

Echinoid distribution and sequence stratigraphy in the Cenomanian (Upper Cretaceous) of southern England

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SMITH, A. B., MONKS, N. E. A. & GALE, A. S. 2006. Echinoid distribution and sequence stratigraphy in the Cenomanian (Upper Cretaceous) of southern England. *Proceedings of the Geologists' Association*, **117**, 207–217. Almost 3500 individual occurrences of echinoid have been recorded and correlated against a sequence stratigraphic framework for the entire Cenomanian and basal Turonian from three regions of southern England, representing onshore, mid-shelf and deeper-shelf habitats. There are marked differences in the composition and diversity of faunas both across the shelf at a single time interval and through time at the same locality, driven primarily by factors such as sedimentary facies, which are controlled by changing sea-levels. The ranges of individual taxa expand and contract across the shelf as sea-levels change. In mid-shelf environments more onshore taxa appear only near sequence bases, at times of lowest sea-level, while those from more outer shelf settings are found during highstand intervals, and this creates a cyclical pattern of diversity. By comparison with modern faunas, the Middle and Upper Cenomanian of the Sussex coast is likely to have been deposited in water depths of between 100 m and 150 m and the amplitude of sea-level change appears to increase through the Cenomanian.

Key words: sea-level, diversity, diachroneity, faunal assemblages

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1. INTRODUCTION

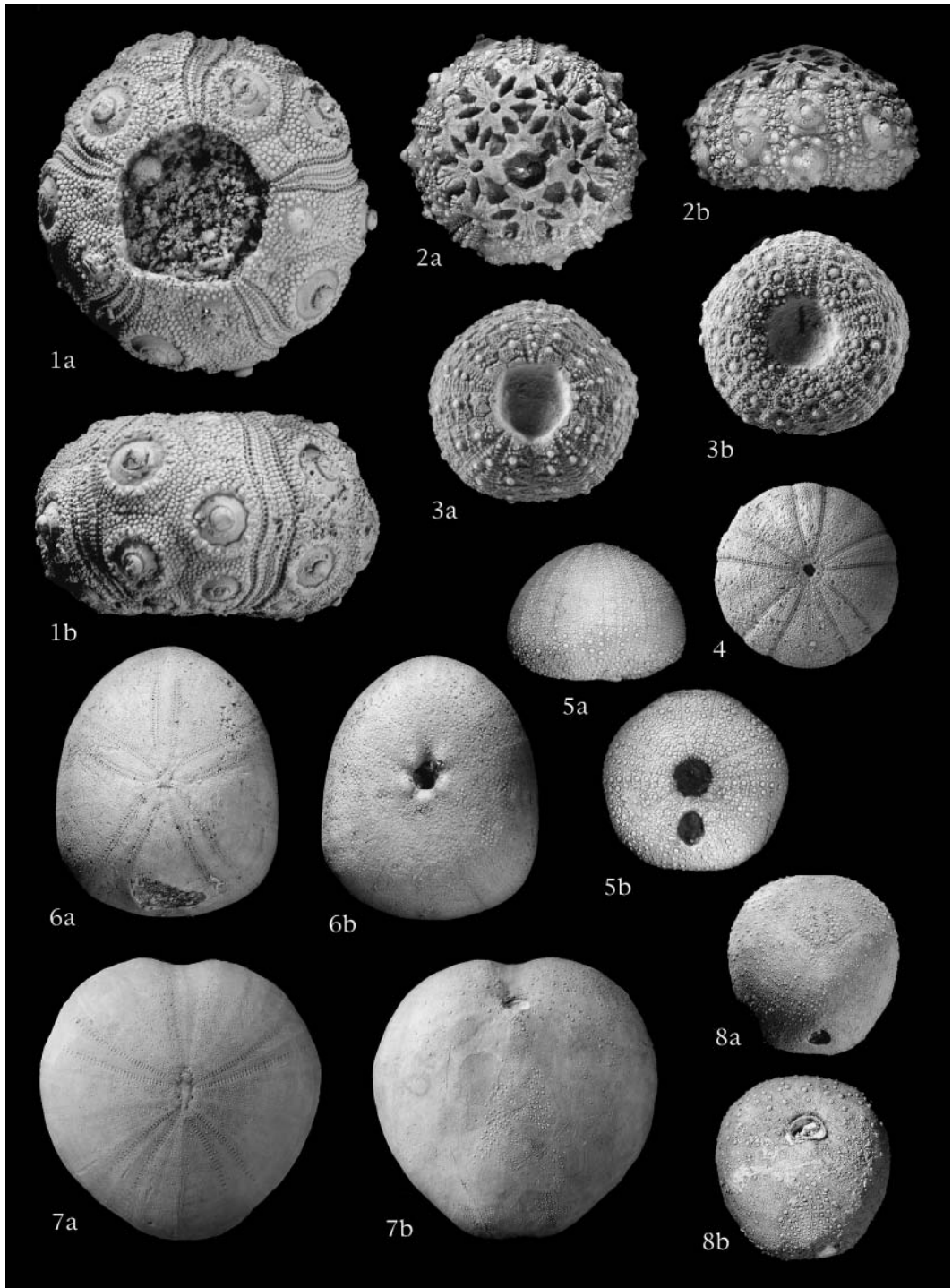
Echinoids have been an important constituent of the modern marine macrobenthic community ever since the Late Triassic, and today are found across the full spectrum of marine habitats, from the intertidal zone down to depths of more than 5000 m. Many factors control the distribution and preservation potential of individual taxa, the most important being nutrient availability, substrate type and turbulence (e.g. Nebelsick, 1995, 1996). All three are directly or indirectly correlated with water depth.

