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## Experimental analysis of soft-tissue fossilization: opening the black box

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**ABSTRACT**

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4 Taphonomic experiments provide important insights into fossils that preserve the remains of  
5 decay-prone soft tissues – tissues that are usually degraded and lost prior to fossilization. These  
6 fossils are among the most scientifically valuable evidence of ancient life on Earth, giving us a view  
7 into the past that is much less biased and incomplete than the picture provided by skeletal remains  
8 alone. Although the value of taphonomic experiments is beyond doubt, a lack of clarity regarding  
9 their purpose and limitations, and ambiguity in the use of terminology, are hampering progress.  
10 Here we distinguish between processes that promote information retention and those that promote  
11 information loss in order to clarify the distinction between fossilization and preservation.  
12  
13 Recognising distinct processes of decay, mineralization and maturation, the sequence in which  
14 they act, and the potential for interactions, has important consequences for analysis of fossils, and  
15 for the design of taphonomic experiments. The purpose of well-designed taphonomic experiments  
16 is generally to understand decay, maturation and preservation individually, thus limiting the number  
17 of variables involved. Much work remains to be done, but these methodologically reductionist  
18 foundations will allow researchers to build towards more complex taphonomic experiments and a  
19 more holistic understanding and analysis of the interactions between decay, maturation and  
20 preservation in the fossilization of non-biomineralized remains. Our focus must remain on the key  
21 issue of understanding what exceptionally preserved fossils reveal about the history of biodiversity  
22 and evolution, rather than on debating the scope and value of an experimental approach.  
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1 ARGUABLY the most scientifically valuable evidence of ancient life on Earth comes from fossils  
2 preserving remains of the decay-prone soft tissues (e.g. integument and muscle) that are usually  
3 degraded and lost prior to fossilization. These examples of 'exceptional preservation', and the  
4 fossil biotas from which they are recovered, represent invaluable fossil archives, giving us a view  
5 into the past that is much less biased and incomplete than the partial picture provided by skeletal  
6 remains alone. Recent technological and methodological advances have allowed the acquisition of  
7 progressively more detailed anatomical and chemical data on fossil soft tissues and, as a result,  
8 reports of high fidelity preservation of anatomy (at micro- and macro- scales) and biomolecules are  
9 expanding the known limits of morphological and chemical fossil preservation. One component of  
10 current advances in the field is a reinvigoration of experimental investigations into the taphonomy  
11 of non-biomineralized organisms and tissues: laboratory-based analyses of post-mortem decay,  
12 maturation and mineralization, and the implications for processes of fossilization of soft tissue  
13 remains and biomolecules (e.g. Raff *et al.* 2008; Sansom *et al.* 2010; Sansom *et al.* 2011;  
14 Cunningham *et al.* 2012a; Cunningham *et al.* 2012b; McNamara *et al.* 2013; Murdock *et al.* 2014;  
15 Colleary *et al.* 2015; Naimark *et al.* 2016). This type of taphonomic experiment, focused on non-  
16 biomineralized remains, is the subject of this contribution; throughout, all references to 'taphonomic  
17 experiments' do not include those designed to address questions of skeletal taphonomy. We use  
18 the terms 'soft tissues' and 'non-biomineralized tissues' interchangeably, and to include sclerotized  
19 tissues.

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40 The application of experimental taphonomy to exceptional preservation has developed over  
41 several decades (see Briggs and McMahon 2016 for a recent review), and has made major  
42 contributions to our understanding of how non-biomineralized tissues become fossilized.  
43 Experiments have provided significant insights, for example, into preservation of soft tissues  
44 through maturation and stabilization of organic compounds (e.g. Gupta *et al.* 2006; Gupta *et al.*  
45 2009), processes of microbially mediated authigenic mineralization (e.g. Sagemann *et al.* 1999),  
46 microbial pseudomorphing of soft tissues (e.g. Raff *et al.* 2008, 2013), and how non-random  
47 patterns of anatomical decay can introduce systematic biases into the interpretation of  
48 exceptionally preserved fossils (e.g. Sansom *et al.* 2010; Murdock *et al.* 2014).

