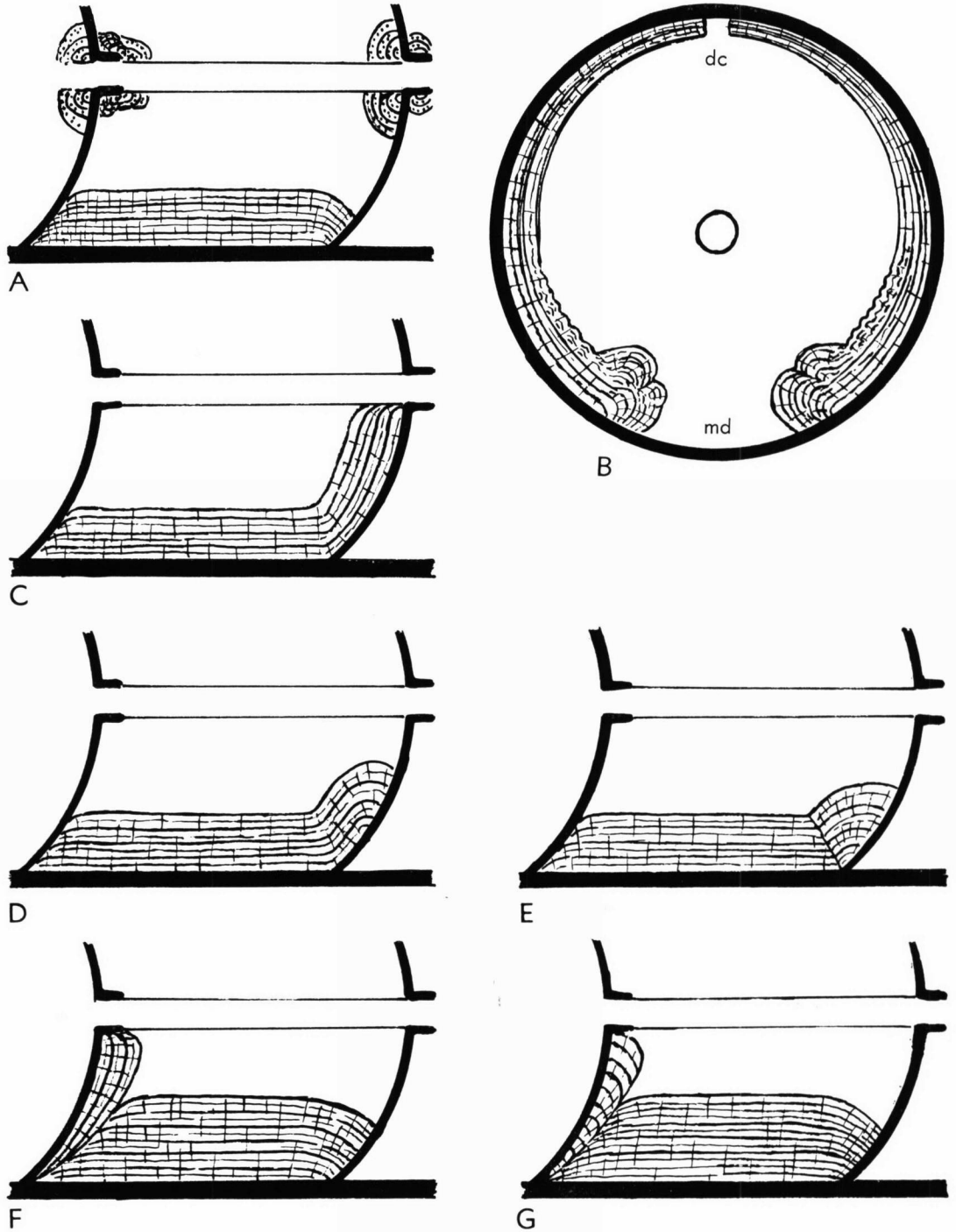


FIG. 7. Diagrammatic sections showing types and nomenclature of cephalopod cameral deposits.

A. Plano-mural deposits, overlapping onto episeptal and hyoseptal surfaces. Hyoseptal and episeptal circuli around siphuncle.

B. Cross section of *Pseudorthoceras*, showing dorsal cleft (*dc*) and mural delta (*md*). Plano-mural deposits become latero-mural and mammillary where they overlap onto the mural delta.

posits along the venter, between the ventrolateral masses, is one of several ways in which the mural delta may come to be expressed in cameral deposits.

VENTRAL CLEFT

The progressive lateral infilling of the mural delta ultimately results in a sharp mid-ventral plane of discontinuity between the right and left latero-mural deposits. This discontinuity (Fig. 2; Pl. 3, fig. 1c) is designated as the **ventral cleft**. In *Pseudorthoceras* showing a mural delta and ventral cleft, the episeptal deposits are of the lateral type, resulting from encroachment of the latero-mural deposits onto the episeptal surface. We should expect these episeptal deposits to show a continuation of the ventral cleft and they do (Pl. 3, fig. 5a,b, 6a,c).

