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Forum

A modern definition of Fossil-Lagerstätten

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Fossil-Lagerstätten are amongst the most important windows onto the paleobiology of ancient ecosystems. Inconsistencies surrounding what constitutes a Lagerstätte limits our ability to compare sites and thus their scientific potential. Here, we provide a modern and utilitarian classification scheme for Konservat-Lagerstätten, allowing for more consistent and improved scientific discourse.

What are Lagerstätten?

In 1970, Adolf Seilacher coined the term Fossil-Lagerstätte (singular; plural: Lagerstätten), defined as 'rock bodies, which in quality and quantity preserve an unusual amount of paleontological information' [1]. His definition included two primary categories: (i) Konservat-Lagerstätten (Box 1), or deposits defined by their fossil quality, often preserving fossils with minimal decomposition of soft tissues, preserving organic skeletal components, such as chitin, and connected or articulated skeletal components, and (ii) Konzentrat-Lagerstätten, or the dense accumulations of disarticulated organismal hard parts. Seilacher *et al.* [2] later elaborated on this classification, and suggested viewing them in the context of **sedimentary facies** (see Glossary) and the major agents involved in the preservation of the fossils (or their **taphonomy** [3]). In the 50 years of research since, we now recognize Lagerstätten throughout the fossil record from nearly all types of aquatic (and a few terrestrial) settings. The paleontological community values these deposits as the most important windows onto ancient ecosystems.

A recent tally of Konservat-Lagerstätten placed their numbers at nearly 700 worldwide [4], up from a sum of <50 that had been documented only a quarter-century prior [5]. However, it is important to recognize that they are not only rare compared with the wealth of known fossil deposits, but also rarely extensive, either geographically or geologically. Rather than occupying broad spatial distributions or an entire geological formation or even member, the exceptional preservation of Konservat-Lagerstätten instead comprises only isolated regions that often represent a unique paleoenvironment or single to few layers within the geologic unit. Historically, when studies refer to geographically extensive Konservat-Lagerstätten, they likely represent an accumulation of several localized fossil deposits that may not necessarily originate from the same fossilization event. As a prime example, the Late **Jurassic** plattenkalk deposits of the 'Solnhofen Archipelago' in Germany are part of numerous Lagerstätten spanning the Jurassic of the Franconian and Swabian Alps. While often mentioned together, these Lagerstätten are distinct in time, occur in different sediments, and have diverse preservational modes [6,7].

What is exceptional preservation?

Seilacher [1] struggled to offer a succinct characterization for what should qualify as an exceptional fossil, though he later clarified [8] that Fossil-Lagerstätten are meant to represent the end-members of fossiliferous deposits that provide additional or extraordinary paleontological information and 'warrant exploitation'.

With considerable growth of taphonomic and paleobiological research into Konservat-Lagerstätten, we should now reflect on whether this original framework remains valuable, appropriate, and informative. Seilacher was writing in a time

Glossary

Aluminosilicification: replication of organism tissues in aluminosilicate minerals, a class of clay minerals that are primarily composed of aluminum, silicon, and oxygen; usually observed in the form of 'templating', or coating the outer surfaces of a fossil organism.

Calcification: replication or replacement of organism tissues in calcareous minerals, such as calcite ($CaCO_3$).

Cambrian: geological period from 539 to 485 million years ago.

Cementation of enveloping sediment: usually 'cast and mold' preservation, where sediment surrounding a fossil is cemented before the organism is lost, decayed, or replaced, leaving an imprint or mold; if this mold is filled by secondary mineralization or cementation, it becomes a cast.

Jurassic: geological period from 201 to 145 million years ago.

Kerogenization: process by which organic precursors are converted and volatilized into inert, geologically robust carbon compounds (e.g., kerogens), usually observed as two-dimensional carbon-rich fossil films occurring after rapid burial into anoxic settings.

Neoproterozoic: geological era from 1000 to 539 million years ago.

Paleozoic: geological era from 539 to 252 million years ago.

Phosphatization: replication or replacement of organism tissues in minerals bearing the phosphate (PO_4^{3-}) ion, such as apatite [$Ca_5(PO_4)_3$(F/Cl/OH)], often driven by fluctuating redox conditions.

