Taphonomy

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Abstract

Taphonomy is the study of how organic remains pass from the biosphere to the lithosphere, and this includes processes affecting remains from the time of death of an organism (or the discard of shed parts) through decomposition, burial, and preservation as mineralized fossils or other stable biomaterials. Taphonomy can be studied in all types of organisms, from protists to complex eukaryotes – microbes, plants, invertebrates, and vertebrates. Although taphonomy usually focuses on the material remains of the organism itself, it can include biomolecules and traces such as trackways, burrows, fecal matter. Only a tiny fraction of the organisms that have inhabited the earth are preserved as fossils, but some organic remains are relatively abundant, while many others are rare to absent. Taphonomy is essential to understanding what the limited samples of past life mean – including biases caused by the types of organisms and habitats that are and are not represented in the fossil record.

The field of taphonomy, broadly speaking, aims to understand all kinds of physical, chemical, and biological processes that cause changes in organic remains, together with evidence (clues) that can be used to identify these processes. It is strongly interdisciplinary and provides many opportunities for research at the intersections of biology, geology, paleontology, anthropology, archaeology, forensic science, ecology, and biogeochemistry in both modern and ancient time periods. Taphonomy continues to expand and gain importance in different scientific arenas, such as Conservation Paleobiology. This new field of study examines human impacts on modern ecosystems, and one approach uses taphonomy in "live-dead" studies to reveal differences between the number of species of

living shelly marine invertebrates and the remains of older communities that flourished prior to the time of human disturbance.

Glossary

Actualistic – relating to the present-day; research on taphonomic processes in modern environments is often referred to as actualistic taphonomy (or neo-taphonomy).

Allochthonous - organic remains that are found outside of the place where the organism lived and were subjected to 'out-of-habitat' transport.

Autochthonous – organic remains that are found in the same place where the organism lived and were not subjected to 'out-of-habitat' transport.

Biostratigraphy - stratigraphy that uses fossils to correlate rock layers and to determine relative geological age. This is done with the aid of guide (index) fossils, in some cases representing successive stages in an evolutionary lineage.

Biostratinomy – the sub-discipline of taphonomy that is focused on sedimentological and biological processes affecting organic remains in the interval between initial decomposition (necrology) and final burial.

Bioturbation – reworking and homogenization of sediment caused by the actions of living organisms, such as plant roots, soil micro-organisms, arthropods, worms and other burrowing animals, and vertebrate trampling.

Bone Modification – features of bones that record the actions of other organisms, such as breakage caused by carnivory and scavenging, and surface damage caused by trampling, chewing, cutting, insects, etc.

Conservation Paleobiology – a field of paleontology that uses knowledge from the fossil and geological record as a source of information about the past to help with conservation planning for the future.

Decomposer – an organism that utilizes dead organisms for energy by breaking down tissues and recycling nutrients, performing a critical service in the ecological cycle of life.

Decomposition – the break-down of organic materials by decomposers, mainly fungi and bacteria.

Detritivore – organisms that feed on dead organic materials by ingesting them, such as earthworms, nematodes, mites, and millipedes.

Diagenesis – the sub-discipline of taphonomy that focuses on changes to organic materials caused by processes that chemically (and sometimes physically) alter the structure and composition of dead biological tissues, usually after burial.

Early post-mortem – the interval of time in necrology when decomposers, detritivores, and scavengers actively break down dead organic remains, mainly soft tissues.

Endogenous – microflora and fauna (microbiome) that occur within living organisms. After an individual's death these microbes can begin the process of decomposition and affect later biostratinomy and diagenesis.

Exceptional preservation – a term applied to fossils with unusually complete anatomical features and preserved soft tissues, sometimes with minimally altered cell structure and biomolecules. Many examples are associated with Lagerstätten.

Exogenous – microbes occurring outside of living organisms that colonize and break down tissues of dead remains.

Isotaphonomy – an approach to analyzing patterns in the fossil record that uses fossil assemblages formed by the same or similar taphonomic processes, with the goal of controlling for potential biases in species representation and other variables affected by differential preservation.

Lagerstätte - (plural Lagerstätten) is a German term that refers to a sedimentary layer with unusual occurrences of well-preserved organic remains, usually including soft tissues.

Live-Dead fidelity – how well ecological census data on living organisms is represented by the organic remains in the same ecosystem, which form the potential or preserved fossil record.

Megabias – a large-scale bias caused by differential preservation of organic remains representing particular organisms or ecosystems, such as the dominance of organisms with hard parts in the fossil record and the scarcity of organisms from upland habitats on land.

Necrology – a sub-discipline of taphonomy focused on the study of death and early decomposition of organisms and their remains. This area of study is sometimes included in biostratinomy but represents a distinct interval of post-mortem decomposition of particular interest to forensic scientists.

Neo-taphonomy – the study of taphonomic processes and material evidence for these processes in modern environments. Paleontologists use neo-taphonomy (actualistic taphonomy) as a source of analogues for interpreting the fossil record.

Obrution – a sedimentary event causing death by smothering and simultaneous rapid burial of organisms or organic remains, sometimes leading to exceptional preservation (e.g., Cambrian fossil organisms of the Burgess Shale).

Paleoecology – the study of ecology in the past using fossils and the geological record.

Permanent burial – being buried in sedimentary environments or other geological circumstances (e.g., caves) without subsequent reworking; permanent generally means long enough to become fossilized.

Recycling – the operation of natural processes of decomposition and consumption that break down organic remains and return their nutrients to the ecosystem.

Space-averaging – refers to the spatial area that is represented by assemblages of fossil organisms, which may or may not coincide with their ecological range and habitat associations while alive.

Taphonomic Feedback – interactions between living organisms and dead organic remains in the same environment that affect the ecology of the living community, e.g., the accumulation of dead shells as substrates for live organisms in marine benthic habitats.

