British Upper Cretaceous Stratigraphy

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Chapter 2

Fossils of the Chalk and the ecology of the Upper Cretaceous Chalk seas

FOSSILS OF THE CHALK

Upper Cretaceous Chalk is remarkable for its diversity of fossils. The ultra-fine fraction (below ten micron size) contains about 30 000 coccoliths (Figure 1.9, Chapter 1) per one millimetre diameter pin head-sized sample. The next size fraction (about 500 microns (0.5 mm) diameter) contains abundant foraminifera, calcispheres (calcareous dinoflagellates; Figure 1.10, Chapter 1) and disaggregated fragments of other fossils. The mesofossil fraction abounds in disaggregated parts of asteroids (starfish), crinoids (sea lilies), and spines and plates of echinoids (sea urchins). The macrofossil fraction contains some horizons so packed with shells they resemble a coquina (e.g. the abundant inoceramid bivalve *Mytiloides* in the Holywell Nodular Chalk Formation). Some of the largest fossils in the Chalk are giant parapuzosid ammonites such as *Parapuzosia* (*Austiniceras*) *austeni* (Sharpe) in the Upper Cenomanian Zig Zag Chalk Formation and *Parapuzosia leptophylla* (Sharpe) in the Santonian–Campanian Newhaven Chalk Formation (Figure 2.1). These ammonites can be up to 3 m in diameter and form spectacular mounds on the wave-cut platform in the **Newhaven to Brighton** GCR site.

The superbly preserved fossils seen in museum collections were obtained when quarries were worked by hand. Some of the finest museum specimens (e.g. starfish), are actually cleverly constructed fakes, put together using components from more than one species.

A feature of the Chalk is the cyclic occurrence of more and less calcareous horizons (couplets; see Figure 2.2). The more calcareous part of the cycle is frequently characterized by abundant fossil sponges (Figure 2.2a). Within such couplets there is a distribution of fossils (Felder, 1981) which may be related to regular climatic shifts. Similar couplets in the Lower Cretaceous of Germany contain dinoflagellates with different degrees of complexity of ornament within the cycle. Ornaments less complex in the marly unit and more complex in the calcareous unit have been interpreted as a response to climatically controlled regular changes in sediment input and agitation of the sea waters (J. Mutterlose, pers. comm.).

There are several anomalies in the distribution of fossils in the Chalk. Some horizons are rich in macrofossils while other horizons appear to be almost barren of any diagnostic forms. Diversity of fossils also changes stratigraphically. The higher parts of the Lower Turonian Holywell Nodular Chalk Formation are dominated by abundant shells of *Mytiloides* species (a relatively low diversity fauna). In contrast, the Upper Turonian strata are characterized by a higher diversity fauna including *Mytiloides* species and other inoceramid bivalves, a variety of echinoids

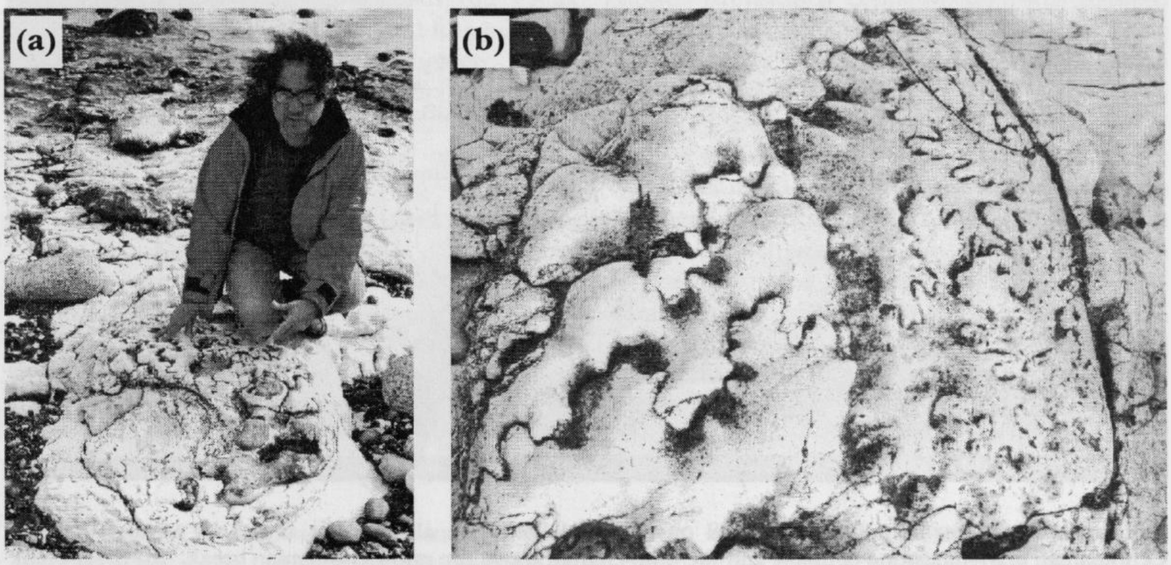


Figure 2.1 (a) Large ammonite (*Parapuzosia*) in the Lower Campanian Newhaven Chalk Formation (Meeching Beds), on the foreshore at Portobello, Sussex. The enlargement (b) shows the septal sutures. (Photos: R.N. Mortimore.)

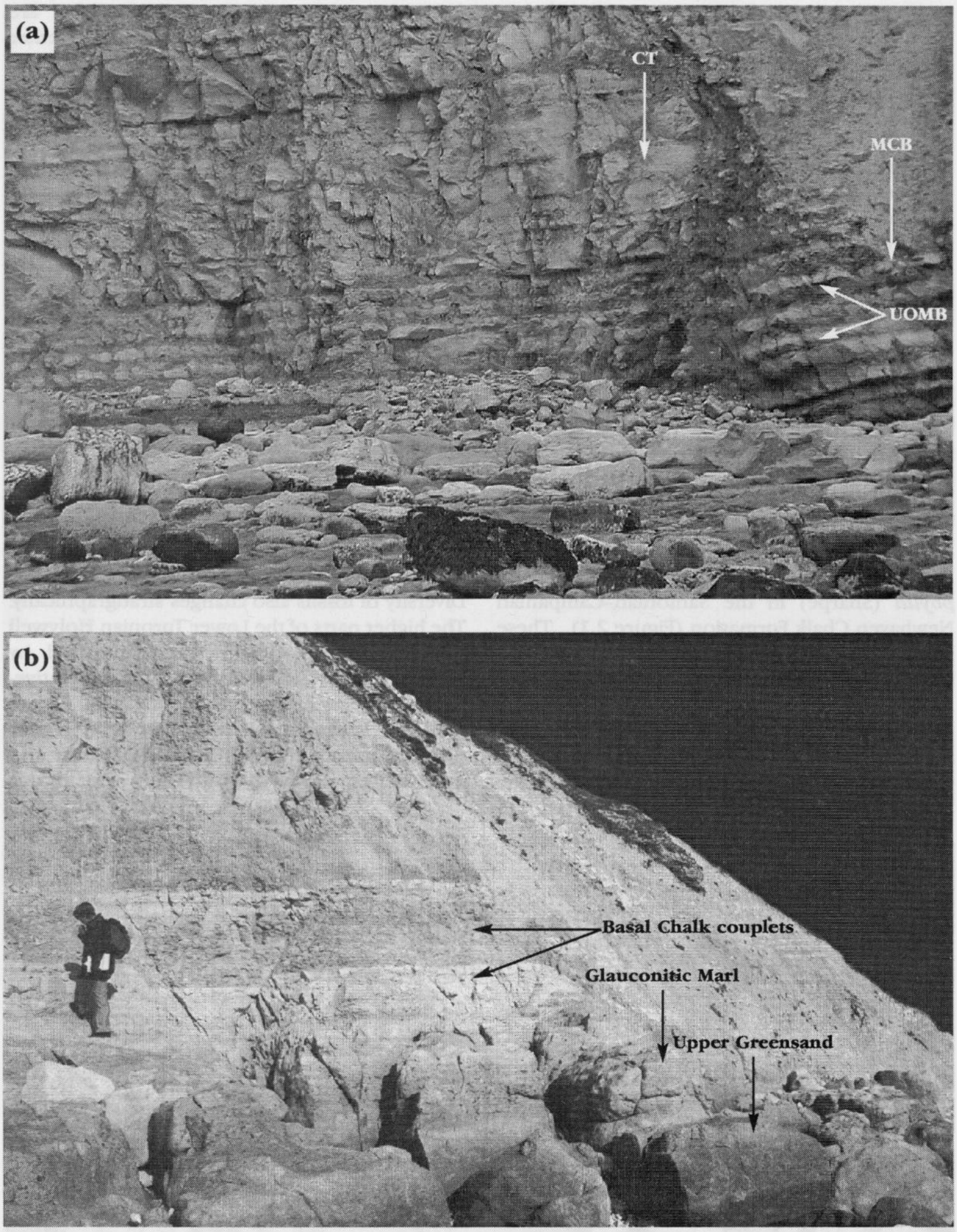


Figure 2.2 Rhythms in the Chalk picked out by marl–limestone alternations at Beachy Head. (a) Mid-Cenomanian marl–limestone couplets and the litho-change above the mid-Cenomanian break. (b) Basal Chalk (Lower Cenomanian) couplets comprise thicker marl bands compared with the Middle Cenomanian couplets above. (CT = change in limestone-marl thickness with increase in carbonate upwards; MCB = mid-Cenomanian Break; UOMB = hard limestones with sponges and heteromorph ammonites (upper *Orbirhynchia mantelliana* band). (Photos: R.N. Mortimore.)

including *Holaster*, *Micraster* and *Echinocorys* and numerous species of brachiopods. Another feature is the change in size from predominantly small forms to predominantly large forms. Such a size change is particularly well developed between the Meeching Marls and Bastion Steps Beds of the Newhaven Chalk Formation. Smaller forms of *Echinocorys* and *Offaster pilula* (Lamarck) in and below the Meeching Marls are replaced upwards by large globose forms of *Echinocorys* and large *Offaster*. Even the brachiopods are larger. A broad alternation of large and small forms of echinoids is present through the Campanian strata, associated with a parallel shift in the concentration of types of trace fossil (Figure 2.3).

Preservation of fossils is also variable. Basin margins where shallow-water calcareous sands developed in the early part of the Cenomanian, such as south-east Devon, are areas where originally aragonitic-shelled fossils, particularly ammonites, are better preserved and more abundant than in the regions where deeper-water chalks formed. Similarly, otherwise extremely rare ammonites are found in the Upper Turonian Chalk Rock hardgrounds of the Chiltern Hills (on the Anglo-Brabant Massif). Right across Europe there is a preservational event at the equivalent level of the Chalk Rock. This type of event is found again in the Catton Sponge Bed and the Trimingham Sponge Bed in Norfolk and Northern Ireland. Not all of the sponge beds and hardgrounds in the Chalk show this type of preservation and it is puzzling why some do whereas others are barren.

Some of the earliest subdivisions of the Chalk (e.g. Barrois, 1876), used the abundance of particular groups of fossils, such as the echinoids *Holaster* (Cenomanian), and *Micraster* (Coniacian, Santonian), the crinoid *Marsupites* (Santonian) and belemnites (Campanian–Maastrichtian). These broad divisions are still useful concepts as they emphasize the conspicuous faunal assemblages present at different times, perhaps reflecting major ecological changes in the Upper Cretaceous oceans.

KEY BIOSTRATIGRAPHICAL INDICES

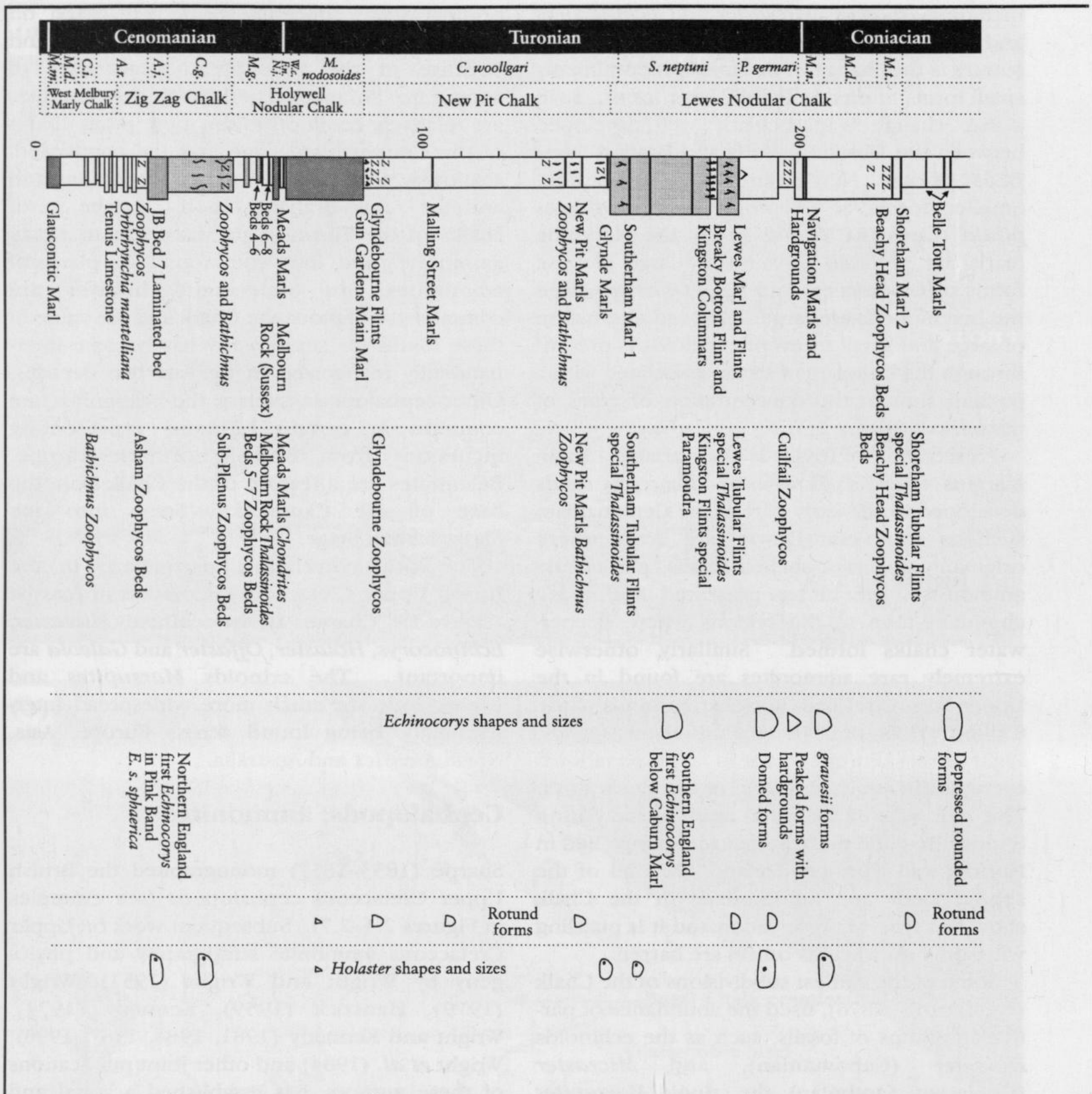
In the Upper Cretaceous Series, as in other parts of the Mesozoic succession, cephalopods, particularly the ammonites, are generally considered to be the most important international stratigraphical index fossils. This is because the original stage concepts are largely based on ammonites (see Appendix, this volume), and because of the widespread occurrence of ammonites in marine sediments. Ammonites are relatively common in the more marly chalks of the Cenomanian Stage and the condensed, shallow-water shelf areas of south-west England and the Anglo-Brabant Massif. In the purer chalks of the Turonian to Maastrichtian strata, ammonites are less common. In place of ammonites, the inoceramid bivalves are common throughout the Chalk and the value of these fossils for stratigraphy has become internationally recognized in the last two decades. Other cephalopods, such as the belemnites, are common at certain horizons representing incursions from Boreal northern Europe. Belemnites are a feature of the Chalk from the base of the Campanian Stage into the Maastrichtian Stage.

For local correlation, particularly in the Boreal Upper Cretaceous succession of Europe (Figure 1.4, Chapter 1), the echinoids *Micraster*, *Echinocorys*, *Holaster*, *Offaster* and *Galeola* are important. The crinoids *Marsupites* and *Uintacrinus* are much more widespread internationally, being found across Europe, Asia, North America and Australia.

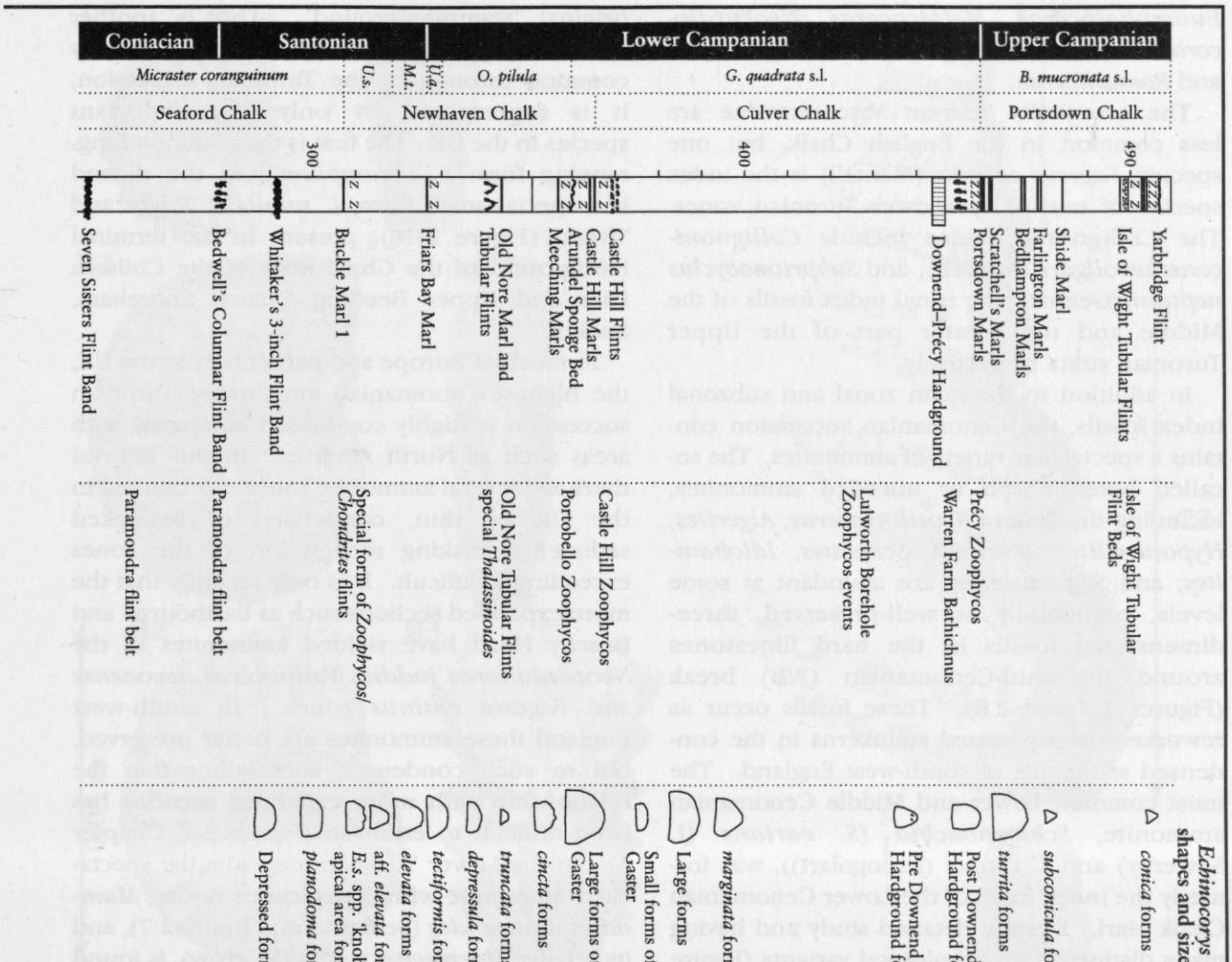
Cephalopods: ammonites

Sharpe (1853–1857) monographed the British Upper Cretaceous cephalopods (see examples in Figures 2.4–2.7). Subsequent work on Upper Cretaceous ammonite stratigraphy and phylogeny by Wright and Wright (1951), Wright (1979), Hancock (1959), Kennedy (1971), Wright and Kennedy (1981, 1984, 1987, 1990), Wright *et al.* (1984) and other joint publications of these authors, has established a zonal and subzonal scheme for the Cenomanian and Turonian stages (Figures 2.8 and 2.9). The family Acanthoceratidae dominates the stratigraphically useful forms, giving rise to numerous genera including *Mantelliceras*, *Sharpeiceras*, *Cunningtoniceras*, *Acanthoceras*, *Protacanthoceras*, *Calycoceras*, *Eucalycoceras*, *Thomelites*,

Figure 2.3 (overleaf) Integration of trace fossil events with shape and size changes in some key benthic fossils, and the magnetostratigraphy for the Upper Cretaceous succession in southern England. See Figure 1.5, Chapter 1, for full details of zonal fossils.


Cenomanian
Turonian
Coniacian
M.m.
M.d.
C.i.
A.r.
A.j.
C.g.
M.g.
W. Fn. N.j.
M. nodosoides
C. woollgari
S. neptuni
P. germari
M.n.
M.d.
M.t.
West Melbury Marly Chalk
Zig Zag Chalk
Holywell Nodular Chalk
New Pit Chalk
Lewes Nodular Chalk
0
100
200
Glauconitic Marl
Tenuis Limestone
Orbirhynchia mantelliana
Zoophycos
JB Bed 7 Laminated bed
Zoophycos and Bathichnus
Beds 4–6
Beds 6–8
Meads Marls
Melbourn Rock (Sussex)
Melbourn
Gun Gardens Main Marl
Glyndebourne Flints
Malling Street Marls
Zoophycos and Bathichnus
New Pit Marls
Glynde Marls
Southerham Marl 1
Kingston Columnars
Breaky Bottom Flint and
Lewes Marl and Flints
Hardgrounds
Navigation Marls and
Beachy Head Zoophycos Beds
Shoreham Marl 2
Belle Tout Marls
Bathichnus Zoophycos
Asham Zoophycos Beds
Sub-Plenus Zoophycos Beds
Beds 5–7 Zoophycos Beds
Melbourn Rock Thalassinoides
Meads Marls Chondrites
Glyndebourne Zoophycos
Zoophycos
New Pit Marls Bathichnus
special Thalassinoides
Southerham Tubular Flints
Paramoudra
Kingston Flints special
special Thalassinoides
Lewes Tubular Flints
Cuilfail Zoophycos
Beds
Beachy Head Zoophycos
special Thalassinoides
Shoreham Tubular Flints
Echinocorys shapes and sizes
E. s. sphaerica
in Pink Band
first Echinocorys
Northern England
below Caburn Marl
first Echinocorys
Southern England
Domed forms
hardgrounds
Peaked forms with
gravesii forms
forms
Depressed rounded
Rotund forms
Rotund forms
Holaster shapes and sizes
Large
Small
Large
Small
Large
Tottenhoe Stone erosion
SB sub I. anglicus –
Hardground
SB sub Eastbourne
SB sub Plenus Marls
Event II Black Shales
Oceanic Anoxic
inoceramids
small and medium-sized
diversity benthonic fauna,
Dysaerobic conditions, low
inoceramids, brachiopods
benthonic fauna, larger
and higher diversity
with flints, erosion surfaces
Aerobic conditions at base,
inoceramids, brachiopods
benthonic fauna, larger
and higher diversity
with flints, erosion surfaces
Aerobic conditions at base,
Anoxic event black shales
inoceramids, brachiopods
benthonic fauna, larger
and higher diversity
with flints, erosion surfaces
Aerobic conditions at base,
Zoophycos soft chalks
Cremnoceramus
Small Mytiloides and
Larger Cremnoceramus
Large flat shells
Long Cretaceous Quiet Zone 34N

Key biostratigraphical indices



Euomphaloceras, *Metoicoceras*, *Neocardioceras*, *Watinoceras*, *Mammites*, *Metasigaloceras* and *Romaniceras*.

The essentially Tethyan Vascoceratidae are less common in the English Chalk, but one species, *Fagesia catinus* (Mantell) is the index species of one of the Lower Turonian zones. The Collignoniceratidae include *Collignoniceras woollgari* (Mantell), and *Subprionocyclus neptuni* (Geinitz), the zonal index fossils of the Middle and the greater part of the Upper Turonian strata respectively.

In addition to the main zonal and subzonal index fossils, the Cenomanian succession contains a spectacular variety of ammonites. The so-called heteromorph or uncoiled ammonites, including the genera *Neostlingoceras*, *Algerites*, *Hypoturrilites*, *Mariella*, *Scaphites*, *Idiohamites*, and *Sciponoceras*, are abundant at some levels, particularly as well-preserved, three-dimensional fossils in the hard limestones around the mid-Cenomanian (P/B) break (Figures 2.2 and 2.8). These fossils occur as reworked, phosphatized steinkerns in the condensed sediments of south-west England. The most common Lower and Middle Cenomanian ammonite, *Schloenbachia* (*S. varians* (J. Sowerby) and *S. coupei* (Brongniart)), was formerly the index fossil of the Lower Cenomanian Chalk Marl. Despite detailed study and having many distinctive morphological variants (Figure 2.4) this frustrating genus has not provided the consistent biostratigraphy originally expected and is not, therefore, used in the modern zonal scheme.

Very large desmoceratid ammonites (*Parapuzosia* (*Austiniceras*) *austeni* (Sharpe); Figure 2.6) are common in the higher, more calcareous part of the Middle Cenomanian succession, and the more strongly ribbed *P.* (*P.*) *leptophylla* occurs relatively commonly in purer chalks of the Upper Santonian and Lower Campanian strata of Kent and Sussex (Figure 2.1). Another large form, *Hauericeras* cf. *pseudogardeni* (Schlüter), is recorded from the Lower Campanian Substage (**Newhaven to Brighton** section, Sussex and at Sewerby, **Flamborough Head**, Yorkshire). Another medium- to large-sized ammonite, belonging to the genus *Lewesiceras* (Pachydiscidae) is *Lewesiceras peramplum* (Mantell). This species is present in the Turonian strata in all areas but particularly in the Lewes pits (from which the genus takes its name), in Sussex, Mantell's original 'stamping-ground'. This is another frustrating genus for, despite being relatively common throughout the Turonian succession, it is represented by only two important species in the UK. The first is the common long-ranging form *L. peramplum* and the second is a special small form, *L. mantelli* Wright and Wright (Figure 2.10), present in the terminal hardground of the Chalk Rock of the Chiltern Hills and Upper Beeding Quarry, Shoreham, Sussex.

In much of Europe and particularly in the UK, the highest Cenomanian and lowest Turonian succession is highly condensed compared with areas such as North America. In this interval there are several ammonite zones represented in the UK by thin, condensed or reworked sediments, making recognition of the zones exceedingly difficult. It is only recently that the more expanded sections such as Eastbourne and Beachy Head have yielded ammonites of the *Neocardioceras juddii*, *Watinoceras devonense* and *Fagesia catinus* zones. In south-west England these ammonites are better preserved, but in such condensed successions that the relationship with more expanded sections has been difficult to establish (Figure 3.4, Chapter 3). In the Lower Turonian deposits the spectacular ammonite with conspicuous nodes, *Mammites nodosoides* (Schlotheim) (Figure 2.7), and its relative *Morrowites wingi* (Morrow), is found relatively frequently throughout the UK. The occurrence in the Chalk of the Middle Turonian ammonites *Collignoniceras woollgari* and *Romaniceras deverianum* (d'Orbigny) (Figure 2.10) has been known since Mantell (1822). However, locating the position of these ammonites and working out their ranges has proved difficult. Only relatively recently have numbers of specimens been collected *in situ*, mainly from the Lewes chalk pits.

Where well-preserved ammonites are found in otherwise ammonite-poor parts of the succession, even as single horizons, then the UK succession can be placed more confidently in the international zonal scheme. Two such horizons are the aragonitic fossils from the Upper Turonian Chalk Rock at **Kensworth Chalk Pit** *Subprionocyclus neptuni* Zone (Woods, 1896; Wright, 1979: Kaplan *et al.*, 1987; see Figure 2.11), and the heteromorph assemblage from the Lower Campanian Downend Main Hardground at **Downend Chalk Pit**, Portsdown (Gale, 1980).

