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ECHINOIDS AS SUBSTRATES FOR ENCRUSTATION – REVIEW AND QUANTITATIVE ANALYSIS

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Abstract: The existing literature, including records of both fossil and extant echinoid encrustation, is quantitatively analysed and reviewed. This shows that echinoid encrustation (number of encrusted echinoid taphocoenoses) has increased nearly continuously and dramatically to the present day, as confirmed by linear regression values of more than 85 per cent. It also demonstrates that current levels of echinoid fouling stabilised by the Miocene, while there has been a more or less continuous record of echinoid encrustation since the Late Cretaceous. Several increases have been identified since echinoid encrustation first noted occurrence from the Late Carboniferous. This trend is explained as the probable result of corresponding increases in productivity (richness, biomass, energetics, ecospace utilisation) and resources in the marine environment, including epibionts and their hosts. This conclusion matches other indicators, including the number and thickness of shell beds, bioerosion and predation intensity or biodiversity. The trajectory might have been altered to some degree by biases (e.g. selective recording, sampling effort, outcrop area, rock volume) in the same way as palaeobiodiversity estimates. Two recognised long-term gaps in echinoid encrustation (Upper Ordovician–Lower Carboniferous and Permian–Lower Cretaceous) are explained in part as bias and as biological and taphonomic signals. These gaps are caused mostly by the rapid disarticulation of Palaeozoic-type echinoids, the methodology applied here, and a lack of interest in the encrustation of Jurassic echinoids. Conversely, three short-term gaps in the Cenozoic are interpreted exclusively as bias. If correct, the present study demonstrates quantitatively the step-wise increase of productivity through time. It also suggests potential focus on further study, including the collection of new data from the field and pre-existing collections, as best for other encrustation proxies (e.g., percent of coverage by epibionts, ratio of encrusted to nonencrusted shells, taxa richness or numerical abundance of sclerobionts) in cases of large-scale analyses.

Key words: Echinoids, encrustation, Recent, fossil record, patterns, meta-analysis, review.

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INTRODUCTION

Echinoids first appeared in the fossil record in the latest Ordovician (e.g., Kier, 1965; Smith, 1984; Smith and Savill, 2001; Sprinkle and Guensburg, 2004), as representatives of the Great Ordovician Biodiversification Event (review in Webby *et al.*, 2004). However, as they have been ecologically significant only since the Mesozoic, they are generally classified as "modern fauna" (e.g., Sepkoski, 1981). On the other hand, in modern settings they are a diverse and abundant group, and successfully serve as one of the fundamental components of many benthic communities around the world, comprising, with other echinoderms, up to 90 per cent of the biomass in equatorial to polar environments (e.g., Smith, 1984). Echinoid history spans various, substantial events (e.g., Kier, 1982; Smith, 1984), including the evolution of the first irregular forms during the Jurassic, related infaunalisation, and the appearance of sand dollars, with numerous morphological innovations during the Cenozoic. In addition, it is worth noting that Foote and Sepkoski (1999) showed that the echinoid fossil record is fairly complete and better than that of any other echinoderm class. Throughout their history, they have provided diverse substrates for colonisation by various sclerobionts (*sensu* Taylor and Wilson, 2002, 2003). This makes them a useful tool for both long-term and large-scale studies.

In spite of a long and rich history of research and apart from phylogenetic analyses, incorporating a geological time scale (see Kroh and Smith, 2010), only about a dozen studies so far have focused on the quantitative treatment of echinoids as a macroecological and macroevolutionary model group, analysed 'through time' (Kier, 1974, 1977a; McKinney, 1986; Greenstein, 1992; Smith, 1992, 2001, 2007a; Smith and Jeffery, 1998; Eble, 2000; Smith *et al.*, 2001; Villier and Eble, 2004; Villier and Navarro, 2004; Smith and Stockley, 2005; Barras, 2008). This is especially

low, by comparison with investigations, focusing on bivalves and many general studies, incorporating echinoids as one of many target groups (e.g., Sepkoski, 1981; Jablonski and Bottjer, 1991; Jablonski, 1993; Benton, 1995; Foote and Sepkoski, 1999; Bambach *et al.*, 2002; Alroy *et al.*, 2008). However, analytical approaches, integrating case studies from the literature or many new, local field investigations in one analysis (meta-analysis), like "through-time analyses", have shaped many issues in geobiological research. Examples of these issues include geochemistry and biomineralogy (e.g., Kiessling *et al.*, 2008; Zhuravlev and Wood, 2008), palaeobiodiversity (e.g., Sepkoski, 1993; Benton, 1995; Powell and Kowalewski, 2002; Alroy *et al.*, 2008), taphonomy (e.g., Allison and Briggs, 1993a) and evolutionary palaeoecology (e.g., Kidwell and Brenchley, 1994; Trammer and Kaim, 1997; Trammer, 2005; Huntley and Kowalewski, 2007; Powers and Bottjer, 2007).

