Supplementary Materials for

Was Paleolake Messel a death-trap? Insight from modern bat drownings and decay experiments

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This PDF file includes:

Other Supplementary Materials for this manuscript include the following:

Data S1. PDF file with survey questions
Data S2. CSV file with survey responses
Data S3. Excel file containing a compilation of surface temperatures in modern tropical water bodies
Data S4. HTML file (RMarkdown output) containing R code and output of data analysis

Available here: https://dataportal.senckenberg.de/dataset/83845977-6728-4348-b4b9-65552d639beb

Supplementary Methods

The surface water temperature of a large number of modern tropical bodies of water was examined to set parameters for the decay experiments with modern bats. Data were taken from lakes and rivers in Indonesia and Vietnam, because model lakes were found in these countries (Rabenstein et al. 2004). We compiled the following data: our own measurements as well as literature data given as deriving from 0–0.25 m depth and those indicated as "surface" or "Oberfläche." When in the literature only maximum and minimum temperature were published, these were entered as independent values in the calculations (Ruttner 1931; Green et al. 1978; Whitten et al. 1987; Le Dien Duc 1989; Giesen and Sukotjo 1991a, b; Usman 1991, 1992; Mai Dinh Yen 1993a, b; Lehmusluoto et al. 1995; Sporrer 1995; Rabenstein et al. 2004).

Most of the data come from Indonesia, whose numerous lakes are relatively well studied. Bodies of water in Sumatra, Java and Bali have been the focus of both national and international research projects since the German Sunda Expedition in 1928–1929 (see Lehmusluoto et al. 1995; Sporrer 1995). The detailed studies published by Ruttner (1931) encompassed 15 lakes and reservoirs of different areal extent, depth and elevation. These were repeatedly sampled in the past decades (e.g., Sporrer 1995) and also formed part of the 38 lakes and reservoirs that were the object of the most extensive and recent research project (Lehmusluoto et al. 1995).

To compensate in part for the dearth of systematic studies in individual bodies of water, which could show, for instance, diurnal and annual fluctuations or long-term changes (cf. Lehmusluoto et al. 1995), our analysis of surface temperatures includes tropical lakes of differing elevation, geographic position, and morphology. Additionally, the measurements took place at different times of day and year. About three quarters of the measurements (N = 362, or 73.9%) derive from lakes most comparable to Messel (Rabenstein et al. 2004). The remaining 128 measurements were taken from the tributaries and drainages of the lakes as well as from other rivers. Most (94.3%) of the data were collected in Indonesian bodies of water (N = 462; 119 from rivers, 343 from lakes), and 5.7% from Vietnamese bodies of water (N = 28; 9 from rivers, 19 from lakes).

A total of 490 individual values for surface temperature were compiled, whose distribution is shown in Figure S1. Of these values, 128 measurements (26.1%) are from the open-water areas of rivers, 306 measurements (62.5%) are from the open areas of lakes, and 56 measurements (11.4%) are from lakes in stands of abundant aquatic vegetation. The mean of surface temperature measurements was 27.0 °C. In rivers the mean was 26.0 °C and in lakes 26.6 °C. In (shallow) areas with dense aquatic vegetation, water temperature was much higher, with a mean of 31.9 °C.

The temperature spectrum of the open-water area of lakes is from 17.0–33.8 °C. In some cases the entire spectrum can be covered by a single lake, such as Lake Ba Be, Vietnam (17.0–33.1 °C; Mai Dinh Yen, 1993a; Rabenstein et al. 2004). At 19.1–31.4 °C, rivers also show a wide temperature spread. Areas with dense aquatic vegetation show a much higher temperature spectrum, for instance 27.2–39.7 °C in Ranu Lamongan, Java (Ruttner 1931).

In open-water areas of modern tropical bodies of water (N = 434), sometimes much higher and lower surface temperatures were measured. Some (N = 27, or 6.2%) were low, ≤20 °C, whereas others were high, ≥32 °C (N = 22, or 5.1%). In light of these results, the experiments were conducted at low (c. 20 °C), medium (c. 25 °C) and high (c. 32 °C) temperatures. No experiments were conducted at higher temperatures, because in modern tropical bodies of water these were only recorded in densely vegetated areas of water; it is possible that water-lilies, *Nuphaea engelhardtii* Gee and Taylor, 2019, formed dense stands along parts of the shore of Paleolake Messel (Wilde and Micklich 2007), but the densely vegetated areas would have been only a tiny proportion of the lake surface and in any case were presumably not used by bats.

Long-term studies of tropical bodies of water are wanting, and diurnal or annual fluctuations in temperature are known only for a few (Lehmusluoto et al. 1995). The greatest number of published data derive from random measurements and short-term studies, which can show considerable variation, depending on the influence of various abiotic and biotic factors (see values in Ruttner, 1931; Sporrer, 1995). Abiotic factors that can greatly influence the surface temperature are latitude, elevation, lake morphology (especially depth and character of the shore), climate and weather (wind, cloudiness, seasonality) and the presence of inorganic suspended matter entering as sediment. The influences of biotic factors come especially from the presence of aquatic vegetation and the vegetation of the shore.

- *Latitude*. Lakes at the equator show a higher surface temperature than lakes at the level of the Tropics (of Capricorn and Cancer). This applies to mean temperature of the body of water as well as temperature at the surface and on the lakebed. The higher water temperature is most clearly manifested at the water surface (cf. Lewis, 1996: fig. 6-7).
- *Elevation*. Lowland lakes show higher water temperatures than lakes at higher elevation. This was clearly shown by the German Sunda Expedition (Ruttner, 1931), according to whose results the temperature of deep water decreases by 6 °C for every 1000 m elevation. On average, the surface temperature is about 1.5 °C higher than the surrounding ground temperature (cf. Lehmusluoto et al. 1995: fig. 10). Similarly, Fricke and Wing (2004: fig. 2) found a systematic 1 °C offset between atmosphere and rivers, the rivers being warmer.
- *Lake morphology*. The surface water of small and shallow lakes shows greater temperature fluctuations than larger and deeper lakes. Sporrer (1995) showed this at four Javanese lakes. In the smallest and shallowest, Telaga Warna (70 m diameter, 10 m depth, situated at 1500 m elevation) the difference between the highest and lowest measured temperature during the year was 6.5 °C. In the larger lakes the difference was about one-half or one-third as great: 3.6 °C at Ranu Lamongan (740 m diameter, 30.5 m depth, 240 m elevation), 2.3 °C at Ranu Klindungan (1800 m diameter, 134 m depth, 10 m elevation), and 2.1 °C at Ranu Pakis (790 m diameter, 156 m depth, and 205 m elevation).
- *Sedimentation*. Suspended matter can contribute to an increase in surface temperature (Lehmusluoto et al. 1995).
- *Climate and weather*. Fluctuations in the surface temperature of tropical lakes are further caused by monsoons, wind and clouds. For instance, higher surface water temperatures were measured in 38 examined Indonesian lakes and reservoirs during the Western Monsoon at the beginning of the year (December to March = wet weather) than during the Eastern Monsoon (June to September = dry weather), because rainclouds inhibit the transport of heat (Lehmusluoto et al. 1995: 15, 20). Wind causes a homogenisation of temperature in the epilimnion, whereas on windless days surface temperature rises. In the measurements of Rabenstein et al. (2004) a maximum value of 33.1 °C was obtained at the North Vietnamese Lake Ba Be at noon on a windless, sunny day.
- *Aquatic vegetation*. Surface water temperature can reach high values of 35 to 40 °C in areas of dense aquatic plant growth. Ruttner (1931) conducted a comparative study of extremes in open water vs. stands of aquatic vegetation – viz., a dense stand of *Hydrilla verticillata* and a sparse stand of "*Eichhornia*" *crassipes* (an invasive species from South America now known as *Pontederia crassipes*) – at Ranu Lamongan from 10–22 Nov. 1928. The temperature minima showed little difference, but there were great differences in daily temperature maxima. Specifically, the highest daily maximum temperatures were found in the aquatic vegetation. Around the submergent *Hydrilla* they had a mean of 36.8 °C (range: 27.5–39.7 °C), followed by the stand of *Pontederia*, where they had a mean of 34.4 °C (range: 27.2–36.9 °C). In open water, in contrast, temperatures at the very surface had a mean of 32.2 °C (maximum: 33.8 °C), and at 25 cm below the surface they had a mean of only 30.6 °C (maximum: 32.4 °C). "The maxima in the stand of *Eichhornia*

[=*Pontederia*] were definitely lower than in *Hydrilla* as a result of the partial shading of the water surface by the subaerial leaves of this floating plant" (original: "Die Maxima lagen innerhalb des *Eichhornia*-Bestandes durchwegs niedriger als in *Hydrilla*, infolge der teilweisen Beschattung der Wasseroberfläche durch die Luftblätter dieser Schwimmpflanzen") (Ruttner, 1931: 230 ff.).