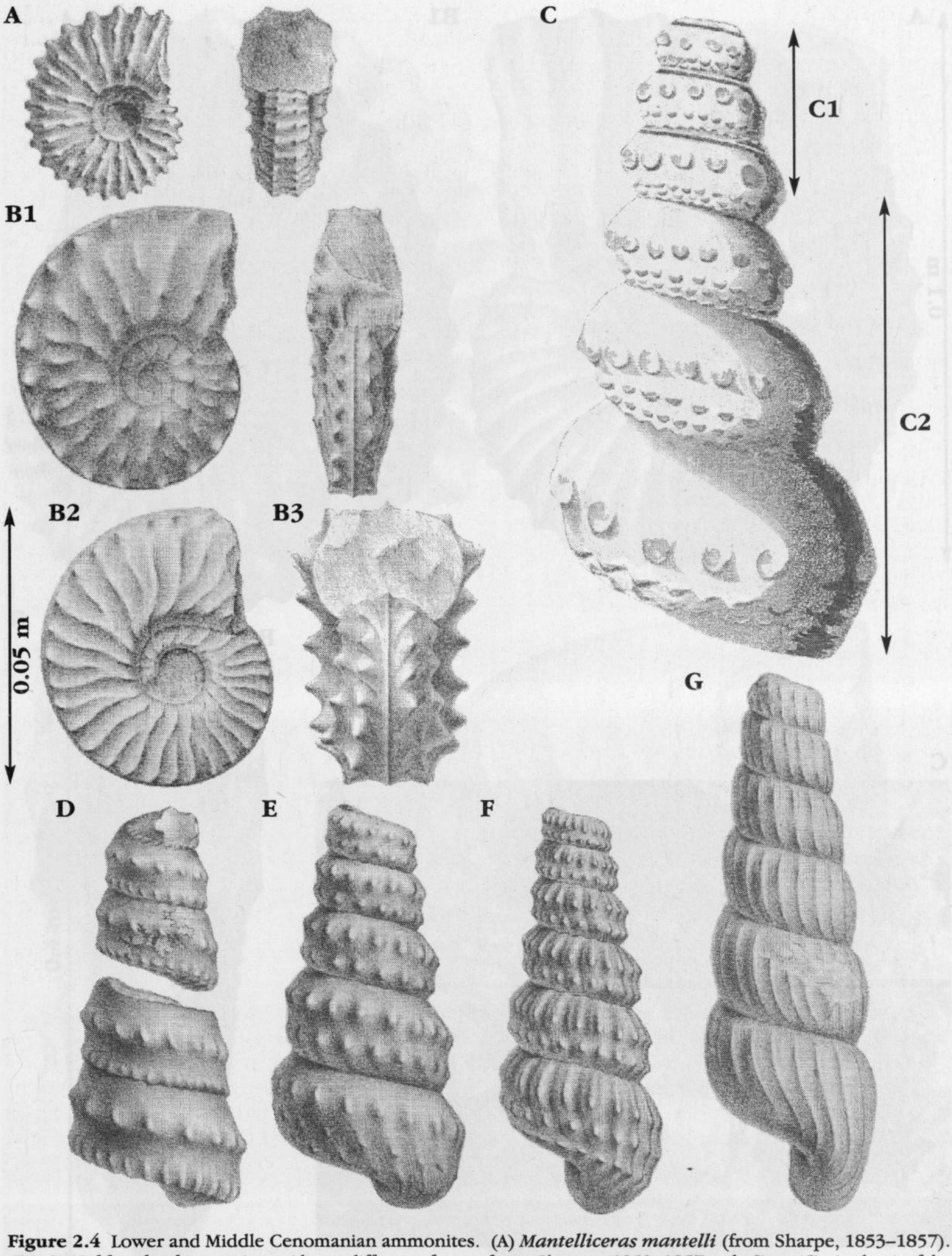


Figure 2.4 Lower and Middle Cenomanian ammonites. (A) ***Mantelliceras mantelli*** (from Sharpe, 1853–1857). (B1–3) ***Schloenbachia varians*** (three different forms from Sharpe, 1853–1857, pl. 8). (C) A classic fake combining two fossils; (C1) ***Hypoturrilites gravesianus*** (from Mantell, 1822, pl. 26, fig. 7); (C2) ***Hypoturrilites tuberculatus*** (from Mantell, 1822, pl. 26, fig. 7). (D) ***Neostlingoceras carcitanense*** (from Sharpe, 1853–1857, pl. 26, figs 7a, 8). (E) ***Turrilites acutus*** (from Sharpe, 1853–1857, pl. 27). (F) ***Turrilites costatus*** (from Sharpe 1853–1857, pl. 27). (G) ***Turrilites scheuchzerianus*** (from Sharpe 1853–1857, pl. 26). Scale bar applies to all specimens.

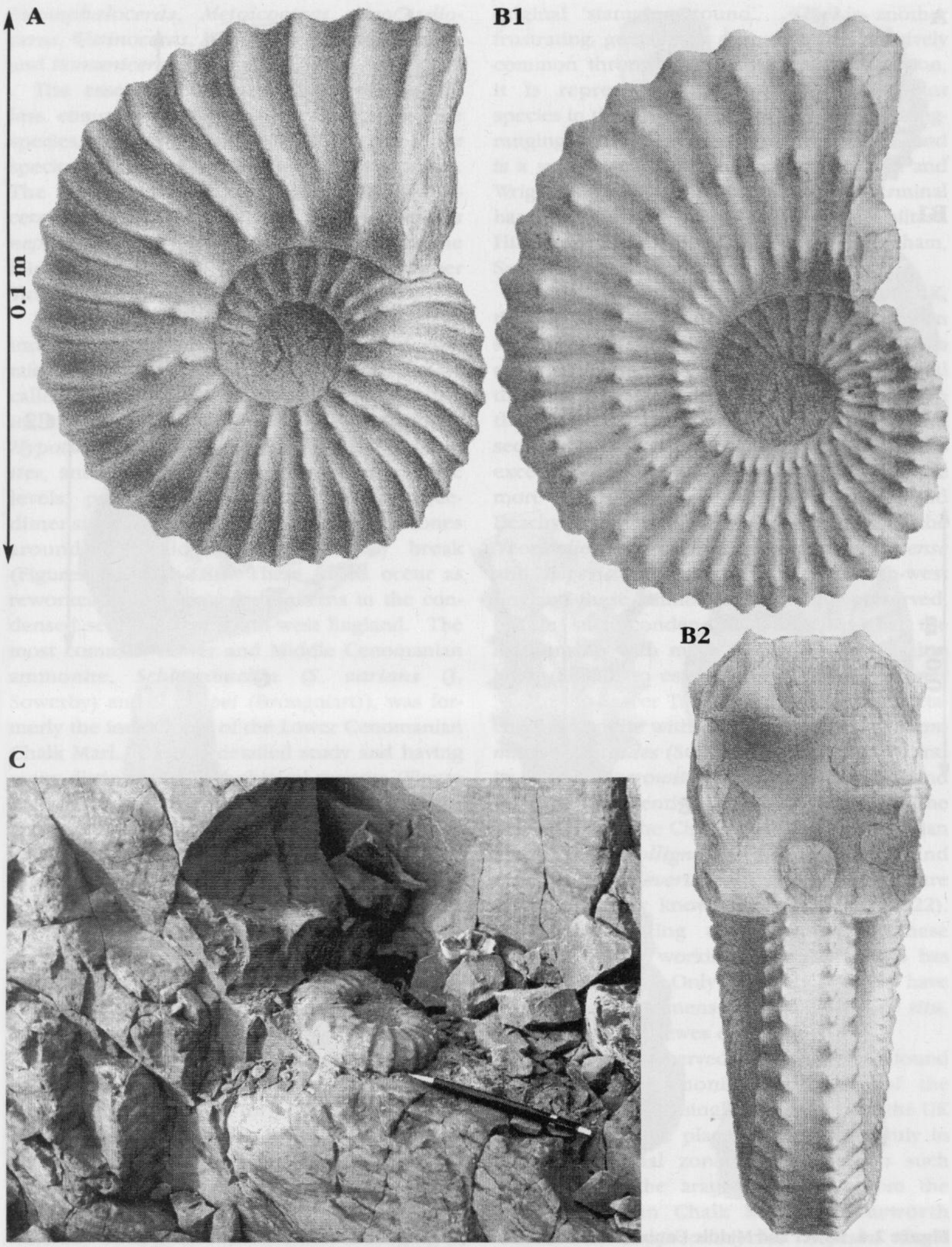


Figure 2.5 Lower and Middle Cenomanian ammonites. (A) *Mantelliceras cantianum* (from Sharpe, 1853–1857, pl. 18). (B1, B2) *Sharpeiceras schlueteri* (from Sharpe, 1853–1857, pl. 14) from the Lower Cenomanian *S. schlueteri* Zone. (C) *Cunningtoniceras inerme* at the base of the Middle Cenomanian, West Melbury Marly Chalk Formation at Beachy Head, Sussex (the pencil is 150 mm long). (Photo: R.N. Mortimore.) Scale bar applies to A and B.

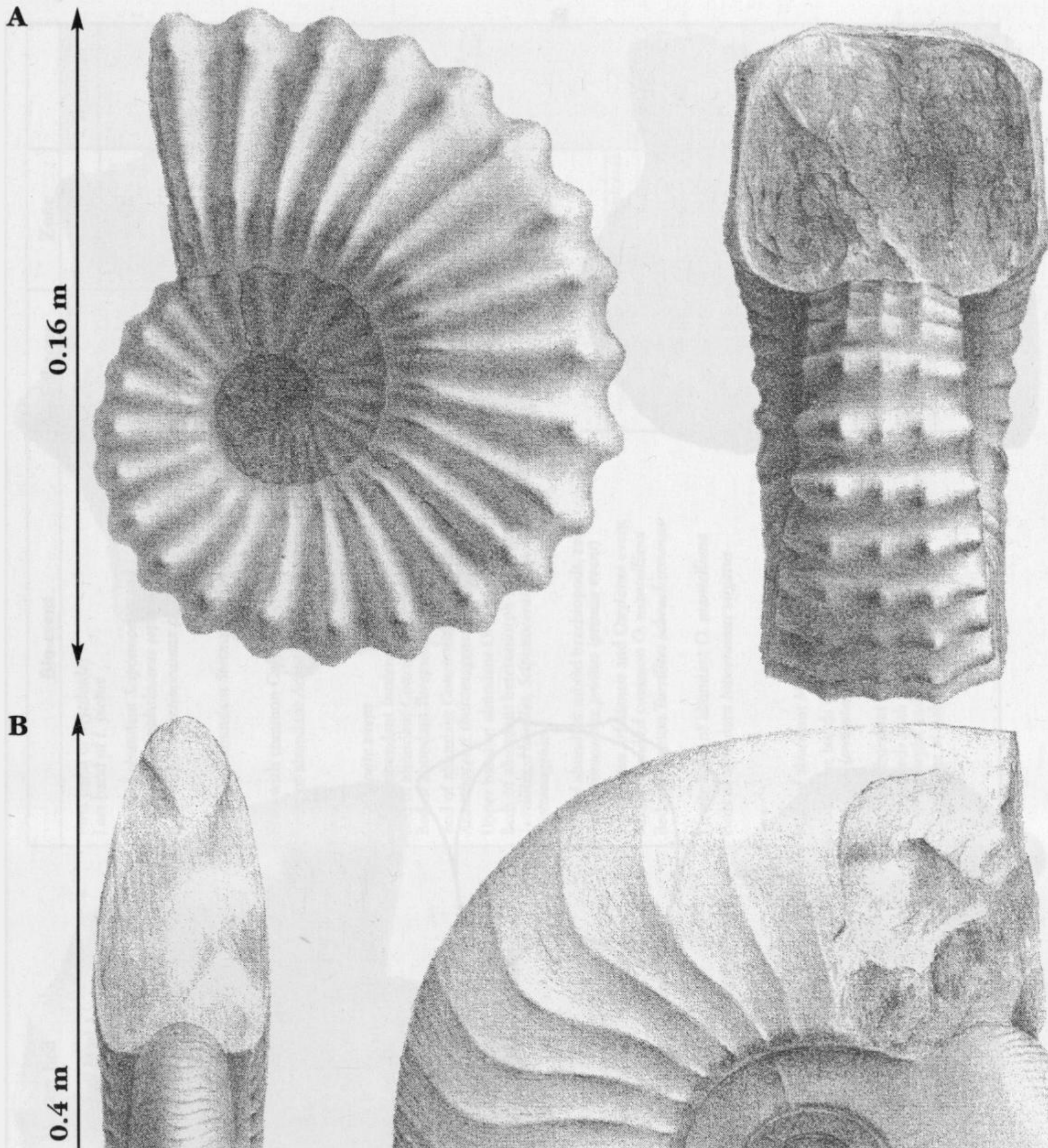


Figure 2.6 Middle Cenomanian ammonites. (A) *Acanthoceras rhotomagense* (from Sharpe, 1853–1857, pl. 16). (B) *Parapuzosia* (*Austiniceras*) *austeni* (from Sharpe, 1853–1857, pl. 12).

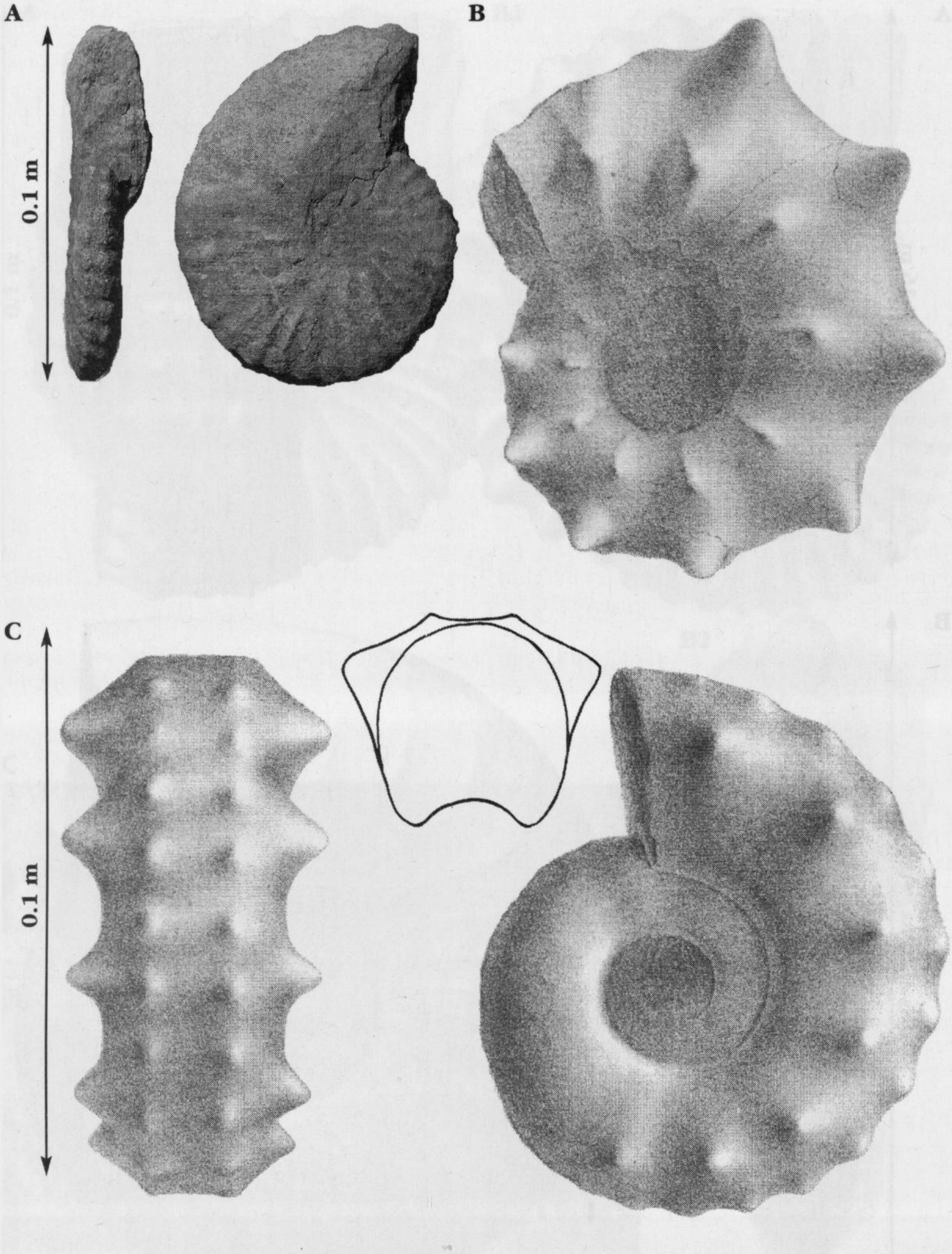


Figure 2.7 Upper Cenomanian and Lower Turonian ammonites. (A) ***Metoicoceras geslinianum*** (from the Plenus Marls Member, Ballard Down, Dorset; from Mortimore Collection). (B) ***Mammites nodosoides*** (from Sharpe, 1853–1857, pl. 15), typical of the higher part of the Holywell Nodular Chalk Formation. (C) ***Metasigaloceras rusticum*** (from Sharpe, 1853–1857, pl. 20) from the higher part of the Holywell Nodular Chalk Formation.

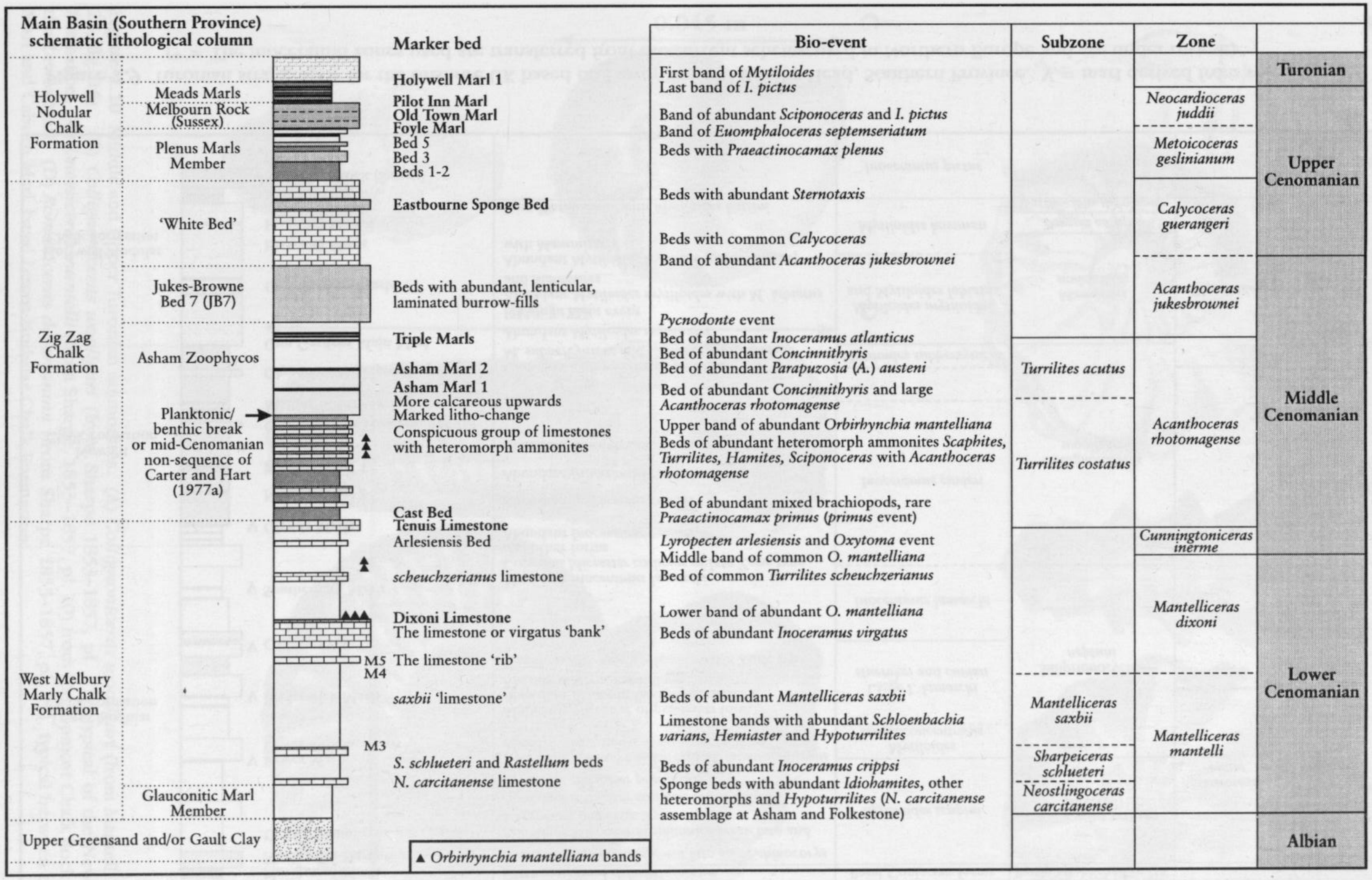
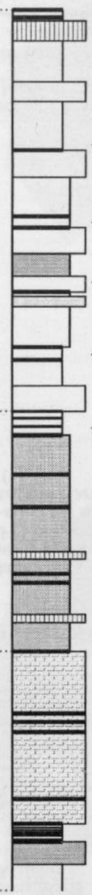


Figure 2.8 Cenomanian stratigraphy for the onshore UK based on Southerham, Asham, Beachy Head and Folkestone. M2, M4 and M5 are Marker Beds of Gale (1995).



Schematic log	Marker bed	Bio-event	Inoceramid Zone*	Ammonite Zone	Traditional Zone	
	Navigation Marls	*Cremnoceramus deformis erectus*	Basal Coniacian forms	Partly established in UK		Coniacian
	Navigation Hardgrounds	*Micraster normanniae sensu lato* and *Echinocorys*				
	Cuilfail Zoophycos soft chalks	Abundant *Micraster normanniae sensu lato* and *Sternotaxis placenta*	*Mytiloides scupini*	*Prionocyclus germari* (inferred)		
		Abundant *Micraster corbovis sensu stricto*			*Sternotaxis plana*	
		Abundant *Micraster praecursor*				
	V Lewes Marl Lewes Tubular Flints	Abundant *Micraster leskei* and *M. labiatoidiformis* Abundant *Mytiloides striatoconcentricus*	*Mytiloides striatoconcentricus*			
Lewes Nodular Chalk Formation		Abundant *Micraster* of pre-*leskei* form				Upper Turonian
	V Bridgewick Marls	Abundant *T. lata* in Bridgewick Marl 1 Abundant *Sternotaxis plana*	Large *I. lamarcki stuemkei* and *cuvieri*	*Subprionocyclus neptuni*		
		Common *Micraster corbovis* of *lata* Zone type				
	V Caburn Marl					
			Inoceramus lamarcki			
	V Southerham Marls	Abundant *Inoceramus lamarcki* Common *Micraster corbovis* of *lata* Zone type and other forms				
		Abundant *Inoceramus cuvieri*			*Terebratulina lata*	
	V Glynde Marls					
	New Pit Marl 2	Abundant *Inoceramus cuvieri*	*Inoceramus cuvieri*			
	New Pit Marl 1	Abundant *Inoceramus cuvieri*		*Collignoniceras woollgari*		Middle Turonian
New Pit Chalk Formation		Abundant *Inoceramus cuvieri*				
	Glyndebourne Hardgrounds 2/3					
	Malling Street Marls					
	Glyndebourne Hardgrounds 1	Common *Collignoniceras woollgari, M. subhercynicus* and *Conulus subrotundus*	*Mytiloides subhercynicus*			
	Gun Gardens Main Marl	Abundant *Mytiloides mytiloides*				
		Filograna avita event				
	Gun Gardens Marls	Abundant *Mytiloides mytiloides* with *M. labiatus* and *Mammites*	*Mytiloides mytiloides* and *Mytiloides labiatus*	*Mammites nodosoides*	*Mytiloides* spp.	Lower Turonian
Holywell Nodular Chalk Formation	Holywell Marls	Abundant *Mytiloides kossmati* [*columbianus*] with *Mammites*				
	Holywell Marl 4		*Mytiloides kossmati*	*Fagesia catinus*		
		Rare *Watinoceras* with *Mytiloides hattini*		*Watinoceras devonense*		
	Meads Marls Melbourn Rock (Sussex) Plenus Marls		*Inoceramus pictus*			Cenomanian

Figure 2.9 Turonian stratigraphy for the onshore UK based on Lewes Pits and Beachy Head, Southern Province. V = marl derived from volcanic ash. (* = The inoceramid zones used are transferred from the current scheme used in Northern Europe and are under review.)

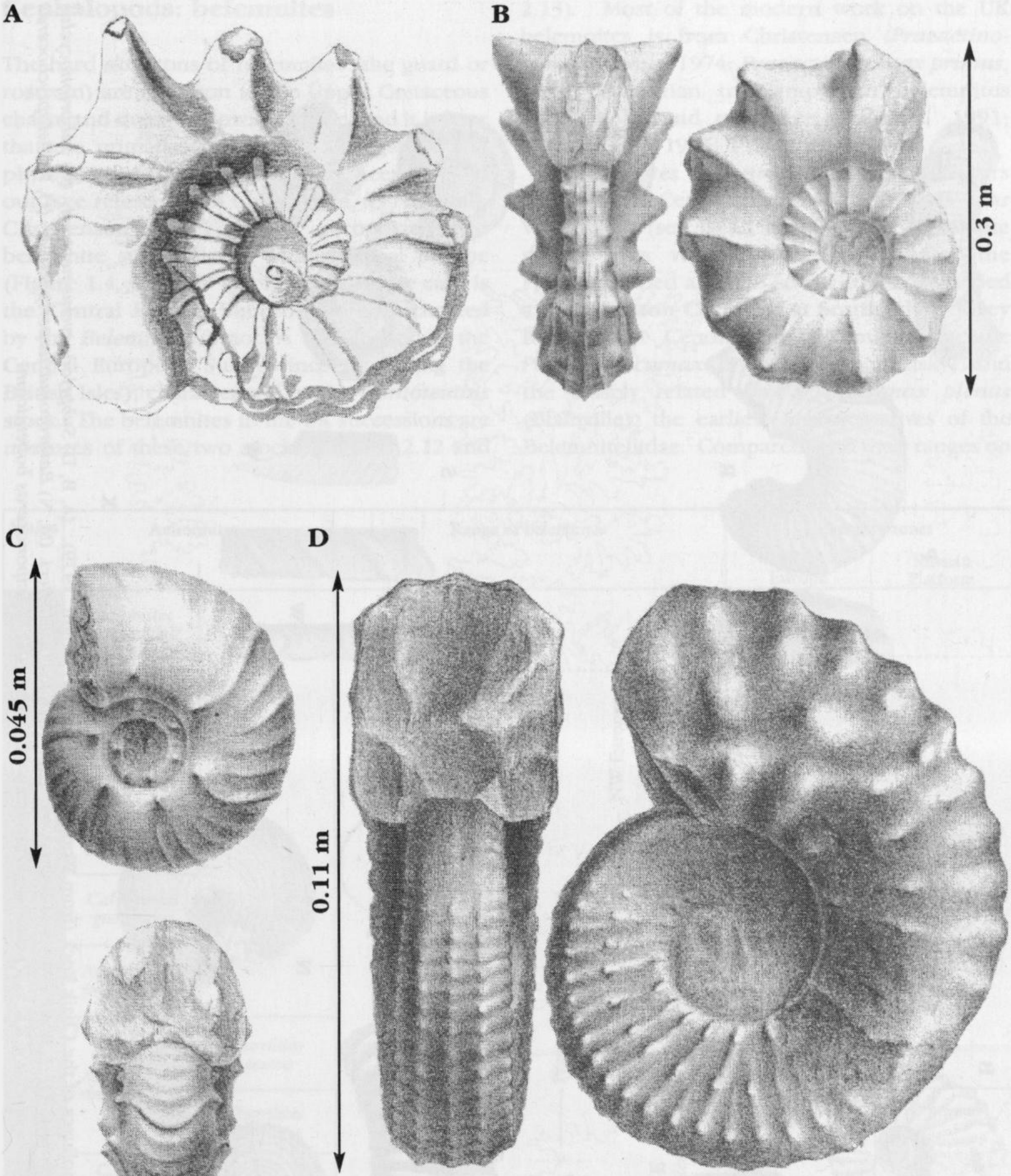


Figure 2.10 Middle and Upper Turonian ammonites. (A) ***Collignoniceras woollgari*** (from Mantell, 1822, Tab. 21, fig. 16). (B) ***Collignoniceras woollgari*** (from Sharpe 1853–1857, pl. 11), typical of the New Pit Chalk Formation. (C) ***Lewesiceras mantelli*** (from Sharpe, 1853–1857, pl. 10) from the topmost Chalk Rock and above the Lewes Marl. (D) ***Romaniceras deverianum*** (from Sharpe 1853–1857, pl. 19), typical between the Glynde Marl and Caburn Marl, basal Lewes Nodular Chalk Formation.

