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Marine arthropod Fossil-Lagerstätten

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Abstract

Fossil-Lagerstätten, or Lagerstätten, have played a critical role in our understanding of the diversity, abundance, evolution, and systematics of marine arthropods. The tendency toward preservation of Phanerozoic marine arthropods as fossils generally increases as a factor of biomineralization. Concentration deposits (Konzentrat-Lagerstätten) tend to have an abundance of biomineralized arthropod taxa, whereas conservation deposits (Konservat-Lagerstätten) tend to produce a higher biodiversity that includes biomineralizing and non-biomineralizing taxa. Some Lagerstätten incorporate aspects of both concentration and conservation deposits, indicating that these concepts are idealizations, or preservational end members. For arthropod occurrences, it is useful to consider another dimension of Lagerstätten: their taphonomic associations. This leads to a more nuanced understanding of arthropod fossilization history. Four taphonomic associations account for a substantial number of marine arthropod occurrences: (1) concretions, (2) clusters, (3) event beds, and (4) microbially sealed sediments. Each of these occurrences can blur the distinctions between, or the means of recognizing, the idealized genetic categories of concentration deposits and conservation deposits.

Non-technical Summary

Fossil-Lagerstätten, or deposits of exceptional preservation, have played a critical role in our understanding of the diversity, abundance, evolution, and systematics of marine arthropods. In general, arthropods that added biominerals to their exoskeletons have left a more complete fossil record than those that had only chitinous exoskeletons. Four types of occurrences account for a substantial number of fossil marine arthropods: (1) concretions, (2) clusters, (3) event beds, and (4) microbially sealed sediments. Understanding how these fossil associations developed shows that concentration deposits (Konzentrat-Lagerstätten) and conservation deposits (Konservat-Lagerstätten) are idealized concepts of fossil preservation, because Lagerstätten commonly incorporate aspects of both concentration and conservation.

Articles

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Introduction

Arthropods have dominated all major animal clades, both in diversity and abundance, in the marine realm since the Cambrian, and in the terrestrial realm since about the Devonian–Carboniferous. Their fossil record, with the exception of the Cambrian record (e.g., Peng et al., 2020, and references therein), however, trifles compared to the records of other major groups, such as mollusks, brachiopods, bryozoans, and corals, that biomineralize more substantially or broadly. The tendency toward biomineralization in panarthropodan taxa varies considerably. In terms of their published record, they can be underrepresented at both ends of a biomineralization spectrum, either related to non-biomineralization or weak biomineralization, or related to under-collecting or under-reporting. In spite of the proportional underrepresentation of arthropodan groups in the fossil record compared to groups that are better biomineralized, our information base is rich, in large part due to the existence of Fossil-Lagerstätten, or simply Lagerstätten (Seilacher, 1970; Seilacher and Westphal, 1971; Seilacher et al., 1985; Itano, 2019).

This paper, which follows a presentation in a theme session held at the Geological Society of America's annual meeting in Pittsburgh, Pennsylvania (Babcock, 2023), honors the remarkable scientific career of the late Prof. Rodney M. Feldmann. Across the span of seven decades, Rod Feldmann documented and advanced concepts that extend across all arthropodan groups and most phyla known from fossils. Much of his publication record is based on fossils derived from Lagerstätten as originally defined and interpreted (Seilacher, 1970, 2007; Seilacher et al., 1985), and that record, although far from treating arthropod remains exclusively, has emphasized the biodiversity and evolutionary record of this large group, and especially that of the decapod crustaceans. In collaboration with students and colleagues, he documented arthropods from numerous Lagerstätten and some "ordinary" marine deposits, weaving together a fascinating picture of the interrelationships among paleoecologic, taphonomic, and sedimentologic factors influencing our perception of the evolutionary history of Earth's most diverse animals.

This paper provides some examples of sedimentary deposits that have produced an unusual amount of paleontological information concerning Phanerozoic marine arthropods, organized

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here as taphonomic associations (Figs. 1–5). These deposits also yield body fossils of other organisms, and trace fossils (see for overviews Muscente et al., 2017, 2023; Kimmig and Schiffbauer, 2024), but these other fossils are de-emphasized here. The terms "arthropod" and "arthropodan" are intended as references to the broad assortment of animals commonly classified today as panarthropods, although the emphasis in the examples given here is on euarthropods. The selection of examples in this paper is quite incomplete, as there are many possibilities (e.g., Allison and Briggs, 1991a; Bottjer et al., 2002; Muscente et al., 2017; Kimmig and Schiffbauer, 2024). Moreover, in the Cambrian System, arthropod fossils greatly outnumber all other macrofossils in many marine deposits (e.g., Peng et al., 2020, and references therein), and they justifiably have been the focus of numerous reports (e.g., Whittington, 1985; Briggs et al., 1994; Hou et al., 2004; Zhao et al., 2011; Robison et al., 2015; Harper et al., 2019). The examples cited here represent a small fraction of the volume of information currently available, and the intent of this paper is not to summarize all that is known about marine Lagerstätten yielding remains of arthropods, but to provide general patterns of their occurrence through the stratigraphic record.

In this contribution, rather than concentrating on Lagerstätten from the standpoint of genetic models, I concentrate on taphonomic associations, or common sedimentary occurrences of marine arthropod fossils in Lagerstätten. The examples provided point to the conclusion that the concepts of conservation deposits (Konservat-Lagerstätten) and concentration deposits (Konzentrat-Lagerstätten; Seilacher, 1970; Seilacher at al., 1985) are idealizations, or preservational end members. Deposits we normally think of as Lagerstätten result from the interplay of various biological and taphonomic factors (e.g., Kidwell and Jablonski, 1983; Seilacher et al., 1985; Allison and Briggs, 1991c, and papers therein; Brett et al., 2012; Vrazo et al., 2017), and some of these factors result in taphonomic associations that transcend the boundaries of the genetic models (compare Seilacher et al., 1985; Nudds and Selden, 2020). Understanding that the factors leading to conservation or concentration underlie the origins of many Lagerstätten in varied proportions leads to a more nuanced view of these deposits, which in turn may further inform us as to how, where, and when strata rich in paleontological information were formed.

Materials and methods

Most specimens were photographed using a Canon EOS R6 Mark II digital camera. The specimen in Figure 5.1 was photographed using a Canon EOS Rebel Xsi digital camera. A portable NeuroLogica CereTom XCT medical scanner was used to image the specimen in Figure 1.6. Images were adjusted and assembled using Adobe Photoshop.

Repository and institutional abbreviation. All illustrated specimens are in the Orton Geological Museum at The Ohio State University (OSU), Columbus, Ohio, USA.

Definition and meaning of Fossil-Lagerstätten

Seilacher (1970, p. 34; translated from German, Itano, 2019) originally defined Fossil-Lagerstätten (plural: Fossil-Lagerstätten; singular: Fossil-Lagerstätte) as rock bodies containing "an unusual amount of paleontological information, in terms of quality or quantity." Seilacher et al. (1985, p. 5) later stated this in English as "rock bodies unusually rich in paleontological information, either in a quantitative or qualitative sense." Strata included may be ones having "an unusual preservation" or be "less spectacular deposits such as shell beds, bone beds and crinoidal limestones" (Seilacher et al., 1985, p. 5). As originally intended, there is "no sharp boundary" between Lagerstätten and "normally" fossiliferous strata, with the preservation of any fossil being perceived as an "unusual accident" (Seilacher et al., 1985, p. 5).

Fossil-Lagerstätten have been classified according to two broad, genetic categories (Seilacher, 1970; Seilacher et al., 1985): concentration deposits, or Konzentrat-Lagerstätten; and conservation deposits, or Konservat-Lagerstätten. Concentration deposits were intended to embrace condensation deposits, placer deposits, and concentration traps. Conservation deposits were intended to embrace stagnation deposits, obrution deposits, and conservation traps.

Various authors (e.g., Allison, 1988; Allison and Briggs, 1991b, c; Kidwell, 1991; Kidwell and Bosence, 1991; Butterfield, 1995, 2003; Brett et al., 1997; Shields, 1998; Schiffbauer and Laflamme, 2012; Muscente et al., 2017, 2023) have modified, amplified, or embellished the concept of "Fossil-Lagerstätten." Conventionally, the term has been applied to sedimentary deposits yielding body fossil remains, but Hunt et al. (2005), Seilacher (2007, p. 8), and Kim et al. (2019) all discussed exceptional trace fossil assemblages as Lagerstätten. Kimmig and Schiffbauer (2024), who significantly updated the concept of Konservat-Lagerstätten, likewise argued that deposits rich in trace fossils are Lagerstätten. This is relevant to the marine arthropod record, because traces of inferred of arthropod origin are abundant at some sites (e.g., Hannibal and Feldmann, 1983; Wiedner and Feldmann, 1985; Babcock et al., 1995, 2000; Hannibal, 1996; King et al., 2019).

Factors influencing the marine arthropod fossil record

The fossil record of marine arthropods varies along a preservational spectrum, from excellent to weak. Studies on Holocene arthropods show that the most significant taphonomic filtering takes place quite early following death or release of body parts (e.g., by exuviation) into the environment (e.g., Plotnick, 1986; Tshudy et al., 1989; Briggs and Kear, 1993; Babcock and Chang, 1997; Babcock et al., 2000; Borkow and Babcock, 2003; Briggs, 2003a, b). Biodegraders, including predators, scavengers, and microbial decay agents, generally work quickly to break down nutrient-rich body parts. Bodily remains that escape breakdown shortly after death or release may be subject to further taphonomic filtering but nevertheless stand an improved chance of retention in sediments, leading in some instances to preservation as fossils. As a general rule, heavily biomineralized remains ("hard parts") tend to be less palatable or more difficult to break down for many biodegraders and are more likely to slip through the early taphonomic filter of biodegradation (e.g., Klompmaker et al., 2017; Plotnick and McCarroll, 2023). For this reason, the most important factors accounting for the extreme variability in the perceived record of marine arthropods are the extent of biomineralization and related taphonomic responses. The effects of collecting bias and of monographic bias also may play roles in our perception of arthropod biodiversity and abundance following the processes that have resulted in successful fossilization.

