

# Decay experiments on shrimps provide insight into the fossilisation potential of arthropod appendages

Nora Corthésy<sup>a,1</sup>, Gaëtan J.-M. Potin<sup>a,1</sup>, Alexandre Torchet<sup>a</sup>, Ian Quintas<sup>a</sup>, Yu Wu<sup>a,b</sup>, Sinéad Lynch<sup>a</sup>, Allison C. Daley<sup>a</sup>, and Farid Saleh<sup>a,2</sup>

Decay experiments on organisms under controlled laboratory conditions provide a powerful tool for understanding the preservation potential of organisms in the rock record. These experiments have been applied to numerous animal groups, including but not limited to echinoderms, annelids, priapulids, chordates, and arthropods. However, little work has focused on the degradation of arthropod appendages, despite their abundance in many fossil sites. Here, we compare the decay of appendages in freshwater and saltwater shrimps. Setae on these appendages are preserved in minute detail and do not exhibit signs of degradation, even after the appendages have separated from the body. The results are then compared to appendage preservation patterns in the fossil record with a particular focus on radiodonts since their taxonomy and palaeoecology largely rely on the shape and fine details of their frontal appendages. We suggest that radiodont appendages with differences in setal number are unlikely to represent taphonomic variations of the same species but are more likely to belong to different taxa.

Experimental taphonomy | Cambrian | Ordovician | Arthropoda | Decay | Radiodonta

Received: 24 March 2025; Accepted: 22 July 2025; Published: 18 August 2025

## Introduction

The description of fossil species is a challenging task since fossilisation is a complex process during which anatomical information can either be retained or lost (Briggs and McMahon, 2016; Purnell et al., 2018), but in the absence of genetic information, the taxonomy of fossil organisms is entirely based on morphology alone. Loss of anatomical information mainly occurs during the first days to weeks following the death of an organism, as it is exposed to environmental factors such as bacteria and scavengers (Briggs and McMahon, 2016; Purnell et al., 2018; Saleh et al., 2021b). Internal conditions specific to each carcass, such as pH levels and the gut microbiome, can also influence decay (Butler et al., 2015; Clements et al., 2022; Purnell et al., 2018). If degradation is not halted, it can lead to the complete loss of morphological features, particularly in non-biomineralised remains, which are more prone to decay than bones and shells (Saleh et al., 2020a).

Arthropods are the most abundant animal phylum on Earth today, as they were in the early eumetazoan-dominated communities of the Cambrian Explosion (Daley et al., 2018). Some Early Palaeozoic fossil sites preserve arthropods in exceptional detail, such as the middle Cambrian Burgess Shale in Canada (Butterfield, 1995, 1990; Caron and Jackson, 2008; Izquierdo-López and Caron, 2022; Moysiuk and Caron, 2019, 2022; Nanglu et al., 2020; Yochelson, 1996), the early Cambrian Chengjiang Biota in China (Cong et al., 2014; Hou et al., 2017; Ma et al., 2012; Schmidt et al., 2021, 2024; Zhao et al., 2010), and the Early Ordovician Fezouata Biota in Morocco (Laibl et al., 2023; Lustri et al., 2024; Perez-Peris et al., 2021; Saleh et al., 2021b; Van Roy et al., 2015). However, even in sites where non-biomineralised arthropods are preserved, body fragments are far more common than complete specimens (Daley and Budd, 2010; Pates et al., 2021; Potin and Daley, 2023; Saleh et al., 2022a, 2024a; Whittington and Briggs, 1985; Zhang et al., 2023). This is the case in the Burgess Shale (Collins, 1996; Daley and Edgecombe, 2014; Daley and Peel, 2010; Whittington and Briggs, 1985), and in other Burgess Shale-type assemblages such as the Fezouata, Chengjiang, and Qingjiang biotas (Fu et al., 2019;

Potin et al., 2023; Saleh et al., 2021a; Wu et al., 2021b, 2024a, 2024b). These isolated body fragments are often used to describe new taxa, even in the absence of whole body specimens, with the most complex example of this coming from Radiodonta (Fig. 1), stem lineage euarthropods whose fossil remains have a tendency to disarticulate into separate specimens of frontal appendages, mouth parts, head carapaces, eyes, lateral flaps and setal blades (Briggs, 1979; Collins, 1996; Daley et al., 2018; Potin and Daley, 2023; Whittington and Briggs, 1985). For radiodonts, the appendages in particular have been most often used to define new taxa, but if these fragments have undergone decay, how confidently can we use them to assign new fossil taxa?

To address similar questions, decay experiments are usually conducted under controlled laboratory conditions. By quantifying post-mortem information loss of modern taxa under different environmental conditions (e.g., Allison, 1988; Briggs et al., 1995; Briggs and Kear, 1993, 1994; Butler et al., 2015; Clements et al., 2017, 2022; Corthésy et al., 2024, 2025a, 2025b; Fraga and Vega, 2025; Hancy and Antcliffe, 2020; Iniesto et al., 2015, 2016, 2017; Klompmaker et al., 2017; Murdock et al., 2014; Naimark et al., 2018, 2016; Newman et al., 2019; Palmer et al., 2024; Sagemann et al., 1999; Sansom, 2014; Sansom et al., 2010, 2013), these experiments help reconstruct the potential degradation sequence of extinct animals. Many previous decay experiments have focused on arthropods (Baas et al., 1995; Briggs and Kear, 1994; Butler et al., 2015; Corthésy et al., 2024, 2025b; Klompmaker et al., 2017; Naimark et al., 2018; Plotnick, 1986; Wilson and Butterfield, 2014).

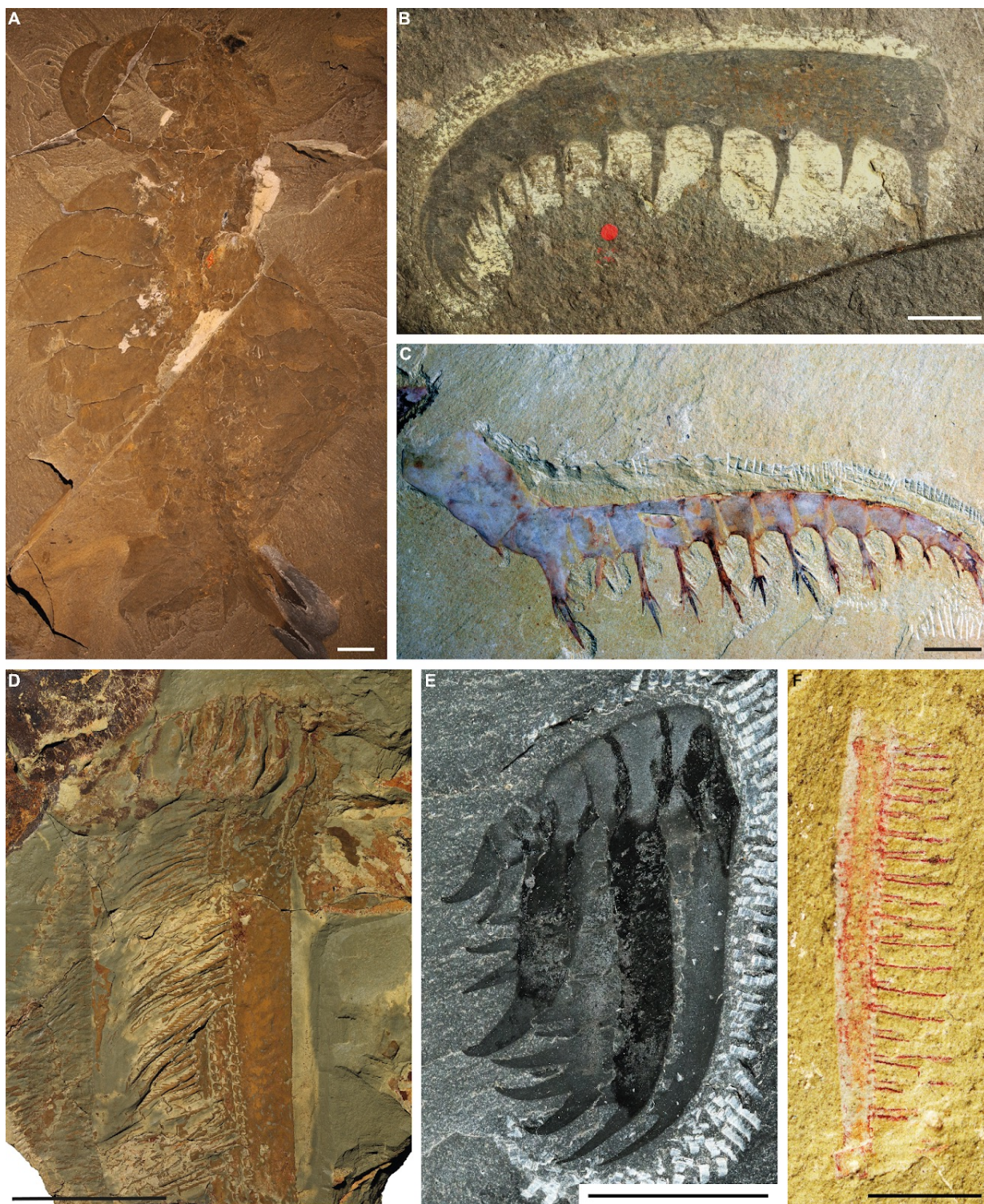
Author affiliations: <sup>a</sup>Institute of Earth Sciences, University of Lausanne, Géopolis, CH-1015 Lausanne, Switzerland; <sup>b</sup>State Key Laboratory of Continental Evolution and Early Life, Shaanxi Key Laboratory of Early Life and Environments, Department of Geology, Northwest University, Xi'an 710069, China

<sup>1</sup>N.C. contributed equally to this work with G.J.-M.P.

