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The skeletal taphonomy of anurans from the Eocene Geiseltal Konservat-Lagerstätte, Germany: insights into the controls on fossil anuran preservation

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Abstract: The Geiseltal biota is an Eocene lacustrine Konservat-Lagerstätte in central Germany. Despite its rich fauna and flora (over 50 000 fossil vertebrates, insects and other invertebrates, plants and trace fossils) the taphonomy of the biota, and of the anurans in particular, is poorly understood. We analysed the skeletal taphonomy of 168 anurans, scoring each specimen for orientation, completeness and articulation. Most are partial skeletons, truncated during preparation. This process introduces measurable artefacts into the taphonomic data, which requires further study. We identified recurring taphonomic states, including disarticulation or loss of abdominal bones, loss of one or more limbs, extensive disarticulation, and extensive loss of elements across the body. Relatively rare states include: loss of distal limb elements only, scattered bones, and isolated, articulated limbs. These data inform a new taphonomic model for the Geiseltal anurans. Comparative analysis of patterns in completeness and articulation in these specimens and anurans from other Cenozoic Lagerstätten reveals repeated patterns in preservation in lacustrine-hosted settings, such as proximal to distal trends in completeness, preferential loss of small peripheral bones, disarticulation of abdominal bones, and reorientation of major body regions. Taphonomic controls in lacustrine systems are surface water temperature, lake depth, vegetation, exposure to bottom currents, transport mechanisms, scavenging, decay regime, bone size and location in the skeleton; all ultimately controlled by palaeoclimate, lake physiography and hydrology, and anuran anatomy. A universal approach to quantitative analysis of skeletal taphonomy metrics will enable comparative testing of the relationship between preservation and palaeoenvironment for diverse fossil vertebrates.

Key words: fossil amphibian, fossil preservation, taphonomy, Geiseltal, Konservat-Lagerstätte, Eocene.

KONSERVAT-LAGERSTÄTTEN are fossil deposits that preserve unusually high-quality palaeontological information, characterized by high-fidelity preservation as (semi-) articulated skeletons and/or soft tissues (Seilacher *et al.* 1985; Muscente *et al.* 2017). These fossil remains can provide insights into the body plan and lifestyle of ancient organisms (Briggs 2014). In particular, an understanding of the skeletal taphonomy of fossil vertebrates can inform on physical and chemical characteristics of the depositional setting and on syndepositional and postdepositional processes. These processes include decay, transport and flotation (Beardmore *et al.* 2012; Briggs 2014), but also include biases related to sampling and taphonomy (Cleary *et al.* 2015; Dean *et al.* 2016). Skeletal taphonomy metrics (e.g. specimen completeness) have important applications in studies of palaeodiversity, phylogeny and historical palaeontology and enable biases in the fossil record to be assessed (Brocklehurst & Fröbisch 2014; Cashmore *et al.* 2020). Skeletal taphonomic data have been investigated systematically for various fossil vertebrates, such as the early tetrapod *Acanthostega* from the Devonian Aina Dal and Britta Dal Formations (Greenland; Coates 1996), the aquatic reptile *Serpianosaurus* from the Triassic Besano Formation (Switzerland; Beardmore *et al.* 2012; Beardmore & Furrer 2018), the bird *Archaeopteryx* and the dinosaur *Juravenator* from the Jurassic Solnhofen biota (Germany; Kemp & Unwin 1997; Reisdorf & Wuttke 2012), rodent-like mammals (multituberculates) from the Cretaceous Jehol biota (China; Kielan-Jaworowska & Hurum 2006), the frog *Pelophylax pueyoi* from the Miocene Libros biota (Spain; McNamara *et al.* 2012*a*) and salamanders from the Miocene Rubielos de Mora biota (McNamara *et al.* 2012*b*).

The middle Eocene Geiseltal biota includes >25 000 vertebrate specimens representing *c.* 125 taxa (Haubold &

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Krumbiegel 1984; Hellmund 2018). The biota includes specimens that are near-fully articulated, near-complete and/or preserve soft tissues (Krumbiegel *et al.* 1983; Voigt 1988; Wilde & Hellmund 2010). Previous studies of the Geiseltal vertebrates focused on systematic palaeontology, anatomy and evolution, applied to hippomorphs and tapiromorphs (Barnes 1926; Franzen 2003; Hellmund 2013; Ring *et al.* 2020), birds (Mayr 2020), fish (Jerzmanska 1977), reptiles (Hervet 2004; Smith 2009; Hastings & Hellmund 2015*a*) and anurans (Hinsche 1941; Kuhn 1941; Rage & Roček 2003). In contrast, there are few studies on the biostratinomy (Weigelt 1932; Krumbiegel 1977; Krumbiegel *et al.* 1983; Hellmund 1997; Hastings & Hellmund 2015*a*) and the palaeoecology (Walter & Weigelt 1931; Krumbiegel *et al.* 1983) of the biota. In particular, the skeletal taphonomy of the Geiseltal vertebrates has not been investigated systematically. As a result, the palaeoecology, mode of death, biostratinomy and diagenesis of the fossil vertebrates are poorly understood and the biases affecting the biota are unknown.

As with many Cenozoic lacustrine-hosted Lagerstätten (e.g. Messel (Eocene, Germany), Enspel (Oligocene, Germany), Bechlejovice (Oligocene, Czech Republic) and Libros (Miocene, Spain)), anurans are abundant in the Geiseltal biota. These are potentially important index fossils for taphonomic studies because their general body plan and ecology has not changed markedly since the Early Jurassic (Roček 2013) and thus variations in their preservation among biotas are likely to reflect primarily environmental factors. Fossil anurans therefore have the potential to provide unique insights into the palaeoenvironment of lacustrine-hosted Konservat-Lagerstätten (e.g. water depth, water temperature, presence/absence of bottom currents). Here, we use systematic data on the skeletal taphonomy of the Geiseltal anurans (especially completeness and articulation) to test the following hypotheses: (1) that the fidelity of preservation is consistent for all skeletal elements, especially between homologous skeletal elements of the fore and hind limbs and between the left and right sides of the body; (2) that the fidelity of preservation is linked to excavation site and taxonomy; (3) that specimens represent a series of repeating taphonomic states; (4) that the cause of death is desiccation or lake overturn; and (5) that comparative analysis of the taphonomy of anurans from Geiseltal and other important Cenozoic biotas (i.e. Messel, Bechlejovice, Enspel and Libros) can identify broad taphonomic trends in anuran preservation in in lacustrine-hosted Cenozoic settings.

GEOLOGICAL SETTING

The middle Eocene Geiseltal Lagerstätte is located *c.* 20 km southwest of Halle (Saale) in Saxony-Anhalt, central Germany (Fig. 1) and has been of scientific interest for almost 100 years (Barnes 1926). The biota is hosted within a *c.* 120-m-thick succession of palustrine, limnic–palustrine and fluvial–terrestrial sediments that were deposited in the large (*c.* 75 km^2) west-northwest–east-southeast-trending Geiseltal inshore basin (Krumbiegel *et al.* 1983; Blumenstengel 2004; Hellmund & Hastings 2014). Basin formation was driven by a combination of three factors: (1) tectonics focused in the north of the basin; (2) local halotectonics linked to the underlying Permian ‘Zechstein’ and Triassic ‘Röt’ deposits; and (3) fluctuations in sealevel of the Palaeo-North Sea located to the east–northeast (Küstermann *et al.* 2008; Krutzsch 2011; Fig. 1). The Geiseltal succession is dominated by repeated intervals (each 3–25 m thick) of claystones, siltstones and sandstones intercalated with lignite intervals (each *c.* 10–50 m thick; Eissmann 2002; Blumenstengel 2004; Krutzsch 2011). The lignites were exploited commercially in a series of open cast mines from the late nineteenth century until 1993. The mine region was flooded in 2003 and the remaining fossiliferous outcrops are no longer accessible.

Most Geiseltal vertebrates are hosted in lignite intervals. Vertebrate remains are relatively rare in the intercalating siltstones and sandstones (‘Hauptmittel’; Haubold &

FIG. 1. Palaeogeography of the Eocene Geiseltal Lagerstätte (modified after Storch 1986; Hastings & Hellmund 2015*b*; Scotese 2016).

Hellmund 1998). The succession includes six lignite intervals, listed here from oldest to youngest: lower lower coal (LLC, 'Untere Unterkohle'), lower middle coal (LMC, 'Untere Mittelkohle'), upper middle coal (UMC, 'Obere Mittelkohle'), upper sandstone/siltstone deposits (UHM, 'Oberes Hauptmittel'), lower upper coal (LUC, 'Untere Oberkohle') and middle upper coal (MUC, 'Mittlere Oberkohle'; Lincke 1977; Haubold & Hellmund 1998; Fig. 2). The Geiseltal succession lacks igneous components and thus cannot be dated radiometrically (Fig. 2). The LLC, LMC, UMC and UHM units are part of the Geiseltalian European Land Mammal Mega Zone (ELMMZ), which comprises the Mammal Palaeogene Zones MP 11 (LC) to MP 13 (UMC; Haubold & Hellmund 1998). The LLC corresponds to the uppermost part of the succession hosting the middle Eocene Messel Lagerstätte (47 Ma; MP 11; Mertz & Renne 2005). The UMC corresponds to the sediments of the middle Eocene Eckfeld Lagerstätte (44 Ma; MP 13; Mertz *et al.* 2000). The LUC and MUC are correlated with the lower Robiacian and MP 14 (Franzen & Haubold 1987; Aguilar *et al.* 1997). These mammal biochronology data are not universally accepted (see Ring *et al.* 2020) but a late early or middle Eocene age is most plausible. This is supported by palynomorph biostratigraphy, which indicates that the Geiseltal strata span up to the entire Lutetian (Krutzsch *et al.* 1992, Krutzsch 2011).

Palaeoclimate was subtropical, usually frost free (but see Grein *et al.* 2011) and humid (Krutzsch 2011) during deposition of the lignites, but semiarid and warm with seasonal precipitation during deposition of the clastic beds (Krutzsch 2011). Analyses of fossil leaves from clastic beds at the base of the Geiseltal profile (most likely MP 11; Mosbrugger *et al.* 2005, supporting table 2) indicate mean annual temperatures of *c.* 23–25°C with cold month mean temperatures of *c.* 17–21°C and mean annual precipitation of *c.* 1000–1600 mm (Mosbrugger *et al.* 2005).

The Geiseltal fossils were recovered during semicontinuous excavations from the mid-1920s to 2000, with breaks in excavation from 1938 to 1949 and the mid-1980s–early 1990s (Haubold 1995; Hellmund 2018). Vertebrate fossils were recovered from 36 sites in the mines 'Cecilie' (Ce), 'Leonhardt' (Leo), 'Neumark-West' (N_W), 'Neumark-South' (N_S), 'Mücheln-West' (M_W) and 'Mücheln-South' (M_S). Excavation sites were usually <100 m^2 and were classified as sinkholes (each *c.* 10–16 m wide and 3–8 m deep), fluvial channel deposits (up to 40 m wide and 15 m thick) or 'dying fields' ('Leichenfelder'; each with an area of *c.* 80 m × 100 m; Weigelt 1933; Krumbiegel 1962*a*, 1975, 1977; Krumbiegel *et al.* 1983; Haubold & Krumbiegel 1984; Weigelt 1989; Haubold & Hellmund 1998; Hellmund 2018).

The sinkholes are considered to have formed due to dissolution of underlying salt and gypsum deposits and subsequent subsidence; the resulting localized depressions were filled with carbonate-rich and saline waters derived from groundwater and surface water during wet periods (Weigelt 1934; Krumbiegel 1975, 1977; Krumbiegel *et al.* 1983). Sinkhole sediments are characterized by alternating layers of lacustrine chalk ('Seekreide') and dysodile lignites with rare diatomites (Weigelt 1934; Krumbiegel 1975, 1977; Krumbiegel *et al.* 1983). Biomarkers for chlorophyll (Dilcher *et al.* 1970) and the sapropelic character of the lignites suggest benthic dysoxia (Krumbiegel 1977). The best-preserved fossils in sinkhole excavation sites are considered to occur in the finely laminated lignites deposited in the central parts of sinkholes (Krumbiegel *et al.* 1983); some fossils are considered to have been exposed subaerially before burial (Weigelt 1935).

Fluvial deposits have been attributed to meandering rivers with low current velocities and unstable banks (Krumbiegel 1977). Carbonate-rich sediments in certain sinkholes and dying fields have been linked to inputs of alkaline waters from inflowing rivers (Krumbiegel 1962*b*; Krumbiegel *et al.* 1983). The river deposits include fossiliferous beds that consist of white, cross-bedded sandstones and brown mudstone (Krumbiegel 1962*b*). Most fossils were recovered from the sandstones, whereas the mudstones preserve only occasional accumulations of bones (Krumbiegel 1962*b*). Fossil wood usually shows a north–south or north-northeast–south-southwest orientation; some fossil tree trunks and branches are associated with accumulations of vertebrate remains and are interpreted as fossil traps (Krumbiegel 1962*b*, 1977). The faunal composition of the river deposits differs from that of the sinkholes and dying fields; for example, the river deposits are usually rich in crocodilian, palaeohippid, and turtle fossils (Krumbiegel 1962*b*; Krumbiegel *et al.* 1983). Floodplain sediments include halophile invertebrates (Krumbiegel 1977).

The dying fields consist of laterally restricted, laminated lignite seams, 0.2–0.8 m thick (Weigelt 1933; Raupach 1948; Krumbiegel *et al.* 1983), with particularly high densities of vertebrate fossils (e.g. *c.* 2200 vertebrate specimens over a surface area of 914 m^2 at site Ce II; Weigelt 1940; Haubold 1995). These deposits are localized to a geomorphological depression striking north-east–south-west in the central region of the Geiseltal basin (Weigelt 1933; Krumbiegel 1977). The dying field sediments are considered to have originated in shallow swampy troughs that formed during wet periods and persisted for tens to hundreds of years (Raupach 1948; Krumbiegel 1977). The lignite seams are usually underlain and overlain by carbonate-rich beds interpreted as lake bank deposits (Raupach 1948), indicating temporal fluctuations in lake level and thus size (Raupach 1948).

The Geiseltal biota shares faunal elements with other important German Cenozoic Lagerstätten, especially Messel

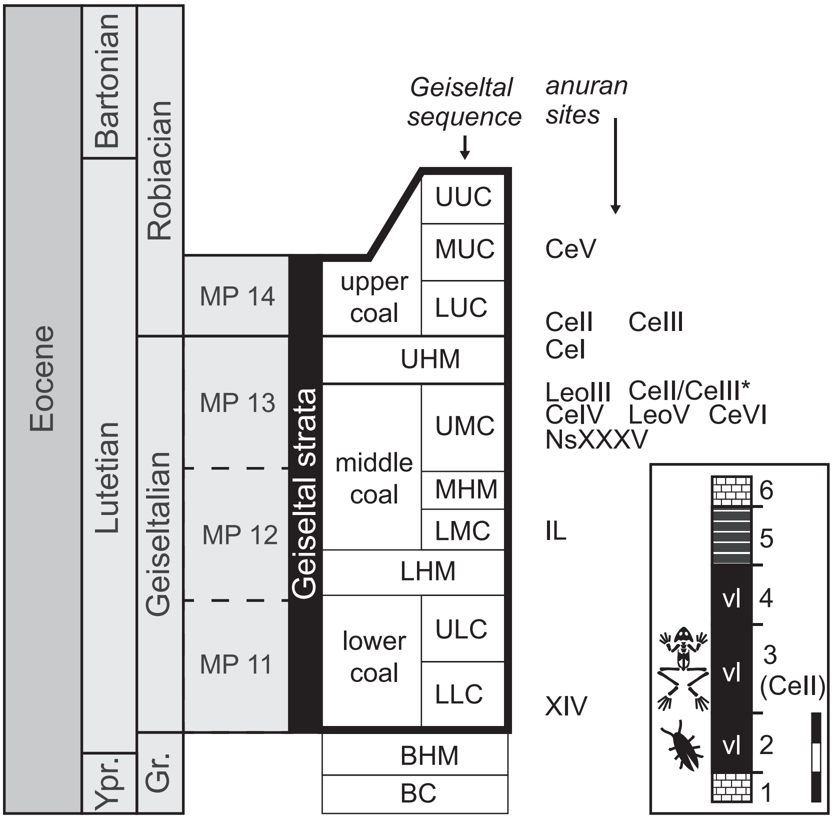

FIG. 2. Stratigraphy of the Geiseltal Lagerstätte (modified after Haubold & Hellmund 1998). Geiseltal sequence and anuran sites. Inset shows stratigraphic section of the interval containing site Ce II ('dying field 1'), drawn using data from Raupach (1948). *Note that Ce II/Ce III was originally assigned to UMC by Krumbiegel (1962*a*). Also note that the mammal biochronology data for the Geiseltal strata (MP) are not universally accepted (Ring *et al.* 2020). *Abbreviations*: BC, basal coal; BHM, basal 'Hauptmittel' ('Hauptmittel': intercalated sandy and silty successions); Ce, 'Cecilie' pit; Gr., Grauvian; IL, 'Geiselröhlitz' site; Leo, 'Leonhard' pit; LHM, lower 'Hauptmittel'; LLC, lower lower coal; LMC, lower middle coal; LUC, lower upper coal; MHM, middle 'Hauptmittel'; MUC, middle upper coal; Ns, 'Neumark-South' pit; Nw, 'Neumark-West' pit; UHM, upper 'Hauptmittel'; ULC, upper lower coal; UMC, upper middle coal; UUC, upper upper coal; v, varve-like; Ypr., Ypresian. 1, 6, carbonate bed; 2, dark lignites rich in insect fossils ('black coal'); 3, lignites rich in vertebrate fossils (site Ce II, dying field 1); 4, lignites; 5, laminated lignites/dysodile coal ('Blätterkohle'). Scale bar in inset represents 0.3 m.

