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BRITISH MIDDLE CRETACEOUS INOCERAMID BIOSTRATIGRAPHY

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INTRODUCTION

Bivalves of the Family Inoceramidae are among the most abundant macrofossils of British Middle Cretaceous successions, especially in the Cenomanian-Turonian and younger carbonate sequences. Virtually all of the known British species are also spread widely in Europe, and most are intercontinental or cosmopolitan in their biogeographic distribution, including abundant representation in at least the Subtropical marginal zones of the Tethyan Tropical seaway. Inoceramidae are sparse to only moderately and locally abundant in Tethys proper, and its western (Caribbean) counterpart ; those that occur there are also widespread species in the Cretaceous North Temperate Realm (including England), allowing detailed correlation of these otherwise highly distinct biogeographic units.

The Inoceramidae thus are important in zonation and regional correlation of the British Cretaceous sequence, and in the identification of European stages, substages, and stage boundaries. Their abundance ; consistently good preservation of at least one of the shell layers (usually the calcitic prismatic layer) and/or steinkerns ; their continuity of stratigraphic occurrence, exceeding that for most other macrofossil groups ; their apparently rapid, widespread dispersal potential (mainly as larvae) ; and their characteristically rapid rates of evolution are all features which enhance the biostratigraphic utility of the Inoceramidae. In the British succession, they have the same potential as the ammonites and microbiota, and in some cases allow more refined zonation and more distant correlations to be made than is possible with co-occurring organisms, including ammonites.

Despite these attributes, no more than a broad, generalized inoceramid biostratigraphy has been published for the English Cretaceous (e.g., Woods, 1912b), derived from data compiled in the last comprehensive systematic treatment of the Family (Woods, 1911, 1912a). The ammonite succession is far more comprehensive (e.g., Kennedy, 1969, 1970, 1971) and is the main basis, today, for zonation of the Middle Cretaceous of Great Britain. An extensive study of the British Inoceramidae by the author in 1970-1971 revealed several reasons for the relatively minor role played by inoceramid bivalves, at present, in Cretaceous biostratigraphy of this region :

(1) The most recent comprehensive systematic treatment of British Inoceramidae (Woods, 1911, 1912a) employs very broad species concepts, invokes a high degree of variability in space and time for most taxa, and fails to separate phenotypic and ecotypic variation on the one hand, from small scale evolutionary change on the other. Collections within lineages from single horizons were not treated separately and compared for micro-evolution ; instead, collections were mixed from many levels within broad lithostratigraphic or biostratigraphic units. Consequently many inoceramid "species" described by Woods (1911, 1912a) appear to be species-groups of several phylogenetically closely related taxa. As a result, individual inoceramid-range-zones, as currently defined, are excessively long compared with ammonite zones or with inoceramid zones elsewhere, as in areas like North America. Population systematic studies of American inoceramid lineages which are also well represented in Europe (e.g., the *Inoceramus pictus* and *Mytiloides labiatus* lineages ; see Kauffman, 1970) demonstrate that much of the "variation" implied by Woods (1911, 1912a) and others for species of Inoceramidae is, in fact, evolutionary change. Studied lineages of inoceramids show rapid evolutionary rates in most cases, equivalent to those of ammonites, and individual species and subspecies show low to moderate levels of phenotypic-ecotypic variability when population systematic analysis is employed.

(2) Historically, collecting preocedures have prohibited precise stratigraphic location of many key specimens of inoceramids. In part, this reflects collecting techniques of early workers, lumping collections together from within broadly prescribed lithological or biostratigraphical units (e.g., within the "Lower Chalk" or the *Micraster coranguinum* zone"). In part, it also reflects the difficulty in precisely extracting large collections of specimens from steep coastal cliff sections and quarry walls which dominate English Cretaceous exposures ; collections of good specimens have largely come from rubble at the foot of these faces which is stratigraphically mixed and can be located only generally within the sequence based on lithologic or biotic similarities. The finest specimens of Inoceramidae, housed in the magnificient collections of the British Museum and various universities, and representing most of the species which elsewhere in the world are important, time-restricted biostratigraphic indices, are largely without precise enough stratigraphic data to allow them to be accurately placed in the English sequence. Only recently have stratigraphically precise collections been made by various workers, and these are now in the process of being studied for systematic and biostratigraphic purposes.

The use of Inoceramidae in biostratigraphic zonation of the English Cretaceous sequence and its detailed correlation with other areas of the world, therefore, depends on a careful collecting program, seeking populations of Inoceramidae at numerous, closely spaced levels, analyzing them separately in search of microevolutionary trends, subsequently revising the systematics of the family, and integrating these data throughout the stratigraphic column with the well defined ammonite and foraminiferal biostratigraphy. From such an integrated biostratigraphic system, highly refined zonation and regional correlation of the English Cretaceous sequence will be possible to an even greater extent than it is now.

Ongoing studies of British Inoceramidae collected in this manner by the author, by W. J. Kennedy of Oxford University, J. M. Hancock of King's Colledge, London, and in the collections of the British Museum, Sedgwick Museum and the Geological Survey of Great Britain have yielded encouraging initial results. The stratigraphic ranges for many described Cenomanian and Turonian species have been redefined and the species concepts, at least informally for the present, have been restricted and revised, allowing a much more refined biostratigraphy based on this fossil group. In the Cenomanian, these have been collected and placed in detail within the framework of W. J. Kennedy's ammonite zonation (1969, 1970, 1971), and most of the new data is available from rocks of this age. The Turonian and Coniacian ammonite and inoceramid succession is still poorly known ; although numerous inoceramid species have been described from the Turonian part of the column, their relative stratigraphic placement and range zones still must be defined. Because of the relative sparcity of available inoceramids from the English Turonian, compared to the Cenomanian, more systematic collecting needs to be done before a confident zonation of the stage is possible. The Albian sequence has yielded abundant collections of inoceramids, well located stratigraphically, and the analysis of these has just begun.

The following remarks on Inoceramid biostratigraphy in the British Middle Cretaceous sequence are therefore intended to be progress report of ongoing research, and should be used with caution until the work is finalized. Greatest confidence should be placed in the Cenomanian data, which represents the research closest to completion.

ALBIAN INOCERAMIDAE

The principal lineages of Albian Inoceramidae with bostratigraphic potential are the *Birostrina concentrica-B. sulcata-B. salomoni* lineage, and the *"Inoceramus" anglicus* lineage. *Birostrina* does not appear to range above Albian over most of the world and is the best bivalve marker for determining the Albian-Cenomanian boundary. *"Inoceramus" anglicus* and its subspecies questionably range into the Lower Cenomanian in North America, Siberia, France, and England, but are more normally found in the Albian. The *Inoceramus tenuis-I. etheridgei* lineage is reported to first appear in the Latest Albian of England, but this is subsequently discredited. The lineage is characteristic of the Cenomanian. Consistent time-stratigraphic changes in all of these "species" suggest they are actually groups or plexi of closely related and derived species which, when studied in detail from individual stratigraphic levels and restricted systematically, will allow a refined biostratigraphic zonation of the Albian sequence nearly equivalent to that available from ammonite data (Fig. 1).

The oldest Middle Cretaceous inoceramid zones of England (Fig. 1) are those of *"Inoceramus" coptensis* Casey (Lower Albian *Leymeriella regularis* subzone ; lower *Douvilleiceras mammilatum* zone), and *Birostrina salomoni* (d'Orbigny) s.s. (Lower Albian : *D. mammillatum* zone only). Together these comprise the broader species concept of *"Inoceramus salomoni"* of Woods (1911). These are divisions of a single evolutionary lineage which arises from the Aptian *"I." neocomiensis* d'Orbigny and which, through *B. salomoni*, gives rise to the *B. concentrica - B. sulcata* lineage of the later Albian throughout the world, according to Casey (1961). *Inoceramus neocomiensis* may also have been the origin point of the distinct Albian-Lowest Cenomanian (?) lineage of *I. anglicus* Woods. Woods' (1912b) report of the *B. salomoni* ranging downward into Aptian strata of the Folkestone beds is probably based on the older, broad concept of this species and must be regarded now as incorrect. Whereas *B. salomoni* does not range above the *D. mammilatum* zone in England, insofar as is presently known, it has been reported by Jones (1960) in probable Middle Albian rocks of Oregon, U.S.A., and by Schlagintweit in rocks of Late Albian ("Vraconian") age in Peru (1911). Jones' (1960) report is based on two specimens with fine concentric ornamentation and at least two radial sulci which might better be placed with the Middle and Upper Albian plexus of *Birostrina subsulcata*. Schlagintweit (1911) did not illustrate his specimen and it has not been reexamined by the author. *Birostrina salomoni* does not occur in collections from the type Vraconian, however, which casts some doubt on this report as well. This species is probably a reliable late Lower Albian marker, as Casey indicates. (1961).

Birostrina salomoni has not been examined yet for microevolutionary trends and is regarded here in the broad sense as ranging throughout the *D. mammilatum* zone. Initial investigations of the *"I." coptensis* collections in the British Museum suggest tentative division into two as yet unnamed subspecies with biostratigraphic value : an older, rounded form (n. subsp.) of the upper *L. tardefurcata* and lowest *D. mammilatum* zones, and a younger, elongate form *(coptensis*, s.s.) of the lower half of the *D. mammilatum* zone. Additional work is needed to verify this apparent evolutionary trend.

The *Birostrina concentrica-B. subsulcata-B. sulcata* lineage is the most common in the British Middle and Late Albian, and throughout much of the world in rocks of this age. *Birostrina concentrica* is the most common and longest ranging of the "species" ; it was presumably derived from *B. salomoni* and ancestral to partially co-occurring *B. subsulcata* and *B. sulcata*. The sulcate forms *(salomoni, subsulcata, sulcata)* may represent a different subgenus, as yet unnamed, than the smooth forms *(concentrica)*.

As currently regarded, the species *B. concentrica* is extremely variable and very likely represents a species plexus rather than a single form. Some attempt has been made to divide the group into more restricted species and subspecies, but without placing these in evolutionary or stratigraphic succession. Some of these "subspecies", e.g. *"I. concentricus costatus"* Nagao and Matsumoto, and *"I. c. nipponicus"* Nagao and Matsumoto are regarded as Cenomanian-Turonian forms in Asia and are doubtfully closely related to the Albian group of *B. concentrica*. Preliminary examination of collections in the British Museum, in the private collection of Mr. Julian Hollis, and in the U.S. National Museum, however, reveals some consistent evolutionary trends within the lineage (*B. concentrica*, s.l.). These suggest that, once studied through population analysis, the lineage will be readily divisible into a succession of species and subspecies with a potential for biostratigraphic refinement of the Albian succession nearly equivalent to that currently based on ammonites, and with greater geographic spread (Fig. 1). Pending detailed systematic study, these trends are represented by tentative division of the *B. concentrica* lineage into informally designated "subspecies" A (oldest) through D (youngest), with possible biostratigraphic utility in England and elsewhere (Fig. 1).

Woods (1911, 1912a, b) and later authors indicated that *B. concentrica*, s.l. had a Middle and Late Albian age range. The collections of the British Museum, however, yield sparse and subspecifically distinct members of the *B. concentrica* lineage in the latest Lower Albian (upper *D. mammilatum* zone) which are small, highly convex, narrow and very elongated along the height axis (nearly tear-drop shaped). These have a prominent, moderately prosogyrous beak and umbo, an anterior sulcus, a very small posterior auricle, and only a few coarse, widely and unevenly spaced, concentric rugae which are more distantly spaced than in any other member of the lineage. These forms are designated *B. concentrica* n. subsp. A and possibly allow biostratigraphic division of the *D. mamillatum* zone into a lower *B.*

salomoni-"I." coptensis concurrent range subzone, and an upper *B. salomoni-B. concentrica* n. subsp. A concurrent range subzone. *Concentricus*-shaped inoceramids also occur with populations of *"Inoceramus" coptensis* Casey in the *regularis* subzone, upper *tardefurcata* zone, in the lower part of the Lower Albian. It is not yet known whether these are normal variants of *"I." coptensis* or early ancestral *B. concentrica.*

In the Middle Albian, three inoceramid zones based on subspecies of *B. concentrica* are tentatively recognized (Fig. 1). The lowest zone, that of *B, concentrica* n. subsp. B, occurs in the *dentatus-?* lower *loricatus* ammonite zones, *lyelli* and *spathi* subzones, of the lower Middle Albian. This subspecies is directely descended from *B. concentrica* n. subsp. A and similar in basic morphology. The shells are moderately small, elongate-subovate to nearly linguiform, with the height appreciably greater than the length, and with the beak and umbo strongly projecting, inflated, and slightly prosogyrous. The valves have moderate convexity, a moderately large posterior auricle, and ornament consisting of strong, equally developed and moderately spaced, coarse raised concentric ridges or small rugae with a rounded trace. According to the literature, the earliest members of the *Birostrina sulcata-subsulcata* lineage also occur in the *Hoplites dentatus* zone.

The overlying Middle Albian is characterized by two inoceramid zones (Fig. 1). The lowest (*intermedius* subzone of *loricatus* zone), is characterized by *Birostrina concentrica brasiliensis* (White) (see Maury, 1936, pl. 8, figs. 9, 10, 13 ; White, 1888, pl. 3, figs. 11, 12) an ovate to subrounded, highly convex form with a very prominently projecting, highly inflated, prosogyrously coiled beak and umbo, and concentric ornamentation consisting dominantly of small, equally developed and evenly spaced, raised growth lines with a nearly symmetrical, rounded trace. This form may range higher in the *loricatus* zone, but initial observations on existing collections have not revealed it. Most of the Middle Albian *loricatus* zone above the *intermedius* subzone seems to be characterized by typical *Birostrina concentrica concentrica* (Parkinson), based on the concept of Sowerby (1814, pl. 305, figs. 1-6) and that illustrated by Woods (1911, pl. 46, figs. 1-7) from the Gault at Folkestone. Parkinson's type is lost and could not be reexamined. Typical *B. concentrica concentrica* may range as high as the base of the Upper Albian (*cristatum* nodule bed), but specimens accredited to this bed in museum collections could also be largely remanie in origin. It is worthy of note that many specimens of *B. concentrica concentrica* from the basal Upper Albian *cristatum* nodule bed are generally broader, more rounded, and more evenly convex than those from the Middle Albian, suggesting the possibility that they are contemporaneous with the *cristatum* zone, and with additional study may constitute the basis for further systematic division of the species, and greater refinement of the inoceramid biostratigraphy.

The Upper Albian seems to be divisible into two inoceramid zones (Fig. 1) based on the *B. concentrica* lineage. In the lower part of the substage (through the *varicosum* subzone of the *inflatum* zone), a new subspecies (*B. concentrica* n. subsp. C) is found which is characterized by its subquadrate outline ; moderately biconvex valves ; only moderately to slightly projecting beaks and umbos ; weak concentric ornamentation of low, widely spaced, subequally developed rugae ; its moderately large triangular posterior auricle ; and especially in having a strong umbonal fold or ridge on both valves extending from the beak to the midventral margin. The trace of the growth lines and rugae is asymmetrical, and bends narrowly over this fold – a character which becomes greatly accentuated in younger members of the lineage. The observed origin points of *B. sulcata* and *B. subsulcata* in many localities are also in the *cristatum* subzone.

The hightest Albian inoceramid zone is coincident with the *Stoliszkaia dispar* zone. It is characterized by *B. concentrica* n. subsp. D (see Woods, 1911, pl. 46, figs. 8-10, and especially pl. 47, figs. 1, 2). This form has a more erect posture than older members of the species, only moderately projecting beaks and umbos, moderately biconvex valves, and is especially characterized by medium size to coarse, prominently raised, equally spaced and evenly developed rugae or raised growth lines which on the left valve tend to have a chevron-shaped growth line trace with a strong median bend. Variants of this subspecies with a more rounded growth line trace and strong rugae may be ancestral to small basal Cenomanian inoceramids (from the *Hypoturrilites carcitanensis* assemblage zone) with moderate convexity, prominent, moderately spaced rugae, and a rounded growth line trace. This form is usually identified as *"Inoceramus* sp. cf. *I. concentricus"* in many older collections. *Inoceramus concentricus costatus* Nagao and Matsumoto from the Cenomanian-Turonian of the western Pacific margin is a probable extension of this basal Cenomanian group. The phylogenetic connection between Upper Albian *Birostrina concentrica* n. subsp. D and superficially similar Cenomanian-Turonian taxa has not been established, however, and the similarity may simply represent yet another case of homeomorphy in the Inoceramidae, this time between late *Birostrina* and early *Inoceramus* s.s.

Preliminary studies of the *B. sulcata* lineage indicate it may undergo evolutionary change in the Late Albian toward broader shells with more radial plicae, and this may eventually form the basis for further biostratigraphic division of the Late Albian. Initial plicae counts on two populations from the *cristatum* subzone at Folkestone indicate an average of 8 plicae (N = 100 specimens) on adult left valves, whereas *B. sulcata* from the *orbignyi* subzone (and probably higher) have an average of 9.5 plicae (N = 10 specimens in one population), many with low sguamae, on adult left valves. More data are needed to confirm this as a consistent trend with biostratigraphic potential.

The *Birostrina sulcata-B. subsulcata* lineage of the *B. concentrica* plexus is much less well known and more poorly studied at present than the more common *B. concentrica* lineage. Sufficient collections have not yet been examined to determine much in the way of microevolutionary trends and therefore to allow these forms to play a very important roll in refined biostratigraphic zonation of the British Albian. For this reason the inoceramid zonation tentatively proposed here is based mainly on the *concentricus* lineage and where relevant, origin and extinction points of other, less well studied inoceramids (including the *I. anglicus* lineage) are noted within the context of ammonite and/or *B. concentrica*-based zones.

Woods (1911) reports both *B. sulcata* and *B. subsulcata* "from the Gault at Folkestone". Much of the general literature since that time (e.g. Cox, 1967) has therefore accredited the two species to the Middle and Upper Albian, presumably from the base of the *Hoplites dentatus* zone to the top of the *Stoliczkaia dispar* zone. Museum collections similarly contain many specimens attributed to the Lower Gault, or Middle Albian. The range zones of these taxa are therefore considered to extend from the *dentatus* through the *dispar* zone in this report, until proven otherwise. Woods (1912b, p. 2) clearly indicated, however, that the range of both species extended from a point half way between the top of the Lower Albian (his *D. mammilatum* zone) to the top of the Upper Albian sequence, i.e. approximately from the Middle-Upper Albian boundary to the top of the stage. The author's observations, and those of active workers in England, have been basically the same. It is probable therefore that the range zones of both *B. sulcata* s.s., and *B. subsulcata* s.s., are restricted to the Late Albian (Fig. 1), and possibly only to the *Mortoniceras inflatum* zones despite the range given by Woods (1912b, p. 2).

