Echinoderms and Oligo-Miocene carbonate systems: potential applications in sedimentology and environmental reconstruction

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ABSTRACT

Echinoderms represent a major ecological component and contribute considerably to Oligocene–Miocene carbonate sediments, both as macrofossils and as skeletal grains. The skeletal morphology of all five extant echinoderm classes (echinoids, asteroids, ophiuroids, crinoids, holothuroids) is reviewed. Disarticulated skeletal elements are much more common in sediments than articulated specimens for all echinoderm classes except for echinoids; studies relying on complete specimens alone may be severely biased. The reproduction and growth of echinoderms, the composition of the skeleton, and the crystallography and diagenesis of echinoderm ossicles are reviewed. The echinoderm skeleton consists of high-Mg calcite with 3–18.5 wt% Mg. The skeleton exhibits strong interlacing of microcrystalline calcite with organic material and non-random orientation of crystals, achieving considerable hardness and durability. Echinoderm biostratigraphy and the identification of disarticulated material are considered. The echinoderm origin of sediment particles can usually be recognised by their characteristic microstructure. Due to the high degree of specialisation, disarticulated remains can often be identified to family or genus level, leading to a more accurate picture of spatial and temporal echinoderm distributions.

Echinoderm geochemistry is reviewed with respect to the Mg-content of the skeleton as a palaeotemperature proxy, and the Mg/Ca ratio as a monitor of ancient seawater composition; Sr/Ca ratios and carbon and oxygen stable-isotopes are considered. The echinoderm skeleton is altered during diagenesis and is transformed to low-Mg calcite. The microstructure of the skeleton is largely unaffected by this process, but changes in the isotopic signature and minor/trace-element contents may occur. These factors, together with physiological effects of isotope intake, hamper geochemical applications. However, echinoderms have been used successfully in studies of Phanerozoic seawater chemistry: the Mg and Sr contents of echinoderm skeletons apparently strongly correlate with temperature. Asteroids and ophiuroids are probably best suited for palaeotemperature reconstructions because of the lack of known fractionation within the skeleton and because genetic effects are less pronounced than in echinoids. Controlled laboratory experiments are needed to establish calibrations.

Echinoderm remains may account for 5–30 % of the particles within specific Oligocene and Miocene carbonate facies. They seem to be more abundant in temperate shelf carbonates than in tropical settings. Diagenetic changes associated with echinoderm ossicles strongly affect the embedding sediment and promote lithification. Bioerosion by grazing echinoids is important for carbonate budgets in coral reefs and influences the modal size-distribution of sediments by the production of carbonate mud. Burrowing echinoderms may cause intensive bioturbation and reworking of sediments. Echinoderms provide valuable evidence for palaeoenvironmental reconstructions. Ecological information can both be gained by actualistic comparisons with modern echinoderms and by a functional morphological approach, allowing the detailed assessment of general life habits, substrate conditions, nutrient availability and hydrodynamic regimes.

Keywords Echinodermata, taphonomy, palaeoecology, skeletal chemistry, Mg/Ca ratio, Sr/Ca ratio, stable isotopes.

INTRODUCTION

Echinoderms are a group of skeleton-bearing organisms that radiated in the early Palaeozoic, where they showed considerable diversity and morphological plasticity. The Permo-Triassic extinction event strongly affected echinoderms leaving only five groups, all of which are still extant today. These groups are the echinoids (sea urchins, sand dollars, heart urchins), asteroids (sea stars), ophiuroids (brittle stars and basket stars), crinoids (sea lilies and feather stars), and holothuroids (sea cucumbers). In each group, a variety of different life styles and feeding habits are realized, allowing their survival in a broad range of marine settings. With few exceptions among ophiuroids (Talbot & Lawrence, 2002) echinoderms are strictly stenohaline organisms.

Due to their peculiar high-Mg calcite skeleton, echinoderms exhibit a high fossilization potential, and are among the most common macrofossils found in Oligocene and Miocene carbonates. This paper presents a review of the current knowledge on the echinoderm skeleton and taphonomy, as well as their potential use in Oligo–Miocene carbonate sedimentology. Possible applications include actualistic and palaeoecological approaches to palaeoenvironmental reconstruction, taphonomic studies for facies analysis, and investigation

of their geochemical signature as palaeoclimate proxies and/or ancient seawater archives.

ECHINODERM SKELETON

Morphology

The echinoderm skeleton is a highly specialized, three dimensional meshwork of high-Mg calcite, called stereom. Its high porosity with an average of 50–60 % volume (the full range is c. 10–70 %: Weber, 1969a; Weber *et al.*, 1969) makes it a lightweight structure, conserving energy resources and facilitating rapid growth and regeneration. The morphology of the stereom network, including the thickness of individual rods and pore size, varies strongly according to position and function of the ossicles (Smith, 1980; Fig. 1). Although only covered by a thin layer of epithelium, the echinoderm skeleton is an endoskeleton of mesodermal origin. During life, the pores within the stereom are filled with tissue, which is termed stroma. This design accounts for high structural integrity and regeneration potential.

Echinoderms possess a multi-element skeleton. The skeleton of *Paracentrotus lividus*, the common stone urchin of the Mediterranean and East Atlantic coasts, for example, encompasses more than 110,000 ossicles (Fig. 2). Most crinoids possess

Fig. 1. Stereom differentiation on an ambulacral plate of an echinoid (*Asthenosoma ijimai*). Pore and trabecle size changes according to the attached soft tissue and its function: e.g. very small pores in the stereom forming the small tubercle on the lower right-hand side, marked by the arrow; rather coarse meshwork on the flanks.

Fig. 2. Number of ossicles and their size in the skeleton in an individual regular echinoid (*Paracentrotus lividus*) and a comatulid crinoid (*Himerometra robustipinna*; data from Meyer & Meyer, 1986).

more than twice as many elements (e.g. Fig. 2: *Himerometra robustipinna*, Meyer & Meyer, 1986). Ossicle shape is in most cases strongly functionally controlled. Due to the fact that the echinoderm skeleton is highly repetitive (with a pentaradial symmetry in most groups), the inventory of different ossicle types is limited (see Figs. 3–5 for characteristic ossicles of Cenozoic echinoderms). Despite this high degree of functional control, the shapes of individual groups are usually well differentiated and allow a rather straightforward identification (e.g. Fig. 6, showing spine cross-sections). The degree of taxonomic resolution that may be reached when working with echino-

derm remains depends on ossicle type and echinoderm group involved, ranging from phylum level at the worst, to species level in the best case. Oligocene, Miocene and Pliocene echinoderm faunas show a modern composition, many genera ranging back in time to the Late Eocene. This facilitates recognition of individual skeletal ossicles, particularly when extant material is used for comparative purposes. This method has been successfully employed in a number of studies dealing with Neogene echinoderms (e.g. Gordon & Donovan, 1993; Donovan *et al.*, 1993; Donovan, 2001; Kroh, 2003a, b, 2004; Kroh & Nebelsick, 2003).

Echinoid skeleton

Echinoids are characterized by a corona made up of 20 columns of perforate (ambulacral) and imperforate (interambulacral) plates. Attached to this corona are spines of variable shape, length and function, as well as tube feet (for locomotion and feeding) and pedicellariae (tiny claw-like defence and sanitary organs). While these appendages are generally lost before fossilization, the coronae often remain intact and are commonly found in Cenozoic sediments. This is due to the presence of organic and skeletal structures tightly interlocking the plates (except in cidaroids, diadematoids and echinothurioids, which are thus usually found as isolated plates or spines only).

Fig. 3. Examples of Neogene echinoids. (a) Spine of the cidaroid *Stylocidaris? polyacantha* (Reuss, 1860); (b) Test fragment of the cidaroid *Stylocidaris? schwabenaui* (Laube, 1869). (c–e) Lantern elements of the “regular” echinoid *Schizechinus hungaricus* (Laube, 1869). (f) and (g) *Parmulechinus hoebbarthi* (Kühn, 1936), a sand dollar. (h) and (i) Corona of the “regular” echinoid *Echinometra mathaei* (de Blainville, 1825). (j) and (k) *Schizaster eurynotus* (Sismonda, 1841), a heart urchin. Scale bars equal 10 mm (upper left scale bar valid for a and b, lower left bar for c–e, upper right bar for f–k). Modified from Kroh (2005).

Fig. 4. Preservation of fossil Neogene asteroids. (a–e) Disarticulated ossicles. (f) A whole specimen. Arrows indicate possible positions of the disarticulated material in the body of an asteroid (specimens shown here are not conspecific). (a) and (b) marginal ossicles of a goniasterid. (c) Astropectinids ambulacral ossicle. (d) Paxilla (abactinal ossicle) of *Luidia* sp. (e) Abactinal ossicle of an asteroid. (f) “*Goniaster*” *muelleri* (Heller, 1858). The scale bar equals 1 mm (for a–e), and 1 cm (f). Modified from Kroh & Harzhauser (1999).

Based on the gross morphology, three different types of echinoids can be identified in Oligo-Miocene deposits: (1) “regular” echinoids, characterized by their radial symmetry (Cidaroida, Diadematoidea, Echinacea; Fig. 3a–i); (2) sand dollars and sea biscuits (Clypeasteroidea) which are often flat and disc-like with a strong corona (Fig. 3f and g); and (3) heart urchins (Spatangoida), usually with a thin-walled corona and sunken ambulacra (Fig. 3j and k). Each of these groups is adapted to a different environment and can be used in facies analysis and palaeoenvironmental reconstruction (see below).

The identification of (fossil) echinoids is based mainly on corona morphology. Although a number of additional features are used in extant forms, identification using literature on recent genera is rather straightforward, at least in Neogene strata. A monograph of utmost importance in this respect is Mortensen’s (1928, 1935, 1940, 1943a, b, 1948a, b, 1950, 1951) “*Monograph of the Echinoidea*”. In most cases, identification of fragments and isolated spines is possible by

comparison with extant material. For further information on echinoids the reader is referred to Smith (1984), a highly useful textbook on echinoid palaeobiology.

Asteroid skeleton

The asteroid skeleton is composed of large, often block-shaped marginal ossicles (Fig. 4a and b) forming a pentagonal or pentastellate frame. The dorsal (aboral) side is covered by smaller polygonal plates (abactinal plates, Fig. 4d and e) set in a flexible membrane, but may also include large ossicles in some forms. The ambulacral grooves are located on the ventral (oral) side, formed by ambulacral (Fig. 4c) and adambulacral ossicles. The region of the mouth is framed by another set of specialized ossicles. After death, the asteroid skeleton disarticulates rapidly resulting in the common occurrence of isolated ossicles in the fossil record. Despite this fact, research has mainly focused on more or less complete asteroids (with the exceptions of Müller, 1953; Hess, 1955; Blake,

Fig. 5. Characteristic ossicles of crinoids (a–f, k–l), ophiuroids (g–j, m) and holothuroids (n–q); (a) and (b) Calyx of the comatulid crinoid *Conometra hungarica* (Vadász, 1915). (c) and (d) Crinoid brachials. (e) and (f) Isocrinoid columnals. (g) and (h) Ophiuroid lateral shields. (i) Ophiuroid vertebra. (j) Ophiuroid ventral shield. (k) and (l) Crinoid cirrals. (m) Vertebra of a gorgonocephalid ophiuroid. (n) and (o) Elements of the calcareous ring of an apodid holothuroid. (p) and (q) Wheel-shaped holothuroid sclerites: (p) *Theelia kutscheri* (Reich, 2003); (q) *Palaeotrochodota jagti* Reich, 2003. Scale bar equals: 1 mm (a–m); 0.5 mm (n–o); and 0.1 mm (p–q). Modified from Kroh (2003a), Kroh & Jagt (2006), Reich (2001, 2003) and Reich and Frenzel (2002).

1973; Breton, 1992; Villier, 1999; Jagt, 2000b). Identification of isolated ossicles is difficult, mainly due to the lack of comparative literature. Detailed descriptions of the ossicle morphology of some, more common forms can be found in Blake (1973).

Asteroids are very common in Oligocene and Miocene marine sediments, occurring mainly in form of isolated ossicles (e.g. Kaczmarzka, 1987; Jagt, 1991; Kroh & Harzhauser, 1999) and, more rarely, as whole skeletons (Nosowska, 1997). In cases these ossicles can constitute a large part of the fossil biomass recovered from sediment bulk samples (e.g. phosphate beds in the Lower-Middle Miocene *Globigerina* Limestone of the Maltese Islands).

Ophiuroid skeleton

Ophiuroids are characterized by their body shape with a usually well delimited disc and five arms. In some forms, the so-called basket stars, the arms may be branched, forming a catch apparatus for filter feeding. The disc is composed of a stout mouth frame, jaw apparatus, bursal ossicles, and a high number of polygonal platelets set in a flexible dorsal membrane. The arms are built of a central structure of longitudinally aligned vertebrae and protective platelets (dorsal, ventral and lateral shields). The structure of the ophiuroid arms is thus highly repetitive, with proximal elements very similar in shape to distal ones, only differing in their size and elongation.

Fig. 6. Cross-sections of fossil and recent echinoid spines illustrating the potential use of spine microstructure for classification in thin section. (a) Cidaroid *Plegiocidaris? peroni*. (b) Cidaroid *Eucidaris zeamays*. (c) Diadematoïd. (d) Echinacean *Paracentrotus lividus*. (e) Echinacean *Tripneustes ventricosus*. (f) Cassiduloid *Echinolampas crassa*. (g) Echinoneoid *Echinoneus cyclostomus*. (h) Spatangoid *Brissopsis otnnangensis* (i) Spatangoid.

As in asteroids, palaeontological research has mainly focused on complete specimens, with the exception of some workers (Hess, 1962a, b, 1963, 1965, 1966, 1975a, b; Jagt, 2000a; Kutscher & Jagt, 2000; Kroh, 2003b, 2004; Kroh & Jagt, 2006) who studied disarticulated ophiuroid material, in particular lateral shields and vertebrae. Identification of these isolated remains is usually difficult, necessitating numerous specimens for evaluation of morphological variation and extant material for comparison. Despite these difficulties, identification to genus level is often possible.

In comparison with asteroid ossicles, ophiuroid remains tend to be less common in Oligocene and Miocene sediments. Locally, however, they can be quite abundant and characteristic (e.g. basket star vertebrae in the Middle Miocene Hartl Formation of Austria; Kroh, 2003a; Kroh *et al.*, 2003).

Crinoid skeleton

The crinoid skeleton often consists of a very large number of ossicles (see Fig. 2), in spite of being composed of a small number of ossicle types. The majority of the ossicles are found in the arms, which basically consist of just two ossicle types, the larger brachials and the smaller pinnulae (Fig. 5c and d). The calyx in contrast, is made up of a small number of ossicles, which are often tightly fused (5 radials, 5 basals, 1 centrodorsale). Attached to the lower side of the calyx there may be a number of cirrae, being composed of numerous individual cirrals (Fig. 5k and l). In stalked forms, a stem consisting of numerous columnals is also present. Considerable information on fossil crinoids can be found in Hess *et al.* (1999), although primarily dealing with Palaeozoic and

Mesozoic forms. A review on comatulids (stalkless crinoids) has been published by Messing (1997).