ORDERLY ADORAL DECREASE OF CAMERAL DEPOSITS

The observation that earliest chambers of nautiloids tend to be completely filled with cameral deposits, and that the extent of chamber filling decreases gradually from chamber to chamber in adoral direction has been confirmed by many workers, among them BARRANDE (1859, 1877), TEICHERT (1933), and FLOWER (1939, 1955, 1964). According to FLOWER, the number of most anterior chambers which lack cameral deposits entirely varies from species to species, but commonly lies between 6 and 14. Our material, being almost entirely fragmentary, does not lend itself to studies of this phenomenon, but the general decrease in chamber fillings is illustrated on Plate 1 for "*Orthoceras*" and *Pseudorthoceras*. Chambers not strengthened by cameral deposits generally were crushed.

CHANGES IN BASIC PATTERN OF CAMERAL DEPOSITS FROM CHAMBER TO CHAMBER

Observations on thin sections of many apical tips reveal consistent changes in cameral deposits

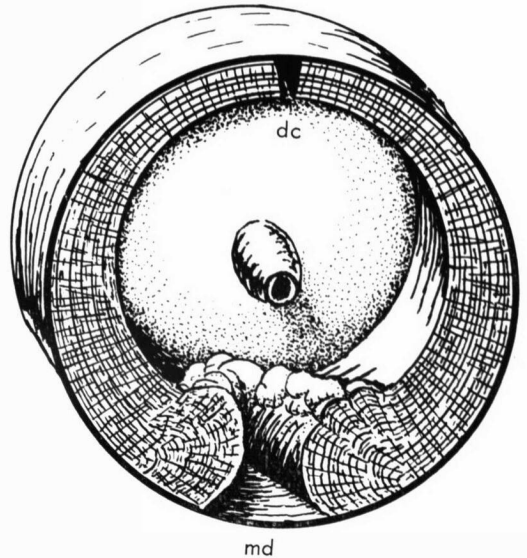


FIG. 8. Diagrammatic cutaway view of a *Pseudorthoceras* shell in early stages of chamber filling, showing dorsal cleft (*dc*) and mural delta (*md*). Plano-mural deposits pass into mammillary latero-mural deposits which overlap the mural delta from sides and join in adoral direction.

from chamber to chamber, as well as marked differences between different species.

In "*Orthoceras*" and *Pseudorthoceras* the first three or four chambers have mural, episeptal, and hyposeptal deposits (Pl. 4). In "*Orthoceras*" these deposits are normally of the planar type, although some deviations occur (e.g., Pl. 4, fig. 5a) in which one of the episeptal surfaces shows an irregular latero-episeptal overgrowth. In *Pseudorthoceras* (Fig. 7, 8) the episeptal deposits are largely planar in the first chamber and they become increasingly lateral thereafter. The hyposeptal deposits in these pseudorthoceratids are strictly of the lateral type.

Beyond the third or fourth chamber, hyposeptal deposits are absent in most species.

In all forms, cameral deposits of small, early chambers tend to be more highly calcareous than those of later, larger chambers.

FIG. 7. (Continued from facing page.)

C. Plano-mural deposits grading into plano-episeptal deposits.
D. Plano-mural deposits grading into short plano-episeptal deposits becoming latero-episeptal.

E. Plano-mural deposits sharply divided from latero-episeptal deposits.
F. Plano-mural and plano-hyposeptal deposits.
G. Plano-mural and latero-hyposeptal deposits.

CORRELATION OF CAMERAL DEPOSITS WITH TAXA

"*Orthoceras*" is characterized by highly calcareous, hard, cameral deposits; only in the larger chambers do we find heavily stained or very dark, soft, crumbly deposits; in *Pseudorthoceras*, on the other hand, hard, clean deposits are confined to the very earliest chambers, and heavily stained, even dark, soft, carbonate-poor deposits appear in the ultimate stages of chamber fill, from a diameter of a few millimeters onward.

In "*Orthoceras*" the hyposeptal deposits found in the earliest chambers are of planar type. In *Pseudorthoceras* they are of lateral type.

In "*Orthoceras unicamera*", episeptal deposits are commonly planar, while in *Pseudorthoceras* latero-episeptal deposits are the rule after the first few chambers. The cancellate "*Orthoceras*," however, developed episeptal, and perhaps mural deposits of a mammillary-lateral type (Pl. 2, fig. 1). The imbricate "*Orthoceras*" is unique among these species in having hyposeptal deposits not only in the earliest chambers but also in intermediate ontogenetic stages of the conch (Fig. 6). "*Orthoceras unicamera*" developed episeptal and hyposeptal circuli in its larger chambers.

Whereas all well-preserved forms show a dorsal cleft, the mural delta and ventral cleft appear to be confined to *Pseudorthoceras*. The strong development of latero-mural deposits along sides of the mural delta and their overlap over planomural deposits adorally and over the episeptal surface adapically, produces the striking spread-eagle pattern which characterizes these *Pseudorthoceras* in cross section.