Life in rocky shore habitats requires special adaptations if epifaunal species are not to get torn off and crushed by powerful wave surge. This includes the development of large numbers of strong oral tube feet, the organs that are used for grip, stout spines for wedging into crevices and, in extreme cases, anen-

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caseament of tessellated aboral spines (as in the Upper Jurassic *Acrocidaris* (Baumeister & Leinfelder, 1998) and the modern *Colobocentrotus*). Life in littoral sediments is equally precarious because of the dangers of being washed out and crushed by wave surge and in these environments deep burial is a common strategy developed by infaunal irregular echinoids.

Below the littoral zone to depths of approximately 30–50 m specialist algal grazers and herbivores are predominant amongst regular echinoids, and bulk sediment swallowers predominate amongst irregular echinoids. The latter ingest sediment more or less wholesale in order to exploit the small quantities of organic particles that it contains (Lawrence, 1987). However, as water depth increases, nutrient supply to the sea floor becomes significantly curtailed and the free organic material available in the sediment diminishes, making bulk sediment swallowing unfeasible. With increasing depth and reducing light penetration, the stands of macroalgae also disappear and algal grazers are confined to areas where there is a supply of drift macroalgae. Consequently, in mid to outer shelf settings the echinoid fauna changes to one dominated by regular carnivore species and irregular phytodetritus browsers that mine organics at the sediment–water



interface and rely on the rain of organic material from surface waters. Within storm wave base there is sufficient lateral transportation of organic material from shallow water to maintain a diverse mixed echinoid fauna and, indeed, highest taxic diversity in Sagami Bay is found at *c.* 100–120 m water depth (Smith *et al.*, 2001). Below this, however, diversity rapidly drops and bulk sediment swallows and algal grazers are lost.

These clear changes in the population structure of echinoids in the present day are also recognizable in the geological past (e.g. Neraudeau & Villier, 1996; Smith *et al.*, 2001). This paper documents the stratigraphic distribution of echinoids across southern England during the Cenomanian, a time when sea-level was rapidly changing.

The aims of the article are two-fold: first to establish the precise ranges of echinoids in each section (summarized at genus level) collected by reference to stratigraphic horizons and tied into biostratigraphic and sequence stratigraphic schemes. Secondly, to explore how changing community structure may be related to sequence stratigraphy.

2. METHODS AND MATERIALS

Echinoid trophic groupings

A general description of the mode of life of Cenomanian echinoids can be found in Smith *et al.* (1988) and Neraudeau & Moreau (1989). Echinoids from the Cenomanian of the UK fall into a number of broad categories.

(i) *Cidaroids* (Fig. 1.1)

Cidaroids are generalist carnivores, feeding on sessile organisms especially sponges (De Ridder & Lawrence, 1982; Jacob *et al.*, 2003). Cenomanian cidaroids fall into two easily distinguishable groups based on their spine morphology: those with long cylindrical spines, equal or greater than their test diameter in length (*Stereocidaris*, *Phalacrocidaris*, *Prionocidaris*, *Hirudocidaris*) and those with stout club-like spines (*Tylocidaris*). Both are widely distributed in all three study regions.

(ii) *Saleniids* (Fig. 1.2)

Today saleniids are restricted to the deep-sea environment and are presumably generalist carnivores,

being much like cidaroids in habits and appearance. Cenomanian saleniids (*Salenia*, *Goniophorus* and *Hypsosalenia*), like cidaroids, occur in small numbers in inshore, mid-shelf and deeper shelf settings.

(iii) *Goniopygids*

These have expanded phyllodes orally and indicate the presence of nearby rocky substrates within wave base. Goniopygids are very rare and have been recorded only from SW Devon in the lowest, most inshore, beds.

(iv) *Other stirodents*

The genera *Tiaromma*, *Allomma*, *Glyphopneustes*, *Echinocyphus* (Fig. 1.3), *Glyptocyphus* and *Cottaldia* (Fig. 1.4) are all forms with a sunken peristome and no phyllodes. Similar forms today are typically neritic in distribution and feed on macroalgae. They are common only in the Devon sections, but are occasionally found in Sussex and Norfolk.

