Biomechanics as a Test of Functional Plausibility:
Testing the Adaptive Value of Terminal-Countdown Heteromorphy in Cretaceous Ammonoids

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14 Text-Figures and 2 Tables

Biomechanics
Adaptation
Functional Morphology
Life Mode

Contents

Biomechanik als Test der Glaubwürdigkeit der Funktion der „Terminal-Countdown"-Heteromorphie bei Kreideammoniten: Überprüfung der Anpassungswerte

Zusammenfassung

Trotz eines Jahrhunderts Publikationstätigkeit zum Thema bleiben die Hypothesen über die Funktion der U-förmigen Wohnkammer vieler Kreideammoniten ungeprüft. Neue Arbeiten über den morphogenetischen „Countdown" und seine Bedeutung für die Lebensgeschichte (z.B. SEILACHER & GUNJI, 1993) bilden die Grundlage, die Countdown-Morphologie als eine adaptive Strategie zu betrachten. Es wird gezeigt, dass Erscheinungen der U-förmigen Wohnkammern auf die Kreidezeit beschränkt sind. Die zeitlich beschränkte Konvergenz zu einer radikalen neuen Morphologie weist auf eine allgemeine autökologische (d.h. Funktions-)Änderung der Lebensweise hin. Funktionsmorphologische Untersuchungen sollten die Überprüfung dieser adaptiven Hypothese ermöglichen. Mehrere Annahmen betreffend der Berechnungen der Schwebefähigkeit und Orientierung werden diskutiert.

Die vor kurzem vorgeschlagene Hypothese der hydrostatischen Destabilisierung (KAKABADZÉ & SHARIKADZÉ, 1993; MONKS & YOUNG, 1998) wird überprüft. Diese Autoren haben angenommen, dass das Tier nach Belieben zwischen den mehreren stabilen Orientierungen schalten könnte, die von der „Terminal-Countdown"-(T-C-)Morphologie angeboten werden. Vorgeschlagene Mechanismen sind
1) die gesteuerte Verteilung von Kammerflüssigkeit und Gas; und
2) die Schwerpunktverlagerung eines kleinen, relativ dichten Körpers innerhalb der Wohnkammer.

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Jeder Mechanismus hat eine benthische Ernährungsweise für eine der Orientierungen zur Folge. Es werden daher verschiedene T-C-Morphologien (hamiticon, scaphiticon, ancylocon, praviticon, heterocon) auf die Möglichkeit überprüft, ob das lebende Tier sich von Benthos ernährt haben könnte. Die morphodynamischen Effekte jedes Mechanismus werden soweit wie möglich (innerhalb der Begrenzung der Nullschwebefähigkeit) erweitert, um dem Ammonitentier den besten Benthoszugriff zu erlauben. Benthoszugriff wird über dem maximalen Winkel der Mündungsneigung (und auch dem minimalen Abstand von der Mündung zum Substrat) gemessen.

Bei den meisten Morphologien erlaubt keiner der vorgeschlagenen Mechanismen einen leistungsfähigen Benthoszugriff (Winkel der Mündungsneigung ≥40°). Folglich kann die konvergente Evolution der T-C-Morphologie nicht durch eine Umstellung auf benthische Lebensweise unter Kreideammoniten erklärt werden. Alternative Anpassungshypothesen müssen gesucht werden. Potentielle Datenquellen sind unter anderem in Epökie, Biogeochemie, Biostratinomie, und in der Ontogenie des Phragmokons zu suchen.

Abstract

Functional hypotheses for the U-shaped body chamber found in many Cretaceous ammonoids remain untested, despite over a century of publications on the subject. Recent work on morphogenetic "countdowns" and their implications for life history strategy (e.g., SEILACHER & GUNJI, 1993) provides the groundwork for consideration of countdown morphologies as adaptive. The "terminal-countdown" U-morphology is shown to be evolutionarily convergent, yet temporally constrained essentially to the Cretaceous period. Temporally constrained convergence to a radical new morphology indicates a functional (ecological) shift in ammonoid habits. Thus, functional morphology should provide adequate tests of this adaptive hypothesis. Assumptions implicit in buoyancy and attitude calculations are discussed.

The hypothesis of hydrostatic destabilization is tested here. Previous authors have supposed that the terminal-countdown ("T-C") morphology allowed the ammonoid multiple stable orientations, between which it could alternate at will. Proposed mechanisms include
1) controlled localization of cameral fluid and gas
2) mobility of a small, dense soft body within the body chamber.
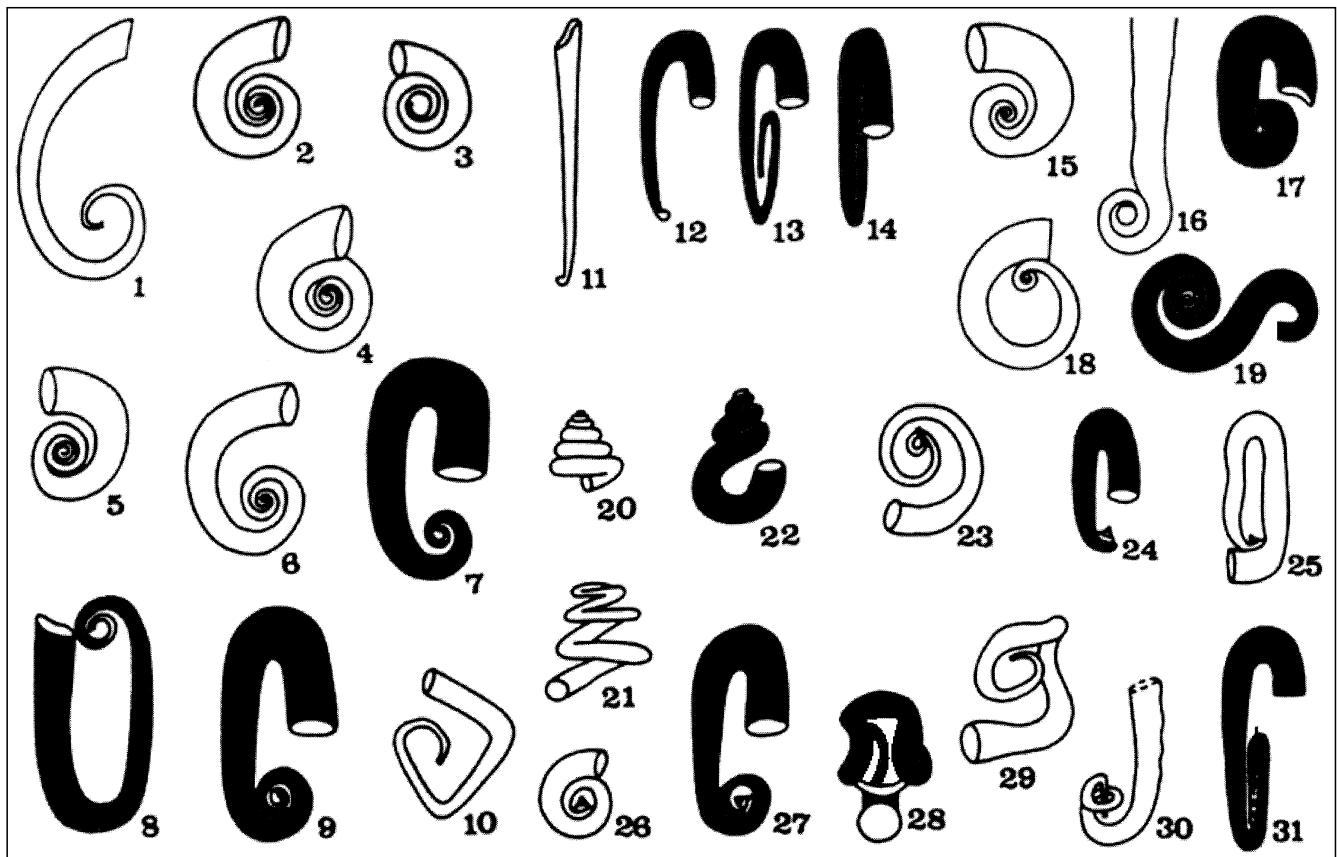
These mechanisms imply a benthic feeding function for one of the orientations. Therefore, various T-C morphologies (hamiticone, scaphiticone, ancylocone, praviticone, heterocone) are tested here for their ability to provide the ammonoid access to the benthos. Morphodynamic effects of each mechanism are extended as far as possible (within the constraint of neutral buoyancy), so as to allow the ammonoid to best access the benthos. Benthos access is measured by maximum angle of declination of aperture.

Neither of the proposed mechanisms provides efficient benthos access (angle of apertural declination measuring ≥40°) in most morphologies. Therefore, the convergent evolution of the T-C morphology cannot be explained by a shift to benthic habits among Cretaceous ammonoids. Alternate functional hypotheses must be sought. Potential sources of data include epibiosis, biogeochemistry, biostratinomy, and phragmocone ontogeny.

