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New ichnotaxa based on tooth impressions on dinosaur and whale bones

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Traces produced by teeth on bones provide a source of information on the feeding behaviour, predator-prey relationships, and tooth morphology of the tracemaking carnivores and scavengers involved. Studies on mammals, both fossil and recent, have used tooth-scratched bones as clues to the feeding behaviour of carnivorous, scavenging, mineral-seeking and tooth-sharpening mammals in various ecosystems. Similarly, theropod tooth traces have the potential of being important for studying the ecology and ethology of both carnivorous and herbivorous dinosaurs. This paper augments the ichnological nomenclature for traces made by teeth on bones. Two new ichnogenera and ichnospecies, *Linichnus serratus* and *Knethichnus parallelum*, are introduced on the basis of the morphology of theropod biting damage, to focus on the resulting trace fossils as an ichnological feature and to encourage further observation and studies of distribution. Using similar ichnological terminology for both theropod and mammalian feeding traces, and even those of selachian sharks preying on whales or scavenging their corpses, will help coordinate biting strategies, jaw mechanism and feeding behaviour for both recent and ancient carnivores and scavengers.

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INTRODUCTION

The study of trace fossils is a well known source of information on the behaviour of ancient animals (e.g., Bromley, 1996; Miller, 2007; Seilacher, 2007; Bromley *et al*., 2007). Likewise, tooth traces or biting traces found on bones of prey animals (and other corpses and bones) have the potential of adding significant information on the feeding behaviour of the animals involved (e.g., Jacobsen, 1998; Rogers *et al*., 2003; Mikuláš *et al*., 2006 and references therein).

The morphology of tooth traces on recent mammal bones is known to provide information on feeding strategy and bone modification of hyenas, wolves, cheetahs, dogs and other animals (Bishop, 1975; Haynes, 1980, 1983; Binford, 1981; Brain, 1981; Noe-Nygaard, 1987). These carnivores commonly crush, chew and consume bones to acquire calcium and phosphorus (Fiorillo, 1991). Theropod tooth traces have mainly been referred to in association with the description of dinosaur bones, and only few studies link theropod tooth traces to feeding strategy and prey preference (Farlow, 1976; Fiorillo, 1991; Erickson *et al*., 1996; Erickson and Olson, 1996; Carpenter, 1998; Jacobsen, 2003; Rogers *et al*., 2003; Happ, 2008; Paul, 2008). Patterns of bone modification made by mammalian carnivores overlap in morphology with the patterns made by theropod dinosaurs. Therefore, it is important to focus on the morphological variety of tooth traces to correlate the information on feeding behaviour and jaw mechanism of recent and extinct animals.

Other organisms than vertebrates, in particular insects, make traces on bone substrates (e.g., Chin and Bishop, 2007; Britt *et al*., 2008 and references therein). But vertebrates lack symmetrical, opposing teeth, and their dental size is much greater than the mandibles of insects, so there is no likelihood of confusing these tracemakers. Likewise, on the sea floor, bones of whales and other large vertebrates show trace fossils deriving from algae, crustacean as well as sharks, but their morphology generally allows the tracemaker groups to be distinguished (e.g., Esperante *et al*., 2009 and references therein).

This paper introduces an ichnological classification of tooth traces found on dinosaur bones from the Horseshoe Canyon and Dinosaur Park Formations (Upper Cretaceous, Campanian) in Alberta, Canada. Comparison is made with tooth traces of sharks on whale bones. Attempts have been made to classify theropod bite traces in different types and categories (Tanke and Currie, 1998; Jacobsen, 2003), and conclusions have been drawn that give insight into feeding behaviour, jaw mechanism and face-biting habits of theropods. It is therefore appropriate to go a step further, using ichnotaxa to emphasize this important part of ancient ethology.

In this paper, two new ichnogenera and ichnospecies are erected: *Linichnus serratus* and *Knethichnus parallelum*. Puncture traces, or punch-holes in bone from a perpendicular biting vector, have been named *Nihilichnus nihilicus* Mikuláš *et al*., 2006, and are not treated in detail here.

APPLYING ICHNOTAXA TO TOOTH IMPRESSIONS AND DAMAGE

The use of ichnotaxonomy for tooth traces (e.g., Mikuláš *et al*., 2006) will focus studies and provide new clues for the behaviour of extinct predators and correlate information on these ethological implications. Thus, this paper treats such structures as trace fossils, and two new ichnogenera and ichnospecies are erected here.

Application of ichnotaxa to trace fossils is a procedure that must vary according to the group of trace fossils under study. Some such groups are easy to name, having a relatively constant morphology showing limited variation. Such groups include invertebrate burrows (e.g., Uchman, 1999), insect nests (e.g., Genise, 2004), carbonate-substrate borings (e.g., Bromley, 2005), and to some extent invertebrate trackways (e.g., Minter *et al*., 2007).

In contrast, the tracks of tetrapods tend to show extreme variation in morphology, due to preservational differences between true tracks, undertracks and ghost tracks (e.g., Manning, 2004, 2008; Milàn and Bromley, 2006, 2008); to rapid variation in the behaviour as revealed by individual trackways (e.g., Bromley, 2001); and to local, rapid variation in substrate consistency (e.g., Fornós *et al*., 2002). Tetrapod tracks have been classified ichnologically for a long time (Hitchcock, 1836), but until recently their morphology has chiefly been used to attempt identification of the tracemaker (e.g., Cruickshank, 1986), whereas generally, trace fossils are considered as evidence of behaviour and substrate consistency, and are thus important in the reconstruction of palaeoenvironment. In recent years the ichnological classification of tetrapod tracks has greatly improved the understanding, distribution and utility of these structures in palaeoenvironmental analysis (e.g., Lockley *et al*., 1994).