IRREGULARITIES AND SIMILARITIES TO AGATES

Notwithstanding the lawful changes from chamber to chamber and the consistent links of certain patterns to specific taxa, examination of the illustrations shows that these cameral deposits show more irregularity and individual variation than normally are seen in skeletal structures (Pl. 4, fig. 2, 5). The third and fourth chambers of these specimens are essentially identical in pattern of cameral deposits, while chamber 5 (Pl. 4, fig. 5) deviates from the normal pattern by development of latero-episeptal and mammillary growth

forms. The "planar" type of growth commonly gives way at random to the "lateral" type, with development of mammillary structures and this "wildness" increases during the history of filling of any one chamber. This trend may develop gradually (e.g., Pl. 4, fig. 4) or suddenly along an "unconformity" (e.g., in Fig. 3,D; Pl. 2, fig. 3). It is as though the controls over deposition which produced symmetry and consistency had been at a maximum when deposition of cameral deposits commenced and had waned as filling of any one chamber proceeded. Furthermore, the general form of the deposits, with surfaces convex toward the interior and with sharp discontinuities ("pseudosepta" of authors) extending from corners toward the center, are strongly reminiscent of agates and other finely fibrous mineral precipitates from solutions in irregular cavities.

RELATIONSHIPS TO ENDOSIPHONAL DEPOSITS

In most of the sections the endosiphonal deposits appear to be entirely discrete from the cameral deposits. However, a section of *Pseudorthoceras knoxense* (Fig. 1; Pl. 2, fig. 4) shows endosiphonal deposits along the ventral side of the siphuncle, with growth lines parallel to and apparently continuous with those of the adjacent cameral deposits. The cameral deposits did not stop growing when they reached the connecting ring but continued to grow through the ring into the siphuncle. In this process the ring was not disrupted but simply incorporated into the deposit. The only major change in the deposits is one of composition. Outside the connecting ring they are very organic-rich, whereas in the siphuncle they are composed of much purer carbonate. Such continuity between cameral and endosiphuncular deposits has been noted by FLOWER (1939) and SWEET (1958) but the connecting rings may have been broken.

In some specimens the dorsoventral plane of symmetry of the siphonal deposits deviates notably from that of the shell and cameral deposits (Fig. 3,B; Pl. 2, fig. 2). We believe that this results from deposition at different times, the endosiphonal deposit having been formed later than most or all of the cameral deposit at this place, and from a slight torsional displacement between

shell and animal in the interval between these depositional episodes. The dorsoventral plane of shell and cameral deposit at this place no longer

corresponded to the precise orientation of the animal as a whole when the endosiphonal deposit was formed.

INTERPRETATION

Here we shall consider two questions: Are cameral deposits in the Buckhorn nautiloids of organic or inorganic origin? If organic, were they secreted by cameral tissues or precipitated from cameral fluids?

ORGANIC OR INORGANIC ORIGIN OF CAMERAL DEPOSITS

So far as most paleontologists are concerned, we may be flogging a dead horse in this question, yet it seems appropriate to round up the evidence once more. It seems to us that an organic origin, that is an origin during life of the animals concerned, is indicated by the following, largely independent lines of evidences.

CAMERAL DEPOSITS PREDATE ENTRANCE OF CLASTIC MATRIX

This observation has been made repeatedly since BARRANDE'S time and is here illustrated (Pl. 1, fig. 2). The clasts, consisting of shell debris and odd grains of quartz in a matrix of tarry material, have not only filled the chambers around the cameral deposits but also surround broken and partly displaced pieces of cameral deposits. Broken pieces of cameral deposits also occur scattered through the matrix along with other shell fragments. Such relationships are to be expected if cameral deposits were original constituents of the shells. Those who would consider them to be secondary, diagenetic, structures must assume sedimentary reworking of the fossils.

CAMERAL DEPOSITS CONSISTED OF ARAGONITE AND ORGANIZED ORGANIC MATTER

Specific gravity and staining tests (FISCHER & FINLEY, 1949) indicated that carbonate minerals of the Buckhorn cephalopod fauna are largely aragonite, a conclusion later confirmed by X-ray study (STEHLI, 1956, checked by LOWENSTAM and FISCHER). As discussed above, some specimens

are partly recrystallized to calcite, and in these recrystallized spots the microstructure has been largely lost (Pl. 4, fig. 3-4).

In addition to carbonate minerals, the cameral deposits contain considerable amounts of brown organic matter as discussed above. The cameral deposits are built up of growth layers, alternately poorer and richer in this organic matter, hence alternately clear and stained, as may be seen in many illustrations.

Aragonite, which is the dominant skeletal material of cephalopods, is not a normal diagenetic mineral. In fact, diagenesis generally destroys aragonite, and it has destroyed some of the Buckhorn aragonite. Secondly, the presence of much organic matter, interlaminated with the aragonite, is not readily explained as a result of inorganic processes but is common in cephalopod shells, resembling, for example, the interlayering in belemnite rostra and nacreous layers of mollusks, including *Nautilus* and fossil nautiloids (GRÉGOIRE, 1957, 1959a,b). Furthermore, GRÉGOIRE'S discovery of reticulate sheets of conchiolin, similar to those in mother-of-pearl, in the Buckhorn nautiloids is virtually final proof of organic origin.

Defenders of the inorganic theory might appeal to very special conditions, such as post-depositional diagenesis in hot rising groundwaters bearing also much organic material, to account for such peculiar diagenetic cavity fillings. But *Pseudorthoceras knoxense* from the St. Louis outlier (MILLER, DUNBAR, & CONDRA, 1933) and Kendrick shale of Indiana shows similar structures, and many of the cameral deposits in nautiloids of ordinary preservation show the blurred type of growth banding which may be seen in recrystallized parts of the Buckhorn material. It is thus clear that the Buckhorn cameral deposits were originally not unique in structure. They have become unusual merely because of their preservation. They are representative of what nautiloid cameral deposits were before alteration, and their composition speaks for an organic origin.