1. Introduction

Heteromorphy, as etymology implies, refers simply to sudden ontogenetic change in an organism's form. The term is derived from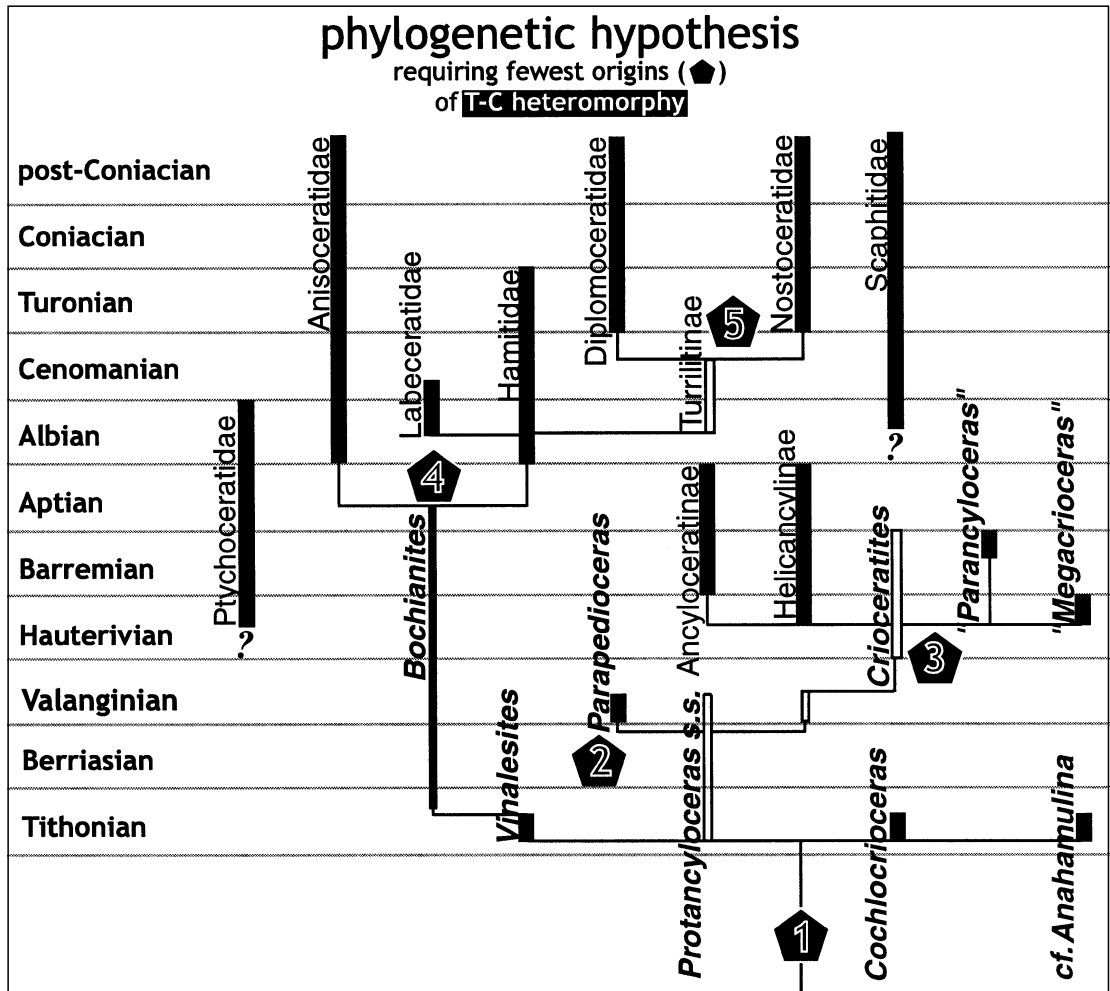 work on accretionary skeletons, in which changes in underlying mode of growth are reflected in radical morphologic changes. The typology of heteromorphy has been laid out by SEILACHER & GUNJI (1993) in

Text-Fig. 1.
Morphological classification of heteromorph ammonoids, modified from KAKABADZÉ (1988).
Note frequency of T-C forms (black) and non-T-C forms (white).

Macroscaphites Ancyloceras Didymoceras Anaklinoceras   Hamulina

Text-Fig. 2.
Examples of T-C heteromorphy in Cretaceous ammonoids, modified from SEILACHER & GUNJI (1993).
Note proximity of mature aperture to phragmocone in some forms.

a lucid and thought-provoking discussion. For ammonoids, "terminal countdown" heteromorphy occurs with the greatest frequency, particularly in the Cretaceous flourish of heteromorph ammonoid evolution (Text-Fig. 1; KAKABADZÉ, 1988). In this type of heteromorphy, the onset of the new mode of growth signals the imminent end of skeletal accretion (SEILACHER & GUNJI, 1993). Most often represented in ammonoids by a U-shaped body chamber

Text-Fig. 3.
Phylogenetic hypothesis of ammonoid evolution through Phanerozoic time, modified from HOUSE (1985).
Note the absence of T-C forms (white) before the Cretaceous.

Text-Fig. 4.
Phylogenetic hypothe-
sis of Cretaceous am-
monoid evolution re-
quiring the fewest ori-
gins of T-C heteromor-
phy, following WIED-
MANN (1973), WRIGHT
(1980, 1996), and KA-
KABADZÉ (1994).
Assuming the points of
phylogenetic consen-
sus among specialists
to accurately represent
ammonoid evolution,
at least five indepen-
dent origins (penta-
gons) are required for
T-C heteromorphy. Gi-
ven the uncertain posi-
tion of Macroscaphites,
the Scaphitidae, and
the Ptychoceratidae,
additional origins may
be necessary in order
to accurately reflect
ammonoid evolutiona-
ry patterns.

(Text-Fig. 2; KLINGER, 1981), this strategy combines deter-minate growth with the development of novel form. This distinctive combination has led evolutionary theorists and paleontologists to conclude that the novel form represents special adaptation to the animal's post-growth life mode. It may be that such adaptation is incompatible with con-tinued growth, as in spider conchs. If so, then the growing organism's ontogeny may be conceptualized as a lead-up to a more highly adaptive, "optimized" adult life mode. The terminal countdown ("T-C"), like any determinate-growth strategy, can be viewed as a trade-off between continued growth and specialized adult form. In theory, then, the adult life mode should be highly specialized in order to make the trade-off "worthwhile" evolutionarily (SEILACHER & GUNJI, 1993).

From a stratigraphic perspective, all appearances of T-C heteromorphy are confined essentially to the Cretaceous Period. These appearances follow 250Ma of ammonoid evolution without a single appearance of T-C hetero-morphy (Text-Fig. 3). If our understanding of Mesozoic ammonoid phylogeny is at all accurate, then we can be sure of at least five independent origins of T-C hetero-morphy from non-T-C forms (Text-Fig. 4). Such rampant convergence to a radical new morphology, constrained within the bounds of the Cretaceous, prompts an adaptive explanation for T-C heteromorphy in ammonoids. The next question is rather obvious (although its answer is certainly not): What is the adult life mode to which this morphology is apparently so well adapted?

Before an exploration of this question can begin, however, we must consider LEWY's (1996) suggestion of a fully necroplanktonic existence for adult T-C morphol-ogies. On the basis of a loose analogy with the egg case of Argonauta, he proposed that the ammonite died upon com-pletion of the U-shaped body chamber, and that the morphology served only as a floating egg case. Because such an assertion has the potential to void all discussion of adult heteromorph life mode, it must be considered seriously. However, positive taphonomic evidence for nec-roplanktonic exposure – in the form of epibiosis, punc-ture, or wave damage (MAEDA & SEILACHER, 1996) – is con-sistently lacking. In fact, only one case of possible epibio-sis is reported for any T-C heteromorph (AGER, 1963). Moreover, adult T-C morphologies tend to exhibit strong facies-control, appearing only in offshore shaley and limy facies (e.g., MATSUMOTO, 1977; BATT, 1989), whereas post mortem flotation would be expected to wash many re-mains into nearshore facies (e.g., CHIRAT, 2000). Finally, the year-round persistence of adults in heteromorph populations is evidenced by their appearance in the pre-ponderance of heteromorph assemblages (WESTERMANN, 1996). Adult heteromorph morphologies must then re-present living, feeding individuals; they thus require an as-sessment of life mode.

Several hypotheses of life mode have been advanced over the past century. HYATT (1889) was the first to write on the life mode of T-C heteromorphs, concluding either a bur-rowing or planktonic mode of life. The former position has since been taken only by FRECH (1915), while the latter has enjoyed a number of proponents (SCHMIDT, 1925, in WARD & WESTERMANN, 1977; BERRY, 1928; DONOVAN, 1964; PACKARD, 1972; TANABE, 1975; WARD & WESTER-

MANN, 1977; WARD, 1979, 1986; KLINGER, 1981; SAUNDERS & SHAPIRO, 1986; BATT, 1989; WESTERMANN, 1996). Still more popular has been BERRY'S (1928) nektobenthic hypothesis (SCOTT, 1940; MORTON, 1958; KAUFFMAN, 1967; WAAGE, 1968; WIEDMANN, 1969; HOLLINS, 1971; TANABE, 1975, 1977, 1979; KENNEDY & COBBAN, 1976; MATSUMOTO, 1977; TANABE et al., 1978, 1981; CHAMBERLAIN, 1981; KLINGER, 1981; LEHMANN, 1981; MATSUMOTO et al., 1981; WRIGHT, 1987; OKAMOTO, 1988b; OKAMOTO & SHIBATA, 1997; MONKS & YOUNG, 1998). A few authors have proposed a crawling or sessile benthic existence (DIENER, 1912; SCOTT, 1940; EBEL, 1992) or a full-out swimming mode (KAKABADZÉ & SHARIKADZÉ, 1993). KLINGER (1981) and OKAMOTO (1996) finally resigned in favor of a diverse set of life modes for the various T-C species.

Save HYATT's burrowing hypothesis, none of the above points to a specific function adaptively fulfilled by the adult morphology yet incompatible with continued growth (SEILACHER & GUNJI, 1993; OKAMOTO & SHIBATA, 1997). As ARKELL (1957), KLINGER (1981), and OKAMOTO (1996) have pointed out, the hook-shaped body chamber seems almost counteradapted to a nektobenthic life mode. At least there seems to be general agreement that some change of life mode took place at the time of morphologic change (CASEY, 1960; WESTERMANN, 1971, 1996; TANABE, 1975; KAKABADZÉ & SHARIKADZÉ, 1993; OKAMOTO, 1996; but see MILLER & CULLISON [1946] and SEILACHER & GUNJI [1993] for a counterexample in *Nautilus*). One proposed function of a U-shaped body chamber incompatible with continued growth is as a hydrostatic stabilizer (TRUEMAN, 1941; WARD, 1979; KLINGER, 1981).
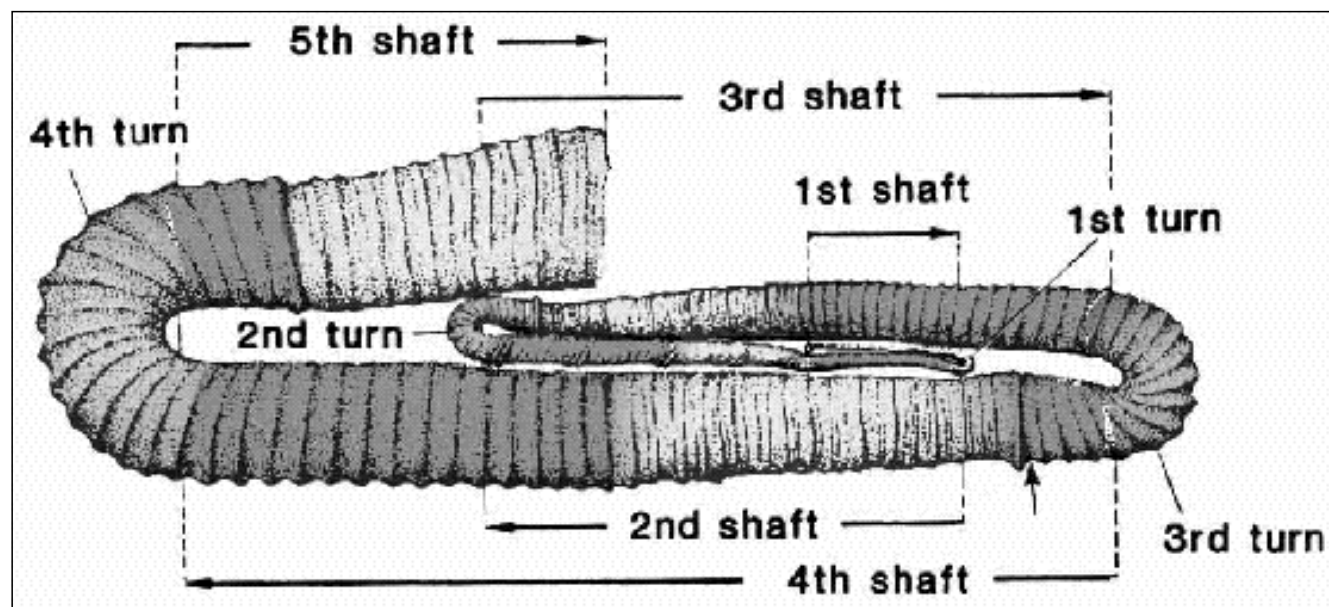
These authors have shown that no planispiral form could attain the hydrostatic stability available to T-C heteromorphs. The advantage of high stability in such non-streamlined forms has yet to be made clear, however. In the last few years, the T-C body plan has been hypothesized to have served quite a different function: it allowed for hydrostatic destabilization and some lability of at-titude (KAKABADZÉ & SHARIKADZÉ, 1993; MONKS & YOUNG, 1998). It is this last hypothesis which is under consideration in the present work. HYATT's (1889) burrowing hypothesis will be examined in future work on in-place vertically inbedded T-C heteromorphs and juvenile (pre-T-C) body chamber lengths.