1 The value of experimental and analytical approaches applied to the study of exceptionally  
2 preserved fossils is beyond doubt, but we identify two issues that are hampering further progress.  
3 First, a lack of clarity regarding the purpose and limits of experimental approaches, and second,  
4 ambiguity in the use of terminology. More precise use of language and greater clarity regarding the  
5 rationale for conducting taphonomic experiments will allow researchers to focus on the key issue of  
6 what exceptionally preserved fossils reveal about the history of biodiversity and evolution, rather  
7 than the scope and value of an experimental approach.  
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## 16 **DECAY, MATURATION, PRESERVATION AND FOSSILIZATION**

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19 Clarity regarding 'fossilization' and 'preservation' are clearly crucial to taphonomic analysis,  
20 otherwise we risk confusing processes with results, yet the terms are used interchangeably by  
21 some authors and to mean distinct and different things by others.  
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26 **Fossilization** is one outcome of the range of processes that affect an organism after death (Figure  
27 1). These processes cumulatively result in both loss and retention of information, and can balance  
28 out in different ways, with the most obvious alternative outcome to fossilization being non-  
29 fossilization - the loss of features or complete absence from the fossil record. Every part of every  
30 organism ends up somewhere on a spectrum from partial to complete non-fossilization. We focus  
31 here on decay, maturation and mineralization as distinct processes resulting in information  
32 retention (preservation) and information loss.  
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41 **Decay** is the post-mortem process by which original biomolecules, tissues and structures are  
42 degraded and lost through abiotic processes (such as chemical thermodynamics) and biotic  
43 processes, such as autolysis and microbially mediated decomposition. For many researchers, the  
44 antithesis of decay is preservation, but preservation is not the same thing as fossilization (see  
45 below).  
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51 **Preservation** refers to the processes that directly result in retention of information (Figure 1);  
52 processes by which inorganic and/or organic chemical activity replicates the form or converts the  
53 remains of non-biomineralized tissues into minerals (mineralization) and organic compounds that  
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1 are stable over geological timescales (maturation). This conversion can be via replacement or  
2 replication by minerals (mineralization), chemical transformation through maturation of organic  
3 compounds, or a combination. Different types of preservation may occur at different stages of  
4 decay and maturation. This definition of preservation is neither new nor out of step with its  
5 widespread use in the taphonomic literature; it serves merely to clarify the distinction between  
6 preservation and fossilization.  
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14 **Mineralization** is replacement or replication of non-biomineralized tissues by minerals. It can  
15 occur at any stage post-mortem, pre- or post-burial, early or late, and different modes of  
16 mineralization can act at different times (and under different conditions) in the taphonomic history  
17 of a fossil. Different modes of mineralization can occur in different parts within the same carcass,  
18 linked to differences in microenvironments (McNamara *et al.* 2009). Although many exceptionally  
19 preserved fossils have been mineralized, mineralization is not a requirement for exceptional  
20 fossilization.  
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29 **Maturation** of organic remains occurs post-mortem, mostly post-burial, primarily in the diagenetic  
30 realm, and can involve processes resulting in degradation and loss of biological information and/or  
31 processes resulting in stabilization of organic compounds such that they can survive over  
32 geological timescales. Maturation thus includes elements of both loss and retention of information,  
33 with preservation of organic remains through maturation involving in situ polymerization of more  
34 labile compounds (e.g. Gupta *et al.* 2006, 2009; McNamara *et al.* 2016).  
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42 Secondary transformations might be considered as an additional stage in the post-mortem history  
43 of a fossil. Like maturation, they can involve either loss or retention of information. Mineral  
44 replacements from early stages of preservation can be lost or altered by subsequent chemical  
45 activity under different conditions of diagenesis (iron sulfides converted to iron oxides, for  
46 example). And organic remains stabilized through low temperature polymerization might be  
47 oxidized, depolymerized or otherwise mobilized and lost during later, higher grades of maturation.  
48 Information loss through weathering will also be a factor, but we do not consider this further here.  
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1 Focussing on these processes of decay, mineralization and maturation clarifies the distinction  
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3 between fossilization and preservation: fossilization of an organism's remains is one outcome of  
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5 the balance and interactions between processes of information loss (decay and maturation) and  
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7 preservation (information retention via maturation and mineralization). This balance can be  
8  
9 expressed as two very simple equations:

- 12 1. processes of information loss > processes of information retention = no fossil
- 13  
14 2. processes of information loss < processes of information retention = fossil
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17 The balance and outcome reflected in equation 1 are far more prevalent than those of equation 2.