Supplementary Results

Further descriptive results of the laboratory experiments (Fig. S2–S4) are given as follows. First are results from experiments 1–3 (Table 1): short-term (3-4 week) experiments at three water temperatures (low: c. 20 °C, medium: c. 25 °C, and high: c. 32 °C), each with 8 individuals, half with water-filled lungs (experimental group) and half with air-filled lungs (control group). Note that radiographic documentation was conducted for all individuals but is shown only for half of them due to space constraints. Plates and descriptions focus on those intervals when radiographs were created, but the experimental containers were checked more frequently. Experiments 4–6 are not described in detail, as they aimed to study not the decay process generally, or the disarticulation sequence of the bones. Rather, they aimed to increase sample size concerning the tendency of carcasses to sink or float (experiments 1–4), and additionally (experiments 2–3 and 5–6) to study the disarticulation of the cochleae and of the teeth.

Experiment 1: Low temperature, c. 20 °C, experimental days 1–25

At the **beginning** of the experiment (Fig. S3, row 1), three of four bats with water-filled lungs sank completely to the bottom of the experimental containers. The fourth animal floated at the surface at first, but then after 24 hr also sank (Fig. S3, a1 and b1). Of the animals with air-filled lungs, two immediately sank completely, whereas two floated at the surface. After 24 hr, this situation is unchanged (Fig. S3, c1 and d1).

On experimental **day 4** (Fig. S3, row 2), all eight bats floated at the surface. The four bats with water-filled lungs floated strongly distended with their bellies down, the body clearly jutting up from the water surface. The skin of the back of the two most strongly distended animals was so taut from the putrefactive gases beneath it that the scapulae no longer stand out (Fig. S2b). The radiographs (Fig. S3, a2) showed the strong development of putrefactive gases in the thorax and abdomen, which extends via the mediastinum into the shoulder and head regions. In the two other animals (e.g., Fig. S3, b2), the putrefactive gases in the thorax and abdomen are less strongly developed. Of the four bats with air-filled lungs, the two that had sunk to the bottom floated up to the water surface between day 2 and 4. These four floating bats appeared hardly distended; only the radiographs showed a marked accumulation of gases and a few isolated gas bubbles in the abdomen and thorax (e.g., Fig. S3, c2 and d2).

Two bats with water-filled lungs and one with air-filled lungs (Fig. S3, d2) rotated from belly-up to belly-down. This postmortem shift could be related to the observation that a substantial minority of the bats – both those with water- and with air-filled lungs – drifted at first beneath the water surface obliquely, or even vertically, with the head pointed downward. The head acts as a weight here. Whether the bats adopt an oblique orientation beneath the water, one way or the other, or even rotate from belly-up to belly-down or vice versa as they float up to the water surface, probably depends on the distribution of the putrefactive gases in the bats' bodies.

On experimental **day 8** (Fig. S3, row 3), all eight bats floated at the surface. In contrast to the previous inspection, however, the development of putrefactive gases was very heterogeneous. In some cases, gas volume had been reduced by degassing (4 bats, 3× with water-filled and 1× with air-filled lungs; e.g., Fig. S3, a3 and d3), had remained the same (1 bat with water-filled lungs; Fig. S3, b3), or had increased substantially (3 animals with air-filled lungs; e.g., Fig. S3, c3). These first indications of decomposition were observed earlier in the bats with water-filled lungs. Probably this fact is related to the injection of unsterile water into the thorax, which would accelerate the development of putrefactive gases there rather than just in the abdomen.

On experimental **day 11** (Fig. S3, row 4), all eight bats continued to float at the surface. Now, the first disarticulations begin to transpire at the exertion of the slightest forces (0–0.7

g). Disarticulation affect three-quarters of the bats, causing the separation in a total of 10 wings or legs (radius: 6× distally, 3× proximally; knee: 1×). In testing for separable elements, the skin of three bats tore, leading to incomplete degassing (Fig. S3, a4–c4). The ultimate cause of joint separability and the accompanying weakening of the ability of the skin to withstand mechanical stress is surely to be sought in decay, working also from the outside in.

On experimental **day 15** (Fig. S3, row 5), all eight bats still continued to float at the surface. Disarticulation now affect all bats, not just the postcranium but now also the cranial skeleton. In three of four bats with water-filled lungs, the craniovertebral joint is disarticulated. Either just the skull separates from the vertebral column (2×), or the skull and both mandibles become separated from the vertebral column and from each other, respectively (1×; Fig. S3, b5). Of the bats with air-filled lungs, only one mandible in one individual became disarticulated.

In the postcranium, disarticulation of the hip and shoulder joints were now observed (e.g., Fig. S3, b5). Of the four bats affected, three were from the group with water-filled lungs, and one from the group with air-filled lungs. At this point, the hip joint was disarticulated in nearly half the cases (7/16 joints, or 43.8%). At the first and thus far only observed disarticulation of the shoulder joint (a bat with water-filled lungs), the radius, humerus, scapula and clavicle together with flight muscles become separated at the exertion of a small force (7.0 g) at the distal end of the radius (Fig. S3, b5).

The total number of disarticulated joints recorded in these decay tests rose greatly. For bats with water-filled lungs, disarticulation affects 57.7% (previously: 7.7%) of joints; for bats with air-filled lungs, disarticulation affects 43.1% (previously: 12.2%) of joints. In the former group – the reader is reminded that unsterile water was injected into the thorax – specifically more disarticulations were observed in the shoulder and hip joints (6×) and at the craniovertebral joint (3×) than in the latter group (2× and 0×, respectively). This observation is presumably the result of decay.

By experimental **day 18** (Fig. S3, row 6), the first of four bats with water-filled lungs had sunk to the bottom, whereas the remaining seven bats (3 with water-filled and 4 with air-filled lungs) still continued to float at the surface. A bat with air-filled lungs floated just beneath the water-line and seemed to be in the process of sinking. Only at this point does the skull become separated from the vertebral column in the first two individuals with air-filled lungs (Fig. S3, d6). Although the shoulder joint in over half of all eight bats has been disarticulated (56.3%), this remains the most common still-intact joint (Fig. S3, a6 and c6). With the application of a force between 0–4.0 g, either the humerus becomes disarticulated together with the scapula, clavicle and musculature (1×), or the humerus, scapula and musculature become separated (1×), or just the humerus and musculature become separated (1×).

One bat from the group with water-filled lungs was already mostly disarticulated; only a few costovertebral joints remained intact (Fig. S3, b6: bent vertebral column to the left of the skull). One individual from the other group was also mostly disarticulated, but in this case ribs, vertebral column and pelvis remained in conjunction (Fig. S3, d6). The conductivity of the water – which nearly reached maximum values of c. 3.0 mS/cm – is consistent with the highly advanced state of decay.

By experimental **day 22** (Fig. S3, row 7), half of the bats had sunk to the bottom (2× in each group). The last cranial articulations become separated (at force 0–4.0 g). For the remaining two bats with once air-filled lungs, the craniovertebral joint had become separated. Moreover, the mandibles had become separated from the skull and the symphyses disarticulated (Fig. S3, c7). The bones of the facial skeleton and neurocranium, in contrast, remain articulated, and seven of eight skulls float at the water surface until the end of the experiment.

Further disarticulation of the main bones of the extremities occurred only at the shoulder joint (force: 0–8.0 g): in two bats with once-water-filled lungs and in the four bats

with once-air-filled lungs. In one bat with once air-filled lungs, the disarticulation does not occur at the shoulder joint, but rather humerus, scapula and musculature became separated together (force: 5.0 g). Thus, the skeletons of five individuals are completely disarticulated. In the remaining bats, the rib cage of one individual (with once water-filled lungs) remains articulated, and its left shoulder joint withstood a force of 8.0 g (Fig. S3, a7). In a second bat in this group, the ribs are mostly disarticulated, and in a third individual (with once air-filled lungs) the torso remains intact (Fig. S3, c7). The proportion of disarticulated joints is 98.0% for bats with once water-filled lungs, and 100% for bats with once air-filled lungs.

By experimental **day 25** (Fig. S3, row 8; end of experiment), all bat carcasses were predominantly or completely disarticulated (Fig. S3, a8–d8). Following the disarticulation of the last remaining glenohumeral joint (cf. Fig. S3, a7 and a8), the skeletons of all four bats with once water-filled lungs are completely disarticulated (100%). In contrast, a few joints remain intact in two of four bats with once air-filled lungs (1× with partly articulated ribs: Fig. S3, c8; 1× left humerus and scapula: Fig. S3, c8), although the shoulder joint capsule that had withstood 8 g of force was now broken. Amongst bones of the bats that were already mostly skeletonized, only small-scale displacements on the bottom of the experimental containers were observed (cf. Fig. S3, b7 and b8, d7 and d8).

Experiment 2: Medium temperature, c. 25 °C, experimental days 1–20

At the **beginning** of the experiment (Fig. S4, row 1), all four bats with water-filled lungs floated at the surface of the water. Air bubbles remained trapped beneath the body or the wings or in the external ears of some individuals, or a thin seam of air bubbles partly or wholly surrounded them (e.g., Fig. S4, a1 and b1). Of the four bats with air-filled lungs, two drifted beneath the water surface obliquely, with the head pointed downward (Fig. S4, d1). The other two bats sank immediately and completely onto the bottom of the experimental container despite the fact that large air bubbles were trapped under both wings (especially) and the uropatagium (Fig. S4, c1).

