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Carnivorous reptile feeding strategies and postmortem food-processing behaviors: tooth traces on bones from the Upper Triassic Grabowa Formation (southern Poland)

Grzegorz Sadlok

Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Bedzińska 60 Street, 41-200, Sosnowiec, Poland
<gregsadlok@gmail.com>

Abstract.—Carnivores make traces on bones with their teeth when feeding. A true predatory bite trace (predichnia) forms when a predator catches and kills its prey or attempts to do so. Both predators and scavengers may leave their nonpredatory feeding traces during postmortem food processing. Despite the interpretative uncertainties as to the ethology such ichnofossils may represent, the bite traces have been traditionally classified as predichnia—traces of predation. Previously, there was no alternative ethological category available for workers to classify them. The present paper fills that gap and describes tooth-made ichnofossils from the continental Upper Triassic Grabowa Formation of southern Poland. It discusses modes the serration and striations might have formed along *Linichnus* edges, potential makers of the trace fossils, feeding strategies, and food-processing behaviors the ichnites may represent. All the bite traces are thought to act as a record of carnivorous behaviors and are classified as sarcophagichnia, a new ethological category (traces of feeding on a body). Finally, all the studied bite traces were likely inflicted postmortem and are classified as necrophagichnia (traces of feeding on an already dead body), most likely produced by scavengers in the studied cases. Data on recent carnivores link these ichnites with postmortem food-processing behaviors, such as dismembering and defleshing. Scavenging could, in fact, have been a preferred carnivorous feeding strategy in the seasonal Norian climate of the area. Dry seasons could have perhaps increased vertebrate mortality rates and provided plenty of carcasses for carnivores to feed on.

Introduction

A tooth trace on the surface of a fossil bone is merely evidence that an interaction took place between the two. However, the behavior that such a trace may represent is up for interpretation. In general, tooth–bone contacts may result from various behaviors. Fighting carnivores may bite hard enough to gouge the bones of their adversaries during nonpredatory biting. Such fight-induced bites may occur in particular areas, such as the head and tail (see Webb et al., 1983; Tanke and Currie, 1998; Avilla et al., 2004; Katsura, 2004; Bell and Currie, 2010; Zammit and Kear, 2011). Signs of tissue recovery (healing) may aid nonfeeding interpretation of such bite traces (see, e.g., Tanke and Currie, 1998; Drumheller et al., 2014, 2020).

Tooth traces may form on bones due to predatory behaviors, mainly prey capturing and killing (see, e.g., Schaller and Vasconcelos, 1978; Njau and Blumenschine, 2006). However, many traces on bones represent postmortem feeding behaviors associated with various phases of food processing, such as gross reduction of the corpse (dismembering) and bone defleshing (Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009; Westaway et al., 2011; Njau and Gilbert, 2016).

Therefore, the teeth may gouge the bones during sarcophagy, and by escaping the swallowing and subsequent ingestion, some of the tooth-marked bones may be abandoned. Those have a potential to preserve bite traces and convey behavioral information into the fossil record (see, e.g., Erickson and Olson, 1996; Boaz et al., 2000; Rogers et al., 2003; Njau and Blumenschine, 2006; Pobiner, 2008; Jacobsen and Bromley, 2009; Bianucci et al., 2010; Bell et al., 2012).

Although ichnology has experienced progress in the naming of fossilized bite traces on bones (e.g., Mikuláš et al., 2006; Jacobsen and Bromley, 2009) and in their behavioral interpretations (see, e.g., Bell and Currie, 2010; Longrich et al., 2010; Hone and Chure, 2018; Scheyer et al., 2018; Drumheller et al., 2020), there have been no similar advances in the ichnological scheme of their ethological classifications. Therefore, despite the interpretative uncertainties associated with ethology of such trace fossils, all have been traditionally classified as predichnia—traces of predation (see definition in Ekdale, 1985; see Vallon et al., 2016 and references therein). Such classification of a bite trace implies it is evidence of a predator–prey interaction. However, this is not necessarily the case.

The present paper discusses examples of bite traces preserved on bone fragments recovered from the continental Upper Triassic (Norian) Grabowa Formation from southern Poland and provides two new terms to aid in future ethological classification of such bite traces (sarcophagichnia and necrophagichnia). The analysis and discussion provided in the present paper focus on morphological features (serration/striations in *Linichnus*) of the ichnites, their potential trace makers, feeding strategies, and postmortem food-processing behaviors that the trace fossils may represent.

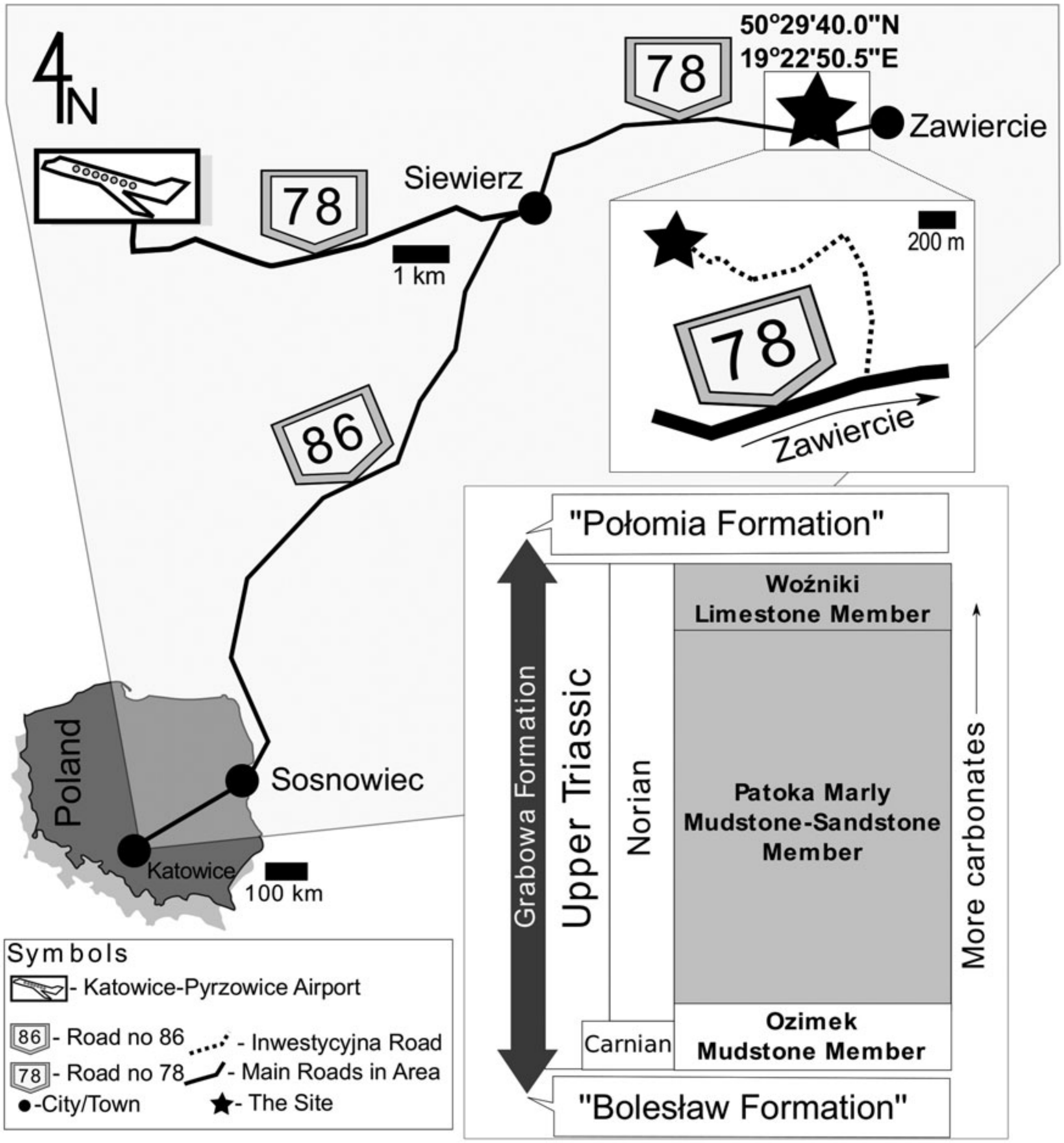

Figure 1. The Zawiercie site in southern Poland. The figure shows generalized stratigraphy of the Upper Triassic strata in the area—grayed members of the Grabowa Formation constitute the Norian profile of Zawiercie (based on Szulc et al., 2006, 2015; Szulc and Racki, 2015).

Geological settings

Location and stratigraphy.—The bite traces described in this paper occur on fragmentary fossil bones recovered from the Upper Triassic deposits exposed in a site close to Zawiercie, a city in southern Poland (Fig. 1, Table 1). The area was part of the Late Triassic sedimentary basin located on the northern shore of the Tethys Ocean (see Szulc, 2007b; McKie and Williams, 2009; Jewuła et al., 2019).

The deposits at the site in Zawiercie represent the continental Grabowa Formation (Fig. 1), which is sandwiched between two informal units (both in a rank of formation): "Bolesław" (below) and "Połomia" (above; see Szulc and Racki, 2015; Szulc et al., 2015). The lower part of the sequence is mud dominated and represents the Patoka Member. This unit grades upward into the Woźniki Limestone Member, which is distinguished by the presence of thicker carbonate beds (see Szulc and Racki, 2015; Szulc et al., 2015). The sedimentary sequence at the site is dominated by freshwater calcareous gray and reddish mudstones. The sequence comprises also subordinate, coarser grained deposits, including sand- and gravel-grade facies (see Szulc et al., 2006; Szulc and Racki, 2015; Szulc et al., 2015).

The deposits at the site in Zawiercie comprise microfossils characteristic for the Polish Upper Triassic, namely components of the palynological zone IVb (see Orłowska-Zwolińska, 1983 for details). This assemblage and correlation with other sites in the formation indicate that the sediments from Zawiercie are Norian (see e.g., Szulc et al., 2006; Szulc, 2007a; Fijałkowska-Mader et al., 2015; Szulc et al., 2015).

Table 1. Summary of studied bite traces.

Ichnotaxa; symbol on figures	Morphological remarks	Example figure	Binford's (1981)	Bone fragment catalog number	Consumed animal	Possible behavior	Proposed ethological classification	References
Linichnus bromleyi; Lb	*Linichnus* with no serration along the edges, short to long and straight to curved grooves, U- to V-shaped cross sections. Length range: ∼0.5-2.2 cm Width range: ∼0.05-0.2 cm	3.2–3.6	Score	WNoZ/S/7/170: distal part of a pubis	Carnivore archosaur (?theropod)	Defleshing	***sarcophagichnia*** *necrophagichnia*	Niedźwiedzki and Budziszewska-Karwowska (2018) and this paper
		4.2	Score	WNoZ/S/7/268: flat bone fragment	Unknown			This paper
		5.1, 5.4, 5.10	Score and furrow	WNoZ/S/7/267: ?rib	Unknown			This paper
Linichnus serratus (a); Ls(a)	Serrated *Linichnus* with serration on both edges of the groove, U- to V-shaped cross sections, short to long and straight to curved grooves. Length range: ∼0.3-3.5 cm Width range: ∼0.1-0.3 cm	3.1	Furrow	WNoZ/S/7/168: distal part of an ischium	Carnivore archosaur (?theropod)	Reduction	***sarcophagichnia*** *necrophagichnia*	Niedźwiedzki and Budziszewska-Karwowska (2018) and this paper
		4.6	Furrow	WNoZ/S/7/268: flat bone fragment	Unknown			This paper This paper
Linichnus serratus (b); Ls(b)	*Linichnus* with striations on one edge of the groove, V-shaped cross sections, typically short and straight groove. Length range: ∼0.6-2.0 cm Width range: ∼0.1-0.6 cm	5.1, 5.2, 5.16, 5.17, 5.19, 5.20	Furrow	WNoZ/S//267: ?rib	Unknown	Defleshing	***sarcophagichnia*** *necrophagichnia*	This paper
Nihilichnus; N	Elongated, oval to diamond shaped *Nihilichnus* – depression in bone with U- to V-shaped cross section, fractured bone around the depression. Length width: ∼0.25-0.93 cm Width range: ∼0.1-0.6 cm	3.2–3.6	Puncture	WNoZ/S/7/170: distal part of a pubis	Carnivore archosaur (?theropod)	Reduction	***sarcophagichnia*** *necrophagichnia*	Niedźwiedzki and Budziszewska-Karwowska (2018) and this paper
		4.2, 4.3, 4.6, 4.7	Pit and puncture	WNoZ/S/7/268: flat bone fragment	Unknown			This paper
		5.6	Puncture	WNoZ/S/7/267: ?rib	Unknown			This paper

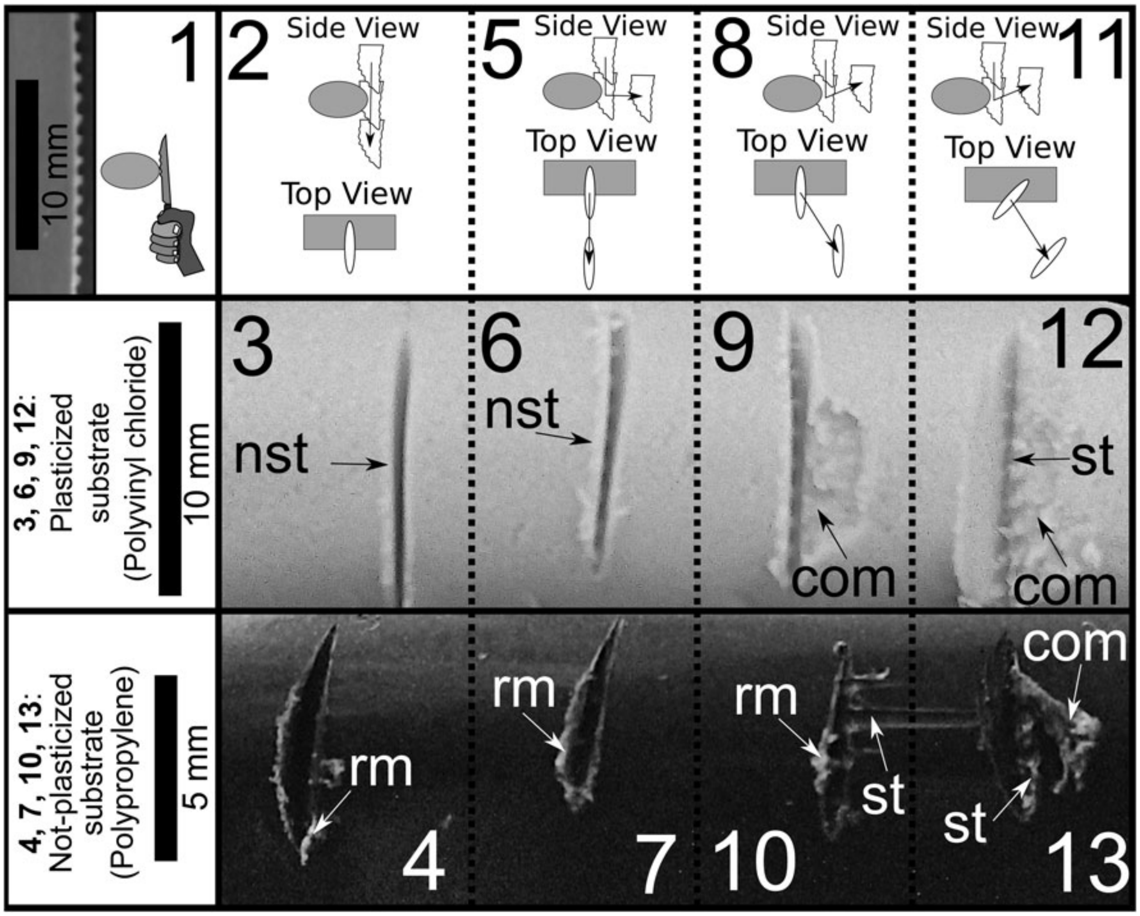

Figure 2. The cut tests: resulting trace morphologies versus blade kinetics. (**1**) Serrated blade representing a tooth in this test (blade was hand held). (**2–13**) Results for different blade kinetics. (**2, 5, 8, 11**) Kinetics of blade in respect to the substrate (shown in gray): side and top views during interaction are illustrated. Two types of substrates, differing in plasticity, were used with comparable results: (**3, 6, 9, 12**) polyvinyl chloride (plasticized); (**4, 7, 10, 13**) polypropylene (not plasticized). (**3, 4**) Cut morphologies resulting from kinetics depicted in (**2**). (**6, 7**) Cut morphologies resulting from kinetics depicted in (**5**). (**9, 10**) Cut morphologies resulting from kinetics depicted in (**8**). (**12, 13**) Cut morphologies resulting from kinetics depicted in (**11**). nst = no striations; com = chipped-off material; st = striations; rm = removed material.