(Franzen 2005) and Eckfeld (Mertz *et al.* 2000). The Geiseltal vertebrate biota includes skeletal remains of mammals, amphibians, reptiles, fish and birds (Krumbiegel *et al.* 1983; Hellmund 2018) with rare crocodilian and avian eggs (Kohring & Hirsch 1996; Hastings & Hellmund 2015*a*; Mayr 2020). Invertebrates include bivalves, gastropods and diverse insects (*c.* 155 species; Krumbiegel *et al.* 1983). Plant fossils are abundant and include cryptogams, gymnosperms and angiosperms (Rüffle *et al.* 1976; Krumbiegel *et al.* 1983; Wilde 1995; Rüffle & Litke 2000). The Geiseltal flora also includes rare fibrous laticifers termed 'monkeyhair' (McCoy *et al.* 2021). Fossil resin and trace fossils are other common components of the Lagerstätte (Krumbiegel 1995; Falk *et al.* 2019; Simoneit *et al.* 2020). Preservation of the Geiseltal fossils has been linked to inputs of carbonate-rich waters (springs and rivers) derived from the Triassic Muschelkalk limestone plateau that crops out to the south and south-west (Krumbiegel *et al.* 1983). Preserved bacteria have been reported from coprolites, frog epidermis, beetle spiracles and fish eyes (Mrugowsky 1936), but these microbodies (at least those in the vertebrates) are likely to represent fossil melanosomes, which commonly define carbonaceous soft tissues of fossil vertebrates (Vinther *et al.* 2008; Rossi *et al.* 2019; Rossi *et al.* 2020).

The vast majority of the Geiseltal anurans were excavated and prepared during the 1930s (Weigelt 1933; Kuhn 1941); the remainder, during the 1950s and 1970s (Falk *et al.* 2022, dataset 1). Almost all specimens were prepared via the transfer method (i.e. Lackfilm method; Fig. S1; Voigt 1933, 1988); records indicate the loss of hundreds of specimens during the transfer process (Krumbiegel *et al.* 1983). Approximately 200 anuran specimens were transferred successfully (Krumbiegel *et al.* 1983) but only 180 specimens (including tadpoles) are accounted for today; the location of the remaining

20 specimens is unknown. Early studies of the fossil anurans reported preservation of skin cells, glands, connective tissue, blood capillaries, melanophores and a pale greenish colouration in some specimens (Voigt 1935, 1937, 1988).

MATERIAL AND METHOD

Fossil material

The Geiseltal Collection of the Natural Sciences Collections (ZNS) of the Martin Luther University Halle-Wittenberg in Halle (Saale) (Saxony-Anhalt, Germany) hosts at least 50 000 specimens from the Geiseltal Lagerstätte including *c.* 25 000 vertebrates. In this study we examined 168 fossil anuran specimens from the collection. Most of the studied anurans (n = 121) were excavated from the dying field deposits at the sites Ce II (lignite interval LUC; Haubold & Hellmund 1998) and Ce III (lignite interval UMC; Krumbiegel 1962*b*; Fig. 2). Forty anurans used in this study are from sinkhole deposits (i.e. Ce I, Ce IV, Ce V, Ce VI, Leo III, Leo V and N_s XXXV; Haubold & Krumbiegel 1984). A single anuran used in this study derives from river bank and flood plain deposits (site XIV (N_w XIV in Haubold & Krumbiegel 1984) of interval LLC; Krumbiegel 1962*b*; Haubold & Krumbiegel 1984; Fig. 2). Stratigraphic data are not available for the remaining six specimens.

Most of the fossil anurans (n = 99) are of undetermined affinity (Falk *et al.* 2022, dataset 1). Of the remainder, most have been previously assigned to the (mainly terrestrial) Pelobatidae (n = 54) and (mainly aquatic) Palaeobatrachidae (n = 15) (Kuhn 1941; Roček & Rage 2000; Roček 2013; Roček *et al.* 2014). Some specimens may represent Discoglossidae (Rage & Roček 2003; Roček 2013).

Completeness and articulation vary considerably. Most specimens are well-articulated skeletons (Fig. 3). Specimens consisting of disarticulated and scattered bones or isolated, articulated limbs are rare. One specimen is conserved *in situ* in sedimentary matrix (with the slab conserved in water); most of the remaining specimens are conserved in nitrocellulose glue (Fig. 3A, C–F, H–J) with a minority in paraffin wax (Fig. 3B, G). Many slabs retain small (<10 mm) patches of dark organic-rich sedimentary matrix; no distinctive sedimentary textures or fabrics are evident (Fig. 3). Most (n = 166) slabs hold one specimen; the remaining two slabs each include two specimens. A single slab includes fish scales.

The Geiseltal Collection includes tadpoles but these are excluded from the current study due to their poor preservation and markedly different Bauplan to the adult anurans. This study focusses exclusively on the anurans that represent post-tadpole developmental stages (n = 168). Unequivocal discrimination of adults, subadults and juveniles is not always possible.

Twenty-eight specimens were omitted from the study because poor preservation precluded confident identification of individual skeletal elements. The remaining 140 specimens comprise 54 pelobatids, 15 palaeobatrachids and 71 undetermined individuals. A total of 106 specimens are truncated either by the edge of the slab and/or the embedding medium.

Skeletal anatomy

The skeleton of adult anurans consists of three major units: the cranium, axial skeleton and appendicular skeleton. The axial skeleton consists of the vertebral column (including eight presacral vertebrae and the sacral vertebra), urostyle, ischium and ilia. The appendicular skeleton consists of the forelimbs (clavicle, coracoid, scapula, humerus, radioulna, carpals, metacarpals and phalanges) and hindlimbs (femur, tibiofibula, tibiale–fibulare, tarsals, metatarsals and phalanges). The torso here refers to the vertebrae, urostyle, ilia and ischium.

Size

The distance from the snout to the distal end of the urostyle (snout–urostyle length: SUL) is a proxy for specimen size (Gvoždík *et al.* 2008). SUL was measured from digital images of specimens (n = 28) using ImageJ v.1.53e (Schneider *et al.* 2012).

Orientation

Orientation was defined as: (1) dorsal, ventral or dorsoventral if the sagittal axis was perpendicular to the bedding on the slab; (2) oblique if it was inclined to the bedding; or (3) lateral if it was parallel to the bedding. Orientation was assessed for 121 specimens. The way up of specimens cannot be determined unequivocally: the transfer process usually results in an inverted way up relative to the presentation of specimens in the field (Fig. S1; Voigt 1933; Weigelt 1933), but whether this applies to all specimens is unclear. Orientation was assessed using the orientation of the scapula, pectoral girdle, teeth in the upper jaw and vertebrae. ‘Left’ and ‘right’ body sides of specimens were coded as per the presentation of the specimen on the transfer/slab.

Completeness

We used a modified form of the Skeletal Completeness Metric (SCM) proposed by Mannion & Upchurch (2010)

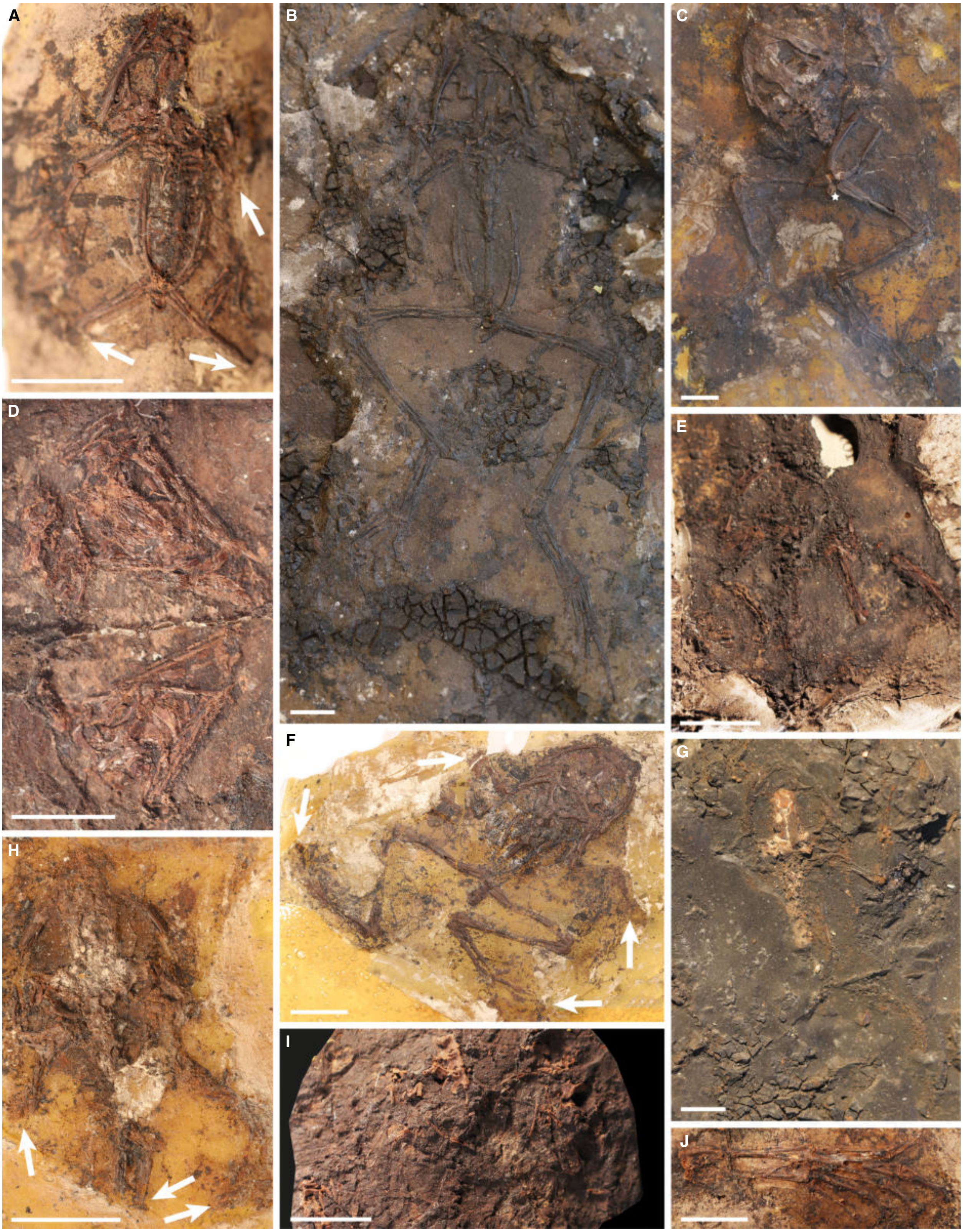
A
B
C
D
E
F
G
H
I
J

FIG. 3. Variation in completeness and articulation among the Geiseltal anurans. Some specimens are truncated by the edge of the slab or embedding medium (arrows). Specimens belong to truncation categories T0–T4; untruncated specimens were assigned to a taphonomic state (for details see text). All slabs retain patches of dark organic-rich host sediment. Interpretative line drawings are shown in Figure S2. A, Ce III-6735-1932; incomplete, near-fully articulated, T2. B, Ce II-4949-1930; near-complete, near-fully articulated with patches of sediment (apparent as dark polygons), T0, states 1, 9. C, Ce III-6728-1932; near-complete, partially articulated (the urostyle is shifted to the left), potential coprolite (star), T0, states 1, 7, 8. D, Ce IV-4953-1933; accumulation of mostly disarticulated bones, T0, states 4, 9. E, Ce III-6720-1932; incomplete, partially articulated anterior body, T0, states 3, 9. F, Ce III-6719-1932; near-complete, near-fully articulated, T2. G, Ce I-4947-1930; incomplete, lacking limbs, near-fully articulated, T0, states 2, 9. H, Ce III-6742-1932; incomplete, near-fully articulated, T4. I, IL 17A-1969; disarticulated and reorientated vertebrae and possible limb elements, T0, states 5, 9. J, Ce III-6737-1932; incomplete, near-fully articulated foot showing digits I–V and several phalanges, states 6, 9. Scale bars represent 10 mm.

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to assess skeletal and specimen completeness in the Geiseltal anurans. The total number of skeletal elements in the body is estimated as 91 for the Geiseltal anurans. This value was derived from the number of bones in fully preserved body regions of different specimens and in the skeleton of the extant frog *Lithobates catesbeiana* (American bullfrog; Ranidae; De Iuliis & Pulerà 2011); its skeletal configuration is near-identical to that of the Geiseltal anurans. Geiseltal specimens differ from *L. catesbeiana* in the shape and dimension of some skeletal elements (i.e. cranial elements, sacral vertebra) and by probably lacking a prepollex and prehallux (neither element is observed in Geiseltal specimens; the prehallux is usually absent in palaeobatrachids; Wuttke *et al.* 2012). Furthermore, *L. catesbeiana* includes partly fused tibiale and fibulare. These are fused in some adult pelobatids (Roček *et al.* 2014) but are usually unfused in palaeobatrachids (Wuttke *et al.* 2012). The Geiseltal pelobatids and palaeobatrachids differ in cranial shape, metacarpal length and tibiofibula–femur length ratio. In addition, pelobatids (but not palaeobatrachids) have sculptured cranial bones and an ossified sternum (Roček *et al.* 2014); palaeobatrachids (but not pelobatids) commonly feature fused vertebrae (i.e. 'synsacrum'; Wuttke *et al.* 2012).

Completeness was not assessed for the following skeletal elements:

1. Individual elements of the cranium. These are usually superimposed and difficult to identify. The cranium is thus coded as present if at least one cranial bone is evident.
2. Individual elements of the pectoral girdle (clavicula, coracoid, scapula, sternum). These are often obscured by vertebrae or cranial elements.
3. Individual carpals and tarsals. These are small, typically overlap and are coded as present if at least one carpal or tarsal is evident.