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20 Original biological tissues, or components thereof, are either lost or transformed into materials that  
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22 are stable over geological timescales, and the existence of a fossil, even the most exquisitely  
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24 preserved, does not imply survival of its biological information without alteration and loss. In these  
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26 terms, 'exceptional preservation' is shorthand for *part of the process* that results in exceptional  
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28 fossilization; we should not ignore the unexceptional aspects of information loss.

### 31 **THE RATIONALE FOR CONDUCTING TAPHONOMIC EXPERIMENTS**

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34 The goal of the vast majority of taphonomic experimental analyses is not 'experimental  
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36 fossilization': their aim is not to *replicate* the fossilization process in the laboratory or field. This is  
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38 because fossilization involves many variables, including both known and unknown unknowns, and  
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40 multiple confounding variables mean that - if our focus is on understanding the processes of  
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42 fossilization - the results of such fossil replication experiments, whether in general or for specific  
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44 Lagerstätten, are unlikely to tell us much of interest. While their success could be evaluated in  
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46 terms of whether they produce something that might look more or less like a fossil, the  
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48 experiments can reveal little if anything about the various processes involved in fossilization. This  
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50 is not to say that observations of what happens when organisms decay under natural conditions  
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52 have no place: these observations can provide useful constraints on the design of taphonomic  
53  
54 experiments, or guidance on what a fossil jellyfish might look like, for example. But crude  
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56 experiments that attempt to replicate fossilization without controlling variables are, in effect,



1 treating fossilization as a Black Box (Figure 2). To understand the processes that control  
2 information loss and information retention, the processes which ultimately produce the outcome of  
3 fossilization, we need to see inside the box.  
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8 This is the focus of robust taphonomic experiments: experimental decay, experimental maturation,  
9 and experimental preservation. The purpose of well-designed taphonomic experiments is generally  
10 to understand these processes individually (thus limiting the number of variables involved and  
11 making experiments tractable). In particular, robust taphonomic experiments investigate how  
12 specific variables, e.g. environmental pH, availability of ions, diffusion rate, burial temperature, etc.,  
13 have potentially affected the loss and retention of anatomical information and biased exceptionally  
14 preserved biotas.  
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23 A simplifying initial assumption of this reductionist approach is that there are no direct causal links  
24 between processes of decay, maturation and preservation. However, it is important to note that  
25 this assumption applies only to the *design* of taphonomic experiments and does not preclude  
26 finding evidence of links between the various processes of decay, preservation and maturation,  
27 either in fossil data or in experimental results (a good example being taphonomic experiments  
28 demonstrating that certain forms of mineralization require decay to establish the geochemical  
29 gradients across which they operate (Sagemann *et al.* 1999)). In general, analysing and  
30 understanding each of these processes is a prerequisite for clear understanding of potential  
31 interactions between them.  
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42 Recognising the distinction between processes, the sequence in which they act (Figure 1), and the  
43 potential for interactions, has important consequences for analysis of fossils; missing this point has  
44 led to some unjustified criticism of experimental approaches. There is no reason to assume, for  
45 example, that sequences of decay should provide a guide to sequences of preservation: decay  
46 commences first (Figure 1) and provides a timeline and pattern of morphological modification and  
47 loss — the products of decay, in the form of incomplete carcasses and decay-modified characters,  
48 are the substrate upon which the processes of maturation and mineralization act. It is the timing  
49 and interplay between processes of loss and retention that govern what anatomical structures,  
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1 tissues and biomolecules are ultimately fossilized, and this can be unravelled only if we understand  
2 the taphonomic patterns resulting from decay. Similarly, claims that decay experiments are not  
3 applicable to the fossil record because either the environment or the experimental taxon used is  
4 not a good analogue for what occurred in deep time are missing the point of controlled taphonomic  
5 experiments. The same is true of criticisms that taphonomic experimental models are not  
6 informative because fossilization in each deposit, taxon and even specimen reflects a suite of  
7 unique conditions. Were these criticisms to be levelled at experiments designed to transform  
8 carcasses into fossils, we would agree, but they carry little weight as arguments against the validity  
9 of taphonomic experiments as an approach to modelling the general parameters that control  
10 decay, maturation and mineralization and their respective roles in fossilization across  
11 environments and taxa.  
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#### 24 **TAPHONOMIC EXPERIMENTS AND COMPARATIVE ANATOMY OF EXCEPTIONALLY** 25 **PRESERVED FOSSILS** 26 27