Biomineralization and taphonomic responses. The spectrum of arthropod preservation in the fossil record spans from taxa that are non-biomineralizing through ones that are well biomineralized.

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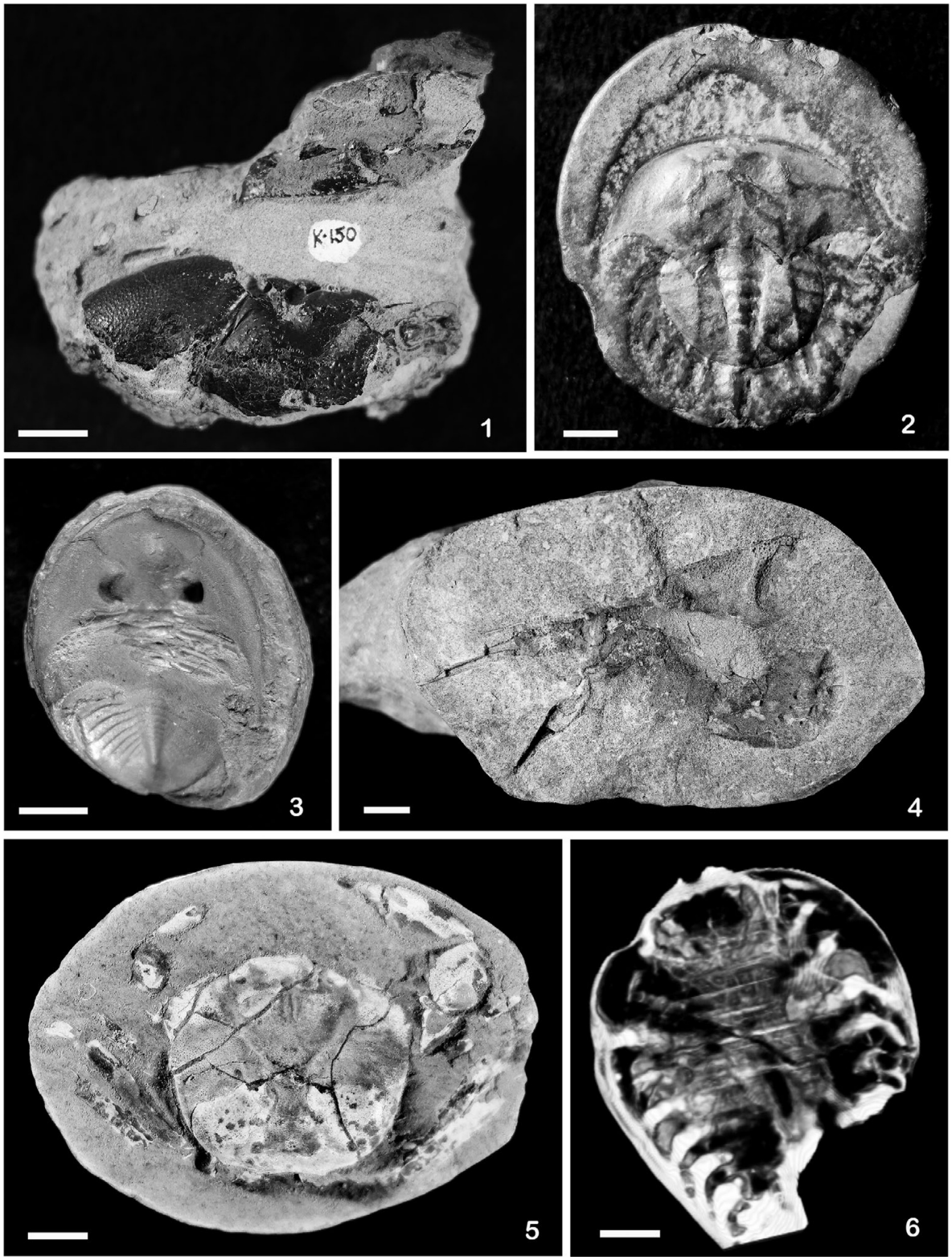


Figure 1. Arthropods preserved in concretions resulting from rapid onset of mineralization mediated by microbial action in "decay halos," biofilms surrounding organic remains. (**1**) *Hoploparia stokesi* (Weller, 1903), a nephropid lobster, incomplete molts in calcite-cemented siliceous and glauconitic concretion from the López de Bertodano Formation (Cretaceous), Seymour Island, Antarctica; OSU 55326. (**2**) *Euproops danae* (Meek and Worthen, 1865), holotype of *Euproops colletti* White, 1884, a belinurid xiphosuran, dorsal view of exoskeleton preserved in siderite Mazon Creek-type concretion from the Carboniferous of Durkee's Ferry, Vigo County, Indiana, USA; OSU 50291. (**3**) *Pseudoasaphus* cf. *P. globifrons* (Eichwald, 1857), a trilobite, external mold, preserved in a calcareous concretion from the Church Hill Formation (Ordovician), Church Hill, Caceres Province, Spain; OSU 55240. (**4**) *Hoploparia stokesi* (Weller, 1903), a nephropid lobster, molt ensemble in calcite-cemented siliceous and glauconitic concretion from the López de Bertodano Formation (Cretaceous), Seymour Island, Antarctica; OSU 55328. (**5**) *Neopilumnoplax hannibalanus* (Rathbun, 1926), a brachyuran crab, preserved in calcareous concretion from the Hoko River Formation (Paleogene, Eocene) of Clallam County, Washington, USA; OSU 51488. (**6**) *Hemirhodon amplipyge* Robison, 1964, a trilobite, XCT scan of specimen preserved in calcite concretion, showing appendages and digestive tract; from the Marjum Formation (Cambrian) of the House Range, Millard County, Utah; OSU 55241A (part; counterpart slab is OSU 55241B). Scale bars = 10 mm.

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Klompmaker et al. (2017), studying present-day arthropods, discussed differences in preservation potential among taxa, stemming largely from their relative extent of biomineralization. In general, biomineralizers suffer the effects of biodegraders less than non-biomineralizers and have a better or more complete fossil record (Mikulic, 1990). Their remains dominate the arthropod faunas of concentration deposits (Konzentrat-Lagerstätten). Notable examples include the trilobites, and certain crustaceans, particularly ostracodes, barnacles, and biomineralizing decapods such as lobsters and brachyuran crabs. Plotnick and McCarroll (2023) recognized that different parts within biomineralized exoskeletons may be variably mineralized and therefore can have different taphonomic outcomes: the thickness and extent of biomineralization, as well as the Mg:Ca ratio and phosphorus content in exoskeletons, are variables influencing the preservation of arthropod remains.

At the other end of the preservational spectrum, non-biomineralizing marine arthropod taxa, which stand a relatively increased probability of complete breakdown through the action of biodegraders, tend to have weak fossil records in most sedimentary environments apart from conservation deposits (Konservat-Lagerstätten). Examples include various crustaceans such as amphipods, copepods, and krill, as well as radiodonts, naraoiids, marrellomorphs, lobopodians other than the armored lobopods, emeraldellids, luolishaniids, and tardigrades. Intermediate intervals along the preservational spectrum are occupied by taxa that have weakly biomineralized exoskeletons, such as some decapods (e.g., certain shrimps and prawns) or heavily sclerotized but non-biomineralized skeletons, such as some xiphosurans.

The relationship between biomineralization and preservation in the fossil record is heavily influenced by the role of biodegraders, which recycle organic materials back into the ecosystem, and are important in the cycles of carbon, calcium, phosphate, oxygen, and even sulfur. Biodegraders include predators, scavengers, herbivores, and microbial agents—organisms that in sum represent all domains and kingdoms (animals, plants, fungi, protistans, and archaeans). Among the variety of organisms that are adapted, or even specialized, for the breakdown of chitin (Beier and Bertilsson, 2013) are some bacteria (e.g., Gooday, 1990; Jiang et al., 2022), fungi (Gooday, 1990), archaeans (e.g., Huber et al., 1995; Tanaka et al., 1999; Gao et al., 2003), algae, including diatoms (Vrba et al., 1996, 1997; Štrojsová and Dyhrman, 2008), rotifers (Štrojsová and Vrba, 2005), and higher animals (Beier and Bertilsson, 2013). In the terrestrial realm, even carnivorous plants can break down chitin (e.g., Gooday, 1990).

Thicker, more resistant, biomineralized skeletal elements generally stand a better chance of long-term survival in sediments than less resistant, non-biomineralized bodily elements. This principle underlies the concept of the "preservation paradox," wherein the most abundant and diverse taxa in a living ecosystem are proportionally underrepresented in the resulting fossil assemblage (Babcock et al., 2006) Among the best examples of this principle are some of the crustaceans, such as amphipods, copepods, and krill, which account for a large percentage of the biomass in Holocene marine ecosystems and presumably were similarly abundant in the geologic past, but which have meagre fossil records.