On experimental **day 3** (Fig. S4, row 2), all four bats with water-filled lungs floated at the surface. In all (e.g., Fig. S4, a2 and b2) the radiographs show a strong development of putrefactive gases, from the abdomen to the thorax and shoulders up to the head. The cause of this early decomposition is probably the injection of unsterile water into the thorax. Of the bats with air-filled lungs, three of four individuals now floated at the water surface (e.g., Fig. S4, d2), whereas the fourth drifted obliquely and head-down beneath the surface because of putrefactive gases (Fig. S4, c2). In three of the four individuals, the volume of putrefactive gases is clearly smaller than in the parallel series of bats with water-filled lungs. In two bats, putrefactive gases occur only in the thorax (e.g., Fig. S4, d2). The strongest development of putrefactive gases was seen in the abdomen, thorax, shoulder region and head of a female that died postpartum (Fig. S4, a2). The cause is presumably bacterial decomposition that proceeds from the open birth canal (see below).

On experimental **day 7** (Fig. S4, row 3), all eight bats floated at the surface, and putrefactive gases were present throughout the body up to the shoulder and head regions. As with the low temperature experiment (see above), there is a very heterogeneous development of putrefactive gases. As a result of the disarticulation tests, degassing occurred in four bats (3× in the group with water-filled lungs, 1× in the group with air-filled lungs; e.g., Fig. S4, a3). In three bats the volume of putrefactive gases is roughly the same as at the previous inspection (three bats: 1× in the group with water-filled lungs, 2× in the group with air-filled lungs; e.g., Fig. S4, b3 and c3), whereas in one individual there was a clear increase in volume (Fig. S4, d3).

For the first time, small forces (0–7.0 g) were capable of producing in five bats disarticulations of the distal or proximal radial joint (6×) and of the knee joint (3×). In all, bats with water-filled lungs showed far more disarticulations (7× in four individuals; e.g., Fig. S4, a3 and b3) than bats with air-filled lungs (2× in one individual; Fig. S4, d3). The first disarticulations occurred at the same joints as in the low-temperature experiment – wrist, elbow and knee joints – but at an earlier point in time (between day 3–7, compared to day 8–11 at low temperature).

On experimental **day 10** (Fig. S4, row 4), seven of eight bats still floated at the surface (three bats with water-filled lungs, all four with air-filled lungs). In all bats, small forces (0–7.0 g) suffice to produce disarticulations in the postcranial and now also cranial skeleton. These cranial disarticulations occurred in all eight bats (six disarticulations each per experimental group) and were highly variable: in two animals with water-filled lungs, the craniovertebral joint was separated, either with (Fig. S4, b4) or without (Fig. S4, a4) disarticulation of the mandibles. In one further individual only the mandibular joint became disarticulated, and in a fourth both the mandibular joints and symphysis were separated. Furthermore, in one bat with air-filled lungs, the craniovertebral and mandibular joint were separated, and in yet another the left mandibular joint and the symphysis were separated (Fig. S4, d4). In the two remaining bats with air-filled lungs, only the conjoined mandibles were disarticulated (Fig. S4, c4).

Thus, at medium temperature the same cranial disarticulations occurred as in the low-temperature experiment, but at an earlier point in time (between day 7–10, compared to day 11–15 at low temperature).

Similarly, all eight bats experienced postcranial disarticulations (force: 0–6.0 g), namely 2× in each group at the hip and shoulder joint. In one bat with once water-filled lungs (Fig. S4, b4) one hip and both shoulder joints were disarticulated, whereas in another bat in this group – the female that died after birth – both hip joints were disarticulated (see below). In two bats with once air-filled lungs, one showed a disarticulated hip joint (Fig. S4, d4) and one a disarticulated shoulder joint. The total number of disarticulated joints was greatly increased in both groups: 60.8% of joints in bats with once water-filled lungs (previously: 13.7%), and 42.3% of joints in bats with once air-filled lungs (previously: 4.0%).

Thus, on experimental day 10 in the medium-temperature experiment, the bats show a similar level of disarticulation to the bats on day 15 of the low-temperature experiment. All bat carcasses show cranial and postcranial disarticulations; the first disarticulations occur in the shoulder and hip joints; and the total number of disarticulated joints is comparable (60.8% at medium temperature vs. 57.7% at low temperature for bats with once water-filled lungs, and 42.3% at medium temperature vs. 43.1% at low temperature for bats with once air-filled lungs).

On experimental **day 14** (Fig. S4, row 5), half of the bats still floated at the water surface (two individuals with once water-filled lungs, three with once air-filled lungs). The bats were largely disarticulated. In the remaining bats with once water-filled lungs, separation of the skull from the vertebral column had transpired. Similarly, the last mandible had separated (Fig. S4, a5). Only the symphysis remains in articulation in this group. Similarly, amongst the bats with once air-filled lungs the symphysis was still intact in two individuals (e.g., Fig. S4, c5). In contrast, the symphysis became disarticulated with application of a small force (0–4.0 g), and the remaining three skulls separated from the vertebral column (e.g., Fig. S4, c5 and d5).

In the postcranium, further disarticulations of the radial and knee joints and now most notably of the hip and shoulder joints transpired at touch (force not measurable). The hip joints were disarticulated in seven individuals; the last individual with intact hip joints once had water-filled lungs. Eight shoulder joints were disarticulated (4× in two individuals with once water-filled lungs, 4× in three individuals with once air-filled lungs). Although the shoulder joint in now two-thirds (11/16, or 68.8%) of all bats are disarticulated, this remains the most commonly still intact joint capsule (cf. 56.3% of shoulder girdles in the low-temperature experiment on day 18; see above).

The total number of disarticulated joints in both groups was comparable at this point: in bats with once water-filled lungs it was 88.2% (previously: 60.8%), and in bats with once air-filled lungs it was 90.4% (previously: 42.3%). The conductivity of the water – which reached maximum values of c. 3.0 mS/cm – is consistent with the highly advanced state of decay. In general, on day 14 of the medium-temperature experiment the water conductivity corresponded to that on day 18 of the low-temperature experiment, and the degree of disarticulation to that on day 18–25. That is, decay proceeded more rapidly at higher temperature, as expected.

On experimental **day 17** (Fig. S4, row 6), only one bat (with once water-filled lungs) still floated at the surface. The last postcranial joints – both hip and shoulder joints together with the ribcage – are disarticulated here, and in another individual the distal radial joint (Fig. S4, a6). Similarly, in one individual in the other group the last shoulder joint is disarticulated, and in a second individual the disarticulation of the last shoulder joint occurred simultaneously with that of the ribcage.

Three days later (experimental **day 20**), the complete skeletal disarticulation of all joints tabulated here (100% in both experimental groups) as well as that of the ribcage was observed. The inspection also showed that the last remaining shoulder joint capsule (in a bat with once air-filled lungs) was no longer intact, and the last three remaining mandibular symphyses (1× in individuals with once-water filled lungs, 2× in individuals with once air-filled lungs) could now be separated with very small forces (0–1.0 g).

In sum, skeletal disarticulation and sinking of the carcasses followed a similar pattern at low and medium temperature, but faster at medium temperature. The complete disarticulation of the joints examined here, including the rib-cage, occurred between day 17–20 of the experiment at medium temperature, and between day 18–25 at low temperature.

Experiment 3: High temperature, c. 32 °C, experimental days 1–28 day

At the **beginning** of the experiment, one bat with water-filled lungs sank immediately to the bottom of the experimental container; two further bats drifted obliquely below the water surface with the head down; and one bat floated at the surface. Of the bats with air-filled lungs, one sank immediately and completely to the bottom, whereas the remaining three floated at the surface.

Already on experimental **day 2** (Fig. S5, row 1), all eight bats floated at the surface (e.g., Fig. S5, a1–d1). The reason for this fact is the clear development of more putrefactive gases already after 24 hr, compared to the low-temperature experiment (day 4; Fig. S3, a2–d2). The radiographs revealed significant development of putrefactive gases in the thorax and abdomen, which also reach the shoulder and head region via the mediastinum. Three bat carcasses were strongly distended (e.g., Fig. S5, b1), one somewhat less so (Fig. S5, a1). Of the four bats with air-filled lungs, the radiographs revealed the distinct development of putrefactive gases in two individuals (e.g., Fig. S5, c1), less so in the other two individuals (e.g., Fig. S5, d1).

As in the experiments at low and medium temperature, putrefactive gases were generally less voluminous in bats with air-filled lungs, compared to those with water-filled lungs (exception: Fig. S5, c1). Moreover, the radiographs showed a predominance of putrefactive gas development in the abdominal region. Probably, in bats with air-filled lungs, early decomposition begins with autolysis in the abdomen (decay by released digestive enzymes), whereas in bats with (unsterile) water-filled lungs bacterial decomposition in the thorax probably accompanies autolysis.

Two bats with water-filled lungs rotated from belly-down to belly-up position (Fig. S5, a1) or vice versa. This postmortem movement transpires (see also low-temperature experiment above) as a result of the development and distribution of putrefactive gases in the carcass. Within very few days – and at high experimental temperature even within hours – there can occur a shift from belly-down to belly-up position (via an obliquely drifting position). This did not occur in the bats with air-filled lungs, probably because of the relatively small volume of putrefactive gases.