2. Materials and Methods

I performed a series of analytic geometric analyses of T-C heteromorph shell morphologies. Analyses were based on the formulae for volumes and centers of mass of spirally coiled shells given by MOSELEY (1838) and RAUP & CHAMBERLAIN (1967). Masses and centers of mass and buoyancy for heteromorphic morphologies was determined by breaking each morphology into its monomorphic segments (Text-Fig. 5). Coiling parameters were consistent within each such section, and could therefore be estimated for use in the aforementioned formulae. Once the mass and the centers of mass and of buoyancy were determined for each segment, the segments were "reassembled." The mass of the whole was taken as the simple sum of the masses of the segments. The coordinates of the overall center of buoyancy were taken as the average, weighted by the volumes of the segments, of the coordinates of the centers of buoyancy of the segments. The coordinates of the overall center of mass were taken as the average, weighted by the masses of the segments, of the coordinates of the centers of mass of the segments. Formulae used in calculating the mass and the centers of buoyancy and mass are given in Appendix and Table 1.

These analyses allowed for the calculation of overall buoyancy, as well as for the determination of the centers of mass and buoyancy. Thus it was possible to restore the ammonoids' life-orientations using a number of safe assumptions (see below) and measurements. Life-orientations for each T-C morphology were compared to those obtained by previous authors (KAKABADZÉ & SHARIKADZÉ,

Text-Fig. 5.
Sample "piecemeal" calculation of buoyancy and attitude in a heteromorph ammonoid, *Polyptychoceras pseudogaultinum*, from data in OKAMOTO & SHIBATA (1997).
Procedure is as follows: Divide conch into cylinders (dark gray), frustra (light gray), tori (medium gray), and "planispiral frustra". For each such section, determine the mass and the positions of the centers of mass and buoyancy. Weighting each section according to its volume, evaluate the overall centers of mass and buoyancy, under conditions of neutral buoyancy. Repeat for distribution of cameral fluid, cameral gas, and soft body. For formulae for evaluating volumes and centers of mass of cylinders, frustra, tori, and "planispiral frustra", see Table 2.

1993; MONKS & YOUNG, 1998); orientation comparisons were made only between pairs of calculations based on the same mechanistic assumptions about T-C heteromorph morphodynamics (see Hypothesized Mechanisms below).

Ultimately, the test of each of these hypothesized mechanisms as an adaptive explanation for T-C heteromorphy must be its functional plausibility across all T-C morphologies. Here the criterion for plausibility is benthos access, since this is the function implied by previous suggestions of an attitude-lability morphodynamic effect. Attitude lability itself is recorded for each morphology

Table 1.
Formulae used in piecemeal calculations of buoyancy and attitude.
Formulae for centers of mass and buoyancy are taken from RAUP & CHAMBERLAIN (1967) and MOSELEY (1838).
For explanation of symbols see Apendix.

	Frustrum	Cylinder	Torus
Volume	$(\pi r^3 L - \pi r^2 r_0 L - \pi r_0^2 L)/(3r-3r_0)$	$\pi r^2 L$	$\pi R r^2 \Theta$
Surface Area	$(\pi r^2 L - \pi r r_0 L - \pi r_0 L)/(r-r_0)$	$2\pi r L$	$2\pi R r \Theta$
Center of Mass of Surface	$X = (3r-L)(r^2+r_0 r+r_0^2)/6(r+r_0)$ $Y = 0$	$X = L/2$ $Y = 0$	$X = r(\cos[\Theta/2])(2\pi-\Theta)/\pi$ $Y = r(\sin[\Theta/2])(2\pi-\Theta)/\pi$
Center of Mass of Solid	$X = (9r-L)(r^2+r_0 r+r_0^2)/12(r+r_0)$ $Y = 0$	$X = L/2$ $Y = 0$	$X = r(\cos[\Theta/2])(2\pi-\Theta)/\pi)$ $Y = r(\sin[\Theta/2])(2\pi-\Theta)/\pi$

	Cone	"Planispiral Frustrum"
Volume	$\pi r^2 L/3$	$\pi R r_0^3 (e^{3\Theta \cot A}-1)\tan A/3r$
Surface Area	$\pi r L$	$2\pi r_0(e^{2\Theta \cot A}-1)/\cos A$
Center of Mass of Surface	$X = (3r-L)/6$ $Y = 0$	$X = \dfrac{R_0\{1+[3(\cot A)\sin\Theta - \cos\Theta][e^{3\Theta\cot A}+1]\}}{(\tan A + 9\cot A)(e^{2\Theta\cot A}-1)}$ $Y = \dfrac{R_0\{1+[3(\cot A)\cos\Theta + \sin\Theta][e^{3\Theta\cot A}-3\cot A]\}}{(\tan A + 9\cot A)(e^{2\Theta\cot A}-1)}$
Center of Mass of Solid	$X = (9r-L)/12$ $Y = 0$	$X = \dfrac{3r r_0\{[4(\cot A)\sin\Theta - \cos\Theta]e^{4\cot A} + 1\}}{2R(\tan A + 16\cot A)(e^{3\cot A} - 1)}$ $Y = \dfrac{3r r_0\{[4(\cot A)\cos\Theta + \sin\Theta]e^{4\cot A} - 4\cot A\}}{2R(\tan A + 16\cot A)(e^{3\cot A} - 1)}$

and each morphology and each mechanism, but is not taken here to be the appropriate measure of functionality of the T-C morphology. Benthos access is most directly measured by the angle between aperture and substrate – the angle of apertural declination. In this study I consider any apertural declination $\geq 40°$ as a potentially functional configuration (see MILLER & CULLISON, 1946; DONOVAN, 1964).

The drawings used for the calculations were taken from KAKABADZÉ & SHARIKADZÉ (1993) and MONKS & YOUNG (1998) when possible, to allow for the closest correspondence of calculations. If the drawings were inaccurate or unclear, then drawings of similar morphologies were used. Morphologies were chosen based on degree of involution, regularity of coiling, planarity of coiling, completeness of figured specimens, and perpendicularity of ribbing to the shaft. Morphologies selected were hamiticone (ptychocone), ancylocone, scaphiticone, heterocone, and praviticone (KAKABADZÉ, 1988).

The examination of a number of Cretaceous morphologies using the same single criterion lends power to hy-

Table 2.
Summary of results.
Using the mobile soft body mechanism of MONKS & YOUNG (1998) and the cameral fluid mechanism of KAKABADZÉ & SHARIKADZÉ (1993), the following results were calculated for maximum attitude lability (MONKS & YOUNG'S [1998] criterion) and maximum angle of apertural declination.

MORPHOLOGY	MECHANISM	LABILITY	DECLINATION	VIABLE?
Ancylocone	Mobile Soft Body	24°	24°	NO
Ancylocone	Cameral Fluid	24°	24°	NO
Hamiticone	Mobile Soft Body	20°	12°	NO
Hamiticone	Cameral Fluid	51°	31°	NO
Scaphiticone	Mobile Soft Body	11°	22°	NO
Scaphiticone	Cameral Fluid	54°	65°	YES?
Heterocone	Mobile Soft Body	34°	49°	YES?
Heterocone	Cameral Fluid	37°	52°	YES?
Praviticone	Mobile Soft Body	21°	30°	NO
Praviticone	Cameral Fluid	52°	39°	YES?

drostatic analyses which might otherwise appear flimsy and equivocal (EBEL, 1999).

3. Hypothesized Mechanisms

3.1. Mobile Soft Body

Paleontologists have long known of the ability of ectocochleate cephalopods to maintain or alter their own attitudes via ontogenetic change. The best evidence for this ability comes from

1) primary aragonite deposits in the apical chambers of Paleozoic nautiloids and

2) Cretaceous "meandering" heteromorphs such as Nipponites (OKAMOTO, 1988c).