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29 It is important to point out here that taphonomic experiments can be designed to address a range  
30 of different questions. For some, the goal is to understand the environmental conditions in which  
31 organisms decayed and were ultimately preserved (e.g. Plotnick 1986; Kidwell and Baumiller 1990;  
32 Hellawell and Orr 2012), or the degree to which a fossil biota is diminished in diversity by the loss  
33 of soft bodied organisms. In such cases taphonomic signatures are a proxy for palaeoenvironment  
34 or for faunal completeness, and the loss of anatomical information translates into gains in  
35 geological data.  
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44 For much recent work, however, the purpose of taphonomic experiments is to provide better data  
45 upon which to base interpretations of the anatomy of fossil organisms and, in turn, more accurate  
46 reconstructions of phylogenetic relationships and evolutionary patterns. These endeavours rely on  
47 comparative anatomical analysis, and when applied to exceptionally preserved non-biom mineralized  
48 fossils, this analysis is predicated on the assumption that differences between taxa are not simply  
49 the result of random taphonomic processes. This is a crucial point that is often overlooked,  
50 particularly in the most fundamental elements of comparative anatomy: the individuation of body  
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1 parts and characters, and determination of the suite of characters present in a taxon (see Rieppel  
2 and Kearney 2002 for discussion of individuation). Comparative analysis is possible only if the  
3 similarities and differences in characters reflect original anatomy and, critically, if taphonomic  
4 factors can be detected and taken into account. Furthermore, because comparative analysis  
5 ultimately requires comparison with extant organisms, investigators must distinguish differences  
6 that arise because of evolutionary history from those that simply reflect the incompleteness of the  
7 fossil (Donoghue and Purnell 2009). This decision can be based either on intuitions and  
8 assumptions, or on the crucial evidence generated by taphonomic experiments. We advocate the  
9 latter approach.

### 20 **TAPHONOMY, EXCEPTIONAL PRESERVATION, AND EXPERIMENTS - A WAY FORWARD**

23 The processes of decay, maturation and mineralization are controlled by diverse factors that vary  
24 both spatially and temporally in how they act. A focus of future studies must be on deconvolving  
25 the relative impact of these processes on our reading of the fossil record of exceptionally  
26 preserved organisms and particular Lagerstätten. In many exceptionally preserved fossils, the  
27 suite of characters present does not correspond to what might be predicted from a simplistic  
28 application of experimental decay results (i.e. the fossils are not simply a collection of the most  
29 decay resistant body parts). This is because the effects of preservational processes, sometimes  
30 highly selective with regard to tissue types, are superimposed upon the results of decay; it is false  
31 reasoning to suggest that fossilization of more than just decay resistant remains in itself indicates  
32 that patterns and sequences of character transformation and loss observed in experimental decay  
33 deviate from those that occurred in particular fossils. To use a specific example, invertebrate  
34 nervous tissues decay rapidly under controlled experimental conditions (e.g. Murdock *et al.* 2014,  
35 Sansom *et al.* 2015), yet mounting evidence supports the interpretation that some exceptionally  
36 preserved biotas include specimens with fossilized nervous tissues (e.g. Ma *et al.* 2012; Strausfeld  
37 *et al.* 2016). There is no conflict here: the fossils do not falsify the experiments, and the  
38 experiments do not falsify the anatomical interpretations of the fossils. Together they highlight a  
39 gap in our understanding of how nervous tissues become fossilized (Murdock *et al.* 2014). We  
40 argue that decay experiments are the best starting point for understanding the biases and filters of