For most specimens, the margins of the slab or transfer are less than 50 mm from the bones in all directions. Some specimens consist of disarticulated associations of bones in which individual bones may be shifted from their original positions *in vivo* by several centimetres. Despite this, the associated bones clearly belong to a single specimen based on their size, anatomy and the presence of pairs of relevant elements. Bones were therefore coded as present if they are preserved <50 mm from life position; complete specimens may thus be disarticulated. The presence or absence of all other skeletal elements was noted for each specimen. In most specimens, unequivocal identification of a limited number of bones (typically 3–4) was difficult due to superimposition, poor preservation and/or incomplete transfer. The assessment of the presence or absence of each skeletal element was therefore coded as 'confident' or 'not confident'. Only skeletal elements identified confidently were included in the study. Furthermore, identification of small elements present as a set of three or more bones (e.g. individual vertebrae and phalanges) was often challenging and it was not always possible to determine the exact number of these elements present. For these bones, specimens were therefore assigned to one of the following completeness categories: vertebrae: 0, 1–3, 4–6 or 7–9 present; forelimb phalanges: 0, 1–3, 4–6, 7–9 or 10 present per hand; hindlimb phalanges: 0, 1–3, 4–6, 7–9, 10–12 or 13–14 present per foot.

Completeness data were assessed using two indices:

1. Specimen completeness. Percentage completeness was assessed for each specimen as follows. The total number of bones preserved in each specimen was expressed as a percentage of the total number of bones in a complete specimen; for example, a specimen completeness value of 43% indicates that the specimen has 43% of the bones present *in vivo* (i.e. is 43% complete). Certain additional elements were excluded due to low confidence and/or truncation (see below). The calculation of specimen completeness may thus not use the potential maximum number of 91 bones; for example, for a specimen lacking a hand due to truncation, the maximum number of 91 bones was reduced (by the number of bones in the hand) to 77 bones. For elements present as a set (e.g. phalanges), the highest number for each completeness category was used in the calculation. For instance, in a specimen with left-hand phalanges

assigned to category ‘1–3’ and right-hand phalanges assigned to category ‘4–6’, the total number of phalanges is recorded as nine. The highest value and not the median value was chosen because the former may lead to an overestimation only, rather than an over- or underestimation when the median is used. Thus, the potential error in the dataset has only one polarity.

2. Skeletal element completeness. Presence–absence data were compiled for each element across the total dataset and expressed as a percentage of the number of specimens used in the calculation; for example, ‘urostyle, 39% (n = 138)’ indicates that the urostyle is present in 39% of specimens in a dataset of 138. In this example, two specimens (out of a total dataset of 140 specimens) were omitted because identification of the urostyle was not confident and/or it was truncated. Bones present as a pair or as a set of three or more elements were considered complete if at least one bone from the pair or set is present. Given that many skeletal elements are paired or present as a set, this index may artificially inflate completeness values. A second measure of element completeness was therefore calculated as follows. First, the total number of bones was calculated for each element in the dataset. In the Geiseltal dataset, some elements and specimens were excluded due to low confidence and/or truncation, so the calculation may not use the potential maximum number of these elements in the dataset. For example, 140 specimens yield a potential maximum of 280 humeri, but our dataset includes a total of only 223 humeri. Presence–absence data for each element are expressed as a percentage of this maximum number of elements; for example, ‘humerus, 29%’ indicates that 29% of all humeri in the dataset (i.e. 29% of 223) are present.

Truncation

Any analysis of the skeletal taphonomy of fossil vertebrates must consider how much of the specimen is present on the slab and to what extent this apparent completeness, and related apparent articulation, may be affected by biases related to taphonomy and/or fossil preparation and conservation. If all skeletal elements are equally likely to be preserved, with similar fidelity, then taphonomic indices such as completeness and articulation should be independent of which bones are present on the slab. If, however, preservation potential varies between skeletal elements (e.g. due to biological factors linked to decay and anatomy) then values for completeness and articulation will vary between specimens depending on which bones are present. It is therefore essential to assess whether or not the skeletal taphonomy of specimens is affected by fossil preparation. In particular, is apparent completeness equal to true completeness, or an artefact of preparation and/or conservation? This is a critical issue for the Geiseltal anurans, for which variations in taphonomy have not been assessed and for which the vast majority of specimens have been subject to invasive conservation via the transfer method. The primary risk during the transfer process is that part of the specimen (including some bones) may not transfer across to the new conserving material, generating a fossil that is ‘truncated’. We therefore assessed the impact of truncation on skeletal taphonomy as follows.

Truncated bones are those for which the edge of the slab or of the nitrocellulose glue/wax transfer passes through the bone (i.e. part, but not all, of the bone is visible) (Figs 3, 4). Most specimens included in the study (76%, n = 140) are truncated; depending on the position and orientation of the torso and limbs, truncation of a skeletal element may affect all elements that are more distal of it. For instance, a specimen with a truncated femur usually lacks the tibiofibula, tibiale–fibulare and foot of that limb. When the truncated element is part of a set (e.g. metatarsals) both the element group itself and more distal elements may be truncated. For instance, the edge of the slab may pass through three metatarsals but lie proximal of the fourth and fifth metatarsal and of the phalanges (which are thus not present).

Truncation was assessed for each skeletal element because it potentially affects values for completeness and articulation (see below), depending on how the latter two indices are assessed (Fig. 4). This applies particularly to skeletal elements distal of truncated elements. For instance, in the case of a truncated femur with the anterior part of the bone on the slab, it is not possible to determine whether more distal skeletal elements are truly absent (i.e. disarticulated and lost), or were indeed preserved as part of the fossil but were subsequently lost during the transfer process. Two potential options for treating this uncertainty are to: (1) omit skeletal elements distal to truncated elements from the analysis; or (2) code all skeletal elements distal to truncated elements as ‘absent’ (Fig. 4G). Both methods have the potential to bias values for specimen completeness. Method 1 is favoured herein because it does not incorporate assumptions regarding the presence or absence of bones distal of truncated elements (note that data are, however, provided for both methods; see Fig. S3). Using method 1, truncated elements were coded as present. Elements distal of truncated elements were omitted from the study (Fig. 4H). In the assessment of specimen completeness, when at least one bone in an element set is truncated, the truncated element(s) was(were) coded as present. For instance, when three out of five truncated metatarsals are present

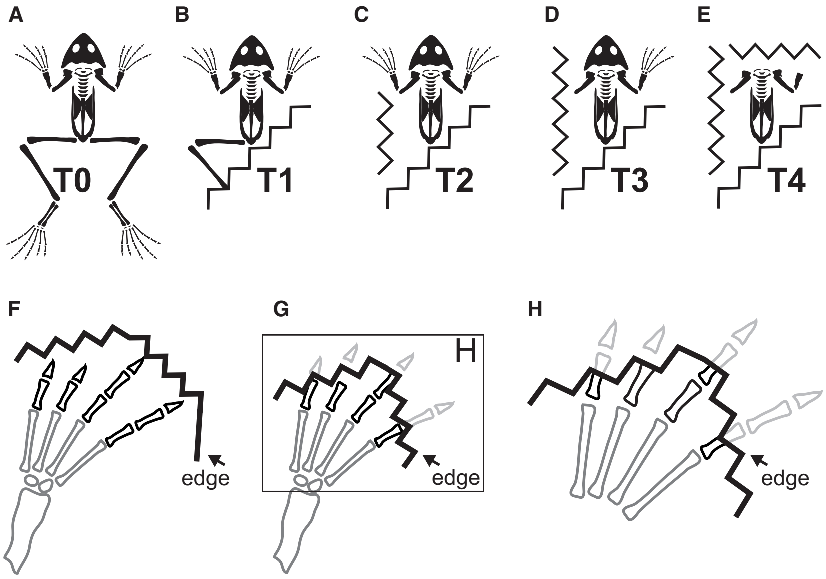

FIG. 4. Truncation. A–E, truncation categories for the Geiseltal anurans: A, T0: no bones truncated; B, T1: 0.1–24.9% of bones truncated; C, T2: 25–49.9% truncation; D, T3: 50–74.9% truncation; E, T4: 75–100% truncation. F–H, impact of truncation on completeness and articulation: F, hand is not truncated and includes 10 phalanges (in black outline); G—H, hand is truncated by the edge of the slab (thick zigzag line); G, truncated hand lacks five phalanges, which are omitted from the study; the presence of five out of a measurable total of five phalanges thus results in a completeness value of 100%; this is the preferred approach for calculating completeness used in this study; the alternative approach is to include the bones truncated by the slab in the study but code them as 'absent' (Fig. S3), in which case the presence of five out of 10 phalanges yields a completeness value of 50%; this approach potentially biases specimen completeness to lower values and is rejected in this study; H, edge passes through three phalanges; these bones are coded as present, whereas bones beyond the edge are omitted.

and two are not visible but are potentially distal of the transfer edge, the latter two metatarsals are omitted from the study. When at least one element in a set is truncated, the set was omitted from the analysis of completeness categories.

Truncation usually affects peripheral elements (i.e. phalanges); these elements are also the most numerous and thus make the greatest contribution to values for specimen percentage completeness and articulation. The values for percentage completeness and articulation of individual specimens may thus be affected markedly by truncation. To assess this, the percentage of skeletal elements omitted from the study due to truncation was calculated for each specimen. Specimens were assigned to one of the following truncation categories (Fig. 4A–E): T0 (no bones truncated), T1 (0.1–24.9% of bones truncated), T2 (25–49.9% truncation), T3 (50–74.9% truncation) and T4 (75–100% truncation).

Articulation

Articulation was assessed only for those joints that are present in the fossils (i.e. when all bones that form the joint are present). The total number of joints present in a complete specimen is 98. A joint was coded as articulated if the relevant bones are juxtaposed in life position. Herein, the term 'shoulder joint' refers to the articulation of the humerus and scapula and 'hip joint' refers to the articulation of the femur and ilium. For certain specimens, unequivocal identification of articulated joints is difficult when bones are superimposed, poorly preserved or incompletely transferred. As with completeness, the assessment of the articulation state of each skeletal element was therefore coded as 'confident' or 'not confident'. Only joints for which articulation could be assessed confidently are included in the study. It was not always possible to determine the exact number of articulated joints between adjacent vertebrae, metacarpals, metatarsals, carpals, tarsals and phalanges. For these joints, specimens were therefore assigned to one of the following articulation categories: vertebrae: 0, 1–3, 4–6 or 7–8 joints articulated; metacarpals–carpals and metacarpals–phalanges: 0, 1–2, 3 or 4 articulated joints per hand; forelimb phalanges: 0, 1–2, 3–4 or 5–6 articulated joints per hand; metatarsals–tarsals and metatarsals–phalanges: 0, 1–2, 3–4 or 5 articulated joints per foot; hindlimb phalanges: 0, 1–3, 4–6 or 7–9 articulated joints per foot. Joint sets were coded as articulated if at least one joint is in life position. When carpals and/or tarsals are absent or were omitted from the study, the articulation of the wrist and/or ankle joint was assessed using the preserved positions of the metacarpals and radioulna (0, 1–2, 3 or 4 articulated joints per hand), or tibiale–fibulare and metatarsals (0, 1–2, 3–4 or 5 articulated joints per foot), respectively.

As for completeness, articulation was assessed using two indices:

1. Specimen articulation. Percentage articulation was assessed for each specimen as follows. The total number of articulated joints in each specimen was expressed as a percentage of the total number of joints in a complete specimen; for example, a specimen articulation value of 48% indicates that 48% of the joints in the specimen are articulated. For joint sets, the highest number for each articulation category was used in the calculation.
2. Joint articulation. Articulation–disarticulation data were compiled for each joint present across the total dataset and expressed as a percentage of the number of specimens used in the calculation; for example, ‘humerus–shoulder, 90% (n = 80)’ indicates that the proximal humerus adjoins the shoulder in 90% of specimens in a dataset of 80. In this example, 60 specimens (out of a total dataset of 140 specimens) were omitted because either at least one adjoining skeletal element is absent, poorly preserved and/or truncated. Joints present as a pair or a set of three or more joints (e.g. phalanges) were considered articulated if at least one bone from the pair or set is articulated. Given that many joints are paired or present as a set, this index may artificially inflate articulation values. Articulation data were therefore also expressed as a percentage of the number of joints across the total dataset. First, the total number of each joint in the dataset was calculated. Some joints and specimens were excluded due to low confidence or absence. For instance, for paired joints (e.g. elbow: humerus–radioulna) the potential maximum number of 280 joints in the dataset (n = 140 specimens) is rarely achieved. Articulation data for each joint were then expressed as a percentage of this total number of joints; for example, a joint articulation value of ‘87% (n = 119)’ indicates that 87% of all elbow joints in a dataset of 119 joints are articulated.

Standard statistical summary data and Pearson’s correlation coefficients were calculated using Microsoft Excel. Significance tests were performed with PAST v4.03 (Hammer *et al.* 2001). For further details of our statistical approach, please see Supporting Information.

Comparative taphonomy

Data on the skeletal taphonomy of anurans from Libros were extracted from McNamara *et al.* (2012*a*). Data for specimens from Lake Bechlejovice and Lake Messel were derived in part from published photographs and in part from study of hand specimens, and digital photographs of anurans in the collections of the National History Museum in Prague, Czech Republic (Bechlejovice) and Senckenberg Research Institute in Frankfurt am Main, Germany (Messel). Skeletal taphonomy data for specimens from Enspel were derived from published photographs only.

RESULTS

Size

SUL data are normally distributed and range from 16 to 79 mm (41 mm ± 16 mm; n = 28) (Falk *et al.* 2022, dataset 1). Differences in SUL between pelobatids (n = 15) and palaeobatrachids (n = 6) are not significant (two-sample t-test, unequal variance, p = 0.304).

Orientation

All specimens (n = 140) are orientated with the sagittal axis of the body parallel to the bedding. It was not possible to determine orientation more precisely for 19 specimens (14%; n = 140). Of the remaining 121 specimens, 23 (19%) are dorsal, 50 (41%) are ventral and 48 (40%), dorsoventral (Fig. S4; Falk *et al.* 2022, dataset 2).

Completeness

Completeness data are presented in two ways: (1) for specimens; (2) for skeletal elements.

Specimen completeness. Most specimens are incomplete, although there is substantial variation in the data (specimen completeness: 44 ± 28% (n = 140); Fig. 5A). Completeness increases when phalanges (64 ± 26% (n = 140); Fig. 5B) and entire hands and feet (75 ± 23% (n = 140); Fig. 5C) are omitted from the calculations. Differences in completeness values between these groups are significant (Kruskal–Wallis, p(same) = 3.92^{-14}).

Fourteen specimens are complete, but all specimens classified as such are truncated (one specimen in category T2, three specimens in T3 and 10 specimens in T4). Approximately one-third of specimens (34%, n = 126) lack at least one entire limb; this is not related to truncation. Furthermore, 12 specimens consist of parts of articulated hindlimbs only. Ten of these show truncated proximal limb elements (one specimen in T2¸ three specimens in T3, six specimens in T4). The remaining two

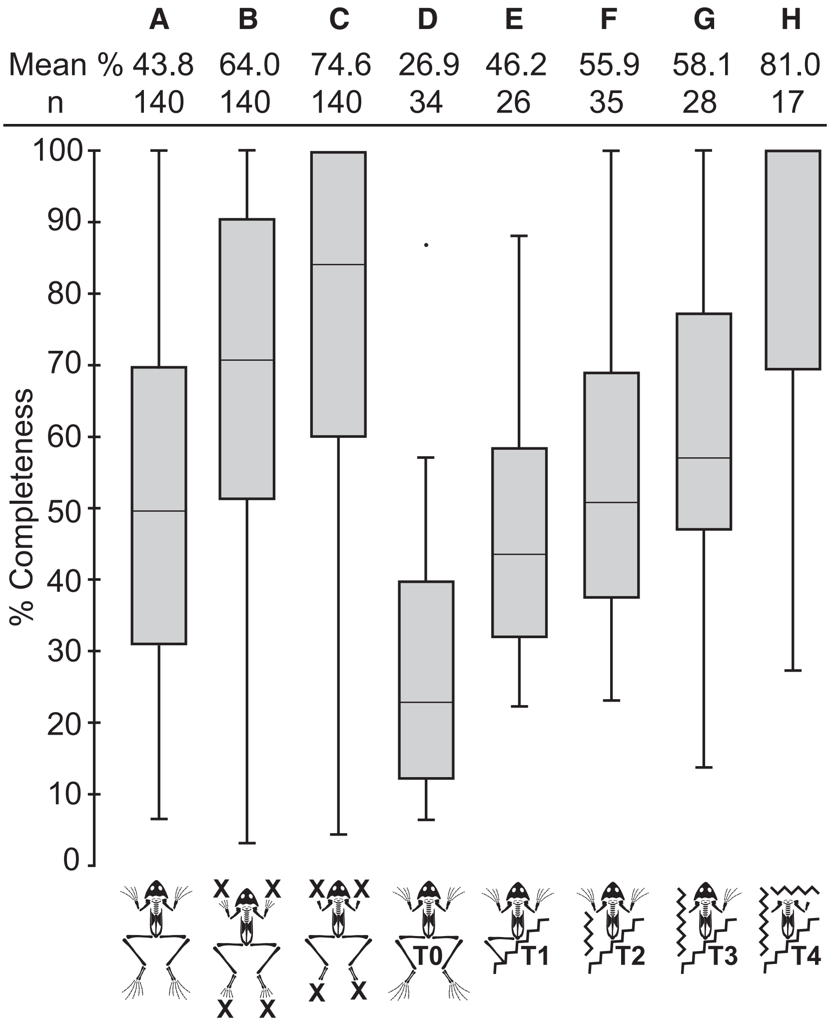

FIG. 5. Impact of truncation on the percentage completeness of individual specimens. A–C, specimen completeness for the entire dataset: A, no elements omitted from the dataset; B, phalanges omitted; C, entire hands and feet omitted. D–H, specimen completeness for truncation categories: D, T0 (no truncation); E, T1 (0.1–24.9% truncation); F, T2 (25–49.9% truncation); G, T3 (50–74.9% truncation); H, T4 (75–100% truncation). Horizontal lines in boxplots denote the median.

specimens are not truncated and consist, respectively, of: (1) the femur, tibiofibula and metatarsals articulated as a unit; and (2) the tibiale–fibulare, metatarsals and phalanges articulated as a unit (Fig. 3J).