The notion of at-will change in attitude is quite another issue, and was not discussed until TRUEMAN (1941) commented on the possibility of soft body extension past the aperture (for normally coiled ammonites). This extension would rotate the aperture down, while retraction would rotate i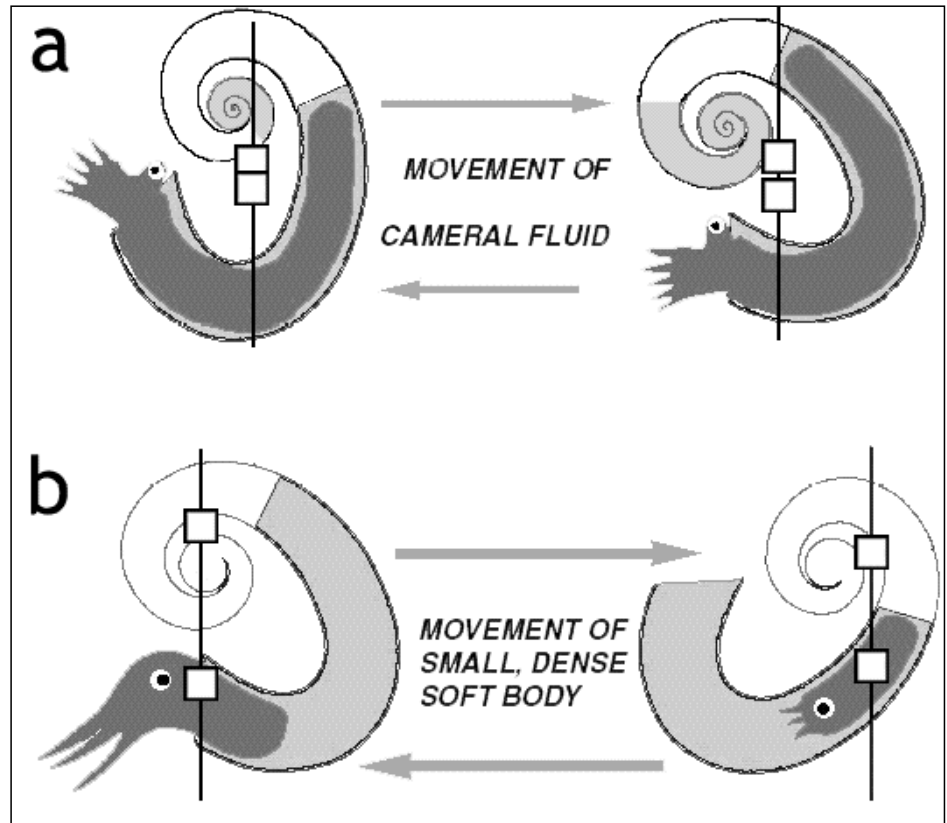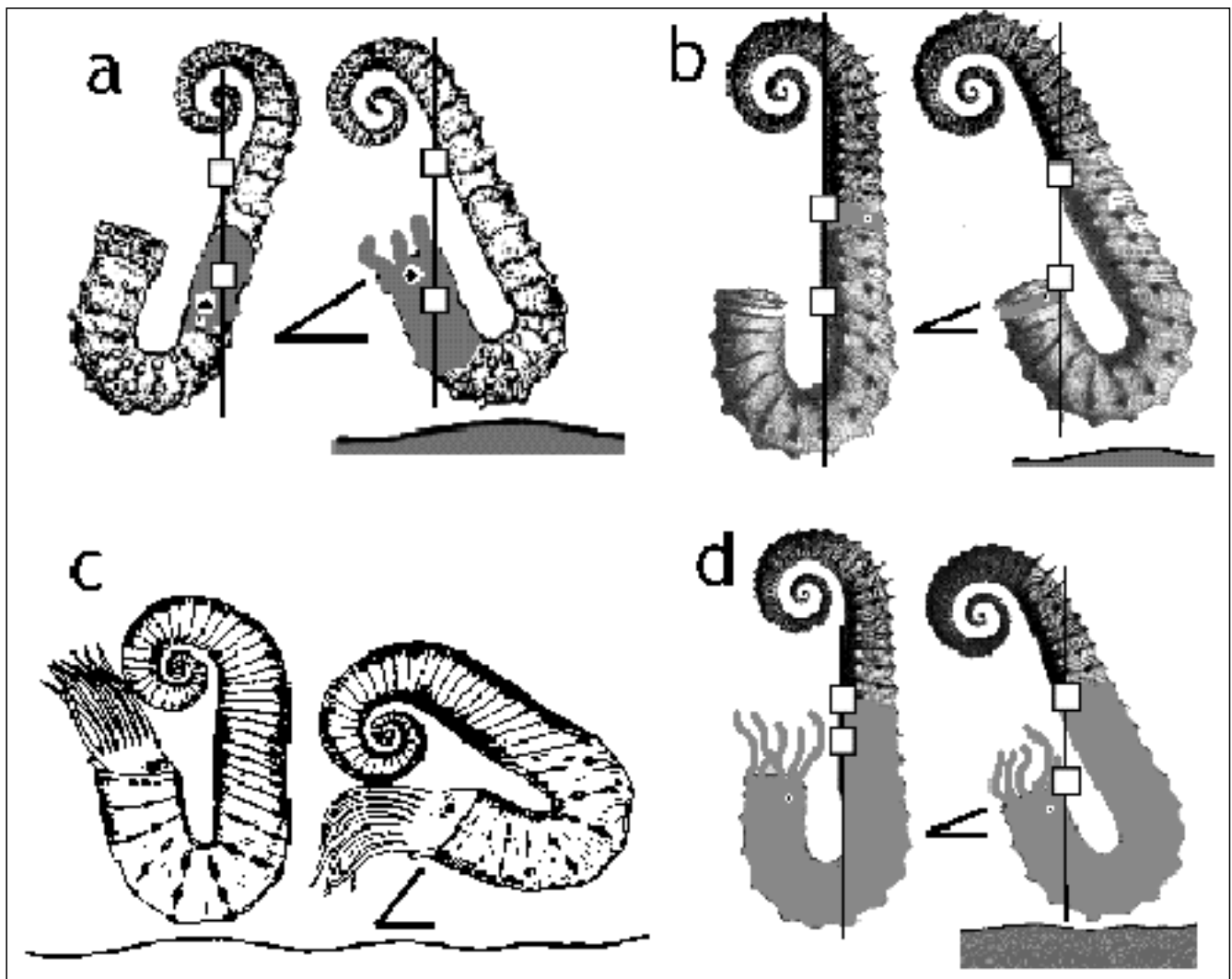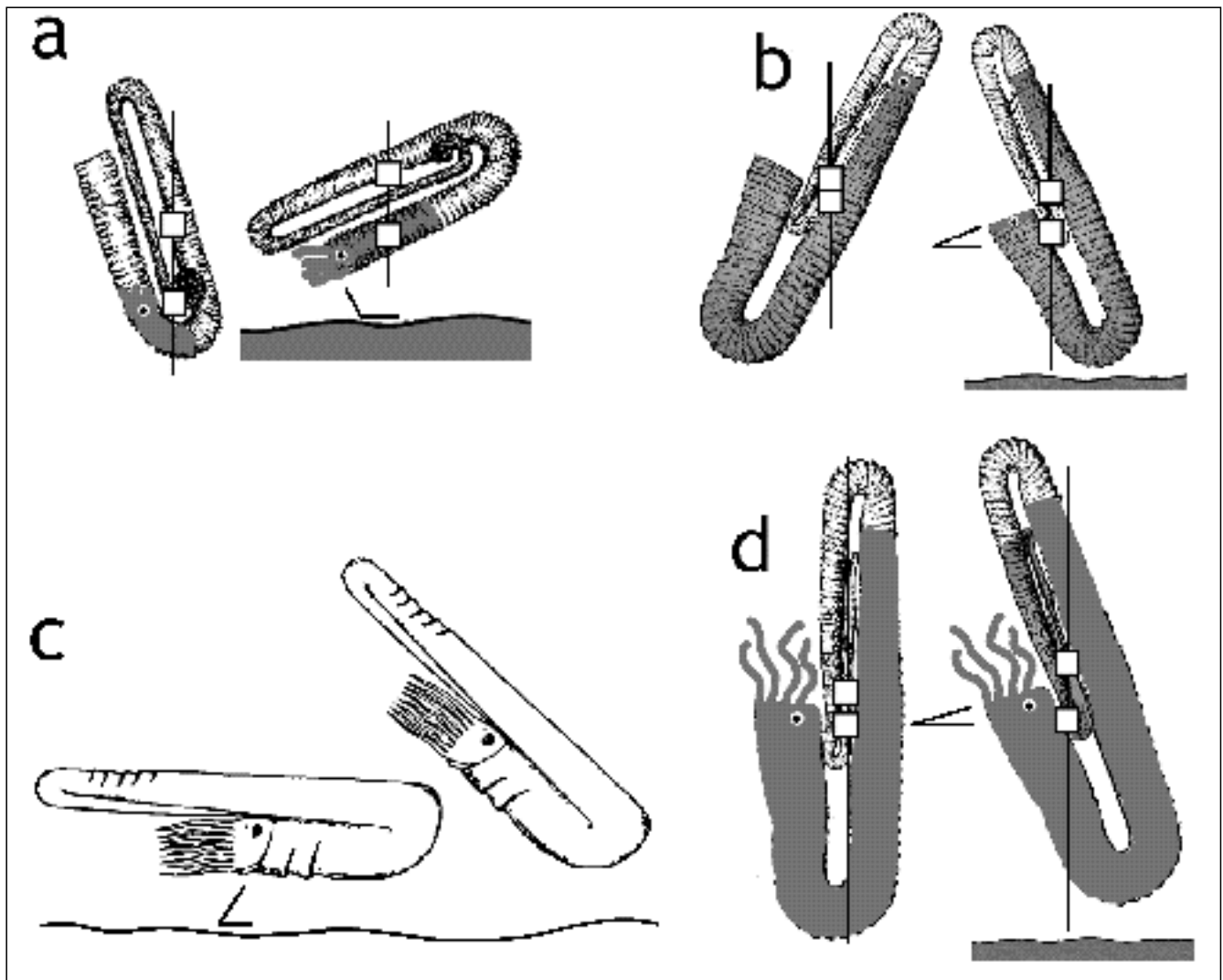t up (EBEL, 1990). As mentioned above, extension of the soft body is often impossible for T-C heteromorphs (WESTERMANN, 1996); however, soft body movement to effect attitude change is certainly possible within the body chamber itself. WESTERMANN (1996) found support for this notion in the highly variable angular position in which aptychi and radulae are found in the body chamber.

MONKS & YOUNG'S (1998) notion of a small heteromorph ammonoid soft body mobile within the body chamber should be examined by inspection before being put to analytic geometric tests. JOYSEY (1961) has commented that changes in an ectocochleate cephalopod's soft body shape should

Text-Fig. 6. ► ▷ ►
Mechanisms for producing at-will attitude lability in T-C heteromorphs, modified from MONKS & YOUNG (1998).
a) The cameral fluid mechanism of KAKABADZÉ & SHARIKADZÉ (1993).
b) The mobile soft body mechanism of MONKS & YOUNG (1998).

Text-Fig. 7. ▼ ▽ ▼
Attitude lability and benthos access in the ancylocones.
a) MONKS & YOUNG's (1998) illustration.
b) Calculations based on MONKS & YOUNG's (1998) mobile soft body mechanism.
c) KAKABADZÉ & SHARIKADZÉ's (1993) illustration.
d) Calculations based on KAKABADZÉ & SHARIKADZÉ's (1993) cameral fluid mechanism.

Text-Fig. 8.
Attitude lability and benthos access in the hamiticones.
a) MONKS & YOUNG's (1998) illustration.
b) Calculations based on MONKS & YOUNG's (1998) mobile soft body mechanism.
c) KAKABADZÉ & SHARIKADZÉ's (1993) illustration.
d) Calculations based on KAKABADZÉ & SHARIKADZÉ's (1993) cameral fluid mechanism.

not affect its overall density; but what impact would these changes have on attitude? As MONKS & YOUNG (1998) rightly illustrate (Text-Fig. 6a), the center of buoyancy of the (shell + animal) should remain unchanged through soft body movement, since the body chamber is filled with (seawater + soft body) in one case and (soft body + seawater) in the other. The center of mass may change, however. Thus the shell can be conceived of as pivoting around the center of buoyancy (= the center of mass of the water which the whole ammonoid displaces) to achieve its new stable attitude.

