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Authors: REISZ, ROBERT R., and TSUJI, LINDA A.

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NOTE

AN ARTICULATED SKELETON OF *VARANOPS* WITH BITE MARKS: THE OLDEST KNOWN EVIDENCE OF SCAVENGING AMONG TERRESTRIAL VERTEBRATES

ROBERT R. REISZ and LINDA A. TSUJI, Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Rd. N. Mississauga, ON, L5L 1C6, Canada; rreisz@utm.utoronto.ca.

The Latest Carboniferous to the Early Permian (305–270 mya) is one of the most important periods in vertebrate evolution because it marks the appearance of the first complex terrestrial vertebrate communities and the initial, rapid evolutionary radiation of amniotes (Sues and Reisz, 1998). In contrast to younger Mesozoic and Cenozoic communities, however, little is known about the trophic structure of these early vertebrate assemblages, or the feeding habits of their constituents. There have been numerous reports and analyses of Mesozoic tooth marks in both terrestrial and marine environments (Erickson, 1996; Fiorillo, 1991), and possible bite marks have been suggested in early aquatic tetrapods (Shubin et al., 2004). Previous reports of evidence of feeding behavior among Paleozoic terrestrial vertebrates, however, have been restricted mainly to the preservation of small tetrapods as supposed stomach contents of large predators such as *Dimetrodon* (Romer and Price, 1940; Reisz, 1986), or the strange preservation of a skull of the early eureptile *Captorhinus* with another, somewhat smaller skull of the same species stuck in its mouth (Eaton, 1964).

We report on the discovery of a new, large articulated skeleton of the early Permian synapsids predator *Varanops* displaying numerous bite marks, indicating that the carcass was scavenged by a large tetrapod. The identity of this scavenger as a temnospondyl, probably a dissorophoid, is confirmed by the anatomy of the bites and the remarkable preservation of a broken single tooth crown lodged in the forelimb of the *Varanops* skeleton.

DESCRIPTION

Skeletal remains of varanopid synapsids are surprisingly rare in the fossil record, especially when considering the longevity of the clade and the wide geographic distribution of its members. The fossil record of this group extends from the Late Pennsylvanian to the Late Permian (Reisz and Dilkes, 2003), and its spatial extent includes North America, Northern Russia, and South Africa. The larger members of this group, *Aerosaurus, Varanops*, *Varanodon*, and *Watongia* form a clade, the Varanodontidae, whose fossil record extends from the base of the Early Permian to the early part of the Middle Permian (Reisz and Laurin, 2001). The specimen described here can be identified as a large individual of *Varanops*, and because it is identical to *Varanops brevirostris* (Williston) in all known respects except for its larger size, we assign it to that taxon.

In addition to the remarkable presence of evidence of scavenging, this new specimen of *Varanops* is significant because of the superb preservation of the skeleton, the first found outside the *Cacops* Bone Bed in Baylor County, Texas. A number of skeletons of *Varanops* were excavated from this locality together with the large dissorophid *Cacops* and the basal synapsid *Casea*, but the fossil-producing pocket has been exhausted (Romer and Price, 1940; Williston, 1911) and the locality is inaccessible beneath Lake Kemp. Although much of the *Varanops* material from this locality is articulated, preservation is relatively poor and consequently the specimens are difficult to study. In addition, most of these specimens appear to have belonged to juvenile and sub-adult individuals. In strong contrast, the new *Varanops* specimen is very well preserved with remarkably good detail in many critical parts of its skeleton. Its identification as a large, fully adult individual of *Varanops brevirostris* is consistent with the high level of ossification of the shoulder girdle, of the manus, and of the pes. It is also remarkable for its size, with long bones measuring at least 15% longer than the largest known articulated individual from the *Cacops* bonebed. The skeleton was found near a partially articulated *Diadectes*, which also displays evidence of scavenging. This new locality is southwest of Abilene, in Taylor County, Texas, also attributable to the Arroyo Formation (Olson 1989).

The remains of this new specimen of *Varanops,* TMM 43628 (Texas Memorial Museum) were left largely in articulation, and are remarkably complete, despite the presence of numerous bite marks on its skeleton that suggest extensive scavenging (Fig. 1). The surface texture of the bones indicates that this individual was not buried immediately after death, the most common taphonomy of well-preserved, articulated skeletons, but was instead exposed for some time permitting weathering of the bones before burial. This taphonomic interpretation is based on the presence of extensive surface cracking of the long bones parallel to fiber structure, and some mosaic cracking occurring on the surface of the bones (Behrensmeyer, 1978). Despite the scavenging and exposure, most of the loss of skeletal material has occurred through recent weathering and the rather abrupt discovery of the specimens with a backhoe. All the skeletal remains were found within a 1-m radius of the articulated vertebral column.

Bite marks have been found on the shoulder girdle, upper arm, pelvic girdle, and hind limb. These bite marks are indicative of feeding behavior because the bitten areas occur where most of the fleshy part of the musculature would have been located. The gut area below the rib cage also seems to have been affected by scavenging, with all the massive ventral scales being bunched up together into a single compact mass, instead of the commonly occurring full extension below the rib cage.