On experimental **day 5** (Fig. S5, row 2), all eight bats floated at the surface. The bats in both groups showed a very different pattern of disarticulation. Two of the individuals with once water-filled lungs were either completely (Fig. S5, a2) or nearly completely disarticulated (Fig. S5, b2). In these individuals, small forces (0–8.0 g) sufficed to disarticulate all cranial joints (1× between atlas and axis). In one skeleton (Fig. S5, a2), the same force sufficed to disarticulate all postcranial joints considered here, including rib joints. As a peculiarity, in this immature individual, one humerus was dislocated in the shoulder joint, whereas in the second the proximal humeral epiphysis was detached and the joint capsule remained undamaged. In the second bat (Fig. S5, b2) only one wrist and one elbow joint remain intact. As a peculiarity, the humerus and radius remain connected by a tendon (that withstood 6.0 g of force), whereas the shoulder joint disarticulated at 5.0 g. The two remaining bats, in contrast, were less disarticulated. In one, the radiograph continued to document significant putrefactive gases in the thorax, abdomen, and shoulder, whereas elbow, knee, and hip joints were already disarticulated. In the fourth bat, the tests of joint separation caused tearing of the skin, which led to partial degassing, but with the exception of one elbow, the joints remained intact.

Two of the individuals with once air-filled lungs were similarly largely disarticulated (Fig. S5, c2 and d2). The craniovertebral and temporomandibular joints disarticulated in both (force: 0–5.0 g), whereas the symphysis remained intact. The postcranial skeleton of one individual – including ribcage – fell apart completely at the touch, and only the shoulder joints disarticulated with small forces (0–4.0 g; Fig. S5, c2). Similarly, in a second individual (Fig. S5, d2) nearly all postcranial joints considered here fell apart at the touch, but both humeri at the shoulder joint resisted a force of 3.0 g. The two remaining individuals, in contrast, were largely unaffected (3.0–6.0 g). In one individual, only the mandibles and one knee disarticulated, and

in the other a wrist (0–5.0 g). The radiographs showed well-developed accumulations of putrefactive gases in these individuals in the whole body (abdomen, thorax, shoulder, and head regions; cf. Fig. S5, a2 and b2) or in the shoulder and head (cf. Fig. S4, c4).

As in the previous two experiments at low and medium temperature, the total number of disarticulations in bats with water-filled lungs (63.3%) was much higher than in bats with air-filled lungs (52.2%). The state of disarticulation on experimental day 5 at high temperature corresponded to that on day 10 at medium temperature (60.8% and 42.3%, respectively) and to that on day 15 at low temperature (57.7% and 43.1%, respectively).

On experimental **day 9** (Fig. S5, row 3), only one bat (with once air-filled lungs) still floated at the surface. All other bats had sunk to the bottom, although the skin of three individuals (two with once water-filled, one with once air-filled lungs) still drifted at the water surface.

All skeletons of bats with once water-filled lungs were completely disarticulated, including the ribcage (Fig. S5, a3 and b3). Only in two individuals does one wrist joint each remain. Similarly, the skeletons of three of four bats with once air-filled lungs are completely disarticulated. In the last individual, both humeri remain articulated to the scapulae of the otherwise disarticulated skeleton. In one further individual the ribcage remains partly intact.

The total number of disarticulated joints considered here is similarly high in bats with once water-filled and those with once air-filled lungs: 95.9% and 92.9%, respectively. Decay of the soft tissues went in concert with the separation of the joints: the conductivity of the water reached a maximum value of 2.5 mS/cm between experimental day 7–9.

As in the previous experiments, the shoulder joint capsule showed itself to be extremely resistant. In half of the bats, the humeri became disarticulated only on day 9 (two bats each with once water-filled and air-filled lungs). In one individual with once air-filled lungs, both capsules remained intact.

Below we describe additional observations and special cases that occurred in the experiments at low, medium and high temperature, which otherwise might be overlooked. These observations could potentially prove useful in the interpretation of new bat fossils from Messel, where isolated wings or disarticulated skulls are known, or elsewhere.

Special cases

Wing disarticulation in an immature individual: In one of the three bats with incompletely fused epiphyses, the wing did not disarticulate at the shoulder joint in a typical fashion. Rather, the proximal epiphysis of the right humerus as well as attached tendon separated on application of a small force (<0.5 g), as briefly noted in the high-temperature experiment (day 5) above. The disarticulation of the left shoulder joint on application of the same force (<0.5 g) occurred between humerus and scapula, as it did as well in the other two individuals with incompletely fused epiphyses.

Incomplete elbow disarticulation: On application of a force of 5.0 g to the wrist of an adult female bat, not only the humerus at the shoulder joint but also the radius were dislocated. The elbow capsule was decayed, to be sure, but a tendon resisted a force of 6.0 g (see high-temperature experiment, day 5 above).

Wing disarticulation beyond the shoulder joint: In four of eight adult bats in the low-temperature experiment above, disarticulation of the wing transpired surprisingly not at the shoulder joint; rather, small forces (<0.5–7.0 g) caused separation either of the entire extremity – comprising lower arm, humerus, scapula, clavicle, and shoulder musculature (1× on day 15; Fig. S3, b5) –, or of the humerus together with scapula, clavicle, and shoulder musculature (1× on day 18), or of the humerus together with scapula and shoulder musculature (1× on day 18 and 1× on day 22).

Cervicovertebral joint with atlas: In one of the 46 bats, disarticulation of the cranium occurred not between cranium and atlas but rather between atlas and axis (high-temperature experiment, day 5). Separation of the skull with cervical vertebrae is also known in a fossil bat from Messel, SMF-ME 1414.

Hip joint disarticulation in pregnant and postpartum females: A small number of bats (N = 6) were pregnant or immediately postpartum females. On the basis of this sample it was tested whether the higher abdominal volume caused by the foetuses resulted in a different pattern of decomposition. Four females showed no differences in the disarticulation of the abdominal region or the hip joints.

In contrast, in one female with a half-produced foetus, both hip joints were the first joints to be separated (low-temperature experiment, day 11; force <0.5 g). This was also the first disarticulation observed in the experimental container, which otherwise held three other bats with air-filled lungs. The cause of hip disarticulation is probably the early opening of the abdomen of the gravid female: the foetus had namely separated from the body of the mother, which was floating in a belly-down position, and sunk to the bottom.

A further example of early disarticulation of the hip joint comes from a female bat that died postpartum. In this individual as well both hip joints became disarticulated (medium-temperature experiment, day 10; force <0.5 g), the first separations observed amongst the four bats in the experimental container. In this case as well, we may postulate that a more rapid bacterially mediated decomposition and disarticulation of the hip joints resulted from the opening of the abdominal cavity during birth.

Special observations

Notes on organ preservation: In the experiments at medium and high temperatures, the integument (skin, patagium) was decomposed, or at least fell apart at the touch, by two weeks at the latest. In the experiments at low temperature, this occurred by the end of the third week, and small pieces of skin could still drift at the water surface after the end of experiment 4 on day 87.

Observations on the musculature could only be made at low temperature. In successive tests the humerus became disarticulated with the shoulder musculature. Pieces of muscle of ≤1 cm^3 could be observed on two individuals on experimental days 22, 24 and 25, and on two further individuals even on day 27. All pieces fell apart at the touch.

Remains of the liver were still present in three bats at the end of experiment 4 on day 87 at low temperature.

The brain decayed rather late. Remains of the brain were still present at the end of all experiments, with the exception of the extreme long-term experiment 6, which ended on day 764.

Degassing through body openings: In rare cases, the spontaneous escape of small gas bubbles (1–2 mm diameter) could be observed. In one postpartum female bat, this occurred through the widened birth canal (low-temperature experiment, day 6). During the same experiment, gas bubbles escaped from the anus of a bat drifting vertically under the water (day 17), precipitated by small water movements resulting from the placement of the experimental container on the X-ray table. In both cases, the volume of escaped gas was too low to lead to a sinking of the carcass.

When lightly touched (contact with the tweezers, measurement with the spring balance), three to four 1-mm-diameter gas bubbles escaped from the mouth of a bat in the medium-temperature experiment (day 7), whereas in two further individuals gas bubbles up to 2-cm in diameter escaped from the anus (day 8). On four occasions even a slight touch caused damage to the abdominal skin, following which in one case the bat continued to float at the surface following a partial degassing (low-temperature experiment, day 11). In the other three cases, in contrast, the bats sank to the bottom (medium-temperature experiment, days 12 and 17; high-temperature experiment, day 5). In the last case the degassing was accompanied by escape of a reddish bodily fluid.

Disarticulation of the cochleae

After the end of decay experiments 2, 3, 5 and 6, the skulls of the 30 individuals involved were taken and examined for the occurrence of articulated cochleae. Surprisingly there was a high proportion of cases in which the cochleae had fallen out (Table S2). Specifically, in 25 of the 30 individuals both cochleae were completely separated from the skull and lay isolated in the experimental containers. Of the 5 remaining skulls, 4 retained one cochlea and only 1 retained the cochlea on both sides.