**CAMERAL DEPOSITS SHOW ORDERLY
DECREASE IN BULK FROM APICAL
CHAMBERS TOWARD LIVING
CHAMBERS**

This observation has been discussed above. The orderliness of change suggests control by the organism and the organic theory holds that the filling proceeded gradually during life of the individual in a zone which was located at some distance behind the body chamber and gradually moved forward as the apical chambers became completely filled, and as new chambers were added at the front.

**CAMERAL DEPOSITS DO NOT FORM
EVEN LININGS OF CHAMBERS BUT
ARE HIGHLY DIFFERENTIATED**

For actinocerids, orthocerids, and other forms, BARRANDE (1859, 1877) and TEICHERT (1933, p. 170) demonstrated that primary, organic cameral deposits never cover the outside of the connecting ring and that only secondary, inorganic deposits form a continuous lining of the entire camerae. When the connecting ring is destroyed, secondary (diagenetic) deposits may form a continuous lining on both sides of the septa and around the septal necks. FLOWER (1939, 1955, 1964) has shown a wide variety of such structures.

A cursory examination of the literature (FLOWER, 1955, 1964), illustrations in this paper, and a series of nautiloid sections, show a bewildering variety of cameral deposits. But one generalization may be made for all: They do not form overall continuous linings. They grew inward from the outer wall of the chamber, and in some cases from the frontal and rear surfaces of the septa, but with exception of distinctive circuli, they did not grow outward from the siphuncle.

**CAMERAL DEPOSITS ARE BILATERALLY
SYMMETRICAL**

When cameral deposits are studied in laterally oriented longitudinal section (Pl. 1, fig. 3), or in cross section (Fig. 2, 3,A, 5; Pl. 2, fig. 2; Pl. 3, fig. 1a-c, 5b, 6b-c; Pl. 4, fig. 3), they are found to have an overall bilateral symmetry, although in detail this may show minor imperfections. This has been pointed out repeatedly by other workers (e.g., BARRANDE, 1877, especially pl. 229; FLOWER, 1939, 1955, 1964; and TEICHERT, 1933, 1961).

The Buckhorn material shows that this symmetry extends not only to general shape but also to internal structure and actually consists of symmetrical variations of two sorts: composition and form.

Perhaps the first character to strike the observer in a study of our thin sections is color distribution within cameral deposits; colors vary from white to yellow and brown, reflecting the amount of admixed organic matter. A fine color lamination of clearer and darker layers occurs through much of the deposits; but, in addition, the various species studied show a notable concentration of pigmentation (organic admixture) on one side of each chamber filling and a notable lack of it on the other.

This change in composition is accompanied by a change in form of the individual growth laminae, which tend to be thicker on the dark side and in *Pseudorthoceras knoxense* may be expanded into one or more bulges; laterally, and toward the opposite side, they thin in a symmetrical fashion. Thus "*Orthoceras*" *unicamera* shows a crescentic pattern in cross section (Fig. 5; Pl. 2, fig. 2; Pl. 4, fig. 3), whereas *Pseudorthoceras* presents a peculiar spread-eagle pattern (Fig. 2; Pl. 3, fig. 1a-c, 5b, 6b-c). In "*Orthoceras*" *unicamera* the circuli also show a bilateral symmetry (Fig. 3,A, 5).

The plane of symmetry is even more sharply defined by the dorsal cleft, described above, and in *Pseudorthoceras* by the mural delta and the associated ventral cleft.

Whereas one can imagine that simple types of bilateral symmetry might be developed in diagenetic fillings of symmetrical cavities, especially if mechanical sedimentation played a role, the development of complex structures such as those found, and serial repetition of features such as the mural delta, seem quite outside the realm of physical-chemical processes.

**PLANE OF SYMMETRY OF CAMERAL
DEPOSITS IS INDEPENDENT OF
POSITION OF BURIAL**

This has been previously mentioned (FLOWER, 1939, 1955, 1964; TEICHERT, 1961). If symmetry had been developed under the influence of gravity in diagenetic cavity fillings, the planes of symmetry might be expected to lie at right angles to

bedding. Instead, the orientation is random, incompatible with the diagenetic theory unless post-diagenetic reworking is assumed to be the rule.

PLANE OF SYMMETRY OF CAMERAL DEPOSITS APPROXIMATELY COINCIDES WITH DORSOVENTRAL PLANE OF OUTER SHELL

This observation, made previously by TEICHERT and by FLOWER, is fully substantiated by the Buckhorn material.