Paleoenvironment.—Central Europe experienced pluvialization during the Carnian–Norian transition, and that climatic shift reflected in the dominant facies: evaporates (representing playas of Carnian age) were replaced by sediments of fluvial channels and lakes, all deposited in Norian wetlands (Szulc et al., 2006). The latter were formed under the seasonal semi-arid to subhumid Norian climate (see Szulc et al., 2006; Szulc, 2007b; Gruszka and Zieliński, 2008; McKie and Williams, 2009; Fijałkowska-Mader et al., 2015; Szulc et al., 2015; Jewuła et al., 2019).

The fine, mud-dominated facies exhibit the deposition of particles suspended within still waters. However, the coarser facies (sand and gravel) had to be deposited by flowing water and some—especially gravel-grade deposits—indicate flooding events (see, e.g., Szulc et al., 2006; Jewuła et al., 2019; Sadlok, 2020).

Materials and methods

The following subsections describe the type and provenience of the fossilized material and methods utilized in the present study, including details of cut tests (see Fig. 2).

Materials.—All the illustrated specimens (Figs. 3–5) were collected at the pail of sediments left after the construction of a local city dump (see also Budziszewska-Karwowska et al., 2010; Niedźwiedzki and Budziszewska-Karwowska, 2018; Sadlok, 2020).

The bones.—The bite-bearing bones are fragmentary, and their proper identification is problematic (see Table 1). The taxonomy of specimens illustrated in Figure 3 has been studied by Niedźwiedzki and Budziszewska-Karwowska (2018). Those authors concluded that the bones likely represented carnivorous archosaurs—potentially theropods (compare Dzik et al., 2008; Niedźwiedzki et al., 2011; Niedźwiedzki and Budziszewska-Karwowska, 2018). According to Niedźwiedzki and Budziszewska-Karwowska (2018), these bone fragments were parts of pelvic girdles, namely, a distal part of an ischium shaft (Fig. 3.1) and a pubic boot (Fig. 3.2–3.6).

Figures 4 and 5 show fragmentary bones of unknown affinities (see Table 1); one is a flat bone fragment (Fig. 4) and the other may represent a short fragment of a rib (Fig. 5).

Methods.—The analyzed bite traces were measured with a caliper to provide a range of observed sizes (lengths and widths; see Table 1 and supplementary materials). Bone specimens bearing the bite traces were photographed with a Canon DS126491 (18-55 lens) and presented in grayscale in Figures 3–5. A few close-up photographs were taken with a

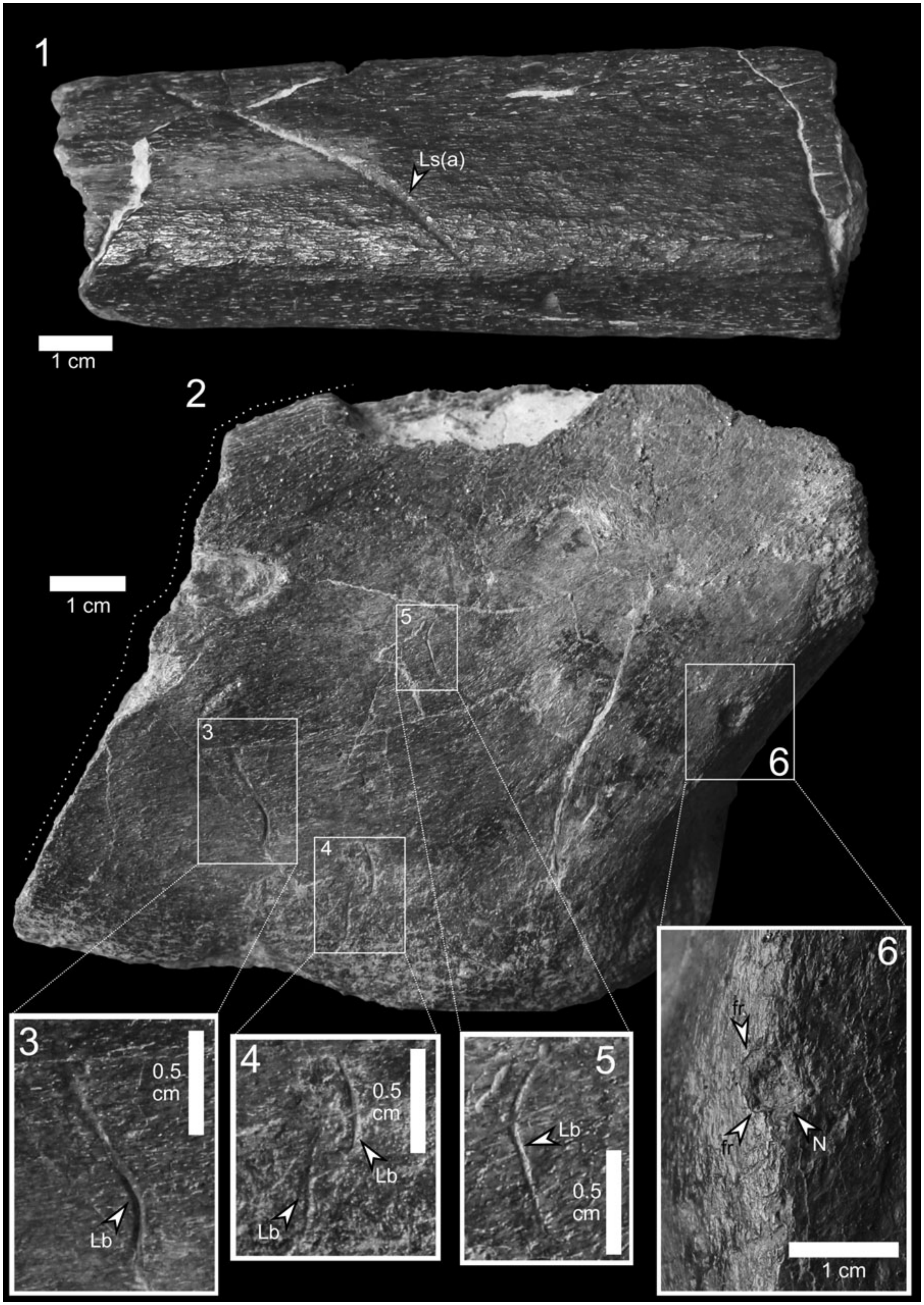

Figure 3. Bite trace fossils on pelvic girdle components: traces of feeding on carnivorous archosaurs. (**1**) An ischium fragment (distal part; specimen WNoZ/S/7/168) of a carnivorous archosaur (?theropod; see Niedźwiedzki and Budziszewska-Karwowska, 2018). (**2**) Pubic bone fragment (distal part; specimen WNoZ/S/7/170) of a carnivorous archosaur (?theropod; see Niedźwiedzki and Budziszewska-Karwowska, 2018). (**3–6**) Magnified details of pubic bone surface from (**2**): (**3–5**) *Linichnus bromleyi*; (**6**) *Nihilichnus*. Ls(a) = *Linichnus serratus* (a); Lb = *Linichnus bromleyi*; N = *Nihilichnus*; fr = bone fracturing around the trace.

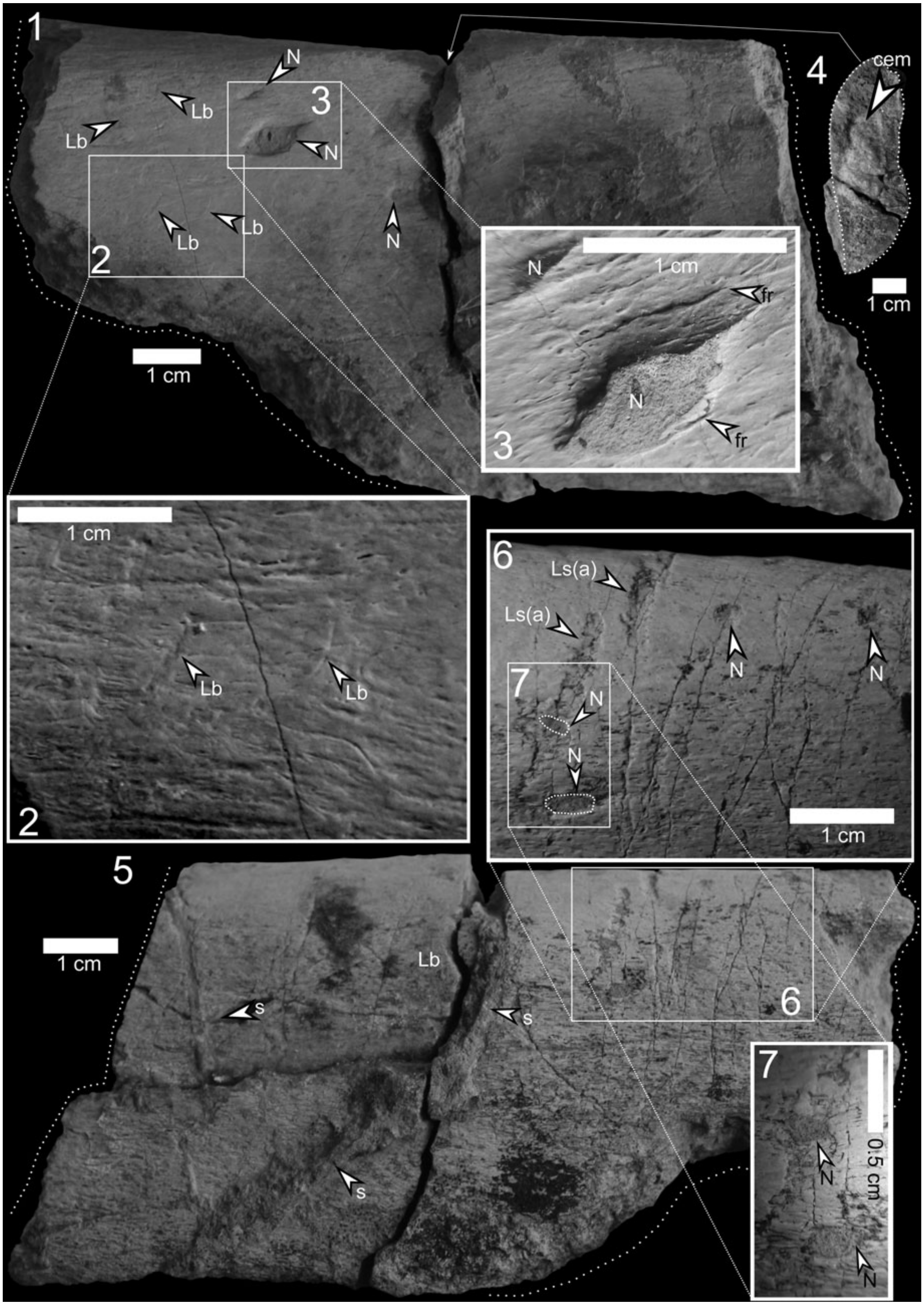

Figure 4. Multiple bite trace fossils on a flat bone fragment (specimen WNoZ/S/7/268). (**1, 5**) Two opposite sides of the bone specimen (dashed lines around the fragment depict those parts of its margins where the bone is missing). (**2, 3**) Enlarged views of areas shown in (**1**). (**4**) Sectional view of the specimen (along the fracture); light-colored calcite cementation is visible. (**6**) Enlarged view of area shown in (**5**). (**7**) Enlarged area from (**6**). Note various sizes of the bites (compare (**2**) and (**6**)). Lb = *Linichnus bromleyi*; Ls(a) = *Linichnus serratus* (a); N = *Nihilichnus*; cem = cement (calcite); fr = bone fracturing around the trace; s = sediment-infilled breakage of bone (?natural).