<sup>2</sup>To whom correspondence should be addressed: farid.nassim.saleh@gmail.com

Managing Editor: Thomas Wong Hearing; Handling Editor: William Gearty; Peer reviewers: Jane Reeves, Silvina Slagter; Typesetter: Farid Saleh





**Figure 1.** Example of radiodont fossils. Full body of *Anomalocaris canadensis* from the Burgess Shale, ROMIP 51214 (A); *Anomalocaris canadensis* frontal appendage from the Burgess Shale, GSC 3418, holotype (B); *Houcaris saron* frontal appendage from the Chengjiang Biota, YKLP 13459 (C); *Aegirocassis benmoulai* frontal appendage from the Fezouata Biota, YPM IP 527125, paratype (D); *Hurdia* sp. frontal appendage from the Burgess Shale, USNM 213880 (E); and *Pseudoangustidontus izdigua* from the Fezouata Biota, MGL 103603, paratype (F). Scale bars: 1 cm (A, B, C, E), 10 cm (D), 0.5 cm (F). ROMIP: Royal Ontario Museum Invertebrate Paleontology, Toronto; GSC: Geological Survey of Canada; YKLP: Yunnan Key Laboratory for Palaeobiology; YPM IP: Yale Peabody Museum Invertebrate Paleontology; USNM: United States National Museum of Natural History; MGL: Muséum Cantonal des Sciences Naturelles, Département de Géologie, Lausanne. Image credits: (A) A. Daley, (B, E, F) G. Potin, (C) P. Cong & S. Pates, (D) A. Daley & P. Van Roy.



However, little research has investigated the decay of arthropod appendages at high resolution, despite appendages being one of the most abundant body fragments of non-biomineralised arthropod groups such as radiodonts (Guo et al., 2019; Pates and Daley, 2019; Potin et al., 2023; Potin and Daley, 2023; Wu et al., 2021a, 2021b) (Fig. 1).

Here, we compare the degradation of shrimp appendages in saltwater and freshwater conditions, since arthropods can tolerate and get preserved in different environments with contrasting salinities. More importantly, although most arthropods from the Cambrian and Ordovician inhabited fully marine environments, some lived in settings influenced by freshwater input, such as deltas (Gaines, 2014; Gaines et al., 2024; Saleh et al., 2020c, 2022b). Since freshwater input in palaeodeltas cannot be easily quantified, we use purely freshwater and marine conditions to investigate if the degradation sequences are similar or significantly different between these environments. We also compare the degradation of appendages to patterns observed in the fossil record, with a particular focus on radiodonts since the morphological characteristics of their appendages are often used for taxonomic and palaeoecological purposes.

## Materials and methods

Five adult marine shrimps [*Palaemon varians* (Caridea); 30 mm long] and sixteen adult freshwater shrimps [*Neocaridina davidi* (Caridea); 15 mm long] were used for this study, which took place at the Animal Origins and Morphology Lab (ANOM Lab) at the Institute of Earth Sciences of the University of Lausanne, Switzerland. Shrimp populations were bred and housed in the Aquarium Research Lab at the University of Lausanne. The *N. davidi* population was maintained at 25°C in non-saline water, while the *P. varians* population was maintained at 22°C with a specific gravity (SG) of 1.024 using Aquarium Systems Reef Crystals (Code 216029; www.aquariumsystems.eu). Specimens were selected randomly from their respective populations. Shrimps were used because of their availability in the aquariums in Lausanne.

All specimens were euthanised by fully submerging them in a solution of magnesium chloride (two parts water to one part  $MgCl_2$ ). The euthanised shrimps were then extensively washed in reverse osmosis deionised water to remove any residuals and debris covering their surface, such as microalgae from the aquarium, without introducing any damage to the surface of the shrimps. *N. davidi* individuals were placed in sterilised polyester boxes of dimensions 6.5 x 4.5 x 2.3 cm, containing fully oxygenated reverse osmosis deionised freshwater and *P. varians* individuals were placed in boxes containing artificial seawater [fully oxygenated reverse osmosis deionised water with a specific gravity (SG) of 1.024 using Aquarium Systems Reef Crystals (Code 216029; www.aquariumsystems.eu)]. All boxes were filled with water to ~80% of their height. The use of reverse osmosis water, which is mostly free of bacteria and has a neutral pH of 7, implies that most bacteria in the experiment originated from the shrimps themselves. All shrimps were allowed to decay for ten days and were stored in a dark chamber to prevent the influence of light on the decay process. The time frame of ten days was chosen since some characters became difficult to monitor after 10 days, which is a typical timeframe for shrimp decay (Corthésy et al., 2024, 2025b). Shrimps were maintained at a stable room temperature between 21 °C and 22 °C for the duration of the experiment. Shrimps were photographed every 24 hours, and changes in their anatomical

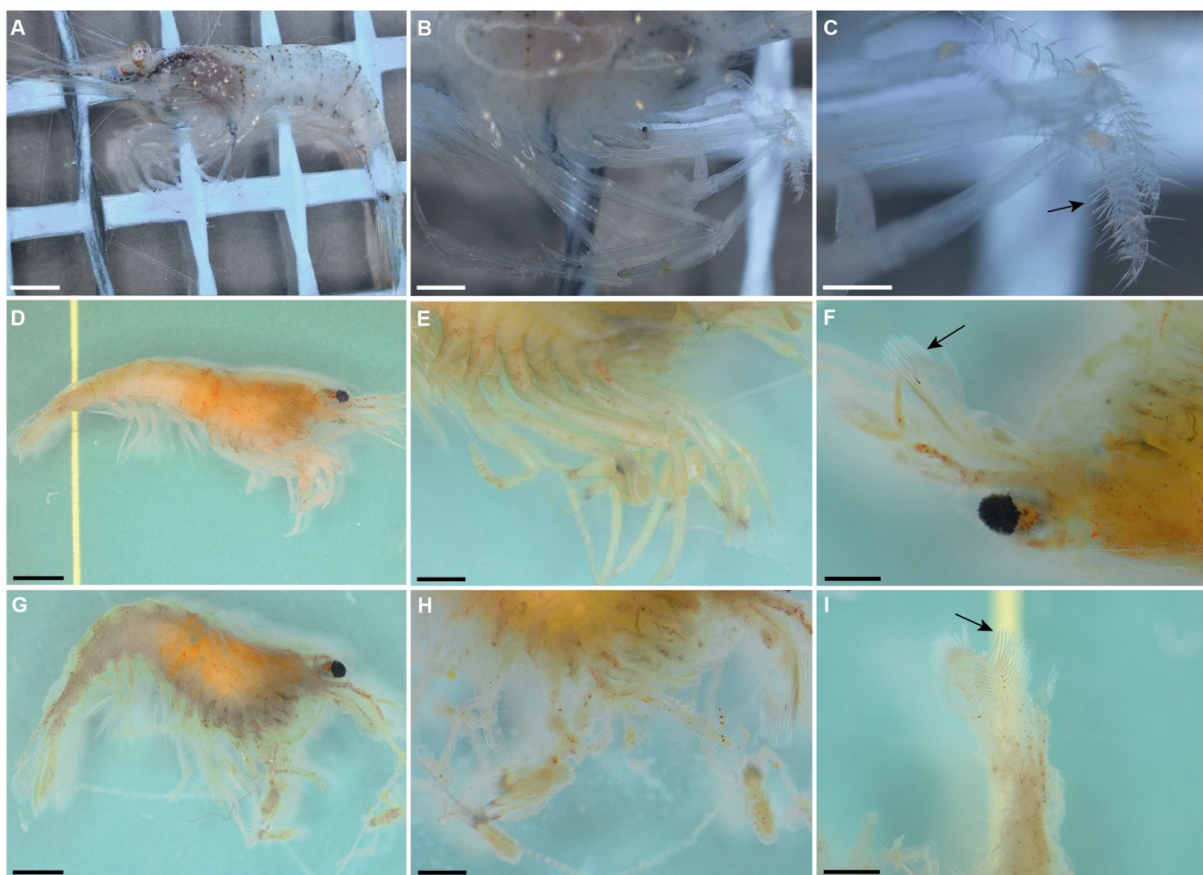
characters were noted using an Olympus Life Science Solutions SC50 5-megapixel camera and the software Olympus Stream Basic 2.2 (Olympus Soft Imaging Solutions).

Three distinct taphonomic characters were investigated: breaking of appendages, detachment of appendages, and detachment of setae. Breaking of appendages describes appendages that broke in the middle of the limb, usually at joints between podomere segments. Appendage detachment refers to appendages that separate from the body at their base while retaining their overall structure. The detachment of setae describes the loss of the fine setal structures found on all appendages. To quantify the decaying state of each of the aforementioned characters, taphonomic scores ranging between 0 and 3 were attributed. A score of 0 means that the taphonomic character is not observed and that appendages did not break or detach and setae are still intact. A score of 1 means that the taphonomic character was observed in less than 50% of the appendages. In other words, less than 50% of the appendages broke, detached, and started to lose their setae. A score of 2 means the taphonomic character was observed in 50% or more of the appendages. A score of 3 means the taphonomic character was observed in all appendages. Overall, an increase in taphonomic scores means an increase in appendage decay (Fig. 2). Each individual shrimp was given a taphonomic score for each of these characters for the ten days of observation (refer to Supplementary Database for further details).

In investigating the decay of marine shrimps to freshwater shrimps, which is the only investigation relying on comparing two datasets with different sample sizes (i.e., comparing sixteen freshwater shrimps with five marine shrimps), a Mann-Whitney U test was performed to compare the values of taphonomic scores between freshwater and saltwater shrimps. Since the results of this test indirectly account for differences in sample size, a significant p-value would imply that differences in decay between the two shrimp species are not only due to sample sizes (Feltovich, 2003). Then, ordinal logistic regressions (OLR) were chosen to analyse the data, as the taphonomic score is an ordinal qualitative variable (Harrell, 2015). A first OLR and a contrast analysis were performed to test whether the decay of each taphonomic character was significantly different between saltwater and freshwater species, with the taphonomic score as the response variable and the water conditions and the taphonomic character as the explanatory variables. The same OLR was used to do another contrast analysis to determine whether the decay is different between taphonomic characters of the same environment (e.g., detachment vs breaking of appendage in marine conditions), also using the water conditions and the taphonomic characters as explanatory variables. Data of all individual shrimp were represented by boxplots (Figs. 3, 4). Statistical analyses and graphs were implemented on the software R 4.2.1 (R Core Team, 2021).