A variety of criteria may be used to locate the dorsoventral plane. Among these are: 1) Curvature of the tip (generally exogastric) (Pl. 4, fig. 1, 4); 2) the "dorsal line" or septal furrow and its corresponding counterpart in the cameral deposits (Pl. 3, fig. 2a, 4b, 6b); 3) the ventral conchal furrow (a faint structure, commonly not recognizable); 4) depressed elliptical rather than circular cross section of shell, a notable feature in some pseudorthoceratids); 5) excentric position of siphuncle in some species (Pl. 4, fig. 1, 2a, 4, 5a); 6) hyponomic sinus (in at least one species of pseudorthoceratids) (Pl. 3, fig. 4a); 7) ventral saddle of suture (in one pseudorthoceratid) (Pl. 3, fig. 5a); 8) ventral concentration of endosiphuncular deposits (Fig. 1-5; Pl. 2, fig. 2-4, Pl. 3, fig. 1; Pl. 4, fig. 3).

In a majority of shell fragments the dorsoventral plane of the phragmocone may be recognized by the septal furrow or by a combination of this and other criteria and in the great majority by the plane of symmetry of the cameral deposits coincident with it. In some cases, the symmetry planes of phragmocone and cameral deposits deviate slightly (Fig. 3,A,B; Pl. 2, fig. 2). In some specimens the symmetry planes of cameral deposits of successive chambers likewise deviate from each other by a few degrees (Pl. 3, fig. 6a). Such deviations we have explained as result of torsional displacements of the shell relative to the organism as a whole which took place during ontogeny.

When cameral deposits are viewed with this orientation, it is clear that the heavily pigmented side, where growth of the deposits was most rapid, is the ventral side, and that the last part of the chamber to be filled is the portion immediately dorsal of the siphuncle, except in "*Orthoceras*" *unicamera*, in which this space tends to be filled by the circuli.

This agrees with observations by TEICHERT (1933, p. 183) who found concentration of cameral deposits in actinoceroids to be heavier on the ventral than on the dorsal side of the camerae. A similar disposition of cameral deposits exists in some discosorids (FLOWER & TEICHERT, 1957), and in other nautiloids (FLOWER, 1955, 1964).

CAMERAL DEPOSITS SHOW DEFINITE CHANGES IN PATTERN FROM APICAL CHAMBERS TOWARD LIVING CHAMBER

Not only the degree to which cameral deposits fill the chambers, but also their organization changes. This matter has been discussed above.

TAXA DIFFERENTIATED ON BASIS OF SHELL ORNAMENTATION, CHAMBER FORM, SIPHONAL CHARACTERS, AND OTHER FEATURES MAY ALSO BE DIFFERENTIATED BY THEIR CAMERAL DEPOSITS

This point has been described in the preceding text. We therefore regard the organic origin of cameral deposits as established. They were functional parts of living organisms. The hydrostatic function of the camerae and their cameral deposits have been discussed by many authors (e.g., BARRANDE, 1859; TEICHERT, 1933; FLOWER, 1939, 1955, 1964). The deposits served as counterweights to bring together the animal's centers of gravity and buoyancy to provide maneuverability. The question remains as to how they were formed.

CONCLUSIONS ON ORIGIN OF CAMERAL DEPOSITS

The question of the origin of cameral deposits has now resolved itself into three simple possibilities: Were they deposited from living tissues present within the chambers as visualized by

TEICHERT and by FLOWER? Were they deposited from cameral fluids secreted by the tissues in the siphuncle? Were some cameral deposits formed by one of these processes, and others by the other?

We are agreed that the structures described by FLOWER (1943) and HOLLAND (1965) in the cameral deposits of *Leurocyloceras* offer very strong support for the theory of cameral tissues in this genus and presumably in other genera. But the next question is whether all cameral deposits, and specifically, the cameral deposits of the Buckhorn nautiloids, were formed in this manner, and here we have come to different interpretations: One of us (TEICHERT) believes that they were and that deposition of cameral deposits from cameral tissues is still the most satisfactory general explanation for cameral deposits in cephalopods. FISCHER, on the other hand, interprets the cameral deposits in the Buckhorn nautiloids as products of precipitation from cameral fluids and advances this as the normal mechanism in cephalopods, to which *Leurocyloceras* and presumably some other groups proved exceptions. We therefore close our joint paper with two sets of conclusions, leaving further clarification to readers and researches of the future.

DEPOSITION FROM CAMERAL FLUIDS (Fischer)

CONNECTING RINGS

Examination of many thin sections and of numerous siphuncles prepared in relief has shown that the connecting rings of Buckhorn nautiloids, while uncalcified, were solid conchiolinic sheaths. Though connecting rings have commonly been broken, no regular system of perforations has been found, through which cameral tissues could have grown from the siphuncle into the chambers, or through which such tissues could have been supplied with arterial blood, relieved by veins or provided with nerves. If these present rings are the original connecting rings, then it seems unlikely that tissues existed in the chambers since their separation from the body chamber. The alternative is that the original connecting rings were broken and perforated after such tissues had died or been resorbed. This alternative is eliminated by observation that cameral deposits in *Pseudorthoceras* (Fig. 1; Pl. 2, fig. 4) may grow across the connecting ring into the siphuncle (thus becoming endosiphuncular deposits by definition) without disrupting the connecting ring in the process. The ring was present when the

cameral deposits were formed and growth lines of the deposits, crossing the connecting ring obliquely, show that it was gradually engulfed as the deposits grew. The ring evidently was sufficiently porous on a molecular scale to offer no barrier to the advancing front of calcification. This observation is, to me, proof positive that the cameral deposits were not secreted in direct contact with a living tissue, for such tissues could not have passed obliquely through the connecting ring in the manner of the deposits.