Encrustation, also known as bioencrustation, biofouling or epibiosis, is a widespread process of permanent attachment by sessile organisms to substrates of biological and non-biological origin, primarily in marine environments, and ranging through geological time to the present day (for reviews see e.g., Wahl, 1989; Taylor and Wilson, 2003; Kukliński, 2009). Until now, only a few studies researched large-scale trends of encrustation through geological time, in spite of a few decades of intensive fieldwork, offering a sufficient database for meta-analysis. For instance, Palmer (1982; updated by Wilson and Palmer, 1992) analysed the diversity of epibionts on hardgrounds from the Cambrian to the Cretaceous. Hansen (1988) investigated the abundance and diversity of sessile suspension-feeding bivalves through time, while McKinney (1995), followed by Barnes and Dick (2000; see also Barnes, 2006), tracked the competitive interactions of bryozoans through the last 100 Ma. Recently, Taylor (2008) tallied a number of studies of hardgrounds as proxies for testing their distribution against past ocean chemistry. There are only a few records of the long-term history of echinoids as substrates for colonisation, which is also true for other patterns of encrustation (see also Lescinsky, 2001; Taylor and Wilson, 2003). Santos and Mayoral (2008, p. 317) pointed out that, 'during a long span in the history of life, tests of dead echinoids have appeared to serve as potential and stable substrata for bioeroders and epibiont colonization'. Nebelsick *et al.* (1997, p. 272) mentioned that 'encrusted fossil echinoids are known in the fossil record, especially from the Miocene and Cretaceous', while Taylor and Wilson (2003, p. 30) merely stated that, 'skeletobionts are common on some post-Paleozoic echinoids'. All of these 'conclusions' were drawn without any rigorous data collection and quantification, but may stand as testable hypotheses, challenged in the present paper.

Here, all existing literature sources on echinoid encrustation are reviewed. This should be treated as complementary to the general comprehensive review by Taylor and Wilson (2003), where in fact the encrustation of echinoids was treated only superficially. Since then significant progress has been made. Furthermore, reviewed data are used to create a quantitative analysis of echinoid encrustation through time. In this literature-based study, the number of communities (taphocoenoses) per time interval, where echinoids served as substrate for colonization, are utilised for deciphering the trajectory of echinoid encrustation through time. This approach of tentatively focusing on one clade is used as a tool towards searching for large-scale trends in encrustation. The author concentrates on quantitative testing of the widely recognised, but untested hypothesis (yet often used as 'hard evidence', see e.g., Finnegan *et al.*, 2011) that "encrustation intensity" has increased through time to the present (e.g., Vermeij, 2004), and focuses on recognising the magnitude and timing of predicted changes.

REVIEW OF ECHINOID ENCRUSTATION

Only recently has Schneider (2003) provided the first insight into echinoid encrustation in the Palaeozoic. She presented data from the Upper Carboniferous Winchell Formation in Texas (USA), based on hundreds of echinoids of the order Cidaroida (see also Schneider *et al.*, 2005), preserved as articulated material. Schneider (2003) showed that only spines were encrusted by numerous commensals, including brachiopods and bryozoans, preferentially located on the proximal portion of spines. In addition, she demonstrated that encrusters showed no host-size preference, and she noted that the costs for echinoids of such an association far outweighed the benefits. In the light of a recent report by Zapalski (2011), such an interpretation is impossible to infer from the fossil material and thus should be rather treated as unproved. Nevertheless, Schneider (2003) provided the sole example from the fossil record to date of the *in vivo* encrustation of echinoids. In that case, encrustation *in vivo* is supported by (*i*) the settlement of episkeletobionts exclusively on echinoid spines, (*ii*) the rapid burial of echinoids during life or shortly after death, precluding post-mortem encrustation, and (*iii*) the non-random distribution of encrusters. A search for records of echinoid encrustation from Permian to Early Cretaceous yielded no results, an observation that is discussed below.