Taphonomy – the study of how biological, chemical, and physical processes preserve and destroy organic remains and affect information in the fossil record.

Time-averaging – refers to information that is combined over time. Taphonomic time-averaging estimates the time interval represented by fossil organisms that co-occur in the same deposit, which may be considerably longer than a one-time census of modern organisms because of taphonomic and sedimentological processes. Analytical time-averaging can represent even longer time intervals and results from combining multiple fossil assemblages for the purpose of paleontological analysis.

Trace Fossil – any evidence resulting from the actions of living organisms on organic parts, organic remains, or sediment substrates, e.g., tracks and trails, burrows, insect damage on leaves or bones, carnivore tooth marks, bioerosion tunnels in shells. Trace fossils (ichnofossils) are a record of fossil behavior and the subject of the paleontological subfield of ichnology.

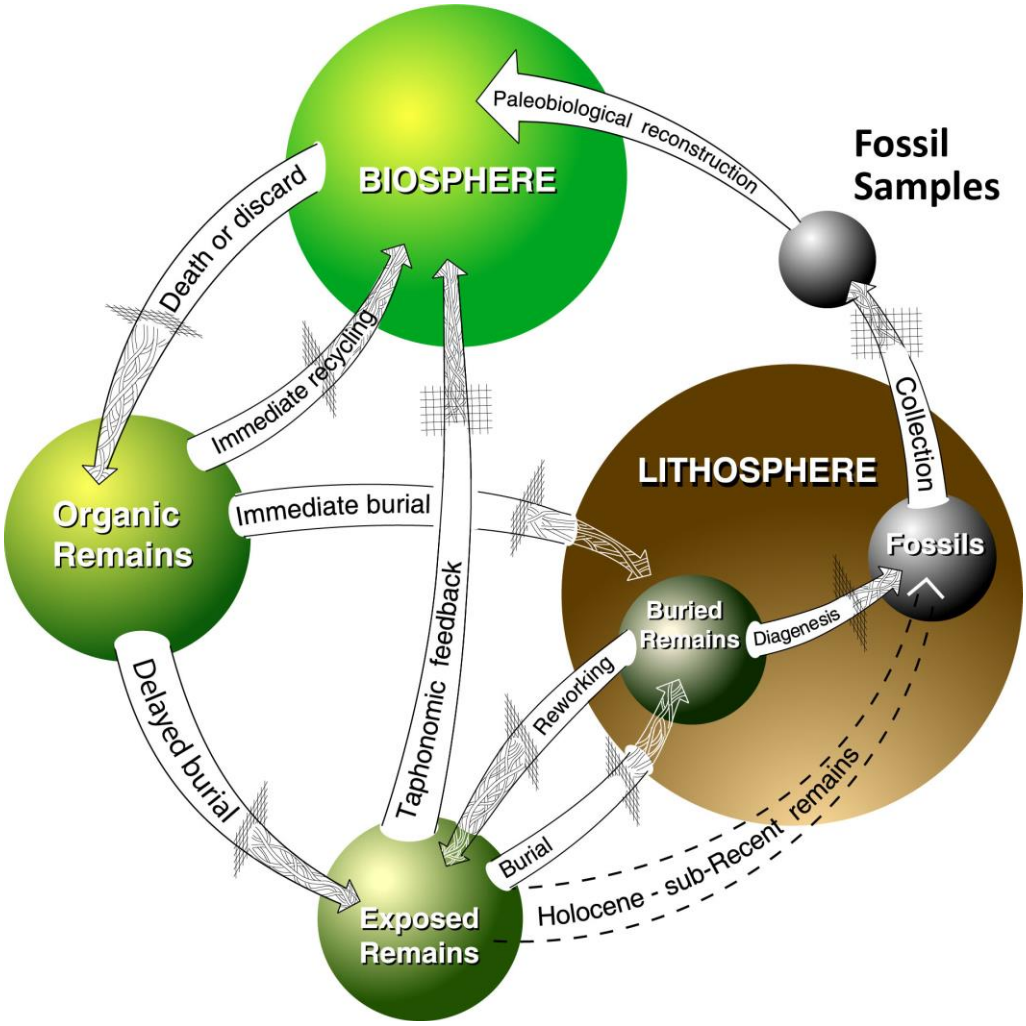

Figure 1. Taphonomy is the study of the transition of organic remains and traces from the biosphere to the lithosphere, and this diagram illustrates alternative pathways in this transition. Biological and geological processes that affect remains are represented by the filters that intervene between each type of organic remains (spheres), and the turbulent flow lines represent alteration in what passes through the filters. The same categories apply for all types of remains and traces in marine or terrestrial systems, although taphonomic processes differ across organisms and environments. Taphonomic feedback recognizes the impact that the direct return of dead remains may have on the living ecosystem. (Adapted from Behrensmeyer and Kidwell, 1985, Fig. 3).

History and Scope of Taphonomy

The word taphonomy is derived from the Greek word for “taphos,” meaning "burial", and “nomos,” meaning "law," and thus literally means (the study of) the laws of burial. It was first proposed as a distinct field of science by Soviet paleontologist Ivan Efremov (1940), who described it as the study of the transition of remains, parts, or products of organisms from the biosphere to the lithosphere (Figure 1). European scientists, including Johannes Weigelt (1890-1948) and Wilhelm Schäfer (1912-1981), investigated taphonomic processes in modern environments to improve understanding of fossil preservation (Weigelt, 1989; Schäfer, 1972). The growth of taphonomy was spurred on in the 1950’s and 1960’s by interest in reconstructing ancient marine and terrestrial environments. It was clear that fossil assemblages of shells, bones, or plant parts often resulted from circumstances that were biased relative to the living communities, so such assemblages could not simply be taken at face value. Investigating taphonomic processes affecting shelly invertebrates became a major focus in marine paleontology (Lawrence, 1968). Interest in human evolution and meat-eating behavior also stimulated research in taphonomic processes affecting bones (Behrensmeyer and Hill, 1980; Shipman, 1981). Archaeologists and paleoanthropologists sought evidence for bone modification patterns (e.g., cutmarks, breakage) that would allow them to distinguish damage caused by early humans from other biological or physical processes. With the expanding scope of the field, taphonomy was redefined as the study of how biological, chemical, and physical processes preserve and destroy organic remains and affect information in the fossil record (Behrensmeyer and Kidwell, 1985). By the 1990’s, taphonomy had established its relevance and importance to a wide range of scientific problems and was recognized as sub-field of palaeontology (Allison and Briggs, 1991) and anthropology (Lyman and Lyman, 1994).

