ASPECTS OF AMMONITE BIOLOGY, BIOGEOGRAPHY, AND BIOSTRATIGRAPHY

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With 11 plates, 5 tables, and
24 text-figures

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ABSTRACT. All ammonites appear to have passed through an initial planktonic larval stage, after which some assumed a nektobenthonic existence while others remained essentially nektonic or planktonic. Many may have lived segregated by sex or age, and juvenile and adult habitats may also have differed. Functional analysis of the shell and of what is inferred about ammonite musculature suggest that ammonites were generally poor swimmers when compared with many extant cephalopods. They were, however, well-adapted for depth changes as a result of their capacity to vary their density in relation to sea-water. Most appear to have exploited low levels in food chains and were perhaps largely benthonic herbivores or plankton feeders; some may have been higher-order carnivores and scavengers. They were in turn preyed upon by a variety of vertebrates and invertebrates, whilst several examples of cannibalism are known.

Distribution patterns shown by the group reflect both the occurrence of living animals and dispersal as a result of post-mortem drift. In general, five types of distribution are recognizable: pandemic, latitudinally restricted, endemic, disjunct, and post-mortem. Broad biofacies associations can sometimes be recognized, but there is no consistent pattern of relationship between morphotypes, or between morphotypes and presumed environments. The group as a whole is highly independent of facies in normal marine sediments, although there are subtle relationships between relative abundance *within* faunas, and sedimentary facies. Some heteromorphs show marked facies-linked distributions, which may reflect their benthic habits; yet others are facies independent.

Ammonites provide a biostratigraphical framework with zonal durations of as little as 0·2 million years, whilst global correlations of Triassic to Cretaceous sequences with a precision of from 0·5 to 3·0 million years zonal duration have been established. Evolutionary rates varied markedly within the group. When measured in terms of species longevity, the range is from 0·2 to 25·0 million years. There is no apparent link between species longevity, zonal duration, and regressive-transgressive cycles, although the broader patterns of evolution and extinction may be so related. Use of the group in biostratigraphy is limited by several factors, including limited geographic distribution, high intraspecific variability which masks geographic *versus* stratigraphical differences in populations, homeomorphy, sexual dimorphism, and problems of preservation and dissolution of the shell.

The broader geological implications of the distribution of ammonites in space and time are illustrated by five examples:

1. The European Boreal and Tethyan 'Realms' of the Jurassic and Cretaceous, where limited distributions and development of endemic elements resulted in a breakdown in correlation between the two areas from late Oxfordian to Hauterivian times.

2. The Western Interior region of North America; where the endemic nature of Late Cretaceous faunas, reflecting regional environmental conditions (including perhaps reduced salinity), allows a very fine biostratigraphy that cannot, for much of the interval, be correlated with sequences elsewhere in the world.

3. The southern limit of the European mid-Cretaceous Boreal 'Realm', which is marked by gradational faunas only in the area west of the Alpine front and corresponds in the east to a plate suture, along which dissimilar faunas are now juxtaposed.

4. A comparison of Late Cretaceous faunas of the western European-North African and the North American Western Interior-Gulf Coast-eastern seaboard, which shows that progressive differentiation and declining similarity coefficients can be linked to the opening of the North Atlantic.

5. A study of mid-Cretaceous distribution patterns along South Atlantic continental margins, where endemism in the southern Proto-Atlantic, developed in the early Late Albian, suggests the presence of barriers to north-south migration; but later Albian, Cenomanian, and post-Cenomanian distributions indicate an open seaway at these times.

INTRODUCTION

A REVOLUTION in our understanding of ammonites has taken place in the two decades which have elapsed since the publication of the Ammonoidea volume of the *Treatise on Invertebrate Paleontology*. Sexual dimorphism, dismissed as unproven at that time, has been demonstrated in a host of taxa and now finds general, if not universal, acceptance. Anaptychi, formerly regarded as operculae, are now known to be jaw structures, as may be calcareous aptychi. Radulae, ink sacs, crop contents, gills, and even egg masses of ammonites are now known, although no remains of tentacles or other external soft tissues, or indeed unequivocal trace-fossils produced thereby, have been described.

Elucidation of the function of the shells of the living *Sepia*, *Spirula*, and *Nautilus* and the mechanism by which they use their shells as a buoyancy apparatus has cast new light on the function of the ammonite shell, which has become the subject of a wide range of theoretical and experimental papers on functional morphology. Application of the relatively new techniques of scanning electron microscopy and isotopic analysis have added yet further insights into our knowledge of this wholly extinct group. The present contribution grew out of a review of the role of ammonites in biostratigraphy presented to the Paleontological Society of America in 1973 (Kennedy and Cobban 1973). We have tried to bring together published and unpublished data on ammonite palaeobiology, to review palaeobiogeographic patterns shown by the group, to discuss their biostratigraphical utility, and to give a series of examples of the broader geological significance of some aspects of their distribution in space and time.

Previous work in this field has been concentrated on Jurassic faunas, and, as well as discussing these, we have attempted to redress the balance by drawing on lesser-known Cretaceous examples. Although the theme of this paper is ammonites (that is to say the Phyllocerata, Lytocerata, and Ammonita of Arkell *et al.* 1957), there is so much data on pre-Jurassic forms which is relevant to our understanding of the biology of the group that we have at times strayed beyond our terms of reference.

In a review of this type there is much that is controversial, and much that is omitted. Literature relevant to topics such as sexual dimorphism, ontogenetic changes, variability, and the like would cover many pages, and produce an indigestible text. Ammonite workers have, however, the advantage of a first-class abstract service in the reviews by Otto Haas which have appeared in the *Journal of Paleontology* at regular intervals since 1958, to which the interested reader may refer, together with more general sources in the form of *Biological Abstracts* and the *Zoological Record*.

AMMONITE BIOLOGY

Ammonites were one of the dominant marine invertebrate groups during the Meso-zoic Era, and their remains are found in sediments deposited in a variety of normal marine environments ranging from the open sea to shore, and including clays through limestones to sandstones and conglomerates. Facies-linked distributions indicate that this wide occurrence is not entirely a reflection of post-mortem drifting, as does their typical absence or rarity in oolite shoal and hermatypic coral-bearing facies. Their absence, rarity, or reduced diversity in quasi-marine deposits indicate that the group was essentially stenohaline, although some recent cephalopod species are known to be tolerant of salinities down to 30% (Mangold-Wirz 1963; Hallam 1969).

Ammonites died out in the late Maastrichtian, and much of our knowledge of their mode of life and anatomy draws heavily on what is known of Recent cephalopods. It is thus particularly unfortunate that only one genus of externally shelled cephalopods survives, *Nautilus*, and this may be a poor model for comparison with ammonites, as is discussed below (Mutvei and Reyment 1973).

Reproduction. Sexes in Recent cephalopods are separate; many are strikingly dimorphic, but others differ only subtly. The existence of such dimorphism in ammonites was first suggested by de Blainville (1840) and d'Orbigny (1847), and after a long period of scepticism (see, for instance, Arkell *et al.* 1957, pp. L487–L490) has now found general if not universal acceptance and has been demonstrated in taxa of Devonian to Cretaceous age, both normally coiled and heteromorphic (Makowski 1962; Callomon 1963, 1969; Cobban 1969; Davis *et al.* 1969; Elmi 1969; Guex 1967*a*, 1968*a*; Lehmann 1966, 1968, 1971*a*; Palframan 1966, 1967, 1969; Sturani 1966; Westermann 1964, 1969*b*; Zeiss 1969*a*; Cope 1967).

The chief manifestation of dimorphism (Pl. 1, figs. 1–5) is size; forms whose early whorls are identical but which reach maturity at consistently different diameters. Large individuals (macroconchs) are thought to represent females; small individuals (microconchs) are believed to represent males (Callomon 1963). In Palaeozoic groups, females are two to four times as large as males (Makowski 1962); in the Jurassic they are often as much as five times larger. There do, however, seem to be


EXPLANATION OF PLATE 1

Sexual dimorphs

Figs. 1, microconch (*Kosmokeras* (*Spinikosmokeras*) *acutistriatum* Buckman) and 2, macroconch (*Kosmo-keras* (*Lobokosmokeras*) *phaenium* Buckman) from the *Peltoceras athleta* Zone Lower Oxford Clay (Callovian) of Christian Malford, Wiltshire (British Museum photographs, kindly supplied by Dr. M. K. Howarth).

Fig. 3, microconch and 4, macroconch of *Borissiakoceras* aff. *orbiculatum* Stephenson from the *Plesia-canthoceras wyomingense* Zone of the Belle Fourche Shale (late Cenomanian) at USGS Mesozoic locality 22871 on the north flank of the Black Hills uplift, south-eastern Montana. Both ×2.

Figs. 5*a–b*, microconch (USNM 131465) and 6*a–b*, macroconch (USNM 16308) of *Scaphites hippocrepis* (DeKay), both from the Cody Shale (early Campanian) at USGS Mesozoic locality 21206, 7 miles east of Hardin, Big Horn County, Wyoming.

1

3

4

2

5a

5b

6a

6b
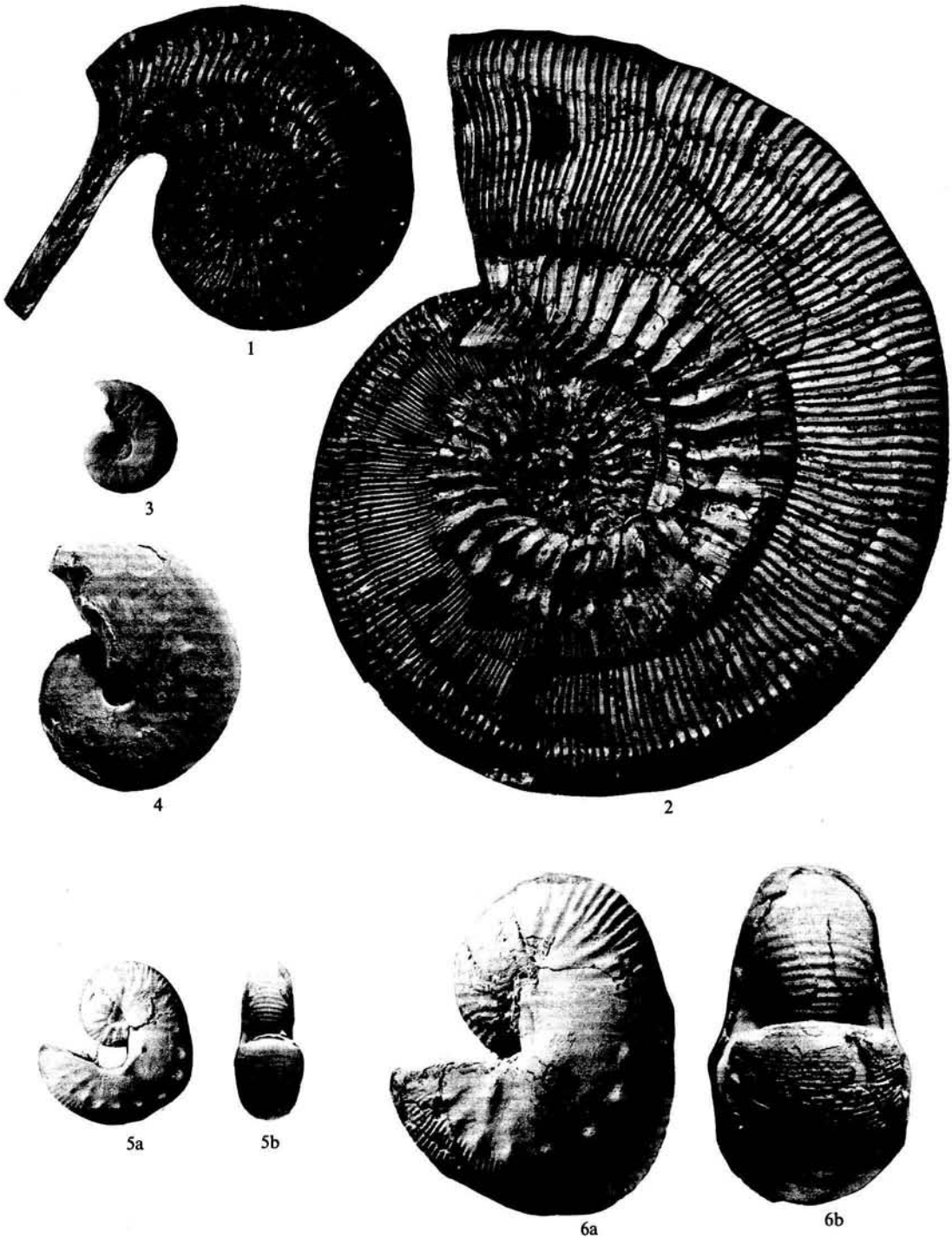
KENNEDY and COBBAN, Sexual dimorphs

some taxa where size differences are less, and only relative proportions differ, as in the case of living *Nautilus* and some extinct nautiloids (Wiley 1902; Teichert *et al.* 1964, with references; Tintant 1969).

Maturity in ammonites (excellent discussion of this topic is given by Hölder 1960 and Callomon 1963) can generally be recognized by:

1. A slowing of growth, indicated by the approximation of the last few septa, which often crowd, interfere with each other, and may simplify, lobes and saddles shortening (Arkell *et al.* 1957, pp. L97–L98, fig. 143; Hölder 1952; Lehmann 1971*a*).

2. A decline in ornament on the adult body chamber or a reversion to that of earlier ontogenetic stages. The body chamber of normally coiled forms may become slightly uncoiled.

3. Development of apertural processes.

Mature females tend to show changes in, or loss of, ornament on their body chambers. Males tend to retain their ornament throughout ontogeny, show a greater tendency toward eccentric coiling, and develop rostra, lappets (which first appear in the Toarcian), or other striking apertural modifications. The reason for these changes is obscure. Slowing growth accompanying sexual maturity is a common feature of organisms, whereas size differences might reasonably be interpreted as a reflection of the greater volume required to accommodate the ovaries of the females. Early workers considered that lappets might serve some grasping function during copulation, like the claspers of Lepidoptera. Lappets are, however, rigid calcareous structures, and such a use seems unlikely. A more reasonable interpretation is that these structures are related in part to modified soft tissues developed by adult males. In Recent *Nautilus*, for instance, the male develops a specialized copulatory apparatus, the spadix. Cope (1967) has suggested that the ventral horn and other ventral processes of microconchs may have housed a modified spadix, and, by insertion of the horn within the venter of the female, more successful fertilization might have been achieved. A. M. Bidder (*in* Westermann 1971) has suggested that ventral processes in male ammonites may have housed an equivalent of Van der Hoeven's organ, a secretory and sensory organ in male *Nautilus*; similarly, structures in female ammonites may have housed an equivalent of Owen's organ, a lamellate accessory sexual organ probably of olfactory function.

A further possible interpretation of the differences between dimorphs may be drawn by analogy with other vertebrate and invertebrate groups that are strongly dimorphic. The striking ornament and modification of the microconch may thus reflect sexual selection of these features and their importance in courtship rituals. Recent cephalopods are known to possess excellent vision for invertebrates; see, for example, Packard (1972, with references), and to have evolved complex courtship behaviour (Tinbergen 1939, 1951; Wells and Wells 1972) involving colour changes amongst other features, whilst colour patterns are a significant aid to intraspecific and inter-sexual recognition. Ammonites may well have possessed such abilities of colour display in addition to having developed ornately sculptured shells and colour bands, in part used in courtship.

One of the problems hindering the acceptance of dimorphism in ammonites has been the absence of 1:1 ratios in some collections, which may be dominated by

females in one case and males in another, and there are some instances in which males are simply very rare (Makowski 1962). These findings are, however, compatible with what little data are available for Recent cephalopods. Mangold-Wirz (1963; see also Westermann 1969a) reported that females significantly outnumbered males in sixteen Recent species studied; the reverse being true in only two instances. These differences are believed to reflect sexual segregation; the preponderance of males reported (in *Octopus vulgaris* and *Eledore moschata*) reflects the earlier withdrawal of females from feeding to egg-laying grounds.

Migration is, of course, widespread among Recent pelagic cephalopods; schools are frequently segregated and may consist of (a) adult males or adult females only, (b) adults of both sexes only, (c) juveniles of both sexes only, or (d) complete populations, mixed without regard to size or sex. The relevance of these associations to many fossil occurrences (e.g. Sturani 1971), which clearly do not represent average cross-sections of populations, is obvious: macroconch- or microconch-dominated fossil assemblages may thus be derived from sexually segregated shoals. Occurrences of adult-dominated fossil assemblages (breeding swarms, or mass-mortality assemblages following breeding?) are also common, as in the case of scaphitid heteromorphs, where most of the populations we have studied consist entirely of complete or fragmentary adults and no juveniles.

Development. Egg-like bodies associated with ammonoids have been reported by a number of workers. Lehmann (1966) described a mass of capsules 0·6–0·7 mm in diameter from within the body chamber of an adult macroconch of the Lower Jurassic ammonite *Eleganticeras*; Müller (1969b) has noted a similar occurrence in the living chamber of the mid-Triassic ammonoid *Ceratites*. The size of capsules is compatible with that known for ammonoid protoconchs, which presumably formed within the egg as in most other molluscs.

The early development of the ammonite shell (text-fig. 1) has been examined in detail by many workers, with recent interest centred on the development of the ultrastructure of the shell wall (early work is reviewed by Erben 1964; see also Birkelund 1967; Birkelund and Hansen 1968, 1974; Palframan 1967; Erben 1962, 1964, 1966; Erben et al. 1969; Grégoire and Voss-Foucart 1970; Bayer 1970; and Howarth 1975). Three basic phases in development are recognized by virtually all workers (although Drushchitz and Khiami (1970) believed that ammonites lacked a larval stage and that only two developmental stages of shell growth can be recognized!).

During the first growth stage, the primary wall of the protoconch was formed. It consists of subprismatic sublayers characterized by irregular distribution of organic matrix (= porcellaneous layer of Birkelund). During the second phase of development, which typically extends for 1·25–1·5 whorls from the protoconch to the nepionic constriction, a secondary wall is secreted within the protoconch and also forms the wall of the initial whorl as far as the nepionic constriction. This wall is built of prismatic sublayers (= porcellaneous layer of the first whorl of Birkelund). Shortly before the second change in growth at the nepionic constriction, the proseptum and flange are secreted as extensions of the innermost prismatic layers. The third phase of growth is marked by the nepionic constriction, which is characterized by a sudden interruption in growth at the aperture and by the first secretion
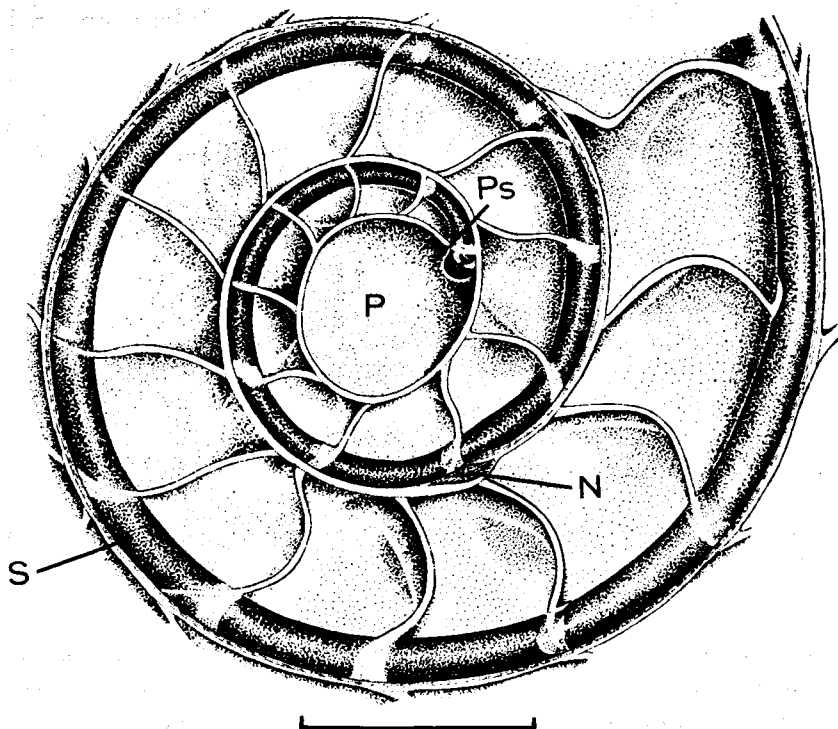
TEXT-FIG. 1. Early stages in ammonite development are illustrated by this specimen of *Discoscaphites* from the Upper Cretaceous of East Greenland (after Birkelund and Hansen 1968). P = protoconch; Ps = proseptum; N = nepionic constriction; S = siphuncle. The protoconch is believed to have developed within the egg, the septate whorls from protoconch to nepionic constriction during a free-living, perhaps planktonic, larval stage, whilst the nepionic constriction may mark a growth halt and metamorphosis to the post-larval state. Bar scale is 500 microns.

of an inner nacreous layer some distance back from the aperture. This nacreous layer thickens rapidly to produce the nepionic constriction, and remains an important shell layer during subsequent growth. As growth proceeds following the hiatus at the nepionic constriction, the primary septum is secreted at the adapical end of the body, and has a prismatic structure. All subsequent septa are built of nacre. The shell of the ammonoid during later growth consists predominantly of nacre with a thin outer prismatic layer, and an inner lining of prismatic habit, possibly equivalent to the myostraca in other molluscs (Taylor *et al.* 1969, 1973). Some groups also developed a 'double shell', lining the lateral and ventral parts of the shell (Guex 1970; Howarth 1973*b*, 1975), whilst Tozer (1972) and Nassichuk (1967) have described umbilical plug deposits and other secondary additions to the basic shell fabric in ceratites and goniatites respectively.

Interpretation of these developmental changes leans heavily on what is known in living *Nautilus*, where a constriction can be distinguished about 1·25 whorls from the apex of the shell, but unlike the constriction in ammonites, it is not characterized

by any marked change in shell secretion. Some workers (Wiley 1896; Stenzel 1957) have suggested that the constriction corresponds with the end of the embryonic stage, but recent work by Eichler and Ristedt (1966) and Davis and Mohorter (1973) has shown that *Nautilus* is only about 12 mm in diameter when it hatches and that the later constriction actually marks a change in life habits corresponding to migration from warmer to cooler water, which in turn might be equated with a change from a planktonic to nektobenthonic mode of life.

Erben (1964, 1966) and Erben *et al.* (1969) have, therefore, suggested that the first change in ammonite growth represents the end of the embryonic stage and hatching from the egg. The second stage represents a free-living, perhaps planktonic, larval stage, and the nepionic constriction, associated growth halt, and major changes in shell fabric, indicate metamorphosis and change to the post-larval state. That *Nautilus* lacks a larval stage and also possesses all of its shell layers from the apex strongly supports Erben's view.

Growth and age. Most living cephalopods, including *Nautilus*, reach maturity in one or two years and probably live several years longer (Denton and Gilpin-Brown 1966; Eichler and Ristedt 1966; Westermann 1971; Packard 1972, pp. 280–282). Growth rates of ammonites have been estimated on a number of independent lines of evidence; all suggest that they grew slower than *Nautilus* and lived longer. Stahl and Jordan (1969) and Jordan and Stahl (1970) have demonstrated cyclic fluctuations in palaeotemperature of secretion of successive septa of a number of Jurassic ammonites on the basis of oxygen isotope determinations on preserved aragonite. Their data show temperatures falling on a regular sinusoidal curve, with differences between temperature maxima and minima of approximately 9 °C. (text-fig. 2). Their data suggest that growth was continuous, and, if the data represent annual temperature fluctuations, the indication is of the addition of approximately five septa, or
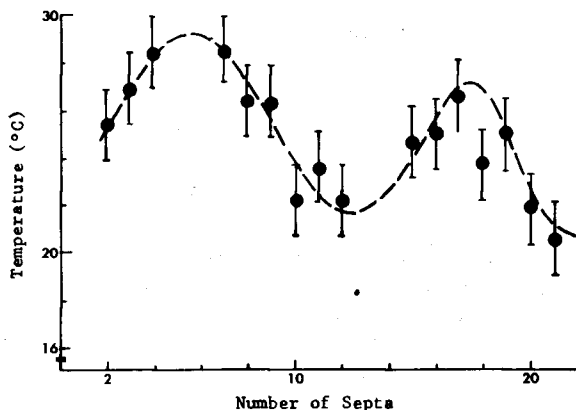
TEXT-FIG. 2. Palaeotemperatures from successive septa of the Jurassic ammonite *Staufenia* (after Jordan and Stahl 1971). Temperatures are based on oxygen isotope measurements of preserved aragonite. Maxima and minima are believed to represent summer and winter extremes; the curve thus covers two years of growth.

from one-third to one-quarter of a whorl (110°) per year. Adult ammonites generally had from five to nine whorls, indicating a minimum age at sexual maturity of between 16 and 30 years. We have, however, a collection of the Upper Cretaceous ammonite *Borissiakoceras* aff. *orbiculatum* Stephenson in which males show all features of maturity between diameters of 3 and 12 mm and females show mature features at diameters of 10–27 mm. These specimens possess at maximum only $3\frac{1}{2}$ whorls, indicating an age of about 11 years at maturity.

These figures for slow development find support from examples where ammonite growth can be related to that of epizoans that have living relatives, such as species of *Ostrea* and *Placunopsis* (Seilacher 1960; Merkt 1966; Meischner 1968; Westermann 1971) or Schindewolf's (1934) now classic account of Lower Jurassic *Schlothemia* growing in parallel with serpulids. Knowing the range of growth rates in living serpulids, Schindewolf estimated one whorl was added to the ammonite's shell during an interval of from four months to three years. This latter figure matches that calculated by Stahl and Jordan from their isotopic studies, and supports their interpretation that temperature fluctuations recorded in septa are seasonal, rather than the result of annual or biannual migration from warmer to cooler waters and vice versa. However, more general evidence, summarized by Westermann (1971; see also Müller 1970a for an estimate of ceratite longevity), suggests a substantially lower estimate of average age at maturity. Westermann noted that four to six cycles, probably reflecting seasonal shell growth, are indicated by (1) whorl section and coiling (Trueman 1941, fig. 5; Raup 1967, text-fig. 10; Raup and Chamberlain 1967, text-fig. 2); (2) spacing of septa (Oechsle 1958, fig. 7; Rieber 1963, figs. 9, 10); and (3) size groupings in what are believed to be mass-mortality associations, as in the case of the Lower Jurassic Marston Marble of England (Trueman 1941). An interesting suggestion from available estimates is that males (microconchs), which generally have fewer whorls than females (macroconchs), reach sexual maturity sooner.

Anatomy. We know little of the body anatomy of ammonoids. No trace of the external soft tissues of ammonites is known, although ammonites are common in sediments famous for the preservation of the soft tissues of coleoids, coelenterates, fish, and reptiles, as in the cases of the famous Upper Jurassic Solnhofen Limestone of Germany, the Lower Jurassic Hölzmaden Shales of Wurttemberg, Germany, and the Upper Cretaceous fish beds of the Lebanon, which have yielded a fossil octopus and coleoids (Roger 1946). No wholly convincing impressions of soft parts are known to be associated with sole marks produced by ammonites, even where they were made in sediments ideal for soft-part preservation, as in the case of the Solnhofen example figured by Rothpletz (1909; see also Arkell *et al.* 1957, fig. 158). A range of tentacular impressions, supposedly produced by ancient nautiloids is known (Flower 1955; Teichert *et al.* 1964), while impressions attributed to coleoid arms (*Asterichnites octoradiatus* Brown and Vokes), occur in the Cretaceous Mowry Shale of the Western Interior of the United States. This trace fossil (Vokes 1941; Brown and Vokes 1944) came from a sequence where coleoids are unknown, and ammonites are locally abundant, but no traces attributable to the latter have been described. Impressions attributed to ammonite arms by Trusheim (1934) and Kolb (1961, 1967) appear to have been produced by the shell alone (Seilacher 1963).

This curious lack of remains may reflect the delicate nature of those soft tissues of the ammonite that projected beyond the shell, or a withdrawal of the soft tissues into the shell at the time of death, or may even indicate that gases derived from decomposition expelled water from the body chamber, inflated tissues, and floated the shell to the surface. Mutvei and Reyment (1973) have suggested that this process may have taken only hours (Yochelson and Copeland (1974) described just this event in gastropods) and that within days shell and body dropped apart. True as this may be, there is evidence, discussed below, of burial of shells including more resistant internal organs, so that our ignorance of tissues external to the shell remains a major problem (although no greater than in the case of bivalves and gastropods). X-ray examination of pyritized Palaeozoic cephalopods (Zeiss 1968, 1969*b*; Stürmer 1967, 1968, 1970) has revealed traces of what appear to be tentacular crowns, mantle sacs, and internal organs. Unfortunately, no similar studies on pyritized ammonites are available.

Ink sacs. Almost all Recent cephalopods possess ink sacs; only the largely nocturnal *Nautilus* and a few deep-sea forms are exceptions. The sacs vary greatly in size; in *Sepia* the sac is 50% of the body length; in *Octopus* and *Loligo* it is less than 25% of body length. The purpose of the ink sac is defensive. In part the ink may affect the olfactory organs of predators; it also serves as a decoy, for the ink cloud resembles the producer in shape and size and is attacked by the pursuer while the pursued animal itself escapes (Packard 1972). The lack of ink sacs in *Nautilus* and others reflects their nocturnal habits or the low light intensities in the abyss they inhabit.

Fossil ink sacs have long been known in coleoids and are now known to occur in ammonoids; Lehmann (1967*b*) has noted sacs in the Lower Jurassic harpoceratinid *Eleganticeras*, whilst Wetzel (1969) described a comparable occurrence in the Lower Cretaceous heteromorph *Bochianites*; their widespread occurrence thus seems very probable. The ink sacs are pear-shaped, with a long narrow tube directed adorally. Lehmann has described remains of glandular tissue in the marginal areas of sacs, ink (black or brown in colour) being concentrated in the centre. Sacs are about one-quarter of the length of the body chamber.

Musculature. The nature of ammonite musculature has been inferred by a number of workers, conclusions being based on the presence of either muscle scars on internal moulds or traces of myostracal layers within the shell. In general, muscle scars are restricted to, or best developed in, adult body chambers; this is presumably a reflection of their permanence as compared to the transient nature of attachment during growth of the phragmocone. Interpretation of musculature is based upon what is known from Recent *Nautilus* (Teichert *et al.* 1964; Mutvei 1957, 1964*a–b*; Mutvei and Reyment 1973). Here, mantle tissues forming the roof of the mantle cavity are intimately associated with a pair of retractor muscles which originate from the lateral, inner faces of the shell wall in front of the edge of the last septum and extend to the head, where they are inserted into the cephalic cartilage. Their function is to attach the soft body to the shell, to withdraw it into the body chamber (as with the columellar muscles in gastropods), and, also, to aid in swimming (Mutvei and Reyment 1973, pp. 632–633). The remaining attachment areas are along the lateral

and ventral parts of the aperture, in a band 1·0–1·5 cm wide; a tract around the back
of the body chamber where the visceral sac is attached by the periphract; and an
attachment tract around the septal contour, where the mantle cover of the visceral
sac is attached.

The classic work on ammonite musculature is Crick's (1898) monograph, in
which muscle impressions in a score of normally coiled and heteromorph forms were
described and early records (Oppel 1862–1863; Trautschold 1870; Waagen 1870;
Eck 1879; Mojsisovics 1873, etc.) discussed. Subsequent workers doubted Crick's
conclusions (see, for instance, Spath 1919; Arkell *et al.* 1957), but recent work by
Mutvei (1957, 1964*b*), Jones (1961), Jordan (1968), Palframan (1969), and Mutvei
and Reyment (1973) have confirmed them.