There are a few papers on encrustation processes of Late Cretaceous age, mostly from Europe (Table 1). Substrates for colonisation are various echinoid clades, preferentially spatangoids and holasteroids (e.g., Kidwell and Baumiller, 1990; Kudrewicz, 1992; Rose and Cross, 1993; Olszewska-Nejbert, 2007), the dominant groups at that time. To date, the best examples from the Upper Cretaceous were provided by Zamora *et al.* (2008) and Borszcz *et al.* (2012). Zamora *et al.* (2008) showed that 94 per cent of echinoids in their material were colonised by epibionts, one of the most intensive encrustations of echinoids ever recorded. Kudrewicz (1992), among others, on the basis of Santonian echinoids from Poland, proposed a taphonomic scenario for echinoids and suggested the role of encrustation in their post-mortem paths. Borszcz *et al.* (2012) introduced new examples for echinoneid and holectypoid clades from the Turonian of Poland, which fill some taxonomic and stratigraphic gaps in the record of encrustation. Among other issues, they found a lesser encrustation intensity than that, shown by Zamora *et al.* (2008), which Borszcz *et al.* (2012) regarded as a "loosening effect" in assemblages, characterised by moderate abundance and low diversity.

Table 1

Literature compilations of Recent and fossil echinoid encrustation examples

PERIOD (STAGE)	LOCALITY	CLADE	REFERENCES
Recent	Scotia Arc	various	Linse *et al.* (2008)
Recent	Gulf of Mexico	Cidaroida	Davis *et al.* (2005)
Recent	Antarctic	Cidaroida	Cerrano *et al.* (2009)
Recent	Antarctic	Cidaroida	Gutt and Schickan (1998)
Recent	Antarctic	various	David *et al.* (2009)
Recent	Panama	Clypeasteroida	Seilacher (1979)
Recent	USA, California	Clypeasteroida	Lescinsky (2001), Giltay (1934), Houk and Duffy (1972)
Recent	Red Sea	Clypeasteroida	Nebelsick (1999a, b)
Recent	Adriatic Sea	Spatangoida	Nebelsick *et al.* (1997)
Recent	France	?Camarodonta	Jagt *et al.* (2007)
Recent	Mediterranean Sea	Spatangoida	Ernst *et al.* (1973)
Miocene/ Lower	France	Clypeasteroida	Philippe (1983)
Miocene	-	-	Mitrović-Petrović and Urošević-Dačić (1963)
Miocene	-	Clypeasteroida	Mitrović-Petrović (1972)
Miocene (Badenian)	Croatia	various	Mikša (2009)
Miocene/ (Eggenburgian)	Austria	Clypeasteroida	Nebelsick (1999a)
Miocene (Eggenburgian)	Austria	Cassiduloida	Nebelsick (1996), Nebelsick *et al.*(1997)
Miocene	Egypt	Cassiduloida + Clypeasteroida	El-Hedeny (2007)
Miocene (Tortonian)	Spain	Clypeasteroida	Santos and Mayoral (2008)
Palaeocene (Danian)	Italy	Spatangoida	Giusberti *et al.* (2005)
Late Cretaceous	-	-	Schmid (1949), Müller, 1969)
Cretaceous/ (Maastrichtian)	Germany	Camarodonta	Jagt *et al.* (2007)
Cretaceous (Maastrichtian)	Belgium	Holasteroida	Jagt *et al.* (2007)
Cretaceous (Santonian)	Poland	Spatangoida	Kudrewicz (1992)
Cretaceous (Santonian)	Spain	Spatangoida	Zamora *et al.* (2008)
Cretaceous (Turonian-Campanian)	England	various	Kidwell and Baumiller (1990), Rose and Cross (1993)*
Cretaceous (Turonian-Coniacian)	Kazakhstan	various	Olszewska-Nejbert (2007)
Cretaceous (Turonian)	Poland	Echinoneida + Holectypoida	Borszcz *et al.* (2012)
Carboniferous (Missourian)	USA, Texas	Archaeocidaridae	Schneider (2003)

* excluded from finer-scale analysis

A loosening effect is a commonly occurring (but rarely investigated) phenomenon and concerns instances, where more substrates are available than necessary, thus a part of available surfaces for encrusters remains unoccupied. Their investigation is the largest study, focusing on the encrustation of such substrates to date, and the planar projections of epibionts that they propose may have a much wider application. On the basis of the division of an echinoid's test surfaces on virtual sectors, such a projection allows the visualization of the distribution of encrusters or other issues (e.g., bioerosion, drill holes, repair scars) on the tests of echinoids (or other organisms).