Pyritization: replication or replacement of organism tissues in the mineral pyrite (FeS_2), often driven by microbial sulfate reduction.

Sedimentary facies: bodies of sediment that are recognizably distinct from other sediments based on their overall appearance, composition, or condition of formation, resulting from different depositional environments.

Siderite mineralization: process by which a decaying organism forms a nucleus for siderite ($FeCO_3$) cementation, usually resulting in a nodule encasing the fossil.

Silicification: includes two different endmembers of fossil preservation: specifically, entombment of organism tissues sealed within microcrystalline or cryptocrystalline quartz (chert), or replacement and/or replication of fossil materials via silicon-bearing minerals.

Taphofacies: sedimentary rocks characterized by the combination of preservational features of the fossils contained within them.

Taphonomy: the study of the processes of fossilization that occur between the death of an organism and its discovery as a fossil.

Trace fossils: fossils that record animal and plant activities and behaviors.

Box 1. Important historic definitions of Konservat-Lagerstätten

1970: Seilacher [1] coined the term Konservat-Lagerstätte, which was then subcategorized based on fossilization processes. Seilacher also emphasized that Fossil-Lagerstätten are created under exceptional circumstances and will therefore present a distinct, but perhaps atypical view of the contemporary life they preserve.

1985: Seilacher *et al.* [2] elaborated on the classification of Konservat-Lagerstätten and brought it into the context of the sedimentary facies and major agents involved in the preservation of the fossils. They also emphasized the scientific potential of Konservat-Lagerstätten.

1988: Allison [10] introduces a mineralogy-based classification.

1990: Seilacher [8] acknowledges that the problem with the term Lagerstätte is that it defines no boundaries and suggests they be treated as fossil deposit end members with additional paleontological information.

1993: Allison and Briggs [5] tabulate and publish a first curve of marine Lagerstätten through the Phanerozoic, and consider rock outcrop availability and sea-level controls.

2003: Butterfield [9] introduces a site-based nomenclature for deposits with exceptional fossil preservation, largely limited to the Neoproterozoic and Paleozoic, referring to six localities with a typical kind of fossil preservation.

2017: Muscente and colleagues [4] build on Allison's definition [10], adding important contexts of sedimentary geochemistry and microbial metabolic pathways.

when any fossil deposit that preserved soft tissues may have been considered exceptional, and perhaps rightly so, but in today's landscape, the wealth of paleobiological information we can achieve from fossils and the ways in which we study them have improved immensely.

In this forum article we propose a suite of criteria to be followed in order to consider a fossil deposit to be 'exceptional', which in turn affects how we should classify Konservat-Lagerstätten. These criteria, by general fossil group, are listed as follows:

Invertebrate fossils:

- Complete, or mostly complete (>75%), specimens preserving fine morphological details of the exoskeleton, shell, or other hard parts.
- Preservation of associated soft tissues of the respiratory, excretory, circulatory, nervous, integumentary, or muscular systems, including but not limited to appendages, digestive tracts, eyes, and/or nervous tissues.

Vertebrate fossils:

- Complete, or mostly complete (>75%), skeletons.
- Preservation of associated soft tissues as mentioned previously, including other vertebrate-specific examples such as connective tissues and feathers.

Plant fossils:

- Associated stems, branches, foliage and leaves, flowers (if appropriate), fruit and seeds, and/or pollen.
- Preserved microstructures (mm scale) in tissues, such as venation in leaves and/or reproductive structures in flowers.

Trace fossils:

- Fine-scale details of trace production, such as excavation or scratch marks in burrows. Associated with little erosion.
- Preserved organic matter from the trace-maker.

To qualify as a Konservat-Lagerstätte, the deposit must contain fossil materials that fulfill either of the aforementioned criteria by group, preferably fulfilling both. Within the horizons that contain them, a minimum of 5% of the fossils found should be those that are considered exceptionally well preserved.

