COMPARATIVE EXPERIMENTAL TAPHONOMY OF EIGHT MARINE ARTHROPODS INDICATES DISTINCT DIFFERENCES IN PRESERVATION POTENTIAL

by ADIËL A. KLOMPMAKER1,2, ROGER W. PORTELL1 and MICHAEL G. FRICK3

1Florida Museum of Natural History, University of Florida, 1659 Museum Road, PO Box 117800, Gainesville, Florida 32611, USA; adielkloampmaker@gmail.com
2Department of Integrative Biology & Museum of Paleontology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, Berkeley, CA 94720, USA
3Archie Carr Center for Sea Turtle Research & Department of Biology, University of Florida, PO Box 118525, Gainesville, FL 32611, USA

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Abstract: Global biodiversity patterns in deep time can only be understood fully when the relative preservation potential of each clade is known. The relative preservation potential of marine arthropod clades, a diverse and ecologically important component of modern and past ecosystems, is poorly known. We tackled this issue by carrying out a 205-day long comprehensive, comparative, taphonomic experiment in a laboratory by scoring up to ten taphonomic characters for multiple specimens of seven crustacean and one chelicerate species (two true crabs, one shrimp, one lobster, one hermit crab, one stomatopod, one barnacle and one horseshoe crab). Although the results are preliminary because we used a single experimental setup and algal growth partially hampered observations, some parts of hermit crabs, stomatopods, swimming crabs and barnacles decayed slowly relative to other parts, implying differential preservation potentials within species, largely consistent with the fossil record of these groups. An inferred parasitic isopod, manifested by a bopyriform swelling within a hermit crab carapace, decayed relatively fast.

We found limited variation in the decay rate between conspecifics, and we did not observe size-related trends in decay rate. Conversely, substantial differences in the decay rate between species were seen after c. 50 days, with shrimps and stomatopods decaying fastest, suggesting a relatively low preservation potential, whereas the lobster, calico crabs, horseshoe crabs and barnacles showed relatively slow decay rates, suggesting a higher preservation potential. These results are supported by two modern and fossil record-based preservation potential metrics that are significantly correlated to decay rate ranks. Furthermore, we speculate that stemward slippage may not be ubiquitous in marine arthropods. Our results imply that diversity studies of true crabs, lobsters, horseshoe crabs and barnacles are more likely to yield patterns that are closer to their true biodiversity patterns than those for stomatopods, shrimps and hermit crabs.

Key words: Arthropoda, biodiversity, Crustacea, decay, preservation, taphonomy.

U N D E R S T A N D I N G the fossil record and its biodiversity hinges on knowing how fossils preserve, the chances of fossilization and the preservation potential between clades. An assessment of the relative preservation potential between taxa can be performed in several ways: (1) comparing the fossil content of Konservat-Lagerstätten to fossils from coeval, nearby deposits; (2) comparing the fossil record to modern biota; and (3) comparative experimental taphonomy.

Whereas interpreting the taphonomy of the fossil record a posteriori can be very insightful, a priori experiments are extremely useful to better explain why organisms do or do not fossilize (Plotnick 1986) and the conditions required for preservation, even though only the initial stages of fossilization can be investigated. This has led to a surge in research involving taphonomic experiments, especially since the 1980s (e.g. Briggs 1995; Sansom 2014; Briggs & McMahon 2016). Experimental taphonomy has been widely used for a variety of clades, to decipher the decay rate of whole organisms or parts thereof (e.g. Raff et al. 2006; Sansom et al. 2010; Murdock et al. 2014; Nangl et al. 2015), the physical and chemical conditions that enhance the preservation potential and early mineralization of soft tissues (e.g. Briggs & Wilby 1996; Briggs 2003; Raff et al. 2006; Darroch et al. 2012), to reconstruct colour (McNamara et al. 2013a, b; Vinther 2015) and its implications for phylogeny including tests of stemward slippage, a process whereby
taphonomic loss of phylogenetically informative characters results in erroneously primitive phylogenetic placement of fossils (Sansom et al. 2010; Sansom & Wills 2013; Murdock et al. 2014; Nanglu et al. 2015), among others. Comparative experimental taphonomy, defined here as decay experiments in which multiple species are used and compared to each other, has been performed within some clades using a few taxa usually (Allison 1986; Sansom et al. 2010; Powell et al. 2011; Sigwart et al. 2014; Nanglu et al. 2015). Conversely, comparative experiments involving a range of species that differ substantially in morphology are rare (e.g. Parsons-Hubbard et al. 2008).

The same applies to experimental taphonomy of marine macroarthropods; rarely more than one species is used (Table 1). Comparing results of existing studies is difficult because of different experimental conditions and setups. This lack of knowledge severely hampers our understanding of the differential preservational biases across arthropod clades and, as a result, their true biodiversity through time, which is already confounded by their lower preservation potential compared to the more heavily calcified molluscs (e.g. Kidwell & Flessa 1995; Stempień 2005) and possibly also to tetrapods and fishes (Wills 2001). First-order biodiversity patterns through time of various arthropod clades have become increasingly well known recently (Sepkoski 2000; Klompmaker et al. 2013; Schweitzer & Feldmann 2014, 2015), but fully taking into account differential preservation between clades to better quantify diversity through time remains challenging. Comparative experimental taphonomy will help to improve our understanding of Phanerozoic arthropod biodiversity.

Although comparisons between taxa are highly problematic, previous work on individual arthropod species not involving tumbling experiments found that swimming shrimp disarticulated and fragmented within weeks to months in experimental setups (Plotnick 1986; Allison 1988; Briggs & Kear 1994). A lobster in the same experiment by Allison (1988) decayed slower: many fragments were left after 25 weeks. Stomatopod carcasses were still complete after 25 weeks into an experiment, but limbs had fallen off (Hof & Briggs 1997). Long-term experiments with true crabs (Callinectes sapidus) deployed in ocean settings within mesh bags showed that claws are the parts that preserve best after 2–13 years (Mutel et al. 2008; Parsons-Hubbard et al. 2008; Krause et al. 2011), and the same species used in an archaeological study on land also resulted in claws being most resistant to decay (Rick et al. 2015). Burial experiments using the crab Panopeus sp. showed disarticulation within two weeks, but fragmentation was still limited after ten months (Plotnick et al. 1988).