In some instances, conservation deposits such as the Burgess Shale (Cambrian; e.g., Walcott, 1912; Conway Morris, 1985, 1998; Whittington, 1985; Briggs et al., 1994), Chengjiang (Cambrian; e.g., Zhang and Hou, 1985; Hou et al., 2004), Sirius Passet (Cambrian; e.g., Budd, 1997; Babcock and Peel, 2007; Harper et al., 2019), Emu Bay (Cambrian; e.g., Bicknell et al., 2022a; Gaines et al., 2024), Kaili (Cambrian; e.g., Zhao et al., 2011), 'orsten' of the Alum Shale (Cambrian; e.g., Müller and Walossek, 1985, 1987), the Fezouata Formation (Ordovician; e.g., Van Roy et al., 2015), Bertie Group dolostones (Silurian; e.g., Clarke and Ruedemann, 1912; Vrazo et al., 2016, 2017), Waukesha (Silurian; Mikulic et al., 1985a, b; Wendruff et al., 2020) and other Silurian plattenkalk deposits (e.g., von Bitter et al., 2007), Mazon Creek and similar deposits (Carboniferous; e.g., Nitecki, 1979; Baird et al., 1985a, b, 1986; Shabica and Hay, 1997; Cotroneo et al., 2016), and the Solnhofen Limestone (Jurassic; e.g., Barthel et al., 1990) provide a counterbalance to the preservation paradox. In these and comparable sedimentary settings, the actions of biodegraders have been limited by a variety and combination of means that include, but may not be limited to, dysoxia or anoxia, salinity fluctuation, desiccation, rapid burial through event deposition or tidal sedimentation, and microbially mediated sedimentary sealing (e.g., Allison and Briggs, 1991a, b, 1993; Feldman et al., 1993; Brett et al., 1997; Babcock et al., 2001; Briggs, 2003a; Schiffbauer and Laflamme, 2012; Vrazo et al., 2016; Wendruff et al., 2020; Albani et al., 2024). Conservation deposits may provide a more realistic picture of the original diversity and abundance of arthropods in ancient marine ecosystems than we might infer from "ordinary" deposits. Conservation deposits have been of incalculable benefit for providing details pertaining to the morphology, origins, phylogeny, systematics, paleoecology, and taphonomy of numerous arthropod clades, as well as many non-arthropodan organisms (e.g., Conway Morris, 1985, Whittington, 1985; Barthel et al., 1990; Allison and Briggs, 1991c; Budd, 1997; Butterfield, 2003; Schiffbauer and Laflamme, 2012; Lerosey-Aubril et al., 2014, 2018, 2020; Robison et al., 2015; Cotroneo et al., 2016; Wendruff et al., 2020; Pates et al., 2021, and references therein).

Fortuitously, some of the well-studied conservation deposits coincide with critical intervals in the evolutionary history of arthropods, and provide important morphologic information, which in turn provides insight into evolutionary processes and driving factors, phylogenetic relationships, morphologic patterns, and other aspects of the biology of ancient arthropods. Our perception of the phylogenetic history and relationships of and within arthropods would be far less complete were it not for conservation deposits, and especially ones in Paleozoic strata.

Collecting and monographic biases. Few studies on marine Fossil-Lagerstätten consider the full suite of body fossils present at a site (see English and Babcock, 2010, for an exception). Often reports emphasize one group of fossils in preference to others, for reasons of monographic priority, perceived abundance or preservational quality at a site, or perhaps because collecting in a truly unbiased fashion would be challenging (Miller, 1997). Indeed, in particularly rich deposits such as the Cincinnatian "series" (Upper Ordovician of Ohio, Kentucky, and Indiana, USA), collecting 100% of body fossils would present enormous logistical and time-related challenges in the field-collection phase, as well as accessioning and storage challenges in museum repositories, where space for collections is commonly at a premium.

Consider stratigraphic units that are rich in arthropod sclerites, of which there are many in the Phanerozoic (e.g., Clarke and Ruedemann, 1912; Eldredge, 1972; Brandt Velbel, 1985; Whiteley et al., 2002; Hunda et al., 2006; Brett et al., 2012; Bonino and Kier, 2024). Specimens in these deposits are commonly separated, and often broken, sclerites (Figs. 3.2, 4.2). Fully articulated exoskeletons are much less common, but even when present they often show some displacement of sclerites (Fig. 2.3–2.5). These sites provide valuable paleobiological or taphonomic information that often is exploited only in part. In particular, such sites may convey useful

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information bearing on questions of predation and scavenging, molting, and non-biologically induced physical breakage (e.g., Brandt, 1993; Pratt, 1998; Babcock, 2003; McCoy and Brandt, 2009; Bicknell et al., 2019a, 2022a, b). Anecdotally, it is my experience that trilobite remains, especially separated sclerites such as thoracic segments, librigenae, hypostomes, and rostral plates, are collected and/or recognized in numbers well below their true abundance, especially in trilobite-rich Cambrian, Ordovician, and Devonian strata. For example, commercial and other heavily collected trilobite quarries in the Cambrian of the Great Basin (see Robison et al., 2015; Bonino and Kier, 2024) are commonly littered with separated trilobite sclerites rejected by collectors. In addition, trilobite grainstones or "coquinas" (e.g., Babcock, 1994; Terfelt, 2003; Babcock et al., 2007, 2015; Calner et al., 2013) are rarely collected intensively except for faunal documentation.

To provide the most complete understanding of arthropod biodiversity through time, and abundance in individual ecosystems, documentation is necessary. Even incomplete materials that cannot be easily assigned to taxa initially, should be documented, because they may provide clues to the identities of other fragments that emerge upon further work. Sometimes rare taxa are documented in preference to the more common taxa, which can lead to a distorted impression of taxic abundance at a site. It is just as important to collect and document the common taxa as the less-common taxa.

Examples of arthropod-rich marine Lagerstätten

Marine stratigraphic units that are rich in paleontological information about arthropods can be classified genetically as either conservation deposits (Konservat-Lagerstätten) or concentration deposits (Konzentrat-Lagerstätten) according to the Seilacher et al. (1985) definitions, although some occurrences incorporate aspects of both categories. Strict application of these original models can result in overlooking important aspects of taphonomic history. As a result, it may be useful to consider types of stratigraphic, sedimentologic, or taphonomic occurrences of fossils, which allows the recombining of information from the original genetic models in novel ways, leading to new interpretations of fossilization history (compare Brett et al., 1997). It is important to recognize, as Vrazo et al. (2017) have emphasized, that successful preservation of remains in Lagerstätten involves the interplay of a variety of ecological and sedimentary factors, including sequence-stratigraphic history and basin-specific geochemistry (e.g., Gaines et al., 2012). These constraints are largely implied in the following discussion.

Do the Seilacher concepts of conservation deposits (Konservat-Lagerstätten) and concentration deposits (Konzentrat-Lagerstätten), together with their subcategories, still have relevance? Should they be considered as end-member conditions of preservation, or should the concepts be supplanted? A practical interim approach would be to retain terms such as Konservat-Lagerstätten and Konzentrat-Lagerstätten but explore further what factors enter into the development of taphonomic associations, and perhaps ultimately modify how we conceptualize their origins.

An overview of the marine arthropod fossil record leads to recognition of at least four types of taphonomic associations that appear repeatedly through the Phanerozoic Eonothem: (1) concretions (Fig. 1); (2) cluster associations (Figs. 2, 3.2, 3.3, 4.2, 5.2, 5.3); (3) event beds (Figs. 2, 3.2, 4, 5.2?, 5.3?); and (4) microbially sealed layers (Figs. 4.1, 4.2?, 5). Each of these associations yields either exceptionally preserved fossils, or large numbers of remains. These associations are not necessarily discrete categories because multiple factors may be involved in their genesis. In this section some common examples of arthropod occurrences are discussed using a highly abbreviated set of examples (Figs. 1–5). Many occurrences of rare arthropod remains, even where those sites yield rich or important information about arthropods, are not considered here.

Concretions. One of the most common sources of well-preserved marine arthropods is in concretions (e.g., Branisa, 1965; Müller, 1979, 1983; Feldmann and McPherson, 1980; Feldmann and McKenzie, 1981; Feldmann and Zinsmeister, 1984; Feldmann, 1985, 1988, 1990, 1992a, b; Müller and Walossek, 1985, 1987; Weidner and Feldmann, 1985; Bishop, 1986; Tucker et al., 1987; Feldmann and Wilson, 1988; Tshudy and Feldmann, 1988; Feldmann et al., 1993, 2003; Hannibal et al., 1993; Walossek and Müller, 1997; Bishop et al., 1998; Schweitzer and Feldmann, 2000a, b; Crawford et al., 2006; Schwimmer and Montante, 2007; Feldmann et al., 2012; Cotroneo et al., 2016; Tashman et al., 2019; Bicknell et al., 2021; Fig. 1). Concretions have varied compositions, among them are calcareous concretions (especially calcite, siderite, or ankerite, e.g., Fig. 1.2, 1.3, 1.5, 1.6), siliceous concretions (often quartz, or quartz sand combined with other minerals such as glauconite; Fig. 1.1, 1.4), phosphatic (e.g., francolite) concretions, and iron sulfide (pyrite or marcasite) concretions. Feldmann et al. (2012) noted, from concretions in the Bearpaw Shale (Cretaceous) of Montana, that concretions often contain more than one mineral, the result of multiple steps in concretion formation. In that specific example, framboidal pyrite, probably resulting from mineralization of a microbial sheath surrounding lobster cuticle, was present, in addition to francolite, which replaced the lobster cuticle. Most of the concretionary mass, however, was composed of calcium carbonate.