Thus the scars (Pl. 2, figs. 1*a–b*, 5) for the attachment of the paired retractor
muscles to the shell wall are typically situated on the dorsal face of the body chamber,
irrespective of coiling and shell shape. As in *Nautilus*, these paired muscles pre-
sumably extended to the head and were attached to the cephalic cartilage, but because
of their dorsal position and the curvature of body chambers, they must have lain
in the dorsalmost portion of the body over much of their length (Mutvei and Rey-
ment 1973, p. 633, text-fig. 8), and thus seem not to have been in juxtaposition with
the roof of the mantle cavity. These differences are of fundamental importance in
determining the possible swimming abilities of ammonites. In addition to the paired
retractor muscles of ammonites, there is commonly a small unpaired ventral scar,
indicating a muscle insertion in this area (Crick 1898; Mutvei *in* Mutvei and Rey-
ment 1973 and our own observations). This muscle finds no equivalent in living
Nautilus nor in Palaeozoic ammonoids; it may, however, be homologous with the

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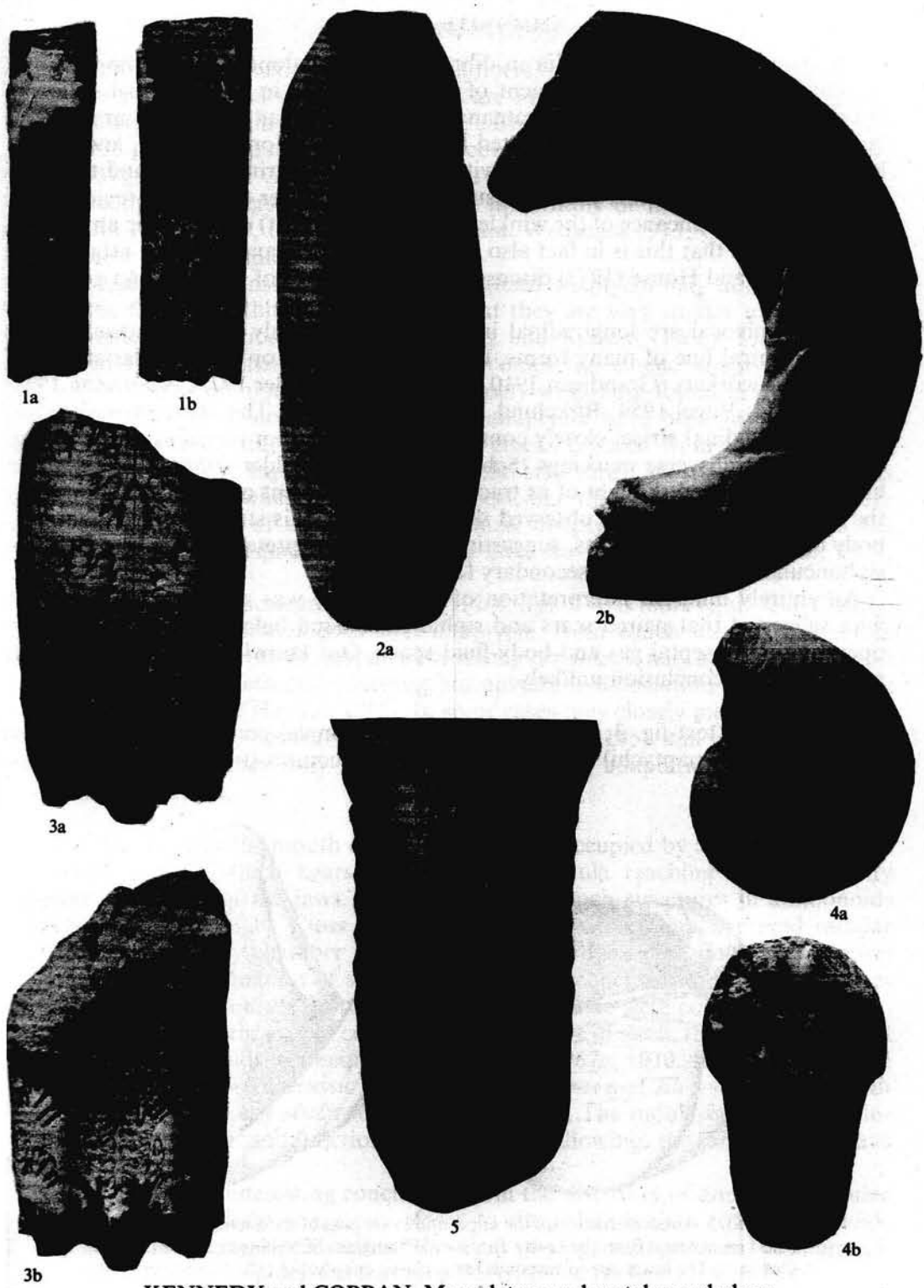*Musculature and septal morphology*

Fig. 1*a–b*. Dorsal and lateral views of an internal mould of the last few chambers and the posterior end
of the phragmocone of *Baculites codyensis* Reeside showing the paired dorsal muscle scars, believed to
represent the sites of insertion of retractor muscles. From the Marias River Shale (Santonian) at USGS
Mesozoic locality 21425 near Shelby, Montana.

Fig. 2*a–b*. Ventral and lateral views of an internal mould of the tetragonitid *Saghalinites cala* (Forbes).
Constrictions on the mould as seen in lateral view represent the site of thickenings of the shell corre-
sponding to growth halts and the development of a temporary apertural position. The ventral view shows
a well-developed siphonal band extending throughout the length of the body chamber. From the late
Campanian, St. Lucia Formation of Zululand, South Africa. BMNH C78863.

Fig. 3*a–b*. Ventral and dorsal views of an internal mould of four successive camerae of a specimen of
Saghalinites cala from the same horizon and locality as in fig. 2*a–b*. Delicate longitudinal striations can
be seen on the siphonal band (Schelppstreifen), believed by some workers to be associated with attach-
ment sites of siphuncular ligaments. Details of the internal suture and delicate septal lobe are visible
in 3*b*. BMNH C78855.

Fig. 4*a–b*. Lateral and apertural views of *Tetragonites subtimotheanus* Wiedmann from the Upper Albian
Mzinene Formation of the Skoenberg region, lower Mzinene River, Zululand, South Africa. The
specimen bears the shell, replaced by calcite; the lateral view shows periodic collars and constrictions
indicating temporary apertural positions. BMNH C88836.

Fig. 5. Dorsal view of the posterior end of the body chamber of *Aegocrioceras quadratum* Crick, showing
paired dorsal muscle scars. BMNH 89102 from the Hauterivian Speeton Clay of Speeton, Yorkshire.

KENNEDY and COBBAN, Musculature and septal morphology

retractor muscles of the ctenidia in dibranchiate cephalopods. Other impressions, possibly associated with attachment of the mantle fold in the apertural region of the shell have been noted by Palframan (1969) and annular attachment areas at the back of the body chamber were noted by Crick (1898), Jordan (1968), and others. In addition, thickenings of the shell within the umbilical rim and around the aperture may represent further aids to tissue attachment. Bayer (1970) has reviewed the structure and significance of the winkle layer (runzelschicht) of Mesozoic ammonites and concluded that this is in fact also an area for muscle and ligament attachment; Tozer (1972) and House (1973) discussed similar features of ceratites and goniatites respectively.

More equivocal are longitudinal impressions commonly found associated with the mid-ventral line of many forms, the 'siphonal band' or 'siphuncular structure' of previous workers (Grandjean 1910, pp. 502–503; Kessler 1923; Neaverson 1927; Hölder 1954; Vogel 1959; Birkelund 1965; Jordan 1968). This structure commonly shows longitudinal striae, closely connected with the minor incisions of the ventral saddle, and transverse markings (Schelppstreifen of Hölder 1954). These features have generally been thought of as traces of the attachment of ligaments supporting the siphuncle, but we have observed the extension of this structure throughout the body chamber in some forms, suggesting that this interpretation is in error, or that siphuncular attachment is a secondary feature.

An entirely different interpretation of musculature was given by Jordan (1968) who suggested that paired scars and siphuncular band belong to a muscle system operating a pre-septal gas and body-fluid space. Our knowledge of living *Nautilus* makes this last conclusion unlikely.

Jaws. Aptychi (text-fig. 3; Pl. 3, figs. 1–3), either single, unmineralized conchiolin objects (strictly anaptychi) or paired calcareous structures (true aptychi) have long
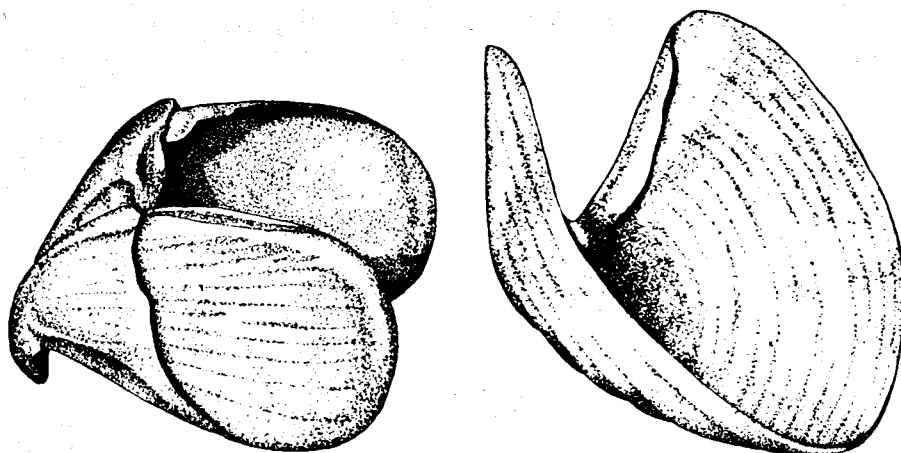
TEXT-FIG. 3. A reconstruction of the upper and lower jaws of the ammonite *Psiloceras*, based on material from the Lower Jurassic (Hettangian) of Nellingen, near Stuttgart, Germany. The lower jaw corresponds to the classic anaptychus (after Lehmann 1970).

been known to occur within the body chambers, or in some cases, closing off the apertures of ammonoid shells. Anaptychi are known from the Devonian to Late Cretaceous; true aptychi first appear in the early Jurassic (Trauth 1927, 1928, 1930, 1931, 1936 provides the most exhaustive account of these structures; see also Arkell *et al.* 1957). The classic view is that these are opercula, but a series of elegant studies by Lehmann and others suggests that they are wholly or in part ammonite jaws (Lehmann 1967*a*, 1970, 1971*a-b*; Lehmann and Weitschat 1973; Closs and Gordon 1966; Closs 1967; Schmidt-Effing 1972).

Lehmann has demonstrated that unmineralized anaptychi may in fact consist of two parts, the one within the other, and that they are very similar to the jaws of Recent coleoids described by Mangold-Wirz and Fioroni (1966). The lower jaw separated from the shell and flattened, becomes the classic anaptychus, whilst the upper jaws of ammonites correspond closely with those found in living octopi. As Lehmann (1971*a*) noted, most isolated anaptychi have been secondarily flattened into a plane, and, as a consequence, cracks proceed from the rim inward, a feature hardly to be expected in originally flat structures. Most anaptychi possess a notch at the apex, whilst others have a beak-like thickening; both features are observed in the jaws of coleoids. In addition, anaptychi never fit well into the apertures of the corresponding ammonites (see, for instance, Arkell *et al.* 1957, fig. 146).

The nature of paired calcareous aptychi (Pl. 4, figs. 1-4) is more equivocal. Clearly, these structures are homologous with anaptychi, from which they have evolved. Their form, especially the development of strong ornament, may suggest an adaptation for specialized methods of feeding, for aptychi in association with upper jaws are known (Meek and Hayden 1865). In some cases they closely match the aperture of shells in which they occur (e.g. Arkell *et al.* 1957, fig. 145), and we would suggest the possibility that they may have indeed undergone adaptation to a secondary function as opercula.

Radula. The floor of the mouth of living *Nautilus* is occupied by a large tongue (the subradular organ) which bears a long-toothed radula reaching into the cavity between the beaks of the jaws. The occurrence of such structures in ammonoids was first documented by Closs and Gordon (1966) who found scattered radular teeth within the body chamber of a specimen of the Permian goniatite *Eosianites* from the Itararé Formation of southern Brazil. Subsequently (Closs 1967) a series of specimens with exquisitely preserved jaws and radulae were collected (Pl. 5, figs. 1-3); they show that the radula consisted of seven rows of teeth, the condition found in most Recent coleoids. Subsequently, Lehmann (1967*a*, 1970, 1971*a-b*) described radulae from the Lower Jurassic ammonites *Arnioceras* and *Eleganticeras*. As with *Eosianites*, there are only seven rows of simple teeth. The radula in living cephalopods is usually simple, and functions as an aid in swallowing: the same seem to have been true in ammonites.

Perhaps the most interesting conclusion from the discovery of ammonite radulae is that their form places the group closer to the coleoids than to the nautiloids (Lehmann 1971*a*) as was predictable from their phylogenetic position, both ammonoids and coleoids being derived from the Bactritoidea (Erben 1964, 1966).

Crop and food. The food of ammonites has been graphically demonstrated by a
number of records of actual crop or stomach contents from *Arnioceras, Hildoceras,*
Oppellia, and *Physodoceras* (Lehmann 1971a; Lehmann and Weitschat 1973).
Perhaps the earliest described occurrence is the specimen of *O. steraspis* from the
Solnhofen Limestone of Germany with a mass of tiny broken aptychi, shell, and
siphuncle fragments within its body chamber figured by Michael (1894). Michael
interpreted this mass as the remains of unborn young; Gürich (1924) and Schwarz-
bach (1936) subsequently suggested the occurrence might represent a case of can-
nibalism. This view has been confirmed by Kaiser and Lehmann (1971); ammonite
crop contents now recorded include masses of ammonite shell debris, radulae and
aptychi, Foraminiferida, and ostracods. Further direct evidence of food may come
from the interpretation of the common Solnhofen trace-fossil *Lumbricaria* as
cephalopod faeces (Müller 1969a; Janicke 1970—although Van Straaten 1971 would
regard them as reptilian faeces) suggesting in this case that the pelagic crinoid
Saccocoma was a major food source.

The jaws and radulae of ammonites resemble those of Recent cephalopods, and
presumably acted in a similar fashion. The jaws cut food (*Nautilus* can deal with
chicken bones (Teichert *et al.* 1964, p. 39)) and the simplified radula helps transport
it to the stomach. There is thus no evidence for a grazing or predatory habit as
developed by gastropods, with consequent radular specialization (although *Octopus*
is known to bore into bivalve and gastropod shells).

If comparisons with *Nautilus* (where food consists largely of fish and arthropods)
are valid, a part carnivorous, part scavenging habit, feeding close to the bottom
seems likely for at least some forms. However, ammonites are a diverse and variable
group, and a single feeding strategy seems unlikely. Their very abundance suggests
they may have exploited the lower levels in feeding pyramids, either as benthonic
herbivores or as plankton feeders. The reduced apertures of some mature forms (see,
for instance, Arkell *et al.* 1957, fig. 131) might suggest that these at least were micro-
phagous (see also Berry 1928; Bayer 1970), or that they broke up their food prior
to ingestion. Lehmann (1971b) has suggested that many ammonites were vegetarian
or carrion feeders, or that they fed upon slow-moving organisms such as gastropods.
Mutvei and Reyment (1973) have suggested that most were plankton feeders, being
influenced by their conclusion that many ammonites possessed poor swimming

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EXPLANATION OF PLATE 3

Jaws and aptychi

Fig. 1a–b. Crushed composite moulds of *Oppellia lingulata* from the Tithonian Solnhofen Limestone of
Solnhofen, Bavaria. In 1a, USNM 1658, the lower jaw—*Lamellaptychus*—is lying in the ventral posi-
tion; in 1b, USNM 29195, the aptychi lie in the apertural position. The former has been considered as
that of the 'operculum' when withdrawn, the latter as the 'opercula' brought forwards to close off the
aperture.

Fig. 2a outer and 2b inner surface of *Laevaptychus latus*—an ammonite lower jaw—from the Tithonian
Solnhofen Limestone of Solnhofen, Bavaria. USNM, unregistered specimens.

Fig. 3a natural mould and 3b silicone squeeze of a crushed lower jaw—*Anaptychus*—attributed to the
hoplitid ammonite *Neogastroplites americanus* (Reeside and Weymouth) from the late Albian Mowry
Shale at USGS Mesozoic locality 17934, Park County, Wyoming. USNM 129548.
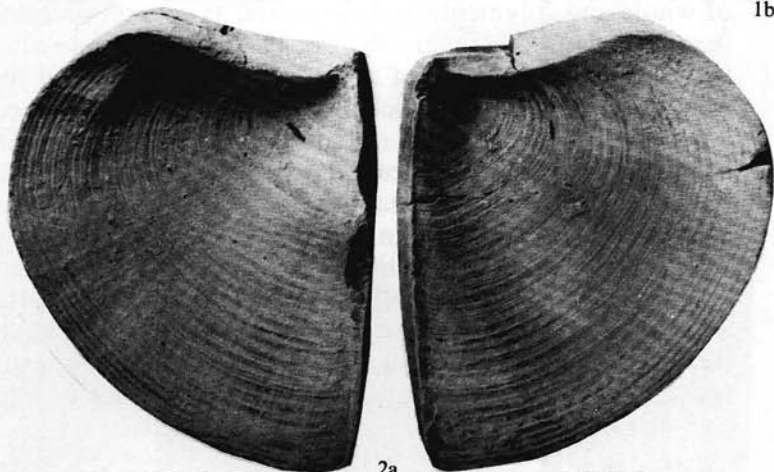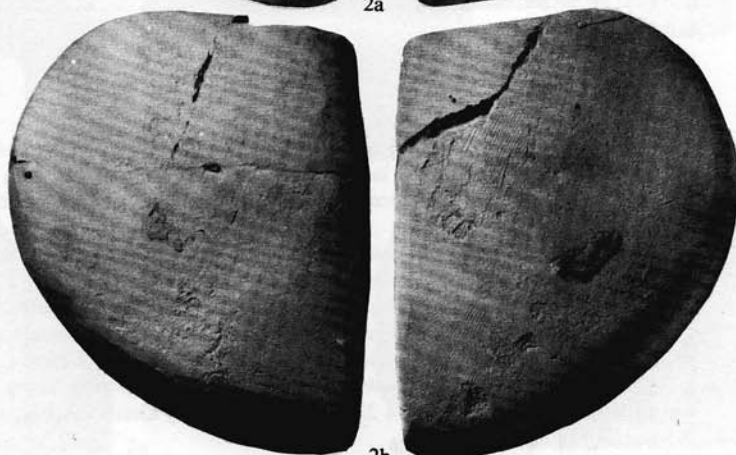
KENNEDY and COBBAN, Jaws and aptychi
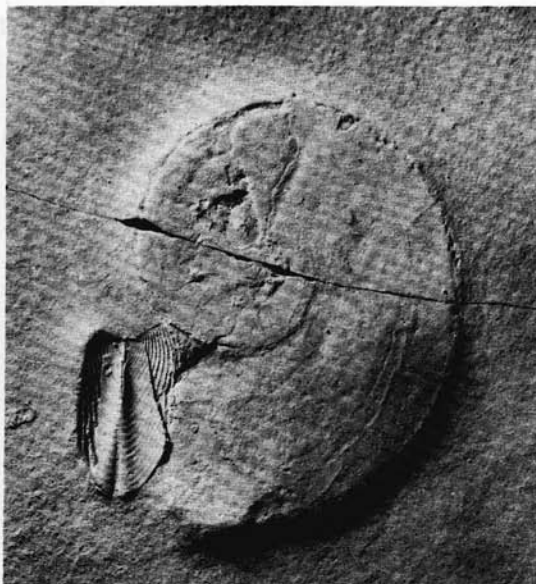
ability but were well adapted to move vertically through the water column. There-
fore, one might envisage feeding habits similar to those known for some Recent
cephalopods, following the diurnal vertical migration of, and feeding on, plankton;
a mode of life like that of the Recent ommastrephid squid *Todarodes*, which migrates
up and down through a water column of 400–700 m, as a light-induced circadian
response as in *Sepia* (Denton and Gilpin-Brown 1961*a–c*; Denton *et al.* 1961). This
species is a second-order carnivore with a mixed diet of fish, crustacea, and molluscs,
and is enormously successful. Clarke (1966) estimated that 24×10^8 individuals of
the common Japanese species *T. pacificus* of average weight 250 gm were caught in
a single year (1952); such habits and consequent success are compatible with the
extraordinary abundance of many ammonites.

Gills. Obscure structures interpreted as gills have been described in a single instance
(Lehmann and Weitschat 1973).

Predators. If feeding habits are poorly known, predators on ammonites are even
less understood. Frentzen (1936) has described specimens of the Lower Jurassic
ammonite *Amaltheus* from saurian stomach contents, and the occurrence of masses
of whole and fragmentary shells (often as concretion nuclei) has led some workers
(e.g. Reeside and Cobban 1960, pp. 25–26) to speculate whether these might represent
the faecal accumulation of some large carnivore, be it reptile, fish, or cephalopod
(see also Barthel and Janicke 1970). Roll (1935) ascribed chunks bitten from the
back of the body chamber of haploceratid and oppellid ammonites to the activities
of predatory decapods; decapod predation on the Cretaceous perisphinctid *Endemo-
ceras* is described by Thiermann (1964), whilst Kauffman and Kesling (1960) described
a large (30 cm) Campanian *Placenticeras meeki* Boehm whose sad fate was to be
bitten (no less than sixteen times) by a platecarpine mosasaur. Their detailed analysis
of the specimen indicates that the mosasaur attacked the ammonite from above,
and, from the changing tooth impressions of successive bites, attempted to swallow
it. They conclude that the mosasaur was in the habit of eating ammonites; Kauffman
(pers. comm.) has subsequently collected further examples of *Placenticeras* and


EXPLANATION OF PLATE 4

Jaw apparatuses

Fig. 1*a–d*. *In situ* jaw apparatus of the heteromorph ammonite *Discoscaphites cheyennensis* (Meek and
Hayden). 1*a* and 1*c* show the lateral aspect, 1*b* the ventral, and 1*d* a natural mould of one-half of the
lower jaw. USNM 386 'Cretaceous no. 5, Moreau River, Dakota'—in fact from the Maastrichtian Fox
Hills Sandstone.

Fig. 2*a*. Natural cast of upper jaw attributed to the hoplitid ammonite *Neogastroplites americanus* from
the late Albian Mowry Shale at USGS Mesozoic locality 17934, Park County, Wyoming. 2*b* is the
counterpart, showing a natural mould of both upper and lower jaws. USNM 12954.

Fig. 3. Natural cast of upper jaw attributed to *Neogastroplites cornutus* (Whiteaves) from the basal part
of the Mowry Shale at USGS Mesozoic locality 23021, Park County, Wyoming.

Fig. 4*a* lateral and 4*b* frontal views of an uncrushed ammonite lower jaw, the holotype of *Anaptychus
knoxvillense* (Stanton), USNM 23095, from the early Cretaceous Knoxville Formation near Knoxville,
Napa County, California.
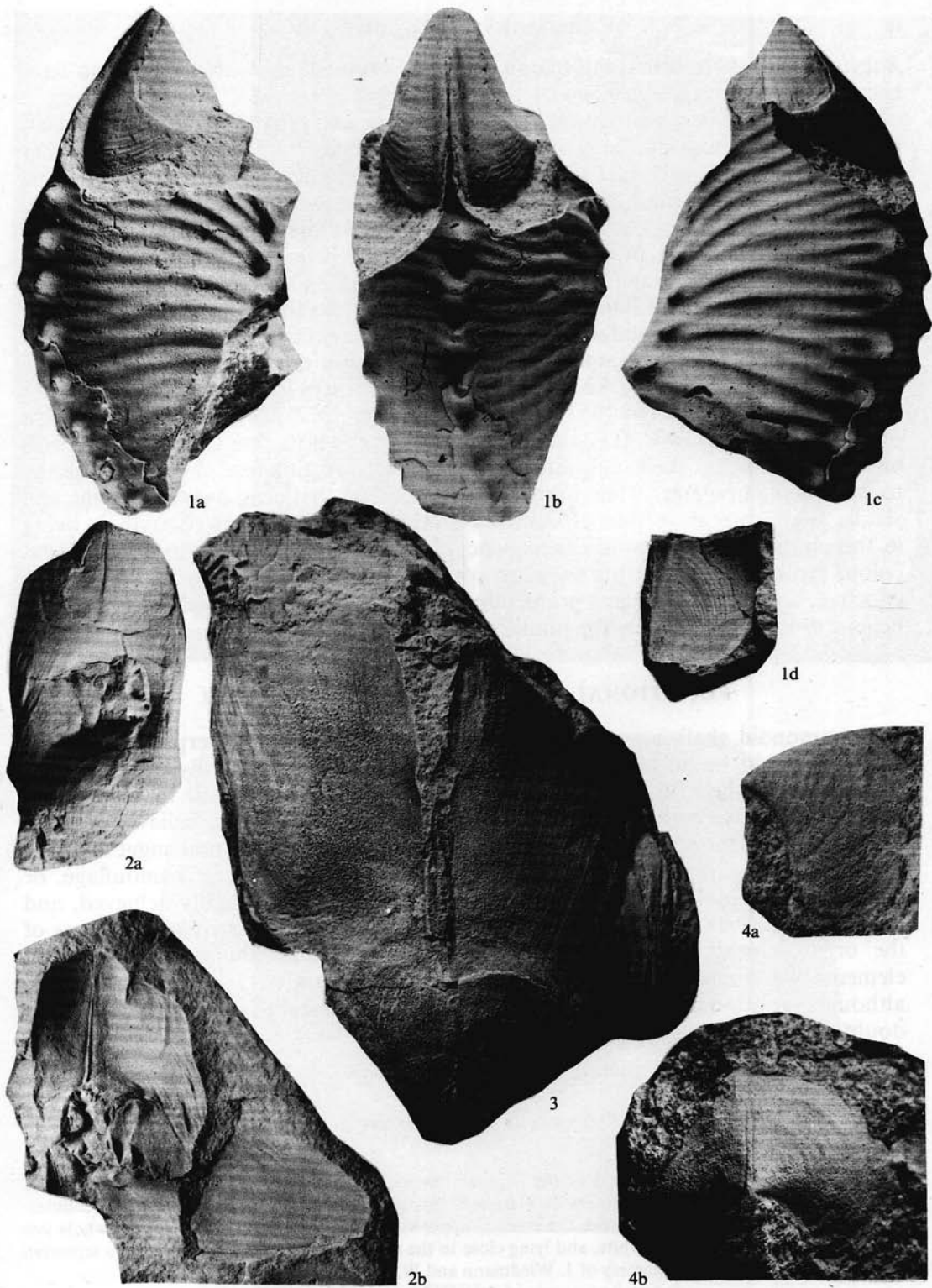
KENNEDY and COBBAN, Jaw apparatuses

Baculites with mosasaur tooth-marks. Cases of cannibalism within the group have been discussed above under *Food*.

There is a considerable literature on shell damage and repair in ammonites (recent papers include those by Nagy 1964; Guex 1967*b*, 1968*b*; Théobald 1958; Müller 1970*a–b*; Bayer 1970; Hölder 1970; Lominadze 1970), leading to various asymmetric individuals, monstrosities and the like, but few of these can be definitely attributed to predation. Some groups, notably hoplitids and scaphitids, appear to show higher frequencies of damage of this type than others such as macrocephalitids (H. S. Torrens, in litt.), although the reason for this remains obscure. Bayer (1970), in a study of Aalenian and Bajocian ammonites, suggested that variation in frequency of damage might reflect different modes of life (e.g. nektonic *versus* benthonic).

Indirect evidence that ammonites suffered predation might be adduced from the presence of colour banding, known in some rare instances (e.g. Spath 1935; Schindewolf 1928, 1931; Reyment 1957; Pinna 1972; Tozer 1972), and presumably a form of protective camouflage. It is, therefore, interesting to note that Cowen *et al.* (1973) have suggested that shell sculpture in ammonites (ribs, tubercles, keels) also serves to provide camouflage. They argue that camouflage patterns deal with light and shade, that sculpture produces shadows and breaks up outlines of animals living in the photic zone and is, in consequence, functionally equivalent to a permanent colour pattern. Colour patterns, when combined with ornament, would be doubly effective, and might also give protection to the smooth forms which these authors believe to have lived below the photic zone.

FUNCTIONAL MORPHOLOGY OF THE SHELL

The ammonoid shell is a complex structure, and any single interpretation of its function would be naïve. Early workers often drew fundamentally opposed conclusions as to shell function; thus Berry (1928) believed the shell to serve in an entirely protective role, while Beurlen, writing in the same year, believed it to be primarily a hydrostatic organ. Subsequent workers have in addition suggested that various features might have been strengthening devices, forms of camouflage, or the result of sexual selection. All of these functions were probably achieved, and individual features contributed in differing degrees towards the over-all success of the organism. The widespread and repeated homoeomorphy seen between all elements of ammonoid shell morphology point to the adaptive value of these features, although variations in relative importance and role throughout ontogeny cannot be doubted.
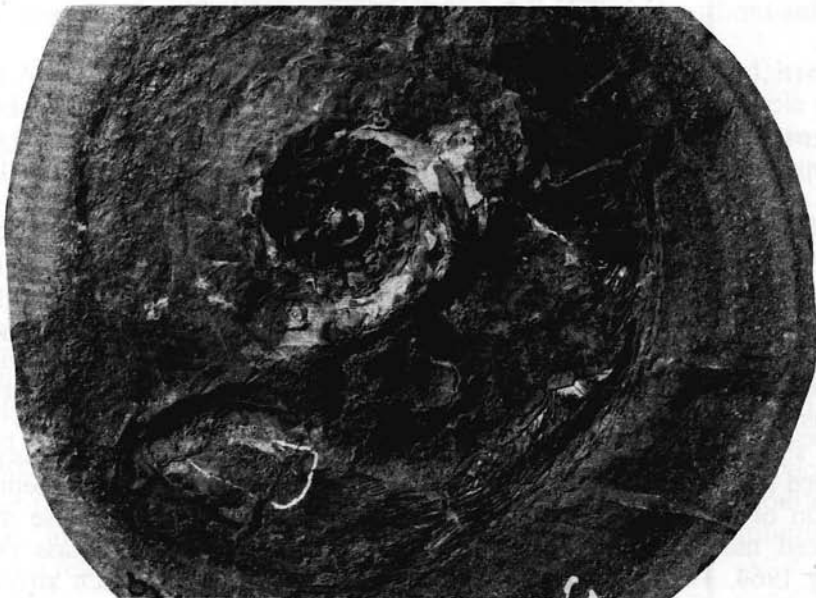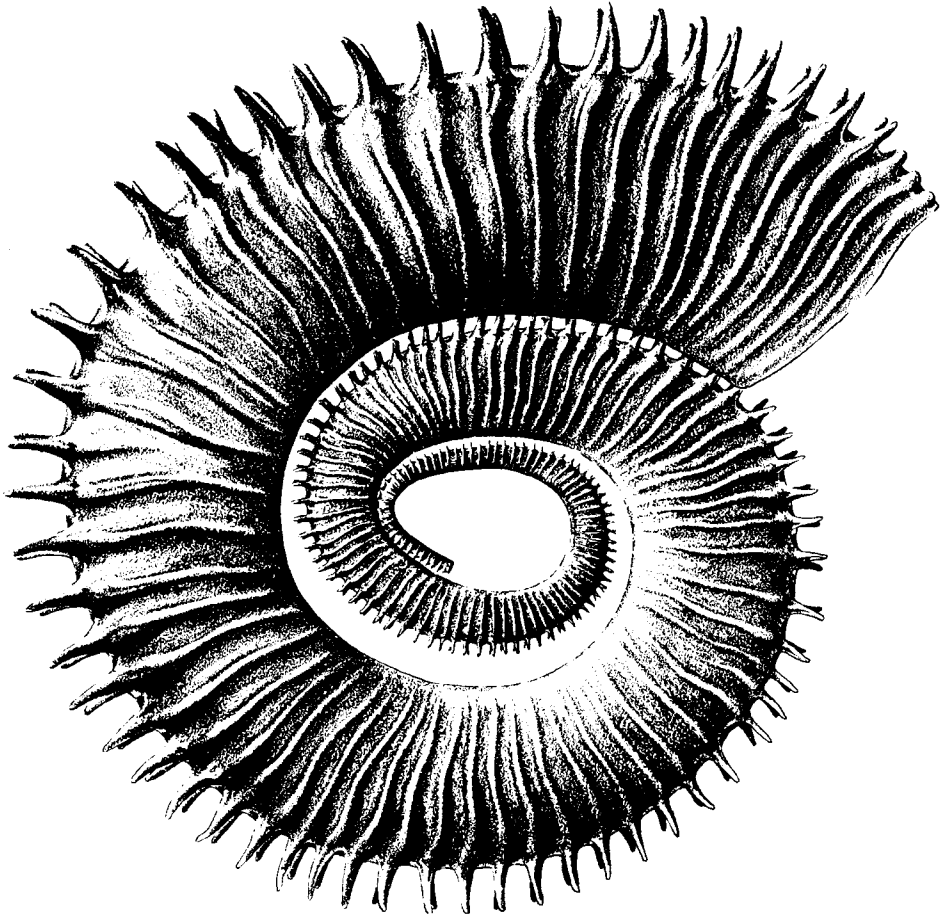

KENNEDY and COBBAN, Jaws and radula

TEXT-FIG. 4. A reconstruction of the Campanian heteromorph *Exiteloceras jenneyi* (Whitfield), based on material from the Pierre Shale of Colorado (after Scott and Cobban 1965).