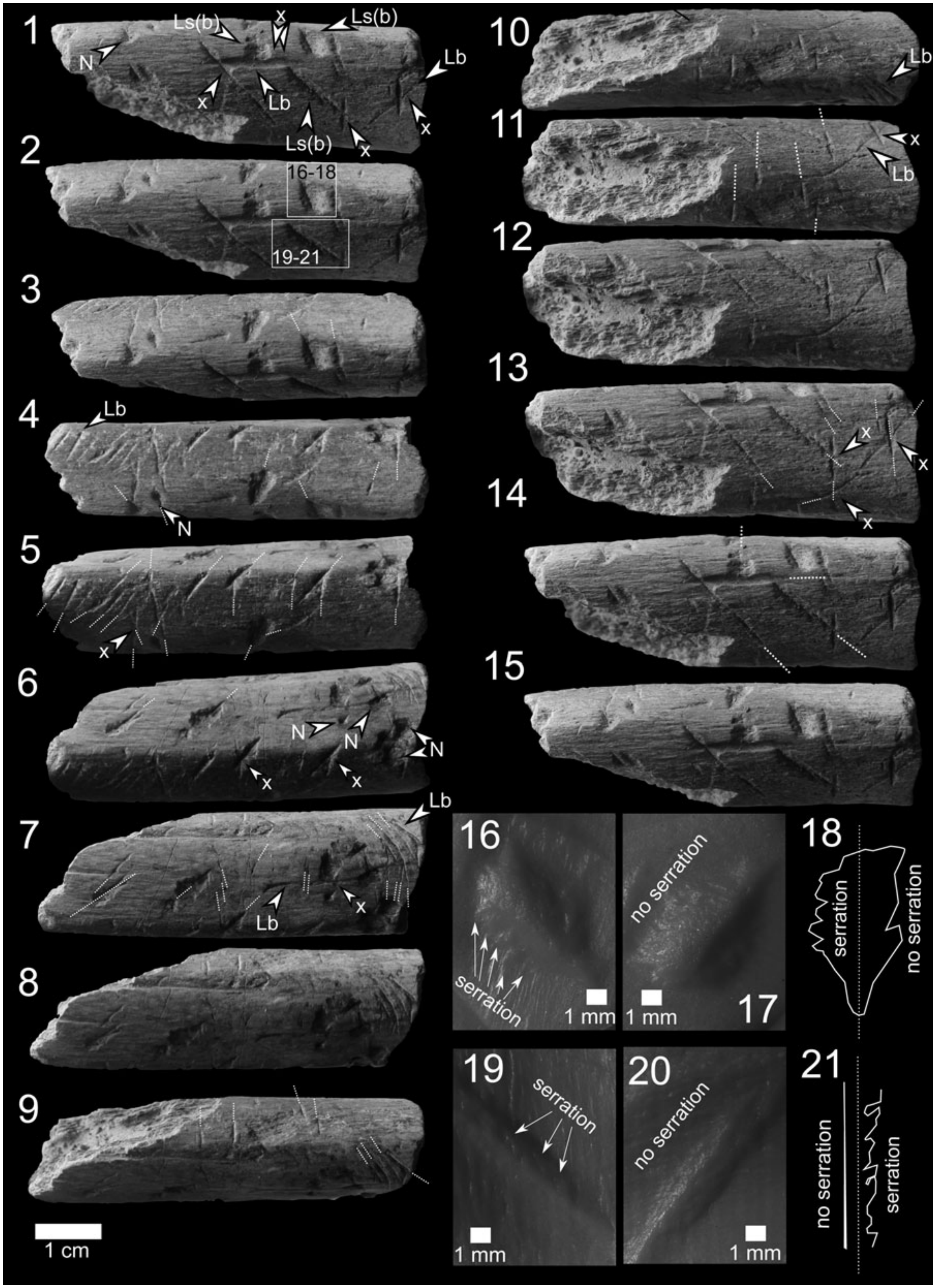

Figure 5. Multiple bite trace fossils on a ?rib fragment (specimen WNoZ/S/7/267). (**1–15**) Various views (360° rotation) of the specimen (bite traces occur on all surfaces). Short dashed lines used in places illustrate axes of the traces (parallel axes may result from a single bite). Note various sizes and orientations of the bite traces and their cross cutting. (**16, 17**) Two views (rotation applied to illuminate/shadow two sides of the plasticine cast made of trace boxed in (**2**)). (**18**) Drawing based on (**16, 17**) (dashed line depicts the trace axis). (**19, 20**) Two views (rotation applied to illuminate/shadow two sides of the plasticine cast made of trace boxed in (**2**)). (**21**) Drawing based on (**19, 20**) (dashed line depicts the trace axis). Ls(b) = *Linichnus serratus* (b); Lb = *Linichnus bromleyi*; N = *Nihilichnus*; x = cross-cutting bite traces.

Leica Wild L10 microscope equipped with a NikCam Pro camera to compose Figure 5.16, 5.17, 5.19, 5.20.

No heavy preparatory work was done in the field or laboratory that could end in formation of artificial tool-induced bone surface modifications. Also, the Triassic age of the material excluded the need for cut–bite mark differentiation (compare Blumenschine et al., 1996). All the figures were prepared with Gimp and Inkscape software (Kimball et al., 2008; Albert et al., 2010).

Cutting tests were performed with a serrated steel blade and two types of polymeric substrate: plasticized (polyvinyl chloride) and nonplasticized (polypropylene). The knife was handheld during the tests (see inset drawing in Fig. 2.1). The cuts were easily produced in room temperature, and no excessive force was required to mark the substrates (polypropylene was harder to cut with the blade than polyvinyl chloride). Figure 2 summarizes the information on used substrates, blade size (see Fig. 2.1), applied kinetics during the blade–substrate contacts (see Fig. 2.2, 2.5, 2.8, 2.11), and resulting cut-mark morphologies (see Fig. 2.3, 2.4, 2.6, 2.7, 2.9, 2.10, 2.12, 2.13).

The aim of the test was to approximate the possible tooth kinetics responsible for bite formations. Therefore, only a simply flat blade with a well-defined edge morphology was used during the tests (9 serrations/cm). One blade was used in all the tests (Fig. 2.1), and only a single sequence of movements (without repetition) was used to obtain each cut (as shown on Fig. 2.2, 2.5, 2.8, 2.11). The test results were particularly useful in analysis and discussion of the modes that serration and striations could form along *Linichnus* bite traces studied in the present work (Fig. 2; see also Bianucci et al., 2010; Muñiz et al., 2020).

Repository and institutional abbreviation.—The material is part of a collection hosted by the Museum of Earth Sciences at the University of Silesia in Sosnowiec, Poland (see Table 1 and figure captions for specimen catalog numbers; collection abbreviation: WNoZ).

Results

The following subsections describe the bite traces encountered on the analyzed fossil bones.

The bite traces on bones.—The studied bite traces display morphologies falling into four main categories of bone modifications recognized by Binford (1981) in his taphonomic studies: pits and scores (shallow surficial modifications) and punctures and furrows (deeper modifications; see Binford, 1981; D'Amore and Blumenschine, 2009). These terms are widely used in taphonomic literature (see, e.g., Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009; Drumheller and Brochu, 2014, 2016; Njau and Gilbert, 2016; Drumheller et al., 2020; Drymala et al., 2021). Therefore, the following descriptions and Table 1 include them to indicate the relationships between the taphonomic terminology and the ichnotaxa.

Linichnus *ichnogenus.*—A single, elongated biogenic groove (score or furrow) on skeletal material (e.g., bones, teeth). The groove is U- or V-shaped in its transverse section. It may be shallow, affecting only the bone surface, or deeper, cutting the bone-fibers, which may become recurved or broken (see Jacobsen and Bromley, 2009). The original diagnosis of this ichnogenus also contained information on serrated edges of the groove (see Jacobsen and Bromley, 2009). However, since Muñiz et al. (2020) established *Linichnus bromleyi*, the edge serration has become a distinguishing feature at the ichnospecific rather than ichnogeneric level. Currently, there are two ichnospecies within *Linichnus*: *L. serratus* (Jacobsen and Bromley, 2009) and *L. bromleyi* (Muñiz et al., 2020). The first one has serrated edges, whereas the edges of *L. bromleyi* are smooth (compare Jacobsen and Bromley, 2009; Muñiz et al., 2020).

Description of Linichnus *traces.*—Table 1 provides a brief descriptive summary for the studied *Linichnus* traces. The scores and furrows on bone ascribed herein to *Linichnus* (Figs. 3–5) are variably elongated, straight to curved. In some instances, they appear to form sets of parallel traces (marked with dashed lines in Fig. 5). Their cross sections are U- to V-shaped (observed on casts made with modeling clay/plasticine). The sizes are also variable. Lengths range from a few millimeters to ∼3.5 cm (measured on a convex bone surface). Widths range from submillimeter to ∼5.6 mm. The depths vary as well and range from submillimeter to ∼1 mm (estimated from plasticine casts). The wider grooves are also deeper (e.g., compare Figs. 3.1 and 4.2). Two ichnospecies of the ichnogenus are present in the material. For example, Figures 3.1 and 4.6 show *L. serratus* whereas Figures 3.2–3.5 and 4.2 illustrate *L. bromleyi*.

The studied *L. serratus* comprises two morphological variants, labeled here as *L. serratus* (a) (e.g., Figs. 3.1, 4.6) with serration along both edges and *L. serratus* (b) (Fig. 5.1, 5.16–5.21) with striations along one edge only (compare this morphology with the Type I bite trace of Collareta et al., 2017). The latter variant is distinct and deserves a more detailed description.

These traces are straight and typically short with their sectional views resembling a wide-gaping "V"; both sides of the "V" sink into the bone at slight angles. However, one of the sides is typically steeper than the other and shows some fine, short striations emanating from the groove (see Fig. 5.1, 5.2, 5.19–5.21). These fine features are approximately perpendicular to the summit line between the two V-forming surfaces (see Fig. 5.16–5.21). The overall outline of these *L. serratus* (b) traces may resemble a teardrop, with one end of the groove being slightly wider than the other (see Fig. 5.16–5.18). The overall morphology (short, straight grooves having V-shaped cross sections) of these traces resembles the so-called edge marks that Komodo monitors may produce on bone edges (D'Amore and Blumenschine, 2009). The edge marks, contrary to the present *L. serratus* (b), rarely display striations. They occur on narrow edges of bones, being approximately transverse to those edges (see D'Amore and Blumenschine, 2009, 2012).

Nihilichnus *ichnogenus.*—Triangular to ovoid holes or external pits or punctures. They occur as individual traces or may form groups; the grouping may be a recurring pattern. The margin of individual pits/punctures shows irregular jags, resulting from a brittle deformation (see Mikuláš et al., 2006). The ichnogenus comprises one ichnospecies, *Nihilichnus nihilicus* Mikuláš et al., 2006, sharing the diagnostic features with the ichnogenus (Mikuláš et al., 2006).

Description of Nihilichnus *traces.*—Table 1 provides a brief description summary for the studied *Nihilichnus*. The trace fossils ascribed here to the ichnogenus (Figs. 3.2, 3.6, 4.1, 4.3, 4.6, 4.7, 5.4, 5.6) are pits/punctures made in bone surfaces. Their outlines are elongated, oval to slightly diamond-like in shape (compare Fig. 3.6 with 4.3, 5.4). The maximal measured dimensions of the traces range from ∼2.5 to ∼9.3 mm. The marginal fracturing (jags) is well visible in some of the traces (see Figs. 3.6, 4.4). The sections of *Nihilichnus* traces are U- to (Fig. 5.14) slightly V-shaped (Figs. 4.1, 5.4; profiles observed with casts of modeling clay/plasticine); some traces are partially filled with sediment that masks their full sectional morphology (e.g., Fig. 4.3).

Results of cutting tests.—The cutting tests were conducted with a serrated blade and two types of synthetic substrates (see Methods). The results of these tests are shown in Figure 2. Only the blade edge–substrate contacts were studied, and therefore the results may be relevant only for some of the studied *Linichnus* traces (see Serration and striations of *Linichnus*).

The cuts illustrated in Figure 2.3, 2.4 resulted from the blade edge penetrating the substrate and passing through (Fig. 2.2). Figure 2.6, 2.7 shows cuts that resulted from the blade entering the substrate (parallel to denticulated edge), stopping within the substrate, and then lifting off, without further surface modification (Fig. 2.5). The cuts in Figure 2.9, 2.10, 2.12, 2.13 resulted from the blade entering the substrate as in Figure 2.3, 2.4, 2.6, 2.7. The blade stopped in these cases (see Fig. 2.9, 2.10, 2.12, 2.13) within the substrate (as in Fig. 2.6, 2.7) but then left it with a sideways movement (Fig. 2.8, 2.11; perpendicular to the denticulated edge). The cuts from Figure 2.9, 2.10, 2.12, 2.13 differ from each other in the angles at which the blade entered and left the substrate. Figure 2.12, 2.13 depicts lower angles (see also Erickson and Olson, 1996 for comments on tooth–bone contact angle).

Discussion

Serration and striations of Linichnus.—Jacobsen and Bromley (2009) used the term "serration" to describe both uneven edges in *Linichnus* and parallel grooves forming *Knethichnus*. D'Amore and Blumenschine (2009, 2012) used the term "striations" to label grooves of *Knethichnus*-like traces. They did not provide any specific term to describe uneven edges of *Linichnus*-like traces. D'Amore and Blumenschine (2012) used "striation" also to label sets of grooves associated with short *Linichnus*-like traces (their edge marks). Forrest (2003) used the term "striations" to name grooves covering the surface of purported tooth trace left by marine crocodile *Metriorhynchus*. Those grooves, however, were thought to match ridges running from tooth tip toward its base (see Forrest, 2003). Therefore, Forrest's (2003) usage of "striations" was different from that of D'Amore and Blumenschine (2009, 2012), and their usage did not match exactly with that of Jacobsen and Bromley (2009).

Although the meanings of "serration" and "striations" overlap to some degree, these are not complete synonyms. Therefore, I use both terms in the following. However, my usage of "serration" is restricted to uneven edges of *Linichnus* (as in Jacobsen and Bromley, 2009) whereas "striations" applies to sets of elongated grooves (as in D'Amore and Blumenschine, 2009).

Jacobsen (1998, 2003) showed that serration and striations of bite traces and tooth denticles may be matched (in terms of size and density), in some cases aiding in identification of carnivorous species that could have made the bite traces. This link between the tooth denticles and serration/striations of a trace has been highlighted also in other works (e.g., Alexander and Burger, 2001; Jacobsen and Bromley, 2009; Bell et al., 2012; see also D'Amore and Blumenschine, 2012; Drumheller et al., 2020).

D'Amore and Blumenschine (2009) showed that scores were the most frequent (81%) type of bone modifications by Komodo monitors (reptile with ziphodont teeth) in their actualistic study. They concluded also that only 5% of bite traces had striations. Komodo monitors do have distinct tooth denticles on both mesial and distal cutting edges of their teeth. The strong backward tooth curvature makes the contact of their mesial carinae with bone surface very likely; indeed, denticles in these parts of carinae appear particularly worn down (see D'Amore and Blumenschine, 2009, 2012). Interestingly, this actualistic study showed that individual bite traces made with denticulated ziphodont teeth are likely to show no striations at all, and a larger sample may be required to detect their presence. D'Amore and Blumenschine (2009, e.g., fig. 6A) illustrated some scores with uneven edges, features resembling serration of *Linichnus* trace fossils (sensu Jacobsen and Bromley, 2009), but no details were provided on frequency of those features.

Muñiz et al. (2020) contributed experimental data and showed that when a denticulated tooth edge cuts through the substrate (moving along its denticulated edge), irregular serration forms on both sides of the emerging *Linichnus*-like trace. Muñiz et al. (2020) illustrated results of cutting tests performed with one kinetic (edge-parallel) shark tooth and plaster serving as a substrate. Bianucci et al. (2010) used plasticine instead of plaster and different tooth kinetics, including one that was edge perpendicular.

The results presented herein (Fig. 2) match those of Bianucci et al. (2010) in terms of: (1) missing striation in a trace produced via a tooth edge-parallel kinetics and (2) striations/irregular grooves formed within the trace made with the edge-perpendicular tooth kinetics; denticles are not mandatory to form such irregular grooves as the tooth edge imperfections may cause them to form (see Bianucci et al., 2010).

The results presented here match also with the results of D'Amore and Blumenschine (2009, 2012) where the striations required a deviation from the tooth-edge-parallel kinetics to form in bite traces of Komodo monitors. The study of bite traces made by Komodo monitors showed also that smooth transition from the tooth-edge-perpendicular to tooth-edge-parallel kinetics results in a set of distinct striations converging into a single score, and an overall branching pattern is the result (see D'Amore and Blumenschine, 2012).