Today, the fields of paleontology, sedimentology, stratigraphy, anthropology, archaeology, forensics, ecology and astrobiology all contribute to, and benefit from, the continuing growth of taphonomy. These areas of study have somewhat different approaches, and there is currently no single source of information or broad synthesis of the field, although numerous treatments are available within specific disciplines (see References and Further Reading). Taphonomy has been built on two main sources of information: 1) studies of modern organisms and environments (referred to as neo-taphonomy or actualistic taphonomy), including both observation and experimentation, and 2) investigation of different types of preservation in the fossil record. Research in taphonomy addresses a wide range of scales, from decomposition sequences of individual plants and animals to large-scale patterns of preservation in the stratigraphic record (e.g., Holland, 2016) and megabiases that affect the fossil record as a whole (Behrensmeyer et al., 2000). In the 1970’s-1980’s, taphonomy was regarded mainly as a source of cautionary tales about information loss in the fossil record (Behrensmeyer and Kidwell, 1985). Though such thinking remains an important check on over-interpretation, there is a growing realization that taphonomic processes also result in valuable information gain (Behrensmeyer et al. 2000). This includes understanding that time-averaged samples of biodiversity and paleoenvironments can filter out short-term "noise" and strengthen signals for longer term trends. Neo-taphonomic research is an important source of data on sedimentary processes as well as how living organisms interact with dead remains (taphonomic feedback). Taphonomy also provides evidence for interactions among species otherwise absent from the fossil record, especially through the study of trace fossils that leave distinctive signatures on preserved remains.

Taphonomy can be a means to an end, or an end in itself. As a tool for paleontologists, it provides methods for understanding filters (Figure 1) that affect information preserved in the fossil record, allowing (for example) more accurate reconstructions of ancient food webs and explanations of concentrations of skeletal or soft-tissue remains. In modern contexts, taphonomic research on the decomposition of individual bodies can have practical applications, such as helping forensic scientists estimate time since death. In these examples, taphonomy becomes a means to an end, helping scientists in different fields understand processes affecting organic remains that relate to their special areas of interest. Taphonomy also can be regarded an end in itself because it focuses on building knowledge of decomposition and nutrient recycling processes as essential components of ecosystems, and investigating how these changed through geological time. Some archaeologists and anthropologists have expanded the scope of taphonomy to include humanity's cultural products, such as stone artifacts, building materials, and tunnels, which are currently forming the record of the Anthropocene. This connects taphonomy with material science and thinking about what humans will leave behind as future fossils. Taphonomic perspectives could contribute to the study of decay in human-made materials (e.g., books, works of art) or how to recycle materials (such as plastic) that are causing world-wide contamination problems.

An early (and on-going) concern of taphonomy is the issue of bias – i.e., recognition that the preserved fossil record provides distorted evidence (Figure 1), which is difficult to interpret accurately in the study of ancient life (Behrensmeyer et al., 2000). What constitutes "bias" in paleontological (or any other) data, however, depends on the question being asked of those data. For example, if a fossil assemblage records a single species of well-preserved fish, and we are asking questions about their skeletal anatomy, then there may be minimal taphonomic bias (e.g., bone distortion) affecting anatomical reconstructions of their skeletons. On the other hand, if we are asking a question about the diversity of fish that lived in the lake at that time, then it is reasonable to suspect a strong taphonomic bias because it is unlikely that only one species lived in the lake. Such a bias could happen, for example, if one species was particularly vulnerable to a sudden change in the water chemistry (e.g., anoxia), especially if that change also helped to preserve their remains. Similar, less extreme variations in the preservation of different species result from skeletal durability, physiological traits, behaviour, and habitat preferences, any of which can affect their presence or absence in the fossil record. Such factors create biases in taxonomic representation and also in population samples (e.g., favouring large individuals over small or immature ones), whether vertebrate, invertebrate, plant or microbe, in marine or terrestrial environments. Once aware of such potential biases, scientists can use knowledge of taphonomic processes to design research that focuses on fossils with similar (isotaphonomic) histories. These subsets provide controlled samples allowing more accurate reconstructions of specific portions of ancient populations and communities (Behrensmeyer et al. 2000). Neo-taphonomic studies have shown that even small samples of skeletal remains within these subsets can provide accurate records of living species diversity (e.g., Western and Behrensmeyer, 2009).

This contribution is aimed at providing readers with a broad overview of taphonomy and glimpses into its diverse areas of on-going research. References and Further Reading were selected to provide access to taphonomic research in different disciplines.