Now it is the turn of the trace fossils produced by tetrapod teeth to receive ichnological nomenclature. The excessive variation in morphology makes this a difficult task, although the undertrack and ghost-track problems are lacking here. But there are plenty of other problems to consider. A tooth can impact the surface of a bone at any angle and with varying degrees of force, producing a wide array of scratch, gouge and puncture morphologies. It may or may not contact the bone surface through a layer of flesh. Thin bones will be crushed whereas the same force will leave but a scratch in a thick bone.

In the case of tracks, it is important to consider if a single pes or manus, or both, preferably preserved as a true track, can adequately represent an ichnospecies. The whole trackway may vary from track to track in many ways, rendering difficult the choice of a holotype.

Some ichnotaxa are characterized by the relative position of a group of scratches. This is the case where regular echinoids scrape substrates with their five teeth, producing with each bite an easily recognizable stellate pattern of five radiating grooves, ideally at an angle of 72°. The individual grooves are not particularly characteristic on their own, but the grouping has been named *Gnathichnus pentax* Bromley, 1975. Similarly, the groups of tooth scrapes that rodents produce on bone that they exploit for calcium carbonate were named *Machichnus* Mikuláš *et al*., 2006, because the grouping of the scratches is functional and characteristic.

On the other hand, the designation of an ichnospecies to a single multitoothed bite, i.e., *Mandaodonites coxi* Cruickshank, 1986, is less definite. The name is based on a single bite in a dicynodont femur, leaving about 33 well preserved tooth traces as pits in the bone surface. The pits are morphologically diverse, and it is "the impressions in" the bone (Cruickshank, 1986, p. 416) that have been chosen as holotype, not an individual pit. The chances that an identical collection of tooth impressions will be found again will be small.

Tooth impressions in general comprise a complex taphonomic time-series that may be said to be initiated before death, in that the breakdown of the corpse by chewing and scraping the bones is a taphonomic process (*cf*. Emig, 2002). Thus, before death, large carnosaurs caused skeletal damage to maybe other individuals of a pack by face biting, which did not necessarily cause death (Tanke and Currie, 1995, 1998).

Some tooth traces may actually represent the cause of death. Carnivores, followed by scavengers, most probably are the source of most of the tooth traces seen on bones (e.g., Happ, 2008; Paul, 2008). But later, maybe much later, mammals in particular may be responsible for mining bone material for its calcium carbonate content, or in the case of rodents, wearing down and sharpening their incisors (Bromley, 1975, pl. 89, fig. 3; Brain, 1981; Fiorillo, 1991) and producing characteristic traces (*Machichnus regularis* Mikuláš *et al*., 2006). Taking these considerations in mind, the use of appropriate ichnotaxa for tooth traces will give important information on feeding behaviour of the tracemaker that otherwise would have been lost.

As is the case with tracks, many of the tooth-traces would not be ideal for analysis, due to erosion, preservation biases, the angle of the tooth/bone contact and many other well known factors for the scientist working with fossils (Fig. 1). But exceptionally there will be a tooth-trace of potential value for understanding ancient environments and tracemakers, and it is of great importance to recognize this when it occurs.

This is the main reason for introducing these new ichnotaxa. Tooth/bone contact will leave traces that — if the right preservational conditions are there — will provide information about the biting animal. Especially *Linichnus serratus* and *Knethichnus parallelum* ispp. nov. are tooth impressions that can be compared to a fingerprint and therefore can reveal the tracemaker (e.g., Figs. 2 and 3). Using this method will provide information on feeding behaviour, predator-prey interaction and co-existence of species because the biting action and agent will be identified (Jacobsen, 2003). And by providing ichnotaxa for these features, morphological differences would be included in the description, providing opportunities to make further studies and observations.

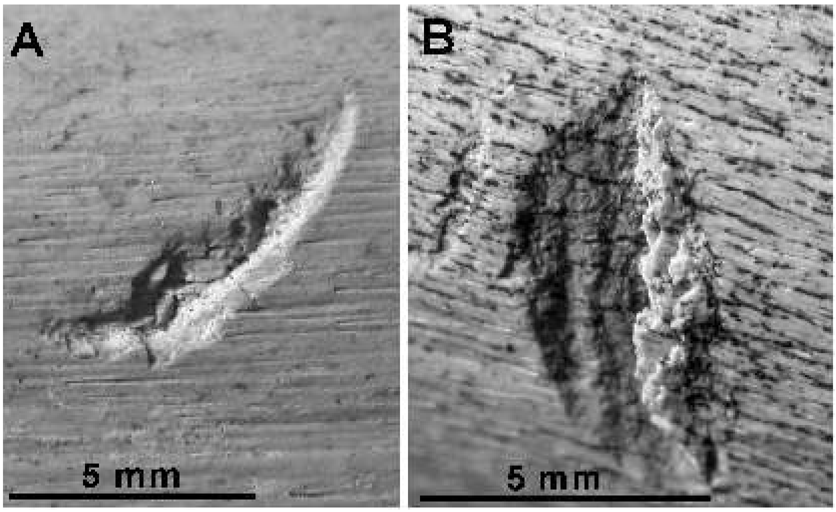

Fig. 1. Simple dental hacks into bone surfaces

A — a small specimen breaking bone fibres, RTMP79.14.733; **B** — another small hack transecting bone fibres on the left side and deforming and bending them on the right, RTMP88.36.39

The other side of the coin is the vast majority of biting trace fossils that have no inherent characteristics for the basis of ichnotaxonomic treatment. Random biting angles and biting strength on varying bone substrates offer a wealth of structures that show no coherent morphology. They merge imperceptibly with the scratches called "trample marks" that are produced not by teeth but by trampling of animals on bones strewn over the ground. These abundant structures have individual value in themselves, but are not suitable for ichnotaxonomic treatment.

