

HYDROSTATICS AND HYDRODYNAMICS OF CEPHALOPOD SHELLS: FORM, STRUCTURE, AND FUNCTION.

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ABSTRACT

This paper discusses the physical properties and potential adaptations of cephalopod shell, together with evolution. From the "simplest design" in ancient nautiloids to the most "complex" in the ammonoids, all parts of the shell were more or less maximized for buoyancy (minimum weight), strength against implosion by ambient pressure, and various functions related to swimming, hovering, feeding, protection etc. Simple engineering principles are applied to explain the structures.

RESUMEN

Este trabajo discute las propiedades físicas y el potencial de adaptación de la conchilla del cefalópodo, junto con su evolución. Desde el "diseño más simple" en antiguos nautiloideos al más "complejo" en los ammonoideos, todas las partes de la conchilla fueron más o menos maximizadas por levedad (mínimo peso), resistencia contra la implosión por presión ambiental, y varias funciones relacionadas con natación, flotación, alimentación, protección, etc. Principios simples de ingeniería son aplicados para explicar las estructuras.

The centuries' old fascination with Ammonites as beautiful and useful fossils in stratigraphy, historical geology and biogeography, has in the last decades been expanded to ecology and oceanography. The complicated shape and internal 'architecture' (macro-structure) of the ammonite shell has given rise to a new discipline that we may call "engineering paleontology": the theoretical and experimental study of fossilized tissues, in our case the mainly nacreous (aragonitic) shell wall and internal septa and the chitinous or chitino-phosphatic tube (connecting rings) of the siphuncle. The three-dimensional shapes, often with anticlastic and sometimes convoluted curvature, together with the mechanical properties based on the ultra-structure of these parts, are the

basic data for analyses: e.g., how much hydrostatic pressure can the empty internal chambers (camerae) of the shell (phragmone) withstand before collapsing or imploding? Under what pressure does the siphuncular tube (connecting rings) explode? What is the hydrodynamic drag on the shell or, better, the entire organism during swimming? And how stable was it submersed in the water?

This paper, more or less in the present form but including colour photographs, was given to the Academy on the occasion of my membership in December 1992 and is essentially a series of notes and comments to diagrams. This article is also heavily biased on my own work over the last two decades, a kind of autobiography, lightly spiced with mathematical flavour giving a slight taste of the recent work of my long-time associate Roger Hewitt.

I will reference the literature only in the captions to copied illustrations.

Conferencia pronunciada durante su incorporación como Académico Correspondiente en Hamilton, Ontario, Canadá, el día 11 de diciembre de 1992.

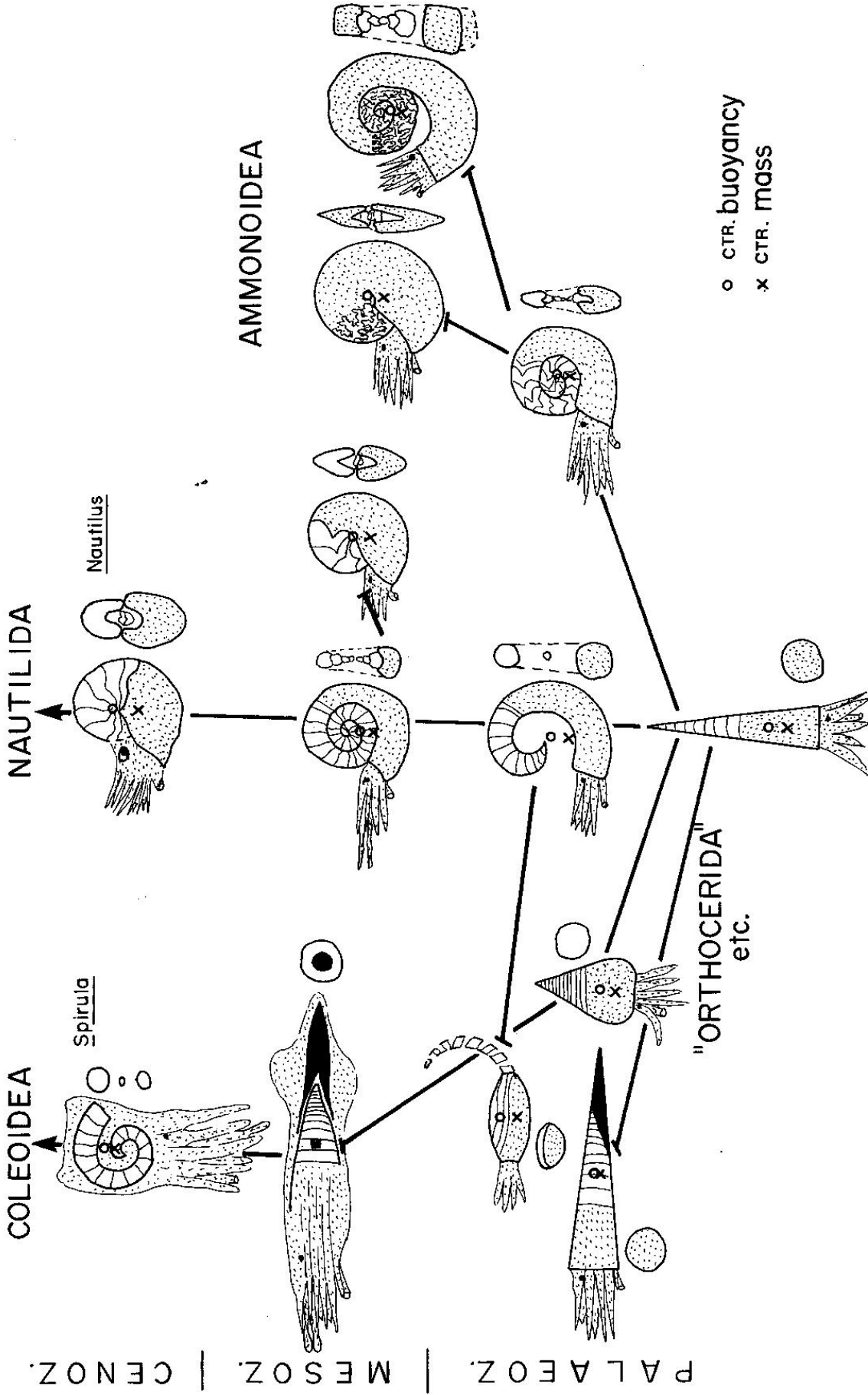


Fig. 1 — The principal adaptive trends in the evolution of the cephalopod shell, greatly simplified. From vertically oriented orthocones, to 'counterweighted' orthocones with internal deposits (black) to achieve neutral equilibrium (diverse Paleozoic nautiloids), to internal shells with 'counterweights' outside of the phragmocone (belemnites); or to cyrtocoenic, gyrogonitic and coiled shells that become increasingly involute and moderately 'streamlined' (nautilids); or to similar but more specialized designs with fluted and, finally, frilled septa that permitted a great diversity of whorl shapes designed for hydrodynamic efficiency, protection against predators, etc. (planispiral ammonoids); and to a great variety of planktonic, often vertically migrating heteromorphs.

Hydrostatics

Basic Shell 'Design'

The rather complicated 'design', or architecture, of the ammonite shell can be better understood by extreme 'simplification' of its principal functional parts. During cephalopod evolution, the shell modified in several unique adaptive trends, which served the organisms in an astonishing variety of ways related to buoyancy and protection (Fig. 1).

The phragmocone basically served as a fixed-volume buoyancy apparatus (in contrast to the fish bladder). The hypothetically simplest structure fulfilling this function — which was indeed present in the ancestral orthoconic and cyrtococonic nautiloids of the Paleozoic — is a cone, subdivided by septa into empty chambers (camerae, so it can grow incremental). Each chamber is water-filled during construction by the posterior mantle

of the body, until the septum has been secreted; then the water (body fluid) is extracted osmotically via the siphuncle, i.e. it is 'pumped' osmotically back into the body. In the real organisms, the last stage consist of diffusing gas slowly into the empty chamber until it slowly reaches the partial pressure of nitrogen in the surrounding seawater (0.9 atm). Cephalopods have no gas pressure glands like some deep-water fish; hence the phragmocone acted as a fixed-volume pressure vessel (strictly speaking a quasi-vacuum vessel) — the ambient pressure tended to crush it by implosion. The resulting stresses can be calculated.

The body-chamber, of course, contained and protected the body, which almost certainly resembled that of squids or octopods. The entire organism was kept at neutral buoyancy throughout the incremental growth, with the aid of a complex system of water exchange between body and phragmocone

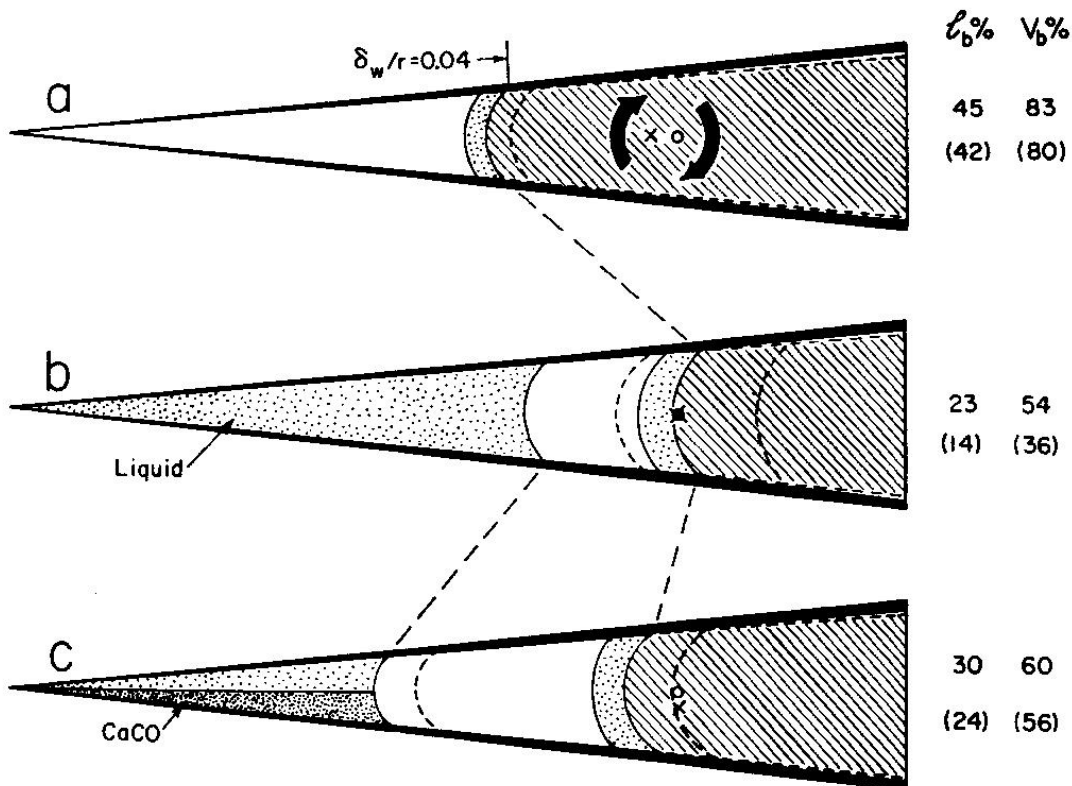


Fig. 2 —Orientation and neutral equilibrium (centres of mass, o, and buoyancy, x, coincide) of orthoconic nautiloids; a, shell in vertical position without neutral equilibrium; b, neutral equilibrium achieved by water only, with great reduction of animal size; c, by calcium carbonate and water (probably the natural state). (From Westermann, 1977)

compensating for buoyancy gain and loss during chamber construction — like building a submarine floating in midwater!