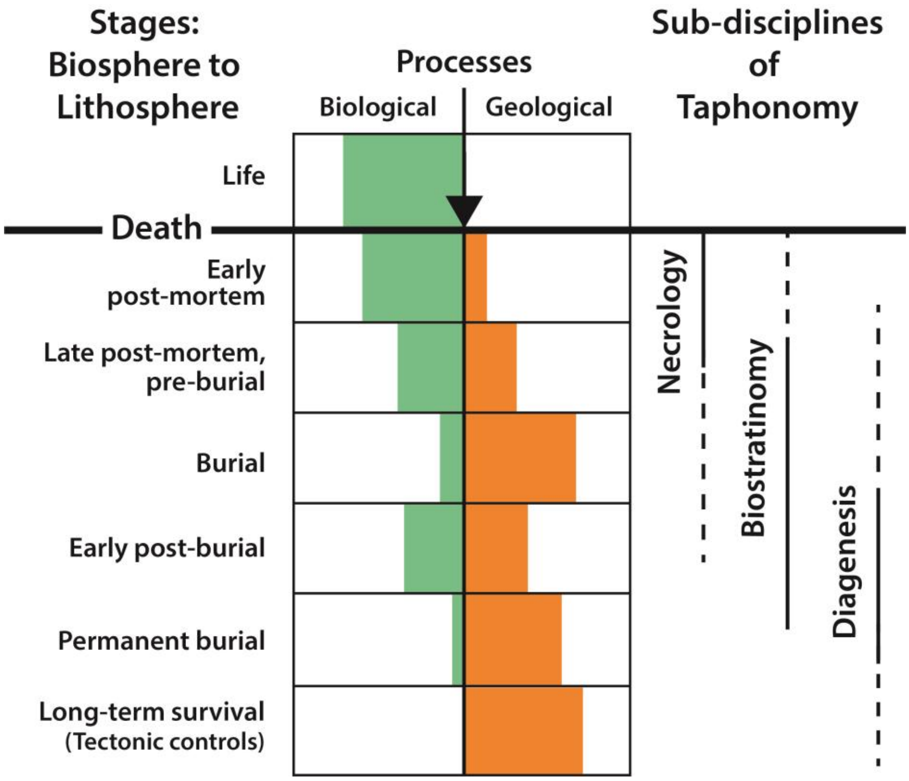

Figure 2. Major stages (top to bottom) that organic remains pass through (left) before becoming part of the fossil record, sub-disciplines of the field of Taphonomy (right), with estimated relative importance of biological (green) versus geological (tan) for each stage (center). During life an organism has control over its body, but after death other biological processes take over to break down tissues and recycle nutrients. Geological processes usually become more important over time as biological processes taper off. Solid lines indicate the main focus in the sequence of stages of the three sub-disciplines of taphonomy, and dashed lines show varability in when different taphonomic processes can affect organic remains. Ultimately the survival of buried fossils (mineralized or not) in the geological record is subject to tectonic controls on the fate of depositional basins.

Divisions of Taphonomy

Taphonomy can be divided into different stages in the progression of remains from biosphere to lithosphere. A common three-part categorization is: 1) necrology – early post-mortem processes such as scavenging and decomposition, 2) biostratinomy – transport and burial, and 3) diagenesis – changes that usually occur after burial, such as mineralization (Figure 2). These categories are a convenient way of organizing evidence according to a natural sequence that leads either to recycling (destruction) or preservation as a fossil, and they can be applied to all types of organic remains and traces. Different fields of study have varying emphasis on necrology, biostratinomy, and diagenesis; for instance, forensic science focuses on necrology, sedimentology on biostratinomy, and geochemistry on diagenesis. Paleontologists tend to study all three so they can understand preservation and potential biases in fossil taxa and paleocommunities. In some cases, necrology and diagenesis are linked by interacting processes of decomposition and mineralization, and many other examples of the biosphere-to-lithosphere transition do not progress neatly through each successive stage to fossilization (Figure 2).

Decades of research in taphonomy have shown that almost any type of organic material can be preserved and stabilized in the deep time geological record. Younger geological age is not necessarily correlated with better preservation. There are many examples of surprisingly well-preserved fossils that are millions to hundreds of millions of years old (Smiley et al. 1975; Allison and Briggs 1993). More exceptionally preserved fossils are coming to light with continuing field exploration and the application of new technology (e.g., CT scanning) that reveals previously unknown examples of special preservation. This includes analysis of biomolecules and how they were changed and preserved by taphonomic processes (Briggs and Summons, 2014).

Two factors have emerged as critical in predicting whether an organism will become a fossil, 1) the composition of its body and 2) the environment where it lives and dies. Organisms with mineralized hard parts are more common as fossils than those made only of soft tissues. While larger organisms such as dinosaurs and trilobites are well known as fossils, diatoms, radiolarians, and foraminiferans are far more abundant, and their uncountable numbers of microscopic skeletons form a significant part of the stratigraphic record. All types of organic remains, whatever their size or composition, can be affected by taphonomic processes that decompose soft parts and modify hard parts through breakage, disarticulation, transport, bioerosion, dissolution, and mineralization and recrystallization. These processes vary, depending on the characteristics of environments where organisms leave their remains. Given the range of chemical and physical processes in surface and burial situations, as well as the diversity of organisms adapted to recycling dead remains, it is a safe assumption that all fossils were affected in some way by taphonomic processes.

This means that in addition to their identities as individual organisms, fossils have much more to say about the past than is commonly recognized.

Necrology - Decomposition

The initial stages of the transition from biosphere to lithosphere are referred to as necrology. This is a dynamic time when scavengers and decomposers (endogenous and exogenous) compete to capture the newly available nutrients in the dead organism, usually resulting in destruction rather than preservation. Necrology focuses on the processes and agents involved in utilizing, dispersing and destroying organic remains. Changes often happen rapidly in minutes to hours but can be prolonged over months to years, depending on the body composition (e.g., soft versus hard parts), the size of the dead organism, the environment where death occurred, and the living organisms available to interact with the remains.

Observations and experiments with modern organisms have been very useful in revealing rates and patterns of change that can be expected during necrolysis (e.g., Greenwood, 1991; Pokines and Symes, 2013; Briggs and McMahon, 2016). This research has shown that often there is a predictable succession of biological and physical processes that decompose dead animals and plants in different environments, which also has helped scientists calibrate the effects of varying climate and water chemistry. In most circumstances, it is a safe assumption that necrological processes begin to interact with organic remains from the moment the individual dies. This also applies to remains that ended up as fossils, and necrology can indicate at what point in the decomposition sequence remains were protected from further change, e.g., by deep burial. Preservation of soft tissues is evidence for special circumstances that stopped these processes soon after death. Survival of bones, teeth, and shells means that early post-mortem necrological processes did their job, but longer-term decomposition and nutrient recycling failed to break down more durable body components.