1 fossilization because it is upon decayed remains that the processes of maturation and preservation  
2 must operate.  
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6 Further work is also required to better understand the processes of mineralization and authigenic  
7 mineral replication of original tissue. Despite experimental studies of the processes of replication of  
8 soft tissues in calcium phosphate (Briggs and Kear 1993a, b; Briggs and Wilby 1996) and in pyrite  
9 (Grimes *et al.* 2001, 2002) other authigenic minerals have received little attention (but see Martin  
10 *et al.* 2004; McCoy *et al.* 2015). Soft tissues may be preserved via multiple pathways in a single  
11 fossil (e.g. Butterfield 2002; McNamara *et al.* 2009) but the controlling factors have yet to be  
12 elucidated experimentally. Future studies focussing on these preservational processes will be  
13 especially critical for attempts to extract tissue-specific and taxonomic signatures from fossil  
14 specimens that preserve different tissues in different minerals. Similarly, greater understanding of  
15 how microbial communities are mediating both decay and mineralization is likely to yield significant  
16 new insights into preservational biases.  
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20 We have attempted here to clarify the essential elements and the terminology that form the  
21 conceptual framework of taphonomic experiments, and the value of considering decay, maturation,  
22 mineralization, and preservation as distinct but interacting processes. Greater emphasis on the  
23 rationale for conducting particular experiments will enhance experimental design, allowing  
24 taphonomists to construct more tightly constrained models of taphonomic processes. This  
25 reductionist approach allows us to see beyond the Black Box view of fossilization, and from these  
26 foundations we can build towards a more holistic understanding of the roles of — and interactions  
27 between — decay, maturation and preservation in the fossilization of non-biomineralized remains.  
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49 *Contributor statement.* MAP, SEG and DJEM outlined the framework for discussions, and these  
50 concepts were subsequently developed by all the authors. MAP produced the initial draft of the  
51 manuscript; all authors contributed to its subsequent development and are listed alphabetically.  
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6  
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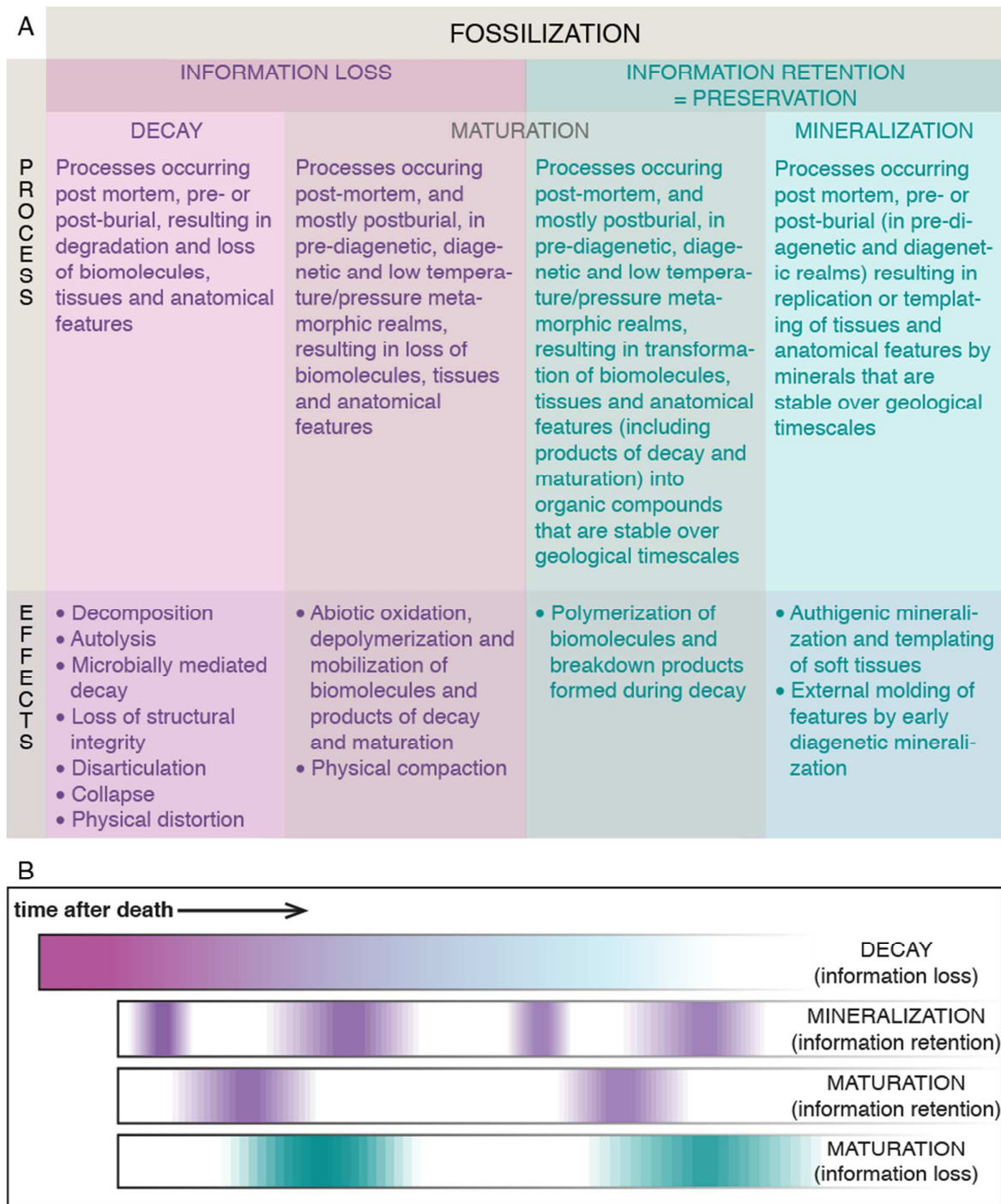