In calculating the angular change in attitude between the two stable orientations proposed by MONKS & YOUNG (1998), I have attempted to obtain as great a change as possible, shrinking the body size suggested by MONKS & YOUNG (1998) while maintaining neutral buoyancy. As shown above, soft body density is extremely poorly known; the present method may shed some light on the likely range of soft body densities in T-C heteromorphs.

The results of all calculations are represented graphically in Figs. 7b, 8b, 9b, 10a, and 11a, and are summarized in Table 2. In general, the orientational labilities described by MONKS & YOUNG (1998) are accurate for the morphol-
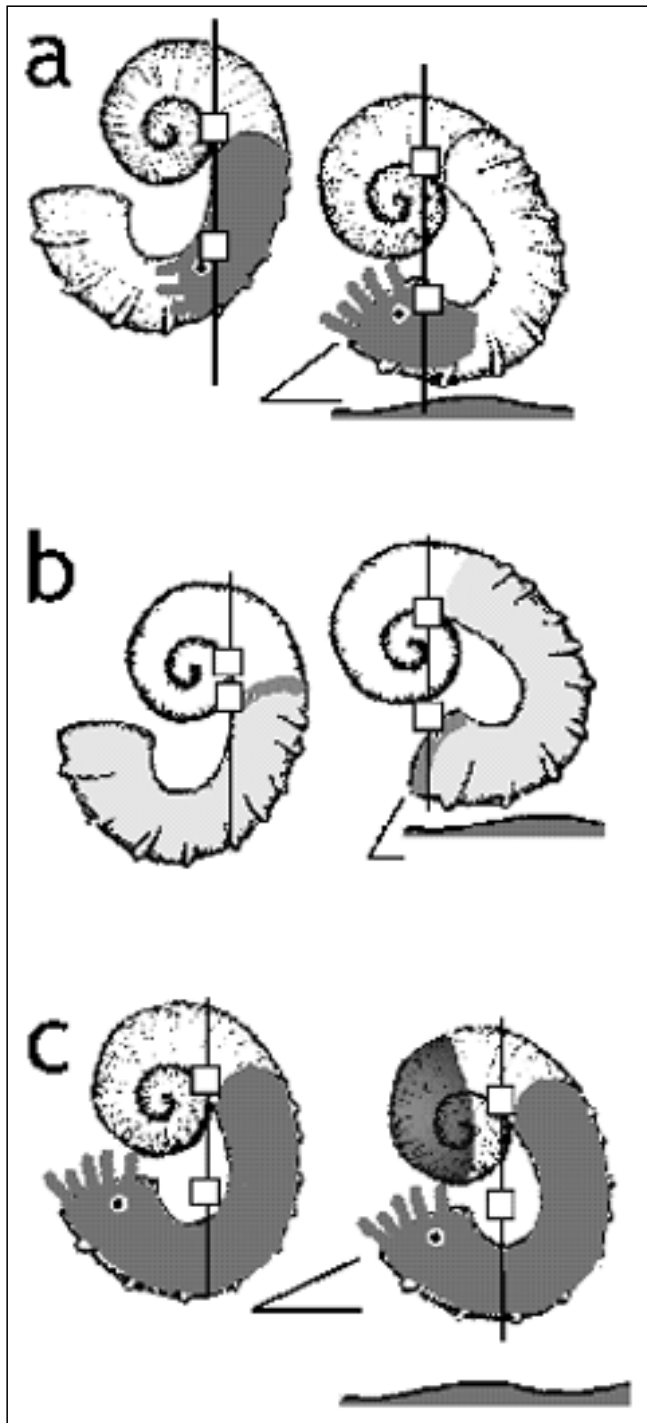
ogies under study. Again, however, this lability does not necessarily translate into functionality. Rather, it is the angular and spatial relationship between the aperture and the substrate that lends the structure functionality.

3.2. Cameral Fluid

In *Nautilus* as well as other recent cephalopods, the amount of fluid present in the camerae is under the strict control of the animal (DENTON & GILPIN-BROWN, 1961, 1967, 1973). However, the ability to regulate the spatial distribution of cameral fluid is known only from cuttlefish and spirulid squids (DENTON & GILPIN-BROWN, 1961, 1973).

Active regulation of cameral fluid distribution in ammonoids has, in fact, been implied by many authors in connection with buoyancy and attitude calculations. JOYSEY (1961), in attempting to give an orthoconic ammonoid a horizontal attitude, suggested that fluid ballast be placed at the shell apex to help counterbalance the relatively heavy soft body (Text-Fig. 12). DONOVAN (1964), KLINGER (1981), CHAMBERLAIN (1991), and WESTERMANN (1996) followed JOYSEY (1961), KLINGER pointing out that the shell must remain neutrally buoyant even after the ballast is
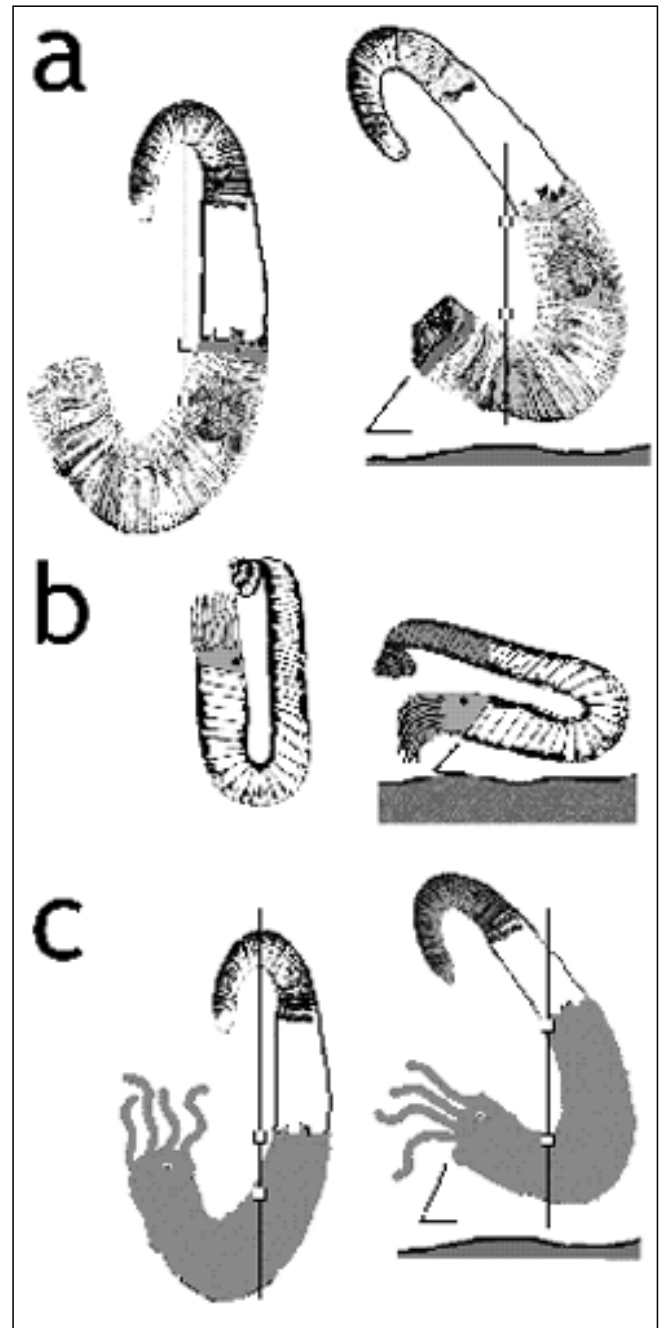
Text-Fig. 9.
Attitude lability and benthos access in the scaphiticones.
a) MONKS & YOUNG'S (1998) illustration.
b) Calculations based on MONKS & YOUNG'S (1998) mobile soft body mechanism.
c) Calculations based on KAKABADZÉ & SHARIKADZÉ'S (1993) cameral fluid mechanism.

Text-Fig. 10.
Attitude lability and benthos access in the heterocones.
a) Calculations based on MONKS & YOUNG'S (1998) mobile soft body mechanism.
b) KAKABADZÉ & SHARIKADZÉ'S (1993) illustration.
c) Calculations based on KAKABADZÉ & SHARIKADZÉ'S (1993) cameral fluid mechanism.

added – the primary constraint on this type of calculation. WESTERMANN (1975a) extended the idea's domain to coiled ammonoids; WARD & WESTERMANN (1977) and KAKABADZÉ & SHARIKADZÉ (1993) applied it to partially uncoiled heteromorphs (Text-Fig. 6b).

In calculating the angular change in attitude between the two stable orientations proposed by KAKABADZÉ & SHARIKADZÉ (1993), I have attempted to obtain as great a change as possible while maintaining neutral buoyancy. In some cases, I find that KAKABADZÉ & SHARIKADZÉ's (1993)

attitude labilities would require negative buoyancy. In such cases, the cameral fluid hypothesis is invalidated, as the selected heteromorphs were neutrally buoyant (see Discussion for explanation.) In these same cases, benthos access is highly restricted by the shell, precluding a feeding function for either life attitude.