Shell function in Nautilus. The shell of *Nautilus* serves two prime functions: as a protection for the soft parts, and as a hydrostatic device. Inasmuch as cephalopods evolved from benthonic ancestors, the protective function would seem to have been original (together with secondary functions such as providing a base for muscle insertion and possibly serving as a frame, making possible the development and maintenance of a mantle cavity). Subsequent evolution has, however, resulted in emphasis of hydrostatic function.

The shell of *Nautilus* is built up of aragonite and proteinaceous organic matrix arranged into outer prismatic and inner nacreous layers, as are the septa. The combination of organic and inorganic materials produces a two-phase material with enhanced mechanical properties analogous to bone or fibreglass (Evans 1957; Currey 1964, 1970; Taylor and Layman 1972). Nacre is much stronger in both bending and compression than bone, and is an ideal construction material; in addition, it possesses a high apparent microhardness. It is also the structure most

widespread in the molluscan classes (Taylor *et al.* 1973; Taylor 1973). Prisms, on the other hand, lack such good mechanical properties, but are a fabric that can be seeded and grown rapidly. The construction of nautiloid shells may thus represent a compromise between growth and strength requisites (Taylor and Layman 1972). Added to this mechanical strength of the building materials is their combination with a geometric form of shell and septa (Moseley 1838; Raup 1966, 1967; Seilacher 1973, 1975) which result in a structure of great strength produced with a high economy of building materials.

The hydrostatic function of the nautiloid shell is obvious. The gas in the chambers counteracts the weight of shell and body, so that the animal is able to devote its energies to locomotion only and need not expend them on the prevention of sinking (Teichert *et al.* 1964). We now know that successive chambers, as produced, are fluid-filled, and that fluid is pumped out by the animal and its place taken by Argon-enriched air (Bidder 1962, 1965). The gas filling is a passive process, the result of diffusion. The work of Bidder (1962) and Denton and Gilpin-Brown (1966) demonstrated that living *Nautilus* possesses slight positive to slight negative buoyancy, and that weight adjustments for shifts in hydrostatic conditions are made by the secretion or transfer of relatively small quantities of liquid via the siphuncle, which also serves to drain fluid from newly formed chambers. Volume of fluid not only controls buoyancy; its distribution also serves to add to shell stability.

The gas in *Nautilus* chambers is close to atmospheric pressure in all but the last-formed chambers; shell and septa serve to prevent implosion at depth (*Nautilus* has been collected live at depths of up to 180 m, see also Raup and Takahashi 1966; Westermann 1973). Calculations and experiments on the weakest part of the phragmocene, the siphuncular tube (Denton and Gilpin-Brown 1966; Collins and Minton 1967) indicate that *Nautilus* can extend to depths of at least 480 m without suffering implosion.

The shell of *Nautilus* bears striking colour markings, consisting of broad, irregular, transverse red, brown, and white stripes. These are present over the whole of the juvenile shell; in adults, the ventral and lateral areas of the body chamber are white. *Nautilus* thus shows classic camouflage patterns (Cowen *et al.* 1973). The stripes are disruptive, breaking up shell outline in profile against the sea-bed, whilst the adults show typical countershading, as in many fish (and other animals, e.g. zebra, wildebeest, etc.). The changing distribution of colour markings during ontogeny probably reflects the differences in life habits of the benthonic juveniles and nektobenthonic adults (Eichler and Ristedt 1966; Cowen *et al.* 1973).

Shell function in ammonites. From the above review of *Nautilus* we may conclude that the shells of ammonites fulfilled similar functions, with protection and flotation the most important. So far as shell structure is concerned, ammonites have reduced the phylogenetically primitive outer prismatic layer, retaining a thickened nacreous layer to which is added a myostracum. The remainder of ammonite shell architecture is, however, far more diverse than that observed in nautiloids, and many additional features developed, as discussed below.

Shell shape. The ammonite shell typically grew as a close approximation to a logarithmic spiral, and can be expressed mathematically in terms of a few simple
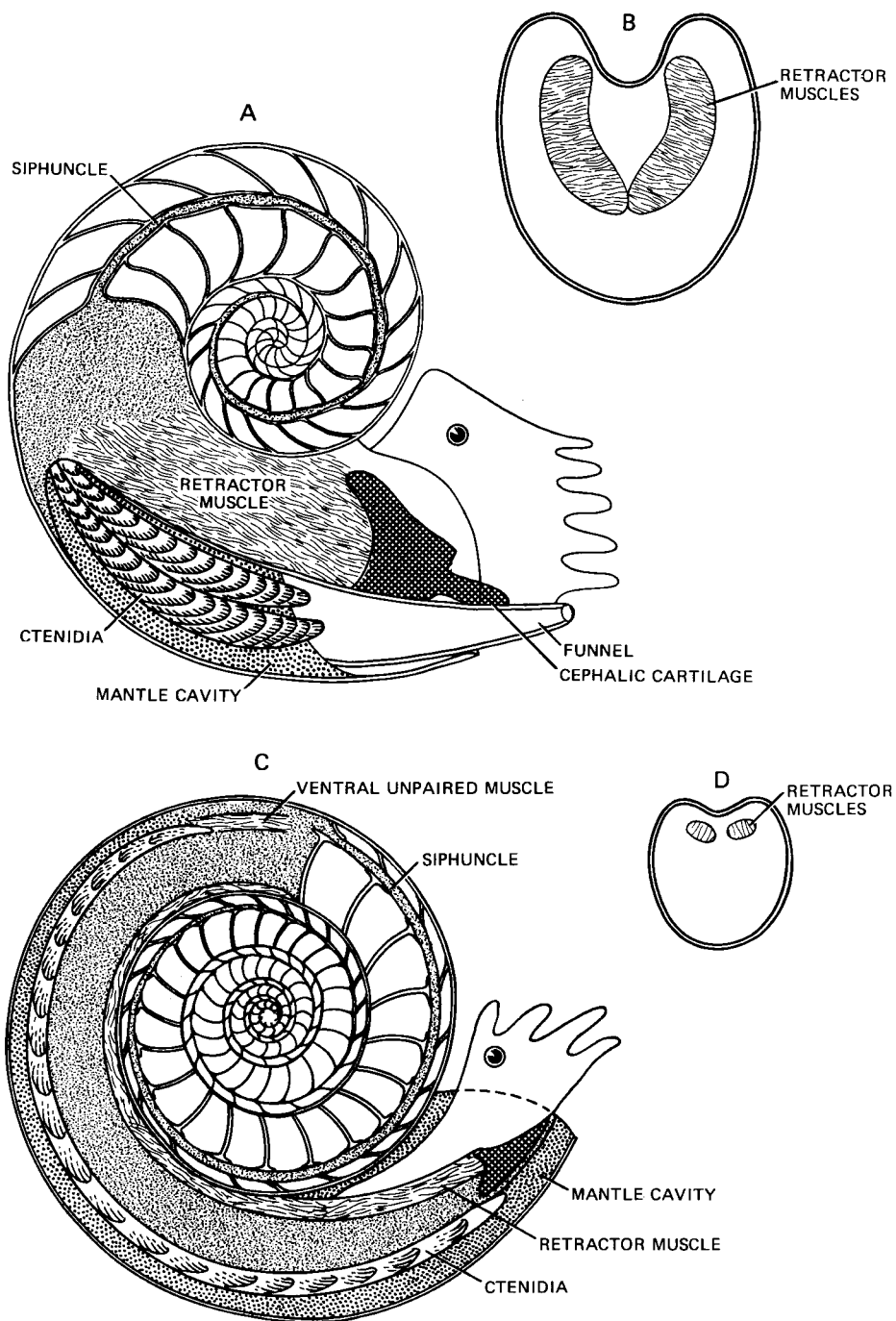
TEXT-FIG. 5. Simplified anatomy and musculature of *Nautilus* (A, B) and a typical ammonite (C, D) compared in median section and transverse sections of the body chamber (after Mutvei 1964 and Mutvei and Reyment 1973).

parameters, as was so elegantly demonstrated by Raup (1966, 1967). Shape of generating curve, expansion rate, translation rate, and distance of generating curve from the axis of coiling suffice to define most morphotypes. In general, ammonite whorl sections are modified ovate or ogival. In ovate sections, the flanks and venter follow a catenary curve, which both economizes on building materials and enhances shell stability by separating centres of gravity and geometry (Trueman 1941; Raup and Chamberlain 1967). Ogival sections are derived from ovate ones by omission of the central (ventral) part of a catenary curve (Westermann 1971).

Calculations based upon theoretical growth models and actual experiments on scale models very clearly show differences between buoyancy and stability of different morphotypes. In general, slowly expanding forms of average coiling have optimum potential buoyancy, and forms with higher expansion rates have higher stability. Adult modification of coiling and whorl shape may thus reflect enhanced stability, as a result of uncoiling of the umbilical seam or whole shell, or by changing the whorl section of the adult body chamber (Mutvei and Reyment 1973).

Streamlining is also dependent on over-all shell shape and size (Kummel and Lloyd 1955); juvenile individuals or small species required more marked modification than large species of similar form, whilst involute shells are better streamlined than evolute. Evolute, compressed shells are, however, fairly well streamlined, while widely umbilicate and robustly ornamented types show poor streamlining.

Septa. The significance of the complexly folded septa of ammonites when compared with nautiloids, has been thought to be either chiefly mechanical or physiological (Westermann 1958, 1971; Raup and Stanley 1971; Seilacher 1973, 1975). Suggestions include:

1. Preventing implosion of the phragmocone and body chamber septum at depth (Pfaff 1911; Spath 1919; Westermann 1956, 1958).
2. Increasing over-all weight for buoyancy control (Reyment 1958; Teichert 1967).
3. Serving to secure efficient body attachment to the shell (Spath 1919).
4. Reflecting the shape of the posterior mantle, the increased area of which may serve for better respiration or other physiological functions (Newell 1949).
5. Providing an increased surface area of wettable conchiolin in the chambers for faster transport of fluid to the siphuncle, aiding in more rapid buoyancy regulation (Mutvei 1967).

Hypothesis 5 can be dismissed in that septal flutings typically run more or less normally to the direction of presumed fluid movement; they diverge from the dorsum, or are transverse (Pl. 6, figs. 1a, 3; Arkell *et al.* 1957, fig. 5), rather than radiating from the siphuncular region. Hypothesis 4 is possible, but no likely physiological function is known to be associated with the posterior part of the mantle in living cephalopods (Westermann 1971). In addition, maximum mantle surface areas would be provided by fluting the entire septum, not merely the margins (Raup and Stanley 1971, p. 179). Hypothesis 3 seems untenable; ammonites, like *Nautilus* were attached to their shells at distinct muscle scars (see p. 10) or along an annular structure in front of the last septum (Jordan 1968; p. 12, above). Hypothesis 2 seems tenable, in that septa do increase in thickness and crowding with maturity. Both septa and

shell are, however, relatively thinner than in *Nautilus*, and a hydrostatic function would thus seem to be secondary.

That septa served a mechanical function is clearly the most attractive alternative. Ammonite shells are thinner than those of nautiloids, and fluted septa clearly represent a close approach to an ideal form of vaulting, both at a superficial level of inspection (Pl. 7, figs. 1-4) and under more rigorous analysis (G. A. Oravas *in* Westermann 1971; Raup and Stanley 1971). The septum not only supports the shell, it is also adorally convex, and thus mechanically better able to withstand hydrostatic pressure transmitted to it via the body where it forms the back wall of the body chamber, a strength enhanced by the fluting. Septal complication thus supports both the shell wall and the septum itself (Raup and Stanley 1971). The development of fluted septa in ammonites enabled them to depart from the ovate whorl section of nautiloids. Forms with compressed sections, flattened sides, and the like are mechanically unsound, and liable to implode if they lacked complex sutures to support the walls (unless they were surface dwellers), while the fluting of the terminal septum again provides a surface of greater strength for accommodating hydrostatic stress transmitted by the body.

Sutural complexity can often (but not invariably) be correlated with other features of shell morphology, increasing as strength of ribbing (another strengthening device against implosion) declines (Buckman 1892). There is some evidence for increasing sutural complexity as septa and shell wall thin (Westermann 1971, p. 22; Seilacher 1973, 1975) and, finally, a trend of increased sutural complexity in some groups as whorl section departs from the mechanical optimum of the ovate to subcircular. That oxyconic pseudoceratites with simple sutures (e.g. *Neolobites, Epengonoceras*), and *Nautilus*-like forms with complex sutures (e.g. *Pseudophyllites, Phyllopachyceras*), are known indicate that more than one selective factor is at work.

A promising approach to understanding the mechanism of formation and function of septa comes from publications by Seilacher (1973, 1975), who noted that the septal surface resembles a soap bubble spread out in the frame of the suture line. The minimum shape of the true soap bubble (which can be simulated by a wire ring shaped like an actual suture, dipped into plastic solution), has been modified; in the real septum the marginal undulations caused by the sutural lobes extend further towards the centre (Seilacher 1963, fig. 7; Pl. 6, figs. 1-2; Pl. 7, figs. 1-4). The septum thus

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EXPLANATION OF PLATE 6

Septal architecture

Fig. 1*a–b* show an internal mould of parts of six chambers of the oxyconic ammonite *Sphenodiscus tirensis* Stephenson from the early Maastrichtian Kemp Clay at USGS Mesozoic locality 12930, 1½ miles southeast of Tira, Hopkins County, Texas, USNM 12930. Note how the somewhat simplified sutures of this oxyconic form are compensated for by the extension of fluting across the whole septal face, normal to the shell walls. ×2.

Fig. 2. Fractured section of *Baculites eliasi* Cobban from the Pierre Shale (early Maastrichtian) at USGS Mesozoic locality D 4481, Black Hills region, Wyoming. This specimen retains its original aragonitic shell wall and septa, with a lining of calcite. The siphuncle is conspicuous at the top of the figure. ×2.

Fig. 3. Lateral view of an internal mould of *Baculites* sp. USNM 13293, from the Campanian part of the Cody Shale, 10 miles (16 km) south-west of Buffalo, Johnson County, Wyoming.
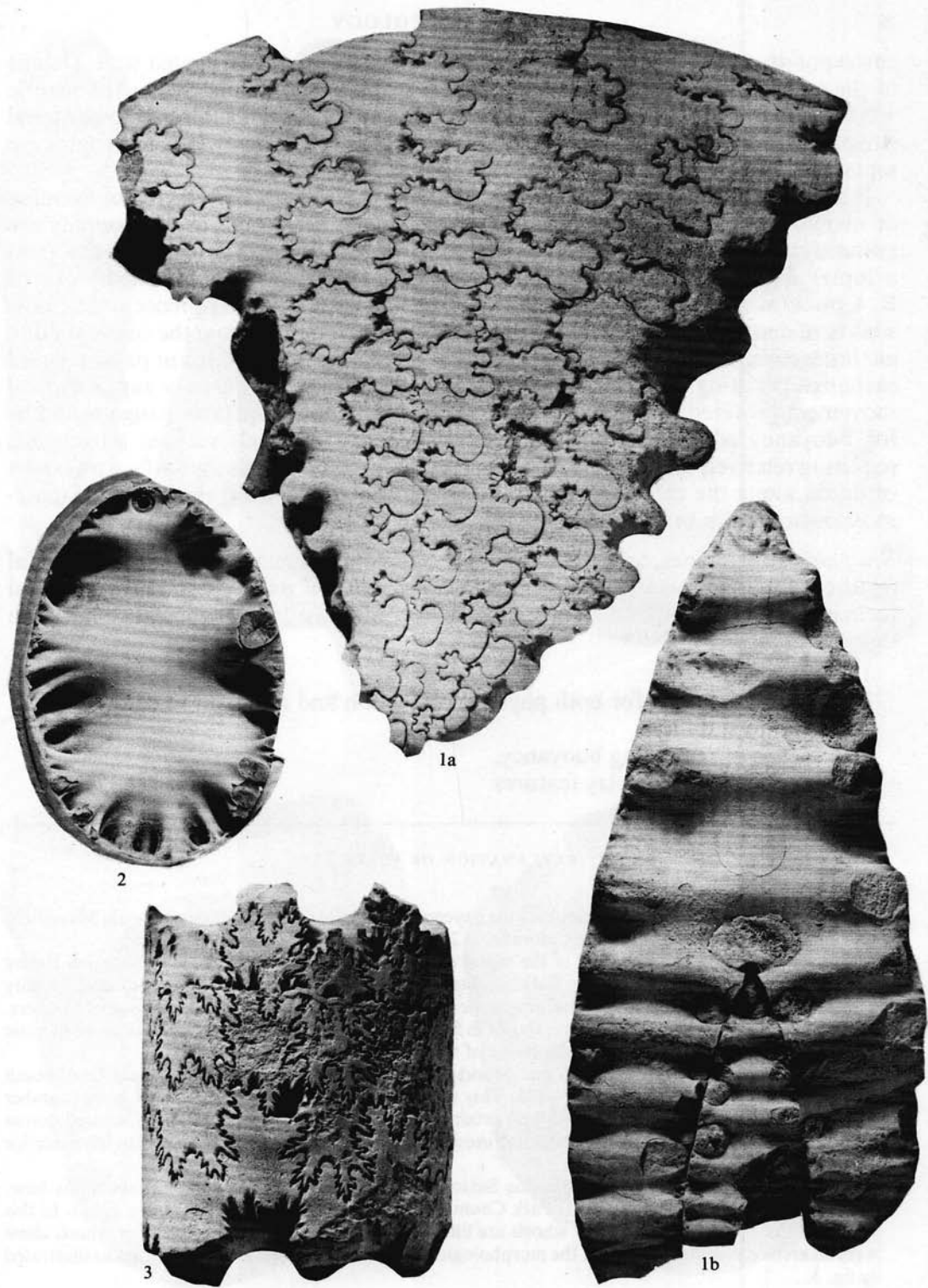
KENNEDY and COBBAN, Septal architecture

corresponds to the functional model of a pressure resistant corrugated wall. Details of the suture can be explained in terms of a series of 'tie points' where the mantle secreting the septum, which behaves as an elastic membrane, is subjected to tensional stresses. Insertion of additional 'tie points' throughout ontogeny lead to progressive septal folding and increased sutural complexity.

It should be noted, however, that current views on buoyancy, degree of flooding of chambers, and indeed mechanism of gas/fluid interchange in ammonoids are currently under critical review. Objections to Mutvei and Reyment's views (and a reply) are made by Westermann (1975), who quotes the unpublished work of R. Cowen at Davis, California, on liquid movement as a consequence of the possibility of decoupling of the connecting rings of the siphuncle from the cameral fluid, *not* immersion in it. Cowen suggests that this would prevent significant passive liquid exchange resulting from pressure differentials during the relatively rapid vertical movement powered by the hyponome; whilst the osmotic liquid exchange would be for buoyancy adjustment and more persistent (e.g. diurnal) vertical movements requiring relatively slow exchange of liquid. Cowen thus regards the surface transport of liquid along the cameral walls towards the ventro-marginal siphuncle in uppermost position as a braking mechanism.

Sculpture. Ribs, spines, tubercles, and other types of ornament were highly functional features of the shell, as is demonstrated by their constant recurrence in near-identical form and combination in distantly related groups (p. 4). Their significance has been thought of as:

1. Mechanical.
2. Protective, serving for both physical protection and as an aid to camouflage.
3. An aid to stability.
4. A means of regulating buoyancy.
5. Sexually selected display features.

EXPLANATION OF PLATE 7

Septal architecture

Fig. 1. Septal surfaces of an internal mould of the oxyconic ammonite *Coahuilites* from the early Maastrichtian Fox Hills Sandstone of eastern Colorado. ×2.

Fig. 2a normal and 2b oblique views of the septal surface of *Placenticeras* from the Campanian Ripley Formation of Lumberyard Creek, Eufaula, Barbour County, Alabama, USGS Mesozoic locality 27883. This specimen retains its original aragonitic shell, with a secondary calcite lining to some chambers. Although oxyconic, like the *Coahuilites* shown in fig. 1, this genus retains a highly subdivided ammonitic suture, and fluting dies out towards the centre of the septal surface. ×2.

Fig. 3. *Anapachydiscus complexus* (Hall and Meek); from the Campanian Pierre Shale near Oral, South Dakota, USGS Mesozoic locality D 1411. This specimen consists of a sediment-filled body chamber retaining the original aragonitic shell, and retains a wholly aragonitic inner whorl, fractured across several camerae to show the original architecture and insertion of the sutures together with the posterior face of the terminal septum. ×3.

Fig. 4. *Scaphites depressus* Reeside; from the Santonian part of the Cody Shale, 630 ft above the base, 6 miles (9·7 km) north-west of Clark, Park County, Wyoming, USGS Mesozoic locality 17955. In this specimen much of the septate outer whorls are filled by sediment or spar whilst the inner whorls show a septal architecture close to that of the morphologically similar but unrelated *Anapachydiscus* illustrated in fig. 3.

KENNEDY and COBBAN, Septal architecture
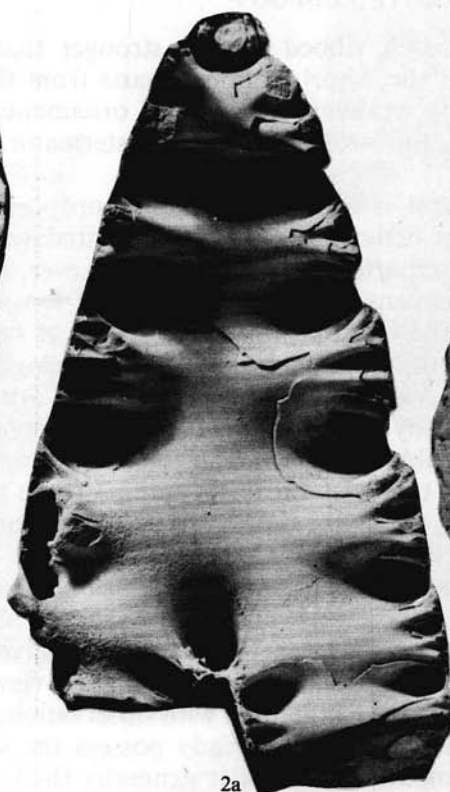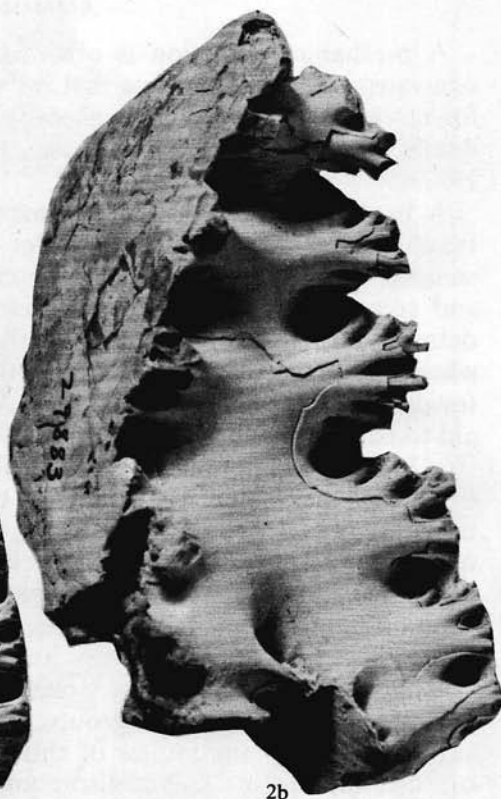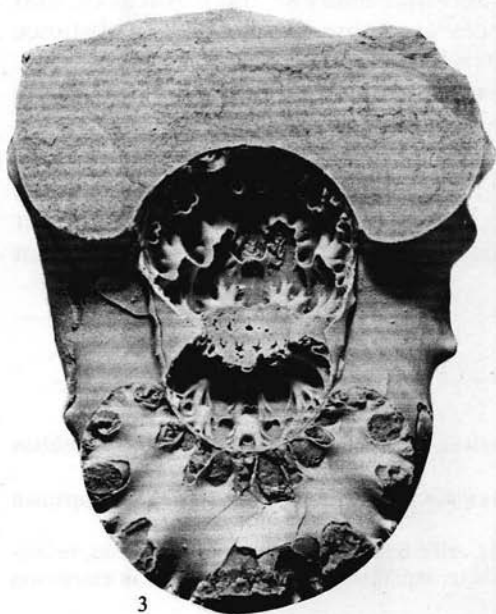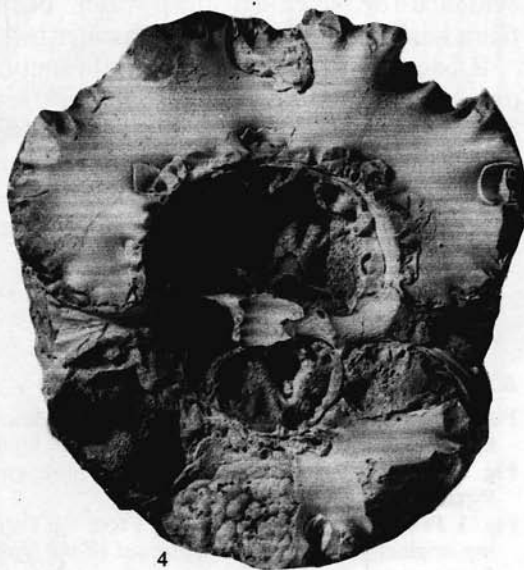
A mechanical function is obvious. A ribbed shell is stronger than a smooth equivalent, but it is curious that, as the whorl section departs from the optimum for strength, the ornament generally weakens. Strength of ornament is thus frequently greatest in what are already the strongest shells (Westermann 1966; Raup 1967).

A protective function for ornament is again an attractive proposition, in that ribbed and spinose shells might offer better protection against predators than their smooth or feebly ornamented counterparts. In many cases, however, the tubercles and spines normally found on specimens are only the bases of longer, far more delicate, structures, broken across the basal septum. The spines of many species, when well preserved, are delicate in the extreme, hollow, and seemingly too fragile for defence (text-fig. 4; Pl. 8, fig. 3). An ingenious interpretation of ornament as an aid to camouflage has been proposed by Cowen et al. (1973), as briefly noted above (p. 18). Viewed laterally, transverse ribbing patterns thus help break up the smooth outline of the venter; ventro-lateral tubercles break up outline when viewed from any direction. In compressed forms the sharp outline is sometimes broken up by crenulations, a groove, offset tubercles, or keels (Cowen et al. 1973, p. 211).

Consequent on this interpretation, these workers consider ribbed forms as benthonic; compressed smooth forms as pelagic; whilst forms such as phylloceratids (and others with rounded whorls and no ornament) are believed to have lived below the photic zone. This last conclusion correlates with the classic view that these leiostracans are deep-water groups, and is compatible with observations of complex sutures in many ammonites of this type, which already possess the mechanically optimal shell form. This is also compatible with their generally thicker shells and more effective siphuncles (Westermann 1971). It must be noted, however, that some of these leiostracans show colour markings, which are functionally equivalent to ornament so far as camouflage is concerned, and that many of the features of, and evidence for, so-called 'deep-water' occurrences are more a reflection of distance from land and terrigenous/freshwater influx than bathymetry.

Ribs appear to have a potential function in enhancing streamlining by decreasing drag under conditions of turbulent flow (J. A. Chamberlain in Westermann 1971). Spines may also serve as balancing aids when the shell rests on the bottom (Pl. 8, fig. 3) or may act as horizontal stabilizers or hydroplanes to prevent yawing when swimming and diving (as in submarines—see Dewey and Loomis 1964). A further function of the large numbers of hair-like spines present in juveniles of some genera

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EXPLANATION OF PLATE 8

Bizarre forms and current orientation

Fig. 1. Part of a concretion crowded with adult microconch and macroconch *Scaphites whitfieldi* Cobban from the late Turonian Ferron Sandstone of Utah.

Fig. 2. Post-mortem accumulation of current-aligned *Baculites perplexus* Cobban from the Campanian Pierre Shale at Red Bird, Wyoming.

Fig. 3. *Prionocyclus hyatti* (Stanton). From the Turonian Carlile Shale, Mitchell County, Kansas, retaining original aragonitic shell and most of the long, delicate, septate spines, normally lost in extraction from matrix.
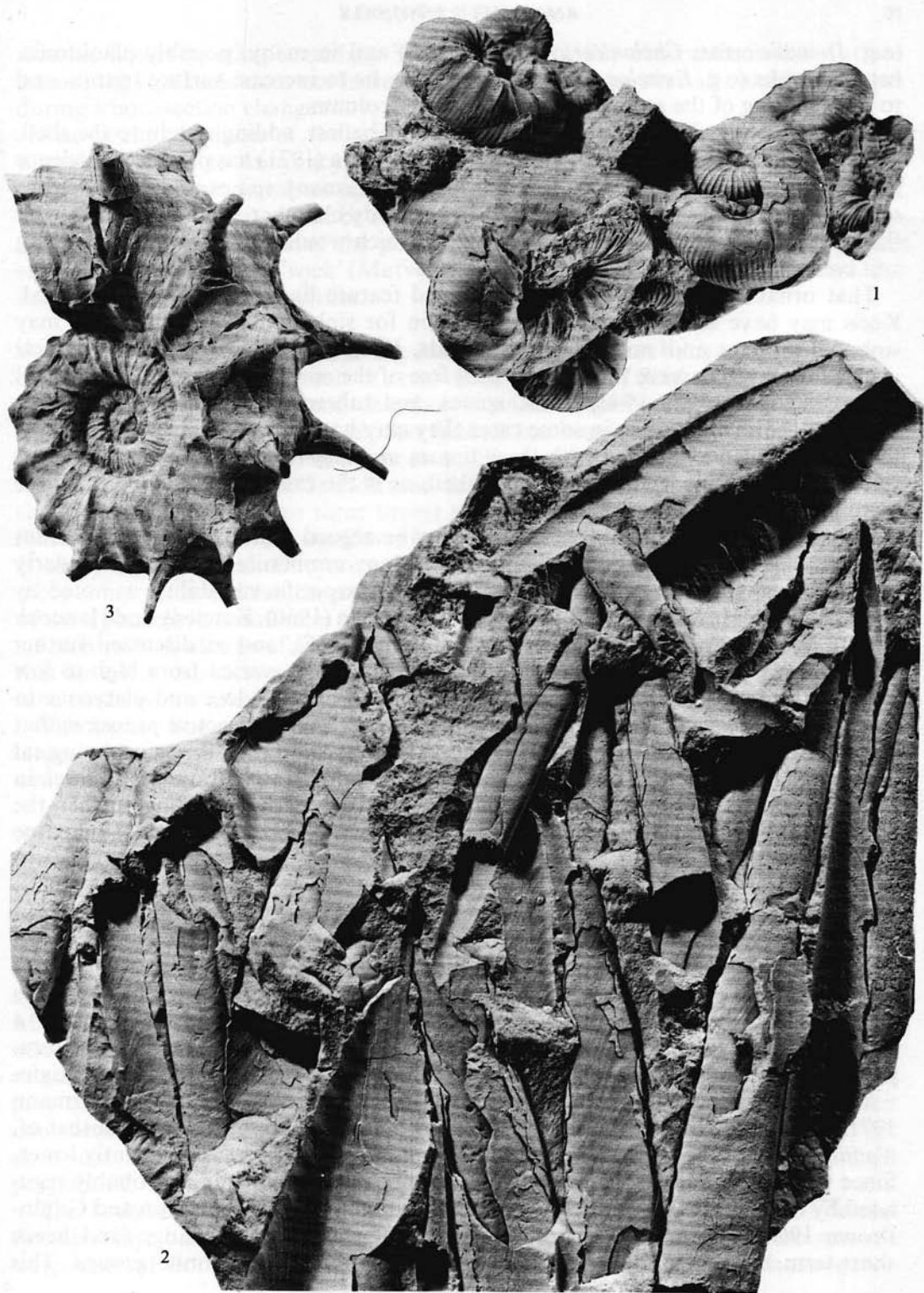
KENNEDY and COBBAN, Bizarre forms and current orientation

(e.g. *Douvilleiceras, Cheloniceras, Kanabiceras*) and in many, possibly planktonic, heteromorphs (e.g. *Exiteloceras*; text-fig. 4) may be to increase surface friction and to slow sinking of the animal through the water column.