As with epibionts from other times, Late Cretaceous echinoids have been illustrated on numerous occasions, but epibionts have not been specifically noted or, more importantly, studied in detail (see e.g., Małecki, 1982; McKinney, 1995; Gale, 2002a, b; Taylor and Wilson, 2002).

Cenozoic records are mainly from Europe (but see e.g., El-Hedeny, 2007) and include numerous, encrusted examples of spatangoids, clypeasteroids and cassiduloids (Table 1). The most spectacular example is that by Santos and Mayoral (2008), who found nearly 1,500 specimens of balanomorph cirripedes, attached to a single test of *Clypeaster* from the Miocene of Spain. Balanomorph barnacles were widespread and common encrusters in the Neogene (see also e.g., Seilacher, 1979; Philippe, 1983). Santos and Mayoral (2008) also carried out numerous analyses, which demonstrated the non-uniform distribution of epibionts, among other patterns. Their study indicated that the settlement of the cirripeds was initially controlled by the availability of free space, while the topography of the echinoid test played a minor role. In fact, the latter issue, i.e., the impact of the topography of echinoid tests on encrustation pattern, should be addressed more rigorously in future works.

All of these examples come from *post-mortem* encrustation. This may be identified by aspects of encrustation that cannot be reconciled with live echinoids: (*i*) During life, echinoid tests are covered by epidermis, producing antifouling substances such as biocides (e.g., McKenzie and Grigolava, 1996). (*ii*) A dense spine canopy in some taxa prevents encrustation. (*iii*) The encrustation of oral sides is precluded during life, because this part of tests is close to the sea floor in epifaunal examples, or is buried in sediment in semi-infaunal representatives (infaunal species buried whole). (*iv*) Inner test surfaces (e.g., Jagt *et al.*, 2007) of live organisms are inaccessible to colonisers. The presence or absence of stereom malformations in places of encrustation or epibionts embedment within test walls/spines provide direct indications of when the echinoderm skeleton was settled upon, i.e. during life (*syn vivo*) or after death (*post-mortem*). An inhibiting (antifouling) role for pedicellariae is debatable (see Campbell, 1983; Schneider, 2003; Coppard *et al.*, 2012). Moreover, Campbell and Rainbow (1977) argued that settlement of the cyprid larvae of barnacles is impossible, when spines and pedicellariae were active, on the basis of experiments with settlement slates, coated with various parts of the echinoid test, including interambulacral plates. They also noted that there was no repulsion, due to the chemical properties of the epithelium or the pedicellariae.

In Recent settings, examples of echinoid encrustation are known mostly in the Antarctic (Gutt and Schickan, 1998; Linse *et al.*, 2008; Cerrano *et al.*, 2009; David *et al.*, 2009), and Red and Mediterranean Seas, while nothing is known from e.g., the Arctic. Among these papers, David *et al.* (2009) questioned the adaptive significance of the cortical stereom layer. Linse *et al.* (2008) showed a great diversity of epibionts on echinoids, with up to 51 species, found on only 70 cidaroid specimens. Echinoid encrustations have been well recognised in Recent settings of the Mediterranean (Ernst *et al.*, 1973), and combined with studies of fossil settings (Nebelsick *et al.*, 1997; Nebelsick, 1999a, b, 2008). These studies recognised encrustation, acting both *syn vivo* and *post mortem*. In their model study, Nebelsick *et al.* (1997) integrated extant and fossil material to develop a taphonomic-encrustation model, and showed a disparity between the two scales of observation, suggesting that investigations of fossil material clearly need modern analogs for comparison purposes. Other examples of echinoid encrustation are listed in Table 1.

QUANTITATIVE ANALYSIS

Data, methods and rationale

The analysis of encrustation intensity is based on sampling of the existing literature. In addition to a library search, including references in existing echinoid encrustation papers, the following electronic databases were used: *Scopus*, *Science Direct*, *Ingenta*, *Georef* and *Google-Scholar*. Echinoid encrustation reports are rather randomly distributed in the literature, but some relevant journals, such as *Palaios*, *Geobios*, *Journal of Paleontology* and *Facies*, were checked in detail. Apart from a few exceptions, mostly peer-reviewed papers were used. Literature data were 'verified' by reading compiled papers and such approach was successfully applied in other case studies (e.g., Schubert *et al.*, 1997; Kiessling, 2001; Powell and Kowalewski, 2002; Harper, 2003; Fraiser and Bottjer, 2007). In the assembled dataset, case studies, based only on single specimens, were also included (e.g., Santos and Mayoral, 2008). Reports, in which encrusted echinoids are occasionally illustrated, but not studied or marked explicitly, were excluded from the analysis. Encrustation intensity in the present study, contrary to that recorded by Rodland *et al.* (2004) for brachiopods (encrustation frequency) and Borszcz *et al.* (2012),where the number of encrusted to non-encrusted echinoids were counted, is analysed on the basis of the number (abundance) of echinoid communities (assemblages) with encrustation per time interval through time, regardless of how many tests were encrusted within particular cases. A compilation of papers, used in the present study, including geographic, stratigraphic and taxonomic details, is presented in Table 1.