Figure 1. A. Terminology for processes involved in fossilization. B. The sequence of action, effects and potential timespan over which processes act. Processes are not continuous; intervals when processes (horizontal bars) are operating more intensely are shown by more intense colours; the relative timing and duration of periods of more intense loss and retention of information (via mineralization and maturation) are schematic. Decay starts before other processes but the potential timespan over which it operates is shorter. It is irreversible, and the rate of decay is not constant. Mineralization can start before maturation, but not before decay has commenced, and can occur at any subsequent point, although not continuously (multiple phases of mineralization are possible). Mineralization that post-dates decay can only preserve information previously retained through either mineralization or maturation. Maturation, both information loss and retention, can start before or after mineralization and can occur at any subsequent point. That maturation is a process that promotes both information loss and information retention does not imply separation of these processes in fossilization. The diagram does not attempt to show

1 interactions between processes, and should not be taken to imply, for example, that information  
2 loss and information retention through maturation occur simultaneously (although maturation can  
3 affect different tissues differently). Late stage information loss through weathering processes is not  
4 shown. 'Information', in the context of this figure, refers to primary anatomical, microanatomical  
5 and biochemical data, not information regarding the geological processes of fossilization and  
6 palaeoenvironment.  
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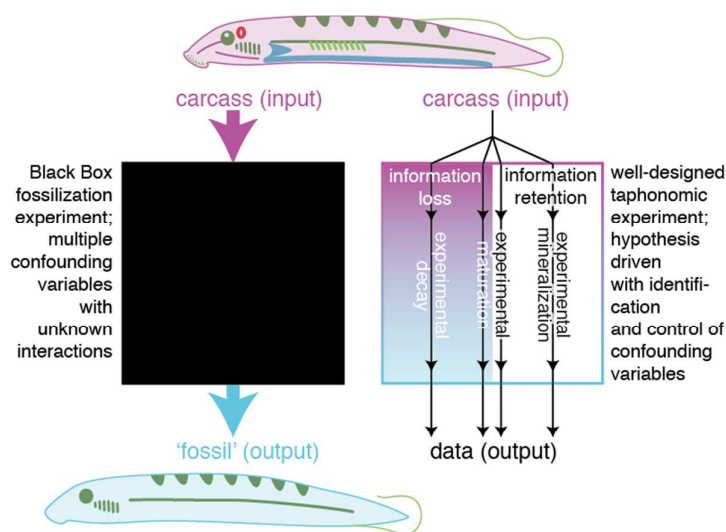