A NOTE ON ICHNOLOGICAL WORD-USE: TRACES AND MARKS

As the discipline Ichnology has grown, there has been increasing attention on unifying terminology and word-use. It is to be hoped that the different branches of ichnology will ultimately share a single terminology, which will promote understanding and help strengthen the discipline.

At an early stage of the development and identification of ichnology, Seilacher (1953) suggested that "trace" and "mark" should not be considered synonyms, and that "trace" should be restricted to biogenic structures, created by the life processes and behaviour of the tracemaker, whereas "mark" should be restricted to structures produced by physical processes. Thus, tool marks, ripple marks, rill marks, raindrop marks *etc*., as opposed to trace fossils, scratch traces, escape traces *etc*. This usage has recently been emphasized by Mikuláš *et al.* (2006). However, tetrapod workers retain many of the colloquial forms such as footmark, tooth mark and bite mark. As the terminology of ichnology is being refined (e.g., Bertling *et al*., 2006), it is hoped that the terms "trace" and "mark" can each retain their widely accepted meaning, and should not be merged as synonyms.

As an experiment, therefore, the term "trace" is used here in a paper on tetrapod trace fossils, to encourage focus on scientific nomenclatorial uniformity.

LOCALITY AND SETTINGS

Dinosaur Park Formation is very rich in fossils (Currie and Koppelhus, 2005) and it has produced body-fossil material of many taxa of dinosaurs, including tyrannosaurids, *Dromaeosaurus albertensis*, *Troodon formosus*, *Saurornitholestes langstoni*, *Richardoestesia gilmorei*, hadrosaurids, ceratopsids and ornithomimids (Ryan and Russel, 2001). Pterosaur bones also occur, although rarely. Bones are preserved as articulated skeletons, in bonebeds and as isolated occurrences. Preservation is excellent, which gives an opportunity for taphonomic studies. Biting traces and tooth scratches occur on this material.

Additionally, fairly common vertebrate fossils include fish scales, *Myledaphus* teeth, crocodile teeth, frog bones, turtle bones, salamander vertebrae, champsosaur vertebrae and, to a lesser degree, mammal teeth. These fossils are found mostly in microsites together with bone fragments and teeth of herbivorous and carnivorous dinosaurs (Brinkman, 1990). So far, theropod tooth traces have not been found on any of these common elements.

SYSTEMATIC ICHNOLOGY

On the basis of a study of 1000 dinosaur bones from Dinosaur Park Formation, Alberta (Jacobsen, 2003), new categories of trace fossils emerged. These are used here to form the basis of new ichnotaxa. The specimens are housed in the collections of The Royal Tyrrell Museum of Palaeontology, Alberta, Canada.

Ichnogenus *Linichnus* igen. nov.
Linichnus serratus, isp. nov.