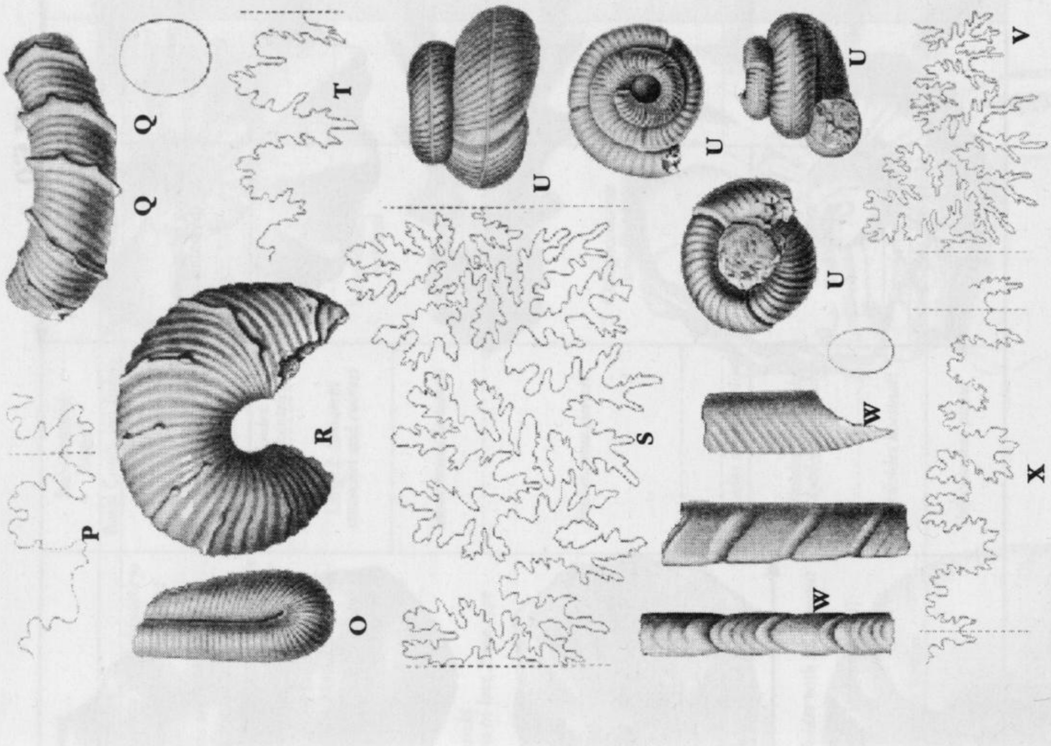


Figure 2.11 Upper Turonian mollusca of the Chalk Rock (from Woods, 1896; see also Wright, 1979). (A, B, D) *Subprionocyclus neptuni*. (C) *Subprionocyclus branneri*. (E, F, G) *Scaphites geinitzi*. (H, I, J) *Allocrioceras angustum*. (K, L) *Turcica? schlueteri*. (M, N) *Bathrotomaria perspectiva*. (O, P) *Metaptychoceras smithi*. (Q, R, S) *Hyphantoceras reussianum*. (T, U, V) *Eubostrychoceras saxonicum*. (W, X) *Sciponoceras bohemicum*.

Cephalopods: belemnites

The hard skeletons of belemnites (the guard or rostrum) are common in the Upper Cretaceous chalks and marls of Boreal Europe, and it is here that the primary work on the stratigraphy and phylogeny of the belemnites has been worked out (see references in Christensen, 1974, 1986). Christensen (1975, 1986) recognizes two belemnite subprovinces within Boreal Europe (Figure 1.4, Chapter 1). The first, in the east, is the Central Russian Subprovince characterized by the *Belemnitella* stock. The second is the Central European Subprovince (including the British Isles), characterized by the *Gonioteuthis* stock. The belemnites in the UK successions are mixtures of these two stocks (Figures 2.12 and 2.13). Most of the modern work on the UK belemnites is from Christensen (*Praeactinocamax plenus*, 1974; *Praeactinocamax primus*, 1990; Coniacian to Campanian belemnites of Norfolk and southern England, 1991; *Belemnitella*, 1995, 1996, 1997, 2000).

Neobibolites ultimus (d'Orbigny) occurs in the basal Cenomanian Rye Hill Sands near Warminster (see **Dead Maid Quarry** GCR site report, this volume), at the base of the Paradoxica Bed and the Lower Inoceramus Bed at **Hunstanton Cliffs** and at **Southerham Grey Pit**. Other Cenomanian belemnites include *Praeactinocamax primus* (Arkhangelsky) and the closely related *Praeactinocamax plenus* (Blainville), the earliest representatives of the Belemnitellidae. Compared with their ranges on

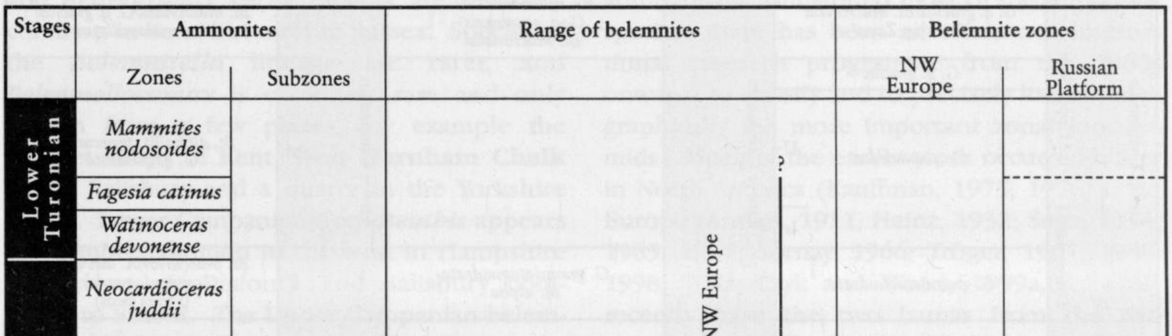


Figure 2.12 Comparison between the ranges of Cenomanian belemnites on the Russian Platform and in north-west Europe. (After Christensen, 1990.)

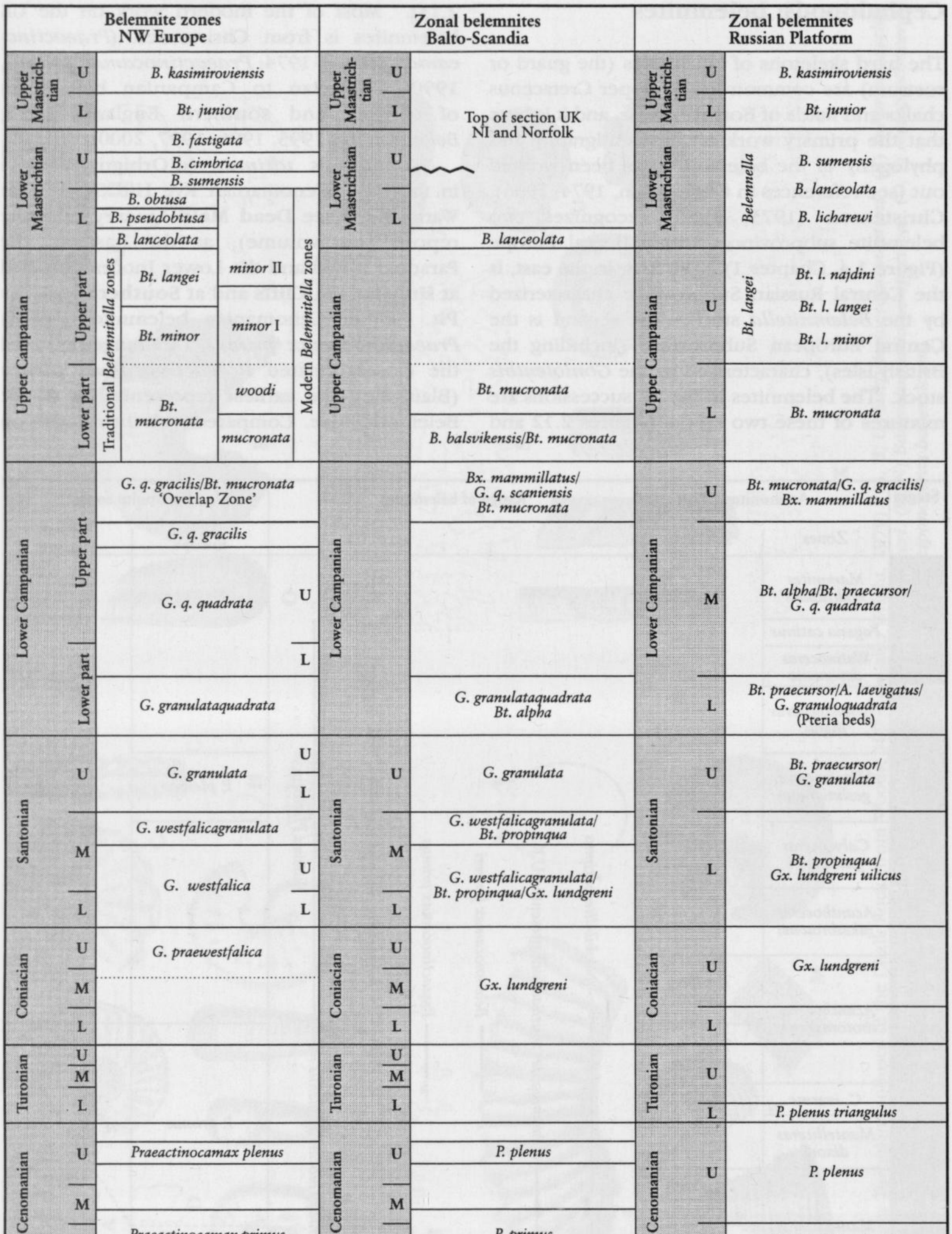


Figure 2.13 Comparison of Upper Cretaceous belemnite zones across Europe, which are only partly represented in the UK and mainly on the Anglo-Brabant Massif. (After Christensen, 1991.) (*A.* = *Actinocamax*; *B.* = *Belemnella*; *Bt.* = *Belemnitella*; *Bx.* = *Belemnellocamax*; *G.* = *Gonioteuthis*; *Gx.* = *Goniocamax*; *N.* = *Neobibolites*; *P.* = *Praeactinocamax*.)

the Russian Platform (Figure 1.4, Chapter 1) these two belemnites have very restricted occurrences in the UK successions. The very unusual, diminutive Middle Cenomanian belemnite *Belemnocamax boweri* Crick, is known from the Totternhoe Stone of Norfolk, Lincolnshire and Yorkshire. This species was once thought to be a pathological form of another Cenomanian species, an idea invalidated by Wright and Wright (1951), and Christensen (1992). *B. boweri* is now considered to be derived from an unknown stock. The very limited ranges of Cenomanian belemnites in the UK probably represent short-lived migrations from the east. Nevertheless, these short-lived events form a good basis for correlation in the UK and in north-west Europe.

In the Coniacian to Lower Campanian chalks of England, species of the *Gonioteuthis* lineage and *Actinocamax verus* (Miller) are relatively common in Kent, but rarer in Sussex. Species of the *Belemnitella* lineage are rarer, and *Belemnellocamax* is extremely rare and only known from a few places, for example the **Thanet Coast** of Kent, **West Harnham Chalk Pit** in Salisbury and a quarry in the Yorkshire Wolds. Lower Campanian *Gonioteuthis* appears to be more common to the west in Hampshire (Portsdown, Mottisfont), and Salisbury compared to Sussex. The Upper Campanian belemnites are restricted to species of *Belemnitella*, and the Maastrichtian faunas of Norfolk and Northern Ireland comprise predominantly of species of *Belemnella* with, in the lower beds, subordinate *Belemnitella* (Schulz, 1982; Christensen, 1999).

The belemnite biostratigraphy in the UK can be linked to the new European Standard Zonation (Figure 2.13). Part of the problem in constructing a satisfactory scheme in the UK is poor and discontinuous exposure of the Campanian strata in the Southern Province and Norfolk and the poor localization of important historical collections. For example the stratigraphy of Brydone's Shawford collection, Hampshire, is very speculative. Only in the Southern Province, however, is the so-called 'overlap' zone (Schmid, 1953, 1959) between *Gonioteuthis quadrata* (Blainville) and *Belemnitella mucronata* (Schlotheim) partly worked out. The key sections for this overlap Zone are **Downend Chalk Pit** and Warren Farm on Portsdown. Recognizing belemnite species is a further problem. Most current workers require populations of well-preserved specimens on which statistical analyses of measurements and parameters can be performed. In the majority of exposures it is not possible to collect statistically significant numbers from any one bed to make reliable species identifications on this basis.

Bivalves: inoceramids

Perhaps the most consistently abundant fossils in the Upper Cretaceous Chalk are the inoceramid bivalves. Even the hinges alone are frequently sufficiently distinctive to have biostratigraphical value. These bivalves exhibit a great variety of forms, which are generally easily identifiable, and have restricted ranges, providing ideal zonal material. Following the monograph of Woods (1911–1912, Volume 2, Parts 7 and 8), which illustrated most of the important species, there has been an enormous international research programme from the 1960s onwards to classify and to precisely locate stratigraphically the more important zonal inoceramids. Much of the earlier work occurred either in North America (Kauffman, 1975, 1976) or in Europe (Andert, 1911, Heinz, 1932; Seitz, 1934, 1965, 1967; Sornay, 1966; Trõger, 1967, 1989, 1998; Walaszczyk and Wood, 1999a,c). Only recently have the two faunas from the two continents been thoroughly compared and synonymies established (Kennedy *et al.*, 2000; Walaszczyk and Cobban, 2000). Studies in the Pacific in Japan (Noda, 1975, 1984; Matsumoto and Noda, 1986), New Zealand (Crampton, 1996), and other regions of the world, including Southern Africa, India and Brazil, have illustrated the global extent of many species of inoceramids. However, because of ongoing research, many of the species names are subject to change and, in most cases, no agreed lineages exist. It is not possible, therefore, to provide diagrams for the phylogeny of inoceramids.

The bivalve family Inoceramidae is first recorded in the Permian System and it died out at the end of the Cretaceous Period. Two broad concepts are accepted within the Inoceramidae, the genera *Mytiloides* and *Inoceramus*. The type species of *Inoceramus* is *I. cuvieri* (J. Sowerby) based on the original *Inoceramus* sp. Mantell from the Lewes chalk pits, Sussex (probably latest Turonian or Lower Coniacian in age from the **Southerham Pit**). *Mytiloides* is essentially a Turonian genus whereas *Inoceramus* ranges throughout the

Upper Cretaceous succession. Other genera include *Cremnoceramus* and *Volviceramus* (Coniacian), *Cladoceramus* (Santonian), *Sphenoceramus* (Santonian–Campanian) and *Cataceramus* (Campanian).

Inoceramids tend to occur in great abundance at particular horizons. The Cenomanian species *Inoceramus crippsi* (Mantell) (Figure 2.14) is abundant, particularly in the Lower Cenomanian marly chalks (Figure 2.2) and tends to alternate at some levels with *I. virgatus* (Schlüter). *I. virgatus* (Figure 2.14) is a feature of the more calcareous 'Bank' (Figure 2.8; Figures 3.4, 3.108 and 3.109, Chapter 3) in the *Mantelliceras dixoni* Zone. *Inoceramus schoendorfi* (Heinz) is common near the top of the West Melbury Marly Chalk. Above this level inoceramids are less common but return as a band of common *I. atlanticus* (Heinz) (Figure 2.14) in the Triple Marls beneath Jukes-Browne Bed 7 (Figure 2.8). In the Upper Cenomanian Substage, *I. pictus* J. de C. Sowerby (Figure 2.14) is a key species and its replacement upwards by *Mytiloides* in the Meads Marls is an international proxy marker for the base of the Turonian Stage.

The most troublesome horizon for stratigraphers and palaeontologists has been that yielding the Lower Turonian *Mytiloides* assemblages (Figure 2.15). Many North American concepts have been applied to the great variety of forms present in European assemblages. Hence there are numerous names in the literature. Gradually the synonymy is becoming clearer and a rationalization of the species names now indicates that a relatively simple stratigraphy may exist (First Inoceramid Workshop, Hamburg 1992; Harries *et al.*, 1996; Kennedy *et al.*, 2000). In the more expanded sections of Lower Turonian chalk in Sussex, *Mytiloides puebloensis* Walaszczyk and Cobban and *M. kossmati* (Heinz) probably occur in a broad zone near the base of the Turonian Stage with a narrow band of *M. hattini* Elder at the base. The detailed stratigraphy of the Lower Turonian inoceramid bivalves is unclear but it is probable that there are some bands dominated by *M. mytiloides* and others by *M. labiatus* (Schlotheim). Other species co-occur in this interval. These *Mytiloides* species are replaced above the Gun Gardens Main Marl by *M. subhercynicus* (Seitz) (Figure 2.16) up to the Glyndebourne Hardground 1 (Mortimore and Pomerol, 1996). Inoceramids then return in the form of *I. cuvieri* for the major part of the Middle Turonian Substage (Figure 2.16). *Inoceramus* dominates in the Middle and lower Upper Turonian (*I. cuvieri*, *I. lamarcki*), with *Mytiloides* (e.g. *M. striatoconcentricus*, *M. herbichi* (Figures 2.17 and 2.18) dominating at the top of the Turonian Stage.

The Second Inoceramid Workshop (held in Freiburg in 1996; Walaszczyk and Wood, 1999a) concentrated on the Upper Turonian and Lower and Middle Coniacian assemblages (Figures 2.17–2.20). The outcomes are included in Figures 2.9 and 2.21. Of particular importance has been the resolution of the vexed problems of the species and subspecies of *Cremnoceramus*, notably the recognition of the American taxon *Cremnoceramus deformis erectus* (Meek) (formerly *C. rotundatus sensu* Tröger *non* Fiege). There is now general agreement on a new zonal scheme for this interval (Walaszczyk and Wood, 1999b,c; Walaszczyk and Cobban, 2000).

In the Middle Coniacian to Upper Santonian interval, the occurrence and ranges of inoceramid species are comparatively well known (Figures 2.20–2.23). In the Campanian succession (Figures 2.24–2.26) there is still much work to be done and the information given in Figure 2.27 is provisional. Figures 2.8, 2.9, 2.21, 2.22 and 2.27 provide detailed information for the first time on many of the inoceramid horizons in the UK Upper Cretaceous Series and will inevitably be subject to revision in the future.

Other bivalves

The Upper Cretaceous Chalk is rich in bivalves other than inoceramids. Oysters are common at many horizons and are used for correlation in the Cenomanian succession (*Pycnodonte* events, see Figure 2.28). In the Upper Santonian and basal Campanian strata the oyster-rich coarse chalks are known as 'Grobkreide facies' and are characterized by *Pseudoperna boucheroni* (Woods *non* Coquand) (Figure 2.28). One unit near the top of the Lower Maastrichtian succession at Trimingham contains abundant *Agerostrea lunata* (Woods *non* Nilsson). A particular feature of the Upper Turonian and Lower Campanian chalks is the occurrence of the spectacularly spiny bivalve *Spondylus spinosus* (J. Sowerby) and the less strongly spinose *Spondylus* cf. *latus* (J. Sowerby) respectively.

The book *Fossils of the Chalk* (Owen and Smith, 1987) contains excellent illustrations of many of the more important fossil bivalves.

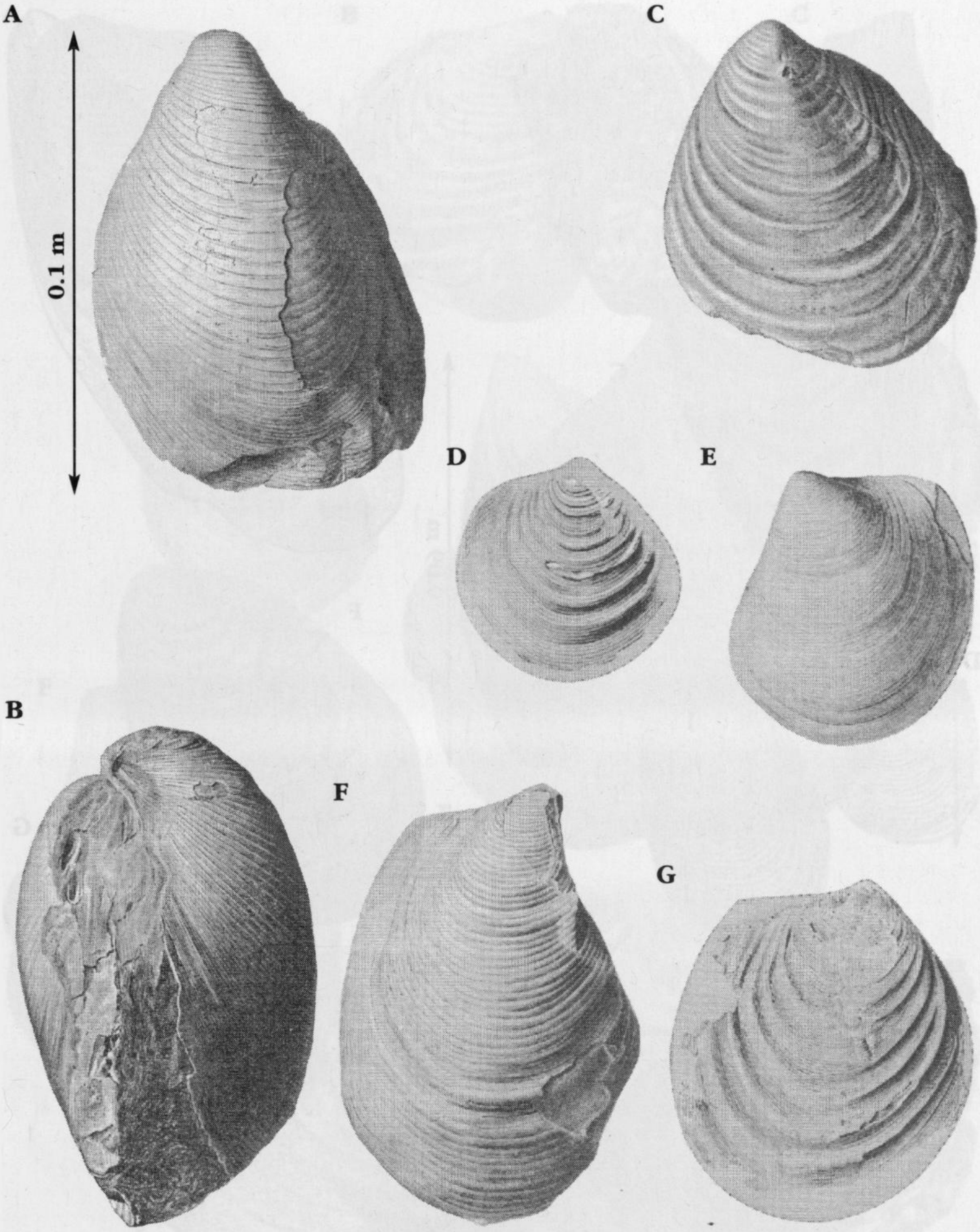


Figure 2.14 Cenomanian inoceramid bivalves. (A, B) Holotype of *Actinoceramus tenuis* (from Woods, 1911, text-fig. 31). (C) *Inoceramus crippsi* (from Woods, 1911, text-fig. 34). (D) *Inoceramus atlanticus* (from Woods, 1911, pl. 48, fig. 5). (E) *Inoceramus virgatus scalprum* (from Woods, 1911, pl. 49, fig. 3a) typical of the Lower Cenomanian 'Bank' of limestones. (F) *Inoceramus pictus* (from Woods, 1911, pl. 49, fig. 5) typical of the Plenus Marls Member and the basal few metres of the Melbourn Rock, Upper Cenomanian. (G) *Inoceramus atlanticus* (from Woods, 1911, pl. 49, fig. 1), typical of the Middle Cenomanian '*atlanticus*' flood. Scale bar applies to all specimens.

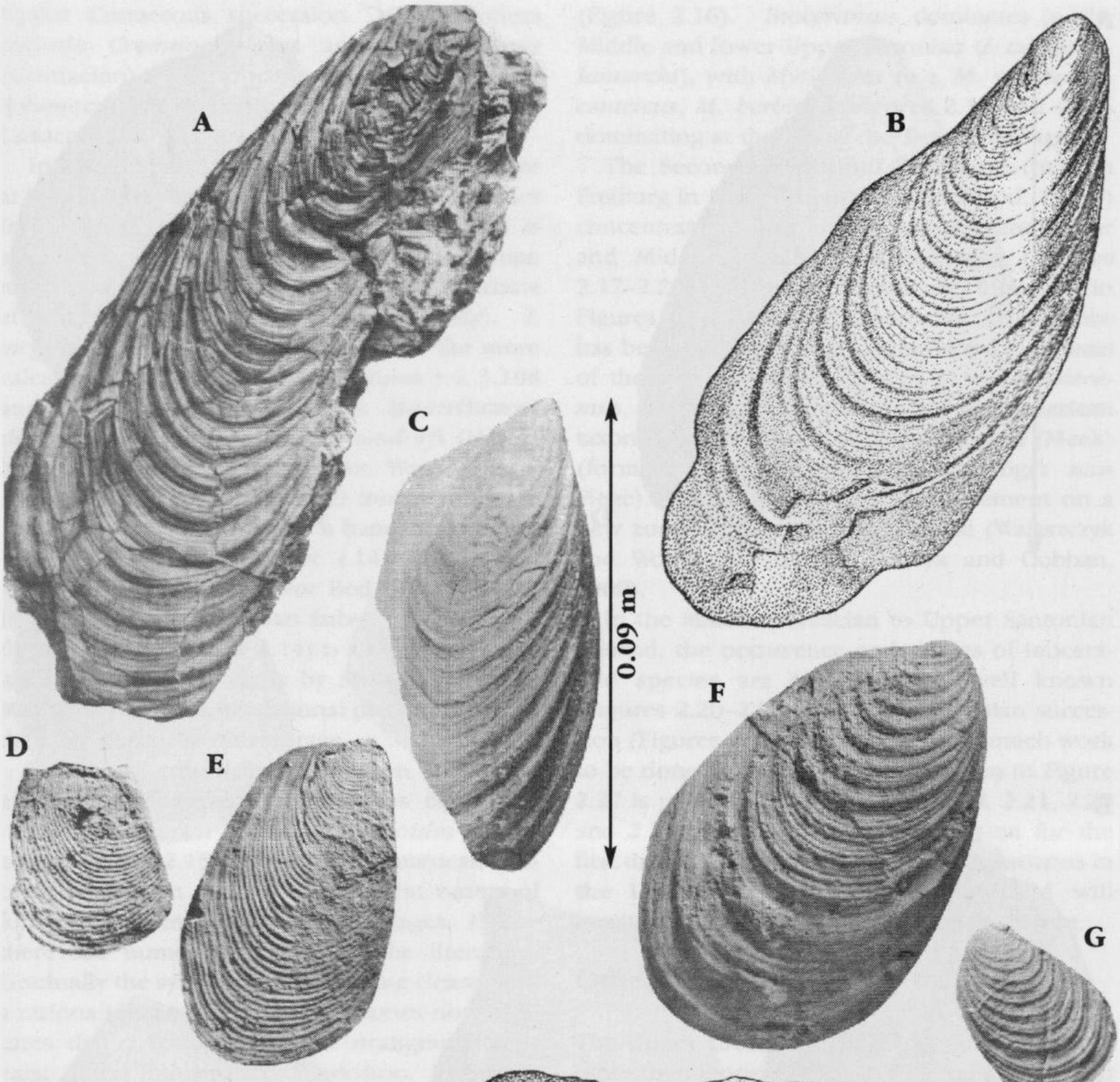


Figure 2.15 Lower Turonian inoceramid bivalves. (A–C) *Mytiloides mytiloides*; (A) left valve (from Seitz, 1934, pl. 36) typical of the Holywell Nodular Chalk; (B) right valve (from Seitz, 1934, text-fig. 2c) from a sandstone steinkern; (C) the type from Woods, 1911, text-fig. 37. (D, E) *Mytiloides hattini* (from Elder, 1991); (E) is the holotype. (F, G) *Mytiloides puebloensis* (formerly *M. opalensis* and/or *M. columbianus* of authors); (F) (Elder, 1991, fig. 4.9) is a typical example; (G) (Elder, 1991, fig. 4.2) shows features transitional to *M. kossmati* (doubling of concentric rugae). (H, I) *Mytiloides labiatus*; (H) from Seitz, 1934, pl. 38, this is closest to the missing type; (I) from a sandstone steinkern (from Seitz, 1934, fig. 9a). Scale bar applies to all specimens.