The oldest nautiloids (Ellesmeroceroidea) and some later planktonic forms (Bactritoida, now considered to have been the first Ammonoidea) resembled the 'simple orthocone' model, described above: the centre of buoyancy was well separated from the centre of mass, and the organisms had vertical orientation, with great stability.

All but the most primitive orthocones secreted calcium carbonate in the apical chambers and so produced also neutral equilibrium (besides neutral buoyancy), i.e. the centres of buoyancy and mass come to coincide and the animal was unstable in any orientation. Limited stability against pitch and rolling was produced by ventro-dorsal (here up-down) asymmetry of secretions, with more weight produced ventrally (below). The amounts of water and/or calcium carbonate required for

neutral equilibrium and neutral buoyancy, as well as the amount of consequent enlargement of the phragmocone (or reduction of body-chamber) have been calculated (Fig. 2).

Shell Strength of Orthocones

Calculations of shell strength are usually based on the internal septa, instead of the external phragmocone wall. The outer shell had to be strong enough also withstand bending pressures, abrasion and, especially, point loads applied by the teeth of predators.

The latest septum (throughout growth) resisted the ambient water pressure applied adorally via the body. In the simplest case, as in the orthocone nautiloids, the septum had the spherical curvature of a membrane, with surface-parallel tensile stress only (Fig. 3). The ideal form maximizing strength and minimizing weight is a 'cap' with height = $1/2$ radius-of-curvature. Its strength is pro-

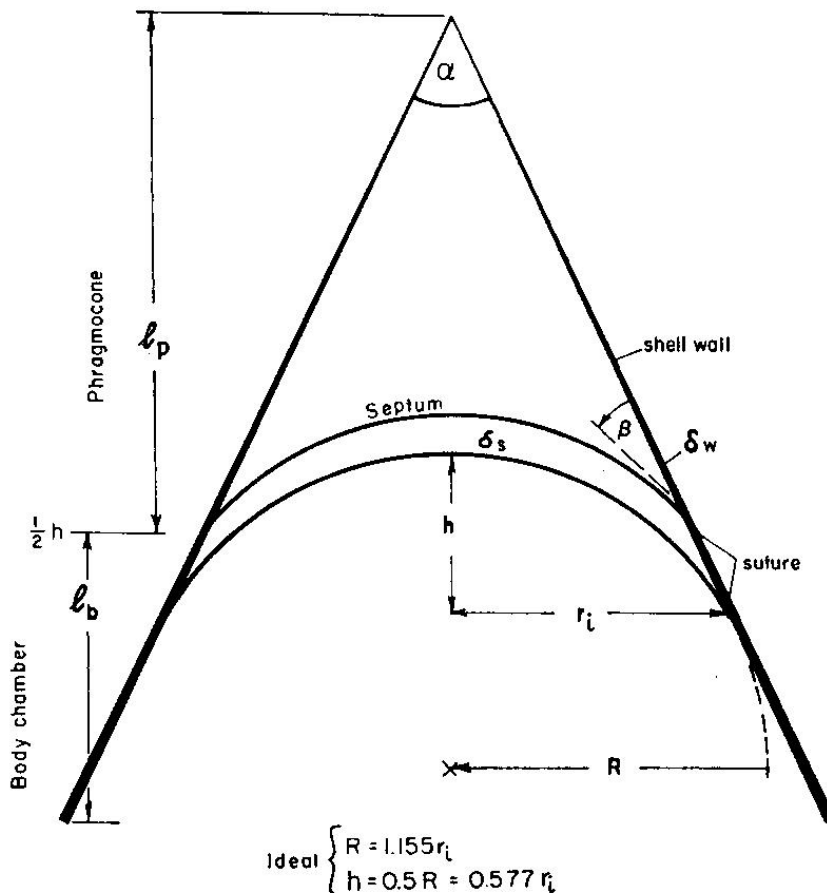


Fig. 3 — The essential dimensions for calculation of the strength of a simple, orthoconic nautiloid shell (From Westermann, 1977).

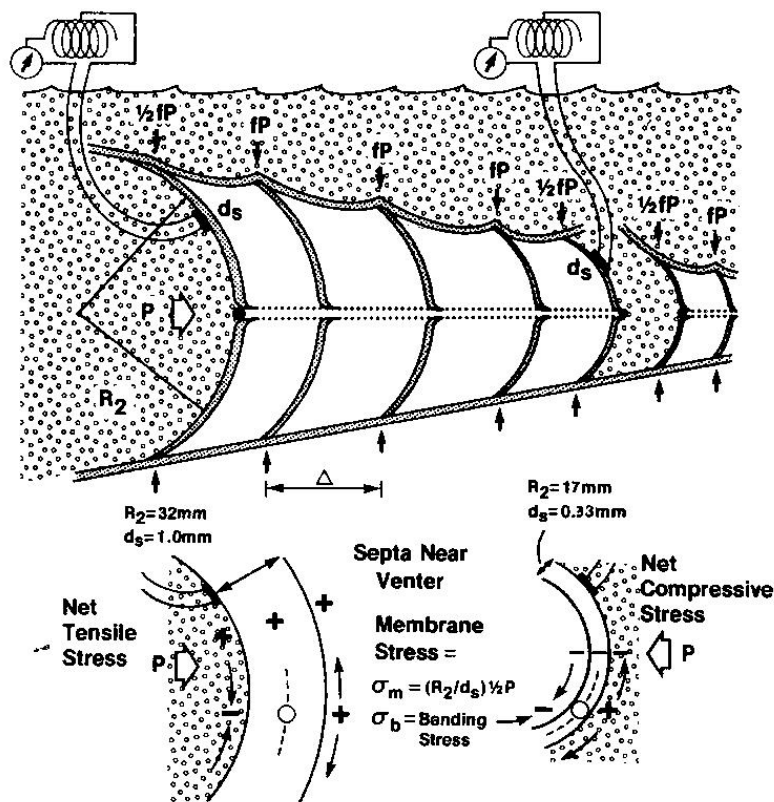


Fig. 4 — Model orthocone illustrating experiments with Nautilus shells using straingauges to measure radial bending and membrane stresses in the septum. fP , force due to water pressure applied at septal suture; P , water pressure applied to septum; R_2 , minimum curvature radius. Note bending of shell wall over septal sutures, see Fig. 4. (From Hewitt and Westermann, 1987b).

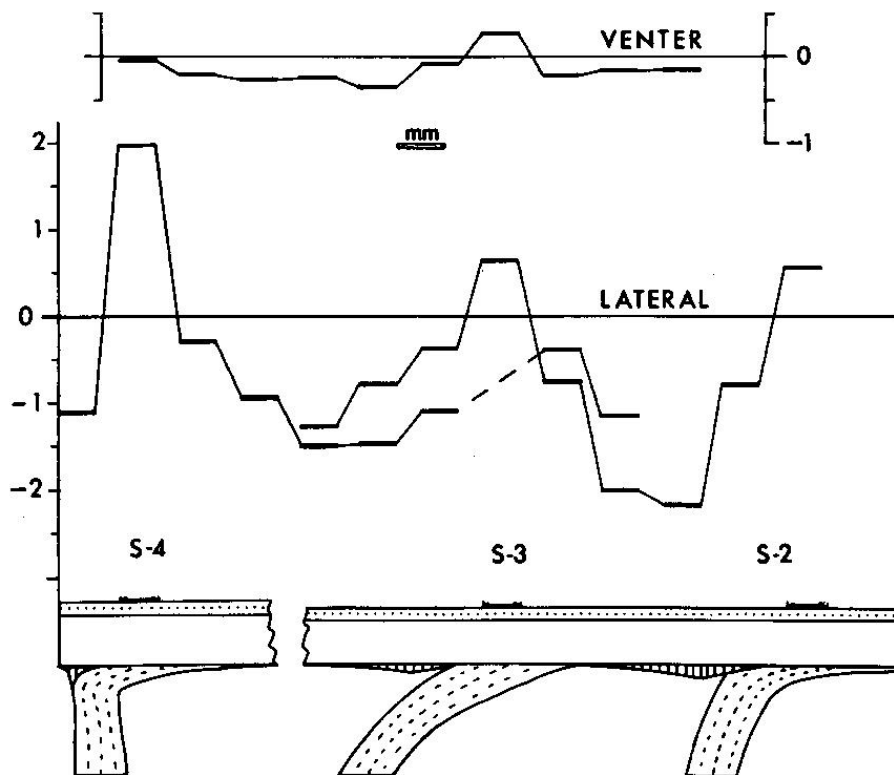


Fig. 5 — Strain variation in the outer layer on the Nautilus shell wall, due to bending stresses related to the position of the septal suture; the stress is highest where the septum meets the shell wall at right angle (lateral lobe), whereas the septum acts elastically at lower angle of incidence. (From Hewitt and Westermann, 1986)

portional to the Radius-of-curvature/shell thickness; the septum brakes at a critical ambient pressure that results in membrane stress in the septum of > 131 MPa, as calibrated on the Nautilus septum (which fails at about $8 \text{ Mpa} = 80 \text{ atm} = 780 \text{ m}$ saltwater column). A number of experiments in pressure chambers have been made by several authors to identify the different parameters of Nautilus nares, which closely resembles fossil cephalopod nares (Figs. 4-5). The radii and thicknesses of the 'simple-convex' (less than hemispherical) septa of many fossil

orthocones, external in the nautiloids and internal in the belemnites, have been measured: the extinct forms imploded at depth ranging from 50 to 800m. We assume that there depth limit was at roughly $3/4$ and there usual habitat at about $1/2$ implosion depth (Fig. 6). Analysis of variance of septal strength during growth and of small populations has recently resulted in more realistic estimates of habitat depth (Hewitt and Westermann, 1990).

Unique examples of septal implosion are known from orthocones in the Silurian of

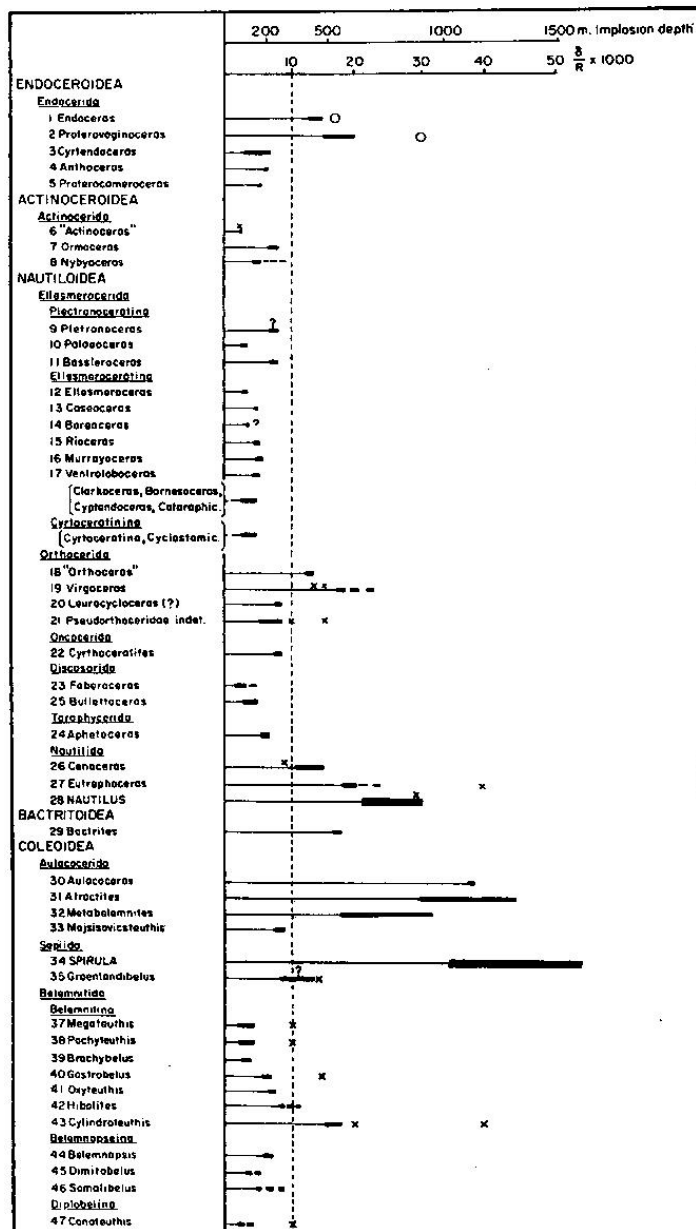


Fig. 6 — The relative strength of simple-concave septa ($1000 \Delta/R$) and the estimated water depth at which implosion would occur, based on experimental data for Nautilus and Spirula (From Westermann, 1973).