Encrustation cases (excluding bioerosion) were recorded by stratigraphic and geographic unit, the latter over a radius of 50 km. Data were analysed at low and high resolutions. In the former, intervals, such as Permian to Early Cretaceous, were used as single time bins. In the latter, data were binned to epochs or intervals, such as "Santonian–Maastrichtian". As a result, six and eight time bins were applied to the lower and higher resolutions, respectively. The variations in duration of time bins do not generate bias (see below). For analyses, 29 and 26 data points were collected for the lower and higher resolutions, respectively. Regression analysis (R^2) was used to explore the relationships between the number of bio/taphocoenoses of echinoids with encrustation (distinct echinoid encrustation cases) *vs* geological time scale. Statistical analyses were done, using Statistica 8 software and $p < 0.05$ was assumed to be significant.

Results

The trajectory of echinoid encrustation through time (Fig. 1A), based on 29 data points (Table 1), shows a trend of significant increase ($R^2 = 0.85$, $p = 0.009$). It is also apparent that recent levels of encrustation stabilised around the Miocene. Since the Late Cretaceous, a more or less continuous record of echinoid encrustation is observed (see Fig. 1). In recent times, however, rather low levels of echinoid encrustation have been recorded, but the post-Miocene time bins are of shorter duration (cf. *c.* 18 myr in the Miocene or *c.* 15 and 20 myr in subsequent Late Cretaceous bins).

Two long-term gaps were identified, from the Late Ordovician to the Early Carboniferous and from the Permian to the Early Cretaceous. Additionally, on a finer time scale, three short gaps were detected in the Cenozoic, viz. in the Eocene, Oligocene and Plio-Pleistocene. If a linear regression were restricted to the Upper Cretaceous–Recent interval (the last *c.* 100 Ma), two distinct patterns arose (based on 26 data points). When analysed for eight intervals (Fig. 1B), linear regression indicated no significant relationship ($R^2 = 0.2$; $p = 0.26$). Alternatively, when analysed for more