This 5% cut-off, while arbitrary, is an imperative benchmark to establish a more formalized definition. We chose this delineation based on assessments of literature data, our own fieldwork experiences, and from discussions with colleagues, as well as from museum collections data reflecting numerous well-described Konservat-Lagerstätten. A major concern with historical collections, which represent a large part of the described Konservat-Lagerstätten, is that many of the deposits have been collected with an 'eye for the exceptional', rather than providing a bulk survey or detailed log of preserved fossil materials within the deposit [9]. As such, we recommend that new classification endeavors should implore comprehensive future revisitations to past described Konservat-Lagerstätten.

How should we categorize Konservat-Lagerstätten?

With the recent uptick in localities being termed Konservat-Lagerstätten, it is more important now than ever to find a concise and consistent way to compare these deposits. Over the years, there have been multiple attempts to classify Konservat-Lagerstätten (Box 1), the most prominent of which was the nomenclature first introduced by Butterfield [10] based on mode of preservation as designated to a 'type section' that exemplifies its taphonomy. For example, 'Burgess Shale-type preservation', named for the famous **Cambrian** locality in the Canadian Rockies, equates, roughly, to two-dimensionally compressed carbonaceous films in marine rocks. This approach permeated the **Neoproterozoic** and **Paleozoic** literature (since Butterfield's types were limited to these eras), because most paleontologists can envision the mode and quality of preservation when the site is mentioned. However, this may be problematic for researchers outside the discipline or focusing within different geological intervals, largely because they are not necessarily familiar with the site names or modes of preservation they typify. Further complications can arise with the unintentional conflation of type with fossil assemblage dynamics, geological time interval, and even collector bias.

The site-based classification itself is underlain by a fossil chemistry-based classification, similar to the one proposed by Allison [11]. This compositional approach has several significant advantages, and – with increasingly cost- and time-effective analytical approaches – no real disadvantages. The biggest advantages are that fossil compositions and mineralogies are easily comparable between sites and are understood by a wide range of scientists. With compositional subtleties that exist between different localities considered to be of the same site-based type, a compositional classification scheme would help to streamline scientific discourse around such distinctions. These subtleties can, and often do, have much broader implications for variations in depositional paleoenvironment and the prevailing sedimentological, oceanographic, and/or preservational geochemistry (e.g. [4,7,12,13]). As a result, site-based types may obscure true distinctions in the summative factors that contribute to the mode of preservation.

Based on the broad spectrum of currently known Konservat-Lagerstätten, we propose the following fossil composition-based categories for classification, listed here in alphabetical order. In some cases, these may apply to the enveloping sediment as well as the fossils themselves, and individual compositions should not be viewed as exclusive of one another.

- **Aluminosilicification**
- Amber
- **Calcification**
- **Cementation of enveloping sediment** (casts and molds)
- Coal balls
- Collagen
- **Kerogenization**
- **Phosphatization**
- **Pyritization**
- **Siderite mineralization**
- **Silicification** (replacement or entombment)

This composition-based classification of Konservat-Lagerstätten (Figure 1) provides the most pertinent information on the first-order controls of fossil preservation, the mineralogical mechanism that provides geological stability of the fossil material over time. However, equally important, because the same mineralization can happen in different settings, this scheme should be bolstered or amended by facies-based descriptions of the depositional