No microevolutionary trends were noted with available material for *B. subsulcata* and only a small change upsection, toward increasing numbers of plicae and rounder shells (subsequently discussed) was noted in examined collections of *B. sulcata*, with the main break between the *cristatum* and *orbignyi* subzones of the *Mortoniceras inflatum* zone.

Similarly, the *Inoceramus anglicus* lineage is not yet well enough known to use it confidently in biostratigraphic subdivision of the English Albian. Woods (1912b, p. 6) reports it as ranging throughout the Upper Greensand and Gault (Middle and Upper Albian). Preliminary observation of specimens from collections in the British Museum suggest that those of the Middle Albian are more erect, with greater relative height and convexity, and have more raised concentric growth lines per unit height (average of 43 in the first 50 mm of shell height) than do those of the Upper Albian (*M. inflatum* zone data?; average of 29 concentric lines in first 50 mm of shell height). More data will be necessary to confirm this apparent evolutionary trend and to apply it to biostratigraphy. The report of *I. crippsi* in the highest Albian by Woods (1912b, p. 6), where it evolves from *I. anglicus*, cannot yet be confirmed.

Finally, Woods (1911, 1912b) reports *Inoceramus tenuis* from the highest part of the Upper Albian sequence (*S. dispar* zone approximately). The *I. tenuis-I. etheridgei* lineage is primarily a Cenomanian group and has important biostratigraphic usage in that stage. The supposed Albian example, from the Red Limestone near Louth, is not *I. tenuis* s.s. but rather an early evolutionary phase of *I. etheridgei* with greater inflation and relatively coarser concentric ornament than the type of that species. It represents a new subspecies and is plotted in this way on the biostratigraphic chart of this report. Further, it is possible that the Red Chalk of Louth may be, at least in part, of Early Cenomanian age, not Albian, for the unit is known to be diachronous across this boundary when traced from Hunstanton to Yorkshire (Kaye, 1964, p. 340-356).

CENOMANIAN INOCERAMIDAE

English Cenomanian Inoceramidae are remarkably diverse, intercontinental to cosmopolitan in distribution, rapidly evolving, abundant, and consistently represented through the stratigraphic sequence in most facies. They are thus a primary tool in Cenomanian biostratigraphy.

Whereas most species were originally described from field and museum collections with relatively general stratigraphic data, the author has had the unique opportunity to collect and analyze large populations of Inoceramidae from closely spaced stratigraphic intervals throughout the British Cenomanian, under the direction of Dr. W. J. Kennedy of Oxford University. Each collection has been located precisely within Kennedy's Cenomanian ammonite zonation (1969, 1970, 1971 ; Kennedy and Hancock, this volume). Systematic research has nearly been completed on these collections, and though formal taxonomy is not yet formulated for all species and subspecies, the concepts are stable and applicable to biostratigraphic zonation, regional correlation, and stage definition. The taxa are tentatively organized into zones, along with ammonite zonal indices, in this report (Fig. 2). Because of the relative status of the systematic work, higher confidence may be placed in the Cenomanian inoceramid zonal scheme than those of the relatively unstudied Albian, Turonian or Coniacian. As in the case of other British Inoceramidae, species concepts previously applied to Cenomanian forms by Woods (1911, 1912a) and others are extremely broad, assuming high levels of variation, and do not take into account the possibility of small-scale evolutionary trends. The present work, testing for such trends, demonstrates that most of the Woods Cenomanian inoceramid "species" concepts (e.g. his *I. pictus, I. crippsi,* or *I. etheridgei* concepts) are really species groups of two or more distinct taxa with narrower, biostratigraphically more useful species ranges.

The principal Cenomanian inoceramid lineages are those of *Inoceramus (Inoceramus) pictus ; "Inoceramus" (Mytiloides ?) crippsi-"I." (M ?) reachensis*, and that of *I. (I.) etheridgei-I. (I.) tenuis*. Secondary lineages include Lower Cenomanian forms questionably derived from and superficially similar to the *Birostrina concentrica* group of the Albian, and possibly some members of the *"Inoceramus" anglicus* lineage. Also, members of the *I. arvanus-I. rutherfordi* lineage, formerly known only from the Cenomanian of the Western Interior of North America, are reported in small numbers from England for the first time here. These diverse, rapidly evolving taxa allow a refined inoceramid biostratigraphy of the English Cenomanian, linked to the current ammonite zonation (Fig. 2 ; from Kennedy, 1969, 1971), as follows (oldest to youngest) :

LOWER CENOMANIAN

Hypoturrilites carcitanensis Zone This is the point of origin for many characteristic Cenomanian inoceramid stocks. The following taxa originate at or near the base of the zone : *"Inoceramus" crippsi crippsi* Mantell (Woods, 1912a, p. 276, figs. 33, 34) and a new subspecies A (Woods, 1911, fig. 35, p. 277) with erect growth form and crowded, small umbonal rugae (subspecies A may originate in latest Albian time) ; *"Inoceramus" (Mytiloides ?) reachensis reachensis* Etheridge (Woods, 1911, pl. 48, fig. 5) ; *"Inoceramus" anglicus conjugalis* Pergament ; *Inoceramus (Inoceramus) heinzi* Sornay ; *I. (I.) tenuis tenuis* Mantell (Woods, 1911, p. 272, 273, figs. 31, 32) and forms transitional between this and the *Birostrina concentrica* lineage; *I. (I.) etheridgei* Woods, n. subsp. A (transitional to *I. (I.) tenuis ;* Woods, 1911, pl. 48, fig. 1, as *I. tenuis*), and n. subsp. B transitional to *I. (I.) conicus* Gueranger, an erect, tall form ; possibly the earliest occurrence of *I. (I.) tenuistriatus ?* Nagao and Matsumoto, *I. (I.)* n. sp. A cf. *I. (I.) arvanus* Stephenson (ancestral form with very weak rugae and sulcus), *I. (I.)* sp. aff. *I. ginterensis* Pergament (weaker rugae than normal), and *I. (I.) pictus,* n. subsp. A aff. subsp. *vardonensis* Sornay (with very coarse, raised growth lines).

Three rare inoceramids are restricted to this zone insofar as they are known: *"Inoceramus" (Mytiloides ?) reachensis,* n. subsp. C transitional to *"I." anglicus conjugalis* Pergament; *I. (I.)* n. sp. B cf. *I. (I.) arvanus* Stephenson (form with coarse, evenly developed, small rugae and a weak broad posteroventral sulcus); and a very finely ornate, early member of the *I. (I.) pictus* lineage-*I. (I.)* n. sp. ex gr. *I. (I.) pictus* Sowerby. The origin of *I. (I.) arvanus* Stephenson in the middle of the *H. carcitanensis* zone may allow biostratigraphic division of this zone into upper and lower subzones.

Mantelliceras saxbii Zone : A second major radiation of new Cenomanian inoceramid stocks apparently takes place at or near the base of the *M. saxbii* zone of Kennedy (1969, 1971). Inoceramids which originate here include *"Inoceramus" (Mytiloides ?) reachensis* n. subsp. A (Woods, 1911, pl. 49, fig. 1), an inclined, ovate form with large, moderately and equally spaced, rounded rugae having fine concentric lines evenly distributed between them; *"Inoceramus" (Mytiloides?) reachensis* n. subsp. B (Woods, 1911, pl. 48, fig. 4 ; a high, erect, slightly sulcate subspecies with closely spaced, subequal rugae and coarse raised growth lines); *I. (I.) tenuistriatus* Nagao and Matsumoto, n. subsp. A, transitional to *I. etheridgei* (see Nagao and Matsumoto, 1939, 1940, pl. 46, fig. 4) ; *I. (I.) rutherfordi* Warren ; *I. (I.) arvanus arvanus* Stephenson ; and *I. (I.) flavus* Sornay, n. subsp. A (ancestral, with erect beaks and umbos, finer concentric ornamentation). *Inoceramus (I.) etheridgei* Woods may originate this low in the sequence (based on fragments) but is first definitely known in the younger zone of *Turrilites costatus.*

Inoceramidae restricted to the *M. saxbii* zone and useful in its identification biostratigraphically are : *"Inoceramus" crippsi* n. subsp. B (nearly smooth to very weakly ornamented) ; *I. (Mytiloides ?) reachensis* n. subsp. D (broad, rounded, non-sulcate, with very sparse, widely separated, low rugae) ; and *"I." anglicus* cf. subsp. *"I." anglicus elongatus* Pergament. Subdivision of the *M. saxbii* zone on the basis of inoceramids is not possible at this time.

Mantelliceras dixoni Zone : This zone is poorly differentiated on the basis of inoceramid origins and extinctions, although it contains rich inoceramid assemblages throughout. Two forms originate at or near the base of the zone : *Inoceramus (Inoceramus) pictus* n. subsp. B (Woods, 1911, pl. 49, fig. 5 ; erect form with subtle, sparsely distributed rugae, coarse evenly developed raised growth lines over the entire shell, and a small posterior auricle without a prominent auricular sulcus); and *I. (I.) etheridgei*, n. subsp. C (large, with low convexity and fine growth lines). *Inoceramus (Inoceramus) etheridgei*, n. subsp. A transitional to *I. (I.) tenuis* (Woods, 1911, pi. 48, fig. 1) dies out at the top of the *M. dixoni* zone, as do *I. (I.) flavus* Sornay n. subsp. A (ancestral, with erect beaks, umbos, finer concentric ornamentation) and *I. (I.)* sp. aff. *I. (I.) ginterensis* Pergament (weaker rugae than normal). No inoceramids are restricted to the zone.

MIDDLE CENOMANIAN

Turrilites costatus Zone : This ammonite zone is also well defined by Inoceramidae and possibly divisible into two subzones utilizing these bivalves. Taxa which originate at or near the base of the zone include The earliest definite occurrence of *Inoceramus (Inoceramus) etheridgei etheridegei* Woods (1911, pl. 49, figs. 3, 4) ; *I. (I.)* n. sp. C aff. *I. (I.) arvanus* Stephenson (small erect form with close small rugae, very shallow, narrow posteroventral and auricular sulci) ; *I. (I.) flavus flavus* Sornay ; *I. (I.) pictus* Sowerby transitional to broader, flatter ancestral forms ; and possibly *I. (I.)* n. sp. D aff. *I. flavus* (with short, erect, finely ornamented beak and umbo). The following become extinct at the top of the zone in England ; *I. (I.) etheridgei* n. subsp. B trans. to *I. conicus* Guéranger ; *I. (I.) heinzi* Sornay ; and *I. arvanus arvanus* Stephenson.

The lower half of the *T. costatus* zone is characterized exclusively by forms of *I. (I.) arvanus* Stephenson with unusually prominent sulci, and by forms of *I. (I.) etheridgei* transitional between subsp. *etheridgei* and n. subsp. A. The upper half of the zone has, at the base, the last occurrence of *I. (I.) pictus* n. subsp. A aff. subsp. *vardonensis* Sornay (erect, narrow, with very coarse, raised growth lines) and the origin point of *I. (I.) tenuistriatus* Nagao and Matsumoto, n. subsp. B with flat, rounded shells and *I. (I.)* n. sp. E aff. *I. (I.) tenuis* Mantell (with prominent, coiled, exogyroid beaks and umbos).

Turrilites acutus Zone : Few inoceramid taxa have their origins or extinctions in the *T. acutus* zone, but they are sufficient to allow recognition of the zone on the basis of inoceramids, and possibly even its subdivision into subzones once the faunas. are better studied. Inoceramidae having their origin point at or near the base of the zone include *Inoceramus (Inoceramus) ginterensis* Pergament, and *Inoceramus (I.)* sp. aff. *I. (I.) prefragilis* Stephenson (concentric ornamentation stronger than typical for species). *Inoceramus (Inoceramus) tenuis* s.s., and *I. (I.) pictus* n. subsp. B (Woods, 1911, pl. 49, fig. 5) die out at the top of the zone, and the last definite occurrence of *I. (I.) etheridgei etheridgei* and *I. (I.)* n. sp. A aff. *I. (I.) arvanus* Stephenson (ancestral forms with weak rugae and sulcae) are also at the top of this zone, although both may range into the *Acanthoceras jukes-brownei* zone, based on questionable fragments. *Inoceramus (I.) tenuis* Mantell, n. subsp. A (with large posterior auricle, blunt beak) is restricted to this zone. *Inoceramus (Inoceramus) rutherfordi* Warren and *I. (I.) etheridgei* n. subsp. C (large, rounded, with low convexity and fine growth lines) both disappear in the middle of the *T. acutus* zone, possibly providing a basis for its division into two subzones.

Acanthoceras jukes-brownei Zone : The upper boundary of the *Acanthoceras jukes-brownei* zone, marking the Middle-Late Cenomanian contact, is an important extinction point for numerous inoceramid species and lineages. A single species, *I. (I.)* n. sp. F aff. *I. (I.) pictus* Sowerby (broad, flat, with coarse equally developed, closely spaced, raised growth lines) has its origin near the base of the zone. *"Inoceramus" anglicus conjugalis* Pergament and *I. (I.) flavus flavus* Sornay become extinct in the middle part of the zone, allowing its division into a lower and an upper subzone. The following taxa become extinct at or near the top of the *A. jukes-brownei* zone *"Inoceramus" crippsi crippsi* Mantell ; *"I." (Mytiloides?) reachensis reachensis* Etheridge ; *"I." (M ?) reachensis* n. subsp. B (Woods, 1911, pl. 48, fig. 4) ; *I. (I.) tenuistriatus ?* Nagao and Matsumoto, and transitional forms of the species into *I. (I.) etheridgei* (see Nagao and Matsumoto, 1939, 1940, pl. 26, fig. 4) ; possibly *I. (I.) etheridgei etheridgei* Woods (fragments only), *I. (I.)* n. sp. E aff. *I. (I.) tenuis* (with prominent, coiled exogyroid beak, umbo), and *I. (I.) arvanus* Stephenson, s.l. No inoceramids are restricted to the zone.

UPPER CENOMANIAN

Calycoceras naviculare Zone A great reduction in inoceramid diversity among all lineages but that of *I. (I.) pictus* Sowerby takes place within or at the base of the *C. naviculare* zone, marking an important evolutionary boundary (and thus substage boundary) for many organisms. The typical Late Cenomanian taxa *I. (I.) pedalinoides* Nagao and Matsumoto and *I. (I.) tenuiumbonatus* Warren have their origins at or near the base of the zone. The following forms become extinct at the top of the *C. naviculare* zone *"Inoceramus" crippsi* n. subsp. A (with erect growth form and crowded small umbonal rugae : Woods, 1911, p. 277, fig. 35), and *I. (I.)* n. sp. D cf. *I. (I.) flavus* Sornay (with short, erect, finely ornamented beak, umbo). *"Inoceramus" (Mytiloides ?) reachensis* n. subsp. A (Woods, 1911, pl. 49, fig. 1) dies out in the middle of the zone, possibly providing a basis for its local subdivision into an upper and a lower subzone.

Metoicoceras geslinianum Zone : Little is known about the Inoceramidae of the *M. geslinianum* zone at present ; similar taxa range below and above it however, so that there appears to be little in the evolutionary history of the inoceramids to help define the zone. A rare species transitional between the *I. (I.) rutherfordi-I. (I.) arvanus* lineage of the older Cenomanian and the *"Inoceramus" (Cordiceramus) cordiformis* lineage of the Latest Coniacian and Santonian probably originates near the base of this zone, and the last representatives of *I. (I.) ginterensis* Pergament or a related form die out at the top of the zone. The last definitely determinate representatives of *I. (I.) tenuimbonatus* Warren and *I. (I.) pedalionoides* Nagao and Matsumoto in England occur near the top of this zone, but poorly preserved specimens questionably assigned to both species range higher (through the *M. gourdoni* zone), and the species are definitely known in younger strata of North America.

Metoicoceras gourdoni Zone No Cenomanian Inoceramidae originate in or are exclusively confined to this zone. The following become extinct in England at or near the upper boundary of the zone and aid in its determination where ammonites are rare or absent The last possible occurrence of *Inoceramus (Inoceramus) pedalionoides* Nagao and Matsumoto and *I. (I.) tenuiumbonatus* Warren ; the last definite occurrence of *I. (I.)* n. sp. C aff. *I. (I.) arvanus* Stephenson (small erect form with close small rugae, very shallow, narrow posteroventral and auricular sulci) ; *I. (I.)* n. sp. transitional between the *I. (I.) arvanus-rutherfordi* lineage and *I. (Cordiceramus) cordiformis* lineage ; *I. (I.) pictus* n. subsp. B (Woods, 1911, pl. 49, fig. 5 ; erect form with subtle, sparsely distributed rugae, coarse evenly developed raised growth lines over entire shell, and small posterior auricle without prominent auricular sulcus) ; and *I. (I.)* sp. aff. *I. (I.) prefragilis*

Stephenson (concentric ornamentation stronger than typical for species).

Beds above the *M. gourdoni Zone* Horizon A (Kennedy and Juignet, 1973), lower part. Kennedy and Juignet (1973) and Kennedy and Hancock (this volume) have recognized the presence of the North American zone fossil, *Sciponoceras gracile*, in the European Middle Cretaceous and assigned it, as in North America, to the Upper Cenomanian based on the large scale evolutionary break between it and the overlying *"Inoceramus labiatus"* zone of the Lower Turonian, and the similarity of many ammonites associated with *S. gracile* to those of the Cenomanian. The Inoceramidae co-occuring with *S. gracile* in the uppermost part of its range are poorly known to date, but are dominantly of Cenomanian stocks. At present the typical Cenomanian *Inoceramus (I.) pictus pictus* Sowerby is known to range only to the top of the *S. gracile* range zone. Further study will probably show that other members of this lineage, such as *I. tenuiumbonatus* Warren, range similarly, as they do in North American section. The evolutionary forerunners of the *Mytiloides labiatus* lineage, *M. submytiloides* Seitz, first appear at the top of the range zone. This is the only inoceramid of Turonian affinities in the fauna.