Forensic anthropologists have contributed a large body of experimental evidence on necrology by observing what happens over time to cadavers of humans (and domestic pigs) in natural settings, both on land and in aquatic environments (Pokines and Symes, 2013). Studies of decomposition by ecologists and paleobiologists in circumstances where some variables can be controlled help to define what conditions allow exceptional preservation (Briggs and McMahon, 2016). Experiments on the necrology of small animals (e.g., lizards, toads) in natural tropical land habitats show how rapidly their carcasses can be reduced to dry remains in a matter of days (Cornaby, 1974). A study of crocodilian carcasses in water revealed how preservation can vary in three different burial situations (Syme and Salisbury, 2014). There are many other examples of observations and experiments on the necrology of different types of organisms, including fish, birds, shrimp, marine worms, and leaves.

There is considerable variation in the decay of different types of organisms under different environmental conditions. The progression of natural decomposition typically leads to rapid loss of soft tissues, slower destruction of more durable materials such as wood or keratin, with mineralized body parts such as bones and shells most resistant to recycling. This depends on the environmental conditions, however, and in acidic water, soft tissue and plant remains may be preserved, but bones dissolved (Greenwood, 1991; Brothwell et al. 2001). Rapid rates of decomposition are typical of warm environments where bacterial activity is accelerated (e.g., in the tropics), and complete removal of soft tissue can reduce the subsequent impact of other scavengers and decomposers on remaining hard parts, which are then available to move to the next taphonomic stage (Figures 1 and 2). Slow decomposition in colder climates or deeper, anoxic water, allows more time for burial and fossilization of the complete organism. Decomposition can be stopped at any stage if the remains are removed from the biologically active environment, for example through burial, freezing, mummification, anoxia, or rapid permineralization.

Different decomposers are adapted to aquatic versus terrestrial settings, marine versus freshwater conditions, and burial environment chemistry. Endogenous microbes, i.e., those inside the body of the animal while it is alive, can become important decomposers after death. Both endogenous and exogenous fungi and bacteria can take over dead tissue by secreting noxious smells or distasteful rot that discourages other organisms from competing for the remains (Janzen, 1977). In some circumstances, microbial activities set the stage for rapid mineralization of soft and hard tissues (e.g., microbial mats, concretion formation) (Briggs and McMahon, 2016; Yoshida et al. 2018). Decomposition can selectively destroy some soft tissues faster than others, creating pseudo-anatomical features that may lead to misinterpretations of morphological traits, which in turn affect understanding of evolutionary relationships (Purnell et al. 2018).

There are common denominators that operate in both marine and terrestrial systems, such as anoxia in limiting disturbance by burrowing organisms (bioturbation), microbes that facilitate mineralization, and rapid burial that shuts down further taphonomic change. The existence and preservation state of fossils thus provide useful information to geologists about biotic and abiotic conditions in the original depositional environments.

Biostratinomy – transport and burial

Taphonomic processes that affect this stage of the biosphere to lithosphere transition are primarily geological and grouped under the term biostratinomy (Figure 2). Organic remains can be rapidly buried or stay exposed on substrate surfaces for long periods after soft-tissue decomposition, increasing the probability that they will be subject to biostratinomic processes. Organic remains can be transported, dispersed or concentrated post-mortem, or they may stay at the site of original death or discard. Chances for dispersal and burial vary greatly depending on the type of organic remains. For example, wind-dispersed pollen can be carried long distances, giving it a higher probability of preservation in a favourable environment, e.g., lake sediments. Insect-dispersed pollen is more likely to remain near its source and not be preserved. Physical processes include water currents, wind, slope wash, landslides, turbidity flows, and volcanic mudflows. Biological transport processes include predation (e.g., owls, other avian raptors), scavengers (e. g., hyenas), collectors of organic remains (e. g., pack rats), and passive transport (e.g., of seeds). Predation by owls or carnivorous mammals concentrates bones under roosts, in dens or in feces, where they may be entrained by water flow or buried in place. In general, a taphonomic trajectory that avoids or minimizes dispersive biostratinomic processes but includes circumstances promoting concentration and/or rapid burial gives organic remains a better chance for becoming part of the fossil record.

Quick burial out of the bio- and geo-active zone is key to shutting down ongoing recycling and protecting remains from further physical and chemical destruction. This can be accomplished through burial in places not subject to erosion, such as deep ocean basins, continental shelves, rivers, deltas or dune fields associated with subsiding continental margins, and areas with active volcanism. Upland areas, especially those with caves and sink holes, offer places for burial and protection from decomposition, but, over long time periods, most uplands with caves erode away. Much of the terrestrial fossil record for the past ~40,000 years in North America is preserved in cave settings (e.g., Plotnick and Koy, 2020), but examples of such assemblages are rare before 2-3 million years ago (Ma). Fossils of extinct animals and plants from upland habitats over the last 40,000 years are much better represented than in the rest of the history of life. This is an example of a taphonomic megabias affecting a major continental environment whose paleobiological diversity is poorly represented in the fossil record (Behrensmeyer et al. 2000).