The edge-parallel tooth kinetics (Fig. 2.2–2.7) failed to replicate serration observed by Muñiz et al. (2020). This is most likely due to different substrates applied in both their tests and those in the present work. Overall, the blade traces obtained during this study are similar (Fig. 2) for both applied types of substrates, despite the differences in their plasticity. Muñiz et al. (2020) used plaster, and therefore it is likely that the serration formed in their tests along edges of *Linichnus*-like groove due to the brittle nature of the substrate they used.

Although it may be unclear how the denticulated edge creates serration along the sides of *Linichnus* during tooth edge–bone contact (as in Muñiz et al., 2020), the way denticles modify the bone is well understood in *Knethichnus* (see D'Amore and Blumenschine, 2009, 2012; Jacobsen and Bromley, 2009; Drumheller et al., 2020). It is a trace fossil formed by dragging a tooth along the bone surface; the tooth movement must not be parallel to its denticulated edge (see D'Amore and Blumenschine, 2012). This way a characteristic regular morphology forms: densely spaced grooves of comparable sizes (see Rogers et al., 2003; D'Amore and Blumenschine, 2009, 2012; Jacobsen and Bromley, 2009). Fine striations may form in bone due to similar kinetics of denticle-free teeth (result of edge defects), but they are irregular and thus distinct from *Knethichnus* (see Bianucci et al., 2010). In the following, I consider two distinct types of tooth–bone interactions that may lead to *Linichnus* formation: tooth tip–bone contacts and tooth edge–bone contacts.

Tooth tip–bone contact.—Some authors have depicted strongly curved (U-shaped grooves), elongated bite traces (hook scores) made by recent crocodylian species (see what are crocodylian taxa in Brochu, 2003, and for their various bit traces, see Njau and Blumenschine, 2006; Drumheller and Brochu, 2014; Njau and Gilbert, 2016). The curved morphology of those hook scores is analogical to that of *Linichnus serratus* holotype, which is a groove following a U-shaped trajectory (see Jacobsen and Bromley, 2009, fig. 2B, C). The teeth making those crocodylian traces (or the one that produced the *Linichnus* holotype) had to change movement direction when gouging the bone to follow their U-like trajectories. A plausible interpretation is that those crocodylian traces (and the holotype of *Linichnus*) might have resulted from an interaction between the tooth tip and bone.

Tooth tip–bone contact would most likely grant higher freedom of movement than the tooth edge–bone contact, for which any deviation from tooth edge-parallel movement would result in *Knethichnus* morphology rather than *Linichnus* (see D'Amore and Blumenschine, 2012). Therefore, *Linichnus* resulting from tooth tip–bone contact could display more curved or even winding trajectories of the groove (see Fig. 4.2).

The U-shaped cross section should also aid in differentiation between traces made with tooth tip and those produced with a tooth's narrow cutting edge (see Fig. 4.6). This is because a sharp-edged tool cuts bone forming a narrow groove (V-shaped cross sections), whereas the action of a blunt cutting tool results in a wider groove (U-shaped cross section; Fig. 6.1; see Mate-Gonzalez et al., 2016).

The hook scores and other scores made by extant crocodylians display commonly irregular serration along their edges (see Njau and Blumenschine, 2006, fig. 6A; Drumheller and Brochu, 2014, fig. 3). Those crocodylian traces resemble the *Linichnus* holotype in this respect (see Jacobsen and Bromley, 2009) and the traces from the Grabowa Formation illustrated in Figure 4.6. Serrations along fossil *Linichnus* edges are interpreted as traces of denticles (see, e.g., Jacobsen and Bromley, 2009). Extant crocodylians, however, do not have denticulated teeth (see Erickson et al., 2003; Njau and Blumenschine, 2006) but still produce serrated scores and furrows. Therefore, the origin of serrated edges of those traces is likely unrelated to the tooth-edge morphology, in contrast to bisected pits, punctures, or striations in scores and furrows; their morphology may owe its origin to carinae or denticles of ziphodont teeth (see, e.g., Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009, 2012; Vasconcelos and Carvalho, 2010; Njau and Gilbert, 2016). In addition, there is no *Knethichnus*-like component associated with the crocodylian-made traces of *Linichnus*-type morphology or the *Linichnus* holotype itself (see Jacobsen and Bromley, 2009; compare D'Amore and Blumenschine, 2012). For this reason, tooth denticulated edges most likely did not participate in the production of any of those bone modifications, and the tooth tip–bone contact is the likely scenario (compare Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009, 2012; Jacobsen and Bromley, 2009; Drumheller and Brochu, 2014; Njau and Gilbert, 2016).

The "tooth tip contact" interpretation could be applied to winding *Linichnus bromleyi* from Figure 3.2 and *Linichnus serratus* (a) from Figures 3.1 and 4.6. If those bite traces indeed originated due to tooth tip–bone contacts, how then can the serration along edges in *Linichnus serratus* (a) traces be explained?

Associations of pits (snags) and scores made by crocodylians (see Njau and Blumenschine, 2006; Drumheller and Brochu, 2014; Njau and Gilbert, 2016) may offer an explanation applicable to tooth tip-made curved, winding traces and/or those having U-shaped cross sections (see Fig. 4.6). Those crocodylian pits (*Nihilichnus*-like traces) are superimposed over scores (*Linichnus*-like traces) and may form a serration-like pattern along the trace edges if their spacing is dense enough. The pattern occurs on both sides of the main groove and is comparable to serration of *Linichnus* holotype (Jacobsen and Bromley, 2009). Some of those superimposed pits show bisected morphologies indicating that indeed it was the tooth tip that punctured and gouged the bone (compare Njau and Blumenschine, 2006; Njau and Gilbert, 2016).

It is proposed here, from comparison with crocodylian bites, that the serration along the edges of *Linichnus serratus* (a) from the Grabowa Formation (Figs. 3.1, 4.6) might have resulted from interrupted movement of the tooth along its path during a tooth tip–bone interaction (Fig. 6.1). The shallow repetitive pits making the serrated edges would represent short pauses in the tooth movement during which the vertical force(s) would temporarily prevail over those trying to pull the tooth along the bone surface (see Figs. 4.6, 6.1). According to the proposed interpretation, the smooth edges of *L. bromleyi* (Fig. 4.2) may suggest that the vertical force component could be negligible (no impact on trace morphology) and that dragging forces dominated the tooth when gouging the bone. In conclusion, crocodylian-made associations of scores and pits (see Binford, 1981; Njau and Gilbert, 2016) support the view that *L. serratus* (a) from the Grabowa Formation may result from a trade between bone-vertical and bone-parallel tooth kinetics.

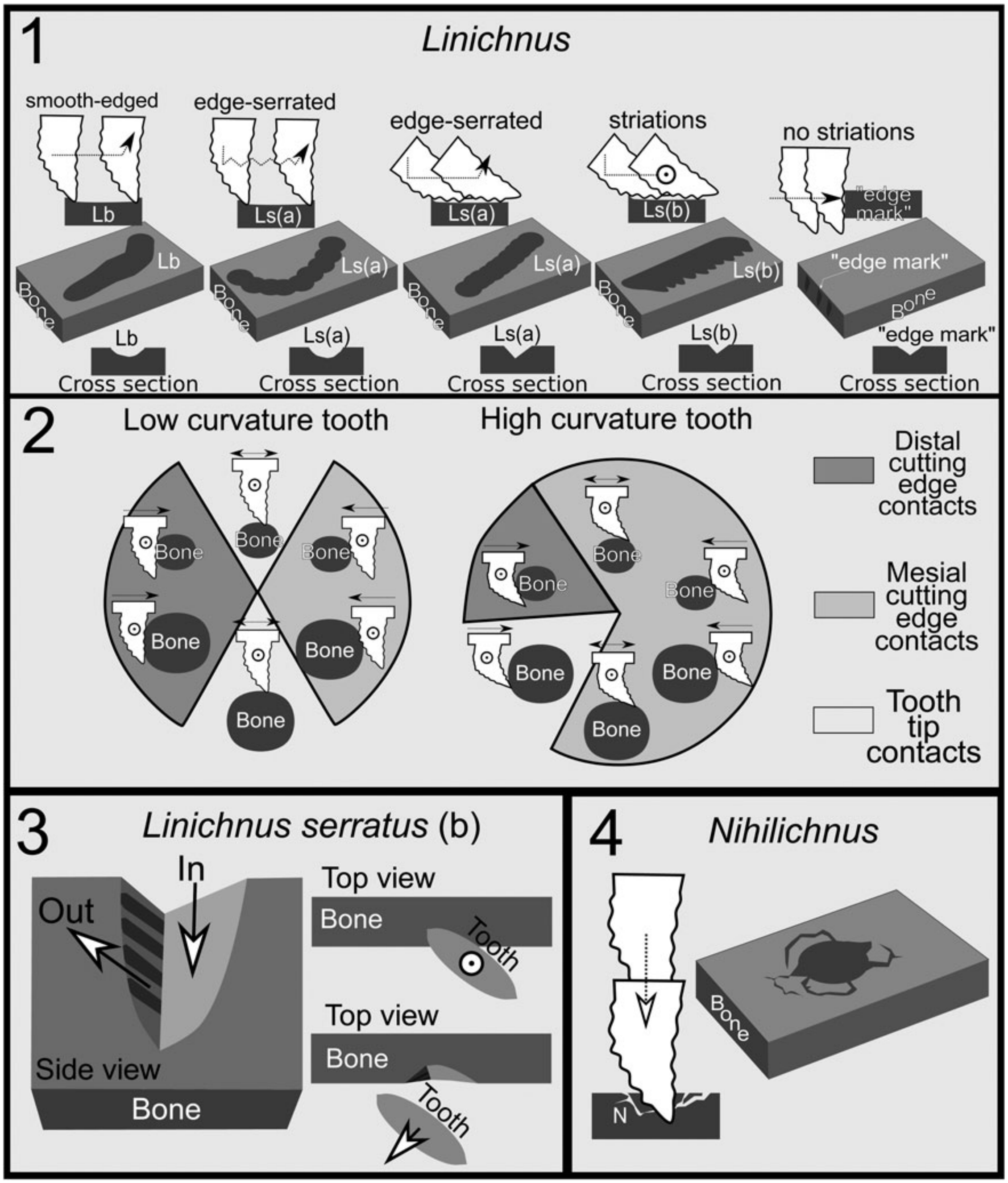

Figure 6. Tooth kinetics and plausible bite trace morphologies. (**1**) *Linichnus* may form due to both tooth tip–bone and tooth edge–bone interaction. Curved versus straight *Linichnus* trajectories and their cross-sectional geometries (see cut cross sections in Mate-Gonzalez et al., 2016) may aid in differentiation between the two contact scenarios. The edge mark is a type of short *Linichnus* (typically without striations) formed due to a distal carina of tooth contacting narrow edge of bone (see D'Amore and Blumenschine, 2012). (**2**) Possible configurations are shown of tooth–bone contacts involving mesial, distal cutting edges (carinae) and tooth tips (teeth in all cases shown in side views). Feasibility of distal cutting-edge contact is lower for curved tooth. Low- and high-curvature teeth and two bone elements differing in cross-sectional areas are considered. Note that adjacent teeth are ignored here, but dental spacing would allow only bones of certain maximal sizes to slip between the teeth. This could limit the mesial and distal cutting-edge contacts to those bone elements that fit in between. (**3**) *Linichnus serratus* (b): formation and morphology ("In" and "Out" refer to the tooth movement in respect to the bone). Top and side views are illustrated for the tooth–bone interaction. The trace is thought to form due to tooth edge–bone contact. (**4**) Tooth kinetics and morphology of *Nihilichnus* with a zone of fractured bone around. Dashed arrows in all depict the general tooth kinetics, and block diagrams show simplified morphologies of resulting traces and their sectional views. Circles with dots are movement vectors (arrow heads are directed toward the page), perpendicular (in (**1**) and (**2**)) and parallel (in (**3**)) to the cutting edges of the teeth (or tooth symmetry plain). Abbreviations used in the figures: Lb = *Linichnus bromleyi*; Ls(a) = *Linichnus serratus* (a); Ls(b) = *Linichnus serratus* (b); N = *Nihilichnus*.

Tooth edge–bone contact.—Tooth edge cutting the bone typically forms a straight groove (following the shape of the edge) with or without serration along its edges (see Fig. 2.1; D'Amore and Blumenschine, 2009, 2012; Bianucci et al., 2010; Muñiz et al., 2020). Some of the short and straight *Linichnus* traces (*L. serratus* (b); see Table 1 and Fig. 5.1, 5.16–5.21) show distinct V-shaped cross sections and fine, trace-axis-perpendicular striation along one of their edges (see

Fig. 5.16–5.21; compare Jacobsen and Bromley, 2009, fig. 2A). These are likely to have formed through cutting-edge contact with bone. Ziphodont tooth may contact bone with mesial or distal cutting edge (carina). D'Amore and Blumenschine (2009, 2012) illustrated short bite traces of Komodo monitors (edge marks) they thought almost certainly formed when the distal carina of the last tooth contacted the edge of bone (e.g., rib) or when a thin bone element slipped between adjacent teeth.

The teeth of the Komodo monitor get shorter toward the back of its jaws. Those at the very back are short and strongly curved backward. Their distal cutting edges have almost no straight parts, making the contact with bone difficult (see D'Amore and Blumenschine, 2009, 2012). The lodging of those rear teeth against the bone appears an unlikely scenario or at least a rare event. However, formation of clusters of parallel edge marks (see D'Amore and Blumenschine, 2009, fig. 7A) would require repetitive tooth–bone contacts. Longer teeth that Komodo monitors have in the middle of their snouts seem to be better suited to produce such clusters in repetitive bites ; their distal cutting edges have straight parts to modify the bone.

Figure 6.2 shows how tooth curvature and size of bone (in relation to the tooth's size and its curvature) may affect the feasibility of mesial and distal carina contacts. The low-curvature teeth are likely to easily engage in tooth-tip contacts (the bone does not need to fit between adjacent teeth to make this contact). Mesial- and distal-edge contacts may easily take place for low-curvature teeth as long as the bone fragment is small enough to slip between the adjacent teeth. The relatively large size of bone when compared with the tooth may hinder distal cutting-edge contacts in high-curvature teeth where, due to a backward movement of the head, tooth tip may contact bone surface first and prevent subsequent proper contact with the tooth cutting edge. The tooth-tip contacts are thought to be hindered for high-curvature teeth. Their tips are directed backward, not ventrally. The high-curvature teeth may easily contact bone with their mesial cutting edges, most likely with the backwardly curved part of their mesial carinae. The curvature brings that part of the mesial cutting edge to a more ventral position. Ziphodonts, strongly curved teeth of Komodo monitors, may be good examples of this; the teeth are heavily worn down in respective parts of their mesial carinae (see D'Amore and Blumenschine, 2012). In general, distal carina contacts require bone to fit between adjacent teeth or to contact the distal carina of the last tooth in the row (see D'Amore and Blumenschine, 2009, 2012). Contact between bone and distal tooth carina is thought to become increasingly less feasible than that with mesial carina with increasing tooth backward curvature (Fig. 6.2).