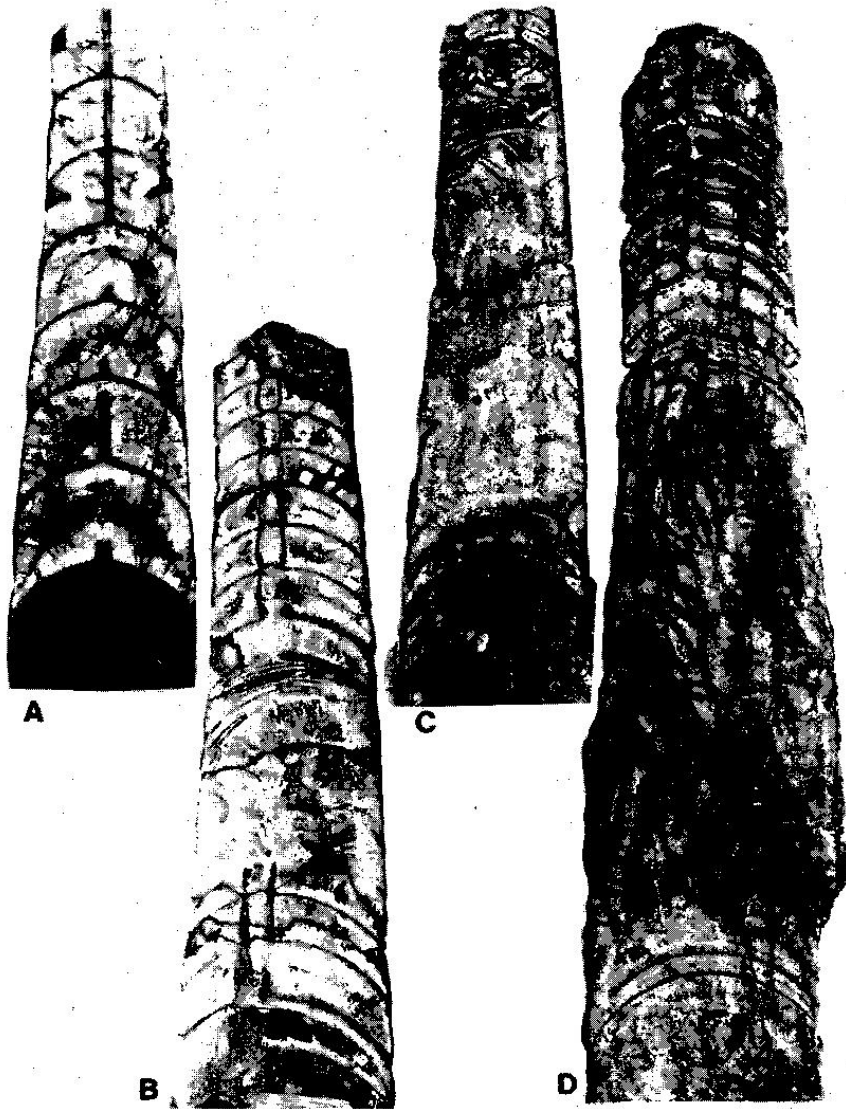


Fig. 7 — Polished section of orthocone nautiloids from the Silurian of Bohemia, without body chambers. A, *Kopaninoceras* has widely spaced, thick septa, that are all intact; B-C, *Geisonoceras* and D, *Michelinoceras*, have wider spaced, thinner septa that broke post-mortem by water pressure overload (see Fig. 8). (From Westermann, 1985).

Bohemia (Figs 7-8). Basin depth can be estimated by the data for minimum and maximum implosion pressures: it was deeper than the failure pressure calculated from the broken 'weak' septa (> 250-300m), and shallower than the potential implosion depth of the intact 'strong' septa (< 400-450 m).

More complex calculations of stresses and strains in simple shells require high-power computers. Finite Element Analysis has been used to estimate stresses in models of actual

orthocone nautiloids (Fig. 9); and in hypothetical models differing in single structures only. The differences in the calculated stresses indicates if the 'design' changes would have been advantages or not.

Shell Coiling and Septal Fluting

Planispiral coiling produces horizontal orientation of the body, without the internal 'counterweights' required in orthocones to

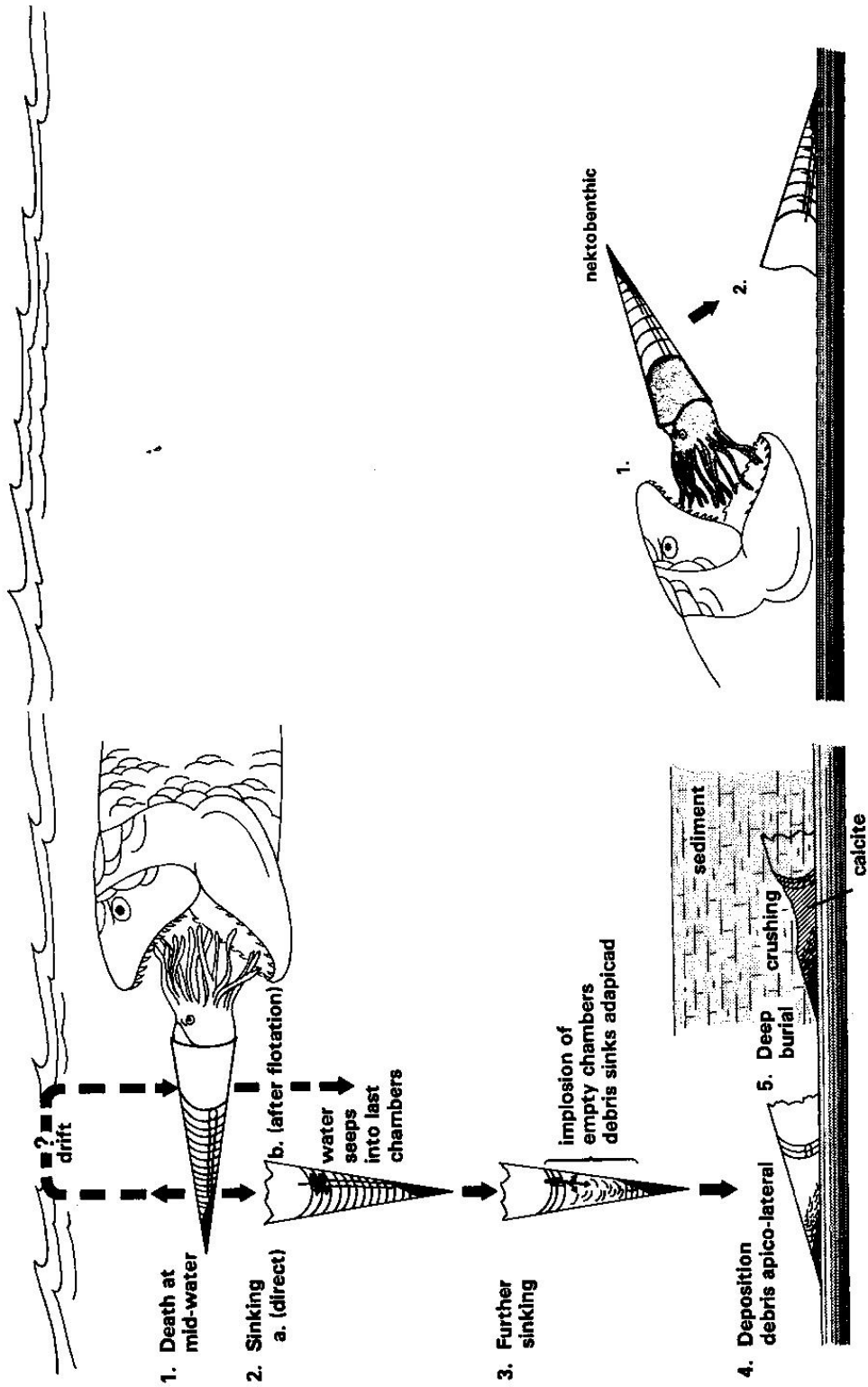


Fig. 8 — Post-mortem models for weak and strong longiconic nautiloids in neutral equilibrium, as illustrated in Figure 7. The longicone at left lived in mid-water (100-200 m) and had thin, weak septa; after death it sank and the last chambers (camerae) filled slowly with sea water through the still permeable mature connecting rings; the earlier ring (s) burst in an immature chamber, which then 'exploded' adapically; the shell debris collected geopetally within the void while the shell sank to the sea floor, apex first because of the cameral deposit (black). The specimen at right lived near the sea floor (400-450 m) and accordingly had thick, strong septa that remained intact after death since there was no marked postmortem sinking. (From Westermann, 1955)

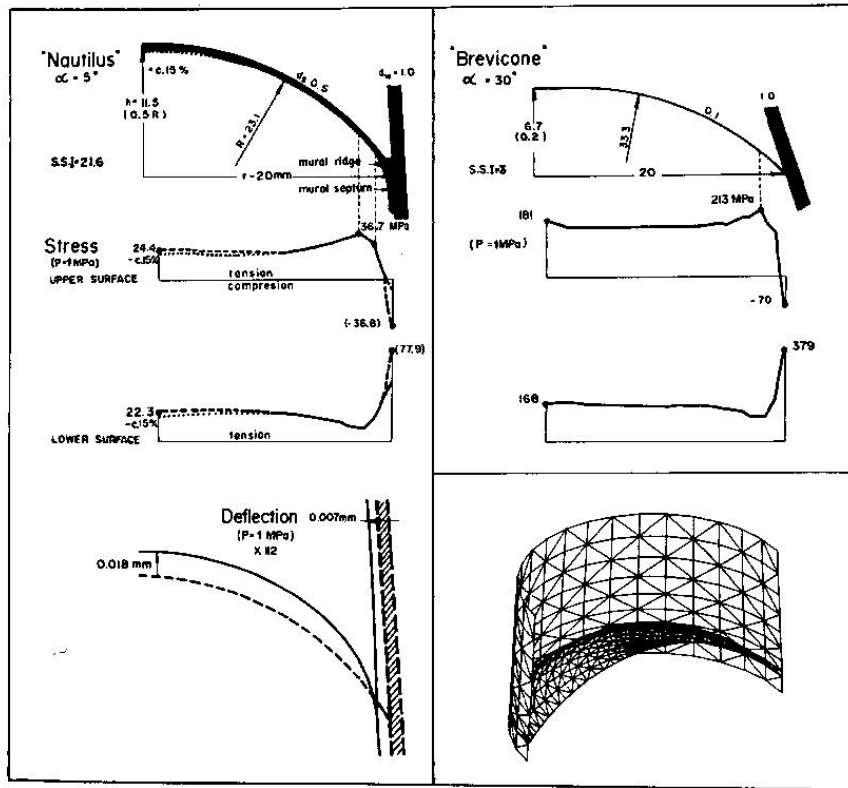


Fig. 9 — Finite element analysis of two hemispherical septa indicating tensile and compressive stress and radial deflection at 1 MPa hydrostatic pressure (100 m depth). Left: uncoiled juvenile Nautilus with no thickness variations within the septum; right: Paleozoic orthocone with weaker septa (alpha, apical angles). (From Hewitt and Westermann, 1987b)

produce neutral equilibrium, i.e. cameral and siphuncular deposits (Fig. 1). As coiling becomes tighter (more involute), the shell becomes more compact, improving “streamlining” and protection against predators. The large diversity of shapes and sizes in the ammonites is well known, greatly influencing orientation, stability, ‘streamlining’, and other features that are all more or less closely related to mode of live and habitat.