Disarticulation of the teeth

The same 30 individuals were also examined for the retention of teeth of the upper dentition. The tooth formula in the genus *Carollia* is I 2/2, C 1/1, P 2/2, M 3/3 = 32 teeth in total and 16 in the upper jaws (Anderson, 1997; Cloutier and Thomas 1992). A substantial number of these teeth fell out during the time the carcasses spent in water (Table S3). In no individual did all 16 teeth remain at the end of the experiment. In five individuals there were still 9–12 teeth, in eleven individuals there were 5–8 teeth, and in fourteen individuals there were 4 teeth or fewer. In particular, these experiments at c. 25 °C or higher for three to four weeks produced a result comparable to overlong maceration, during which the fixation of the teeth by Sharpey's fibres is destroyed. The length of time in water seems to be unimportant – at least above a threshold of c. 3 weeks – in controlling the extent of tooth loss: the two individuals left in water until day 764 retained 3 and 8 teeth, respectively, in the middle of the sample spectrum.

Supplementary Figures

Figure S1. Histogram (overlapping bars) of surface temperature measurements in tropical rivers and lakes (open-water areas of both) as well as in stands of aquatic vegetation in lakes. The temperature in open-water areas of lakes most similar to Paleolake Messel ranges from 17–34 °C with a mode between 28–29 °C. Temperatures >35 °C are only found in areas of dense stands of aquatic vegetation in some lakes.

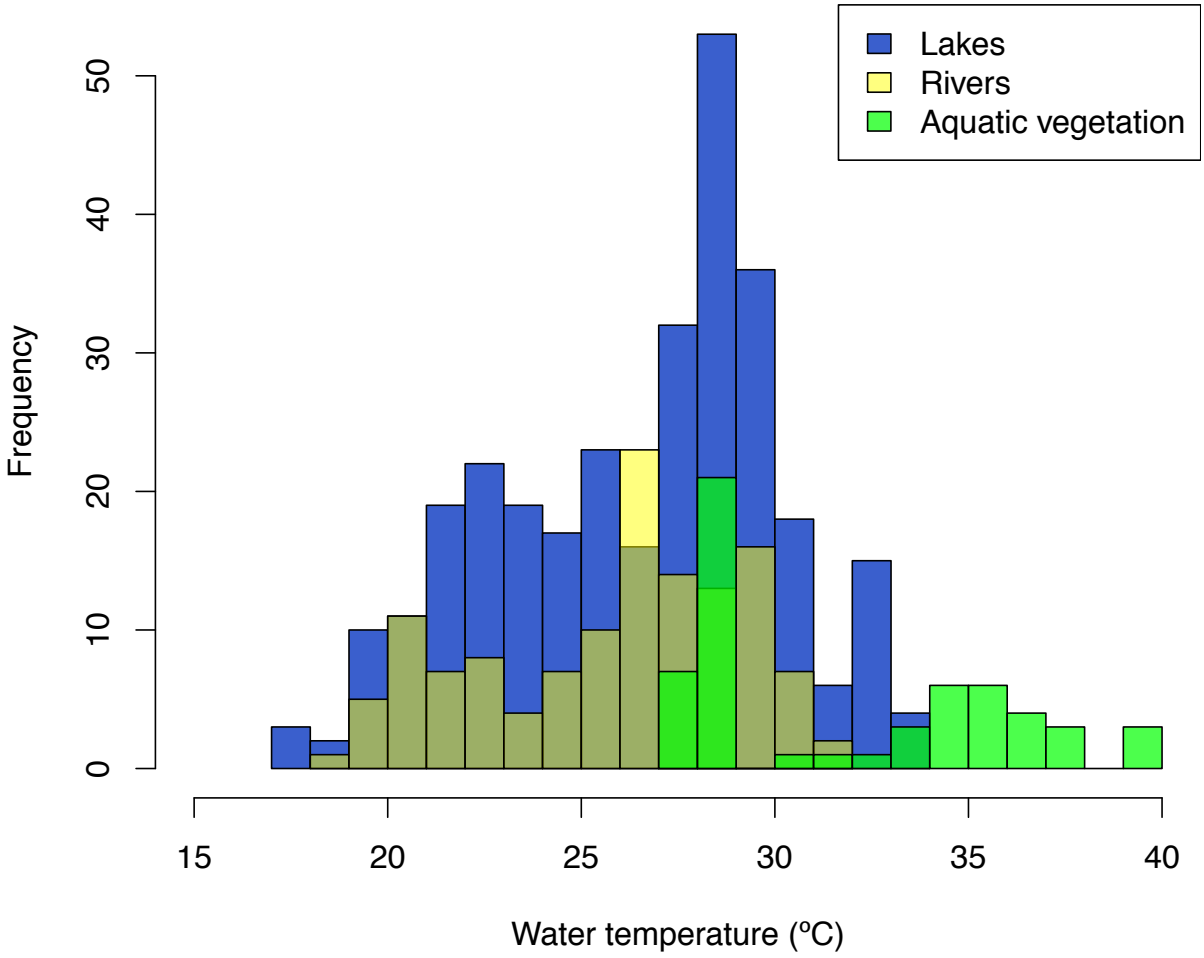


Figure S2. Decay experiments using carcasses of an extant bat species (*Carollia perspicillata*): set-up and early decompositional phenomena. **a** Experimental set-up in the radiographic laboratory at the Research Station Messel. Bat carcasses were allowed to decompose in two water baths at a time. Temperature varied depending on the experiment but was guided by Supplementary Methods and results summarised in Figure S1. The experimental containers were opened to check conductivity and pH and to document the condition of the carcasses photographically and radiographically. **b** Overview of a bat on experimental day 4 at low temperature (c. 20 °C). The carcass is floating belly-down at the water surface. Due to the accumulation of putrefactive gases, the carcass is strongly distended dorsally and juts up well over the surface of the water. **c** The same carcass, turned carefully onto its back for photographic documentation. The abdominal skin is intact and shows no build-up of putrefactive gases. **d** Isolated wing fragment of another bat carcass from (long-term) experiment 6 (at 25.4 °C) on day 9. The distal and proximal radial articulations are separated and, surrounded by large parts of the patagium, have sunk to the bottom. Only one animal is present in the container, in comparison with the previous two panels, and the relatively clear water permits visual inspection down to the bottom. **e** The same carcass at in previous panel. It is distended by putrefactive gases and still floats at the water surface. A small force (2.5 g) suffices to separate the skull by disarticulating the craniovertebral joint. The skull also floats at the surface, and the brain is not yet fully decomposed. Photos: R. Rabenstein, image processing: A. Vogel (Senckenberg).

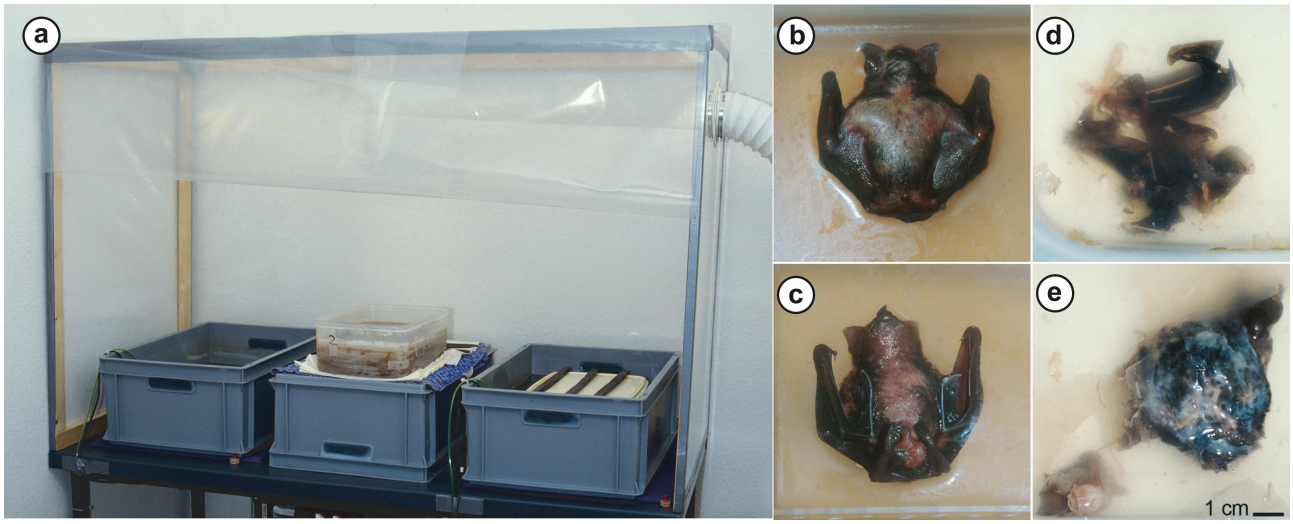


Figure S3. Decay of carcasses of an extant bat (*Carollia perspicillata*) at low temperature (experiment 1). In the left half of the image are bats with water-filled lungs, in the right half bats with air-filled lungs. The panels show typical decompositional phenomena for two individuals in each series on a particular experimental day. Radiographs: R. Rabenstein/M. Ackermann; image processing: A. Vogel (Senckenberg).