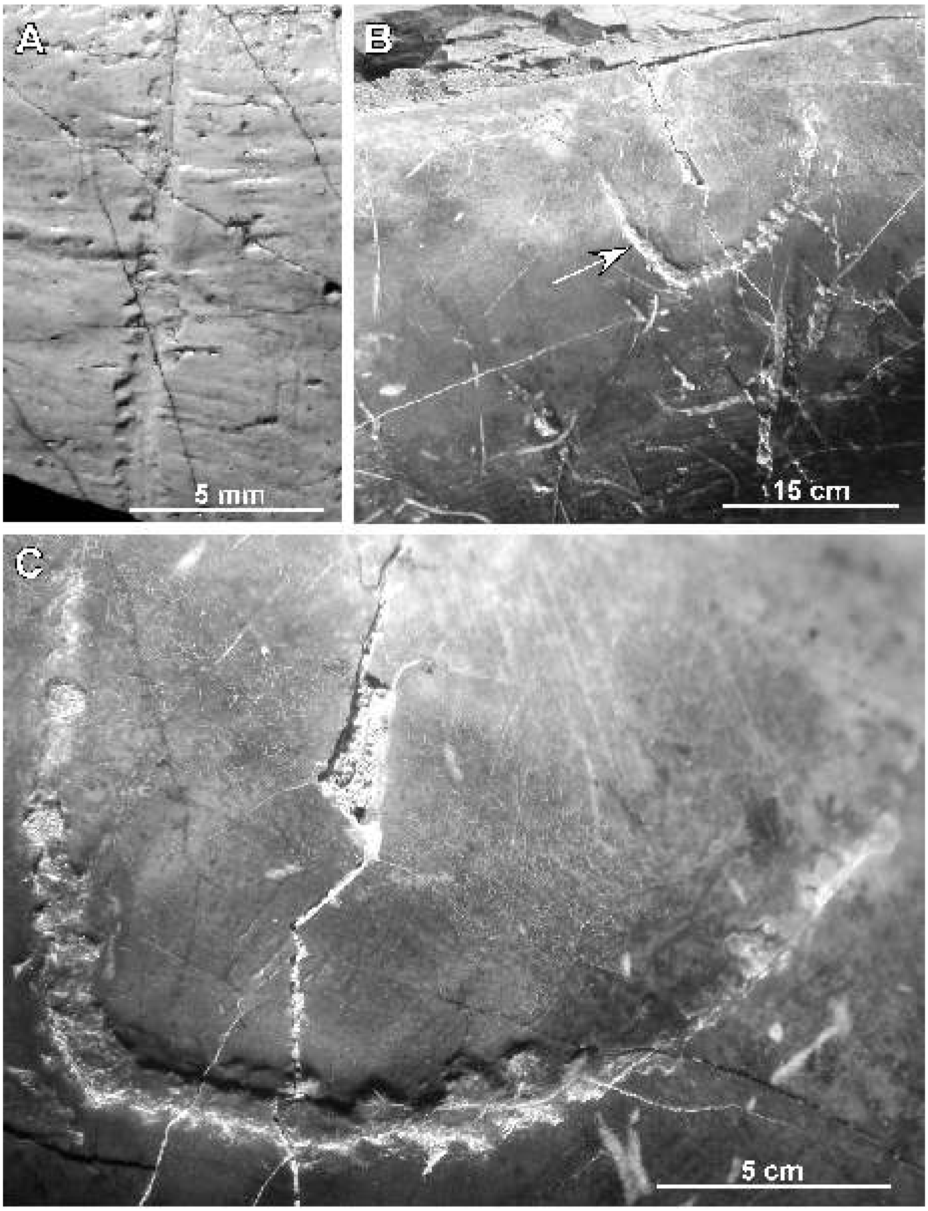

Fig. 2. *Linichnus serratus*

A — a small but well preserved example, produced by *Troodon* sp., RTMP81.22.24; **B** — a very large *L. serratus*, the holotype (large arrow), among a host of minor tooth scratches and probable trample marks, RTMP84.82.01, the trace fossil was made by a tyrannosaurid in a tyrannosaurid bone; **C** — enlarged view of the holotype in B

Etymology. — Latin, *linea*, *linum*: line, thread; Greek, *ikhnos*: trace, footprint.

Diagnosis. — Single elongate groove of biogenic origin on skeletal material (e.g., bones, teeth). The groove, U- or V-shaped in transverse section, may only affect the surface of the bone, or bone-fibres may be cut through, recurved or broken within the groove. The groove has a serrated morphology.

Discussion. — The groove derives from a tooth penetrating and cutting into the surface of the bone substrate during a bite. The trace fossil is similar to "type 2 tooth trace" described by Tanke and Currie (1998) and Jacobsen (2003), and "isolated tooth score" or "U-shaped groove" of Fiorillo (1991, fig. 2), and at a much larger scale, the "puncture and pull" impressions of Erickson and Olson (1996, figs. 1, 2 and 4) and Erickson *et al*. (1996), on dinosaur bones.

Linichnus serratus isp. nov.
(Figs. 2 and 5)

Holotype. — The specimen RTMP 84.82.01, illustrated in Figure 2B and C.

Etymology. — Latin, *serratus*: saw-edged, serrated.

Diagnosis. — As for the ichnogenus.

Description. — The holotype (Fig. 2B and C), from the Horseshoe Canyon Formation, comprises a curved groove, U-shaped in cross-section, 4.5 cm long and 0.5 mm deep. Serration traces are sharply defined, symmetrical and 1 mm wide.

Discussion. — In some *Linichnus serratus*, serration traces do not occur in all of the grooves (Fig. 2C). This may be due to preservation, erosion, preparation, or histological differ-