The bite marks show a variety of morphologies, including evidence of punctures, pits, scoring, and furrows on the limb bones, the pectoral, and pelvic girdles (Fig 1.1–9). The pectoral girdle shows obvious evidence of scavenging, most notably with the presence of a large puncture mark on the posterior side towards the dorsal end of the left scapula, where a significant chunk of bone has been removed (Fig. 1.1). Multiple bite marks also occur on the limbs, with a large, deep furrow near the proximal end of the femur (Fig. 1.5), near the proximal ends of the radius and ulna (Fig. 1.3 and 1.4), near the proximal end of the tibia (Fig. 1.8), as well as near the distal end of the fibula (Fig 1.9). The joint surfaces also show evidence of scavenging, most prominently where a large furrow extends across the proximal end of the humerus (Fig. 1.2). Other prominent furrows can be seen on the proximal articular surfaces of the right tibia, and on the distal surface of the left radius. Posteriorly, there are two major bite marks located on the pelvic girdle, both located on the ischium. The first occurs on the swollen lip on the posteroventral border of the acetabulum (Fig. 1.6) and is characterized by scoring in a posteroventral direction, ending in a small puncture at the terminus of the mark. The other major bite mark on the ischium consists of a series of small punctures on the lateral side, opposing scratch marks on the medial side, the evidence that helps with the identification of the predator (Fig. 1.7).

DISCUSSION

Although it is impossible to prove that each of the tooth marks were produced by a single individual, it appears that most, if not all the bite marks were made by one specific type of tetrapod. This identification is possible because the marks have a distinctive morphology, entirely consistent with the anatomy of a single tooth that has apparently broken off, and its tip has been found lodged between the proximal ends of the left

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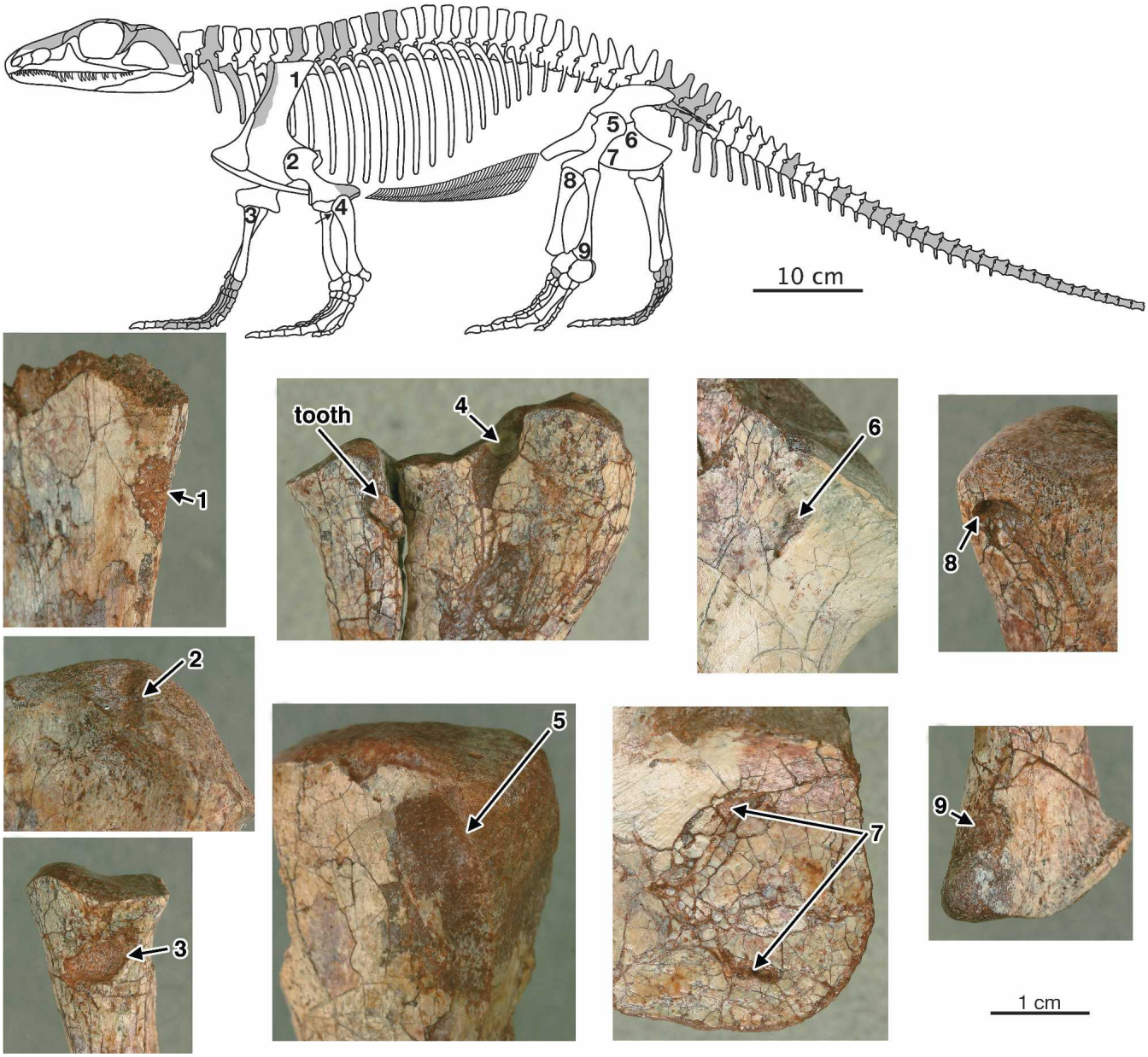