## Results

When comparing appendage decay through time, the overall taphonomic scores slowly increase (Fig. 3A, B), except for the taphonomic character “detachment of setae” where almost no evidence of decay was observed (Fig. 3C). For the taphonomic characters “breaking of appendages” and “detachment of appendages”, the decay rate is significantly higher for freshwater shrimps than for marine shrimps (Contrast analysis of OLR; Breaking of appendages,  $p = 0.0037$ , z-ratio = 2.899; Detachment of appendages,  $p < 0.0001$ , z-ratio = 4.713; Tab. S2). On the other hand, for the



**Figure 2.** Examples of shrimp decay over time. On day 0, shrimp body (A), appendages (B), and setae (C) are intact and the three taphonomic characters have a taphonomic score of 0. After five days, appendages start to break (D, E), and setae are still intact (F). After ten days, almost all appendages are detached and broken (G, H), and setae are still intact (I). The setae are stable on the different part of the shrimp body (C, F, I). Scale bars: 1 mm (A-E, G, H), 2 mm (F, I). Image credit: (A-C) O. Bath-Enright, (D, H, I) A. Roland, (E) B. Pioger, (F, G) I. Quintas.

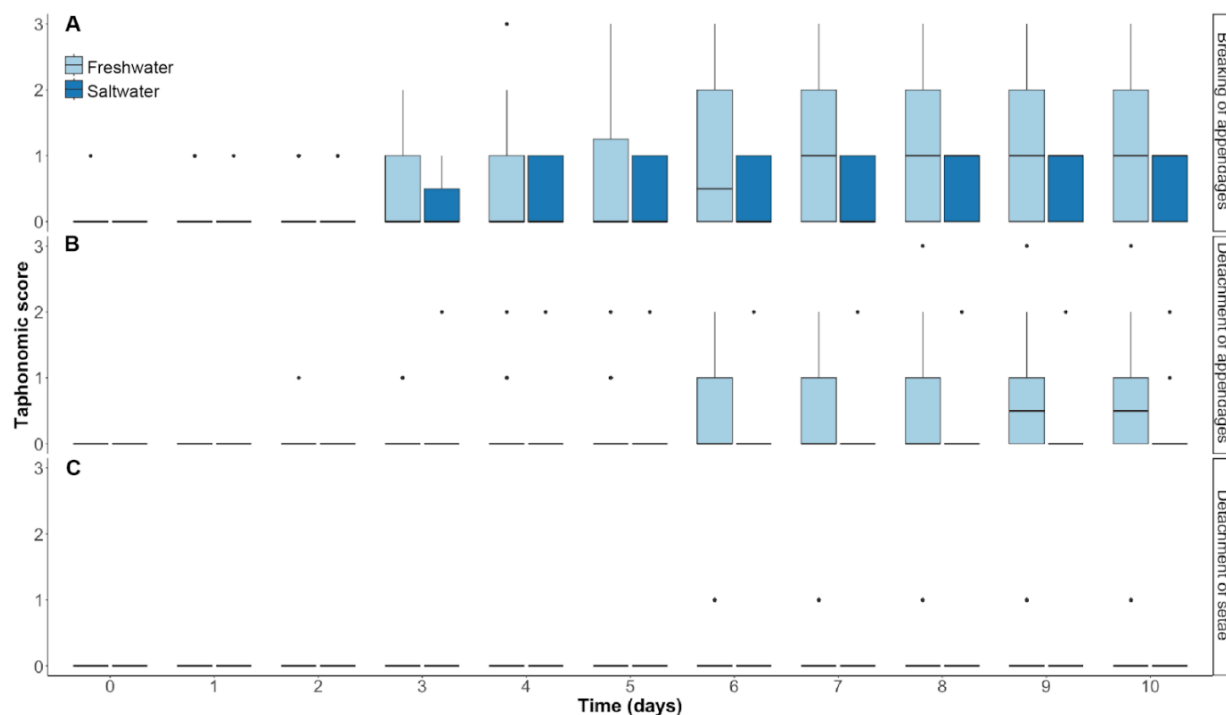
“detachment of setae”, there is no significant difference in decay between marine and freshwater shrimps (Contrast analysis of OLR; Detachment of setae,  $p = 0.8523$ ,  $z\text{-ratio} = 0.186$ ; Tab. S2), since the decay is almost non-existent for this character (Fig. 3C). None of these comparisons between freshwater and saltwater shrimps is influenced by differences in sample size as the result of the Mann-Whitney U test was significant as well (Tab. S1 in Supplementary Material). Moreover, differences in sample sizes have no impact on subsequent comparisons between the different taphonomic characters (Fig. 4), as these comparisons do not involve comparing freshwater to saltwater conditions and are conducted separately for each environmental condition.

When comparing the decay between the three taphonomic characters in freshwater, the decay is fastest for “breaking of appendages”, then “detachment of appendages” and it is slowest for “detachment of setae” (Fig. 4A). In freshwater, “breaking of appendages” has a decay rate significantly higher than “detachment of appendages” (Contrast analysis of OLR;  $p < 0.0001$ ,  $z\text{-ratio} = 6.703$ ; Tab. S2) and “detachment of setae” (Contrast analysis of OLR;  $p < 0.0001$ ,  $z\text{-ratio} = 12.409$ ; Tab. S2). The decay rate of “detachment of appendages” in freshwater is significantly higher than “detachment of setae” (Contrast analysis of OLR;  $p < 0.0001$ ,  $z\text{-ratio} = 8.293$ ; Tab. S2). In saltwater, the taphonomic scores slowly increase for “breaking of appendages”, while the values remain around zero for “detachment of appendages” and “detachment

of setae” (Fig. 4B). The decay is significantly more pronounced for “breaking of appendages” than “detachment of appendages” (Contrast analysis of OLR;  $p < 0.0001$ ,  $z\text{-ratio} = 5.468$ ; Tab. S2). However, the taphonomic scores of “breaking of appendages” are not significantly different from “detachment of setae” (Contrast analysis of OLR;  $p = 0.9715$ ,  $z\text{-ratio} = 0.229$ ; Tab. S2).

## Discussion

The major observations regarding shrimp decay are that the appendages of freshwater shrimps detach and/or break more rapidly than saltwater shrimps (Fig. 3A, B); and the setae remain relatively stable even when appendages break or detach from the body (Fig. 3C; 4A, B). The slower decay of saltwater shrimps compared to freshwater shrimps cannot be attributed to the different environmental conditions in which they were placed, even though salt is known to be a natural preservative and can act as a conservation agent at high concentrations (Wijnker et al., 2006). Salt is even considered a catalyst for the replication of non-biomineralised morphologies in authigenic minerals (Corthésy et al., 2025b). The role of increased salinity in the fine-scale preservation of arthropod bodies can be observed in sites like the Jurassic Solnhofen Lagerstätte in Germany, which preserved a large number of arthropods with their appendages attached, particularly shrimps (Pazinato et al., 2021; Winkler, 2014). Numerous taphonomic models and experiments



**Figure 3.** Decay comparisons between freshwater and saltwater shrimps. Taphonomic scores through time for breaking of appendages (A), detachment of appendages (B), and detachment of setae (C). Boxplots represent the observations of all specimens at each time point, with the median as the bold bar, the edges of the rectangles as the first and third quartiles, the whiskers as the minimum and maximum values of the data, and the dots as the outliers of the data.