Row 1: day 2. No decomposition is evident after 24 hr in water, but air bubbles can be discerned outside the body (e.g., in a1 in the external ear and the elbow region beneath the right wing).

Row 2: day 4. Strong development of putrefactive gases in all carcasses (light areas in radiographs) and rising of the carcasses to the water surface (cf. Figs. S2b, c).

Row 3: day 8. Carcasses of all bats continue to be distended by putrefactive gases. Degassing is already occurring for some individuals (a3, d3), although in one individual gas volume continues to increase (c3).

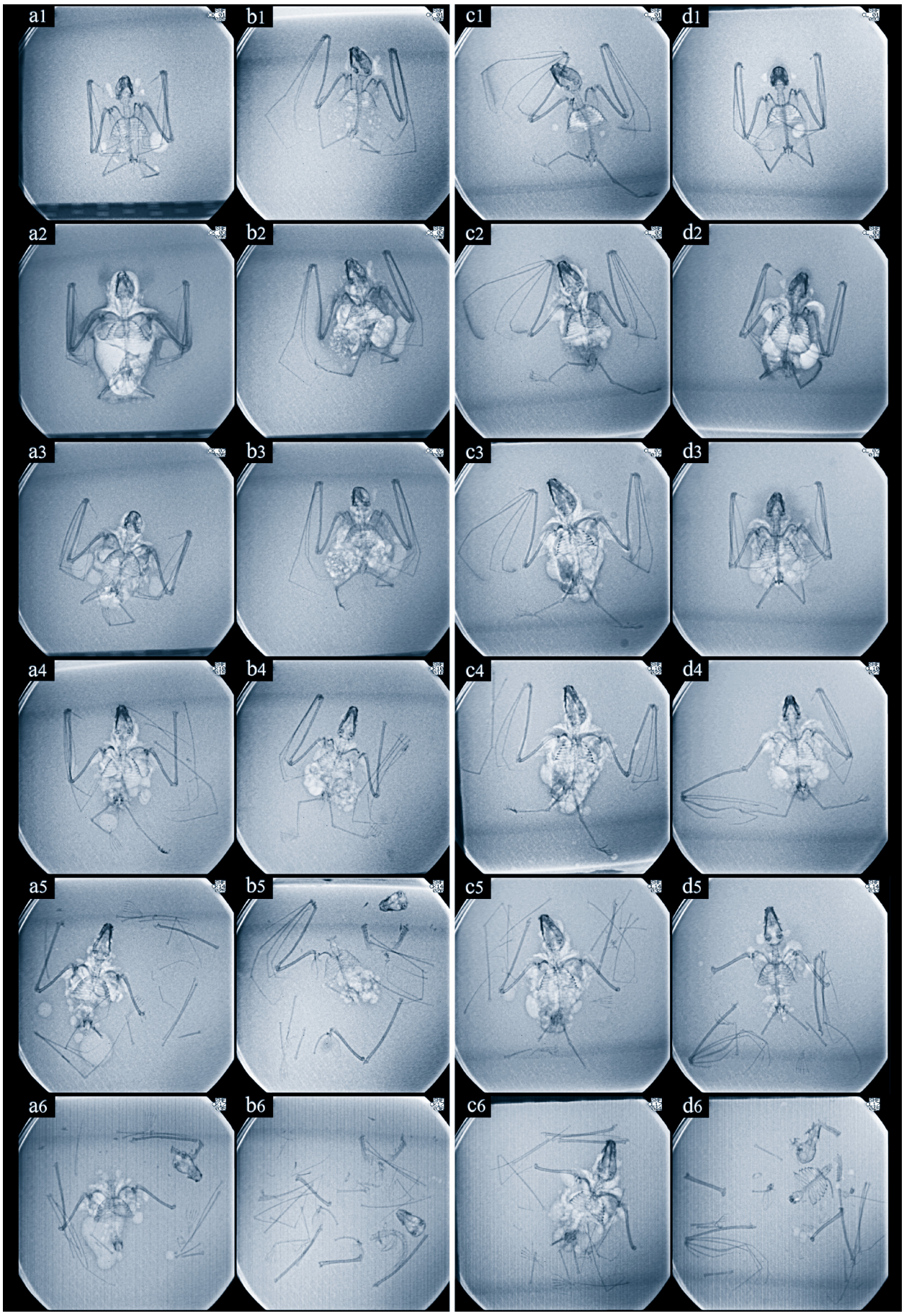
Row 4: day 11. First disarticulations of the wings in the wrist (a4–c4) with small exerted forces. Asymmetrical form of the abdomen (a4–c4) caused by incomplete degassing during disarticulation tests.

Row 5: day 15. All carcasses show disarticulations of the postcranium. For the first time there is disarticulation of the skull at the craniovertebral joint (b5), of the whole wing (b5, bottom: unit comprising radius, humerus, scapula, clavicle, and musculature), and of the hip (b5: both femora). In bats with water-filled lungs, there is more disarticulation of the skeleton as a whole than in bats with air-filled lungs.

Row 6: day 18. Disarticulation continues. Separation of the cranium from vertebral column occurs in the last of the bats with once water-filled lungs (a6). The same now occurs for the first bat with once air-filled lungs (d6). The most stable joint (glenohumeral) remains connected in both shoulders of a6 and c6. The skeleton of b6 is already mostly disarticulated.

Row 7: day 22. Disarticulation of the skeleton is predominant (a7, c7) to complete (b7, d7). The main joints of the skull (craniovertebral and temporomandibular) as well as the symphysis are separated (now also in c7). Further disarticulation mostly affects the shoulder joint and the costovertebral joints (a7, c7).

Row 8: day 25 and termination. The skeletons of all eight bats are predominantly (c8–d8) or completely (a8–b8) disarticulated. Parts of the rib-cage of one individual with once air-filled lungs remains connected to the vertebral column (c8).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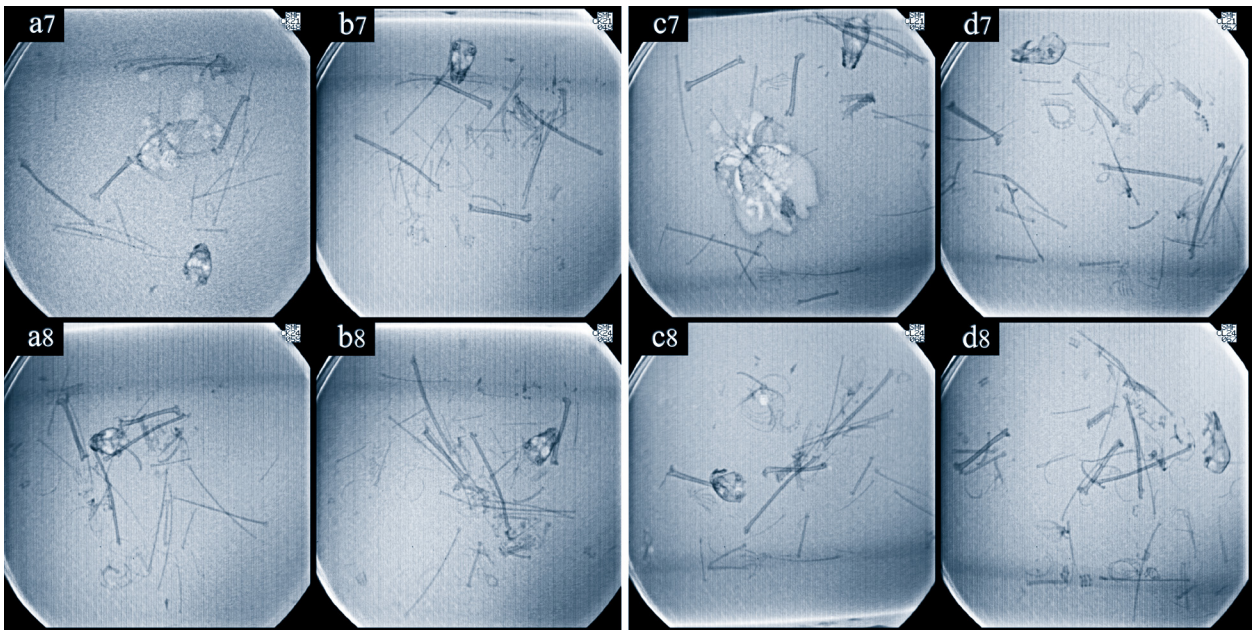
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Figure S4. Decay of carcasses of an extant bat (*Carollia perspicillata*) at medium temperature (experiment 2). In the left half of the image are bats with water-filled lungs, in the right half bats with air-filled lungs. The panels show typical decompositional phenomena for two individuals in each series on a particular experimental day. Radiographs: R. Rabenstein/M. Ackermann; image processing: A. Vogel (Senckenberg).

Row 1: beginning and day 2. Air in the lungs is mostly driven out by the injection of water (a1), although a little air sometimes remains (light areas in radiographs: b1). Air bubbles outside the body are most clearly seen in the external ears (a1, b1) and under the wings (a1, c1).