The aim of this research was to evaluate the relative preservation potential of eight marine macroarthropod clades by carrying out comprehensive comparative taphonomic experiments using multiple specimens of seven crustacean and one chelicerate species. Taphonomic experiments have also been carried out on a mm-sized brine shrimp which primarily lives in lakes (e.g. Gostling et al. 2009; Butler et al. 2015). Unlike our experiment, other investigations of marine arthropods were performed primarily to infer chemical changes or alteration of the cuticle (Poulicek et al. 1986; Schimmelmann et al. 1986; Baas et al. 1995; Stankiewicz et al. 1998; Gupta et al. 2006, 2009; Gupta 2014). We determined decay rate within and between macroarthropod species, and compared our results to the preservation of fossils from each clade and two preservation potential metrics based on the number of fossil and modern taxa.

### MATERIAL AND METHOD

#### Trial experiment

Because this is the first time that decay rates have been compared for different extant clades of arthropods in the

<table>
<thead>
<tr>
<th>Common name(s)</th>
<th>Taxon name(s)</th>
<th>Reference(s)</th>
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<tr>
<td>Shrimp</td>
<td>Pandalus danae Stimpson, 1857</td>
<td>Plotnick (1986)</td>
</tr>
<tr>
<td>Shrimp</td>
<td>Crangon crangon (Linnaeus, 1758)</td>
<td>Sagemann et al. (1999)</td>
</tr>
<tr>
<td>Lobster and shrimp</td>
<td>Nephrops norvegicus (Linnaeus, 1758) and Palaemon adspersus Rathke, 1837</td>
<td>Allison (1986, 1988)</td>
</tr>
<tr>
<td>True crab</td>
<td>Panopeus sp. Neogonoioactulus oerstedii (Hansen, 1895)</td>
<td>Plotnick et al. (1988)</td>
</tr>
<tr>
<td>True crab</td>
<td>Linulus polyphemus (Linnaeus, 1758)</td>
<td>Babcock &amp; Chang (1997); Babcock et al. (2000); Tashman (2014)</td>
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same experimental setup, a trial experiment was run first to determine the morphological characters best suited for comparing decay rates between arthropods and to test a compartmented saltwater aquarium (see below). One specimen each was used of the calico crab *Hepatus epheliticus* (Linnaeus, 1763), the swimming crab *Portunus gibbesii* (Stimpson, 1859), the pink shrimp *Penaeus duorarum* Burkenroad, 1939, the striped hermit crab *Clibanarius viitatus* (Bosc, 1802) as well as other arthropods including the mantis shrimp *Squilla empusa* Say, 1818, and the Atlantic horseshoe crab *Limulus polyphemus* (Linnaeus, 1758).

**Full experiment**

For the full experiment, five differently-sized live specimens of each species mentioned above were dispatched by freezing (as in Plotnick (1986), Plotnick *et al.* (1988), Gupta *et al.* (2006) and Krause *et al.* (2011)) in freshwater for c. 20 h and subsequently put on the bottom of saltwater aquarium compartments in a lab at the University of Florida (Fig. 1). Additionally, tens of specimens of the barnacle *Amphibalanus eburneus* (Gould, 1841) and one specimen of the blue spiny lobster *Panulirus versicolor* (Latreille, 1804) were added using the same procedure. Additional conspecific lobsters were not available at the start of the experiment. All species belong to marine arthropod clades (Crustacea and Chelicerata) that have an existing fossil record and these taxa are here considered to be morphologically representative of the clades they belong to. The specimens were not scrubbed or rinsed prior to placement into the aquarium to minimize damage to the specimens, but algae and invertebrates were removed around the barnacles where possible. All specimens originated from the Gulf of Mexico in the Florida panhandle region, except for *P. versicolor* from the Western Pacific or Indian Ocean. The live specimens were purchased from a local marine lab and an aquarium shop for the lobster. Transparent lids with holes for aeration were put on the compartments containing specimens to minimize the settling of dust and other particles into the aquarium. Four specimens were put in the lower and larger compartments, whereas two specimens were put into the smaller upper compartments. Specimens were placed about equidistantly and next to electrical tape with a width of 19 mm for scale. A pump in a separate basin allowed for continuous through-flow of artificial seawater at c. 36‰, especially in the uppermost part of the water column where the compartments were interconnected, whereas circular flow occurred in the rest of the water column. Through-flow ensured mixing of waters resulting in similar conditions for all specimens throughout the experiment. Artificial seawater was made by mixing dry or granular salt and dechlorinated freshwater. The aquarium lacked large-bodied scavengers and natural perturbations such as storms so that the decay process was dominated by microorganismal activities because microbial decay is a major determinant of preservation potential (Briggs & McMahon 2016, and references therein). No sediment was added to the bottom of the tank to ensure that all appendages could be readily observed. The specimens were not handled during the experiment and algal growth was not removed once it formed. The specimens were observed and photographed (requiring temporary removal of the transparent lids) about three times per week for the first three months. After these months, during which all relatively fast changes had occurred, the same procedure occurred about once a week until the end of the experiment after 205 days, when algal growth was judged to have become too pervasive to continue the experiment. Salinity was measured each time and distilled freshwater and saline water was added as needed to keep salinity levels near that of normal seawater. Temperature and other characteristics of the water, using an API saltwater master test kit (marine), were measured 4–5 times during the experiment. Experimental conditions in the water column were as follows (Klompmaker *et al.* 2017, table S1): salinity: 36.2 ± 1.7‰ (1 SD), n = 57; temperature = c. 21.3°C (n = 4); light conditions: 12 hours dark and 12 hours light per day; pH = 8.2 (n = 5); ammonia (NH₃/NH₄⁺): 0 ppm (n = 5); nitrate (NO₃⁻): ≤ 10 ppm (n = 5); nitrite (NO₂⁻): ≤ 5 ppm (n = 5). Since the compartments were in contact with the ambient air in the lab during the entire experiment, oxygen levels of the saltwater should not have varied and be in equilibrium with oxygen levels in the atmosphere (~9 mg/L; this does not necessarily apply to fluids within and around the

![FIG. 1. Full experimental setup of the compartmented aquarium. The basin with the pump for through-flow is located on the other side of the aquarium (not visible). Colour online.](image-url)
carcasses as demonstrated by Sagemann et al. 1999). The presence of oxygen does not appear to be a major control on the decay rate of arthropods (Plotnick 1986; Briggs & Kear 1994).