In Oligo-Miocene sediments, crinoids play only a subsidiary role. Stalked crinoids (isocrinids and bourgueticrinids) are rare, except in deep-water settings (Oji, 1990; Eagle, 1993; Donovan, 1995; Donovan & Veltkamp, 2001; Kroh, 2003a). Stalkless forms, the comatulids, are more common, especially in reefal environments (Meyer & Macurda, 1997). Identification of these forms, however, is severely limited by the lack of adequate illustrations of the individual ossicles of most extant forms. Isolated brachial and cirral ossicles, as well as pinnulae, in most cases cannot be related to a specific taxon. Useful compendia on Cenozoic crinoids have been published by Gislén (1924), Biese & Sieverts-Doreck (1939), and Rasmussen (1972).

Holothuroid skeleton

In contrast to all other echinoderm groups discussed above, holothuroids have a highly reduced skeleton composed from numerous, minute sclerites (<1 mm) embedded in the body wall, tube feet and tentacles (Fig. 5p and q). Apart from these tiny ossicles, the only hard parts present are those of the calcareous ring, a structure usually composed of 10 elements (Fig. 5n and o). While widespread and common in extant settings, fossil holothuroids are much less abundant, particularly in the Cenozoic. Holothuroid body fossils are especially rare. Usually only isolated sclerites are found in micropalaeontological samples. In most cases, an artificial classification (parataxonomy) is used for the identification of fossil sclerites (Gilliland, 1993). A wide range of sclerites may occur in a single animal and individual sclerite types may occur in more than one species. A review of holothuroid skeletal morphology, systematics and evolutionary history was provided by Gilliland (1993) and the reader is referred to that work.

Reproduction and growth

Echinoderms, like many other invertebrates, usually reproduce by external fertilization, i.e. by the release of vast numbers of sperm and eggs into the water column. Fertilization is followed by a planktonic larval stage (except in direct developing forms) and finally metamorphosis and settlement. After a short lag-phase in early juvenile growth, a period of rapid growth followed by a long interval of declining growth can be observed in most echi-

nodermers. Growth in echinoderms, unlike most vertebrates, does not seem to stop at maturity although rather strongly decrease in rate (Lawrence, 1987; Pearse & Pearse, 1975; Russell & Meredith, 2000).

Growth in echinoderms is realized not only by enlargement of individual skeletal elements, but also by the continuous addition of new ossicles (Lawrence, 1987; Smith, 1984). Due to this, the position of an individual element may change considerably during growth (e.g. an interambulacral plate of an echinoid may migrate from a position near the apex to the underside of the animal). As a consequence, ossicle shape also changes during growth, both through lateral deposition of new skeletal material and by resorption. This change of shape is well illustrated by the growth lines present in many echinoderm ossicles (Fig. 7). These growth lines form by episodic growth breaks, injury and regeneration, as well as by other, unexplained causes. An interpretation of these growth lines as annual increments might seem tempting, but recent studies, employing tagging experiments, showed that this is not necessarily true (Russell & Meredith, 2000; Ebert, 2001, 2007). Slow growth rates in older individuals are especially problematic in this respect, and it now appears that the age of echinoids and, possibly most other echinoderms may have been seriously underestimated (Ebert, 1998, 2001; Russell *et al.*, 1998; Russell & Meredith, 2000).

For more information on echinoderm growth and mathematical models, in particular concerning echinoids, the reader is referred to Ebert (2001) and references therein. Further details on echinoderm biomineralization can be found in the comprehensive review provided by Smith (1990).

Mineralogy of the echinoderm skeleton

The skeleton of all known echinoderms is composed of high-Mg calcite, with MgCO₃ contents ranging from ~3 to 18.5 weight % (wt%; Weber, 1969b; Ebert, 2007). In the so-called “stone zone” of echinoid teeth, a primary protodolomite with Mg-values of up to 40 mol% occurs (Schroeder *et al.*, 1968, 1969; Märkel *et al.*, 1971). Transmission electron microscopic (TEM) studies of crinoid stereom revealed that Mg incorporation into the calcite structure of the echinoderm stereom is random and homogeneous to at least the 20 nm level (Blake & Peacor, 1981). Iron and strontium are incorporated as minor elements

Fig. 7. Growth lines in interambulacral plates of an extant *Strongylocentrotus pallidus* as revealed in thin section. Modified from Raup (1966a). Scale bar equals approx. 10 mm (no scale given in original paper).

with contents <1 wt% (e.g. SrCO_3 content ranging from 0.296 to 0.354 wt% in the sand dollar *Dendraster excentricus*, Pilkey & Hower, 1960; $1329\text{--}1645\ \mu\text{g g}^{-1}$ (parts per million) Sr, and $32\text{--}164\ \mu\text{g g}^{-1}$ Fe in stalked crinoids, Roux *et al.*, 1995). Manganese, aluminium and silicon are trace elements that occur at concentrations of $<100\ \mu\text{g g}^{-1}$ (e.g. $0\text{--}22\ \mu\text{g g}^{-1}$ Mn in stalked crinoids, Roux *et al.*, 1995).

Crystallography of echinoderm ossicles

Echinoderm ossicles are peculiar among other invertebrates with calcite skeletons as each echinoderm ossicle behaves optically like a single calcite crystal (West, 1937; Raup, 1966a; Donnay & Pawson, 1969; Nissen, 1969). Although parts of the echinoderm skeleton may be polycrystalline and composed of tiny crystallites with preferred orientation (e.g. cortex of spines in cidaroid echinoids, parts of the echinoid teeth, and the calcareous ring of holothurians), the overwhelming part of the echinoderm skeleton is monocrystalline (Märkel *et al.*, 1971) at a micro-optical scale. The polycrystalline parts are usually associated with structures and elements exposed to considerable wear or strain and are the hardest parts of the echinoderm skeleton. This hardness, which lies distinctly above the mineralogical hardness of calcite and protodolomite, is achieved by strong interlacing of the microcrystalline calcite with organic material (Märkel *et al.*, 1971). Individual skeletal plates of crinoids examined with single-crystal X-ray diffraction analysis by Blake & Peacor (1981) yielded diffuse and imperfect X-ray reflections due to a mosaic structure. Close inspection with TEM revealed crystallites within an order of magnitude of about $1\ \mu\text{m}$ in size, but it remains to be shown if this is true for all echinoderms. The observed mosaic structure together with incorporated organic material might be responsible for the lack of cleavage in fracture surfaces of extant echinoderm skeletal material (Blake & Peacor, 1981). In fossil specimens, by contrast, such cleavage is present due to diagenetic alteration resulting in (slight) mineralogical and crystallographical transformation.

Crystallographic orientation is non-random in most ossicles of the echinoderm skeleton, with empirical data showing clear genetic control in the echinoderms studied so far (echinoids: Raup, 1959, 1960, 1962a, 1966a, b; blastoids: Bodenbender, 1996). How exactly this control is achieved by the echinoderms is not completely understood, and several mechanisms have been discussed (see Smith, 1990; Bodenbender, 1996). Crystallographic data may be employed to address palaeobiological questions (e.g. mode of larval development in echinoids, see Raup, 1965; Raup & Swan, 1967; Emlet, 1985, 1989), classification and phylogeny (Raup, 1962a, b; Fisher & Cox, 1988; Bodenbender, 1996), as well as to assess diagenetic alteration.

GEOCHEMISTRY OF THE ECHINODERM SKELETON

As outlined above, echinoderms possess a relatively durable skeleton of high-Mg calcite and are common in many marine deposits. Due to these favourable attributes they represent a potential tool for the investigation of palaeotemperatures, geochemical cycles and ancient seawater composition. Despite their potential usefulness, only a small number of geochemical studies have actually employed echinoderm material (e.g. Bill *et al.*, 1995). This is probably related to the generally incomplete knowledge of the formation of the echinoderm skeleton in relation to seawater chemistry. Although a number of studies on this topic have been published, many of the basic principles are still poorly understood. Furthermore, detailed studies on the vital effects and intra- and interspecific variation are mostly missing (with a few exceptions: e.g. Pilkey & Hower, 1960; Weber & Raup, 1966a, b; Weber, 1968, 1969b, 1973). Nevertheless, echinoderms represent an unexploited source of original data on ancient seawater chemistry and palaeotemperature, as emphasized by Dickson (2004).

Magnesium content as a palaeotemperature proxy

Initial studies on the chemistry of recent echinoderm skeletons (Clarke, 1911; Clarke & Wheeler, 1914, 1915, 1917, 1922) suggested a good correlation between Mg content and water temperature in crinoids, asteroids, echinoids, and ophiuroids (listed according to the quality of the fit). The investigation of fossil echinoderms, in contrast, resulted in highly ambiguous and unexpectedly low values. Nevertheless, the potential of the apparent magnesium-temperature correlation for “studies of climatology” (Clarke & Wheeler, 1917, p. 56) was cautiously highlighted. Chave (1954), in a major paper on the biogeochemistry of a wide range of marine organisms, identified three major factors influencing the Mg content in the skeleton: mineralogy; water temperature; and phylogenetic level. However, the results of these studies (Clarke & Wheeler, 1922; Chave, 1954) were based on a limited dataset, and intraspecific as well as individual variation remain to be investigated. The first systematic investigation in this direction was undertaken by Pilkey & Hower (1960) on a large number of sand dollars (*Dendraster excentricus*) from the US west coast. They found that although

a magnesium-temperature correlation existed, Mg content was also influenced by salinity. Furthermore, they showed that the slope of the magnesium-temperature regression line in *Dendraster* differed strongly from that of the entire class and that the different species living at the same temperature showed considerable difference in skeletal MgCO_3 concentration (larger differences than the range shown by *Dendraster* over its entire temperature range). It could thus be deduced that a genetic control of Mg-uptake exists, an inference substantiated by subsequent studies (e.g. Raup, 1966b; Weber, 1969b, 1973). New data, albeit preliminary, indicate a negative correlation between growth rate (expressed by the Brody-Bertalanffy growth constant) and Mg content in echinoids (Ebert, 2007).

Weber (1969b) was the first to investigate the variation of MgCO_3 content within individual animals on a larger scale. Although it was known from early on that there were differences between spines, coronal plates and lantern elements in echinoids (Clarke & Wheeler, 1915) this had not been investigated in detail. Weber (1969b) showed that variation within individual skeletal elements was low (with the exception of echinoid spines; see below). The existence of a systematic variation of Mg content in the different skeletal elements of echinoids was also confirmed (Fig. 8). These differences were small in some species, but could

Fig. 8. Systematic variation of MgCO_3 content in the different skeletal elements of echinoids (data from Weber, 1973).

amount of up to 8.7 wt% in others (spines vs. coronal plates in *Echinometra mathaei*). In contrast to echinoids, no significant variation was detected in ophiuroids and asteroids. Magnesium content variation within individual populations was found to be rather low (Weber 1969b, Table 7), which confirmed earlier results by Pilkey & Hower (1960, Table 2). Surprisingly, asteroids and ophiuroids, in contrast to echinoids, showed only small differences between different species collected from the same locality (Weber, 1969b, Table 8) and thus genetic control of Mg-uptake seems to be less pronounced in these groups (compare also Weber, 1973, Fig. 4). Additionally, echinoid skeletal elements (even the coronal plates) are generally less rich in Mg than asteroids and ophiuroids from the same sample locations and seem, as a class, to be displaced towards lower Mg values at given temperatures (Weber, 1969b, 1973).

Data on crinoids, and even more so holothurians, are scarce. Roux *et al.* (1995) showed that MgCO_3 content in crinoids decreases with depth (Fig. 9) and provided also the first evidence for fractionation of Mg between different parts of the crinoid skeleton. They concluded that the incorporation of Mg in crinoid calcite was not necessarily a direct function of temperature, but is influenced also by metabolic rate and energy allocated to biomineralization in a given adaptive strategy. This is corroborated by newer data presented by Ebert (2001), that show that there is an inverse relationship between growth rate and MgCO_3 content. Additionally, regeneration may also have an important impact on Mg-uptake in the echinoderm skeleton.

Fig. 9. Decreases of MgCO_3 content in crinoids with water depth.

Based on the analysis of regenerated echinoid spines, Davies *et al.* (1972) and Weber (1973) demonstrated that Mg is not uniformly incorporated during regeneration and that the original MgCO_3 content is only reached in the final stage of regeneration.

In light of the data available at present, the use of MgCO_3 content as a palaeotemperature proxy is complicated by several factors, and the interpretation of its variation is not as simple as once thought. Particular problems are the poorly understood physiological effects causing strong scatter in echinoid data, the influence of factors other than temperature (including food availability, growth rate and regeneration), and difficulties in calibration between measured MgCO_3 content and temperature (as growth is temperature dependent and temperature varies seasonally). Slight variations of salinity may also pose a problem. Studying the geochemistry of recent tests of *Echinocyamus* from North Atlantic European localities, Richter & Bruckschen (1998) noted that the Mg content of the skeletons strongly correlated with the average annual temperature but not with salinity. Regarding the different echinoderm groups, asteroids and ophiuroids may be best suited for palaeotemperature reconstructions because fractionation between different skeletal elements is not known and genetic effects are apparently less pronounced than in echinoids (Weber, 1969b, 1973). In any case, controlled laboratory experiments are needed to establish well-founded calibrations for any echinoderm group that is to be used.

There is potentially a wide range of other research issues addressing the use of Mg content in echinoderm skeletons, in addition to palaeoclimatic research. An innovative approach utilizing the Mg content of fossil echinoderm skeletal material, for example, was employed by Richter (1974), who made use of the Mg-loss under subaerial diagenesis for the relative dating of Pleistocene carbonate terraces.

Mg/Ca-ratio as a monitor of ancient seawater composition

Initially, the major ionic composition of seawater was presumed to have been constant throughout the Phanerozoic (Holland, 1978). More recently, however, major changes in ancient seawater chemistry have been discovered by investigation of sediment mineralogy (Sandberg, 1983), geochemical modelling (Wilkinson & Algeo, 1989; Hardie,

1996) and fluid inclusion studies (Lowenstein *et al.*, 2001; Horita *et al.*, 2002).

Recently, Dickson (1995, 2002, 2004) and Ries (2004) employed fossil echinoderm skeletal material as an independent monitor for Mg/Ca oscillation of ancient seawater. Based on 29 specimens, Cambrian to Eocene in age, Dickson (2002, 2004) was able to reconstruct a Phanerozoic Mg/Ca-curve closely resembling first-order Mg/Ca seawater oscillations derived from earlier studies (Wilkinson & Algeo, 1989; Hardie, 1996; Horita *et al.*, 2002). At a finer scale, however, (<100 Myr) considerable differences exist and additional data, as well as improved understanding of Mg partitioning in echinoderms is required. These studies have demonstrated that, despite the uncertainties involved, echinoderms have a high potential as a “seawater archive” and represent an underused resource in this context.

Sr/Ca-ratio

Like magnesium, the strontium/calcium ratio may be used as palaeotemperature proxy (Lea, 2003) and has been successfully utilized in living and fossil corals (e.g. Beck *et al.*, 1992; Linsley *et al.*, 2000). Unlike corals, data on the Sr-uptake and content in echinoderms is largely missing. Pilkey & Hower (1960) found an inverse relationship between Sr and temperature in the sand dollar *Dendraster excentricus* with Sr/Ca ratios decreasing at roughly 0.3×10^{-4} per °C. Contrary to Turekian (1955), they could not detect any consistent influence of salinity.