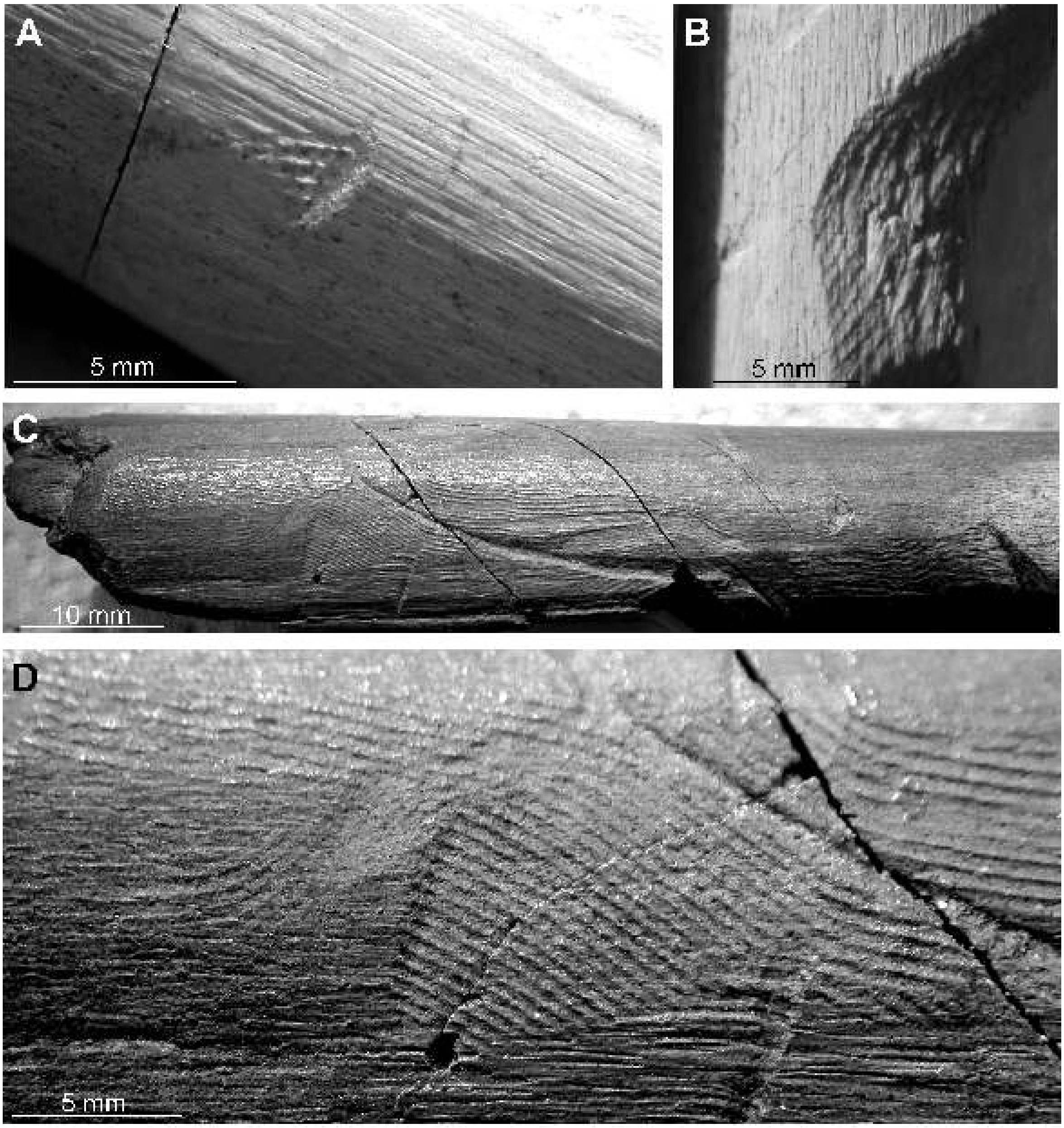

Fig. 3. *Knethichnus parallelum*

A — a gouge into a bone showing striation ornament, RTMP66.17.30; **B** — a small *K. parallelum* comprising a hack into a bone surface showing parallel grooves leading to a terminal scrape, RTMP88.36.39; **C** — the holotype, a bone extensively covered with *K. parallelum*, RTMP88.36.39; **D** — close view of C depicting the extensive *K. parallelum*; a theropod tooth has been dragged across the bone surface leaving striations as the tracemaker twisted its head as revealed by the varying orientation of the groups of striations

ences. It might also represent anatomical characteristics of an individual predator that produced the trace. Size varies from a few millimetres to several centimetres long, from 1–10 mm wide, and commonly less than 1 mm deep.

Ichnogenus *Knethichnus* igen. nov.
Knethichnus parallelum isp. nov.

Etymology. — Greek, *Knethos*: a scrape.

Diagnosis. — Scraping structures in which serration traces extend as parallel grooves leading in some cases away from an initial groove.

Knethichnus parallelum isp. nov.
(Fig. 3)

Holotype. — The specimen RTMP 88.36.39, Figure 3C and D.

Etymology. — Latin, *parallelus*: side by side equidistantly.

Diagnosis. — As for the ichnogenus.

Description. — The holotype, from the Dinosaur Park Formation, has a 4.5 mm long depression from which parallel grooves (serration traces) extend laterally to at least 8 mm away from the initial depression; these grooves are slightly curved, but remain strictly parallel. The serration traces on the holotype are symmetrical and 0.4 mm wide, but in other specimens the size and symmetry can vary.

Discussion. — *Knethichnus parallelum* consists only of serration traces, which originate when a theropod tooth, or other denticulate tooth, was dragged across a bone at an angle at which only the denticles on the tooth meet the bone. Depending on bone structure, preservation, erosion and preparation, the area showing serration traces may be the only preserved feature of the tooth trace. Size varies from a few millimetres to several centimetres long, from 1 to 10 mm wide, and commonly less than 1 mm deep. This form is similar to type 3 tooth traces described by Tanke and Currie (1998).

Knethichnus parallelum can superficially resemble *Machichnus regularis*, which also consists of aligned grooves. However, being produced by pairs of rodent incisors, the grooves of *Machichnus* are not precisely parallel but occur as slightly deviating, subparallel sets of paired grooves. The grooves also have a shorter maximum length than those of *K. parallelum*.

DISCUSSION

When analyzing the morphology of tooth traces, it is important to recall that the dentitions of theropods and mammalian carnivores are basically different. Theropod maxillary teeth are usually simple, bladelike and are aligned in a single row, making them suitable for grabbing prey or ripping flesh, but not for the gnawing or crushing of bone (Fiorillo, 1991; Abler, 1992, 2001; Erickson *et al*., 1996; Jacobsen, 2003). The conclusion has therefore been made that bite traces on dinosaur bones generally originate from accidental tooth-bone contact, as opposed to repeated tooth-bone interaction as when dogs chew bones. Each tooth has rows of denticles, anterior and posterior, that in the Dinosaur Park Formation, are species specific (Currie *et al*., 1990). In contrast, the dentition of most mammalian predators is suited for bone crushing and gnawing, owing to more precise occlusion and more complex tooth shapes. The morphology of mammalian canines is comparable to theropod teeth, but generally they lack denticles.

These differences in tooth morphology will obviously affect the morphology of tooth traces left on bone. In addition, the morphologic variety within these tooth trace types originates in the forces and dynamics of the tooth/bone contact during a bite, which again gives clues of tooth strength and biting forces.

Denticles on theropod teeth can leave serration traces within the tooth trace or even clear imprints of the denticles on the outer surface (Figs. 2 and 3), making it possible to identify the theropod that produced *Linichnus serratus* and *Knethichnus parallelum* (Jacobsen, 2001, 2003). This method is useful where the theropods are well known from the body-fossil record (represented by teeth) and the preservation of the bone is sufficiently good to show tooth traces. In addition, the inter-tooth distances of theropods are ontogenetically and species-specific, making it possible to correlate *Nihilichnus* (Fig. 4) and series of parallel traces of *Linichnus serratus* type (Fig. 5) to inter-tooth distances of theropods (Erickson and Olson, 1996; Jacobsen, 2003; Rogers *et al*., 2003).