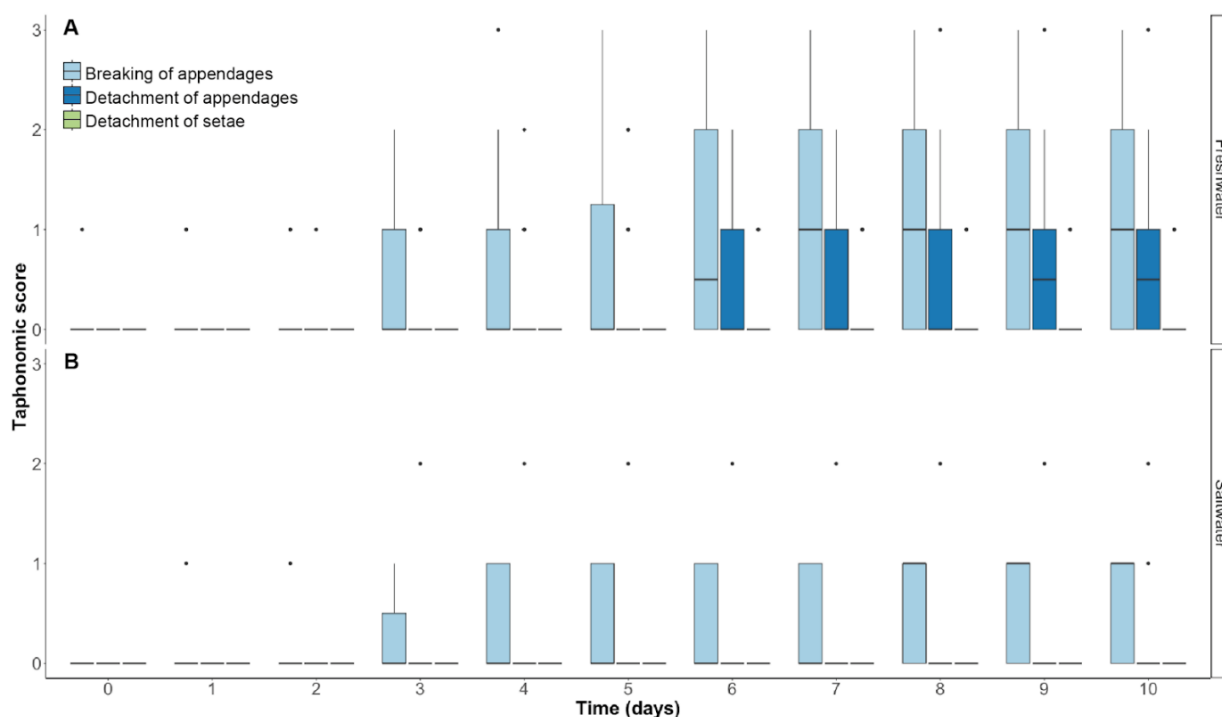
developed to explain preservation in Solnhofen attribute the high degree of articulation in fossils to elevated salinity levels (Gäb et al., 2020; Gerschermann et al., 2021). However, salt is also known to increase the degradation rate of proteins under normal salinities (Corthésy et al., 2025a). As such, the relationship between salinity and decay rates is not linear. For these reasons, and because the experiments were not designed to investigate the role of salinity in the decay process, we attribute the differences in decay rates between freshwater and marine shrimps to variations in their organic composition rather than to differences in salinity. For instance, considering that calcium is more limited in freshwater compared to saltwater, it is possible that freshwater shrimp appendages contain fewer biominerals and are, therefore, more prone to decay and disarticulation than marine shrimp appendages. Additionally, the thickness of the freshwater shrimp cuticle may be lower than that of marine shrimps, making the latter more resistant to degradation. Other factors, such as the quantity of polysaccharides in the cuticle, may also influence decay, as this material is not easily recyclable by bacteria (Corthésy et al., 2024). It is also worth noting that factors other than salinity and the nature of the organic matter also influence decay rates. These include pH, oxygen concentration among other parameters (Allison, 1988; Clements et al., 2017, 2022; Corthésy et al., 2024; Fraga and Vega, 2025; Hancy and Antcliffe, 2020; Mähler et al., 2023).

The detachment and breakage of appendages in both freshwater and saltwater experiments explain patterns observed in the fossil record (Fig. 4A, B). Although fossil carideans often preserve appendages both in marine water (Bravi et al., 1999; Garassino and Bravi, 2003; Winkler, 2013) and in freshwater (Barros et al., 2021; de Mazancourt et al., 2022; Feldmann et al., 1981; Garassino et

al., 2002), most of them do not preserve all of their appendages. For instance, cretaceous freshwater caridean showed that the cephalothoracic appendages were poorly preserved or absent in many specimens, while abdominal appendages were visible in almost all samples (Garassino, 1997). However, this pattern is not observed in all decapods. For example, in an astacidean taxon from the same locality, cephalothoracic appendages were relatively well-preserved and attached to the body in most specimens, while abdominal appendages were only observed in a few (Garassino, 1997). This indicates that different appendages are lost to varying degrees before the stabilisation of the carcass and its fossilisation.

The detachment/breakage of appendages from the body is not limited to Cretaceous arthropods; similar patterns can also be observed as far back as the Cambrian. For instance, complete carcasses of animals such as *Anomalocaris* and *Hurdia* are rare. Fossils of this taxon are primarily represented by frontal appendages, mouthparts, and head carapaces (Daley et al., 2009, 2013; Daley and Edgecombe, 2014; Saleh et al., 2021a) found in isolation or in disarticulated assemblages (Daley et al., 2009, 2013; Daley and Budd, 2010; Daley and Edgecombe, 2014). In the Chengjiang Biota, over 800 isolated frontal appendages of *Amplectobelua symbrachiata* have been discovered, yet only one nearly complete body has been found (Wu et al., 2021b). In this sense, isolated radiodont appendages are the norm rather than the exception, with articulated bodies being extremely rare (Paterson et al., 2023, p. 202; Wu et al., 2024a, 2024b), and it is even possible to distinguish between detached from broken appendages in the fossil record. For example, in *Anomalocaris*, some appendages display 13 podomeres instead of the typical 14, which is a result of breakage between the most proximal podomeres (Daley and Edgecombe, 2014; Whiteaves,





**Figure 4.** Decay comparisons between the three taphonomic characters. Taphonomic scores through time for breaking of appendages, detachment of appendages, and detachment of setae in freshwater (A), and saltwater (B). Boxplots represent the observations of all specimens at each time point, with the median as the bold bar, the edges of the rectangles as the first and third quartiles, the whiskers as the minimum and maximum values of the data, and the dots as the outliers of the data. Note that no green boxplots representing setae detachment are shown in the figure, as the taphonomic scores for this character did not increase significantly enough to warrant representation in a boxplot.

1892; Whittington and Briggs, 1985). Isolated appendages with 14 podomeres likely represent those that detached from the body, with those showing fewer podomeres corresponding to appendages that broke apart between segments. This taphonomic pattern is not exclusive to *Anomalocaris* and other radiodont taxa, such as *Hurdia*, *Peytoia*, *Pseudoangustidontus*, and *Tamisiocaris*, exhibit similar trends, with both broken and detached appendages frequently observed in the fossil record (Briggs, 1979; Collins, 1996; Daley et al., 2009, 2013; Daley and Legg, 2015; Daley and Peel, 2010; Potin et al., 2023; Potin and Daley, 2023).

Interestingly, the setae in both freshwater and saltwater showed minimal degradation (Fig. 4A, B), which is consistent with data from the fossil record. For example, setae are found preserved in crustaceans from the Cambrian “Orsten” fauna (Garm and Watling, 2013; Müller and Walossek, 1985, 1988; Walossek, 1993). This degree of minute preservation of setae is also observed in decapod fossils (Audo et al., 2021; Jauvion et al., 2017; Moreau et al., 2022). Setae can also be preserved when the rest of the body has suffered from pronounced degradation. For instance, radiodont appendages can be significantly decayed yet still show setae [Plate 81, Fig. 11 in Briggs (1979); Fig. 5 in Wu et al. (2022)]. This stability of setae is particularly relevant in palaeontological and palaeoecological research. The absence of setae on a particular radiodont frontal appendage was used to describe *Lenisicaris* (Wu et al., 2021b), which shares many morphological similarities with *Houcaris magnabasis* [previously referred to as *Anomalocaris magnabasis*; Pates et al. (2021)]. The most distinguishing feature between the two taxa is the absence of setae in *Lenisicaris* compared to *H. magnabasis*, which might imply that *Lenisicaris*

material represents a taphonomic variant that underwent greater decay than *H. magnabasis* material (Pates et al., 2021). The results of our study do not support this hypothesis and suggest that *Lenisicaris* and *H. magnabasis* are indeed distinct taxa.

The aforementioned case of *Lenisicaris* vs *H. magnabasis* is not the only one where decay information may provide insights into the preservation potential of radiodont appendages in the fossil record. For example, the first *Tamisiocaris borealis* appendage material was described as having only a pair of thin endites (Daley and Peel, 2010). However, material subsequently discovered and assigned to *T. borealis* was found to have setae attached to the endites (Vinther et al., 2014). Given the relative stability of setae observed in our experiment, it seems unlikely that the appendages with and without setae both belong to the same *Tamisiocaris* species. It further suggests that the absence of setae in the possible counterpart (*Tamisiocaris* aff. *borealis*) from the Kinzers Formation (Pates and Daley, 2019) may reflect a taxonomic differentiation rather than a taphonomic bias. However, we do not rule out the taphonomic explanation, as decay experiments do not replicate natural environments, and generalisations about natural systems should be made cautiously (Purnell et al., 2018). Taphonomic processes operating over geological time are far more complex than those observed in laboratory decay experiments (Purnell et al., 2018; Sansom, 2014), and Cambrian radiodonts have an anatomy that is very different from modern shrimps.

Factors other than decay can influence the preservation potential of anatomical features in the fossil record. For instance, some transport processes are known to fragment skeletal elements while only slightly affecting the preservation of certain taxa, such as

annelids (Bath Enright et al., 2017, 2021) and arthropods (Allison, 1986). Authigenic post-mortem mineralisation could also play a role, with some structures being more prone than others to replication by aluminosilicates, pyrite, or phosphate (e.g., Anderson et al., 2018, 2020; Barling et al., 2023; Butterfield, 1990, 2003; Corthésy et al., 2025a, 2025b; El Khoury et al., 2025a, 2025b; Gabbott et al., 2004; Gaines et al., 2008; McNamara et al., 2009; Nielsen et al., 2022; Orr et al., 1998; Saleh et al., 2019, 2020b, 2023, 2024b; Schiffbauer et al., 2014; Slagter et al., 2024). A limitation of our work might be the choice of the model organism, as shrimp appendages are likely to be less sclerotised than radiodont appendages and their morphology is different in almost every aspect. Radiodonts also had unsclerotised bodies, given a large contrast in material hardness between their frontal appendages and the soft body to which they attach, and this difference is less pronounced between the shrimp appendages and body. Despite this discrepancy in the degree of sclerotisation, which certainly impacts decay and influences preservation (Saleh et al., 2020a, 2022c), there is no reason to expect that more heavily sclerotised appendages, such as those observed in Cambrian radiodonts or modern lobsters and crabs, would decay more rapidly than the less sclerotised appendages of shrimps. In other words, if shrimp appendages demonstrated some resistance in retaining their setae (Figs. 3, 4), the more sclerotised appendages of other taxa would probably be even more resistant to degradation and retain their setae better than the investigated shrimp taxa, as it has been previously shown that animals like lobsters and crabs have a higher preservation potential than shrimps (Klompaker et al., 2017). Experiments on the brachyuran *Callinectes sapidus* showed that the claws, mandibles, and certain partial spines of this taxon are very resistant to degradation (Mutel et al., 2008). Considering the different abiotic and biotic conditions that can influence decay and preservation, the results presented here should not be automatically generalised to all preserved arthropod appendages in the fossil record. Instead, they can serve as a baseline for assessing the likelihood of certain palaeontological scenarios.

