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1 EXPERIMENTAL INVESTIGATION OF INSECT DEPOSITION IN LENTIC  
2 ENVIRONMENTS AND IMPLICATIONS FOR FORMATION OF  
3 KONSERVAT-LAGERSTÄTTEN

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13

14 **Abstract:** Terrestrial insects are often remarkably well preserved in lacustrine Konservat-  
15 Lagerstätten. However, the assumption that carcasses should sink fast through the water  
16 column seems to contradict evidence that this scenario is unlikely due to excessive buoyancy  
17 and surface tension. The mechanisms that promote rapid and permanent emplacement onto  
18 the sediment surface (RPESS) of such terrestrial animal remains are not fully understood.  
19 Here we use taphonomic experiments to show that floating in water, growth of microbial  
20 biofilms and reception of rapid sediment load promote RPESS of terrestrial insect remains in  
21 lentic water bodies. Our results show that the optimum conditions for RPESS occur when  
22 terrestrial insects enter a lentic water body in articulation, experience brief decay in  
23 association with growth of microbes, then are buried rapidly by airborne volcanic ash. These  
24 results provide a model for preservation of articulated terrestrial insects and emphasize the

1 importance of microbial activity and volcanism for insect preservation in lacustrine

2 Konservat-Lagerstätten.

3

4 **Key words:** experimental taphonomy, Konservat-Lagerstätten, decay, microbes, ashfall.

5

6 KONSERVAT-LAGERSTÄTTEN are characterized by a high quality of fossil preservation,  
7 notably the preservation of articulated skeletons, sometimes in association with soft tissues  
8 (Seilacher *et al.* 1985). These biotas are often likened to a series of rare snapshots of ancient  
9 life that provide much more complete data on the diversity of ancient communities than the  
10 remainder of the fossil record (Briggs 2001). Preservation of soft tissues has been a focus of  
11 recent research on such biotas; skeletal preservation (e.g. completeness, articulation) has  
12 received less attention. Early models considered the principal mechanisms leading to soft  
13 tissue preservation to include anoxia (stagnation), rapid burial (obrution), early diagenetic  
14 concretion growth, and microbial coverings, in addition to more localized decay-inhibitory  
15 media such as tar, permafrost, and amber (Seilacher *et al.* 1985). Over the past three decades,  
16 publication of a comprehensive body of experimental taphonomic studies has added nuance to  
17 these models and provided detailed information on how various processes operate.  
18 Experiments have shown that anoxia and obrution cannot inhibit degradation (Allison 1988)  
19 and thus cannot in isolation result in soft-tissue preservation. Instead, soft-tissue preservation  
20 is understood to reflect a complex interplay of factors, including decay, mineralization and/or  
21 maturation of organic material (Allison 1988; Briggs 1995; Briggs and McMahon 2016;  
22 Purnell *et al.* 2018 and references therein). Decay is a major factor in preservation via the  
23 generation of steep geochemical gradients necessary for replication of soft tissues in  
24 authigenic minerals (Sagemann *et al.* 1999) and for certain types of organic preservation  
25 (McNamara *et al.* 2016). The impact of sediment composition on soft tissue preservation has

1 also been investigated (Anderson *et al.* 2011; Wilson and Butterfield 2014; Murdock *et al.*  
2 2016).

3 In contrast, controls on the preservation of articulated skeletons are less well  
4 understood. Taphonomic experiments have shown that freshly killed animals may remain  
5 articulated after long-distance transport, whereas they disarticulate readily if transported  
6 following a period of decay (Allison 1986; Bath Enright *et al.* 2017). Decay and subsequent  
7 disarticulation of animal remains on the water surface begins rapidly (commonly within 3–10  
8 weeks; e.g. Duncan 1997; Peñalver 2002; Brand *et al.* 2003; Syme and Salisbury 2014), thus  
9 rapid and permanent emplacement onto the sediment surface (RPESS) of the animal remains  
10 is an important factor in the preservation of articulated skeletons under water.

11 Insects are of particular importance as they are the most diverse taxon in terrestrial  
12 ecosystems (Gaston 1991; Stork 2009) and are abundant in many lacustrine Konservat-  
13 Lagerstätten (Zherikin 2002). Decay sequences and taxonomic biases of insects have been  
14 studied (Martínez-Delclòs and Martinell 1993; Duncan 1997; Peñalver 2002; Duncan *et al.*  
15 2003; Smith *et al.* 2006; Wang *et al.* 2013), but other aspects of their taphonomy are less well  
16 understood. Notably, depositional mechanisms – particularly those relating to sinking – have  
17 not been investigated systematically. Previous studies have suggested that in the absence of  
18 transport, turbulence and sediment influx, terrestrial insects rarely sink onto, and remain on,  
19 the sediment-water interface without first disarticulating at the water surface (Martínez-  
20 Delclòs and Martinell 1993; Duncan 1997; Duncan *et al.* 2003). Studies in natural lake  
21 systems also support the hypothesis that terrestrial insects rarely sink (Rolla *et al.* 2017).  
22 Transport increases rates of both sinking and disarticulation but does not impact the trend for  
23 sinking to occur after disarticulation of the abdominal or leg segments (Duncan *et al.* 2003;  
24 Smith *et al.* 2006).

1           Whether a floating animal carcass can sink to the sediment surface in standing water  
2 depends on the contrast between the downward force (a product of carcass mass  $mg$  plus any  
3 external downward force  $F$  exerted on it) and upward resistance force (a product of surface  
4 tension  $ST$  plus buoyancy  $B$ ; Fig. 1):  $F + mg$  vs.  $B + ST$ . The carcass will float until the  
5 downward force overcomes the resistance force. The force contrast varies depending on the  
6 biological characteristics of the floating carcass (e.g. size, shape, hydrophilicity and mass;  
7 Sansom 2014; Vella 2015), water conditions (e.g. pH, salinity, extent of microbial biofilms,  
8 temperature, and depth; Allison 1990; Allison *et al.* 1991; Raff *et al.* 2014), and the amount  
9 and nature of physical disturbances (e.g. wind, rainfall and sediment load; Martínez-Delclòs  
10 and Martinell 1993; Beattie 2007). After a carcass enters a lentic water body, several of these  
11 parameters (e.g. submerged volume, contact area, hydrophobicity and mass) change over time  
12 due to the effects of decay, absorption of water and development of biofilms (Martínez-  
13 Delclòs and Martinell 1993; Duncan 1997); this, in turn, could potentially reduce the force  
14 contrast, but could not overcome the resistance force alone. Extrinsic factors, such as waves,  
15 fungi and algae, have been suggested to promote sinking (Martínez-Delclòs and Martinell  
16 1993).

17           Among these physical disturbances, rapid sediment load may significantly enhance the  
18 downward force and has been identified as a factor in the rapid burial of articulated carcasses  
19 (Smiley *et al.* 1975; Beattie 2007; Yang *et al.* 2019). Beattie (2007) investigated ash load on  
20 freshly killed insects, and most insects remained floating. In this study, we test whether: 1)  
21 development of microbial biofilms on floating carcasses can reduce the force contrast, and 2)  
22 rapid sediment load, mimicking volcanic ashfall, can promote RPESS of terrestrial insect  
23 remains. Our results are compared with lacustrine-hosted Lagerstätten that contain articulated  
24 preserved terrestrial insects. Other extrinsic factors, such as rainfall, wind, predation and  
25 attaching bivalve larvae, may contribute to external downward forces (Martínez-Delclòs and

1 Martinell 1993; Ilger 2011), but these are not tested here as they do not yield a sustained  
2 force, easily cause disarticulation or are not applicable widely.