Unnamed single cuts or scratches can also occur in pairs or groups of parallel cuts or scratches, showing regular spacing. Where the scratches occur on dinosaur bones as parallel grooves, it would be possible to correlate tooth trace distance with inter-tooth distance of the theropod tracemaker (Jacobsen, 2003). When several *Linichnus serratus* occur as parallel scratches, correlations can be made with the inter-tooth distances of the predator that left the trace. In addition, the serration-traces can be correlated with the denticles on theropod teeth, and these two methods of identification can provide further information on the predator that left the trace (Fig. 5; Jacobsen, 2001, 2003).

Matching pairs of parallel *Linichnus serratus* of tyrannosaurids (Fig. 5B) were seen on 6 specimens in the collections at The Royal Tyrrell Museum of Palaeontology. One ornithomimid bone (Fig. 5A) had serration traces comparable in shape and size and suggestive of teeth from *Saurornitholestes*, and parallel traces matching the intertooth distance of *Saurornitholestes* (Jacobsen, 2001).

Insight into the feeding behaviour of theropods can be obtained if the prey dinosaurs can be identified. Using these methods of identifying tooth traces, it has been possible to correlate some predator-prey interactions for the Judith River Group in Alberta. These include one ceratopsid bone carrying a *Linichnus serratus* matching denticles of *Troodon* (Fig. 2A), and tyrannosaurid tooth-impression on other tyrannosaurid bones (Fig. 2B and C), hadrosaurid, ceratopsid, and *Saurornitholestes* bones, making these dinosaurs prey animals or scavenged corpses for tyrannosaurids (Jacobsen, 2003, 2005).

Mammalian carnivores are not expected to be capable of making *Linichnus serratus* and *Knethichnus parallelum* because, with few exceptions, their teeth lack denticles. Even though they have different dentition, mammalian and dinosaurian carnivores are both capable of making similar damage to bones, e.g. *Nihilichnus*. This ichnogenus represents biting behaviour, but derives from a single tooth-bone contact. This may add new and important information to studies of histology, jaw mechanism, biting forces, and tooth strength of theropods. But it can also help in differentiating theropod tooth traces and patterns of bone modification that can be species specific, as they are in hyenas, wolves and large cats (Haynes, 1983).

Another vertebrate group that possesses prominent denticulate teeth is the selachian sharks. Rare instances are documented of selachian shark teeth broken off and left embedded in whale bone (e.g., Bianucci *et al*., 2002 and references therein; Ehret *et al*., 2009; Cicimurri and Knight, 2009 and references therein). It is thus surprising to see the remarkable similarity of ornament produced by a tooth of the Pliocene great white shark (*Carcharodon sulcidens*) that is scraped over a paraffin wax surface (Deméré and Cerutti, 1982). The same ornament was found by these authors on a whale dentary bone from the same sediment that contained the shark teeth (Fig. 6C).