Ornament may also have functioned in part as ballast, adding weight to the shell, as suggested by Teichert (1967), although Westermann (1971) has produced evidence that this is at best a secondary function. However, many spines and tubercles are septate, and the basal septum is added in the body chamber some way back from the aperture. These would thus be fluid-filled which would enhance their stabilizing and balancing role.

That ornament may be a sexually selected feature has already been discussed. Keels may have served a supporting function for siphuncular attachment as may siphonal grooves and smooth ventral bands. Keels and other features of ventral ornament may also serve to raise the shell free of the sea-floor, as may some rostral processes (Spath 1923–1943). Ribs, spines, and tubercles are secreted by mantle tissues at the shell margin; in some cases they may have served in a support or protective role when associated with these tissues *in an apertural position* and in a different role when incorporated into the shell, as is the case with many comparable features of bivalves and gastropods.

Interesting as these possibilities are, it may be argued that in some groups ornament was of limited functional significance. Many ammonite species (particularly endemic taxa) show an extraordinary range of intraspecific variability, as noted by Sturani (1971), Howarth (1973b), Reeside and Cobban (1960), Kennedy and Hancock (1970), Wiedmann (1969), Wiedmann and Dieni (1968), and as discussed further below. Many populations thus contain individuals which varied from high to low efficiency in terms of streamlining: from smooth to hypernodose and platycone to cadicone. Such variations may reflect a milieu free from the selective pressures that acted on those groups where intraspecific variability is low. If this morphological variability is a reflection of genetic variability it opens fascinating possibilities in terms of understanding extinction and the like, and perhaps testing further the conflicting views on the evolutionary significance of polymorphism (Valentine 1971a; Ayala *et al.* 1975).

Siphuncle. The siphuncle in *Nautilus* consists of calcareous crystallites in a proteinaceous matrix. Its function is to house the siphuncular cord, the epithelium of which is responsible for withdrawal or addition of fluid to chambers, and in part to act as a wick, aiding fluid movements. In contrast, the siphuncle of ammonites may not have been mineralized. Birkelund and Hansen (1968) have recorded a carbonate outer tube, while Andalib (1972) records the presence of carbonate fluorapatite; Erben *et al.* (1969) and others regard these as of a secondary, diagenetic origin.

The relative diameter of siphuncle to shell in ammonites is variable (Westermann 1971, pp. 25–29); that of the Ammonitina is comparable to, or higher than that of, *Nautilus*, that of the Phylloceratina and of some Lytoceratina is significantly lower. Since the rate of fluid exchange between haemocoel and camerae is probably regulated by the siphuncular epithelium inside the siphuncular tube (Denton and Gilpin-Brown 1966), this may reflect differing rates of short-term exchange (and hence short-term buoyancy adjustment and control) in various ammonite groups. This

view is, however, complicated by Westermann's (1971) observations that surface area of the siphuncle does not increase at the same rate as over-all chamber volume during whorl-section changes.

The ventral position of the siphuncle in all ammonoids save the clymeniids is probably related to buoyancy regulation, as discussed below. If regulation took place only in those chambers where the siphuncle lay topographically on the floor of the chamber, then it would be continually bathed in cameral fluid. This may also explain the probable lack of the porous calcareous layers present in the *Nautilus* siphuncle which acts as a 'wick' (Mutvei and Reyment 1973); this aid to fluid removal being unnecessary in ammonites.

Buoyancy regulation. Work on living *Nautilus* indicates that buoyancy regulation is by density alteration as a result of removal or addition of fluid to the chambers via the siphuncle, the last-formed chamber being completely fluid-filled, and earlier chambers containing progressively less fluid. It has been generally assumed that this mechanism also functioned in ammonites (Guex and Rakus 1971). Recent work by Mutvei and Reyment (1973) indicated that the buoyancy of an empty ammonite shell is significantly (up to three times) greater than that of *Nautilus*, and that to function in the same way a significantly greater number of chambers must have been filled by cameral fluid. Buoyancy decreases with increase in shell involution; the more compressed and evolute a shell is, the greater the lift. Growth and development of the siphuncle in ammonites appears to have been slower than in nautiloids (many ammonites lack all sign of a siphuncular tube in the last few chambers), and it may be that these last chambers were flooded in life and that lack of a supporting siphuncular tube rendered the animal unable to pump out cameral fluid.

The higher buoyancy may also be reflected in the proportionately longer and larger body chamber (and hence body and body weight) of ammonites as compared with nautiloids.

Swimming ability. *Nautilus* swims in two ways: gently, and very rapidly (the latter presumably as an escape response). Gentle movement is accomplished by expulsion of water from the mantle cavity as a result of contraction of the funnel; the mechanism of rapid jet propulsion is poorly understood. In contrast to living dibranchiates, where rapid movement is possibly by virtue of the contraction of a muscular mantle wall, the mantle of *Nautilus*, lining an external shell, is reduced, and contractions appear insufficient for the violent expulsion of water. An ingenious argument by Mutvei and Reyment (1973) suggested that rapid reduction of mantle cavity volume, and hence rapid swimming, is in fact accomplished by contraction of the powerful retractor muscles that roof the mantle cavity (text-fig. 5). In dibranchiates, these may contract simultaneously with the muscles of the mantle (ibid., p. 633); their contraction in *Nautilus*, aided perhaps by withdrawal of the animal's head into the shell and consequent reduction of mantle-cavity volume, may enable rapid jet propulsion.

The body chamber of ammonites, and hence body shape (text-fig. 5), varied considerably, but in most it was elongate and worm-like. The retractor muscles were inserted dorsally, and hence appear not to have roofed the mantle cavity

(text-fig. 6; Mutvei 1964b, fig. E; Mutvei and Reyment 1973, fig. 8). This relationship suggests that many members of the group may have been very poor swimmers indeed.

Similar conclusions have been reached independently by other workers, as noted elsewhere (e.g. Lehmann 1971a; Westermann 1971). Disappearance of a hyponomic sinus and development of ventral rostra have also been interpreted as indicating the loss of a funnel necessary for jet propulsion (Mutvei and Reyment 1973). Donovan (1964) claimed that all post-Permian ammonoids lack a hyponomic sinus, it being replaced by a projecting rostrum and the change occurring somewhere near the point of origin of the Xenodiscidae. He concluded that 'in view of the presence of the sinus in all other shelled cephalopods, its loss is likely to have been a significant evolutionary change, and may have accompanied the disuse of the funnel as a locomotory organ' (1964, p. 268). We would point out that a rostrum is lacking in many Mesozoic forms, while others developed apertural structures which might be interpreted as ideal for housing a funnel (as in many baculitids and turrilitids). A. M. Bidder (in Westermann 1971, p. 9) has suggested that some ventral projections may indicate the development of a paired propulsive organ.

Life orientation of ammonites. The classic investigation of the life orientation of ammonoids is that of Trueman (1941) who calculated centres of gravity, centres of buoyancy and hence shell attitude for a range of morphotypes (text-fig. 6). However, Trueman's work (and that of Raup and Chamberlain 1967) ignored the weight of adult shell modifications, and, of necessity, the presence/absence and distribution of cameral fluids. Trueman also made an incorrect assumption regarding ammonite body density, which was probably close to that of sea-water. In spite of these problems, his calculations find confirmation in the known examples of ammonite strandings (Rothpletz 1909) and in Seilacher's (1960) work on epizoans as a key to ammonoid ecology (although Reyment 1973 suggested the latter observations were not demonstrably an indication of life habits; the case is also discussed by Heptonstall 1970). Many bathypelagic squid have evolved chemical 'floats' (Packard 1972); such a device may also have been exploited by some ammonites.

THE MODE OF LIFE OF AMMONITES

A number of generalizations about the mode of life of ammonites can be drawn from the observations and speculation on anatomy and functional morphology outlined above. Ammonites were diverse, variable, and successful exploiters of a number of regions within marine ecosystems; although no doubt many palaeontologists would take exception to the following conclusions.

1. After hatching, many ammonites underwent a planktonic larval stage, as do most gastropods and bivalves. In this respect they differed markedly from *Nautilus*. The length of their larval life was equivalent to the time of secretion of the second phase of shell growth, from protoconch to nepionic constriction. The duration of this larval stage can only be guessed at; in other molluscan groups it varies from hours to months (Ekman 1953, with references; Scheltema 1968, 1971a–b; Thorson 1961).
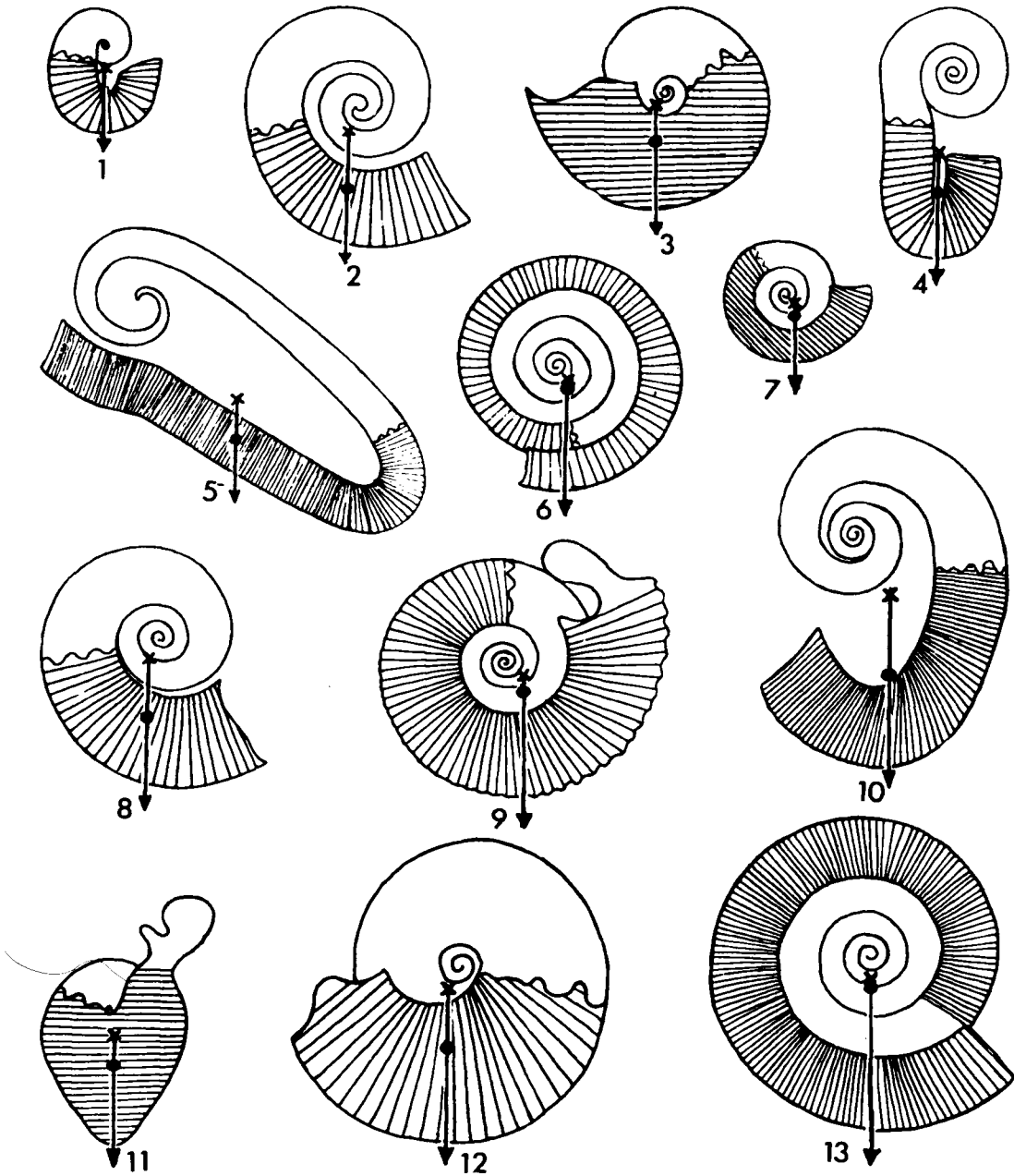
TEXT-FIG. 6. Probable flotation positions of some representative ammonite morphotypes, after Trueman (1941) and Arkell *et al.* (1957). 1, *Scaphites equalis*; 2, *Crioceras duvali*; 3, *Ludwigia* sp.; 4, *Macroscaphites yvanii*; 5, *Lytocrioceras jauberti*; 6, *Caloceras* sp.; 7, *Promicroceras marstonense*; 8, *Crioceras fissicostatum*; 9, *Normannites* sp.; 10, *Crioceras mulsanti*; 11, *Oecoptychius* sp.; 12, *Sigaloceras micans*; 13, *Dactylioceras commune*. Cross marks approximate position of centre of buoyancy. Dot marks approximate positions of centre of gravity. For discussion see text.

2. After metamorphosis a number of possible life styles emerged:

(*a*) Geographic distribution of many groups and strong substrate controls on the distribution of others suggest a benthonic habit during post-larval life, especially for some heteromorphs and strongly ornamented forms. In these groups, intra-specific variation is high, and ornament may reflect evolution of camouflage patterns designed for a benthic life. These are the classic Trachyostraca of early workers. Groups with simplified or pseudoceratitic sutures may also have been shallow-water benthonic forms (Mutvei and Reyment 1973).

(*b*) A planktonic or nektonic life habit continued into post-larval life in many taxa, both normally coiled and heteromorph. Washings of sediments deposited many miles from shore often yield abundant juvenile ammonites (A. J. Lloyd, pers. comm.), and we know of many cases of huge concentrations of juveniles, complete with body chambers, preserved in pelagic deposits. For example we have a collection from the Marias River Shale (Santonian) of north-western Montana, which is a mass of juvenile *Baculites codyensis* Reeside and *Clioscaphites vermiformis* (Meek and Hayden). These specimens are complete with body chambers and aper-tures; they died possibly 150 km east of the western shoreline of the Western Interior epeiric sea. We also have a comparable collection of *B. codyensis* from the Cody Shale of south-central Wyoming, found at a locality at least 300 km east of the strandline. These are the only collections of juveniles of these species known to us.

(*c*) Morphological features of shell, siphuncle, and sutures of some groups, especially the phylloceratids and lytoceratids, together with their lack of camouflage, suggest that these—the classic Leiostraca of early workers—may have been able to occupy deep-shelf habitats, perhaps below the photic zone. Their local abundance in what are clearly shallow-water deposits indicates, however, that they were not confined to deeper-water situations (Hallam 1969 and our observations). 'Offshore' rather than 'deep water' may have been the milieu of these forms.

3. In many cases, ammonites appear to have lived segregated by sex or age in varying degrees, as is the case for many living cephalopods. Recorded occurrences indicate:

(*a*) Partial segregation of adult males and females in some cases, although 1:1 ratios are common, and records exist in which either sex may have dominated.

(*b*) Segregation of adults and juveniles in many cases, although all developmental stages of both sexes can also be found together. We know of many fossil occurrences where juveniles are absent, and where only specimens near maturity, adults or fragments thereof, are present in collections (Pl. 8, fig. 1). In some cases, as in the Upper Cretaceous of the Western Interior, U.S.A., this absence of juveniles can be traced at the same horizon over thousands of square kilometres. This lack of juveniles is not, in our experience, due to any collection failure or to the selective post-depositional destruction of larval shells, nor is it a result of minimal post-larval mortality. Rather, it indicates that some groups spent their early life far from land, moving on to inner shelf areas only when adult. This pattern matches what is known of migratory behaviour in Recent cephalopods (e.g. Packard 1972), and is supported by the striking morphological differences between juveniles and adults found in many ammonites (e.g. text-fig. 7), a reflection of life habits that changed through ontogeny.

Didymoceras nebrascense
(Meek and Hayden)

Didymoceras cheyennense
(Meek and Hayden)
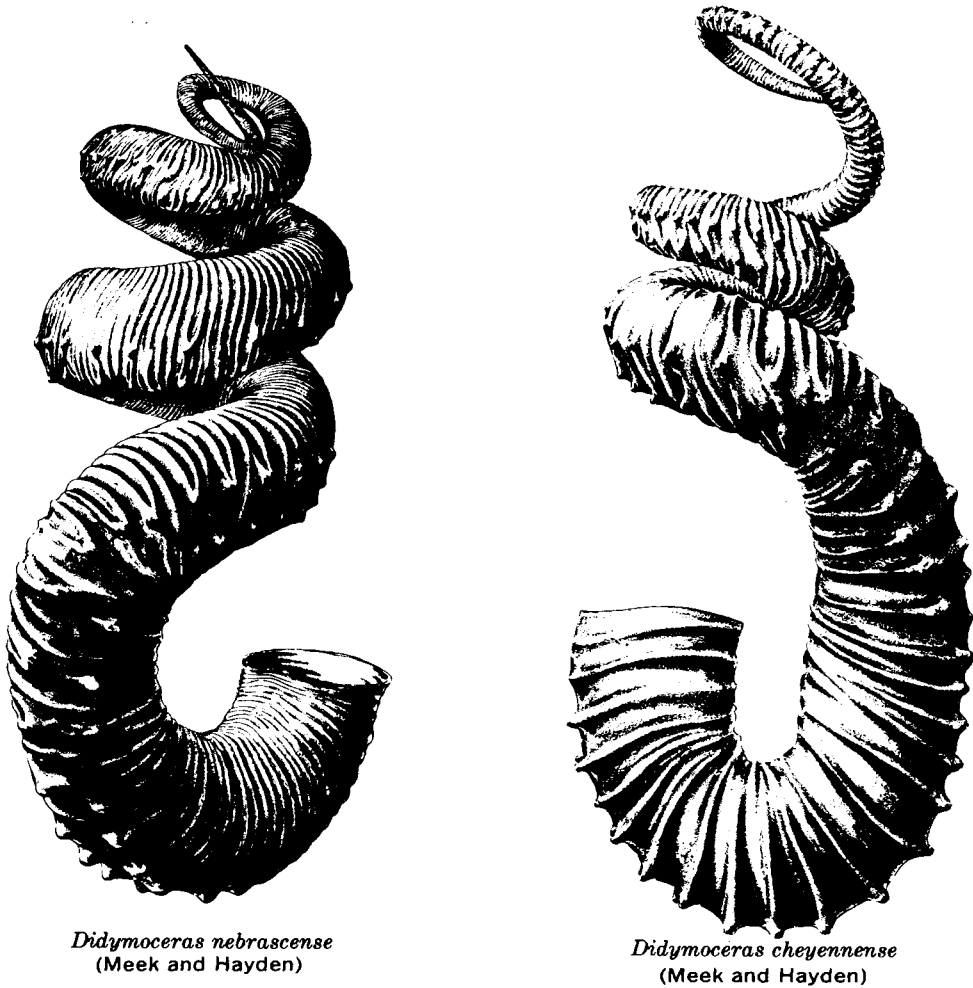
TEXT-FIG. 7. A reconstruction of the Campanian nostoceratid heteromorphs *Didymoceras cheyennense* (Meek and Hayden) and *D. nebrascense* (Meek and Hayden), based on material from the Pierre Shale of Colorado (after Scott and Cobban 1965).

4. Ammonites possessed variable powers of locomotion. Some forms may have been capable of rapid jet-propulsion, as in coleoids; in most, however, this must have been an occasional escape mechanism, if developed at all. Generally, the groups were poorly adapted for swimming, moving slowly as a result of water expelled from the mantle cavity by contraction of the funnel. Several lines of evidence suggest that many ammonites were adapted for slow vertical migration as a result of alteration of relative density by addition or subtraction of cameral fluid.

5. The majority of ammonites exploited the low levels of food pyramids; some were planktonic feeders, eating both plankton and first-order carnivores feeding thereon; others were benthonic and perhaps microphagous, yet others were probably

vegetarian browsers. A few may have been carnivores and scavengers like Recent *Nautilus* and coleoids, but most probably lacked the ability to capture large active prey or jaws and radulae capable of breaking up this type of food.


POST-MORTEM HISTORY

Post-mortem drifting. Shells of recently dead *Nautilus* do not contain appreciable amounts of cameral liquid (Bidder 1962; Denton and Gilpin-Brown 1963, 1966; Mutvei and Reyment 1973). How this fluid disappears is not known, but its loss results in the shell rising to the surface (if death did not occur there), whilst decomposition and scavengers feeding on the carcass also reduce weight. Until the shell becomes waterlogged, punctured, or weighted down by epizoans, it is free to float and may become widely distributed as a result of drifting by ocean currents. House (1973), Toriyami *et al.* (1966), and Reyment (1973) summarized the relationship between the known distribution of living *Nautilus* and dead shells, and their data indicate that dead shells drift for considerable distances (text-fig. 8). Early observations suggested that dead shells found on the east African coast and islands of the Indian Ocean had drifted thousands of kilometres since death. Knowing the surface velocity of oceanic currents in these areas, House (1973, p. 308) concluded that shells floated for periods of years. His view is incompatible with Reyment's (1958) earlier experiments where it was demonstrated that holes develop in empty shells floating in sea-water for periods as short as 32 days. Furthermore, those *Nautilus* we have seen from the western Indian Ocean are relatively free from epizoans, whilst glass and plastic floats from Japanese long-line fishing operations in the area often bear massive growths. These observations lend credibility to the recent reports of live *Nautilus* in the western Indian Ocean (Bidder *in* Reyment 1973). Post-mortem drift of *Nautilus* may thus be less than assumed, although the distances travelled may involve hundreds of kilometres.

Distribution patterns in ammonites suggest a variable post-mortem history (see below; also Walther 1897; Scupin 1912; and particularly Reyment 1958 with discussion). Some species distribution patterns indicate that extensive drift did not occur (Scupin 1912; Diener 1912; Kessler 1923; Gill and Cobban 1966), whilst the abundance of ammonites in off-shore, relatively deep-water sediments without signs of damage or puncture suggests that many either did not float at all after death, or became rapidly waterlogged. We cannot agree with the views of Reyment (1958; *in* Reyment and Tait 1972) that many ammonite shell beds represent coastal or strandline deposits; associated faunal and sedimentological evidence indicates that such occurrences are the exception.

Extensive post-mortem drift of ammonite shells would in some cases be aided by their greater buoyancy when compared with *Nautilus*. Extensive drift may also explain the frequent separation of ammonites and aptychi; decay of tissues led to jaws simply falling from the shell. This long-held view is discussed by Reyment (1958, pp. 161–162, with references). There are, however, *mineralogical* differences between ammonite shells and aptychi which offer an alternative explanation.

Further evidence of post-mortem drift out to sea from shelf areas (or perhaps
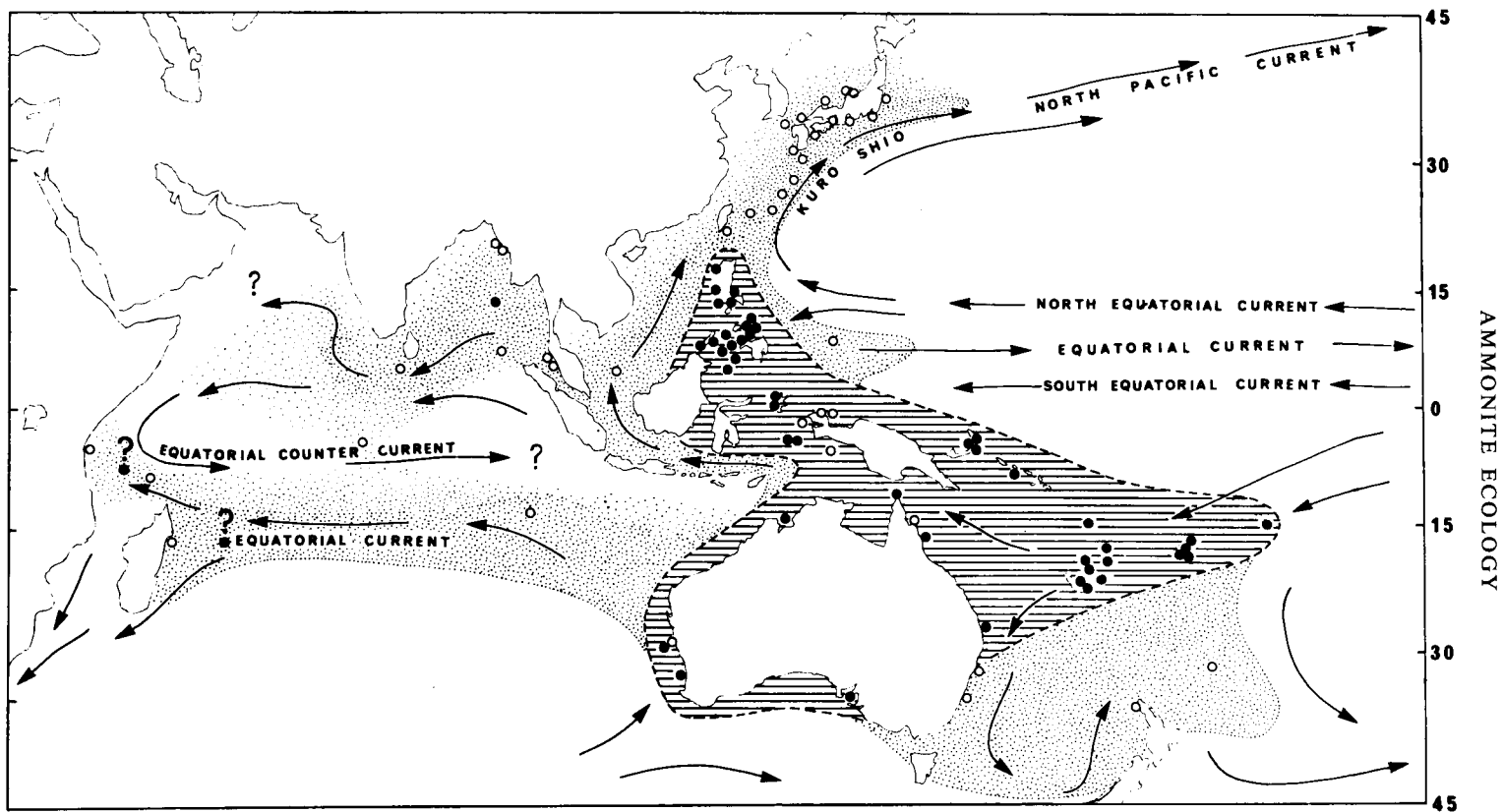
TEXT-FIG. 8. Distribution of Recent *Nautilus*. Black dots show records of live specimens, open circles drifted shells. Based on House (1973) and Reyment (1973). Horizontal shading shows known life area; note, however, possible records off Madagascar and Arabia. Even if confirmed, the area covered by dead shells (stippled) suggests post-mortem drift of at least hundreds, if not thousands, of kilometres.

merely an oceanic habit) may come from recent records of ammonites from cores recovered during the Deep-Sea Drilling Project (e.g. Renz 1972*a–b*).

Pre-burial dissolution. A number of workers (see discussion in Hallam 1967*a*) have explained the lack of originally aragonitic ammonite shells but the common occurrence of calcitic aptychi in supposed deep-water deposits as a result of their accumulation below the aragonite compensation depth. Recent work has suggested that aragonite dissolution may occur at depths of only a few hundred metres (Jefferies 1962, 1963; Hudson 1967; Kennedy 1969; Bathurst 1971). Perhaps the best examples of such pre-burial destruction of ammonites in relatively shallow-water deposits comes from the Upper Cretaceous chalks of western Europe. Here, remains of originally aragonitic fossils (generally preserved as moulds) are known through limited intervals only. They are common throughout much of the Cenomanian part of the sequence (the English Lower Chalk and its equivalents), but above this they usually occur only at horizons of shallowing and early cementation (hardgrounds: see Bathurst 1971). Evidence of their former presence is, however, widespread. Aptychi are known throughout the sequence, as are xenomorphic oysters and other calcitic epizoans; their attachment areas show traces of the form and ornament of diverse ammonites, gastropods, and other originally aragonitic shells, all other indication of which has now vanished. Further examples of this type are recorded by Lewy (1972). We suspect that the great rarity of ammonites in many ancient open marine sediments may reflect diagenetic removal rather than their original absence (e.g. Niobrara Chalk of the Western Interior, U.S.A.).

Post-burial history and reworking. The sedimentary infilling of cephalopod shells has puzzled workers for more than a century, but the complexity of infilling, post-burial exhumation, and reinterment has been largely overlooked. These problems are beyond the context of this review, but the reader is referred to a series of articles on draught infilling, and burial diagenesis of ammonite shells by Seilacher (1963, 1966, 1968, 1971; see also Mundlos 1970, and Schindewolf 1967).

TAXONOMIC PROBLEMS

Variability. Ammonites, perhaps more than most groups, have suffered extensive taxonomic splitting, and authors have frequently divided intergrading populations into a whole range of species and even genera. Buckman (1892) divided morphologically intergrading series into differing 'species', although admitting they probably belonged to what would now be termed a single biospecies. Spath (1923–1943) made similar statements and commented on the problems of identifying species when large numbers of specimens were available; whole monographs have thus been devoted to descriptions of what are now regarded as but a few species.

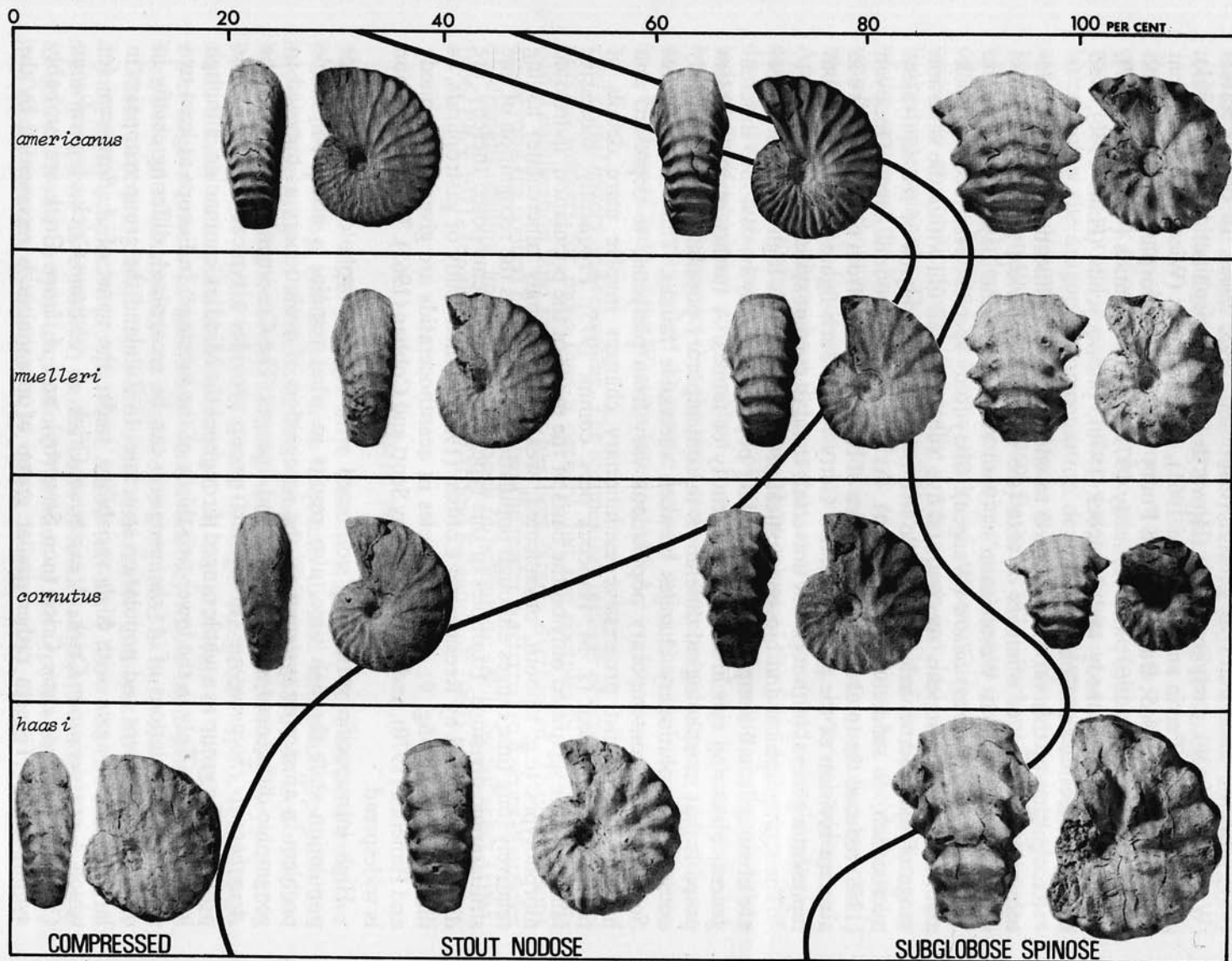These problems result from the truly remarkable intraspecific variability seen among many ammonite groups, Plate 9 and text-fig. 9 show the end members of some groups we have studied; on the basis of small samples, even their congeneric assignment would be open to question! Variation of this type has been widely noted; in Triassic ceratites (Silberling 1959, 1962; Wenger 1957; Tozer 1961; Kummel

1961), Jurassic ammonites in general (Callomon 1963, 1969), in phylloceratids (Wiedmann 1963*b*), dactylioceratids (Howarth 1973*b*), perisphinctids (Geyer 1961), grammoceratids (Perrin and Théobold 1961), desmoceratids (Wiedmann and Dieni 1968; Jones *et al.* 1965; Busnardo and Foury 1966), heteromorphs (Wiedmann and Dieni 1968; Cobban 1969; and Kennedy 1972), placenticeratids (Wolleben 1967), acanthoceratids (Kennedy and Hancock 1970), prionocyclids (Haas 1946), and hoplitids (Reeside and Cobban 1960).