3

#### 4 **MATERIALS AND METHODS**

##### 5 *Experimental materials*

6 *Specimens.* Our experiments used commercially available specimens of the cockroach  
7 *Periplaneta americana* (Blattodea: Blattidae; n = 580) and the butterfly *Danaus chrysippus*  
8 (Lepidoptera: Nymphalidae; n = 510). We selected these taxa because they differ strongly in  
9 mass, geometry and hydrophobicity (Table 1). Specimens were euthanized via asphyxiation  
10 as in Duncan *et al.* (2003). To ensure that specimens were dead, they were left within the  
11 airtight chambers for 24 h after their last movement. All specimens died in the wing-folded  
12 posture.

13

14 *Experimental media.* Two different media were used in our experiments to evaluate the effect  
15 of microbial activity: natural eutrophic lake water and commercially available distilled water  
16 (Table 2). The former contains aquatic microbes in contrast to the latter, which contains no  
17 detectable microbes (Table 2). The lake water was collected from Lizhao Lake at the Xianlin  
18 campus of Nanjing University one or two days prior to the experiments and filtered through a  
19 150 µm mesh to remove macroscopic debris. Filtered lake water was stored at 20–25°C until  
20 the experiments commenced; no other treatment was applied.

21

22 *Sediment.* Tuffs and tuffaceous sediments are a common component of the sedimentary  
23 successions hosting many lacustrine Konservat-Lagerstätten (e.g. Yixian Formation,  
24 Haifanggou and Tiaojishan Formations and Florissant Formation; Hethke *et al.* 2012; Yang *et*  
25 *al.* 2019; McLeroy and Anderson 1966) and volcanic ashfall has been proposed as a death

1 mechanism for some biotas (Sinichenkova and Zherikhin 1996; Beattie 2007; Jiang *et al.*  
2 2011; Beattie and Avery 2012; Yang *et al.* 2019; Wang *et al.* 2019). Commercially available  
3 volcanic tephra (grain size 10–150  $\mu\text{m}$ , mean 40  $\mu\text{m}$  (Hess pumice, Idaho, USA)) was used in  
4 this study.

5

### 6 *Experimental setup*

7 Our experiments used plastic basins 258 mm in diameter, each containing ca. 4500 ml water.  
8 Basins with lake water were covered by 1 mm mesh to avoid potential physical disturbance,  
9 while those with distilled water were washed by hot water ( $> 80^\circ\text{C}$ ) prior to experiments and  
10 covered by saran wrap to minimize contamination by environmental microbes. All basins  
11 were placed in the basement of the School of Earth Sciences and Engineering, Nanjing  
12 University and were not moved during the experiment. Water temperature was maintained at  
13  $20\text{--}25^\circ\text{C}$  using ambient air-conditioning units. In each experiment, ten carcasses of either  
14 cockroaches or butterflies were placed in each basin. The resulting carcass density was 145  
15 insects/ $\text{m}^2$ , which is in the range of observations during mass mortality events (e.g. 10–200  
16 cicadas/ $\text{m}^2$ , Nowlin *et al.* 2007; 200–500 ants/ $\text{m}^2$ , Carlton and Goldman 1984). During  
17 emplacement in the basins, carcasses were positioned carefully to prevent mutual contact.  
18 During the experiment, 78% of carcasses (calculated based on photographs of total 540  
19 specimens) were spaced  $> 10$  mm apart, which is ca. three times the capillary length for an  
20 air-water interface (2.7 mm; Cooray 2014). As lateral capillary forces between floating  
21 objects decay approximately exponentially over the capillary length (Velev *et al.* 1993),  
22 interactions among most of the carcasses were therefore negligible. The other 22% of  
23 carcasses ( $n = 540$ ) were spaced  $< 10$  mm apart. The antennae and body margins of 13% of  
24 carcasses ( $n = 540$ ) locally came into contact, but no overlap of body parts was observed.



1 Four independent experiments were designed (Fig. 2A). All experiments were run  
2 with cockroaches and butterflies separately.

3 Experiment 1 was designed to make continuous taphonomic observations (of indices  
4 including decay state, articulation, sinkage and presence of microbial films, etc.) on both taxa  
5 placed in different media without treatment. Observations were recorded daily for one month,  
6 and then after an additional two weeks.

7 Experiment 2 was designed to test the effects of media type (predictor variable 1  
8 (nominal) with two levels: lake and distilled water) and flotation duration (predictor variable  
9 2 (ratio) with 8 and 7 levels for cockroaches and butterflies respectively;  $T_2$  in Table 3) on  
10 mass (response variable 1 (ratio)) and resistance force (response variable 2 (ratio)) of the  
11 insects. The experimental design incorporated a longer flotation duration for butterflies: pilot  
12 experiments revealed that their wet mass continued to increase for a longer time than  
13 cockroaches.

14 Experiment 3 was designed to test the effects of media type (predictor variable 1  
15 (nominal) with two levels of lake and distilled water) and flotation duration before  
16 introduction of 200 g sediment (predictor variable 2 (ratio) with 12–16 levels;  $T_3$  in Table 3)  
17 on the flotation state (sink / not sink (response variable (nominal))) of the insects. Intervals of  
18 flotation duration were more closely spaced in the early part of the experiment in order to  
19 better define the shortest duration required for sinking.

20 Experiment 4 was designed to test the effects of mass of sediment introduced  
21 (predictor variable 1 (ratio) with 8 and 7 levels for cockroaches and butterflies respectively; Q  
22 in Table 3) on the flotation response (sink / not sink (response variable (nominal))) of the  
23 insects that had already floated for 14 days in lake water. Among the fifteen basins, more  
24 basins were treated with only 10–70 g of sediment in order to identify the minimum thickness

1 required for sinking. The flotation duration of 14 days was selected because most carcasses  
2 sank by that time in Experiment 3.

3

#### 4 *Measurements, sediment loading, observations, and data processing*

5 In Experiment 2, measurements of resistance force (buoyancy and surface tension) were based  
6 on the physical principles used by Hughes (2005) and Wang *et al.* (2015) (Fig. 2B).

7 Individual carcasses (including any attached microbial films) were transferred from the basins  
8 to a paper cup of water on a scale for weighing using sterile tweezers. To reduce confounding  
9 influences on surface tension, carcasses were placed horizontally onto the water surface in the  
10 cup to replicate as closely as possible the orientation of the insect in the basin relative to the  
11 air-water interface. All specimens remained floating after transfer. Each carcass was then  
12 pushed downward at a speed of 0.05 mm/s by a slider that was automatically manipulated by  
13 a wire bracket until fully submerged. The scale readings and the slider block positions were  
14 recorded once per second by G&G electronic balance sampling software. Carcasses that  
15 disarticulated or failed to submerge during the measurements were excluded from subsequent  
16 analyses.

17       After subtracting the resistance force exerted on the wire bracket, a resistance force-  
18 submerged depth curve was obtained for each carcass (Fig. 1B shows a schematic curve; the  
19 full dataset is available in Tian *et al.* 2019, S6–S9). The maximum resistance force was  
20 always reached when the insect broke through the water surface. The mean values and 95%  
21 confidence intervals of (1) wet weight, (2) buoyancy, (3) the force contrast between wet  
22 weight and buoyancy and (4) the contrast between wet weight and the maximum resistance  
23 force were plotted versus flotation duration using OriginPro (OriginLab, Northampton, MA).  
24 Linear regression using the Ordinary Least Squares algorithm was performed in PAST  
25 (Hammer *et al.* 2001) to test the effects of flotation duration on the force contrast between wet

1 weight and buoyancy, and the contrast between wet weight and the maximum resistance  
2 force, respectively.