FIGURE 1. Skeletal outline of *Varanops brevirostris*, showing level of completeness of the articulated skeleton (missing parts in grey), and distribution of bite marks, as indicated by numbers on the reconstructions, and the same numbers with arrows in the specimen photographs. Arrow without a number in the reconstruction indicates position of dissorophoid tooth. **Abbreviations**: **1**, bite mark along the posterior edge of scapula, near its distal end; **2**, large furrow-like bite mark on proximal articular surface of humerus; **3**, large gouge on proximal head of right radius; **4**, bite mark on proximal end of the ulna; tip of dissorophoid tooth lodged between the radius and ulna; **5**, proximal head of femur with two bite marks, one along its dorsal surface, a second extending onto the articular surface; **6**, posteroventrally directed scoring on the body of ischium, near the posteroventral border of the acetabulum, that ends in a small puncture mark; **7**, elongate tooth mark extending along the surface of the ischium, with associated, typical collapse of the bone surface along the presumed path of the tooth tip; **8**, massive bite mark on the proximal head of the tibia, with associated crushing of the bone along the leading edge of the bite path; **9**, gouge-like bite mark at the distal end of left fibula along its anterior edge. All to scale.

radius and ulna (Fig. 1.4). The tooth has a simple, conical outline, and is only slightly recurved. This morphology indicates that it did not belong to either of the top two amniote predators of the time, a sphenacodontid or another varanopid, because the teeth of the former are massive, with serrated cutting edges even near the tip, and the teeth of the latter are strongly recurved and also possess cutting edges (Reisz, 1986). Because only these large, top predators would have been able to kill the large varanopid described here, it is reasonable to interpret the feeding traces to be the result of scavenging rather than predation. The part and counterpart of each bite mark and the morphology of the tooth are entirely consistent with a relatively large temnospondyl amphibian, most likely a dissorophoid (Berman et al., 1985; Sullivan and Reisz, 2000). Although the tooth could belong to another large temnospondyl, such as an eryopoid, it is too slender to have belonged to a form like *Eryops*. In addition, the skeletal morphology of Early Permian non-dissorophoid temnospondyls indicates that they were probably aquatic organisms that rarely ventured onto land. Thus, a fully terrestrial dissorophoid temnospondyl was the most likely candidate as the source of the bite marks.

On one side of the bone the mark was made by a large single tooth, but on the opposite side of the same bone the bite mark is either absent or is little more than a gentle breaking of the bone surface along a relatively larger surface area, indicating the presence numerous opposing smaller

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teeth. In contrast to other contemporary large faunivores that have large teeth on both upper and lower jaws, temnospondyl amphibians are characterized by the presence of a single tusk near the tip of each lower jaw, the ad-symphyseal tusk, and numerous smaller teeth along the jaw margins (Berman et al. 1985; Sumida et al., 1998). This dental pattern is therefore entirely consistent with the bite marks. Although there are large palatal tusks in the skull, their positions on the roof of the mouth, lingual to the marginal dentition suggests that they would have been used mainly to hold struggling prey.

The morphology of the bite marks indicates that the tetrapod that caused them, although it may have been scavenging, did not crush the bones, like modern scavenging mammals often do, but was certainly modifying the bones during feeding. If our identification of the scavenger is correct, it requires that we reevaluate the position of large armored terrestrial dissorophoids in Early Permian terrestrial vertebrate communities. Instead of considering these amphibians as the 'last brave attempt' of anamniotes to compete for a short time directly with the amniotes (reptiles and synapsids) before they disappeared at the end of the Early Permian, we should instead consider that these widely occurring forms were an important component of their terrestrial vertebrate communities (Sumida et al., 1998). This find shows that large dissorophoids were at least scavengers of top predators, and the anatomy of the bite marks may indicate that these terrestrial tetrapods had a larger role in the ecosystem than is conventionally regarded for these creatures.

CONCLUSION

These bite marks provide direct evidence about the feeding behavior of vertebrates during the initial, dramatic diversification of tetrapods on land. Their first identification in the Permian is important, but it is likely that it is not an isolated occurrence. In our opinion, few Paleozoic tetrapods have been prepared with the kind of care required to readily identify bite marks, or studied with these taphonomic features in mind. We predict that reexamination of Permian material will yield additional evidence of these traces, and thus provide new insights into the trophic structure of these early terrestrial vertebrate communities.

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