The first ammonites (in the Devonian) were ‘streamlined’, with compressed, involute, planispiral shells (Fig. 1). With the disappearance of the self-supporting, circular whorl section of the orthocones, however, the flattened flanks (increased radius of curvature) of the whorls required internal support against implosion. This was the second function of the septa (the first was body support), which formed transverse folds and flutes producing stiff supporting structures that fused with the shell wall in the suture with lobes

and saddles (Fig. 10). The complicated loading conditions — at first lateral (1. function) and later peripheral (2. function) — and the rounded outline of the whorl cross-section, resulted in the anticlastic (negative Gaussian) septal curvature forming flutes, with alternating convex and concave fold axes, instead of simple corrugation. A single cross-bracing fold axis is present also in Nautilus; the corresponding lateral lobe in the suture is placed at the largest curvature radius (flattest part) of the flanks. There is, therefore, a strong dependence of the flute ‘design’ from the whorl cross-section and whorl overlap (Fig. 11).

Simple, first-order or ‘goniatitic’ fluting has two principal modes or ‘strategies’, both reducing the area of shell supported by the suture, i.e. ‘zig-zag’, with a few, broad v-shaped telescoping lobes and saddles, and ‘meander’, with many, narrow u-shaped lobes and saddles (Fig. 12). Examples for the first mode are the Goniatitina, for the second the

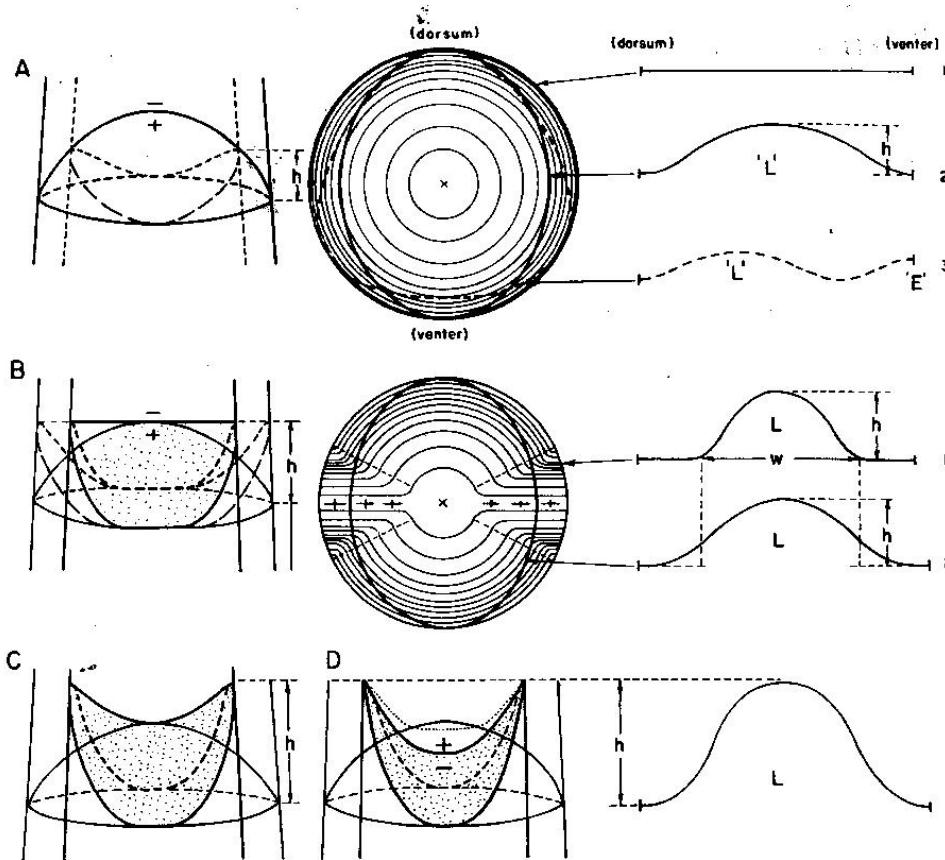


Fig. 10 — Origin of fluted, anticlastic septa. Schematic lateral and plain views of hemispherical septum and its derivatives, with part of the shell wall and corresponding sutures; the slight pressure differential between new cameral liquid and body during the membranous stage is indicated. A, hemispherical septum with shell walls of circular, elliptical and subtriangular cross-sections, resulting in straight and sinuous sutures; B, pillar flutes with straight crests in circular and compressed shells, resulting in more sinuous sutures; C-D, flutes with adorally convex crests in compressed shells, C under neutral pressure and D with inverse pressure differential, shape of a 'soap bubble' (dotted), and suture. (From Westermann, 1975)

Prolecanitina. Because the septal surface has to retain minimal curvature for its primary (1st) function, further lengthening for improved buttressing of the shell wall is by second-order ('ceratitic'- 'subammonitic') and third- to fourth-order ('ammonitic'), marginal fluting. The septum thins out rapidly toward its fluted margin, so that septum weight does not increase (Fig. 13). The fluted and 'frilled' septum makes possible the relative thinning of the shell wall, for improved buoyancy, without loss to overall strength against implosion. More importantly, it allows for planar and even concave wall surfaces whenever these are advantages for hydrodynamics (see below) or other functions (Fig. 14).

Bathymetric Indices

The bathymetric methods based on ammonite septa differ, of course, from those for nautiloids with simple-concave (near-hemispherical) septa. Here the Septal Flute Strength Index (SSI) and the Siphuncle Strength Index (SiSI) have been used for rough estimates of implosion depth. Both were based on simple equations for cylinder wall strength. The former is a function of the ratio of shell thickness near septum centre, divided by the minimum diameter of the whorl cross-section; the second of the thickness of the connecting ring of the siphuncle, divided by its inner radius (Figs. 15-16).

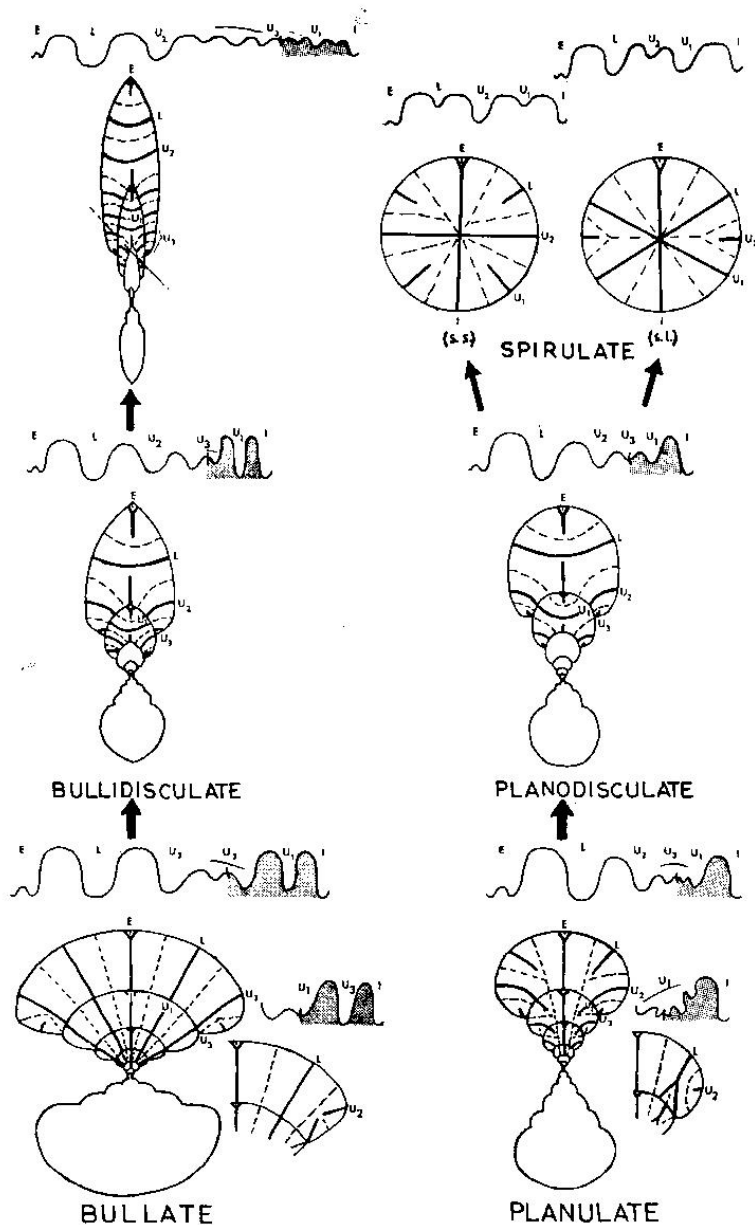


Fig. 11 — Whorl cross-sections of Jurassic ammonites with septa showing the lobe (solid) and saddle (dashed) flute axes, and the corresponding, simplified sutures (frilling omitted and internal parts shaded); major differences in fluting patterns (with terminology) partly depend on the shape of cross-sections and are in common to family-level taxa; note 'design' of flute axes according to mechanical principles, within and between whorls. (From Westermann, 1965)

Both were, again, roughly calibrated on *Nautilus*, the latter with an ontogenetic correction. There is a surprisingly close correlation between the two indices, taken from the same shells, supporting their usefulness as relative depth indicators (Fig. 17). More sophisticated measurements and calculations on different parts of the shell, especially the septal lobe flutes and their lobules (Fig. 18),

have recently been developed by Hewitt (1993 and in preparation). These simple indices have, nevertheless, resulted in valid estimates of relative ammonite implosion depth, while statistical work on the Septal Strength Index in *Nautilus* from different populations (Hewitt and Westermann 1990) has indicated the relationship between living depth and implosion depth. The general con-