Vital effects affecting the Sr-uptake in the echinoderm skeleton are, so far, unknown. In corals, at least, growth rate and symbiont activity appear to influence Sr-uptake from seawater (Cohen *et al.*, 2001, 2002). Diagenetic alteration, likewise, is poorly investigated in echinoderms, but it seems likely that, as in corals, subaerial exposure and vadose diagenesis result in Sr-loss from the skeletal calcite (compare McGregor & Gagan, 1994). When employing Sr/Ca-ratio in fossil echinoderms, secular changes in seawater strontium content have to be taken into account. As with Mg, there are data suggesting that the Sr/Ca-ratio changed through time, in particular due to glaciation events (Stoll & Schrag, 1998; Stoll *et al.*, 1999).

Carbon and oxygen isotopes

One of the most powerful methods for reconstructing palaeoenvironmental parameters is the study

of stable isotopes of oxygen ($^{18}\text{O}/^{16}\text{O}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) in carbonate shell material. Oxygen isotopes are used as temperature and salinities proxies, and carbon isotopes for the reconstruction of water bodies and palaeoproductivity (e.g. Wefer & Berger, 1991; Hoefs, 1997; Brenchley & Harper, 1998).

Despite this, stable-isotope studies on echinoderm skeletons are relatively rare. There is only a small number of research papers dating back to the beginning of biogenic stable isotope research dealing with echinoderm material (e.g. Weber & Raup, 1966a, b, 1968; Weber, 1968). In these initial studies, a wide range of interspecific, intraspecific and even intraindividual variability was detected. In general, echinoderms are enriched in ^{12}C and ^{16}O with respect to inorganically precipitated calcium carbonates under the same environmental conditions. Ophiuroids however, are an exception to this “rule” and show similar isotopic values to calcium carbonates precipitated abiotically at ambient seawater conditions (Weber, 1968).

According to Weber & Raup (1966a) echinoids show considerable fractionation of stable isotopes, especially in the coronal plates. The isotopic values of spines, in contrast, coincide better with data of other marine invertebrates than do other elements of the echinoid skeleton (Weber & Raup, 1966a; Ebert, 2007). During growth, the variation of the isotopic values seems rather small. Similar results were obtained for asteroids, ophiuroids and crinoids (Weber & Raup, 1968; Roux *et al.*, 1995; Baumiller, 2001), which also show large and systematic variation for different skeletal elements. Weber & Raup (1966b, 1968) found both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values to be largely genetically controlled. Oxygen-isotope values and, to a lesser extent, $\delta^{13}\text{C}$ values, are also controlled by temperature (Weber & Raup 1966b; Weber, 1968). If present, the correlation of carbon with temperature is positive, while in oxygen isotopes the correlation is negative. In asteroids, crinoids and echinoids $\delta^{13}\text{C}$ is negatively correlated with depth, while a positive correlation has been found for $\delta^{18}\text{O}$ (Weber & Raup 1966b; Weber, 1968; Roux *et al.*, 1995; Baumiller, 2001). According to Roux *et al.* (1995) the $\delta^{13}\text{C}$ depth correlation is related to the metabolic rate in crinoids, which in turn is controlled by the inter-related parameters, depth, temperature, food supply, and changing $\delta^{13}\text{C}$ levels of dissolved CO_2 at different depths.

Similar to other geochemical parameters (see above), diagenesis represents a potential severe

problem in using echinoderm skeletons because the skeletal elements consist of high-Mg calcite, an unstable carbonate mineral under meteoric conditions. Weber & Raup (1968), based on a study on the isotopic composition of fossil echinoids, concluded that distinct patterns may be found in isotopic signals despite diagenesis changing absolute isotopic values, especially when the extent of diagenetic alteration is known.

Despite all the problems mentioned, carbon-isotope data of crinoid stems and echinoid spines have more recently been used successfully to reconstruct environmental parameters in Upper Jurassic sediments from Switzerland (Bill *et al.*, 1995). Apart from isotope stratigraphy, isotope analysis in echinoderms may be applied to a wide range of palaeontological and (palaeo-)biological issues. Oji (1989), for example, used $\delta^{18}\text{O}$ values in living crinoids to identify seasonal temperature variation in bottom seawater and annual stem growth rates, while Baumiller (2001) utilized the isotope signature of the crinoid skeleton to recognize regenerated parts and different soft-tissue types.

ECHINODERM TAPHONOMY

Biostratinomy

Echinoderms have been the subject of a number of studies dealing with taphonomic aspects, as reviewed by Lewis (1980), Donovan (1991), Brett *et al.* (1997), Ausich (2001) and, most recently, Nebelsick (2004). Echinoderm skeletons can rapidly fall apart after death in a matter of days (Kier, 1977; Allison, 1990; Kidwell & Baumiller, 1990; Donovan, 1991; Greenstein, 1992; Nebelsick & Kampfer, 1994). The degree of disarticulation is related to intrinsic (type of connective tissues, structural integrity of the skeleton) as well as extrinsic factors (temperature, water agitation, scavenging). While holothuroids, ophiuroids, crinoids, and asteroids, as a rule, disarticulate into their separate, single ossicles, many echinoids can be preserved as denuded coronas, devoid of spines. This is related to the presence of interlocking skeletal supports and tight suturing of skeletal plates in some echinoid coronas. The skeletons of clypeasteroids are especially durable due to the added presence of internal supports that connect the oral and aboral surfaces (Seilacher, 1979).

Under certain circumstances (e.g. rapid burial, dysoxic conditions) articulated specimens of even

the most fragile echinoderms are preserved. Examples of exceptional preservation include holothuroid body fossils (Smith & Gallemí, 1991; Haude, 2002), articulated crinoid communities (numerous examples discussed in Hess *et al.*, 1999), the famous Devonian Hunsrück slates (Lehmann, 1957; Bartels *et al.*, 1966; Hess, 1999a; Glass & Blake, 2004), and the Upper Cretaceous *Uintacrinus* beds of Kansas (Hess, 1999b; Meyer & Milsom, 2001). In some instances, conditions may be exceptionally favourable, leading to the formation of so-called echinoderm-“Lagerstätten” (Rosenkrantz, 1971; Seilacher *et al.*, 1985) including the famous complete crinoids (*Seirocrinus* and *Pentacrinites*) from the Lower Jurassic Posidonian shales of southwestern Germany. Exceptional preservation of Oligo-Miocene echinoderms seems to be limited to concentrated deposits of echinoids, especially that of clypeasteroids (see below). A rare example of Oligocene crinoids preserved as articulated specimens is the famous Oregon sea-lily fauna (Moore & Vokes, 1953; Hess, 1999c).

Due to the properties of the stereo, the echinoderm skeleton is very durable during life, but is easily abraded and transported after death (Chave, 1964). Small ossicles, in particular, are easily lost due to winnowing or dissolution. Transportation however, can often be recognized by ossicle wear and assessing abrasion thus represents a useful tool to separate autochthonous elements from allochthonous ones. Another application, involving assessment of abrasion and transport, was demonstrated by Meyer & Meyer (1986), who showed that comatulid crinoid ossicle abundance and wear might serve as an indicator for reef proximity (Fig. 10).

Identification of disarticulated material

The echinoderm origin of individual skeletal components can be easily recognized by their peculiar skeletal structure (stereom). Echinoderm components in the mud-fraction are less easily identified, as the stereom structure may not be readily recognized in small fragments. If unaltered, skeletal mineralogy (high-Mg calcite) may aid identification. Due to the high degree of specialization of the individual ossicles, even disarticulated remains can often be identified to family or genus level (Nebelsick, 1992b, c; Donovan, 1996). Sometimes identification to species level is possible by comparison with complete fossil and/or extant specimens (e.g. Kroh, 2005). Inclusion of data from

Fig. 10. Comatulid crinoid ossicle abundance and preservation as a potential palaeoenvironmental tool to indicate reef proximity. Modified from Meyer and Meyer (1986).

fragmentary and/or disarticulated specimens leads to a much more accurate picture of spatial and temporal echinoderm distributions (Nebelsick, 1992a, b, 1966; Gordon & Donovan, 1993; Donovan, 2001, 2003; Kroh, 2005). In this respect, the analysis of sediment bulk samples is of special importance. Typical size classes of echinoderm skeletal elements are shown in Fig. 2.

Diagenesis of the echinoderm skeleton

The skeleton of echinoderms consists of high-Mg calcite, which is thermodynamically metastable. Nevertheless, recrystallization of echinoderm calcite during early diagenesis is usually inhibited by organic or inorganic coatings, and stabilizing effects due to the interaction of Mg-ions in the seawater with the skeletal calcite (Berner, 1966, 1996a, b; Bischoff, 1968; summary in Weber, 1969b). The growth of cement crystals, in contrast, usually starts very early, commonly as soon as the soft tissue has decomposed. A peculiarity of calcite cements growing on echinoderm skeletal material is their syntaxial nature (Fig. 11). Depending on Ca-ion availability, pore-water chemistry and available space, individual cement crystals may attain considerable size (Fig. 12A and B), usually completely filling the pores of the stereom. Larger cavities in the echinoderm skeleton may also be filled if they are free from sediment, and eventually so-

called “crystal apples” (Donovan & Portell, 2000; Donovan *et al.*, 2005, plate 1, figs. 2–7) may be formed. These are especially common in Palaeozoic forms like *Echinospaerites*, but also occur in

Fig. 11. Thin section from the Lower Miocene Zogelsdorf Formation of Austria showing two crinoid brachials (arrows) with extensive syntaxial cement. Crossed polarized light view (after Nebelsick, 1989).

Fig. 12. Syntaxial cement growth on echinoid tests. (a) and (b) On the inside of the corona of *Echinolampas manzoni* (scale bar = 1 cm). (c) and (d) On the outside of *Echinocyamus pseudopusillus* (scale bar = 1 mm).

Cenozoic echinoids. The outlines of these crystals often precisely follow the distribution of skeletal plates (Fig. 12; see also Donovan & Portell, 2000, fig. 1), and may thus sometimes be useful recognizing plating patterns. Neugebauer (1979) recognized two types of cement growth, the dog tooth cement (“Zahnzement” of Neugebauer, 1979a) mentioned above, and rim cement (“Facettenzement” of Neugebauer, 1979a). The development of large cement crystals on the outside of individual ossicles is initiated only after large parts of the pore space within the ossicle are closed.

Apart from cement growth, the mineralogy of the echinoderm skeleton itself changes during diagenesis. In most cases, fossil echinoderms are transformed to low-Mg calcite (Weber, 1969b, 1973; Neugebauer, 1979a, b, c), especially during vadose meteoric diagenesis (Richter, 1974). For example, Weber & Raup (1968) found only one single skeleton consisting of high-Mg calcite (a Pleistocene sand dollar of the genus *Mellita*) in a survey of 83 fossil echinoids from the Carboniferous to Pleis-

tocene. However, echinoderm skeletal material can be altered along different diagenetic pathways (Dickson, 2004). In some cases, high-Mg calcite is preserved (examples dating back to the Silurian are known, e.g. Dickson, 1995, 2004), others are altered to calcite and dolomite, but retain their original bulk composition (Bruckshen *et al.*, 1990; Dickson, 2001b, 2004). Cement coating plays an important role in this respect, as so called “crystal caskets” (Dickson, 2001b) may be formed that prevent ion-exchange with surrounding pore water.

Macro- and microscopic structure of the echinoderm stereom is often preserved, even in mineralogically altered ossicles. Even primary growth banding in individual stereom trabeculae may be preserved (Neugebauer, 1979a; Dickson, 2001b). Transformation however, is usually texturally not perfect, and often a finely mottled or granular texture is observed (contrary to the homogenous texture in unaltered samples). This granular texture resolves into large calcite crystals enclosing many microdolomite blebs (few μm in diameter)

Fig. 13. Diagenetic changes of echinoderm skeletons shown by the example of a tubercle from the dwarf sea urchin *Echinocyamus*. Stages shown: (a) Fresh, unaltered corona; (b) Initial cement growth begins, here in the form of syntaxial rim cement; (c) Strong cementation with dog tooth cement; (d) Marginal micritization.

and micropores ($\sim 1\mu\text{m}$ in diameter) in the Backscatter Scanning Electron Microscope (BSEM) (compare Dickson, 2001b, 2004). A similar texture can be observed in modern echinoderm ossicles artificially transformed by heating (Gaffey *et al.*, 1991; Dickson, 2001a). More commonly, however, another type of texture consisting of single calcite crystals with homoaxially well-defined microrhombic dolomite crystals occurs in fossil echinoderms (Macqueen & Ghent, 2003; Richter, 1974; Blake *et al.*, 1982). Contrary to the former texture type, which is the result of transformation with little or no involvement from material external to the skeleton, the latter type forms due to open-system transformation.

Similarly to the Mg-loss during vadose diagenesis, changes in the isotopic signature of the echinoderm skeletal remains may occur. Again the microstructure of the skeleton is largely unaffected by the process. Manze & Richter (1979) documented a loss of ^{13}C correlated to Mg-loss under meteoric-vadose conditions. Weber & Raup (1968), by contrast, found no evidence for a correlation of

Mg-loss and alteration of the stable-isotope signature in a survey of 191 fossil echinoids spanning an age range from the Devonian to the Pleistocene. The degree of diagenetic alteration of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values cannot be predicted by Mg content, except in special cases involving conspecific fossil and recent specimens (Weber & Raup, 1968).

Apart from the geochemical alteration discussed above, echinoderm ossicles may also become subject to micritization during diagenesis, be it biogenic (Bathurst, 1990) or abiogenic (Neugebauer, 2001). While complete micritization as described by Neugebauer (2001) is rather rare (at least in the Cenozoic), marginal micritization is commonly observed (Fig. 13). Hand-in-hand with micritization, a considerable loss of volume may occur due to pressure dissolution. This loss may amount to up to 80% of the original skeletal mass in the example of the Cretaceous crinoid *Uintacrinus socialis* investigated by Neugebauer (2001). A similar alteration has been observed in Miocene echinoids (Fig. 14) where the corona is micritized and strongly leached due to pressure solution.

Fig. 14. Vertical cross section through a "Prägesteinkern" of *Clypeaster campanulatus*. The corona is nearly completely micritized and leached due to pressure solution, only traces remain of the original shell. Modified from Kroh (2005).

Diagenetic changes associated with echinoderm ossicles strongly affect the embedding sediment and promote lithification. This especially applies when echinoderm syntaxial cements extend out into the surrounding pore space. Cementation with syntaxial cement is an important factor in sediments where: (1) echinoderms are common; (2) the sediments show high interparticulate porosity (grainstones and rudstones); and (3) there is little or no primary marine cementation. In the Oligo-Miocene, this has been most often described from non-tropical limestones (e.g. Nelson, 1978; James & Bone, 1989; Nebelsick, 1989; Nicolaides, 1995; Nicolaides & Wallace, 1997; Knoerich & Mutti, 2003).