The results of all calculations are represented graphically in Figs. 7d, 8d, 9c, 10c, and 11b, and are summarized in Table 1. In general, the cameral fluid mechanism is insufficient to generate the attitude changes described by KAKABADZÉ & SHARIKADZÉ (1993). Moreover, the mechanism tends to leave the ammonoid aperture well out of contact with the substrate. Thus the mechanism can be con-

189
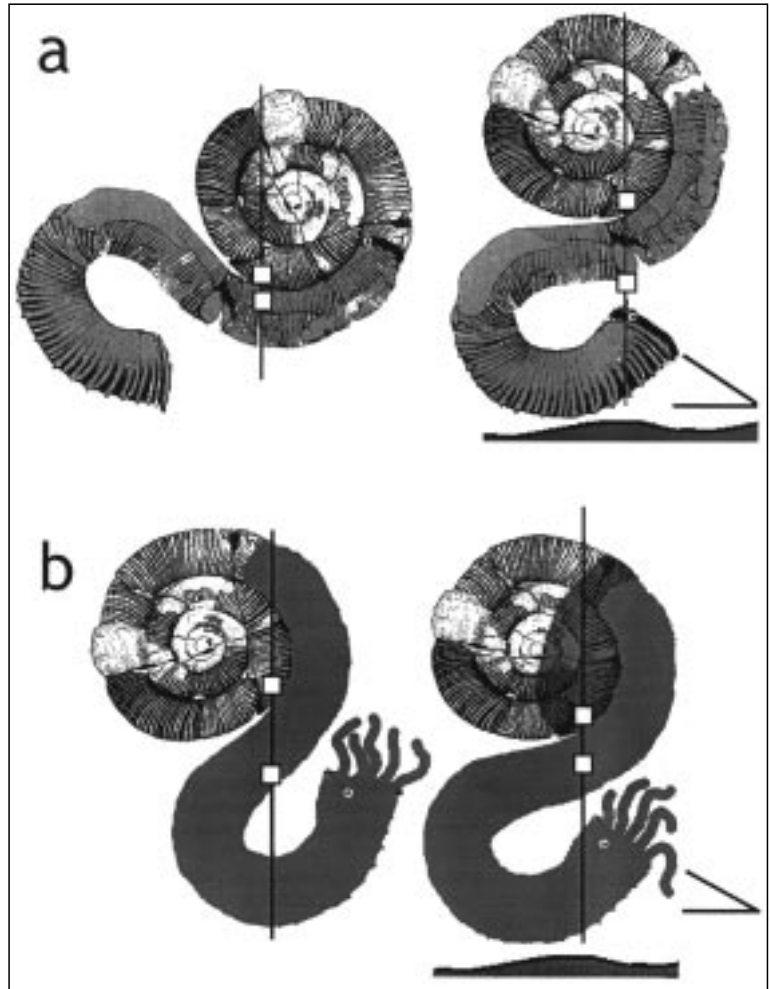
sidered neither general nor adaptive for T-C heteromorphs.

4. Assumptions

The calculation of ectocochleate cephalopod buoyancy and attitude is one of the diciest, most assumption-laden lines of research condoned by the functional-morphologic community. Careful selection of taxa and morphologies (Fig. 1) is necessary in order to provide a worthwhile and fruitful analysis while avoiding the pitfalls of unsatisfied assumptions. Below I present a list of the assumptions necessary to the technique, along with the corresponding reasons why the choice of certain T-C heteromorphs should lend the results an unusual degree of robustitude.

4.1. Neutral Buoyancy

The resulting buoyancy (EBEL, 1999) of the shell-animal system is neutral. For a given morphology, a particular buoyancy must be indicated before an attitude can be calculated. Classically, the assumption has been neutral buoyancy for all ectocochleate cephalopods, though the method certainly allows for other a priori assumptions (EBEL, 1983; SAUNDERS & SHAPIRO, 1986; OKAMOTO & SHIBATA, 1997). However, the neutral buoyancy assumption was based initially on evidence from recent forms. Further evidence for the validity of neutral buoyancy has come from the series of ammonoid buoyancy calculations themselves (TRUEMAN, 1941; CURRIE, 1957; RAUP, 1967; HEPTONSTALL, 1970; MUTVEI & REYMENT, 1973; TANABE, 1975; WARD & WESTERMANN, 1977; CHAMBERLAIN, 1981; MATSUMOTO et al., 1981; EBEL, 1983, 1990, 1992; SAUNDERS & SHAPIRO, 1986; LANDMAN, 1987; SHAPIRO & SAUNDERS, 1987; SWAN & SAUNDERS, 1987; OKAMOTO, 1988b, 1996; OLIVERO & ZINSMEISTER, 1989; SHIGETA, 1993; WESTERMANN, 1993; TANABE et al., 1995; KAKABADZÉ & SHARIKADZÉ, 1996; OKAMOTO & SHIBATA, 1997; MONKS & YOUNG, 1998), which have tended to corroborate the neutral buoyancy assumption by independent means.
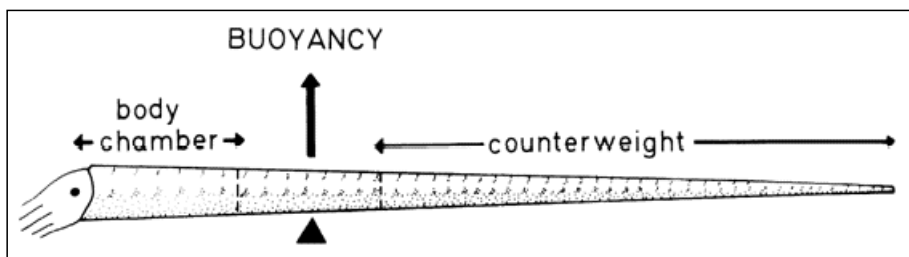
The morphologies under study here were probably neutrally buoyant at least during the secretion of the shaft, as can be discerned from the perpendicularity of ribbing (and thus growth lines [OKAMOTO, 1988b]) to the shaft (OKAMOTO & SHIBATA, 1997). These forms were therefore nektoplanktonic, or perhaps nektobenthic with only slight contact with the sediment. If planktonic, then they were neutrally buoyant or nearly so (WESTERMANN, 1993). If they were nektobenthic, then buoyancy assumptions are less clear (but see Discussion).

4.2. Soft Body Volume

The soft body fills and is essentially contained within the body chamber. This assumption has its roots in *Nautilus*, whose body chamber is so short that dramatic retraction or extension is hardly possible. In order to run the algorithms from the literature, this assumption becomes a necessity. However, it is not at all clear that ammonoid soft parts either filled the body chamber (MONKS & YOUNG, 1998) or were contained within it (EBEL, 1990, 1992; JACOBS & LANDMAN, 1993, and references therein). For calculations of overall buoyancy and attitude, the only soft body data needed are density, center of mass, and center of buoyancy. Therefore assumption 2 is relaxed in this study, unidirectionally: I allow for a small soft body mobile within the body chamber. The possibility of extension of the soft body is disregarded, as it is precluded in many T-C heteromorphs by space constraints outside the mature aperture (see Fig. 2; KLINGER, 1981; MATSUMOTO et al., 1981; WESTERMANN, 1996).

BUOYANCY

body
←chamber→   ←——— counterweight ———→

4.3. Position of Center of Mass

The overall center of mass lies near the center of mass of soft body. TRUEMAN (1941) mentioned that for his mostly low-stability monomorphic ammonoids, the displacement of the (shell + animal)'s center of mass from the soft body's center of mass would be minuscule and hardly worth calculating. However, he stressed that this might not be the case for open-coiled or especially heteromorphic forms, where the mass of the shell might come to play a greater role (CURRIE, 1957; see also WARD, 1976b). Despite his caveats, many subsequent studies have taken the center of mass of the soft body as that of the system (though MONKS & YOUNG [1998] appear to make some variable correction for the shell). Here I dismiss assumption 3 and proceed to calculate the overall center of mass as the sum of the centers of mass of the animal's parts, hard and soft alike. Attitude and stability might be influenced by any of the following factors: ratio of volumes of phragmocone and body chamber, soft body size and displacement by mantle fluid or seawater, filled vs. unfilled chambers, aperture shape, septal thickness, soft body density, number of septa, shell density, aptychus density, shell thickness, or aptychus size. For a fuller discussion of the individual effects, the reader is advised to consult SAUNDERS & SHAPIRO (1986) and SWAN & SAUNDERS (1987).

4.4. Uniform Densities

Each component in the buoyancy calculation is of uniform density.

4.4.1. Shell Material

TRUEMAN's (1941) value for shell aragonite density, 2.94 g/cm^3, assumed a solid crystalline structure with no organic matrix. Later studies incorporated the organic component, bringing the aragonite density down to about 2.63 g/cm^3 (RAUP & CHAMBERLAIN, 1967). All subsequent studies have employed this value or similar values, despite recent evidence for microstructural heterogeneity in cephalopod aragonite (MUTVEI, 1983). As this complexity is just too difficult to account for in studies of overall shell hydrostatics, the value of 2.63 g/cm^3 is taken as a reasonable estimate.

4.4.2. Soft Body

Crop contents, organs, aptychi, and the size of the mantle cavity all contribute to an acknowledged heterogeneity of soft body density. However, as above, the only necessary data concerning the soft body are overall density, center of mass, and center of buoyancy. Here I ignore TRUEMAN's (1941) figure of 1.13 g/cm^3 and instead take RAUP & CHAMBERLAIN's (1967) figure of 1.06 g/cm^3 for the overall soft body density, a figure adopted by nearly all subsequent workers.

4.4.3. Whole Phragmocone and Soft Body

OKAMOTO (1988b, 1996; OKAMOTO and SHIBATA, 1997) assumed a homogeneous density for the (shell + gas + liquid) of the phragmocone, and a second homogeneous density for the (shell + soft body) of the body chamber! Since his computer models produced forms highly similar to those seen in nature, the assumption of homogeneous density is probably insignificant among this list of assumptions. Most other workers have kept the shell, gas, and soft body separate.

4.4.4. Chamber Contents

The phragmocone's chambers are nearly always assumed to be empty of fluid for calculations of buoyancy and attitude (but see SAUNDERS & SHAPIRO [1986] and KAKABADZÉ & SHARIKADZÉ [1993]). Chamber gas is always assumed to be under less than 1atm pressure, as in recent taxa. Here I address the possibility of fluid-filled chambers in the context of allowing the ammonoid to achieve some particular attitude.

4.5. Geometric Approximations

Whorl sections are represented by simple geometric forms. TRUEMAN's (1941) and RAUP & CHAMBERLAIN's (1967) formulae are applicable only to shells of circular to elliptical whorl section. EBEL's (1983) routine approximates whorl sections as truncated trapezoids, while SAUNDERS & SHAPIRO (1986) take some account of the overlap of whorls and the non-elliptical shape of overlapping whorl sections. However, these latter two methods yield approximations only slightly better than RAUP & CHAMBERLAIN's (1967) formulations. It would seem advantageous to restrict initial studies, at least, to forms which can be accurately modelled with elliptical whorl sections. T-C heteromorphs satisfy this condition nicely; their uncoiled shapes allow the whorl to take on a circular to elliptical section (WARD & WESTERMANN, 1977).

4.6. Shell Thickness

Shell thickness is constant around the whorl perimeter. Once again, TRUEMAN's (1941) and RAUP & CHAMBERLAIN's (1967) formulae implicitly assume a constant thickness for shell wall around the whorl section. As most ammonoids lack a full dorsal shell wall (WESTERMANN, 1971), this assumption seems largely unwarranted. SWAN & SAUNDERS (1987) attempted to correct for this overgeneralization, but the resulting formulae prove useless unless shell thickness data are available for entire whorl sections. However, uncoiled forms and "lytoceratines" tend to possess a dorsal shell wall (BIRKELUND, 1981) – a necessity for an uncoiled ammonoid (WESTERMANN, 1971). The simple circular to elliptical whorl sections mentioned above imply an equable distribution of shell material around the whorl section for "lytoceratine" T-C heteromorphs (BIRKELUND, 1981).