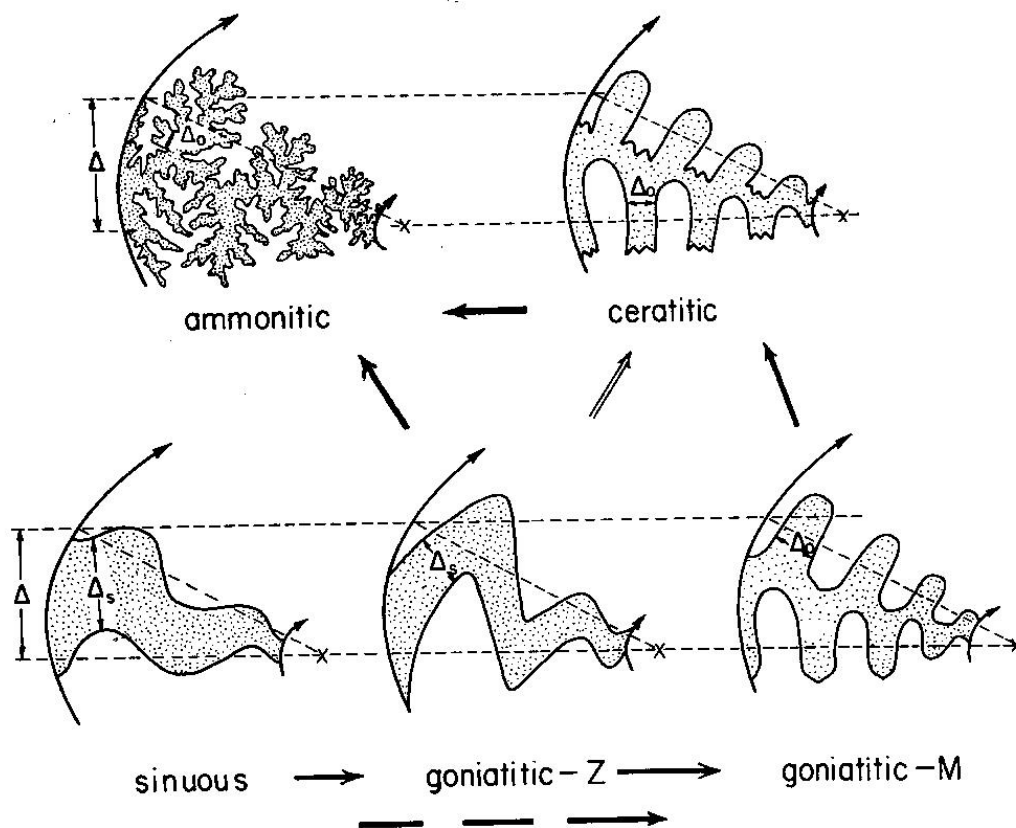


Fig. 12 — Model for the evolution of ammonoid sutures, according to their function to support the shell wall; all pairs in identical shells and with identical septal spacing. Sinuous : corresponding to simple pillar flutes with initial supporting function (see Fig. 10); goniatitic-Z, "zigzag" strategy and telescoping to reduce spacing between sutures; goniatitic-M, simple-meander strategy to reduce spacing between parts of same suture; ceratitic, similar to last but with serrated lobe basis (function unclear); ammonitic, complicated-meander strategy to reduce spacing between parts of same and between sutures, probably derived from last and goniatitic-Z. Note that reverse trends occurred during sutural simplification, i.e. origin of "neoceratites". (Modified from Westermann, 1975)

clusions are that the "geosynclinal", i.e. oceanic and "leiostraca", i.e. many phylloceratids, lytoceratids and desmoceratids, lived at depth of 200 - 500 m; most goniatites and ammonites at 80 - 200 m; most oxycones and ceratites at 30 - 80 m.

Qualitative indicators for habitat depths of Mesozoic ammonites, e.g. whorl shape, have to be considered in conjunction and with great care (Fig. 19):

1. Shallow

- Septal sutures uncomplicated and irregularly spaced
- Whorls strongly compressed, square or triangular and with flat to concave surfaces.
- Sculpture very prominent

2. Deep

- Complicated and narrow spaced septal suture (relative to size) (Fig. 12).
- Evolute whorls with rounded to circular section; involute shells globular.
- Sculpture reduced to superficial lirae and striae: internal varices (pseudoconstrictions) often present.

Hydrodynamics

The degree of hydrodynamic efficiency in the ammonites is a function of (1) whorl shape and sculpture, both controlling drag, as well as of (2) the jet-producing hyponome and its muscular tissues. Naturally, only (1) is well preserved in fossils and (2) can only

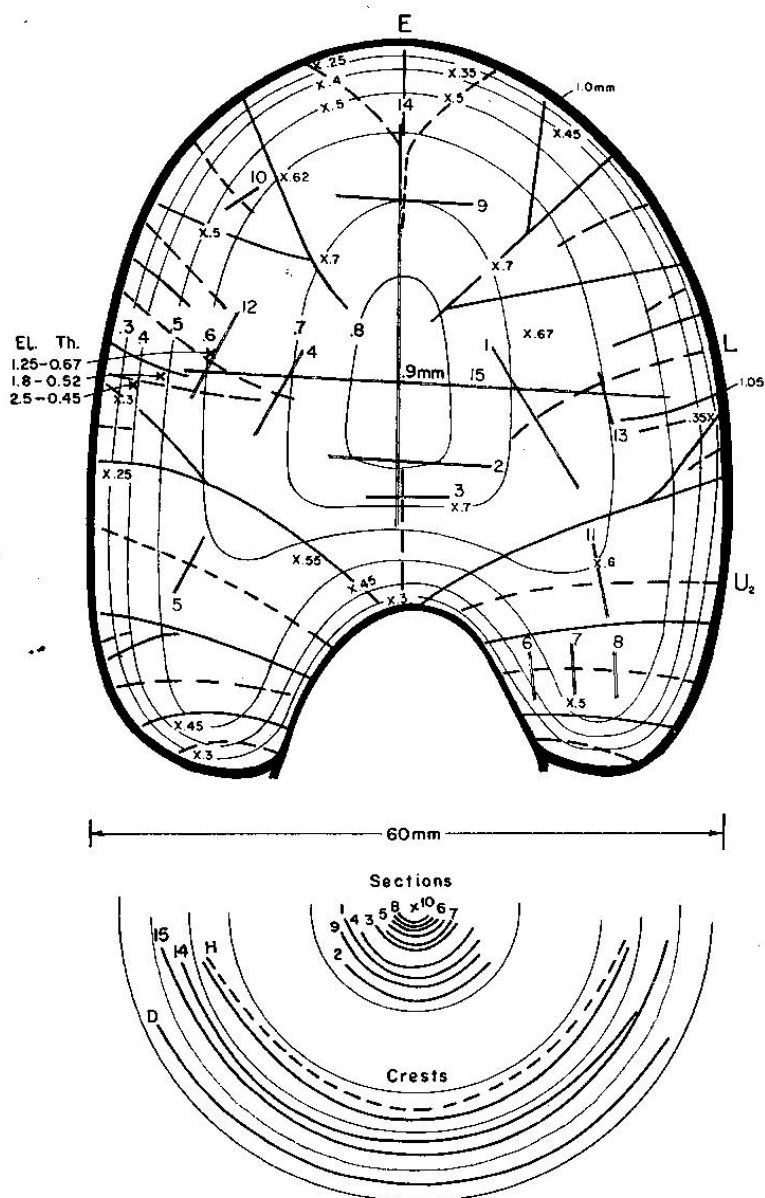


Fig. 13 — Ammonitic septum of a Pachydiscus; detail of the lobe (solid) and saddle (dashed) flute axes, shell thickness and the curvature of the axes resembling hemicircles. Note that septal thickness decreases rapidly toward the margin, so that fluting and frilling do not increase weight (or simple-concave septum). (From Westermann, 1975)

be guessed from body-chamber shape and muscle scars. Other essential features required for locomotion that can be deduced from fossil shells the relative position of centres of buoyancy and mass controlling stability and orientation of the shell; soft-body volume can be estimated only on the assumption that the body could be withdrawn in the body-chamber (supported by aptychi/mandibles and radulae found within body-chamber). The water flow around the shell

can be visualized with the use of dye in a flume using models or real shells (Figs. 20-21).

Nektonic vs. Planktonic Ammonite Habitats

The highly diversity in ammonite size, shape and surface (smooth or sculpture) is closely interrelated with the principal functions of stability, drag ('streamlining'), and protection against implosion and/or preda-

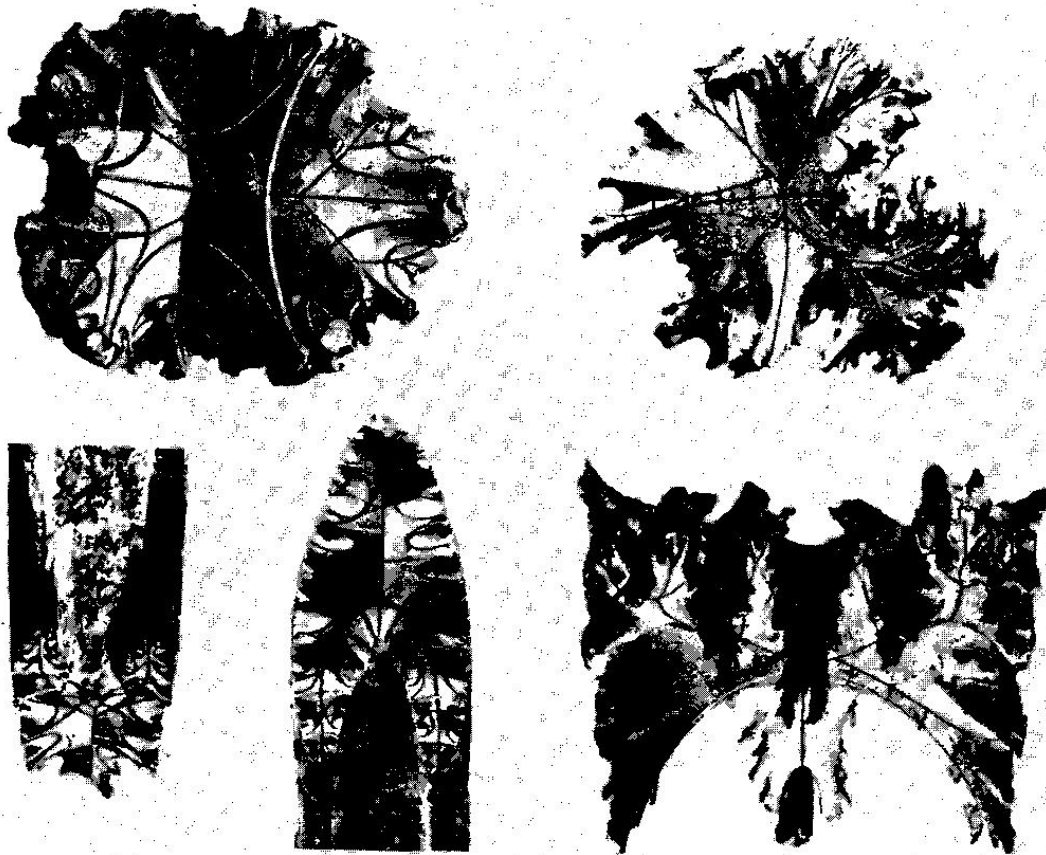


Fig. 14 — Septal surfaces of Jurassic and Cretaceous ammonites (*Leymeriella*, *Crioceras*, *Dorsetensia*) with saddle flute axes, reproduced from original paper by Pfaff, 1911. (From Hewitt and Westermann, 1986)

tors; probably also sexual selection, camouflage, etc. In the different modes of life and habitats, anyone or a combination of these basic functions dominates.