## Data availability

All data necessary to replicate this work are available in the main text and the supplementary material files.

## Acknowledgements

The team thanks various members of the AnomLab (Lausanne) for helpful discussions. We are grateful to D. Rudkin, P. Fenton, J.-B. Caron (ROM), H. Gene (USNM), and M. Coyne (GSC) for the curatorial assistance during ACD and GJMP collection visits to take photos. We also thank P. Cong (Yunnan University) and S. Pates (University of Exeter) for sharing the picture of *Houcaris saron*. Orla Bath Enright (State Museum of Natural History Stuttgart), Alexandre Roland, and Blanche Pioger are thanked for helpful discussions and for providing images of marine shrimps.

## Author contributions

Conceptualization FS, ACD, GJMP, IQ; Formal analyses IQ, AT, NC, GJMP; Funding acquisition FS, ACD; Investigation NC, GJMP, AT, IQ, YW, SL, ACD, FS; Methodology NC, GJMP, IQ, AT; Supervision FS, ACD; Visualization NC, GJMP; Writing original draft NC, GJMP, AT, FS; Writing review and editing NC, GJMP, AT, IQ, YW, SL, ACD, FS.

## Competing interests

FS is a Steering Committee member at Open Palaeontology.

## Ethics and AI use

Artificial intelligence powered by a large language model was used to check for grammatical errors. Unlike some other decapods such as crabs and lobsters, experimental work on shrimps in Switzerland does not require any special permission. Nevertheless, shrimp individuals were euthanised ethically, and the experiments adhered to the 3Rs principle of research (Replacement, Reduction and Revision).

## Funding

NC and FS work is funded by an SNF Ambizione Grant (PZ00P2-209102). GJMP work is funded by the Canton of Vaud (Switzerland). YW work is supported by a Swiss Government Excellence Scholarship and the National Science Foundation of China (42202011). SL work is supported by an SNF Sinergia Grant (198691) awarded to ACD and three other co-PIs.

## References

- Allison, P.A., 1986. Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport. *Geology* 14, 979. [https://doi.org/10.1130/0091-7613\(1986\)14<979:SAITFR>2.0.CO;2](https://doi.org/10.1130/0091-7613(1986)14<979:SAITFR>2.0.CO;2)
- Allison, P.A., 1988. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology* 14, 139–154. <https://doi.org/10.1017/S009483730001188X>
- Anderson, R.P., Tosca, N.J., Gaines, R.R., Mongiardino Koch, N., Briggs, D.E.G., 2018. A mineralogical signature for Burgess Shale-type fossilization. *Geology* 46, 347–350. <https://doi.org/10.1130/G39941.1>
- Anderson, R.P., Tosca, N.J., Saupe, E.E., Wade, J., Briggs, D.E.G., 2020. Early formation and taphonomic significance of kaolinite associated with Burgess Shale fossils. *Geology* 49, 355–359. <https://doi.org/10.1130/G48067.1>
- Audo, D., Winkler, N., Charbonnier, S., 2021. *Pseudodrobnia natator* n. comb., a new link between crustacean faunas from the Jurassic of Germany and Cretaceous of Lebanon. *geod* 43, 209–218. <https://doi.org/10.5252/geodiversitas2021v43a8>
- Baas, M., Briggs, D.E.G., Van Heemst, J.D.H., Kear, A.J., De Leeuw, J.W., 1995. Selective preservation of chitin during the decay of shrimp. *Geochimica et Cosmochimica Acta* 59, 945–951. [https://doi.org/10.1016/0016-7037\(95\)00012-7](https://doi.org/10.1016/0016-7037(95)00012-7)
- Barling, N., Saleh, F., Ma, X., 2023. A unique record of prokaryote cell pyritization. *Geology*. <https://doi.org/10.1130/G51352.1>
- Barros, O.A., Viana, M.S.S., Viana, B.C., Silva, J.H. da, Paschoal, A.R., Oliveira, P.V. de, 2021. New data on *Beurlenia araripensis* Martins-Neto & Mezzalana, 1991, a lacustrine shrimp from Crato Formation, and its morphological variations based on the shape and the number of rostral spines. *PLOS ONE* 16, e0247497. <https://doi.org/10.1371/journal.pone.0247497>
- Bath Enright, O.G., Minter, N.J., Sumner, E.J., 2017. Palaeoecological implications of the preservation potential of soft-bodied organisms in sediment-density flows: testing turbulent waters. *Royal Society Open Science* 4, 170212. <https://doi.org/10.1098/rsos.170212>
- Bath Enright, O.G., Minter, N.J., Sumner, E.J., Mángano, M.G., Buatois, L.A., 2021. Flume experiments reveal flows in the Burgess Shale can sample and transport organisms across substantial distances. *Communications Earth & Environment* 2, 1–7. <https://doi.org/10.1038/s43247-021-00176-w>
- Bravi, S., Coppa, M.G., Garassino, A., Patricelli, R., 1999. *Palaemon*

- vesolensis* n. sp. (Crustacea, Decapoda) from the Plattenkalk of Vesole Mount (Salerno, Southern Italy). *Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano* 140, 141–169.
- Briggs, D.E.G., 1979. *Anomalocaris*, the largest known Cambrian arthropod. *Palaeontology*, 22, 3, 631–664.
- Briggs, D.E.G., Kear, A.J., 1993. Decay and preservation of polychaetes: taphonomic thresholds in soft-bodied organisms. *Paleobiology* 19, 107–135. <https://doi.org/10.1017/S0094837300012343>
- Briggs, D.E.G., Kear, A.J., 1994. Decay and Mineralization of Shrimps. *PALAIOS* 9, 431–456. <https://doi.org/10.2307/3515135>
- Briggs, D.E.G., Kear, A.J., Baas, M., Leeuw, J.W., Rigby, S., 1995. Decay and composition of the hemichordate *Rhabdopleura*: implications for the taphonomy of graptolites. *Lethaia* 28, 15–23. <https://doi.org/10.1111/j.1502-3931.1995.tb01589.x>
- Briggs, D.E.G., McMahon, S., 2016. The role of experiments in investigating the taphonomy of exceptional preservation. *Palaeontology* 59, 1–11. <https://doi.org/10.1111/pala.12219>
- Butler, A.D., Cunningham, J.A., Budd, G.E., Donoghue, P.C.J., 2015. Experimental taphonomy of *Artemia* reveals the role of endogenous microbes in mediating decay and fossilization. *Proceedings of the Royal Society B: Biological Sciences* 282, 20150476. <https://doi.org/10.1098/rspb.2015.0476>
- Butterfield, N.J., 1990. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* 16, 272–286. <https://doi.org/10.1017/S0094837300009994>
- Butterfield, N.J., 1995. Secular distribution of Burgess-Shale-type preservation. *Lethaia* 28, 1–13. <https://doi.org/10.1111/j.1502-3931.1995.tb01587.x>
- Butterfield, N.J., 2003. Exceptional Fossil Preservation and the Cambrian Explosion. *Integrative and Comparative Biology* 43, 166–177. <https://doi.org/10.1093/icb/43.1.166>
- Caron, J.-B., Jackson, D.A., 2008. Paleoecology of the Greater Phyllopod Bed community, Burgess Shale. *Palaeogeography, Palaeoclimatology, Palaeoecology, The Dawn of Animal Life: Evolutionary and Palaeoecological Patterns in the Neoproterozoic-Cambrian Animal Fossil Record* 258, 222–256. <https://doi.org/10.1016/j.palaeo.2007.05.023>
- Clements, T., Colleary, C., De Baets, K., Vinther, J., 2017. Buoyancy mechanisms limit preservation of coleoid cephalopod soft tissues in Mesozoic Lagerstätten. *Palaeontology* 60, 1–14. <https://doi.org/10.1111/pala.12267>
- Clements, T., Purnell, M.A., Gabbott, S., 2022. Experimental analysis of organ decay and pH gradients within a carcass and the implications for phosphatization of soft tissues. *Palaeontology* 65, e12617. <https://doi.org/10.1111/pala.12617>
- Collins, D., 1996. The “evolution” of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). *Journal of Paleontology* 70, 280–293. <https://doi.org/10.1017/S0022336000023362>
- Cong, P., Ma, X., Hou, X., Edgecombe, G.D., Strausfeld, N.J., 2014. Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513, 538–542. <https://doi.org/10.1038/nature13486>
- Corthésy, N., Antcliffe, J.B., Saleh, F., 2025a. Taxon-specific redox conditions control fossilisation pathways. *Nat Commun* 16, 3993. <https://doi.org/10.1038/s41467-025-59372-3>
- Corthésy, N., Saleh, F., Antcliffe, J.B., Daley, A.C., 2025b. Kaolinite induces rapid authigenic mineralisation in unburied shrimps. *Communications Earth & Environment* 6, 1–8. <https://doi.org/10.1038/s43247-024-01983-7>
- Corthésy, N., Saleh, F., Thomas, C., Antcliffe, J.B., Daley, A.C., 2024. The effects of clays on bacterial community composition during arthropod decay. *Swiss Journal of Palaeontology* 143, 26. <https://doi.org/10.1186/s13358-024-00324-7>
- Daley, A.C., Antcliffe, J.B., Drage, H.B., Pates, S., 2018. Early fossil record of Euarthropoda and the Cambrian Explosion. *Proc. Natl. Acad. Sci. U.S.A.* 115, 5323–5331. <https://doi.org/10.1073/pnas.1719962115>
- Daley, A.C., Budd, G.E., 2010. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* 53, 721–738. <https://doi.org/10.1111/j.1475-4983.2010.00955.x>
- Daley, A.C., Budd, G.E., Caron, J.-B., 2013. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology* 11, 743–787. <https://doi.org/10.1080/14772019.2012.732723>
- Daley, A.C., Budd, G.E., Caron, J.-B., Edgecombe, G.D., Collins, D., 2009. The Burgess Shale Anomalocaridid *Hurdia* and Its Significance for Early Euarthropod Evolution. *Science* 323, 1597–1600. <https://doi.org/10.1126/science.1169514>
- Daley, A.C., Edgecombe, G.D., 2014. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology* 88, 68–91. <https://doi.org/10.1666/13-067>
- Daley, A.C., Legg, D.A., 2015. A morphological and taxonomic appraisal of the oldest anomalocaridid from the Lower Cambrian of Poland. *Geological Magazine* 152, 949–955. <https://doi.org/10.1017/S0016756815000412>
- Daley, A.C., Peel, J.S., 2010. A possible anomalocaridid from the Cambrian Sirius Passet Lagerstätte, North Greenland. *Journal of Paleontology* 84, 352–355. <https://doi.org/10.1666/09-136R1.1>
- de Mazancourt, V., Wappler, T., Wedmann, S., 2022. Exceptional preservation of internal organs in a new fossil species of freshwater shrimp (Caridea: Palaemonoidea) from the Eocene of Messel (Germany). *Sci Rep* 12, 18114. <https://doi.org/10.1038/s41598-022-23125-9>
- El Khoury, A., Somogyi, A., Chi Fru, E., Saleh, F., Chraiki, I., Fontaine, C., Aubineau, J., Rollion-Bard, C., Harzhauser, M., El Albani, A., 2025a. A battle against arsenic toxicity by Earth's earliest complex life forms. *Nat Commun* 16, 4388. <https://doi.org/10.1038/s41467-025-59760-9>
- El Khoury, A., Saleh, F., El Albani, A., Fontaine, C., Rollion-Bard, C., Chraiki, I., Aubineau, J., Ngwal'ghoubou Ikouanga, J., Bhilisse, M., Zguaid, M. and Somogyi, A., 2025b. Pyrite morphology and sulfur isotopes refine taphonomic models for the 2.1 Ga Francevillian biota, Gabon. *Scientific Reports*, 15(1), pp.1–11.
- Feldmann, R.M., Grande, L., Birkhimer, C.P., Hannibal, J.T., McCoy, D.L., 1981. Decapod Fauna of the Green River Formation (Eocene) of Wyoming. *Journal of Paleontology* 55, 788–799.
- Feltoch, N., 2003. Nonparametric Tests of Differences in Medians: Comparison of the Wilcoxon–Mann–Whitney and Robust Rank-Order Tests. *Experimental Economics* 6, 273–297. <https://doi.org/10.1023/A:1026273319211>
- Fraga, M.C., Vega, C.S., 2025. Decay and preservation in marine basins: A guide to small multi-element skeletons. *International Biodeterioration & Biodegradation* 196, 105904. <https://doi.org/10.1016/j.ibiod.2024.105904>
- Fu, D., Tong, G., Dai, T., Liu, W., Yang, Y., Zhang, Y., Cui, L., Li, L., Yun, H., Wu, Y., Sun, A., Liu, C., Pei, W., Gaines, R.R., Zhang, X., 2019. The Qingjiang biota—A Burgess Shale-type fossil Lagerstätte from the early Cambrian of South China. *Science* 363, 1338–1342. <https://doi.org/10.1126/science.aau8800>
- Gäb, F., Ballhaus, C., Stinnesbeck, E., Kral, A.G., Janssen, K., Bierbaum, G., 2020. Experimental taphonomy of fish - role of elevated pressure, salinity and pH. *Scientific Reports* 10, 7839. <https://doi.org/10.1038/s41598-020-64651-8>
- Gabbott, S.E., Xian-guang, H., Norry, M.J., Siveter, D.J., 2004. Preservation of Early Cambrian animals of the Chengjiang biota. *Geology* 32, 901–904. <https://doi.org/10.1130/G20640.1>
- Gaines, R.R., 2014. Burgess Shale-type Preservation and its Distribution in Space and Time. *The Paleontological Society Papers* 20, 123–146. <https://doi.org/10.1017/S1089332600002837>
- Gaines, R.R., Briggs, D.E.G., Yuanlong, Z., 2008. Cambrian Burgess Shale-type deposits share a common mode of fossilization. *Geology* 36, 755–758. <https://doi.org/10.1130/G24961A.1>