Entrapment of a bone element between adjacent teeth should result in a set of bite traces on both sides of that element: one resulting from bone contact with distal and one with mesial carina of adjacent teeth. However, no such set of *L. serratus* (b) is distinguishable in the studied material (see Fig. 5).

The straight shape of the grooves ascribed to *L. serratus* (b) and their striation pattern (including its presence along one edge of the trace) could be explained by the tooth-edge contact scenario (see Fig. 5.16–5.21). Results of the performed cutting tests (Fig. 2) may help to match the bite morphology with the tooth kinetics.

Cuts illustrated in Figure 2.9, 2.10, 2.12, 2.13 show morphologies comparable to *L. serratus* (b); the cuts display striation along one of their edges emanating from the axis toward the edge of each cut (trace-axis perpendicular). Morphologies of cuts from Figure 2.12, 2.13, due to their distinct V-shaped cross sections, are especially similar to the studied *L. serratus* (b). Kinetics similar to those from Figure 2.8, 2.11 are proposed herein as models for tooth kinetics that produced *L. serratus* (b) from the Grabowa Formation (see Fig. 5.1, 5.16–5.21).

D'Amore and Blumenschine (2012, fig. 3D) illustrated a cast of Komodo monitor-made edge mark with striations. The pattern, as in *L. serratus* (b), resembled grooves of *Knethichnus*. Therefore, formation of the edge marks likely required not only that the tooth edge contact the bone (see D'Amore and Blumenschine, 2009, see fig. 10C therein) but also that the tooth kinetic include a movement component at an angle to the denticulated tooth edge (see Fig. 6.1; compare D'Amore and Blumenschine, 2012). The denticles on the distal cutting edge of a tooth would most likely produce *Knethichnus*-like striations in an edge mark during the initial phase of tooth–bone contact, when the tooth exerted force on the bone due to the head being pulled backward. This kinetics seems to be different from the one proposed here for *L. serratus* (b). Most of the edge marks made by Komodo monitors show no striations (see D'Amore and Blumenschine, 2009). Thus, detailed interpretation and comparison is hindered for the tooth–bone interactions and the tooth kinetics.

Potential tracemakers.—Morphologically fairly uniform conical teeth, like those filling jaws of extant and extinct carnivorous reptiles (including reptilian ancestors of mammals; see, e.g., Benton, 2005), might contact bones and modify their surfaces through a tooth tip–bone or a tooth edge–bone contact, leaving various traces (see, e.g., D'Amore and Blumenschine, 2009, 2012; Njau and Gilbert, 2016). In contrast to bites made by mammalian carnivores, those of reptiles are typically morphologically plain, representing pits, punctures, scores, and furrows not unique enough to allow easy identification of the tracemakers (see Murmann et al., 2006; Smits and Evans, 2012; Evans and Pineda-Munoz, 2018).

However, a study by Aramendi et al. (2017) shows that even pits made by various reptilian and mammalian carnivores may be distinguished with dedicated three-dimensional modeling and visualization techniques (see also Pante et al., 2017; Souron et al., 2019). Bite traces made by recent large carnivorous reptiles on bones match the general morphologies of traces studied in the current fossil sample comprising *Linichnus* and *Nihilichnus* ichnogenera from the Grabowa Formation (compare Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009; Westaway et al., 2011; Baquedano et al., 2012; Drumheller and Brochu, 2014; Njau and Gilbert, 2016).

The Grabowa Formation has provided bone fragments of various reptiles, including carnivorous archosaurs and herbivores—dicynodontids (see, e.g., Niedźwiedzki et al., 2011; Sulej et al., 2011; Niedźwiedzki and Budziszewska-Karwowska, 2018; Sulej and Niedźwiedzki, 2018). The skeletal remains recovered from the formation included teeth of semi-aquatic and fully terrestrial carnivorous archosaurs, such as phytosaurs and plausible large theropods, respectively (see Niedźwiedzki et al., 2010; Sulej et al., 2011; Niedźwiedzki and Budziszewska-Karwowska, 2018). Fossilized tracks from the Grabowa Formation render a fauna composition image matching the one emerging from the bone findings, which indicates the presence of archosaurs and dicynodontids (see Sadlok and Wawrzyniak, 2013). Overall, the makers of studied bite traces are likely to be found among carnivorous archosaurs whose fossil remains and footprints have been recovered from the deposits of the unit (including plausible theropods; see also Niedźwiedzki et al., 2010).

Carnivorous feeding strategies and bite traces.—A predator kills its prey to feed. Therefore, it may put selective pressure on the population of its prey species by removing some genes from the pool (see, e.g., Berryman, 1992; Lima, 1998). Scavengers employ an opportunist strategy by feeding on carcasses found in the environment. A scavenger, in contrast to a predator, does not exert selective pressure on the population of animals it feeds on. This highlights the importance, especially in the paleoecological context, of distinguishing between true predichnia (see Carpenter, 1998) and postmortem feeding tooth traces, including scavenging (compare Vallon et al., 2016).

Despite the fundamental differences between predatory and nonpredatory carnivorous ethologies, predation and scavenging may be practiced by the same species (see, e.g., Jędrzejewska and Jędrzejewski, 2001; Ordiz et al., 2020). Not surprisingly, one carnivore may produce predichnia and/or nonpredatory, postmortem feeding bites, depending on the chosen strategy and performed behavior.

Disentanglement between the bio- and ichnotaxa is a well-known phenomenon in the realm of trace fossils (compare Bromley, 1990). Traces of predator(s) are not necessarily traces of predation as a predator may kill and then feed on the pray, leaving bite traces one could associate with predatory and with postmortem feeding behaviors, respectively. The general feeding strategy a carnivore applies may depend on the prey/carcass availability in the environment; increased mortality may favor scavenging, as carcasses could be a predictable food source and are certainly easier to catch than living prey (see, e.g., Henschel and Skinner, 1990; Jędrzejewska and Jędrzejewski, 2001).

Ethology of bite traces from the Grabowa Formation.—Tooth-marked bones from the Grabowa Formation have previously been reported and provided some data on trophic interactions. Work by Budziszewska-Karwowska et al. (2010) and the subsequent paper by Niedźwiedzki et al. (2010) both assessed bite traces on bones assignable exclusively to the first-order consumers of this Late Triassic habitat, the so-called dicynodontids, which were unique large-bodied reptiles (see Cox and Parrington, 1965; Thulborn and Turner, 2003; Wawrzyniak, 2010).

Niedźwiedzki et al. (2010) postulated that the bite marks they studied represented predichnia left by large theropods on dicynodontid bones (see also Sulej and Niedźwiedzki, 2018). However, supporting evidence of predation was missing. Moreover, the circular outline of some bites (*Nihilichnus*; see Niedźwiedzki et al., 2010, fig. 1H) was not typical of the trace made by narrow teeth of theropods (see Avilla et al., 2004; Smith et al., 2005), including teeth from the same formation (see Niedźwiedzki and Budziszewska-Karwowska, 2018).

Budziszewska-Karwowska et al. (2010) made a detailed size analysis of various bite traces and their spacing on a single dicynodontid limb to infer a minimal number of tracemakers involved. They analyzed the possible impact of jaw–bone kinetics on the inferred dental spacing and concluded that the specimen could have been scavenged as bite traces suggested that more than one size class of carnivores likely fed on the reptile corpse.

Hone and Chure (2018) conducted a similar analysis of spacing between tooth traces and jaw–bone kinetics in their study whereas D'Amore and Blumenschine (2012) applied similar geometrical analysis in their actualistic studies of tooth–bone kinetics and its impact on resulting spacing of striations in bite traces (see also Buffetaut, 1983; Erickson, 1984; Cisneros, 2005; Hone and Watabe, 2010; Noto et al., 2012; Casal at al., 2013; Botfalvai et al., 2014; Hone and Chure, 2018). Works of Budziszewska-Karwowska et al. (2010) and D'Amore and Blumenschine (2012) show that spacing of tooth traces and spacing of striations in most cases are poor indices of interdental and interdenticle spacing. Both works showed also that spacing of tooth traces and striations may be used as proxies of minimal interdental and minimal interdenticle spacing, respectively.

Sarcophagichnia.—The present report includes two tooth-marked bone fragments assignable to carnivorous archosaurs (see Fig. 3.1, 3.2; Table 1; see also Niedźwiedzki and Budziszewska-Karwowska, 2018). These fragmentary bones are the first direct indication of second- or third-order consumers serving as a food source for other meat eaters in that Late Triassic habitat.

According to Niedźwiedzki and Budziszewska-Karwowska (2018), the two bone fragments represent elements of archosaurian pelvic girdles. The belly sides of the animals could be accessible to the carnivores most likely after they had died and were rested on their sides. The location of the bites suggests they are probably not predichnia (killing bite traces) and that the traces were most likely inflicted postmortem due to feeding behavior rather than inter- or intra-specific fights (compare Webb et al., 1983; Jacobsen, 1998; Tanke and Currie, 1998; Avilla et al., 2004; Katsura, 2004; Longrich et al., 2010; Zammit and Kear, 2011; Drumheller et al., 2020).

The upper parts of hindlimbs and tail bases of archosaurs' bodies would be associated with considerable mass of edible muscle tissues (see, e.g., Carrano and Hutchinson, 2002; Schachner et al., 2011). Easily accessible body parts of high muscle content would represent high nutrition value to carnivores (see, e.g., Blumenschine, 1986) and would be likely targeted early during the carcass consumption (see Longrich et al., 2010; Drumheller et al., 2020). However, muscles originating on distal pubis and ischium could be less attractive due to hindered access (hidden under shallower upper hindlimb musculature; see, e.g., pelvis and hindlimb myological reconstruction of archosaur in Schachner et al., 2011).

Data provided by Drumheller et al. (2020, table 4) showed that pectoral and pelvic girdle elements of various tetrapods (including theropods) provided consistently fewer tooth traces than easily accessible ribs of the same tetrapod group—the other high-economy element. A size comparison of muscle origin points on distal pubis and ischium in crocodiles, theropods, and birds (see, e.g., Carrano and Hutchinson, 2002) may also suggest that muscle nutrition value could be low for these distal elements.

The other two bone fragments (Figs. 4, 5) display bite traces of variable sizes, occurring on all the available (preserved) surfaces. Some of the traces (see Fig. 5.4–5.7, 5.11–5.14) appear to form sets of parallel traces (see dashed lines in Fig. 5). Thinner traces (e.g., Fig. 5.5) also display denser packing (smaller trace spacing) than do thicker traces (e.g., Fig. 5.14). It seems reasonable to assume that at least some of those surfaces would be inaccessible for carnivores during lifetimes of the bone-source animals. Those fragments would be still embedded within soft tissues and/or articulated with other bones. Seemingly unrestricted access may suggest that at least some of the bite traces represent wounds inflicted postmortem (compare Forrest, 2003), perhaps even after the bone-containing part of the carcass had been detached from the rest of a corpse, e.g., because of ongoing dismembering that could be due to activity of predator(s) that made the kill and/or scavengers (see comments on carcass reduction in Jacobsen, 1998).

The bite traces on the bone fragments studied herein (Figs. 3–5) most likely represent a record of feeding by carnivorous archosaurs. A new ethological category is proposed herein for these traces to not classify them as predichnia. The category is sarcophagichnia (traces of feeding on a body). The category includes predichnia as a subcategory and is supposed to provide a more neutral way of classifying tooth traces on bones than the predichnia used to (no distinction between predatory and non-predatory tooth traces is needed at this point).

Predichnia.—It is extremely challenging to distinguish between true predatory traces (predichnia) with no signs of healing and postmortem bites (see also Vallon et al., 2016). However, it is worth the effort even though classifying the bite traces can be problematic (see Avilla et al., 2004).

Positive identification of a fatal bite is not trivial, even when it concerns forensic analysis of recent cases (see Chattopadhyay et al., 2013), let alone the fossil material (see Hone and Chure, 2018). The bite location may aid in predichnia identification. Predators may target the throat, neck, head (e.g., felids), abdomen, or tail fin (e.g., sharks) to neutralize the prey, overcome its defensive adaptations, and kill (see Schaller and Vasconcelos, 1978; Steklis and King, 1978; Seidensticker and McDougal, 1993; Clevenger et al., 1994; Antón and Galobart, 1999; Martin et al., 2005; Bianucci et al., 2010; Milàn et al., 2010; Antón et al., 2019). None of the studied bite-trace-bearing bone fragments represent the head or neck area, a plausible target for terrestrial predators using killing bites. Therefore, the location requirements are not met for predichnia.

Another way of identifying predichnia would be to look for signs of bone tissue recovery. Healing is evidence that the bite was not lethal and was inflicted antemortem. Such bone modifications would represent good candidates for true predatory ichnites (see, e.g., Erickson, 1984; Carpenter, 1998; Lebedev et al., 2009; DePalma et al., 2013; Drumheller et al., 2014). However, the present material shows no sign of bone tissue regrowth. Therefore, the supportive evidence for predatory interpretation (predichnia) is missing here.

Necrophagichnia.—The consumption of a small animal does not present any difficulties for carnivorous reptiles, especially if the prey constitutes a food item small enough to be swallowed in one piece. However, larger corpses may require some preswallowing processing, including reduction and defleshing. Those take place postmortem due to activity of the predator(s) and/or scavenger(s) (Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009; Westaway et al., 2011). The fossilized tooth traces that originated on bones during those activities are a record of postmortem feeding behaviors. The proposed ethological category for such trace fossils is necrophagichnia (traces of feeding on an already dead body). The relations between the newly proposed ethological categories/subcategories and predichnia are as follows: sarcophagichnia = predichnia (made by predators only) + necrophagichnia (made by predators and scavengers). The studied bite traces on bones from the Grabowa Formation are found on elements that could represent low nutrition value to carnivores (distal pubis and ischium; compare, e.g., Longrich et al., 2010; Drumheller et al., 2020) and on all preserved surfaces, likely also including those hardly accessible during the animal life (compare, e.g., Forrest, 2003; Longrich et al., 2010). Therefore, the bite traces are interpreted as postmortem feeding and for this reason are classified as necrophagichnia.

Food-processing behavioral patterns and bite traces.—Behavior is a complex and hierarchical phenomenon, and trace fossil morphology may, in some cases, reflect aspects of that hierarchy (see Fürsich, 1974; Miller, 2003). Bite trace fossils are not different. Such ichnites result from tooth and bone interaction, and they may convey a good deal of information on food-processing behavioral patterns that manifested during trace production. Those patterns (e.g., related to teeth and jaw kinetics) may be deciphered from the fossilized material (see, e.g., Fig. 7.1–7.3) with the knowledge of food-processing behavior of recent carnivores and associated tooth traces. Reptiles, such as crocodylians and large varanids, process large food items before swallowing and their teeth leave traces on bones during dismembering and defleshing (see, e.g., Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009; Westaway et al., 2011).