1. Relatively good swimmers - nekton or --
? nekto-benthos
 - a) Planispiral whorls compressed, involute (low pressure drag or 'wake')
 - b) Venter keeled or fastigate (improved maneuverability)
 - c) Body-chamber 'short', ca. 1/2 whorl (high stability, aperture in lateral orientation)
 - d) Sculpture fine or shell smooth (low friction drag)
 - e) Large (increased velocity)
2. Sluggish swimmers — nekto-benthos or nekton

- a) Planispiral whorls not compressed
- b) Venter rounded (lower maneuverability, but greater strength against implosion; i.e. subcircular or ovate whorl section)
- c) Body-chamber usually 3/4 whorls (? improved protection)
- d) Sculpture with prominent ribs and/or nodes (protection against predators); may be reduced at large adult size.
3. Vertical migrators — plankton (? potential plankto-benthos)
 - a) Planispiral, round whorls with strong adult uncoiling; or orthocone or gyrocone (stable vertical position, with aperture down or up; high drag)
 - c) Body-chamber moderately 'long', in adult uncoiled, often hooked (increased stability)

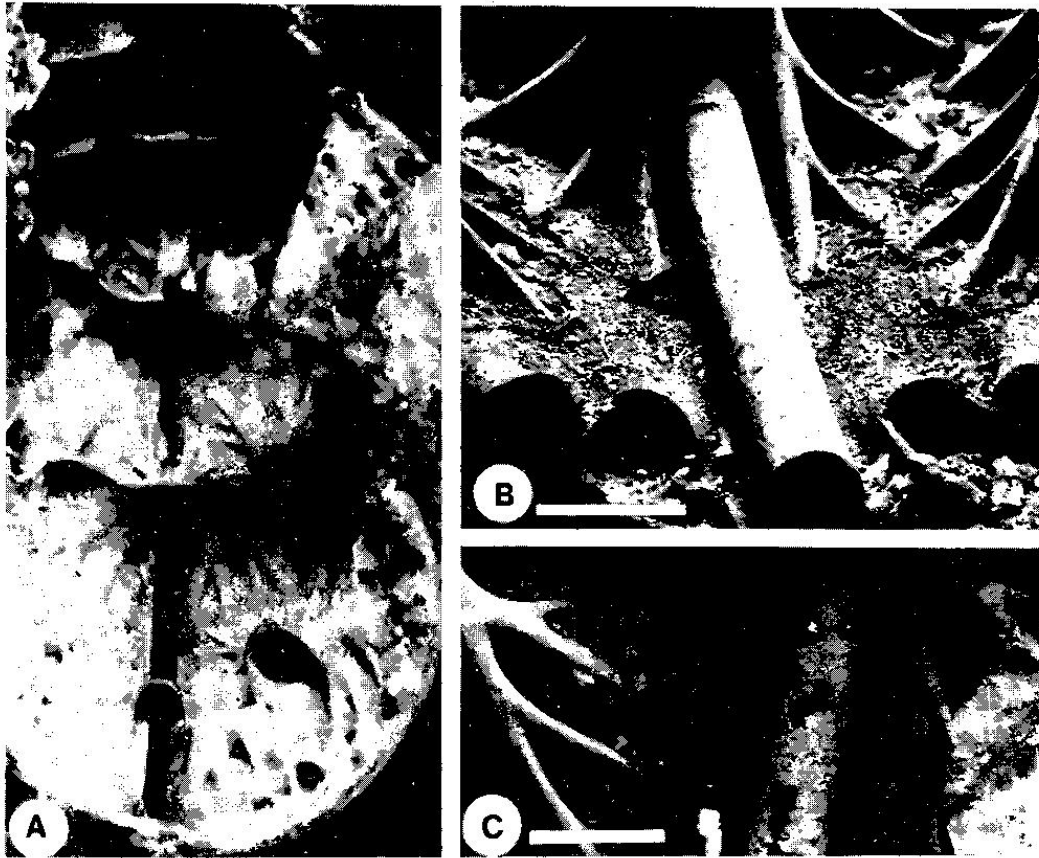


Fig. 15 — Siphuncle and folioles and lobules of ventral septa in an empty shell of *Haploceras strigile*, Tithonian of Sula Islands, Indonesia. A, light photograph of chambers with conchiolinous connecting rings; B-C, SEM micrographs of undamaged ultimate (B) and perforated penultimate (C) connecting rings; all bars = 1 mm. (From Westermann, 1982)

d) Sculpture prominent (shallow water forms) or reduced (pressure resistant deep water forms)

4. Planktonic drifters —plankton

a) Serpenticone with body-chamber of at least 1 whorl (very low stability, ? voluntary rotation) or typical heteromorph of juvenile and adult (extremely high drag)

d) Sculpture present, may include long thin spines, or smooth.

Reconstruction of Ammonite Organism and Habitat

Organism

One the best reconstruction of an epipelagic rapid swimmer has recently been

made by Doguzaeva and Mutvei (1991), based on the new finds of surprisingly large muscle scars in some oxyconic Ammonitina. This strongly supports the hypothesis that these compressed ammonites with acute venter were better, more manuevrable swimmers than *Nautilus*.

Habitat

Only one 'panorama' of possible ammonite habitats is represented here (Fig. 22). The possible life cycles are shown in Figure 23.

Ammonite habitat interpretation, however, is developing rapidly, shifting from the conviction that most epicontinental ("shelf") ammonites were benthopelagic, to suggesting

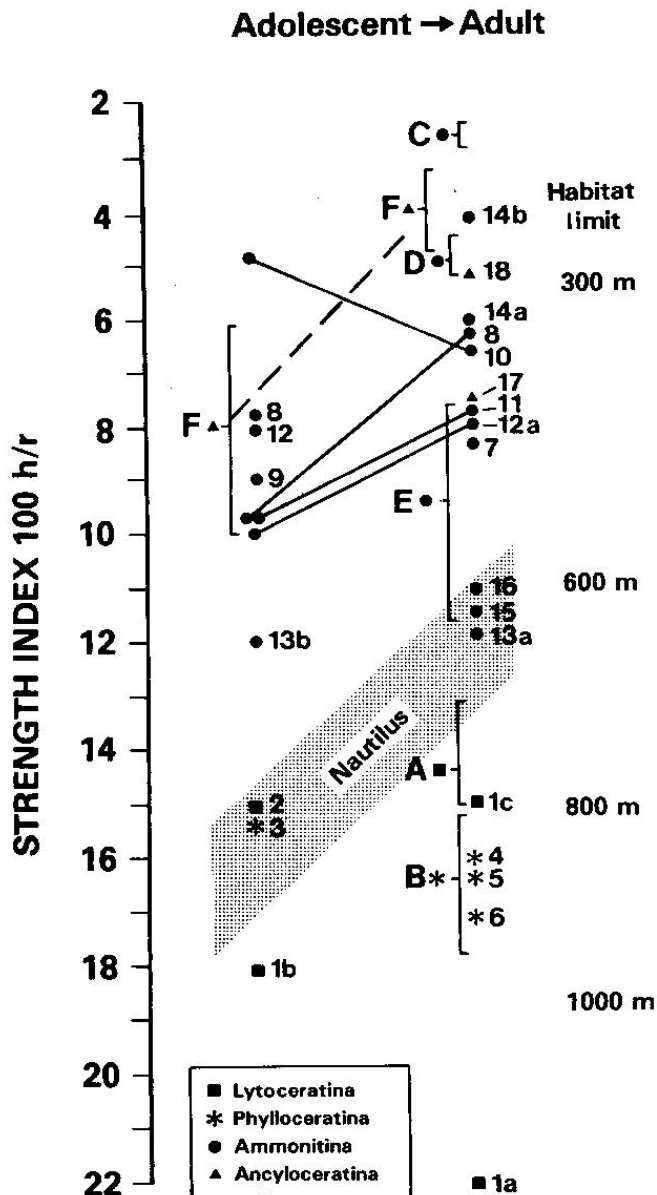


Fig. 16 — Plot for adolescent to adult siphuncular strength indices (SiSI = 100 wall thickness/inner radius) for Nautilus and ammonoids. Assuming that habitat depth was limited to roughly 2/3 of the depth limit set by connecting ring fracture, the data indicate that Ammonitina and Ancyloceratina lived maximally about half as deep as Nautilus (80-400 m), except for the Desmocerotaceae *Metapuzosia* and *Canadoceras*; and that Phylloceratina and Lytoceratina could live as deep or deeper (600-1000 m). Note that average habitat depth was about half of maximal depth. (From Westermann, 1982)

that most were pelagic, with much less dependence on the seafloor. This includes spawning into midwater or possible 'brooding' in the bodychambers of 'oversized' pelagic females (macroconchs), hatchlings and very young individuals (neaniconchs, Westermann

in press) in the deeper, zooplankton, and even the larger nektonic or planktonic immatures of the majority of species; whereas probably only a minority of ammonite species become benthopelagic when adult (unpublished).

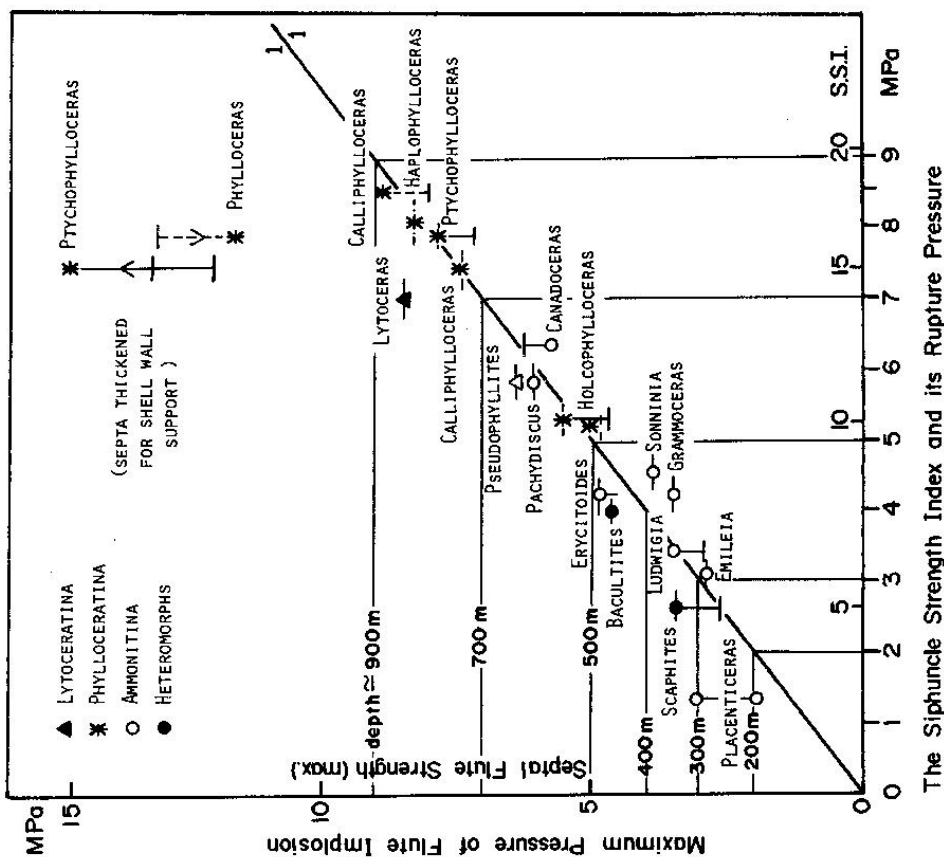
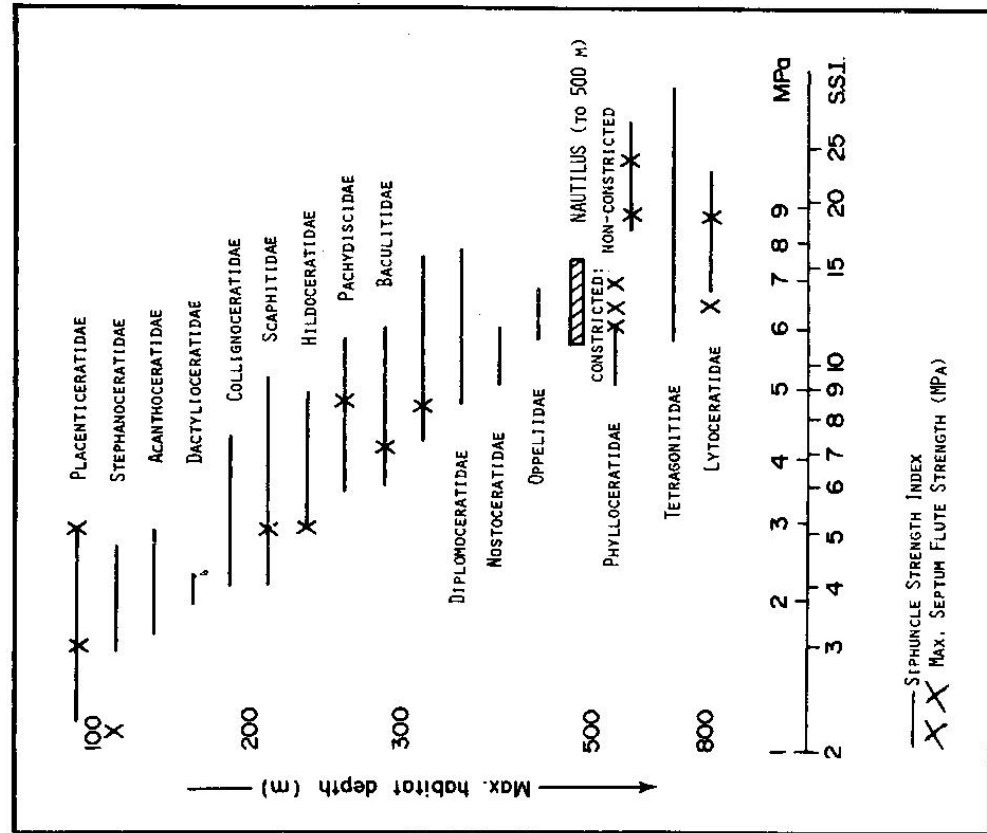