- Gaines, R.R., García-Bellido, D.C., Jago, J.B., Myrow, P.M., Paterson, J.R., 2024. The Emu Bay Shale: A unique early Cambrian Lagerstätte from a tectonically active basin. *Science Advances* 10, eadp2650. <https://doi.org/10.1126/sciadv.adp2650>
- Garassino, A., 1997. The macruran decapod crustaceans of the Lower Cretaceous (Lower Barremian) of Las Hoyas (Cuenca, Spain). *Atti Soc. it. Sci. nat. Museo civ. Stor. nat. Milano* 137, 101–126.
- Garassino, A., Bravi, S., 2003. *Palaemon antonellae* new species (Crustacea, Decapoda, Caridea) from the lower Cretaceous “Platydolomite” of Profeti (Caserta, Italy). *Journal of Paleontology* 77, 589–592. [https://doi.org/10.1666/0022-3360\(2003\)077<0589:PANSCD>2.0.CO;2](https://doi.org/10.1666/0022-3360(2003)077<0589:PANSCD>2.0.CO;2)
- Garassino, A., Yanbin, S., Schram, F.R., Taylor, R.S., 2002. *Yongjicaris zhejiangensis* n. gen. n. sp. (Crustacea, Decapoda, Caridea) from the Lower Cretaceous of Zhejiang Province, China.
- Garm, A., Watling, L., 2013. The crustacean integument: setae, setules, and other ornamentation, in: *Functional Morphology and Diversity*. Oxford University Press, pp. 167–198.
- Gerschermann, S., Ballhaus, C., Gäb, F., 2021. Rheological properties of calcite oozes: Implications for the fossilisation in the plattenkalks of the Solnhofen-Eichstätt lagoons in the Franconian Alb, Germany. *PLOS ONE* 16, e0252469. <https://doi.org/10.1371/journal.pone.0252469>
- Guo, J., Pates, S., Cong, P., Daley, A.C., Edgecombe, G.D., Chen, T., Hou, X., 2019. A new radiodont (stem Euarthropoda) frontal appendage with a mosaic of characters from the Cambrian (Series 2 Stage 3) Chengjiang biota. *Papers in Palaeontology* 5, 99–110. <https://doi.org/10.1002/spp2.1231>
- Hancy, A.D., Antcliffe, J.B., 2020. Anoxia can increase the rate of decay for cnidarian tissue: Using *ctinia equina* to understand the early fossil record. *Geobiology* 18, 167–184. <https://doi.org/10.1111/gbi.12370>
- Harrell, F.E., 2015. Ordinal Logistic Regression, in: Harrell, Jr., Frank E. (Ed.), *Regression Modeling Strategies: With Applications to Linear Models, Logistic and Ordinal Regression, and Survival Analysis*, Springer Series in Statistics. Springer International Publishing, Cham, pp. 311–325. [https://doi.org/10.1007/978-3-319-19425-7\\_13](https://doi.org/10.1007/978-3-319-19425-7_13)
- Hou, X.-G., Siveter, David J, Siveter, Derek J, Aldridge, R.J., Cong, P.-Y., Gabbott, S.E., Ma, X., Purnell, M.A., Williams, M., 2017. The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. Wiley Blackwell.
- Iniesto, M., Buscalioni, Á.D., Carmen Guerrero, M., Benzerara, K., Moreira, D., López-Archilla, A.I., 2016. Involvement of microbial mats in early fossilization by decay delay and formation of impressions and replicas of vertebrates and invertebrates. *Scientific Reports* 6, 25716. <https://doi.org/10.1038/srep25716>
- Iniesto, M., Laguna, C., Florín, M., Guerrero, M.C., Chicote, A., Buscalioni, A.D., López-Archilla, A.I., 2015. The impact of microbial mats and their microenvironmental conditions in early decay of fish. *PALAIOS* 30, 792–801. <https://doi.org/10.2110/palo.2014.086>
- Iniesto, M., Villalba, I., Buscalioni, A.D., Guerrero, M.C., López-Archilla, A.I., 2017. The Effect Of microbial Mats In The Decay Of Anurans With Implications For Understanding Taphonomic Processes In The Fossil Record. *Scientific Reports* 7, 45160. <https://doi.org/10.1038/srep45160>
- Izquierdo-López, A., Caron, J.-B., 2022. Extreme multisegmentation in a giant bivalved arthropod from the Cambrian Burgess Shale. *iScience* 25. <https://doi.org/10.1016/j.isci.2022.104675>
- Jauvion, C., Charbonnier, S., Bernard, S., 2017. A new look at the shrimps (Crustacea, Decapoda, Penaeoidea) from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte. *geod* 39, 705–716. <https://doi.org/10.5252/g2017n4a3>
- Klompmaier, A.A., Portell, R.W., Frick, M.G., 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology* 60, 773–794. <https://doi.org/10.1111/pala.12314>
- Laibl, L., Drage, H.B., Pérez-Peris, F., Schöder, S., Saleh, F., Daley, A.C., 2023. Babies from the Fezuota Biota: Early developmental trilobite stages and their adaptation to high latitudes. *Geobios*. <https://doi.org/10.1016/j.geobios.2023.06.005>
- Lustri, L., Gueriau, P., Daley, A.C., 2024. Lower Ordovician synziphosurine reveals early euchelicerate diversity and evolution. *Nat Commun* 15, 3808. <https://doi.org/10.1038/s41467-024-48013-w>
- Ma, X., Hou, X., Edgecombe, G.D., Strausfeld, N.J., 2012. Complex brain and optic lobes in an early Cambrian arthropod. *Nature* 490, 258–261. <https://doi.org/10.1038/nature11495>
- Mähler, B., Janssen, K., Lönart, M.I., Lagos, M., Geisler, T., Rust, J., Bierbaum, G., 2023. Time-dependent microbial shifts during crayfish decomposition in freshwater and sediment under different environmental conditions. *Scientific Reports* 13, 1539. <https://doi.org/10.1038/s41598-023-28713-x>
- McNamara, M.E., Orr, P.J., Kearns, S.L., Alcalá, L., Anadón, P., Peñalver Mollá, E., 2009. Soft-tissue preservation in Miocene frogs from Libros, Spain: insights into the genesis of decay microenvironments. *PALAIOS* 24, 104–117. <https://doi.org/10.2110/palo.2008.p08-017r>
- Moreau, J.-D., Vullo, R., Charbonnier, S., Jattiot, R., Trincal, V., Néaudeau, D., Fara, E., Baret, L., Garassino, A., Gand, G., Lafaurie, G., 2022. Konservat-Lagerstätten from the Upper Jurassic lithographic limestone of the Causse Méjean (Lozère, southern France): palaeontological and palaeoenvironmental synthesis. *Geological Magazine* 159, 761–781. <https://doi.org/10.1017/S0016756821001382>
- Moysiuk, J., Caron, J.-B., 2019. A new hurdiid radiodont from the Burgess Shale evinces the exploitation of Cambrian infaunal food sources. *Proceedings of the Royal Society B: Biological Sciences* 286, 20191079. <https://doi.org/10.1098/rspb.2019.1079>
- Moysiuk, J., Caron, J.-B., 2022. A three-eyed radiodont with fossilized neuroanatomy informs the origin of the arthropod head and segmentation. *Current Biology* 32, 3302–3316.e2. <https://doi.org/10.1016/j.cub.2022.06.027>
- Müller, K.J., Walossek, D., 1985. Skaracarida, a new order of Crustacea from the Upper Cambrian of Västergötland, Sweden, in: Skaracarida, a New Order of Crustacea from the Upper Cambrian of Västergötland, Sweden, Fossils and Strata. Universitetsforlaget, pp. 1–65. <https://doi.org/10.18261/8200074986-1985-01>
- Muller, K. J., Walossek, D., 1988. External morphology and larval development of the Upper Cambrian maxillopod *Bredocaris admirabilis*. *Fossils and Strata* 23, 1–70. <https://doi.org/10.18261/8200374122-1988-01>
- Murdock, D.J., Gabbott, S.E., Mayer, G., Purnell, M.A., 2014. Decay of velvet worms (Onychophora), and bias in the fossil record of lobopodians. *BMC Evolutionary Biology* 14, 222. <https://doi.org/10.1186/s12862-014-0222-z>
- Mutel, M.H.E., Waugh, D.A., Feldmann, R.M., Parsons-Hubbard, K.M., 2008. Experimental taphonomy of *Callinectes sapidus* and cuticular controls on preservation. *PALAIOS* 23, 615–623. <https://doi.org/10.2110/palo.2008.p08-024r>
- Naimark, E., Kalinina, M., Boeva, N., 2018. Persistence of external anatomy of small crustaceans in a long term taphonomic experiment. *PALAIOS* 33, 154–163. <https://doi.org/10.2110/palo.2017.083>
- Naimark, E., Kalinina, M., Shokurov, A., Boeva, N., Markov, A., Zaytseva, L., 2016. Decaying in different clays: implications for soft-tissue preservation. *Palaeontology* 59, 583–595. <https://doi.org/10.1111/pala.12246>
- Nanglu, K., Caron, J.-B., Gaines, R.R., 2020. The Burgess Shale paleocommunity with new insights from Marble Canyon, British Columbia. *Paleobiology* 46, 58–81. <https://doi.org/10.1017/pab.2019.42>
- Newman, S.A., Daye, M., Fakra, S.C., Marcus, M.A., Pajusalu, M., Pruss, S.B., Smith, E.F., Bosak, T., 2019. Experimental preservation of muscle tissue in quartz sand and kaolinite. *PALAIOS* 34, 437–451. <https://doi.org/10.2110/palo.2019.030>
- Nielsen, M.L., Lee, M., Ng, H.C., Rushton, J.C., Hendry, K.R., Kihm, J.-H., Nielsen, A.T., Park, T.-Y.S., Vinther, J., Wilby, P.R., 2022. Metamorphism obscures primary taphonomic pathways in the early Cambrian Sirius Passet Lagerstätte, North Greenland. *Geology* 50, 4–9.
- Orr, P.J., Briggs, D.E.G., Kearns, S.L., 1998. Cambrian Burgess