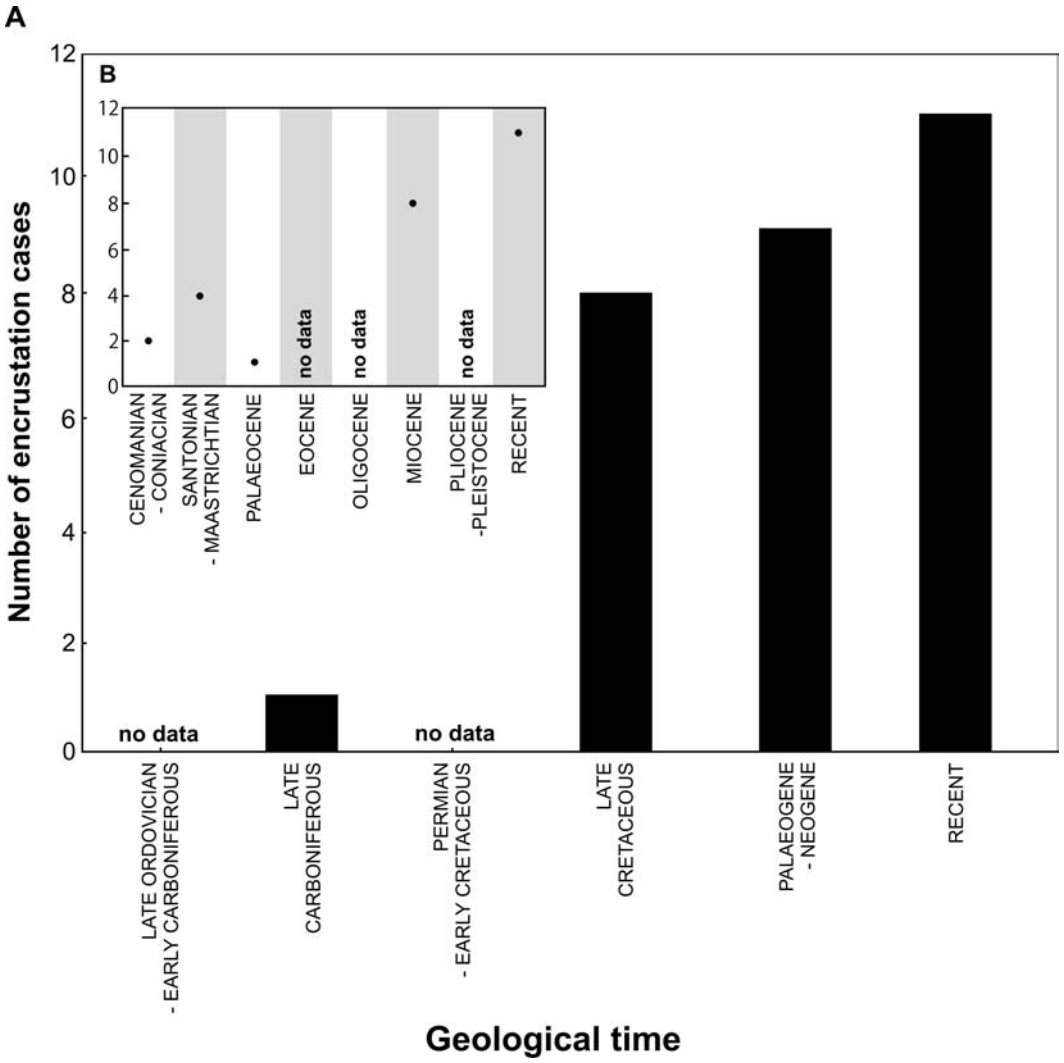

Fig. 1. Number of encrustation cases per time interval, plotted against geological time scale. (A) lower time resolution for data, since echinoids first appeared to Recent (N = 29 data points) and (B) higher time resolution for last *ca*. 100 Ma of echinoid encrustation (N = 26 data points). Data from Table 1

or less timely, standardised intervals, with the Palaeocene, Eocene, Oligocene, Pliocene and Pleistocene grouped to adjacent intervals in five time bins, the same analytical technique showed a strong relationship near to or exactly 1 ($R^2 \approx 1$; $p < 0.01$; and $R^2 = 0.97$; $p = 0.02$), depending on how the bins were amalgamated. The latter analysis, i.e., for standardised time bins, should be regarded as valid.

The dynamics of encrustation rate (Fig. 1B), specifically the magnitude of variation in the number of encrustation cases, varies between intervals. Between two bins in the Upper Cretaceous, a two-fold increase was observed, while there was a decrease in encrustation rate by a factor of about 2.5 from the Santonian–Maastrichtian bin to the Paleocene bin. This transition, crossing the Cretaceous–Paleogene boundary, is the sole example of a decreasing trajectory, since the start of continuous records of echinoid encrustation in the Late Cretaceous. From the Paleocene to the Miocene, the rate of encrustation increased eight times, and from the Miocene to the present, this increase was about 30 per cent.

On the basis of available data (Table 1), in the past and present, encrusters have utilised various echinoid clades as substrate, without strong preferences. During the Carboniferous, encrusters used cidaroids as they do today. In Recent communities, clypeasteroids, spatangoids, and camarodonts are also occupied by encrusters. In the Cretaceous, various existing clades, such as spatangoids, holasteroids, echinoneids, and holectypoids, among others, were settled upon. During the Cenozoic, most encrustation took place on clypeasteroids and associated cassiduloids and spatangoids.

DISCUSSION

Benton (2009), among others, showed that patterns, inferred from the fossil record, may be interpreted as biological and geological signals, that is, as real, biological phenomena and biases. In the present investigation, the trends detected may result from both. Two major points must be discussed: (*i*) the trend of increased echinoid encrustation

towards the present and the related stabilisation of "recent level", timing and magnitude of recognised changes and (*ii*) the detected time gaps in echinoid encrustation.