Most specimens (76%; n = 140) are truncated by the edge of the slab or of the nitrocellulose glue/wax transfer (Fig. S5). Truncation of distal limb elements (i.e. forelimb phalanges and hindlimb phalanges) is common (65% (n = 105) and 94% (n = 106) of truncated specimens, respectively). Truncation of proximal limb elements (e.g. humerus and femur) is relatively rare (39 and 53% of truncated specimens, respectively; n = 106) (Falk *et al.* 2022, dataset 1). Similar numbers of specimens are assigned to each of the truncation categories T0–T3 (Fig. 5D–G; Fig. S5); few specimens are assigned to T4 (Fig. 5H). Specimen completeness increases progressively from T0 (27 ± 18%; n = 34) to T1 (46 ± 18%; n = 26), T2 (56 ± 21%; n = 35), T3 (58 ± 24%; n = 28) and T4 (81 ± 22%; n = 17; Fig. 5D–H). These differences in completeness values are significant (ANOVA d.f. = 4; F = 24.77; p(same) = 2.18×10^{-15}).

Differences between the specimen completeness values for palaeobatrachids (62 ± 6%; n = 15) and pelobatids (50 ± 3%; n = 54) are not significant (t-test (equal variance): t = 1.70, p(same mean) = 0.09). Furthermore, there is no significant difference in the completeness of specimens from the upper coal (Ce II, Ce III, Ce V; 44 ± 28%; n = 111) and middle coal units (Ce IV, Ce VI, Leo III, Leo V, IL, N_s XXXV; 46 ± 27%; n = 23; Mann–Whitney U-test: p(same median) = 0.64; see Supporting Information).

Skeletal element completeness. Most skeletal elements are present in most specimens, although there is wide variation in the data (mean element completeness: 77 ± 20%; Figs 6, 7A). The most complete skeletal elements are the cranium, femur and vertebrae (93–98% of specimens; n = 108, 122 and 112, respectively). Most specimens with

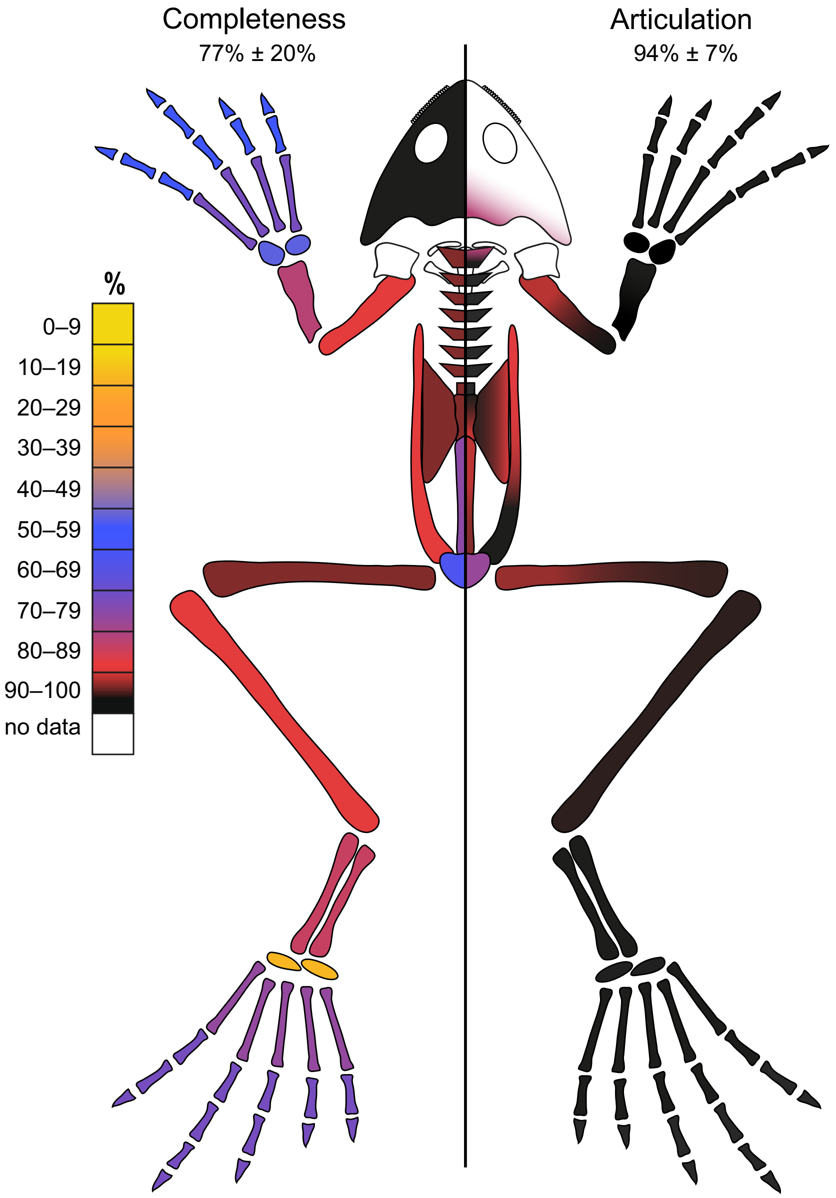

FIG. 6. Schematic frog skeleton summarizing the percentage completeness and articulation values for each type of skeletal element in the Geiseltal anurans (n = 140). A black and white version of this figure is provided in Figure S6.

vertebrae (63%; n = 102) have a (near-)complete vertebral column (i.e. 7–9 vertebrae). Skeletal elements of the abdomen and distal limbs show lower completeness values. Most specimens include at least one (88% of specimens; n = 118) or both (73%; n = 118) ilia and the urostyle (75% of specimens; n = 103). Just over half of specimens include the ischium (62% of specimens; n = 76; Figs 6, 7A), carpals (53% of specimens; n = 93) and forelimb phalanges (54% of specimens; n = 97). The tarsals are the least complete elements (17% of specimens; n = 58; Figs 6, 7A).

There is a general trend for completeness to decrease progressively towards the distal parts of the forelimbs (humerus: 87% complete (n = 117); radioulna: 81% (n = 110); carpals: 53% (n = 93); metacarpals: 70% (n = 96); forelimb phalanges: 54% (n = 97)). Hindlimbs show a similar trend (femur: 93% (n = 122); tibiofibula: 88% (n = 112); tibiale–fibulare: 84% (n = 99); tarsals: 17% (n = 58); metatarsals: 76% (n = 82); hindlimb phalanges: 70% (n = 77); Figs 6, 7A). Hindlimb elements are usually more complete than homologous forelimb elements (Figs 6, 7A).

Completeness values for skeletal elements are generally lower (mean 62 ± 24%) when completeness is assessed relative to the total number of elements (not specimens; Fig. 7B), given that many specimens contain only one element of a pair and few of a set. Trends in the data for skeletal elements, however, are similar to those described above for specimens (compare Fig. 7).

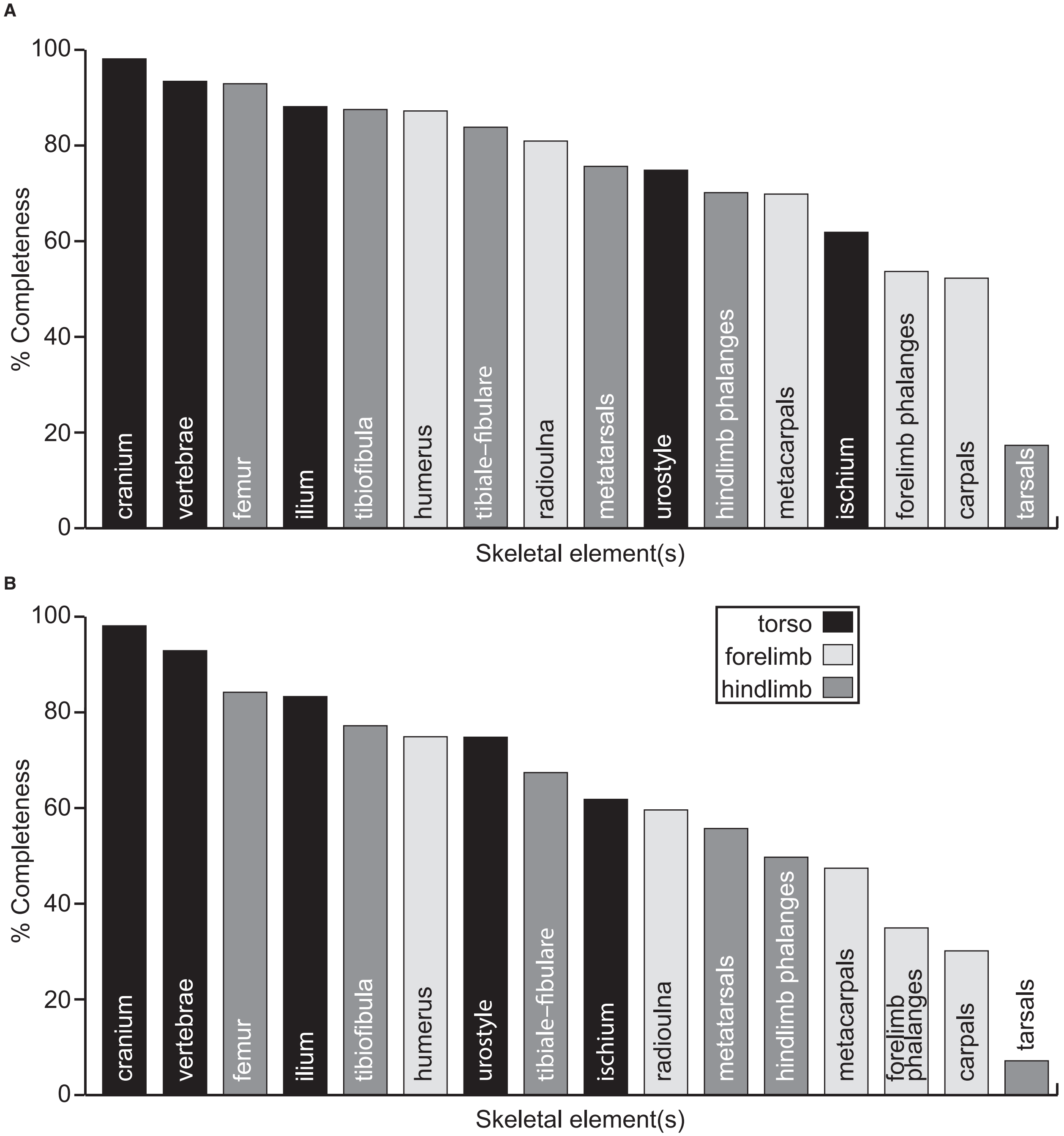

FIG. 7. Percentage completeness of skeletal elements. A, percentage of specimens in the dataset for which each skeletal element is complete (i.e. represented by at least one element); for example, the completeness value for the femur is 93%, indicating that 93% of specimens have at least one femur. B, percentage of skeletal elements present (i.e. complete) based on the total number of those elements in the dataset; for example, the completeness value for the femur is 84%, indicating that 84% of all femora are present.

Phalanges are absent from 75% of hands (n = 171), and when present they are usually represented by three or fewer bones (mean 2.4 phalanges per specimen; n = 69) (Fig. S7). When forelimb phalanges are present in both hands, specimens show a mean of 7.0 phalanges (n = 24). No specimen has the full complement of 10 forelimb phalanges in either hand. Similarly, phalanges are absent from 69% of feet (n = 106) (Fig. S7), and when present they are usually represented by 1–3 phalanges (mean 2.8 phalanges per specimen; n = 36). When hindlimb phalanges are present on both feet, specimens show a mean of 7.9 phalanges (n = 13). No

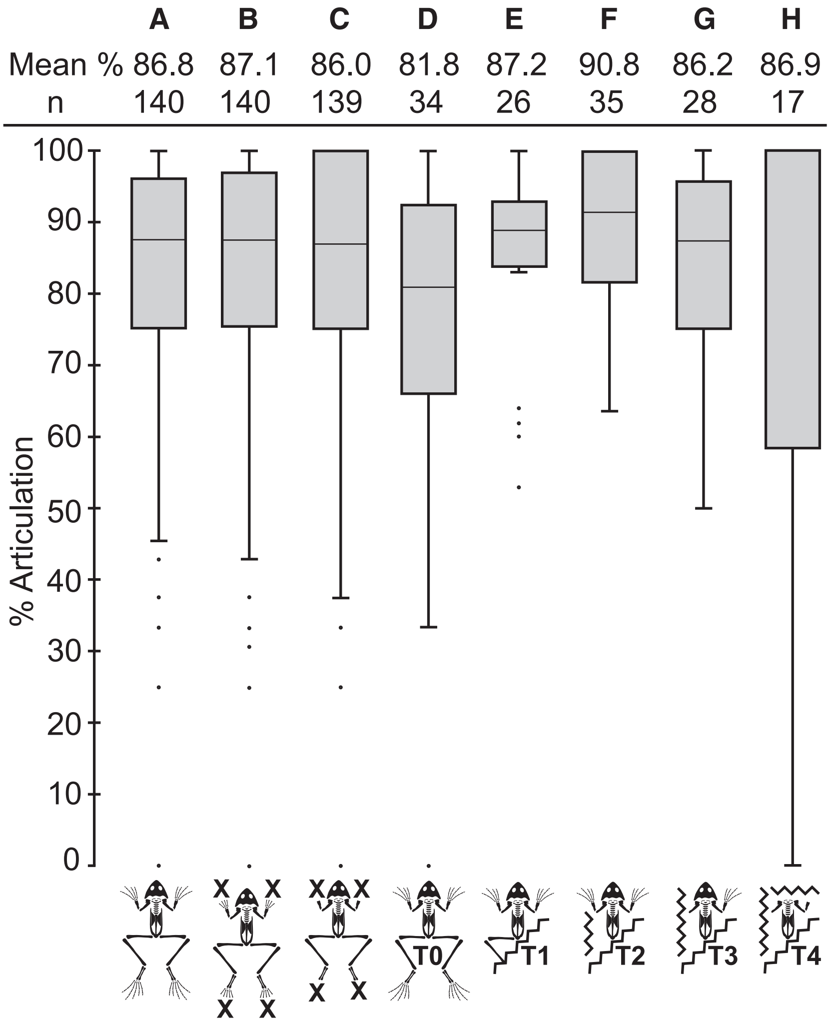

FIG. 8. Impact of truncation on the percentage articulation of individual specimens. A–C, specimen articulation for the entire dataset: A, no elements omitted from the dataset; B, phalanges omitted; C, entire hands and feet omitted. D–H, specimen articulation for truncation categories: D, T0 (no truncation); E, T1 (0.1–24.9% truncation); F, T2 (25–49.9% truncation); G, T3 (50–74.9% truncation); H, T4 (75–100% truncation). Horizontal lines in boxplots denote the median.

specimen has the full complement of 13–14 phalanges in a foot (Fig. S7).