Originally, Seilacher at al. (1985, p. 19) referred to concretions as "a subset of stagnation (and obrution?) deposits," a form of conservation deposit, and some may have such an origin. However, a range of biological and biostratinomic circumstances may result in concretion development. Dhami et al. (2023) reviewed recent literature pertaining to the compositions of fossil-bearing concretions and factors involved in their formation, including microbial mediation and geochemical pathways. As for the origin of the specimens illustrated here (Fig. 1), obrution and biofilm-mediated early mineralization are likely, but compelling evidence for stagnation is lacking. Some concretions may qualify, in part, as skeletal concentration deposits, owing in part to event deposition followed by early diagenesis (Brett et al., 1997, 2012).

One unifying characteristic of concretions is the tendency for their stratigraphic occurrence to be along horizons that have wide lateral extent (e.g., Babcock and Speyer, 1987; Hellstrom and Babcock, 2000; Whiteley et al., 2002), indicating an origin with physical events, coupled with biological processes of decay and microorganism-mediated mineralization in sediment where porewater conditions or chemical microenvironments within biofilm "decay halos" took place (e.g., Allison and Briggs, 1991b; Borkow and Babcock, 2003; Briggs, 2003a; Babcock et al., 2015; Cotroneo et al., 2016). Obrution, condensation plus obrution, and perhaps anoxia, in addition to biological factors, played central roles in the development of certain concretion beds that are rich in marine arthropod remains. Some carbonate concretions evidently developed in places, or during times, of siliciclastic sediment starvation (e.g., Babcock et al., 2015).

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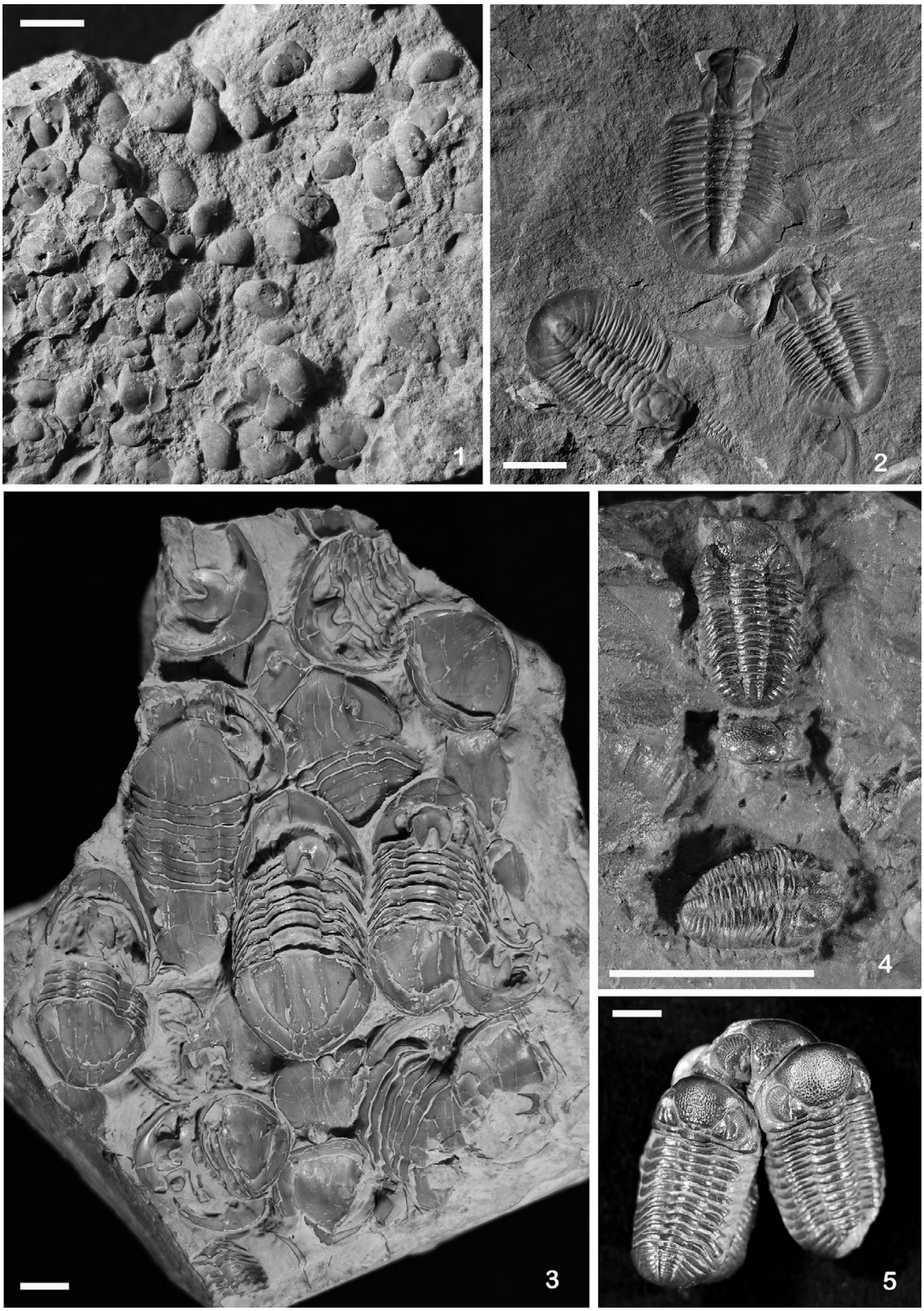


Figure 2. Cluster associations of ostracodes (**1**) and trilobites (**2–5**), all inferred to be molted exoskeletons of adults. (**1**) *Leperditia angulifera* Whitfield, 1882, from the Greenfield Dolomite (Silurian), Greenfield, Highland, County, Ohio; OSU 3502. (**2**) *Athabaskia wasatchensis* (Resser, 1939), three molts lacking the librigenae, and separated exoskeletal elements including librigenae (one with hypostome attached); from the Spence Shale (Cambrian), Wellsville Mountain, Utah; OSU 55242. (**3**) *Homotelus bromidensis* (Esker, 1964), outstretched and loosely folded exoskeletons showing roughly bidirectional alignment; the cephala are displaced in most specimens, suggesting they are molts; from the Pooleville Member of the Bromide Formation (Ordovician), Criner Hills, Carter County, Oklahoma (previously illustrated by Laudon, 1939); OSU 47616. (**4**) *Eldredgeops rana* (Green, 1832), outstretched exoskeletons and separated sclerites; cephalon of specimen near bottom of photograph is displaced, suggesting that it is a molt; from a calcareous distal tempestite bed, one of "Grabau's trilobite beds," lower Wanakah Shale Member of the Ludlowville Formation, South Branch of Smoke Creek, Windom, Erie County, New York; OSU 55243. (**5**) *Eldredgeops milleri* (Stewart, 1927), three outstretched, overlapping exoskeletons, two of which have displaced cephala suggesting they are molts; from the Silica Shale (Devonian), Silica, Lucas County, Ohio; OSU 17673. Scale bars = 10 mm.

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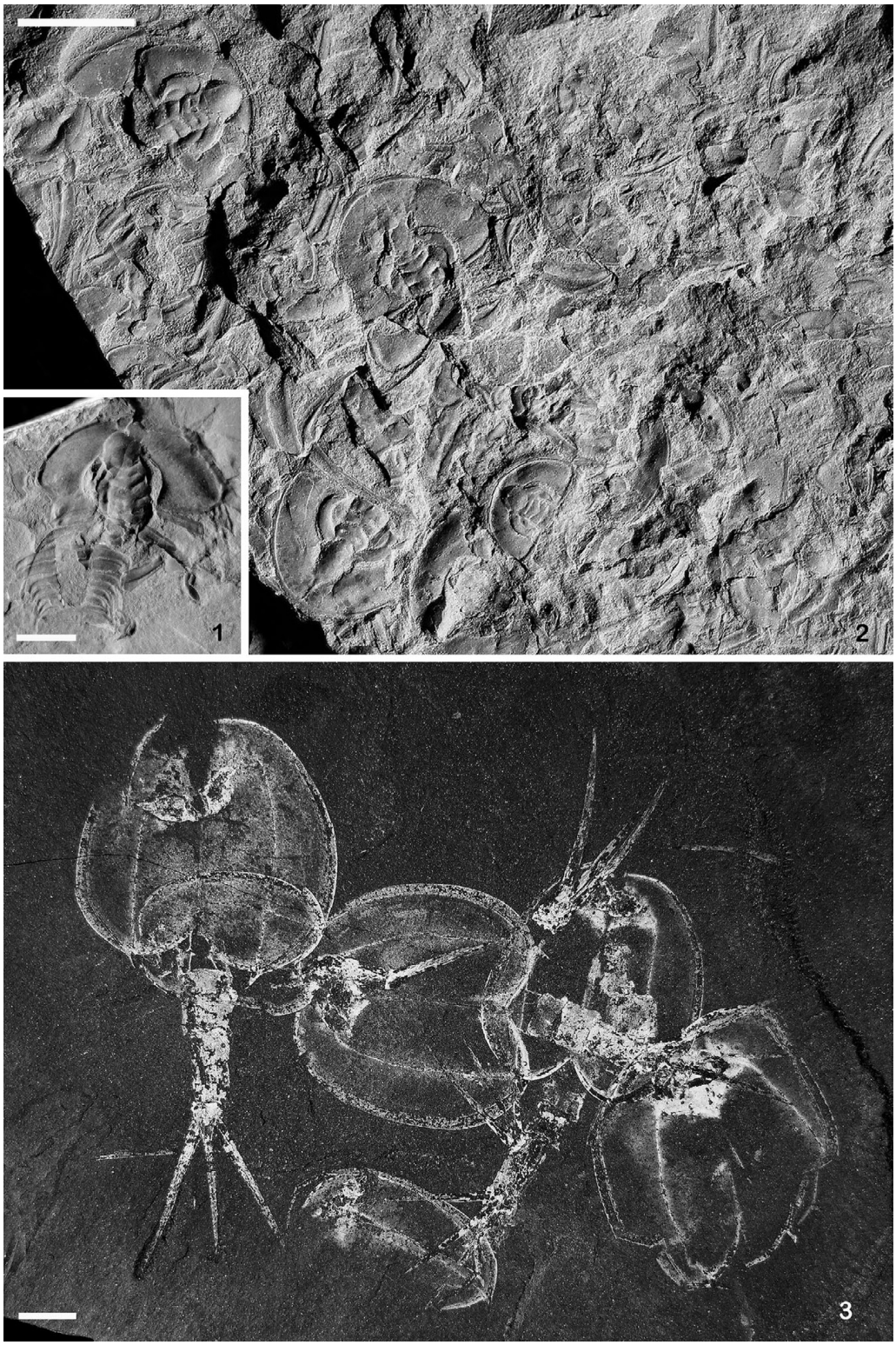