3 In Experiment 3 and 4, sediment was introduced through a 150  $\mu\text{m}$  sieve, which was  
4 held by hand at a distance of ca. 0.3 m above the water surface (Fig. 2C). This distance is  
5 sufficient to accelerate all clasts in our experimental sediment to speeds of over 88% of the  
6 maximum falling speed for that grain size in natural ashfall (Tian *et al.* 2019, S2). Sediment  
7 was introduced in pulses of 10 g, with each pulse lasting  $26 \pm 7$  s ( $n = 25$ ) and an interpulse  
8 interval of  $33 \pm 7$  s ( $n = 25$ ). The mean mass flux in each treatment ( $6.7 \pm 0.7$  kg/m<sup>2</sup>/h,  $n = 5$ ,  
9 calculated based on the area of water surface  $6.88 \times 10^{-2}$  m<sup>2</sup>, and 30% loss of sediment from  
10 the vessel) has a similar magnitude to that of a natural volcanic ash fallout (1–2 kg/m<sup>2</sup>/h;  
11 Scheidegger *et al.* 1982). Introduction of 200 g sediment took  $18 \pm 2$  min ( $n = 5$ ) in total and  
12 resulted in the formation of a lamina ca. 4 mm thick.

13 In Experiments 3 and 4, carcasses that sank onto the sediment surface were monitored,  
14 and those that remained there three days after the treatment were considered as having  
15 experienced RPESS. The effects of flotation duration and microbial activity on RPESS of  
16 individual specimens were tested by performing binary logistic regression analyses and  
17 likelihood ratio tests (the null hypothesis is that the probability of RPESS is independent of  
18 one predictor variable) in R using the functions `glm {stats}` (R Core Team 2018) and `lrtest`  
19 `{lmtree}` (Zeileis and Hothorn 2002). The proportion of specimens experiencing RPESS in  
20 each basin was plotted versus (1) duration before sediment loading (Experiments 3; with  
21 logistic regression lines for different water types) and (2) sediment thickness calculated from  
22 the mass of introduced sediment (Experiment 4) using OriginPro.

23 Representative sedimentary laminae containing carcasses from Experiments 3 and 4  
24 were dried and embedded in epoxy resin; polished and thin sections were prepared from the  
25 resin blocks. For comparison, a typical laminated tuffaceous mudstone with fossil insects

1 from the Jurassic Haifanggou Formation was also sectioned. The sections were examined  
2 with a Nikon SMZ25 stereomicroscope and a Nikon ECLIPSE LV100N POL polarizing  
3 microscope.

4

#### 5 *Scanning electron microscopy*

6 To test for the presence of microbial films on butterfly carcasses in lake water, small  
7 fragments (ca. 5 mm × 5 mm) of the hind wing between veins M<sub>3</sub> and Cu<sub>1</sub> were dissected  
8 from representative butterfly specimens using sterile tools after performing the measurements  
9 in Experiment 2. Samples were mounted on carbon tape, dried and sputter-coated with Au and  
10 examined with a Zeiss Supra 55 scanning electron microscope (SEM) at 15 kV and a working  
11 distance of 8.8–9.1 mm.

12

#### 13 *Lacustrine-hosted Lagerstätten*

14 Terrestrial insect fossil records from deposits in lentic environments (“lacustrine”, “crater  
15 lake” and “pond”) were downloaded from the Paleobiology Database (PaleoDB:  
16 <http://paleobiodb.org>) on 19th May 2019 (Tian *et al.* 2019, S10). Among these deposits, 27  
17 Lagerstätten hosted in laminated sediments and with well-studied sedimentary backgrounds  
18 and fossil records were selected for investigation. Data collected include location, age,  
19 lithology, and the thickness, organic carbon content and microbial component of the fossil-  
20 bearing laminae (Tian *et al.* 2019, S4). For “large-winged” insects (adult Lepidoptera,  
21 Ephemeroptera, Odonata, Neuroptera and Tricoptera) such as butterflies, RPESS is rare in  
22 normal situations (Martínez-Delclòs and Martinell 1993; Duncan 1997). The presence or  
23 absence of articulated “large-winged” insects in each Lagerstätte was also noted. Specimens  
24 assigned to “body” in “specimen\_part” in the PaleoDB records were counted as articulated.  
25 The proportion of “body” specimens was calculated for each Lagerstätte as a proxy for the

1 proportion of articulated specimens in the fossil assemblage. As the PaleoDB includes only  
2 published specimens, the stated articulated proportion may be artificially inflated, but all  
3 Lagerstätten should have similar biases (Karr and Clapham 2015). The diversities of the  
4 articulated insect fossils were calculated for each Lagerstätte. The Lagerstätten were grouped  
5 into “microbe-bearing laminae” or “not determined” based on the presence / absence of  
6 microbial fossils.

7         The data were analysed as follows. Welch’s t test was performed to compare the  
8 proportion and diversity of articulated specimens in the two groups of Lagerstätten (“microbe-  
9 bearing laminae” and “not determined”). Fisher's exact test was performed to assess the  
10 association between the preservation of articulated “large-winged” insects (“present” or “not  
11 determined”) and the presence of microbial fossils (“microbe-bearing laminae” or “not  
12 determined”). The statistical analyses were performed in PAST (Hammer *et al.* 2001).

13

## 14 **RESULTS**

### 15 *Experiment 1: observations*

16 In lake water, the decay sequences for both cockroaches and butterflies are similar to  
17 sequences reported previously (Fig. 3; Martínez-Delclòs and Martinell 1993; Duncan 1997;  
18 Duncan *et al.* 2003):

19         Decay stage 1 (0–5 days): For both taxa, the legs and antennae became flaccid and the  
20 abdomen, swollen; microbial films were apparent on the carcass. Microbial films also  
21 appeared on the water surface in the basin with cockroaches. Most of the butterfly wings lost  
22 their iridescence.

23         Decay stage 2 (5–21 days): For both taxa, the antennae began to disarticulate.  
24 Microbial films covered the surface of the water in the basin with cockroaches and appeared  
25 on butterfly wings (Fig. 3C, 3F, 3H).

1           Decay stage 3 (> 21 days): Cerci of cockroaches, and heads, abdomens and distal  
2 segments of legs of butterflies started to disarticulate.

3           In distilled water, for both taxa, the decay sequence was identical to that in lake water  
4 but the rate of decay was slower. Microbial films were relatively rare on cuticles and were not  
5 observed on the water surface (Fig. 3B, 3E). Decay stage 1 lasted ca. 10 days. In both types of  
6 water, no RPESS of articulated carcasses was observed during the experiment.

7

### 8 *Experiment 2: measurements*

9           During decay, the wet weight and resistance force of specimens of both taxa showed similar  
10 trends in both types of water. Wet weight and buoyancy increased progressively for 9–18  
11 days, then stabilized or decreased slightly (Fig. 4A–D). Buoyancy exceeded wet weight for all  
12 specimens except one cockroach (in distilled water, 12 days), but the contrast between  
13 buoyancy and wet weight has a negative relationship with flotation duration in water (Fig.  
14 4E–F). The maximum resistance force exceeded the wet weight for each specimen and the  
15 contrast between the two forces does not correlate with duration except for the cockroaches in  
16 distilled water (Fig. 4G–H).

17

### 18 *Experiment 3: flotation duration and sediment load*

19           Sediment influx did not lead to RPESS of the freshly killed carcasses. During sediment influx,  
20 some carcasses were submerged, but refloated in less than 20 seconds when the overlying  
21 sediments slipped away from the wing surface (Fig. 5A, 5D). The initial submergence is  
22 consistent with the force contrast calculations, which show that the calculated maximum  
23 value of the external force generated by the sediment load exceeds the mean value of the force  
24 contrast for the carcasses floating on the water surface, thus submerging the carcasses (Fig.  
25 4E–H).