The observed increase in encrustation towards the present may be understood both as a real signal, e.g. caused by parallel increase in productivity towards the present, and as a result of biases (see Kidwell, 2001). Some of these latter may include an increase in outcrop area toward the present and related fluctuations over time, improvements in the quality and fidelity of the fossil record, observed as a "Pull of the Recent" effect (but see Jablonski *et al.*, 2003), or selective recording, which may also serve as an explanation for the gaps, detected in echinoid encrustation. Other factors (see also e.g., Signor, 1982; Allison and Bottjer, 2010), biasing palaeobiodiversity estimates, may also include heterogeneous worker efforts (the "paleontologic interest units" of Sheehan [1977]; see also Bernard *et al.* [2010]), fluctuations in rock lithification through time (Hendy, 2009; Sessa *et al.*, 2009), sampling intensity (e.g., Westrop and Adrain, 2001), and socio-economic effects.

Trends, inferred in the present study, are in agreement with predictions of increases in productivity, energetics, ecospace and guild occupation (utilisation), and nutrient levels throughout the Phanerozoic (e.g., Vermeij, 1977, 1995; Bambach, 1993, 1999; Wood, 1993; Martin, 1996, 2003; Finnegan *et al.*, 2011). This prediction is probably the most adequate, biological explanation for this trend and is regarded as their numerical representation. This is also strongly supported by evidence from modern environments. For example, Lescinsky *et al.* (2002) showed that modern encrustation was linked with productivity. The rising trend is also in agreement with other known patterns in the fossil record that show increases to the present day, such as palaeobiodiversity and drilling predation intensity (e.g., Huntley and Kowalewski, 2007), maximum body size (Payne *et al.*, 2009), number of shell beds per time interval and their thickness (Kidwell and Brenchley, 1994; Oji *et al.*, 2003), and echinoid biodiversity (e.g., Kier, 1974, 1977a; Smith, 1984). This fact points to two possibilities: all of these trends represent biases, arising from the same source – the fossil record (= 'common cause'), or all of them are true signals that are affected, only by individual biases to some degree. Encrustation trajectory, like inferences of productivity in the fossil record and other patterns, may be biased by a number of factors. Sheehan (1977) noted that there were many more researchers, working on Cretaceous and Cenozoic strata, than on older rocks. In fact, virtually all reports, used in this study, concern the Cretaceous and the Cenozoic, so sampling effort is probably not a sufficient explanation. Further, serious issues are outcrop area, quality and completeness of the fossil record. Numerous studies (e.g. Raup, 1972; Smith, 2007b; McGowan and Smith, 2008; Smith and McGowan, 2007; Wall *et al.*, 2009; Hannisdal and Peters, 2010; Peters and Heim, 2010; Dunhill, 2011) suggest an increase in outcrop area or rock exposure for younger deposits and in their influence on the perception of patterns, inferred from the fossil record. On the other hand, between the Jurassic and the Cretaceous, as well as in particular adjacent intervals of the Cenozoic, there are no such drastic differences between outcrops, available for the sampling of encrusted echinoids. These changes may cause discrepancies in encrustation patterns. For example, there are few encrustation cases in the Late Cretaceous, but twice as many in the Miocene. Detected trajectories are therefore regarded as biological indicators. Other types of bias, such as a concentration of records from Europe, might affect the results. Traditions of studying echinoids, great interest in studying encrustation and other agents, related to education or funding level, all of which may be regarded as 'socio-economic' effects, are expected to be important factors in perception (see also Allison and Briggs, 1993b). The observed trend may also be the result of differences in sampling intensity (i.e. sampling effort), which probably could be detected, when compared to general tendencies of encrustation investigations, recorded in the "marine hard substrate bibliography" (Wilson, 2008). Furthermore, interest in encrustation in Jurassic and Cretaceous cases is high and comparable to levels in studies of the Cenozoic. Therefore, differences in the number of encrustation cases for particular intervals of the Late Mesozoic and Cenozoic should not be regarded exclusively as the result of sampling effort. Selective recording in this case is linked to the fact that Cretaceous and Cenozoic materials are encrusted by more diverse epibionts and are more abundant and more heavily colonised, than those of the Jurassic and earlier materials, thus increasing their attractiveness to researchers. This bias may have a strong effect on perceptions of the distribution of echinoid encrustation.

The primary objective of the present study was to find how many examples of echinoid encrustation occurred through geological time. The intense focus by previous researchers on cases, where encrusted echinoids were frequent and widespread, in fact may have created a realistic picture of the extent, to which each of these intervals was productive for echinoid encrustation.