TURONIAN INOCERAMIDAE

Turonian Inoceramidae are abundant and well preserved, moderately well described, but very poorly known biostratigraphically in the English Middle Cretaceous sequence. They have not been thoroughly restudied in the same manner as those from the Cenomanian, and so the following is a generalization of available data with certain biostratigraphic relationships implied from other areas, but not yet observed in the British sequence. Highly detailed stratigraphic collecting of the Turonian sequence in England will be required to refine the zonation and stage and substage implications.

LOWER TURONIAN

"Inoceramus labiatus" and *Orbirhynchia cuvieri* Zone : Throughout the world, the appearance of the cosmopolitan stock of *Mytiloides labiatus* (Schlotheim) marks the basal Turonian. Whereas most workers recognize this as a single variable species, Seitz (1934) recognized it correctly as a species plexus and divided it into a series of distinct species and subspecies with potential for refined biostratigraphic zonation and regional correlation. Kauffman (see Kauffman, Cobban, and Eicher in this volume ; Kauffman and Powell, 1977, in press ; and work in progress) has subsequently established the zonal sequence in North America and traced it widely into Europe and North Africa. In descending order, the *Mytiloides labiatus* plexus incorporates the following Middle and Lower Turonian zones in these areas :

- Youngest : Middle Turonian
  - Zone of *Mytiloides "latus"* (Mantell) (concept of Woods, 1911, p. 285, fig. 41, and Hattin, 1962, pl. 14, figs. A, C, E) and *Inoceramus cuvieri* Sowerby
  - Zone of *Mytiloides hercynicus* (Petrascheck), *Inoceramus cuvieri* Sowerby
  - Zone of *Mytiloides subhercynicus* (Seitz) with *M. hercynicus* (Petrascheck) overlapping in the upper half of the zone.
- Lower Turonian
  - Zone of *Mytiloides labiatus* (Schlotheim) with *M. subhercynicus* Seitz
  - Zone of *Mytiloides mytiloides* (Mantell)
  - Zone of *Mytiloides opalensis* (Böse) with (locally) *M. duplicostatus* (Anderson)
- Oldest : Lowest Turonian and highest Cenomanian (?)
  - Zone of *Mytiloides submytiloides* (Seitz)

Slight overlap between zonal taxa near zone boundaries is possible and has been locally recognized in North America and Western Europe.

Many of these taxa have been recognized in the British Turonian, mainly in older museum and university collections where precise stratigraphic data and relationships are not available. They are simply listed as "Middle Chalk", "Melbourn Rock", *"Orbirhynchia cuvieri* zone" or *"Inoceramus labiatus* zone". The relative stratigraphic positions of these taxa are thus poorly known, and must be largely assumed from the zonal scheme as established outside of Britain. Present data allows the following subzonation of the Lower Turonian *"Inoceramus labiatus* zone" in England (oldest to youngest).

Subzone of Mytiloides submytiloides (Seitz) - At the top of the Cenomanian, in the uppermost part of the *I. pictus pictus* and *Sciponoceras gracile* Zone (basal Melbourn Rock), inoceramids indentified as *Mytiloides submytiloides* (Seitz) first appear in small numbers with late occurrences of *I. pictus*, as previously noted. These are the ancestral forms of the *M. labiatus* (Schlotheim) lineage which characterizes the Lower Turonian throughout the world. *M. submytiloides* ranges upward and becomes somewhat more abundant above the *I. pictus-S. gracile* Zone, in the higher parts of Kennedy and Juignet's Horizon A (1973) of northwest France and southern England. Here *M. submytiloides* is associated with *Watinoceras* in beds corresponding to the base of the classic *"Mammites nodosoides-Inoceramus labiatus"* (s.l.) zone. This *Watinoceras*-bearing sequence has been recently separated from the *M. nodosoides* zone by Cobban and Scott (1972) as the *W. coloradoense* zone (basal Turonian), and further divided (Kauffman, Cobban and Eicher, this volume) into a lower *W. reesidei* zone and an upper *W. coloradoense* zone. All of these occur in the United Kingdom and a similar zonation should be demonstrable here. The *Mytiloides submytiloides* range zone therefore possibly extends from the highest Cenomanian (if *I. pictus* is truly restricted to the Cenomanian) and definitely into the base of the Turonian, lower half of the *W. reesidei* zone, in North America and presumably in Britain as well. The *M. submytiloides* zone or subzone is thus established in England for the first time here. *Mytiloides submytiloides* underlies the lowest occurrences of *M. mytiloides* and *M. labiatus* s.s.

Subzone of Mytiloides opalensis (Böse). - No specimens definitely identifiable as *M. opalensis* (Böse) or *M. duplicostatus* (Anderson) are yet known from England, but a single specimen of *M.* sp. cf. *M. opalensis* is recorded from the *Orbirhynchia cuvieri* zone; possibly this inoceramid zone is greatly compressed and/or locally missing in England. *Mytiloides mytiloides arcuata* (Seitz), which occurs in the upper part of the *M. opalensis* zone and lower *M. mytiloides* zone of North America, is well represented in Britain, however (Woods, 1911, pl. 50, figs. 2, 3), further suggesting the presence of at least part of the *M. opalensis* zone there.

Subzone of Mytiloides mytiloides (Mantell. - This is one of the most common *Mytiloides* in the British Lower Turonian sequence (Woods, 1911, pl. 50, fig. 1 is typical; Mantell's type, ibid., p. 283, fig. 37 similar but crushed). Most museum specimens are listed as coming from the *"Orbirhynchia cuvieri* zone", or *"I. labiatus zone"* of the Middle Chalk.

Subzone of Mytiloides labiatus Schlotheim. - Specimens resembling closely the type concept of the *M. labiatus* (compare Woods, 1911, pl. 50, fig. 5 with Seitz, 1934, pl. 38, fig. 1, and text-fig. 5a) occur commonly in museum collections labeled as being from the "Middle Chalk", "Melbourn Rock", and *"O. cuvieri-I. labiatus* zone", but their stratigraphic relationship to *M. mytiloides* (which has a lower range elsewhere) is not yet precisely known in England.

MIDDLE TURONIAN : ZONE OF TEREBRATULINA LATA

Subzone of Mytiloides subhercynicus, M. hercynicus, and Inoceramus cuvieri cuvieri Sowerby. - These taxa constitute two distinct zones in Western Interior North America, but so little is known about their distribution in Britain that they are combined here. *Mytiloides subhercynicus* (Seitz) is represented in museum collections by rare specimens from the "Middle chalk" and the *"O. cuvieri* zone". *Mytiloides hercynicus* (Petrascheck) is also rare in the upper part of the Middle Chalk ; it's stratigraphic relationships to *M. subhercynicus* are unknown in England. *Inoceramus (Inoceramus) cuvieri cuvieri* Sowerby (Woods, 1911, p. 315, fig. 73 ; p. 317, fig. 75) is extremely abundant in this zone however, as it is elsewhere in the early Middle Turonian in association with the widespread ammonite *Collignoniceras woollgari* (Mantell). It is characterized by smooth to faintly rugate shells of low convexity, with fine subequal flat growth lamellae over the entire shell.

Subzone of Mytiloides "latus" (of Woods, non Sowerby, non Mantell) *and Inoceramus cuvieri Sowerby, n. subsp.* - Specimens identical to the concept of *M. "latus"* used widely in North America and parts of Europe for Middle Turonian forms (e.g., Woods, 1911, p. 285, fig. 41 ; Hattin, 1962, pl. 14, figs. A, C, E) occur in museum collections where they are labeled as coming from the upper part of the Middle Chalk, zone of *Terebratulina lata*, and from the Chalk Rock (Upper Turonian), at the base of the *H. planus* zone, the basal unit of the Upper Chalk. This is not the type concept of *I. labiatus latus* of Sowerby (1828) based on specimens from Swaffham (Woods, 1911, p. 284, figs. 39, 40 ; the type) which is closely related to the Lower Coniacian species *I. rotundatus* Fiege. Nor does it correspond to the type concept of *I. latus* Mantell (1822, pl. 27, fig. 10), which belongs in the *I. cuvieri-I. lamarcki* lineage.

An evolutionary derivative of *Inoceramus (Inoceramus) cuvieri* Sowerby (i.e., n. subsp., rugate form), also occurs in this subzone. In North America, the *cuvieri* lineage is divisible into at least three subspecies which are the basis for distinct biostratigraphic zonation a lower subzone of *Inoceramus (Inoceramus) cuvieri* s.s. – characterized by nearly smooth valves lacking coarse, evenly developed rugae (i.e. the type of *I. cuvieri* ; Woods, 1911, text-fig. 73, Middle Chalk, *T. lata* zone). *Inoceramus (Inoceramus) cuvieri* n. subsp. (rugate form) is the next taxon and co-occurs with *Mytiloides "latus"* (sensu Woods, 1911, fig. 41) in the middle Middle Turonian, dominantly above the smooth, more typical forms, in America and Europe. This distribution seems to generally be the case in Britain, where typical evenly and prominently rugate forms of *I. (I.) cuvieri* (Woods, 1911, p. 319, fig. 77 ; p. 320, fig. 78) occur widely. In America, this form ranges from the upper *C. woollgari* zone into the basal *Prionocyclus hyatti* zone.

Subzone of Inoceramus (Inoceramus) flaccidus White. - In North America this species, with its very prominent, angular, unevenly curved rugae (Woods, 1911, p. 323, fig. 82, as *I. cuvieri),* occurs above more evenly rugate *I. (I.) cuvieri*, n. subsp. with *Prionocyclus hyatti* (lower part of range) in the late Middle Turonian. Identical forms occur in Britain along with coarsely rugate *I. (I.) cuvieri* and early *I. (I.) lamarcki*, but their stratigraphic relationship to *I. cuvieri cuvieri* and its subspecies is not yet known.

ZONE OF HOLASTER PLANUS, LOWER PART

Subzone of Inoceramus costellatus Woods. - In many parts of the world, *I. (I.) costellatus* marks the highest Middle Turonian inoceramid zone (upper part, zone of *Prionocyclus hyatti* in U.S. ammonite succession). This species occurs abundantly in the Chalk Rock of England and appears to have a comparable stratigraphic position, although the exact spatial relationships to other inoceramids are not known. Woods (1911, pl. 54, figs. 5-7) illustrates typical Chalk Rock specimens. Early, small, weakly rugate and sulcate members of the *I. (I.) lamarcki* s. l. plexus also occur in this zone, as do early *I. apicalis* s.l.

UPPER TURONIAN ZONE OF HOLASTER PLANUS, UPPER PART

The Upper Turonian sequence in Britain is characterized by a variety of taxa belonging mainly to the plexus of *Inoceramus (Inoceramus) lamarcki* Parkinson, and to a lesser degree, forms attributable to the *I. apicalis* Woods species group and derivatives from the *I. costellatus* lineage. The apparently rapid evolution and wide biogeographic spread of these taxa suggest that they will have great value in refined biostratigraphic division of the British sequence, but the detail of the systematics, relative stratigraphic position of various forms, and the degree of expected population variation within species are still largely unknown and further division of this substage is not yet possible based on inoceramids. Woods (1911, p. 312, 313, figs. 63-67) illustrates a range of examples of *I. lamarcki* s.l.

Representatives of much of the North American Late Turonian inoceramid succession do occur in the British Chalk, including, in ascending zonal succession elsewhere, *I. (I.) dimidius* White, *Mytiloides striatoconcentricus* (Gümbel), and *I. (I.) kleini* Andert associated with *I. (I.) waltersdorfensis* Andert. But present stratigraphic data is too imprecise to allow their relative positions to be determined. Further careful work will obviously allow more refined zonation of the Late Turonian.

As in the United States, France, and elsewhere, the Turonian-Coniacian boundary in England is best drawn at the major evolutionary break in inoceramid stocks. This break lies everywhere at the termination point of most members of the *I. (I.) lamarcki* plexus, and the origin of the *I. rotundatus-erectus-deformis-schloenbachii* lineage. The position of this inoceramid break is not yet clearly known in the English succession, mainly because the precise succession of the dominant Inoceramidae is still so poorly known. It is thought to lie somewhere in the lower part of the classic *Micraster cortestudinarium* zone, presumably at or somewhat below the *M. normanniae-M. decipiens* zone boundary of Stokes (1975, fig. 19). This inoceramid boundary lies well below the North German Turonian-Coniacian boundary based on Inoceramidae, and corresponds with the first appearance of typical Coniacian ammonites (*Peroniceras, Forresteria, Barroisiceras*) in many parts of the world (i.e., Kennedy and Hancock, this volume, tab. 4).

CONIACIAN

The Coniacian inoceramid succession is critical to global correlation of the temperate zones because ammonites are so rare in dominantly chalk sequences. Detailed inoceramid zonations have been worked out in North Germany (e.g., Tröger, 1967 ; Lower Coniacian of our usage = Upper Turonian-"Emscherian" above the origin point of *I. rotundatus* Fiege) and North America (Kauffman, 1966; 1975, and *in* Kauffman, Cobban and Eicher, this report), but not in England, where the relative stratigraphic position of most collections is still vaguely known, and precise stratigraphic collecting has not yet been done.

Collections of the British Museum, Geological Survey, and various universities, however, do contain many elements of the German and/or North American zonation so that with future studies the English Coniacian should also be divisible into a refined biostratigraphy. The standard American Coniacian inoceramid zonation is given below, and compared with counterpart taxa known from the English sequence, based on existing collections.

COMPARISON OF GENERAL EURAMERICAN AND BRITISH CONIACIAN INOCERAMIDAE

Euramerican Coniacian Inoceramid Zonation	British Counterparts and Stratigraphic Levels in the Upper Chalk as currently known
Upper Coniacian	
Zone of *Inoceramus (Magadiceramus) subquadratus*, with *Volviceramus involutus*	*Volviceramus involutus* (part), Upper Chalk, especially *"Micraster cor-anguinum"* zone (Woods, 1912a, p. 330-333, figs. 90-94).
Middle Coniacian	
Zone of *Volviceramus involutus* (? = *V. grandis*), with *Cremnoceramus ? wandereri, Volviceramus ? koeneni* (upper limit of range), *Cremnoceramus inconstans woodsi* and var. (upper limit of range), and *Platyceramus platinus* s.l. (lower limit of range).	*Volviceramus involutus*, Upper Chalk (Woods, 1912a, p. 329, fig. 88) ; *Cremnoceramus inconstans* (part), Upper Chalk (Woods, 1912a, p. 287, figs. 44, 45).
Zone of *"Inoceramus" schloenbachii*, with *Cremnoceramus inconstans woodsi, Volviceramus ? koeneni*, and ancestral forms of *V. involutus*.	*Cremnoceramus inconstans* (part), Upper Chalk, ? *"M. coranguinum* zone (probably older) (Woods, 1912a, p. 287, figs. 44, 45). *Volviceramus "involutus" (= koeneni)*, Upper Chalk (Woods, 1912a, p. 329, fig. 89).
Zone of *"Inoceramus" browni* and *Cremnoceramus inconstans inconstans.*	*Cremnoceramus inconstans* s.s., Upper Chalk (Woods, 1912a, p. 286, figs. 42, 43).
Lower Coniacian	
Zone of *"Inoceramus" deformis*, n. subsp. (prosogyrous anterior beak, asymmetrical rugae), with *Cremnoceramus inconstans*, n. subsp. A (small, flat, finely ribbed early growth stage). *Mytiloides dresdensis labiatoidiformis* occurs in upper limit of its range zone.	*Cremnoceramus inconstans* (part), Upper Chalk.
Zone of *"Inoceramus" deformis deformis.*	None yet known.
Zone of *"Inoceramus" erectus*, n. subsp. (large, moderately inflated, with coarse rugae and prominent posterior auricle), with *I. waltersdorfensis hannovrensis* in upper limit of its range zone.	*"Inoceramus inconstans"* (Woods, 1911, p. 287, fig. 46), Upper Chalk.
Zone of *Inoceramus" erectus erectus.*	None yet known.
Zone of *Inoceramus rotundatus*, with *Inoceramus lueckendorfensis. I. waltersdorfensis walterdorfensis, Mytiloides fiegei fiegei*, and *M. striatoconcentricus*, s.s. occur here in the upper part of their range zones.	*Inoceramus "latus"* (Woods, 1911, p. 284, figs. 39, 40) lower part of Upper Chalk ; *I. websteri* (Woods, 1911, pl. 53, figs. 1, 2), lower part of Upper Chalk. *"Inoceramus labiatus* var. *latus" (= waltersdorfensis) (ibid*, p. 283, fig. 38). Lower part of Upper Chalk.
Late Turonian	
Zone of *Mytiloides lusatiae, M. dresdensis dresdensis, M. fiegei fiegei*, and *M. fiegei mytiloidiformis.*	None yet known.

REFERENCED CITED

CASEY R., (1961).— The stratigraphical palaeontology of the Lower Greensand. Palaeontol., v. 3, p. 487-621, pls. 77-84.

COX L. R., (1967). — British Mesozoic fossils. British Mus., Nat. Hist. Pub., 3rd ed., 207 pp., 73 pls.

HATTIN D. E., (1962). — Stratigraphy of the Carlile Shale (Upper Cretaceous) in Kansas. Kansas Geol. Surv. Bull. 156, p. 1-155.

JEFFRIES R. P. S., (1963). — The stratigraphy of the *Actinocamax plenus* Subzone (Turonian) in the Anglo-Paris Basin. Proc. Geol. Assn., v. 74, pt. 1, p. 1-34, 9 text-figs.

JONES D. L., (1960). — Lower Cretaceous (Albian) fossils from southwestern Oregon and their paleogeographic significance. Jour. Paleont., v. 34, n. 1, p. 152-160, pl. 29, text-figs. 1, 2.

KAUFFMAN E. G., (1966). — Notes on Cretaceous Inoceramidae (Bivalvia) of Jamaica. Jour. Geol. Soc. Jamaica, v. 8, p. 32-40, p. 32-40, tab. 1.

(1970). — Population systematics, radiometrics, and zonation - - a new biostratigraphy. Proc. N. American Paleont. Conv., pt. F, p. 612-666, 10 text-figs.

(1975).— Dispersal and biostratigraphic potential of benthonic Bivalvia in the Western Interior. *In* Caldwell, W.G.E. (Ed.) The Cretaceous System in the Western Interior of North America. Spec. Pap. no. 13, Geol. Assn. Canada, pp. 143-194, text-figs. 1-4.