Metacarpals are usually either absent (56% of hands; n = 187) or complete (32% of hands); few specimens retain some, but not all, metacarpals. The mean number of metacarpals per specimen is 2.9 in the total dataset (n = 78) and 4.6 (n = 49) when specimens lacking metacarpals are excluded. Similarly, metatarsals are usually either absent (47% of feet; n = 142) or complete (41% of feet); few specimens retain some, but not all, metatarsals (Fig. S7). The mean number of metatarsals per specimen is 4.2 in the total dataset (n = 49) and 7.1 (n = 29) when specimens lacking metatarsals are excluded.

The tibiale–fibulare unit is present in 84% (n = 99) of specimens and is complete in 64% (n = 181) of all hindlimbs (Fig. 7; Fig. S7). The mean number of tibiale–fibulare bones per specimen is 2.6 in the total dataset (n = 72) and 3.3 (n = 56) when specimens lacking these elements are excluded.

In the total dataset, completeness values are positively correlated between the left and right sides of the body (Pearson's $r(10) = 0.99$, $p < 0.001$) and between homologous skeletal elements in the fore and hind limbs (Pearson's $r(3) = 0.89$, $p < 0.04$) (Fig. 6; Fig. S8). Differences in completeness values between individual skeletal elements of palaeobatrachids and pelobatids are not significant (Mann–Whitney U-test: p(same median) = 0.097) (see Supporting Information).

Articulation

Articulation data are presented in two ways: (1) for individual specimens; (2) for individual skeletal elements.

Specimen articulation. Most specimens are well articulated (specimen articulation 87 ± 19%; n = 140; Figs 8A, 9). Unlike completeness, articulation values do not vary

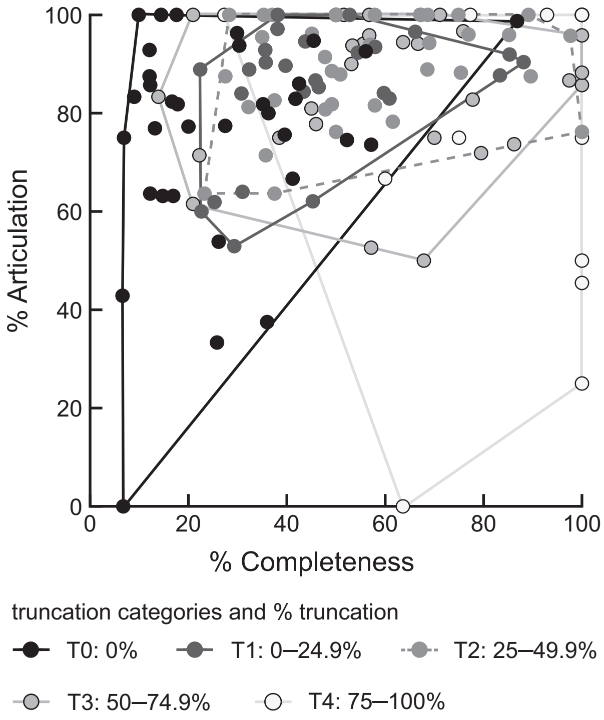

FIG. 9. Percentage articulation versus percentage completeness for each specimen (n = 140).

significantly (Kruskal–Wallis; p(same) = 0.89) when phalanges (87 ± 21%; n = 140; Fig. 8B) and the entire pes and manus (86 ± 22%; n = 139; Fig. 8C) are omitted from the calculations.

Few specimens are fully articulated (21%, n = 140); most specimens classified as such are truncated (90%; n = 30) (Figs 8D–H, 9). Specimen articulation differs between the truncation categories: T0 (82 ± 22%; n = 34), T1 (87 ± 13%; n = 26), T2 (91 ± 11%; n = 35), T3 (87 ± 14%; n = 28) and T4 (87 ± 32%; n = 17) (Fig. 8D–H). These differences are significant (Kruskal–Wallis; p(same) = 0.034). Only five specimens have articulation values <40%; two of these are fully disarticulated (Figs 8, 9).

Differences between specimen articulation of palaeobatrachids (92 ± 9%; n = 15) and pelobatids (84 ± 18%; n = 54) are not significant (Mann–Whitney U-test: p (same median) = 0.053).

Joint articulation. Overall, most joints present are well articulated (94 ± 7% of specimens; Figs 6, 10A). When present, the joints of the fore and hind limbs are articulated in >90% of specimens (Figs 6, 10A). Articulation values for distal limb joints are usually higher than for proximal limb joints (Fig. 6). Values are slightly lower (76–90% of specimens) for many joints in the pelvic region (Figs 6, 10A). The vertebrae are usually well articulated (96% of specimens; n = 98; Figs 6, 10A).

Articulation values for skeletal elements are only slightly lower (mean articulation for the total dataset: 86 ± 8%) when articulation is assessed relative to the total number of joints (not specimens) present in the dataset (Fig. 10B). Most specimens, therefore, have articulation of both elements of a pair, or all elements of a set. When assessed in this way, articulation values for joints in the hip region, shoulder and limbs are usually only 10–20% lower than when assessed per specimen (Fig. 10B). Unlike completeness, articulation values are high for the phalanges. Forelimb phalanges are articulated in all specimens (n = 31) and in 79% (n = 47) of hands. Hindlimb phalanges are articulated in all specimens (n = 34) and in 86% (n = 43) of feet (Fig. 10).

Even when carpals and tarsals are absent, the adjacent bones are *in situ* (and thus considered articulated) in most hands (85%; n = 33) and feet (93%; n = 69; Fig. 10B).

For elements occurring as a set, the number of articulated elements present was considered. The vertebrae are usually well articulated: 56% of specimens show (near-) full articulation (7–8 joints articulated, n = 96). Less articulated states are relatively rare (Fig. S9). In contrast, most phalanges are poorly articulated: 76% of hands have two, or fewer, articulated phalangeal joints (n = 37; Fig. S9). Similarly, 72% of feet have two, or fewer, articulated phalangeal joints (n = 25; Fig. S9). Furthermore, for joints between the phalanges and metacarpals, and phalanges and metatarsals, usually only 1–2 bones are articulated (41% of hands (n = 51) and 37% of feet (n = 54), respectively; Fig. S9). The metacarpal–carpal joints are fully articulated in 51% (n = 55) of hands (i.e. four joints articulated) and metatarsals–tarsals, in 75% (n = 12) of feet (i.e. five joints articulated); poorly articulated states are less common (Fig. S9).

Using the dataset for all joints, articulation values are positively correlated for the left and right sides of the body (Pearson's r(16) = 0.897, p < 0.001) and for homologous joints of the fore and hind limbs (Pearson's r(5) = 0.773, p = 0.042; Fig. 6; Fig. S8). Differences in articulation values between individual skeletal elements of palaeobatrachids and pelobatids are significant (Mann–Whitney U-test: p(same) = 0.007; see Supporting Information).

Relationship between completeness, articulation and truncation

Plotting articulation versus completeness shows that specimens have consistently high articulation values, albeit with a wider range in completeness values (Fig. 9). Six specimens do not fit this pattern (with values 0–42.9%; Figs 8A, 9). Four of these specimens belong to truncation category T0 (no truncation; Fig. 9) and two belong to truncation category T4 (highly truncated). The data fields for

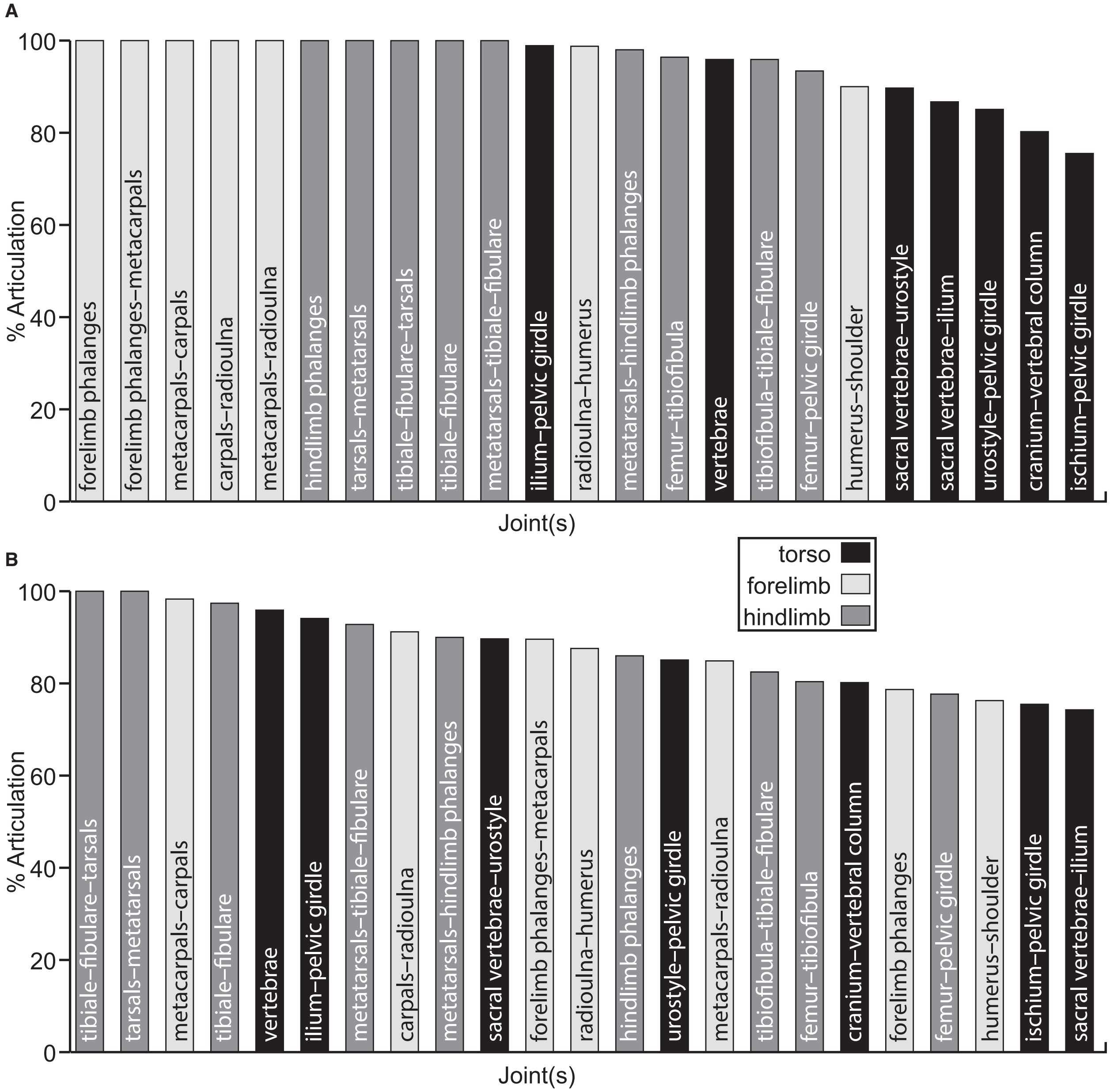

FIG. 10. Percentage articulation of joints. A, percentage of specimens in the dataset for which each joint is articulated (i.e. represented by at least one articulated element); for example, the articulation value for the femur–tibiofibula (knee joint) is 96%, indicating that at least one knee joint is articulated in 96% of specimens. B, percentage of articulated joints, based on the total number of those joints in the dataset; for example, the value for the femur–tibiofibula joint is 80%, indicating that 80% of all knee joints in the dataset are articulated.

specimens belonging to truncation categories T1, T2 and T3 overlap almost completely, reflecting a similar range of values for completeness and articulation in each category (Fig. 9). Closer inspection of the articulation data does not show an obvious link with truncation. Thirty-five specimens plot below 75.2% articulation (outliers included), which is the lower quartile of the data (Q_1; Fig. 8A). Almost half of these specimens (n = 17) have little or no truncation (i.e. belong to T1 (n = 5) or T0 (n = 12)). Thirty-four specimens plot above the upper quartile (Q_3; Fig. 8A) and are thus >96.3% articulated; almost half of these specimens (n = 16) are strongly affected by truncation (i.e. belong to T3 (n = 6) and T4 (n = 10)).

In contrast to articulation, the relative proportions of specimens in different truncation categories differ strongly for completeness. For instance, 35 specimens plot in the lower quartile for completeness (Q_1; <30.8% complete; Fig. 5A). Most of these specimens belong to T0 (n = 22; Fig. 5D). In contrast, many specimens in the upper quartile (Q_3; >69.7% complete; n = 35; Fig. 5A), belong to T4 (n = 13; Fig. 5H).

Distal limb bones (e.g. phalanges, carpals) are usually absent but, when present, are usually articulated (Fig. 6). In contrast, proximal limb elements (e.g. humerus, femur) are often complete but, when present, are less well articulated (with the torso, i.e. shoulder and hip joint, respectively). Vertebrae are nearly always present and usually form articulated units of two or more vertebrae (Figs 6, 10; Fig. S9). Bones adjacent to the vertebral column (e.g. urostyle, ilia), however, are less complete and joints where the vertebrae articulate with other elements (i.e. atlas vertebra–cranium, sacral vertebrae–urostyle, sacral vertebrae–ilium) are less articulated (Fig. 6). The ilium is usually present and articulated with the hip, but the urostyle and the ischium have lower values for both articulation and completeness (Fig. 6).

There is no significant difference in the completeness and articulation of specimens grouped in the following ways: (1) preserved at different sites (completeness: Kruskal–Wallis p(same) = 0.84; articulation: Kruskal–Wallis p(same) = 0.15; sinkholes, n = 25; dying field 1, n = 18; dying field 2, n = 92; Fig. S10); (2) embedded in different materials (completeness: Kruskal–Wallis p(same) = 0.90; articulation: Kruskal–Wallis p(same) = 0.58; nitrocellulose glue, n = 104; nitrocellulose glue on gypsum, n = 6; paraffin wax, n = 29); (3) determined (n = 69) and undetermined (n = 71) (Mann–Whitney U-test, completeness: p(same median) = 0.47; articulation: p(same median) = 0.13); and (4) percentage truncation for different embedding materials (Kruskal–Wallis p(same) = 0.28; Supporting Information).

DISCUSSION

The data show that the Geiseltal anurans vary markedly in their skeletal taphonomy. Some or all taphonomic features identified may relate, at least in part, to collector bias, study design, missing specimens and/or taxonomy. These potential biases are discussed at length in the Supporting Information. Alternatively, at least some of the data presented here could reflect taphonomic factors linked to the mode of death and biostratinomy of the fossils. These taphonomic factors are the focus of the discussion here, which is organized according to the key hypotheses that underpin this study.

> **Hypothesis 1:** The fidelity of preservation is consistent for all skeletal elements, especially between homologous skeletal elements of the fore and hind limbs and between the left and right sides of the body.

According to the present data this hypothesis is false: preservation varies among skeletal elements and is strongly linked to bone size and anatomical location.

The completeness values for individual specimens vary markedly depending on whether all or a subset of skeletal elements (i.e. omitting phalanges or entire hands and feet) are used in the analysis (Fig. 5A–C). Although the range of completeness values is similar for all three scenarios, mean values vary from 43.8% (no omissions) to 74.6% (omitting hands and feet; Fig. 5A–C). This variation reflects much lower completeness values for peripheral, rather than proximal, skeletal elements; omitting the former elements clearly biases the data towards higher values (Fig. 7). Indeed, there is a strong proximal to distal trend in completeness, whereby both the fore and hind limbs show progressively lower completeness values from proximal to distal bones (Fig. 6). Similar patterns have been reported from fossil vertebrates in marine (Beardmore *et al.* 2012) and lacustrine (McNamara *et al.* 2012*a*, *b*) settings.