1           In lake water, some butterfly carcasses sank after one day of flotation and subsequent  
2 sediment loading, and for cockroaches after three days (Fig. 6A–B). The proportion of  
3 carcasses that sank following sediment influx increased progressively with increased flotation  
4 duration; after 14 days of flotation, almost all carcasses of both taxa sank after sediment  
5 loading (Fig. 6A–B, 7). In distilled water, butterfly carcasses sank with sediment load after  
6 three days of flotation, and cockroaches after seven days (Fig. 6A–B). The proportion of  
7 carcasses of both taxa that sank increased progressively with increased flotation duration but  
8 more slowly than in lake water (Fig. 6A–B). The likelihood ratio tests showed that flotation  
9 duration and media type both had significant effects on the probabilities of RPRESS of both  
10 cockroaches (flotation duration,  $\chi^2 = 160.5$ ; media type,  $\chi^2 = 91.4$ ; both  $p$  (independent)  $<$   
11  $0.001$ ) and butterflies (flotation duration,  $\chi^2 = 58.3$ ; media type,  $\chi^2 = 70.5$ ; both  $p$   
12 (independent)  $< 0.001$ ). The resulting sedimentary laminae were ca. 4 mm thick (Fig. 7).

13

#### 14 *Experiment 4: minimum sediment load*

15 For the carcasses that had floated in lake water for 14 days, carcasses of cockroaches and  
16 butterflies sank after only 10 g and 100 g of sediment influx, respectively; the resulting  
17 sedimentary laminae were ca. 0.2 mm and 2 mm thick, respectively (Fig. 6C–D).

18

#### 19 *Analyses of lacustrine Lagerstätten*

20 Analyses of the PaleoDB terrestrial insect fossil records from the “lacustrine”, “crater lake”  
21 and “pond” environments showed that 48% of all specimens (total  $n = 20947$ ) are from the 27  
22 selected Lagerstätten. Among these Lagerstätten, seven are associated with tuffaceous  
23 deposits, and eight formed in pre-existing calderas or maars where most fossiliferous laminae  
24 are not tuffaceous (Tian *et al.* 2019, S4). Statistical analyses show that Lagerstätten with  
25 microbe-bearing laminae have a higher proportion of articulated preserved terrestrial insects

1 compared with those from the 'not determined' group (Welch's  $t = 2.252$ ,  $p$  (same mean) =  
2 0.037). Further, the presence of microbe-bearing laminae is positively associated with the that  
3 of articulated "large-winged" insects (Fisher's exact test,  $p$  (no association) = 0.004).  
4 Lagerstätten with microbe-bearing laminae do not have a significantly higher diversity of  
5 articulated preserved specimens compared with the others (Welch's  $t = 1.701$ ,  $p$  (same mean)  
6 = 0.112).

7

## 8 **DISCUSSION**

9 Our experiments are subject to several potential confounding variables: temperature (20–  
10 25°C) and humidity during the experiments; abundance of microbes in the lake water prior to  
11 the experiments; and sedimentation rate in each pulse of sediment loading ( $15 \pm 5 \text{ kg/m}^2/\text{h}$ ,  $n$   
12 = 25). However, these variables do not undermine our results because (1) temperature does  
13 not significantly affect decay sequence between 15–25°C (Sansom *et al.* 2010) and there was  
14 a statistically robust sample size in each experiment; (2) experimental results of different taxa  
15 and water types had similar patterns; (3) mean flux during each treatment was similar among  
16 basins ( $6.7 \pm 0.7 \text{ kg/m}^2/\text{h}$ ,  $n = 5$ ) and calculations suggest that the momentary impact provides  
17 little downward force on floating insects (Tian *et al.* 2019, S3).

18 Our results show that floating in water can reduce the force contrast of fully  
19 submerged carcasses but – critically – in isolation cannot lead to RPESS. Rapid sediment  
20 loading can significantly increase the downward force, submerging carcasses, but does not  
21 usually result in RPESS of freshly killed carcasses, as observed previously (Beattie 2007).  
22 Rapid sediment loading can, however, trigger widespread RPESS where carcasses have  
23 floated in water for as little as 1–3 days. Most carcasses experience RPESS following  
24 flotation in natural lake water for two weeks, followed by sediment loading. Floating in water  
25 thus plays an important role in RPESS by reducing the force contrast exerted on the



1 submerged carcasses as measured in this experiment. This suggests that most well-preserved  
2 terrestrial insects in lacustrine sediments, though articulated, are likely to have experienced a  
3 phase of floating (and decaying) at the water surface.

4 Growth of microbial films on the carcasses promoted RPESS; this likely reflects  
5 enhanced retention of sediment via adhesion to the biofilm surface (Gerbersdorf and  
6 Wieprecht 2015) and, for the cockroaches, increased surface area for sediment adhesion on  
7 the extensive regions of biofilm surrounding carcasses (Fig. 5C). It is plausible that surficial  
8 biofilms (i.e. biofilms at the air-water interface) trapped additional sediment when the carcass  
9 was submerged, resulting in larger downward forces if the biofilms were better developed.  
10 These aspects of the biofilms may contribute to the positive association between the  
11 probability of specimens experiencing RPESS and flotation duration, and to the higher  
12 probability of specimens experiencing RPESS in lake water than in distilled water (where  
13 fewer microbial films were observed on carcasses; Figs. 3C, 3H, 6A–B). The highest  
14 probabilities of RPESS are associated with flotation in natural eutrophic lake water for over  
15 two weeks and with sediment load > 0.2 mm thick for cockroaches and > 2 mm for butterflies  
16 prior to substantial disarticulation.

17 The probability of RPESS was also influenced by certain biological characteristics of  
18 the insects, particularly their geometry and hydrophobicity. The higher wing surface-body  
19 mass index (wing surface/(body mass)<sup>0.67</sup>; Wagner *et al.* 1996; Table 1) and enhanced  
20 hydrophobicity of the butterflies relative to the cockroaches (Table 1) results in a greater  
21 contrast between the downward and resistance forces applied to the carcasses (Fig. 4E–H),  
22 thus requiring a higher mass of sediment to overcome the force contrast than for the  
23 cockroaches (Fig. 6C–D). Further, the high surface area:volume ratio (relating to the large flat  
24 wings) of the butterflies relative to the cockroaches (Table 1; Fig. 3) mean that the overlying

1 sediment is less likely to slip away, so the sediment load can submerge butterflies after shorter  
2 flotation durations than the cockroaches in both types of water (Fig. 6A–B).

3 Collectively, these results demonstrate that RPESS of insect remains that are floating  
4 in static water bodies depends on their biological characteristics, flotation duration in water,  
5 intensity of microbial activity, and availability of sufficient sediment load. RPESS contributes  
6 to the preservation of articulated terrestrial insects in lacustrine Konservat-Lagerstätten. For  
7 the carcasses of terrestrial insects that remain articulated and floating on a eutrophic or  
8 hypereutrophic water surface for a sufficient duration (e.g. two weeks in our experiments), a  
9 rapidly deposited sediment load on the insect carcasses as little as 0.2 mm thick may enable  
10 RPESS. This process may have contributed to the preservation of articulated terrestrial insects  
11 in lacustrine Konservat-Lagerstätten with surficial biofilms and sediment load deposits over  
12 0.06 mm thick, considering the density of compacted deposits as ca. 1.7 g/cm<sup>3</sup> (Duncan and  
13 Vucetich 1970). This is consistent with our statistical results that show that the presence of  
14 microbe-bearing laminae is associated with articulated preservation of terrestrial insects and  
15 the presence of articulated “large-winged” terrestrial insects in lacustrine Lagerstätten. The  
16 presence of microbe-bearing laminae suggests that microbial films existed around floating  
17 carcasses, which promote RPESS of terrestrial insects, especially the “large-winged” ones, as  
18 shown in our experiments. Microbial films not only make sediments adhere to the carcass to  
19 increase the external force for sinking, but they also delay decay and bind carcasses to reduce  
20 disarticulation before burial (Iniesto *et al.* 2016; Martínez-Delclòs and Martinell 1993).