Extant large carnivore archosaurs swallow food items with bones via the so-called inertial feeding mechanism. They execute repetitive cycles of jaw closing–opening and head rising–lowering to pass the food item down the esophagus (see Cleuren and De Vree, 1992, 2000). It is likely that some bite traces form as the food item is repositioned in jaws during inertial feeding. It would be difficult to discern morphologically between such bite traces and those made during dismembering or defleshing. However, it is very likely that bite traces of archosaurs dismembering or defleshing the corpse and those originating during the inertial feeding would have different preservation potential in natural settings and hence representation in fossil material. This is because, contrary to mammalian carnivores, large extant archosaurs have very aggressive stomach acids and food passes slower through their digestive tracts (see Fisher, 1981). They tend to completely digest bones they managed to swallow before they pass stomach content further down into intestines (compare Fisher, 1981; Schmitt and Juell, 1994; Milàn, 2012). As a result, no bone fragments are to be found in extant crocodylian feces (see Milàn, 2012), and any potential bite traces on swallowed

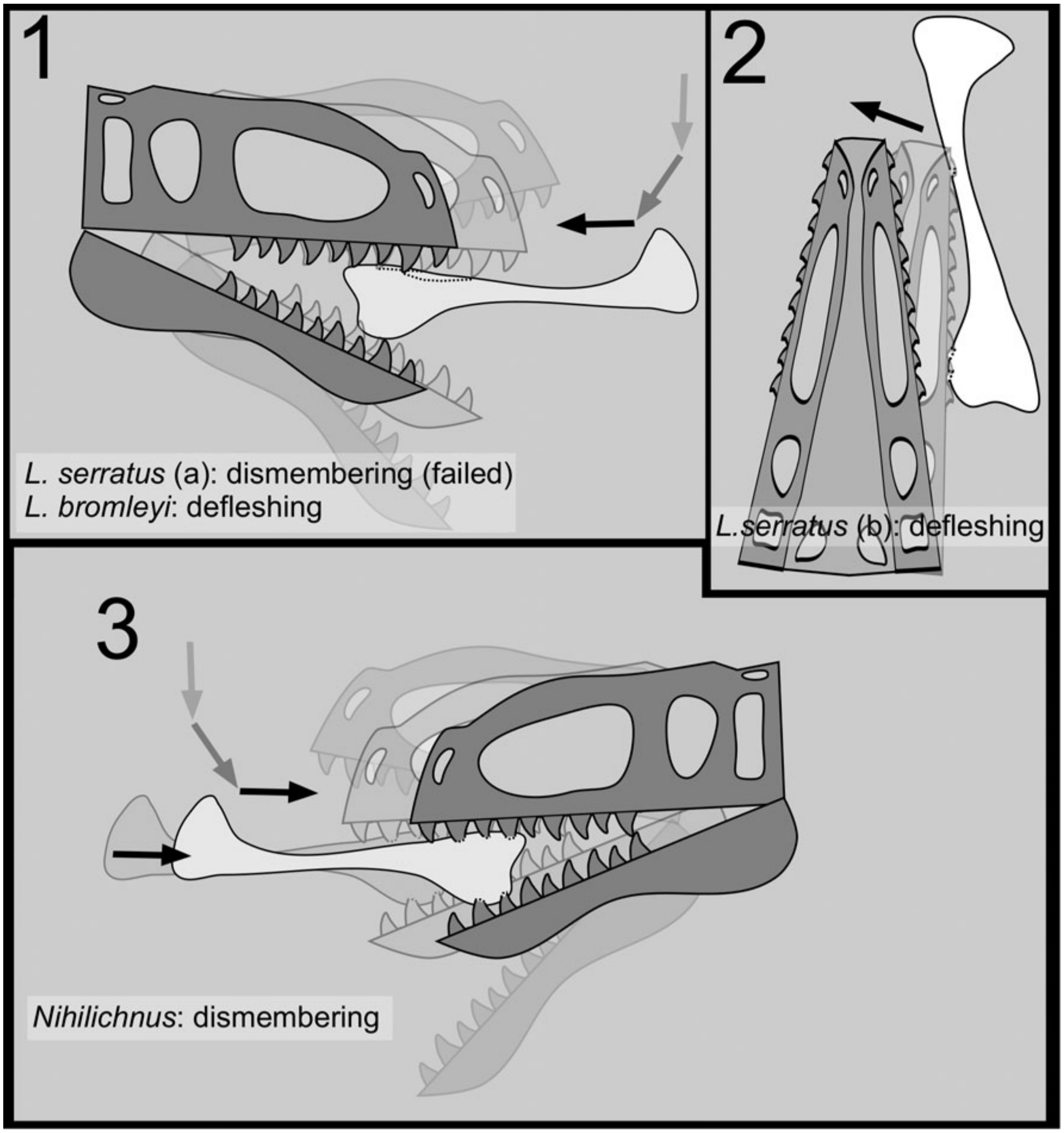

Figure 7. Food-processing behavioral pattern and resulting trace fossil. (**1**) *Linichnus serratus* (a) and *L. bromleyi* as results of dismembering (reduction) and defleshing, respectively; cartoon bone = trace-bearing specimen; cartoon skull = carnivorous archosaur. (**2**) *Linichnus serratus* (b) as a result of defleshing of a corpse (cartoon bone) by a carnivorous archosaur (cartoon skull). (**3**) *Nihilichnus* as a result of dismembering (reduction behavior) of a corpse (cartoon bone) by a carnivorous archosaur (cartoon skull). The fractured zones visible around some *Nihilichnus* traces suggest a large force applied to close the jaw (solid and firm grip on the bone). Arrows show generalized head movement (and bone movement in (**3**)). Note that in (**3**), the skull and the bone move as a unit (no bone gouging; compare with (**1**)).

and digested bones are lost, including those made during inertial feeding. No edge rounding or polishing of bone fragments is observed in studied examples to provide evidence for swallowing and subsequent partial digestion (compare Schmitt and Juell, 1994; Chin et al., 1998). Moreover, some of the studied thin and shallow surficial bite traces (Fig. 4.2) would likely be easily destroyed by the action of digestive acids.

Still, bite traces resulting from inertial feeding could potentially be preserved on abandoned bone elements (if somehow they avoided swallowing). Positive identification of such traces would pose a major challenge in fossil material. As the purpose of inertial feeding is to swallow the food, not abandon it, such instances should be rare. Therefore, a parsimonious approach is taken here, and studied tooth-marked bone fragments are thought to have been abandoned during dismembering and defleshing rather than resulting from inertial feeding.

Nihilichnus *from the Grabowa Formation as a trace of dismembering.*—Data on feeding behaviors of recent large meat-eating reptiles, such as crocodylian species and Komodo monitors (see Njau and Blumenschine, 2006; D’Amore and Blumenschine, 2009; Westaway et al., 2011; Baquedano et al., 2012; Drumheller and Brochu, 2014; Njau and Gilbert, 2016) suggest that the studied *Nihilichnus* (Figs. 3.6, 4.1–4.3) was likely the result of tooth-tip pushing with a vertical force on the bone surface (see also Mikuláš et al., 2006). Such traces, especially those with fractured bone margins (Figs. 3.6, 4.3), may indicate that a significant force was applied to close the jaws (compare Mikuláš et al., 2006).

A forceful bite on the bone could lead to a strong and firm grip on the prey/carcass body; the teeth would be well immobilized (locked) inside the pits they had formed in bone surface, preventing them from slipping off and gouging the bone surface. This way, relative tooth–bone movements are inhibited; teeth (jaws) and the bone move as a single unit (Fig. 7.3). This is a condition mandatory for a successful reduction, a behavior performed to tear the corpse apart and ultimately bring the food item sizes down to manageable pieces, small enough for swallowing and ingestion (see Njau and Blumenschine, 2006).

L. serratus *(a) from the Grabowa Formation as a trace of failed dismembering.—Linichnus serratus* (a) in the present sample (Figs. 3.1, 4.6) also could have formed during reduction behavior. However, contrary to the *Nihilichnus* case, the tooth tips had to grip the bone with insufficient force (compare, e.g., Njau and Gilbert, 2016). In other words, to form *Linichnus serratus* (a), the teeth (jaws) and bone must not move as a single unit (see Fig. 7.1, 7.2). A grip that is too weak would be necessary to allow the teeth to leave the pits they had formed in the bone (compare Taylor, 1987; Njau and Blumenschine, 2006; Njau and Gilbert, 2016). Therefore, fossil *Linichnus serratus* (a) (e.g., Fig. 4.6) may represent a failed grip during a dismemberment attempt (see also “puncture and pull” traces in Erickson and Olson, 1996).

In crocodylians, jaw-closing force could be exceeded by torsional forces appearing during death rolls or due to forces resulting from side-to-side head shakes; both are examples of behavioral patterns associated with reduction. The resulting bite traces on bones resemble *Linichnus* trace fossils, including some (Figs. 3.1, 4.6) from the Grabowa Formation (see Taylor, 1987; Njau and Blumenschine, 2006; Baquedano et al., 2012; Njau and Gilbert, 2016).

Unlike terrestrial carnivores, crocodiles typically reduce their food items in water where they must deal with corpse buoyancy (see Taylor, 1987). They may use forceful side-to-side head shakes or death rolls to reduce a buoyant corpse. The latter behavior is sometimes executed with a kind of cooperation between carnivores; two animals may catch the large corpse on its two ends and execute their death rolls in opposite directions (see Taylor, 1987; Njau and Blumenschine, 2006). Reduction of a corpse resting on land is an easier task than reducing one in water as the land-dwelling carnivores may utilize their limbs and the inertial mass of a corpse itself to stabilize it during reduction and counteract their own pulling forces.

Varanus komodoensis Ouwens, 1912 is an example of a large carnivorous reptile that feeds and processes the corpse on land (see Moreno et al., 2008; D’Amore and Blumenschine, 2009). This carnivore uses its broad snout and sharp, narrow teeth to execute a specific type of medial–caudal strikes on the carcass it feeds upon (see D’Amore and Blumenschine, 2009). The reptile repeats this behavior and removes chunks of flesh using mainly the corpse’s weight to counteract pulling forces generated by the muscle apparatus of its own body (see Moreno et al., 2008; D’Amore and Blumenschine, 2009; D’Amore et al., 2011). Most of the resulting bite traces resemble *Linichnus* and *Knethichnus*, but only a few are like *Nihilichnus* (see D’Amore and Blumenschine, 2009, 2012). This may indicate a true behavioral pattern (avoiding strong biting), but it may also be the result of experimental settings in which Komodo monitors were fed parts of goat prepared (already dismembered to some degree) by researchers (see D’Amore and Blumenschine, 2009). It is also likely that if multiple individuals were feeding on one goat at the same time (compare D’Amore and Blumenschine, 2009), then dismembering could result from competition between them, and perhaps more bite traces of this sort would be observed as a result.

L. serratus *(b) from the Grabowa Formation as a trace of defleshing.*—The analysis of *V. komodoensis* bite traces by D’Amore and Blumenschine (2009, 2012) clearly showed that some *Linichnus*-type traces on fossil bones may result from accidental tooth–bone interactions during defleshing (compare also theropod behavior in Fiorillo, 1991; Jacobsen, 1998). The *L. serratus* (b) traces (Fig. 5.1, 5.16–5.20) with their V-shaped cross sections resemble (in terms of their general morphology) the so-called edge marks made by *V. komodoensis* (D’Amore and Blumenschine, 2009). The data available (see D’Amore and Blumenschine, 2009, 2012) on the internal morphology and striation pattern of those edge marks is sufficient at this stage to allow a gross comparison with the material from the Grabowa Formation. Although detailed interpretation of tooth kinetics for the edge marks is hindered as most of them have no striations, the rare instances where striations are preserved show that some lateral movements were taking place during defleshing effort (see D’Amore and Blumenschine, 2009, 2012). Therefore, this actualistic study showed that bite morphologies combining *Linichnus* (a groove in bone) with *Knethichnus* (striations on bone) may result from defleshing of bone with ziphodont teeth (D’Amore and Blumenschine, 2009, 2012). Similar interpretation may also apply to some bite traces from the Grabowa Formation, with *L. serratus* (b) being a good candidate morphology.

The results of cutting tests (Fig. 2) suggest the tooth making *L. serratus* (b) had to (Fig. 2.8, 2.11): (1) contact and penetrate the surface of bone with its denticulated edge and (2) leave the bone substrate with a sideways movement (compare Bianucci et al., 2010, fig. 1). This particular tooth kinetics may explain striation on one edge of *L. serratus* (b) from the Grabowa Formation and suggests that it may represent a side pull of jaws/head, likely taking place during defleshing behavior (compare Njau and Blumenschine, 2006; D’Amore and Blumenschine, 2012), when the carnivore was targeting soft tissues rather than the bone itself; the tooth–bone contact could be accidental (Fig. 7.2; compare Erickson and Olson, 1996).

L. bromleyi *from the Grabowa Formation as a trace of defleshing.*—The lack of serrated edges and the curved to winding shape of these traces (Fig. 4.2) may suggest negligible vertical forces operated during trace formation, whereas the main force components dragged the tooth along the bone. This suggests that soft tissues could be the target (defleshing). These *L. bromleyi* traces are closely associated with *Nihilichnus* (Fig. 4.1–4.3). This close association may suggest that the *L. bromleyi* are shallow traces due to negligible vertical force gouging bone rather than suboptimal bone density (compare Bell and Currie, 2010; Drumheller and Brochu, 2014).

Feeding strategies and paleohabitat.—Crosscutting of bites (Fig. 5.1, 5.6, 5.11, 5.13) suggests time difference between the bites. It may be due to one individual biting the same spot in a repetitive manner (see D'Amore and Blumenschine, 2009) or more than one individual feeding on the corpse at different times (scavenging involved). The first interpretation may apply when crosscutting bites are of comparable widths (see, e.g., Fig. 5.5). The second interpretation may apply when the sizes of crosscutting bite traces (e.g., depths and widths) are different (see, e.g., Fig. 5.6) and therefore do not favor a multiple-bites scenario; size difference is likely not due to a variation in bone density as bites crosscut each other and modify the same substrate (compare Drumheller and Brochu, 2014).

Sets of parallel bite traces (see Fig. 5) could result from a single bite, and therefore they could convey information on spacing between the tracemaker's teeth. However, repetitive biting on the same spot (by one individual) may decrease the trace spacing below the interdental spacing of the tracemaker (see D'Amore and Blumenschine, 2009). Differentiation between sets emerging due to one bite and those from multiple bites could be difficult (a subtle angular difference could be used for that). Budziszewska-Karwowska et al. (2010) showed that spacing of parallel bite traces is very likely to be smaller than the actual spacing of teeth even if a set originated due to a single bite; the spacing was dependent on jaw-bone kinetics (see also Hone and Chure, 2018).