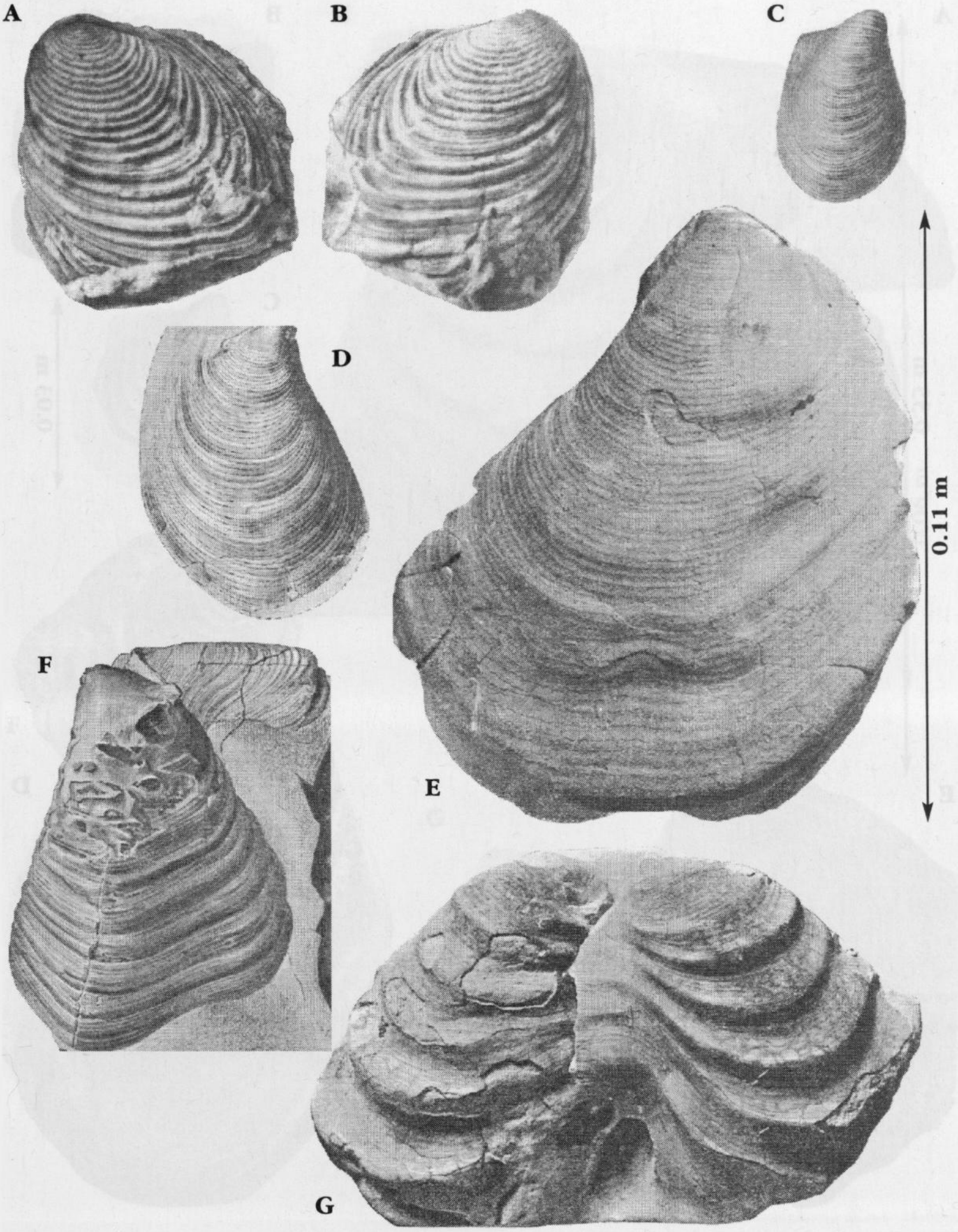


Figure 2.16 Middle Turonian inoceramid bivalves. (A, B) *Mytiloides subhercynicus*, typical of the lowest New Pit Chalk (from Seitz, 1934, pl. 40). (C) *Inoceramus apicalis* (lectotype, from Woods, 1912, pl. 53, fig. 4a), Holywell Nodular Chalk, Hitchin. (D, E) *Inoceramus cuvieri*; (D) typical of *cuvieri* (from Woods, 1912, pl. 53, fig. 7), New Pit Chalk, Royston; (E) the holotype of *cuvieri* (from Woods, 1912, holotype, text-fig. 73), New Pit Chalk, Royston. (F, G) *Inoceramus lamarcki*; (F) the holotype of *lamarcki* from the Glynde Marls–Southerham Marls interval, Dover (Woods, 1912, text-fig. 63); (G) form typical of mid-New Pit Chalk around Lewes (Woods, 1912, text-fig. 69). Scale bar applies to all specimens.

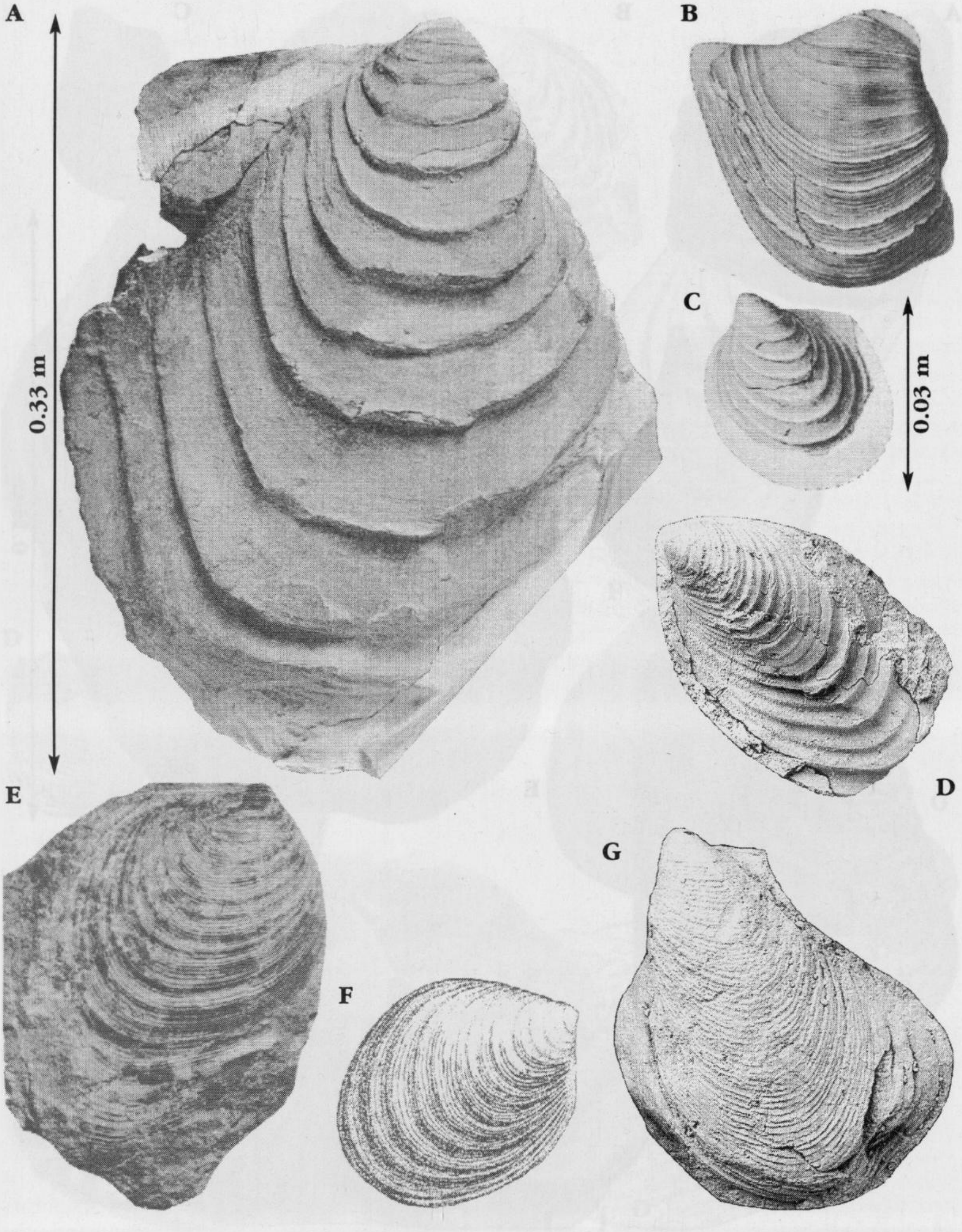


Figure 2.17 Upper Turonian inoceramid bivalves. (A) ***Inoceramus lamarcki stuemkei***, typical between Caburn and Bridgewick marls, (from Woods, 1912, text-fig. 82). (B) ***Inoceramus websteri sensu*** Woods ***non*** Mantell, typical of the beds above the Lewes Marl (from Woods, 1912, pl. 53, fig. 1). (C) ***Mytiloides costellatus sensu stricto*** (from Woods, 1912, pl. 54, fig. 5). (D) ***Mytiloides labiatoidiformis***, typical of the Lewes Marl and the beds above (from Walaszczyk and Wood, 1999b, pl. 1, fig. 8). (E, F) ***Mytiloides incertus*** (from Noda, 1984). (G) ***Mytiloides striatoconcentricus***, typical of the Kingston Nodular Beds, (from Walaszczyk and Wood, 1999b, pl. 1, fig. 11). Large scale bar applies to A, E; small scale bar applies to B, C, D, F and G.

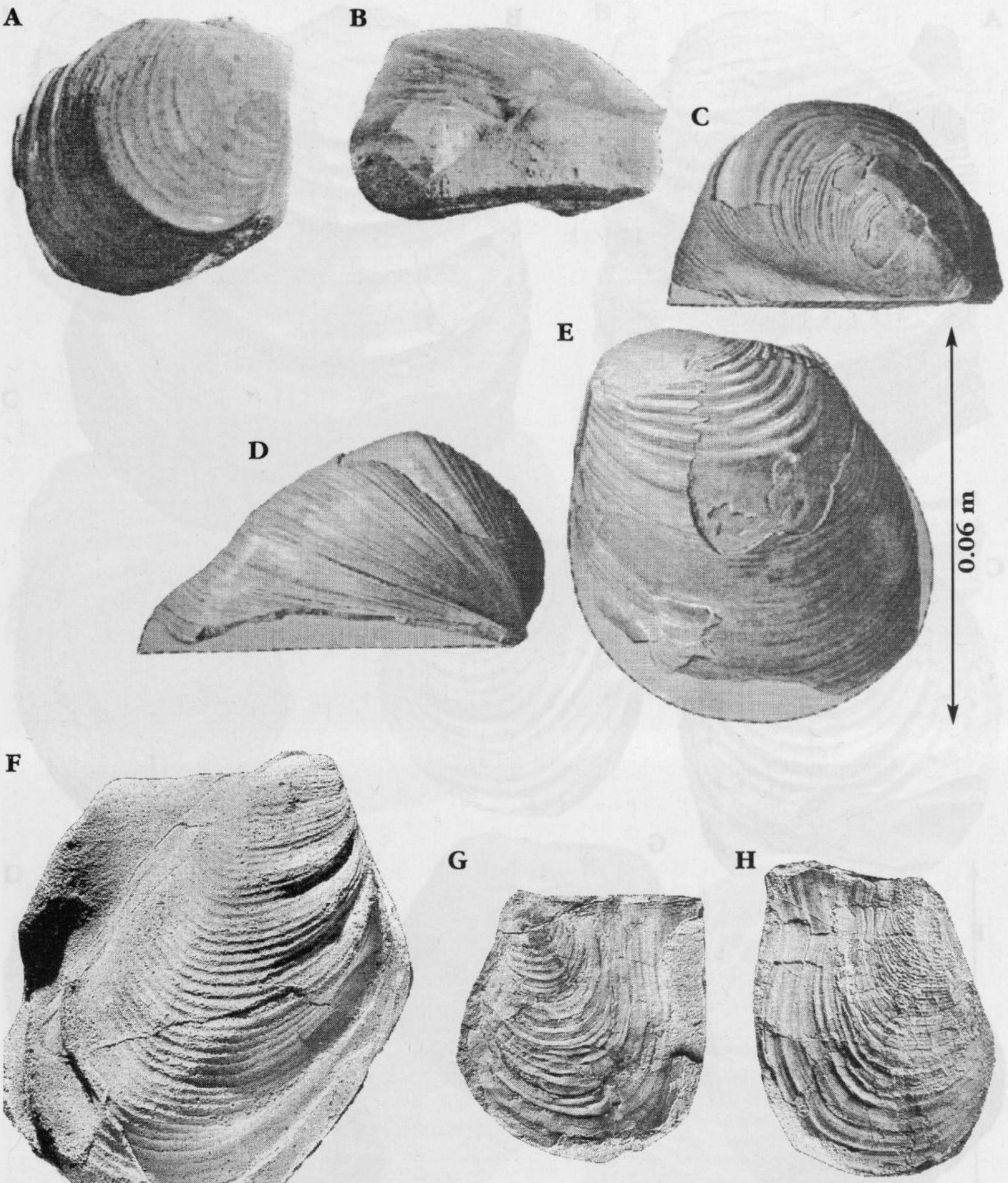


Figure 2.18 Upper Turonian and Lower Coniacian inoceramid bivalves. (A–E) ***Cremnoceramus crassus inconstans***; (A, B) the lectotype, the original of *Inoceramus* sp., Mantell, 1822 (from Woods, 1912, text-fig. 42); (C–E) from Woods, 1912, text-fig. 43. (F) ***Inoceramus lusatiae***, holotype: typical of the Navigation Hardgrounds (from Walaszczyk and Wood, 1999b, pl. 2, fig. 4). (G, H) ***Mytiloides herbichi***, probably typical of the beds around the Cuilfail Zoophycos (from Walaszczyk and Wood, 1999b, pl. 1, fig. 5). Scale bar applies to all specimens.

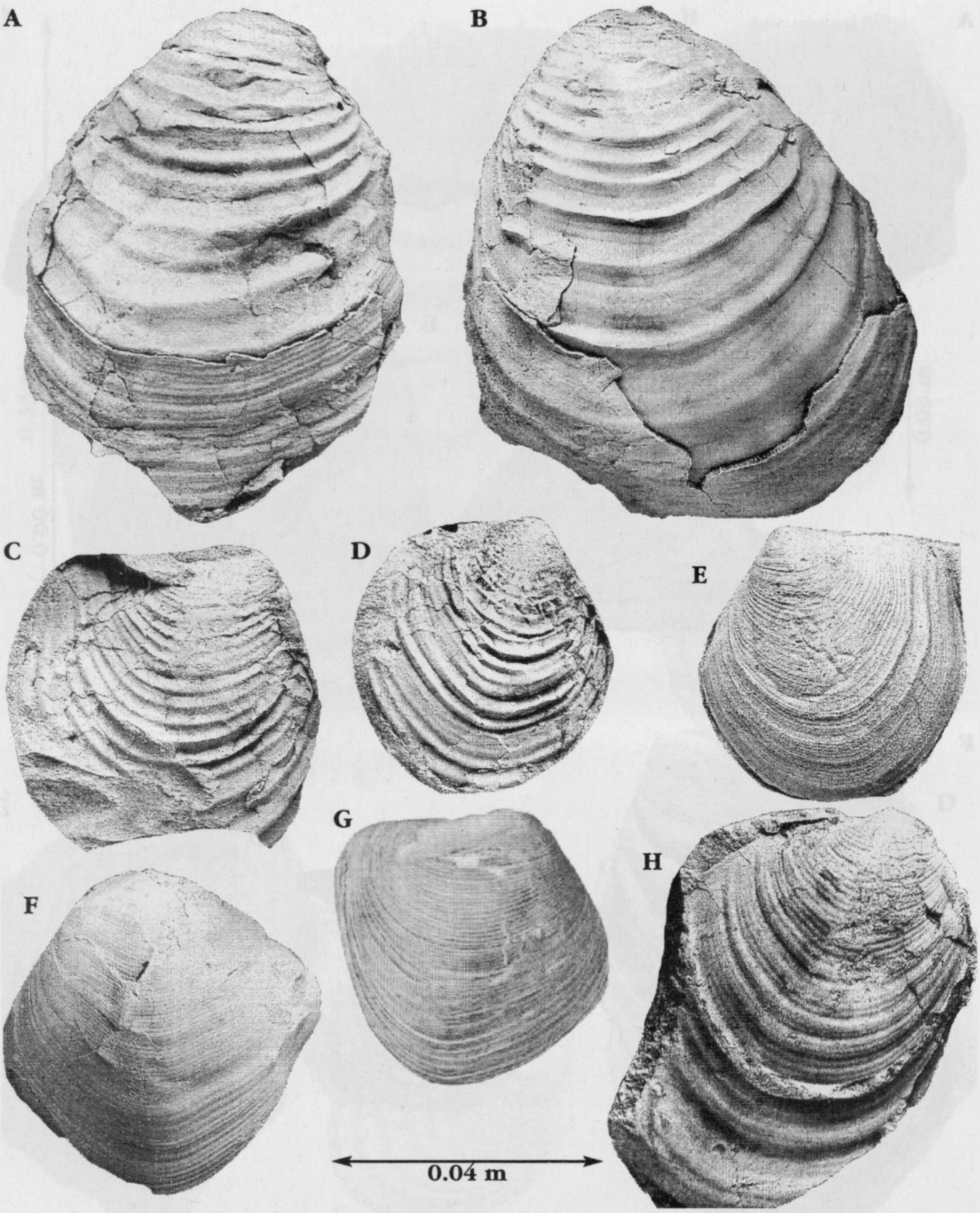


Figure 2.19 Topmost Turonian and basal Coniacian inoceramid bivalves. (A, B) *Cremnoceramus deformis erectus* typical of beds just above the Navigation Hardgrounds and the larger forms from the Hope Gap Hardground (from Walaszczyk and Wood, 1999b, pl. 7, figs 7, 8). (C, D) *Cremnoceramus deformis erectus*, typical of Navigation Marls, (from Walaszczyk and Wood, 1999b, pl. 7, figs 1, 2). (E–G) *Cremnoceramus waltersdorfensis waltersdorfensi*; (E) typical of the Southern Province (from Walaszczyk and Wood, 1999b, pl. 15, fig. 2); (F) typical of beds below the Navigation hardgrounds (from Walaszczyk and Wood, 1999b, pl. 17, fig. 3); (G) typical of beds between Navigation and Cliffe hardgrounds in the Southern Province (from Woods, 1912, pl. 52, fig. 1). (H) *Cremnoceramus waltersdorfensis bannovrensis* typical of beds between Cliffe and Hope Gap hardgrounds (from Walaszczyk and Wood, 1999b, pl. 11, fig. 2). Scale bar applies to all specimens.

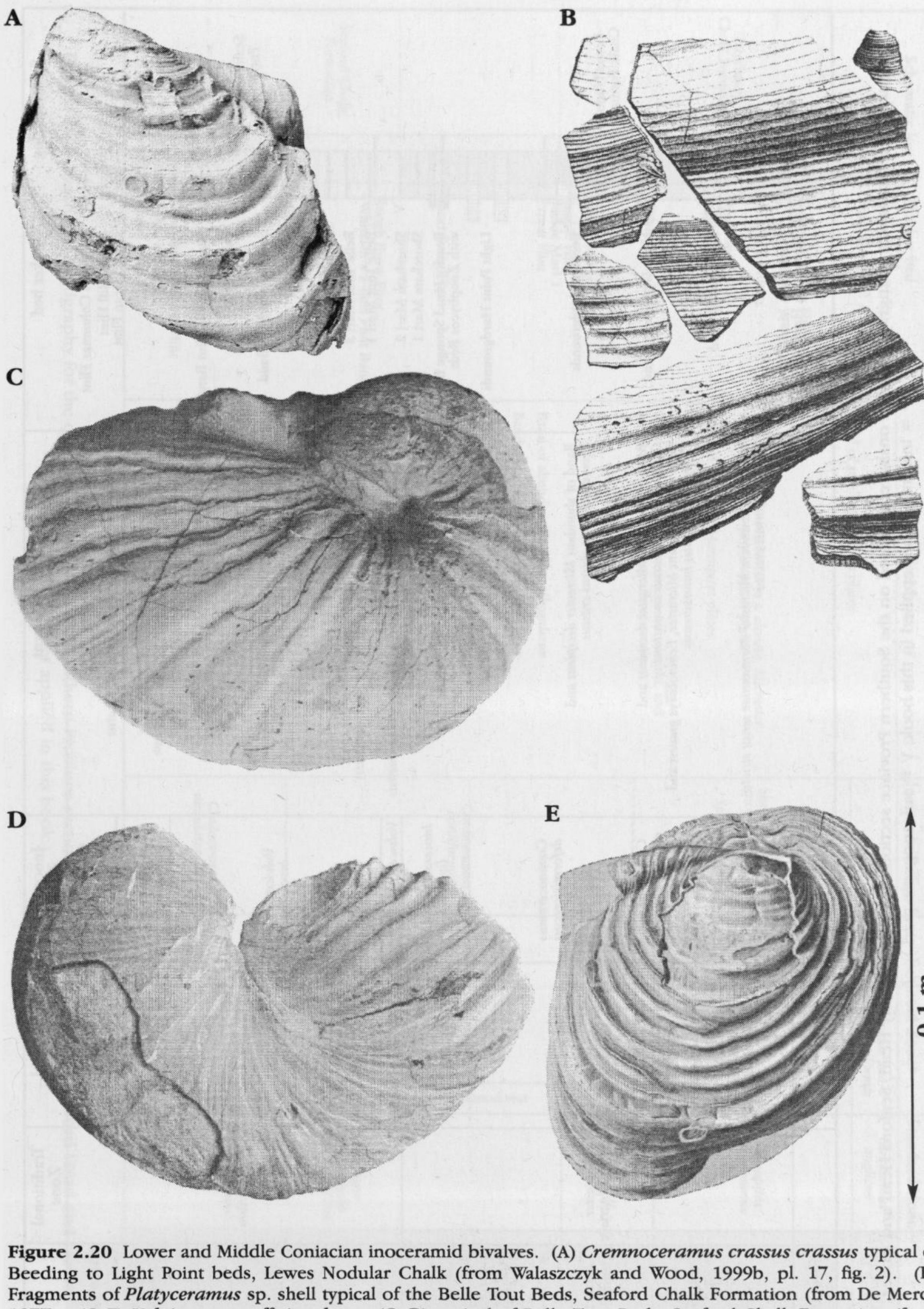


Figure 2.20 Lower and Middle Coniacian inoceramid bivalves. (A) *Cremnoceramus crassus crassus* typical of Beeding to Light Point beds, Lewes Nodular Chalk (from Walaszczyk and Wood, 1999b, pl. 17, fig. 2). (B) Fragments of *Platyceramus* sp. shell typical of the Belle Tout Beds, Seaford Chalk Formation (from De Mercy, 1877). (C–E) *Volviceramus* aff. *involutus*; (C, D) typical of Belle Tout Beds, Seaford Chalk Formation (from Woods, 1912, text-figs 93, 90); (E) typical cap valve in Belle Tout Beds, Seaford Chalk Formation, common 1.8–2 m below the Seven Sisters Flint Band (from Woods, 1912, text-fig. 94). Scale bar applies to all specimens.

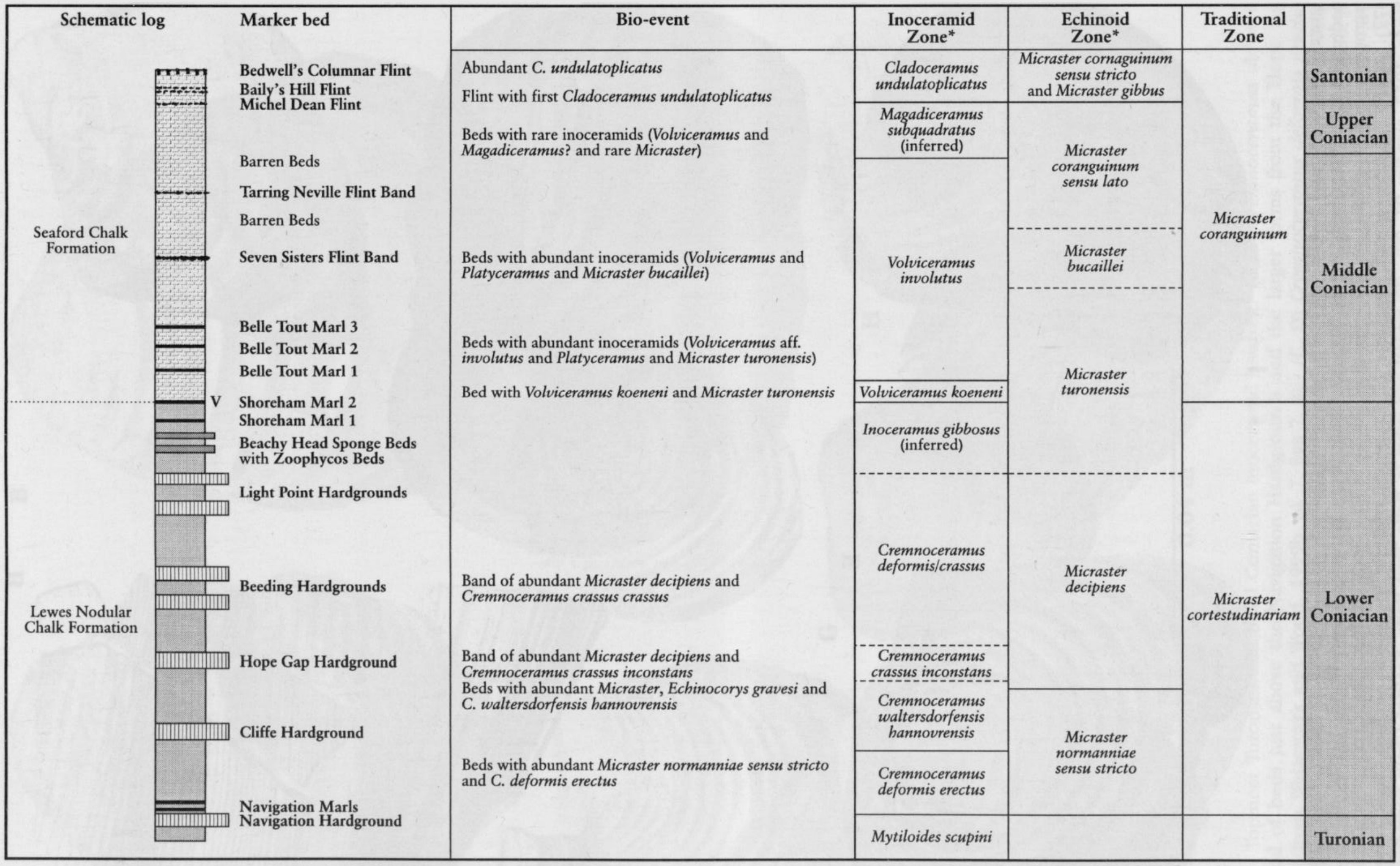


Figure 2.21 Coniacian stratigraphy for the onshore UK based on the Southern Province sections at Lewes, Beachy Head, Seaford Head and Dover. (* = informal zones applied in this book; V = vulcanogenic marl.)

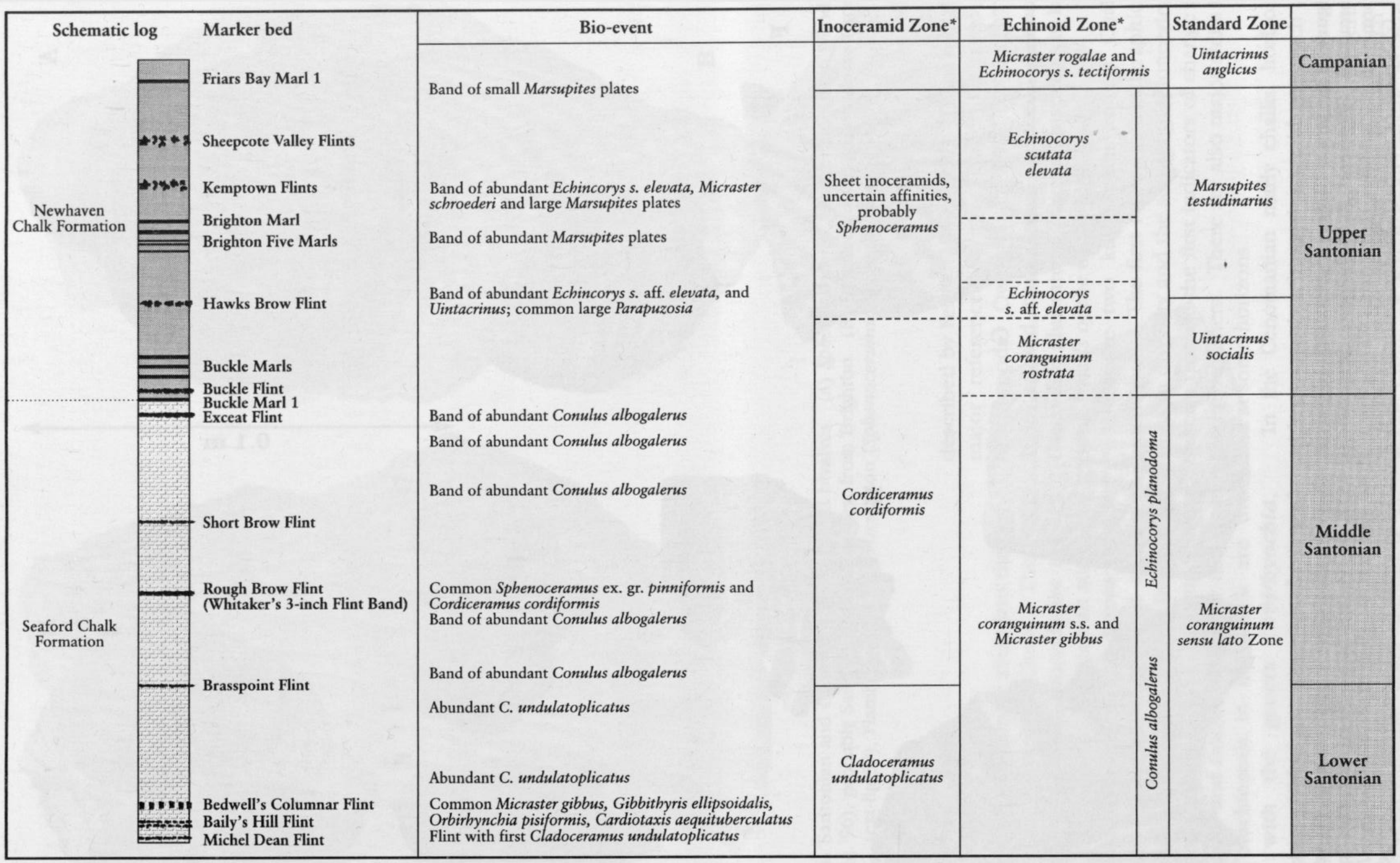


Figure 2.22 Santonian stratigraphy for the onshore UK based on the Southern Province sections at Lewes, Beachy Head, Seaford Head and Dover. (* = informal zones applied in this book.)