4.7. Septa and Siphuncle

Septa and siphuncular tube account for a portion of the mass of the shell material. TRUEMAN (1941) included the mass of septa (6 % of the shell wall mass) in his calculations but dismissed that of the siphuncular tube (1 % to 1.5 % of the shell wall mass). RAUP & CHAMBERLAIN (1967) and subsequent workers have adopted these values and included both septa and siphuncular tube, but without assigning them any particular spatial distribution. It is well known that the siphuncular tube undergoes extinction as much as a full whorl prior to the ultimate septum (TRUEMAN, 1920). Septa would appear to be more regularly (logarithmically) distributed (WESTERMANN, 1975a), but would not the increasing complexity of sutures through ontogeny also increase each successive septum's weight disproportionately? WESTERMANN (1971, 1975b) shows that this is not the case; the septum's thinness near its periphery more than makes up

for its increased fluting (i.e., surface area). All in all, there is far too much spatial distribution information to possibly take into the analysis; moreover, analyses distributing the septum/siphuncular tube material evenly over the phragmocone have predicted fairly accurate attitudes and buoyancies for *Nautilus* (SAUNDERS & SHAPIRO, 1986; SHAPIRO & SAUNDERS, 1987). The assumption remains that septa and siphuncle account for approximately 7 % of the total shell mass, but their distribution will continue to be conceived of as homogeneous within the phragmocone.

4.8. Coiling Parameters

Coiling parameters must be constant and derived from shell form. TRUEMAN's (1941) and CURRIE's (1957) work to show the inconstancy of coiling parameters proved nothing new to paleontologists. This inconstancy was already well known; these workers merely quantified it into a series of growth phases. TANABE (1975) obtained the discouraging result that coiling parameters change gradually even within a single growth phase. However, the formulae of RAUP & CHAMBERLAIN (1967) and especially TRUEMAN (1941) rely on the ability of the researcher to assign a single value to each parameter for the whole ontogeny. Fortunately, the determination of covariations between parameters is possible through rigorous measurement schemes (STONE, 1997). Striking perhaps more at the heart of this entire line of research is the assumption that the mathematical information we can glean from shells "after the fact" (JACOBS & CHAMBERLAIN, 1996) informs our understanding of the biological processes involved in their secretion. Humbling as such a statement may be, it asserts an assumption paleontologists must be willing to make.

4.9. Ontogenetic Change

All morphological parameters and components are insensitive to ontogenetic change. This assumption is made readily and often in the literature (HEPTONSTALL, 1970; TANABE, 1975; WARD & WESTERMANN, 1977; CHAMBERLAIN, 1981; SAUNDERS & SHAPIRO, 1986; SHAPIRO & SAUNDERS, 1987; SWAN & SAUNDERS, 1987; OLIVERO & ZINSMEISTER, 1989; WESTERMANN, 1993; TANABE et al., 1995; KAKABADZÉ & SHARIKADZÉ, 1993; MONKS & YOUNG, 1998), often without justification. The functions of the various components in maintaining overall buoyancy and attitude had to be active at all times during ontogeny; therefore the postulation of a particular buoyancy at the adult stage is not enough (EBEL, 1992). For example, it is widely known that soft body densities decrease through ontogeny for swimming organisms (JACOBS & CHAMBERLAIN, 1996), and especially for JACOBS & LANDMAN's (1993) coleoid-like mantle model, in which a greater and greater proportion of the body chamber might be taken up by the mantle cavity, through ontogeny. TRUEMAN's (1941) assertion of constant body chamber volume to phragmocone volume through ontogeny was shown to be false many years ago (REYMENT, 1973; MUTVEI & REYMENT, 1973). And as stated above, most (if not all) coiling parameters undergo sudden, coordinated changes at various points in ontogeny (TRUEMAN, 1941).

4.10. Intraspecific Variation

Characters controlling buoyancy have low intraspecific variability. For the calculations to have meaning, they should apply to some morphology which accurately represents one or more ammonoid species. However, if intraspecific variability for buoyancy-controlling characters is high, then buoyancy and attitude calculations may be poor predictors of actual buoyancy and attitude. In *Hamites*, for example, the body chamber length is known to be highly variable even within a single species (C. SPATH, fide TRUEMAN 1941). *Hamites* is, in fact, one of the taxa examined by MONKS & YOUNG (1998). OLIVERO & ZINSMEISTER (1989) observed a similar pattern for *Diplomoceras*, and H. KLINGER (pers. comm., 1998) has observed the same in *Didymoceras, Myloceras* and *Labeceras*. High variability in these characters indicates that a range of attitudes (or even buoyancies) may have been present in the population. Variability in the angle of apertural declination itself (e.g., RICCARDI, 1983) represents yet another confounding factor in functional analysis.
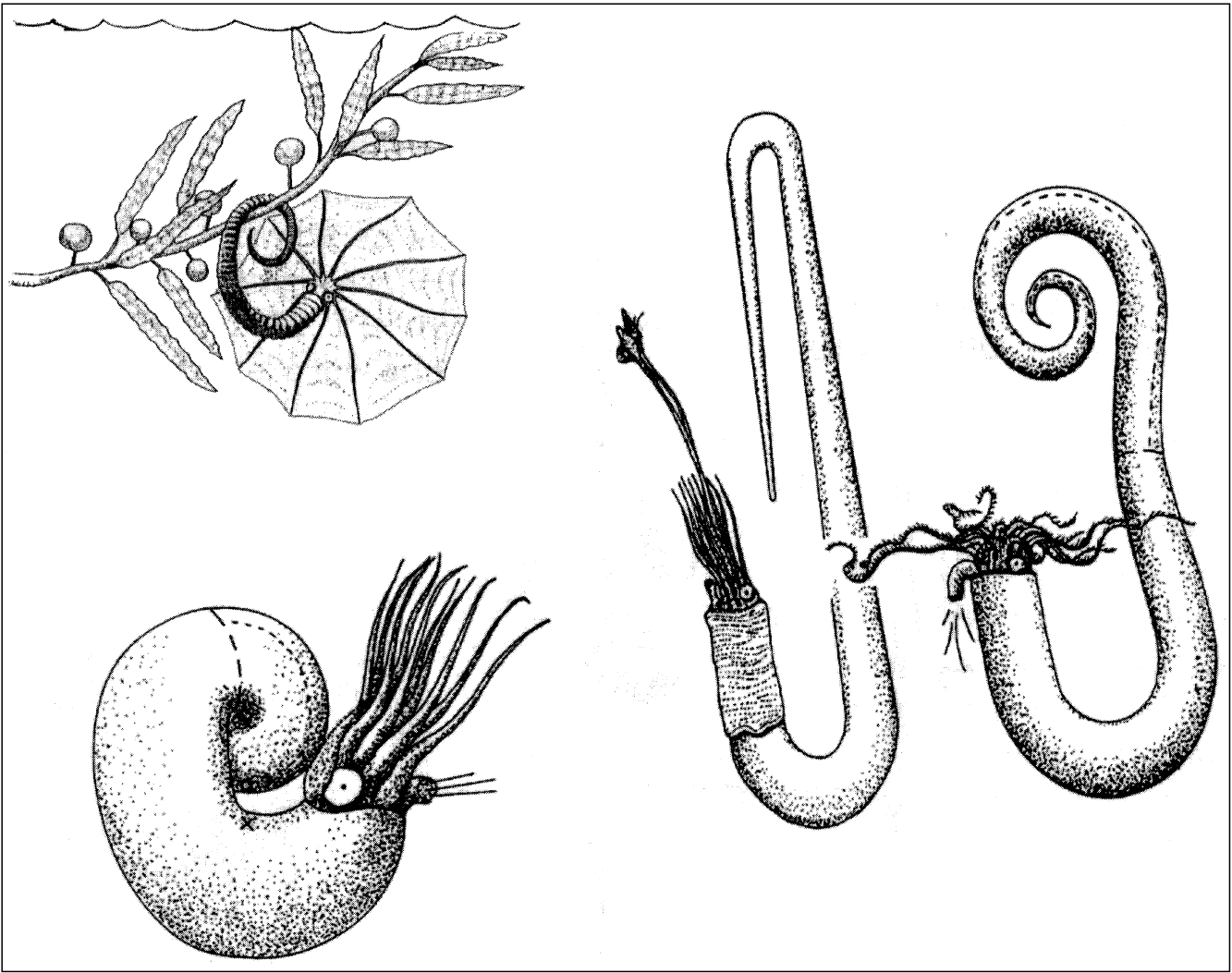
5. Discussion

The problem of heteromorph ammonoid attitude is a difficult one to solve by inspection, due to
1) the highly irregular geometries,
2) the influence of "fudge factors" such as septal complexity and ornament thickness, and
3) the nearly equal contributions of shell material and soft body to the negative buoyancy of the system.
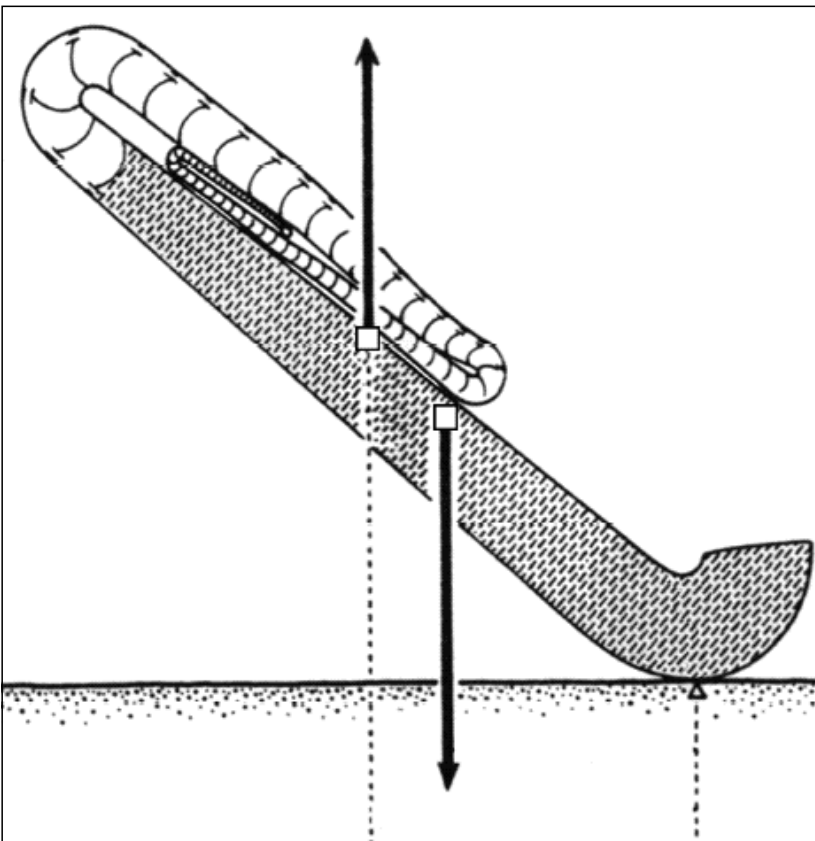
These considerations make analytic calculations necessary; these calculations, in turn, necessitate detailed measurements of morphologic features. Once complete, the analytic calculations may allow us to rule out certain functional hypotheses for certain morphologies. The falsification of such an hypothesis in multiple morphologies implies that the mechanism cannot be generally applied to all T-C heteromorphs. When multiple falsifications of the same explanatory functional hypothesis can be made in multiple phylogenetically independent cases, this compound falsification provides grounds for falsification of the corresponding hypothesis of overarching adaptation, namely, "The appearances of the T-C morphology represent an adaptive shift to benthic life habits."

