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Disarticulation and Preservation of Fossil Echinoderms

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1 Introduction

The multielement echinoderm skeleton disarticulates in a predictable progression, which renders echinoderms model organisms for taphonomic studies. Consequently, much has been written on this topic, including thorough reviews, such as Lewis (1980), Donovan (1991), Brett et al. (1997), and Ausich (2001). Rather than attempt another full review, this Element will concentrate on understanding the following questions: When you find a fossil echinoderm – from a complete, articulated specimen to completely disarticulated and abraded ossicles (Figures 1 and 2) – what do you see? What data are encapsulated in fossil echinoderm occurrences? Initial observation of skeletal material clarifies morphology, but what other data are preserved – biologic, ecologic, biostratinomic, and diagenetic? Are the fossils



Figure 1 Buried paleocommunity from the Mississippian (Tournaisian) Maynes Creek Formation of Legrand, Iowa. Crinoids and blastoids occur together, and different species preserved characteristically in different colors: large white crinoid, *Elegantocrinus symmetricus*, large very dark crinoid *Cribanocrinus watersianus*, intermediate-colored crinoid in bottom center *Cusacrinus nodobrachiatus*, two very small cladids white, and white blastoids. (BC-173; scale bar 10 mm).

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Figure 2 Fossiliferous bedding surfaces from Anticosti Island, Québec,
Canada. (1) Mill Bay Member, Vauréal Formation, Ordovician (Katian) (OSU 54743). (2) Goéland Member, Menier Formation, Silurian (Aeronian) (OSU 54744) (scale bar 10 mm).

preserved where they lived or are they transported; if transported, how far? All echinoderm clades provide taphonomic information but because of their high relative abundance in the fossil record, the taphonomy of crinoids (e.g., Lewis, 1980; Donovan, 1991; Brett et al., 1997; Ausich, 2001; and Baumiller, 2003), and echinoids (e.g., Kier, 1977; Seilacher, 1979; Smith, 1984; Telford, 1985a, 1985b; Kidwell & Baumiller, 1990; Nebelsick, 1992, 1995a, 1995b, 1995c, 1996, 2008; Kroh & Nebelsick, 2003; Smith & Rader, 2009; Balaústegui et al., 2012; Mancousa & Nebelsick, 2013, 2015, 2017; Nebelsick et al., 2015; Grun et al., 2018; and Nebelsick & Mancosu, 2021) have been studied more extensively. The

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basic principles of these two clades are applicable for understanding the taphonomy of other echinoderm clades.

2 Echinoderm Skeleton

As noted, an echinoderm has a multielement mesodermal skeleton. Individual ossicles (skeletal plates) may be floating independently in mesodermal tissue (e.g., holothurians), imbricated (e.g., helicoplacoids, gogiids, edrioasteroids, ophiocistioids), or tessellate (abutting against one another). Tessellate plates abut one another in various configurations (Donovan, 1991); are bound together by either ligaments, muscles, or ligaments and muscles; or have interlocking stereom with varying degrees of strength. The strength of the bond between two plates by interlocking stereom is commonly correlated with plate thickness.

When secreted, the echinoderm skeleton is a high-magnesium calcite (see Gorzelak et al., 2012 and references therein). The magnesium content is variable and has been attributed to many causes (MacQueen et al., 1974; Gorzelak et al., 2012). Gorzelak et al. (2012) reported magnesium content between 1.83 and 3.55 wt.%. Variability existed between individuals as well as within a single ossicle, with higher concentrations in the center of ossicles (Weber, 1969; Stolarski et al., 2009; and discussion in Gorzelak et al., 2012).

Individual echinoderm ossicles have a stereom microstructure (Roux, 1970, 1974a, 1974b, 1975; Macurda & Meyer, 1975; Macurda et al., 1978; Smith, 1980) that is a porous arrangement of calcite trabeculae (Figure 3). When alive, space within the stereom was filled with mesodermal tissue. Each ossicle behaves optically as a single crystal of calcite despite the fact that each ossicle is a composite of nanograins (Gorzelak et al., 2016). Savarese et al. (1997) calculated the porosity of columnals in extant crinoids to range from 52–72%.

Echinoderm high-magnesium calcite is metastable, not in equilibrium with ambient conditions. Both the chemistry and stereom microstructure may be transformed during diagenesis as a function of local diagenetic conditions. Important diagenetic factors for echinoderm ossicle preservation include the following: primary magnesium content; porosity, permeability, and chemistry of the enclosing sediment; Eh, pH, and oxic chemistry of pore fluids; temperature, etc. (Gorzelak et al., 2016). Dickson (2001a) and Gorzelak et al. (2016) outlined several transformation pathways yielding different types of echinoderm ossicle preservation. Despite chemical and nanostructural changes, original single-crystal optical properties are typically maintained after occlusion of the original porosity during cementation. Dickson (1995, 2001a, 4

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Figure 3 Stereom microstructure of the extant crinoid *Metacrinus* sp. (1) Upper portion of a brachial plate with axial canal to lower left and adoral groove to

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Caption for Figure 3 (cont.)

upper right; ligamentary stereom to left an most of image muscular stereom (OSU 54740) (scale bar 500 μ m). (2) Lower portion of a brachial plate with aboral ligament fossa beneath articular ridge and additional ligamentary fossae above articular ridge on either side of the adoral groove (OSU 54740) (scale bar 500 μ m). (3) Central portion of a columnal with lumen in center of image, all ligamentary stereom (OSU 54739) (scale bar 1 mm). (SEM images taken by

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2001b, 2002, 2004, 2009) argued that the chemistry of well-preserved echinoderm calcite was correlated with ancient ocean Ca/Mg ratios; but Gorselak et al. (2016) argued that the echinoderm diagenesis system was too complex to reliably make this assumption.

3 Accumulations of Fossil Echinoderms

In shallow-water marine facies, echinoderms are among the more common bioclasts in many carbonate and siliciclastic settings. This was especially true during the Paleozoic, when crinoid bioclasts in rocks varied from seemingly random constituents (Figures 1 and 2) to beds comprised exclusively of crinoidal ossicles (Figure 4). Echinoderm-dominated beds include both allochthonous and autochthonous facies. Allochthonous facies range from thin to massive beds deposited by storms to areally extensive sediment gravity flows.

Within an autochthonous facies, individual fossils may be either autochthonous (preserved at the site where they lived) or parautochthonous (not preserved at their living site but fossilized within the sedimentary facies where they lived) (Kidwell et al., 1986). A typical autochthonous facies may contain a combination of autochthonous and parautochthonous individual fossils. Autochthonous echinoderm facies include a wide array of siliciclastic, carbonate, and mixed carbonate-siliciclastic depositional settings. Echinoderms may have been attached to a hard substratum during life. Hard substrata may be hardgrounds, shell pavements, or living organisms (Figures 5 and 6, Table 1). Rapid burial of both uncemented sessile or mobile organisms was varied and common. Such occurrences may contain only autochthonous organisms or a combination of autochthonous and parautochthonous organisms (Figures 7–10). A few examples are listed in Table 2.