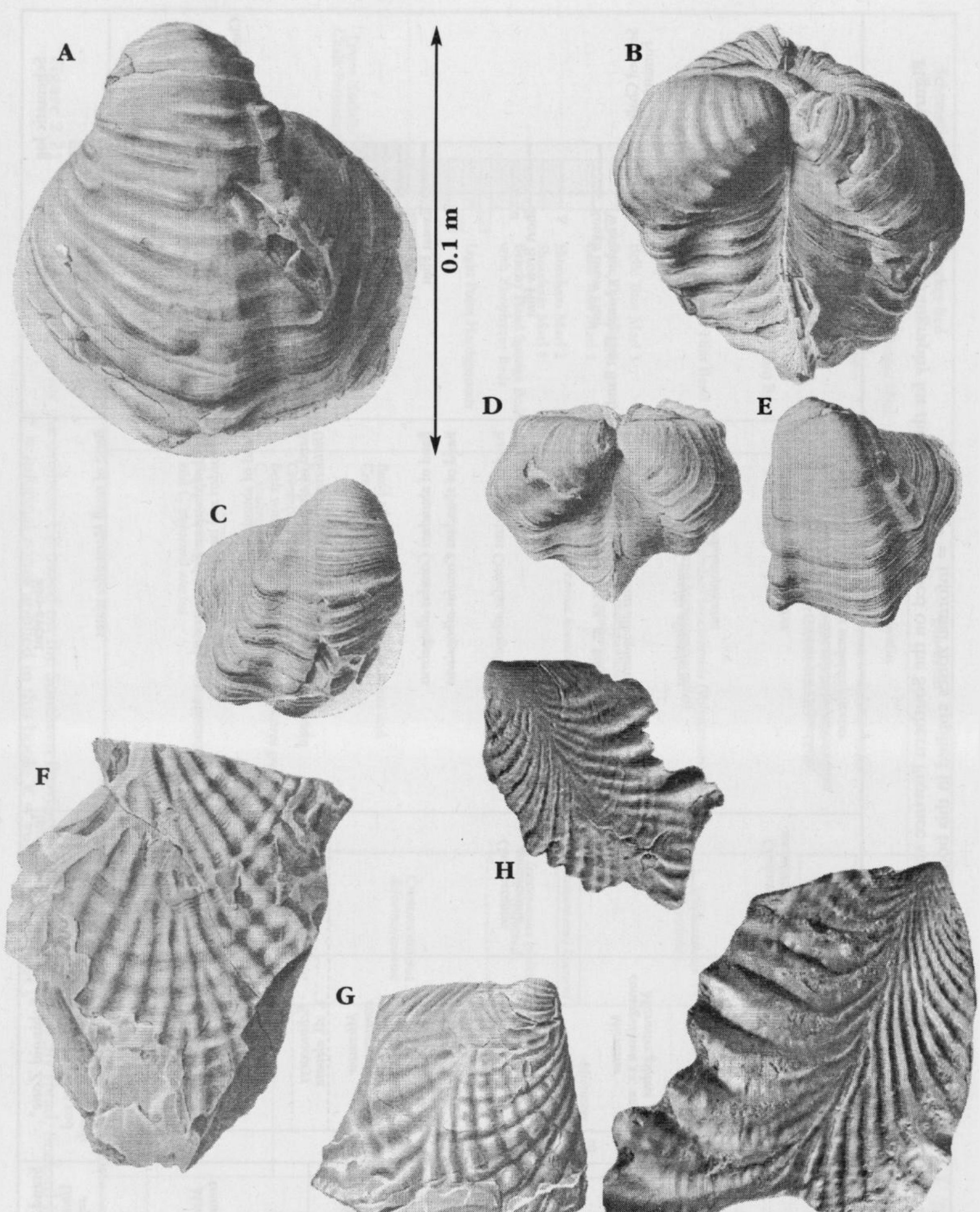


Figure 2.23 Lower Santonian inoceramid bivalves. (A–E) *Cordiceramus cordiformis*; (A, B) Seaford Chalk Formation, Gravesend, Kent (holotype from Woods, 1912, pl. 53, figs 8a,b); (C–E) from the Seaford Chalk Formation, Micheldever, Hants (from Woods, 1912, pl. 54, figs 3a,b, 4). (F–I) *Cladoceramus undulatoplicatus*; (F, G) typical of the basal Santonian including Bedwell's Columnar Flint Band (from Woods, 1912, text-figs 60, 61), from Haldon, Devon; (H, I) typical of the basal Santonian (from Seitz, 1961). Scale bar applies to all specimens.

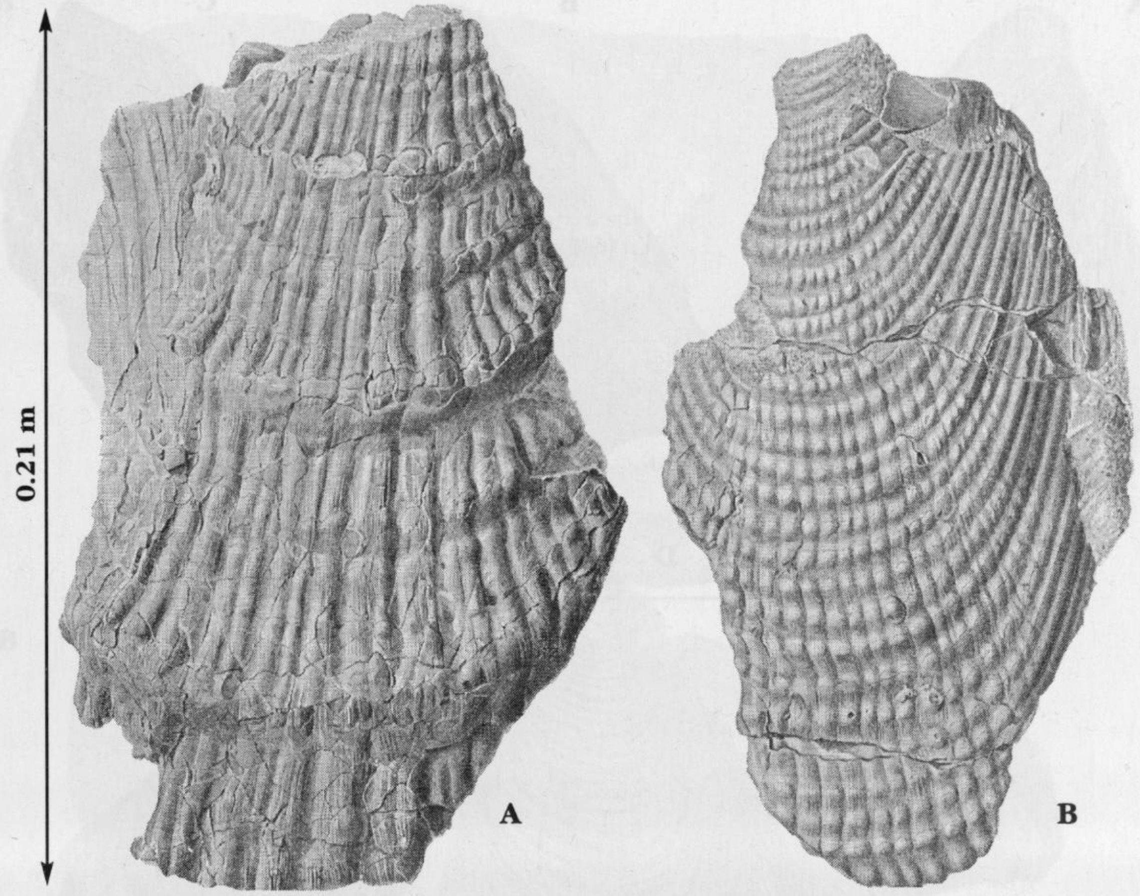


Figure 2.24 Santonian and Campanian inoceramid bivalves. (A) *Sphenoceramus pinniformis* (from Woods, 1912, text-fig. 96), probably Santonian crinoid zones, from Brighton. (B) *Sphenoceramus tuberculatus* (from Woods, 1912, text-fig 59), Flamborough Chalk Formation (*Sphenoceramus lingua* Zone), Sewerby.

Brachiopods

Brachiopods are surprisingly abundant throughout the Upper Cretaceous Chalk. There are some horizons where brachiopods are the key indices for correlation and provide an additional environmental indicator of conditions on the chalk seabed. Both inarticulate and articulate brachiopod classes are present, the Inarticulata being represented by the long-ranging genera *Ancistrocrania* and *Isocrania*. By far the most abundant brachiopods in the Chalk are the Articulata with the genera *Orbirhynchia*, *Cretirhynchia*, *Gibbithyris*, *Concinnithyris* and *Terebratulina* being the most widely used for stratigraphy. Following Davidson's monographs of British Brachiopoda (1852–1854, 1874), the Chalk Terebratulidae were described by Sahni (1929) and the Rhychonellidae were described by Pettitt (1949, 1954). These remain major references for the Upper Cretaceous brachiopods. Owen (1962, 1968, 1970, 1977, 1988) revised many Upper Cretaceous genera. Owen also illustrated all the major species in his book *Fossils of the Chalk* (1987).

There are two key aspects to the Chalk brachiopods. The first relates to stratigraphical shifts in diversity and the second to 'pioneering' species that are the first indicators of change in the environment. There are also major shifts in size at some horizons.

In the Cenomanian marly chalks, horizons with diverse brachiopod assemblages, such as the Cast Bed (Figure 2.8) contrast with the *Orbirhynchia mantelliana* (J. de C. Sowerby) dominated horizons above and below. Each of these types of brachiopod event is stratigraphically consistent and widespread across

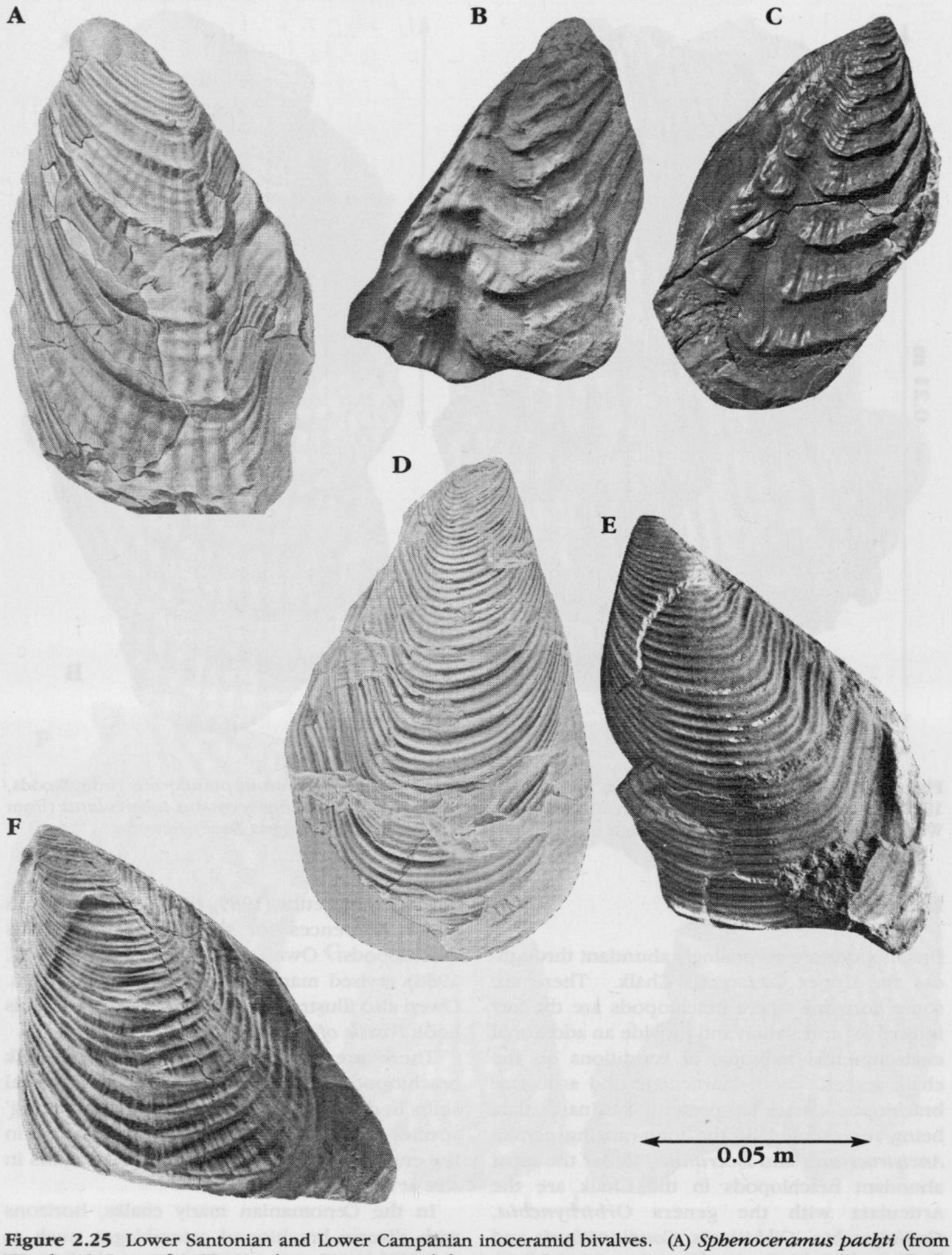


Figure 2.25 Lower Santonian and Lower Campanian inoceramid bivalves. (A) ***Sphenoceramus pachti*** (from Woods, 1912, text-fig. 57), Northern Province, Yorkshire coast, Santonian ***Micraster coranguinum*** Zone. (B, C) ***Sphenoceramus pachti pachti*** (from Seitz, 1965). (D, E) ***Sphenoceramus lingua***; (D) typical of the upper Flamborough Chalk Formation, Lower Campanian, Northern Province (from Woods, 1912, text-fig. 54); (E) typical of the upper Flamborough Chalk Formation, Lower Campanian (from Seitz, 1965). (F) ***Sphenoceramus patootensiformis*** typical of the Lower Campanian, Northern Province (from Seitz, 1965). Scale bar applies to all specimens.

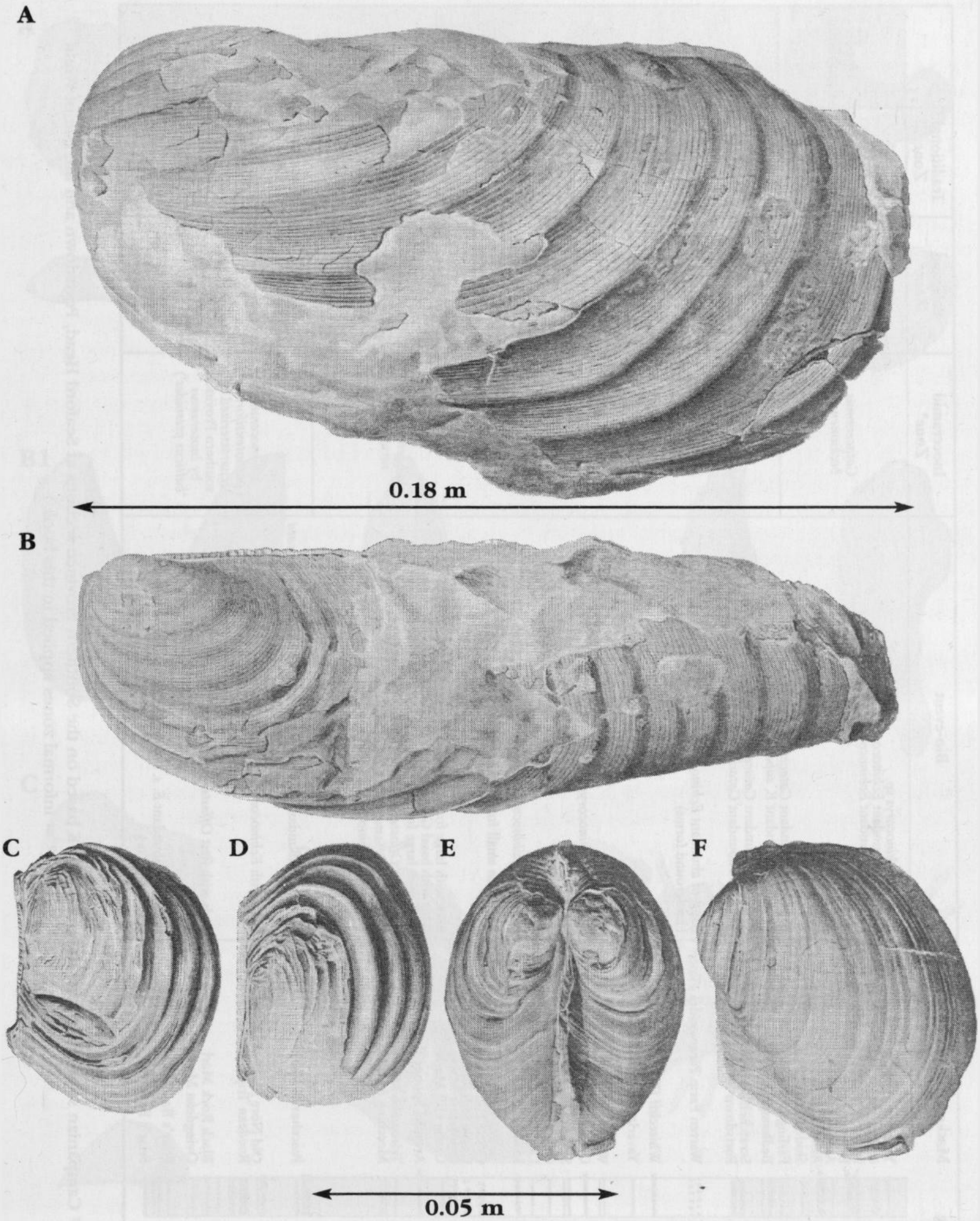


Figure 2.26 Campanian inoceramid bivalves. (A, B) *Inoceramus balticus pteroides* (name is uncertain) typical of the top Old Nore Beds and the Peacehaven and Meeching Beds, Newhaven Chalk (*Offaster pilula* Zone, lower belt) (from Woods, 1912, text-fig. 51). (C, D) *Cordiceramus*? sp. (co-occurs with *Sphaeroceramus sarumensis* in the *Hagenowia blackmorei* Subzone at East and **West Harnham**, Salisbury (from Woods, 1912, pl. 51, figs 3a,b). (E, F) *Sphaeroceramus sarumensis*; (F) from the Newhaven Chalk Formation, *Hagenowia blackmorei* Subzone, at East and **West Harnham**, Salisbury (from Woods, 1912, pl. 52, figs 2a,b). Large scale bar applies to A, B; small scale bar applies to C–F.

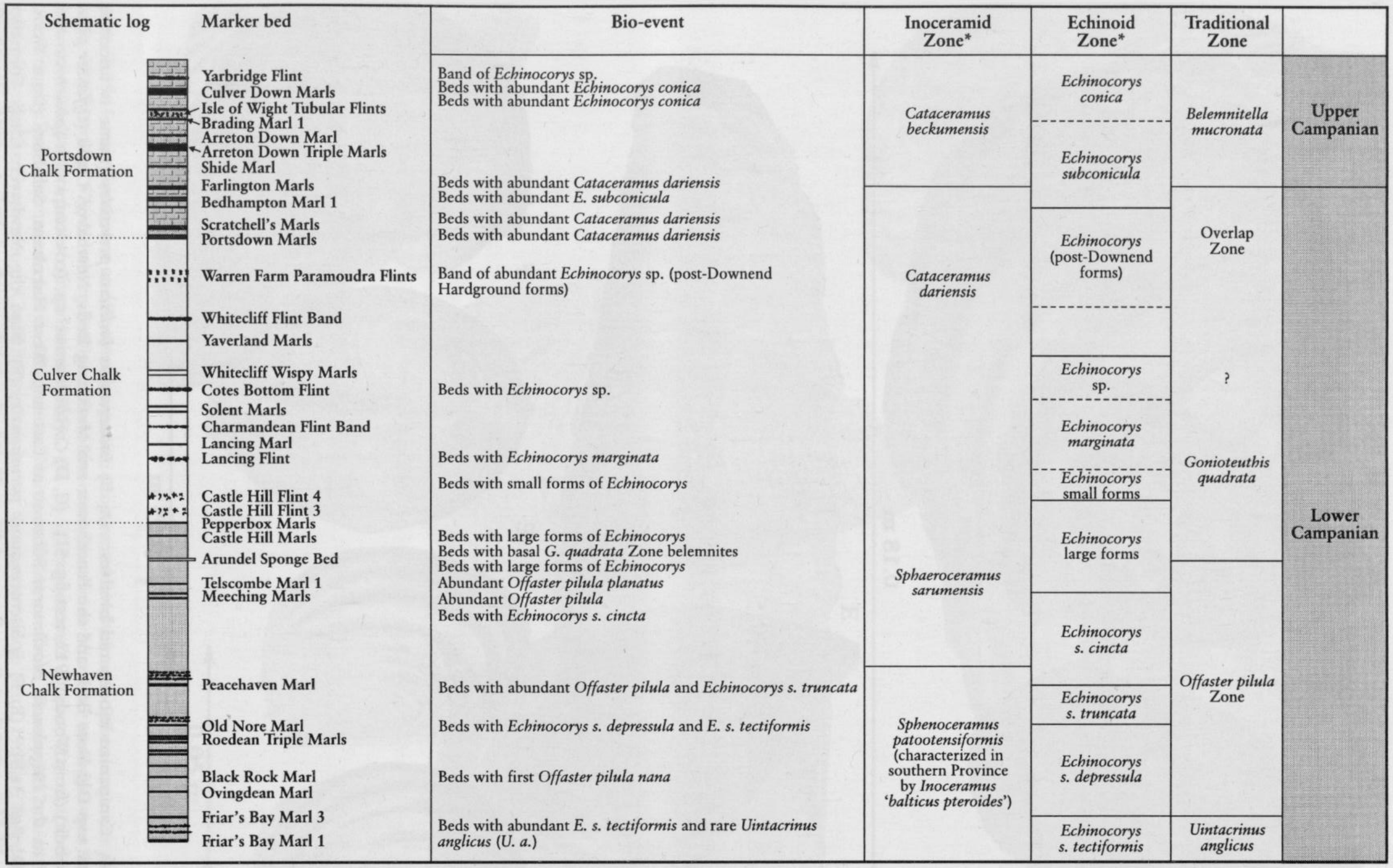


Figure 2.27 Campanian stratigraphy for the onshore UK based on the Southern Province sections at Seaford Head, Portsdown and the Isle of Wight. (* = informal zones applied in this book.)

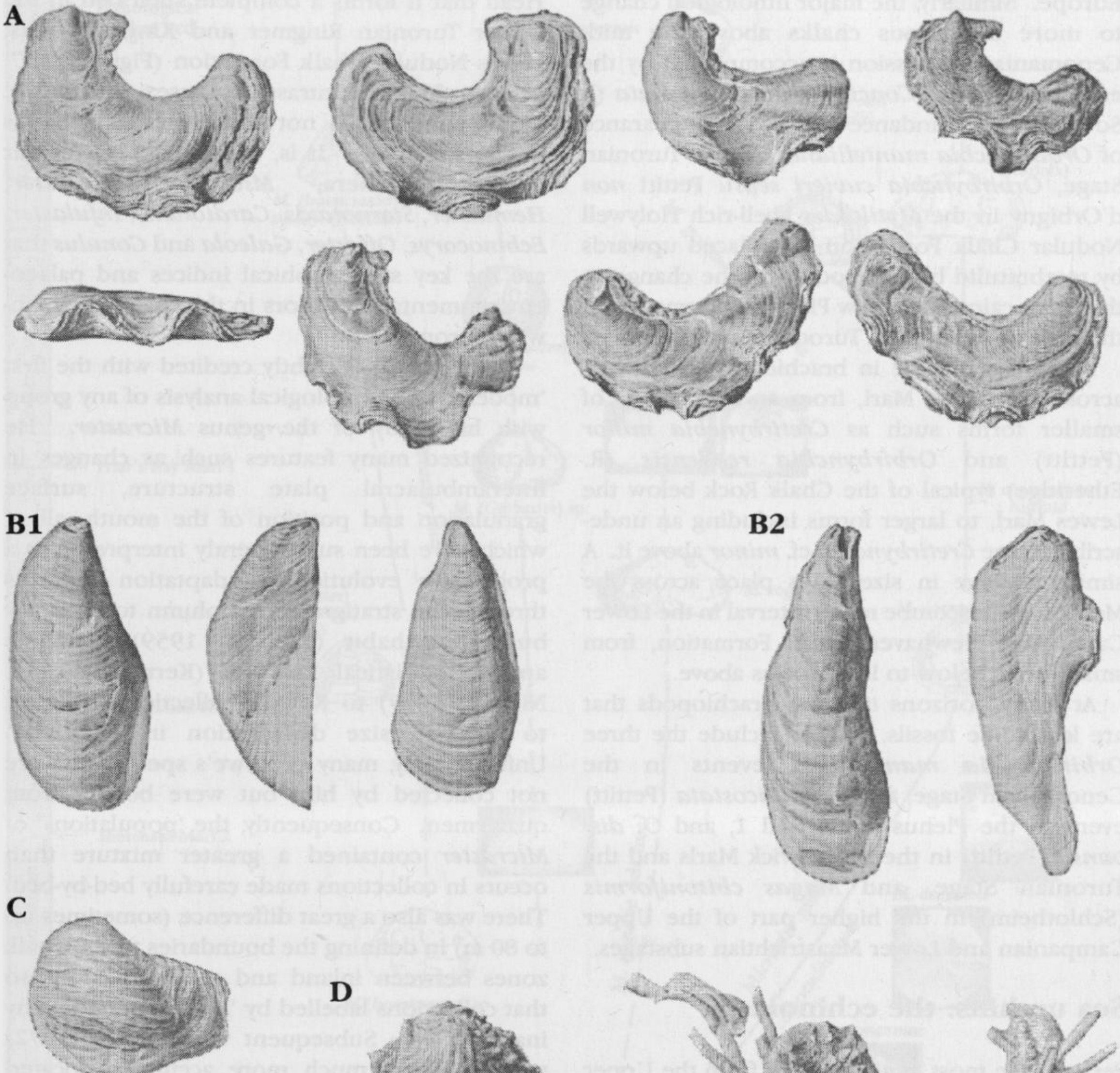


Figure 2.28 Key Upper Cretaceous Chalk oysters. (A) *Agerostrea lunata*, Lower Maastrichtian, Norfolk (from Woods, 1912, pl. 61, figs 1–5). (B1, B2) *Pseudoperna boucheroni* from the Santonian–Campanian boundary 'Grobkreide' facies (from Woods, 1912, pl. 60, figs 1–3). (C) *Pycnodonte* from the Cenomanian *Pycnodonte* event (Woods, 1912, pl. 55, figs 8, 9). (D) *Rastellum colubrinum*, Lower Cenomanian *Sharpeiceras schlueteri* Subzone (from Woods, 1912, text-fig. 122). All specimens natural size.

Europe. Similarly, the major lithological change to more calcareous chalks above the mid-Cenomanian succession is accompanied by the entry of the large *Concinnithyris subundata* (J. Sowerby) in abundance and the disappearance of *Orbirhynchia mantelliana*. In the Turonian Stage, *Orbirhynchia cuvieri sensu* Pettitt *non* d'Orbigny in the *Mytiloides* shell-rich Holywell Nodular Chalk Formation is replaced upwards by terebratulid brachiopods with the change to the more calcareous New Pit Chalk Formation at the base of the Middle Turonian Substage.