KAUFFMAN E. G., COBBAN W. A. AND EICHER D. L., (1977) — Albian through Lower Coniacian strata and biostratigraphy, Western Interior United States. This volume, 50 ms. pp., 8 pls., 5 text-figs.

KAUFFMAN E.G. and POWELL J.D., (1977) in press — Upper Cretaceous fossils from Cimarron County, northwestern Oklahoma. Memoir, Geol. Soc. America, 175 ms. pp., 12 pls., 8 text-figs.

KAYE PETER, (1964). — Observations on the Speeton Clay (Lower Cretaceous). Geol. Mag., v. 101, n. 4, p. 340-356, 6 text-figs.

KENNEDY W. J., (1969). — The correlation of the Lower Chalk of south-east England. Proc. Geol. Assoc., V. 80, p. 459-560, pls. 15-22, text-figs. 1-16.

(1970). — A correlation of the Uppermost Albian and the Cenomanian of south-west England. Proc. Geol. Assoc., v. 81, pt. 4, p. 613-677, 20 text-figs.

(1971). — Cenomanian ammonites from southern England. Spec. Pap. Palaeontol., n. 8, Palaentol. Assoc., 133 pp., 64 pls., 5 tabs.

KENNEDY W. J. AND JUIGNET P., (1973). — Obsservations on the lithostratigraphy and ammonite succession across the Cenomanian-Turonian boundary in the environs of Le Mans (Sarthe, N.W. France). Newsl. Stratigr., v. 2, n. 4, p. 189-202, 2 text-figs., 2 tabs.

MAURY CARLOTTA, (1936). — O Cretaceo de Sergipe. Brazil Servico Geol. e Mineral., mon 11, p. 1-25.

NAGAO T. AND MATSUMOTO T., (1939, 1940). — A monograph of the Cretaceous *Inoceramus* of Japan ; Pts. 1, 2. Jour. Fac. Sci., Hokkaido Imp. Univ., ser. 4, v. 4, n. 3-4, p. 241-299, pl. 23(2)-34(12) ; v. 6, n. 1, p. 1-64, pls. 1-23.

SCHLAGINTWEIT OTTO, (1911). — Die fauna des Vracon und Cenoman in Peru. *In* Steinman, G., Beitrage zur Geologie und Paläontologie von Südamerika : XVII. Neues Jahrb. Min., Geol., Paläontol., bd. 33, p. 43-135, pls. 5-7, 4 text-figs.

SEITZ OTTO, (1934). — Die Variabilität des *Inoceramus labiatus* v. Schloth. Pal. Zentralbl., v. 4, n. 229, p. 429-474, pls. 36-40, 9 text-figs., 9 tabs.

SOWERBY J., (1814). — The mineral conchology of Great Britain. p. 1-689, pls. 1-395.

STEPHENSON L. W., (1955). — Basal Eagle Ford fauna (Cenomanian) in Johnson and Tarrant Counties, Texas. U. S. Geol. Surv., Prof. Pap. 274-C, p. 53-67, pls. 4-7.

STOKES R. B., (1975). — Royauines et Provinces Fauniques du Crétacé établis sur la base d'une étude systématique du genre *Micraster*. Mém. Mus. Hist. Nat. Paris, n. ser., ser. C. tome 31, 'ê p., 12 pls.

TRÖGER K.-A., (1967). — Zur Paläontologie, Biostratigraphie und faziellen Ausbildung der unteren Oberkreide (Cenoman bis Turon). Teil 1. Paläontologie und biostratigraphie der Inoceramen des Cenomans bis Turon Mitteleuropas. Abh. Staatl. Mus. Mineral. geol., Bd. 12, p. 13-207, pls. 1-14, 43 text-figs.

WHITE C. A., (1888). — Contributions to the paleontology of Brazil ; comprising descriptions of Cretaceous invertebrate fossils, mainly from the Provinces of Sergipe, Pernembuco, Para, and Baha. Archiv. Mus. Nac. Rio de Janeiro, v. 7, p. 1-273, 28 pls.

WOODS HENRY, (1911). — A monograph of the Cretaceous Lamellibranchia of England. vol. 2, pt. 7. *Inoceramus.* Mon. Palaeontograph. Soc., 1910, London, p. 261-284, pls. 4à-50.

(1912a). — A monograph of the Cretaceous Lamellibranchia of England. vol. 2, pt. 8. *Inoceramus* (continued). Mon. Palaeontograph. Soc., 1911, London, p. 285-340, pls. 51-54.

(1912b). — The evolution of *Inoceramus* in the Cretaceous Period. Quart. Jour. Geol. Soc., v. 68, p. 1-19, text-figs. 1-94.

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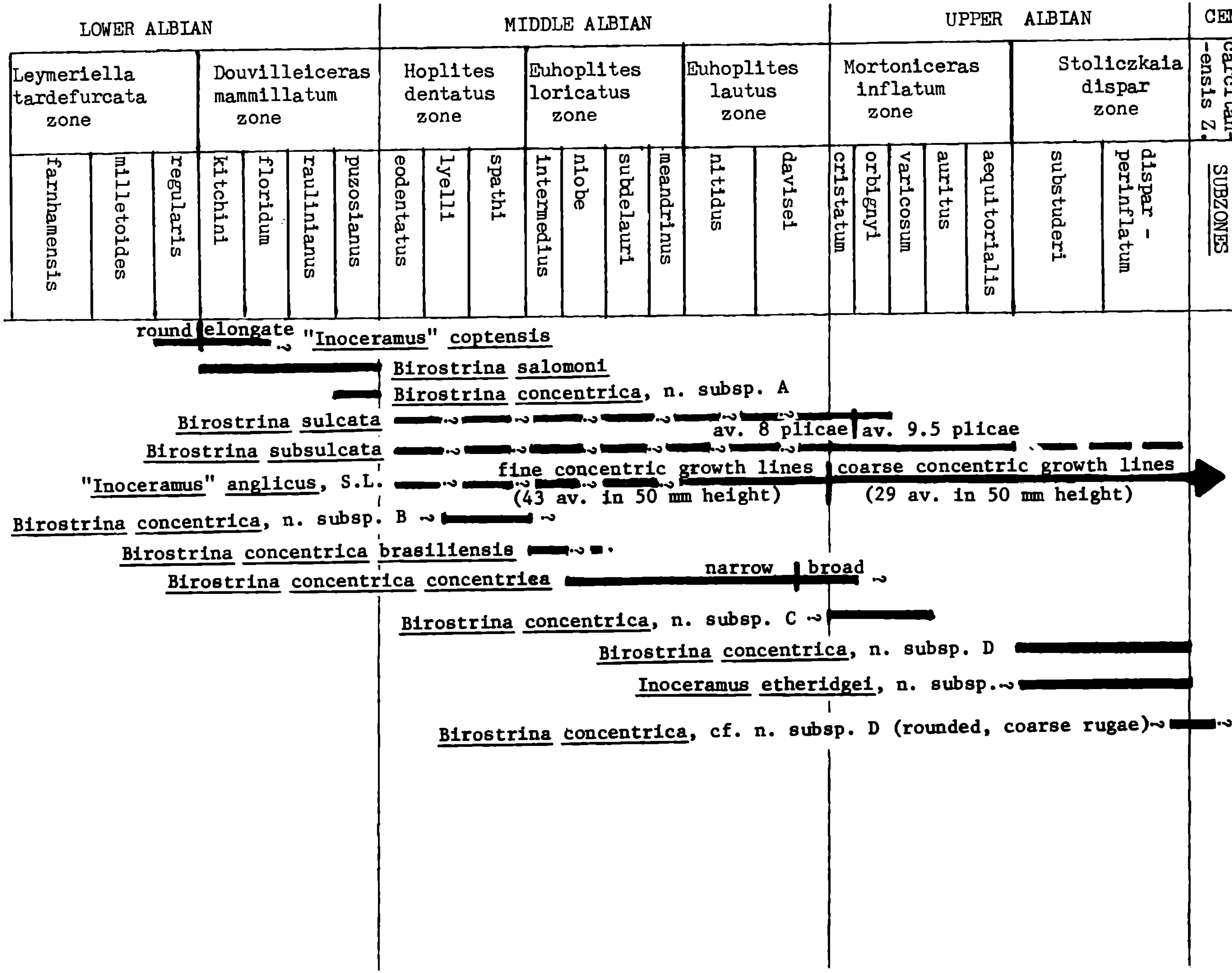


FIGURE I: ALBIAN INOCERAMID BIOSTRATIGRAPHY

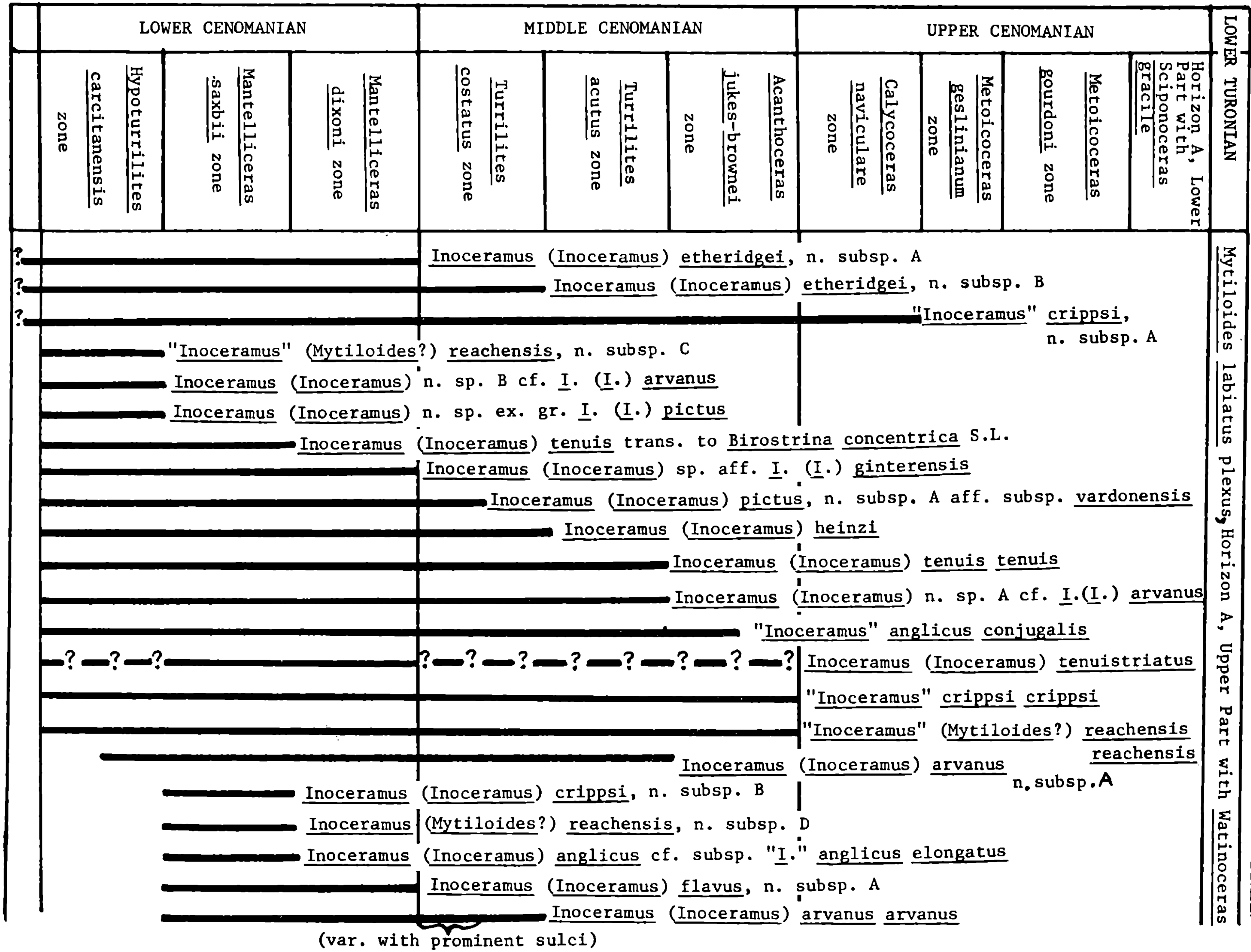
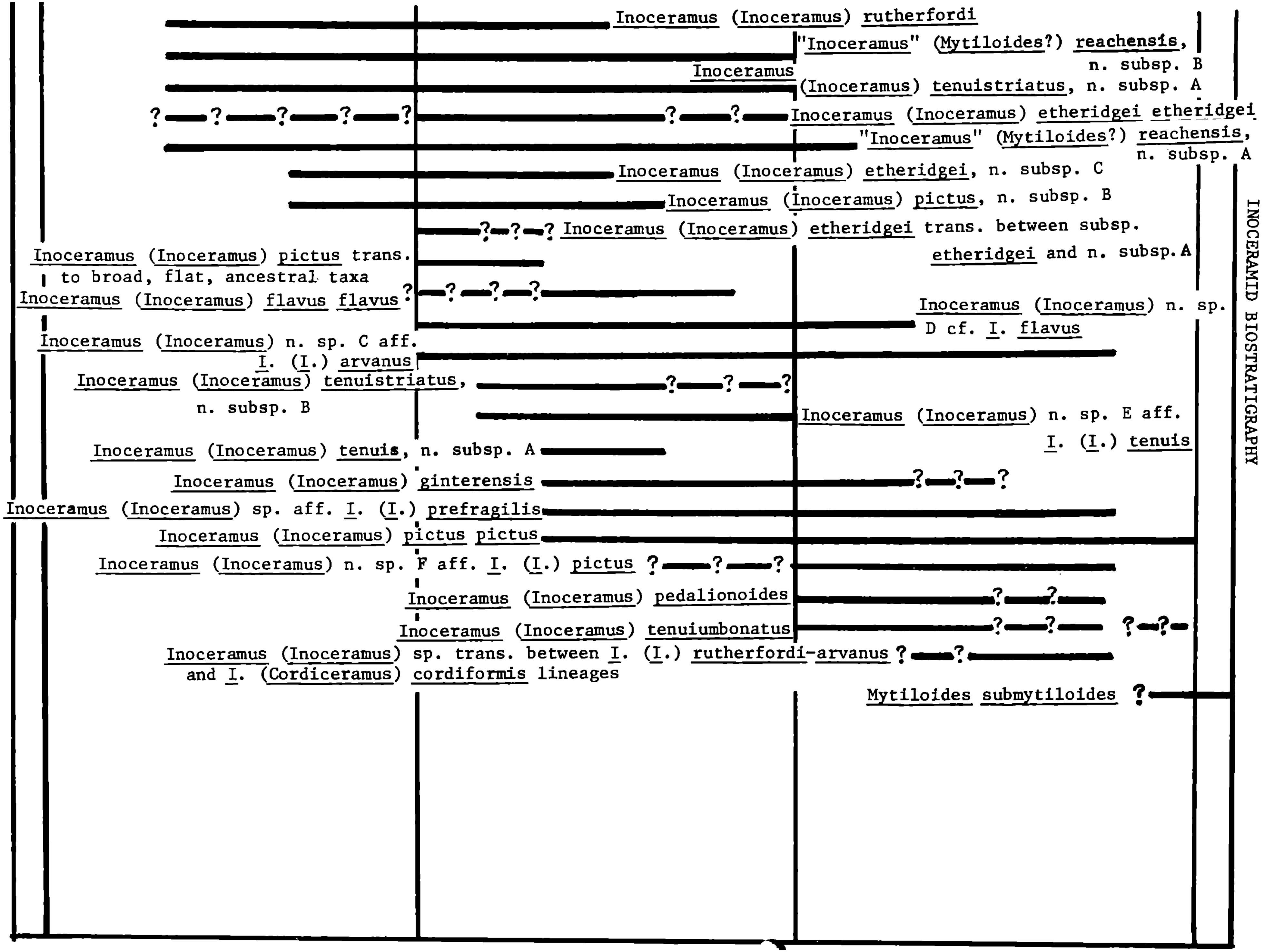


FIGURE 2: BRITISH CENOMANIAN



INOCERAMID BIOSTRATIGRAPHY

«ANNALES DU MUSÉUM D'HISTOIRE NATURELLE DE NICE - TOME IV - 1976»

AN OUTLINE OF MIDDLE CRETACEOUS MARINE HISTORY AND INOCERAMID BIOSTRATIGRAPHY IN THE BOHEMIAN BASIN, CZECHOSLOVAKIA

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Klein and Soukup (1966, p. 489-504) and Müller (1974) have outlined the Middle Cretaceous and Coniacian sedimentation, stratigraphy, and paleoenvironments, and have listed the principal marine fossils of the Cretaceous Bohemian Basin. Whereas the sedimentary history of the Bohemian Basin near its center is complex, and reflects shallowing and deepening trends that are strongly influenced by basinal tectonics, the more marginal Middle Cretaceous facies clearly depict a series of transgressive and regressive pulses which can be precisely correlated, biostratigraphically, with epicontinental cyclothems all over the world. It is assumed from this that the cyclothems preserved in marginal facies of the Bohemian Basin reflect major eustatic changes of sea level. These were probably generated by plate tectonics and the alternating construction of oceanic ridges or broad uplifts during active plate movement (inducing eustatic rise and epicontinental transgression), and their subsequent collapse during tectonically "quiet" periods (inducing eustatic fall, and regression). Transgressive-regressive peaks of these global cyclothems and eustatic fluctuations are outlined by Kauffman (1973a, figs. 6-10). The Bohemian pattern of cyclothems is characteristic of stable cratonic areas during the Cretaceous (Kauffman, 1973b, p. 687).