Figure 3. Trilobites (**1, 2**) and phyllocarid crustaceans (**3**) in various states of disarticulation. (**1**) *Olenellus clarki* (Resser, 1928) showing healed, sublethal injury to the left genal angle, and partly disarticulated exoskeleton with displaced and broken sclerites, inferred to be the result of scavenging; from the Latham Shale (Cambrian) of the Marble Mountains, San Bernardino County, California; OSU 55244. (**2**) Olenelline trilobites, including *Olenellus gilberti* (Meek in White, 1874) and *Olenellus chiefensis* Palmer, 1998, mass accumulation of separated sclerites, many of them broken, perhaps through predation or scavenging, and deposited in an inferred tempestite layer; from the Pioche Shale (Cambrian), Ruin Wash, Nevada; OSU 55245. (**3**) *Dithyrocaris* sp., accumulation of exoskeletons, some with mandibles in place, and disarticulated sclerites; from the Breathitt Formation (Carboniferous), Kentucky Highway 546, Greenup County, Kentucky; OSU 55246. Scale bars = 10 mm.

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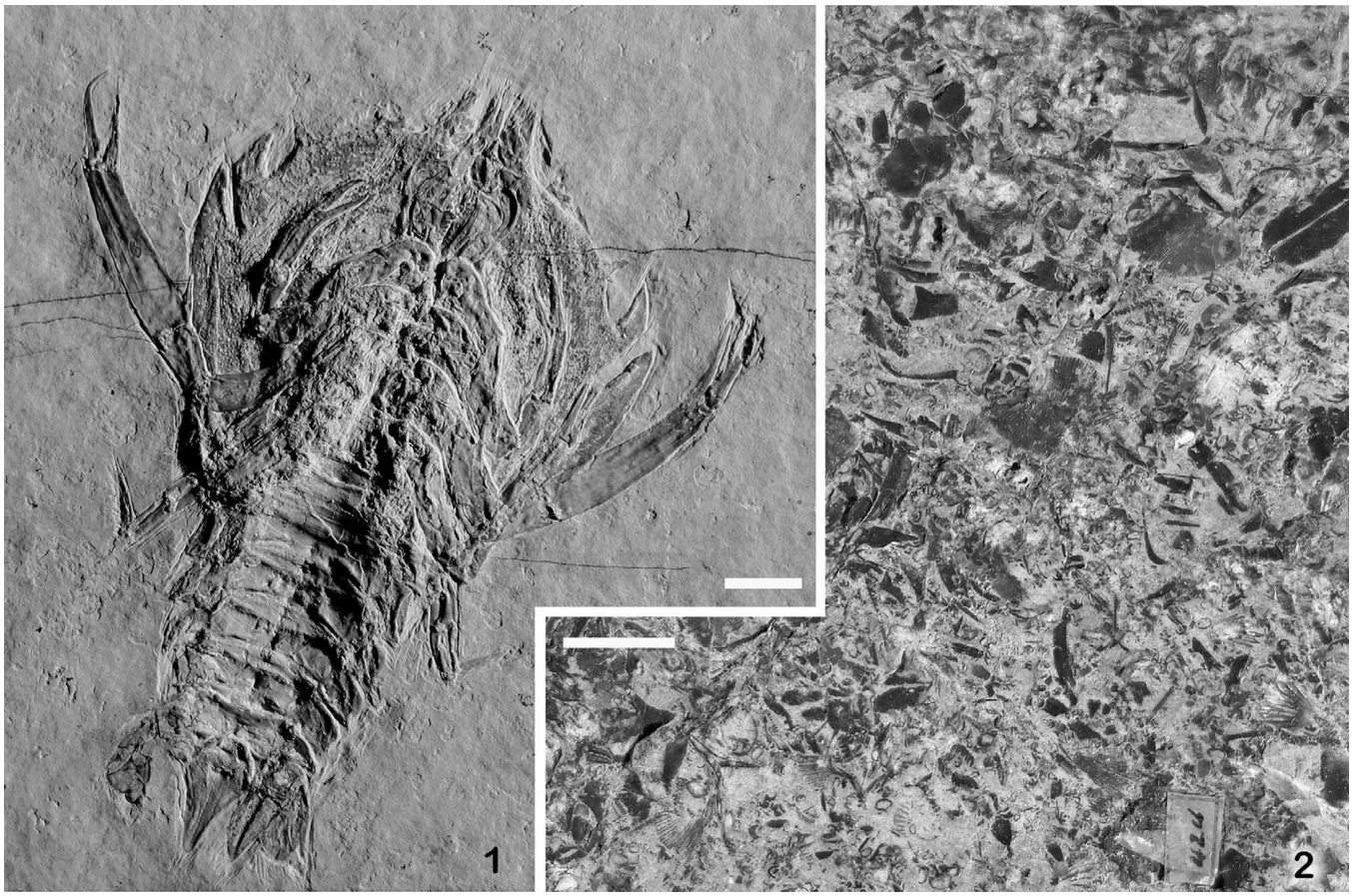


Figure 4. Arthropods preserved through an inferred combination of episodic burial and microbial sealing or stabilization of sediment. (**1**) *Cycleryon propinquus* (Schlotheim, 1822), a decapod crustacean, from the Solnhofen Limestone (Jurassic), Bavaria, Germany; OSU 19804. (**2**) Upper surface of limestone tempestite bed showing numerous disarticulated trilobite and ostracode sclerites, and hard parts of brachiopods, echinoderms, tentaculitids, and other marine organisms; many of the trilobite sclerites are broken, perhaps through predation, and include *Calymene niagarensis* Hall, 1843, and *Trimerus delphinocephalus* Green, 1832; the ostracodes are *Bollia symmetrica* Hall, 1852; from the Rochester Shale (Silurian), Lockport, Niagara County, New York; OSU 12732. Scale bars = 10 mm.

Certain concretionary horizons rich in enrolled trilobite remains have been ascribed a relationship to storm events. In an example from the Alden Pyrite Bed in the Ledyard Shale Member of the Ludlowville Formation (Devonian) of New York, Babcock and Speyer (1987) inferred that phacopine trilobites became buried in sediment, enrolled, as advancing storm conditions stirred up sediment. Burial in anoxic muds and failure to emerge from the bottom-smothering sediment following the storm resulted in the trilobites succumbing in their enrolled postures. Concretion growth followed shortly thereafter. This obrution model can be invoked for other instances of beds rich in enrolled trilobite corpses, including ones known from the Cambrian of Missouri (Stitt, 1983), the Ordovician of southwest Ohio and adjacent Kentucky and Indiana (Osgood, 1970; Brandt Velbel, 1985; Hunda et al., 2006; Brett et al., 2012), the Devonian of Ohio, Michigan, and Indiana (Stewart, 1927; Kesling and Chilman, 1975), and the Permian of Kansas (Whittington, 1992).

Apart from the examples from the Alden Pyrite Bed, these occurrences of enrolled trilobites from the United States have not been commonly considered as concretions, but indeed they seem to be, because the fossils are preserved in rounded masses of, or containing, mineralized material, and their origins appear to be related to microorganism–sediment interactions. There are varied ways enrolled trilobites have been preserved, however. In the Alden Pyrite Bed, the trilobites are fully to partly pyritized except for the calcite-reinforced exoskeleton. In the Silica Shale (Devonian, e.g., Stewart, 1927; Kesling and Chilman, 1975) and the Cincinnatian "series" (Ordovician, e.g., Brandt Velbel, 1985; Babcock, 1996; Hunda et al., 2006), pyrite accompanies mud-size carbonate and occasionally carbonate spar. Pyrite is present is much greater quantity within the "capsules" formed by the Silica Shale trilobites than in the Cincinnatian trilobites, where it preserves appendages and internal soft tissues (Vayda and Babcock, 2022). Preservation of non-biomineralized anatomy of trilobites is rare in outstretched trilobites from these two deposits. In both the Missouri (Cambrian) and Kansas (Permian) examples, preservation is almost exclusively in mud-sized sediment, now calcite.