Tetragramma and *Polydiadema* are slightly different, having weak phyllodes a flush peristome and a strongly flattened form. They are likely to be algal grazers living on or around hard substrata in the neritic zone. Both are common in the lower parts of the succession in Devon.

(v) *Discoidids and conulids*

There are no modern equivalents to *Discoides*, *Camerogalerus* (Fig. 1.5) or *Conulus* and so their mode of life and diet can only be guessed at. They were possibly epifaunal opportunists living on unconsolidated sediments and feeding on detached algal debris and small benthic organisms on the sea floor.

(v) *Cassiduloids*

The cassiduloids *Catopygus* (Fig. 1.6), *Ochetes* and *Penesticta* were all probably bulk sediment swallows living in shallow-water clastic habitats within fair weather wave base. *Echinogalerus* is more likely to have been an epipsammic grazer (i.e. feeding on the organic particles adhering to individual grains without ingesting the grains themselves) judging from its size. Like modern cassiduloids, both fed on the organic material coating sediment grains (De Ridder & Lawrence, 1982; Lawrence, 1987).

(vi) *Holasterids and spatangoids*

Cenomanian holasteroids are represented by flat-based *Holaster* and the rounded-based *Crassiholaster*

Fig. 1. Typical elements of the echinoid fauna of the Cenomanian–early Turonian of southern England. **1a, b**, *Hirudocidaris uniformis* (Sorignet), NHM E76261. *M. dixonii* Zone, Lower Cenomanian, Wilmington, Devon: **a**, apical; **b**, lateral; $\times 2.25$. **2a, b**, *Hyposalenia clathrata* (Woodward), NHM E10296. Lower Cenomanian [?Cast bed], Dover, Kent: **a**, apical; **b**, lateral; $\times 2.7$. **3a, b**, *Echinocyphus rotatus* Cotteau, SM B98. Grey Chalk, Dover, Kent: **a**, apical; **b**, oral; $\times 1.8$. **4**, *Cottaldia benettiae* (König) NHM E42304. *M. dixonii* Zone, Lower Cenomanian, Wilmington, Devon; apical, $\times 1.35$. **5a, b**, *Camerogalerus minimus* (Desor), NHM E59654. *I. labiatus* Zone, Lower Turonian, Charring, Kent: **a**, lateral; **b**, oral; $\times 2.7$. **6a, b**, *Catopygus columbarius* (Lamarck), NHM E80657. *M. dixonii* Zone, Lower Cenomanian, Wilmington, Devon: **a**, apical; **b**, oral; $\times 2.0$. **7a, b**, *Crassiholaster subglobosus* (Leske). Grey Chalk, *A. rhotomagense* Zone, Oxted, Surrey: **a**, apical; **b**, oral; $\times 0.9$. **8a, b**, *Hemaster (Bolbaster) nasutululus* Sorignet, NHM E80642. *I. labiatus* Zone, Lower Turonian, Wilmington, Devon: **a**, apical; **b**, oral; $\times 2.25$.