The temporal gaps in echinoid encrustation, noted earlier, arise in part from problems in methodology, but in part they also reflect real absences. Some gaps reflect low sampling effort. For example, there are a number of records of encrusted Jurassic echinoids (e.g., Hess, 1975), yet the reports are not explicitly presented and they were therefore omitted from the data compilation. However, this approach was also applied to data from other time intervals for similar reasons and thus the omissions are probably of rather low significance. Furthermore, from the personal field experience of the author, there are numerous locations in south-central Poland, where Middle and Late Jurassic encrusted tests and spines have been found, sometimes even abundantly, but these have never been reported in the literature. An analysis of published data, especially plates in selected papers describing Palaeozoic echinoids (e.g., Jackson, 1912; Hawkins, 1946; Kier, 1965), echinoid bibliographic compilations (Weisbord, 1971) and taphonomic papers, dealing with echinoids and/or echinoderm content (e.g., Donovan, 1991; Ausich, 2001), did not show any other examples like those in Schneider's (2003) work and did not include epibionts, preserved on illustrated specimens from the Palaeozoic. Only Smith and Hollingworth (1990, fig. 3.1) illustrated (without comment) an interambulacral segment of a Late Permian echinoid, colonised by epibionts on

its inner surface, indicating encrustation after death. Additionally, there are no studies that focused specifically on the encrustation of echinoids in Triassic and Lower Cretaceous deposits. Illustrations in studies of Triassic echinoids (e.g., Bather, 1909; Kier, 1968, 1977b, 1984; Hagdorn, 1995; Salamon and Niedźwiedzki, 2003) show no examples of encrustation. There may be several explanations for the apparent rarity of echinoid encrustation in the Palaeozoic and the Triassic, including biological signals, taphonomic or literature artifacts (sampling biases). Attention should be paid to the fact that echinoids were a group of minor, ecological importance, with very low abundance and richness, in Palaeozoic communities, indicated e.g., by diversity estimates (e.g., Smith, 1984), but awaiting more reliable quantification. They were characterised by short, thin spines, so colonising organisms preferences may have been skewed to other benthic groups that were more abundant, more resistant, and more stable on the sea floor after death, such as brachiopods (e.g., Zatoń and Borszcz, 2012). Additionally, this lack of encrustation may be the result of the anti-fouling properties of echinoids, specifically the covering of tests and appendages by an epidermis, which precluded colonisation. Cidaroid-like echinoids are suitable for hosting colonising organisms, while alive. They lack an epidermal covering on their spines and have only been known to exist from the Late Devonian (e.g., Schneider *et al.*, 2005) to the Permian, a time interval, also lacking samples with encrustation of them. Permian gaps may be also explained simply by the overall rarity of echinoids. This probably explains why all other Palaeozoic echinoids had spines and tests, covered by this anti-fouling protection, while they were alive, and so they were not encrusted. It should also be noted that tests of all Paleozoic echinoids consist of imbricated plates (e.g., Smith, 1984, 2005) that rapidly disarticulate into isolated ossicles after death, and these may have been too small to serve as a stable colonisation ground. This is in contrast to brachiopods, which were one of the main hard substrates of the Palaeozoic (e.g., Bordeaux and Brett, 1990; Taylor and Wilson, 2003). A third probable interpretation could be that isolated ossicles of echinoids, which might preserve epibionts, are of minor significance to researchers, who neglect them, in favour of others groups and articulated material if available, thus masking the real picture (see also e.g., Donovan, 2001 for similar reasoning in another case). It is also worth noting that the "sampling artifact" explanation extends to a suggestion that palaeontologists may have preferred to illustrate clean, unencrusted specimens, and that they may have ignored information, other than the taxonomic context of their finds, which may be especially true in cases, where epibionts were overlooked (see also Lescinsky, 1996).

CONCLUSIONS

Echinoids and their encrusters have been poorly explored as a potential tool for assessing quantitative, large-scale patterns in the marine environment. The present study fills this gap, and shows an increase in echinoid encrustation through time. This rise is more or less parallel to the trajectory of palaeobiodiversity and other increasing trends in the fossil record, and is interpreted mainly as a probable response to a simultaneous rise in productivity and concomitant opportunities for organisms and ecosystems. The encrustation intensity level has stabilised since the Miocene, yet since the Late Cretaceous there is nearly a continuous record. Such a continuous record for nearly one hundred million years makes echinoids a model group for this time interval. Future works (see also Brett *et al.*, 2012) should include a larger diversity of animals, as well as a larger number of parameters, including, for example, the percentage of encrustation coverage or encrustation intensity, measured as a ratio of encrusted to non-encrusted shells. Additionally, the present study has identified some gaps in the timeline of echinoid encrustation that warrant further field study, specifically in the Jurassic.

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