Another important instance of trilobite preservation in concretions is the layers of outstretched trilobites in the Wheeler and Marjum formations (Cambrian) of Utah (Bright, 1959; Gaines and Droser, 2003; Robison and Babcock, 2011; Robison et al., 2015). Both corpses and molts are preserved in the concretions, with cone-in-cone development extending stratigraphically downward (Gaines and Droser, 2003; Robison and Babcock, 2011). Babcock et al. (2015) remarked that cone-in-cone development is commonly associated with anoxic or dysoxic conditions, and Gaines and Droser (2003) inferred that the *Elrathia*-rich beds of the Wheeler Formation represented sedimentation in the exaerobic zone during

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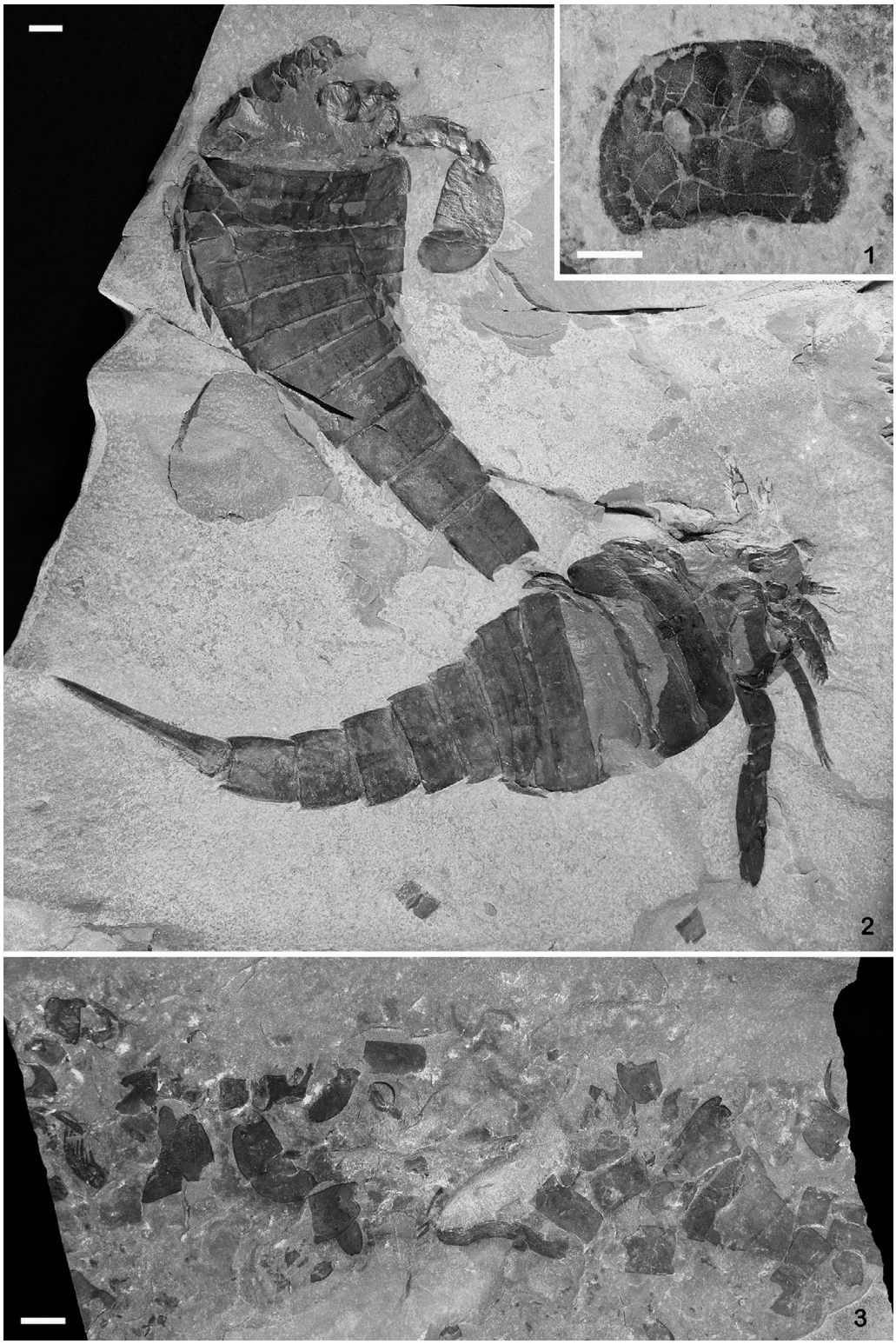


Figure 5. Eurypterids from plattenkalk deposits inferred to have been preserved through microbial sealing. (**1**) *Eriopterus eriensis* (Whitfield, 1882), prosoma retaining moderate relief and showing cracks perhaps related to desiccation after microbial sealing in sediment, followed by compaction; from the Bass Islands Group (Silurian), Huntsville, Logan County, Ohio; OSU 49974. (**2**) *Eurypterus lacustris* Harlan, 1834, two partly disarticulated exoskeletons, in dorsal view (upper left) and ventral view (lower), inferred to have been washed into final resting place and stabilized in sediment through microbial covering; from the Williamsville Formation of the Bertie Group (Silurian), Buffalo area, Erie County, New York; OSU 55247. (**3**) Eurypterid exoskeletal fragments, mostly *Eurypterus remipes* DeKay, 1825, inferred to have been broken through predation, scavenging, and possibly physical processes, then deposited along a strandline or wind row and stabilized in sediment through microbial action; from the Fiddler's Green Formation of the Bertie Group (Silurian), Ilion, Herkimer County, New York; OSU 55248. Scale bars = 10 mm.

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the Cambrian. Preservation of appendages and internal soft tissues is common in the concretions from the Wheeler and Marjum formations (Fig. 1.6).

In another example of concretionary development, Babcock et al. (2015) noted that large "orsten"-type concretions in the Cambrian of Scandinavia and China may have a relationship to eustatic sea level, coinciding with transgressive systems or maximum flooding, and siliciclastic sediment starvation in basinal areas. "Orsten"-type carbonate concretions have produced exquisitely preserved, small arthropods that sometimes retain appendages and soft, non-biomineralized tissues (e.g., Müller, 1979, 1983; Müller and Walossek, 1985, 1987; Walossek and Müller, 1997, 1998; Babcock et al., 2005).

Arthropods and many other organisms have been documented from sideritic Mazon Creek-type concretions of North America and Europe (e.g., Meek and Worthen, 1865, 1866; Lesquereux, 1866; Johnson and Richardson, 1966; Nitecki, 1979; Baird et al., 1985a, b, 1986; Brett et al., 1997; Cotroneo et al., 2016; Bicknell et al., 2021; Fig. 1.2). Most of these concretions formed in marginal-marine to shallow-marine, siliciclastic-dominated deltaic paleoenvironments. The concretions preserve a combination of marine, nonmarine aqueous, and terrestrial biota. Together, these concretions probably result from a variety of biologic factors and incorporate aspects of both concentration and conservation models. Cotroneo et al. (2016) introduced a model for the formation of the sideritic Mazon Creek concretions, involving encasement of decaying organic remains by early diagenetic pyrite and siderite, which was mediated by sulfate-reducing bacteria. High-porosity proto-concretions were cemented prior to compaction by siderite resulting from the methanogenic production of bicarbonate. Proto-concretion formation must have occurred on the order of days after settling of organic remains on the sediment surface, because details of the soft anatomy of arthropods and other organisms are commonly preserved (e.g., Nitecki, 1979; Baird et al., 1986; Bicknell et al., 2021).

In numerous Mesozoic and Cenozoic examples, arthropods, and especially decapods, are common in concretions (e.g., Feldmann and McPherson, 1980; Feldmann and Zinsmeister, 1984; Feldmann, 1985; Bishop, 1986; Tucker et al., 1987; Feldmann and Wilson, 1988; Tshudy and Feldmann, 1988; Feldmann et al., 1993, 2003, 2012; Bishop et al., 1998; Schweitzer and Feldmann, 2000a, b; Crawford et al., 2006; Babcock et al., 2024). Many of these occurrences are inferred molt ensembles or incomplete exoskeletons (Fig. 1.1, 1.4, 1.5), although some corpses are undoubtedly represented. Among many excellent examples, the Cretaceous–Paleogene and Eocene deposits of Seymour Island, Antarctica, are particularly noteworthy (Feldmann and Zinsmeister, 1984; Feldmann, 1985, 1988; Feldmann and Wilson, 1988; Feldmann et al., 2003; Babcock et al., 2024). Here, mostly large adult decapods are preserved in dense, siliceous and glauconitic concretions from shallow siliciclastic marine environments. Most remains appear to be molted exoskeletons in various states of completeness, from fully intact to separated sclerites. Some lobsters have been preserved as molt ensembles in "Salterian" position, suggesting that concretionary growth was rapid following the time of molting (Feldmann et al., 1993; Babcock et al., 2024; Fig. 1.4).

Growth of concretions, at least initially, has been demonstrated experimentally to be related to the rapid development of a microbial biofilm or microbial sheath (a so-called "decay halo") surrounding recently dead or shed organic remains (Borkow and Babcock, 2003; Briggs, 2003a, b). The decay halo, in studied examples, comprises a network of intertwined fungal hyphae that form a three-dimensional, rounded envelope around decaying matter. Bacterial cells associated with this consortium can include inferred autolithifiers (Borkow and Babcock, 2003; see also Feldmann et al., 2012) that mediate the early stages of lithification in the decay halo, ultimately resulting in early diagenesis of a concretion. Experiments on the timing of arthropod decay and disarticulation (e.g., Plotnick, 1986; Briggs and Kear, 1993; Babcock and Chang, 1997; Babcock et al., 2000, 2005; Borkow and Babcock, 2003; Briggs, 2003b) indicate that, for soft tissues to be preserved, mineral replication (for example, precipitation of a thin layer of mineral over soft tissue) must take place within about 7–10 days of death (Babcock et al., 2000, 2005). Disarticulation along arthrodial membranes is a longer process but normally completes in about 30–40 days. The implication is that arthropods preserved with soft tissues, such as internal organs, muscles, or some connective tissues intact, were, in many instances, corpses that were quickly preserved by taphonomic processes including mineral replication and perhaps early burial, sediment sealing, or even microbial sealing. Articulated exoskeletons lacking these true soft tissues, in many instances, probably represent molts or corpses that remained at or near the sediment–water interface that underwent decay for up to several weeks.