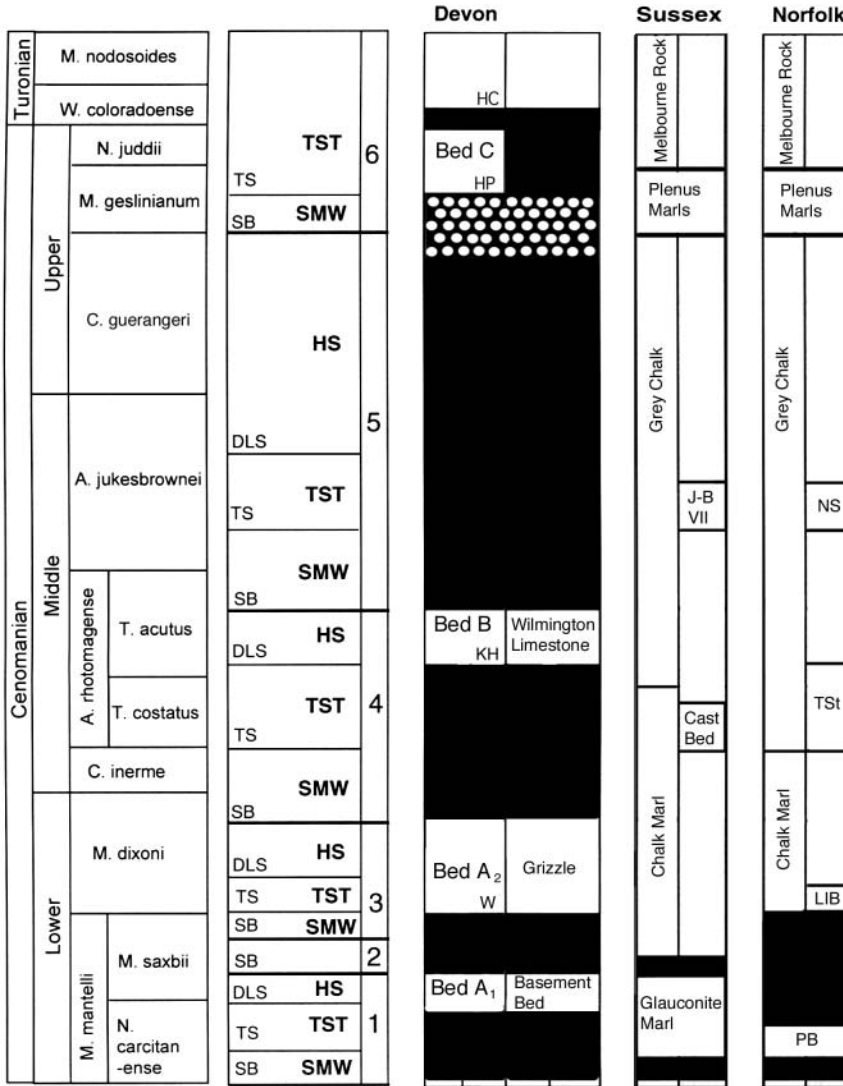


Fig. 2. Ammonite biostratigraphy and sequence stratigraphic framework for Cenomanian–basal Turonian sections in SE Devon (Branscombe–Beer and Wilmington), S. Sussex (Southerham and Beachy Head) and Norfolk (Hunstanton). Ammonite zonation follows Wright *et al.* (1984); systems sequences tracts are numbered 1–6 following Robaszynski *et al.* (1998). Note that only HS deposits of Sequence 2 are present in the UK. Abbreviations: DLS, downlap surface; HC, Haven Cliff hardground; HP, Humble Point hardground; HS, highstand system tract; J-B VII, Jukes-Brown Bed VII; KH, Kings Hole hardground; LIB, Lower Inoceramid bed; NS, Nettleton Stone; PB, Paradoxides bed; SB, sequence boundary; SC, Small Cove hardground; SMW, shelf margin wedge; TS, transgressive surface; Tst, Totternhoe Stone; TST, transgressive systems tract; W, Weston Hardground. Note that phosphatized fossils originating from the *C. guerangeri* Zone (white circles) can occur as reworked elements in Bed C.

(Fig. 1.7), *Cardiaster*, *Cardiotaxis* and *Labrotaxis*. *Holaster* was probably surface dwelling, feeding on accumulations of organic debris at the sediment–water interface. The others were infaunal deposit feeders. Spatangoids are represented by species of *Hemiaster* (Fig. 1.8) and *Micraster*. Both are infaunal detritivores, the former being deep-sea in distribution today.

Sequence stratigraphic framework

The Cenomanian was a time interval when sea-level was rising rapidly (Carter & Hart, 1977; Hancock, 1989; Hart *et al.*, 1992). Gale (1995), Gale *et al.* (1999) and Robaszynski *et al.* (1998) have constructed a detailed sequence stratigraphic framework for this time interval, recognizing five cycles during the