21 All factors being equal, the likelihood of RPESS depends on the availability of  
22 sediment load. Carcasses decaying at the air-water interface in lakes that frequently receive  
23 rapid airborne sediment loads of silt and fine sand are more likely to experience RPESS than  
24 carcasses in lakes that rarely receive rapid airborne sediment load; frequent RPESS is likely to  
25 result in more abundant and diverse insect faunas. This may contribute to the abundance of

1 articulated terrestrial insects preserved in some lacustrine Konservat-Lagerstätten, as over half  
2 of the listed lacustrine Lagerstätten were formed in a volcanic background and about 25%  
3 contain tuff or tuffaceous deposits. Volcanic eruptions may contribute to the abundance of  
4 articulated fossils in three main ways. First, strong eruptions can cause mass mortalities  
5 (Elizalde 2014) that increase the number of articulated carcasses available for burial, and  
6 second, volcanic eruptions can trigger eutrophication of adjacent lake waters (Baross *et al.*  
7 1982) which may promote biofilm development and sinking of insects in these lakes. Third,  
8 volcanic ashfall or remobilization of fresh pyroclastic sediments by wind (Wilson *et al.* 2011)  
9 can dump airborne sediment loads on the carcasses.

10         Apart from tuffaceous lacustrine Lagerstätten, some diatomites, oil shales and  
11 laminated limestones also produced diverse and highly-articulated terrestrial insect fossil  
12 assemblages, which include articulated “large-winged” insects (Tian *et al.* 2019, S4). It is  
13 possible that microbial films on the water surface adhere other terrestrial detritus or  
14 suspended grains around floating carcasses as sediment load to promote RPESS (Gall 2001).  
15 The mechanism was supported by experiments on floating plastic pieces (Chen *et al.* 2019)  
16 but the efficiency on insects requires further study.

17         As different taxa have various conditions for RPESS, preservation biases will exist in  
18 a fossil assemblage. If the flotation duration is between 1–3 days in lake water, only  
19 butterflies can experience RPESS while cockroaches cannot (Fig. 6A–B); if the sediment load  
20 is less than 1 mm thick, only articulated cockroaches will be preserved but butterflies will not  
21 (Fig. 6C–D). With a longer floating period (but before disarticulation) or thicker sediment  
22 load, more diverse insects will be preserved in articulation in a fossil assemblage. Thus  
23 sedimentary conditions may skew our reconstructions of the community diversity.

24

## 25 **CONCLUSIONS**

1 Here, we address the conundrum of the excellent preservation of insects in Lagerstätten  
2 despite evidence that their carcasses generally do not sink in an undamaged condition  
3 (potentially because of resistance forces of the water). Our experiments show that the force  
4 contrast between the downward and resistance forces of fully submerged carcasses reduces  
5 with prolonged floating in lentic water body. We focus on the finding that rapid sediment  
6 loads can significantly increase the downward forces exerted on carcasses and pushes them  
7 fully beneath the water. In contrast to freshly killed carcasses that were buoyed up again,  
8 rapid sediment loads can lead to RPESS of carcasses that had floated for 1–3 days in natural  
9 eutrophic lake water and 3–7 days in distilled water. The proportion of RPESS triggered by  
10 rapid sediment load gradually increased with prolonged floating over 1–2 weeks, after which  
11 rapid sediment load dumping commonly led to RPESS of almost all carcasses. The proportion  
12 of RPESS increased with prolonged floating in both lake and distilled water but remained  
13 lower in the latter than in the former with the same flotation duration. For the carcasses that  
14 had floated in natural eutrophic lake water for 14 days, RPESS occurred when the  
15 experimental vessels received a rapid sediment load of as little as the amount that could form  
16 deposits about 0.2 mm thick for cockroaches and 2 mm for butterflies. Biological  
17 characteristics of the animal, flotation duration, intensity of microbial activity, and availability  
18 of sufficient and rapid sediment load are important factors that determine whether RPESS will  
19 happen or not to carcasses floating in static water bodies. These experimental results are  
20 supported by analysis of the spatiotemporal occurrences and relative abundances of  
21 articulated terrestrial insects in lacustrine Konservat-Lagerstätten.

22  
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9

#### 10 **DATA ARCHIVING STATEMENT**

11 Data for this study are available in the Dryad Digital Repository:

12 <https://datadryad.org/review?doi=doi:10.5061/dryad.6c2fk58>

13

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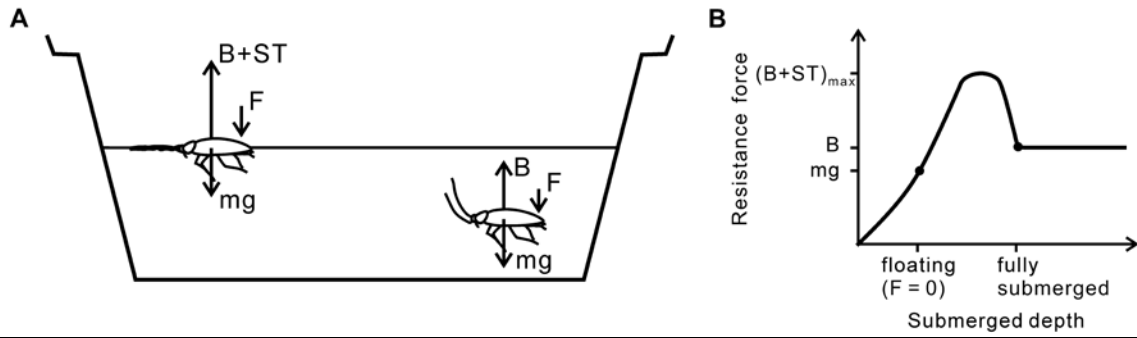
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- 3
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- 5