Clusters. Clustered associations of trilobite remains have been well documented (e.g., Laudon, 1939; Esker, 1964; Ludvigsen, 1979; Speyer and Brett, 1985; Speyer, 1990; Whittington, 1992; Levi-Setti, 1993; Karim and Westrop, 2002; Whiteley et al., 2002; Babcock, 2003; Robison and Babcock, 2011; Brett et al., 2012; Robison et al., 2015; Corrales-García et al., 2020; Secher, 2022; Bonino and Kier, 2024; Randolfe and Gass, 2024; Figs. 2.2–2.5, 3.2, 4.2). Most such occurrences are dominated by exoskeletons within narrow size classes, inferred to have been molted (for recognition criteria, see Henningsmoen, 1975; McNamara and Rudkin, 1984; Speyer, 1985; Brandt, 1993; Babcock, 2003; Brett et al., 2012). In most examples, the trilobites are outstretched and, with rare exception (Corrales-García et al., 2020), are adult (holaspid) exoskeletons (e.g., Speyer and Brett, 1985; Speyer, 1990; Karim and Westrop, 2002; Babcock, 2003; Brett et al., 2012). Clusters may consist of complete exoskeletons or incomplete ones (lacking, for example, the librigenae).

Horizons yielding clusters of trilobites commonly have wide aerial extents, indicating an origin with physical events, coupled with biological processes of decay and microorganism-mediated mineralization (Brett et al., 2012). In some classic examples, such as in the Hamilton Group (Devonian) of New York (Speyer and Brett, 1985; Brett et al., 2012), and the "butter beds" of the Arnheim Formation (Ordovician) of Ohio, Kentucky, and Indiana (e.g., Osgood, 1970; Brandt Velbel, 1985; Babcock, 1996; Hunda et al., 2006; Brett et al., 2012), the occurrence of large numbers of outstretched trilobites in single sedimentary beds has been attributed to obrution (sediment smothering) on storm-prone shallow marine shelves (Speyer and Brett, 1985; Babcock, 1996; Whiteley et al., 2002; Brett et al., 2012). In some instances, biological activity, such as synchronized mass molting, likely preceded the accumulation of molts, which was then followed by obrution and diagenesis (Speyer and Brett, 1985; Karim and Westrop, 2002; Babcock, 2003; Gutiérrez-Marco et al., 2009; Robison and Babcock, 2011; Brett et al., 2012; Corrales-García et al., 2020). Biological mediators and anoxia may have also played roles in the taphonomic history of clusters.

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Most cluster associations probably qualify as short-term condensation (concentration) deposits, perhaps on the order of hours to days to weeks. Others, especially where separated and time-averaged suites of sclerites are present (Figs. 3.2, 4.2), likely reflect longer time intervals, perhaps through years in duration. Where non-biomineralized parts are preserved in specimens buried soon after death, such as in pyritized trilobites from the Ordovician of New York (Brett et al., 2012), they also may qualify as conservation deposits.

Trilobite cluster associations could have been the result of animal behavior, current activity, sediment smothering, and potentially other factors. Cluster associations were among the earliest taphonomic associations to be discussed for fossil arthropods: clusters of trilobites in discrete, fine-grained limestone layers in the lower Wanakah Shale (Devonian) of western New York came to be known as "Grabau's trilobite beds" (Whiteley et al., 2002), following their documentation in the late nineteenth century by Grabau (1899). Most occurrences of trilobite clusters in "Grabau's trilobite beds" and elsewhere in the Hamilton Group (Devonian) of New York, are either monospecific or disproportionately dominated by one species (Speyer and Brett, 1985; Fig. 2.4). Speyer and Brett (1985) attributed this pattern to the aggregation of animals at the time of mating, during which time older exoskeletons were cast off and abandoned. Shortly afterward, the abandoned molts were buried under a cloud of sediment introduced by storm activity (obrution). Karim and Westrop (2002) reached a similar conclusion for Ordovician trilobites from Oklahoma that are preserved in large clusters. Gutiérrez-Marco et al. (2009) documented large clusters of Ordovician trilobites from Portugal and suggested this gregarious behavior offered temporary refuge from predators and represented synchronous molting and reproduction. In contrast, Corrales-García et al. (2020) documented clusters of trilobites from the Cambrian of South China that exhibited gregarious activity attributed to the need for protection during synchronized molting, which was unrelated to reproductive behavior.

Robison and Babcock (2011) documented non-random orientations in trilobite clusters from the Cambrian of Utah that suggest bidirectional or multidirectional current redistribution prior to sediment covering. This tends to support the inference that the remains were molted, although the possibility that some corpses were present cannot be ruled out entirely. These exoskeletal remains may have accumulated at the sediment–water interface over a period of days to a few weeks prior to rapid, event-related sediment covering. Remains could have been initially scattered over a rather broad area and concentrated to some extent by current activity prior to burial.

Some clustered associations of arthropods can be reasonably attributed to events involving mass mortality. Robison et al. (2015) illustrated a cluster of Cambrian trilobites from Utah with opisthoparian facial sutures and retaining their librigenae in place, indicating a mass mortality rather than an accumulation of molts. Similarly, Crawford et al. (2008) documented a mass mortality of decapod crustaceans from the Miocene of Argentina, citing Andean volcanism as a factor in the mortality and burial event.

Clusters of non-trilobite arthropods in marine or other aquatic settings have received less attention. Obrution can be invoked as a major factor in their occurrence, but prior concentration of remains through current activity and/or biologic activity is likely in various instances. Layers in Paleozoic carbonates that are unusually rich in monospecific assemblages of ostracodes may be explained as coterie assemblages of crustaceans that gathered in mass aggregations for mating, events that were accompanied by synchronized molting. Alternatively, these could represent mass mortality events. One such layer, from the Greenfield Dolomite (Silurian) of Ohio is illustrated here (Fig. 2.1). The exoskeletons may have been concentrated by currents. Afterward, rapid sedimentary influx, perhaps by storm suspension and smothering, led to sedimentary sealing and, ultimately, preservation.

Similar to mass accumulations of trilobites and ostracodes reviewed above, Vrazo and Braddy (2011) ascribed some accumulations of eurypterid remains to mass molting and mating events, followed by burial of the molted exoskeletons. Vrazo et al. (2017) placed these associations in a broader ecological–sedimentary context, interpreting the mass fossilization of eurypterids in Silurian and Devonian deposits of the Appalachian Basin to be a result of the interplay of several factors, including habitat preference, burial by storms or microbialite sediment baffling, and sequence-stratigraphic history. Vrazo et al. (2017) interpreted the eurypterids as preferentially inhabiting nearshore marine ecosystems following freshening of water during times of transgression. After burial of molted exoskeletons, long-term preservation of remains was facilitated by regression and cyclical shallowing-upward deposition that promoted hypersalinity and anoxia.

Bicknell et al. (2019b) documented a cluster of the belinurid xiphosuran *Euproops* from the Carboniferous of England, inferring that they exhibited mass mating behavior. They speculated that this gregarious behavior may have helped decrease the effect of predation, increased genetic diversity, or both.

Another example of arthropod clusters is illustrated by phyllocarid remains from a cannel-coal-type bed, described as a marine horizon (Bennington, 1992) in the Breathitt Formation (Carboniferous) of Kentucky. One slab (Fig. 3.3) illustrates outstretched exoskeletons in various states of completeness with a nearly orthogonal arrangement of their long axes. The valves of the carapace are opened in a "butterflied" pattern and internal non-biomineralized parts are not preserved. The mandibles are in place in some specimens. This concentration of exoskeletons, which are probably molts, is inferred to have been influenced by currents. Burial leading to preservation may have been storm related, although their introduction to a dysoxic or anoxic channelform deposit in a transitional marine–nonmarine environmental setting indicates that low oxygen conditions played a significant role in their preservation. Naimark et al. (2018) documented the role of clay minerals, especially kaolinite, in facilitating preservation of arthropod remains in sediments. It is likely that clay minerals present in the cannel coal also played an important role in preservation of these phyllocarids.

Event beds. Tempestites, or storm deposits, sediment–gravity flow deposits, and ash beds resulting in rapid burial of remains, and sediment sealing are important sources of arthropod fossils (Taylor, 1976; Speyer and Brett, 1985; Babcock, 1994; Robison, 1994; Brett et al., 1997, 2012; Peng et al., 2004a, b; Albani et al., 2024). Event-bed deposition was discussed in part in connection with both concretionary horizons and cluster associations (above). Beds enriched in fossils can accumulate over temporal scales ranging from geologically "instantaneous" to thousands of years (Kidwell and Jablonski, 1983; Kidwell, 1991; Kidwell and Bosence, 1991). Those containing arthropod remains, however, tend to represent shorter time spans. They are primarily event-bed concentrations, but occasionally composite concentrations, in the terminology of Kidwell (1991). Brett et al. (1997) recognized that short-term events can incorporate live burial of organisms (mass mortality events), or

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passive burial of separated body parts (skeletal concentrations). Skeletal concentrations can be either parautochthonous or allochthonous.