Distal limb bones (e.g. phalanges) are usually absent; somewhat unexpectedly, distal bones that are present are better articulated than proximal elements (e.g. humerus); in other words, they are usually in life position (Figs 6, 10). This reflects loss of distal, small elements soon after disarticulation, probably by weak bottom currents (Dodson 1973; McNamara *et al.* 2012*a*), resulting in a scenario in which distal elements are either complete and articulated, or absent. In contrast, proximal bones such as the humerus are larger and are surrounded by more tissue, promoting their association with the carcass (and thus higher completeness values) even when they are disarticulated.

The low completeness values for carpals and tarsals (Figs 6, 7) may reflect difficulties in identification due to their small size (*c.* 1–4 mm) and one, or a combination, of associated factors. These include poor preservation, potential loss during preparation (Fig. S1), fusion *in vivo* to adjacent elements, reduction (Špinar 1972; Fabrezi 1993; Fabrezi & Alberch 1996) and/or incomplete ossification in juveniles (Špinar 1972; Fabrezi & Alberch 1996; Henrici & Haynes 2006; Roček *et al.* 2014). Preferred disarticulation and loss of carpals and tarsals during decay is less likely because the adjacent elements do not show similarly low completeness values or disarticulation (Fig. 10).

Similar completeness and articulation values for paired skeletal elements from opposite sides of the body indicate consistent broad taphonomic controls across the body. Except for carpals and tarsals, the completeness values for forelimb bones are usually lower than for the homologous elements of the hindlimbs (Fig. 6). This feature has been discussed previously (Dodson 1973; McNamara *et al.* 2012*a*) and probably reflects the smaller size of most forelimb elements relative to hindlimb elements, facilitating removal of the former bones by weak bottom currents.

There is no link between either completeness or articulation and specimen orientation; the dorsal, ventral or dorsoventral aspect of specimens reflects the most hydrodynamically stable orientation for anurans (McNamara *et al.* 2012*a*) and is independent of other skeletal taphonomy metrics.

Analysis of the data for specimen articulation, completeness and truncation reveals interesting results. Specimen articulation is independent of truncation (Fig. 8). This probably reflects the fact that articulation values do not show a single strong trend linked to anatomical location of bones in the body, but rather reflect several factors. In contrast, specimen completeness is strongly linked to truncation (Fig. 5), whereby less truncated specimens usually have lower percentage completeness values. This usually reflects the real absence of several, or many, phalanges. In such specimens, the apparent completeness is a close approximation of true completeness. In contrast, highly truncated specimens usually have higher completeness values. This is because many bones, typically numerous phalanges, are truncated and thus omitted from the completeness calculation (see Material and Method, Supporting Information). This highlights the critical importance of assessing truncation in studies of the skeletal taphonomy of fossil vertebrates.

Hypothesis 2: The fidelity of preservation is linked to excavation site and taxonomy.

According to the data this hypothesis is false: preservation is independent of local variations in fossil locality and anuran group.

Similar completeness and articulation values for specimens from different types of fossil locality (e.g. sinkholes and dying fields) suggest similar taphonomic processes in operation across the Geiseltal basin. Similarly, completeness and articulation are broadly consistent among specimens from different stratigraphic levels at a single locality. The general suite of taphonomic processes and thus the controls on preservation are consistent through space and time and are not subject to short-term or spatially localized variations.

Similar completeness and articulation values for the Geiseltal pelobatids and palaeobatrachids (Supporting Information) suggest that differences in the absolute abundance of the two groups are not taphonomic in origin. The relatively paucity of palaeobatrachids is therefore likely to reflect a real biological signal, whereby they were simply less abundant members of the lake fauna. Pelobatids were numerically dominant (possibly due to behavioural factors, see the Hypothesis 4 discussion below). The articulation values of individual skeletal elements in pelobatids and palaeobatrachids, however, differ significantly. Palaeobatrachids usually have higher articulation values for abdominal bones than pelobatids (Supporting Information). The reasons for this difference are not clear but may relate to the relatively stable construction of the vertebral column and sacral body region due to the fusion of vertebrae (forming a synsacrum) in palaeobatrachids. In addition, and/or alternatively, the differences in abdominal articulation may reflect differences in the activity of gut-derived decay bacteria linked to original gut flora and ultimately diet. There is no significant difference in preservation between specimens that were determined taxonomically and those that were not. The data suggest that the embedding material has no major impact on truncation, completeness and articulation values (Supporting Information).

Hypothesis 3: Specimens represent a series of repeating taphonomic states.

The data confirm this hypothesis: the Geiseltal anurans represent a series of nine repeating taphonomic states (Fig. 11). These states were identified based on distinct qualitative patterns in disarticulation and loss of skeletal elements.

States 1–3 form a sequence that represents the progressive disarticulation and loss of elements from distal to proximal body regions with potential transitions to states 4, 5 and/or 6. Completeness and articulation values of states 1–6 overlap (Fig. S11) but differences are statistically significant (Supporting Information). States 7, 8 and 9 may be superimposed on any of the other taphonomic states (Fig. 11).

State 1. This state comprises 18% of specimens (n = 34). Specimens are generally well-articulated and complete except for peripheral and distal limb elements, which are disarticulated and/or lost (Fig. 3B, C). This taphonomic pattern indicates preferred loss of smaller and lighter elements at the body margins and is likely to reflect one, or a combination, of the following factors:

1. Transport dynamics. Small and/or light bones are easier to transport than large and/or heavy bones (Dodson 1973).
2. Bottom currents. Peripheral elements are not protected by the body mass and are thus more susceptible to current-induced displacement while the carcass is residing on the floor of the water body prior to deposition of the next sedimentary layer.
3. Less soft tissue. Peripheral elements are associated with a low mass of soft tissues: muscles and connective tissue that promote the retention of articulation. Specimens belonging to state 1 reflect burial prior to substantial decay of soft tissues.

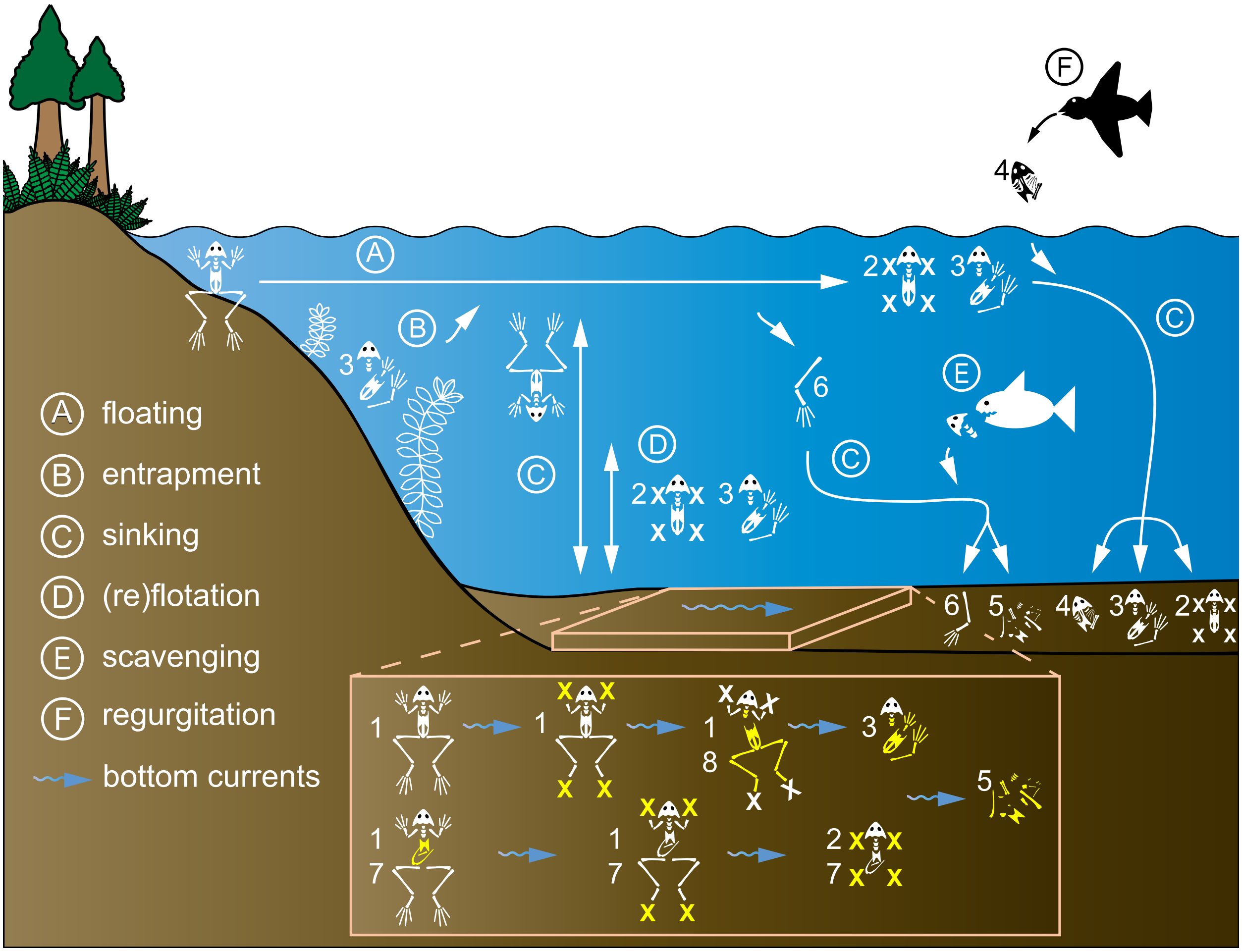

FIG. 11. Distinct qualitative patterns in disarticulation and loss of skeletal elements in Geiseltal specimens reveal the controls on preservation and taphonomic pathways (A–F) in sinkhole and dying field deposits. See text for detailed characterization of taphonomic states (1–9). States 1–3 form a genetically related sequence that represents the progressive disarticulation and loss of elements from distal to proximal body regions with potential transitions to states 4, 5 and/or 6. States 7, 8 and 9 may be superimposed on any of the other taphonomic states.

The relative timing of decay and deposition of vertebrate carcasses in aquatic environments is controlled, in large part, by ambient temperature (Wuttke 1983; Kidwell & Baumiller 1990; Carter & Tibbett 2006; Carter *et al.* 2008), which regulates microbial metabolism and abiotic reactions. Mean annual temperatures >20°C (Mosbrugger *et al.* 2005) during the middle Eocene are likely to have been associated with lake surface temperatures >16°C (Elder & Smith 1988). These in turn would have promoted rapid decay of organic material and high rates of decay gas production, probably followed (in many cases) by (re)floating of carcasses after initial sinking (Wuttke 1983; Elder & Smith 1984; Elder & Smith 1988).

For state 1, although a brief period of (re)floating cannot be excluded, prolonged (re)floating is not plausible because it would generate widely dispersed skeletal elements and specimens missing part, or all, of limbs. State 1 specimens probably represent death and deposition during periods when (re)flotation is inhibited by high water pressures (i.e. deposition in deep waters) or low temperatures (suppressing generation of decay gases), for example, during a relatively cool and/or wet climatic regime. The proximate control is the exposure to bottom currents because these lead to disarticulation and loss of elements. Specimens were probably exposed for an extended period on the lake floor prior to burial by sediment. This is supported by the fine lamination of the host sediments (up to 4 laminae/mm in dying field 1; Raupach 1948), which is consistent with low sedimentation rates (Raupach 1948). Some laminae may reflect intermittent fine-grained debris flows and turbidites (Smith 1986) following collapse of riverbanks or sinkhole slopes

(Krumbiegel *et al.* 1983). It is not possible, however, to test this hypothesis by examination of petrographic sections because almost all specimens are on transfers. Specimens in dying fields 1 and 2 typically exhibit preferred orientations (Weigelt 1933), probably generated during transport and/or by bottom currents.

State 2. This state comprises 29% of specimens (n = 34). These specimens lack at least one entire limb but are otherwise well articulated (Fig. 3G). This state reflects more extensive decay of specimens than state 1 and probably some (re)flotation at the lake surface (or within the water column) prior to deposition. Such specimens are likely to represent deposition in relatively shallow and/or warm waters, where low water pressure was insufficient to prevent refloating and/or where warm temperatures enhanced the production of decay gas. Death and deposition therefore occurred during relatively warm and/or arid climatic regimes compared with those prevailing during deposition of state 1 specimens.

State 3. This state comprises 29% of specimens (n = 34). These specimens are largely incomplete and partially disarticulated (Fig. 3E). These represent prolonged (re)floating of the carcass due to production of abundant decay gases and/or low water pressure (see above). This in turn reflects warmer and/or shallower waters than for state 2. Alternatively, state 3 specimens may represent a longer period of decay prior to transport, potentially due to entrapment of carcasses in littoral vegetation. Patterns of skeletal element loss are consistent with vertical settling from floating carcasses, with no evidence for directional scattering.

State 4. This state comprises 9% of specimens (n = 34), which are clusters of densely packed bones including partly articulated elements (Fig. 3D). These may represent regurgitated digestive material/gastric pellets.

State 5. This state comprises 9% of specimens (n = 34), which are widely disarticulated and reorientated skeletal elements (Fig. 3I). These represent either prolonged (re) floating favoured by warmer and/or shallower waters than in taphonomic states 2 and 3, or an extended period of pre-transport decay.

State 6. A total of 6% of specimens (n = 34), consisting of isolated articulated limbs (Fig. 3J), are categorized in this state. These presumably are the missing skeletal elements of state 2 and state 3 specimens and comprise mostly articulated body units spatially separated from the (missing) remaining skeleton. Isolated limbs originate during decay of soft tissue at the shoulder joint and/or the hip joint. Weak bottom currents may disarticulate smaller limb elements (i.e. phalanges) after final deposition.

State 7. This state consists of 21% of specimens (n = 34). Specimens frequently show disarticulation and/or loss of bones in the abdominal region (Fig. 3C), often despite the rest of the body being relatively well articulated and complete. This could reflect one, or both, of the following processes:

1. Abdominal collapse. Decay-induced collapse of the prismatic configuration of the urostyle, ilia and sacral vertebra inside the abdominal skin sac (McNamara *et al.* 2012*a*). This is unlikely to be sufficiently violent to rupture the skin; in such cases (i.e. when the skin remains intact) no abdominal bones should be lost.
2. Abdominal rupture (Fig. 3C). Violent eruption of decay gases from the abdomen (Wuttke 1983; McNamara *et al.* 2012*a*; Smith & Wuttke 2012). This probably reflects warm water temperatures (promoting production of decay gases); other factors include differences in diet among specimens (and thus variation in the composition of intestinal flora potentially affecting the decay rate). When abdominal rupture is accompanied by tearing of the skin, this may promote further disarticulation and loss of bones.

State 8. A total of 18% of specimens (n = 34). Reorientation of the lower body (Fig. 3C). The bones of the pelvic girdle (e.g. ischium, ilia) and usually hindlimbs are reorientated relative to the sagittal axis as defined by the head and vertebrae, typically with a single major disarticulation between the pelvic girdle and vertebrae. This represents disturbance of the carcass by either stronger bottom currents than those referred to in state 1 and/or disturbance of carcasses by weak currents at relatively advanced stages of decay prior to burial.

State 9. Articulated body units. Certain skeletal elements (e.g. tibiale–fibulare, metatarsals, metacarpals and vertebrae) are usually either complete and articulated as a unit, or all elements in the group are absent (Fig. S7). This may reflect fusion of bones, as in the vertebrae of palaeobatrachids (Wuttke *et al.* 2012) and the tibiale–fibulare of anurans (Fabrezi 1993; Fabrezi *et al.* 2017) (although this may not be a feature of pelobatids (Roček *et al.* 2014) and palaeobatrachids (Wuttke *et al.* 2012)). Articulated units may also reflect differences in the resistance of soft tissues to decay within and external to the unit (Wuttke 1983).

Hypothesis 4: The cause of death is desiccation or lake overturn.