- Shale Animals Replicated in Clay Minerals. *Science* 281, 1173–1175. <https://doi.org/10.1126/science.281.5380.1173>
- Palmer, B., Karačić, S., Low, S.L., Janssen, K., Färber, H., Liesegang, M., Bierbaum, G., Gee, C.T., 2024. Decay experiments and microbial community analysis of water lily leaf biofilms: Sediment effects on leaf preservation potential. *PLOS ONE* 19, e0315656. <https://doi.org/10.1371/journal.pone.0315656>
- Paterson, J.R., García-Bellido, D.C., Edgecombe, G.D., 2023. The early Cambrian Emu Bay Shale radiodonts revisited: morphology and systematics. *Journal of Systematic Palaeontology* 21, 2225066. <https://doi.org/10.1080/14772019.2023.2225066>
- Pates, S., Daley, A.C., 2019. The Kinzers Formation (Pennsylvania, USA): the most diverse assemblage of Cambrian Stage 4 radiodonts. *Geol. Mag.* 156, 1233–1246. <https://doi.org/10.1017/S0016756818000547>
- Pates, S., Leroosey-Aubril, R., Daley, A.C., Kier, C., Bonino, E., Ortega-Hernández, J., 2021. The diverse radiodont fauna from the Marjum Formation of Utah, USA (Cambrian: Drumian). *PeerJ* 9, e10509. <https://doi.org/10.7717/peerj.10509>
- Pazinot, P.G., Jauvion, C., Schweigert, G., Haug, J.T., Haug, C., 2021. After 100 years: a detailed view of an eumalacostracan crustacean from the Upper Jurassic Solnhofen Lagerstätte with raptorial appendages unique to Euarthropoda. *Lethaia* 54, 55–72. <https://doi.org/10.1111/let.12382>
- Pérez-Peris, F., Laibl, L., Vidal, M., Daley, A., Vidal, M., Daley, A.C., 2021. Systematics, morphology, and appendages of an Early Ordovician pilekiine trilobite *Anacheirurus* from Fezouata Shale and the early diversification of Cheiruridae. *Acta Palaeontologica Polonica* 66, 857–877. <https://doi.org/10.4202/app.00902.2021>
- Plotnick, R.E., 1986. Taphonomy of a Modern Shrimp: Implications for the Arthropod Fossil Record. *PALAIOS* 1, 286. <https://doi.org/10.2307/3514691>
- Potin, G.J.-M., Daley, A.C., 2023. The significance of *Anomalocaris* and other Radiodonts for understanding paleoecology and evolution during the Cambrian explosion. *Frontiers in Earth Science* 11.
- Potin, G.J.-M., Gueriau, P., Daley, A.C., 2023. Radiodont frontal appendages from the Fezouata Biota (Morocco) reveal high diversity and ecological adaptations to suspension-feeding during the Early Ordovician. *Frontiers in Ecology and Evolution* 11.
- Purnell, M.A., Donoghue, P.J.C., Gabbott, S.E., McNamara, M.E., Murdock, D.J.E., Sansom, R.S., 2018. Experimental analysis of soft-tissue fossilization: opening the black box. *Palaeontology* 61, 317–323. <https://doi.org/10.1111/pala.12360>
- Sagemann, J., Bale, S.J., Briggs, D.E.G., Parkes, R.J., 1999. Controls on the formation of authigenic minerals in association with decaying organic matter: an experimental approach. *Geochimica et Cosmochimica Acta* 63, 1083–1095. [https://doi.org/10.1016/S0016-7037\(99\)00087-3](https://doi.org/10.1016/S0016-7037(99)00087-3)
- Saleh, F., Antcliffe, J.B., Birolini, E., Candela, Y., Corthésy, N., Daley, A.C., Dupichaud, C., Gilbert, C., Guenser, P., Laibl, L., Lefebvre, B., Michel, S., Potin, G.J.-M., 2024a. Highly resolved taphonomic variations within the Early Ordovician Fezouata Biota. *Scientific Reports* 14, 20807. <https://doi.org/10.1038/s41598-024-71622-w>
- Saleh, F., Antcliffe, J.B., Lefebvre, B., Pittet, B., Laibl, L., Pérez-Peris, F., Lustrì, L., Gueriau, P., Daley, A.C., 2020a. Taphonomic bias in exceptionally preserved biotas. *Earth and Planetary Science Letters* 529, 115873. <https://doi.org/10.1016/j.epsl.2019.115873>
- Saleh, F., Bath-Enright, O.G., Daley, A.C., Lefebvre, B., Pittet, B., Vite, A., Ma, X., Mángano, M.G., Buatois, L.A., Antcliffe, J.B., 2021a. A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas. *Earth and Planetary Science Letters* 569, 117061. <https://doi.org/10.1016/j.epsl.2021.117061>
- Saleh, F., Daley, A.C., Lefebvre, B., Pittet, B., Perrillat, J.P., 2020b. Biogenic Iron Preserves Structures during Fossilization: A Hypothesis. *BioEssays* 42, 1900243. <https://doi.org/10.1002/bies.201900243>
- Saleh, F., Lefebvre, B., Dupichaud, C., Martin, E.L.O., Nohejlová, M., Spaccesi, L., 2023. Skeletal elements controlled soft-tissue preservation in echinoderms from the Early Ordovician Fezouata Biota. *Geobios*. <https://doi.org/10.1016/j.geobios.2023.08.001>
- Saleh, F., Lustrì, L., Gueriau, P., Potin, G.J.-M., Pérez-Peris, F., Laibl, L., Jamart, V., Vite, A., Antcliffe, J.B., Daley, A.C., Nohejlová, M., Dupichaud, C., Schöder, S., Bérard, E., Lynch, S., Drage, H.B., Vaucher, R., Vidal, M., Monceret, E., Monceret, S., Lefebvre, B., 2024b. The Cabrières Biota (France) provides insights into Ordovician polar ecosystems. *Nat Ecol Evol* 1–12. <https://doi.org/10.1038/s41559-024-02331-w>
- Saleh, F., Ma, X., Guenser, P., Mángano, M.G., Buatois, L.A., Antcliffe, J.B., 2022a. Probability-based preservational variations within the early Cambrian Chengjiang biota (China). *PeerJ* 10, e13869. <https://doi.org/10.7717/peerj.13869>
- Saleh, F., Pittet, B., Perrillat, J.-P., Lefebvre, B., 2019. Orbital control on exceptional fossil preservation. *Geology* 47, 103–106. <https://doi.org/10.1130/G45598.1>
- Saleh, F., Pittet, B., Sansjofre, P., Guéria, P., Lalonde, S., Perrillat, J.-P., Vidal, M., Lucas, V., El Hariri, K., Kourais, K., Lefebvre, B., 2020c. Taphonomic pathway of exceptionally preserved fossils in the Lower Ordovician of Morocco. *Geobios* 60, 99–115. <https://doi.org/10.1016/j.geobios.2020.04.001>
- Saleh, F., Qi, C., Buatois, L.A., Mángano, M.G., Paz, M., Vaucher, R., Zheng, Q., Hou, X.-G., Gabbott, S.E., Ma, X., 2022b. The Chengjiang Biota inhabited a deltaic environment. *Nature Communications* 13, 1569. <https://doi.org/10.1038/s41467-022-29246-z>
- Saleh, F., Vaucher, R., Antcliffe, J.B., Daley, A.C., El Hariri, K., Kourais, K., Lefebvre, B., Martin, E.L.O., Perrillat, J.-P., Sansjofre, P., Vidal, M., Pittet, B., 2021b. Insights into soft-part preservation from the Early Ordovician Fezouata Biota. *Earth-Science Reviews* 213, 103464. <https://doi.org/10.1016/j.earscirev.2020.103464>
- Saleh, F., Vaucher, R., Vidal, M., Hariri, K.E., Laibl, L., Daley, A.C., Gutiérrez-Marco, J.C., Candela, Y., Harper, D.A.T., Ortega-Hernández, J., Ma, X., Rida, A., Vizcaíno, D., Lefebvre, B., 2022c. New fossil assemblages from the Early Ordovician Fezouata Biota. *Sci Rep* 12, 20773. <https://doi.org/10.1038/s41598-022-25000-z>
- Sansom, R.S., 2014. Experimental Decay of Soft Tissues. *The Paleontological Society Papers* 20, 259–274. <https://doi.org/10.1017/S1089332600002886>
- Sansom, R.S., Gabbott, S.E., Purnell, M.A., 2010. Non-random decay of chordate characters causes bias in fossil interpretation. *Nature* 463, 797–800. <https://doi.org/10.1038/nature08745>
- Sansom, R.S., Gabbott, S.E., Purnell, M.A., 2013. Atlas of vertebrate decay: a visual and taphonomic guide to fossil interpretation. *Palaeontology* 56, 457–474. <https://doi.org/10.1111/pala.12037>
- Schiffbauer, J.D., Xiao, S., Cai, Y., Wallace, A.F., Hua, H., Hunter, J., Xu, H., Peng, Y., Kaufman, A.J., 2014. A unifying model for Neoproterozoic–Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. *Nature Communications* 5, 5754. <https://doi.org/10.1038/ncomms6754>
- Schmidt, M., Hou, X., Mai, H., Zhou, G., Melzer, R.R., Zhang, X., Liu, Y., 2024. Unveiling the ventral morphology of a rare early Cambrian great appendage arthropod from the Chengjiang biota of China. *BMC Biol* 22, 96. <https://doi.org/10.1186/s12915-024-01889-y>
- Schmidt, M., Liu, Y., Hou, X., Haug, J.T., Haug, C., Mai, H., Melzer, R.R., 2021. Intraspecific variation in the Cambrian: new observations on the morphology of the Chengjiang euarthropod *Sinoburius lunaris*. *BMC Ecol Evo* 21, 127. <https://doi.org/10.1186/s12862-021-01854-1>
- Slagter, S., Konhäuser, K.O., Briggs, D.E.G., Tarhan, L.G., 2024. Controls on authigenic mineralization in experimental Ediacara-style preservation. *Geobiology* 22, e12615. <https://doi.org/10.1111/gbi.12615>
- Van Roy, P., Briggs, D.E.G., Gaines, R.R., 2015. The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society* 172, 541–549. <https://doi.org/10.1144/jgs2015-017>
- Vinther, J., Stein, M., Longrich, N.R., Harper, D.A.T., 2014. A suspension-feeding anomalocarid from the Early Cambrian. *Nature* 507, 496–499.