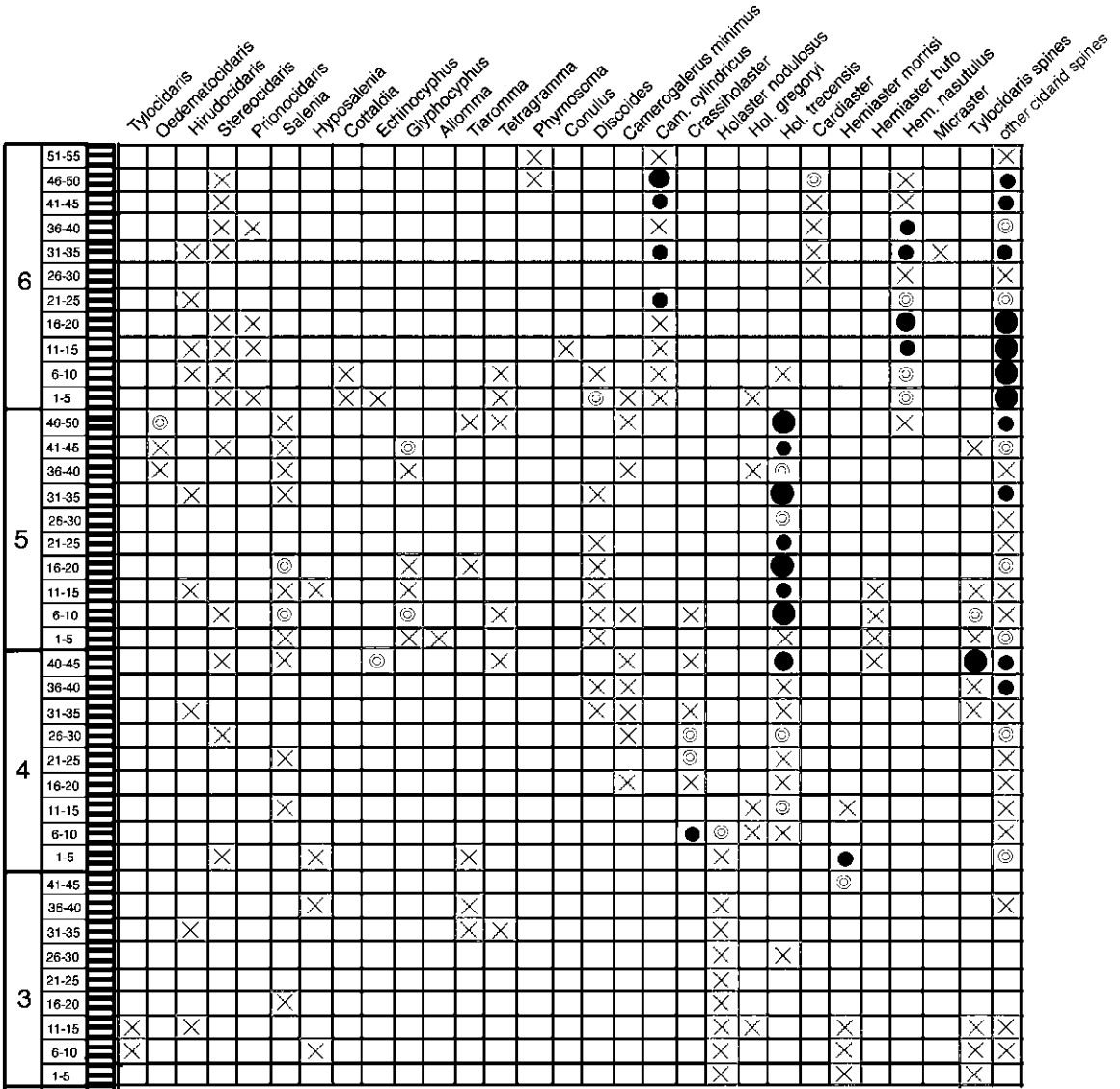


Fig. 4. Distribution of echinoid genera in the Cenomanian to early Turonian of S. Sussex. Symbols as in Fig. 3; abbreviations as in Fig. 2. Scale bar on left is in chalk-marl couplets (c. 20 000-year time intervals) which are grouped into bundles of five and numbered within each sequence.

of the sections at Beachy Head. Throughout this succession chalk-marl couplets are very pronounced and individual specimens were collected by reference to specific chalk-marl couplets (individually numbered). A total of 689 identifiable echinoid tests and 437 cidaroid spines were collected.

- **Norfolk** – The cliff sections lying between the town of Hunstanton eastwards to St Edmund’s Point [TF 672 413 to 677 424] yielded the core of the collections from here, but additional sampling of the higher Cenomanian succession was made at Hillington and Barrett Ringstead (see Gallois (1994)

for details of all of these localities). Some 145 specimens were collected and their height recorded with respect to a series of easily recognizable marker horizons. The onset of pure chalk facies occurs earlier here than elsewhere and, although the succession is thin, deposition was in a more offshore environment.

The surface area of rock available at outcrop for fossil collection in these three areas does not differ greatly, except for the rather small representation of the higher beds available in the Devon sections.

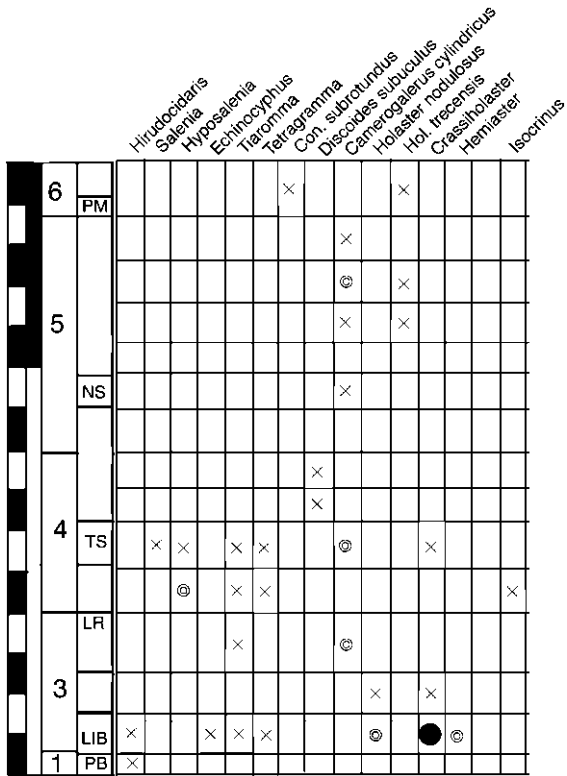


Fig. 5. Distribution of echinoid genera in the Cenomanian to early Turonian of N. Norfolk. Symbols as in Fig. 3; abbreviations as in Fig. 2 except for LR=Lower Orbirhynchia and PM=Plenus Marl; box shading as in Figure 3. Scale bar on left is in metres.