We next turn to the cameral deposits proper, with the question of whether their composition and form requires us to assume precipitation in direct contact with living tissues, or whether precipitation from fluids at some distance from tissues is a conceivable explanation.

MOLLUSCAN SHELL SECRETION

The rapidly growing literature on molluscan shell secretion has been summarized by WILBUR (1964). Shell secretion in mollusks is an extracellular process. The mantle epithelium secretes an *extrapallial fluid* which has essentially the composition of molluscan blood, containing various inorganic ions as well as one or more proteins, mucopolysaccharides, and probably other organic substances. Into this extrapallial fluid the mantle epithelium secretes soluble organic substances, calcium salts, and carbon dioxide.

In ways which are not well understood, the organic substances become polymerized into the insoluble material grossly termed conchiolin, a material of highly complex chemical structure, varying from species to species, and from place to place within the same shell. It contains a protein, a scleroprotein, a polypeptide, and polysaccharides. The assortment of amino acids varies from species to species and from place to place within the same skeleton. Physically, this polymerization occurs on the shell surface and forms there solid or fenestrate sheets and may or may not form a matrix between carbonate grains.

Carbonate deposition occurs by precipitation of calcite or aragonite (rarely vaterite) from the extrapallial fluid onto this organic base. The chemical structure of the conchiolin substrate appears to dictate the mineralogy of the precipitate: Several investigators have shown that the sites of calcite and aragonite precipitation, in

shells in which both occur, are correlated with differences in conchiolin composition; furthermore, insertion of organic matrix from an aragonite-precipitating shell into the pallial fluid of a calcite-precipitating shell results in precipitation of both aragonite and calcite. Not only the mineralogy but also the orientation and habit of the crystals and the fabric of the resulting skeleton are strongly influenced by the organic matrix. The crystals commonly grow in specific crystallographic orientations. This control over deposition by the substrate is generally known as **epitaxis**.

Shell growth normally occurs in very small spaces. The inner lining of the bivalve shell is formed from a thin film of extrapallial fluid between mantle and shell surface and the growth at the shell margin takes place in a kind of pocket, triangular in cross section, running around the edge of each valve and bounded by the mantle edge, the recurved edge of the periostracum, and the growing shell surface. It seems conceivable to me that the same processes would operate in large spaces, such as the chambers of phragmocones: that a fluid, similar in composition to the extrapallial fluid, could be secreted from the siphuncle through the molecularly permeable connecting ring to fill the chamber partly or wholly; and that polymerization of organic substances and the crystallization of aragonite on this organic matrix could lead to a growth of cameral deposits which differ in no essential manner from other molluscan shell deposits, despite their greater distance from the secreting tissues. If reticulated sheets of conchiolin are not formed in direct contact with the living epithelial surface, then distance from tissues should play no role in their origin.

There is nothing haphazard about the deposition of cameral deposits in this model; presumably cameral fluids served initially as a counterweight to awkward apical buoyancy and the systematic deposition of calcareous cameral deposits came as an evolutionary improvement by providing more weight and a more stable ballast. The rate of growth of deposits in any one chamber could be controlled by the amount of organic and inorganic substances secreted into that chamber. Only the form of the deposits could not be controlled as accurately as that of the normal shell.

FORM OF DEPOSITS

Let us now consider the form of the cameral deposits, in the light of this model of deposition from cameral fluids. Three general features characterize the growth of cameral deposits:

1) They definitely grew inward from the chamber walls, in inwardly convex patterns, much like agate fillings of cavities. This is what we should expect in precipitation from cameral fluids, although it seems possible that similar patterns would have developed had cameral tissues been present, and that this character is not a diagnostic one.

2) The cameral deposits are not even and continuous chamber linings, but show very distinctive patterns, avoiding the dorsal line, and the mural delta, and, in most chambers of most species, the hyposeptal surface. At first differentiation into areas of deposition and areas of no deposition had impressed me as very strong evidence of control by cameral tissues, but discussions, with GRÉGOIRE, MUTVEI, and SEILACHER have convinced me (FISCHER) that it is not a serious obstacle to the cameral fluid theory. We need only imagine that the chamber lining, left when the animal vacated the end of the body chamber and sealed it off as a camera, was not uniform in terms of its electrochemical configuration, in that it possessed areas receptive to polymerization of conchiolin which served as base for aragonite crystallization as well as areas not receptive to such overgrowth, i.e., that it was epitaxially differentiated.

3) While beginning as regular and symmetrical structures, the cameral deposits became irregularly botryoidal as the filling of a given chamber proceeded. In particular, the areas favorable to aragonite nucleation and thereby to the growth of "planar" deposits tend to decrease in the history of a given chamber. The development of irregular botryoidal growths in particular suggests free precipitation in an open, fluid-filled space rather than precipitation in close proximity to a controlling tissue surface, and therefore, it seems to me (FISCHER), favors the theory of cameral fluids over that of cameral tissues.