Row 2: day 3. Putrefactive gases (light areas) and rising of the carcasses to the water surface (a2, b2, d2). In bats with water-filled lungs (a2, b2) putrefactive gases develop strongly in the thorax and abdomen. In bats with air-filled lungs there is little (c2) or only thoracic (d2) putrefactive gases. As a result of gases in the abdomen, the first bat (c2) is now drifting obliquely and head-down beneath the water surface.

Row 3: day 7. The carcasses of all bats remain distended by putrefactive gases. Degassing is already occurring for some individuals (a3); gas volume stays about the same (b3, c3) or continues to rise slightly (d3). First disarticulations of the wing in the wrist and elbow (a3, b3, d3) and in the knee (c3) caused by small forces. The development of putrefactive gases is comparable to the low temperature experiment (cf. Fig. S3, row 3, day 8), but disarticulations at medium temperature (here) occur earlier (cf. Figs. S3, row 4, day 11).

Row 4: day 10. All carcasses show disarticulations of the postcranium and cranial skeleton. In each experimental series the first disarticulations are observed in one hip joint (b4, d4) and in both shoulder joints (b4). Disarticulation of the skull is variable (a4: only craniovertebral joint; b4: craniovertebral and temporomandibular joints; c4: only temporomandibular joint; d4: temporomandibular joint and symphysis). In bats with water-filled lungs there are more disarticulations in the skeleton overall than in bats with air-filled lungs. The state of disarticulation of the skeleton corresponds to that on day 15 at low water temperature (cf. Fig. S3, row 5).

Row 5: day 14. Continued disarticulation results in skeletons that have mostly fallen apart. Cranial disarticulation affects the temporomandibular (a5) and craniovertebral (c5, d5) joints as well as the symphysis (b5). With the exception of one intact wrist (a5) and one shoulder joint (c5), disarticulation of the skeletons is nearly complete, including ribcage (a5–d5), and the state of disarticulation already correspond to that on days 22 and 25 at low water temperature (cf. Fig. S3, rows 7 and 8).

Row 6: day 17. No further disarticulations of the joints considered here (hence, individual d was not newly documented, d6 is a placeholder). Only in one skeleton do the humerus and scapula still articulate with parts of the vertebral column (c6: upper left). The bones lying on the bottom of the experimental container have shifted slightly (cf. a5 and c5 with a6 and c6), and the cranium, which still floats at the surface, is more variable in position. The remaining intact symphyses (a6 and c6) and one remaining shoulder joint (c6) separated on day 20.

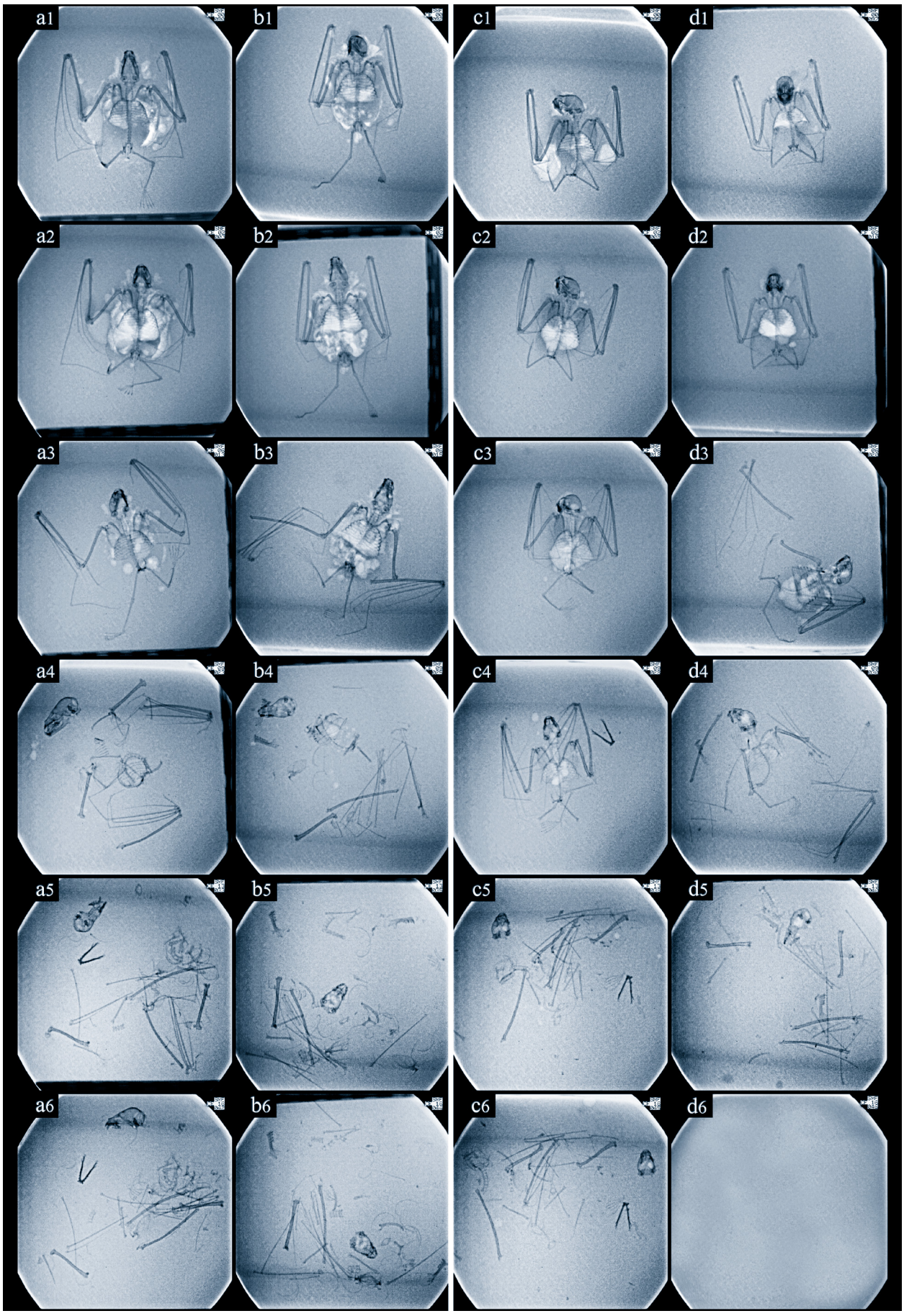
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Figure S5. Decay of carcasses of an extant bat (*Carollia perspicillata*) at high temperature (experiment 3). In the left half of the image are bats with water-filled lungs, in the right half bats with air-filled lungs. The panels show typical decompositional phenomena for two individuals in each series on a particular experimental day. Radiographs: R. Rabenstein/M. Ackermann; image processing: A. Vogel (Senckenberg).

Row 1: day 2. Already after 24 hr, putrefactive gases (light areas in radiographs) have developed in all carcasses, which rise to the water surface. Gas volume in carcasses with water-filled lungs (a1 and b1) is higher than in bats with air-filled lungs (c1 and d1). Decomposition is already notable here, comparable to day 3 of the medium-temperature experiment (Fig. S4, row 2) and day 4 of the low-temperature experiment (Fig. S3, row 2).

Row 2: day 5. The skeleton is predominantly (b2–d2) or completely (a2) disarticulated. In bats from both series, all cranial and nearly all postcranial joints considered here are separated. The few remaining articulated joints are one wrist and one elbow (b2) and one wrist and both shoulder joints (d2). The separation of one skull (d2) occurred together with the atlas. Comparable levels of disarticulation were observed on day 14 of the medium-temperature experiment (Fig. S4, row 5) and day 18 of the low-temperature experiment (Figs. S3, row 6).

Row 3: day 9. Disarticulated skeletons (a3–c3) and last intact shoulder joint (d3). Disarticulation of the last postcranial joints and of the ribcage (b3, d3). The last remaining joint capsules – both shoulder joints – remain intact (d3). The bones lying on the bottom of the experimental containers seen in the previous inspection (row 2) have shifted slightly. The crania generally float at the water surface (especially clear in occipital view in a3). Note that in a3, both humeri and radii had been removed (after a2). In b3, the right humerus, radius and mandible had been removed (after b2). In c3, the mandibles had been removed (just prior to radiography).