Based on observations from the trial experiment and previous taphonomic work on crustaceans (Plotnick 1986; Hof & Briggs 1997; Mutel et al. 2008; Krause et al. 2011) ten taphonomic characters were assigned scores as listed in Table 2. The wall plates of barnacles were herein considered analogous to the carapaces of other arthropods because they protect the soft tissues inside. Measurements were taken from each arthropod specimen prior to the start of the experiment using digital callipers (Klompmaker et al. 2017, table S2): carapace length, width and height; abdominal length and width; telson length and width; hermit crab gastropod shell height and width; minimum and maximum diameters of barnacles at the base. All experiments were carried out in accordance with local ethical guidelines.

**Data treatment**

The data (Klompmaker et al. 2017, table S3), consisting of 58 days during which observations were made over a time span of 205 days, were treated in multiple ways after digitization. For missing scores bracketed by scores on both ends (typically due to temporary algal coverage) the conservative lower score was chosen for all missing scores. In the rare case of missing scores bracketed by scores with a difference of two (e.g. 0 and 2), those scores and the mean are used divided evenly among the missing scores (for example, for 0, −, −, −, 2, the three missing scores are filled out as follows: 0, 0, 1, 2, 2), and when evenly dividing was not possible, the lowest score(s) were used to fill out the remaining missing scores (for example, 0, −, −, −, −, 2 becomes 0, 0, 0, 1, 2, 2). Specimens lifted by strings of algae (Fig. 2A) were typically not easily observable and remained floating. Scores attributed to these specimens, when recorded, were not included.

**Analytical methods**

After normalization of the data (i.e. each taphonomic character is equally weighted), two data sets were used: those with all taphonomic characters included (method 1) and a subset based on the articulation and fragmentation of calcified/chitinous parts of each taxon only (#1, 4, 6, 7, 9 and 10 from Table 1, method 2) because these parts have the highest chance of fossilization. Taphonomic scores were compared per species per character after normalization.

The data were analysed within species to assess whether differences in size affect decay rates. Additionally, possible differences between species were evaluated and we assessed whether variation within species differs from variation between species. Between species comparisons were done in two ways: first, scores from all conspecifics were averaged and, second, the lowest and highest score for each species was used to determine a range of taphonomic variability within a species. The low number of specimens per species (five as the maximum, except for barnacles that were not scored individually) in combination with the fact that only 73 days could be observed for all specimens due to algal growth does not allow for meaningful statistical analyses between species. Analyses were carried out in RStudio v 0.99.902 (https://www.rstudio.com).

To test whether the fossil record of the eight clades may be explained by the relative decay rate of the arthropod clades as found in our study, we calculated two preservation potential indices: (1) number of extant species/number of species in the Cenozoic fossil record (to reduce the possible influence of long-term changes in diversity in certain clades, the possible influence of mass extinctions and different times of origination); and (2) following Valentine et al. (2006), the percentage of genera with a missing fossil record. We then compared those metrics to the provisional rank based on our experiment using Spearman’s rank correlation coefficient and associated p-values using PAST 2.17 (https://folk.uio.no/ohammer/past/).

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**Table 2.** Taphonomic characters scored for the full experiment using marine macroarthropods.

<table>
<thead>
<tr>
<th>Taphonomic character</th>
<th>Score</th>
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<tr>
<td>1. Soft tissue presence</td>
<td>All present (0); some (1); none (2)</td>
</tr>
<tr>
<td>2. Cuticle colouration</td>
<td>Original (0); faded (1); discoloured/white (2)</td>
</tr>
<tr>
<td>3. Separation abdomen and carapace</td>
<td>No (0); yes (1)</td>
</tr>
<tr>
<td>4. Carapace completeness</td>
<td>Intact (0); abundant fragments (1); few fragments (2); no fragments (3)</td>
</tr>
<tr>
<td>5. Carapace translucency</td>
<td>No (0); yes (1)</td>
</tr>
<tr>
<td>6. Claw completeness</td>
<td>Whole, articulated (0); disarticulated, nearly whole (1); badly fragmented (2); absent (3)</td>
</tr>
<tr>
<td>7. Other appendage completeness</td>
<td>Whole, articulated (0); disarticulated, nearly whole (1); badly fragmented (2); absent (3)</td>
</tr>
<tr>
<td>8. Appendage translucency</td>
<td>No (0); yes (1)</td>
</tr>
<tr>
<td>9. Abdomen completeness</td>
<td>Whole, articulated (0); disarticulated, nearly whole (1); badly fragmented (2); absent (3)</td>
</tr>
<tr>
<td>10. Telson completeness</td>
<td>Intact (0); fragmented (1); absent (2)</td>
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RESULTS

Per-character per-taxon observations

Klompmaker et al. (2017, table S3, figs S1–S10) provide the full details of the per-character per-taxon decay scores, and the following summarizes the trends observed in Figure 3.