The initial Cretaceous marine flooding in Bohemia resulted from the great Cenomanian transgression (T6 of Kauffman, 1973a, figs. 6-10), which began in latest Albian time near cratonic margins, reaching central cratonic areas by Cenomanian time and peaking in the Early Turonian. In Bohemia, the earliest marine rocks are of late Middle and Late Cenomanian age and depict the time at which this transgression reached the Central European craton. Müller (1974) presents a detailed history of Middle Cretaceous marine facies fluctuations near the margin of the Bohemian Basin. He documents late Middle to Late Cenomanian strand margins being transgressed in Late Cenomanian and Early to early Middle Turonian time successively by marine sandstones, silty shales, clay shales and calcareous shales (onshore to offshore; Early Turonian) grading upward and seaward into maximum transgressive calcareous shales and local limestones (zones of *Mytiloides mytiloides and M. labiatus,* Middle to latest Early Turonian; ?earliest Middle Turonian). Regression follows, peaking in the late Middle and possibly early Upper Turonian in deposition of the nearshore Quader Sandstone and its lateral tongues, and more offshore silty shale : zones of *Inoceramus (I.) costellatus* and *I. (I) lamarcki,* s.l. Renewed Late Turonian transgression involving nearshore sandstones and silty shales, peaked in deposition of a series of deeper water clay and carbonate shales and localised pelagic limestones of latest Turonian and Coniacian age, zones of *M. lusatiae* through *I. (M.) subquadratus.* The final marine regression began in the Late Cenomanian and apparently terminated in Bohemia in the Santonian. Only Lower to possibly early Middle Santonian marine fossils are as yet known. The peaks of Cenomanian transgression and Turonian regression are precisely correlative and/or only one faunal zone younger than similar peaks in North America and Western Europe, strongly suggesting that they correlate with global eustatic fluctuations.

Albian through Middle Cenomanian deposits, dominantly or exclusively of fresh water origin, have not yielded marine Mollusca. The marine late Middle Cenomanian through Coniacian sequence of shallow water sandstones, and offshore shales and argillaceous limestones, is moderately to richly fossiliferous and contains abundant and diverse Inoceramidae except in certain parts of the regressive Quader Sandstone facies. Ammonites are relatively rare so that the macrofaunal zonation has been largely based on inoceramids historically, and these still provide the best basis for refined zonation and regional correlation of the Bohemian Cretaceous inasmuch as all of the known taxa are of Euramerican or cosmopolitan distribution, and they represent very rapidly evolving stocks.

Considering this, the status of Bohemian Cretaceous biostratigraphy utilizing Inoceramidae and other fossils is still relatively crude in comparison to that developed in Germany, France, Russia, Japan and North America. For example, Klein and Soukup (1966, tab. 20) divide the marine Middle Cretaceous and Coniacian sequence into eight zones, in descending order :

Coniacian
    Inoceramus subquadratus Zone
    Inoceramus involutus Zone
    Inoceramus koeneni Zone
    unzoned interval with Inoceramidae
Upper Turonian (most of which is equivalent to the Lower Coniacian of the North American and Western European, but not North German, usage)
    Inoceramus schloenbachi - I. inconstans Zone
Middle and early Upper Turonian
    unzoned glauconite-phosphorite interval
Middle Turonian
    Inoceramus lamarcki - I. costellatus Zone
Lower Turonian
    Inoceramus labiatus Zone
Cenomanian-Turonian transition sequence
    Actinocamax plenus Zone
Upper Cenomanian-brackish and marine interval
    Inoceramus pictus -Neithea aequicostata Zone

Lower and Middle Cenomanian non-marine interval, unzoned

Soukup (1968) has slightly increased the list of taxa that characterize each zone.

In this same interval, 28 biostratigraphic zones based on Inoceramidae associated with ammonites have been recognized in North America and many parts of Western Europe. This strongly suggests that the Czechoslovakian Middle Cretaceous succession is deserving of very careful collecting, at closely spaced stratigraphic intervals, for the purpose of obtaining precisely located collections of Inoceramidae. From these, a refined regional zonation with high correlation potential should result.

Such a project is currently under way in cooperation with Drs. Jiří Kříž, and Vlastimil Müller of the Geological Survey of Czechoslovakia. In 1971, the author was able to study in detail the Inoceramidae collections of the Geological Survey and the National Museum in Prague, and to visit and collect briefly from selected Middle Cretaceous sections in the Bohemian Basin area with Dr. Kříž. This preliminary work provided a basic knowledge of the inoceramid taxa present in the Bohemian Cretaceous, and to a limited extent, their biostratigraphic relationships. But stratigraphic data for most of the collections examined, many made years before, are generalized and the precise biostratigraphic relationships of most Czechoslovakian Inoceramidae still needs to be worked out through intensive field work and studies in Cretaceous well cores. The author has begun such a study in association with Dr. Kříž. In the meantime, a preliminary inoceramid zonation for the Bohemian Basin Middle Cretaceous can be constructed from available data collected by the author and from past literature, with the stratigraphic relationships of these taxa inferred partially from their occurrence elsewhere in the world, and partially from actual field observations and collection data.

Change in the position of the Turonian-Coniacian boundary over that applied by Klein and Soukup (1966) and used widely in North Germany (e.g. Tröger, 1967), is made by utilizing the concept that this stage boundary should be placed at the point of greatest evolutionary discordance between typical Turonian and Coniacian biotas (d'Orbigny's original intent). This point lies, in Czechoslovakia, at or somewhat below the base of the Klein and Soukup (1966) *Inoceramus schloenbachi -I. inconstans* Zone. In North America and much of Western Europe this is considered as the boundary and coincides with the first appearence of the *I. rotundatus-erectus-deformis-schloenbachi* lineage (base of *I. rotundatus* and *I. ernsti* in the Western Interior United States and North Germany ; see Tröger,, 1967, fig. 43, who nevertheless puts these taxa in the Upper Turonian).

The following zonation and stage boundaries are tentatively proposed for this area.

Upper Coniacian

- Zone of *Inoceramus (Magadiceramus) subquadratus, I. (M.) subquadratus crenistriatus, Platyceramus cycloides cycloides, P. cycloides ahsensis*
- Zone of *Volviceramus involutus (*late evolutionary forms), *Platyceramus mantelli*

Middle Coniacian

- Zone of *Cremnoceramus inconstans woodsi* with late evolutionary variants of *C. inconstans* s.s. and *Inoceramus frechi*
- Zone of *Volviceramus koeneni*, with *Mytiloides mytilopsis, Cremnoceramus ? wandereri, C. inconstans,* and *"Inoceramus" (Mytiloides ?) kleini ?*
- Zone of *Inoceramus schloenbachi, "Inoceramus" gibbosus, Cremnoceramus inconstans* s.l.

Lower Coniacian (mostly "Upper Turonian" of Soukup, 1966, Klein and Soukup, 1966, and Tröger, 1967)

- Zone of *Inoceramus ? deformis* and *Inoceramus waltersdorfensis waltersdorfensis*
- Zone of *Mytiloides ? lusatiae, M. striatoconcentricus striatoconcentricus* and subsp. *carpathicus, "Inoceramus*; *vancouverensis vancouverensis"* (of Tröger, 1967), *I. waltersdorfensis* ss., subsp. *hannovrensis*, and n. subsp. (coarse rugae) ; possibly *I. rotundatus*

Upper Turonian

- Zone of *Inoceramus (Inoceramus) apicalis* s.s. and subsp. trans. to *I. (I.) lamarcki ; "I. vancouverensis"*, and subsp. *parvus* (of Tröger, 1967), *I. protractus* transitional to *I. winkholdioides, Mytiloides mytilopsis, M. fiegei ?, I.* aff. *I. glatziae*
- Zone of *Mytiloides striatoconcentricus, "I. vancouverensis"* (of Tröger, 1967)
- Zone of *Inoceramus (Inoceramus) lamarcki*, s.s. and subsp. trans. to *I. frechi, I. (I.) apicalis, I. (I.) brongniarti, I. inaequivalvis,* and *I. (I.) costellatus* (late form), *I. (I.) cuvieri*, rugate n. subsp. trans. to *I. (I.) lamarcki, I. undulatus* trans. to *I. (I.) lamarcki.*

Middle Turonian

- Zone of *Inoceramus (Inoceramus) costellatus costellatus ; I. (I.) cuvieri* s.s. and subsp.
- Zone of *Mytiloides ? hercynicus*
- Zone of *Mytiloides subhercynicus* and subsp. *transiens* with *M? hercynicus* s.s.

Lower Turonian

- Zone of *Mytiloides labiatus*, s.s. and new subsp. (Finely ribbed), *M. subhercynicus*, and *Inoceramus saxonicus*
- Zone of *Mytiloides mytiloides* s.s., and n. subsp. (elongate)
- Zone of *Mytiloides opalensis* s.s., and subsp. *elongata*

Upper Cenomanian (?) - Lower Turonian transition

- Zone of *Mytiloides submytiloides*, ?with *Actinocamax plenus*

Upper Cenomanian

- Zone of *Inoceramus (Inoceramus) pictus, Inoceramus (Inoceramus) pictus bohemicus, I. (I.) pictus concentricoundulatus*

Middle Cenomanian

- Zone of *"Inoceramus" crippsi* s.s. and subsp. trans. to *Mytiloides opalensis*

REFERENCES CITED

KAUFFMAN E.G., (1973a) — Cretaceous Bivalvia. In Hallam, A. (Ed.), Atlas of Palaeobiogeography. Elsevier Sci. Pub. Co., Amsterdam, p. 351-383, 10 text-figs.

(1973b) — Stratigraphic evidence for Cretaceous eustatic changes. Abstr., 1973 Ann. Mtng. Geol. Soc. Amer.,Dallas, Tex., p. 687.

KLEIN V. and SOUKUP J, (1966) — The Bohemian Cretaceous Basin. In Svoboda, J., et al. Regional Geology of Czechoslovakia, p. 1-667, 100 pls., 120 text-figs.

MÜLLER V., (1974) — Stratigrafie a faciálni vývoj ceské křídove pánve. In Malkovský, M., editor, et al., Geologie české křídové pánve a jejiho poudlozi. Oblastní Reg. Geol. CSSR, Vydal Ústřed. geol., v Acad., naklad. Česko Akad. věd, Praha, p. 101-115, maps 7-9.

SEITZ Otto, (1934) — Die variabilitat des *Inoceramus labiatus* v. Schloth. Pal. Zentralbl., v. 4, n. 229, p. 430-474, pl. 36-40.

SOUKUP J., (1968) — Bohemian Massif. In Lexigue Stratigraphique International, Vol. 1, Europe, pt. 6bl, Tab. 1 Paris.

TRÖGER K.-A., (1967) — Zur Palaontologie, biostratigraphie und faziellen Ausbildung der Unteren Oberkreide (Cenoman bis Turon). Teil 1. Palaontologie und biostratigraphie der Inoceramen des Cenomans bis Turons Mitteleuropas. Abh. Staatl. Mus. Mineral. Geol., bd. 12, p. 13-207, 14 pls., 43 text-figs.

WOODS H., (1911) — A monograph of the Cretaceous Lamellibranchia of England. Palaeontgr. Soc. Mon., v. 2, pt. 7, *Inoceramus*, p. 261-284, pl. 45-50.

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PLATE 1

BOHEMIAN MIDDLE CRETACEOUS INOCERAMIDAE

FIG. 1. — *Inoceramus (Inoceramus) pictus concentricoundulatus* Tröger

Hypotype, composite mold of left valve (xl), CSSR National Museum, Prague, Akc.
Kat. 36675, Late Cenomanian, zone of *I. (I.) pictus*, lower Quader Sandstone, from Broumov Pickensteigs, Bohemia, CSSR.

FIG. 2, 7, 8. — *Mytiloides submytiloides* (Seitz)

Hypotypes, internal molds
Latest Cenomanian (?), earliest Turonian, zone of *M. submytiloides.*
2. left valve (xl), CSSR National Museum, Akc. Kat. 36675, earliest Turonian, Quader Sandstone (?), locality unknown ;
7. typical right valve of a co-attached pair (xl) ; note shallow sulci ; CSSR National Museum, Prague, Akc. Kat. 25196, Inv. No. 1167,
Earliest Turonian, lower Quader Sandstone, at Martineves, near Jilore, Bohemia ;
8. right valve (xl) transitional to *M. mytiloides* (Mantell), CSSR National Museum, Prague, Akc. Kat. 30207, Inv. No. 0 1118,
lower Quader Sandstone, at Děčín, Kvádrová hora, Bohemia, CSSR.

FIG. 3.— *Inoceramus (Inoceramus) lamarcki* Seitz s.l. (juvenile)

Composite internal mold of left valve (× 1), CSSR National Museum, Prague, Akc. Kat. 36675,
early Late Turonian ("Middle Turonian IXa"), zone of *I. (I.) lamarcki*, from Hodkovice nad Mohelkou, Bohemia, CSSR.

FIG. 4, 12.— *Mytiloides mytiloides mytiloides* (Mantell) sensu Seitz, 1934

Hypotypes (× 1), internal molds of right valves, zone of *M. mytiloides*,
middle Early Turonian.
4. CSSR National Museum, Prague, Akc. Kat. 36675, with exceptionally truncated anterior, showing features transitional to *M. submytiloides* (Seitz),
locality unknown, probably Quader Sandstone, Bohemia, CSSR ;
12. typical form, CSSR National Museum, Akc. Kat. 36675, from Quader Sandstone (?), locality unknown, Bohemia.

FIG. 5. — *Mytiloides subhercynicus subhercynicus* (Seitz)

Hypotype (xl), composite mold, right valve, latest Early to early Middle Turonian, *M. subhercynicus* zone, from Rychnov and Kněžnou, Bohemia, CSSR
National Museum, Prague, Akc. Kat. Inv. No. 01080.

FIG. 6. — *Mytiloides subhercynicus transiens* (Seitz)

Hypotype (xl), composite mold, right valve,
early Middle Turonian, zone of *M. subhercynicus*, from Bíla hora, Bohemia, CSSR National Museum, Prague, Akc. Kat. 36675, inv. No. 0 1186.

FIG. 9. — *Inoceramus waltersdorfensis hannovrensis* Heinz

variant with ornament transitional to *I. kleini* Müller (part), hypotype (xl), CSSR National Museum, Prague, Akc. Kat. 659/62, Inv. No. 0 1358,
composite internal mold, left valve, Early Coniacian, probably zone of *Mytiloides lusatiae* and above, from Okřešice V-615, Bohemia, CSSR.

FIG. 10 — *Mytiloides ? hercynicus* (Petrascheck)

Hypotype (xl), internal mold of right valve, CSSR National Museum, Prague, Inv. No. 0 1101, B236,
middle Middle Turonian, *M. ? hercynicus* zone, from Bíla hora, Bohemia, CSSR.

FIG. 11.— *Mytiloides mytiloides* (Mantell) n. subsp., late elongate form

Hypotype (× 1/2), internal mold of right valve, CSSR National Museum, Prague, Akc. Kat. 36675,
middle Early Turonian, *M. mytiloides* zone, locality unknown, probably lower Quader Sandstone, Bohemia, CSSR.

FIG. 13.— *Inoceramus (Inoceramus) apicalis* Woods n. subsp. with equal rugae

Hypotype (× 1), composite internal mold of right valve,
Late Turonian IXa, *I. (I.) apicalis* zone, from Hodkovice nad Mohelkou, Bohemia, CSSR National Museum, Prague, Akc. Kat. 36675.

PLATE 2

BOHEMIAN MIDDLE CRETACEOUS INOCERAMIDAE

FIG. 1. —*Mytiloides (?) crippsi* (Mantell)

Late form transitional to *M. opalensis* (Böse), hypotype (xl), internal mold of left valve, CSSR National Museum, Prague, Akc. Kat. 22937/2, Inv. No. 0 1169, from Slavetín nad Ohří, zone of "*Inoceramus" crippsi*, Late Cenomanian (*M. opalensis* is Early Turonian and this transitional form may occur near or at stage boundary), Bohemia, CSSR.

FIG. 2, 7. —*Mytiloides subhercynicus transiens* (Seitz)

Hypotypes, composite internal molds of right valves (xl),
early Middle Turonian, *M. subhercynicus* zone.
2. CSSR National Museum, Prague, Akc. Kat. 36675, Inv. No. 0 1176, B223 (fig. 2), from Bílá hora.
7. Akc. Kat. 36675, Inv. No. 0 1175, B226, Bíla hora, Bohemia, CSSR.

FIG. 3.— *Inoceramus (Inoceramus) apicalis* Woods n. subsp. (rugate transitional to *I. lamarcki*

Hypotype (X 1), internal mold of left valve, CSSR National Musuem, Prague, Akc. Kat. 36675. Late Turonian, *I. (I.) lamarcki-I. (I.) apicalis* zones, from Hodkovice nad Mohelkou ("Middle Turonian IXa"), Bohemia, CSSR.

FIG. 4. — *Inoceramus frechi* Flegel

Hypotype (xl), internal mold, left valve, Early (elsewhere) to Middle Coniacian, CSSR National Musuem Prague, Akc. Kat. 2894, Inv. No. 0 1196, from Miskovice, near Kutná Hora, Bohemia, CSSR.

FIG. 5. —*Mytiloides (?) lusatiae* (Andert)

Hypotype, (xl), internal mold, right valve, erect variety, *M. lusatiae* zone, earliest Coniacian, CSSR National Museum, Prague, Akc. Kat. 63/68, from Krompach, near Horni Sveltá, Luz Hill, Bohemia, CSSR.

FIG. 6.— *Mytiloides labiatus* (Schlotheim) n. subsp. (late, elongate, finely ribbed form)

Hypotype (X 1), CSSR National Museum, Prague, Akc. Kat. 36675. late Early Turonian, *M. labiatus* zone, locality unknown, Bohemia, CSSR.

PLATE 3

BOHEMIAN MIDDLE CRETACEOUS INOCERAMIDAE

FIG. 1, 6. —*Mytiloides labiatus labiatus* (Schlotheim)

Hypotypes (xl), composite internal molds of left valves, zone of *M. labiatus*,
late Early Turonian, both from the upper spongilitic and sandy marlstones in quarries in the Kunstat and Velim areas, Bohemia, CSSR.
1. paired, gaping valves, USNM 240357 ;
6. typical left valve, USNM 240358.

FIG. 2.— *Mytiloides mytiloides* (Mantell) n. subsp. (late form, elongate shell)

Hypotype (X 1), CSSR National Museum, Prague, Akc. Kat. 25263, Inv. No. 01166, middle Early Turonian, zone of *M. mytiloides*, from Růžový hřeben u Děčína, Bohemia, CSSR.

FIG. 3. —*Mytiloides subhercynicus subhercynicus* (Seitz)

Hypotype(xl), internal mold of right valve, latest Early to Middle Turonian, zone of *M. subhercynicus*, from Bíla hora, Bohemia. CSSR National Museum, Prague, Akc. Kat. 36675, Inv. No. 1181.