Early research in taphonomy suggested that out-of-habitat transport of organic remains was an important source of bias in fossil assemblages (Behrensmeyer et al., 2000). Remains from animals living in different environments, such as fish, plant debris, and terrestrial mammals, were found together in the same fossil deposit. This showed that water transport could mix organisms from different life habitats, creating obvious biases in representation of the original communities. Animal carcasses as well as trees and other plant debris can be washed into rivers, lakes, and oceans by storms and deposited far from their life habitats (e.g., Brown et al. 2017). Further observations and experiments combined with increased understanding of hydrological processes, however, indicate that taphonomic biases caused by transport have been over-estimated (Behrensmeyer et al. 2000). Large vertebrate remains from a floodplain may be buried in a nearby channel but still remain within the original geographic range of the living animals. Water transport of invertebrate remains - shells and other hard parts - can remove them from their original habitat, but this usually can be inferred from sedimentary context (Behrensmeyer et al. 2000). Biological transport also occurs, but predators and other hard-part collectors operate within limited territories, although prey species may come from different habitats within that territory. Whether or not transport is important as a potential bias thus depends on the scale of the question being asked of the paleontological data.

Time-averaging is now regarded as a more important source of taphonomic bias than transport of durable remains (Behrensmeyer et al. 2000). It occurs when organic remains from different time periods are combined through sedimentary and/or biological processes operating within a geographic location (Kidwell et al. 1991). Bioturbation by burrowing or trampling organisms is an important process that disperses remains vertically through the substrate. Durable skeletal elements such as shells, bones, and teeth are more subject to time-averaging than non-durable materials such as leaves. Previously fossilized remains are even more durable and can be mixed with first cycle organic remains from an ecosystem, resulting in long periods of time-averaging. Mixing caused by time-averaging processes can lead to errors in interpreting which organisms occurred together in life, potentially inflating the numbers of species compared with modern communities. On the other hand, time-averaging can be an advantage because it provides more complete samples of the organisms that inhabited an ecosystem, in contrast to snap-shot samples representing a specific time and place, i.e., wildlife censuses of modern species present in a given day or year (Behrensmeyer et al. 2000). As with transport, whether time-averaging is regarded as a bias or an advantage depends on the question being asked of the data.

Diagenesis and Fossilization

Many people (including scientists) assume that fossilization, in the sense of 'being turned to stone,' takes a long time. A corollary assumption is that all fossils are old. Neither is an accurate characterization. There are many fossils that are not mineralized at all and retain original preserved biomolecules or biominerals (e.g., Otto et al. 2005). Mineralization of both hard and soft organic remains occurs over varying periods of time, and in some cases is very rapid. Fine details (cellular structure) of muscle, organ, and plant tissue can be preserved in organisms many hundreds of millions of years old (Martill, 1988, Brown, 2017), and such extraordinary preservation shows what is possible given the right conditions. The fact that soft tissues can be preserved with biological structures intact implies very rapid mineralization, because normal processes of decomposition by micro-organisms quickly destroy these tissues. Experiments and observations have shown that under certain environmental and chemical conditions, mineralization can occur in weeks to months (Briggs, 2003; Mustoe, 2017). There is good evidence that microbes, primarily bacteria, facilitate rapid mineralization of organic remains, even though bacterial activity also is a primary cause of degradation and recycling. There are many kinds of bacteria, and how they interact with dead organisms varies under different conditions. Current understanding of how this affects fossilization is expanding through the study of unusual fossils and increased experimentation with the biogeochemistry of decomposition (Briggs, 2003; Briggs and McMahon, 2016).

Fossil diagenesis can be characterized as a race between processes that preserve organic materials and those that destroy them. There are many different types of fossils and taphonomic pathways leading to preservation, not all of which involve mineralization. Preservation can happen when remains are sealed off in chemically inert burial environments, where some original tissues such as lignin and leaf structure in plants can survive for millions of years (Smiley et al. 1975; Greenwood, 1991). Burning can reduce organic structures to inert carbon, which, if buried, can last unchanged for hundreds of millions of years (Glasspool et al. 2006). Diagenetic effects also occur over different spans of time, and the mineral composition of some fossils continues to change after deep burial, while that of others remains stable. Interest in Carbon-14 dating and recovering original stable isotope signals (e.g., $\delta^{13}C$, $\delta^{18}O$, Strontium) from fossilized invertebrate and vertebrate hard tissues and plant remains led to extensive testing for diagenetic changes in the isotopic composition of these materials. Serious interpretive errors could result if these were chemically open systems that exchanged isotopes with their burial environment over time. This research resulted in standards for assessing the quality of the isotopic signals and demonstrated that many fossils retain original biominerals with unaltered isotopic ratios formed when the animals and plants were alive (e.g., Kohn and Cerling, 2002).

Lagerstätten

Lagerstätte (plural Lagerstätten) is a German term that refers to a sedimentary layer with unusual occurrences of relatively well-preserved organic remains. They may consist of complete bodies or parts with soft tissues (Konservat-Lagerstätten) or densely concentrated skeletal remains (Konzentrat-Lagerstätten). Such occurrences have been the focus of much paleontological attention because of the wealth of information they provide on extinct organisms and also because deciphering the causes of exceptional preservation is intriguing science. These deposits reflect special circumstances of necrolysis, biostratinomy, and diagenesis that combined to preserve relatively intact organic remains, usually representing one time and place. There are many taphonomic processes that can form Lagerstätten, but one of the best understood involves anoxic conditions in marine or lacustrine bottom waters that prevented the normal activities of scavengers and decomposers while continuing sedimentation buried the remains. Rapid burial of transported live organisms (e.g., obrution) is another way to generate Lagerstätten, a classic example being the Cambrian Burgess Shale (Caron and Jackson, 2006). Assemblages of insects and other fossils in amber are also considered to be Lagerstätten. Mass mortality due to drought, accident, volcanic eruptions, poisoning or other lethal circumstances forms concentrations of organic remains that can become densely fossiliferous sedimentary deposits. Each new Lagerstätte offers insights and puzzles that contribute to taphonomic research on geo- and biochemical processes leading to exceptional preservation, a current growth area in paleontology (Bottjer et al., 2002).