In the Gambier Limestone, for example, syntaxial cements on echinoderm fragments are the only cements of any importance (James & Bone, 1989). In the Oligo-Miocene Clifton Formation of southern Australia, syntaxial calcite overgrowths on echinoderm fragments represent one of three morphological cement types along with scalenohedral and blocky equant calcite spar (Nicolaides & Wallace, 1997). Knoerich and Mutti (2003) noted two phases of syntaxial cements growing on echinoderm fragments as part of a complex diagenetic history in Oligocene heterozoan limestones from Malta: a thin rim (30 μm) of inclusion-rich crystals and a later phase of inclusion-free syntaxial calcite with larger crystals (200 μm). The first phase is attributed to marine diagenesis, the second to possible burial marine cementation. In all cases, high degrees of primary pore space allow syntaxial cement to develop far beyond the primary component, often enclosing surrounding biotic and terrigenous components.

Sediment production, erosion and reworking

Echinoderms play an important role both in the production of carbonate (skeleton, faeces) and the reworking of sediment (bioturbation, erosion). The total production of carbonate by echinoderms and their contribution to the carbonate budget is difficult to ascertain. However, disarticulated remains may account for a significant portion of the sediment particles (up to 45% in some instances) as revealed by modal analysis of components (see below). Carbonate mud from echinoderm faeces contributes to the fine fraction of the sediment.

Echinoids are major bioeroding organisms and are important for carbonate budgets in coral reefs (Otter, 1932, 1937; Russo, 1980; Bak, 1993, 1998;

Glynn, 1997; Carreiro-Silva & McClanahan, 2001). The jaw mechanisms of echinoids (Aristotle's lantern) contain hardened teeth which are continuously produced at the base in order to replace the eroded distal tips. Jaws are present in all regular echinoids as well as in many irregulars, including the clypeasteroids. Many regular echinoids are non-specific grazers exploiting plants and animals with both soft and hard skeletal surfaces. The eroded material is then excreted as pellets of fine carbonate mud.

Echinoid bioerosion as a structuring force in the coral reef environments was reported by Mokady *et al.* (1996) from the Red Sea. Typically, the echinoid *Diadema setosum* erodes 310 mg per individual per day, while *Echinometra mathaei* abrades 120 mg per individual per day (see also Muthiga & McClanahan, 2007; McClanahan & Muthiga, 2007). Both echinoids occur in high densities and are thus major converters of carbonate skeletons to carbonate sediments in both reef flats and reef slopes. In a study of echinoid bioerosion and herbivory on Kenyan coral reefs, Carreiro-Silva and McClanahan (2001) showed the importance of regular echinoids (in this case *Echinothrix diadema*, *Diadema setosum*, *Diadema savignyi* and *Echinometra mathaei*) in reef development. Bioerosion was generally found to be higher than herbivory rates. The highest bioerosion rates ($1180 \pm 230 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) were found in unprotected reefs with highest echinoid densities at 6.2 ± 1.5 individuals m^{-2} due to low fish predation pressures. Intermediate bioerosion rates ($711 \pm 157 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) were recorded at newly protected reefs with 1.2 ± 0.1 individuals. Lowest bioerosion rates ($50.3 \pm 25.8 \text{ g CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) were found in protected reefs with 0.06 ± 0.01 individuals m^{-2} .

There has been a dramatic evolution of teeth form and efficiency within echinoids through time (compare Smith, 1984). Steneck (1983) correlated increased bioerosive efficiency of organisms including echinoids during the Mesozoic to adaptive trends in calcareous algal crusts, including the development of sunken conceptacles within the skeletons. Direct evidence of echinoid bioerosion such as five pointed, star-shaped scratch marks (Bromley, 1975) are rare and not conducive to quantification. Although, clypeasteroid teeth do not erode surficial hard substrates as such, they are employed in crushing ingested sand-sized particles (Kampfer & Tertschnig, 1992). This leads to the production of finer sediments, thus influencing the modal size distribution of the sediments.

Echinoids may also produce distinct burrows which can potentially be recognized in the fossil record. The Indopacific echinoid *Echinostrephus molaris* erodes deep burrows in reefal environments (Russo, 1980; Campbell, 1987). Their burrowing activity can also exert an influence on coralline algal growth inducing rhodolith production in the Red Sea (Piller & Rasser, 1996).

Finally, members of the echinoids (especially the irregulars), asteroids, ophiuroids and holothuroids are major infaunal elements and can cause intensive bioturbation of the sediments in calcareous environments (Scheibling, 1982). High maximum individual reworking rates have been recorded for the irregular echinoid *Meoma ventricosa* ($8520 \text{ cm}^3 \text{ day}^{-1}$) and the clypeasteroid *Encope michelini* ($960 \text{ cm}^3 \text{ day}^{-1}$) from Caribbean lagoons (Thayer, 1983). This bioturbation can be shallow, as for most clypeasteroids, or deep, as for many spatangoids, which can result in characteristic trace fossils (Bromley and Asgaard, 1975; Bertling *et al.*, 2006).

ECHINODERMS AS COMPONENTS IN OLIGO-MIOCENE CARBONATES

Echinoderms are important components in carbonate environments, usually comprising between 5 and 30 % of the sediment particles. They seem to be more abundant in non-tropical than in tropical settings. In temperate shelf carbonates, echinoderms constitute one of the major groups of skeletal fragments together with bryozoans, benthic foraminifera, barnacles, brachiopods, bivalves, and coralline algae (Nelson, 1978). This is not only reflected by quantitative modal analysis of component distributions, but finds its expression also in facies nomenclature as well as in the names of general facies associations (see below). In tropical settings, echinoderms, though common as macrofaunal elements, are rare as components in the sediments. A recent example from the Red Sea shows mean concentrations of <1% and maximum values of <5% within sediment samples (Piller, 1994).

One of the most distinct occurrences of echinoderms in Oligo-Miocene sediments is that of mass occurrences of clypeasteroids in shallow-water environments (Nebelsick & Kroh, 2002; Kroh & Nebelsick, 2003). These mass occurrences are often found within shoreface sequences and can include very large numbers of individuals, leading to sand-dollar beds ranging from a few centimetres to a

number of metres in thickness. The origin of these shell beds has been tied to high population densities and concentration processes, including tempestites or winnowing in higher energy environments. Other echinoids can also be included in these special lagerstätten, which can be spectacular in nature and are readily noticed within sedimentary sequences. Encrinites, consisting of mass accumulation of crinoid remains, though common in the Palaeozoic and Mesozoic (Ausich, 1997), are missing in Cenozoic sediments, probably owing to the declining importance of stalked crinoids in shallow-water settings.

Modal distribution of echinoderms

An exact comparison of the modal presence of echinoderms in different Oligo-Miocene carbonates is difficult to accomplish due to the wide variety of qualitative and quantitative assessment methods applied to determine component distribution. Even those studies including multivariate statistical analysis of component distributions differ widely in the exact methods used to accumulate the respective data sets (e.g. by use of semi-quantitative comparative methods or quantitative point-counting methods). However, high numbers of echinoderms are reflected by nomenclature; e.g. “molechfor” facies type of Carannante *et al.* (1988) or “echinofo” facies type of Hayton *et al.* (1995). The ability to distinguish echinoderms in thin section is limited to distinct plates and spines (Fig. 15).

Oligocene carbonates seem to be generally poor in echinoderms, at least in the circum-alpine area. Average concentrations of around 1 % echinoderms are found in the Lower Oligocene Gornji Grad Beds of Slovenia, with maximum values of near 4 % being reached in grainstones of a foraminiferal-coralline algal facies (Nebelsick *et al.*, 2000). Similarly, echinoderm remnants in thin sections from in the Lower Oligocene Werlberg Member of the Paislberg Formation from the Lower Inn Valley show values ranging from 3 to 7 % (Nebelsick *et al.*, 2001). Oligocene carbonates of the Lower Coralline Limestone of Malta consist of packstones to rudstones and are dominated by coralline red algae, bryozoans, echinoids and benthic foraminifera (Knoerich & Mutti, 2003). Modal analysis revealed echinoid dominance between 2 and 29 % within individual samples. These echinoids are especially important for diagenetic pathways including two generations of

Fig. 15. Echinoderms in thin section. (a) Half of a broken regular echinoid with distinct plates and tubercles cupped around a coral fragment (from Nebelsick *et al.*, 2000). (b) Single regular echinoid plate showing differential stereom construction. (c) Slightly oblique sections through a cidaroid spine (regular echinoid; from Löffler & Nebelsick, 2001). (d) Strongly oblique sections through a cidaroid spine (regular echinoid), note thin crust of coralline algae. (a) Lower Oligocene, Gornji Grad Beds. (b–d) Lower Oligocene, Werlberg Member (Paislberg Formation) from the Lower Inn Valley. All views, plain polarized light.

syntaxial cements. Echinoid content is equally high in samples from Ragusa Island (5–16 %, averaging around 9 %; see Knoerich & Mutti, 2006).

An example from Lower Miocene bryomol carbonates is the “Echinoderm-Foraminiferal Facies” within the Lower Miocene Zogelsdorf Formation (Nebelsick, 1989, 1992a). In this facies, echinoderm remnants comprise more than 30% of the biogenic components. The occurrence of echinoderms is linked to high amounts of bryozoans, which may be due to the fact that dead echinoids represent important sites for incrustation not only for bryozoans, but also for barnacles, serpulids and coralline algae, as they represent relatively large substrates within otherwise highly mobile, particulate skeletal sediment (Nebelsick *et al.*, 1997). Tortonian, nearshore, temperate, carbonate depositional systems from southern Spain contain packstones and rudstones in part rich in echinoderms (e.g. Brachert *et al.*, 1996; Martín *et al.*, 1996). Quantitative data from thin sections show average concentrations of echinoderms near 10 %, with maximum values of 28 % (Betzler *et al.*, 1997); packstones below volcanic palaeocliffs are

locally dominated by echinoderm debris, which contributes up to 45 % of the components.

The importance of echinoderms within facies in a non-tropical setting has been reported by Lukasik *et al.* (2000) from the Murray Supergroup in southern Australia. These deposits originated from a shallow, low-energy, mesotrophic, epeiric ramp. Echinoderms are generally common within four facies associations, but especially within the echinoid-bryozoan facies association. This association comprises four echinoderm-dominated subfacies deposited at shallow to moderate depths to the base of the euphotic zone.

Facies associations

Echinoderms are common members of “non-tropical”, “warm temperate” (Nelson, 1988) or “heterozoan” communities (James, 1997). They have played an increasing role in facies models used to describe the component associations. These include the “bryomol” (Nelson *et al.*, 1988), the “rhodalgal” (Carannante *et al.*, 1988) and “molechfor” facies types (Carannante *et al.*, 1988).

The latter association is dominated by molluscs, echinoids and (small) benthic foraminifera.

A more detailed classification, based on component dominance, was introduced by Hayton *et al.* (1995) for non-tropical carbonate deposits using data from New Zealand Cenozoic limestones. Seven assemblages were recognized by cluster analysis of abundance data of skeletal components. Of these, two include echinoderms as denominating components: the “echinoform” (echinoderm/benthic foraminiferal) and the “rhodochform” (calcareous red algal/echinoderm/benthic foraminiferal) assemblages. The echinoform assemblage, which is dominated by echinoid plates and spines with occasional complete sea urchins, is widely distributed in Oligo-Miocene sediments and is interpreted to reflect frequent reworking and high suspension loads that prevented the settlement of bryozoans (Hayton *et al.*, 1995). The rhodochform assemblage is generally rare in Miocene sediments. Lower light intensity is interpreted to be responsible for an increase in non-algal components compared to a rhodalgial assemblage (Hayton *et al.*, 1995). This terminology has been applied in other studies, for example in Eastern Crete where an echinoform-type lithofacies was recognized in Neogene non-tropical carbonates deposited in a warm-temperate biogeographic province (Pomoni-Papaioannou *et al.*, 2002).

Echinoderms in aphotic sediments

The presence of echinoderms is generally not restricted by depth. Members of all five extant echinoderm classes belong to the most dominant benthic organisms in larger depths below the photic zone where phototrophic (e.g. coralline algae) and symbiont-bearing organisms (e.g. larger foraminifera) cannot exist due to the lack of light. This is demonstrated by Miocene rhodalgial and molechform sediments from the “Briozoi e Litotamni” Formation from the Latium-Abruzzi Platform of the central Apennines (Brandano & Corda, 2002; Corda & Brandano, 2003). While carbonate production and accumulation in the inner to middle ramp is dominated by coralline algae with rhodoliths, larger benthic foraminifera and molluscs; sediments of the outer ramp below the photic zone are co-dominated by echinoderms (a bryozoan–echinoid unit, a benthic foraminiferal–echinoid unit, and a planktonic foraminifera–echinoid unit). Deep-water,

basinal sediments also show a large number of echinoderms in calcarenites, together with siliceous sponge spicules and planktonic foraminifera.

ECHINODERMS AS PALAEOECOLOGICAL TOOLS IN OLIGO-MIOCENE SEDIMENTS

Echinoderms have great potential as palaeoecological tools in Oligo-Miocene carbonate environments. Ecological information can not only be gained by actualistic comparisons with recent echinoderms, but also by using a functional morphological approach (e.g. Kier, 1972; Boggild & Rose, 1984; Kroh & Harzhauser, 1999; Néraudeau *et al.*, 1979c; Kroh & Nebelsick, 2003). Both approaches allow the detailed assessment of general life habits, substrate relationships (grain-size parameters, stability and sorting), nutrient factors (food availability and organic content) and hydrodynamic regime including current velocity and water turbulence (Boggild & Rose, 1984; Kroh & Nebelsick, 2003). Studies of echinoderms in Oligo-Miocene habitats have largely focussed on echinoids (Kier, 1972; Boggild & Rose, 1984; McNamara, 1970; Kroh & Harzhauser, 1999; Carter, 2003; Kroh & Nebelsick, 2003) due to their higher preservation potential, but other echinoderms, especially comatulid crinoids, if present, should also be included.

A combination of morphological description, taxonomic treatment, functional morphological interpretation, and interpretative assignment to habitat occupation, were shown in the classic study of Kier (1972) from the Yorktown Formation of eastern North America (originally held to be Late Miocene in age, now attributed to the Pliocene; Dowsett & Wiggs, 1992). The existence of various habitats was demonstrated, based on the ecological demands of two regular echinoids: *Arbacia liorocera*, *Psammechinus phillipsianus* (both occupying an intertidal nearshore habitat); and three irregular echinoids: *Echinocardium orthonotum* (burrowing deeply in a nearshore habitat), *Mellita aclinensis* (burrowing shallowly in a nearshore habitat) and *Spatangus glenni* (burrowing shallowly echinoid in an offshore habitat).