Soft tissue presence. Soft tissue decayed relatively uniformly commencing shortly after the start of the experiment (Fig. 3A). Within-species variation was limited to non-existent (Klompmaker et al. 2017, fig. S1). It appeared to occur slower within well-calciﬁed taxa (lobster, crabs) so that not all soft tissue had fully decayed at the end of the experiment. Soft tissue of other taxa (shrimp, stomatopods, barnacles, hermit crabs) had decayed entirely after c. 100 days. The first phase of decay in every arthropod studied was the development of a white coating (bacterial or fungal) around the parts that contain soft tissue, leading to a swollen appearance of specimens, although bottom currents also have some influence on the extent of the coating (Fig. 2B). This process occurred within days of putting the specimens into the aquarium and could take tens of days depending on the amount of decaying soft tissue inside the exoskeleton. A higher amount of decaying soft tissue resulted in a thicker coating, and odour was limited during the entire

FIG. 2. Various crustaceans in different stages of decay highlighting either important decay processes or differential preservation. A, the middle-sized specimen of the swimming crab *Portunus gibbesii* lifted by black algae 101 days into the full experiment; the ventral side of the crab with the abdomen of up to 10.4 mm wide can still be seen. B, the second largest swimming crab *P. gibbesii* with a white coating 7 days into the full experiment; note that the appendages, containing a limited amount of soft tissue, do not exhibit much coating; direction of bottom current is up. C, the smallest hermit crab specimen of *Clibanarius vittatus*, after losing its original colour, shows a better preserved anterior carapace compared to the posterior part, and has its telson and uropods preserved, whereas the abdomen had fully decayed after 75 days into the full experiment. D, raptorial dactyli preserve better than the remainder of the stomatopod body of *Squilla empusa* (diagonally toward upper left corner) 68 days into the full experiment; the two white points sticking out of the body remains, left of the centre of the image, most likely represent partly covered mandibles. E, the smallest swimming crab specimen of *P. gibbesii* showing translucent non-cheliped appendages and translucent eyes that have fallen out of their sockets 92 days into the full experiment. F, the chela and dactyli of other appendages decay slower than the rest of the hermit crab *C. vittatus* (photo from the trial experiment); length of left chela c. 10–15 mm. Scale bars (B–E) represent 10 mm. Colour online.
decay process. Some opercular plates (scuta and terga) of barnacles fell out of the wall plates surrounding them due to the swelling of internal tissue in the early phase of decay or due to their upside-down orientation after soft tissue holding them in place had decayed (Fig. 3, c. 100 days). The relatively soft eyes decayed relatively fast for each taxon: after c. 75 days most eyes had fully decayed, becoming translucent or shrinking substantially (Figs 2C, E, 4–5). The smallest hermit crab specimen exhibited a bopyriform swelling in the right branchial chamber (Fig. 6), almost certainly caused by a soft-bodied parasitic isopod such as a member of the Entoniscidae or, more likely, Bopyridae (e.g. McDermott et al. 2010; Williams & Boyko 2012; Boyko & Williams 2016). An outline of this isopod was seen at 25 days into the full experiment when the cuticle of the hermit crab appears to have been partially decayed, and a red spot marked the former position of this isopod at 75 days when the isopod had further decayed (Fig. 4).

**Cuticle colouration.** Cuticle discoloured in most species except for pink shrimp and barnacles, and was particularly apparent for both crabs and the hermit crabs (Fig. 3B; Klompmaker et al. 2017, fig. S2). Discolouration started within 100 days for nearly all specimens, with larger specimens losing their colour more slowly in some taxa. Within-species variation was limited to non-existent, with most variation occurring within both crab species and hermit crabs (Klompmaker et al. 2017, fig. S2).

**Separation of abdomen and carapace.** Separation of the abdomen from the carapace was observed for shrimps, stomatopods and hermit crabs, while this was not observed for other taxa (Fig. 3C). When it does occur, separation is visible usually within 50–100 days. Intraspecific variation is limited to non-existent with most variation occurring within hermit crabs (Klompmaker et al. 2017, fig. S3).

**Carapace completeness.** Disintegration of the carapace (Fig. 3D) commenced after c. 50 days for shrimps, stomatopods and hermit crabs, while it took 100–150 days for it to occur in swimming crabs. Other species showed no sign of carapace disintegration over the duration of the experiment (Fig. 3D). Intraspecific variation is limited to non-existent with most variation occurring within hermit crabs (Klompmaker et al. 2017, fig. S4).

**Carapace translucency.** It took c. 50 days for increases in the translucency of carapaces of shrimps, hermit crabs and horseshoe crabs to occur, while other taxa did not show any change throughout the experiment (Fig. 3E) with the exception of a single swimming crab (Klompmaker et al. 2017, fig. S5). Intraspecific variation is limited to non-existent for each taxon (Klompmaker et al. 2017, fig. S5). The anterior part of the carapace of hermit crabs became translucent at a slower pace than the less calcified posterior part (Fig. 2C).

**Claw completeness.** Claw fragmentation could not be recorded for horseshoe crabs, shrimps, barnacles and the lobster because these taxa did not exhibit a major claw. For other taxa, the claws of stomatopods decayed fastest (starting at c. 60 days), followed by those of hermit crabs and swimming crabs (starting at c. 75 days), while those of calico crabs started to disintegrate only after c. 110 days (Fig. 3F). Intraspecific variation is limited to non-existent for each taxon (Klompmaker et al. 2017, fig. S6). The raptorial dactyli and, most likely, the mandibles decayed much slower than the rest of the stomatopods (at least these dactyli were observed after 205 days) (Fig. 2D).

**Other appendage completeness.** The non-claw appendages, or all appendages for some taxa, decayed fastest for barnacles because they are non-calcified, followed by those of stomatopods and shrimps after c. 60 days (Fig. 3G). Appendages of other taxa disintegrated from 60 to 100 days onward. There is some variation within species, especially for horseshoe crabs, calico crabs, swimming crabs and hermit crabs, unrelated to the size of the arthropod (Klompmaker et al. 2017, fig. S7).

**Appendage translucency.** It was not possible to judge the translucency of appendages for barnacles (very small) and horseshoe crabs (covered by the carapace), but it increased for only the lobster and swimming crabs after c. 60 days (Fig. 3H). There was no variation within species for any taxa except for the swimming crabs in which limited variation was seen during days 60–85 (Klompmaker et al. 2017, fig. S8). The non-cheliped appendages of the swimming crabs became translucent first and may decay faster than other parts of this taxon (Fig. 2E). The chela and dactyli of other appendages of hermit crabs became translucent at a slower rate than other parts of the exoskeleton (Fig. 2F).