Evolution of Taphonomic Processes

Although studies in modern systems is critical for understanding taphonomic processes, it is also important to realize that these processes may differ from those of other parts of the geological record (Behrensmeyer et al. 2000; Allison and Bottjer, 2010). Dead tissue is a valuable source of nutrients for many kinds of organisms, and since life (and death) began, this has led to competition and natural selection for efficient utilizers of this resource. Much of our information on necrology is based on modern analogues, but biological agents that decompose and scavenge have evolved over time, with important consequences for the fossil record. For example, given that 170 species (in 49 families) were recorded at single carcasses by Cornaby (1974), it is highly probable that competition was a force in carrion-feeding insect evolution. Bone-cracking capabilities appeared in different mammalian lineages in the Cenozoic, changing bone-modification processes that affected vertebrate remains. This contrasts with the Mesozoic, when dinosaur predators such as *Tyrannosaurus rex* were equipped to consume flesh and bone in giant bites rather than chewing, leaving little for the fossil record. Much farther back in time, the Ediacaran to Cambrian transition is a well-studied example of how the evolution of different body types, consumers and decomposers changed the nature of the fossil record. Ediacaran organisms of 550-580 Ma were entirely soft-bodied, and their preservation as impression fossils is attributed to microbial mats combined with the absence of mat consumers (Kenchington and Wilby, 2014). This type of preservation was drastically reduced when mobile mat-grazers and bioturbators diversified at the beginning of the Phanerozoic (Brasier et al. 2011), and the appearance of biomineralized skeletons also contributed to a very different fossil record from the early Cambrian onward.

Ongoing Research Topics in Taphonomy

Taphonomy is an actively growing field that cuts across disciplinary boundaries and brings together diverse researchers to generate new understanding of the history of life. Below are five examples of questions in taphonomy that currently provide exciting areas for further exploration and discovery.

What can we do about taphonomic bias?

Taphonomy is about much more than bias, but there is no denying that this is a central question affecting many things that we would like to know about the past. One example is Earth's biodiversity and its ups and downs over hundreds of millions of years. We know that samples from the fossil record are not the same as censuses of modern species diversity, but sometimes the importance of taphonomic filters on taxon representation is overlooked. Big data analyses use counts of fossil taxa to represent particular time periods and often assume that large samples will overcome problems with taphonomic bias. This is basically the same as assuming that taphonomic processes create random noise around a stronger biological signal. In some cases this may be true, but in others it is not, leading to errors in reconstructing diversity patterns and other paleobiological phenomena. Many important analyses have been based on taphonomically similar subsets of Earth's biota, such as shelly marine invertebrates, which provide some control on biases resulting from differential preservation. This 'de facto' isotaphonomy means that we have been able to measure biodiversity trends over time, which also must take into account a rock record that is patchy in time and space. Recent interest in examining locality-based biodiversity (for organisms represented by hard parts) is helping to control for large-scale sampling biases, but differential preservation affecting taxon counts may still be an issue. Although tracking the better-preserved components of life over time is informative, it also is important to remember that these are subsets of the true diversity of ancient life. To achieve a broader assessment of life through time, we could: 1) define with more precision the isotaphonomic components of the fossil record to document biodiversity trends, and 2) explore in modern marine and terrestrial ecosystems how preservable taxa represent taxonomic groups and ecological functions that are rare to absent as fossils.

How important is selective preservation of large individuals?

For many fossil vertebrates, as well as other organisms, only the most durable elements are preserved, and these represent one end of the spectrum of carcass sizes and body parts produced by the original species. What would we understand about modern trees, or whales, if we could only study the largest and the strongest? The big individuals are the survivors from earlier growth stages that were much more numerous, and natural selection acts on all life stages to shape the traits of survivors over evolutionary time. The largest individuals often lived the longest and likely had many offspring, so their traits matter as representatives of the species. But reproductive success not only depends on the largest individuals, but on surviving through all life stages. The fossil record of the largest individuals can't tell the whole story of species adaptations and evolutionary history. Therefore, we need to understand how the largest, most durable individuals represent populations as a whole in modern ecosystems, and use this to improve interpretations of the fossil record of taxa and populations represented only by the most preservable specimens.

Can taphonomy distinguish damage caused by predation versus scavenging?

Vertebrate paleontologists and archaeologists would like to determine carnivore behavior using damage patterns from dental processing and human artifacts on bones, and invertebrate paleontologists are similarly interested in causes of damage to invertebrate hard parts. Interpreting such evidence is important to forensic scientists investigating cause of death (e.g., accident, homicide) versus later scavenging. Extensive experimentation and observation of agents of bone modification over the past decades has provided a wealth of evidence for taphonomic 'signatures' of different biological agents, but it has also shown that similar traces can have different causes, such as overlapping features of cut-marks, tooth-marks, and trample scratches on bones. Computer modelling and GIS analysis, together with artificial intelligence (AI) are being used to help distinguish subsets of nonoverlapping signatures of bone modifying agents. This methodology, combined with larger sample sizes from the fossil record, holds promise for distinguishing different causes of bone modification. Certainty in determining cause of death remains elusive, and this is particularly true for fossil remains of extinct organisms where modern analogues may not be relevant. Combining multiple lines of taphonomic evidence, including careful documentation of fossil remains from excavated sites, further study of bone-modifying agents, and advances in image-analysis technology has the potential to improve identification of scavenger and predator signatures on fossil bones, in some cases even the probable cause of death.

How have taphonomic processes evolved over time?

Taphonomic processes have changed as ecosystems and their component organisms evolved over geological time, and the efficiency of nutrient recycling has been affected by changes in both physical (climatic and tectonic) and biological processes. Although we understand important shifts in the taphonomy of organic remains relating to biological innovations, such as the transition from the Ediacaran to Cambrian marine biota, there is much more to learn about how taphonomic processes modulated the long term quality and quantity of the fossil record. Each innovation in organic structures, such as mineralized hard parts in animals and lignin in plants, provided new challenges to nutrient recycling and new opportunities for organisms to utilize these sources of energy for their own survival. Large scale changes in Earth's tectonic plates and climate have interacted with the taphonomic processing of organic carbon, sometimes (for example) leading to long-term storage of unrecycled plant remains in the form of coal. The Phanerozoic history of decomposer – i.e. taphonomic – players in the evolution of life and the workings of ecosystems offers many new opportunities for investigating how this critical ecological process helped to shape not only the fossil record but broader patterns of change in biological and geological systems over time.