Figure 2. Cartoon illustrating the difference between experiments that attempt to replicate fossilization, treating the process as a black box, and those that focus on the processes of decay, maturation or mineralization. The black box approach reveals little about the processes of information loss and information retention, the cumulative effects and interactions of which ultimately results in a fossil (or, more often, not). Well-designed taphonomic experiments do not attempt to replicate fossilization and do not result in a fossil, but provide reproducible data concerning the processes of fossilization. An ideal taphonomic experiment, with all variables identified and controlled for, is rarely attainable in practice.

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### FOSSILIZATION

#### INFORMATION LOSS

#### INFORMATION RETENTION = PRESERVATION

##### DECAY

##### MATURATION

##### MINERALIZATION

Processes occurring post mortem, pre- or post-burial, resulting in degradation and loss of biomolecules, tissues and anatomical features

Processes occurring post-mortem, and mostly postburial, in pre-diagenetic, diagenetic and low temperature/pressure metamorphic realms, resulting in loss of biomolecules, tissues and anatomical features

Processes occurring post-mortem, and mostly postburial, in pre-diagenetic, diagenetic and low temperature/pressure metamorphic realms, resulting in transformation of biomolecules, tissues and anatomical features (including products of decay and maturation) into organic compounds that are stable over geological timescales

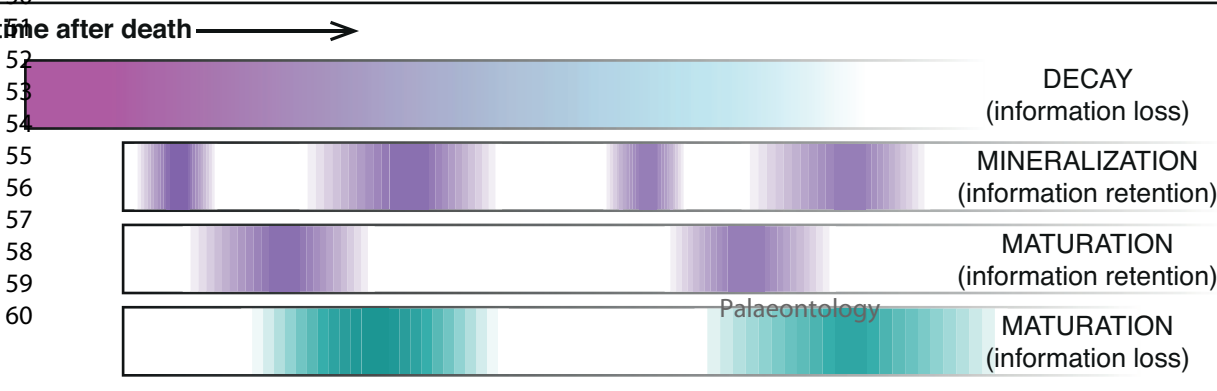
Processes occurring post mortem, pre- or post-burial (in pre-diagenetic and diagenetic realms) resulting in replication or templating of tissues and anatomical features by minerals that are stable over geological timescales

- Decomposition
- Autolysis
- Microbially mediated decay
- Loss of structural integrity
- Disarticulation
- Collapse
- Physical distortion

- Abiotic oxidation, depolymerization and mobilization of biomolecules and products of decay and maturation
- Physical compaction

- Polymerization of biomolecules and breakdown products formed during decay

- Authigenic mineralization and templating of soft tissues
- External molding of features by early diagenetic mineralization



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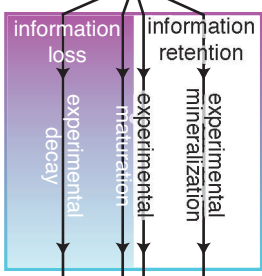


carcass (input)

carcass (input)



'fossil' (output)



data (output)

well-designed taphonomic experiment; hypothesis driven with identification and control of confounding variables

Palaeontology