Fig. 17 — Left, correlation of the Siphuncular Strength Index with the Septum Flute Strength Index (a function of maximal septum thickness and 1/2 minimum whorl diameter that approximates the radius of curvature of the saddle axis); the anomalous group at upper-right are mesopelagic Phylloceratina that compressed 'streamlined' shells with flat sides. Right, ranges for the same indices compiled by family, from different sources. Note that the simple Septum Flute Strength Index is currently being replaced with much more detailed and sophisticated methods for estimating septal strength (e.g. Hewitt and Westermann, 1990. and Hewitt, in press and unpublished) and that the calculated strength of septa and siphuncle as well as the estimated habitat depth have now been lowered by as much as 30-40%. (From Westermann, 1990)

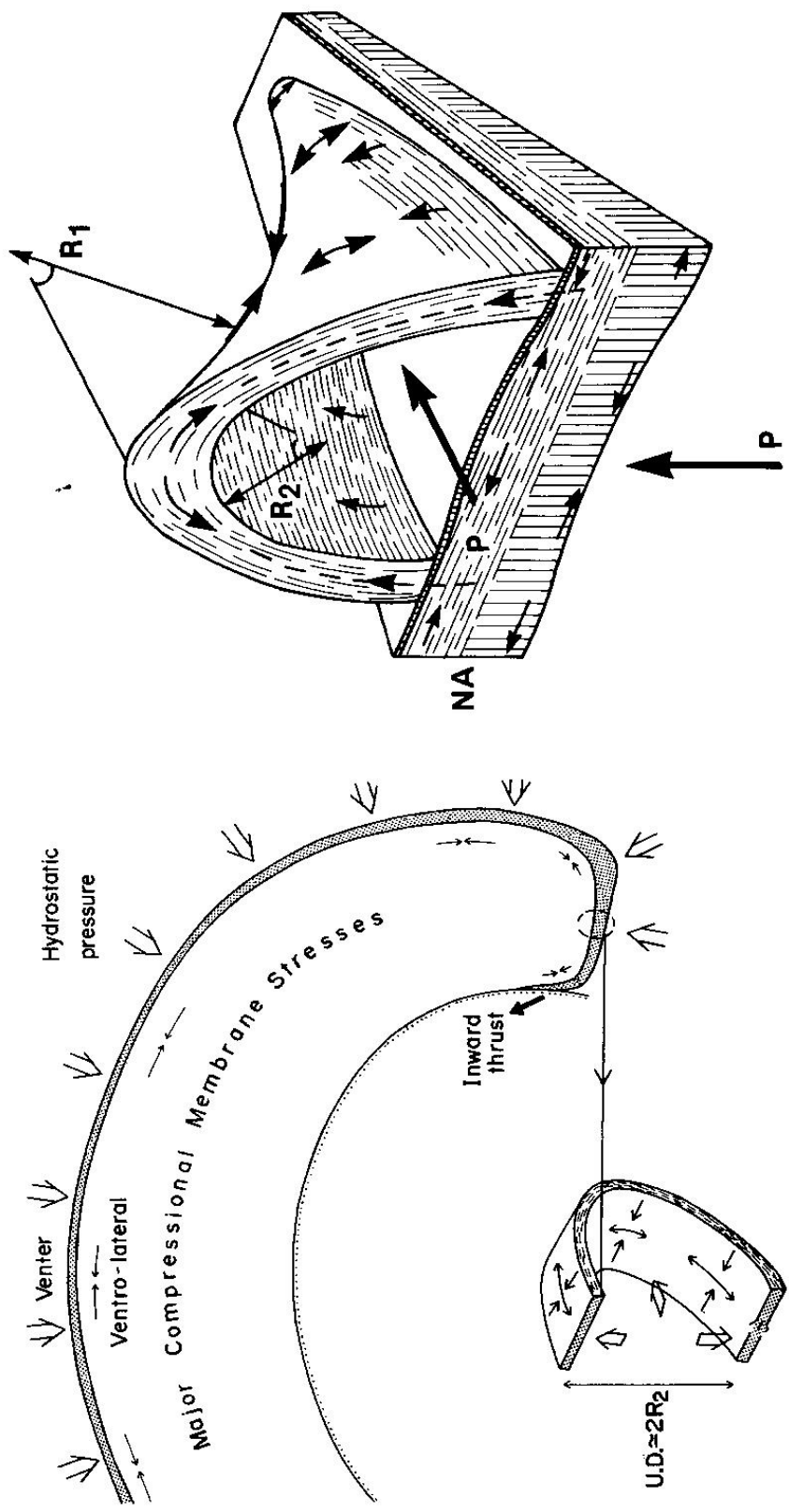


Fig. 18 — Diagrams illustrating, left, the forces and stresses in the phragmocone wall of an ammonite with depressed whorl section; and, right, within a lobule (smallest flute in a septal flute) of a last septum, due to ambient water pressure (P) on the shell wall and through the soft body. P (1 MPa = 100 m water depth) is a function of shell thickness, R_1 and R_2 (the axial and variable transverse radii of curvature) of the lobule, and the constants for nacre strength. (From Hewitt and Westermann, 1986, 1987a)

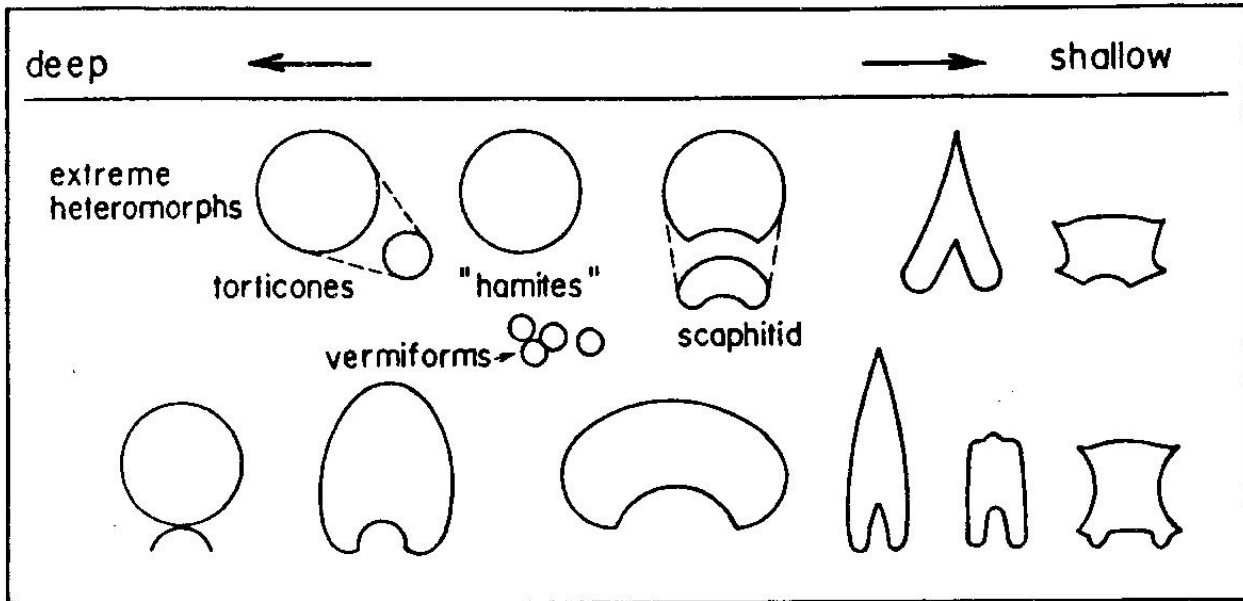


Fig. 19 — Strongly generalize depth distribution of ammonoid whorl sections; but cross-section is not in itself a usefull indicator of habitat, except for some extreme forms with concave surfaces that are restricted to shallow water. (Modified from Ward and Westermann, 1985)

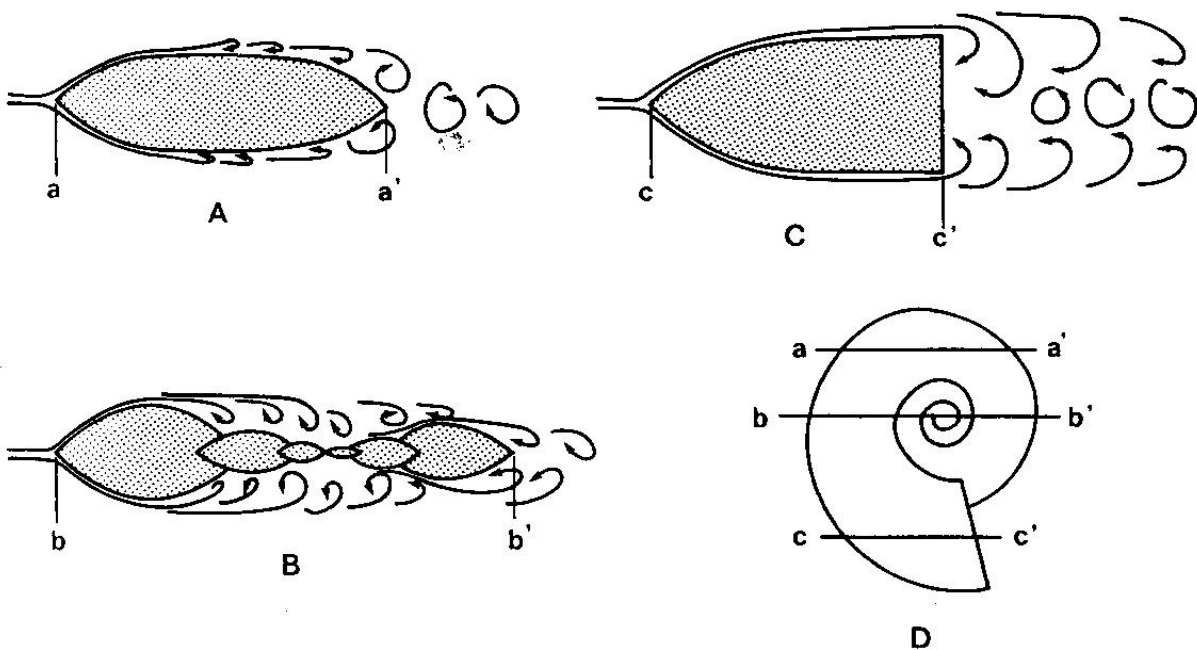


Fig. 20 — Hydrodynamics of a 'streamlined', evolute-platyconic ammonite shell. Cross-sections (shown in D) through the flow field showing water movement near the shell surface; A, at top of shell; B, through umbilicus; and C, bottom of shell with aperture. Note that the strong wake in C, causing most of the drag, is actually considerably reduced by the conically shaped soft-body. (From Chamberlain, 1976)