Recognition of this variation has led to widespread simplification of nomenclature and reduction of numbers of taxa (see references above); perhaps the most impressive example is Westermann's (1966) revision of the Bajocian ammonite *Sonninia* (*Euhoploceras*) *adicra* (Waagen). Sixty-four 'species' described by Buckman, nine other European 'species', and five 'subspecies' all fall within the variation range of the macroconch form, while five others are synonyms of the equivalent microconch, *S. subdecorata* (Buckman). At a higher taxonomic level, Donovan (1958) reduced the total number of genera of Echioceratidae from nineteen to five in a recent revision of the group (see also Getty 1973). Such figures are extreme, but represent a general (although not universal) trend in current systematics.

The stratigraphical and biogeographical problems that this high variability poses are obvious: small samples of intergrading populations may be cast into different genera, obscuring synchroneity and identity of faunas. A further major problem posed is that morphological differences in contemporary populations often greatly exceed the evolutionary changes between successive faunas. Thus in the genus *Schloenbachia*, contemporary populations vary from platycone to depressed and hypernodose, whilst progressive evolutionary changes involve mere details of tubercle arrangement (J. M. Hancock pers. comm. 1975). Frequently, successive faunas can be separated only on the basis of the mode of the population, individual morphotypes (e.g. smooth, ornamented, weakly or strongly tuberculate) having relatively long time ranges although population shift enables the recognition of fine stratigraphic divisions. Examples of this type, and the problems posed thereby, are discussed in detail by Reeside and Cobban (1960) in their study of gastroplitids, as illustrated in text-fig. 9; other examples in acanthoceratids are given by Kennedy and Hancock (1970), and in baculitids by Scott and Cobban (1965). The phenomenon is widespread.

High intraspecific variability, combined with slight morphological change or population shift through time, also results in what remains a near insuperable problem in ammonite systematics: the recognition of evolutionary as opposed to geographic differences within species and lineages. The Cenomanian species of the *Acanthoceras rhotomagense* (Brongniart) group provides a typical example of the problem. The group as a whole ranged throughout the Middle Cenomanian, although it was common only in the lower two-thirds of the substage. In Europe at least two successive populations of *A. rhotomagense* can be recognized, differing chiefly in details of ornament and population structure. In Zululand the group reappears in large numbers, again with high variability, under the name of *A. flexuosum* (of which *A. crassiornatum* Crick, *A. expansum* Crick, *A. robustum* Crick, *A. quadratum* Crick, *A. hippocastanum* Crick (non Sowerby), and *A. latum* Crick are probably synonyms). In Texas a rather similar group of ammonites is represented by the

0   20   40   60   80   100 PER CENT

americanus

muelleri

cornutus

haasi

COMPRESSED   STOUT NODOSE   SUBGLOBOSE SPINOSE

A. stephensoni Adkins, *A. adkinsi* Stephenson–*A. eulessanum* Stephenson–*A. tarrantense* Stephenson complex.

Individuals from any one population would pass unnoticed in any other, but over-all population structures are clearly different. All faunas are of Middle Cenomanian age, but correlation of these widely separated areas is too imprecise to determine their relative ages accurately. We cannot tell if these population differences reflect different stratigraphical horizons, or if they are merely geographic subspecies of *A. rhotomagense*. When other small samples, again from different areas, are considered the problem becomes acute. Thus the few *Acanthoceras* of the *rhotomagense* group described from northern Australia (Wright 1963) fall within the range of variation of the populations discussed above, but to which do they belong, or are they a further geographically or stratigraphically distinct species or subspecies of which we have an inadequate sample?

Homoeomorphy. Since they possess only an external shell, it is scarcely surprising that homoeomorphy is widespread within ammonites, and indeed they are one of the groups to which the term was first applied (Buckman 1895, 1898). Evolutionary and functional aspects of the phenomenon of homoeomorphy are discussed by George (1962, with references), while examples in ammonites have been widely noted, in particular in reviews by Schindewolf (1938, 1940), Haas (1942), and Reyment (1955). Homoeomorphy may be restricted to a specific feature such as sutures, for example, *Buchiceras* (a Coniacian acanthoceratid) and *Czekanowskites* (a Scythian noritid), or may extend to the whole shell. Synchronous and heterochronous homoeomorphy of taxonomically distant groups is common, as is homoeomorphy between stratigraphically separated members of the same lineage. We figure here some of the more perfect examples known to us (Pls. 10–11), and would also point to the following examples, readily available in the *Treatise* (Arkell *et al.* 1957), among a host of others:

1. *Ptychites* (Anisian to Ladinian ceratitid) and *Neoptychites* (Turonian acanthoceratid).

2. *Balatonites* (Anisian ceratitid), *Tropiceltites* (Carnian tropitid), *Arietites* (Sinemurian psiloceratid), and *Mortoniceras* (Albian acanthoceratid).

3. *Discotropites* (Carnian tropitid), *Grammoceras* (Toarcian hildoceratid), and *Neoharpoceras* (Albian acanthoceratid).

4. *Episageceras* (Triassic medlicottid) and *Pseudotissotia* (Turonian acanthoceratid).

TEXT-FIG. 9. Intraspecific variation and population changes in four successive species of the late Albian hoplitid ammonite *Neogastroplites*, showing the shifting proportions of compressed, stout nodose and subglobose spinose variants, from the *Neogastroplites haasi* Zone (oldest) to *N. americanus* Zone (youngest). Based upon material from the Mowry Shale of the United States Western Interior. Sample sizes are: *N. haasi*, 333 individuals from USGS Mesozoic locality 24566; *N. cornutus*, 2471 individuals from USGS Mesozoic locality 23021; *N. muelleri*, 3708 individuals from USGS Mesozoic locality 24056; *N. americanus*, 1248 individuals from USGS Mesozoic locality 23042. For full details see Reeside and Cobban (1960).

5. *Kelnerites* (Anisian ceratitid), *Mortoniceras* (Albian acanthoceratid), and *Schloenbachia* (Cenomanian hoplitid).

6. *Trachyceras* (Ladinian to Carnian clydonitid) and *Discoscaphites* (Campanian to Maastrichtian scaphitid heteromorph).

7. The initial coils of *Cochloceras* (Norian clydonitid), *Colchidites* (Barremian heteroceratid heteromorph), and *Anaklinoceras* (Campanian nostoceratid heteromorph).

8. *Boeseites* (Pennsylvanian prolecanitid), *Gyrophiceras* (Scythian noritid), and *Flickia* (Cretaceous pseudoceratitic acanthoceratid).

Homoeomorphy poses problems for the systematist, and it is becoming clear that the *Treatise* classification (Arkell *et al.* 1957) is in part no more than a series of groupings of polyphyletic homoeomorphs (Wiedmann 1963*a–b*, 1966, 1968, 1970; Kullmann and Wiedmann 1970). There are also many cases where failure to recognize homoeomorphs has led to either the misdating of strata or of the species concerned. Thus Reeside and Weymouth (1931) dated the Aspen Shale of south-eastern Wyoming as Turonian on the basis of '*Kanabiceras*', '*Metoicoceras*', and '*Acompsoceras*' species. Discovery of better specimens subsequently showed their collection to belong entirely to a single Albian species, *Neogastroplites cornutus* (Whiteaves). Douvillé (1931) recognized the presence of Barremian, Albian, Cenomanian, and Turonian genera and species in a fauna from Salinas (Angola); we now believe that the association is from a high Cenomanian horizon, consisting of a series of Cenomanian homoeomorphs of well-known Barremian, Albian, and Turonian forms alongside morphologically distinctive Cenomanian elements. Many similar examples could be cited.

Homoeomorphic developments have also led to misconceptions about the stratigraphical ranges of taxa. Examples are numerous: there are, for instance, many records of the Cenomanian genus *Schloenbachia* from the Albian, based upon *Mortoniceras* species. Van Hoepen (1966) recorded the otherwise exclusively Turonian genus *Selwynoceras* from the Aptian, whereas the specimen is actually a *Lyelliceras* of Albian age! Homoeomorphy has led even the most experienced workers to erroneous conclusions, especially when they have dealt with poor material; it will no doubt continue to do so.

Sexual dimorphism. Widespread recognition of sexual dimorphism in ammonites (Pl. 1, figs. 1–5) has led to a number of taxonomic problems, for dimorphs have usually been referred to different species, and frequently to different genera or even

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EXPLANATION OF PLATE 9

Intraspecific variation

Figs. 1*a–c*, 2*a–c*. *Tropites subquadratus* Silberling. USNM 128262 and 128265. Compressed and depressed end members of the variation series from the late Triassic Luning Formation of the Shoshone Mountains, Nevada.

Figs. 3*a–c*, 4*a–c*. Compressed and depressed end members of the *Neogastroplites muelleri* variation series, USNM 129417, 129514. From the late Albian Mowry Shale at USGS Mesozoic locality 24065, 2½ miles (4 km) south-east of Teigen, Petroleum County, Montana.
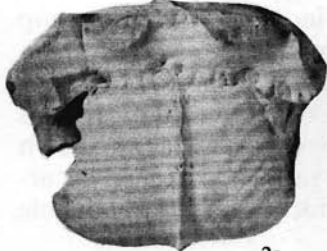
KENNEDY and COBBAN, Intraspecific variation

families. Two fundamentally different philosophies have emerged on the taxonomic treatment of dimorphs; some authors would apply the same name, differentiated only by ♂ and ♀, the specific name adopted for a dimorphic pair being that which has priority (e.g. Makowski 1962; Palframan 1966, 1967; Cobban 1969). Others would retain both names as a species pair. A full discussion of the subject is given in Westermann's book (1969b).

AMMONITES AS FACIES FOSSILS

The inferred life habits of ammonites already reviewed indicate that the group should show a variation in facies-linked distributions. Minimal facies controls on distribution reflect either nektonic or planktonic life habits or post-mortem drifting. Close facies controls suggest a benthonic habit and limited post-mortem drift as factors limiting distribution. The almost complete independence of facies shown by many species is demonstrated in Table 1, where we have tabulated known occurrences of a series of Cretaceous forms we have studied, which illustrate the whole range of distribution patterns.

When studied in detail, species that seem at first sight independent of facies in fact vary in their relative abundances between facies. For example, work on the Cenomanian of Haute-Normandie and southern England has shown a tendency for certain groups to vary in relative abundance between pelagic chalk facies and higher energy, condensed and often glauconitic phosphatic Basement Beds. Table 2 summarizes distributions for two horizons in the Middle Cenomanian. Differences are slight, but can be matched with similar tabulations from higher and lower Cenomanian horizons in the area. Turrilitid, anisoceratid, scaphitid, and hamitid heteromorphs, although occurring in several facies, do show a tendency towards higher diversity and greater abundance in Basement Bed facies, but *Sciponoceras*, a baculitid, is largely facies independent, and, if anything, more common in pelagic chalks; these conclusions are different to those reached by Drummond (1969). Among normally coiled forms, distribution data are harder to assess, but *Calycoceras* appears to be commoner in Basement Bed facies than in pelagic chalks.

EXPLANATION OF PLATE 10

Intraspecific variation and homoeomorphy

Figs. 1a–b, 2a–b. *Collignoniceras woollgari* (Mantell). 1a–b, the costate var. *regularis* Haas and 2a–b, the typical form. From the mid-Turonian Carlile Shale of the Black Hills at USGS Mesozoic locality 21792.

Figs. 3, *Oxytropidoceras* (*Manuaniceras*) *hubbardi* Knetchel, USNM 261065, from the mid-Albian of Peru and 4, *Discotropites sandlingensis* Hauer, USNM 74009, from the late Triassic Hosselkus Limestone, Shasta County, California.

Figs. 5, *Dobrodgeiceras broggianum* (Lissón), holotype, from the Valanginian of Huaylas, Peru (after Riccardi and Westermann 1970) and 6, *Clioscaphites vermiformis* (Meek and Hayden) from the Santonian Marias River Shale near Shelby, Montana, USNM 23682.

Figs. 7, *Baculites rugosus* Cobban from the Campanian Pierre Shale of south-eastern Montana at USGS Mesozoic locality 23054 and 8, *Baculites perplexus* Cobban from the Campanian Steele Shale near Glenrock, Wyoming, USGS Mesozoic locality D 255.
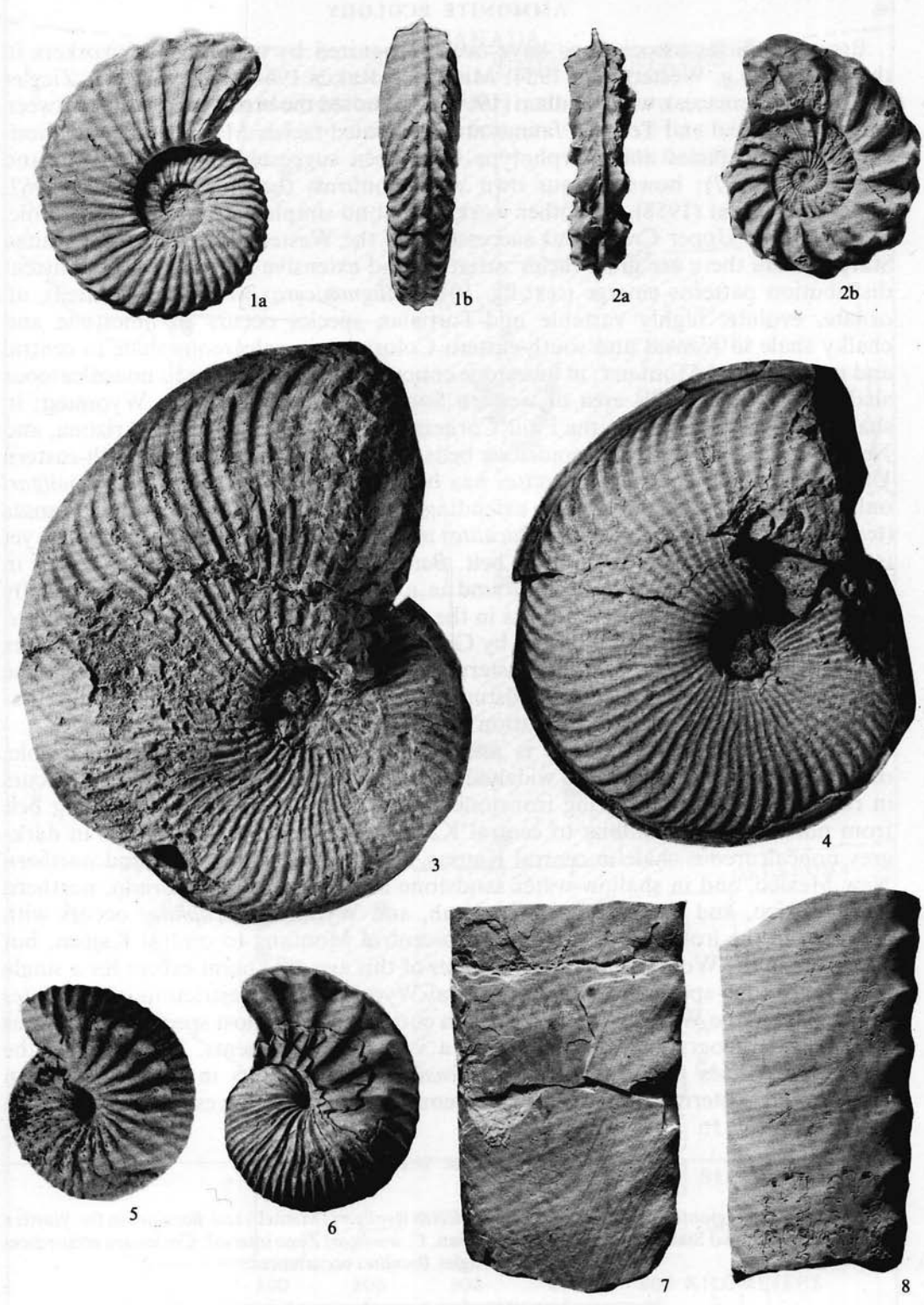
KENNEDY and COBBAN, Intraspecific variation and homoeomorphy

Broad biofacies associations have been recognized by a number of workers in the Jurassic (e.g. Westermann 1954; Misik and Rakús 1964; Torrens 1967; Ziegler 1967, with references), while Hallam (1969, 1971) noted the broad correlation between European Boreal and Tethyan faunas and associated facies. More detailed relationships between facies and morphotype have been suggested by Scott (1940) and Kauffman (1967); however, our own work confirms the view of Ziegler (1967, p. 460), Reyment (1958), and other workers that no simple patterns are discernible.

Thus in the Upper Cretaceous successions of the Western Interior of the United States, where there are great facies variation and extensive sampling, no consistent distribution patterns emerge (text-fig. 10). *Collignoniceras woollgari* (Mantell), an ornate, evolute, highly variable mid-Turonian species occurs in limestone and chalky shale in Kansas and south-eastern Colorado; in calcareous shale in central and north-central Montana; in limestone concretions in calcareous to noncalcareous shale in the Black Hills area of western South Dakota and eastern Wyoming; in shaly olive-grey siltstone in the Four Corners area of Utah, Colorado, Arizona, and New Mexico; and in littoral sandstone beds in western Wyoming and north-eastern Utah. In striking contrast, *Baculites* has been found associated with *C. woollgari* only in a narrow east–west belt extending from central Utah to central Kansas (text-fig. 10). This distribution of *Baculites* is curious in that it crosses facies and yet is confined to a narrow geographic belt. *Baculites* at other stratigraphical levels in the Western Interior are not only found in a variety of lithologies but are usually widely distributed geographically, as in the case of the older of the two undescribed smooth Campanian *Baculites* listed by Gill and Cobban (1966). This species occurs in chalk in western Kansas and eastern Colorado, in noncalcareous shale in the Black Hills area, and in littoral sandstone beds in central Wyoming. These distributions suggest no rational interpretation at present.

Prionocyclus hyatti (Stanton) is another moderately evolute, highly variable, ornate Turonian species that is widely distributed in the Western Interior. It occurs in red- and orange-weathering ironstone concretions in a south-east-trending belt from north-central Montana to central Kansas; in limestone concretions in dark-grey noncalcareous shale in central Kansas, south-eastern Colorado, and northern New Mexico, and in shallow-water sandstone in south-central Colorado, northern New Mexico, and parts of Arizona, Utah, and Wyoming. *Scaphites* occurs with *P. hyatti* in the ironstone belt from north-central Montana to central Kansas, but elsewhere in the Western Interior, *Scaphites* of this age are absent except for a single occurrence (one specimen) in south-central Wyoming. The restriction of *Scaphites* to one part of the Western Interior is again curious, in that most species of the genus have a wide geographic distribution in a variety of sediments. For example the Santonian species *Clioscaphites choteauensis* Cobban occurs in chalk in western Kansas and eastern Colorado, in calcareous shale in north-western Colorado, in

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TEXT-FIG. 10. The regional distribution of *Collignoniceras woollgari* (Mantell) and *Baculites* in the Western Interior of the United States during the mid-Turonian, *C. woollgari* Zone interval. Circles are occurrences of *C. woollgari*; triangles *Baculites* occurrences.

EXPLANATION

▨	Calcareous shale
☐	Clay shale
▨	Silty shale
▨	Sandstone
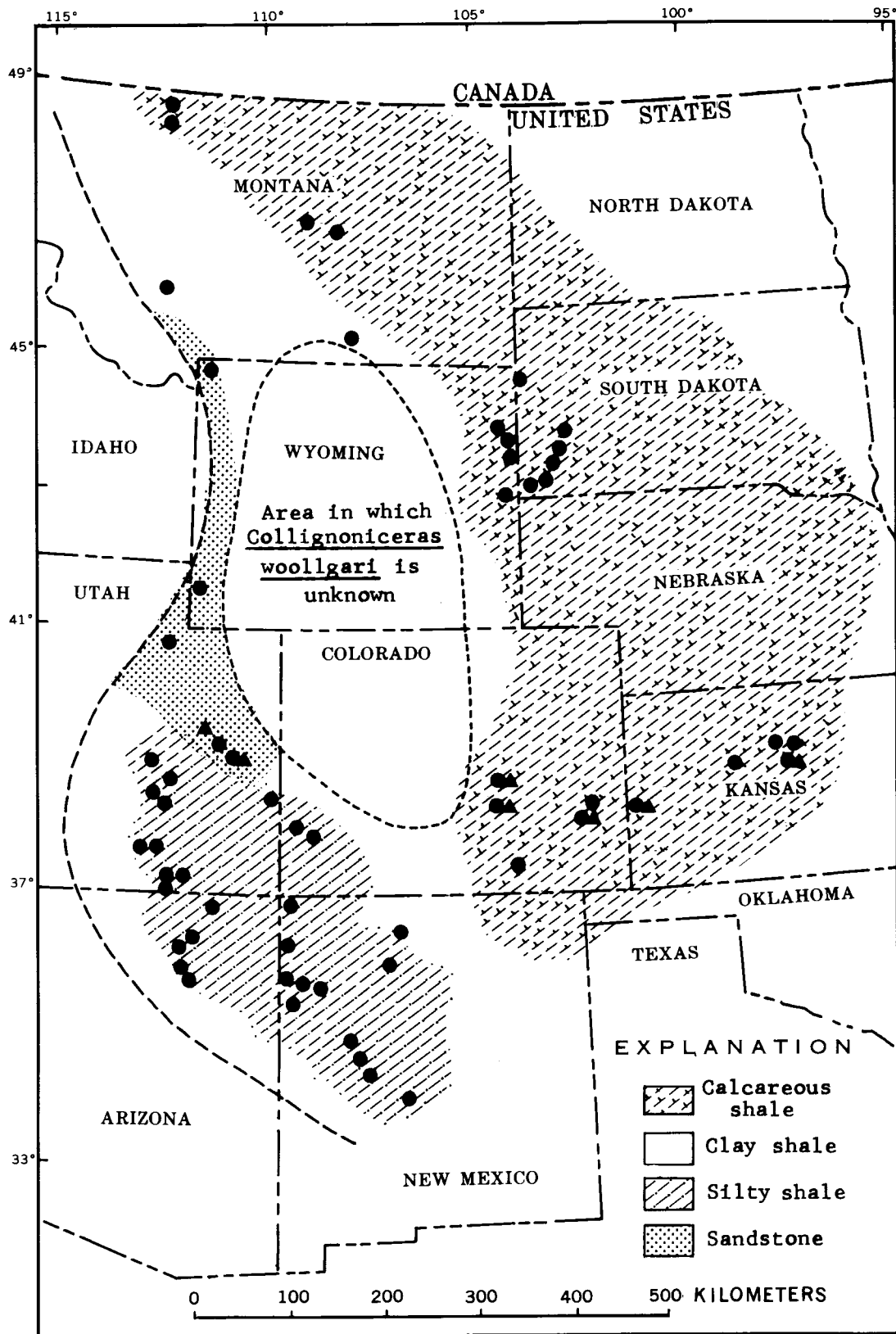
● *Collignoniceras woollgari* ▲ *Baculites* sp.

noncalcareous shale in north-western Montana, and in sandy shale and sandstone in north-western Wyoming and south-central Montana.

However, strict facies-linked distributions are also known (Table 1): certain North American Campanian heteromorphs provide good examples. *Anaklinoceras reflexum* (Stephenson) occurs only in near-shore sandstones in Delaware and

TABLE 1. Facies distribution of selected Cretaceous ammonite genera, based on personal observations; all occurrences recorded are of some numbers of specimens, rather than stray individuals.

GENUS	CHALKS	GLAUCONITIC CHALKS	PHOSPHATIC FACIES	CALCARENITIC LIMESTONES	CLAYS	NONCALCAREOUS SHALES	CALCAREOUS SHALES	SILTSTONES	SANDSTONES	GREENSANDS
DOUVILLEICERAS	O	O	●	●	●	●	●	●	●	●
SCHLOENBACHIA	●	●	●	●	●	●	●	●	●	●
PLACENTICERAS	●	●	●	●	●	●	●	●	●	●
MORTONICERAS	O	O	●	●	●	●	●	●	●	●
MANTELLICERAS	●	●	●	●	●	●	●	●	●	●
ACANTHOCERAS	●	●	●	●	●	●	●	●	●	●
CALYCOCERAS	●	●	●	●	●	●	●	●	●	●
METOICOCERAS	●	●	●	●	●	●	●	●	●	●
COLLIGNONICERAS	●	●	●	●	●	●	●	●	●	●
HYPOPHYLLOCERAS	●	●	●	●	●	●	●	●	●	●
TURRILITES	●	●	●	●	●	●	●	●	●	●
SCAPHITES	●	●	●	●	●	●	●	●	●	●
SCIPONOCERAS	●	●	●	●	●	●	●	●	●	●
TEXANITES	●	●		●		●		●	●	●
SPHENODISCUS	●			●	●	●		●	●	●
COILOPOCERAS	●	●			●	●			●	●
GAUDRYCERAS	●	●	●		●			●	●	
MAMMITES	●	●		●		●			●	
FORRESTERIA	●		●					●	●	
PRIONOCYCLOIDES					●		●			
BUDAICERAS					●					
NEOSAYNOCERAS					●	●				
FLICKIA					●					
FISCHEURIA					●					

● OCCURRENCE   O FACIES OF SUITABLE AGE NOT DEVELOPED

Colorado and in a shallow-water marl in north-eastern Texas. A small unnamed species of *Nostoceras*, moderately common in a near-shore sandstone member of the Pierre Shale in central Colorado, is represented by a few specimens in the deeper-water shale equivalents in south-eastern Colorado and central Wyoming; otherwise it is unknown in the Western Interior, although synchronous fossiliferous marine deposits outcrop over wide areas. A further classic and widely cited example of this type is the restriction of micromorphic genera to 'deep-water' or 'off-shore' clays during the Cretaceous. Thus Albian-Cenomanian clays containing faunas of minute pyritized forms are well known from North Africa (for Algeria and Tunisia, see Pervinquière 1907, 1910; Dubourdieu 1953, 1956; Sornay 1955), Texas (Adkins 1918; Böse 1928), and Madagascar (Collignon 1928-1929, 1932, 1963, 1964). In each of these regions a series of micromorph genera have been described which are limited to the facies, and many are common to these widely separated areas. Examples are *Cottreauites*, *Submantelliceras*, *Prioncycloides*, *Flickia*, *Adkinsia*, *Ficheuria*, *Algericeras*, *Algerites*, *Neosaynoceras*, and *Neopulchellia*. Subsequent work has shown that several of these 'genera' are merely nuclei of forms well known in other facies, and thus *Cottreauites* may be a synonym of *Paracalycoceras*, *Submantelliceras* of *Graysonites*, and *Neopulchellia* of *Forbesiceras*. However, the others remain a group largely or wholly limited to the same facies in three widely separated regions.

GEOGRAPHICAL DISTRIBUTION PATTERNS

The distribution patterns shown by ammonites reflect the interaction of a number of factors, chief among which are:

1. Distribution of the living animals:

   (*a*) As larvae, dispersal patterns of which reflect length of larval life and prevailing surface currents.

   (*b*) The settlement after metamorphosis in forms leading a benthonic mode of life, where their distribution will reflect the occurrence of suitable bottom environments.

   (*c*) A continued nektonic life, when distribution reflects limiting factors such as environmental stability and predictability.

   (*d*) A continued planktonic life when distribution reflects the same factors as (*c*) as well as dispersal by surface currents.

2. Post-mortem distribution, which may be:

   (*a*) Minimal, in which case the occurrence closely reflects the original life distribution.

   (*b*) Extensive, the resulting post-mortem drift producing a distribution pattern far wider than in life, as in Recent *Nautilus*.

   (*c*) Tectonic separation or juxtaposition of regions as a result of plate motions.

Much information on ammonite distributions has been published in three recent compilations: *Faunal Provinces in Space and Time* (Middlemiss and Rawson 1971), the *Atlas of Palaeobiogeography* (Hallam 1973*b*, specifically Cariou 1973; Enay 1973; Dietl 1973; Howarth 1973*a*; Kummel 1973; Matsumoto 1973; and Wiedmann

1973*a–b*), and *The Boreal Lower Cretaceous* (Casey and Rawson 1973). The reader is referred to these papers and to compilations by Hallam (1969) and Donovan (1967).

We have approached the subject in this review in terms of *kinds* of distribution, rather than total distribution patterns at instants in time. In general, the following pre-Continental Drift distribution patterns of ammonites can be recognized: (1) Pandemic. (2) Latitudinally limited. (3) Endemic and provincial. (4) Disjunct. (5) Post-mortem.

Pandemic distributions. As examples of pandemic distribution we cite Arkell's (1956) observations on the near world-wide occurrence of many Jurassic ammonites at generic and sometimes specific level, together with similar distributions given for Jurassic heteromorphs by Dietl (1973) and for a variety of Cretaceous forms by Matsumoto (1973). Many of these distributions involve widespread occurrences in large numbers, and consequently an explanation in terms of post-mortem drift can be dismissed. The chief limitation on these taxa is their absence in high latitudes; this reflects the generally observed decline in faunal diversity from equator to poles resulting from the progressive elimination of stenotopic forms (e.g. Stehli *et al.* 1967; Valentine 1967; Sanders 1968, 1969; Kauffman 1973).

The distribution of some pandemic taxa is truly remarkable; two typical examples are cited in detail.