MODEL IN DETAIL

Let us then review the growth of cameral deposits in a *Pseudorthoceras*, according to the cameral fluid theory, beginning with a young

animal, still living in a part of the shell which was later to become filled with cameral deposits. We imagine this animal as just having vacated the end of its "body chamber," and being in the process of depositing a septum. It left this chamber with a chemically differentiated surface: The outer walls were left receptive to conchiolin polymerization of the type favorable to aragonite overgrowth except in the triangular area of the mural delta, and along the dorsal line. The episeptal surface was receptive only near the outer wall, and the hyoseptal surface was not receptive to such overgrowth.

No such growths developed as yet anywhere in the chamber. This may have been filled with fluid, but was gradually converted into a buoyant gas chamber and served as such for a length of time. Then, becoming more and more "apical" as the growth of animal and its shell continued, it came into the zone of counterweighting, was partly filled with cameral fluids, and came to be again a zone of skeletal deposition, this time by "remote control." The cameral fluids were essentially similar to the extrapallial fluids from which the shell is formed, and were charged from the siphuncle with dissolved organic substances, calcium salts, and carbon dioxide. Deposition of conchiolin and aragonite occurred on the chamber walls which exercised epitaxial control. Certain sites—the hyoseptal and part of the episeptal surface, the dorsal line, and the mural delta—rejected such overgrowths, but were gradually covered by lateral encroachment.

Amount of cameral fluid exercised another control on the growth of cameral deposits—presumably it wetted all the chamber walls during times of violent motion, but collected at the bottom of the chamber during quiet times, and thus led to a more rapid growth of cameral deposits there. The strong botryoidal deposits along sides of the mural delta suggest that at times the fluid level in the chamber was very low, just enough to fill the pit formed by the mural delta. As filling progressed, the deposits became more irregular and botryoidal, and the amount of organic matter gradually increased at expense of the carbonate, so that the latest deposits, closing round the siphuncle, were generally soft and dark.

In part of the phragmocone, growth of cameral deposits did not stop at the connecting

rings, but engulfed these and extended into the siphuncle.

Extending this model to other chambers, we would conclude that the hyoseptal surface of the first three chambers possessed a receptive edge immediately adjacent to the suture, leading to a latero-hyoseptal deposit in these chambers, and that the episeptal surface was largely receptive in the early chambers, but not receptive to direct overgrowth in later ones.

In "*Orthoceras*" the hyoseptal surface was receptive to overgrowth only in the first four chambers except in the imbricately ornamented species. "*Orthoceras*" *unicamera* developed receptive spots in more mature chambers at the end of the septal neck, in front of the septal foramen, and along the dorsal side of the connecting ring, and deposits extending outward from these places formed circuli. The cancellate "*Orthoceras*" had receptive spots on the episeptal surface, arranged in radiating lines, leading to the crenulate episeptal deposits which characterize it.

SUMMARY

I have thus come to the conclusion that the cameral deposits in the orthocerid nautiloids of the Buckhorn asphalt were deposited from cameral fluids, secreted by the siphuncular tissues through the connecting ring (FISCHER).

When such cameral deposits are associated with siphuncles that show no regular system of perforations through which tissues could have grown into the chambers and through which they could have been supplied with blood and nerves, the cameral fluid hypothesis seems preferable to the alternative of assuming presence of lining tissues without visible means of support. This is the case in the Buckhorn nautiloids, and, so far as we now know, in most cephalopods containing cameral deposits.

The cameral deposits of *Leurocycloceras*, containing radial canals, would appear to have been built in a different manner, namely by cameral tissues. Presumably it was not unique in this, amongst nautiloids. I am willing to predict that the connecting rings of such cephalopods having cameral deposits formed from cameral tissues will show systematic perforations or other evidences of communication between siphuncle and camera (FISCHER).

This conclusion, in turn, leads to the view that cameral deposits were independently developed by two or more stocks of cephalopods—which is not at all surprising in view of their obvious functions as instruments of balance, and in view of the various other ways which other groups of cephalopods found toward the same end.

DEPOSITION FROM CAMERAL TISSUE (Teichert)

FISCHER has a valid point when he states that “cameral deposits were independently developed by two or more stocks of cephalopods.” This conclusion seems to be indisputable, inasmuch as cameral deposits are found in the Orthocerida, Oncocerida, and Discosorida, all of which had independent origins in the Ellesmerocerida, in which cameral deposits have so far been reported from only one genus, *Protocycloceras*, which is not in the line of ancestry of any of the mentioned three orders. Further, the Actinocerida, of doubtful derivation, have well-developed cameral deposits and so have several families of the Belemnitida, which are now believed to be derived from the bactritids lacking known cameral deposits. Therefore, it is conceivable that in different stocks different mechanisms evolved for the purpose of depositing cameral deposits and that these may be analogous, not homologous, structures.

This conclusion receives support from the observation that not very closely related Recent cephalopod groups have developed different mechanisms to store liquids in their shells. In *Sepia*, the amount of liquid in the chambers of the cuttlebone is variable and an osmotic exchange with body fluids takes place through the siphuncular membrane. The liquid is concentrated in the posterior part of the cuttlebone (DENTON & GILPIN-BROWN, 1961a, 1961b; DENTON, GILPIN-BROWN & HOWARTH, 1961).