FIG. 4, 5.— *Mytiloides labiatus* (Schlotheim) n. subsp. (elongated, finely ribbed, late form)

Hypotype (X 1), internal composite mold of right valves,
late Early Turonian, *M. labiatus* zone.
4. form transitional to subsp. *labiatus* (Schlotheim) in shape, USNM 240359 ;
5. typical specimen, USNM 240360. Both specimens from the upper spongilitic and sandy marlstone units in limestone quarries of the Kunstat and Velim areas, Bohemia, CSSR.

FIG. 7. —*Mytiloides hercynicus* (Petrascheck)

Hypotype (xl), CSSR National Museum, Prague, Akc. Kat. 36675, Inv. No. 0 1180, composite internal mold of right valve, early to middle Middle Turonian, zone of *M. hercynicus*, from Bíla hora, Bohemia, CSSR.

PLATE 4

BOHEMIAN MIDDLE CRETACEOUS INOCERAMIDAE

FIG. 1, 8, 10.— *Inoceramus (Inoceramus) cuvieri* Sowerby (Sensu Woods, 1911, fig. 78), n. subsp. (late rugate form)

Transitional to *I. (I.) lamarcki* Parkinson; hypotypes (× 1), internal molds.
late Middle to (?) early Late Turonian, upper Quadar Sandstone at Chutnovka, Bohemia, zones of *I. (I.) lamarcki* and/or *I. costellatus*.
1. antérior view, left valve, USNM 240346 ;
8. lateral view, right valve, typical form, USNM 240347 ;
10. lateral view, moderately large right valve lacking umbo, auricle, USNM 240348.

FIG. 2, 11.— *Inoceramus (Inoceramus) pictus pictus* Sowerby Sensu Tröger, 1967

Hypotype (× 1), somewhat deformed composite internal molds, left and right valves, respectively, of co-attached pair, latex cast (USNM 240350) of unnumbered specimen, Macák collection, Geological Survey of Czechoslovakia, latest Cenomanian, *I. (I.) pictus* zone, locality unknown, Bohemia.

FIG. 3.— *Inoceramus undulatus* Mantell n. subsp. transitional to *I. lamarcki* Parkinson

Hypotype (× 1), internal mold of left valve, Geological Survey of Czechoslovakia, Macák collection, latex cast (USNM 240351), zone of *I. lamarcki* Parkinson, Late Turonian, from a fracture in the "Stena Wall" at Telnice, Bohemia.

FIG. 4.— *Inoceramus (Inoceramus) lamarcki* Parkinson n. subsp. trans. to *I. frechi* Flegel

Lateral view, right valve, USNM 240349, from the upper Quadar Sandstone at Chutnovka, Bohemia, *I. (I.) lamarcki* zone, early Upper Turonian.

FIG. 5. —*Mytiloides (?) lusatiae* (Andert)

Hypotype (xl), left valve of co-attached pair, Geological Survey of Czechoslovakia, Macák collection, latex cast (USNM 240352), Early Coniacian, possibly ranging into the latest Turonian as it does elsewhere, zone of *M. (?) lusatiae*, from Jitrava, Bohemia.

FIG. 6.— *Inoceramus cuvieri* Sowerby (weakly rugate variety)

Hypotype (× 1/2), internal mold, right valve, Middle Turonian, zones of *I. costellatus* and *I. lamarcki*, from "Callianassa Sandstone" at Litomysl, Bohemia, USNM 240356.

FIG. 7. —*Inoceramus (Inoceramus) pictus bohemicus* Leonhard

Hypotype (xl), Macák collection, Geological Survey of Czechoslovakia, latex cast (USNM 340353), internal mold, right valve, zone of *I. (I.) pictus*, latest Cenomanian, possibly ranging to Early Turonian, from Telnice, Bohemia.

FIG. 9. —*Mytiloides labiatus labiatus* (Schlotheim)

Hypotype (xl), left valve, composite internal mold of co-attached pair, USNM 240354, *M. labiatus* zone, late Early Turonian, from calcareous sandstones, sandy marlstone, Velim, Bohemia.

FIG. 12. —*Mytiloides opalensis elongata* (Seitz)

Hypotype (xl), internal mold of right valve, Dvorák collection, Geological Survey of Czechoslovakia, latex cast, USNM 240355, zone of *M. opalensis*, middle Early Turonian, from Cervená Voda, Bohemia.

PLATE 5

BOHEMIAN MIDDLE CRETACEOUS-CONIACIAN INOCERAMIDAE

FIG. 1, 2.— *Inoceramus walterdorfensis* Andert n. subsp. with coarse regular rugae

Transitional to *I. apicalis* Woods; hypotypes (× 1), latex casts of composite internal molds of left valves, probably zone of *Mytiloides lusatiae*, earliest Coniacian.
1. Geological Survey of Czechoslovakia, Macák collection from Bykev, Bohemia ; latex cast, USNM 240377 ;
2. Specimen with exceptionally coarse rugae, mold and latex cast, USNM 240378, upper mudstones and shales in bluffs on the River Ohře at Brezno, CSSR.

FIG. 3, 15.—*Inoceramus waltersdorfensis hannovrensis* Heinz

Hypotypes, Geological Survey of Czechoslovakia, Macák collection, left valves (latex casts), earliest Coniacian, probably zone of *Mytiloides lusatiae.*
3. USNM 240361 (xl), from Lenesice ;
15. USNM 240362 (x2), from Lenesice, Bohemia.

FIG. 4. —*Mytiloides opalensis elongata* (Seitz)

Hypotype (xl), latex cast (USNM 240364) of specimen from Macák collection, Geological Survey of Czechoslovakia, small left valve,
middle Early Turonian, *M. opalensis* zone, Kutna Hora, Bohemia, CSSR.

FIG; FIG. 5. —*Mytiloides (?) kleini* (Müller)

Hypotype (xl), mold and external latex cast (USNM 240365), partial left valve,
Middle Coniacian, probable zone of *Volviceramus koeneni*, near top of river bluff section along River Ohre at Brezno, Bohemia, CSSR.

FIG. 6, 7. —*Inoceramus waltersdorfensis waltersdorfensis* Andert

Hypotypes (xl), external molds of left valves, latex casts, USNM 240365 and USNM 240366, respectively
Early Coniacian, probably zone of *Mytiloides lusatiae* (Andert).
6. from middle of limestone section in cement quarry at Cizkovice ;
7. Ohre River bluffs, lower part, at Brezno, CSSR.

FIG. 8. —*Mytiloides labiatus labiatus* (Schlotheim) ?

Deformed hypotype (xl), USNM 240367, composite internal mold of right valve,
from latest Early Turonian, *M. labiatus* zone, sandy marlstone at top of quarry at Orlicko-Ždárský development, Bohemia, CSSR.

FIG. 9. —*Inoceramus* sp. aff. *I. weisi* Andert

Hypotype (xl), USNM 240368, internal mold of right valve, possible zone of *Mytiloides hercynicus* or above,
Middle to (elsewhere) latest Turonian, from upper spongilitic and sandy marlstone units in quarries of the Kunstat and Velim areas, Bohemia, CSSR.

FIG. 10.— *Inoceramus protractus* Scupin n. subsp. transitional to *I. winkholdioides* Andert

Hypotype (× 1), latex cast (USNM 240369) of internal mold of right valve
probably latest Turonian, ranging to earliest Coniacian (most likely) ; zone of *I. (I.) apicalis*, Macák collection,
Geological Survey of Czechoslovakia, from Rýdeč borehole UB-7 at depth of 78.4 m, CSSR.

FIG. 11. —*Inoceramus* sp. aff. *I. glatziae* Flegel

Hypotype (xl), Müller collection, Geological Survey of Czechoslovakia, latex cast (USNM 240370) of internal mold of left valve,
latest Turonian or earliest Coniacian (?), possibly zone of *I. (I.) apicalis*, from Krásné Pole, in borehole Lo-Jc-5 at depth of 23.0-24.0 m, Bohemia, CSSR.

FIG. 12.— *Mytiloides opalensis opalensis* (Böse); sensu Seitz, 1934

Hypotype (× 1), silicone latex cast (USNM 240371) of left valve, Macák collection, Geological Survey of Czechoslovakia,
middle Early Turonian, zone of *M. opalensis*, from Decin/Podmokly, Bohemia, CSSR.

FIG. 13, 21.— *Cremnoceramus inconstans* (Woods) and subspp.

Hypotypes (× 1), shell exterior (Fig. 13) and composite internal mold,
late Early Turonian (elsewhere) to mainly Middle Coniacian, zone of *"I." schloenbachi*, *Volviceramus koeneni*, and *C. inconstans.*
13. subsp. *inconstans*, typical left valve, early growth stage and first slope break, USNM 240372, from Ohře River bluffs at Brezno, unit 6 clays at top of bluff :
21. (?) subsp *woodsi* Fiege, anterior view of compressed right valve showing juvenile and adult ornament on either side of characteristic slope break,
USNM 240373, from middle glauconitic shales, unit 4, Ohře River bluffs at Brezno, CSSR.

FIG. 14. —*Mytiloides labiatus labiatus* (Schlotheim)

Hypotype (xl), USNM 240375, dorso-ventrally compressed internal mold of left valve with typical ornament, latest Early Turonian,
zone of *M. labiatus*, from upper spongilitic and sandy marlstone units in quarries in the Kunstat and Velim areas, Bohemia, CSSR.

FIG. 16.— *Inoceramus walterdorfensis* Andert n. subsp. transitional to *I. rotundatus* Fiege

Hypotype (× 1). USNM 240363, left valve, internal mold, earliest Coniacian, probably zone of *Mytiloides lusatiae*,
middle of river sections at Brezno, Bohemia, CSSR.

FIG. 17, 18.— *Mytiloides labiatus* (Schlotheim) n. subsp.

Late elongate form with fine, close-spaced concentric ornament, hypotypes (× 2, × 1, respectively), composite internal molds of left valves,
latest Turonian, zone of *M. labiatus*, from upper spongilitic sandy marlstone in the stone quarries of the Kunstat and Velim area, Bohemia, CSSR.
17. USNM 240379 ;
18. USNM 240380.

FIG. 19. —*Inoceramus* sp. aff. *I. rotundatus* Fiege

Figured specimen (x2), USNM 240376, anteriorly compressed right vlave, lateral view,
Early Coniacian, zone of *Mytiloides lusatiae*, river bluffs at Brezno, silty shales (unit 3) in lower middle part of bluff, CSSR.

FIG. 20. —*Inoceramus rotundatus* Fiege

USNM 240381, hypotype (xl), composite internal mold of right valve,
earliest Coniacian, zone of *Mytiloides lusatiae* (Andert), guidebook locality 8, Trupelník Hill, just above Kuříň Village,
Bohemia, in limestones and marls crossing Turonian-Coniacian boundary.

FIG. 22. —*Mytiloides mytilopsis* (Conrad)

Hypotype (x1), Müller collection, Geological Survey of Czechoslovakia, latex cast (USNM 240374) of composite internal mold, right valve,
Latest Turonian to Middle Coniacian in various parts of the world : known only from Mid-Coniacian in Czechoslovakia,
zone of *Volviceramus koeneni*, from Krásné Pole, borehole Lo-Jc-5, at depth of 22.0-23.0 m. Bohemia, CSSR.

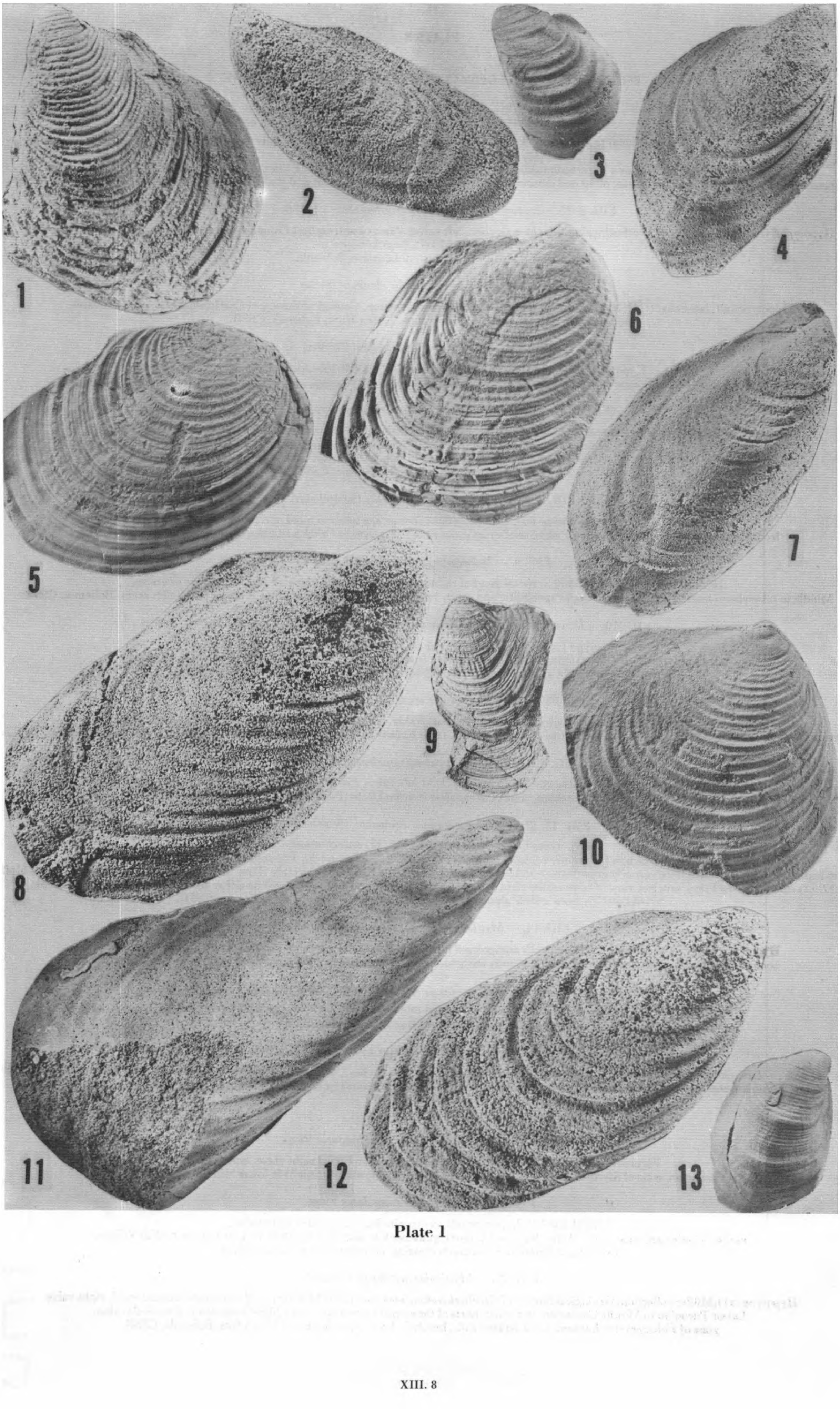

Plate 1

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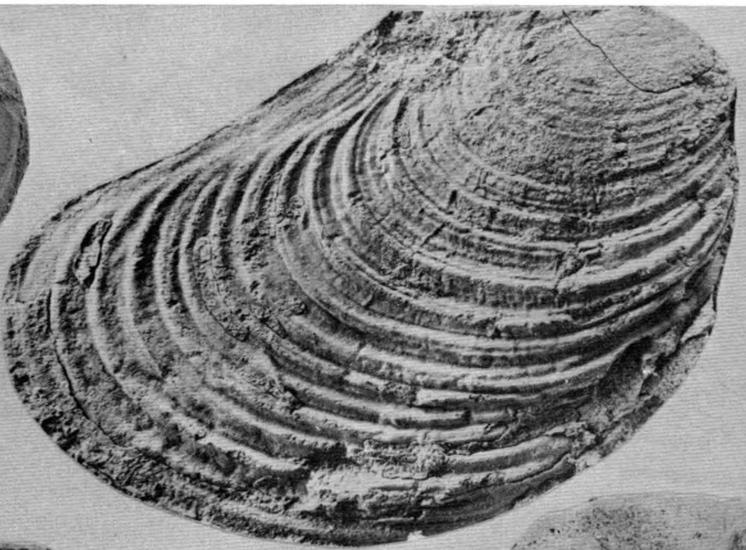

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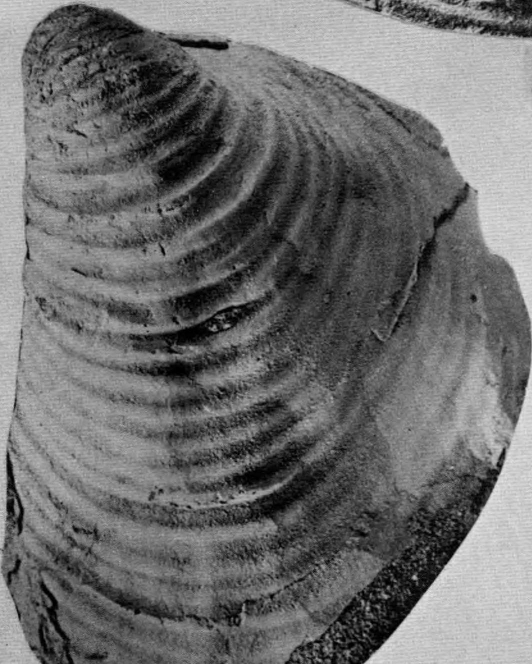

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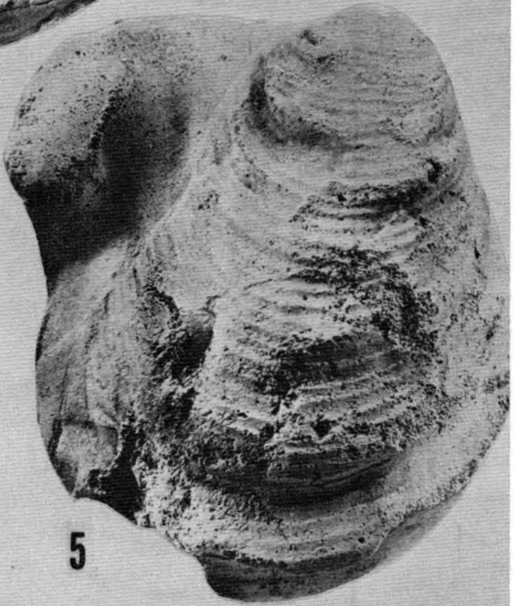