A marked change in brachiopod size occurs across the Lewes Marl, from an assemblage of smaller forms such as *Cretirhynchia minor* (Pettitt) and *Orbirhynchia reedensis* (R. Etheridge) typical of the Chalk Rock below the Lewes Marl, to larger forms including an undescribed large *Cretirhynchia* cf. *minor* above it. A similar change in size takes place across the Meeching–Telscombe marls interval in the Lower Campanian Newhaven Chalk Formation, from small forms below to large forms above.

At many horizons it is the brachiopods that are key guide fossils. These include the three *Orbirhynchia mantelliana* events in the Cenomanian Stage, the *O. multicostata* (Pettitt) event in the Plenus Marls Bed 1, and *O. dispansa* (Pettitt) in the Bridgewick Marls and the Turonian Stage, and *Magas chitoniformis* (Schlotheim) in the higher part of the Upper Campanian and Lower Maastrichtian substages.

Sea urchins: the echinoids

Perhaps the most famous fossils from the Upper Cretaceous Chalk are sea urchins ('shepherd's crowns') and, of these, the heart-shaped urchin *Micraster* and the less glamorous *Echinocorys* are the most well known. The great diversity of Chalk echinoids, both regular and irregular (monographed by Wright, 1881), includes numerous regular cidarids whose spines also act as stratigraphical indices. A bed of cidarid spines in the uppermost Cenomanian Melbourn Rock is a conspicuous marker bed. Club-shaped spines (*Tylocidaris clavigera*) characterize the Lower Coniacian Hope Gap Beds in the Lewes Nodular Chalk Formation and 'long-spines' characterize the Lewes–Seaford Chalk boundary at the base of the Middle Coniacian Substage. The abundance of some cidarids is also geographically restricted. *Gautheria radiata* (Sorignet) is so abundant in Dorset sections such as Ballard Head that it forms a complete shell bed in the Upper Turonian Ringmer and Kingston beds, Lewes Nodular Chalk Formation (Figure 3.117, Chapter 3). In contrast, in Sussex *G. radiata*, whilst common, is not concentrated in bands in the same way. It is, however, the irregular echinoid genera, *Micraster*, *Holaster*, *Hemiaster*, *Sternotaxis*, *Cardiotaxis*, *Infulaster*, *Echinocorys*, *Offaster*, *Galeola* and *Conulus* that are the key stratigraphical indices and palaeoenvironmental indicators in the chalks of north-west Europe.

Rowe (1899) is rightly credited with the first 'modern' palaeontological analysis of any group with his study of the genus *Micraster*. He recognized many features such as changes in interambulacral plate structure, surface granulation and position of the mouth, all of which have been subsequently interpreted as a progressive evolutionary adaptation upwards through the stratigraphical column to a deeper burrowing habit (Nichols, 1959). Others applied statistical analyses (Kermack, 1954; Nichols, 1959) to Rowe's collection and tried to show a size distribution in *Micraster*. Unfortunately, many of Rowe's specimens were not collected by him but were bought from quarrymen. Consequently, the 'populations' of *Micraster* contained a greater mixture than occurs in collections made carefully bed-by-bed. There was also a great difference (sometimes up to 80 m) in defining the boundaries to the Chalk zones between inland and coastal sections so that collections labelled by 'Zone' contain many inaccuracies. Subsequent work (Ernst, 1972) was based on much more accurately located samples and, in addition, began to recognize the key stratigraphical changes in the plastronal plate structure of *Micraster*. This work was further developed by the late Dr Drummond (1983, and unpublished manuscript). From these studies has emerged a very refined *Micraster* stratigraphy for the Upper Turonian to Lower Campanian strata (Figures 2.9, 2.21, 2.22 and 2.29).

Rowe's work (1899) was not the only important study of *Micraster* at that time. Lambert (1878, 1882a,b, 1895, 1901; Lambert and Thiéry, 1924) described the *Micraster* from the eastern Paris Basin and other echinoids in the Chalk including *Echinocorys*. Brydone (1912, 1914, 1915, 1930) and Gaster (1924) also recognized the stratigraphical importance of shape changes in *Echinocorys*. Brydone (1912,

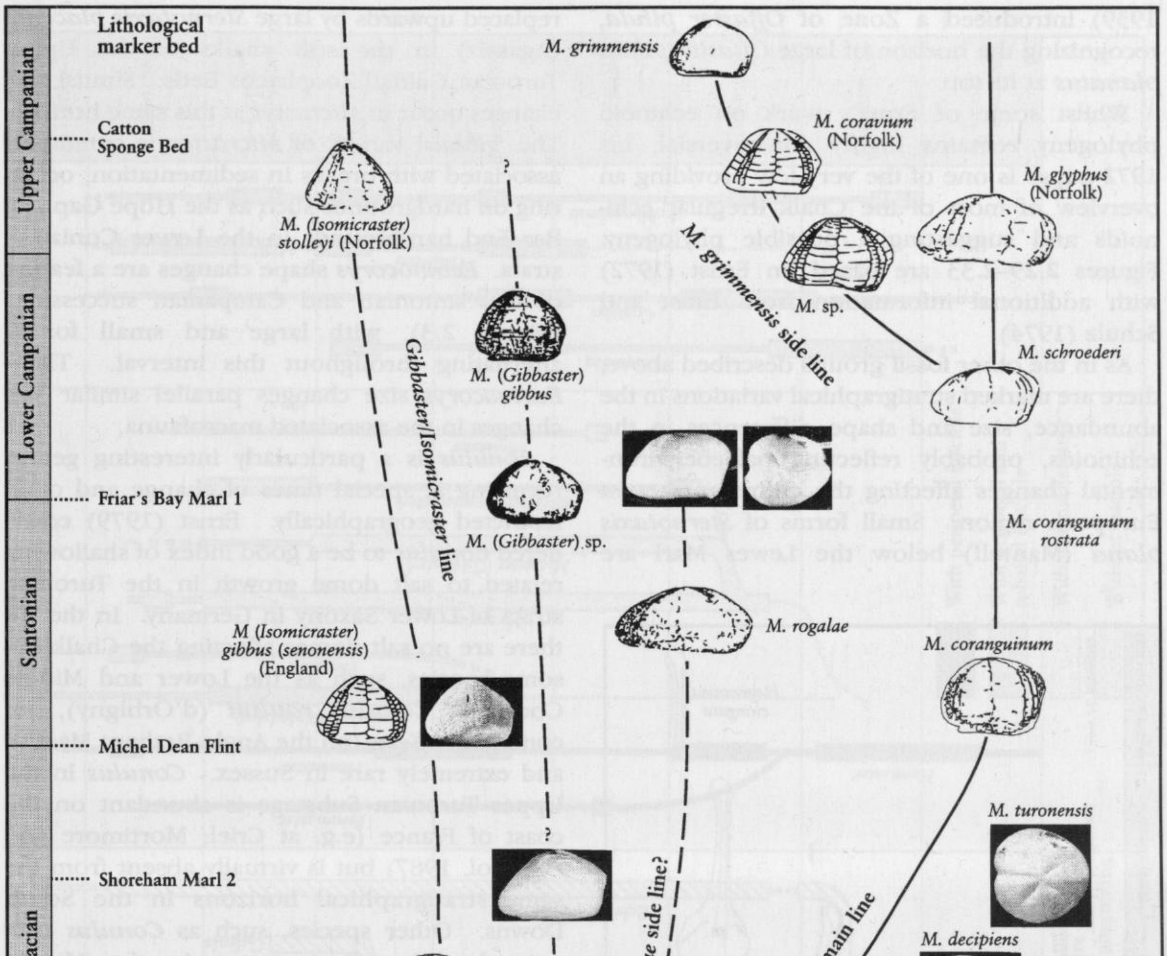


Figure 2.29 Stratigraphy and possible phylogeny of *Micraster* in the Upper Cretaceous Chalk, plotted against English stratigraphical markers. (After Ernst, 1972, fig. 25.)

1939) introduced a Zone of *Offaster pilula*, recognizing the horizon of large *Offaster pilula planatus* at its top.

Whilst some of Ernst's work on echinoid phylogeny remains highly controversial, his 1972 paper is one of the very few providing an overview of most of the Chalk irregular echinoids and suggesting a possible phylogeny. Figures 2.29–2.33 are based on Ernst (1972) with additional information from Ernst and Schulz (1974).

As in the other fossil groups described above, there are marked stratigraphical variations in the abundance, size and shape differences in the echinoids, probably reflecting palaeoenvironmental changes affecting the entire north-west European region. Small forms of *Sternotaxis plana* (Mantell) below the Lewes Marl are replaced upwards by large *Sternotaxis placenta* (Agassiz) in the soft chalks of the Upper Turonian Cuilfail Zoophycos Beds. Similar size changes occur in *Micraster* at this same horizon. The '*gibbus*' variety of *Micraster* is commonly associated with breaks in sedimentation, occurring on hardgrounds such as the Hope Gap and Bar End hardgrounds in the Lower Coniacian strata. *Echinocorys* shape changes are a feature of the Santonian and Campanian successions (Figure 2.3), with large and small forms alternating throughout this interval. These *Echinocorys* size changes parallel similar size changes in the associated macrofauna.

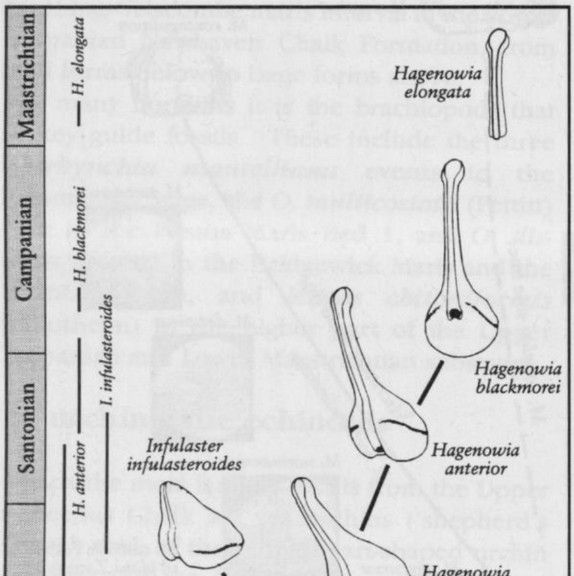


Figure 2.30 Stratigraphy and possible phylogeny of *Infulaster* and *Hagenowia* in the Boreal Upper Cretaceous succession. (After Smith, 1984; Ernst, 1972, fig. 22.)

Conulus is a particularly interesting genus, recurring at special times of change and often restricted geographically. Ernst (1979) considered *Conulus* to be a good index of shallowing related to salt dome growth in the Turonian strata of Lower Saxony in Germany. In the UK there are no salt domes affecting the Chalk but some species, such as the Lower and Middle Coniacian *Conulus raulini* (d'Orbigny), are common in Kent (on the Anglo-Brabant Massif), and extremely rare in Sussex. *Conulus* in the Upper Turonian Substage is abundant on the coast of France (e.g. at Criel; Mortimore and Pomerol, 1987) but is virtually absent from the same stratigraphical horizons in the South Downs. Other species, such as *Conulus subrotundus* Mantell, common in the Middle Turonian Substage (lower part of the New Pit Chalk), are more widespread and perhaps reflect broader changes in the environment represented by the Holywell–New Pit chalk transition. Another widespread index fossil of the Santonian strata is *Conulus albogalerus* (Leske).

Other extraordinary Chalk echinoids are the small, very fragile-shelled, *Infulaster* and *Hagenowia* (Wright and Wright, 1949; Ernst, 1972; Ernst and Schulz, 1974; Gale and Smith, 1982; Figure 2.30). Both genera are considered to be more common in the Northern Province where they have been used as a guide fossil or a zonal index fossil (*Infulaster* in the Upper Turonian; *Hagenowia rostrata* in place of the *M. coranguinum* Zone). *Hagenowia* seem to be more common in the *M. coranguinum* Zone of Kent compared with Sussex and Wessex. In the Lower Campanian strata, however, a *Hagenowia blackmorei* Subzone is recognized throughout the Southern and Transitional provinces (Figure 2.30) at the base of the *Gonioteuthis quadrata* Zone. *Hagenowia* develops a rostrum as an

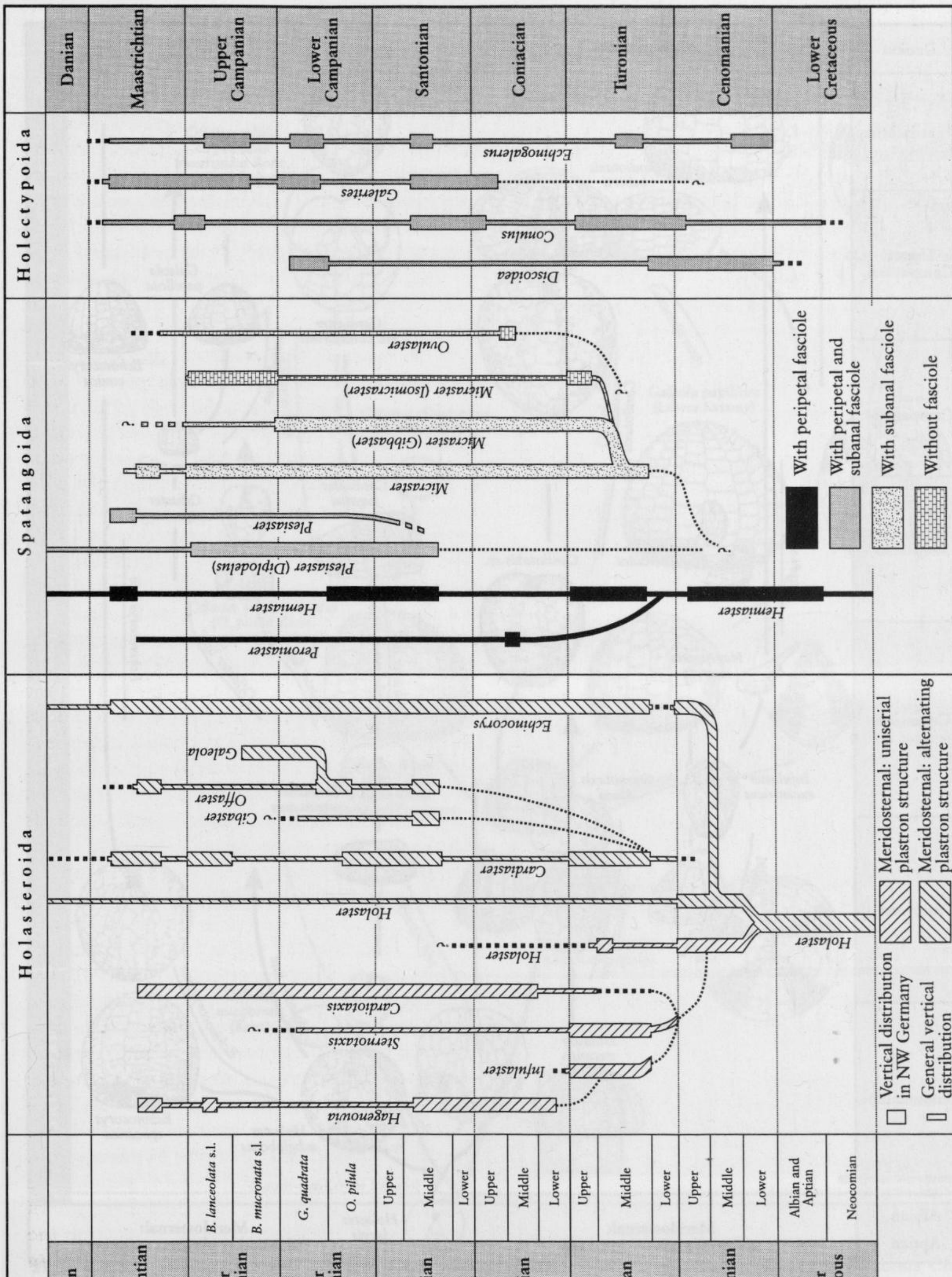


Figure 2.31 Irregular echinoid phylogeny in the Upper Cretaceous Chalk. (After Ernst, 1972.)

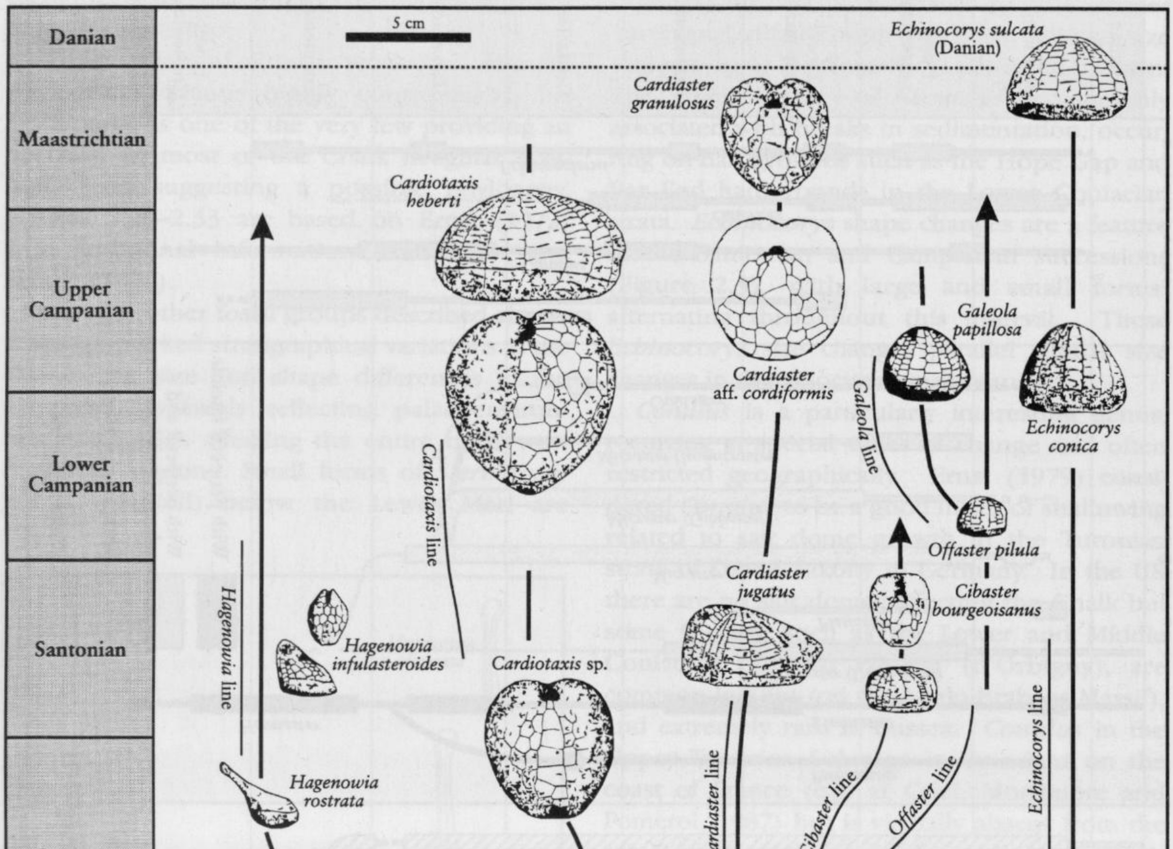


Figure 2.32 Stratigraphy and possible phylogeny of Holasteroidea in the Upper Cretaceous Chalk; note the revised interpretation in Figure 2.30. (After Ernst, 1972, fig. 20.)

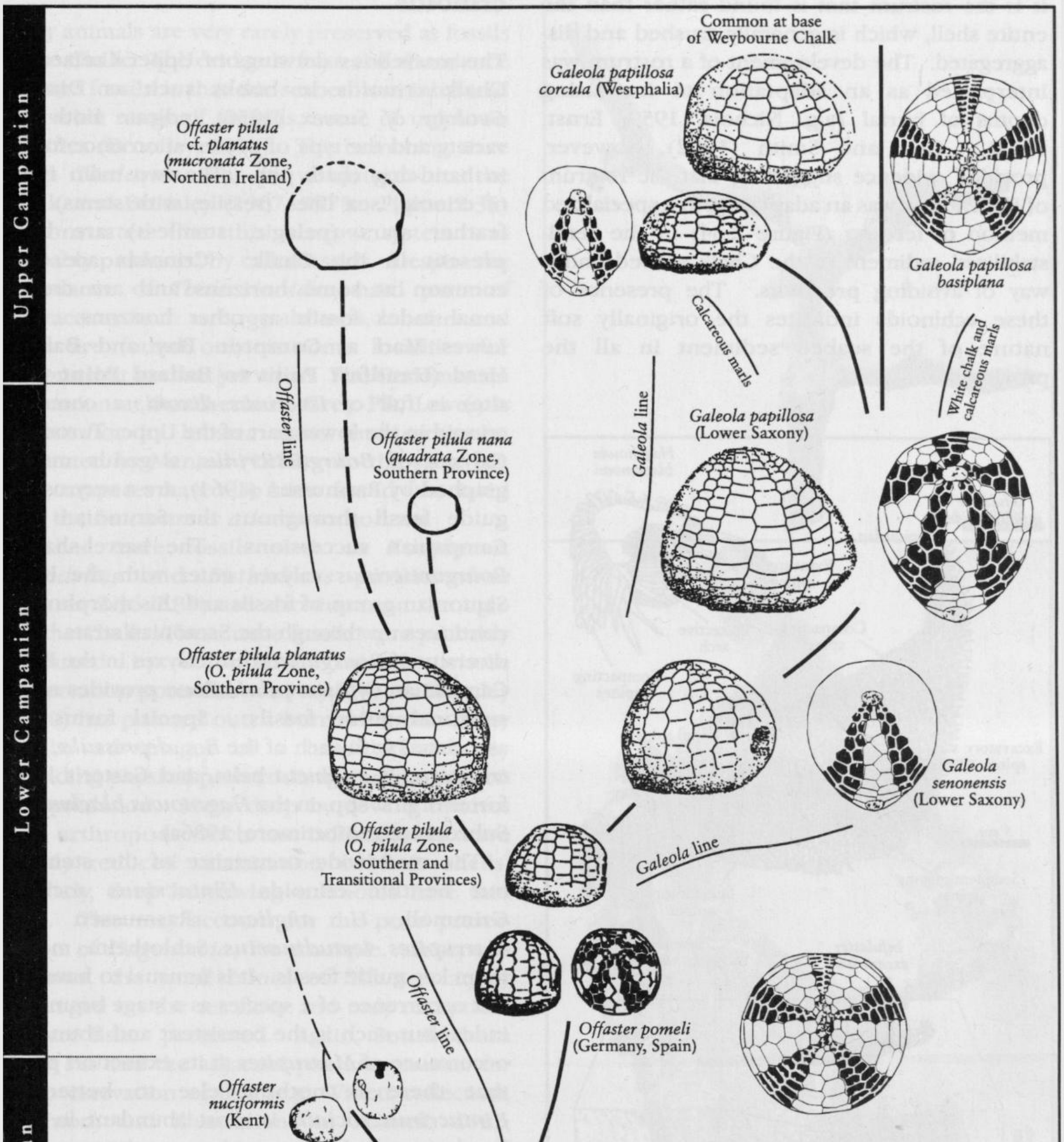


Figure 2.33 Stratigraphy and possible phylogeny of *Offaster* and *Galeola* in the Upper Cretaceous Chalk. (After Ernst, 1972, fig. 21.)

extension of the apical area of the shell. Usually it is the rostrum that is found rather than the entire shell, which is generally crushed and disaggregated. The development of a rostrum was interpreted as an adaptation to increasing depths of burial (e.g. Nichols, 1959; Ernst, 1972). Gale and Smith (1982), however, provided evidence suggesting that the rostrum of *Hagenowia* was an adaptation to a specialized method of feeding (Figure 2.34) in the semi-stabilized sediment of the Chalk seabed and a way of avoiding predators. The presence of these echinoids indicates the originally soft nature of the seabed sediment in all the provinces.

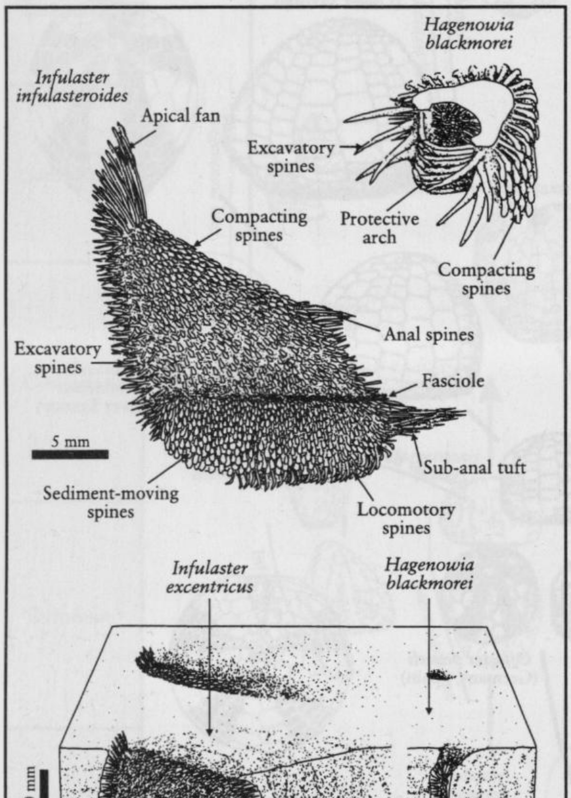


Figure 2.34 Mode of life of *Infulaster excentricus* (S. Woodward) and *Hagenowia blackmorei* Wright and Wright indicating possible depth in the sediment of each species in relation to the development of their different apical elongations (from Gale and Smith, 1982, after Ernst, 1972). Their modes of life can be contrasted with the probable shallower 'ploughing' of *Micraster*.

Sea lilies and feather stars: the crinoids

The marvellous drawings of Upper Cretaceous Chalk crinoids in books such as Dixon's *Geology of Sussex* (1850) indicate both the variety and the type of preservation once found in hand-dug chalk pits. The two main types of crinoid, sea lilies (sessile, with stems) and feather stars (pelagic, stemless) are both present in the Chalk. Crinoids are very common at some horizons and are crucial zonal index fossils at other horizons. The Lewes Marl at **Compton Bay** and Ballard Head (**Handfast Point to Ballard Point** GCR site) is full of *Isocrinus dixoni*, a common crinoid in the lower part of the Upper Turonian. Calyxes of *Bourgueticrinus*, a genus monographed by Rasmussen (1961), are a very useful guide fossil throughout the Santonian and Campanian successions. The barrel-shaped *Bourgueticrinus* calyxes enter with the basal Santonian group of fossils and this morphotype continues up through the Santonian strata. The diversity of *Bourgueticrinus* calyxes in the basal Campanian *Offaster pilula* Zone provides many subzonal guide fossils. Special forms are associated with each of the *E. s. depressula*, *E. s. truncata*, *E. s. cincta* belts, and Gaster's large forms of *E. s.* spp. in the *Hagenowia blackmorei* Subzone (e.g. Mortimore, 1986a).

The worldwide occurrence of the stemless but benthic crinoids *Uintacrinus socialis* Grimmell, *U. anglicus* Rasmussen and *Marsupites testudinarius* Schlotheim makes them key guide fossils. It is unusual to have the last occurrence of a species as a stage boundary index, but such is the consistent and abundant occurrence of *Marsupites* at its extinction point that there is nothing else to better it. *Uintacrinus socialis* is most abundant in two bands, one at the base and one at the top of its range. *Marsupites* is relatively abundant throughout its range but has two bands of maximum abundance. There are also two stratigraphically distinct morphotypes of *Marsupites*. The first morphotype, in the basal part of the *Marsupites testudinarius* Zone, has calyx plates with a simple fold in the centre of each edge, whereas the second morphotype has complex plates with complex folds providing crinkled edges. There is also a stratigraphically useful size change in *Marsupites,* which tends to be smaller at the base and top of its range.

Trace fossils

Many animals are very rarely preserved as fossils in the Chalk. The evidence from the abundance of trace fossils is that the seabed was inhabited by a wide range of animals, some of unknown affinities (Bromley, 1990). The branching trace fossil *Thalassinoides* is ubiquitous in the Chalk, and Bromley (1967, 1975a; Figure 2.35) demonstrated that this burrow system was probably produced by callianassids. Despite the abundance of *Thalassinoides*, hard parts of crustaceans such as large shrimps, lobsters and crabs are found only at some localities for reasons that are not yet clear. The Cenomanian succession at **Southerham Grey Pit**, Lewes, is famous for its lobster claws and carapaces, illustrated by Mantell (1822). In the same pit, crab carapaces have also been found associated with the *Inoceramus atlanticus* horizon.