(*a*) *Pseudophyllites* (text-fig. 11). The tetragonitid genus *Pseudophyllites* has a time range from late Santonian/early Campanian to early Maastrichtian. Nine species have been attributed to the genus, but unpublished work by Kennedy and Klinger suggests that only three appear to merit separation as distinct morphospecies. These species have overlapping stratigraphical and geographical ranges, and may represent no more than variants or subspecies of a *P. indra* (Forbes) biospecies. *Pseudophyllites* is common in the Campanian/Maastrichtian of Alaska, the then North Pole (Smith *et al.* 1973), British Columbia, and East Greenland. It is also common in Antarctica (Graham Land), South Africa, Madagascar, Australia, and New Zealand, at that time in high southern latitudes. These areas of abundance are linked by records from Brazil, Japan, central-southern Europe, and the western shores of the Caspian,
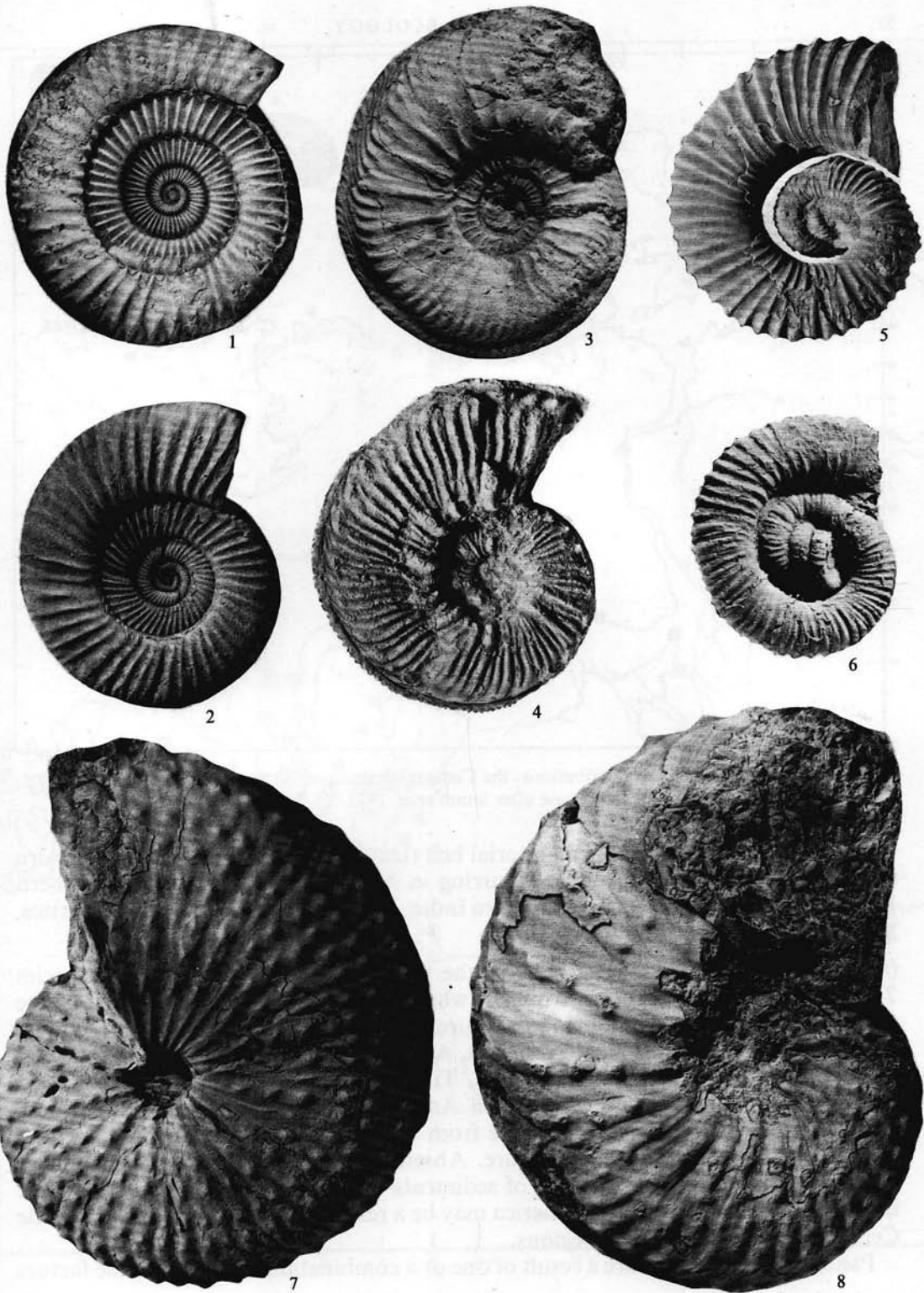

Homoeomorphy

Figs. 1, *Dactylioceras* sp. from the Toarcian Grey Shales near Whitby, Yorkshire, and 2, *Perisphinctes* sp. from the Oxfordian Cordatus Schichten, Alois, Zuber-Oberlé, Oensingen, Switzerland.

Figs. 3, *Cardioceras* sp. from the Oxfordian Cordatus Schichten, Alois, Zuber-Oberlé, Oensingen, Switzerland, and 4, *Prionocyclus wyomingensis* Meek from the Turonian Carlile Shale near Red Bird, Niobrara County, Wyoming.

Figs. 5, *Colchidites* sp. from the Barremian of Boyaca, Columbia (J. P. Conlin Collection), and 6, *Axonoceras* sp. ×2, from the Campanian Pierre Shale near Kremmling, Colorado, USGS Mesozoic locality D 1351.

Figs. 7, *Discoscaphites conradi* (Meek), USNM 696, from the Maastrichtian Fox Hills Sandstone of South Dakota and 8, *Trachyceras* (*Protrachyceras*) *meeki* Mojsisovics, USNM 74380, from the mid-Triassic of Cottonwood Canyon, Nevada.

KENNEDY and COBBAN, Homoeomorphy
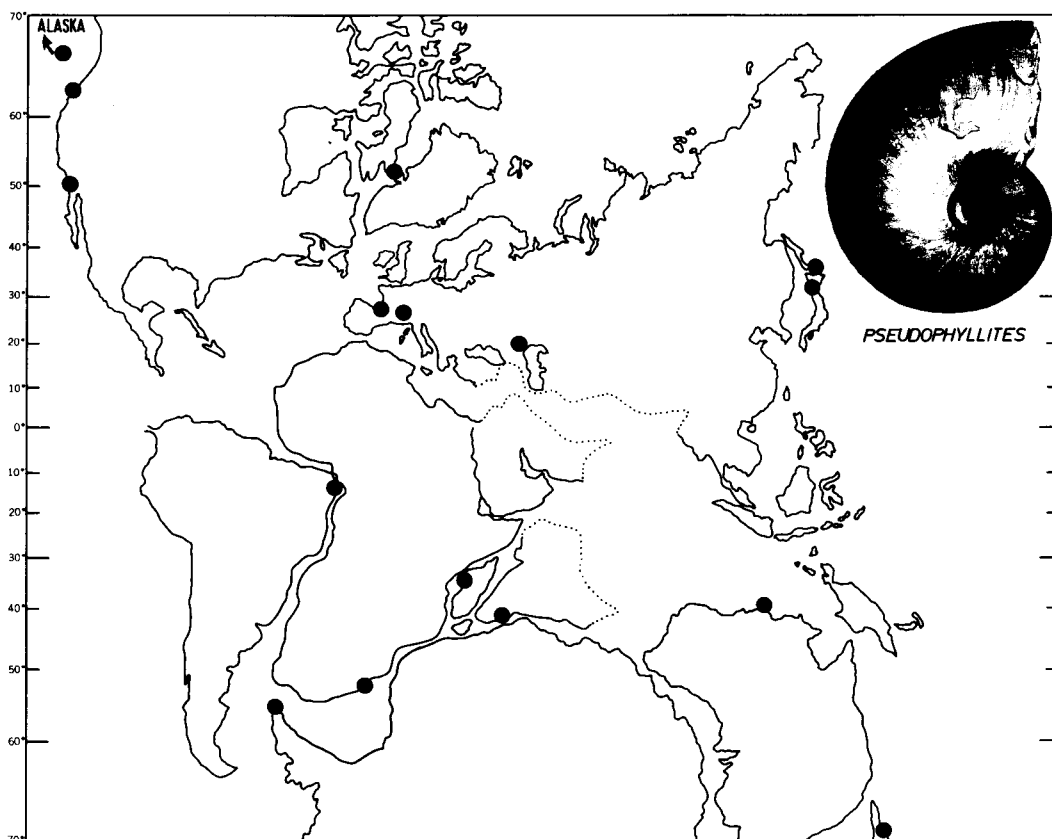
TEXT-FIG. 11. Pandemic distributions: the Campanian tetragonitid genus *Pseudophyllites*.
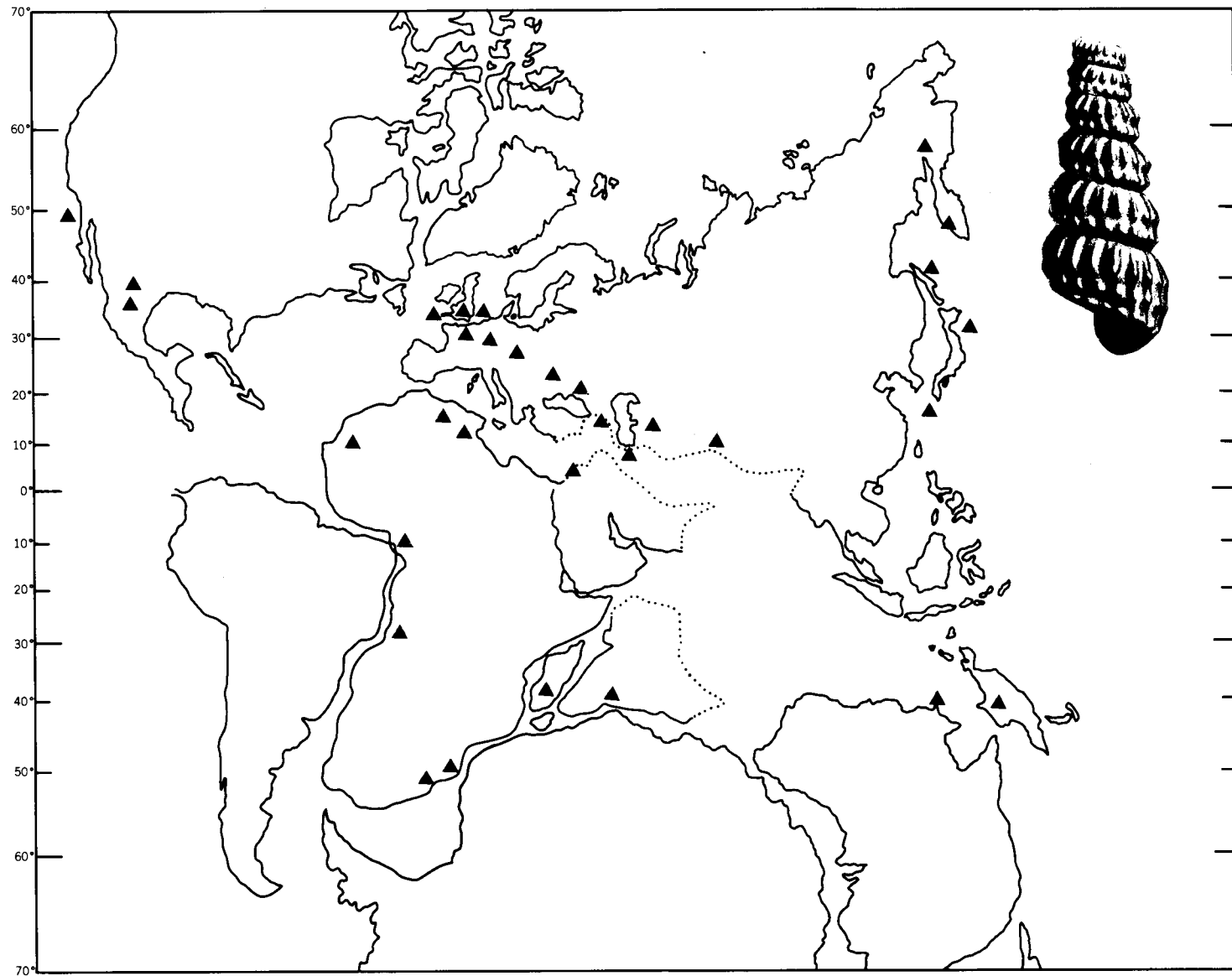Map base after Smith *et al.* 1973, fig. 7.

which span what was then the equatorial belt (text-fig. 11). Even the species *P. indra* (Forbes) has an extensive range, occurring in Alaska, British Columbia, southern France, Zululand, Madagascar, southern India, Japan, western Australia, Antarctica, and Brazil.

(*b*) *Turrilites costatus* (text-fig. 12). In the Cenomanian, the heteromorph species *T. costatus* Lamarck is known from the whole of western Europe as far east as the Caspian and Iran, north of the Zagros suture, the Middle East, North Africa (Algeria, Tunisia, Morocco), West Africa (Nigeria, Angola), South Africa (Mozambique and Zululand), Madagascar, southern India, Tibet, Kamchatka, Sakhalin, Japan, and northern Australia. However, in North America it is only known from Mexico, Texas, and California; and its absence from the Western Interior and Alaska does not appear to reflect collection failure. Absence of records from west Greenland and Antarctica reflect the absence of sediments of suitable ages; apparent absence from New Zealand and South America may be a result of poor knowledge of Middle Cenomanian faunas of these regions.

    Pandemic occurrences are a result of one or a combination of several of the factors

TEXT-FIG. 12. Pandemic distributions: the Cenomanian heteromorph *Turrilites costatus* Lamarck. Map base after Smith *et al.* 1973, fig. 7.
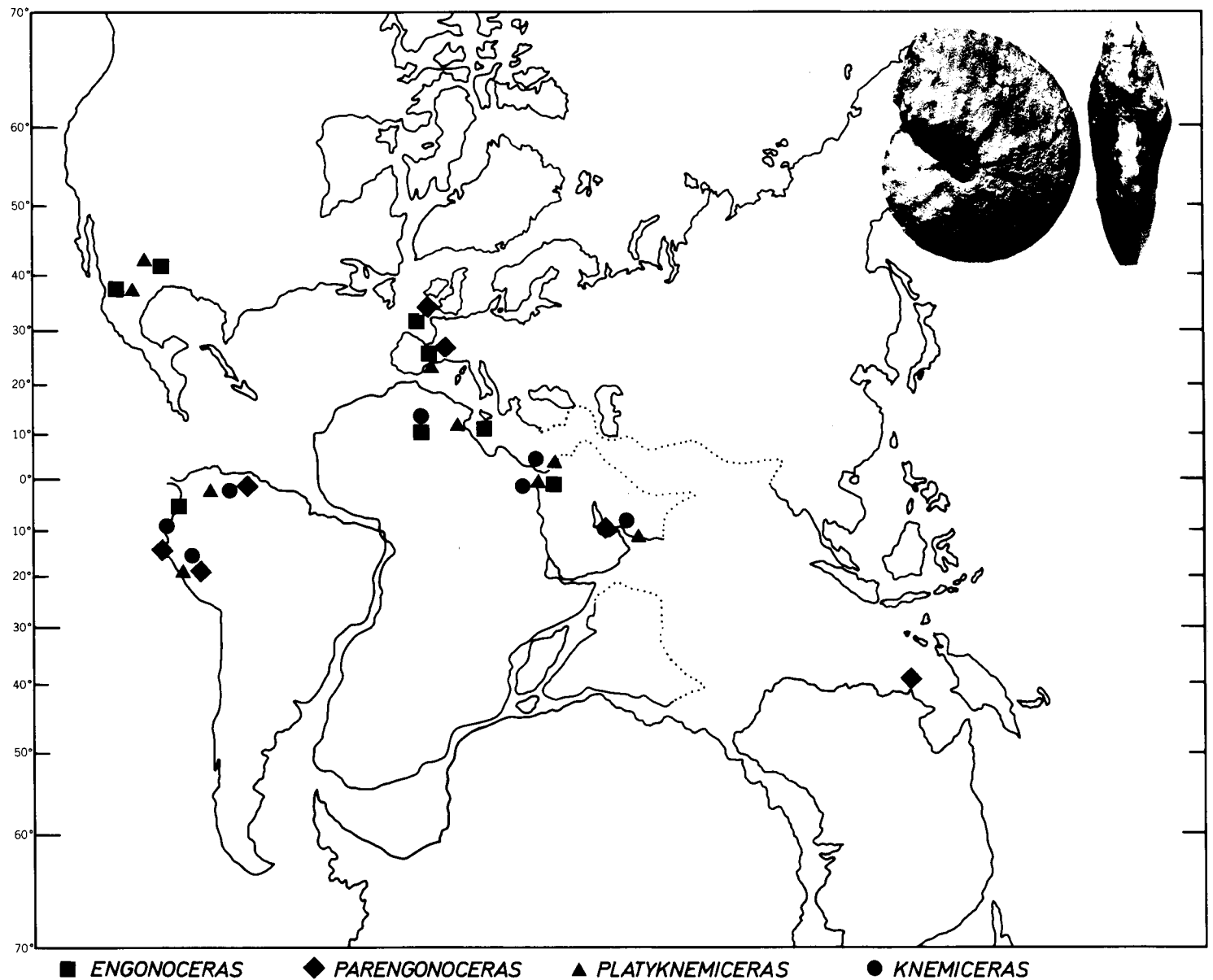
noted in our introductory statement, in particular larval and post-larval planktonic nektonic life habits and post-mortem drift by ocean currents. Pandemic forms generally exhibit a high degree of facies independence (we have collected *T. costatus* in calcareous and noncalcareous shales (crushed, in concretions, and pyritized), bioclastic limestones, chalks, greensands, phosphatic conglomerates, and clastic sediments ranging from silt to gravel. It occurs in geographical situations ranging from outer shelf to near shore); and, from its wide latitudinal spread it would seem to have been eurytopic. The absence of these forms from the Western Interior of the United States indicates that they may, however, have been stenohaline.

As tolerance of environmental fluctuation and instability decreases, pandemic ammonites grade into the latitudinally limited types discussed below.

Latitudinally limited distributions. Ammonites, like other elements of marine biota, show decreasing diversities towards the pole, and some taxa are limited to particular latitudinal belts, reflecting their tolerance or intolerance of fluctuating environmental conditions; they are, to varying degrees, stenotopic. The classic distributions of this type are those associated with the Tethyan belt, a distribution paralleling that known for Mesozoic hermatypic corals (Beauvais 1973), rudistids (Coates 1973) and other bivalves (Kauffman 1973), larger Foraminiferida (Dilley 1971, 1973) and other groups (Hallam 1971). Ammonite distributions of this type are reported for a host of classic 'Tethyan' indicators; Hallam (1969, 1971), Cariou (1973), Enay (1973), and Howarth (1973*a*) have illustrated such distributions for Jurassic forms; Wiedmann has shown such distributions for Upper Triassic heteromorphs (1973*a*, fig. 3) and Kummel (1973) suggests a similar distribution for some Lower Triassic ammonoids. Distribution patterns of this type in the Cretaceous are less well known, although Matsumoto (1973) and Basse (1940) have noted the limited, apparently Tethyan distribution of pseudoceratites. Text-fig. 13 shows the distribution of a series of such genera.

Endemic and provincial distributions. This group includes taxa whose geographical distribution is limited both latitudinally and longitudinally. Examples from the Jurassic are well known, such as the restriction of *Bouleiceras* to a Mediterranean-east African 'Ethiopian' Province (Hallam 1967*b*; Howarth 1973*a*); recognition of Boreal, sub-Boreal, sub-Mediterranean, Mediterranean, Indo-Malagasy, Cuban, and Pacific Provinces in the Middle Jurassic (Cariou 1973), or Mediterranean, Himalayan (Indo-Pacific), and Ethiopian Provinces of the Tithonian (Enay 1973). In the Cretaceous, similar distributions are clearly indicated on Matsumoto's (1973) illustrations and, in particular, by the distribution of Lower Turonian forms plotted by Freund and Raab (1969).

The distinctness of these faunas varies from slight, as in the case of Arkell's Pacific 'Realm' (reduced to a 'Province' by Hallam 1969), to those which are persistent and which are characterized by a high percentage of endemic forms. In this latter category are the Upper Cretaceous faunas of the Western Interior of the United States and the Boreal Jurassic–Cretaceous faunas of western Europe. Ammonites in these two areas are highly endemic; well-known Cretaceous examples are north-west European hoplitid ammonites of the Albian (text-fig. 14: Owen's (1971, 1973) hoplitinid faunal Province), the gastroplitid ammonites of the Western Interior (text-fig. 14), and

TEXT-FIG. 13. Latitudinally restricted distribution: the Albian pseudoceratitic hoplitids *Knemiceras, Engonoceras, Platyknemiceras*, and *Parengonoceras*. Map base after Smith *et al.* 1973, fig. 7. Inset: a typical engonoceratid from the Albian of Texas.

■ ENGONOCERAS   ◆ PARENGONOCERAS   ▲ PLATYKNEMICERAS   ● KNEMICERAS

TABLE 2. Percentages of various normally coiled and heteromorph ammonite genera in Chalk Basement Beds (phosphatic conglomerates) and normal Chalk facies of southern England. Figures are cited for two successive zones in the Middle Cenomanian sequences of the area; data for chalks comes from collections made in southeast England; data for Basement Beds comes from the south-west. For details see Kennedy (1969, 1971). The same range of genera occur in these two dissimilar facies, but there are subtle differences in relative proportions of genera and in the proportions of normally coiled to heteromorphs.

Turrilites costatus assemblage Zone

	Basement beds %	Chalks %
Sciponoceras	65	90+
Schloenbachia	15	5
Turrilites	10-12	2
Acanthoceras	5	2
Calycoceras	1-2	less than 1
Others	1	less than 1
Heteromorphs	75	90
Normally coiled forms	25	10

If *Sciponoceras* is omitted, figures are:

Schloenbachia	45	50
Turrilites	30-35	20
Acanthoceras	15	20
Calycoceras	3-5	1
Others	1	1
Heteromorphs	30-35	20
Normally coiled forms	65-70	80

Turrilites acutus assemblage Zone

	Basement Beds %	Chalks %
Schloenbachia	40-45	50-55
Turrilites	20	5
Scaphites	18	5-7
Acanthoceras	6	25
Calycoceras	10	3
Stomohamites	3	1
Anisoceras	1-2	1
Sciponoceras	1-2	less than 1
Others	1	less than 1
Heteromorphs	40-45	15
Normally coiled forms	55-60	85

many of the baculitid, scaphitid, and acanthoceratid groups of the same area. In the Jurassic, a whole range of taxa are more or less restricted to the Boreal Realm of Hallam (1969) and earlier workers: the Liparoceratidae and Amaltheidae (Pliensbachian), Cadoceratinae (Bathonian to Callovian), Kosmoceratinae (Callovian), Cardioceratinae (Oxfordian), Dorsoplanitidae and many aulacostephanids (Kimmeridgian), Craspeditinae and Virgatitinae (Volgian/Tithonian). No single taxonomic feature links these groups together.

A feature of faunas characterized by a high degree of endemism is that diversities are often low; a few genera or even species dominate assemblages. For example, in Cretaceous occurrences we have studied gastroplitid ammonites which form over 99% of the ammonites from Middle to Upper Albian faunas of the Western Interior of the United States and Canada, whereas *Schloenbachia* forms over 95% of the Boreal Lower and Middle Cenomanian ammonite faunas of northern north-western Europe. A further feature of endemic forms is that they exhibit a high degree of intraspecific variability (p. 38). Endemic and provincial distributions reflect latitudinal restriction of taxa as a result of variation of environmental factors with latitude, whilst longitudinal distribution is a reflection of limitation by barriers, such as north–south land masses, deep ocean basins, and perhaps other topographical features (e.g. Young 1972), as well as circulatory patterns, and perhaps regional salinity gradients.

The controls on two such faunal regions, the Boreal 'Realm' of the Jurassic/ Cretaceous and the Western Interior endemic centre are further discussed below as illustrations of distributions of this type.

Boreal ammonite distribution during the Jurassic and Cretaceous. During the Jurassic, the Boreal 'Realm' occupied the northern part of the Northern Hemisphere, its southern boundary running through Europe along the line of the Alpine fold belts, and through northern California and between Japan and eastern Siberia in the North Pacific region. The rest of the world belongs to the Tethyan 'Realm' (Hallam 1969). Table 3 (from Hallam 1969) summarizes the differences between the ammonite faunas of the two realms. These differences first appeared in the Pliensbachian (Donovan 1967; Hallam 1969; Howarth 1973a), before which Boreal faunas were only an impoverished version of Tethyan. The two faunas become increasingly distinct throughout the Jurassic. Up to and including the Toarcian, correlation between the two areas is possible; above this, different zonal and (in the post-Kimmeridgian) stage systems are recognized in northern and southern Europe. Thus there is an interval extending from Bajocian to early Valanginian within which precise correlation is impossible, and indeed the Jurassic/Cretaceous boundary is drawn at different points in the two areas—the Boreal Volgian/Ryazanian and the Tethyan Tithonian/Berriasian boundaries do not correspond (Casey 1963, 1971; Hancock 1972, etc.).

The degree of exclusion of Tethyan forms from northern Europe (see quantitative curves in Gordon 1975) is truly remarkable. Phylloceratid and lytoceratid ammonites are locally common in the Hettangian to Toarcian of southern Britain, and occur occasionally in the Bajocian. Above this level we know of three *Phylloceras* from the Oxfordian–Callovian (Arkell 1939; Hancock, pers. comm.), one from the Hauterivian (Rawson 1966), a handful from the Albian, and two from the Cenomanian (Kennedy 1971). The distribution of lytoceratids in the post-Bajocian is similar, although there are some remarkable records such as *Lytoceras* and *Hypophylloceras* from the Cenomanian of Greenland (Donovan 1954).

The development of the Boreal 'Realm' has normally been considered a result of temperature gradients (Sato 1960; Stevens 1965a–b, 1967; Ziegler 1963; Saks et al. 1964; Jeletzky 1965; Donovan 1967; Reid 1973; Gordon 1975), yet, as Hallam

(1969, 1972) has demonstrated, there is convincing palaeobotanical evidence indicating that this is not so. Declining faunal diversity within the Boreal 'Realm' took place at a far greater rate with increasing latitude than is seen at present. This is the reverse of that expected when comparing the present glacial and the Jurassic non-glacial situations. It is also clear that there are no geographical barriers preventing faunal migrations into the area, and Hallam produced evidence that suggested to him that the curious geography of the times, with an almost land-locked Boreal epeiric sea, produced an area in which there was great fluctuation in environmental conditions (e.g. temperature, salinity, food supply) and that this was responsible for

TABLE 3. Families and subfamilies of ammonites typifying Jurassic Boreal and Tethyan faunas. Cosmopolitan groups are omitted (from Hallam 1969).

Ammonite families and subfamilies

Stages	Boreal			Tethyan
Tithonian and Volgian	Craspeditidae Virgatitinae			Berriasellidae Spiticeratinae Virgatosphinctinae
Kimmeridgian	Dorsoplanitidae Certain Aulacostephaninae (*Aulacostephanus*, *Rasenia*)			Ataxioceratinae Virgatosphinctinae Simoceratidae
Oxfordian	Cardioceratinae			Peltoceratinae Perisphinctinae Aspidoceratinae
Callovian	Kosmoceratidae Cadoceratinae			Peltoceratinae Aspidoceratinae Reineckiidae Macrocephalitidae
Bathonian	Cadoceratinae			Sphaeroceratidae Tulitidae Morphoceratidae, etc.
Bajocian	Cadoceratinae (Upper Bajocian)			Hammatoceratidae Sonniniidae Leptosphinctinae
Toarcian				Hammatoceratidae Bouleiceratinae
Pliensbachian	Amaltheidae Liparoceratidae			Hildoceratidae Dactylioceratidae Juraphyllitidae
Sinemurian and Hettangian				Juraphyllitidae Ectocentritidae

(Vertical labels between Boreal and Tethyan columns: Oppeliidae; Phylloceratidae and Lytoceratidae)

TEXT-FIG. 14. Endemic distributions. The Albian boreal hoplitids *Hoplites* and *Anahoplites* represent the predominantly Old World Hoplitinae; the contemporary *Gastroplites* and *Neogastroplites* represent the predominantly New World Gastroplitinae. The two groups are recorded together in East Greenland and Spitzbergen, whilst a single *Gastroplites* is known from England. Inset: *Neogastroplites haasi* from Montana; *Gastroplites kingi* McLearn from British Columbia; *Hoplites dentatus* (J. Sowerby) and *Anahoplites planus* (Mantell) from Kent.
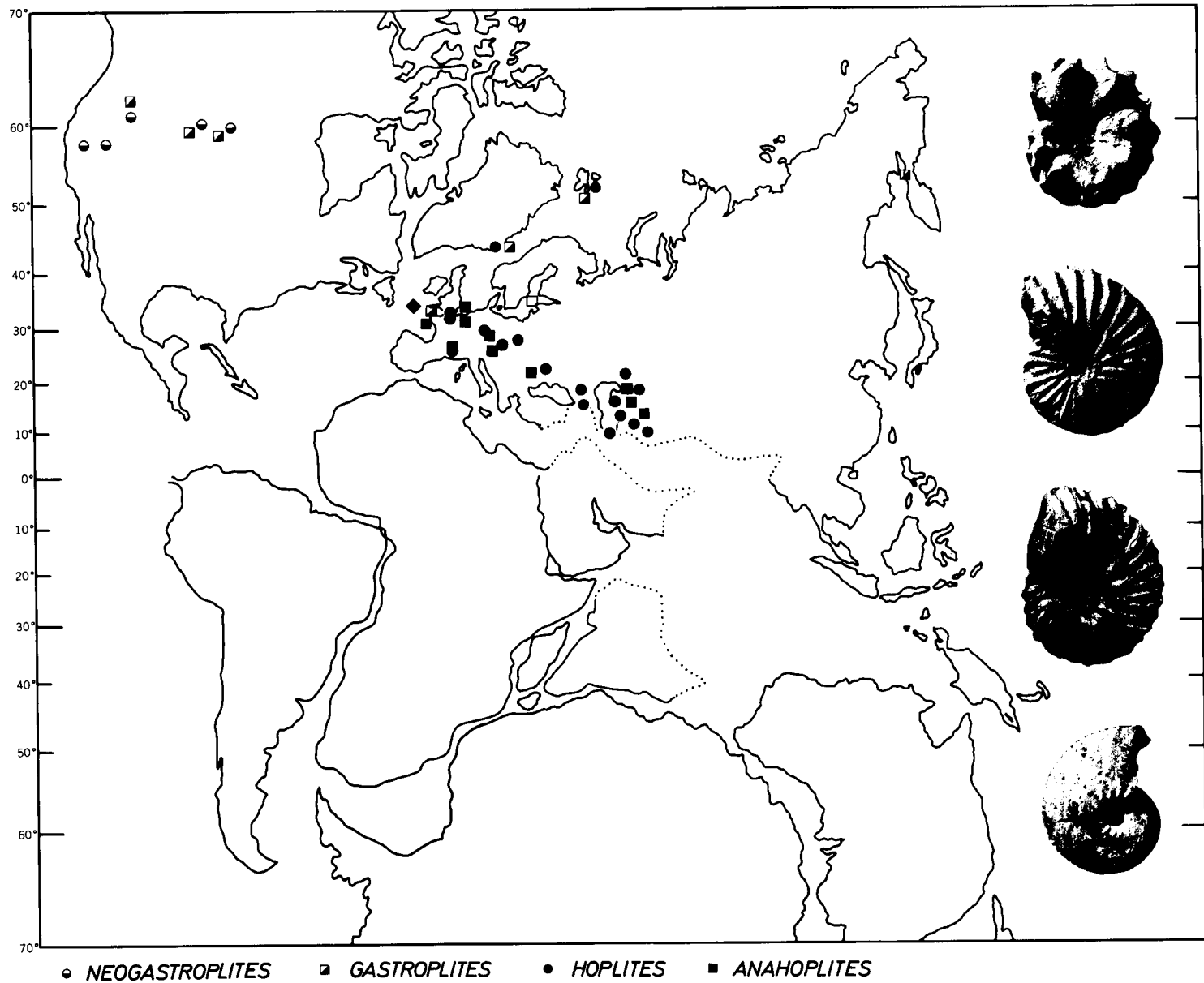
observed changes—an application of current ecological concepts of environmental stability and predictability and trophic resource availability (Valentine 1971b, 1973). This more sophisticated view explains the continuance of a marked Boreal 'Realm' during the Cretaceous, when mid-oceanic rifting resulted in an open sea-way through the middle of the Boreal inland sea.

Endemism in Cretaceous ammonite faunas of the Western Interior of North America. During the Middle and Late Cretaceous, a broad, shallow epeiric sea extended from the Gulf of Mexico to the Arctic Ocean, splitting North America into a low-lying eastern region and western highlands (for map, see Gill and Cobban 1966, fig. 15, 1973). At times, an arm of the sea may also have extended north-eastward across the Canadian Shield via Hudson Bay to western Greenland (Williams and Stelck 1973), whilst a peninsula extending south-westward from the eastern lowland region probably restricted access to the Gulf area, and this connection may indeed have been wholly or partially severed at times. Little is known concerning connections with the Arctic area to the north, but these too may have been restricted from time to time.

The faunas of the Western Interior sea-way suggest that salinities were below normal, probably as a result of the restricted connections with the open sea. Thus stenohaline groups such as echinoderms, articulate brachiopods, bryozoans, corals, sponges, and belemnites are typically rare or absent in the sea-way, whilst those groups that are present are often of relatively low diversity, as is the case with ammonites. The latter may well represent forms that evolved a tolerance for lower salinities than normal. Reduced salinities are also suggested by microfaunas, as inferred by Eicher (1965) and others. Endemic elements first appeared in late Albian times, when the sea-way extended southwards from the Arctic to northern Wyoming (Reeside and Cobban 1960, fig. 13) and a single species, *Neogastroplites haasi* Reeside and Cobban, was present (text-fig. 9). Continued transgression spread across Wyoming, and a successional species, *N. cornutus* (Whiteaves), dominated faunas. The only other ammonites known are two specimens of the pseudoceratite *Metengonoceras* from north-western Wyoming. *Metengonoceras* is common in the Gulf Coast region, and this occurrence may represent drifted dead shells; that *Neogastroplites* did not spread into the Gulf Coast region suggests that it may have been limited to the reduced salinities and lower water temperatures of the northern parts of the sea-way. The dominance of a single *Neogastroplites* species persists through the *N. americanus* and *N. muelleri* Zones, although *Metengonoceras* becomes more widespread.