1 **FIGURES**

2



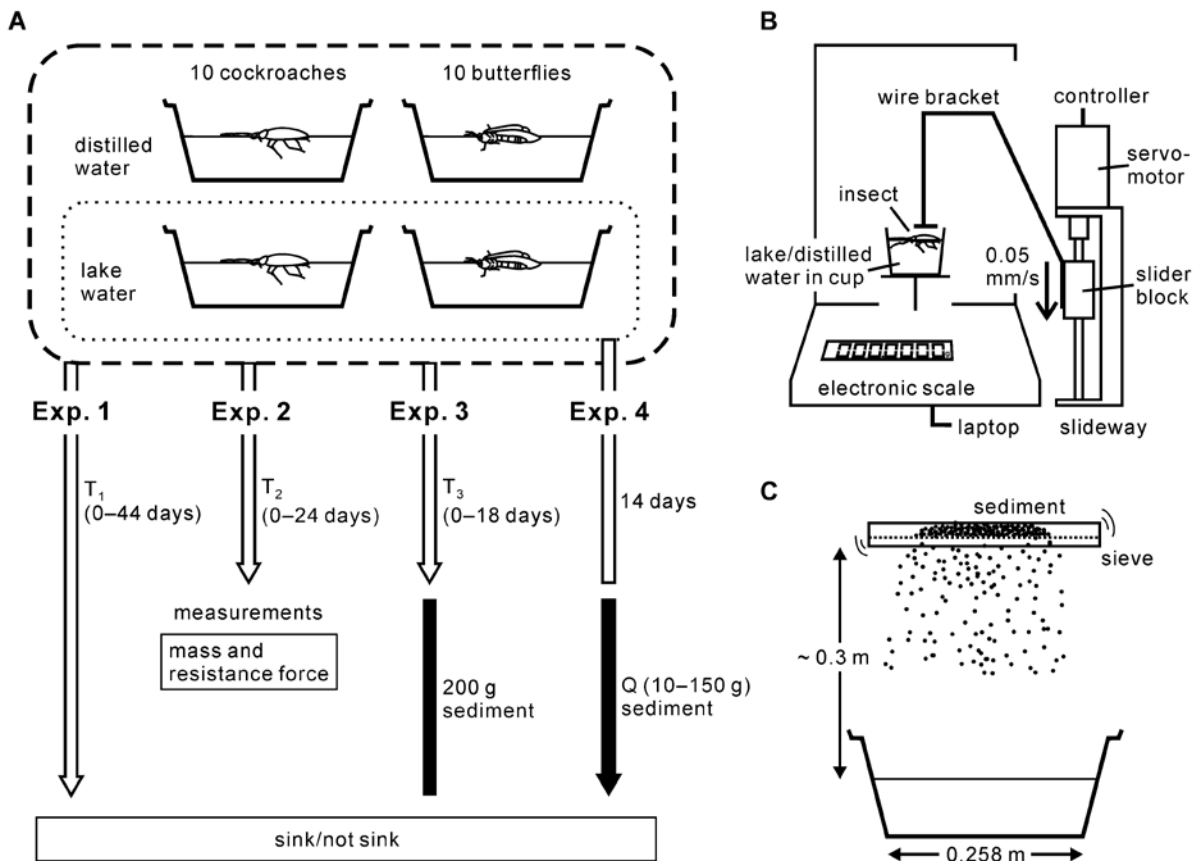
3

4 **FIG. 1.** Schematic showing the forces exerted on floating and submerged carcasses (A) and

5 change in resistance force exerted by water on a carcass versus submerged depth (B). B:

6 buoyancy; ST: surface tension; F: external force;  $mg$ : weight.

7



8

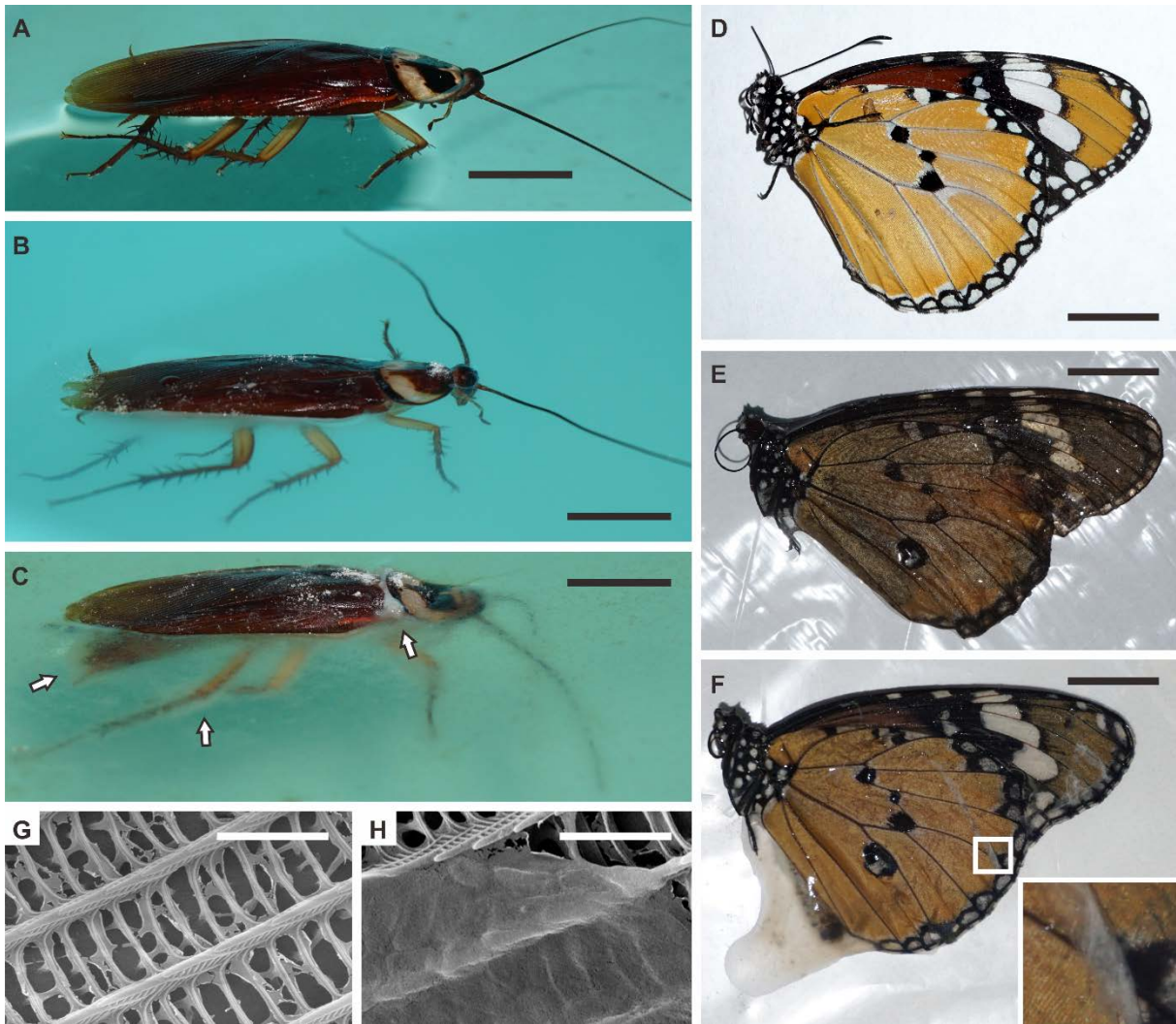
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10 **FIG. 2.** Schematic diagrams of the experimental setup (A) and apparatuses for measurements

11 (B) and sediment loading (C). Exp., Experiment. White and black arrows or bars represent

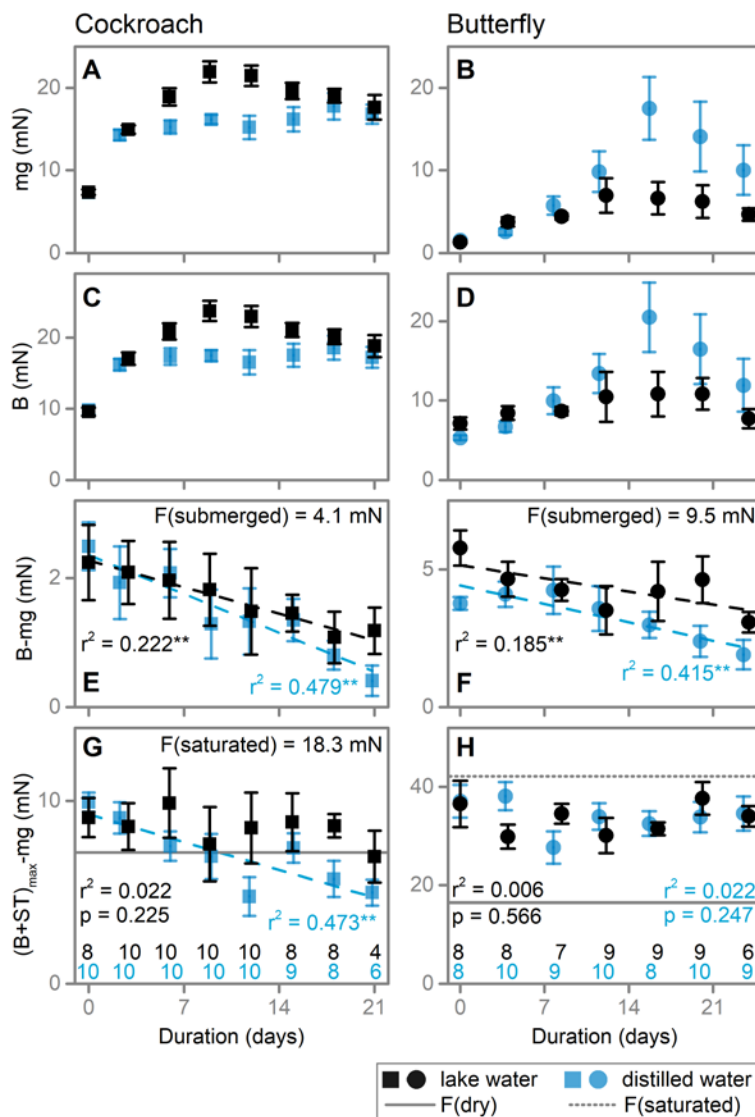
12 floating in water and sediment loading, respectively. Predictor variables are beside the arrows:

1  $T_1$  is flotation duration prior to each observation;  $T_2$  and  $T_3$  are flotation durations prior to  
2 treatment for each basin in Experiments 2 and 3;  $Q$  is mass of sediment introduced to each  
3 basin in Experiment 4. Values of  $T_2$ ,  $T_3$  and  $Q$  for each basin are listed in Table 3. Response  
4 variables are in rectangles.  
5



6  
7 **FIG. 3.** Morphology and flotation of decaying carcasses. A–C: Selected cockroaches in  
8 Experiment 1, photographed in the experimental basins. Freshly killed (A), 14 days in  
9 distilled water (B), 14 days in natural lake water (C; the same specimen as in (A)). Note  
10 microbial film at the water surface and enveloping the carcass in (C; marked by arrows). D–F:  
11 Submerged surfaces of selected butterflies in Experiment 2, photographed following removal  
12 from the experimental basin. Freshly killed (D), 12 days in distilled water (E), 12 days in

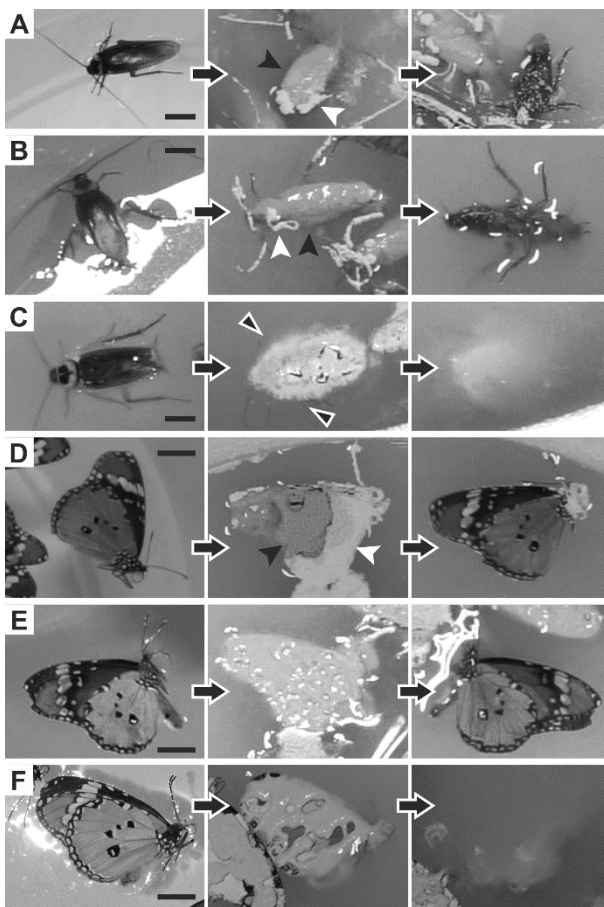
1 natural lake water (F). Note microbial films, associated with the abdomen, and film-like  
 2 structure on the wings (boxed area enlarged in inset) in (F). G–H: Scanning electron  
 3 micrographs showing wing scales on freshly killed (G) and decayed (for 12 days in natural  
 4 lake water; H; Experiment 2) butterfly carcasses. Note the microbial film in (H). Scale bars:  
 5 10 mm for A–F and 2  $\mu\text{m}$  for G and H.  
 6



7  
 8 **FIG. 4.** Changes in wet weight (A, B), buoyancy (C, D), force contrast exerted by water on  
 9 submerged carcasses (E, F) and maximum force contrast (G, H) during decay. B: buoyancy;  
 10 mg: wet weight; ST: surface tension. The number of specimens represented by each whisker

1 is annotated in G or H for corresponding water type and duration. Points are mean values and  
 2 error bars are 95% confidence intervals. Dashed lines are linear regression models for  
 3 significantly correlated variables; \*\*:  $p$  (uncorrelated)  $< 0.001$ . F(dry), F(saturated) and  
 4 F(submerged): the calculated maximum external downward force exerted by 200 g rapid  
 5 sediment load on a carcass when the sediment is under different conditions (calculations in  
 6 Tian *et al.* 2019, S3).