One might consider both sizes of individual traces and spacing between them to aid interpretation. Thin, densely spaced bites (Fig. 5.5, 5.7) and thicker, less densely spaced traces (Fig. 5.5, 5.13) are very likely products of carnivores having different sizes of jaw apparatuses. If such bites co-occur on a small bone fragment, as in the present case (see Fig. 5), then the variation in sizes of individual bite traces (e.g., depths) is likely not due to variation in bone density (compare Drumheller and Brochu, 2014) but rather reflects different jaw force capabilities of involved carnivores.

The present results supplement previous data on carnivore (scavenger) activity in the Late Triassic paleoecosystem represented by the Grabowa Formation (Budziszewska-Karwowska et al., 2010). A significant number of various bites on some of the specimens (Figs. 4, 5) and their variable sizes, crosscutting relationships, and spacing (e.g., in sets of parallel bite traces; see Fig. 5) may suggest that more than one size class of carnivores fed on and modified the bone surfaces (see Figs. 4, 5; compare Budziszewska-Karwowska et al., 2010). This could reflect predators hunting and feeding in a pack (e.g., individuals at different ontogenetic stages). However, there are no data from the Grabowa Formation to support this possibility (no such potential carnivore recorded yet). Multiple bites on bone fragments also may form due to various carnivores utilizing the carcass for some time (scavenging involved). This scenario seems more likely in the present cases.

The Norian seasonal climate of the study area could periodically become harsh (e.g., during occasional droughts) and increase the mortality rates among vertebrate populations (see, e.g., Szulc et al., 2006, 2015; Szulc, 2007b; Gruszka and Zieliński, 2008; McKie and Williams, 2009; Fijałkowska-Mader et al., 2015; Jewuła et al., 2019). Elevated death rates would result in many carcasses being available, making scavenging an easy and profitable way of subsisting for the carnivores (compare Jędrzejewska and Jędrzejewski, 2001; Drumheller et al., 2020).

Conclusions

This report describes bite traces on bone fragments recovered from the Upper Triassic (Norian) Grabowa Formation from southern Poland (Zawiercie site; Table 1). The bite morphologies represent two ichnogenera: *Linichnus* and *Nihilichnus*. These trace fossils have been analyzed and discussed in terms of their morphological details (serration of *L. serratus* (a) and striation of *L. serratus* (b)), the potential tracemakers, feeding strategies, and food-processing behavioral patterns).

Serration in some of the presented *L. serratus* (a) traces (Fig. 4.6) could be unrelated to denticles covering the cutting edges of the teeth making these traces. The serration may have resulted from tooth tip–bone contacts rather than a tooth edge–bone interaction (no involvement of denticulated tooth edge), possibly from interrupted movement of the tooth along its path when gouging the bone with the tip. Associations of pits and scores made by crocodylian carnivore species as illustrated by Njau and Gilbert (2016) may be recent analogs explaining the formation of such bite traces from the Grabowa Formation (see Fig. 4.6). However, *L. serratus* (b) displays a striation pattern (see Fig. 5.16–15.20) that is compatible with the tooth edge–bone contact scenario (Fig. 2.8–2.13).

The analyzed bite traces record meat-eating behaviors of Late Triassic archosaurs and are classified ethologically as sarcophagichnia (traces of feeding on a body). These bite traces were most likely induced postmortem and would represent feeding trace fossils, here classified as necrophagichnia (traces of feeding on an already dead body). In the proposed scheme, sarcophagichnia comprises both necrophagichnia and predichnia (with respective subcategories; see, e.g., Vallon et al., 2016).

Two fragments of pelvic girdle elements likely represent carnivore archosaurs (Niedźwiedzki and Budziszewska-Karwowska, 2018), and therefore the bite traces on them are likely from carnivores targeting the carcasses of second- or third-order consumers; this is the first such record from the Upper Triassic Grabowa Formation.

In addition, the studied *Nihilichnus*, unlike *Linichnus*, is thought to originate from a solid and a firm grip on the bone, sometimes resulting in fracturing of the bone surface around the trace (see Figs. 3.6, 4.3). The grip could be part of a reduction behavior (dismembering), when the food item had to be brought down to sizes manageable for swallowing and ingestion. Studied *L. serratus* (a) traces may represent insufficient strength of the grip during failed reduction (see, e.g., Figs. 3.1, 4.6). Other interpretations may apply to *L. bromleyi* from the Grabowa Formation (e.g., Fig. 4.2), where the lack of serration/striations and the curved to winding shape of some grooves may suggest the traces resulted from tooth tip–bone interaction but with a negligible contribution from forces acting vertically on the tooth pressing on bone (Fig. 4.2). The studied *L. serratus* (b) traces could have resulted from accidental tooth–bone contacts (see, e.g., Figs. 4.2, 5.3) and may represent defleshing behavior (e.g., targeting of soft tissues rather than the bone). Finally, the seasonal Norian climate could have favored scavenging as a feeding strategy. The periodic droughts could have stimulated the animals' mortality rates and increased the number of carcasses available in the habitat, improving their predictability and usability as a source of nutrients.

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3ffbg79kj

Competing interests

The author declares none.

References

Albert, M., et al., 2010, Inkscape v. 0.47. http://www.inkscape.org

Alexander, J.P., and Burger, B.J., 2001, Stratigraphy and taphonomy of Grizzly Buttes, Bridger Formation, and the middle Eocene of Wyoming, *in* Gunnell, G.H., ed., Eocene Biodiversity: Boston, Springer, p. 165–196.

Antón, M., and Galobart, À., 1999, Neck function and predatory behavior in the scimitar toothed cat *Homotherium latidens* (Owen): Journal of Vertebrate Paleontology, v. 19, p. 771–784.

Antón, M., Siliceo, G., Pastor, J.F., Morales, J., and Salesa, M.J., 2019, The early evolution of the sabre-toothed felid killing bite: the significance of the cervical morphology of *Machairodus aphanistus* (Carnivora: Felidae: Machairodontinae): Zoological Journal of the Linnean Society, v. 188, p. 319–342.

Aramendi, J., Maté-González, M.A., Yravedra, J., Ortega, M.C., Arriaza, M.C., González-Aguilera, D., Baquedano, E., and Domínguez-Rodrigo, M., 2017, Discerning carnivore agency through the three-dimensional study of tooth pits: revisiting crocodile feeding behaviour at FLK-Zinj and FLK NN3 (Olduvai Gorge, Tanzania): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 488, p. 93–102.

Avilla, L.S., Fernandes, R., and Ramos, D.F.B., 2004, Bite marks on a crocodylomorph from the Upper Cretaceous of Brazil: evidence of social behavior?: Journal of Vertebrate Paleontology, v. 24, p. 971–973.

Baquedano, E., Domínguez-Rodrigo, M., and Musiba, C., 2012, An experimental study of large mammal bone modification by crocodiles and its bearing on the interpretation of crocodile predation at FLK Zinj and FLK NN3: Journal of Archaeological Science, v. 39, p. 1728–1737.

Bell, P.R., and Currie, P.J., 2010, A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism?: Lethaia, v. 43, p. 278–281.

Bell, P.R., Currie, P.J., and Lee, Y.N., 2012, Tyrannosaur feeding traces on *Deinocheirus* (Theropoda: ?Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia: Cretaceous Research, v. 37, p. 186–190.

Benton, M.J., 2005, Vertebrate Palaeontology (third edition): Oxford, Blackwell, 455 p.

Berryman, A.A., 1992, The origins and evolution of predator–prey theory: Ecology, v. 73, p. 1530–1535.

Bianucci, G., Sorce, B., Storai, T., and Landini, W., 2010, Killing in the Pliocene: shark attack on a dolphin from Italy: Palaeontology. v. 53, p. 457–470.

Binford. L.R., 1981, Bones: Ancient Men and Modern Myths: New York, Academic Press, 320 p.

Blumenschine, R.J., 1986, Carcass consumption sequences and the archaeological distinction of scavenging and hunting: Journal of Human Evolution, v. 15, p. 639–659.

Blumenschine, R.J., Marean, C.W., and Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces: Journal of Archaeological Science, v. 23. p. 493–507.

Boaz, N.T., Ciochon, R.L., Xu, Q., and Liu, J., 2000, Large mammalian carnivores as a taphonomic factor in the bone accumulation at Zhoukoudian: Acta Anthropologica Sinica, v. 19, p. 224–234.

Botfalvai, G., Prondvai, E., and Ősi, A., 2014, Inferred bite marks on a Late Cretaceous (Santonian) bothremydid turtle and a hylaeochampsid crocodilian from Hungary: Cretaceous Research, v. 50, p. 304–317.

Brochu, C.A., 2003, Phylogenetic approaches toward crocodylian history: Annual Review of Earth and Planetary Sciences, v. 31, p. 357–397.

Bromley, R.G., 1990, Trace Fossils: Biology and Taphonomy: London, Unwin Hyman, 280 p.

Budziszewska-Karwowska, E., Bujok, A., and Sadlok, G., 2010, Bite marks on an Upper Triassic dicynodontid tibia from Zawiercie, Krakow-Częstochowa Upland, southern Poland: Palaios, v. 25, p. 415–421.

Buffetaut, E., 1983, Wounds on the jaw of an Eocene mesosuchian crocodilian as possible evidence for the antiquity of crocodilian intraspecific fighting behaviour: Paläontologische Zeitschrift, v. 57, p. 143–145.

Carpenter, K., 1998, Evidence of predatory behavior by carnivorous dinosaurs: Gaia, v. 15, p. 135–144.

Carrano, M.T., and Hutchinson, J.R., 2002, Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda): Journal of Morphology, v. 253, p. 207–228.

Casal, G.A., Martínez, R.D., Ibiricu, L.M., Riga, B.G., and Foix, N., 2013, Tafonomía del dinosaurio terópodo *Aniksosaurus darwini*, Formación Bajo Barreal, Cretácico Tardío de Patagonia (Argentina): Ameghiniana, v. 50, p. 571–592.

Chattopadhyay, S., Shee, B., and Sukul, B., 2013, Fatal crocodile attack: Journal of Forensic and Legal Medicine, v. 20, p. 1139–1141.

Chin, K., Tokaryk, T.T., Erickson, G.M., and Calk, L.C., 1998, A king-sized theropod coprolite: Nature, v. 393, p, 680–682.

Cisneros, J.C., 2005, New Pleistocene vertebrate fauna from El Salvador: Revista Brasileira de Paleontologia, v. 8, p. 239–255.

Cleuren, J., and De Vree, F., 1992, Kinematics of the jaw and hyolingual apparatus during feeding in *Caiman crocodilus*: Journal of Morphology, v. 212, p. 141–154.

Cleuren, J., and De Vree, F., 2000, Feeding in crocodilians, *in* Schwenk, K., ed., Feeding: Form, Function, and Evolution in Tetrapod Vertebrates: London, Academic Press, p. 337–358.

Clevenger, A.P., Campos, M.A., and Hartasanchez, A., 1994, Brown bear *Ursus arctos* predation on livestock in the Cantabrian Mountains, Spain: Acta Theriologica, v. 39, p. 267–278.

Collareta, A., Lambert, O., Landini, W., Di Celma, C., Malinverno, E., Varas-Malca, R., Urbina, M., and Bianucci, G., 2017, Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 469, p. 84–91.

Cox, C.B., and Parrington, F.R., 1965, New Triassic dicynodonts from South America, their origins and relationships: Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, v. 248, p. 457–514.

D'Amore, D.C., and Blumenschine, R.J., 2009, Komodo monitor (*Varanus komodoensis*) feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology: Paleobiology, v. 35, p. 525–552.

D'Amore, D.C., and Blumenschine, R.J., 2012, Using striated tooth marks on bone to predict body size in theropod dinosaurs: a model based on feeding observations of *Varanus komodoensis*, the Komodo monitor: Paleobiology, v. 38, 79–100.

D'Amore, D.C., Moreno, K., McHenry, C.R., and Wroe, S., 2011, The effects of biting and pulling on the forces generated during feeding in the Komodo dragon (*Varanus komodoensis*): PLoS ONE, v. 6, e26226, https://doi.org/10.1371/journal.pone.0026226

DePalma, R.A., Burnham, D.A., Martin, L.D., Rothschild, B.M., and Larson, P.L., 2013, Physical evidence of predatory behavior in *Tyrannosaurus rex*: Proceedings of the National Academy of Sciences: v. 110, p. 12560–12564.

Drumheller, S.K., and Brochu, C.A., 2014, A diagnosis of *Alligator mississippiensis* bite marks with comparisons to existing crocodylian datasets: Ichnos, v. 21, p. 131–146.

Drumheller, S.K., and Brochu, C.A., 2016, Phylogenetic taphonomy: a statistical and phylogenetic approach for exploring taphonomic patterns in the fossil record using crocodylians: Palaios, v. 31, p. 463–478.

Drumheller, S.K., Stocker, M.R., and Nesbitt, S.J., 2014, Direct evidence of trophic interactions among apex predators in the Late Triassic of western North America: Naturwissenschaften, v. 101, p. 975–987.

Drumheller, S.K., McHugh, J.B., Kane, M., Riedel, A., and D'Amore, D.C., 2020, High frequencies of theropod bite marks provide evidence for feeding, scavenging, and possible cannibalism in a stressed Late Jurassic ecosystem: PLoS ONE, v15, e0233115, https://doi.org/10.1371/journal.pone.0233115

Drymala, S.M., Bader, K., and Parker, W.G., 2021, Bite marks on an aetosaur (Archosauria, Suchia) osteoderm: assessing Late Triassic predator–prey ecology through ichnology and tooth morphology: Palaios, v. 36, p. 28–37.

Dzik, J., Sulej, T., and Niedźwiedzki, G., 2008, A dicynodont–theropod association in the latest Triassic of Poland: Acta Palaeontologica Polonica, v. 53, p. 733–738.

Ekdale, A., 1985, Paleoecology of the marine endobenthos: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 50, p. 63–81.

Erickson, B.R., 1984. Chelonivorous habits of the Paleocene crocodile *Leidyosuchus formidabilis*: Scientific Publications of the Science Museum of Minnesota, v. 5, p. 3–9.

Erickson, G.M., and Olson, K.H., 1996, Bite marks attributable to *Tyrannosaurus rex*: preliminary description and implications: Journal of Vertebrate Paleontology, v. 16, p. 175–178.

Erickson, G.M., Lappin, A.K., and Vliet, K.A., 2003, The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*): Journal of Zoology, v. 260, p. 317–327.

Evans, A.R., and Pineda-Munoz, S., 2018, Inferring mammal dietary ecology from dental morphology, *in* Croft, D.A., Su, D.F., and Simpson, S.W., eds., Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities: Cham, Springer, p. 37–51.

Fijałkowska-Mader, A., Heunisch, C., and Szulc, J., 2015, Palynostratigraphy and palynofacies of the Upper Silesian Keuper (southern Poland): Annales Societatis Geologorum Poloniae, v. 85, p. 637–661.

Fiorillo, A.R., 1991, Prey bone utilization by predatory dinosaurs: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 88, p. 157–166.

Fisher, D.C., 1981, Crocodilian scatology, microvertebrate concentrations, and enamel-less teeth: Paleobiology, v. 7. p. 262–275.