The data show that this hypothesis is false. Previous studies have suggested that the Geiseltal anurans died during the desiccation of lakes and/or oxygen depletion of the water column during overturn of lake waters (Voigt 1934; Weigelt 1934). This, however, is unlikely because the anurans could presumably migrate to other water bodies during adverse conditions (Henrici & Fiorillo 1993; Todd *et al.* 2009). Furthermore, the evidence for (re)flotation of carcasses is not consistent with desiccation.

Alternative modes of death for the Geiseltal anurans therefore must be considered. These include:

1. Elevated salinity, as indicated by halophile ferns (Barthel & Rüffle 1970) and ostracods (Krumbiegel 1962*a*). As with the desiccation hypothesis, however, elevated salinity is unlikely to have killed many anurans because the animals could have migrated during adverse conditions; furthermore, some modern pelobatids tolerate brackish water (Stănescu *et al.* 2013).
2. Starvation. This is not plausible because anurans typically migrate if food is scarce (Buchacher 1993; Todd *et al.* 2009). Furthermore, certain Geiseltal anurans are associated with potential coprolites (e.g. Fig. 3C), suggesting death after a recent meal. Starvation during hibernation does not apply because the palaeoclimate was unlikely to have been sufficiently cold to promote enduring hibernation (Grein *et al.* 2011; Krutzsch 2011).
3. Poisoning by algal blooms. Diatomite beds in some sinkhole deposits and records of abundant dinoflagellates (Krumbiegel *et al.* 1983) are direct evidence for algal blooms, which can be toxic to aquatic fauna (Carty & Parrow 2015; López-Cortés *et al.* 2015; Watson *et al.* 2015). The relative stratigraphic positions of the diatomite beds and the fossiliferous strata, however, are unclear. Furthermore, extant pelobatids are terrestrial (Lizana *et al.* 1994) and therefore are unlikely to be affected by algal blooms (Henrici & Fiorillo 1993).
4. Storm or flood events. Some specimens may have died due to high water turbulence during floods (Duellman & Trueb 1994; La Marca 2021); this may apply especially where specimens show a preferred orientation (Weigelt 1933), although the latter feature may originate postmortem (Henrici & Fiorillo 1993).
5. Freezing. The Eocene greenhouse climate may have included rare weather events including temperatures below 0°C (Grein *et al.* 2011; Hu *et al.* 2018), which can be harmful to anurans. The Geiseltal water bodies, however, were probably sufficiently deep to remain ice free at depth. This would have provided shelter (Manion & Cory 1952; Voituron *et al.* 2009), which is important for tropical, mainly aquatic taxa with low cold tolerance (Brattstrom 1968; Costanzo *et al.* 2013) such as the Geiseltal palaeobatrachids. Terrestrial taxa, such as pelobatids, are unlikely to shelter in water bodies (Swanson & Graves 1995; Costanzo & Lee 2013), except during mating season (Lizana *et al.* 1994).
6. Disease. Mass mortalities in extant anurans can result from disease, including chytridiomycosis (Lips 1999; Scheele *et al.* 2019) and Ranavirus (Price *et al.* 2017). Mass mortalities such as the dying fields at Geiseltal could therefore potentially reflect disease, but verification of this hypothesis is difficult because many diseases lack a physical expression that can be readily fossilized (Densmore & Green 2007).
7. Predation or scavenging. A single fish specimen from Geiseltal contains anuran remains in the abdomen, presumably representing gut contents (Voigt 1934, table 3, fig. 1 no. A299). This, plus a limited number of specimens comprising accumulations of densely packed bones (Fig. 3D) or anterior–posterior body halves (Fig. 3E), represent limited evidence for predation or scavenging.
8. Old age. The SUL data are normally distributed, confirming that the specimens represent a wide range of sizes and presumably ages (although there is no direct linear relationship between SUL and age; Liao *et al.* 2011). Death by old age therefore cannot be excluded as a cause of death of at least some specimens.
9. Mating behaviour. Mating-related mass mortality caused by drowning or exhaustion is common in extant anurans (Verrell & McCabe 1986; Trauth *et al.* 2000; Menin *et al.* 2006; Izzo *et al.* 2012) and has been invoked as the primary cause of death for some fossil anurans (McNamara *et al.* 2012*a*). Mating-related mortalities are plausible even for terrestrial anurans (e.g. pelobatids) given that these return to the water to reproduce (Lizana *et al.* 1994).

Collectively, these data suggest that many Geiseltal anurans represent mating-related deaths, at least some of which may have occurred in mass mortalities. Evidence for recurring mass mortality events includes reports of tens to hundreds of specimens on individual bedding planes at many excavation sites (Haubold & Krumbiegel 1984; Hellmund & Hastings 2014). Furthermore, the SUL data presented here (Falk *et al.* 2022, dataset 1) are consistent with a wide range of body sizes and presumably ages. The most plausible taphonomic scenario therefore involves a biological cause of death linked to anuran behaviour (homing instinct to return to the lake to breed) and subsequent accumulation of carcasses via normal sedimentological processes (sinking, transport and deposition of carcasses in profundal lake regions). We cannot, however, exclude the possibility that some specimens (especially those preserved as isolated individuals) died due to freezing, disease or old age, but these three causes of death are difficult to verify.

TABLE 1. Percentage of specimens from Libros and Geiseltal for which each skeletal element is complete or joint is articulated.

Skeletal element(s)	Completeness Libros (%)	Completeness Geiseltal (%)	Joint(s)	Articulation Libros (%)	Articulation Geiseltal (%)
Cranium	100	98.1	Cranium	100	n/a
Forelimb phalanges	25.0	53.6	Cranium-vertebrae	n/a	80.2
Metacarpals	n/a	69.8	Forelimb phalanges	21.0	100
Carpals	78.0	52.7	Forelimb phalanges–metacarpals	n/a	100
Radioulna	95.6	80.9	Metacarpals–phalanges	n/a	100
Humerus	100	87.2	Phalanges–carpals	78.0	n/a
Vertebrae	98.1	92.9	Carpals–radioulna	89.1	100
Urostyle	100	74.8	Radioulna–humerus (elbow)	75.0	98.8
Ilium	100	88.1	Humerus–shoulder	95.3	90.0
Ischium	n/a	61.8	Vertebrae	84.4	95.9
Femur	100	93.4	Urostyle–sacral vertebra	71.9	89.7
Tibiofibula	100	87.5	Ilium–sacral vertebra	89.1	86.7
Tibiale–fibulare	100	83.8	Urostyle–pelvic girdle	75	85.1
Metatarsals	n/a	17.2	Pelvic girdle–femur (hip)	82.8	93.4
Tarsals	81.0	75.6	Femur–tibiofibula	84.4	96.4
Hindlimb phalanges	28.0	70.1	Tibiale–fibulare	64.1	95.9
			Tibiale–fibulare–tarsals	66.8	100
			Tarsals–metatarsals	n/a	100
			Metatarsals–phalanges	n/a	98.0
			Hindlimb phalanges	27.5	100

Data from McNamara *et al.* (2012*a*).

Hypothesis 5: Comparative taphonomic analysis of anurans from various Cenozoic biotas can identify broad taphonomic trends in anuran preservation.

The data confirm this hypothesis: anurans preserved in the different biotas studied share common, repeated, taphonomic patterns. Irrespective of biota-specific taphonomic features (detailed below), this allows identification of the primary controls on the skeletal taphonomy of anurans from Cenozoic lacustrine-hosted Konservat-Lagerstätten.

Fossil anurans have been reported from several key Cenozoic Konservat-Lagerstätten, including Messel (middle Eocene, Germany; Wuttke 1983, 2018), Enspel (late Oligocene, Germany; Roček & Wuttke 2010), Bechlejovice (early Oligocene, Czech Republic; Špinar 1972; Roček 2013) and Libros (Late Miocene, Spain; McNamara *et al.* 2009, 2012*a*). This provides an opportunity to conduct a comparative analysis of the taphonomy of anurans from different biotas to better understand the overarching controls upon preservation. Systematic data on skeletal taphonomy are available only for specimens from Libros, which are therefore the focus of this analysis.

Libros versus Geiseltal

The Libros frogs analysed by McNamara *et al.* (2012*a*) are monospecific (*Pelophylax pueyoi*) and hosted within deep-water laminated mudstones deposited in a perennial palaeolake (McNamara *et al.* 2012*a*). The Libros anurans have higher completeness values for most skeletal elements (McNamara *et al.* 2012*a*; Table 1) than those from Geiseltal. This could be a real taphonomic signal or an artefact of collection bias. If real, the higher completeness of the Libros frogs could reflect: (1) shorter residence time at the water surface due to cooler water temperatures (climate was cool during the Late Miocene relative to the middle Eocene), enhancing sinking and mitigating against substantial decay and disarticulation prior to deposition; (2) the deep nature and high alkalinity of the Libros lake (at least several tens of metres deep; Ortí *et al.* 2003), thus preventing refloating; (3) the large area of the Libros lake and the deposition of the carcasses in central zones where bottom currents would have been weak and rare (McNamara *et al.* 2012*a*); and (4) the absence of fish and other scavengers.

It is possible that the differences in completeness between the anuran assemblages could reflect, at least in part, differences in the analytical approach in this study and in McNamara *et al.* (2012*a*). For the Libros study, specimens consisting of isolated anuran bones were omitted, but such specimens are included in the Geiseltal analysis. In addition, truncated specimens comprise a minority (35%) of the Libros dataset, but most (76%) of the Geiseltal dataset. Furthermore, specimens with moderate truncation (at least two truncated feet) were omitted from the Libros study but included herein.

TABLE 2. Comparative taphonomy of the anurans from Geiseltal, Messel (Eocene, Germany), Enspel (Oligocene, Germany), Bechlejovice (Oligocene, Czech Republic) and Libros (Miocene, Spain).

	Geiseltal lacustrine system	Lake Messel	Lake Bechlejovice	Lake Enspel	Lake Libros
Age/location	Eocene, *c.* 45 Ma, Germany	Eocene, *c.* 47 Ma, Germany	Oligocene, 26.8–25.5 Ma, Czech Republic	Oligocene, *c.* 24.7 Ma, Germany	Miocene, 11.2–8.7 Ma, Spain
Mean annual temperature	23–25°C (Mosbrugger *et al.* 2005)	16.8–23.9°C (Grein *et al.* 2011); 18 ± 2.5°C (Tütken 2014); surface water temperature: 25 ± 3°C (Tütken 2014)	Likely to be similar to Enspel: similar palaeolatitude	15–17°C	Unknown during deposition; 16–17°C reported for Vallesian sites Abezames (NW Spain) and Burgos (Central Spain)
Environment	Swamps, ponds, rivers	Volcanic maar	Thermal spring environment	Volcanic maar	Perennial bench-type lake
Size	Individual water bodies *c.* several hundreds of meters wide	*c.* 0.7 × 1.4 km	Several hundreds of metres wide	*c.* 2 km²	30–40 km²
Depth	Up to 15 m	200–300 m	50–60 m according to profile in Špinar (1972)	Several tens of metres to up to 240 m	Up to 100 m
Hydrology	Hydrologically open	Hydrologically closed	Hydrologically open	Hydrologically closed	Hydrologically open
Excavated facies	Swamps/ponds: littoral to profundal; rivers: channel & overbank deposits	Littoral to profundal	Profundal	Profundal	Littoral to profundal
Profundal sediments	Swamps/ponds: laminated, black lignites and dysodile coal (including varve-like couplets) with intercalated carbonate beds; rivers: white, cross-bedded sandstone & brown mudstone	Organic rich pelites ('oil shale') & fine laminated claystones/siltstones (with slumping structures, drainage structures); intercalated coarse-grained volcanoclastic turbiditic inclusions (increased for lake margins)	Laminated carbonaceous claystones, with intercalated volcaniclastics/pyroclastics	Black shales & coarse-grained volcaniclastics/pyroclastics	Limestones (wackestones & packstones) & laminated mudstones (including oil shales and varves)
Bottom currents	Weak	Rare	No reference	Weak/absent	Weak/absent
Anuran taxonomy	Pelobatidae, Palaeobatrachidae & potentially Discoglossidae	Pelobatidae, Palaeobatrachidae & one unassigned species	Palaeobatrachidae, Discoglossidae, Pelobatidae, Ranidae	Pelobatidae, Palaeobatrachidae & Ranidae	Ranidae
Anuran abundance	Hundreds of adults & at least 12 tadpoles in swamps/ponds; few in fluvial deposits	n ≈ 250 adults & 2 tadpoles	n > 1000 adults & about 200 tadpoles	n = 8 adults & several hundred (mainly pelobatid) tadpoles	n > 73 adults & n > 79 tadpoles

(continued)

TABLE 2. (Continued)

	Geiseltal lacustrine system	Lake Messel	Lake Bechlejovice	Lake Enspel	Lake Libros
Associated fish fauna	Swamps/ponds: abundant (up to four species); rivers: none	Abundant (eight genera & species)	Monospecific species *Umbra prochazkai* (Umbridae)	Monospecific species *Palaeorutilus enspelensis* (Cyprinidae)	None
Truncation	Many specimens	Many specimens	Many specimens	Many specimens	Many specimens
Completeness	Varying; few near-complete specimens (all lack phalanges)	Similarly complete to Geiseltal; few near-complete specimens (including near-complete phalanges)	More complete than Geiseltal; many near-complete specimens include peripheral & small elements (phalanges, carpals, tarsals)	More complete than Geiseltal; some near-complete specimens include near-complete phalanges & small elements such as carpals, tarsals	More complete than Geiseltal; some near-complete specimens include near-complete phalanges & small elements such as carpals, tarsals
Proximal-distal trend	Yes	Yes	Yes	Yes	Yes
Lack of distal elements	Common	Common	Rare; although missing elements commonly include peripheral elements	Common; mainly peripheral elements	Common; mainly peripheral elements
Lack of entire limbs	Common	Common	Rare	Common	Not reported
Articulation	High articulation for most elements present	Less articulated than Geiseltal	More articulated than Geiseltal; high articulation for most elements present	Similarly articulated to Geiseltal; high articulation for elements present (including distal limb elements)	Less articulated than Geiseltal; especially for limb elements
Disarticulation of limb elements or entire limbs	Occasional	Common	Occasional for phalanges and/or single limb joints (limb elements stay as unit)	Occasional	Common
Abdominal disarticulation	Common for the joints associated with the sacral vertebrae & ilia and/or the urostyle–hip joint	Common for the joints associated with the sacral vertebrae & ilia and/or the urostyle–hip joint	Common for the joints associated with the sacral vertebrae & ilia and/or the urostyle–hip joint	Common for the joints associated with the sacral vertebrae & ilia and/or the urostyle–hip joint	Common for the joints associated with the sacral vertebrae & ilia and/or the urostyle–hip joint
Reorientation of the lower body	Common	Common	Occasional; some posterior bodies slightly reorientated	Common	Not reported
Anterior and posterior body halves are independent units	Occasional; clearly separated anterior or posterior body halves	Common; separated anterior or posterior body halves often overlap; one body half can occur in isolation	rare	Occasional; clearly separated anterior or posterior body halves	Never

(continued)

TABLE 2. (Continued)