7

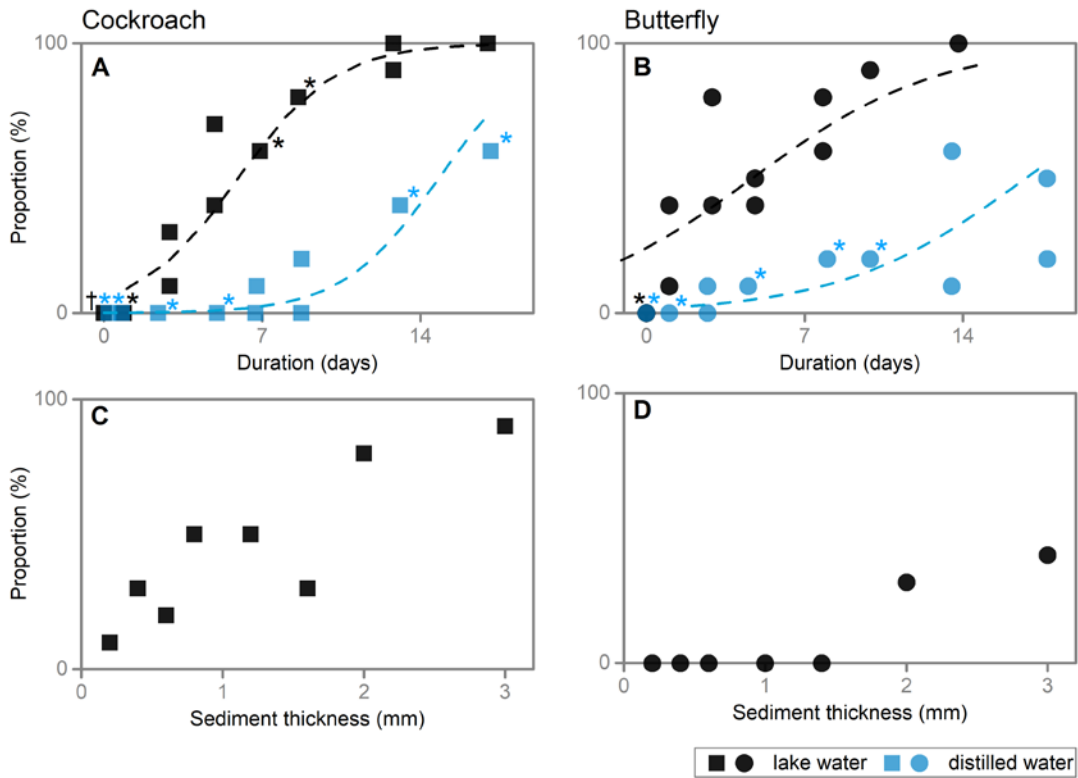


8

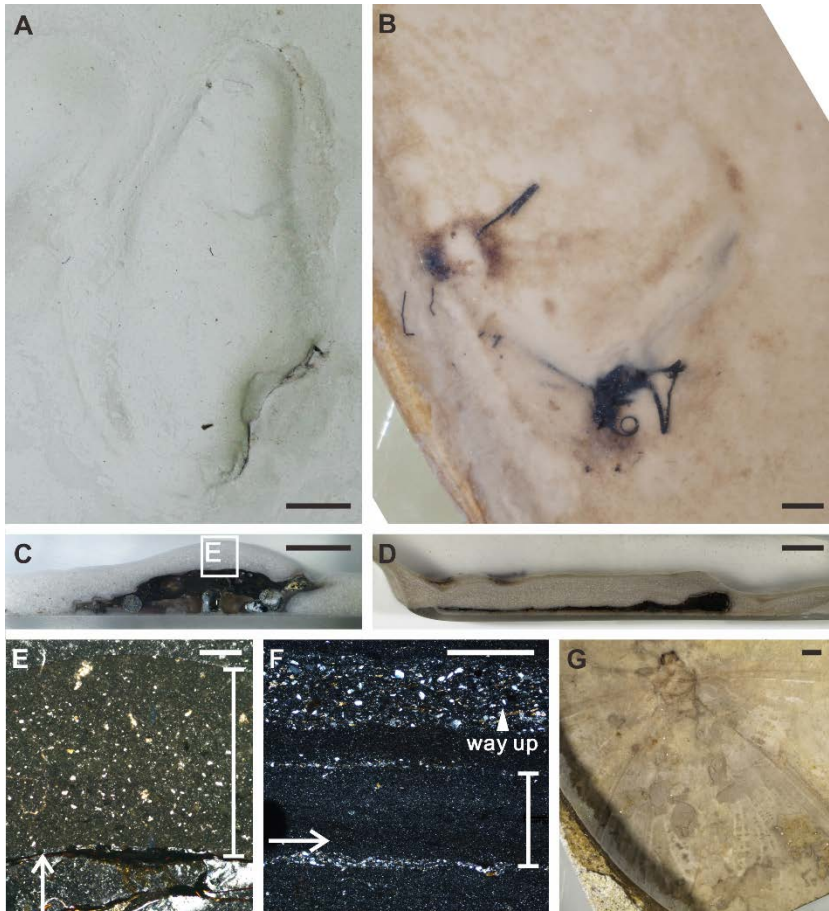
9 **FIG. 5.** Photographs showing the impact of sediment load on carcasses in Experiment 3. A–  
 10 C, Cockroaches. Freshly killed (A), 13 days in distilled water (B), 13 days in lake water (C).  
 11 D–F, Butterflies. Freshly killed (D), 10 days in distilled water (E), 10 days in lake water (F).  
 12 Images in each row show the condition of the carcass before sediment influx (left), 2–10  
 13 seconds before submergence (middle), and 0–20 seconds after submergence (right). The  
 14 carcasses in (A, B, D, E) refloated after submergence, while the carcasses in (C) and (F) sank



1 to the bottom. Saturated sediment (black arrow heads) shows darker colour compared with  
 2 adjacent dry sediment (white arrow heads). More sediment is attached to the carcasses in (C)  
 3 presumably due to the presence of microbial films around the cockroach (marked by  
 4 triangles) in the natural lake water. Scale bars, 10 mm.  
 5



6  
 7 **FIG. 6.** Proportion of carcasses experiencing RPES following sediment influx (Experiment  
 8 3; A–B) and sediment quantities introduced to carcasses that had floated in lake water for 14  
 9 days (Experiment 4; C–D). A, C: cockroach; B, D: butterfly. Dashed lines in (A) and (B) are  
 10 the binary logistic regression models. The sediment thickness in (C) and (D) is based on the  
 11 mass of sediment introduced (200 g of sediment forms a lamina ca. 4 mm thick in the basin).  
 12 Each datapoint represents one basin (datapoints with an asterisk or a dagger represent two or  
 13 three overlapping points, respectively).  
 14



1  
 2 **FIG. 7.** Comparison of sediment hosting experimental and fossil insects. A–B, Cockroach (A)  
 3 and butterfly (B) in plan views; carcasses had floated in lake water for 17 days (Experiment 3,  
 4 200 g sediment) and 14 days (Experiment 4, 150 g sediment), respectively; the butterfly  
 5 antennae and the legs disarticulated during resin block preparation. C–D, Vertical sections of  
 6 the carcasses in (A) and (B). E, Cross-polarized photomicrograph of the region indicated in  
 7 (C), with the overlying lamina and cockroach carcass indicated by a white whisker and an  
 8 arrow, respectively. F–G, Cross-section and plan views of an articulated neuropteran fossil  
 9 (NJU-DHG-NH48) from the Jurassic Haifanggou Formation. F, Cross-polarized  
 10 photomicrograph, the fossil is indicated by a white arrow. Scale bars represent: 5 mm (A–D,  
 11 G); 0.5 mm (E, F).

12  
 13  
 14

1 **TABLES**  
2

**TABLE 1.** Characteristics of experimental specimens.

Taxa	Mass (g)	Dorsal surface area (mm <sup>2</sup> )	Static contact angle (°)
Cockroach	0.76 ± 0.04, n = 180	358 ± 34, n = 7	92 ± 1, n = 2
Butterfly	0.15 ± 0.02, n = 150	827 ± 144, n = 7	130 ± 6, n = 4

Cockroaches were all adult male. Butterflies were all adult of both sexes. Errors are standard deviations. Measuring methods are available in Tian *et al.* 2019 S1.

3

**TABLE 2.** Properties of the water used in the experiments.

Water properties	Natural lake water	Distilled water
Density* (kg/m <sup>3</sup> )	998	996
Total dissolved solids (mg/L)	76	9
pH	7.52	5.91
Ammoniacal nitrogen (mg/L)	0.2	Not detected
Nitrate nitrogen (mg/L)	1.1	0.006
Orthophosphate (mg/L)	0.056	Not detected
Chemical oxygen demand (mg/L)	73.5	8.2
Microorganisms	Diatoms ( <i>Navicula cryptocephala</i> , <i>Melosira</i> , <i>Pinnularia</i> , <i>Synedra</i> , <i>Rhopalodia gibba</i> ), cryptomonads ( <i>Cryptomonas rostrate</i> and <i>C. erosa</i> ) and green algae ( <i>Marimo</i> ) <sup>†</sup>	Colonies number 0 cfu/mL; coliform <3 MPN/100mL; <i>Salmonella</i> , <i>Shigella</i> , <i>Staphylococcus aureus</i> , moulds and yeasts not detected <sup>‡</sup>

\* Measured with a glass hydrometer (Shanghai Loikaw, China).

<sup>†</sup> From an unpublished report (GAO, P., JI, J., JIANG, K. and ZENG, L. 2015. Study Report of Water Environment of Tianlai River. School of the Environment, Nanjing University).

<sup>‡</sup> From an unpublished test report (2008; No. W08061004188) by Shanghai Institute of Quality Inspection and Technical Research.

4

**TABLE 3.** Flotation duration prior to treatment for each basin in Experiment 2 (T<sub>2</sub>) and Experiment 3 (T<sub>3</sub>) and mass of sediment introduced to each basin in Experiment 4 (Q).

T <sub>2</sub> (days)		T <sub>3</sub> (days)				Q (g)			
lake water		distilled water		lake water		distilled water		lake water	
cc	bt	cc	bt	cc	bt	cc	bt	cc	bt
0	0	0	0	0	0	0	0	10	10
3	4	3	4	0	0	0	0	20	20

6	8	6	8	0	1	1	1	30	30
9	12	9	12	1	1	1	1	40	50
12	16	12	16	1	3	3	3	60	70
15	20	15	20	3	3	3	3	80	100
18	24	18	24	3	5	5	5	100	150
21		21		5	5	5	5	150	
				5	8	7	8		
				7	8	7	8		
				7	10	9	10		
				9	14	9	10		
				9		13	14		
				13		13	14		
				13		17	18		
				17		17	18		

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Abbreviations "cc" and "bt" represent "cockroach" and "butterfly", respectively.

1