Numerous echinoid biofacies were recognized in Upper Oligocene to Upper Miocene sediments of Malta by Boggild & Rose (1984). These contain a rich echinoid fauna with at least 47 echinoid

species. The echinoid biofacies are each characterized by a distinctive echinoid assemblage, associated biota and lithology and were related to the standard facies belts and standard microfacies types as defined by Wilson (1975). The 13 different echinoid biofacies are found in restricted platform lagoons (one echinoid biofacies), open platform lagoons (three biofacies), winnowed edge sands (one biofacies), organic reefs (one biofacies), foreslope (three biofacies) and in the deep shelf margin to open shelf (four biofacies). The Lower Globigerina Limestones, for example, are characterized by a wackestone with a *Schizaster parkinsoni*/*Ditremaster*/*Pecten* assemblage and were ascribed to Standard Facies Belt Zone 3-2 of Wilson (1975) due to its massive, fine-grained, wackestone to mudstone lithology with pelagic microfossils. Both *Schizaster* and *Ditremaster* are irregular echinoids adapted to burrowing into fine, soft substrates as found in the Globigerina Limestone (see also Rose & Watson, 1998). These echinoid biofacies have also been recognized in other Oligo-Miocene successions of the Mediterranean (e.g. Crete, Libya; Rose, 1974; Marcopoulou-Diacantoni, 1979; Boggild & Rose, 1984) and Caribbean region (Boggild & Rose, 1984; Poddubiuk & Rose, 1984).

Late Miocene Messinian irregular echinoids from the Sorbas Basin of southeast Spain were analysed by Néraudeau *et al.* (1979c) with respect to morphological and palaeoecological gradients including detailed biometrical analysis. An ecomorphological gradient from shallow to deeper water was postulated following the succession of: (1) a *Clypeaster altus* association from the upper infralittoral zone; (2) an association from the lower infralittoral zone with *Clypeaster marginatus*, *Schizaster* and *Spatangus*; (3) a *Brissopsis* gr. *lyrifera* association from the upper-cirralittoral zone; and (4) the deepest association from the medium ciralittoral to bathyal zone with *Brissopsis* gr. *atlantica*. Furthermore, changes in echinoid diversity are used to record sea-level changes and discuss the existence of marine connections between different marine basins across the Messinian salinity crisis.

Seven different echinoid assemblages were recognized in Lower Miocene siliciclastic and carbonate-dominated sediments from the Gebel Gharra section, Egypt (Kroh & Nebelsick, 2003). These assemblages were based on a wide variety of echinoderms representing distinct ecological habitats. The dominating echinoids include both epibenthic as well as various endobenthic forms

from different burrowing depths. Comatulid crinoids and rare marginal ossicles of the sea star *Astropecten* were also present. Changes in echinoderm diversity were related to substrate variations, burrowing depths, taphonomic factors as well as the general deepening and subsequent shallowing of the depositional environment. These findings, based on echinoderms, complemented those based on microfacies analysis and other macrobenthic invertebrate studies from the same section (Abdelghany & Piller, 1999; Mandic & Piller, 2001).

An example of using the complete echinoderm record in palaeoenvironmental reconstruction was shown by Kroh & Harzhauser (1999) from Lower Miocene sediments of Austria. Here, palaeoecological interpretations were based on complete and fragmentary material from echinoids, crinoids, ophiuroids and asteroids. Aut- and synecological analysis of the assemblages allowed the differentiation of a shallow, wave-dominated sand bottom fauna of low diversity, and a rich fauna from more sheltered, diverse habitats.

CONCLUSIONS

The study of echinoderm skeletal remains offers a variety of potentially useful applications for sedimentology and palaeoenvironmental reconstruction. Compared with many other macrofossil groups, echinoderms show many advantages including a durable skeleton, moderate diversity and easy recognition. Once the faunal spectrum present in a given area or time slice has been established and documented by a specialist, usage of disarticulated echinoderm material for sedimentological applications is rather straightforward.

Researchers working on the Oligo-Miocene benefit from the high similarity of fossil echinoderm remains to extant faunas, facilitating element and taxon recognition based on comparison to recent specimens. Many of the potential uses outlined in this paper have not been, or have very rarely been, applied to Oligo-Miocene echinoderms and sedimentary systems thus far. This is, in part, due to the limited awareness of the possibilities and limitations of echinoderms in a sedimentological context and in part due to the lack of communication between echinoderm specialists on the one hand and sedimentologists on the other. The present paper is intended to improve this situation.

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REFERENCES

- Abdelghany, O. and Piller, W.E.** (1999) Biostratigraphy of Lower Miocene sections in the Eastern Desert (Cairo - Suez district, Egypt). *Rev. Micropaléontol.*, **18**, 607–617.
- Allison, P.A.** (1990) Variation in rates and decay and disarticulation of Echinodermata: Implications for the application of actualistic data. *Palaaios*, **5**, 432–439.
- Ausich, W.I.** (1997) Regional encrinurites; a vanished lithofacies. In: *Paleontological Events; Stratigraphic, Ecological and Evolutionary Implications* (Eds C.E. Brett and G. C. Baird), pp. 509–519. Columbia University Press, New York.
- Ausich, W.I.** (2001) Echinoderm taphonomy. In: *Echinoderm Studies*, **6**, (Eds M. Jangoux and J.M. Lawrence), pp. 171–227. Balkema, Lisse.
- Bak, R.P.M.** (1990) Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Mar. Ecol. Prog. Ser.*, **66**, 267–272.
- Bak, R.P.M.** (1993) Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs*, **13**, 99–103.
- Bartels, C., Briggs, D.E.G. and Brassel, G.** (1998) The fossils of the Hunsrück Slate – Marine Life in the Devonian. *Cambridge Palaeobiol. Ser.*, **3**, Cambridge University Press, Cambridge, 309 pp.
- Bathurst, R.C.G.** (1966) Boring algae, micrite envelopes and lithification of molluscan biosparites. *Geol. J.*, **5**, 15–32.
- Baumiller, T.K.** (2001) Light stable isotope geochemistry of the crinoid skeleton and its use in biology and paleobiology. In: *Echinoderms 2000* (Ed. M.F. Barker), pp. 107–112. Swets & Zeitlinger, Lisse.
- Beck, J.W., Edwards, R.L., Ito, E., Taylor, F.W., Recy, J., Rougerie, F., Joannot, P. and Henin, C.** (1992) Sea-surface temperature from coral skeletal strontium/calcium ratios. *Science*, **257**, 644–647.
- Berner, R.A.** (1966) Chemical diagenesis of some modern carbonate sediments. *Am. J. Sci.*, **264**, 1–36.
- Berner, R.A.** (1996a) Diagenesis of carbonate sediments: interaction of magnesium in sea water with mineral grains. *Science*, **153**, 188–191.
- Berner, R.A.** (1996b) Chemical diagenesis of some modern carbonate sediments. *Am. J. Sci.*, **264**, 1–36.
- Bertling, M., Braddy, S.J., Bromley, R.G., Demathieu, G. R., Genise, J., Mikuláš, N.J.K., Nielsen, K.S.S., Rindsberg, A.K., Schlirf, M. and Uchman, A.** (2006) Names for trace fossils: a uniformitarian approach. *Lethaia*, **39**, 265–286.
- Betzler, C., Brachert, T.C. and Nebelsick, J.H.** (1997) The warm temperate carbonate province: a review of the facies, zonations, and delimitations. *Cour. Forsch.-Inst. Senckenb.*, **201**, 83–99.
- Biese, W. and Sieverts-Doreck, H.** (1939) *Crinoidea caenozoica. - Fossilium Catalogus, I: Animalia*. W. Junk., 's-Gravenhage, 151 pp.
- Bill, M., Baumgartner, P.O. and Hunziker, J.C.** (1995) Carbon isotope stratigraphy of the Liesberg Beds Member (Oxfordian, Swiss Jura) using echinoids and crinoids. *Eclogae Geol. Helv.*, **88**, 135–155.
- Bischoff, J.L.** (1968) Kinetics of calcite nucleation: magnesium ion inhibition and ionic strength catalysis. *J. Geophys. Res.*, **73**, 3315–3322.
- Blake, D.B.** (1973) Ossicle morphology of some recent asteroids and description of some West American fossil asteroids. *Geol. Sci. Univ. Calif. Publ.*, **104**, 1–59.
- Blake, D.F. and Peacor, D.R.** (1981) Biomineralization on crinoid echinoderms. Characterization of crinoid skeletal elements using TEM and STEM microanalysis. *Scan. Electron Microsc.*, **1981**, 321–328.
- Blake, D.F., Peacor, D.R. and Wilkinson, B.H.** (1982) The sequence and mechanism of low-temperature dolomite formation: Calician dolomites in a Pennsylvanian echinoderm. *J. Sed. Petrol.*, **52**, 59–70.
- Bodenbender, B.E.** (1996) Patterns of crystallographic axis orientation in blastoid skeletal elements. *J. Paleontol.*, **70**, 466–484.
- Boggild, G.R. and Rose, E.P.F.** (1984) Mid-Tertiary echinoid biofacies as palaeoenvironmental indices. *Ann. Géol. Pays Hellén.*, **22**, 57–67.
- Brachert, T.C., Betzler, C., Braga, J.C. and Martín, J.M.** (1996) Record of climatic change in neritic carbonates: turnover in biogenic associations and depositional modes (Late Miocene, Southern Spain). *Geol. Rundsch.*, **85**, 327–337.
- Brandano, M. and Corda, L.** (2002) Nutrient, sea level and tectonics, constraints: for the facies architecture of Miocene carbonate ramp in Central Italy. *Terra Nova*, **14**, 257–262.
- Brenchley, P.J. and Harper, D.A.T.** (1998) *Palaeoecology: Ecosystems, Environments and Evolution*. Chapman & Hall, London, 402 pp.
- Breton, G.** (1992) Les Goniasteridae (Asteroidea, Echinodermata) jurassiques et crétacés de France: taphonomie, systématique, paléogéographie, évolution. *Bull. Trim. Soc. Géol. Normandie Amis Mus. Havre*, **78**, 1–590.
- Brett, C.E., Moffat, H.A. and Taylor, W.L.** (1997) Echinoderm taphonomy, taphofacies, and Lagerstätten. In: *Geobiology of Echinoderms* (Eds J.A. Waters and C.G. Maples). *Paleont. Soc. Pap.*, **3**, 147–190.
- Bromley, R.G.** (1975) Comparative analysis of fossil and recent echinoid bioerosion. *Palaeontology*, **18**, 725–739.
- Bromley, R.G. and Asgaard, U.** (1975) Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bull. Geol. Soc. Denmark*, **24**, 261–281.
- Bruckshen, P., Noeth, S. and Richter, D.K.** (1990) Tempered microdolomites in crinoids: a new criterion for high-grade diagenesis. *Carbonates Evaporites*, **5**, 197–207.
- Campbell, A.C.** (1987) Echinoderms of the Red Sea. In: *Red Sea (Key Environments)* (Eds A.J. Edwards and S.M. Head), pp. 215–232. Pergamon Press, Oxford.

- Carannante, G., Esteban, M., Milliman, J.D. and Simone, L.** (1988) Carbonate lithofacies as paleolatitude indicators: problems and indicators. *Sed. Geol.*, **60**, 333–346.
- Carreiro-Silva, M. and McClanahan, T.R.** (2001) Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. *J. Exp. Mar. Biol. Ecol.*, **262**, 133–153.
- Carter, B.D.** (2003) Diversity Patterns in Eocene to Oligocene Echinoids. In: *From Greenhouse to Icehouse - The Marine Eocene-Oligocene Transition* (Eds D.R. Prothero, L.C. Ivany and E.A. Nesbitt), pp. 354–365. Columbia University Press, New York.
- Chave, K.E.** (1954) Aspects of the biogeochemistry of magnesium: 1. Calcareous marine organisms. *J. Geol.*, **62**, 266–283.
- Chave, K.E.** (1964) Skeletal durability and preservation. In: *Approaches to Paleocology* (Eds J. Imbrie and N. Newell), pp. 377–382. Wiley, New York.
- Clarke, A.H.** (1911) The inorganic constituents of the skeleton of two recent crinoids. *Proc. US Nat. Mus.*, **39**, 487–488.
- Clarke, F.W. and Wheeler, W.C.** (1914) The composition of crinoid skeletons. *US Geol. Surv. Prof. Pap.*, **90D**, 33–37.
- Clarke, F.W. and Wheeler, W.C.** (1915) The inorganic constituents of echinoderms. *US Geol. Surv. Prof. Pap.*, **90L**, 191–196.
- Clarke, F.W. and Wheeler, W.C.** (1917) The inorganic constituents of marine invertebrates. *US Geol. Surv. Prof. Pap.*, **102**, 1–56.
- Clarke, F.W. and Wheeler, W.C.** (1922) The inorganic constituents of marine invertebrates. *US Geol. Surv. Prof. Pap.*, **124**, 1–62.
- Cohen, A., Layne, G., Hart, S. and Lobel, P.** (2001) Kinetic control of skeletal Sr/Ca in a symbiotic coral: implications for the paleotemperature proxy. *Paleoceanography*, **16**, 20–26.
- Cohen, A., Owens, K.E., Layne, G. and Shimizu, N.** (2002) The effect of algal symbionts on the accuracy of Sr/Ca paleotemperatures from coral. *Science*, **296**, 331–333.
- Corda, L. and Brandano, M.** (2003) Aphotic zone carbonate production on a Miocene ramp, Central Apennines. Italy. *Sed. Geol.*, **161**, 55–70.
- Davies, T.T., Crenshaw, A. and Heatfield, B.M.** (1972) The effect of temperature on the chemistry and structure of echinoid spine regeneration. *J. Paleontol.*, **46**, 874–883.
- de Blainville, H.M.D.** (1825) Oursins. In: *Dictionnaire des Sciences Naturelles*, **37**, pp. 59–245. F.G. Levrault, Strasbourg, Paris.
- Dickson, J.A.D.** (1995) Paleozoic Mg calcite preserved: Implications for the Carboniferous ocean. *Geology*, **23**, 535–538.
- Dickson, J.A.D.** (2001a) Diagenesis and crystal caskets: Echinoderm Mg calcite transformation, Dry Canyon, New Mexico, U.S.A. *J. Sed. Res.*, **71**, 764–777.
- Dickson, J.A.D.** (2001b) Transformation of echinoid Mg calcite skeletons by heating. *Geochim. Cosmochim. Acta*, **65**, 443–454.
- Dickson, J.A.D.** (2002) Fossil echinoderms as monitor of the Mg/Ca ratio of Phanerozoic oceans. *Science*, **298**, 1222–1224.
- Dickson, J.A.D.** (2004) Echinoderm skeletal preservation: Calcite-aragonite seas and the Mg/Ca ratio of Phanerozoic oceans. *J. Sed. Res.*, **74**, 355–365.
- Donnay, G. and Pawson, D.L.** (1969) X-ray diffraction studies of echinoderm plates. *Science*, **166**, 1147–1150.
- Donovan, S.K.** (1991) The taphonomy of echinoderms: calcareous multi-element skeletons in the marine environment. In: *The Processes of Fossilisation* (Ed. S.K. Donovan), pp. 241–269. Belhaven Press, London.
- Donovan, S.K.** (1995) Isocrinid crinoids from the late Cenozoic of Jamaica. *Atlantic Geol.*, **30**, 195–203.
- Donovan, S.K.** (1996) Use of the SEM in interpreting ancient faunas of sea urchins. *Eur. Microsc. Anal.*, **1996**, 29.
- Donovan, S.K.** (2001) Evolution of Caribbean echinoderms during the Cenozoic: Moving towards a complete picture using all of the fossils. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **166**, 177–192.
- Donovan, S.K.** (2003) Completeness of a fossil record: the Pleistocene echinoids of the Antilles. *Lethaia*, **36**, 1–7.
- Donovan, S.K. and Portell, R.W.** (2000) Incipient “crystal apples” from the Miocene of Jamaica. *Caribb. J. Sci.*, **36**, 168–170.
- Donovan, S.K. and Veltkamp, C.J.** (2001) The Antillean Tertiary Crinoid Fauna. *J. Paleontol.*, **75**, 721–731.
- Donovan, S.K., Gordon, C.M., Veltkamp, C.J. and Scott, A.D.** (1993) Crinoids, asteroids, and ophiuroids in the Jamaican fossil record. In: *Biostratigraphy of Jamaica* (Eds R.M. Wright and E. Robinson). *Geol. Soc. Am. Mem.*, **182**, 125–130.
- Donovan, S.K., Portell, R.W. and Veltkamp, C.J.** (2005) Lower Miocene echinoderms of Jamaica. West Indies. *Scripta Geol.*, **129**, 91–135.
- Dowsett, H.J. and Wiggs, L.B.** (1992) Planktonic Foraminiferal Assemblage of the Yorktown Formation, Virginia, USA. *Micropaleontology*, **38**, 75–86.
- Eagle, M.K.** (1993) A new fossil isocrinid crinoid from the Late Oligocene of Waitete Bay, northern Coromandel. *Rec. Auckland Inst. Mus.*, **30**, 1–12.
- Ebert, T.A.** (1998) An analysis of the importance of Allee effects in management of the red sea urchin *Strongylocentrotus franciscanus*. In: *Echinoderms: San Francisco* (Eds R. Mooi and M. Telford), pp. 619–627. A.A. Balkema, Rotterdam.
- Ebert, T.A.** (2001) Growth and survival of post-settlement sea urchins. In: *Sea Urchins: Biology and Ecology Edible Developments in Aquaculture and Fisheries Science* (Ed. J.M. Lawrence), pp. 79–102. Elsevier, Amsterdam.
- Ebert, T.A.** (2007) Growth and Survival of Postsettlement Sea Urchins. In: *Edible Sea Urchins: Biology and Ecology. 2nd Edn. Developments in Aquaculture and Fisheries Science* (Ed. J.M. Lawrence), pp. 95–134. Elsevier, Amsterdam.
- Emlet, R.B.** (1985) Crystal axes in recent and fossil adult echinoids indicate trophic mode in larval development. *Science*, **230**, 937–940.
- Emlet, R.B.** (1989) Apical skeletons of sea urchins (Echinodermata: Echinoidea): two methods for inferring mode of larval development. *Paleobiology*, **15**, 223–254.
- Fisher, D.C. and Cox, R.S.** (1988) Application of skeletal crystallography to phylogenetic inference in fossil echinoderms. In: *Echinoderm Biology* (Eds R.D. Burke, P.V. Mladenov, P. Lambert and R.L. Parsley), pp. 797. A.A. Balkema, Rotterdam.