	Geiseltal lacustrine system	Lake Messel	Lake Bechlejovice	Lake Enspel	Lake Libros
Other body regions are articulated units	Common: astragalus–calcaneum, metacarpals, metatarsals, vertebrae	Common: body halves, astragalus–calcaneum, metacarpals, metatarsals, vertebrae	Common: astragalus–calcaneum, metacarpals, metatarsals, vertebrae	Common: astragalus–calcaneum, metacarpals, metatarsals, vertebrae	Common: astragalus–calcaneum, metacarpals, metatarsals, vertebrae
Isolated limbs/parts of limbs	Rare	Rare	Rare	Not reported	Never
Extensively disarticulated skeletons or disarticulated bones	Rare	Rare	Rare in layers with abundant anurans; common in certain other layers (Špinar 1972)	Not reported	Rare (unidirectional scattered)
Other taphonomic characteristics	Specimen orientation always dorsoventral; specimens often show ’spread-eagled’ attitude (term after Smith 1986); clusters of bones are rare	Common displacement of entire limbs (unnatural limb orientations especially at the shoulder & hip joint)	Not reported	Not reported	Joints can exhibit angles less than the minimum value possible *in vivo* (as a result of osmotic dehydration)
Geiseltal taphonomic state	States 2, 3, 9 > State 1 > States 7–8 > States 4, 5, 6	States 3, 9 > State 2 > States 6–8 > States 1, 4, 5	States 1, 9 > State 2 > State 7 > State 8 > States 4, 6	States 1, 2, 9 > States 7–8	States 1, 9 > State 2 > State 7 > States 3, 4, 5
References	Kuhn (1941); Raupach (1948); Weigelt (1933); Krumbiegel (1962*a*); Krumbiegel *et al.* (1983); Roček & Rage (2000); Rage & Roček (2003); Franzen (2005); Mosbrugger *et al.* (2005); Wuttke *et al.* (2012); Roček (2013); Roček *et al.* (2014)	Nix (2001); Pirrung *et al.* (2001); Franzen (2005); McNamara (2007); Grein *et al.* (2011); Gruber (2011); Tütken (2014); Smith & Lehmann (2014); Smith *et al.* (2018); Wuttke (2018)	Špinar (1972); Bellon *et al.* (1998); Roček (2003); Roček *et al.* (2006); Přikryl (2010); Gardner (2016); McNamara (2007, data)	Böhme (1996, 2000), Wedmann (2000); Pirrung *et al.* (2001); Maus & Wuttke (2002; 2004); Mertz *et al.* (2007); Roček & Wuttke (2010); Schindler & Wuttke (2010); Poschmann *et al.* (2010); Uhl & Herrmann (2010)	Anadòn *et al.* (1992); de las Heras *et al.* (2003); Ortí *et al.* (2003); Bruch *et al.* (2004); McNamara *et al.* (2006, 2009, 2012*a*)

Completeness values for the cranium, vertebrae and femora are similar for specimens in both sites; completeness shows a proximal–distal trend in both. This probably reflects a common taphonomic process: the preferential loss of peripheral elements due to their small size and exposed position in the body (McNamara *et al.* 2012*a*). Both sites show similar articulation patterns for joints in the shoulder and hip region, which are less articulated than others. This reflects the similar anatomical configuration of the bones at these joints and similar taphonomic history (i.e. featuring decay-related collapse of the three-dimensional architecture of the hip bones and compaction during burial). In both sites few specimens show evidence for abdominal rupture; many Libros specimens show gut contents.

In contrast to the completeness data and general patterns of articulation, the articulation values for Geiseltal anurans are usually higher than those for Libros anurans (McNamara *et al.* 2012*a*; Table 1). This probably reflects the inclusion of truncated specimens in the Libros study. Other potential factors include collection bias or the strength of bottom currents (ultimately resulting in lower completeness but higher articulation values).

A major biological (intrinsic) control on the skeletal taphonomy of the Libros anurans is the quality of preservation of the skin: better preserved skin is associated with higher values for completeness and articulation (McNamara *et al.* 2009). Future studies should assess any such taphonomic links for the Geiseltal anurans.

Other Cenozoic biotas

The skeletal taphonomy of anurans from Messel, Enspel and Bechlejovice has not been studied systematically. That said, some general qualitative statements are possible regarding the comparative taphonomy of these and the Geiseltal anurans (Table 2).

Anurans from all four Lagerstätten share a common proximal–distal trend in completeness (Table 2) (e.g. Fig. 3C; Špinar 1972, pl. 102 no.608a; McNamara 2007, data; Roček & Wuttke 2010, fig. 6h; Köhler 2011, fig. 3) that results from the preferred disarticulation of small and peripheral bones (probably linked to the low amount of surrounding soft tissue). Abdominal disarticulation is also common in all four biotas (Table 2) (Fig. 3C; Špinar 1972, pl. 83 no.6210; McNamara 2007, fig. 17.1; Roček & Wuttke 2010, fig. 8a) and is probably linked to the collapse of the three-dimensional structure of the abdominal bones; loss of some of these elements in a limited number

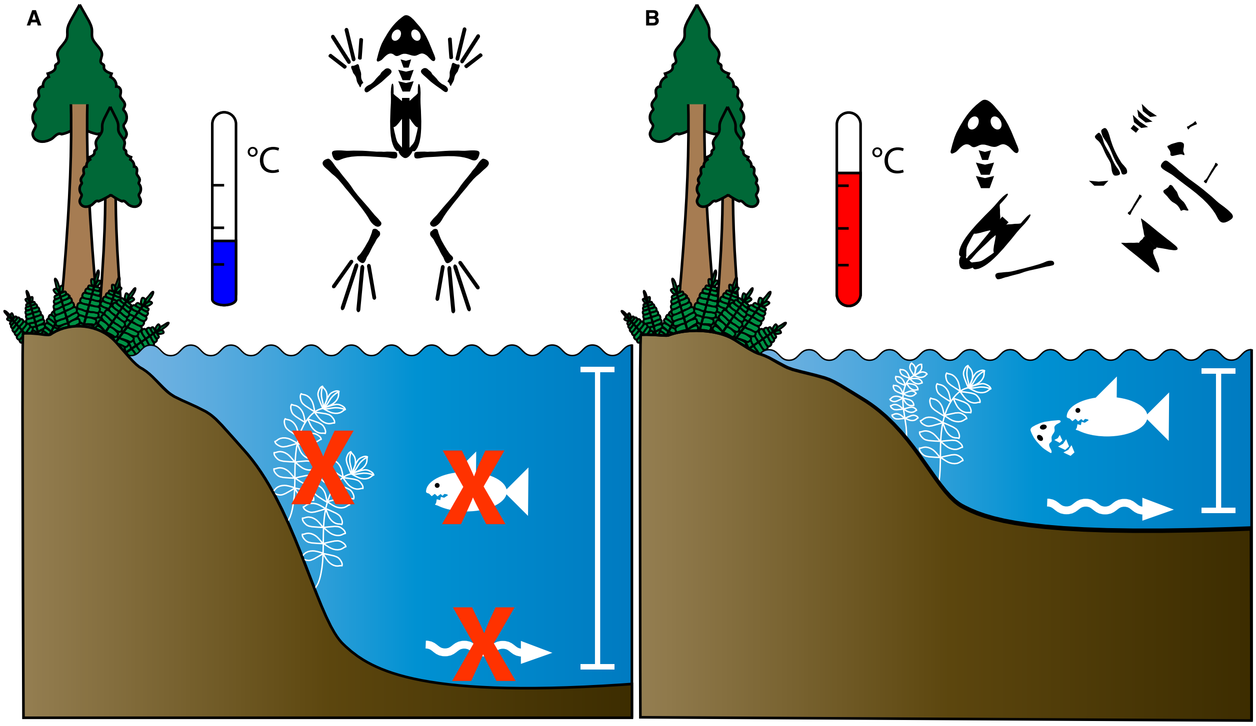

FIG. 12. Controls on preservation for anurans in lacustrine-hosted Cenozoic biotas. A, fossils are more complete and articulated when carcasses were deposited during cooler climatic phases in deep, cool lakes, with inhibited scavenging, bank vegetation and/or post-depositional disturbance. B, fossils are usually less complete and articulated when carcasses were deposited during warmer climatic phases in shallow, warm lakes, with scavengers present, pronounced bank vegetation and powerful post-depositional disturbance.

of specimens suggests rare abdominal rupture. Weak bottom currents (e.g. those generated by inflowing streams, landslides, storm events or lake overturn) may reorientate anterior and posterior body halves and limbs (e.g. Špinar 1972, pl. 76 no.35b; Wuttke 1988, fig. 154; McNamara 2007, fig. 17.1; Roček & Wuttke 2010, fig. 4i; Wuttke 2018, fig. 8.4).

All specimens were deposited in profundal lake regions characterized by low sedimentation rates (Špinar 1972; Pirrung *et al.* 2001; Wuttke & Poschmann 2010). The palaeolakes differ, however, in key environmental parameters such as size, temperature, depth and the presence and absence of fish (Table 2) (Špinar 1972; Pirrung *et al.* 2001; Roček *et al.* 2006). Variations in lake characteristics can be directly related to taphonomic patterns (Fig. 12). Water temperature controls the rate of decay and decay gas production (i.e. lower temperatures inhibit (re)floating; Smith & Elder 1985). Surface water temperature is controlled by the broad palaeoclimatic setting. Deposition in deeper waters also inhibits refloating and abdominal rupture (Smith & Elder 1985) (e.g. Messel, Enspel). Littoral vegetation can trap carcasses (e.g. Enspel) (Wuttke & Poschmann 2010). This may prolong floating/decay and scavenging at or close to the water surface, delaying or preventing deposition in profundal regions (Wuttke & Poschmann 2010). This ultimately results in less complete specimens, isolated limbs and low numbers of specimens. Water depth, lake size, vegetation and presence or absence of scavengers are controlled by lake physiography and lake hydrology, which are both ultimately controlled by the climate. Larger lakes may yield a higher proportion of carcasses deposited soon after death, given that the proportion of vegetated margins to lake area is lower than in a system with interconnected smaller water bodies (e.g. Geiseltal). Furthermore, in larger lakes the profundal region is often deeper, inhibiting decay due to lower water temperatures and inhibiting generation of decay gases due to higher water pressure (Elder & Smith 1988). The extent of scavenging relates to the presence and absence of predators and scavengers (e.g. fish) in the lake. When these are absent, specimens are more complete and articulated and scattered bones are rare (e.g. Enspel (Roček & Wuttke 2010), Bechlejovice (Špinar 1972)).

CONCLUSION

Most of the Geiseltal anurans are likely to have died during or after mating. Most specimens are partially complete, partially articulated and truncated by the edge of the fossil slab/nitrocellulose glue transfer. Omitting truncated specimens in the taphonomic analysis introduces bias towards higher completeness values for truncated specimens. All specimens lack at least some phalanges; some specimens lack limb elements or entire limbs. Taphonomic extremes, such as near-complete, near-articulated specimens, isolated limbs and entirely disarticulated specimens are rare. Specimens show a proximal–distal trend in completeness, and low completeness and articulation values for some abdominal bones. These data are the basis of a new taphonomic model for the Geiseltal anurans. Specimens represent nine taphonomic states based on distinct patterns in disarticulation and loss of skeletal elements. These states reflect different taphonomic pathways related to subtle variation in the depositional environment. The fidelity of preservation is consistent between stratigraphic levels and excavation sites. Potential biases in the dataset include collection history, truncation and taxonomy.

Comparative analysis of patterns in completeness and articulation in the Geiseltal specimens and in fossil anurans from other Lagerstätten reveals recurring taphonomic trends in anuran preservation in Cenozoic lake settings. These include proximal–distal trends for completeness in the limbs, abdominal disarticulation and/or the reorientation of the anterior or posterior body. The inter-biota skeletal taphonomy of Cenozoic anurans is ultimately controlled by climate (especially ambient temperature), lake physiography and anuran anatomy. Anurans are more complete and articulated in Lagerstätten from cooler climatic phases where decay, floating, scavenging and post-depositional disturbance of carcasses were inhibited by deposition in relatively cool and/or deep lakes. These ultimate taphonomic controls are likely to apply to diverse vertebrates decaying in lacustrine settings.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.2bvq83brt

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.1453):

Appendix S1. Supporting information.

Fig. S1. Schematic illustration of the resin transfer method ('Lackfilm' method; after Voigt 1933). For some specimens, the fossil was removed after step 2 by peeling away the lacquer and the attached fossil (Krumbiegel *et al.* 1983). Step 1: Exposure of fossil. Step 2: Application of clay and gypsum ring followed by nitrocellulose lacquer or paraffin wax. Step 3: Application of paper or mesh and gypsum cover. Step 4: Exposure of fossil from reverse side and removal of sediment cover, gypsum and clay. Step 5: Fossil is exposed on a lacquer/wax backing; lower surface of the fossil is now exposed on top.

Fig. S2. Line drawings for specimens shown in Fig. 3. A, Ce III-6735-1932. B, Ce II-4949-1930. C, Ce III-6728-1932. D, Ce IV-4953-1933. E, Ce III-6720-1932. F, Ce III-6719-1932. G, Ce I-4947-1930. H, Ce III-6742-1932. I, IL 17A-1969. J, Ce III-6737-1932. All scale bars represent 10 mm.

Fig. S3. Trends in completeness for Geiseltal anurans where elements distal to truncated elements are coded as 'absent' (rather than being omitted). A–C, specimen completeness for the entire dataset; D–H, specimen completeness for truncation categories. A, no elements omitted from the dataset. B, phalanges omitted. C, entire hands and feet omitted. D–H, specimens in truncation categories T0–T4. D, no truncation. E, truncation group T1 (0.1–24.9% truncation). F, truncation group T2 (25–49.9% truncation). G, truncation group T3 (50–74.9% truncation). H, truncation group T4 (75–100% truncation). The horizontal line in each boxplot denotes median value for each category.

Fig. S4. Specimen orientation (n = 140).

Fig. S5. Distribution of specimens among truncation categories T0–T4 (n = 140).

Fig. S6. Schematic frog skeleton summarizing the percentage completeness and articulation values for each type of skeletal element in the Geiseltal anurans (n = 140). Percentage values indicate the percentage of specimens that show the skeletal element or the articulated joint; for paired elements or elements in a set, at least one element of the pair or set must be visible in order to be coded as present.

Fig. S7. Distribution of skeletal elements among completeness groups. Values in the plots are percentages. Numbers in the key refer to the number of skeletal elements that are present in the hands, feet or torso. Grey tones denote different completeness groups or truncation categories, respectively. For instance, the phalanges are absent in 74.9% of hands and the vertebral column shows 7–9 vertebrae in 58% of specimens. *Abbreviations*: fp, forelimb phalanges; hp, hindlimb phalanges; mc, metacarpals; mt, metatarsals; tb, tibiale–fibulare; v, vertebrae.

Fig. S8. Percentage completeness for each element and percentage articulation for each joint, on the left and right sides of the body. 'Left' and 'right' are as presented in the hand specimen, with the cranium at top. Light grey shading denotes data for the left-hand side of the body, and dark grey shading denotes data for the right-hand side of the body. Elements present as a pair or as a group are coded as complete if at least one of the elements is present. Joints present as a pair or as a group are coded as articulated if at least one of the joints is in life position. A, percentage completeness for each element. B, percentage articulation for each joint. *Abbreviations*: c, cranium; f, femur; fp, forelimb phalanges; hp, hindlimb phalanges; h, humerus; i, ischium; mc, metacarpals; mt, metatarsals; pg, pelvic girdle; r, radioulna; s, shoulder; sv, sacral vertebrae; t, tarsals; tb, tibiale–fibulare; tf, tibiofibula; v, vertebrae.

Fig. S9. Distribution of joints among articulation groups. Pie chart values are percentages. Numbers in the key refer to the number of joints that are articulated in a given hand, foot or torso, respectively. Grey tones denote different articulation groups. For instance, 27% of hands show no articulated phalanges and 48% of hands have 1–2 articulated joints.

Fig. S10. Trends in completeness (A–D) and articulation (E–H) for Geiseltal anurans among excavation sites. A & E, sinkholes (i.e. Ce I, Ce IV, Ce V, Ce VI, Leo III, Leo V and N_s XXXV). B & F, dying field 1 (Ce II), C & G, dying field 2 (Ce III). D & H, combined data for dying field 1 (Ce II) and 2 (Ce III). The horizontal line in each boxplot denotes the median for each site.

Fig. S11. Percentage articulation versus percentage completeness for specimens that are not truncated (n = 34).

Table S1. Percentage completeness and articulation per skeletal element and joint. Data are provided as a percentage of total specimens, total elements (for completeness) and total joints (for articulation). For instance, the forelimb phalanges are present in 53.6% of specimens, but only 34.9% of the theoretical maximum number of forelimb phalanges are present.

Table S2. Percentage completeness and articulation per skeletal element and joint, respectively, in pelobatids and palaeobatrachids. For instance, the forelimb phalanges are present in 62.8% of specimens of pelobatids.

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