**Abdomen completeness.** The abdomina of hermit crabs, stomatopods and shrimps decayed fast after c. 50 days, whereas no noticeable fragmentation was observed for horseshoe crabs or the lobster (Fig. 3I). It was not feasible to quantify the decay of the abdomina for either of the crab species or the barnacles (not visible in all cases). Variation within species is limited to non-existent, except for hermit crabs, where the abdomen of the smallest hermit crab decayed faster than that of conspecifics (Klompmaker et al. 2017, fig. S9).
Telson completeness. Disintegration of the telson was fastest for shrimps, followed by that of stomatopods and the lobster (Fig. 3J). The telson of the horseshoe crab did not change noticeably and neither did that of the hermit crabs, although the telson of hermit crabs is relatively small. Telson decay could not be scored for either the

<table>
<thead>
<tr>
<th>0 days</th>
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**FIG. 4.** Differential decay rates during the full experiment over the course of 100 days for the smallest specimens of eight clades of marine arthropods. Algal growth changed the colour of the bottom of the aquarium, and black algae surrounded and lifted some specimens (Fig. 2A). All scale bars (first column) represent 10 mm. Colour online.
crabs or the barnacles. Variation within species is limited to non-existent (Klompmaker et al. 2017, fig. S10). Not only the telson but also the uropods of the hermit crabs decayed more slowly than the abdomen, the posterior

**FIG. 6.** The smallest specimen of the hermit crab *Clibanarius vittatus*, with a bopyriform swelling (ichnotaxon *Kanthyloma crusta*) in its right branchial chamber, almost certainly caused by a parasitic isopod. A, dorsal view. B, right lateral view. Both scale bars represent 10 mm. Colour online.

**FIG. 5.** Rapid fragmentation within six days of a specimen of the stomatopod *Squilla empusa* (A–D) after soft tissue had decayed during the trial experiment. Carapace length = 22.6 mm; abdomen length = 51.1 mm; telson length = 15.0 mm. See also Klompmaker et al. (2017) for time-lapse movie of this process. Colour online.
carapace region and the non-cheliped appendages (Fig. 2C).

Comparative taphonomic analyses

Comparison within taxa. Under the experimental conditions, distinct increases in the taphonomic scores occurred from c. 50 days for most specimens and both methods (Figs 7–8). Differences in decay rates between conspecific specimens appeared to be limited as the trajectories of most taxa are tightly spaced, except for the swimming and hermit crabs where the smallest specimen of both taxa decayed relatively fast. No obvious size-related structuring of decay trajectories was observed, although the geometric size differences of carapaces are limited for some taxa (the largest was 33–132% larger than the smallest, see Klompmaker et al. 2017, table S2). This lack of size-related structuring suggests that comparisons between taxa may be meaningful.

Comparisons between taxa. Differences between species appeared after c. 50 days (Fig. 9) when using all ten scored taphonomic characters (Fig. 9A) as well as for the six characters with the highest chance of fossilization (Fig. 9B). Subsequently, pink shrimps decayed fastest followed by stomatopods for both methods. There is separation between the lowest scores of the five shrimp specimens and the highest scores for stomatopods for the first method, suggesting that decay differences are meaningful, whereas there is some overlap using the second method. Barnacles show different trajectories for the two methods because the non-calcified appendages decayed fast, but only calcified parts were included for the second method. The swimming crabs, horseshoe crabs, hermit crabs and the lobster show overlap for the available trajectories. Using method 1, the calico crabs appear to have experienced the slowest decay rates and show no overlap with others, even for their highest taphonomic scores. Horseshoe crabs show overlapping scores with calico crabs for method 2, even though the horseshoe crabs could be observed for <100 days only. In summary, shrimps and stomatopods decayed fastest, whereas calico crabs experienced the slowest decay rate for method 1. The fastest decaying taxa were the same for method 2, but barnacles decayed more slowly than calico crabs.

The results are supported by the modern and fossil record of these arthropods based on two preservation potential metrics (Table 3). Both the decay rate rank vs percentage of genera missing from fossil record and decay rate rank vs extant species/species in Cenozoic fossil record are significantly correlated (Spearman $r_s = 0.955$, $p = 0.003$; Spearman $r_s = 0.937$, $p = 0.005$; respectively). These results suggest that decay rate is an important factor of the apparent diversity of fossil arthropods.

DISCUSSION

Sources of variation

Algal growth occurred frequently during the full experiment. Black and green covers on the bottom of the compartmented aquarium and specimens temporarily hampered observations, and later dark green–black masses and strings developed in the water column and ultimately lifted multiple specimens. This lifting is the prime reason that observations could not be continued for those specimens. As none of the specimens were scrubbed prior to placement into the aquarium, algae could have grown from insignificant amounts on any of the specimens. However, the most likely source of algal growth were the barnacles, having the most noticeable amounts of algae on both them and their attachment substrate (plastic hose), even though an attempt was made to remove algae. This hypothesis is supported by the fact that the trial experiment, for which algal growth was more limited during the first 100 days, did not include barnacles with algae growing on them. Although we were primarily interested in decay rate between taxa instead of absolute decay rates, algal growth may have influenced the decay rate by encasing the specimens when the specimens were still on the bottom so that disarticulation was inhibited. Future work will attempt to minimize algal growth so that the decay process can be observed more continuously and for a longer duration.

It is possible that the absolute decay rate was influenced by the method of dispatching the specimens. Freezing in freshwater may have loosened the cuticle, although we did not note any major damage afterwards, and may have harmed microbes that are critical in the decay process so that results may not entirely mimic of what would happen on the seafloor. The relative decay rate, the main factor of interest herein, may not have been altered substantially because circumstances were similar for each specimen. Additionally, the sequence of morphological changes is unlikely to be affected by different boundary conditions (e.g. Briggs 1995).