Ad hoc assumptions concerning body shape and extension past the aperture are tempting in these cases (Fig. 13); it does seem awfully stringent to require every T-C morphology to conform to a single morphodynamic mechanism. But if a single skeletal morphodynamic effect – in response to a single set of selection pressures – were not at work, we would not expect such an observable flourish of convergent T-C skeletal morphologies in the Cretaceous. In other words: if soft-part adaptations contributed variably to function in these forms, then the morphologically convergent pattern evident in their skeletons would not be so striking. The strength of the observable pattern in skeletal morphology indicates that our hypotheses of adaptation should be tested against skeletal evidence alone.

KAKABADZÉ & SHARIKADZÉ's (1993) cameral fluid hypothesis is intriguing but does not provide the necessary morphodynamic function, in most forms. One exception appears to be *Pravitoceras*, in which the addition of apical cameral fluid would allow direct contact between soft body and benthos. In this case KLINGER (1981) may be right: the U-shaped body chamber may serve to protect the respiratory system from mud when the ammonoid is not feeding. MONKS & YOUNG (1998) commented on the cameral fluid hypothesis based on an argument from

Text-Fig. 13. ▲ △ ▲
Fanciful restorations of heteromorphs by C. Tsujita, modified from Westermann (1996).
Proposing different soft body morphologies and sizes for different T-C skeletal morphologies is useful when supported by paleontological evidence. However, such proposals would be unwarranted if serving merely as ad hoc dismissals of evidence against an explanatory functional hypothesis.

Nautilus: cameral fluid transport is too slow even to assist diurnal vertical migration by adjusting overall buoyancy. Could ammonoids have been better at cameral fluid transport? Probably yes, thanks to their complex septa and unmineralized proximal siphuncle; but even this efficiency may have been insufficient to produce the required attitude changes.

Monks & Young (1998) hinted at a further implication of multiple stable orientations in T-C heteromorphs. They implied that the "leaning over" attitude (Okamoto & Shibata,

Text-Fig. 14. ◄ ◁ ◄
Nektobenthic T-C heteromorph "leaning" on the substrate, modified from Okamoto & Shibata (1997).
Constant buoyancy adjustment through ontogeny would allow heteromorph growth lines to parallel the substrate, even if the heteromorph were at all times "touching down" on the substrate ever so lightly.
See Okamoto & Shibata (1997) for full discussion.

1997) was used for feeding, while the "leaning back" attitude was used for defense against predators. Assuming a non-opercular function for aptychi (MONKS & YOUNG, 1998), this explanation of the two attitudes appears highly pertinent from an evolutionary-ecological perspective. Lacking apertural defense and caught in the Mesozoic marine revolution (VERMEIJ, 1977), ammonoids needed a defense strategy. Within a short span of time a number of ammonoid lineages evolved the T-C morphology, perhaps as an anti-predatory tactic.

Since these ammonoids have been hypothesized to have been nektobenthic predators, it might also seem reasonable to allow the bottom of the ammonoid's hook to rest on the substrate while the rest of the ammonoid leans over, pivoting around the point of substrate contact (Fig. 14; OKAMOTO & SHIBATA, 1997; EBEL, 1999). Such a mechanism would allow a greater range of attitudes, and in fact make almost any attitude possible in many forms (note, however, that a "leaning-over" posture would actually be more stable in normally coiled ammonoids than in the longer buoyancy lever arms of T-C heteromorphs). While this mechanism should not be discounted, it should be examined from the viewpoint of synecologic analysis: Do T-C heteromorphs often bear fractures and healed injuries along this pivot point, or, indeed, anywhere along the U-shaped body chamber? This would seem the most likely region for attack by the benthic durophages evolving during the Mesozoic. Yet, apart from anecdotal reports (KENNEDY & HENDERSON, 1992; K. TANABE, personal communication), few injuries have been observed on T-C heteromorph body chambers (e.g., LANDMAN & WAAGE, 1986, 1993; MONKS, 2000).

As stated in the introduction, adult heteromorphs seem to represent living, feeding animals; the sparseness of injuries cannot be ascribed to a wholly necroplanktonic (or even necrobenthic) existence of the adult morphology.

The independent check of MONKS & YOUNG's (1998) results indicates that the evolution of a small adult soft body might have been useful for controlling attitude in some T-C heteromorphs. Further checks on the robustitude of the results might be made by varying the shell parameters to see if the buoyancy or attitude estimates break down easily. Since this study's parameter values were more secure than those of most buoyancy calculations, I find it likely that MONKS & YOUNG's (1998) results would hold up for a range of values for any variable. Benthos access could be further improved by including the heavy aptychus in the geometric analysis; data on the size relationship between jaw and conch are available for ammonoids (MORTON & NIXON, 1986) and living cephalopods (CLARKE, 1962). Additionally, hydrostatic experiments can be performed with life-size or scale models to corroborate or refute analytical results (REYMENT, 1973; WARD, 1976a).

I have shown above that T-C heteromorphy was most likely an adaptive response to some novel selective pressure. However, even the attitude lability attained by MONKS & YOUNG (1998) does not provide functional access to the benthos for all forms. If the benthos was inaccessible to many of these forms, then the temporally constrained, morphologically convergent appearance of T-C heteromorphs cannot be ascribed to an opening of benthic ecospace. Instead, an alternative life mode must be hypothesized – a life mode with its own large-scale Cretaceous ecomorphospacial opportunity. I favor a trophism-related ecosystematic change, in which T-C heteromorphs were able to take advantage of the newly abundant pelagic foraminifera and nannoconida (CECCA, 1997, and references therein). Other explanations for the flurry of T-C origins in the Cretaceous lack either the magnitude or the scale necessary to bring about such a drastic and widespread revolution in ammonoid shape.

6. Conclusions

The functional hypothesis of hydrostatic destabilization in T-C heteromorph ammonoids was examined in terms of its proposed mechanisms. Using neutral buoyancy as a constraining endpoint in the analysis, the range of attainable attitudes was examined for each of a number of T-C heteromorph morphologies: baculiticone, hamiticone, ptychocone, ancylocone, scaphiticone, heterocone, and pravitocone. Analytic-geometric analysis proceeded twice through each morphology, each time with a different assumption about the mechanism of achieving multiple stable orientations:

1) cameral fluid localization;
2) mobile soft body of reduced size.

Cameral fluid localization was found incapable of producing the desired attitude lability; soft body mobility, on the other hand, produced labilities similar to those reported by MONKS & YOUNG (1998), despite a different mass-distribution assumption on the part of these authors.

However, imposition of a benthos-access criterion for T-C heteromorph function leads to inconsistent results for both mechanisms. Neither cameral fluid localization nor soft body mobility was found capable of producing a useful second stable orientation in most morphologies. In these cases, the aperture remained removed from the substrate, even when the mechanism's morphodynamics were effected as strongly as possible. Neither mechanism's function (in this sense) was generally applicable across all T-C morphologies under examination.

Phylogenetic and biostratigraphic support was found for an adaptive aspect of the evolution of the T-C morphology. However, the adaptation itself cannot be definitely identified. Here it has been shown that appearances of the T-C morphology cannot represent a single adaptive response to a shift to b e n t h i c life habits. Some other functional (ecological) shift in life habits was likely responsible for this Cretaceous phenomenon. Phylogenetically independent occurrences of T-C heteromorphy were used here as "replicate" cases in which to test an overarching adaptive hypothesis. Falsification of adaptive hypotheses can play an important part in discussions of functional morphology, phylogeny, and morphospace occupation.

Analytic geometric methods can substitute for biomechanical models when the study has as its purpose the examination of a functional hypothesis's feasibility. Here the analytic method was able to discriminate between two closely related hypotheses. The sensitivity implied by this rejection recommends the use of analytic-geometric methods in functional morphology. Future research should be directed toward additional explicit tests of heteromorph functional morphology, such as epibiosis and taphonomy. The adaptive function of heteromorphy in Cretaceous terminal-countdown forms remains equivocal, but now, at least, less open to debate.

Appendix

Volumes and surface areas can be defined geometrically for monomorphic segments of heteromorph ammonoid shells. The following variables are used in the formulae in Table 2:

r = radius of aperture at adapical end of segment
R = radius of aperture at adoral end of segment
L = length of segment, measured as the average of the lengths along the dorsal and ventral surfaces
a = spiral angle with which shell coils; constant along a given segment

The mass of a segment is simply the product of its volume and its material density. For shell material, mass was taken as the product of density and surface area, producing a "thin shell" estimate.

"Reassembling" the segments allows for an assessment of the overall mass and of the overall centers of mass and of buoyancy. The overall center of buoyancy is calculated as a weighted sum of the coordinates of the segments' centers of buoyancy, as follows. This sum gives the coordinates of the overall center of buoyancy for a reassembly of n segments:

$$\left(\frac{\sum\limits_{j=1}^{n} \left(\text{volume}_j \cdot \text{abscissa of center of buoyancy}_j \right)}{\sum\limits_{j=1}^{n} \text{volume}_j} \ , \ \frac{\sum\limits_{j=1}^{n} \left(\text{volume}_j \cdot \text{ordinate of center of buoyancy}_j \right)}{\sum\limits_{j=1}^{n} \text{volume}_j} \right)$$

Likewise, The overall center of mass is calculated as a weighted sum of the coordinates of the segments' centers of mass, as follows. This sum gives the coordinates of the overall center of mass for a reassembly of n segments:

$$\left(\frac{\sum\limits_{j=1}^{n} \left(\text{mass}_j \cdot \text{abscissa of center of mass}_j \right)}{\sum\limits_{j=1}^{n} \text{mass}_j} \ , \ \frac{\sum\limits_{j=1}^{n} \left(\text{mass}_j \cdot \text{ordinate of center of mass}_j \right)}{\sum\limits_{j=1}^{n} \text{mass}_j} \right)$$

Acknowledgements

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