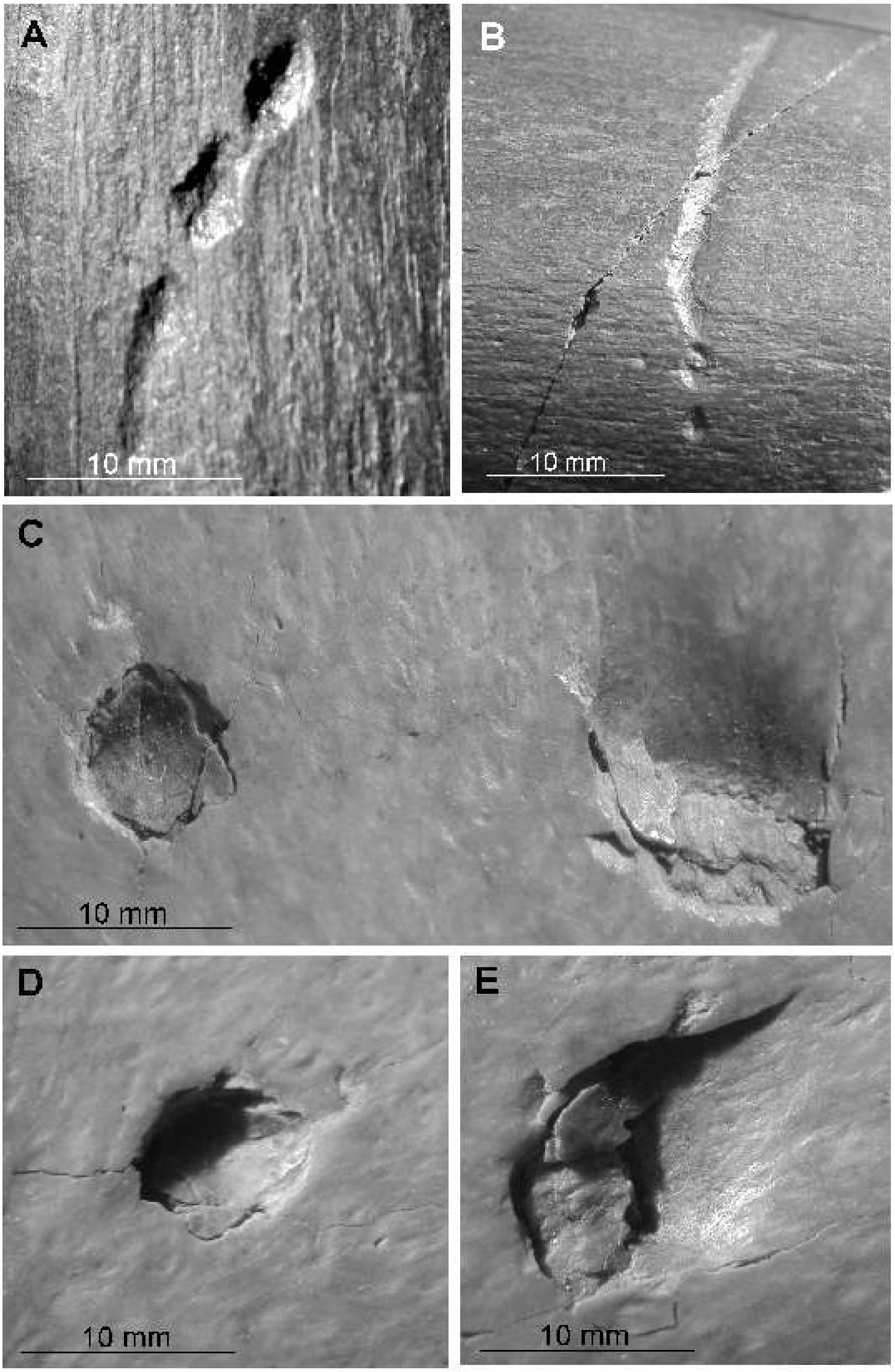

Fig. 4. *Nihilichnus nihilicus*

A — a group of three tooth impressions, probably corresponding to three teeth and a single bite; the upper two are *N. nihilicus*, but the lowest shows lateral movement to produce a short groove, RTMP67.15.21; **B** — likewise a group of depressions probably caused by a single bite. Three *N. nihilicus* can be distinguished below, but the one tooth has skidded across the bone surface to produce a groove, RTMP67.15.21; **C** — two *N. nihilicus* showing different details of crushing, the specimen on the left indicates pressure more or less at right angles to the substrate surface, the specimen to the right shows a more diagonal pressure direction, RTMP85.36.314; **D** — the left-hand specimen in C in contrasting lighting; **E** — the right-hand specimen in C in contrasting lighting

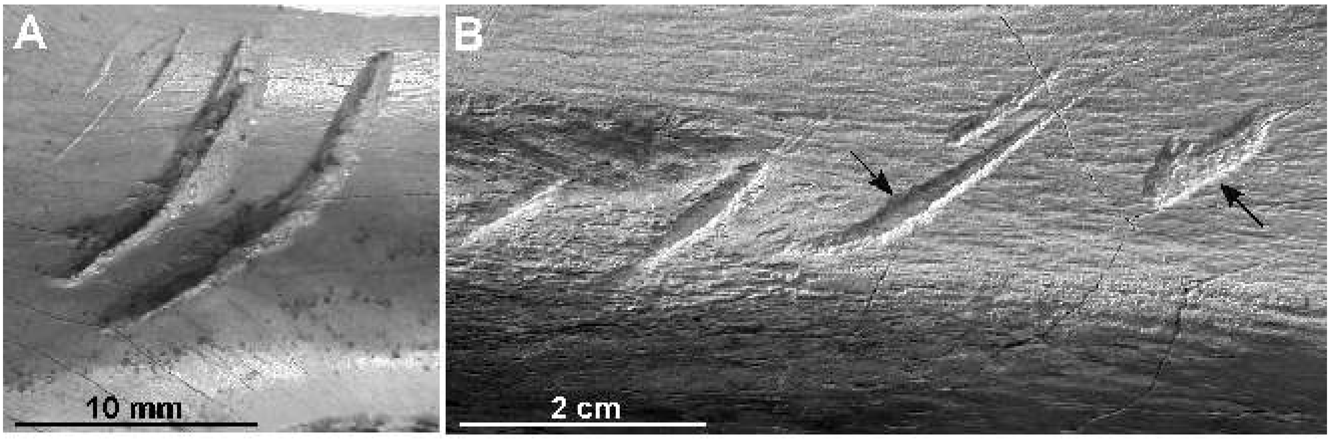

Fig. 5. Two groupings of *Linichnus serratus*

A — an ornithomimid bone bitten possibly by *Saurornitholestes*, RTMP85.06.158; **B** — serrated traces of tyrannosaurid teeth, RTMP79.14.733, these specimens only weakly show serration structure (arrows)