Implication for the preservation of eyes

The study of the evolution of vision hinges largely on preserved eyes (e.g. Aberhan et al. 2012) although socket size has been used as a proxy for eye size (e.g. Klompmaker et al. 2016). Ample research on the vision of other arthropods such as trilobites has been performed (e.g.
FIG. 7. Per-specimen per-species scores using all taphonomic characters. Carapace size represents the geometric mean of the length, width and height. The lines discontinue once a specimen is picked up by algal strings. A, horseshoe crabs (*Limulus polyphemus*). B, calico crabs (*Hepatus epheliticus*). C, swimming crabs (*Portunus gibbesii*). D, hermit crabs (*Clibanarius vittatus*). E, pink shrimps (*Penaeus duorarum*). F, stomatopods (*Squilla empusa*). G, barnacles (*Amphibalanus eburneus*). H, lobster (*Panulirus versicolor*).
Clarkson 1979; Schoenemann & Clarkson 2013, 2017; Tanaka et al. 2015) due to the calcified lenses of their compound eyes. Although the primarily less-calcified eyes of other marine arthropod groups including crustaceans can preserve in Konservat-Lagerstätten, the stratigraphic record of such eyes is patchier (e.g. Tanaka et al. 2009; Paterson et al. 2011; Schoenemann et al. 2012; Anderson et al. 2014; Audo et al. 2016; Poschmann et al. 2016; Vannier et al. 2016). Our experiment suggests that the relatively fast decay of eyes relative to other parts of the arthropod body explains the patchy record of poorly calcified eyes. Specimens that do show such eyes were preserved under favourable taphonomic conditions.

**Implications for the preservation of individual taxa**

Little differential decay within species was observed for pink shrimps, horseshoe crabs, calico crabs and the lobster, but longer experiments for the latter three taxa may show that some hardened parts decay faster than others. Since most pink shrimps had largely or entirely decayed without leaving identifiable hard parts during the trial and full experiments prior to being lifted by algae, either none or a great portion of the shrimp body could be expected to be preserved as a fossil. This hypothesis is largely consistent with the fossil record of shrimp that are capable of swimming (Dendrobranchiata and Caridae) which yields specimens that are often complete or nearly so (e.g. Carriol & Riou 1991; Schweigert & Garassino 2004; Feldmann & Schweitzer 2010; Audo & Charbonnier 2013; Garassino et al. 2013; Huang et al. 2013; Pinheiro et al. 2014; Schweitzer et al. 2014; Winkler 2016). Such specimens are predominantly preserved under favourable preservational conditions in thinly-bedded limestones of Konservat-Lagerstätten.

Conversely, differential preservation potential of parts of specimens of barnacles, swimming crabs, hermit crabs and mantis shrimps were observed. As would be expected based on the outcome of the full experiment, barnacle

![Graph A: Comparisons of taphonomic scores between arthropod species. Mean taphonomic scores per species using ten (A) and six (B) characters. Shaded bands represent the minimum and maximum scores for five specimens per species using ten (C) and six (D) characters (barnacles and lobster are excluded). The lines and bands discontinue when one of the specimens per species is lifted by algal strings.](image)
Data on the modern and fossil record of the marine macroarthropod clades studied followed by metrics of preservation potential including one based on our experiment with the lowest number representing the lowest observed decay rate.

<table>
<thead>
<tr>
<th>Common name(s)</th>
<th>Clade name(s)</th>
<th>Extant species</th>
<th>Extant genera</th>
<th>Species found as fossils</th>
<th>Species in Cenozoic fossil record</th>
<th>Extant species with fossil record</th>
<th>Extant genera with fossil record</th>
<th>Extant species/species in Cenozoic fossil record</th>
<th>% Genera missing from fossil record</th>
<th>Provisional rank our experiment (using Fig. 9B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hermit crabs</td>
<td>Paguroidea</td>
<td>1057</td>
<td>120</td>
<td>128</td>
<td>60</td>
<td>16</td>
<td>13</td>
<td>17.6</td>
<td>89.2</td>
<td>5</td>
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<tr>
<td>True crabs</td>
<td>Brachyura</td>
<td>6559</td>
<td>1298</td>
<td>2057</td>
<td>1564</td>
<td>276</td>
<td>253</td>
<td>4.2</td>
<td>80.5</td>
<td>3</td>
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<tr>
<td>Swimming shrimps</td>
<td>Caridea and Dendrobranchiata</td>
<td>3808</td>
<td>436</td>
<td>155</td>
<td>32</td>
<td>0</td>
<td>10</td>
<td>119.0</td>
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<td>Lobsters</td>
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<td>833</td>
<td>74</td>
<td>515</td>
<td>37</td>
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<tr>
<td>Horseshoe crabs</td>
<td>Xiphosura</td>
<td>4</td>
<td>3</td>
<td>46</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>4.0</td>
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<td>2</td>
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<td>Stomatopods or mantis shrimps</td>
<td>Stomatopoda</td>
<td>449</td>
<td>111</td>
<td>33</td>
<td>18</td>
<td>0</td>
<td>7</td>
<td>24.9</td>
<td>93.7</td>
<td>6</td>
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<tr>
<td>Barnacles</td>
<td>Cirripedia (Thoracica)</td>
<td>809</td>
<td>152</td>
<td>497</td>
<td>364</td>
<td>64</td>
<td>62</td>
<td>2.2</td>
<td>40.8</td>
<td>1</td>
</tr>
</tbody>
</table>

The ranks for lobsters and crabs are the same because the trajectory for the lobster is in between that the two crabs (Fig. 9B). Data sources: Foster & Buckeridge (1987); Hauschke & Wilde (2004); Schram & Müller (2004); De Grave et al. (2009); Klompmaker et al. (2013); Lamsdell (2016); Paleobiology Database.
wall plates and opercular plates are often found in the fossil record (e.g. Darwin 1855; Buckeridge 1983; Zullo 1992; Carriol & Schneider 2013; Collins et al. 2014; Gale & Sørensen 2015; Klompmaker et al. 2015a; Koči et al. 2015) whereas soft tissue preservation (including the appendages) is extremely rare (Briggs et al. 2005). The same applies to swimming crabs because often only the chelipeds, carapace and/or ventral side of fossil members of swimming crabs (Portunidae) are preserved (e.g. Vega et al. 1999; Schweitzer & Feldmann 2000; Beschin et al. 2001; Nyborg et al. 2003; Varela & Schweitzer 2011). However, chelipeds and carapaces are more diagnostic and therefore end up more often in the taxonomic literature than other appendages do.