Other trace fossils such as *Zoophycos*, *Chondrites* and *Bathichnus paramoudrae* (Figures 2.36–2.39) are also common throughout the Chalk. These trace fossils were probably produced by soft-bodied animals whose preservation potential was very low. As Bromley (1990) has pointed out, a burrow confers many of the advantages of a hard skeleton by providing physical protection against dessication and predation. Many deep burrowing bivalves and arthropods such as callianassids have greatly reduced calcitization of their shells. Similarly, deep burrowing echinoids have thin tests. This may account for the poor preservation of *Hagenowia*, for example. Except in burrows, the small bones of fish are largely scavanged on the sea floor and only exceptionally are fishes preserved. Again, **Southerham Grey Pit** and the adjacent pits are unusual for the preservation of fish (e.g. Willett collection, Brighton, and illustrations in Mantell, 1822; Dixon, 1850).

Just as body fossils have levels of abundance used for stratigraphical correlation, so the trace fossils have conspicuous horizons of abundance. These include the abundant *Zoophycos* levels, called 'Tiger' chalk in the Crimea and Bänderkreide in Germany. Similarly, Paramoudra is stratigraphically restricted (Mortimore and Pomerol, 1991b).

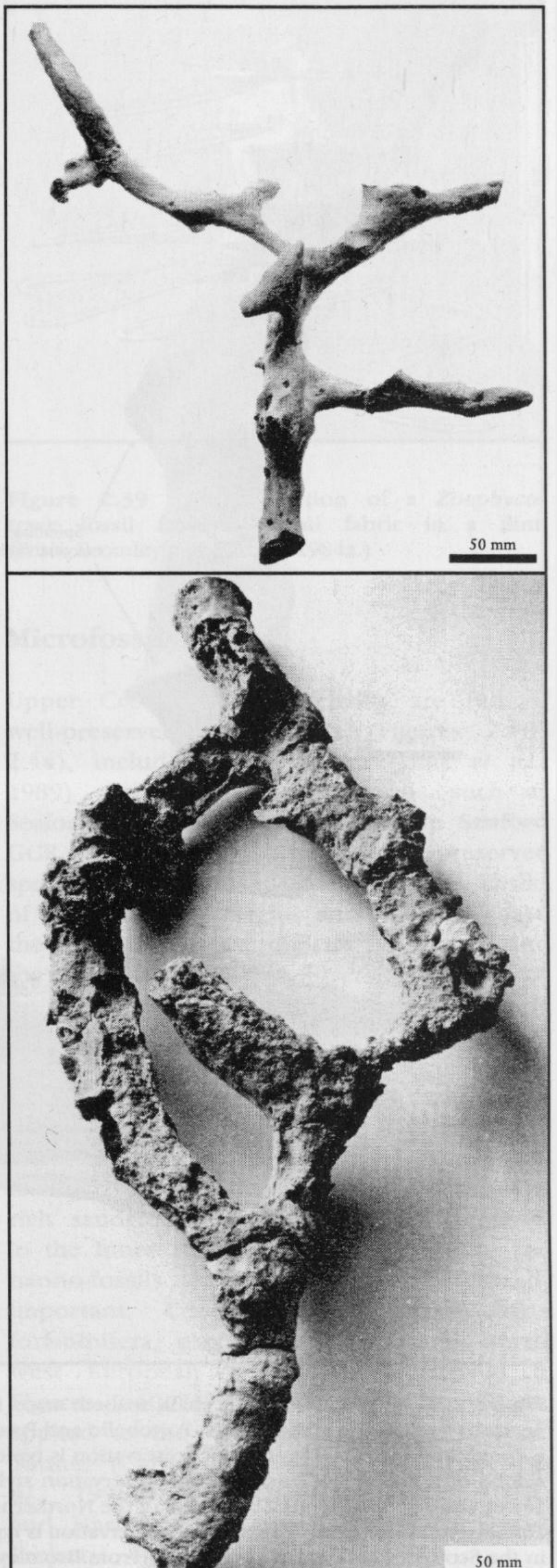


Figure 2.35▸ Branching *Thalassinoides* burrow-replacement flints. (From Bromley and Ekdale, 1984a.)

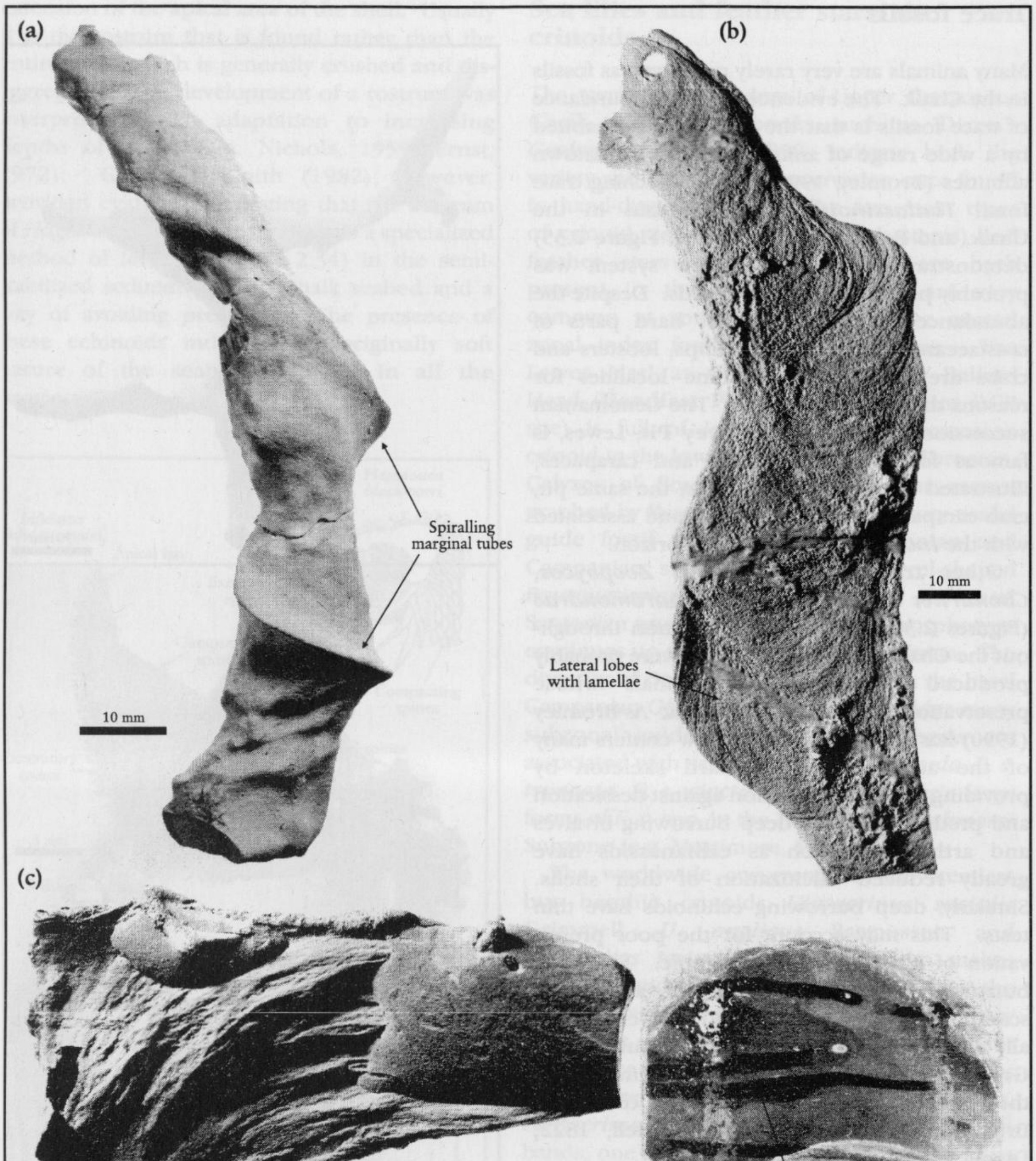


Figure 2.36 Ecology of a soft chalk seabed: trace fossils in flint. (a) A spiral *Zoophycos* typical of many horizons such as the Tavern Flints, Portobello and Précy Zoophycos. (b) Silicified lateral lobes with lamellae of a *Zoophycos* spreite. This type of preservation is typical of the Cuilfail and Beachy Head Zoophycos beds. (c) A lobe of a *Zoophycos* burrow with preservation style typical of the Asham Zoophycos at **Southerham Pit**, Lewes and the Sub-Plenus Zoophycos of the Northern Province. (d) Four tiers of a *Zoophycos* system within a *Thalassinoides* burrow. This style of preservation is typical of many horizons including the bands of *Zoophycos* in the Scottish Chalk at **Gribun**, Mull. (From Bromley and Ekdale, 1984a.)

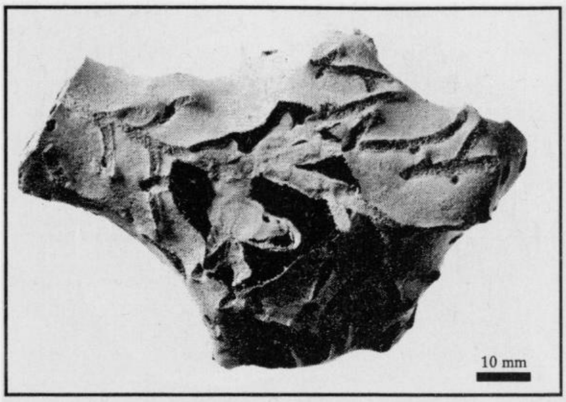


Figure 2.37 A typical '*Chondrites*' flint showing a branching *Chondrites* network in a *Thalassinoides suevicus* network. (From Bromley and Ekdale, 1984a.)

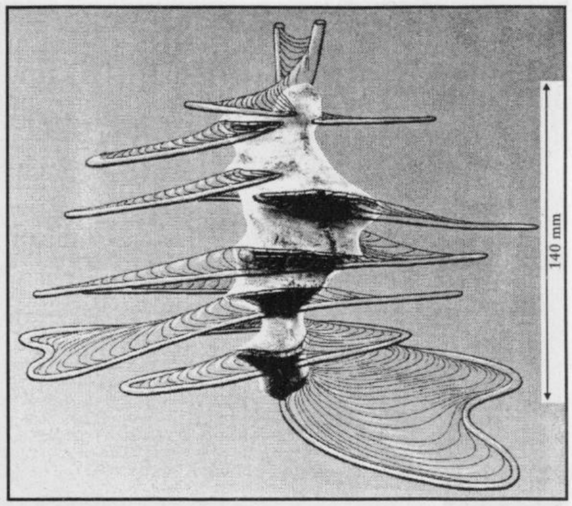


Figure 2.39 Reconstruction of a *Zoophycos* trace fossil from a spiral fabric in a flint. (From Bromley and Ekdale, 1984a.)

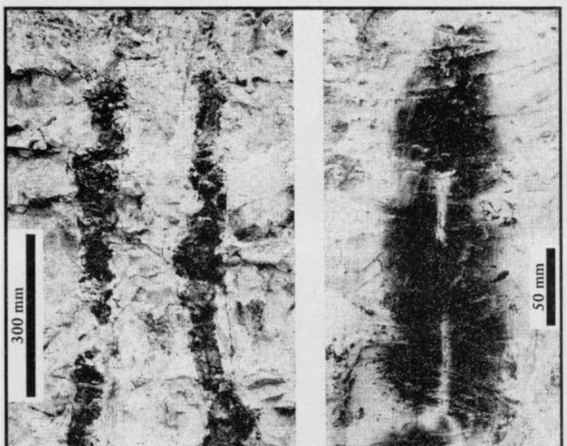


Figure 2.38 *Bathichnus paramoudrae* in various forms. (a) A vertical cylinder of flint (Paramoudra) at **Caistor St Edmunds Chalk Pit**, Norwich. (b) Dark pyritic aureole around the trace fossil (vertical section). (c) Horizontal section of (b). (From Bromley *et al.*, 1975.)

Microfossils

Upper Cretaceous soft chalks are full of well-preserved microfossils (Figures 2.40–2.44), including foraminifera (Hart *et al.*, 1989) and ostracods. Sections such as Seaford Head, Sussex (**Cuckmere to Seaford** GCR site), yield beautifully preserved specimens. In contrast, in the hard chalks of the Isle of Wight and Dorset coast, the microfossils are difficult to extract and the species range and diversity appears to be reduced. Modern techniques, using Glauber salt to help break down the hard chalk, shows that a similar diversity exists in hard and soft chalks. In contrast, in many greensands and the Lochaline White Sands (Inner Hebrides), the calcareous microfossils have been dissolved away in the quartz-rich sandstones. However, the limestones in the Inner Hebrides are full of micro- and nanno-fossils. Selected, stratigraphically important, Cenomanian to Maastrichtian foraminifera used in the UK and north-west European region are illustrated in Figures 2.40–2.44. Microfossils have been applied to the construction of the Channel Tunnel (Carter and Hart, 1977a; Harris *et al.*, 1996b), the Thames Barrier (Carter and Hart, 1977b) and the Ipswich Orwell Project.

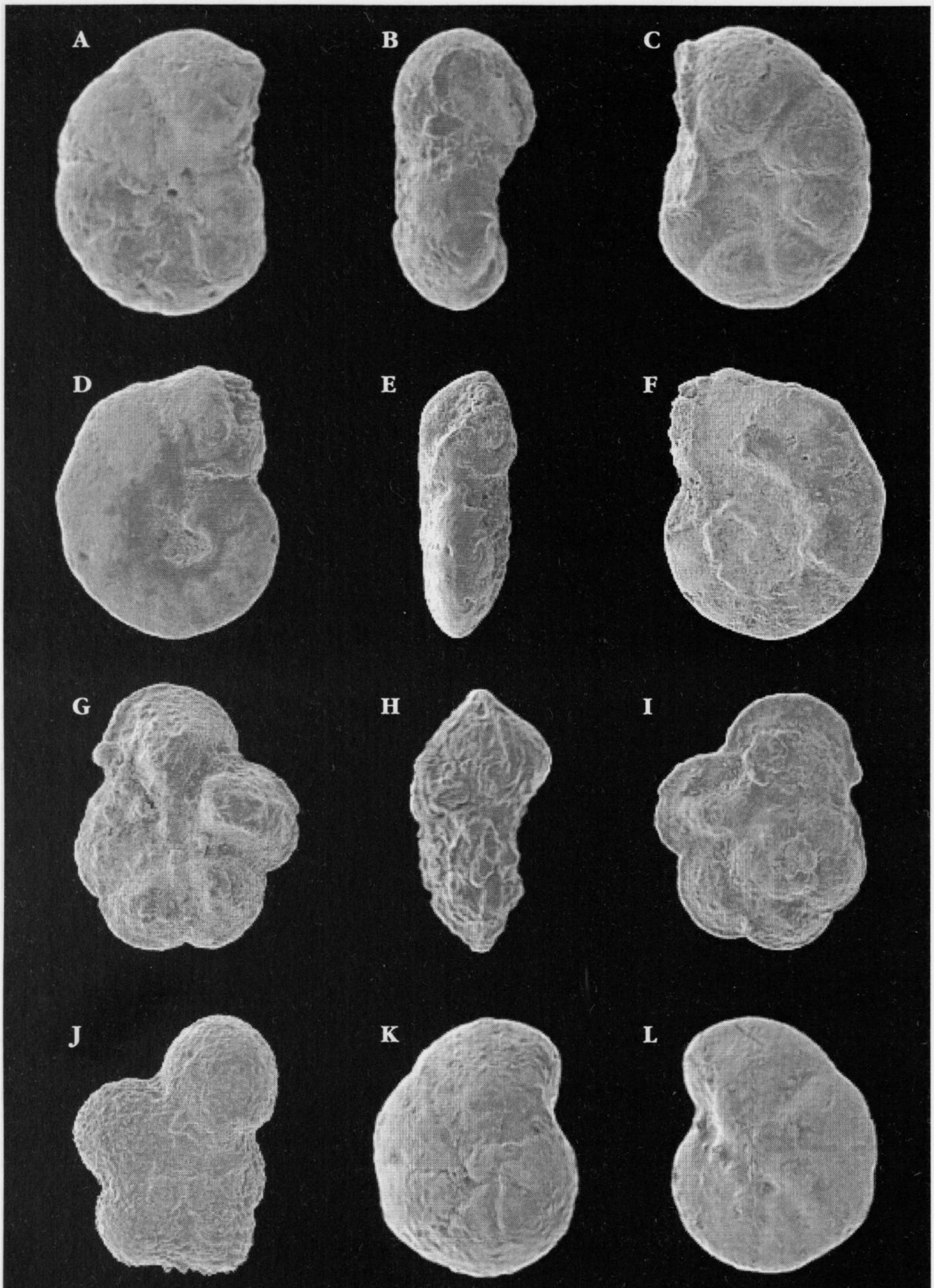


Figure 2.40 Cenomanian and Turonian foraminifera (see page 77 for details).

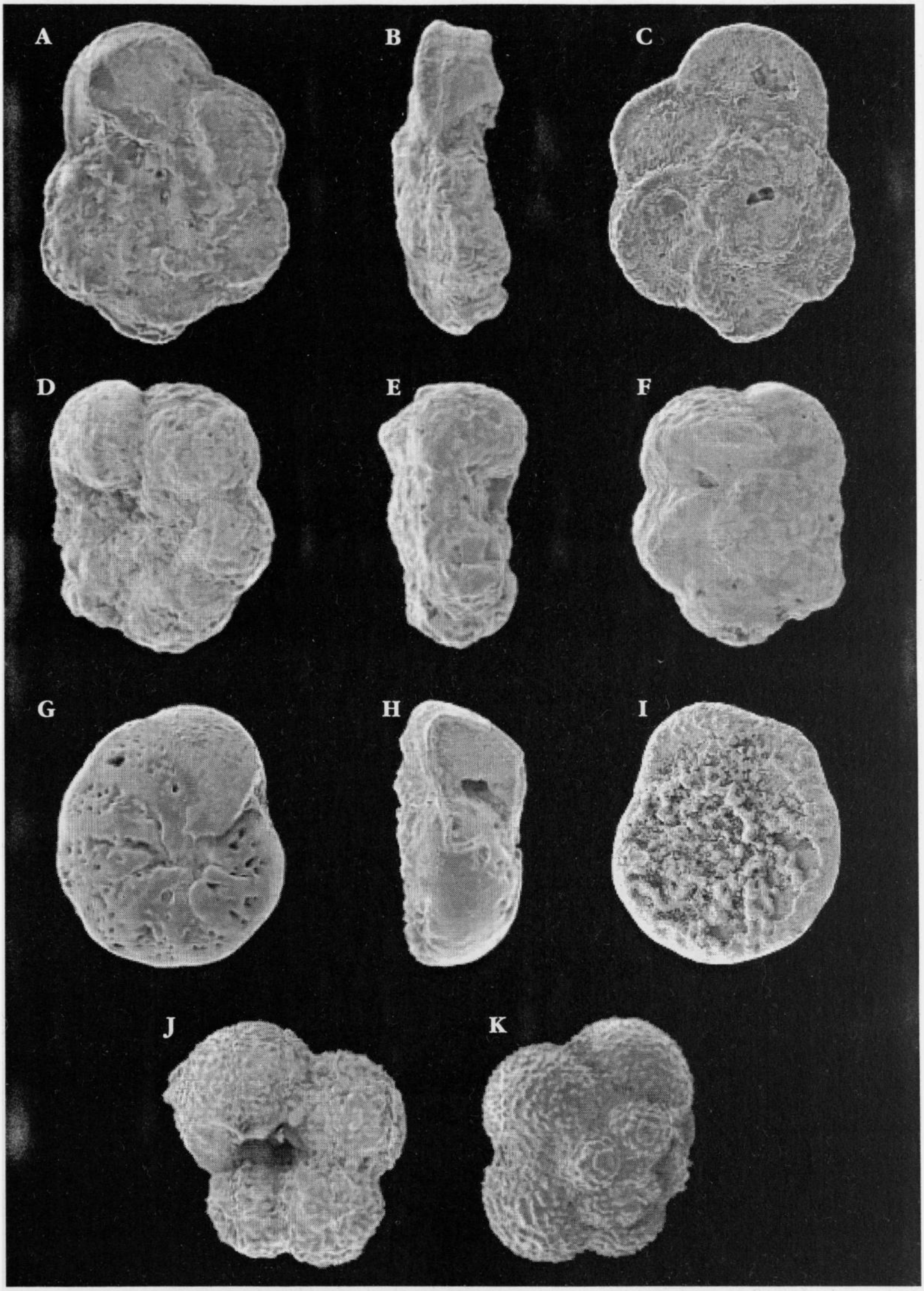


Figure 2.41 Turonian and Coniacian foraminifera (see page 77 for details).

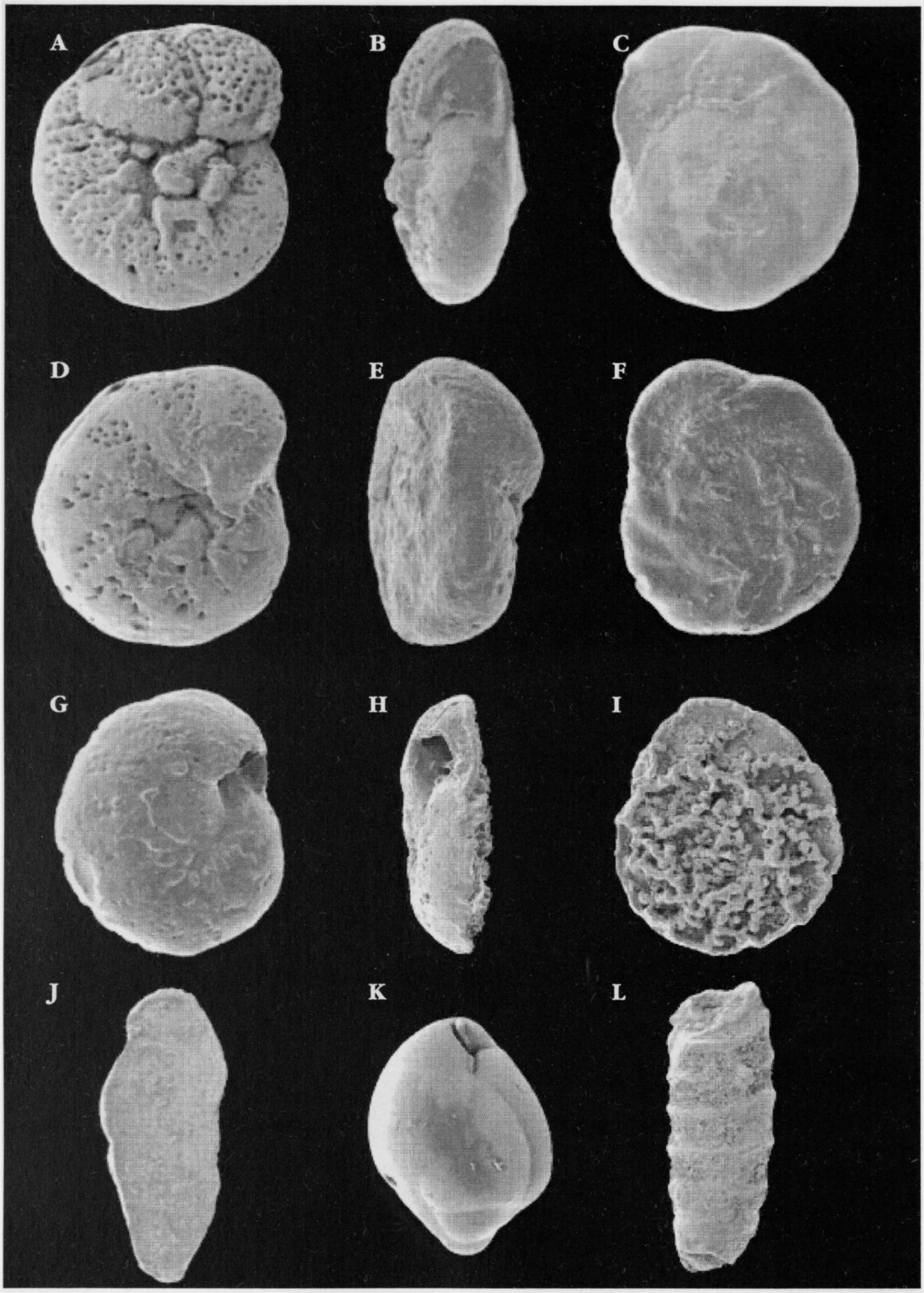


Figure 2.42 Santonian foraminifera (see page 77 for details).

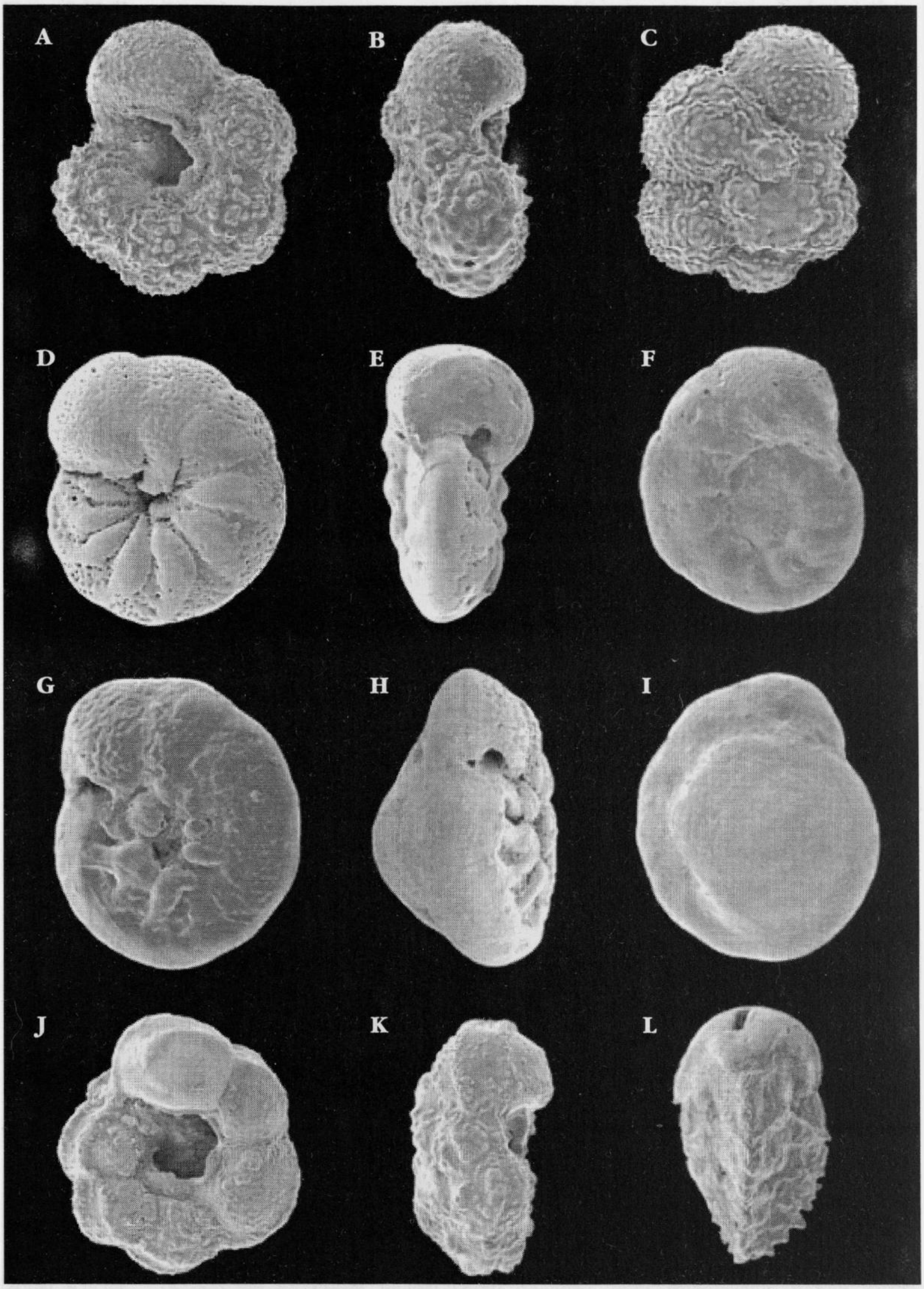


Figure 2.43 Campanian foraminifera (see page 77 for details).