<https://doi.org/10.1038/nature13010>

Walossek, D., 1993. The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea, in: The Upper Cambrian *Rehbachella* and the Phylogeny of Branchiopoda and Crustacea, Fossils and Strata. Scandinavian University Press, pp. 1–202. <https://doi.org/10.18261/8200374874-1993-01>

Whiteaves, J.F., 1892. Description of A New Genus and Species of Phyllocarid Crustacea From The Middle Cambrian of Mount Stephen, B.C. Canadian Record of Science 205–208 — PDF. The Canadian Record of Science 205–208.

Whittington, H.B., Briggs, D.E.G., 1985. The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British-Columbia. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 309, 569–609. <https://doi.org/10.1098/rstb.1985.0096>

Wijnker, J.J., Koop, G., Lipman, L.J.A., 2006. Antimicrobial properties of salt (NaCl) used for the preservation of natural casings. Food Microbiol 23, 657–662. <https://doi.org/10.1016/j.fm.2005.11.004>

Wilson, L.A., Butterfield, N.J., 2014. Sediment Effects on the Preservation of Burgess Shale-Type Compression Fossils. PALAIOS 29, 145–154. <https://doi.org/10.2110/palo.2013.075>

Winkler, N., 2013. A new genus and species of caridean shrimps from the Upper Jurassic Solnhofen Lithographic Limestones of Schernfeld (S Germany). Zitteliana 77–83. <https://doi.org/10.5282/ubm/epub.19015>

Winkler, N., 2014. A new caridean shrimp (Crustacea: Decapoda: Dendrobranchiata) from the Upper Jurassic Solnhofen Lithographic Limestones of Schernfeld (South Germany). Zitteliana 83–90. <https://doi.org/10.5282/ubm/epub.22325>

Wu, Y., Fu, D., Ma, J., Lin, W., Sun, A., Zhang, X., 2021a. *Houcaris* gen. nov. from the early Cambrian (Stage 3) Chengjiang Lagerstätte expanded the palaeogeographical distribution of tamisiocaridids (Panarthropoda: Radiodonta). PalZ 95, 209–221. <https://doi.org/10.1007/s12542-020-00545-4>

Wu, Y., Ma, J., Lin, W., Sun, A., Zhang, X., Fu, D., 2021b. New anomalocaridids (Panarthropoda: Radiodonta) from the lower Cambrian Chengjiang Lagerstätte: Biostratigraphic and paleobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 569, 110333. <https://doi.org/10.1016/j.palaeo.2021.110333>

Wu, Y., Pates, S., Liu, C., Zhang, M., Lin, W., Ma, J., Wu, Yuheng, Chai, S., Zhang, X., Fu, D., 2024a. A new radiodont from the lower Cambrian (Series 2 Stage 3) Chengjiang Lagerstätte, South China informs the evolution of feeding structures in radiodonts. Journal of Systematic Palaeontology 22, 2364887. <https://doi.org/10.1080/14772019.2024.2364887>

Wu, Y., Pates, S., Ma, J., Lin, W., Wu, Yuheng, Zhang, X., Fu, D., 2022. Addressing the Chengjiang conundrum: A palaeoecological view on the rarity of hurdiid radiodonts in this most diverse early Cambrian Lagerstätte. Geoscience Frontiers 13, 101430. <https://doi.org/10.1016/j.gsf.2022.101430>

Wu, Y., Pates, S., Zhang, M., Lin, W., Ma, J., Liu, C., Wu, Yuheng, Zhang, X., Fu, D., 2024b. Exceptionally preserved radiodont arthropods from the lower Cambrian (Stage 3) Qingjiang Lagerstätte of Hubei, South China and the biogeographic and diversification patterns of radiodonts. Papers in Palaeontology 10, e1583. <https://doi.org/10.1002/sp2.1583>

Yochelson, E.L., 1996. Discovery, Collection, and Description of the Middle Cambrian Burgess Shale Biota by Charles Doolittle Walcott. Proceedings of the American Philosophical Society 140, 469–545.

Zhang, M., Wu, Yu, Lin, W., Ma, J., Wu, Yuheng, Fu, D., 2023. Amplectobeluid Radiodont *Guanshancaris* gen. nov. from the Lower Cambrian (Stage 4) Guanshan Lagerstätte of South China: Biostratigraphic and Paleobiogeographic Implications. Biology 12, 583. <https://doi.org/10.3390/biology12040583>

Zhao, F., Zhu, M., Hu, S., 2010. Community structure and composition of the Cambrian Chengjiang biota. Sci. China Earth Sci. 53, 1784–1799. <https://doi.org/10.1007/s11430-010-4087-8>