How can taphonomy contribute to understanding our planet's future?

The field of Conservation Paleobiology (Dietl et al. 2015) is actively exploring how the dead, i.e., fossil and sub-fossil organic remains, can contribute to understanding what is happening to living organisms in recent environments affected by human impact. Shelly remains from marine communities accumulated over the past decades, centuries, and millenia provide evidence for biodiversity in the recent past and often are the only means of calibrating human impact. Pollen and spore records from similar time spans also document shifts in vegetation correlated with climate cycles, and surveys of bones in National Parks record decadal changes in animal populations. All of this evidence requires taphonomic analysis to show that observed differences are real signals of biological and environmental change and not the result of differential preservation or sampling biases. There is more information in taphonomic data that could indicate recent shifts in decomposition rates, time-averaging (e.g., through bioturbation), and levels of predation and scavenging – i.e., evidence of human impact on the workings of ecosystems as a whole. Such data can help us understand the interconnectedness and resilience of human-impacted ecosystems and use this knowledge to foster longer-term perspectives that will contribute to more informed conservation planning in the future.

Can taphonomy help us find evidence for life on other planets?

The rover-facilitated exploration of the surface of Mars, as well as other remote sensing methods, have led to questions about how evidence of Martian life might be recorded in rocks and surface chemistry. If there was life on early Mars, then we can expect that there were ecosystems with cycles of life, death, and decomposition, even if these were quite different from those on Earth. This new field of 'astropaleontology' includes taphonomy, and experts in microbial and chemical processes of decomposition and preservation are being consulted about the potential for fossils on Mars (McMahon et al., 2018). We cannot expect that fossils on other planets or moons (in the case of Jupiter) will be the same as on Earth, but knowing what occurs to preserve simple organic structures, such as microbial mat traces and stable isotopic biosignatures, provides important clues. In the case of Mars, consideration of preservation processes and sedimentology indicates that mudstones rich in silica and iron-bearing clays are promising sites for identifying fossils. Experimental work replicating geochemical conditions of early Mars, when conditions were more favorable for supporting life, offers another approach to inferring taphonomic processes on another planet. Continuing work on the preservation of simple organic traces and chemical signals in Earth's own early geological history will also be instructive. Expanded thinking about fossil preservation beyond our own planet is an exciting prospect for future taphonomic research.

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Smithsonian's Evolution of Terrestrial Ecosystems Program - people, research, publications, and databases, https://naturalhistory2.si.edu/ETE/index.html; https://naturalhistory.si.edu/research/paleobiology/research/evolution-terrestrial-ecosystems-program

Smithsonian's National Museum of Natural History tool for documentation of human skeletal remains, https://osteoware.si.edu/guide/taphonomy

University of California Museum of Paleontology information about fossilization and different kinds of fossils, https://ucmp.berkeley.edu/paleo/fossils/

Figure Captions

Figure 1. Taphonomy is the study of the transition of organic remains and traces from the biosphere to the lithosphere, and this diagram illustrates alternative pathways in this transition. Biological and geological processes that affect remains are represented by the filters that intervene between each type of organic remains (spheres), and the turbulent flow lines represent alteration in what passes through the filters. The same categories apply for all types of remains and traces in marine or terrestrial systems, although taphonomic processes differ across organisms and environments. Taphonomic feedback recognizes the impact that the direct return of dead remains may have on the living ecosystem. (Adapted from Behrensmeyer and Kidwell, 1985, Fig. 3)

Figure 2. Major stages (top to bottom) that organic remains pass through (left) before becoming part of the fossil record, sub-disciplines of the field of Taphonomy (right), with estimated relative importance of biological (green) versus geological (tan) for each stage (center). During life an organism has control over its body, but after death other biological processes take over to break down tissues and recycle nutrients. Geological processes usually become more important over time as biological processes taper off. Solid lines indicate the main focus in the sequence of stages of the three sub-disciplines of taphonomy, and dashed lines show varability in when different taphonomic processes can affect organic remains. Ultimately the survival of buried fossils (mineralized or not) in the geological record is subject to tectonic controls on the fate of depositional basins.

Biography and Photo

Anna K. Behrensmeyer (Photo credit: D. Patterson)

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Anna Katherine "Kay" Behrensmeyer is a Curator of Vertebrate Paleontology in Paleobiology at the Smithsonian's National Museum of Natural History and is recognized as a pioneer in taphonomy and the study of land environments and paleocommunities through geological time. Her paleontological and geological field research includes terrestrial deposits from Permian to Pleistocene age in North America, Pakistan, and Africa, with particular focus on the ecological context of human evolution. She also works in modern ecosystems to understand taphonomic processes that affect vertebrate preservation in the fossil record. Kay received her B.A. in geology from Washington University, St. Louis, and her Ph.D. in vertebrate paleontology and sedimentology from the Department of Geological Sciences, Harvard University. At NMNH, she has served as Acting Associate Director for Science, co-Director of the Evolution of Terrestrial Ecosystems (ETE) Program, and Deep Time Initiative Lead Scientist. She has established a National Taphonomy Reference Collection and mentored many individuals of diverse backgrounds in taphonomy, paleontology, and geology. She has over 160 scientific publications and has received career awards from the Society for Sedimentary Geology, Society of Vertebrate Paleontology, the Paleontological Society, and National Academy of Sciences. She was elected to the National Academy of Sciences in 2020.