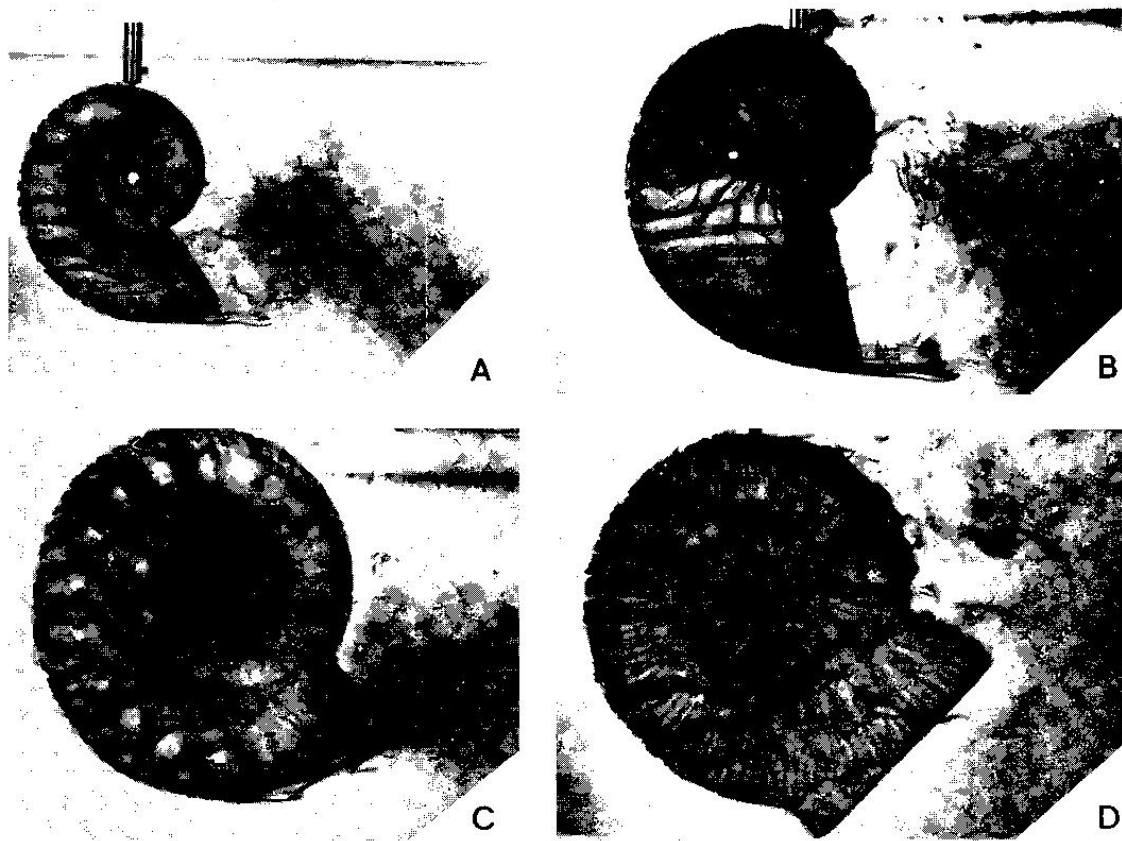


Fig. 21 — Flume experiment showing flow patterns of smooth and sculpted shells, with separation of dye streams (produced by potassium permanganate crystals attached to shell edge) along flank of outer whorl; turbulence shown by swirls of dye in umbilicus and behind shell. A, smooth evolute model shell; B, smooth involute shell of *Nautilus*; C, coarsely costate and nodose ('coronate'), depressed evolute shell of the stephanoceratid *Zemistephanus*; and D, densely costate, roundwhorled evolute shell of *Stephanoceras*. The 'coronate' shell C produces by far the highest drag. (From Chamberlain and Westermann, 1976)

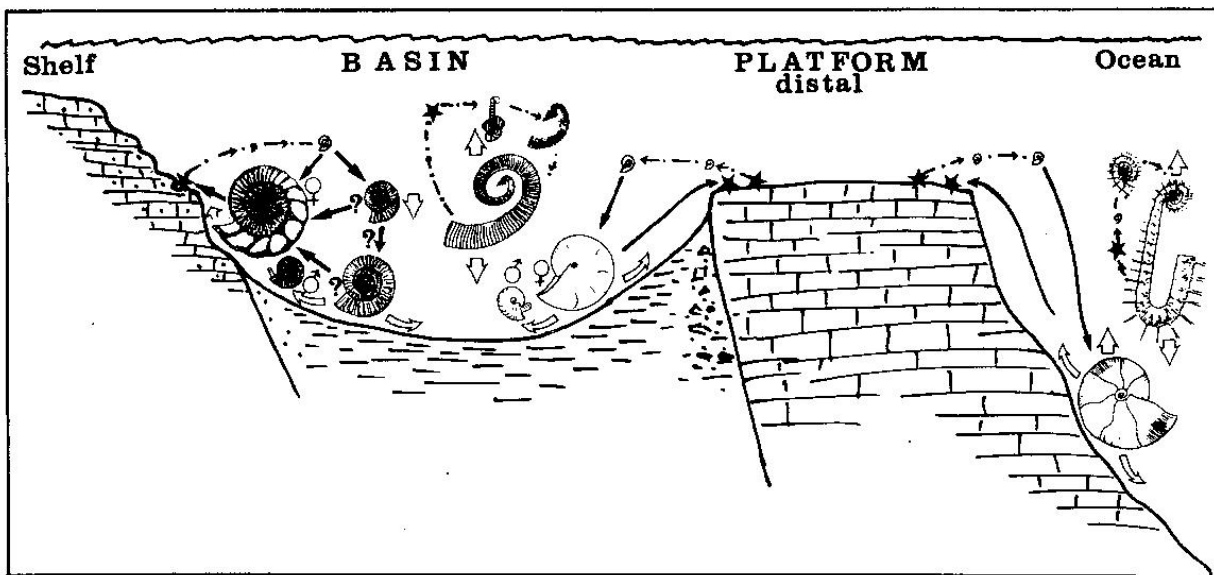


Fig. 23 — Possible life histories of ammonoids, explaining the association in the same fossil assemblages in, e.g., ammonitico-rosso facies, of a mixture of epicontinental *Ammonitina* together with oceanic deep-water 'leiostraca' (represented only by a *Phylloceras*) and heteromorph *Ancyloceratina*. The distal carbonate platforms may have been the common breeding ground for basinal and mesobathyal species; pelagic species, especially the planktonic heteromorphs, presumably had complete life cycles at different midwater levels (including above the distal platforms) and their shells sank post-mortem. (From Westermann, 1990). Note that I presently assume that pelagic habits were more widespread among the ammonoids, from spawning to adult (captions to Fig. 22).

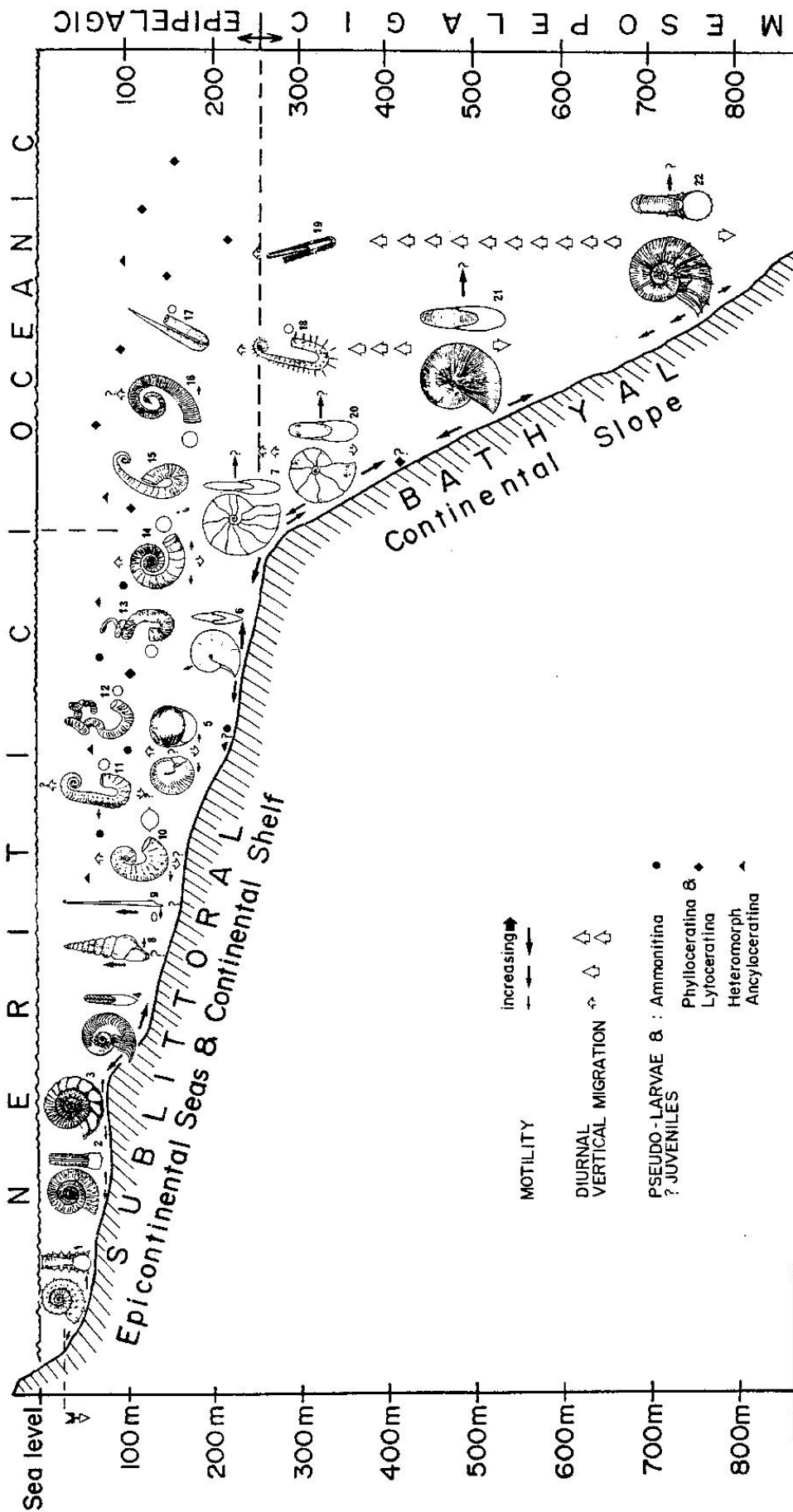


Fig. 22 — Stylized panorama of Jurassic-Cretaceous ammonoid habitats. All hatchlings, the juveniles of most, and the adults of the majority of taxa were probably pelagic, rather than benthic-pelagic as here and generally assumed (in press). Note that only a small selection of habitats and taxa is illustrated and that near-shore habitats excluded ammonoids; hollow vertical arrows imply that migration was vertical or along a gradient. Ammonitina: 1, Peltoceras; 2, Arietites; 3, Perisphinctes; 4, Harpoceras; 5, Sphaeroceras; 6, Oxycerites; 7, Barremites. Ancyloceratina: 8, Turritites; 9, Baculites; 10, Scaphites; 11, Ancyloceras; 12, Nipponites; 13, Didymoceras; 14, Criooceratites; 15, Labeceras; 16, Glyptoxoceras; 17, Hamulina; 18, Anisoceras; 19, Pseudoxybeloceras. Phylloceratina: 20, Holcophylloceras; 21, Phylloceras. Lytoceratina: 22, Lytoceras. (From Westermann, 1990)

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