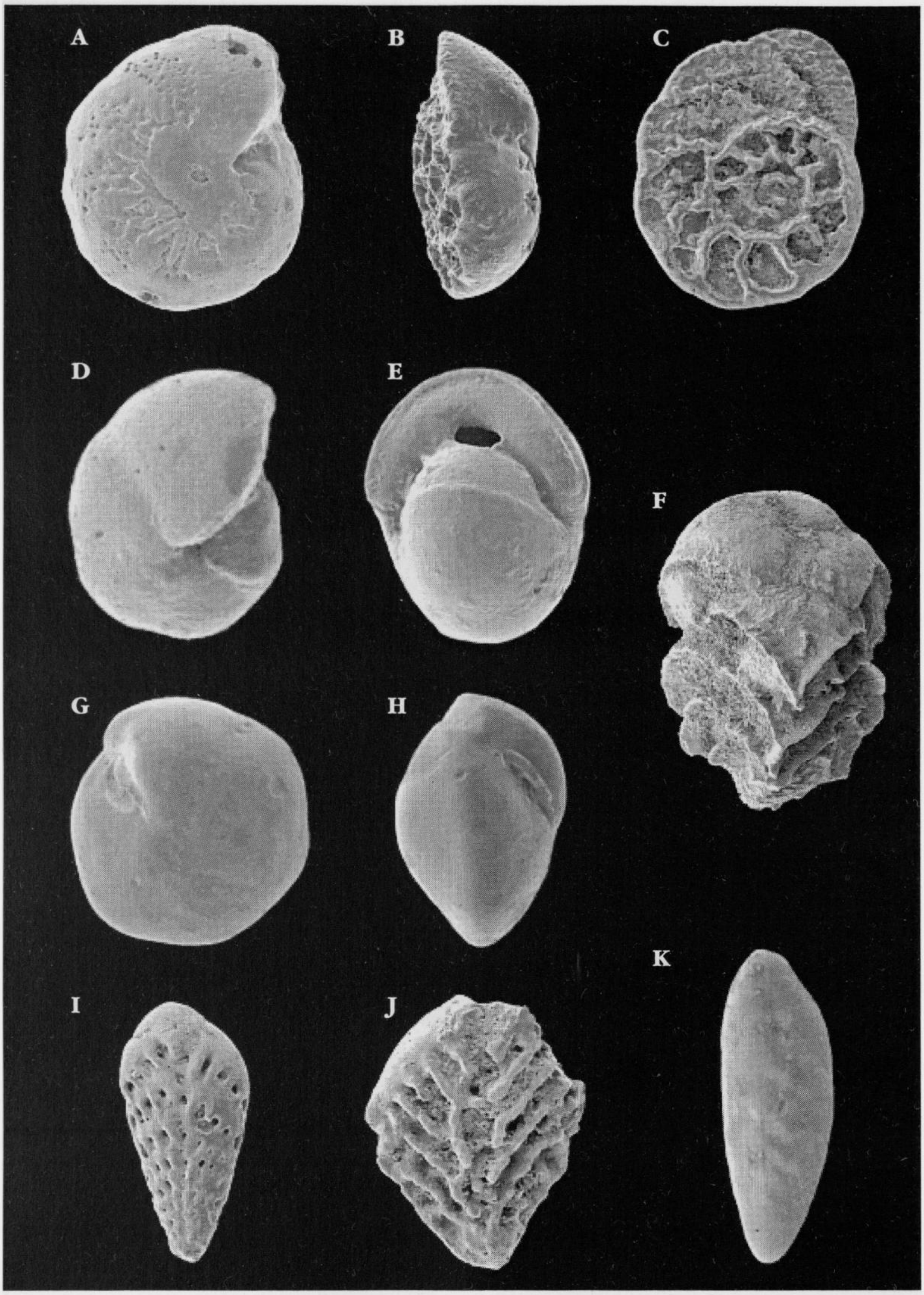


Figure 2.44 Campanian and Maastrichtian foraminifera (see page 77 for details).

Figure 2.40 (Page 72) Scanning electron microscope (SEM) images of Cenomanian and Turonian foraminifera. (A–C) *Gavelinella baltica* (Brotzen) (×200) (benthic), from Beachy Head, East Sussex (Plenus Marls Member, Jefferies Bed 1), Upper Cenomanian *Metoicoceras geslinianum* Zone. Range: Uppermost Albian *Stoliczkaia dispar* Zone to Upper Cenomanian. (D–F) *Gavelinella cenomanica* (Brotzen) (×100) (benthic), from **Southerham Grey Pit**, Lewes, East Sussex, (Zig Zag Chalk Formation), Middle Cenomanian. Range: Upper Albian to Upper Cenomanian. (G–I) *Rotalipora cushmani* (Morrow) (×100) (globally important Tethyan planktonic species) from Beachy Head, East Sussex, (Plenus Marls Member, Jefferies Bed 4), *Metoicoceras geslinianum* Zone. Range: Middle to Upper Cenomanian. Remarks: Enters in the Middle Cenomanian (just below P/B break) and goes up to Plenus Marls Member, Jefferies Bed 4, Upper Cenomanian. (J) *Hedbergella simplex* (Morrow) (×200) (planktonic), from Beachy Head, East Sussex (Plenus Marls Member, Jefferies Bed 4), Upper Cenomanian *Metoicoceras geslinianum* Zone. Range: Cenomanian. (K, L) *Lingulogavelinella globosa* (Brotzen) (×200) (benthic), from Beachy Head, East Sussex (Plenus Marls Member, Jefferies Bed 4), Upper Cenomanian *Metoicoceras geslinianum* Zone. Range: Upper Cenomanian to Middle Turonian.

Figure 2.41 (Page 73) SEM images of Turonian and Coniacian foraminifera. (A–C) *Marginotruncana pseudolinneiana* (Pessagno) (×150) (planktonic), from New Pit, Lewes, East Sussex, (New Pit Chalk Formation), Middle Turonian *Collignoniceras woollgari* Zone. Range: Turonian to Santonian. Remarks: key zonal form in Europe, entry marks a planktonic foraminiferal zone in the Turonian. (D–F) *Helvetoglobotruncana helvetica* (Bolli) (×150) (typical Tethyan planktonic), from New Pit, Lewes, East Sussex, (New Pit Chalk Formation), Middle Turonian *Collignoniceras woollgari* Zone. Range: Lower to Middle Turonian. Remarks: key entry zonal index fossil. (G–I) *Stensioeina granulata granulata* (Olbertz) (×150) (benthic), from Seaford Head (**Cuckmere to Seaford** GCR site) East Sussex (Seaford Chalk Formation), Middle Coniacian *Micraster coranguinum* Zone. Range: base of Middle Coniacian to Middle Santonian. Remarks: key marker at base of Seaford Chalk Formation (Bailey *et al.*, 1983, 1984). (J, K) *Whiteinella baltica* (Douglas and Rankin) (×150) (planktonic), from Euston, Suffolk, *M. coranguinum* Zone. Range: Base of Coniacian to Upper Santonian.

Figure 2.42 (Page 74) SEM images of Santonian foraminifera. (A–C) *Gavelinella cristata* (Goel) (×100) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Upper Santonian to Lower Campanian. Remarks: entry is approximately coincident with base of *Uintacrinus socialis* Zone (Bailey *et al.*, 1983). (D–F) *Stensioeina granulata polonica* (Witwicka) (×150) (benthic), from Euston, Suffolk (Seaford Chalk Formation), Upper Coniacian *M. coranguinum* Zone. Range: entry in Upper Coniacian. Remarks: zonal index in UKB scheme (Bailey *et al.*, 1983). (G–I) *Stensioeina exsculpta exsculpta* (Reuss) (×150) (benthic), from Euston, Suffolk (Seaford Chalk Formation), Upper Coniacian *M. coranguinum* Zone. Range: Benthic Foraminiferal Zone in the Middle and Upper Coniacian. Remarks: ranges from just above the Shoreham Marls to the Flat Hill Flint, Seaford Chalk Formation. (J) *Loxostomum eleyi* (Cushman) (×150) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Santonian to Upper Campanian. (K) *Praebulimina reussi* (Morrow) (×150) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Santonian to Upper Campanian. (L) *Vaginulinopsis scalariformis* (Porthault) (×50) (benthic), from Euston, Suffolk, Seaford Chalk Formation *M. coranguinum Zone*. Range: Middle Coniacian and Lower Santonian.

Figure 2.43 (Page 75) SEM images of Campanian foraminifera. (A–C) *Archaeoglobigerina cretacea* (d'Orbigny) (×150) (planktonic), from Ipswich, Suffolk, lower Upper Campanian Overlap Zone. Range: Upper Santonian to Campanian. (D–F) *Gavelinella lorneiana* (d'Orbigny) (×100) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Upper Turonian to Upper Campanian. Remarks: important gap in Lower Campanian in the English Chalk; absent between Lancing Flint and the Whitecliff Marl, Culver Chalk Formation. (G–I) *Gavelinella trochus* (Goel) (×100) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Upper Santonian to Lower Campanian. (J, K) *Globotruncana bulloides* (Vogler) (×100) (planktonic), from Ipswich, Suffolk, Lower Campanian Overlap Zone. Range: Coniacian to Campanian. (L) *Reussella kelleri* (Vasilenko) (×100) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Upper Turonian to Lower Campanian.

Figure 2.44 (Page 76) SEM images of Campanian and Maastrichtian foraminifera. (A–C) *Stensioeina pommerana* (Brotzen) (×150) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Lower Campanian to Maastrichtian. Remarks: enters in *Offaster pilula* Zone (Bailey *et al.*, 1983), upper limit Lower Maastrichtian. (D, E) *Pullenia quaternaria* (Reuss) (×150) (benthic), from Ipswich, Suffolk, Lower Campanian. Range: Middle Campanian to Maastrichtian. Remarks: entry a critical marker low in the *Gonioteuthis quadrata* Zone (*Apflinocrinus cretaceus* Subzone. (F) *Reussella szajnochae szajnochae* (Grzybowski) (×80) (benthic), from Overstrand, Norfolk. Range: Upper Campanian to Upper Maastrichtian. Remarks: two key flood events, one at base of Maastrichtian at Overstrand Upper Marl, another one in Southern North Sea Basin near base of the Upper Maastrichtian (Bailey *et al.*, 1983, 1984). (G, H) *Eponides beisseli* (Schijfsma) (×80) (benthic), from Overstrand, Norfolk, Lower Maastrichtian. Range: Upper Upper Campanian to Lower Maastrichtian. Remarks: enters on top of Catton Sponge Bed. (I) *Bolivinoides sidestrandensis* (Barr) (×100) (benthic), from Overstrand, Norfolk, Lower Maastrichtian. Range: Upper Campanian to Lower Maastrichtian. Remarks: enters with *B. draco miliaris* at the bio-event just below the base of the Paramoudra Chalk. (J) *Bolivinoides draco miliaris* (Hiltermann and Koch) (×100) (benthic) from Trimingham, Norfolk, Lower Maastrichtian *Belemnella sumensis* Zone. Range: Upper Campanian to Lower Maastrichtian. Remarks: entry is a bio-event within the UKB zonal scheme. (K) *Bolivina incrassata* (Reuss) (×80) (benthic), from Trimingham, Norfolk, Lower Maastrichtian. Range: upper Upper Campanian to Maastrichtian. Remarks: critical species enters in the Catton Sponge Bed.

THE ECOLOGY OF THE CHALK SEAS

There are environmental effects on fossil distribution and preservation before the chalk sediment even forms a substrate on the seabed. Chalk is made primarily from pelagic nannofossils (especially coccoliths; Figure 1.9, Chapter 1), and their skeletons are presumed to have rained down onto the seabed. Before reaching the seabed, however, many nannofossils may have passed through the gut of plankton-eaters such as copepods (Hattin, 1971; Honjo, 1975). Diversity of preserved nannofossils is partly a function of selective species tolerance to dissolution in the water column, dissolution on the seabed and subsequent pressure solution. The greatest diversity of nannofossils is obtained from soft white chalks that have not undergone major diagenetic changes, such as those at Seaford Head, which contrast with the harder chalks of the Isle of Wight and the Northern Province. The amount of organic matter associated with the original nannoplankton sediment is very uncertain but this must have contributed to the availability of food buried in the sediment, in turn attracting a particular infauna and exerting a control on diagenetic processes.

The evidence from both trace fossils (Bromley, 1975a) and from the type of granulation on the tests of echinoids such as *Hagenowia* (Gale and Smith, 1982), indicate that the initial 'chalky-soup' became a partly consolidated soft- to firm-ground relatively rapidly. Only a millimetre to centimetre thin layer was probably available for re-suspension at the sediment–water interface. This was the environment for soft-sediment colonizers. Some burrowed into and through the sediment (e.g. *Hagenowia*, Figure 2.34), some such as the sea urchin *Micraster* are thought to have initially 'ploughed' through the sediment but may have become a deeper burrower. Other animals were adapted to a surface without sinking in (e.g. the large, plate-like inoceramid bivalve *Platyceramus*). Other bivalves developed spines (*Spondylus spinosus*) whose function is uncertain (Figure 2.45). Burrowers cycled both water and sediment through the top layers of the seabed, aiding diagenesis and the formation of hardgrounds and flints.

Some surfaces on the seabed progressed from soft- to firm- to hard-grounds (Figures 2.46 and 2.47). These early diagenetic changes provided the niche for boring sponges and algae and for encrusting oysters and bryozoa. Bromley (1975a) found at least sixteen phases of sediment in the burrow-fills of one hardground. Voigt (1959, 1974; Bromley, 1990) found beautifully preserved bryozoans in *Thalassinoides* burrow-fills that were not present outside these burrows.

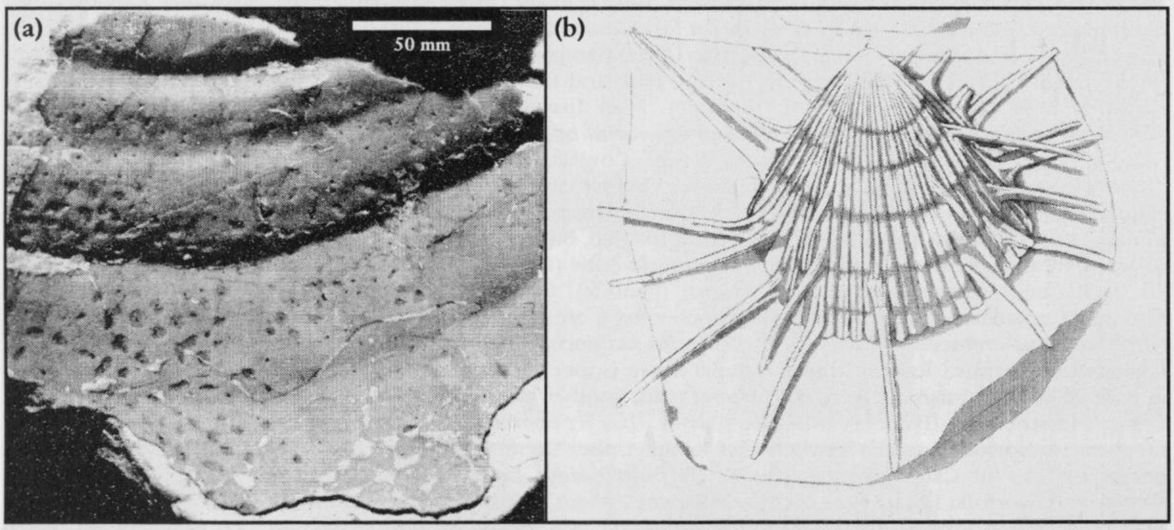


Figure 2.45 Adaptations to a chalky seabed. (a) The shell of *Cremnoceramus crassus* in the Lower Coniacian Lewes Chalk at Seaford Head is a 'hard-surface' and home to the boring *Entobia cretacea* (from Ekdale and Bromley, 1984). (b) The bivalve *Spondylus spinosus* has developed spines whose purpose is uncertain (from Mantell, 1822).

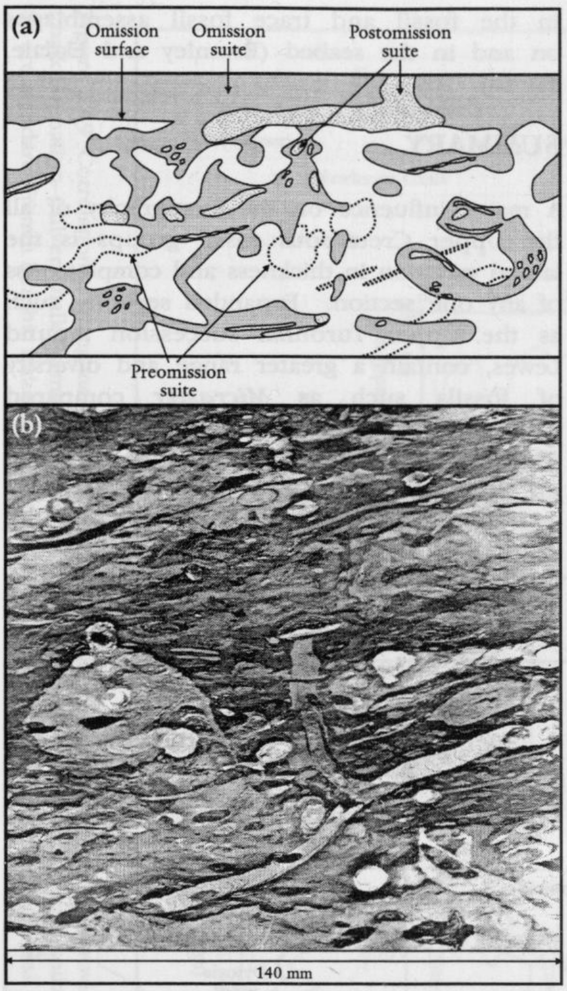


Figure 2.46 (a) Ecology of a soft chalk seabed: an unlithified omission surface with a greyer chalk overlying and filling the underlying whiter bed. The pre-omission suite of burrows is barely visible, the omission suite of trace fossils are pale grey, and the post-omission suite is dark grey (from Bromley, 1975a). (b) Complex trace fossil fabric (ichnofabric) of a soft chalk with successive cross-cutting burrows including two stages of *Planolites*, *Thalassinoides*, *Zoophycos* and *Chondrites* (from Ekdale and Bromley, 1984).

The inoceramids in particular are thought to have been especially adapted, partly by chemosymbioses, to oxygen-poor conditions on the seabed including Mesozoic 'black-shale' events (Kauffman, 1988; Kauffman and Harries, 1992). The low-diversity ***Mytiloides labiatus sensu lato*** fauna in the Holywell Nodular Chalk is cited as one example of this adaptation and these special seabed conditions may be related to major sea-level fluctuations.

Westermann (1990) identified the ecological niches occupied by Mesozoic (including Upper Cretaceous) ammonites (Wiedmann, 1996). Heteromorph ammonites such as the turrilitids and scaphitids might represent shallow water grazers on algae or seaweed, an idea also proposed by others such as Drummond (1967). The large parapuzosid ammonites may have been adapted to a greater range of depths.

In contrast to the deeper-water chalks, a much greater diversity of fossils is found on shallower water shelf areas (e.g. **Wilmington Quarry**) of south-west England during the Cenomanian Age, where calcareous sands were the substrate.

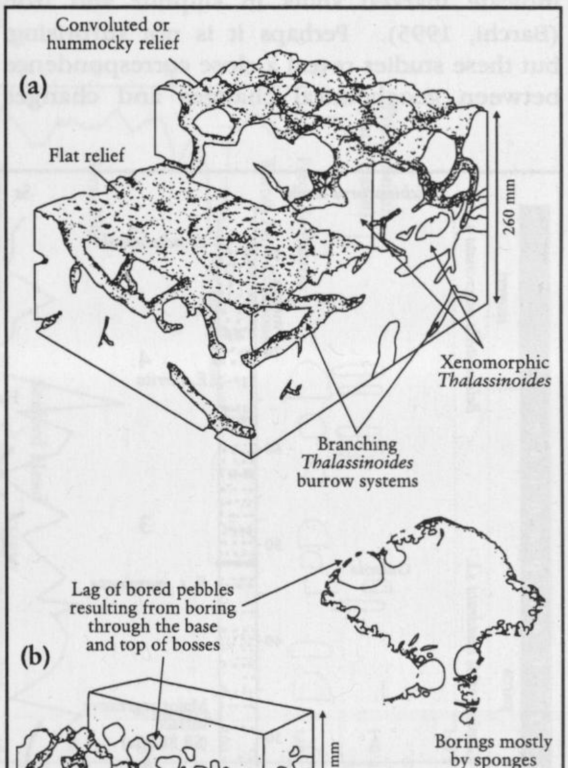


Figure 2.47 Ecology of a hard chalk seabed: burrows and borings in hardgrounds. (a) Hardgrounds from the Chalk Rock at **Charnage Chalk Pit**, Mere, Wiltshire, showing the difference between a convoluted and a flat surface. (b) Hardground with a convoluted surface of irregular bosses between *Thalassinoides* burrow systems. (From Bromley, 1975a.)

INTEGRATED ECOLOGY; BODY FOSSILS, TRACE FOSSILS AND ISOTOPES

By combining the evidence from the stratigraphical and geographical distribution of body fossils and trace fossils a picture of the ecology of the Chalk seabed can be constructed. In addition, studies of the stable isotopes of oxygen and carbon have identified the changes in seawater temperature (Jenkyns *et al.*, 1994) during the Upper Cretaceous Epoch, and the major shifts in burial of organic carbon. Other studies of the stratigraphical distribution of elements (Figures 2.48 and 2.49) indicate marked shifts in sulphur and iron (Barchi, 1995). Perhaps it is not surprising, but these studies reveal a close correspondence between geochemical changes and changes in the fossil and trace fossil assemblages on and in the seabed (Bromley and Ekdale, 1984b).

SUMMARY

A major influence on the stratigraphy of all the Upper Cretaceous fossil groups is the lateral variation in thickness and completeness of any one section. Expanded sections, such as the Upper Turonian succession around Lewes, contain a greater range and diversity of fossils such as *Micraster* compared with more condensed sections in Kent and Wessex. Major erosional channels have reduced the completeness of the stratigraphy at many localities. The Upper Santonian succession of the Anglo-Brabant Massif on the Isle of Thanet and in East Anglia has a

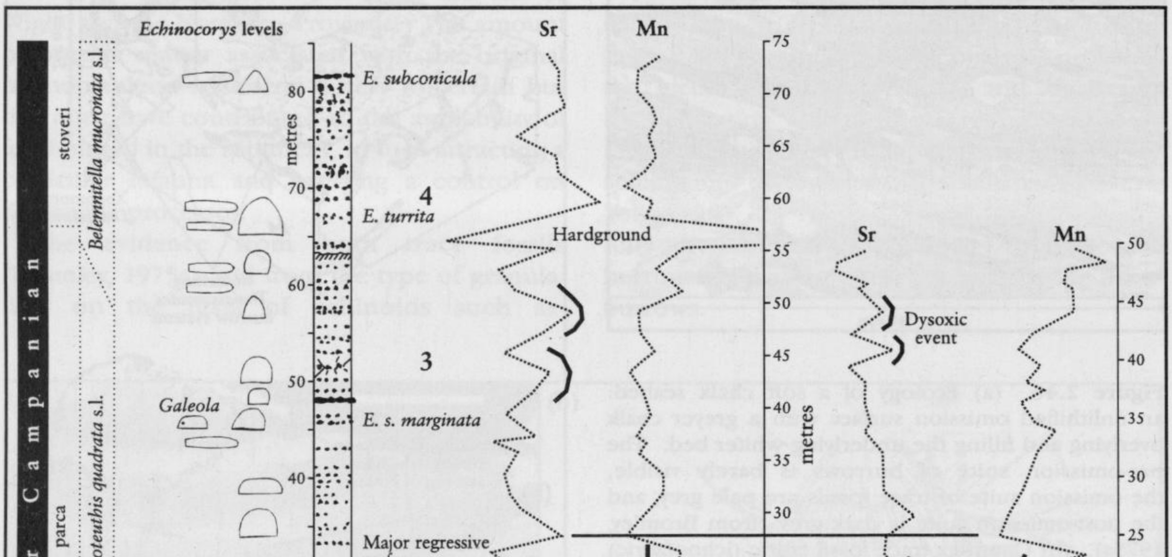


Figure 2.48 Correlation of strontium and manganese and major ecological events 1–4 in the Campanian Chalk of the Anglo-Paris Basin. (Based on field sections of Mortimore and Pomerol, 1987; and geochemistry of Barchi, 1995.)

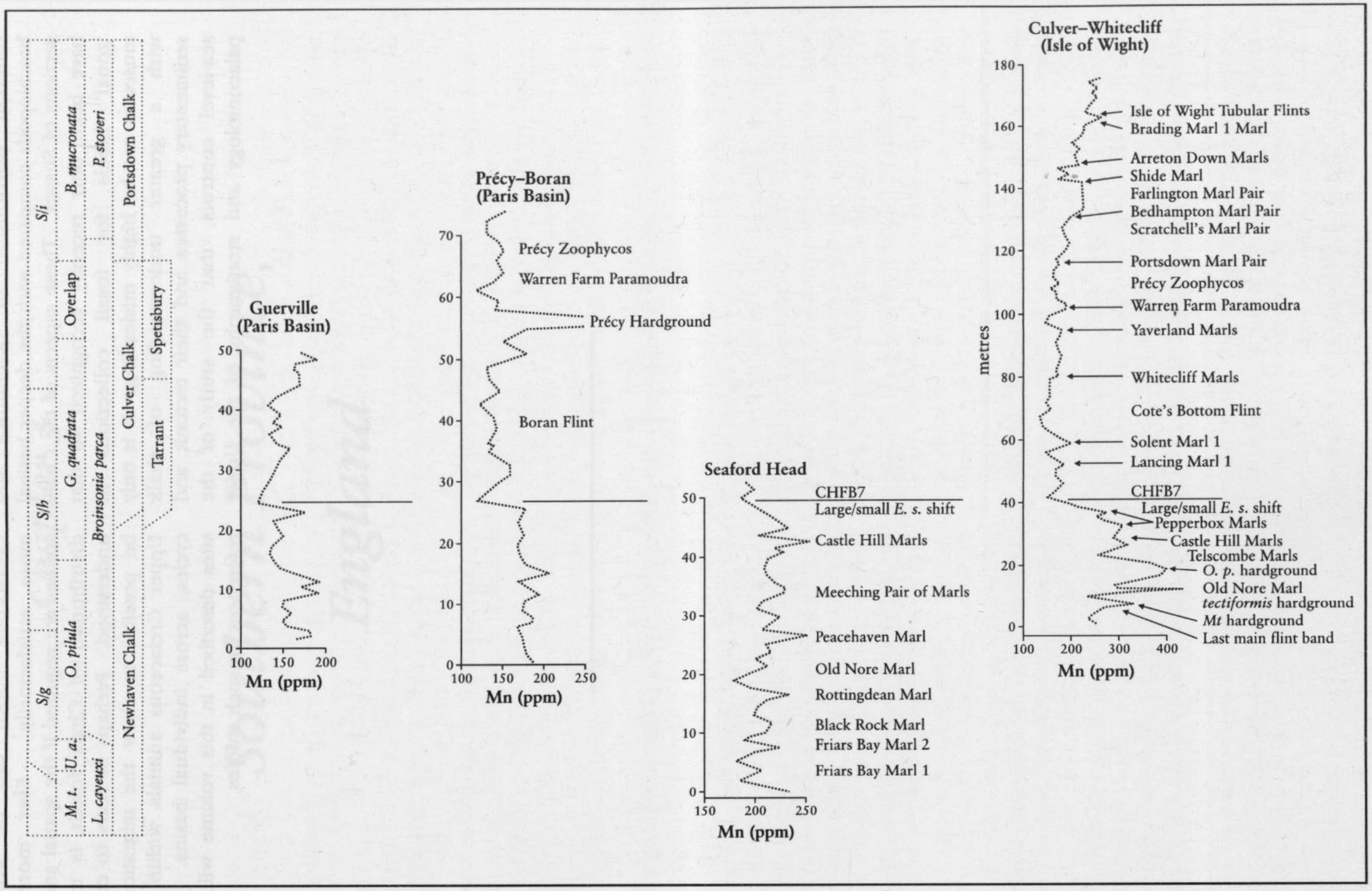


Figure 2.49 Correlation of manganese curves for the Campanian Chalk in the Southern Province and Paris Basin indicating the key event close to the Newhaven Chalk Formation–Culver Chalk Formation boundary, the conspicuous Précy Hardground 'spike', and the marked shift at the base of the Portsdown Chalk. S/g to S/i are standard French benthic foraminiferal zones. The third column refers to nannofossil zones. (CHFB7 = Castle Hill Flint (Band) 7; *M. t.* = *Marsupites*; *E. s.* = *Echinocorys scitula*; *U. a.* = *Uintacrinus anglicus*). (Based on field sections of Mortimore and Pomerol, 1987; and geochemistry of Barchi, 1995).

different distribution of belemnites and brachiopods compared with the deeper basinal sections of Sussex. These aspects of the Chalk have been only recently recognized so that 'zonal' labels for fossil collections in museums can be highly misleading. It is only with a greater understanding of chalk sedimentary processes and their tectonic and sea-level controls, that the study of the palaeontology and stratigraphy of the Upper Cretaceous Epoch can be accomplished more satisfactorily. Ever more detailed studies are required if the spatial and temporal distribution of Chalk fossils is to be fully understood. Perhaps in years to come it will be possible to show the migration rates of Upper Cretaceous animals within individual cycles, across individual basins. The GCR sites described in this volume will be major references for such studies.