- Gaffey, S.J., Kolak, J.J. and Bronnimann, C.E. (1991) Effects of drying, heating, annealing, and roasting on carbonate skeletal material, with geochemical and diagenetical implications. *Geochim. Cosmochim. Acta*, **55**, 1627–1640.
- Gilliland, P.M. (1993) The skeletal morphology, systematics and evolutionary history of holothurians. *Spec. Pap. Palaeontol.*, **47**, 1–147.
- Gislén, T. (1924) Echinoderm studies. *Zool. Bidr. Uppsala*, **9**, 1–316.
- Glass, A. and Blake, D.B. (2004) Preservation of tube feet in an ophiuroid (Echinodermata) from the Lower Devonian Hunsrück Slate of Germany and a redescription of *Bundenbachia beneckeii* and *Palaeophiomys grandis*. *Paläontol. Z.*, **78**, 73–95.
- Glynn, P.W. (1997) Bioerosion and coral reef growth: a dynamic balance. In: *Life and Death on Coral Reefs* (Ed. C. Birkeland), pp. 68–95. Chapman & Hall, New York.
- Gordon, C.M. and Donovan, S.K. (1992) Disarticulated echinoid ossicles in paleoecology and taphonomy: The last interglacial Falmouth Formation of Jamaica. *Palaos*, **7**, 157–166.
- Greenstein, B.J. (1993) Is the fossil record of regular echinoids really so poor? A comparison of living and sub-fossil assemblages. *Palaos*, **8**, 597–601.
- Hardie, L.A. (1996) Secular variation in seawater chemistry: An explanation for the coupled secular variation in the mineralogies of marine limestones and potash evaporates over the past 600 my. *Geology*, **24**, 279–283.
- Haude, R. (2002) Origin of holothurians (Echinodermata) derived by constructional morphology. *Mitt. Mus. Naturk. Berlin Geowiss. Reihe*, **5**, 141–153.
- Hayton, S., Nelson, C.S. and Hood, S.D. (1995) A skeletal assemblage classification system for non-tropical carbonate deposits based on New Zealand Cenozoic limestones. *Sed. Geol.*, **100**, 123–141.
- Heller, C. (1858) Über neue fossile Stelleriden. *Sitzber. Kaiserl. Akad. Wiss. Math.-naturwiss. Cl. Abt. 1*, **28**, 155–170.
- Hess, H. (1955) Die fossilen Astropectiniden (Asteroidea). Neue Beobachtungen und Übersicht über die bekannten Arten. *Mém. Soc. Paléontol. Suisse*, **71**, 1–113.
- Hess, H. (1962a) Mikropalaeontologische Untersuchungen an Ophiuren – I. Einleitung. *Eclogae Geol. Helv.*, **55**, 595–608.
- Hess, H. (1962b) Mikropalaeontologische Untersuchungen an Ophiuren. II. Die Ophiuren aus dem Lias (Pliensbachien – Toarcien) von Seewen (Kt. Solothurn). *Eclogae Geol. Helv.*, **55**, 609–656.
- Hess, H. (1963) Mikropalaeontologische Untersuchungen an Ophiuren. III. Die Ophiuren aus dem Callovien-Ton von Liesberg (Berner Jura). *Eclogae Geol. Helv.*, **56**, 1141–1164.
- Hess, H. (1965) Mikropalaeontologische Untersuchungen an Ophiuren. IV. Die Ophiuren aus dem Renggeri-Ton (Unter-Oxford) von Chapois (Jura) und Longcombe (Ain). *Eclogae Geol. Helv.*, **58**, 1059–1082.
- Hess, H. (1966) Mikropalaeontologische Untersuchungen an Ophiuren. V. Die Ophiuren aus dem Argovien (unteres Ober-Oxford) vom Guldenthal (Kt. Solothurn) und von Savigna (Dépt. Jura). *Eclogae Geol. Helv.*, **59**, 1025–1063.
- Hess, H. (1975a) Mikropaläontologische Untersuchungen an Ophiuren. VI. Die Ophiuren aus den Günsberg-Schichten (oberes Oxford) von Guldenthal (Kt. Solothurn). *Eclogae Geol. Helv.*, **68**, 591–601.
- Hess, H. (1975b) Mikropaläontologische Untersuchungen an Ophiuren. VII. Die Ophiuren aus den Humeralis-Schichten (Ober-Oxford) von Raedersdorf (Ht-Rhin). *Eclogae Geol. Helv.*, **68**, 603–612.
- Hess, H. (1999a) Lower Devonian Hunsrück Schales of Germany. In: *Fossil Crinoids* (Eds H. Hess, W.I. Ausich, C.E. Brett and M.J. Simms), pp. 111–121. Cambridge University Press, Cambridge.
- Hess, H. (1999b) *Unitacrinus* beds of the Upper Cretaceous Niobrara Formation, Kansas, USA. In: *Fossil Crinoids* (Eds H. Hess, W.I. Ausich, C.E. Brett and M.J. Simms), pp. 225–232. Cambridge University Press, Cambridge.
- Hess, H. (1999c) Tertiary. In: *Fossil Crinoids* (Eds H. Hess, W.I. Ausich, C.E. Brett and M.J. Simms), pp. 233–236. Cambridge University Press, Cambridge.
- Hess, H., Ausich, W.I., Brett, C.E. and Simms, M.J. (Eds) (1999) *Fossil Crinoids*. Cambridge University Press, Cambridge, 275 pp.
- Hoefs, J. (1997) *Stable Isotope Geochemistry*. 4th Edn. Springer-Verlag, Berlin-Heidelberg, 201 pp.
- Holland, H.D. (1978) *The Chemistry of the Atmosphere and Oceans*. John Wiley, New York, 351 pp.
- Horita, J., Zimmermann, H. and Holland, H.D. (2002) Chemical evolution of seawater during the Phanerozoic: Implications from the record of marine evaporates. *Geochim. Cosmochim. Acta*, **66**, 3733–3756.
- Jagt, J.W.M. (1991) Early Miocene luidiid asteroids (Echinodermata, Asteroidea) from Winterswijk-Miste (The Netherlands). *Contrib. Tert. Quatern. Geol.*, **28**, 35–43.
- Jagt, J.W.M. (2000a) Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 3: Ophiuroids. With a chapter on: Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by M. Kutscher and J.W.M. Jagt. *Scripta Geol.*, **121**, 1–179.
- Jagt, J.W.M. (2000b) Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 5: Asteroids. *Scripta Geol.*, **121**, 377–503.
- James, N.P. (1997) The cool-water carbonate depositional realm. In: *Cool-water Carbonates* (Eds N.P. James and J. A.D. Clarke). *SEPM Spec. Publ.*, **56**, 1–22.
- James, N.P. and Bone, Y. (1989) Petrogenesis of Cenozoic, temperate water calcarenites, South Australia: a model for meteoric/shallow burial diagenesis of shallow water calcite sediments. *J. Sed. Petrol.*, **59**, 191–203.
- Kaczmarek, G. (1987) Asteroids from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polonica*, **37**, 131–144.
- Kampfer, S. and Tertschnig, W. (1992) Feeding biology of *Clypeaster rosaceus* (Echinoidea, Clypeasteroidea) and its impact on shallow lagoon sediments. *Echinoderm Research 1991 – Proc. 3rd Eur. Echino. Conf., Lecce, Italy, 1991* (Eds L. Scalera-Liaci and C. Canicatti), pp. 197–200. A.A. Balkema, Rotterdam.
- Kidwell, S.M. and Baumiller, T. (1990) Experimental disintegration of regular echinoids: roles of

- temperature, oxygen and decay thresholds. *Paleobiol.*, **16**, 247–271.
- Kier, P.M.** (1972) Upper Miocene echinoids from the Yorktown Formation of Virginia and their environmental significance. *Smithson. Contrib. Paleobiology*, **13**, 1–41.
- Kier, P.M.** (1977) The poor fossil record of the regular echinoids. *Paleobiology*, **3**, 168–174.
- Knoerich, A.C. and Mutti, M.** (2003) Controls of facies and sediment composition on the diagenetic pathway of shallow-water Heterozoan carbonates: the Oligocene of the Maltese Islands. *Int. J. Earth Sci.*, **92**, 494–510.
- Knoerich, A.C. and Mutti, M.** (2006) Missing aragonitic biota and the diagenetic evolution of heterozoan carbonates: a case study from the Oligo-Miocene of the Central Mediterranean. *J. Sed. Res.*, **76**, 871–888.
- Kroh, A.** (2003a) First record of gorgonocephalid ophiuroids (Echinodermata) from the Middle Miocene of the Central Paratethys. *Cainoz. Res.*, **2**, 143–155.
- Kroh, A.** (2003b) The Echinodermata of the Langhian (Lower Badenian) of the Molasse Zone and the northern Vienna Basin (Austria). *Ann. Naturhist. Mus. Wien*, **104A**, 155–183.
- Kroh, A.** (2004) First fossil record of the family Euryalidae (Echinodermata: Ophiuroidea) from the Middle Miocene of the Central Mediterranean. In: *Echinoderms: München* (Eds T. Heinzeller and J.H. Nebelsick), pp. 447–452. Taylor & Francis, London.
- Kroh, A.** (2005) *Catalogus Fossilium Austriae*, **2**. *Echinoidea neogenica*. Österreichische Akademie der Wissenschaften, Wien, 210 pp.
- Kroh, A. and Harzhauser, M.** (1999) An echinoderm fauna from the Lower Miocene of Austria: Paleogeology and implications for Central Paratethys paleobiogeography. *Ann. Naturhist. Mus. Wien*, **101A**, 145–191.
- Kroh, A. and Jagt, J.W.M.** (2006) Notes on North Sea Basin Cainozoic echinoderms, Part 3. Pliocene gorgonocephalid ophiuroids from borehole IJsselmuiden-1 (Overijssel, the Netherlands). *Cainoz. Res.*, **4**, 67–70.
- Kroh, A. and Nebelsick, J.H.** (2003) Echinoid assemblages as a tool for palaeoenvironmental reconstruction – an example from the Early Miocene of Egypt. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, **201**, 157–177.
- Kroh, A., Harzhauser, M., Piller, W.E. and Rögl, F.** (2003) The Lower Badenian (Middle Miocene) Hartl Formation (Eisenstadt - Sopron Basin, Austria). In: *Stratigraphia Austriaca* (Ed. W.E. Piller). *Schriftenr. Erdwiss. Komm.*, **16**, 87–109.
- Kühn, O.** (1936) Eine neue Burdigalaausbildung bei Horn. *Sitzber. Akad. Wiss. Math.-naturwiss. Kl. Abt. 1*, **145**, 35–45.
- Kutscher, M. and Jagt, J.W.M.** (2000) Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark). In: *Late Cretaceous-Early Palaeogene Echinoderms and the K/T Boundary in the Southeast Netherlands and Northeast Belgium – Part 3: Ophiuroids* (Ed. J.W.M. Jagt). *Scripta Geol.*, **121**, 45–107.
- Laube, G.C.** (1869) Die Echinoiden der österreichisch-ungarischen oberen Tertiärlagerungen. *Verh. k.-k. Geol. R.-A.*, **3**, 182–184.
- Lawrence, J.M.** (1987) *A Functional Biology of Echinoderms*. Croom Helm, London & Sydney, 340 pp.
- Lea, D.W.** (2003) Elemental and isotopic proxies of marine temperatures. In: *The Oceans and Marine Geochemistry* (Ed. H. Elderfield), *Treat. Geochem.*, **6**, 365–390.
- Lehmann, W.M.** (1957) Die Asterozoen in den Dachschiefern des rheinischen Unterdevons. *Abh. Hessisch. Landes. Bodenforsch.*, **21**, 1–160.
- Lewis, R.** (1980) Taphonomy. In: *Echinoderms, Notes for a Short Course* (Eds T.W. Broadhead and J.A. Waters). *Univ. Tenn. Stud. Geol.*, **3**, 27–39.
- Linsley, B.K., Wellington, G.M. and Schrag, D.P.** (2000) Decadal sea surface temperature variability in the subtropical South Pacific from 1726 to 1997 A.D. *Science*, **290**, 1145–1148.
- Löffler, S.-B. and Nebelsick, J.H.** (2001) Palaeoecological Aspects of the Lower Oligocene “Zementmergel” Formation based on Molluscs and Carbonates. In: *The Paleogene of the Eastern Alps* (Eds W.E. Piller and M.W. Rasser), pp. 641–670. Verlag der Österreichischen Akademie der Wissenschaften, Vienna.
- Lowenstein, T.K., Timofeeff, M.N., Brennan, S.T., Hardie, L.A. and Demicco, R.V.** (2001) Oscillations in Phanerozoic seawater chemistry: evidence from fluid inclusions. *Science*, **294**, 1086–1088.
- Lukasik, J.L., James, N.P., McGowan, B. and Bone, Y.** (2000) An epeiric ramp: low-energy, cool-water carbonate facies in a Tertiary inland sea, Murray Basin, South Australia. *Sedimentology*, **47**, 851–881.
- McClanahan, T.R. and Muthiga, N.A.** (2007) Ecology of *Echinometra*. In: *Edible Sea Urchins: Biology and Ecology*. 2nd Edn. *Developments in Aquaculture and Fisheries Science* (Ed. J.M. Lawrence), pp. 297–317. Elsevier, Amsterdam.
- McGregor, H.V. and Gagan, M.K.** (2003) Diagenesis and geochemistry of *Porites* corals from Papua New Guinea: implications for palaeoclimate reconstruction. *Geochim. Cosmochim. Acta*, **67**, 2147–2156.
- McNamara, K.J.** (1994) Diversity of Cenozoic marsupiate echinoids as an environmental indicator. *Lethaia*, **27**, 257–268.
- Macqueen, R.W. and Ghent, E.D.** (1970) Electron microprobe study of magnesium distribution in some Mississippian echinoderm limestones from Western Canada. *Can. J. Earth Sci.*, **7**, 1308–1316.
- Mandic, O. and Piller, W.E.** (2001) Pectinid coquinas and their palaeoenvironmental implications – examples from the early Miocene of northeastern Egypt. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **172**, 171–191.
- Manze, U. and Richter, D.K.** (1979) Die Veränderung des C^{13}/C^{12} - Verhältnisses in Seeigelcoronen bei der Umwandlung von Mg-Calcit in Calcit unter meteorisch-vadosen Bedingungen. *Neues Jb. Geol. Paläontol. Abh.*, **158**, 334–345.
- Marcopoulou-Diacantoni, A.** (1979) Biofacies au moyen des échinides du Miocene supérieur dans l'île de Crète (Grèce) (Recherche biostratigraphique et paléontologique). *Ann. Géol. Pays Hellén, Tome hors Sér.*, **2**, 745–854.
- Märkel, K., Kubanek, F. and Willgallis, A.** (1971) Polykristalliner Calcit bei Seeigeln (Echinodermata, Echinoidea). *Z. Zellforsch. Mikroskop. Anat.*, **119**, 355–377.
- Martín, J.M., Braga, J.C., Betzler, C. and Brachert, T.C.** (1996) Sedimentary model and high-frequency cyclicity in a Mediterranean, shallow-shelf, temperate-