3. RESULTS

The stratigraphical ranges of the echinoid fauna from the three areas are summarized in Figures 3–5. Clear differences are seen between these areas, both in the composition of the faunas and in their relative diversities.

In the onshore settings of Devon (Fig. 3) a diverse community dominated by regular echinoids and cassiduloids is present in the early transgressive systems tracts (TST) sediments of Sequences 1 and 3, but this is replaced by a much lower diversity holasteroid-cidaroid-spatangoid community in later cycles. The only other time that an epissammic grazer or stirodont is found is close to the sequence boundary of Sequence 4.

In Sussex (Fig. 4) and Norfolk (Fig. 5), cassiduloids and epissammic grazers are absent due to the absence of sandy facies, and the cyclicity in diversity is driven almost exclusively by the rise and fall in diversity of algal grazer species (irregulars being present throughout). A variety of regular echinoids appear at the sequence boundaries of Sequences 4, 5 and 6 in Sussex,

but regulars are rarer in the silty transgressive sediments of Sequence 3.

In Norfolk regular algal grazer species are found at only two levels, immediately above the sequence boundaries of Sequences 3 and 4. In the upper beds just three species (*Tylocidaris* (spines only), *Holaster trecentis* and *Camerogalerus cylindricus*) co-occur in low numbers.

4. DISCUSSION

Diversity and sequence stratigraphy

Neraudeau *et al.* (1997), working at somewhat coarser resolution on the Cenomanian fauna of Charentes, France, concluded that echinoid diversity reached highest diversities at times of highest sea-levels. They were working in an inshore environment and their highest sea-levels corresponded to deep inner-shelf (neritic) settings. Comparing the three UK sections (Fig. 6) it is clear that greatest diversity of species is present in the transgressive system tracts (TST) of inshore settings and is lowest in the highstand system tracts (HS) of outer shelf settings. This pattern is most clearly seen in the mid-shelf setting at Eastbourne, Sussex where there are no significant breaks in sedimentation. Here a clear cyclicity in species diversity is apparent, with lows at the start of HST and peaks coinciding with system bases. This is apparent in the 100 000 year plots (i.e. five chalk-marl couplets; Fig. 7). A weak cyclicity is also evident in the data of Neraudeau *et al.* (1997).

In inshore habitats diversity peaks during the TST of Sequence 3 and falls rapidly approaching the HS. It remains low in Sequence 4 (possibly in part an artefact of restricted outcrop area), but shows a small peak at the start of the TST of Sequence 6 before dropping once more to low levels.

In outer shelf habitats diversity is always low, but peaks twice – once in the TST of Sequence 3, where species diversity is at its greatest, and a second, smaller peak associated with the TST of Sequence 4. In contrast to Eastbourne and Devon, no increase in diversity is associated with the sequence boundary at the base of Sequence 6, suggesting that in this part of the shelf water remained relatively deep.

In comparison to both Norfolk and Devon, the faunal diversity of the Early Cenomanian in Sussex is anomalously low. This may be because of the high silt content of the beds that presumably indicates highly turbid waters. The fauna of spatangoids, holasteroids and cidaroids found in these beds is typical of a community living below the photic zone.

Diachronous distributions and range expansions

During a transgressive-regressive cycle, as water depth changed over the shelf, one might expect to find evidence for changes in the geographical range of