Marine Lower Cenomanian macrofaunas are unknown in the United States Western Interior, but three successive gastroplitid faunas occur in Alberta and British Columbia (Warren and Stelck 1958), and these successive assemblages are present in the *N. septimus, Irenicoceras bahani*, and *Beattonoceras beattonense* Zones. These endemic hoplitids die out at the close of the early Cenomanian, but endemic elements also became important from late Turonian times onwards. Their evolutionary patterns are best documented in the closely studied baculitid and scaphitid lineages. The endemic *Baculites* (text-figs. 15–16) have their origin in *B. yokoyamai* Tokunaga and Shimizu, a species first described from the Coniacian of Japan. In

the Interior, it first appears in the Lower Turonian (*M. nodosoides* Zone) at many localities from the north end of the Black Hills uplift south through eastern Colorado and central Kansas. By the mid-Turonian, *C. woollgari* Zone times it is restricted to a narrow belt extending from central Utah to central Kansas (text-fig. 10) and is absent in the succeeding *Prionocyclus hyatti* Zone. The species reappears in the late Turonian *Scaphites warreni* Zone, surviving in this area until the close of the Turonian.

B. yokoyamai is a small, smooth species, with an elliptical or subelliptical cross-section and a moderately simple suture. The only detectable evolutionary change seen during the Turonian was a gradual increase in size, but at the beginning of the Coniacian it gave rise to *B. mariasensis* Cobban (a species characterized by a narrower venter) from which evolved the Santonian species *B. codyensis* Reeside and *B. asper* Morton, forms which developed flank ornament, and show slight increases in size, sutural complexity, and changes in whorl section. The lineage culminated in the late Campanian *B. rugosus* Cobban, which reaches diameters of as much as 110 mm. Although later forms show a gradual decrease in size and simplification of sutures, the last representative of the lineage, *B. eliasi*, died out in the early Maastrichtian. Most of the twenty or so species recognized in this lineage are restricted to the Western Interior. The original small, smooth forms seem to have been completely restricted during the late Turonian and early Coniacian, although some Coniacian to early Campanian species do occur in the Caribbean Gulf Coast area. There *Baculites* evolved relatively slowly, and species tend to be small and to retain a simple suture. These species occasionally strayed into the Western Interior but seldom migrated (or drifted?) as far north as the Black Hills. During the late Campanian these Gulf Coast forms showed progressive size increases although retaining simple sutures; by Maastrichtian time they greatly exceed their Western Interior contemporaries in size. A few individuals of these species actually occurred in the late Campanian faunas of the Interior, but with the disappearance of *B. eliasi*, the last endemic Interior species, they became predominant.

The endemic scaphitid record of the Western Interior (text-fig. 17) has its origins in the late Cenomanian. The earliest species, *S. delicatulus* Warren, is found at the top of the Cenomanian where it was widely distributed in the sea-way ranging from the Arctic slope of Alaska south through Canada to New Mexico and Texas. In the early Turonian it was restricted to the Western Interior and gave rise to the early mid-Turonian species *S. patulus* Cobban, *S. larvaeformis* Meek and Hayden, and *S. praecoquus* Cobban. These forms are restricted to the Dakota Black Hills area, Montana and Alberta, but *S. carlilensis* Morrow, a late Middle Turonian descendant of *S. larvaeformis*, spread south across Kansas and into Texas. By contrast the later Turonian *S. warreni* Meek and Hayden, *S. ferronensis* Cobban, *S. whitfieldi*, and *S. nigricollensis* Cobban extend to an area from central New Mexico to north-western Montana. This fluctuating range of the endemic scaphitids continues, and during the latest Turonian to Coniacian, the group was restricted northwards, *S. corvensis* being unknown south of Wyoming but possibly occurring in western Greenland, whilst the succeeding *S. preventricosus* Cobban and *S. ventricosus* Meek and Hayden have a similar Western Interior distribution and definitely occur in Greenland. The lineage reaches its greatest size with the early Santonian
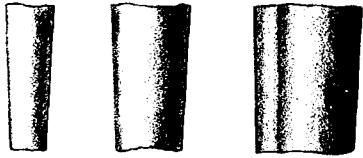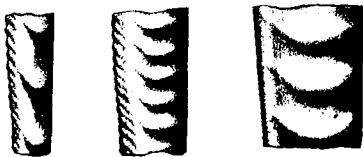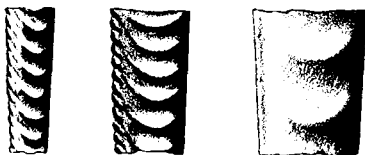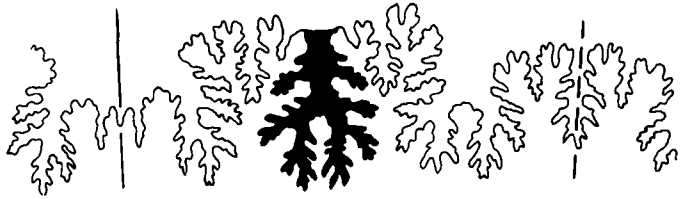
Baculites scotti Cobban
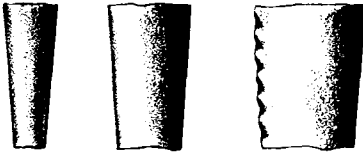
Typical suture

Baculites gregoryensis Cobban

Baculites asperiformis Meek

Baculites mclearni Landes

Typical suture

Baculites obtusus Meek

TEXT-FIG. 15

Baculites eliasi Cobban

Baculites reesidei Elias

Baculites jenseni Cobban

Baculites cuneatus Cobban
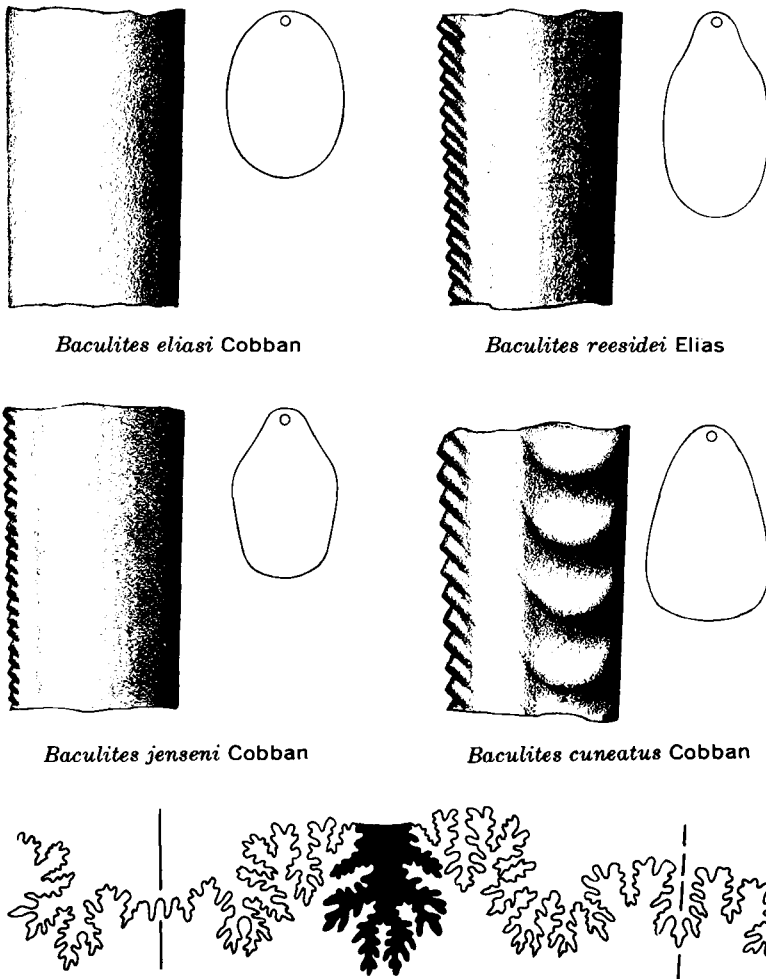
Typical suture

TEXT-FIG. 16.

TEXT-FIGS. 15-16. Representative endemic baculitids from the United States Western Interior Region. *Baculites obtusus*, *B. mclearni*, and *B. asperiformis* are successive mid-Campanian species; *B. gregoryensis* and *B. scotti* are two successive early late Campanian species. *B. cuneatus* is a latest Campanian species; *B. reesidei*, *B. jenseni*, and *B. eliasi* are of early Maastrichtian age. These species are representative of more than twenty endemic species which evolved in the early Turonian to early Maastrichtian interval. The illustrations show the progressive size increase and increased sutural complexity of the lineage together with growth stages of some of the species. As can be seen from comparing the growth stages of *obtusus/mclearni/asperiformis* and *scotti/gregoryensis*, a series of specimens is needed to determine actual horizon and species (after Scott and Cobban 1965).

S. depressus Reeside, a moderately tightly coiled species with the most complex sutures, confined to the Western Interior of the United States and Alberta. By mid-Santonian times the endemic *Scaphites* developed tight coiling and trifid lobes, characters which lead to the grouping of their descendants into a separate genus, *Clioscaphites*, known only from North America and western Greenland. This genus in turn is the origin of a minor radiation, which gave rise to two further endemic genera in late Santonian times: *Desmoscaphites*, a form with constricted inner whorls and compressed later whorls, and the planulate *Haresiceras*. Both died out leaving no descendants.

In contrast, scaphitids outside of the Western Interior remained simple during the Turonian to Santonian interval, did not show progressive re-coiling or develop complex sutures, constrictions, or tabulate peripheries. However, at the close of the Santonian one of these species, *S. leei* Reeside, migrated into the Western Interior from the Gulf Coast region and is found first alongside *Desmoscaphites* and *Haresiceras* and subsequently with *Haresiceras* alone. Its descendant, *S. hippocrepis* (DeKay), and *Haresiceras* both died out suddenly in Lower Campanian times.

Disjunct distributions. The local abundance of the same genera, or even the same species, in widely separated areas has attracted comment from several workers. Many of these distributions represent no more than the result of subsequent tectonic separation of once contiguous faunal regions, and their relevance is discussed elsewhere (p. 50). There are, however, some distribution patterns that remain disjunct and often widely separated even after continental reassembly. Many of these may represent no more than collection failure or our ignorance of the literature, but some appear to be valid distributions. The following examples are drawn from stratigraphical horizons with which we are familiar, and that have been studied in detail over wide areas (text-fig. 18).

1. The Turonian genus *Ampabakites*. The only records are from Ampakabo in Madagascar and from Colorado in the United States.

2. The late Cenomanian genus *Sumitomoceras*, known only from Japan, southern India, Turkestan, southern England, and Texas. The type species, *S. faustum* Matsumoto and Muramoto is known only from Japan and Dorset (England).

3. The Middle Cenomanian *Acanthoceras cornigerum* Crick, known from the unique holotype from Zululand, South Africa, and from a further specimen from Hokkaido, Japan.

4. The largely Cenomanian genus *Marshallites*, known from Japan, Kamchatka, Sakhalin, Alaska, southern California, and southern India.

These examples, and many others, deal with normally coiled, moderately ornamented forms, and we can detect neither facies, environmental nor palaeogeographic features that might account for their distribution.

Post-mortem distributions. All the distributions noted above may in part reflect the post-mortem drifting of floating shells, and many original distributions may be 'blurred' in this way. There are a number of records of otherwise endemic groups known from individual records at great distances from the principal centres of the groups. Some of these may reflect collection failure; others clearly do not. Among

TEXT-FIG. 17. Simplified representation of the phylogeny of endemic Late Cretaceous United States Western Interior endemic scaphitid genera. *Scaphites patulus* Cobban is a late Turonian species; the specimen is from the Carlile Shale; *S. ventricosus* Meek and Hayden is late Santonian species; the specimen is from the Cody Shale. *Clioscaphites vermiformis* (Meek and Hayden) and *C. platygastrus* Cobban are both Santonian species; specimens are from the top of the Colorado Shale. *Haresiceras natronense* Reeside is an early Campanian species from the Pierre Shale; *Desmoscaphites erdmanni* is of late Santonian age, the figured specimen is from the Marias River Shale. *Scaphites hippocrepis* DeKay is of early Campanian age; the illustrated specimen is of an example of *S. hippocrepis* II, from the Eagle Sandstone.

the latter, we would cite the following occurrences of abundant endemic North American Cretaceous forms that also occur as what appear to be post-mortem, drifted specimens in western Europe, analogous in their way to the drifted Recent *Nautilus* of the East African mainland and Japan (text-figs. 8, 19).

1. The single *Gastroplites* from the English Gault recorded by Spath (1937); the genus is abundant in the Western Interior and is known from Spitsbergen and east Greenland.

2. A single *A. amphibolum* (Morrow) recorded by Matsumoto *et al.* (1969) from Chardstock in southern England. This species is abundant in the Western Interior of the United States is widely distributed in north Texas, and also known from two Japanese specimens.

3. A single *Borissiakoceras* recorded from the Cenomanian of Haute-Normandie, France (text-fig. 19; Kennedy and Juignet 1973). This genus is abundant in the Western Interior of the United States and northern Alaska and rare in Canada and Texas. The only other Cenomanian records are in central Asia, Turkestan, and possibly northern Australia and New Zealand.

These examples of largely endemic North American forms occurring in western Europe are especially convincing, because they confirm the theoretically predicted surface current patterns for the Atlantic during this part of the Cretaceous as shown by Luyendyk *et al.* (1972). As other examples of probably post-mortem distribution one may cite the stray Tethyan forms known from the Boreal Realm during the Jurassic (p. 57) or the rare specimens of otherwise Tethyan *Eogaudryceras*, *Anagaudryceras*, *Hypophylloceras*, and *Tetragonites* from the northern European Aptian to Cenomanian (Spath 1923–1943; Kennedy 1971; Owen 1971; Casey 1960, Juignet and Kennedy (in press)) amongst a large number of references to occurrences of this type. Interesting discussions of this mode of dispersal are given by Reyment (1958, 1964) and Willard (1965).

THE ROLE OF AMMONITES IN BIOSTRATIGRAPHY

Zonal duration. Ammonites form the basis for standard zonal schemes of the Triassic, Jurassic, and Cretaceous Periods. As a general indication of their stratigraphical worth, we have calculated average duration of zones for each of these intervals using zonal schemes given in Arkell *et al.* (1957) and radiometric ages given in Harland and Francis (1971). Average zonal duration during the Triassic and Jurassic is thus approximately 1·2 million years but is closer to 2·0 million years during the Cretaceous. The zonations used in this calculation are, however, 'standards' for various parts of the world and do not give an accurate measure of the value of the group.

TEXT-FIG. 18. Disjunct distributions are illustrated by these plots of the Cenomanian ammonites *Marshallites*, *Acanthoceras cornigerum* Crick, and *Sumitomoceras*. Inset are *M.* aff. *olcostephanoides* Matsumoto from Alaska; *A. cornigerum* from Zululand; and *S. faustum* Matsumoto and Muramoto from England (map base after Smith *et al.* 1973, fig. 7).
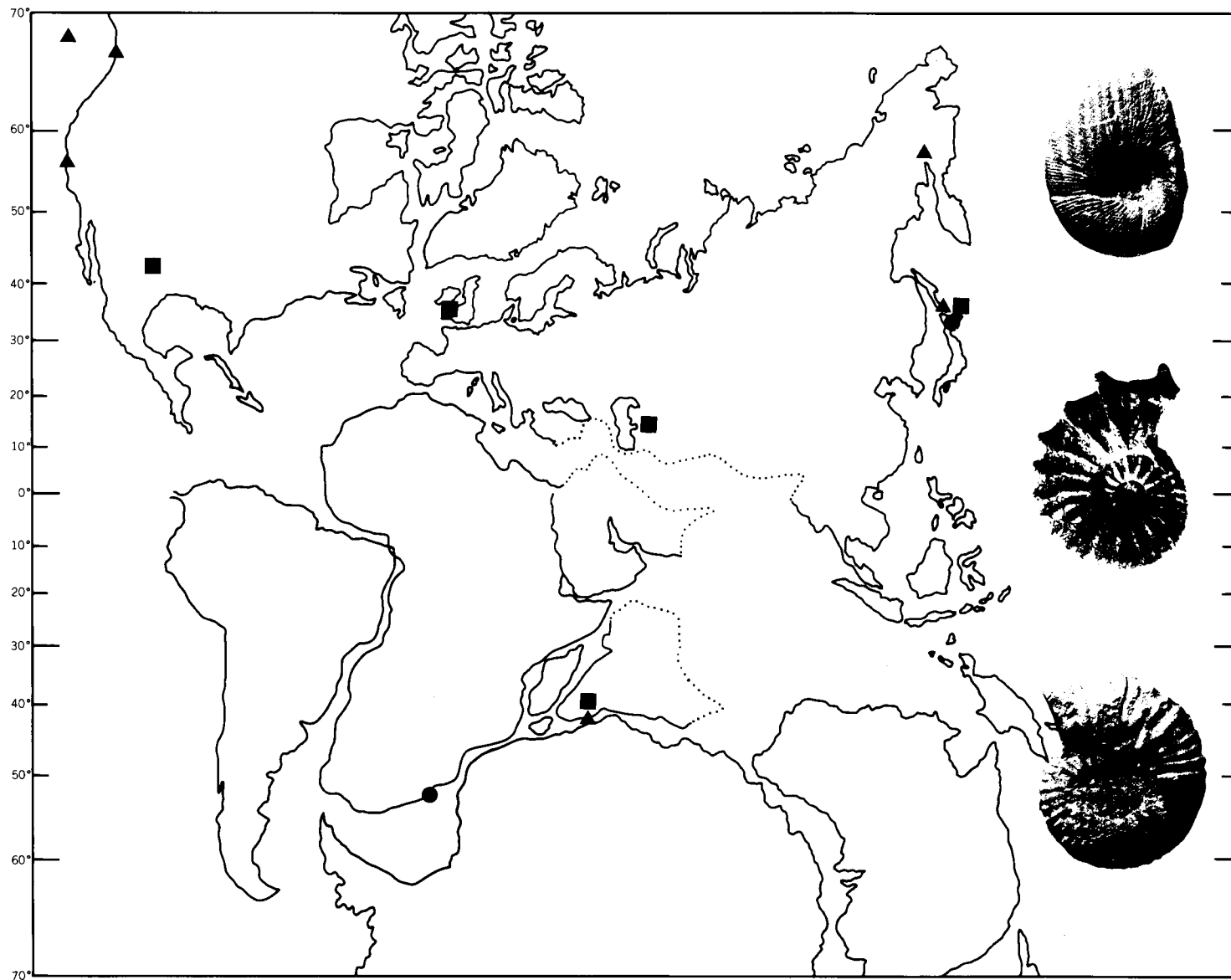
▲ *MARSHALLITES* spp.   ● *ACANTHOCERAS CORNIGERUM*   ■ *SUMITOMOCERAS* spp.

BORISSIAKOCERAS
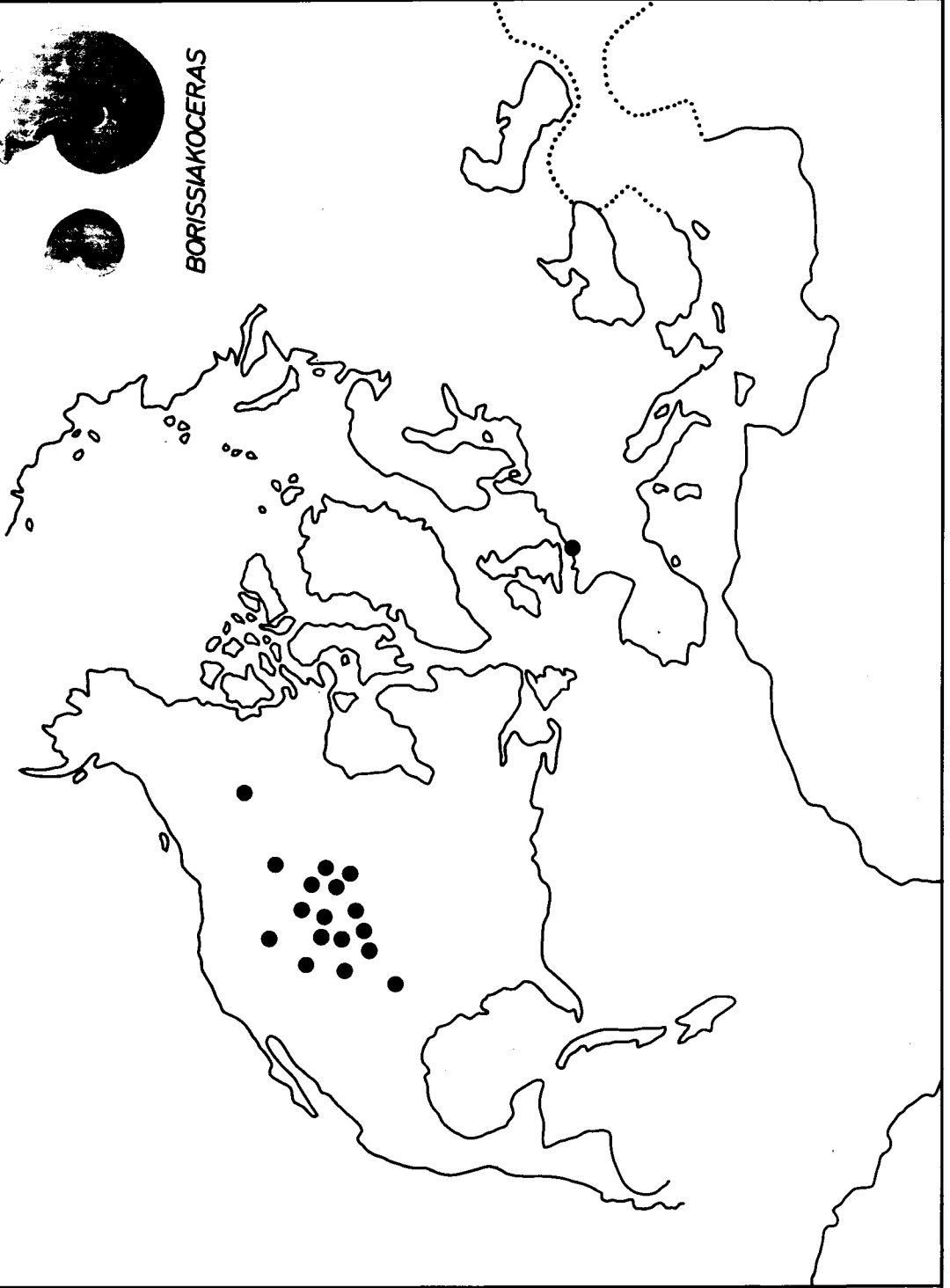
A far more precise picture of the relationship between ammonite biostratigraphy and chronostratigraphy can be gained from the work of Gill and Cobban (1966) and Obradovich and Cobban (1975). Working with the Upper Cretaceous sequences of the Western Interior of North America, these authors were able to integrate Potassium–Argon dates from bentonites very precisely with ammonite successions. Their results are summarized in Tables 4 and 5; they indicate average zonal durations of from 0·2 to 0·9 million years, with an average over the Upper Cretaceous as a whole of 0·6 million years. This figure is for a limited region where detailed studies of evolutionary lineages have produced a very fine zonal scheme. However, the scheme can be integrated with a broader sequence that can be traced globally, as shown in Table 5. At this level, global correlation of the Upper Cretaceous is possible with a precision of from 0·5 to 3·0 million years, with an average of 1·8 million years for the whole interval. Optimum precision of correlation during the Jurassic is best calculated from the detailed sequences available in the European Lias (Dean *et al.* 1961). During the Hettangian to Toarcian interval, some twenty zones with an average duration of 1·2 million years, and forty-nine subzones, with average duration of 0·5 million years, are recognized. Thus at best zonal durations are as short as 0·2 million years, and on average vary between 0·5 and 3·0 million years.

Rates of evolution. Simpson (1952) produced a plausible guess for the life-span of a species; his best average was around 2·75 million years, with probable limits set as low as 0·5 million years and as high as 5·0 million years. Without entering into detailed discussions of species concepts, figures for the average life-span of individual species within a number of ammonite lineages can be derived from Table 4. Thus in the Western Interior region, baculitid species have a life-span of the order of from 0·5 to 0·9 million years, while scaphitid species have a life span of from 0·6 to 0·7 million years. These appear to represent the bottom of the scale in these groups. By contrast, the species *Baculites undatus* Stephenson, a Gulf Coast immigrant into the Western Interior during the late Campanian, ranges throughout a series of ammonite zones, totalling an interval of 3·3 million years. Equally, the range of the Old World species *Hoploscaphites constrictus* (J. Sowerby) is said to be coextensive with the Maastrichtian stage, nearly 4·0 million years.

Life spans of these orders of magnitude appear to be standard; short durations find a match, so far as can be determined, in detailed lineage studies such as those of Brinkmann (1929, 1937) on Callovian kosmoceratids and Albian hoplitids. Upper limits of species longevity are set by long-ranging phylloceratid, lytoceratid, and desmoceratid species, although here ranges reflect the state of the art of taxonomy and the lack of obvious morphological features upon which to base divisions of lineages. *Phylloceras thetys* (d'Orbigny) has a recorded range of Valanginian to Cenomanian—25 million years (Wiedmann 1963*b*); *Neophylloceras ramosum*

TEXT-FIG. 19. The possibility of post-mortem drift of dead shells is suggested by this plot of the distribution of the genus *Borissiakoceras* during middle Cenomanian times. It is locally common in the Western Interior of North America, occurs infrequently in Texas, and is represented by a single specimen from the Normandy coast. Did this last individual drift eastwards on some proto-Gulf Stream prior to burial (map base after Smith *et al.* 1973, fig. 7)?

TABLE 4. United States Western Interior ammonite zonation from the mid-Cenomanian to Maastrichtian, estimated ages in millions of years and average duration of zones during transgressive (T) and regressive (R) phases. Arrows indicate K/Ar determinations on bentonites, taken from Obradovich and Cobban (1975).

CRETACEOUS STAGES (PART)	MILLIONS OF YEARS	WESTERN INTERIOR AMMONITE ZONES	TRANSGRESSIVE (T) OR REGRESSIVE (R)	AVERAGE LENGTH IN MILLIONS OF YEARS
	65			
	66			
MAESTRICHTIAN (LOWER)	67	← *HOPLOSCAPHITES* AFF. *H. NICOLLETI* *BACULITES CLINOLOBATUS*	R	0·2
	68	← *BACULITES GRANDIS* *BACULITES BACULUS* *B. ELIASI*		
?	69	← *B. REESIDEI* *B. JENSENI*		
	70	*B. CUNEATUS*	T	0·5
	71			
	72	← *B. COMPRESSUS* *DIDYMOCERAS CHEYENNENSE* ← *EXITELOCERAS JENNEYI* *DIDYMOCERAS STEVENSONI* ← *DIDYMOCERAS NEBRASCENSE*		
	73	*BACULITES SCOTTI*		
	74	*B. GREGORYENSIS*	R	0·9
	75	*B. PERPLEXUS*		
CAMPANIAN	76	*B. SP. (SMOOTH)*		
	77	*B. ASPERIFORMIS* *B. MACLEARNI*		
	78	← *B. OBTUSUS* ← *B. SP. (WEAKLY RIBBED)*	T	0·8
	79	*B. SP. (SMOOTH)*		
	80	*SCAPHITES HIPPOCREPIS* III		
	81	*S. HIPPOCREPIS* II		0·7
	82	*S. HIPPOCREPIS* I	R	
	83	← *DESMOSCAPHITES BASSLERI* *D. ERDMANNI* *CLIOSCAPHITES CHOTEAUENSIS*		0·7
SANTONIAN	84	*C. VERMIFORMIS*		
	85	*C. SAXITONIANUS* *SCAPHITES DEPRESSUS*		
	86	*S. VENTRICOSUS*	T	0·7
CONIACIAN	87	← *SCAPHITES PREVENTRICOSUS* *S. CORVENSIS* *S. NIGRICOLLENSIS* *S. WHITFIELDI* *PRIONOCYCLUS WYOMINGENSIS*		
?	88	← *P. MACOMBI* *P. HYATTI*	R	0·4
TURONIAN	89	*COLLIGNONICERAS WOOLLGARI* ← *MAMMITES NODOSOIDES* *WATINOCERAS COLORADOENSE*		
	90	*SCIPONOCERAS GRACILE* *DUNVEGANOCERAS ALBERTENSE*		
CENOMANIAN (PART)	91	← *DUNVEGANOCERAS PONDI* *PLESIACANTHOCERAS WYOMINGENSE*	T	0·4
	92	← *ACANTHOCERAS AMPHIBOLUM*		

(Meek), Turonian to Coniacian—12 million years (Matsumoto 1959); *Damesites sugata* (Forbes), Coniacian to Lower Campanian—8 million years (Matsumoto 1959); *Austiniceras austeni* (Sharpe), Cenomanian to Turonian—8 million years (Wright and Wright 1951); whilst *P. serum* Oppel has a range from late Tithonian to Barremian, a span of over 20 million years.

Regressions, transgressions, and zonal duration. Many workers have attempted to relate rates of evolution and zonal durations to cycles of regression and transgression. Kauffman (1970, 1973) dealing with the published and unpublished data of many workers in the United States Western Interior concluded that zonal durations were consistently less during periods of regression than periods of transgression. However, it is clear from Table 4, using the time scale proposed by Obradovich and Cobban (1975), that there is no significant difference between zonal durations during periods of regression and transgression in the Western Interior region, and Kauffman's attractive theory remains unproven at present.

TABLE 5. Upper Cretaceous ammonite assemblage zones which are recognizable world-wide, and their probable duration in millions of years. Dates at stage boundaries in left-hand column are from Obradovich and Cobban (1975).