Although hermit crab inhabitation of now fossilized gastropods can be recognized (Walker 1992), the hermit crab body fossil record is dominated by chela (e.g. Aguirre-Urreta & Olivero 1992; Fraaije 2003; Crónier & Courville 2004; Beschin et al. 2007; Schweigert et al. 2013; Hýzny et al. 2016) but also increasingly by isolated sixth abdominal tergites (mostly ascribed to (para)pylochelids) and anterior parts of carapaces (e.g. Van Bakel et al. 2008; Fraaije et al. 2012a, b, 2013, 2014; Fraaije 2014) whereas only two nearly complete fossil hermit crab specimens are known to date (Garassino et al. 2009; Schweigert et al. 2013). The hermit crab in this study, Clibanarius vitatus, is a member of the Diogenidae and does not have a strongly calcified sixth abdominal tergite (rather, weakly calcified remnants of the abdominal segment(s) are present), but our observations indicate that chela, dactyli of other appendages, the anterior part of the carapace and the telson have a relatively high preservation potential for this taxon. This hypothesis largely agrees with the fossil record of paguroids (see references above) but isolated fossil non-cheliped dactyli and telsons would be difficult to ascribe to hermit crabs because of a lack of diagnostic characters for assigning them to hermit crabs. Moreover, hermit crab telsons are difficult to find due to their small size.

In agreement with Hof & Briggs (1997, p. 435), our results indicate that raptorial dactyli of stomatopods have a relatively high preservation potential. These dactyli have indeed been fairly well-documented in the fossil record of stomatopods, either as part of the stomatopod body under favourable preservational circumstances (e.g. De Angeli & Messina 1996; Hof & Schram 1998; Jenner et al. 1998; De Angeli & Beschin 2006; Ahyong et al. 2007; Cunningham et al. 2008; Haug et al. 2010) or as isolated elements (e.g. Hof & Briggs 1997; De Angeli & Beschin 2006; Ando et al. 2013, 2015, 2016, Haug et al. 2013, 2016). We also noted the presence of likely mandibles well after the stomatopod body had disintegrated (Fig. 2D) and they have been found as fossils in (near) complete specimens occasionally (Jenner et al. 1998; Haug et al. 2010, 2015) but also in isolation (Ando et al. 2013, 2015, 2016). The fact that isolated raptorial dactyli and mandibles are not often figured relative to (nearly) complete stomatopods in the fossil record (Hof & Briggs 1997, table 4) despite their higher preservation potential, suggests that these dactyli are under-represented in the literature, probably because they are not recognized and/or related to the fact that isolated raptorial dactyli may have limited taxonomic value (see also below).

Bopyriform swellings (Fig. 6), termed Kanthyloma crusta Klompmaker et al., 2014, are well-known from the fossil record (e.g. Wienberg Rasmussen et al. 2008; Klompmaker et al. 2014; Klompmaker & Boxshall 2015) but body fossils of the inferred isopod culprits are unknown from within decapod fossils. Our results directly show that these isopods decay fast, also compared to their host, and are unlikely to preserve unless early mineralization has halted decay.

**Implications for biodiversity patterns**

Although our results are preliminary because of one experimental setup and algal growth hampering observations, the differences in relative decay rates between the eight clades may shed light on the abundance and diversity of fossil arthropods. The different decay rates may at least in part be explained by the degree of calcification and the overall cuticle thickness (cf. Amato et al. 2008; Mutel et al. 2008). The moderate to low decay rates of horseshoe crabs, as also observed by others in mostly tumbling experiments (Babcock & Chang 1997; Babcock et al. 2000; Tashman 2014), are consistent with the suggestion that the chitinous exoskeleton of horseshoe crabs is resistant to decay (Baas et al. 1995) compared to other arthropods studied herein. Moreover, chitin is known from the fossil record (Stankiewicz et al. 1997; Ehrlich et al. 2013). Thus, the observed relatively low genus and species richness of xiphosurids through the Phanerozoic (Rudkin & Young 2009; Lamsdell 2016, fig. 2) is not as severely influenced by preservational factors as hypothesized (Rudkin & Young 2009), but may have some biological implication in that their fossil record, although incomplete, was never as rich as for the other crustacean clades studied herein.

Similarly, our experiment suggests that barnacles have a relatively high preservation potential, although their genus and species richness throughout the Phanerozoic is not extremely high with 93 genera and 497 species reported (Foster & Buckeridge 1987; Sepkoski 2000). This pattern of low diversity can at least in part be explained because sediments deposited in the intertidal range, where many barnacles live today, are prone to erosion. There is also a paucity of barnacle systematists.
As for the horseshoe crabs and barnacles, the two brachyuran crabs and the lobster species also show relatively low decay rates, indicating that they may preserve reasonably well. Unlike xiphosurids and the Cirripedia however, at least the true crabs have a relatively rich fossil record with >2000 species of true crabs (infraorder Brachyura), whereas c. 550 lobster species (infraorders Polychelida, Glyphheida, Astacidea and Achelata) are known (De Grave et al. 2009; Schweitzer & Feldmann 2014). The diversity and body size of true crabs and lobsters first increased significantly as part of the Mesozoic decapod revolution (Klompmaker et al. 2013, 2015b), followed by a decrease in raw genus richness for lobsters (Schweitzer & Feldmann 2014) and an increase in raw brachyuran species richness (Schweitzer & Feldmann 2015).

The preservation potential of hermit crabs, as determined by our experiment, relative to other clades requires more research because many of the specimens were covered by too much algae during the greater portion of the 205 day survey, except for the smallest specimen. Nevertheless, their decay rate appears to have been slower than that of shrimps and stomatopods, supported by observations during the trial experiment. This hypothesis is confirmed by their comparatively decent fossil record starting in the Jurassic (e.g. Schweigert et al. 2013; Fraaije 2014) although taxa are often based on isolated chela, carapaces and sixth abdominal tergites (i.e. parataxonomies), and linking carapaces to tergites (as attempted first by Fraaije et al. 2013) and ultimately chela will be necessary to assess the true diversity of paguroids. This relatively decent fossil record is supported by the preservation potential metrics based on the modern and fossil record (Table 3).

The relatively fast decay rates of stomatopods and shrimps suggest a low preservation potential for these taxa. Indeed, the fossil record of stomatopods consists of 33 species while only 155 fossil species of Caridea and Dendrobranchiata were known in 2009 (Table 3). Preservational circumstances must be ideal for entire stomatopods to preserve, which is consistent with the fact that they are often reported from Konserat-Lagerstätten (Hof & Briggs 1997; Hof 1998). Our experiment shows that raptorial dactyli have a relatively high preservation potential, yet their fossil record is sparse (Hof & Briggs 1997; Hof 1998). Assigning isolated raptorial dactyli to lower taxonomic ranks appears to be difficult, especially for taxa that may not have modern representatives (see also Haug et al. 2013, 2016), but further investigation appears warranted.