Current-related transportation, stunning or killing of live animals, and obrution have been invoked for some deposits such as the Burgess Shale (Conway Morris, 1985, 1998), where animals may have been transported from shallow shelf areas into deeper anoxic water and buried. Such transport by means of turbidites or other forms of sediment-gravity flow, would have resulted in an aggregation of both corpses and molts that had concentrated near the sediment–water interface.

Some of the richest sources of Cambrian trilobites, mostly disarticulated sclerites, are from sediment-gravity deposits on distal to marine carbonate shelves to slopes. The Henson Gletscher Formation of North Greenland (Babcock, 1994; Robison, 1994) and the Huaqiao Formation of South China (Peng et al., 2004a, b) both show concentrations of remains, high in abundance and species richness, in carbonate-hosted, gravity-flow deposits. Separated sclerites that are transported and buried in sediment-gravity flows are sometimes more numerous towards the upper portions of flow beds. In these instances, relatively light sclerites, easily suspended in a water-charged turbid flow of sediment, evidently settled out of suspension as part of the relatively light fraction of particles. This pattern contrasts with winnowed shell-bed-type concentrations, where less grading of particles may have occurred.

On stormy marine shelves, clouds of suspended sediment are inferred to have buried organismal remains present at the sediment surface, sealing them in sediment, and leading to their preservation near the bases of tempestite beds (Speyer and Brett, 1985). Alternatively, storm-related currents may have picked up, winnowed (washed) or concentrated remains, and redeposited the parautochthonous remains some distance from their prior resting sites. Thin limestone beds rich in disarticulated and often broken trilobite sclerites plus other fossils are a persistent feature of such deposits as the Rochester Shale (Silurian) of New York and Ontario, and the Cincinnatian "series" (Ordovician) of Ohio, Kentucky, and Indiana. These tempestite beds may be rich in arthropod remains but for the most part remain understudied for their taphonomic and paleobiologic potential (see Miller, 1997). Whereas broken trilobite sclerites in such deposits could be assumed to be related to physical transport, it is at least equally likely that they were broken through the action of predators (see Pratt, 1998; Babcock, 2003). If so, remains preserved in tempestites could offer interesting insights into predator–prey relationships.

Albani et al. (2024) documented Cambrian trilobites that were entombed in volcanic ash from Morocco. Extraordinarily well-preserved specimens from this deposit have yielded remarkable details about their non-biomineralized anatomy and its relationship to biomineralized morphology.

In the context of event deposition, a noteworthy trace-fossil-rich Lagerstätte pertains in part to the fossil record of arthropods. Tempestite beds, cemented with carbonate (commonly siderite) in the Chagrin Shale Member of the Ohio Shale (Devonian) of Ohio, yield a rich and diverse trace fossil assemblage (Hannibal and Feldmann, 1983; Stukel, 1987; Hannibal, 1996). Some of these traces, *Chagrinichnites*, record the burial of phyllocarid crustaceans under a rapidly deposited sediment layer, followed by the animals burrowing through the sediment layer, emerging from the surface (Feldmann et al., 1978; Hannibal and Feldmann, 1983). This example of live arthropods extricating themselves from under rapidly deposited sediment serves as a model for other marine arthropods that had the capacity for burrowing in sediment. Many other arthropods, such as trilobites, if they were live animals at the time of burial, were probably able to escape to safety. This was not necessarily true for trilobites enrolled below the sediment surface under inhospitable conditions, however.

Microbial sealing. In certain fine-grained carbonate (limestone or dolostone) deposits, arthropod and other remains have been preserved through a combination of factors that include microbial sealing (Barthel et al., 1990; Allison and Briggs, 1991b; Vrazo et al., 2016). Such deposits commonly are described as lithographic-type carbonates (Barthel et al., 1990; Wendruff et al., 2020). Seilacher et al. (1985) referred to exceptional preservation in the Solnhofen Limestone (Jurassic) of Germany, a true lithographic limestone, as deposition that took place under obrutionary stagnation conditions, citing a depauperate benthos, few sediment-penetrative traces, and features consistent with cyanobacterial mats such as thin laminations, near-lack of erosion, rip-ups, and ruffling of sediment surfaces.

Wendruff et al. (2020) attributed exceptional preservation in the lithographic dolostone of the Waukesha Lagerstätte (Silurian of Wisconsin; Mikulic et al., 1985a, b), to "microbial entombment." As described by Wendruff et al. (2020), microbial entombment is a microorganism-mediated sedimentary and early diagenetic process, incorporating elements of microbial sealing, microbially mediated mineral precipitation (sometimes accompanied by carbonate dissolution), and physical sediment accumulation within a microbial mat. The Waukesha Lagerstätte shows exceptional preservation of arthropod cuticle, characteristic of a conservation deposit, but the most common remains, trilobite exoskeletons in disarticulated or complete but outstretched condition (Wendruff et al., 2020; Randolfe and Gass, 2024), imply a concentration of these remains at the sediment surface. Dissolution of carbonate from skeletal materials, including trilobite exoskeletons, can be attributed to geochemical conditions within microbial mats (Wendruff et al., 2020). Because the trilobites retain moderate but not original convexity, and lack exoskeletal fracturing, their remains must have become stuck on mat surfaces, covered rapidly by cyanobacteria and perhaps other microbes, then endured loss of carbonate.

The celebrated eurypterid-rich layers of the Bertie Group, a Silurian lithographic-type dolostone cropping out in New York and Ontario (Clarke and Ruedemann, 1912; Kluessendorf, 1994; Tetlie et al., 2007; Vrazo and Braddy, 2011; Vrazo et al., 2016, 2017), and the Eramosa Formation (Silurian of Ontario; von Bitter et al., 2007), another fine-grained dolostone, both show features broadly similar to those reported from the Waukesha Lagerstätte (Wendruff et al., 2020) (see also Vrazo et al., 2017, and discussion above in the section titled "Clusters"), therefore it can be inferred that similar preservational circumstances (conservation and concentration) prevailed. In these microbial-sealing associations, a combination of sedimentary and microbially mediated processes led to fossilization of accumulated or freshly dead organic remains, molted exoskeletons, and traces.

Final thoughts: refining conceptual models of Lagerstätten and the temporal distribution of marine Lagerstätten

Seilacher (1970), when introducing the concept of Fossil-Lagerstätten, offered hope that the classification would be improved upon and refined as new information became available. A number of

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authors have contributed to improving, expanding, or refining the concept, as summarized by Kimmig and Schiffbauer (2024), who also provided a good, multifaceted, and utilitarian means of recognizing Konservat-Lagerstätten. Conservation deposits have received an outsized amount of attention, because they have yielded a wealth of paleobiological data, not just about arthropods, but about a broad range of organisms preserved in exceptional condition. This has contributed to what could be perceived as an overextension of the Konservat-Lagerstätte concept to strata that have yielded quite rare examples of exceptionally preserved fossils. As Seilacher et al. (1985) noted, there is no sharp boundary between Lagerstätten and "normally" fossiliferous strata, so the Kimmig and Schiffbauer (2024) criteria place reasonable constraints on which deposits shall qualify as Konservat-Lagerstätten.

Similarly, as an overview of the record of marine arthropods in Lagerstätten illustrates, there is not always a sharp boundary between the processes operating to preserve organic remains in concentration deposits as compared to those operating in conservation deposits. Concretionary formation, clustering of organic remains, event-bed deposition, and microbial sealing, along with other factors, are facets of the taphonomic processes that contribute in important ways to the preservation of unusual amounts of paleontological information in sedimentary deposits. Some, if not all, of these facets can contribute to the fossilization process in both genetic categories (conservation and concentration deposits), and it is perhaps best to regard these as preservational endmembers or idealizations.

Recognition of taphonomic associations provides another dimension of information useful for interpreting the ecological, taphonomic, sedimentary, and geochemical context in which Lagerstätten deposits form. With further work, it may prove useful to supplant the current conservation-deposit and concentration-deposit models with more nuanced concepts. Further understanding of the multidimensional factors underlying the origin of Lagerstätten may lead to an enhanced ability to identify likely stratigraphic positions of previously unknown Lagerstätten (see Kluessendorf, 1994; Babcock et al., 2001; Vrazo et al., 2017, who discussed semiquantitative, sedimentologic, and stratigraphic parameters used in characterizing or searching for Lagerstätten).

Work leading to a more refined, multidimensional understanding of Lagerstätten has already begun. The work of Allison and Briggs (1991c) and Muscente et al. (2017), as examples, addressed a spectrum of Lagerstätten, but their results certainly apply to deposits containing remains of marine arthropods. Allison and Briggs (1991c) summarized a sizable number of Lagerstätten according to a temporal scale. Their work highlighted the uneven distribution of marine Lagerstätten through geologic time, which implies certain evolutionary, paleoenvironmental, paleoceanographic, geochemical, and stratigraphic controls. More recently, Muscente et al. (2017) compiled and analyzed a large data set of conservation deposits and showed that assemblages with similar ages and depositional settings tend to occur in clusters. Muscente et al. (2017) proposed a relationship between oxygenation and bioturbation in the oceans, which would have affected taphonomic pathways, plus changes in seawater chemistry that affected processes leading to conservation of non-biomineralized anatomy. These factors have had a significant effect on the record of non-biomineralizing or weakly biomineralizing marine arthropods. After the Cambrian–Ordovician transition interval, exceptional preservation is inferred to have occurred rarely in open-marine settings, except at times of widespread oceanic anoxia, or when low oxygen levels were present locally. One outcome is that from the Ordovician on, the marine arthropod fossil record is characterized by a greatly increased proportion of biomineralizing taxa.

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