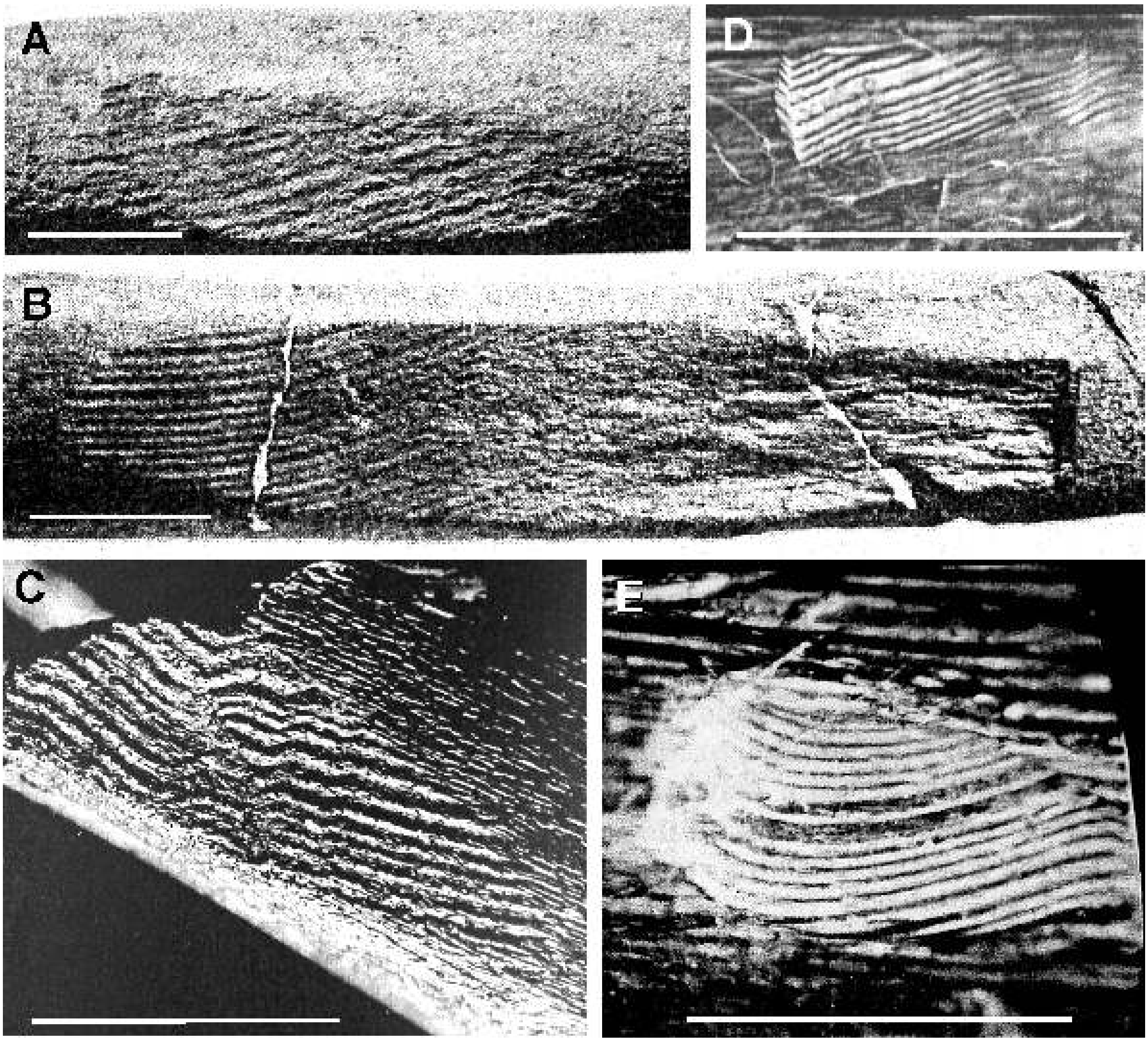

Fig. 6. *Knethichnus parallelum* on bones of cetaceans and a mosasaur

A, **B** — scrape trace fossils produced by the great white shark, *Carcharodon carcharias*, on bones of the extinct bottlenosed dolphin, *Tursiops cortesii*, Pliocene of Italy, modified after Cigala-Fulgosi (1990, pl. 2, figs. 4, 10); **C** — attack by a Pliocene great white shark, *Carcharodon sulcidens*, on bones of a cetotheriid whale, San Diego, California, modified after Deméré and Cerutti (1982, text-fig. 1C); **D**, **E** — ribs of the mosasaur, *Platecarpus ictericus* scraped by the teeth of sharks, Niobrara Formation, Kansas, Campanian, modified after Schwimmer *et al*. (1997, fig. 3F, G)

Further examples of this bone-scraping behaviour in sharks producing *Knethichnus parallelum* have subsequently been provided by Cigala-Fulgosi (1990) in Pliocene dolphin material (Fig. 6A and B), and Schwimmer *et al*. (1997), and Corral *et al*. (2004) on Cretaceous mosasaur bones (Fig. 6D and E). It would seem that the distinctive ichnospecies *Knethichnus parallelum* is equally applicable to the work of theropods on bones in the continental Cretaceous and the feeding of sharks on bones of whales and mosasaurs from the marine Cretaceous to today. In both cases, the feeding method is similar: the lateral scraping of flesh from bone by denticulate teeth.

The possibility that fossil material may have been reworked from older sediments, or brought in by flowing water from upstream ecosystems, is a potential problem when analyzing ancient environments, especially when analyzing predator/prey interaction (Farlow and Pianka, 2002). When analyzing fauna from fossil records, the fossil assemblage could represent a taphocoenosis where the fossils may have come together after death, or a thanatocoenosis where the fossils may have come together at death (Shipman, 1981). Teeth are quite resistant to physical and chemical alteration, but the amount of reworking and transport can only be indicated by observing the relative degree of postmortem wear.

Tooth traces that can be related to feeding theropods will reveal a “true” co-existence of dinosaurs in the palaeoecosystem, similar to the rare specimens having theropod teeth embedded within fossil bone (Currie and Jacobsen, 1995; Buffetaut *et al*., 2004). Using the ichnotaxa defined in this paper can focus attention on the identification of predation traces and may provide additional information for determining the interactions and coexistence of certain carnivores and herbivores in ancient ecosystems. Combined with other methods of studying theropod ethology and ecology, we are confident that the ichnotaxa introduced here will be useful descriptors for evidence of predation on bones, especially on fossil dinosaurs and whales.

CONCLUSIONS

1. It is possible to collect evidence on the feeding habits of extinct predatory animals through study of their tooth trace fossils.

2. This paper introduces new ichnotaxonomy based on theropod tooth trace fossils and shows that the identification of theropod tooth trace fossils with the tracemaker can provide further insight into feeding behaviour of the animals involved.

3. The trace fossils are designated as *Linichnus serratus* igen. et isp. nov. and *Knethichnus parallelum* igen. et isp. nov.

4. The location on the substrate for the new ichnotaxa and the morphology of tooth traces has the potential of correlating this with the tooth morphology of well known theropods. In some cases, this will make it possible to identify the tracemaker.

5. It is hoped that future research on theropod tooth traces, in a wider scope, will be found to be related to predation habits of both recent and ancient carnivorous mammals through ichnological analysis of the tooth traces.

6. The presence of *Knethichnus parallelum* on whale bones, sculpted by selachian sharks, is a striking example that emphasizes the characteristics of trace fossils in sensitivity to behaviour and substrate, but less dependence on the nature of the tracemaker and the ambient environment.

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