In *Nautilus*, as shown by DENTON & GILPIN-BROWN (1966), it is the last, most anterior, ten chambers that are filled with liquid, the amount of which decreases from the newest camera to the older camerae. Apparently, when construction of a septum has been completed, the then last camera remains filled with a liquid which is different in composition from blood, as well as

sea water. As new liquid-filled camerae are added, liquid is gradually drained from the older camerae through the connecting ring into the siphuncle. It seems that no osmotic exchange of liquids takes place between siphuncle and camerae. At the same time it is difficult to imagine how anything resembling cameral deposits could be precipitated in the camerae of *Nautilus* from the liquids contained therein. Further, cameral deposits are never present in the youngest camerae of a phragmocone.

If liquids were present in the camerae of orthoconic cephalopods, they are unlikely to have been distributed in the same way as in the *Nautilus* shell. Rather, it must be assumed that they were concentrated in the apical portion of the shell as was first postulated by HERMANN SCHMIDT (1930). It is difficult to believe that in such forms genesis of liquid formation should have been the same as in *Nautilus*. Instead, one would have to assume that early camerae were filled with liquid pumped through the connecting ring some time after their formation.

FISCHER (see Conclusion 1) postulates that in some cephalopods cameral deposits were secreted by cameral tissue, while in others they were deposited from cameral fluids. He predicts that in the former category the connecting rings will eventually be found to have perforations to allow passage of vascular organs. I am not convinced of this, because it seems to me that, if perforated connecting rings existed, they would have been observed by this time (TEICHERT). Several decades ago, paleontologists believed that the radial canals in the siphuncles of actinocerids penetrated the connecting rings and opened into the camerae. However, in 1933 I was able to show that the canals did not communicate with the camerae but ended in a narrow void space, the perispantium, which extends along the inside of the connecting rings (TEICHERT, 1933, 1935). Most probably the perispantium contained body fluids which could have interacted with fluids in the camerae somewhat in the way FISCHER postulates for the Buckhorn cephalopods.

In the Discosorida the situation is quite different. Here we find cameral deposits coupled with endosiphuncular deposits of parietal type which completely cover the inside of the connecting ring. The latter is thick and complex in many forms, but no perforations have ever been ob-

served. With its inner surface sealed by parietal deposits, no way to account for presence of cameral deposits by either fluid precipitation or by the cameral tissue hypothesis seems to be offered. However, it is possible that in such forms, formation of cameral deposits ceased when the parietal deposits were completed.

The greatest difficulty of FISCHER's fluid precipitation hypothesis seems to lie in the geometrical shape of the cameral deposits—their orderly progression from apical to mature parts of the shell and their symmetrical arrangement within camerae, two features which have been discussed in detail above. To achieve such geometrical balance through precipitation from extrapallial fluid, it is almost necessary to assume that all camerae were at all times completely filled with this fluid. It does not seem possible to account for the orderly arrangement of cameral deposits in only partly filled camerae by occasional wetting of portions of their walls "during times of violent motion." No orderly organic deposit can be formed in this way. On the other hand, if the entire phragmocone were filled with fluid from which deposits of conchiolin and aragonite were precipitated in bulk, the animal would probably have been condemned to immobility.

SCHINDEWOLF (1967), when discussing conchiolin membranes discovered by him in camerae of ammonites, considered, but rejected, the possibility of their precipitation by cameral fluids.

If we were to assume that the amount of fluid was reduced gradually in the apical camerae as the animal advanced in its shell, gas would have to be pumped into the camerae through the siphuncular wall. At such a stage the remaining liquid would accumulate in the ventral portions of the camerae, gas in the dorsal portions, and secretion of cameral deposits would continue in the ventral portions only. Such an assumption might account for the fact that cameral deposits generally are thicker on the ventral side of

camerae than on the dorsal side. To prove this point, however, it would have to be shown that thinning of deposits is due to decrease in number of laminae from ventral to dorsal regions of the camerae.

One further point is to be considered. WILBUR (1964, p. 248) states that the extrapallial fluid forms "a thin layer." He (1964, fig. 2) shows it to be somewhat thinner than the shell wall. The total amount of extrapallial fluid in the body chamber of an ectocochlian cephalopod, therefore, is small. Since the extrapallial fluid presumably is present only in a narrow band near the aperture of the body chamber, its bulk is very small. In a body chamber 20 mm. in diameter it might have been of the order of 100 mm³. If such a body chamber was 40 mm. long, the corresponding phragmocone might have been about 10 cm. long and, if straight, would have had a volume of more than 10 cm.³, enclosing perhaps 8 cm.³ of void space before formation of cameral deposits, this space to be filled with extrapallial fluid. It is difficult to speculate on the capacity of the animal to produce this amount of extrapallial fluid, but the problem should be recognized.

All things considered, it seems to me that most of the facts which we have cited and discussed as proof of the organic nature of cameral deposits at the same time tend to support their origin from body tissues present in the camerae. How this tissue was connected with the siphuncle from which it must have been supplied with blood, is at present unknown. Many more detailed investigations should be made to determine the exact geometrical shape of cameral deposits and the microscopic structure of the connecting ring in fossil cephalopods. Until such studies have been made on a great many different groups in which cameral deposits are present, the fluid precipitation hypothesis as postulated by FISCHER, may at least be considered as a possible alternative for some ectocochlian cephalopods.

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