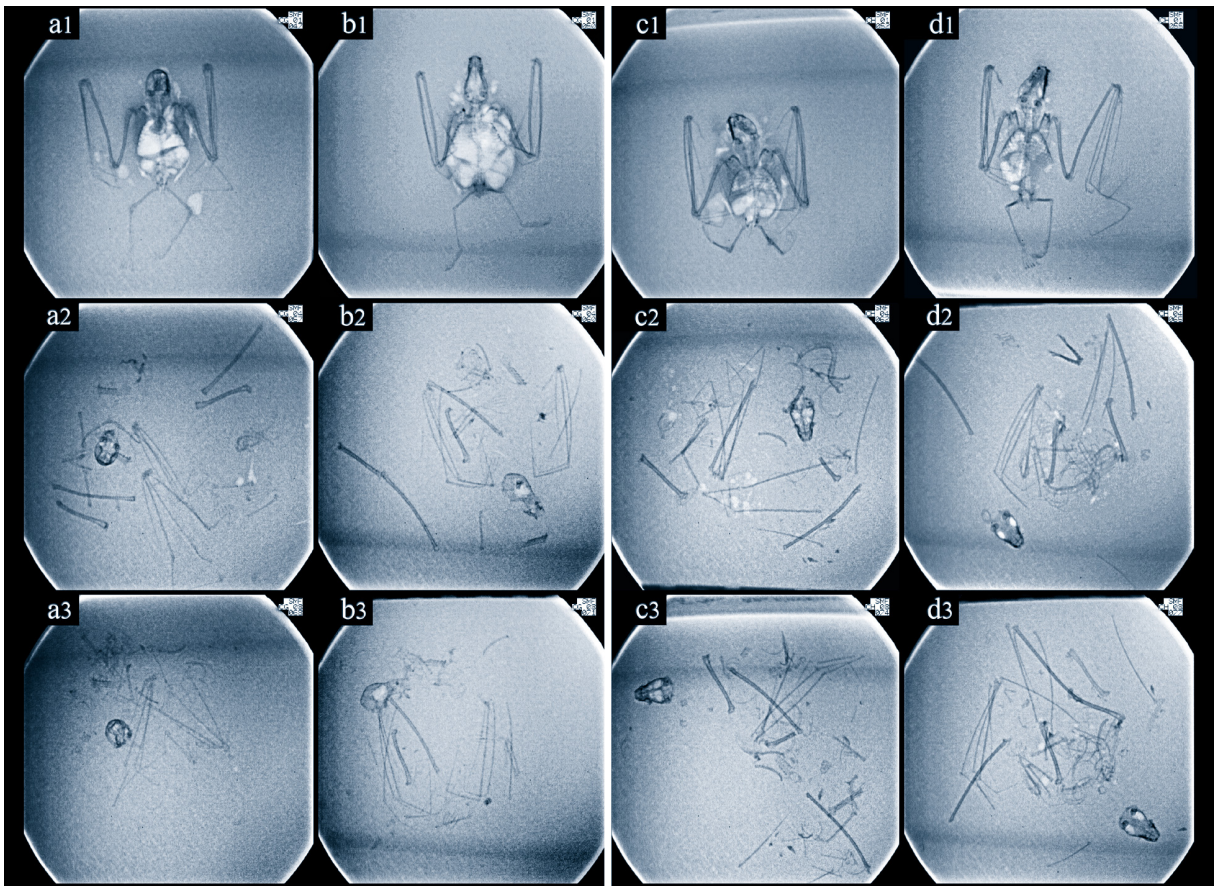
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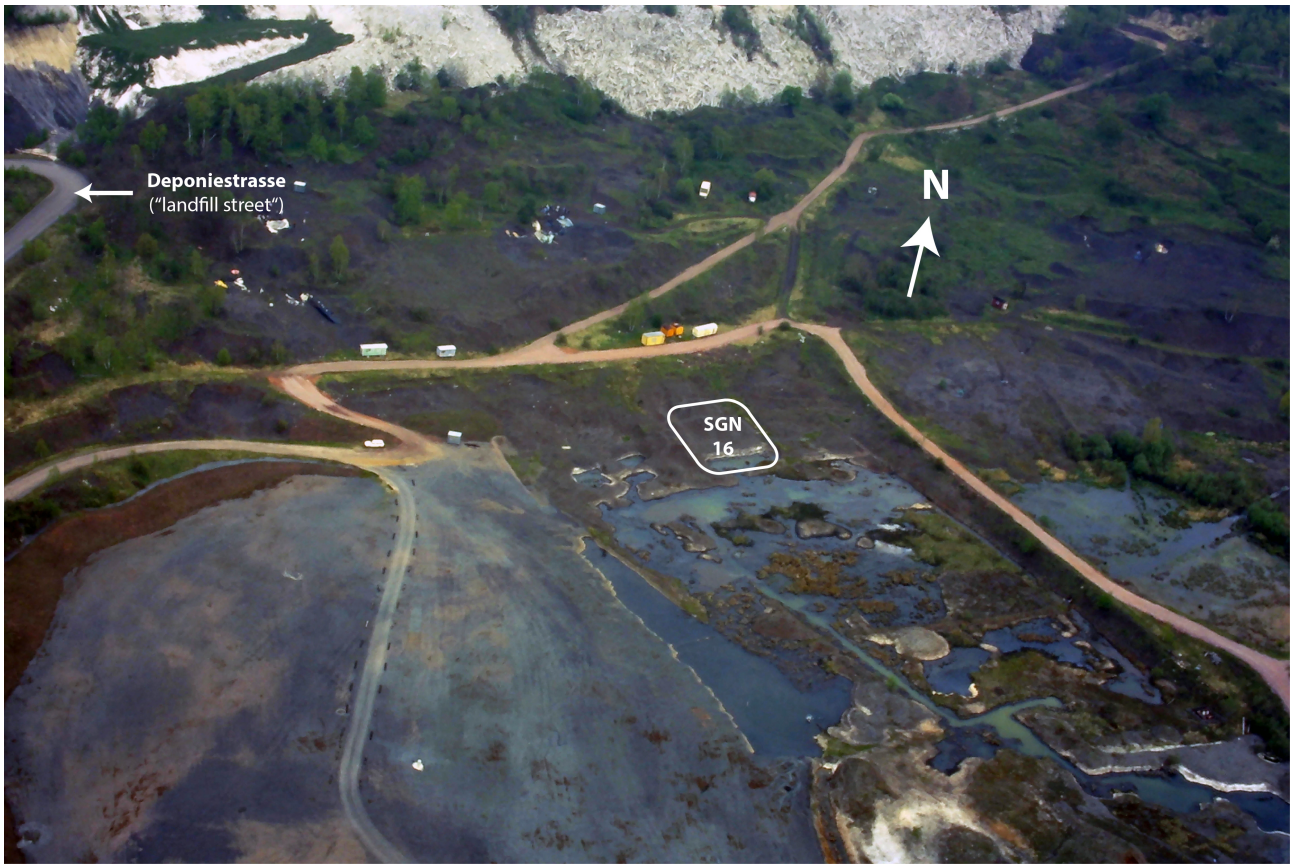
Figure S6. Old aerial photograph showing the location of Senckenberg pit 16. The margins of the pit, last excavated in 1991, were walked out, including wading into the trench remaining at the base. (The strata here dip roughly toward the bottom of the photograph.)



Supplementary Tables

Table S1. Body mass and sex distribution of the 46 individuals of the extant bat *Carollia perspicillata* used in the decay experiments. Body mass measured to 0.5 g, and binned in 1-g classes. With the exception of three individuals of 11.0 g (N = 1) and 12.0 g (N = 2) with incompletely fused epiphyses, all individuals are skeletally mature, as demonstrated by radiologic examination.

Body mass (g)	Male	Female
11.0–11.9	1	0
12.0–12.9	3	1
13.0–13.9	2	2
14.0–14.9	1	3
15.0–15.9	1	2
16.0–16.9	1	9
17.0–17.9	1	7
18.0–18.9	1	3
19.0–19.9	2	1
20.0–20.9	2	0
21.0–21.9	2	1
Totals:	**17**	**29**

Table S2. Number of articulated cochleae remaining in skull at end of experiment. The three subadult animals are in square brackets. Experiments are ordered here by temperature, from highest to lowest.

Experiment Nr.	End of experiment on day	Water Temperature (°C), mean	Number of animals	Number of skulls with *X* (of 2) articulated cochleae		
				0	**1**	**2**
3	28	31.4 - 32.0	5[3]	5[3]		
6	764	28.0	1	1		
6	764	25.4	1		1	
5	21	24.5	12	9	2	1
2	20	24.5	8	7	1	
		Totals:	**30**	**25**	**4**	**1**

Table S3. Number of teeth in upper dentition remaining in skull at end of experiment. Individual tooth positions were not considered. The three subadult animals are in square brackets. Experiments are ordered here by temperature, from highest to lowest.

Experiment Nr.	End of experiment on day	Water Temperature (°C), mean	Number of animals	Number of animals with *X* teeth (of 16) remaining in the upper jaws																
				0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
3	28	31.4 - 32.0	5[3]	1 [1]	[1]	[1]	1		1	1			1							
6	764	28.0	1				1													
6	764	25.4	1									1								
5	21	24.5	12	1	1	1	1	1	1	1	3		1	1						
2	20	24.5	8			1	1	1	1	2					1	1				
		Totals:	**30**	**3**	**2**	**3**	**4**	**2**	**3**	**4**	**3**	**1**	**2**	**1**	**1**	**1**	**0**	**0**	**0**	**0**

Captions for Data Files

Data S1. Comma-delimited text (CSV) file with survey responses.

Data S2. PDF file with survey questions.

Data S3. Compilation of measurements on surface temperature for tropical Southeast Asian bodies of water. Measurements rounded to the nearest tenth of a degree, where necessary. See Additional Literature Cited for full references.

Data S4. RMarkdown file (HTML) containing R code as well as the results of statistical analyses.

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