The fossil record of the shrimps (Caridea and Dendrobranchiata) is very fragmentary with major occurrences in Mesozoic Konserat-Lagerstätten (e.g. Carriol & Riou 1991; Schweigert & Garassino 2004; Klompmaker et al. 2013; Santana et al. 2013). However, they also occur as fairly complete specimens in Cenozoic deposits occasionally (e.g. Garassino & Teruzzi 1996; Garassino & Jakobsen 2005; Garassino et al. 2014). Since they usually have no parts with a high preservation potential, this pattern is not expected to change with targeted searches in other deposits. Diversity analyses focusing on shrimps or including shrimps as a major component will not yield biologically meaningful patterns. The fact that shrimps decay faster than stomatopods was also pointed out by Hof & Briggs (1997), who compared results from a previous study with the same experimental setup as theirs. This similarity suggests that relative decay rates based on one or a few taxa may be generalized for this entire group. The difference in decay rate between stomatopods and shrimps appears to be related the larger proportion of decay-resistant chitin in stomatopods (Hof & Briggs 1997).

### Table 4

<table>
<thead>
<tr>
<th>Common name(s)</th>
<th>Clade name(s)</th>
<th>Characters commonly used for species-level assignment in fossils</th>
<th>Well-preserved at end experiment or last element preserved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hermit crabs</td>
<td>Paguroidea</td>
<td>Carapaces and/or claws or sixth abdominal tergites</td>
<td>Claw, anterior part carapace</td>
</tr>
<tr>
<td>True crabs</td>
<td>Brachyura</td>
<td>Carapaces and/or claws</td>
<td>Carapaces and claws</td>
</tr>
<tr>
<td>Swimming shrimps</td>
<td>Caridea and Dendrobranchiata</td>
<td>Rostrum, carapace, abdomen and/or appendages</td>
<td>All</td>
</tr>
<tr>
<td>Lobsters</td>
<td>Polychelida, Glyphheida, Astacidea and Achelata</td>
<td>Carapace, abdomen and/or claws</td>
<td>Carapace and abdomen</td>
</tr>
<tr>
<td>Horseshoe crabs</td>
<td>Xiphosura</td>
<td>Prosome and opisthosoma</td>
<td>Prosome, opisthosoma and telson</td>
</tr>
<tr>
<td>Stomatopods or mantis shrimps</td>
<td>Stomatopoda</td>
<td>Telson, abdomen and/or carapace</td>
<td>Raptorial dactyli and mandibles</td>
</tr>
<tr>
<td>Barnacles</td>
<td>Cirripedia (Thoracica)</td>
<td>Wall and opercular plates</td>
<td>Wall and opercular plates</td>
</tr>
</tbody>
</table>
Stemward slippage in arthropods?

Stemward slippage can occur when phylogenetically important characters decay faster than less informative characters, as shown for chordates and vertebrates (Sansom et al. 2010, 2011) but not for hemichordates and velvet worms (Murdock et al. 2014; Nanglu et al. 2015; Bel et al. 2017). Of the ten taphonomic characters scored (Table 2), four may be used to evaluate stemward slippage: carapace completeness, claw completeness, abdomen completeness and telson completeness. These are all characters that are used frequently in erecting fossil species of the arthropod clades herein (Table 4). Pronounced differential decay occurred in the hermit crab and stomatopod species. The characters that decay relatively slowly for hermit crabs are frequently used to determine fossil taxa to the species-level (Table 4). Conversely, the decay-resistant elements of stomatopods, isolated raptorial dactyls and mandibles, cannot be used for species-level ascription generally, but genus- and family-level assignments may be possible (Ahyong et al. 2013; Ando et al. 2013, 2015, 2016; Haug et al. 2016). Thus, stemward slippage may occur for stomatopods. Other arthropods herein showed a lower degree of differential decay and the parts that appear to preserve best are often used for species-level ascriptions (Table 4). Although more detailed analyses are needed to determine whether stemward slippage is an issue for arthropods, we speculate that stemward slippage may not be ubiquitous in marine arthropods because decay-resistant characters are usually phylogenetically informative for low taxonomic ranks.

CONCLUSIONS

1. Some parts of the exoskeletons decayed slower than others, and thus have a higher preservation potential for that taxon. For the taxa studied herein, these include the claws, non-cheliped dactyls, anterior portion of the carapace and the telson/uropod region of hermit crabs; the raptorial dactyls and probably also mandibles of stomatopods; the carapace and chelipeds of swimming crabs; and the wall and opercular plates of barnacles. The fossil record of these groups is largely consistent with these observations.

2. An inferred parasitic isopod inside a bopyriform swelling (ichnotaxon *Kanthyloma crusta*) in the right branchial chamber of the smallest hermit crab carapace decayed relatively fast. Such isopods are unlikely to be preserved.

3. Limited variation existed within the decay rate between specimens of the same arthropod species in our experiment, and we did not observe obvious size-related trends in decay rates.

4. Major differences were apparent in the decay rates between species, with shrimps and stomatopods decaying fastest, whereas the lobster, calico crabs, horseshoe crabs and barnacles showed relatively slow decay rates. Barnacles had the slowest decay rate when only calcified/chitinous parts were evaluated.

5. The results of our experiment are supported by two preservation potential metrics using the modern and fossil record of the studied arthropod clades.

6. We speculate that stemward slippage may not be ubiquitous in marine arthropods.

7. Our results provide an improved framework for understanding arthropod biodiversity through time. Diversity studies of brachyuran crabs, lobsters, horseshoe crabs and barnacles are more likely to yield patterns that are closer to their true biodiversity than those for stomatopods, shrimps and hermit crabs.

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DATA ARCHIVING STATEMENT

Data for this study (3 supplementary tables, 10 figures and 1 movie) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4j7r

Editor. Andrew Smith

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