STAGE	ZONE	ZONAL DURATION
64-65 MAESTRICHTIAN	*SPHENODISCUS* SP. *PACHYDISCUS NEUBERGICUS*	2.5 - 3.0
——— 70-71 ——— CAMPANIAN	*HOPLITOPLACENTICERAS VARI* *MENABITES DELAWARENSIS* *DIPLACMOCERAS BIDORSATUM*	2.7± - 3.0±
——— 82± ——— SANTONIAN	*PLACENTICERAS SYRTALE* *TEXANITES TEXANUS*	2.0±
——— 86± ——— CONIACIAN	*PARABEVAHITES EMSCHERIS* *BARROISICERAS HABERFELLNERI*	0.5±
——— 87± ——— TURONIAN	*SUBPRIONOCYCLUS NEPTUNI* *COLLIGNONICERAS WOOLLGARI* *MAMMITES NODOSOIDES*	0.67 - 1
——— 89-90 ——— CENOMANIAN	*SCIPONOCERAS GRACILE* *CALYCOCERAS* GR. *NAVICULARE* *ACANTHOCERAS RHOTOMAGENSE* *MANTELLICERAS MANTELLI*	1 - 1.25
——— 94± ———		

AMMONITE DISTRIBUTIONS AND CONTINENTAL DRIFT

Ammonites were limited in their distribution to varying degrees by environmental gradients and by physical barriers such as land masses and deep ocean basins, as well as by local factors which included ocean current patterns and salinity gradients.
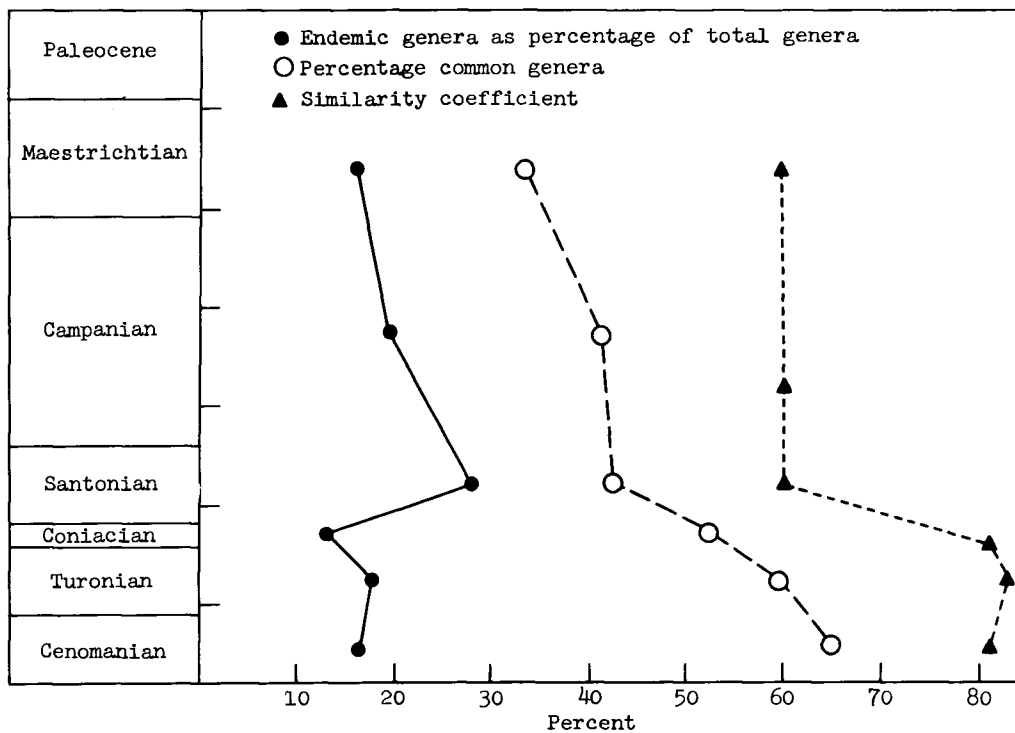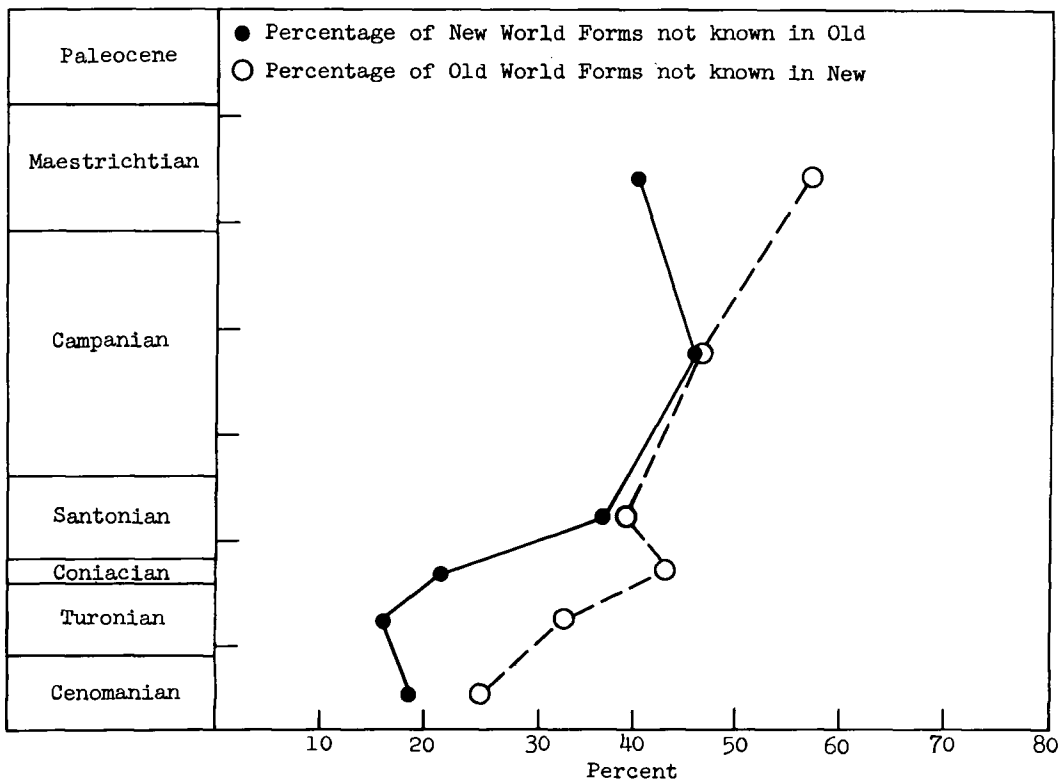
The distribution of barriers and the effects of other factors varied throughout the Mesozoic as plate movements brought about the fragmentation and collision of continents and their associated shelf seas. To a degree, the changing patterns of ammonite distributions reflect changing geography, and present distribution patterns enable the testing of reconstructed continental configurations. The use of ammonoids in this way has been attempted by House (1973) for the Devonian and Hodson and Ramsbottom (1973) for the Carboniferous. Hallam (1967b, 1971) has drawn attention to some aspects of Jurassic ammonite distributions explicable only in terms of continental drift, as have other workers (e.g. Howarth 1973a; Cariou 1973; Enay 1973) while Reyment (1969) and Reyment and Tait (1972) have used changing distribution patterns as a key to the early history of the South Atlantic. Rather than review earlier work, we discuss below how three of the fundamental situations predicted by plate tectonic theory may be tested by the study of the distribution of Cretaceous ammonite faunas in space and time. These examples are (1) changes associated with the separation of two shelf areas, taking the Upper Cretaceous faunas of western Europe/North Africa and the United States/Caribbean as our example, (2) changes associated with an area of continental collision, taking as our example the suture between the Asian and Arabian Plates, and (3) ammonite distributions as a test of the date of origin of the South Atlantic.

Upper Cretaceous distributions and the opening of the North Atlantic (text-fig. 20). There is general agreement on the opening of the North Atlantic during the latter part of the Mesozoic, although the date of initiation of rifting remains disputed. Faunal studies on a number of benthonic groups with pelagic larval stages of variable duration have demonstrated very clearly that there is faunal divergence as a result of the appearance of a deep ocean barrier; divergence increasing as the width of the North Atlantic increased. Thus Dilley (1973), dealing with larger Foraminiferida, Kauffman (1973), dealing with bivalves in general, and Coates (1973), dealing with rudistids and with scleractinian corals, have all shown progressive increases in endemism between faunas of the tropical Mediterranean and Caribbean provinces during this time.

In text-fig. 20 we give a preliminary compilation of distribution data for Upper Cretaceous ammonite genera of two areas, one in the Old World, including North Africa and western Europe; the other in the New World, including the United States Atlantic Seaboard and Western Interior, Texas, the Gulf Coast, and Mexico. This compilation includes all genera known to us, irrespective of abundance, so that taxa introduced as a result of post-mortem dispersal and the like have been included. In a general way, the percentage of genera common to the two areas and similarity coefficients (Simpson 1947) decline throughout the Upper Cretaceous: fairly rapidly during the Cenomanian to Santonian, and at a lesser rate during the post-Santonian interval. Similarly, the percentage of Old World forms that are

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TEXT-FIG. 20. Endemism, common taxa, and similarity coefficients of Upper Cretaceous ammonite faunas on the two sides of the North Atlantic area. The 'Old World' encompasses Western–Central Europe and North Africa; the 'New World' includes Canada, the Western Interior, Gulf Coast, and Atlantic Seaboard of North America.

Top figure — legend:
● Percentage of New World Forms not known in Old
○ Percentage of Old World Forms not known in New

Vertical axis (top to bottom): Paleocene, Maestrichtian, Campanian, Santonian, Coniacian, Turonian, Cenomanian

Horizontal axis: Percent (10 20 30 40 50 60 70 80)

Bottom figure — legend:
● Endemic genera as percentage of total genera
○ Percentage common genera
▲ Similarity coefficient

Vertical axis (top to bottom): Paleocene, Maestrichtian, Campanian, Santonian, Coniacian, Turonian, Cenomanian

Horizontal axis: Percent (10 20 30 40 50 60 70 80)

unknown in North America increases fairly evenly, but with a sharp kink in the curve during the Coniacian. The New World curve shows a continuous increase through Turonian to Campanian time, and a continuous decrease in the Maastrichtian. These data are thus compatible with trends demonstrated in other groups. They suggest rapid faunal divergence throughout the early Late Cretaceous, slowing during post-Santonian times.

The decreasing divergence of New World forms from Campanian to Maastrichtian may be a reflection of the sparsity of the described faunas (ten genera only). The kink in the trend of increasing divergence of Old World faunas from Coniacian to Campanian is entirely a reflection of flowering of the family Tissotidae during the Coniacian; the group was widespread in southern Europe and North Africa at this time, but unknown in the area of North America studied, although present in South America. Less readily explained is the curve for endemic genera, which might be expected to show an increase in total endemic taxa for the two areas as the Atlantic opened. It may, however, reflect two interacting phenomena: first, the generally low endemism of western Europe and North Africa as a whole (only *Schloenbachia* (Boreal) and *Ficheuria* (Tethyan) during the Cenomanian for instance) and second, the over-all decline in ammonite diversity during the late Cretaceous. Considering the Western Interior alone, the proportion of endemic forms does show a progressive increase through the Upper Cretaceous. Figures are: Cenomanian 14%, Turonian 9%, Coniacian 13%, Santonian 28%, Campanian 22%, Maastrichtian 30%.

Ammonite distributions thus suggest continued opening of the North Atlantic throughout the Upper Cretaceous, leading to a general decrease in migration of ammonites between the two areas. The data suggest rapid movement from Cenomanian to Santonian times, followed by a slowing of separation. This closely matches known changes in spreading rate as summarized by Hays and Pitman (1973).

Faunal changes at a plate suture: the southern boundary of the Boreal Realm during the mid-Cretaceous (text-fig. 21). Analysis of Albian–Cenomanian faunas from the Boreal Realm (for sources see Spath 1923–1943; Vinogradov 1968; Owen 1971; Kennedy 1971; Kennedy and Juignet in press; Matsumoto 1973) indicates that three basic groups of ammonites occur in mid-Cretaceous Boreal faunas.

Group 1 are endemic forms; taxa that are abundant, often dominating faunas, and that show a high degree of intraspecific variation (usually masked by taxonomic splitting). These are generally limited to the Boreal Realm or are known only as rarities elsewhere. Examples during the Albian are *Hoplites, Anahoplites, Dimorphoplites, Euhoplites, Lepthoplites, Callihoplites,* and *Pleurohoplites*; Cenomanian representatives are *Schloenbachia* and *Hyphoplites*.

Group 2 are pandemic or latitudinally restricted forms, scarce to common in Boreal faunas, tending to show a gradual reduction in diversity northwards. Examples during the Albian are *Protanisoceras, Mariella, Douvilleiceras, Mortoniceras, Hysteroceras,* and *Stoliczkaia*; Cenomanian representatives are *Turrilites, Anisoceras, Mantelliceras, Acanthoceras,* and *Calycoceras*.

Group 3 are strays, mesogean forms either having lived at the northern limits of their range or having drifted into the area after death. Examples during the Albian include various *Hypophylloceras, Desmoceras, Tetragonites,* and *Engonoceras*

species; Cenomanian representatives are *Hypophylloceras, Tetragonites, Anagaudry-ceras,* and *Neolobites.* In addition, rare exotics like *Gastroplites* (Albian) and *Boris-siakoceras* (Cenomanian) are also known. The change from these Boreal faunas to Tethyan or Mesogean assemblages followed the same course during the Cretaceous as during the Jurassic, running through southern France, and from a point east of Nice, following closely the Alpine fold belts through southern and south-eastern Europe, Iran, and beyond (text-fig. 21). Two distinct types of faunistic junction can
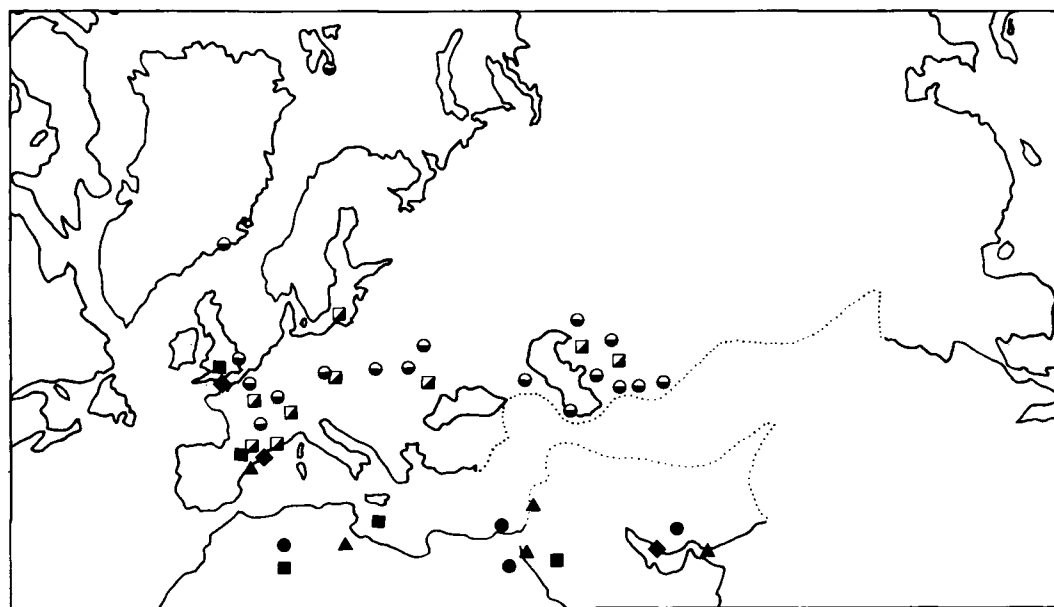
BOREAL HOPLITIDS:

◔ *HOPLITES*   ▨ *ANAHOPLITES*

'TETHYAN' PSEUDOCERATITES:

■ *ENGONOCERAS*   ● *KNEMICERAS*   ◆ *PARENGONOCERAS*   ▲ *PLATYKNEMICERAS*

TEXT-FIG. 21. Distribution of selected Albian boreal hoplitinid and tethyan egonoceratid pseudoceratites around the Tethys sea-way (map base after Smith *et al.* 1973, fig. 7).

be recognized. In France there is a transition, moving from north to south. In the Middle Albian, rich hoplitid faunas extended down the Rhône Valley as far south as the region around Escragnolles and Gourdon (Alpes-Maritimes) (see Jacob 1908; Breistroffer 1940, 1947; Collignon 1949). Moving southward, however, there is a change in relative proportions, Mesogean elements becoming more diverse, and increasingly dominating the faunas. Similar changes are seen in the Upper Albian.

In the Cenomanian, *Schloenbachia* extended as far south as the area around Estéron (Alpes-Maritimes (Thomel 1965; Porthault *et al.* 1966)), while *Hyphoplites* occurred on the Mediterranean coast at Cassis. Again, tracing faunas southward, Boreal elements simply decline in abundance down the Rhône corridor; at Cassis, only two *Hyphoplites* are known, accompanying a range of typically mesogean forms, including frequent to common *Hypophylloceras* and *Desmoceras* together with

Lytoceras, *Anagaudryceras*, *Mesogaudryceras*, *Gaudryceras*, and *Phyllopachyceras* (Fabre 1940). South of this point, the only exotic records of Boreal hoplitids are a *Dischoplites* occurrence in the Upper Albian of North Africa and a single Cenomanian *Hyphoplites* from Israel (Avnimelech 1965).

Traced eastward, this gradation between Boreal and Mesogean faunas disappears. The classic Upper Albian faunas of La Vraconne, Switzerland (Renz 1968) are Boreal, and Mesogean elements are rare, while the Cenomanian faunas of the Neuenberger Jura (Renz *et al.* 1963) are entirely Boreal in aspect. Boreal faunas extend as far east as the southern Urals and eastern borders of the Kopet Dagh in the border region with Iran. In the Albian, these yield abundant hoplitids (Semenov 1899; Sinzov 1909, 1915; Glazunova 1953*a–b*; Owen 1973). Albian hoplitids occur with occasional *Hypophylloceras* in Mangyshlak and between the south-western shores of the Caspian and the Crimea. In Iran, however, there is an apparently abrupt boundary between typically Boreal and Mesogean faunas along the line of the Zagros Thrust complex. *Hoplites dentatus* and other typical Albian Boreal elements occur with *Tetragonites* in the area round Esfahan, 350 km south of Tehran (Seyed Emami *et al.* 1972) as do typical Boreal Cenomanian *Schloenbachia* and *Hyphoplites*. *Schloenbachia* is recorded from the Tobas area (Stoklin *et al.* 1965; Stoklin and Nabavi 1971), and there is a doubtful record of the same genus from the Sarvak Formation on the north-eastern flank of the Kabir Kuh Range near the Iraq/Iran border. South of the Zagros, faunas are wholly Tethyan in aspect, being dominated by pseudoceratites. The Kazdumi Formation yields knemiceratids in the coastal Fars; *Knemiceras uhlighi* (Choffat), *K. syraicum* (Buch), *Spathiceras*, and other forms are recorded from the area north of Gachsaran (James and Wynd 1965), while Spath (1923–1943) records *Platyknemiceras* of the *attenuatum-gabbi* group from Hamiran.

This sharp faunal discontinuity at the Boreal–Mesogean boundary thus corresponds to a line of tectonic discontinuity (Takin 1972) along a plate suture; the line of the Zagros thrust. The same discontinuity, traceable around the Alpine fold belts of southern Europe, follows a comparable junction as far west as the Italian/French border; beyond this point the gradational nature of the Boreal–Tethyan boundary in France and the strong links between some of the Mesogean elements of southern-most France and North Africa are compatible with the inferred pattern of closure of the Tethys (Smith *et al.* 1973, figs. 7–10). That some of the marked differences between northern and southern faunas appear to diminish in some respects during the latest Cretaceous (see maps in Vinogradov 1968) may reflect the narrowing oceanic barrier during the latter stages of the closure of Tethys.

Ammonite faunas of the South Atlantic margins (text-figs. 22–24). There is consider-able dispute over the timing of separation of South America from Africa. Valencio and Vilas (1970) have inferred from palaeomagnetic and spreading data that it began in early or mid-Cretaceous times, although stratigraphical studies (Allard and Hurst 1969) suggested that the two areas did not separate significantly until late in the Cretaceous. Reyment and Tait (1972) have provided the most detailed analysis, basing their conclusions in part upon ammonite distributions as the key to the link-up of northern and southern arms of the proto-Atlantic. Their analysis indicated
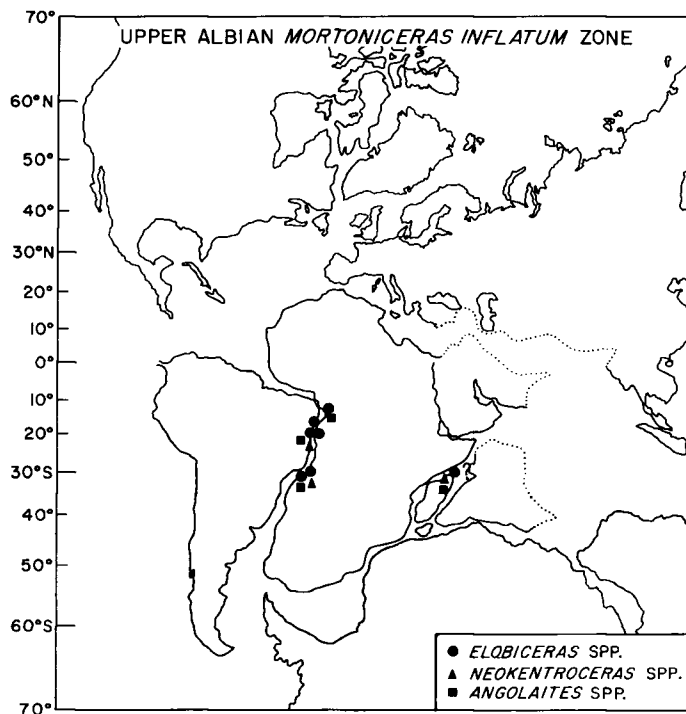
TEXT-FIG. 22. Distribution of selected characteristic southern proto-Atlantic genera during late Albian, *Mortoniceras inflatum* Zone times (map base after Smith *et al.* 1973, fig. 7).

that linking of northern and southern seas finally occurred as late as early Turonian times.

A reappraisal of their data, together with information now available on faunas from Angola (Cooper 1972, 1973; Kennedy and Cooper 1975) and South Africa (W. J. Kennedy and H. C. Klinger, unpublished data 1975) allows the following conclusions.

1. Albian, *Mortoniceras inflatum* Zone times (text-fig. 22). The southern proto-Atlantic area is characterized by widely distributed genera such as *Diploceras*, *Hysteroceras*, *Mortoniceras*, *Hamites*, and *Anisoceras*, together with endemic taxa such as *Elobiceras*, *Angolaites*, and *Neokentroceras*, which are restricted to Brazil, Nigeria, and Angola (Reyment and Tait 1972, p. 63). This distribution pattern suggests the presence of a barrier between the southern and northern proto-Atlantic at least at the beginning of the Upper Albian.

2. Albian, *Stoliczkaia dispar* Zone times (text-fig. 23). There are no endemic forms save a single record of *Angolaites* in the southern proto-Atlantic area, while there are a number of key species common to both areas. *S. africana* (Pervinquière) is thus known from England, North Africa, Nigeria, Brazil (although said to be Cenomanian), South Africa (Zululand), and Texas. The report of this genus from the Cenomanian of Angola (Kennedy 1971; Reyment and Tait 1972) is in error (Cooper

1973), *S. dispar* (d'Orbigny) *attenuata* Douvillé (1931) being an earliest Turonian acanthoceratid. The subgenus *M.* (*Durnovarites*) extends from England south through Europe and North Africa to Nigeria and South Africa, as does the species *Anisoceras perarmatum* (Pictet and Campiche). These distributions point to a marine link along the line of the proto-Atlantic.

3. Lower Cenomanian, *Mantelliceras mantelli* Zone times. Lower Cenomanian faunas are sparse in this area, being poorly represented in both Angola and Nigeria. However, of recorded forms, *Sharpeiceras* of the *laticlavium* group are widespread in western Europe, Texas, Mexico, and North Africa, and are recorded from Brazil, Angola, South Africa, and Madagascar. *Euhystrichoceras* is known from Europe, North Africa, Texas-Mexico, and Madagascar while the only other recorded possible Lower Cenomanian form, *Desmoceras* (*Pseudouhlighella*), ranges from Texas via Nigeria to Madagascar. All evidence points to a continuous marine connection.

4. Middle Cenomanian, *Acanthoceras rhotomagense* Zone times. Extensive faunas are known from Texas, North Africa, Nigeria, Angola, and South Africa. Species of *Euomphaloceras*, *Acanthoceras*, *Forbesiceras*, and *Turrilites* range throughout the area from England to South Africa. There are no endemics in the Southern proto-Atlantic area; all evidence points to continued connection.

5. Upper Cenomanian, *Eucalycoceras pentagonum* Zone times. Described faunas are too sparse for useful comment in most areas.

6. Upper Cenomanian, *Sciponoceras gracile* Zone times (text-fig. 24). Following recent revisions of the position of Cenomanian-Turonian boundary, a number of faunas once regarded as lowest Turonian are included here (it should be noted that beds of this age are absent in South Africa). As evidence of continued marine connection and the presence of a distinct proto-Atlantic, we would note the following distributions: *Kanabiceras septemseriatum* (Cragin) known from northern Europe, the U.S. Western Interior, California, Texas, Angola; *M. whitei* itself, known from Texas, the Western Interior, North Africa, Nigeria, Brazil (*M. ornatum* Moreman of authors), and Angola (*Pulchellia caicedoi* of Douvillé 1931); *Pseudocalycoceras* of the *dentonense* (Moreman)-*harpax* (Stoliczka) group occur in northern Europe, North Africa, the U.S. Western Interior, Texas, Mexico, Venezuela, Bolivia, Angola, and Madagascar. Other species such as *C. naviculare* (Mantell) are equally widespread, while '*Austiniceras*' *dibleyi* Spath is known *only* from England and Angola. These occurrences again indicate a continued marine connection.

7. Lower Turonian, *Mammites nodosoides* Zone times. Faunas of this age are unknown in South Africa and very sparsely represented in Angola. As evidence of probable continued marine connection along the proto-Atlantic we would cite occurrences of *Watinoceras* species throughout western Europe and the Western Interior of the United States, and in Nigeria, Angola, Brazil, and Morocco; also occurrences of *Mammites* in Europe, the United States, Morocco, Nigeria, and Angola. Reyment and Tait (1972) have argued that faunal similarities between the vascoceratid faunas of the Middle East and of the southern Atlantic at this time indicate a trans-Saharan connection, and that a land barrier separated these faunas from those of Texas, north-west Africa, and north-eastern South America. We would point, however, to distributions such as those shown by the early Turonian species *Pachyvascoceras compressum* (Barber) and *P. globosum* Reyment, which
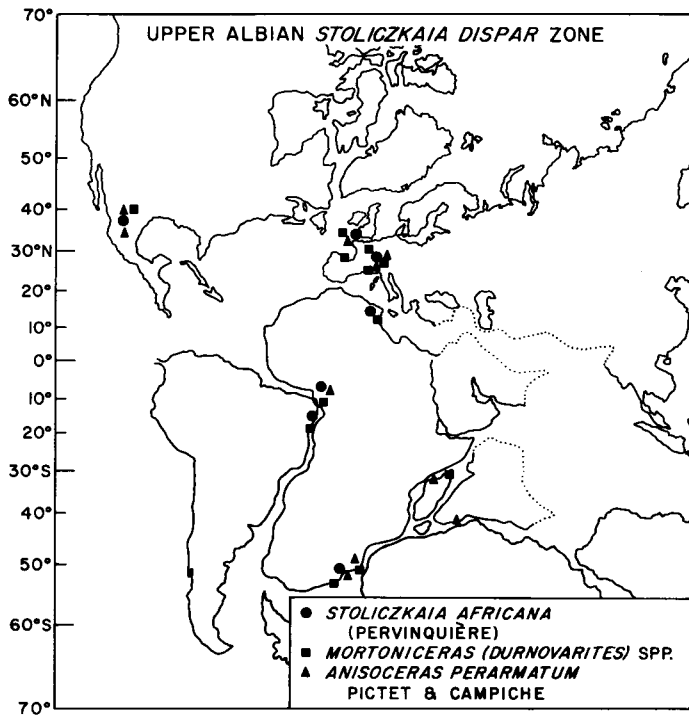
TEXT-FIG. 23. Distribution of selected late Albian *Stoliczkaia dispar* Zone ammonites (map base after Smith *et al.* 1973, fig. 7).
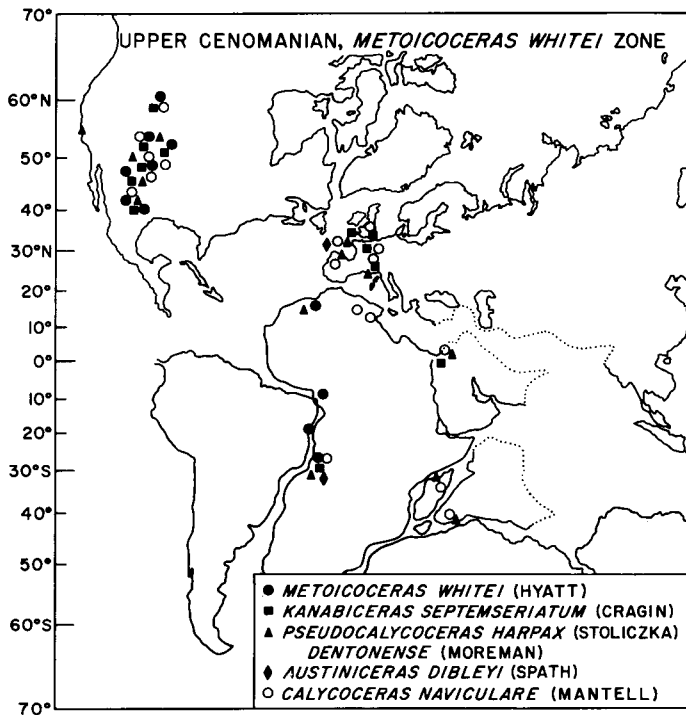
TEXT-FIG. 24. Distribution of selected late Cenomanian *Sciponoceras gracile* Zone ammonites (map base after Smith *et al.* 1973, fig. 7).

have been recorded in numbers from Texas, Nigeria, and Brazil, and nowhere else, although contemporary North African faunas are well known.

Thus our detailed discussions suggest that ammonite distributions during early Late Albian times are compatible with a separation of northern and southern proto-Atlantic marine basins, as suggested by previous workers. From late Late Albian times onward there are many distributions at generic and specific level that extend from western Europe, central to south-eastern North America, down the line of the proto-Atlantic to South Africa. These distributions suggest that an open marine connection appeared during the latest Late Albian and was maintained thereafter, a view directly opposed to previous conclusions on ammonite distribution patterns. This conclusion does not necessarily date the rifting of the South Atlantic, but it is compatible with palaeomagnetic and spreading data.

EXTINCTION

The evolutionary history of ammonoids is depicted as one of alternate episodes of 'explosive' radiation, continued evolution, and widespread extinction. These latter episodes generally correspond approximately with major stratigraphical boundaries, as at the Permian–Triassic, Triassic–Jurassic, and Jurassic–Cretaceous boundaries. The Cretaceous–Palaeocene boundary, it may be argued, is a fourth such event, which the group did not survive. This last event is thus suitable for a concluding section of this review.

Hancock (1967) and Wiedmann (1969, 1973c) have reviewed the general pattern of extinction. There are some 22 ammonite families present in the Cenomanian and only 11 in the Maastrichtian, although most of the decline is pre-Santonian. At generic level, the decline is rather more striking; Hancock noted 78 Campanian genera, but only 34 from the Maastrichtian as a whole, and only 11, distributed amongst 5 families, from the Upper Maastrichtian alone. Thus the Late Cretaceous extinction of the ammonites is not the disappearance of a group at, or even close to, its acme, but rather the disappearance of a group in decline. As Hancock noted, however, this reduction in diversity is no greater than that seen at the base of the Cretaceous, where only 35 genera, distributed amongst 9 families, are known from the Berriasian.

Declining diversity is matched by decreasing abundance of surviving species. Records of Upper Maastrichtian ammonites are thus sparse (Hancock 1967, pp. 92–93), whilst Wiedmann has recorded a tendency towards dwarfism at this time. Assessment of the causes of this slow decline is difficult, and many of the 'reasons' for extinctions at the Cretaceous–Palaeocene boundary are too sudden to be acceptable, whilst others are equally unsatisfactory because they fail to explain changes in both marine and terrestrial spheres. Biological competition, food-chain deficiency, orogeny, transgressions and regressions, changes in salinity, oxygen shortage, increase in cosmic rays, supernovae, magnetic reversals, and even meteorite impacts are only a selection of the more recent suggestions (Wiedmann 1973c, pp. 159–160). So far as ammonite faunas are concerned, there does seem to be a link between 'crises in evolution' and regressions. Transgressions, as during the early Jurassic

and early Cretaceous are marked by phases of adaptive radiation and differentiation of faunas, which are followed, on regression, by provincialism and extinction. Final extinction might thus be considered the result of a coincidence of over-all decline and major regression (Wiedmann 1973c, fig. 11), the latter associated with a decrease in rates of sea-floor spreading (Hays and Pitman 1973).

CONCLUSIONS

1. All ammonites appear to have passed through a planktonic larval stage, followed by adoption of a nektobenthonic, nektonic, benthonic, or planktonic mode of life.

2. Many lived segregated by age or sex; changing morphology throughout ontogeny indicate similar changes in life habits.

3. Functional morphology suggests that ammonites possessed rather poor powers of locomotion, although they were well adapted for slow movements vertically through the water column.

4. Most ammonites appear to have exploited low levels in food chains, as herbivores, plankton feeders, or second-order carnivores. Others may have been benthonic scavengers and carnivores.

5. In turn the group were preyed on by marine saurians, arthropods, and fish, and by other ammonites, although actual records of evidence of predation are few.

6. Distribution patterns shown by ammonites reflect original life habitats modified to varying degrees by post-mortem drift. Some taxa have a virtual pandemic distribution; others are latitudinally restricted or have restricted endemic or provincial occurrences. Yet others show curiously disjunct distributions, whilst there are some instances of distribution as a result of post-mortem drift.

7. No general relationship between morphotypes and sedimentary facies can be recognized; most groups are facies independent, although relative abundance is often facies linked.

8. Species longevity varies from 0·2 to 25·0 million years, and in general the group allow global correlations with a precision of from 0·5 to 3·0 million years, and local correlations of the order of from 0·2 to 0·9 million years.

9. There is no apparent link between species longevity, zonal duration, and cycles of regression and transgression.

10. Extinction of the group was a gradual event and must be explained in general terms as part of the widespread late Cretaceous extinctions. Some causal factor linking the general late Cretaceous regression and the decline of the ammonites appears most plausible.

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ADDENDA

Since this paper went to press, the proceedings of a symposium on Cephalopod Palaeobiology held at the University of Tübingen have appeared.

The reader is referred to the following relevant papers:

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