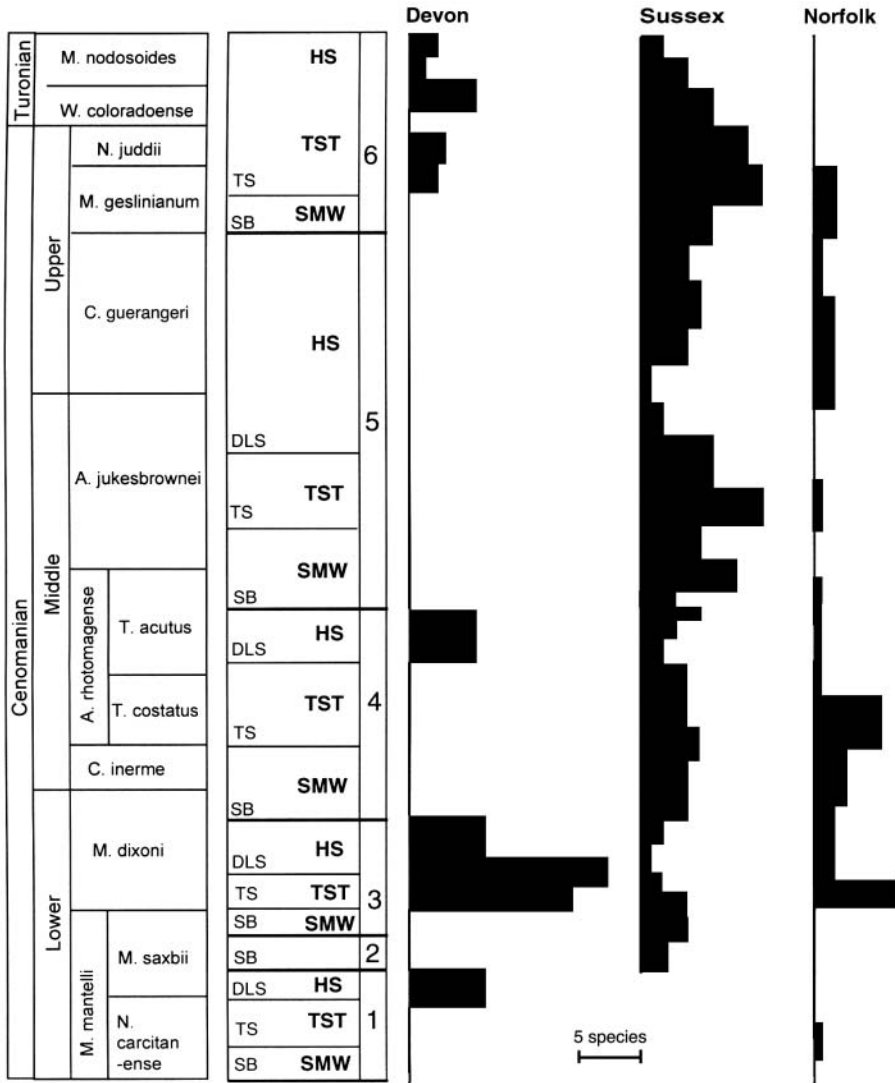


Fig. 6. Comparative diversity of echinoids in onshore, mid-shelf and deeper-shelf settings plotted against sequence stratigraphy. Abbreviations as in Figure 2.

species during different parts of the sequence stratigraphy (see Patzkowsky & Holland, 1993, 1996; Brett, 1995; Neraudeau & Villier, 1996). Deeper-water species should appear first in offshore settings and migrate into more onshore settings only later, once sea-levels have risen. Similarly, one might expect to see shallow-water taxa migrating into more outer shelf settings during times of lowest sea-level stand. Both patterns can be identified during the Cenomanian.

Range expansion of deep-water taxa during transgressive phases

There are two clear examples of deeper-water taxa that migrate over time into more onshore settings as water

depth increased. The earliest record of the holectypoid *Camerogalerus* in the three regions is in HS of Sequence 3 in Norfolk, and it continues to occur in higher beds through to the top of Sequence 5. In Sussex the first *Camerogalerus* does not appear until the HS of Sequence 4, where it becomes moderately common. In Devon rare small individuals are found in the upper parts of the TST of unit 4 and as *remanié* specimens in overlying transgressive beds of Sequence 5.

A similar pattern is shown by the holasteroid *Crassiholaster*, which first appears at the base of the TST of Sequence 3 in Norfolk and reappears in TST of Sequence 4. In Sussex, *Crassiholaster* does not appear

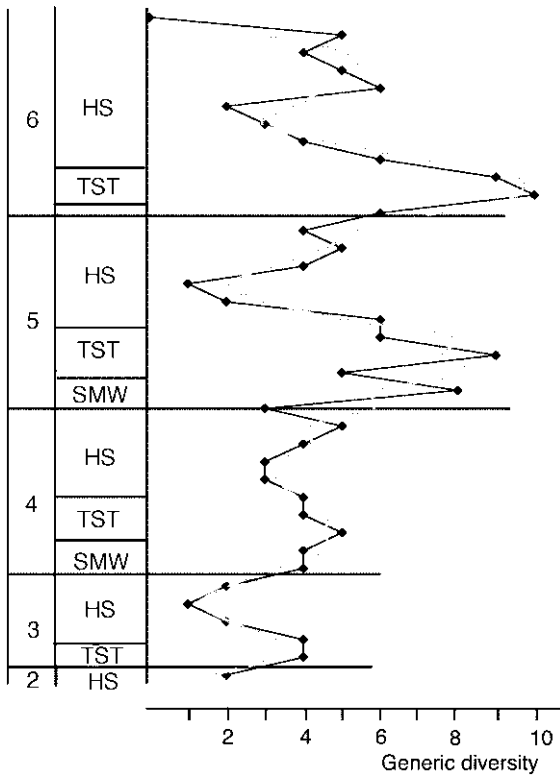


Fig. 7. Diversity of echinoids in southern Sussex grouped into bundles of five chalk-marl couplets (approximately 100 000-year intervals) plotted against sequence stratigraphy. The grey dashed line indicates a three-point moving average. Abbreviations as in Figure 2.

until the top of the TST of Sequence 4 and, like *Camerogalerus*, is moderately common throughout the HS of that cycle. In Devon, *Crassiholaster* comes only in the HST of Sequence 3, and is also found in the HST of Sequence 4.