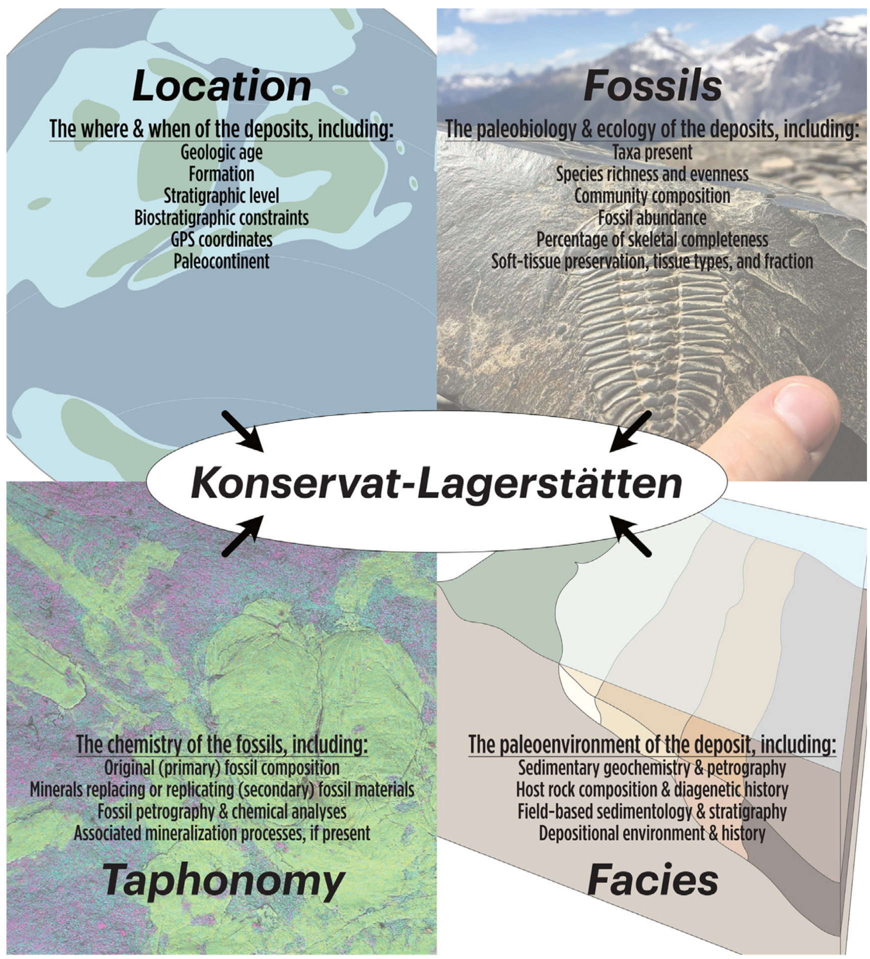

Figure 1. Roadmap for providing all pertinent metadata when evaluating or describing a Lagerstätte to assure maximum comparability between sites. Upper left: 400 million years ago paleocontinental reconstruction with details that should be included for describing the location of a Lagerstätte. Upper right: photograph of a Burgess Shale trilobite at the Walcott Quarry, Yoho National Park, British Columbia, Canada, provided by M. Pulsipher, with details that should be included for describing the fossil community composition of a Lagerstätte. Lower left: elemental map of a spider fossil from the Oligocene Aix-en-Provence deposit, France [15] with details that should be included for describing the taphonomy and mineralogy of fossils preserved in a Lagerstätte. Lower right: generalized onshore profile with details that should be included for describing the facies preserving a Lagerstätte.

paleoenvironment. This records the second-order controls that allow for the preservational mode to occur. Additionally, diagenesis, metamorphism, and weathering impart post-taphonomic effects on the original composition of fossils, and thus need to be considered when classifying deposits. Together these data, effectively following a **taphofacies** approach, will enable comprehensive and quantifiable comparisons of Konservat-Lagerstätten through time and space.

In instances where multiple preservation modes co-occur, such as kerogenized arthropods with phosphatized guts in the Burgess Shale [14] or both pyritized and kerogenized tubular fossils of the Gaojiashan [13], the dominant preservation mode throughout the deposit would take precedence for classification. In the case of the Burgess Shale, this would be kerogenization, with isolated anatomical features preserved through phosphatization. In the Gaojiashan, a large majority of the tubes have been pyritized, thus representing the prevailing mode. With consistency in providing geochemical analyses, we expect this situation to occur regularly, reinforcing the importance of analyzing a suite of specimens from each deposit to appreciate the patterns and modes of preservation. Attention to detail in fossil examination will ultimately afford better comparisons between deposits.

A framework for comparison

Given the rapid pace at which our knowledge of Konservat-Lagerstätten, and deposits categorized as such, has grown over the last several decades, we find it imperative to establish a mechanism not only to quantify what defines them, but also to facilitate their comparison in time and space. We regard our proposed framework as a means to improve the recognition of Fossil-Lagerstätten, to better assess their similarities and differences, and to maximize what further insights these most important fossil deposits can offer us onto the history of life.

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No conflicts of interests are declared.

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