Forrest, R., 2003, Evidence for scavenging by the marine crocodile *Metriorhynchus* on the carcass of a plesiosaur: Proceedings of the Geologists' Association, v. 114, p. 363–366.

Fürsich, F.T., 1974, On *Diplocraterion* Torell 1870 and the significance of morphological features in vertical, spreiten-bearing, U-shaped trace fossils: Journal of Paleontology, v. 48, p. 952–962.

Gruszka, B., and Zieliński, T., 2008, Evidence for a very low-energy fluvial system: a case study from the dinosaur-bearing Upper Triassic rocks of Southern Poland: Geological Quarterly, v. 52, p. 239–252.

Henschel, J.R., and Skinner, J.D., 1990, The diet of the spotted hyaenas *Crocuta crocuta* in Kruger National Park: African Journal of Ecology, v. 28, p. 69–82.

Hone, D.W.E., and Chure, D.J., 2018, Difficulties in assigning trace makers from theropodan bite marks: an example from a young diplodocoid sauropod: Lethaia, v. 51, p. 456–466.

Hone, D.W.E., and Watabe, M., 2010, New information on scavenging and selective feeding behaviour of tyrannosaurids: Acta Palaeontologica Polonica, v. 55, p. 627–634.

Jacobsen, A.R., 1998, Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones: Historical Biology, v. 13, p. 17–26.

Jacobsen, A.R., 2003, Predatory behaviour of carnivorous dinosaurs: ecological interpretations based on tooth marked dinosaur bones and wear patterns of theropod teeth: Judith River Group (Upper Cretaceous, Campanian), Alberta, Canada [Ph.D. thesis]: Aarhus, University of Aarhus, 79 p.

Jacobsen, A.R., and Bromley, R.G., 2009, New ichnotaxa based on tooth impressions on dinosaur and whale bones: Geological Quarterly, v. 53, p. 373–382.

Jędrzejewska, B., and Jędrzejewski, W., 2001, Ekologia zwierząt drapieżnych Puszczy Białowieskiej: Warsaw, Wydawnictwo Naukowe PWN, 461 p.

Jewuła, K., Matysik, M., Paszkowski, M., and Szulc, J., 2019, The Late Triassic development of playa, gilgai floodplain, and fluvial environments from Upper Silesia, southern Poland: Sedimentary Geology, v. 379, p. 25–45.

Katsura, Y., 2004, Paleopathology of *Toyotamaphimeia machikanensis* (Diapsida, Crocodylia) from the Middle Pleistocene of central Japan: Historical Biology, v. 16, p. 93–97.

Kimball, S., Mattis, P., and GIMP Development Team, 2008, Gimp v. 2.6.8, http://www.gimp.org/

Lebedev, O.A., Mark-Kurik, E., Karatajūtė-Talimaa, V.N., Lukševičs, E., and Ivanov, A., 2009, Bite marks as evidence of predation in early vertebrates: Acta Zoologica, v. 90, p. 344–356.

Lima, S.L., 1998, Nonlethal effects in the ecology of predator–prey interactions: Bioscience, v. 48, p. 25–34.

Longrich, N.R., Horner, J.R., Erickson, G.M., and Currie, P.J., 2010, Cannibalism in *Tyrannosaurus rex*: PLoS ONE, v. 5, e13419, https://doi.org/10.1371/journal.pone.0013419

Martin, R.A., Hammerschlag, N., Collier, R.S., and Fallows, C., 2005, Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa: Journal of the Marine Biological Association of the United Kingdom, v. 85, p. 1121–1136.

Mate-Gonzalez, M.A., Palomeque-Gonzalez, J.F., Yravedra, J., Gonzalez-Aguilera, D., and Dominguez-Rodrigo, M., 2016, Micro-photogrammetric and morphometric differentiation of cut marks on bones using metal knives, quartzite, and flint flakes: Archaeological and Anthropological Sciences, v. 10, p. 805–816.

McKie, T., and Williams, B., 2009, Triassic palaeogeography and fluvial dispersal across the Northwest European Basins: Geological Journal, v. 44, p. 711–741.

Mikuláš, R., Kadlecová, E., Fejfar, O., and Dvořák, Z., 2006, Three new ichnogenera of biting and gnawing traces on reptilian and mammalian bones: a case study from the Miocene of the Czech Republic: Ichnos, v. 13, p. 113–127.

Milàn, J., 2012, Crocodylian scatology—a look into morphology, internal architecture, inter-and intraspecific variation and prey remains in extant crocodylian feces, *in* Hunt, P., Milàn, J., Lucas, S.G., and Spielmann, J.A., eds., Vertebrate Coprolites: New Mexico Museum of Natural History and Science, Bulletin 57, p. 65–72.

Milàn, J., Kofoed, J., and Bromley, R.G., 2010, Crocodylian-chelonian carnivory: bite traces of dwarf caiman, *Paleosuchus palpebrosus*, in red-eared slider, trachemys scripta, carapaces, *in* Milàn, J., Kofoed, J., Bromley, R.G., Lucas, S.G., Lockley, M.G., and Spielmann, J.A., eds., Crocodile Tracks and Traces: New Mexico Museum of Natural History and Science, Bulletin 51, p. 195–199.

Miller, M.F., 2003, Styles of behavioral complexity recorded by selected trace fossils: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 33–43.

Moreno, K., Wroe, S., Clausen, P., McHenry, C., D'Amore, D.C., Rayfield, E.J., and Cunningham, E., 2008, Cranial performance in the Komodo dragon (*Varanus komodoensis*) as revealed by high-resolution 3-D finite element analysis: Journal of Anatomy, v. 212, p. 736–746.

Muñiz, F., Belaústegui, Z., Toscano, A., Ramirez-Cruzado, S., and Vintaned, J.A.G., 2020, New ichnospecies of *Linichnus* Jacobsen & Bromley, 2009: Ichnos, v. 27, p. 344–351.

Murmann, D.C., Brumit, P.C., Schrader, B.A., and Senn, D.R., 2006, A comparison of animal jaws and bite mark patterns: Journal of Forensic Sciences, v. 51, p. 846–860.

Niedźwiedzki, G., and Budziszewska-Karwowska, E., 2018, A new occurrence of the Late Triassic archosaur *Smok* in southern Poland: Acta Palaeontologica Polonica, v. 63, p. 703–712.

Niedźwiedzki, G., Gorzelak, P., and Sulej, T., 2010, Bite traces on dicynodont bones and the early evolution of large terrestrial predators: Lethaia, v. 44, p. 87–92.

Niedźwiedzki, G., Sulej, T., and Dzik, J., 2011, A large predatory archosaur from the Late Triassic of Poland: Acta Palaeontologica Polonica, v. 57, p. 267–276.

Njau, J.K., and Blumenschine, R.J., 2006, A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania: Journal of Human Evolution, v. 50, p. 142–162.

Njau, J., and Gilbert, H., 2016, Standardizing terms for crocodile-induced bite marks on bone surfaces in light of the frequent bone modification equifinality found to result from crocodile feeding behavior, stone tool modification, and trampling: FOROST Occasional Publications, v. 3, p. 1–13.

Noto, C.R., Main, D.J., and Drumheller, S.K., 2012. Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: example from the Woodbine Formation of Texas: Palaios, v. 27, p. 105–115.

Ordiz, A., Milleret, C., Uzal, A., Zimmermann, B., Wabakken, P., Wikenros, C., Sand, H., Swenson, J.E., and Kindberg, J., 2020, Individual variation in predatory behavior, scavenging and seasonal prey availability as potential drivers of coexistence between wolves and bears: Diversity, v. 12. p. 356–372.

Orłowska-Zwolińska, T., 1983, Palinostratygrafia epikontynentalnych osadów wyższego triasu w Polsce: Warsaw, Prace Instytutu Geologicznego CIV, 89 p.

Ouwens, P.A., 1912, On a large *Varanus* species from the Island of Komodo: Bulletin du Jardin Botanique de Buitenzorg, v. 6, p. 1–3.

Pante, M.C., Muttart, M.V., Keevil, T.L., Blumenschine, R.J., Njau, J.K., and Merritt, S.R., 2017, A new high-resolution 3-D quantitative method for identifying bone surface modifications with implications for the Early Stone Age archaeological record: Journal of Human Evolution, v. 102, p. 1–11.

Pobiner, B., 2008, Paleoecological information in predator tooth marks: Journal of Taphonomy, v. 6, p. 373–397.

Rogers, R.R., Krause, D.W., and Rogers, K.C., 2003, Cannibalism in the Madagascan dinosaur *Majungatholus atopus*: Nature, v. 422. p. 515–518.

Sadlok, G., 2020, Putative crayfish burrows from the Upper Triassic Grabowa Formation of southern Poland: Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, v. 298, p. 235–249.

Sadlok, G., and Wawrzyniak, Z., 2013, Upper Triassic vertebrate tracks from Kraków–Częstochowa Upland, southern Poland: Annales Societatis Geologorum Poloniae, v. 83, p. 105–111.

Schachner, E.R., Manning, P.L., and Dodson, P., 2011, Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (Archosauria: Poposauridea): Journal of Morphology, v. 27, p. 1464–1491.

Schaller, G.B., and Vasconcelos, J.M.C., 1978, Jaguar predation on capybara: Zeitschrift Säugetierkunde, v. 43, p. 296–301.

Scheyer, T.M., Delfino, M., Klein, N., Bunbury, N., Fleischer-Dogley, F., and Hansen, D.M., 2018, Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene: Royal Society Open Science, v. 5, n. 171800, https://doi.org/10.1098/rsos.171800

Schmitt, D.N., and Juell, K.E., 1994, Toward the identification of coyote scatological faunal accumulations in archaeological contexts: Journal of Archaeological Science, v. 21, p. 240–262.

Seidensticker, J., and McDougal, C., 1993, Tiger predatory behaviour, ecology and conservation: Symposium of the Zoological Society of London, no 65, p. 105–125.

Smith, J.B., Vann, D.R., and Dodson, P., 2005, Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth: The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology, v. 285A, p. 699–736.

Smits, P.D., and Evans, A.R., 2012, Functional constraints on tooth morphology in carnivorous mammals: BMC Evolutionary Biology, v. 12, p. 146–157.

Souron, A., et al., 2019, A new geometric morphometrics-based shape and size analysis discriminating anthropogenic and non-anthropogenic bone surface modifications of an experimental data set: IMEKO TC-4 International Conference on Metrology for Archaeology and Cultural Heritage, Florence, Italy, December 4–6, https://www.researchgate.net/publication/338120115_A_new_geometric_morphometrics-based_shape_and_size_analysis_discriminating_anthropogenic_and_non-anthropogenic_bone_surface_modifications_ of_an_experimental_data_set

Steklis, H.D., and King, G.E., 1978, The craniocervical killing bite: toward an ethology of primate predatory behavior: Journal of Human Evolution, v. 7, p. 567–581.

Sulej, T., and Niedźwiedzki, G., 2018, An elephant-sized Late Triassic synapsid with erect limbs: Science, v. 363, p. 78–80.

Sulej, T., Bronowicz, R., Tałanda, M., and Niedzwiedzki, G., 2011, A new dicynodont-archosaur assemblage from the Late Triassic (Carnian) of Poland: Earth and Environmental Science Transactions of the Royal Society of Edinburgh, v. 101, p. 261–269.

Szulc, J., 2007a, Keuper, *in* Szulc, J., and Becker, A., eds., Proceedings, International Workshop on the Triassic of Southern Poland, Pan-European Correlation of the Epicontinental Triassic, 4th Meeting, September 3–8: Cracow, Polish Geological Society, Polish Geological Institute, Institute of Geological Sciences, Jagiellonian University, p. 33–34.

Szulc, J., 2007b, Chronological outline of evolution of the eastern Germanic Basin in late Ladinian–Rhaetian times, *in* Szulc, J., and Becker, A. eds., Proceedings, International Workshop on the Triassic of Southern Poland, Pan-European Correlation of the Epicontinental Triassic, 4th Meeting, September 3–8: Cracow, Polish Geological Society, Polish Geological Institute, Institute of Geological Sciences, Jagiellonian University, p. 34–41.

Szulc, J., and Racki, G., 2015, Formacja grabowska–podstawowa jednostka litostratygraficzna kajpru Górnego Śląska: Przegląd Geologiczny, v. 63, p. 103–113.

Szulc, J., Gradziński, M., Lewandowska, A., and Heunisch, C., 2006, The Upper Triassic crenogenic limestones in Upper Silesia (southern Poland) and their paleoenvironmental context, *in* Alonso-Zarza, A.M., and Tanner, L.H., eds., Paleoenvironmental Record and Applications of Calcretes and Palustrine Carbonates: Geological Society of America Special Paper, v. 416, p. 133–151.

Szulc, J., Racki, G., and Jewuła, K., 2015, Key aspects of the stratigraphy of the Upper Silesian Middle Keuper, southern Poland: Annales Societatis Geologorum Poloniae, v. 85, p. 557–586.

Tanke, D.H., and Currie, P.J., 1998, Head-biting behavior in theropod dinosaurs: paleopathological evidence: Gaia Ecological Perspectives for Science and Society, v. 184, p. 167–184.

Taylor, M.A., 1987, How tetrapods feed in water: a functional analysis by paradigm: Zoological Journal of the Linnean Society, v. 91, p. 171–195.

Thulborn, T., and Turner, S., 2003, The last dicynodont: an Australian Cretaceous relict: Proceedings of the Royal Society of London B, v. 270, p. 985–993.

Vallon, L.H., Rindsberg, A.K., and Bromley, R.G., 2016, An updated classification of animal behaviour preserved in substrates: Geodinamica Acta, v. 28, p. 5–20.

Vasconcellos, F.M., and Carvalho, I.S., 2010, Paleoichnological assemblage associated with *Baurusuchus salgadoensis* remains, a Baurusuchidae Mesoeucrocodylia from the Bauru Basin, Brazil (Late Cretaceous): Bulletin of the New Mexico Museum of Natural History and Science, v. 51, p. 227–237.

Wawrzyniak, Z., 2010, What could eat dicynodonts (Dicynodontia, Therapsida) from Lipie Śląskie (Upper Silesia, Poland)? Preliminary results of research of the Late Triassic macroflora, *in* Nowakowski, D., ed., Morphology and Systematic of Fossil Vertebrates: Wrocław, DN Publisher, p. 118–124.

Webb, G.J.W., Manolis, S.C., and Buckworth, R., 1983, *Crocodylus johnstoni* in the McKinlay River Area Northern Territory Australia 5: abnormalities and injuries: Australian Wildlife Research, v. 10, p. 407–420.

Westaway, M.C., Thompson, J.C., Wood, W.B., and Njau, J., 2011, Crocodile ecology and the taphonomy of early Australasian sites: Environmental Archaeology, v. 16, p. 124–136.

Zammit, M., and Kear, B.P., 2011, Healed bite marks on a Cretaceous ichthyosaur: Acta Palaeontologica Polonica, v. 56, p. 859–863.

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