- carbonate environment (uppermost Miocene, Agua Amarga Basin, Southern Spain). *Sedimentology*, **43**, 263–277.
- Messing, C.G.** (1997) Living Comatulids. In: *Geobiology of Echinoderms* (Eds J.A. Waters and C.G. Maples). *Paleont. Soc. Pap.*, **3**, 3–30.
- Meyer, D.L. and Macurda, D.B. Jr.** (1997) Adaptive radiation of the comatulid crinoids. *Paleobiology*, **3**, 74–82.
- Meyer, D.L. and Meyer, K.B.** (1986) Biostratigraphy of recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia. *Palaaios*, **1**, 294–302.
- Meyer, D.L. and Milsom, C.V.** (2001) Microbial sealing in the biostratigraphy of Uintacrinus Lagerstätten in the upper Cretaceous of Kansas and Colorado, USA. *Palaaios*, **16**, 535–546.
- Mokady, O., Lazar, O. and Loya, Y.** (1996) Echinoid Bioerosion as a Major Structuring Force of Red Sea Coral Reefs. *Biol. Bull.*, **190**, 367–372.
- Moore, R.C. and Vokes, H.E.** (1953) Lower Tertiary crinoids from northwestern Oregon. *US Geol. Surv. Prof. Pap.*, **233-E**, 113–148.
- Mortensen, T.** (1928) *A Monograph of the Echinoidea. I. Cidaroida*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 551 pp.
- Mortensen, T.** (1935) *A Monograph of the Echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta*. C.A. Reitzel & Oxford Univ. Press, Copenhagen & London, 647 pp.
- Mortensen, T.** (1940) *A Monograph of the Echinoidea. III, 1. Aulodonta, with Additions to Vol. II (Lepidocentroida and Stirodonta)*. C.A. Reitzel, Copenhagen, 370 pp.
- Mortensen, T.** (1943a) *A Monograph of the Echinoidea. III, 2. Camarodonta. I. Orthopsidæ, Glyphocyphidæ, Temnopleuridæ and Toxopneustidæ*. C.A. Reitzel, Copenhagen, 553 pp.
- Mortensen, T.** (1943b) *A Monograph of the Echinoidea. III, 3. Camarodonta. II. Echinidæ, Strongylocentrotidæ, Parasaleniidæ, Echinometridæ*. C.A. Reitzel, Copenhagen, 446 pp.
- Mortensen, T.** (1948a) *A Monograph of the Echinoidea. IV, 1. Holcotypoida, Cassiduloida*. C.A. Reitzel, Copenhagen, 371 pp.
- Mortensen, T.** (1948b) *A Monograph of the Echinoidea. IV, 2. Clypeasteroida. Clypeasteridæ, Arachnoidæ, Fibulariidæ, Laganidæ and Scutellidæ*. C.A. Reitzel, Copenhagen, 471 pp.
- Mortensen, T.** (1950) *A Monograph of the Echinoidea. 1. Spatangoida I. Protosternata, Meridosternata, Amphisternata I. Palæopneustidæ, Palæostomatidæ, Aëropsidæ, Toxasteridæ, Micrasteridæ, Hemiasteridæ*. C.A. Reitzel, Copenhagen, 432 pp.
- Mortensen, T.** (1951) *A Monograph of the Echinoidea. 2. Spatangoida II. Amphisternata II. Spatangidæ, Loveniidæ, Pericosmidæ, Schizasteridæ, Brissidæ*. C.A. Reitzel, Copenhagen, 593 pp.
- Müller, A.H.** (1953) Die isolierten Skelettelemente der Asteroidea (Asterozoa) aus der obersenen Schreiekreide von Rügen. *Beih. Z. Geol.*, **8**, 1–66.
- Muthiga, N.A. and McClanahan, T.R.** (2007) Ecology of *Diadema*. In: *Edible Sea Urchins: Biology and Ecology*. 2nd Edn. *Developments in Aquaculture and Fisheries Science* (Ed. J.M. Lawrence), pp. 205–225. Elsevier, Amsterdam.
- Nebelsick, J.H.** (1989) Temperate water carbonate facies of the Early Miocene Paratethys (Zogelsdorf Formation, Lower Austria). *Facies*, **21**, 11–40.
- Nebelsick, J.H.** (1992a) Components analysis of component distribution in Lower Miocene temperate carbonates of the Zogelsdorf Formation, Lower Austria. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **91**, 59–69.
- Nebelsick, J.H.** (1992b) Echinoid distribution by fragment identification in the Northern Bay of Safaga, Red Sea, Egypt. *Palaaios*, **7**, 316–328.
- Nebelsick, J.H.** (1992c) The northern Bay of Safaga (Red Sea, Egypt): an actiopaleontological approach III. Distribution of echinoids. *Beitr. Paläontol. Österr.*, **17**, 5–79.
- Nebelsick, J.H.** (1996) Biodiversity of shallow-water Red Sea Echinoids: implications for the fossil record. *J. Mar. Biol. Assoc. UK*, **76**, 185–194.
- Nebelsick, J.H.** (2004) Taphonomy of Echinoderms: introduction and outlook. In: *Echinoderms: München* (Eds T. Heinzeller and J.H. Nebelsick), pp. 471–477. Taylor & Francis, London.
- Nebelsick, J.H. and Kampf, S.** (1994) Taphonomy of *Clypeaster humilis* and *Echinodiscus auritus* from the Red Sea. In: *Echinoderms Through Time* (Eds B.A. David, J.-P. Guille and M. Roux), pp. 803–808. Rotterdam, Balkema.
- Nebelsick, J.H. and Kroh, A.** (2002) The stormy path from life to death assemblages: The formation and preservation of mass accumulations of fossil sand dollars. *Palaaios*, **17**, 378–394.
- Nebelsick, J.H., Schmid, B. and Stachowitsch, M.** (1997) The encrustation of fossil and recent sea-urchin tests: ecological and taphonomic significance. *Lethaia*, **30**, 271–284.
- Nebelsick, J.H., Drobne, K. and Bassi, D.** (2000) Microfacies analysis and Palaeoenvironmental Interpretation of Lower Oligocene, shallow water carbonates (Gornji Grad Beds, Slovenia). *Facies*, **43**, 157–176.
- Nebelsick, J.H., Stingl, V. and Rasser, M.** (2001) Facies and component distribution in and autochthonous and allochthonous Lower Oligocene Carbonates. *Facies*, **44**, 31–46.
- Nelson, C.S.** (1978) Temperate shelf carbonates in the Cenozoic of New Zealand. *Sedimentology*, **29**, 737–772.
- Nelson, C.S.** (1988) An introductory perspective on non-tropical shelf carbonates. *Sed. Geol.*, **60**, 3–14.
- Nelson, C.S., Keane, S.L. and Head, P.S.** (1988) Non-tropical deposits on the New Zealand Shelf. *Sed. Geol.*, **60**, 71–94.
- Néraudeau, D., Goubert, E., Lacour, D. and Rouchy, J.M.** (2001) Changing biodiversity of Mediterranean irregular echinoids from the Messinian to Present-Day. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **175**, 43–60.
- Neugebauer, J.** (1978) Micritization of crinoids by diagenetic dissolution. *Sedimentology*, **25**, 267–283.
- Neugebauer, J.** (1979b) Drei Probleme der Echinodermen-diagenese: Innere Zementation, Mikroporenbildung und der Übergang von Magnesiumcalcit zu Calcit. *Geol. Rundsch.*, **68**, 856–875.
- Neugebauer, J.** (1979b) Echinodermen-Diagenese. *Neues Jb. Geol. Paläontol. Abh.*, **157**, 193–195.

- Neugebauer, J.** (1979c) Fossil-Diagenese in der Schreibkreide: Echinodermen. *Clausthaler Geol. Abh.*, **30**, 198–229.
- Nicolaides, S.** (1995) Cementation in Oligo-Miocene non-tropical shelf limestones. Otway Basin, Australia. *Sed. Geol.*, **95**, 97–121.
- Nicolaides, S. and Wallace, M.W.** (1997) Pressure-dissolution and cementation in an Oligo-Miocene non-tropical limestone (Clifton Formation) Otway Basin, Australia. In: *Cool-water Carbonates* (Eds N.P. James and J.A.D. Clarke). *SEPM Spec. Publ.*, **56**, 249–261.
- Nissen, H.-U.** (1969) Crystal orientation and plate structure in echinoid skeletal units. *Science*, **166**, 1150–1152.
- Nosowska, E.** (1997) Asteroids from the Nawodzice Sands (Middle Miocene); Holy Cross Mountains, Central Poland). *Acta Geol. Pol.*, **47**, 225–241.
- Oji, T.** (1989) Growth rate of stalk of *Metacrinus rotundus* (Echinodermata: Crinoidea) and its functional significance. *J. Fac. Sci. Univ. Tokyo, Sect. II*, **22**, 39–51.
- Oji, T.** (1990) Miocene Isocrinidae (stalked crinoids) from Japan and their biogeographic implication. *Trans. Proc. Palaeontol. Soc. Japan New Ser.*, **157**, 412–429.
- Otter, G.W.** (1932) Rock-burrowing echinoids. *Biol. Rev. Camb. Phil. Soc.*, **7**, 89–107.
- Otter, G.W.** (1937) Rock-destroying organisms in relationship to coral reefs. *Sci. Rep. Gt. Barrier Reef Exped., 1928–1929; Brit. Mus. Nat. Hist.*, **1**, 232–352.
- Pearse, J.S. and Pearse, V.B.** (1975) Growth zones in the echinoid skeleton. *Am. Zool.*, **15**, 731–753.
- Pilkey, O.H. and Hower, J.** (1960) The effect of environment on the concentration of skeletal Magnesium and Strontium in *Dendraster*. *J. Geol.*, **68**, 203–216.
- Piller, W.E.** (1994) The Northern Bay of Safage (Red Sea, Egypt): an actuopalaeontological approach. IV. Thin section analysis. *Beitr. Paläontol.*, **18**, 1–73.
- Piller, W.E. and Rasser, M.** (1996) Rhodolith formation induced by reef erosion in the Red Sea, Egypt. *Coral Reefs*, **15**, 191–198.
- Poddubiuk, R.H. and Rose, E.P.F.** (1984) Relationships between Mid-Tertiary echinoid faunas from the Central Mediterranean and eastern Caribbean and their palaeobiogeographic significance. *Ann. Géol. Pays Hellén.*, **31**, 115–127.
- Pomoni-Papaioannou, F., Drinia, H. and Dermizakis, M.D.** (2002) Neogene non-tropical carbonate sedimentation in a warm temperate biogeographic province (Rethymnon Formation, Eastern Crete, Greece). *Sed. Geol.*, **154**, 147–157.
- Rasmussen, H.W.** (1972) Lower Tertiary Crinoidea, Asteroidea and Ophiuroidea from northern Europe and Greenland. *Biol. Skr. Kong. Dan. Vidensk. Selskab.*, **19**, 1–83.
- Raup, D.M.** (1959) Crystallography of echinoid calcite. *J. Geol.*, **67**, 661–674.
- Raup, D.M.** (1960) Ontogenetic variation in the crystallography of echinoid calcite. *J. Paleontol.*, **34**, 1041–1050.
- Raup, D.M.** (1962a) Crystallographic data in echinoderm classification. *Syst. Zool.*, **11**, 97–108.
- Raup, D.M.** (1962b) The phylogeny of calcite crystallography in echinoids. *J. Paleontol.*, **36**, 793–810.
- Raup, D.M.** (1965) Crystal orientations in the echinoid apical disc. *J. Paleontol.*, **39**, 934–951.
- Raup, D.M.** (1966a) Crystal orientations in the echinoid coronal plates. *J. Paleontol.*, **40**, 555–568.
- Raup, D.M.** (1966b) The endoskeleton. In: *Physiology of Echinodermata* (Ed. R.A. Boolootian), pp. 379–395. Interscience Publishers, New York.
- Raup, D.M. and Swan, E.F.** (1967) Crystal orientation in the apical plates of aberrant echinoids. *Biol. Bull.*, **133**, 618–629.
- Reich, M.** (2001) Holothurians from the Late Cretaceous of the Isle of Rügen (Baltic Sea). In: *Echinoderms 2000* (Ed. M. Barker), pp. 89–92. A.A. Balkema Publishers Lisse/Abingdon/Exton (PA)/Tokyo.
- Reich, M.** (2003) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 3. Chiridotidae Östergren, 1898. *Neues Jb. Geol. Paläontol., Abh.*, **228**, 363–397.
- Reich, M. and Frenzel, P.** (2002) Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Arch. Geschiebek.*, **3**, 73–284.
- Reuss, A.E.** (1860) Die marinen Tertiärschichten Böhmens und ihre Verseinerungen. *Sitzber. Kaiserl. Akad. Wiss. Math.-naturwiss. Cl. Abt. 1*, **39**, 207–288.
- Richter, D.K.** (1974) Zur subaerischen Diagenese von Echinodenskeletten und das relative Alter pleistozäner Karbonatterassen bei Korinth (Griechenland). *Neues Jb. Geol. Paläontol. Abh.*, **146**, 51–77.
- Richter, D.K. and Bruckschen, P.** (1998) Geochemistry of recent tests of *Echinocyamus pusillus*: Constraints for temperature and salinity. *Carbonates Evaporites*, **13**, 157–167.
- Ries, J.B.** (2004) Effect of ambient Mg/Ca ratio on Mg fractionation in calcareous marine invertebrates: A record of the oceanic Mg/Ca ratio over the Phanerozoic. *Geology*, **32**, 981–984.
- Rose, E.P.F.** (1974) Stratigraphical and facies distribution of irregular echinoids in Miocene limestones of Gozo, Malta, and Cyrenaica. Libya. Bur. Rech. Géol. Min. Mém., **78**, 349–355.
- Rose, E.P.F. and Watson, A.C.** (1998) Burrowing adaptations of schizasteroid echinoids from the Globigerina Limestone (Miocene) of Malta and their evolutionary significance. In: *Echinoderms: San Francisco* (Eds R. Mooi and M. Telford), pp. 811–817. A.A. Balkema, Rotterdam.
- Rosenkranz, D.** (1971) Zur Sedimentation und Ökologie von Echinodermen-Lagerstätten. *Neues Jb. Geol. Paläontol. Abh.*, **138**, 221–258.
- Roux, M., Renard, M., Améziane, N. and Emmanuel, L.** (1995) Zoobathymetrie et composition chimique de la calcite des ossicules du pèdoncule des crinoïdes. *CR Acad. Sci. Paris Sér. Ila*, **321**, 675–680.
- Russell, M.P. and Meredith, R.W.** (2000) Natural growth lines in echinoid ossicles are not reliable indicators of age: a test using *Strongylocentrotus droebachiensis*. *Inv. Biol.*, **119**, 410–420.
- Russell, M.P., Ebert, T.A. and Petraitis, P.S.** (1998) Field estimates of growth and mortality of the green sea urchin *Strongylocentrotus droebachiensis*. *Ophelia*, **48**, 137–153.
- Russo, A.R.** (1980) Bioerosion by two rock boring echinoids (*Echinometra mathaei* and *Echinostrephus aciculatus*) en Enewetak Atoll, Marshall Islands. *J. Mar. Res.*, **38**, 99–110.
- Sandberg, P.A.** (1983) An oscillating trend in Phanerozoic nonskeletal carbonate mineralogy. *Nature*, **305**, 19–22.
- Scheibling, R.E.** (1982) Habitat utilization and bioturbation by *Oreaster reticulatus* (Asteroidea) and *Meoma*