For both *Camerogalerus* and *Crassiholaster*, their earliest appearances are in the deeper-water sediments of Norfolk and they have only expanded their ranges across into Sussex and Devon during periods of high sea-level stand.

Range expansion of shallow-water taxa during regressive phases

A number of regular echinoids that appear commonly in the TST and HS beds of Sequences 1 and 3 in Devon appear only later in the late SMW or basal TST parts of sequences in Sussex. *Cottaldia*, for example, is moderately common in the TST part of Sequence 3 in Devon, after which it more or less disappears. However, it does occur rarely close to the system base of Sequence 6 in Sussex, when conditions there were at their shallowest. *Echinocyphus* and *Tetragramma* show a similar pattern, with the latter also appearing in the

late SMW Sequence 4 and basal TST of Sequence 5 in Sussex and Norfolk, but only in the late SMW Sequence 5 and basal TST of Sequence 6 in Sussex. These represent shallow-water taxa that have expanded over the shelf during periods of low sea-level stand.

Palaeobathymetric interpretation of cycles

In Devon the presence of a diverse fauna of stirodont echinoids indicates proximity to macroalgal stands probably within *c.* 50 m water depth. Similarly, the presence of epipsammic grazers and bulk sediment-swallowing cassiduloids imply unconsolidated sediments within the same sort of depth range. These two groups predominate in the TST and HS parts of Sequences 1 and 3 in Devon but are absent from younger deposits, implying that water depths were greater than 50 m during the later TST and HS periods. However, phosphatized cassiduloids and stirodons are known from *remanié* deposits representing Bed C elsewhere in Devon (data not presented) and suggest that shallow-water conditions may have returned briefly during the regression at the end of Sequence 5.

By contrast, in Sussex, faunal diversity was low in the early sequences and algal grazers are extremely rare. This may be because the area was initially too deep to support a diverse community, or because the high silt content made the waters turbid, severely reducing light penetration. Higher in the section, when the silt content of the sediments was lower and the waters presumably clearer, there is a clear oscillation between more diverse faunas that include small numbers of algal grazers, and low diversity faunas dominated by surface-feeding holasteroids. The high diversity faunas coincide with the shallowest parts of each cycle, around the sequence boundaries, while the lowest diversities occur during the HS intervals. In present-day settings algal grazers more or less disappear at depths greater than about 100–120 m (Smith *et al.*, 2001) to be replaced by spatangoid-cidaroid communities. So the marked oscillation in diversity and the presence of a small number of algal grazers at the shallowest parts of the sequences, suggest water depths were in the range of 100–150 m.

Interestingly the amplitude of the diversity cycles increases through the Cenomanian, suggesting that sea-level fluctuations were becoming more extreme over time.

In Norfolk, echinoid diversity was never great, but was at its maximum when sea-level was lowest during the earlier sequences. A low diversity community dominated by holasteroids, cidaroids and *Camerogalerus* was the only community present throughout most of the succession. This suggests that during the regression at the end of Sequence 5 water depth remained greater than 100–120 m in this region of the shelf.

Holland (1995), in a pioneering paper, first established through computer modelling that sequence stratigraphic architecture would have a major controlling influence over taxonomic diversity and the distribution of first and last occurrences. Empirical work by Patzkowsky & Holland (1993, 1996) on the distribution of Ordovician brachiopods lent support. The analysis here of shelf echinoid faunas during the Cenomanian, together with earlier studies of the Cenomanian–Turonian boundary (Gale *et al.*, 2000, Smith *et al.*, 2001), confirms the close connection that exists between sequence stratigraphic architecture and faunal diversity patterns.

5. CONCLUSIONS

Because the composition and preservational potential of echinoid communities is controlled by factors that are predominantly depth-related, a strong correlation exists between species diversity and the sequence stratigraphic cycles that make up the rock record. Diversity in onshore environments is high in the Cenomanian but restricted largely to transgressive and early high-

stand intervals, as these are the only times when significant sedimentary deposits were preserved. Diversity decreases significantly below about 100–120 m water depth in modern settings, and is lowest in the deeper-water parts of the continental shelf during the Cenomanian.

Changing sea-level creates a cyclical diversity curve in mid-shelf environments of south Sussex in the Cenomanian primarily because of the expansion of the diverse fauna of algivores and other predominantly onshore taxa across the shelf during times of low sea-level stand (i.e. close to the sequence boundaries). Conversely, at times of high sea-level stand, a low diversity fauna typical of outer shelf settings expands into this region. The pattern of taxonomic appearances and disappearances is also highly predictable from the sequence stratigraphic architecture.

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