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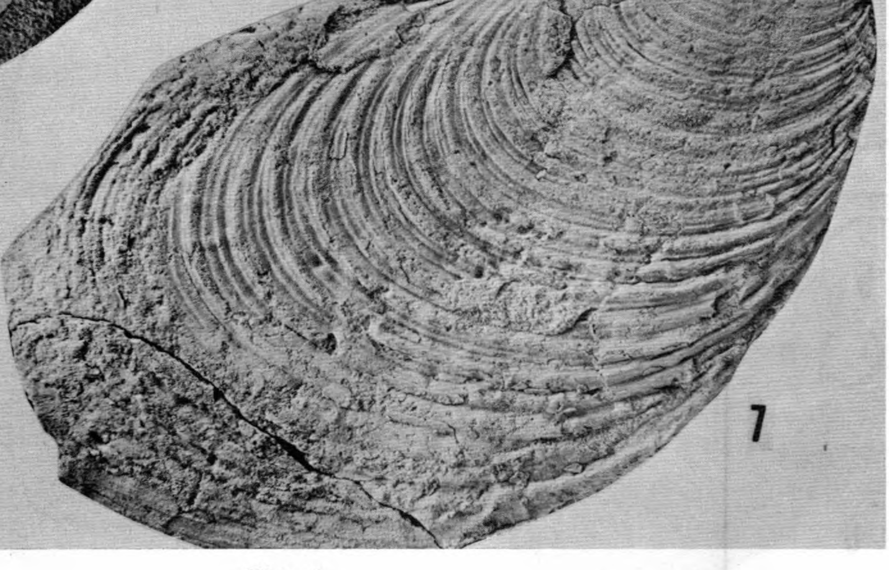

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Plate 2

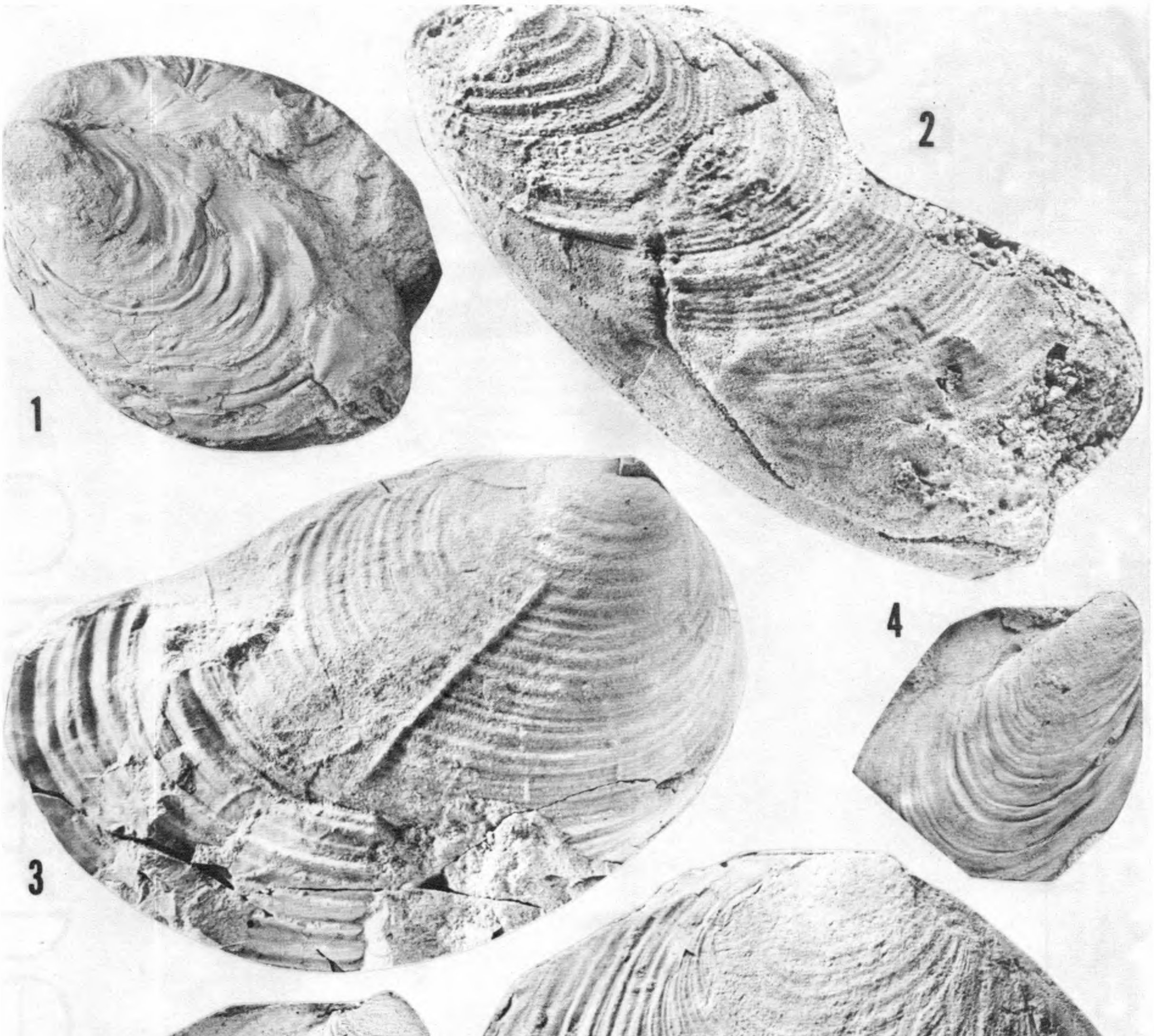

Plate 3

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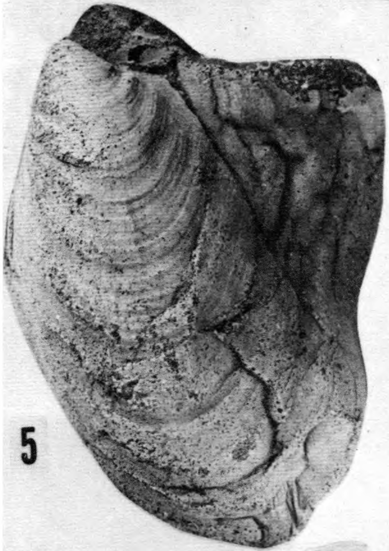

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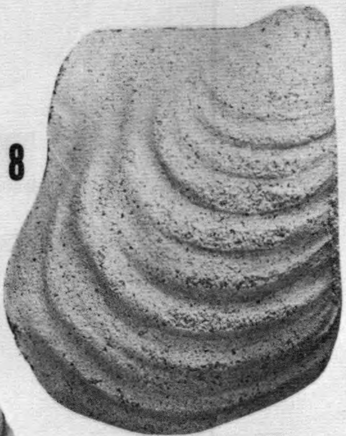

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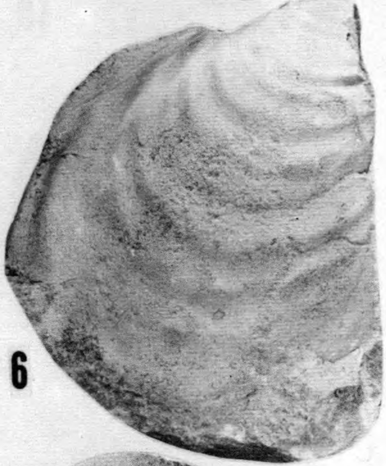

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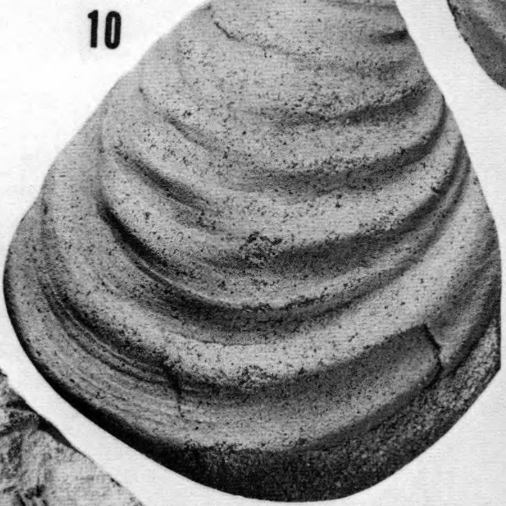

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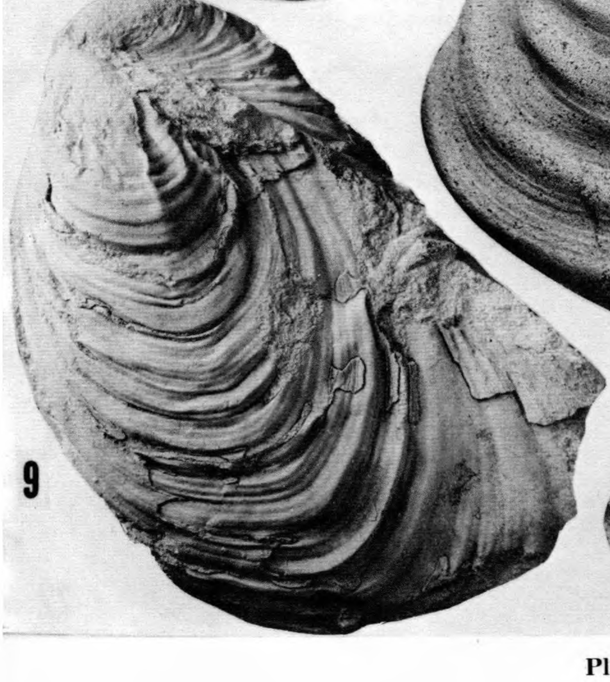

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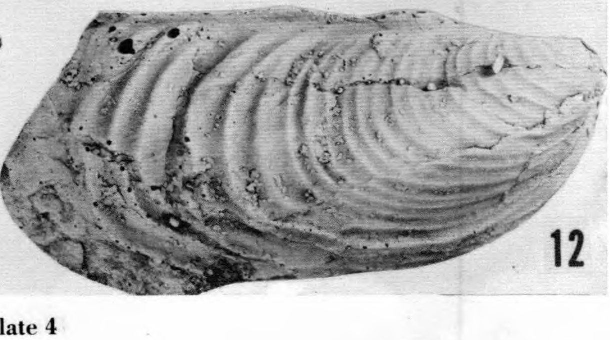

Plate 4

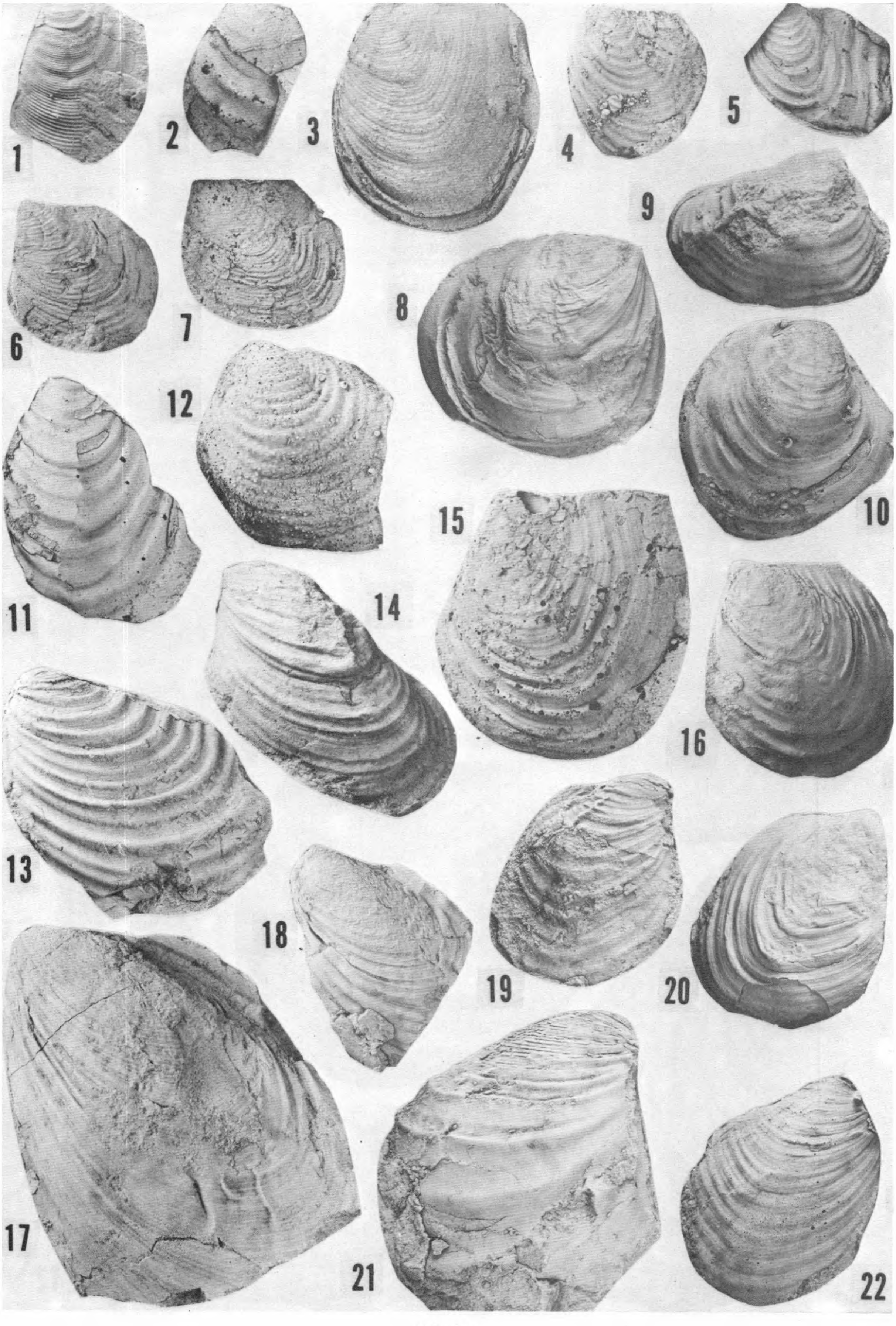

Plate 5

«ANNALES DU MUSÉUM D'HISTOIRE NATURELLE DE NICE - TOME IV - 1976»

SOUTH AFRICAN MIDDLE CRETACEOUS INOCERAMIDAE

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ABSTRACT

Well preserved Inoceramidae co-occur with ammonite faunas in the Albian, Cenomanian, and Coniacian of South Africa. These largely belong to widely distributed Temperate Zone taxa which form the bases for detailed biostratigraphic zonations in North America, Europe, and Japan. Inoceramids thus allow broad, precise correlation of the South African Middle Cretaceous, yielding age determinations which are highly compatible with those based on ammonites. Four Albian zones, three Cenomanian zones, and three Coniacian zones based on Inoceramidae are recognizable in South Africa.

INTRODUCTION

Middle Cretaceous Inoceramidae of South Africa are totally represented by intercontinentally distributed to cosmopolitan species, subspecies, and/or lineages which allow broad regional correlation and relatively precise dating of beds in Zululand and Natal. Integrated with ammonite data compiled by W.J. Kennedy for the same sections, the Inoceramidae have, as elsewhere in the Cretaceous, significant biostratigraphic importance. The few undescribed taxa found in the South African section are also known to be distributed as far north as Europe.

Collections of Dr. W.J. Kennedy and Dr. H.C. Klinger obtained from this area during the summers of 1970-1971 contain very well preserved Albian, Cenomanian and Coniacian taxa. The inoceramids are normally well preserved internal molds with varying amounts of nacreous shell layer retained, and in some cases the entire nacre intact. Prismatic layers are missing or poorly preserved on many specimens. The detail or morphology preserved is excellent and allows confident specific and subspecific identification in most cases. The inoceramids, in their diversity, abundance, and taxonomic composition are clearly part of a South Temperate Realm assemblage (Anti-Boreal of authors) equivalent to that found in the North Temperate Realm throughout much of central and northern Europe, Greenland, and the Western Interior of North America.

Albian (mainly Middle and Upper) Inoceramidae all belong to the cosmopolitan *Birostrina concentrica* (Parkinson) and *B. sulcata* (Parkinson) - *B. subsulcata* (Wiltshire) lineages. Cenomanian Inoceramidae of South Africa are dominantly those of the *Inoceramus (Inoceramus) pictus* Sowerby lineage, also cosmopolitan in distribution. The Lower and Middle Coniacian assemblage is more diverse in South Africa, as it is in many parts of the North Temperate Realm in Europe and America. It contains forms relatable to the *Cremnoceramus inconstans* (Woods) lineage, the *Volviceramus ? koeneni* (Müller) lineage, the *Mytiloides ? striatoconcentricus* (Gümbel) lineage, the *Inoceramus ernsti* Heinz *I. costellatus* Woods lineage, and the *Inoceramus waltersdorfensis* Andert lineage. These all have Euramerican North Temperate, and a more restricted South Temperate Realm biogeographic distribution.

The taxonomic data, keyed to the South African ammonite succession (Kennedy, this volume), are given for Inoceramidae below. The stratigraphy of Middle Cretaceous localities in South Africa is discussed in detail by Kennedy and Klinger (1975).

ALBIAN

The earliest Inoceramids recorded from Zululand are from Albian III level (Kennedy, this volume), and include *Birostrina concentrica* (Parkinson) n. supsp. B of the English sequence and *Birostrina concentrica* (Parkinson) subsp. *brasiliensis* (White). These characterize the early Middle Albian, the upper part of the *Hoplites dentatus* Zone, and the *Anahoplites intermedius* Subzone of the *Euhoplites loricatus* Zone in England ; this date is in good agreement with the associated ammonite fauna, which compares with that of the European early Middle Albian.

Albian IV has yielded *Birostrina concentrica concentrica* (Parkinson), a form ranging from late Middle to earliest Late Albian in Europe ; the associated ammonites suggest a late Middle Albian date.

The lowest part of Albian V has yielded forms of *Birostrina concentrica* (Parkinson) comparable to the new subspecies C of the English sequence (Kauffman, this volume), suggesting an early Upper Albian age. Forms from higher in the Albian sequence include subspecies of *Birostrina subsulcata* (Wiltshire), *B. sulcata* (Parkinson) and *B. concentrica* (Parkinson) s.l. The occurrence of *B. sulcata* with or without associated inoceramids suggests levels low in the *Mortoniceras inflatum* Zone. *B. concentrica* and/or *B. subsulcata* occur without *B. sulcata* higher in the *M. inflatum* Zone. This is in keeping with the ammonite evidence.