- ventricosa* (Echinoidea) in a subtidal sand patch. *Bull. Mar. Sci.*, **32**, 624–629.
- Schroeder, J.H., Papike, J.J., Dwornik, E.J. and Lindsay, J.R.** (1968) Compositional and crystallographic aspects of the echinoid skeleton. *Trans. Am. Geophys. Union*, **49**, 219.
- Schroeder, J.H., Dwornik, E.J. and Papike, J.J.** (1969) Primary protodolomite in echinoid skeletons. *Geol. Soc. Am. Bull.*, **80**, 1613–1618.
- Seilacher, A.** (1979) Constructional morphology of sand dollars. *Paleobiology*, **5**, 191–221.
- Seilacher, A., Reif, W.E. and Westphal, F.** (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten. In: *Extraordinary Fossil Biotas: Their Ecological and Evolutionary Significance* (Eds H.B. Whittington and M.S. Conway Morris). *Phil. Trans. Roy. Soc. London Ser. B: Biol. Sci.*, **311**, 5–24.
- Sismonda, E.** (1841) Monografia degli Echinidi Fossili del Piemonte. *Mem. R. Accad. Sci. Torino Ser.*, **2**, **4**, 1–54.
- Smith, A.B.** (1980) Stereom microstructure of the Echinoid test. *Spec. Pap. Palaeontol.*, **25**, 1–81.
- Smith, A.B.** (1984) *Echinoid Palaeobiology*. George Allen and Unwin, London, 191 pp.
- Smith, A.B.** (1990) Biomineralization in echinoderms. In: *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, I* (Ed. J.G. Carter), pp. 170–175. Nosstrand Reinhold, New York.
- Smith, A.B. and Gallemí, J.** (1991) Middle Triassic Holothurians from Northern Spain. *Palaeontology*, **34**, 49–76.
- Steneck, R.S.** (1983) Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology*, **9**, 44–61.
- Stoll, H.M. and Schrag, D.P.** (1998) Effects of quaternary sea level cycles on strontium in seawater. *Geochim. Cosmochim. Acta*, **62**, 1107–1118.
- Stoll, H.M., Schrag, D.P. and Clemens, S.C.** (1999) Are seawater Sr/Ca variations preserved in quaternary foraminifera. *Geochim. Cosmochim. Acta*, **63**, 3535–3547.
- Talbot, T.D. and Lawrence, J.M.** (2002) The effect of salinity on respiration, excretion, regeneration and production in *Ophiophragmus filigraneus*. *J. Exp. Mar. Biol. Ecol.*, **275**, 1–14.
- Thayer, C.W.** (1983) Sediment-mediated biological disturbance and the evolution of marine benthos. In: *Biotic Interactions with Recent and Fossil Benthic Communities* (Eds M.J.S. Tevesz and P.L. McCall), pp. 478–625. Plenum, New York.
- Turekian, K.K.** (1955) Paleoeological significance of the strontium-calcium ratio in fossils and sediments. *Geol. Soc. Am. Bull.*, **66**, 155–158.
- Vadász, E.** (1915) Die mediterranen Echinodermen Ungarns. *Geol. Hung.*, **1**, 79–253.
- Villier, L.** (1999) Reconstitution du squelette d'astérides fossiles à partir d'ossicules isolés: intérêt taxinomique et phylogénétique. *CR Acad. Sci. Paris*, **328**, 353–358.
- Weber, J.N.** (1968) Fractionation of stable isotopes of carbon and oxygen in calcareous marine invertebrates – the Asteroidea, Ophiuroidea, and Crinoidea. *Geochim. Cosmochim. Acta*, **32**, 33–70.
- Weber, J.N.** (1969a) Origin of concentric banding in the spines of the tropical echinoid *Heterocentrotus*. *Pacific Sci.*, **23**, 452–466.
- Weber, J.N.** (1969b) The incorporation of magnesium into the skeletal calcite of echinoderms. *Am. J. Sci.*, **267**, 537–566.
- Weber, J.N.** (1973) Temperature dependence of magnesium in echinoid and asteroid skeletal calcite: a reinterpretation of its significance. *J. Geol.*, **81**, 543–556.
- Weber, J.N. and Raup, D.M.** (1966a) Fractionation of stable isotopes of carbon and oxygen in marine calcareous organisms – the Echinoidea. Part I. Variation of C^{13} and O^{18} content within individuals. *Geochim. Cosmochim. Acta*, **30**, 681–703.
- Weber, J.N. and Raup, D.M.** (1966b) Fractionation of stable isotopes of carbon and oxygen in marine calcareous organisms – the Echinoidea. Part II. Environmental and genetic factors. *Geochim. Cosmochim. Acta*, **30**, 705–736.
- Weber, J.N. and Raup, D.M.** (1968) Comparison of C^{13}/C^{12} and O^{18}/O^{16} in skeletal calcite of recent and fossil echinoids. *J. Paleontol.*, **42**, 37–50.
- Weber, J., Greer, R., Voight, B., White, E. and Roy, R.** (1969) Unusual strength properties of echinoderm calcite related to structure. *J. Ultrastruct. Res.*, **26**, 355–366.
- Wefer, G. and Berger, W.H.** (1991) Isotope paleontology: growth and composition of extant calcareous species. *Mar. Geol.*, **100**, 207–248.
- West, C.D.** (1937) Note on the crystallography of the echinoderm skeleton. *J. Paleontol.*, **11**, 458–459.
- Wilkinson, P.A. and Alego, T.J.** (1989) Sedimentary carbonate record of calcium-magnesium cycling. *Am. J. Sci.*, **289**, 1158–1194.
- Wilson, J.L.** (1975) *Carbonate Facies in Geologic History*. Springer-Verlag, New York. 471 pp.

ADDENDUM

A major focus of research since the submission of this manuscript has been marine acidification and the ability of marine organisms to cope with dramatic changes in ocean chemistry (e.g. Pörtner *et al.*, 2004; Orr *et al.*, 2005; Fabry, 2008; Fabry *et al.*, 2008; Doney *et al.*, 2009). Published studies have dealt primarily with anthropogenically induced increases in CO_2 and their effect on recent organisms, but this work has profound implica-

tions for interpreting the fossil record during past phases of long-term and short-term change in ocean chemistry.

Echinoderms have attracted particular attention during discussions of ocean acidification; they may be especially sensitive to changes in ocean chemistry because: (1) their skeletons are constructed of high-Mg calcite; and (2) various echinoderm larval forms possess extremely delicate skeletal support elements, which may be adversely affected by acidification. Echinoderms are also

common in various marine environments with differing temperature and ocean chemistry regimes, where acidification may have different consequences. Studies have been conducted on the effects of ocean acidification on echinoderms in general (e.g. Gooding *et al.*, 2009; Dupont *et al.*, 2010), as well as specifically on aspects of their metabolism (Miles *et al.*, 2007), fertilization and development (Dupont *et al.*, 2008; Havenhand *et al.*, 2008; Kurihara, 2008; Wood *et al.*, 2008; Byrne *et al.*, 2009; Clark *et al.*, 2009; O'Donnell *et al.*, 2009, 2010), and sediment/animal relationships (Dashfield *et al.*, 2008).

There has been little corresponding research published on the implications of ocean acidification for the fossil record of echinoderms. New work has emphasized the role of echinoderm skeletons as carbon sinks, since large amounts of echinoderm remains are committed to sediments (Lebrato *et al.*, 2009). The fact that echinoderms play a significant role in the CO₂ budget is amply demonstrated by the rich fossil record of echinoderms, and the significant contribution they make to ancient sediments (see main text). Longer term, secular changes in ocean chemistry occurred through the Phanerozoic, but short term, drastic changes have also been put forward as contributors to mass extinction events (see e.g. Knoll *et al.*, 2007; Veron, 2008). Such events have significantly affected the evolutionary development of echinoderms in the past (e.g. Twitchett, 2007). To what extent ocean acidification has contributed to these mass extinction events and how echinoderms are affected remain to be studied in detail.

- Byrne, M., Ho, M., Selvakumaraswamy, P., Nguyen, H.D., Dworjanyn, S.A. and Davis, A.R. (2009) Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *Proc. Roy. Soc.*, **276**, 1883–1888.
- Clark, D., Lamare, M. and Barker, M. (2009) Response of sea urchin larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate and a polar species. *Mar. Biol.*, **156**, 1125–1137.
- Dashfield, S.L., Somerfield, P.J., Widdicombe, S., Austen, M.C. and Nimmo, M. (2008) Impacts of ocean acidification and burrowing urchins on within-sediment pH profiles and subtidal nematode communities. *J. Exp. Mar. Biol. Ecol.*, **365**, 46–52.
- Doney, S.C., Fabry, V.J., Feely, R.A. and Kleypas, J.A. (2009) Ocean acidification: the other CO₂ problem. *Ann. Rev. Mar. Sci.*, **1**, 169–192.
- Dupont, S., Havenhand, J., Thorndyke, W., Peck, L. and Thorndyke, M. (2008) Near-future level of CO₂-driven radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Mar. Ecol. Prog. Ser.*, **373**, 285–294.
- Dupont, S., Ortega-Martinez, O. and Thorndyke, M. (2010) Impact of near-future ocean acidification on echinoderms. *Ecotoxycology*, **19**, 449–462.
- Fabry, V.J. (2008) Marine calcifiers in a high-CO₂ ocean. *Science*, **320**, 1020–1022.
- Fabry, V.J., Seibel, B.A., Feely, R.A. and Orr, J.C. (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.*, **65**, 414–432.
- Gooding, R.A., Harley, C.D.G. and Tang, E. (2009) Elevated water temperature and carbon dioxide concentration increase the growth of a keystone echinoderm. *PNAS*, **106**, 9316–9321.
- Havenhand, J.N., Buttler, F.R., Thorndyke, M.C. and Williams J.E. (2008) Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Curr. Biol.*, **18**, R651–R652.
- Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S. and Fischer, W.W. (2007) Paleophysiology and end-Permian mass extinction. *Earth Plan. Sci. Lett.*, **256**, 295–313.
- Kurihara, H. (2008) Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Mar. Ecol. Prog. Ser.*, **373**, 275–284.
- Lebrato, M., Iglesias-Rodriguez, D., Feely, R., Greeley, D., Jones, D., Suarez-Bosche, N., Lampitt, R., Cartes, J., Green, D. and Alker, B. (2009) Global contribution of echinoderms to the marine carbon cycle a re-assessment of the oceanic CaCO₃ budget and the benthic compartments. *Ecological Monographs*. e-View.
- Miles, H., Widdicombe, S., Spicer, J.I. and Hall-Spencer, J. (2007) Effects of anthropogenic seawater acidification on acid–base balance in the sea urchin *Psammechinus miliaris*. *Mar. Poll. Bull.*, **54**, 89–96.
- O'Donnell, M.J., Hammond, L. and Hofmann G.E. (2009) Predicted impact of ocean acidification on a marine invertebrate: elevated CO₂ alters response to thermal stress in sea urchin larvae. *Mar. Biol.*, **156**, 439–446.
- O'Donnell, M.J., Todgham, A.E., Sewell, M.A., Hammond, L.M., Ruggiero, K., Fangue, N.A., Zippay, M.L. and Hofmann, G.E. (2010) Ocean acidification alters skeletogenesis and gene expression in larval sea urchins. *Mar. Ecol. Prog. Ser.*, **398**, 157–171.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L. and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.
- Pörtner, H.O., Langenbuch, M. and Reipschläger, A. (2004) Biological impact of elevated ocean CO₂ concentrations: lessons from animal physiology and earth history. *J. Oceanogr.*, **60**, 705–718.
- Twitchett, R.J. (2007) The Late Permian mass extinction event and recovery: biological catastrophe in a greenhouse world. In: *Advances in Earth Science - from earthquakes to global warming* (Eds P.R. Sammonds and J.M. T. Thompson). *Roy. Soc. Ser. Adv. Sci.*, **2**, 69–90. London: Imperial College Press.
- Veron, J.E.N. (2008) Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–472.
- Wood, H.L., Spicer, J.I. and Widdicombe, S. (2008) Ocean acidification may increase calcification rates, but at a cost. *Proc. R. Soc., B* **275**, 1767–1773.