No Inoceramids were found in the highest Albian, level VI.

CENOMANIAN

In contrast to the good correlation between ammonites and inoceramids in the Albian, the Cenomanian inoceramids from Zululand, notably from the Ndumu area, pose some problems.

No inoceramids are known from the earliest Cenomanian, but Cenomanian II has yielded what is normally regarded as a Middle (mainly) to Late Cenomanian assemblage in North America and much of Europe. These include *Inoceramus (Inoceramus) pedalionoides* Nagao and Matsumoto, s.l. , *I. (I.) pictus* Sowerby, and *I. (I.) heinzi* Sornay ? Ammonites co-occuring in the same concretions, however, include *Mantelliceras*, *Sharpeiceras* and *Forbesiceras* species which are indicative of the mid-Early Cenomanian. The inoceramid assemblage in South Africa may, therefore, represent earlier evolutionary stages of these lineages than are known, to date, elsewhere in the world (assuming consistency in the ammonite zonation).

Cenomanian III contains sparse *I. (I.) pictus* Sowerby (Middle-Upper Cenomanian) associated with diverse Middle Cenomanian ammonites.

The age relationships of Cenomanian IV, yielding sparse ammonites of Upper Cenomanian aspect, are confirmed by the occurrence of *Inoceramus (Inoceramus)* n. sp. aff., *I. (I.) pedalionoides* Nagao and Matsumoto (form with strong posteroventral sulcus) at this level.

This form typifies the Late Cenomanian elsewhere in the world.

CONIACIAN

Coniacian I has yielded no inoceramids to date. Coniacian II-III have yielded inoceramids from several horizons which represent three zones elsewhere in the world. These include : *I. (I.)* n. sp. ex. gr. *I. costellatus* - *I. ernsti* (lowest zone, uppermost Turonian, Lower Coniacian) *Inoceramus waltesdorfensis hannovrensis* Heinz, *Mytiloides ? striatoconcentricus striatoconcentricus* (Gümbel) and forms transitional to *"Inoceramus" inconstans woodsi* Fiege (second zone, Lower Coniacian) ; and *Cremnoceramus* sp. cf. *C. inconstans* Woods with *Volviceramus* n. sp. aff. *V. koeneni* (Müller) (early form), and *I. waltersdorfensis*. This represents the highest (earliest Middle Coniacian) of the three zones. Coniacian III-IV have yielded *Cremnoceramus inconstans* (Woods) and subspecies, together with *Volviceramus* n. sp. aff. *koeneni*, an early Middle Coniacian assemblage. No Late Coniacian inoceramids are yet known.

The presence of so many widespread and biostratigraphically important inoceramids in South Africa, tied to good ammonite and stratigraphic data, is important in that it allows the first detailed correlation of the Middle Cretaceous in the South Temperate Realm with the standard zonation of the Cretaceous North Temperate, Euramerican biostratigraphic sequence.

REFERENCE CITED

KENNEDY W.J. and KLINGER H.C., (1975) — Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. Bull. British Mus. (Nat. Hist.), Geol., v. 25, n. 4, pp. 266-315, 10 text-figs., 1 pl.

Dépôt du manuscrit : 30 Septembre 1975

PLATE 1

SOUTH AFRICAN MIDDLE CRETACEOUS INOCERAMIDAE

FIG. 1, 2, 6, 7 — *Birostrina concentrica* (Parkinson)

subsp. B, form transitional to *B. concentrica concentrica*, in being more quadrate and more weakly rugate than normal ; early Middle Albian III, levels equivalent to *Hoplites dentatus* Zone and overlying *intermedius* Subzone of the *loricatus* Zone in England.
1, 6. Lateral and anterior views, respectively, of a specimen from locality 176 of Kennedy and Klinger, 1975
2, 7. Lateral and anterior views, respectively, of a specimen from localty 51 of Kennedy and Klinger, 1975. All figures X1. Hypotypes ; internal molds.

FIG. 3. — *Birostrina concentrica* (Parkinson)

Juvenile, subsp. indet, internal mold of hypotype (X2), lateral view of left valve;
middle Late Albian, upper part of *Mortoniceras inflatum* zone, from locality 51 of Kennedy and Klinger, 1975.

FIG. 4. — *Birostrina (?) coptensis* Casey

Hypotypes (X1), internal mold of right valve, *Douvilleiceras mammillatum* Zone, late Early Albian, at locality 175 of Kennedy and Klinger, 1975

FIG. 5, 10. — *Birostrina concentrica* (Parkinson)

n. subsp. B, typical form ; hypotype (X1), lateral and posterior views, respectively, internal mold of left valve, early Middle Albian, in beds equivalent to the *H. dentatus* zone and lower part of the *loricatus* zone (*intermedius* subzone) of the English sequence ; from locality 176 of Kennedy and Klinger, 1975.

FIG. 8. — *Inoceramus* sp. aff. *I. heinzi* Sornay

internal mold of left valve, lateral view, Cenomanian II, middle Early Cenomanian (ranging elsewhere to Middle Cenomanian)
from locality 61 of Kennedy and Klinger, 1975.

FIG. 9. — *Birostrina concentrica* (Parkinson)

subsp. indet., smooth convex variant ; hypotype (X2), internal mold of left valve, late Late Albian, *S. dispar* zone, locality 179 of Kennedy and Klinger, 1975.

FIG. 11, 16. — *Birostrina concentrica brasiliensis* (White)

Hypotypes (X1), composite molds of left valve, middle Middle Albian, levels equivalent to *Euhoplites loricatus* Zone
(mainly *intermedius* Subzone), of the English sequence. From locality 51 of Kennedy and Klinger, 1975.

FIG. 12, 14. — *Birostrina concentrica* (Parkinson)

n. subsp. D, broad variant ; hypotype (X1), lateral and anterior views, respectively, of left valve, Late Albian, *Stoliczkaia dispar* Zone equivalent (?)
from locality 67 of Kennedy and Klinger, 1975.

FIG. 13. — *Birostrina concentrica* (Parkinson)

aff. subsp. *brasiliensis* (White) older and lacking rugae ; hypotype (X1), anterior view of shell of left valve with ventral half missing,
early Middle Albian, *Hoplites dentatus* Zone equivalent of the English sequence, locality 177 of Kennedy and Klinger, 1975.

15. — *Birostrina* n. sp. aff. *B. sulcatus* (Wiltshire)

Figured specimen, (X1), internal mold of left valve with posterodorsal margin broken;
Late Albian, *S. dispar* zone, from locality 181 of Kennedy and Klinger, 1975.

FIG. 17, 19, 21. — *Birostrina subsulcatus* (Wiltshire)

Hypotypes (X1), early Late Albian, mainly *Mortoniceras inflatum* zone.
***17.* lateral view, internal mold of left valve with shell adhering, posterior margin missing**
***19.* lateral view, internal mold of right valve.**
***21.* lateral view, internal mold of coarsely ribbed right valve.**
All from locality 51 of Kennedy and Klinger, 1975.

FIG. 18. — *Birostrina concentrica* (Parkinson)

n. subsp. C, transitional to n. subsp. D in having moderately coarse rugae, hypotype (X1), internal mold of left valve, lateral view;
early Late Albian, probably equivalent to middle *Mortoniceras inflatum* Zone of the English sequence, locality 51 of Kennedy and Klinger, 1975.

FIG. 20. — *Inoceramus (Inoceramus) pictus* Sowerby

s.l.. hypotype (X1), lateral view, internal mold of right valve,
Middle Cenomanian, locality 59 of Kennedy and Klinger, 1975.

FIG. 22. — *Birostrina sulcata* (Parkinson)

hypotype (X1), lateral view, internal mold of right valve, early form with average of 8 radial plicae,
early Late Albian, *Mortoniceras inflatum* zone equivalents, locality 51 of Kennedy and Klinger, 1975.

FIG. 23, 26, 27. — *Inoceramus (Inoceramus) pedalionoides ?* Nagao and Matsumoto

(= *I. tenuis* Mantell, 1822, i.e. figs. 31, 32 in Woods, 1911), figured specimens (X1), internal molds with pieces of shell adhering
from middle Early Cenomanian II, locality 185 of Kennedy and Klinger, 1975.
***23.* lateral view, left valve ;**
***26.* lateral view; left valve, with weak ornament, form transitional to *I. heinzi* Sornay ;**
***27.* lateral view, right valve.**

FIG. 24. — *Inoceramus* sp. aff. *I. tenuistriatus* Nagao and Matsumoto

Late form with coarser rugae and posteroventral sulcus ; juvenile figured specimen (X1), internal mold, right valve ;
Late Cenomanian IV, locality 60 of Kennedy and Klinger, 1975.

FIG. 25. — *Inoceramus tenuis* Mantell ?

Figured specimen (X1), internal mold of right valve ;
Early Cenomanian, locality 181 of Kennedy and Klinger, 1975.

All specimens in the British Museum Collections.

PLATE 2

SOUTH AFRICAN MIDDLE CRETACEOUS AND CONIACIAN INOCERAMIDAE

FIG. 1, 4, 8. — *Inoceramus (Inoceramus)*
n. sp. aff. "*I. costellatus* Woods" of Fiege, 1930, pl. 5, fig. 10, and *I. uwajimensis* Yehara, 1924, pl. 3, fig. 2 ; fig. 4, fig. 2 ;
Figured specimens (X1), internal molds with some shell adhering,
Early Coniacian, locality 71 of Kennedy and Klinger, 1975.
***1.* lateral view, small right valve ;**
***4.* lateral view, small left valve ;**
***8.* lateral view, adult right valve.**

FIG. 2, 10. — *Inoceramus waltersdorfensis hannovrensis* Heinz
Hypotypes (xl, 2), exterior lateral views of nacreous shell layer, left and right valves, respectively ;
early Early Coniacian, locality 13 of Kennedy and Klinger, 1975.

FIG. 3. — *Mytiloides (?)* sp. aff. *M. lusatiae* (Andert)
Figured specimen (xl), internal mold of left valve with shell adhering, lateral view ;
Early Coniacian, locality 13 of Kennedy and Klinger, 1975.

FIG. 5, 6. — *Mytiloides (?) striatoconcentricus striatoconcentricus* (Gümbel)
hypotypes (xl), lateral views of left and right valves, respectively (nacreous layer exterior),
Early Coniacian, False Bay, Zululand.

FIG. 7, 11, 15. — *Inoceramus* n. sp. aff. *I. ernsti* Heinz, - *"I" koeneni* Müller and *I. selwyni* McLearn
Figured specimens (xl), internal molds with shell adhering, lateral views, Early Coniacian.
***7, 15.* locality 13 of Kennedy and Klinger, 1975 ;**
***11.* from False Bay, Zululand.**
7. small left valve ;
***11.* right valve with typical ornament ;**
***15.* right valve.**

FIG. 9. — *Mytiloides (?) striatoconcentricus* (Gümbel)
n. subsp. transitional to early growth stage of *Cremnoceramus inconstans* (Woods), hypotype (xl), lateral view of left valve, internal mold ;
Early Coniacian.

False Bay Zululand

FIG. 12, 13. — *Cremnoceramus inconstans* (Woods)
Hypotype (X1), lateral views of early growth stage prior to break in slope of left and right valves, respectively ;
early Middle Coniacian, False Bay, Zululand. This form, with alternating rugae and equal growth lines, is called subsp. *woodsi* Fiege.

FIG. 14. — *Mytiloides (?) striatoconcentricus carpathicus* (Simionescu)
Sensu Tröger (1967, pl. 9, fig. 18). hypotype (X1), internal mold, lateral view of right valve ; False Bay, Zululand.

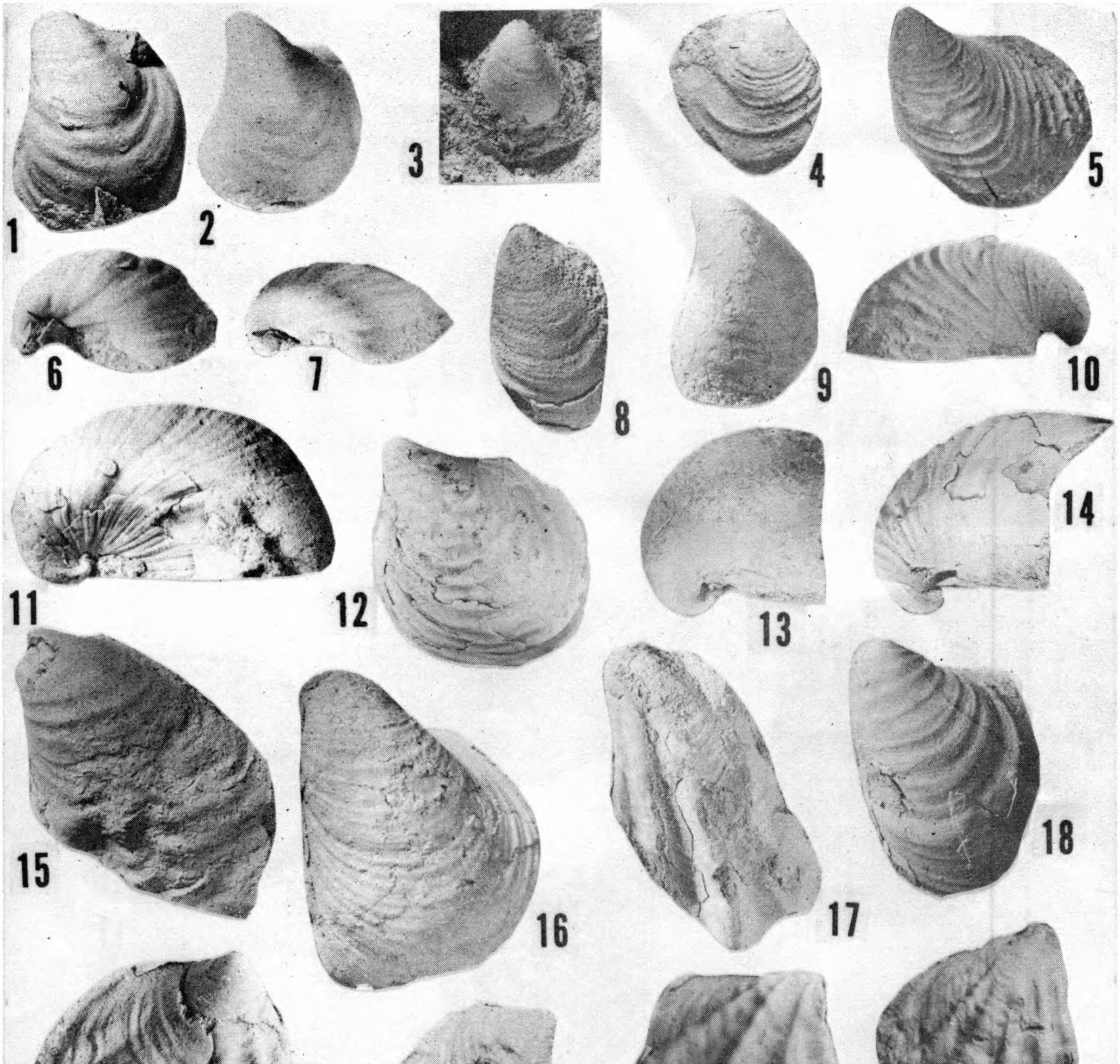
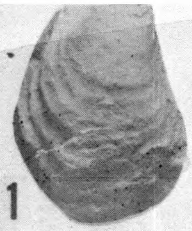


Plate 1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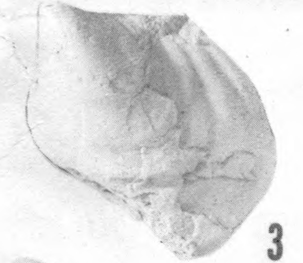
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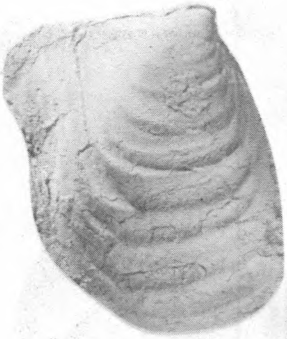
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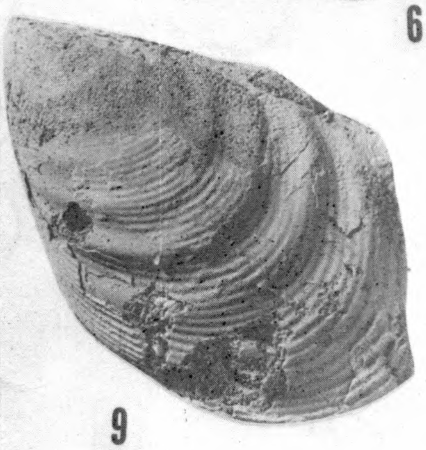
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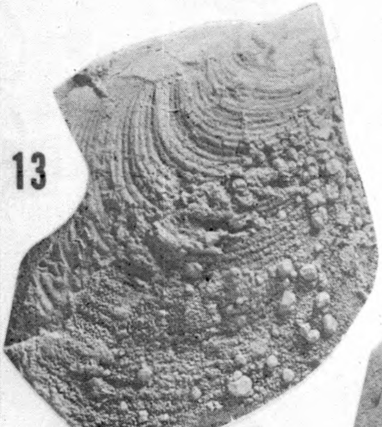
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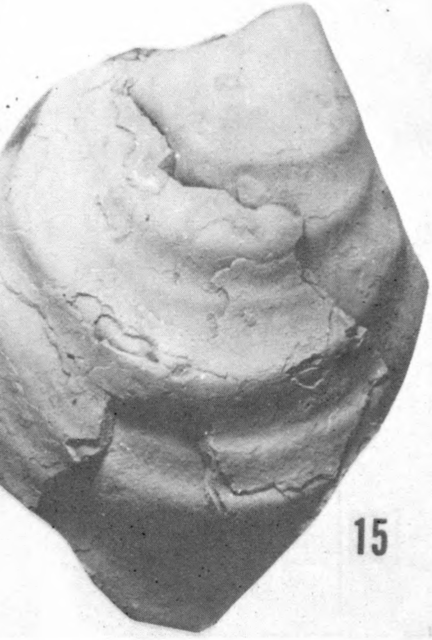
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Plate 2