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CROCODILE *LEIDYOSUCHUS FORMIDABILIS*

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**ABSTRACT**— That the Paleocene crocodile *Leidyosuchus formidabilis* fed upon turtles is clearly demonstrated by its association with turtle shell remains. At least two species of turtles show injuries that are interpreted as evidence of predation by *Leidyosuchus*. These injuries are examined and the method by which they were sustained is discussed.

INTRODUCTION

Crocodylians eat turtles today (Cott, 1961; Neill, 1971). The paleontological literature also contains numerous references to this relationship between fossil forms. Because of the general lack of accompanying paleoecological data however, abnormalities such as “bite marks” are usually given little note.

A feature of fossil crocodylians that is a common basis for diagnosing chelonivorous habits is the presence of enlarged, blunt posterior teeth. These were used, presumably, for crushing the shells of turtles. Teeth of this type are found in a number of short-faced, late Cretaceous and early Tertiary genera and show a range in their degree of development. Examples of these are *Brachychampsia* (Gilmore, 1911), *Allognathosuchus* (Mook, 1921) and *Ceratosuchus* (Schmidt, 1938). It is noted that most of these forms probably frequented stream banks and beaches that were utilized by a variety of turtles for nesting; hence a steady supply of young, convenient-sized turtles was available to them as food. Turtle-eating, as a behavior for which the rear teeth of such small brevirostine forms were specialized, is not the main concern of this discussion however.

Extant crocodylians, many of which are relatively large, include some known to feed on turtles. They do not possess oversized posterior teeth and rely on size and sheer force of their opposing jaws to crush the shells. Certain large

fossil crocodiles, also without specialized teeth, apparently fed on turtles as well. One such form is *Leidyosuchus formidabilis* from the late Paleocene of western North America. Its association with a sizable population of turtles provided ample opportunity for predation and left a remarkable suite of specimens as a record of this behavior.

### EVIDENCE OF PREDATION

*Leidyosuchus formidabilis* is a large eusuchian crocodile with an average adult skull length of about 65 cm and general proportions of *Crocodylus acutus* (the American crocodile). Its posterior teeth are undistinguished. Several teeth near the front of the jaws (viz: numbers 4 in the premaxilla; 4 and 5 in the maxilla; and 1, 3 and 4 in the dentary) are large and caniniform. Its remains have been recovered in abundance from lacustrine deposits that represent a local environment exhibiting a river-lake succession. Here it comprised the principal vertebrate component of the Wannagan Creek Quarry Fauna (Erickson, 1982). In that publication I make reference to predation upon turtles, noting the invulnerability of the high-domed carapace of the genus *Protochelydra*. New materials now at hand warrant further discussion of the feeding behavior of *Leidyosuchus*.

Turtles make up the next largest group of vertebrates at Wannagan Creek Quarry, although fishes may have outnumbered them. Chelonian genera present in descending order of relative abundance include *Protochelydra*, a trionychid and at least two other forms. Diversity of size within each of these suggests that the area was a well-established nesting ground for turtles. Measurements of complete shells range from 7 cm to 50 cm for the breadth of the carapace. Many additional elements indicate that a full size-range, including individuals no more than one season old, was present for each of the mentioned forms.

Among several hundred separate shell fragments are numerous partial, as well as a few complete, shells. A most interesting aspect of this material is the presence of abnormalities, the character of which points to traumatic injury rather than erosion by fungal infection and mycosis as a cause (Figs. 1 and 2). In the immediate areas of the wounds the bone is thickened as part of the regeneration process (Danini, 1946). Figure 2 shows a wound which has been almost completely healed by regeneration of new bony tissue (Hunt, 1957). Occurring as puncture wounds in which penetration of the shell was complete, these are attributed to encounters with *Leidyosuchus* owing to the following: (1) there was no other form present that could have inflicted such wounds; (2) the punctures agree in size with the largest teeth of the crocodile; (3) the punctures are also spaced in a manner which corresponds to the spacing

of these teeth; and (4) occurrence on the posterior and posterodorsal surfaces of the carapace and not on the plastron suggests that, in attempting evasion, the turtle was traveling away from the crocodile's jaws. Capture involved grasping the rear part of the shell by piercing it with its long teeth. Lack of injury to the plastron is explained by the protection afforded it by the wide overhang of the carapace and the fact that all of the turtles present have reduced plastra.

Once the capture was made, the turtle had to be repositioned farther back between the jaws to be crushed. Unlike the soft bodies of other reptiles and fishes, the shell of a turtle is difficult to manipulate in the mouth even for a large crocodile. Carpenter (1928) observed a crocodile taking a large fish to the shore of a lake before adjusting it to swallow. This could be interpreted as a method of lessening the chance of the fish escaping.

In releasing the turtle from its grip, which involved snapping the jaws above the water's surface to make readjustment for swallowing (Cott, 1961; Hubbard, 1927), loss of the living turtle often occurred. Healed mutilations on the shells are evidence of this. If *Protochelydra* was more difficult for the crocodile to handle because of its relatively higher shell, it probably had a better survival rate than the other turtles and that could account for its greater representation.

Carpenter and Lindsey (1980) offer as evidence for chelonivorous habits of the small Cretaceous alligator, *Brachychampsa*, pieces of etched and pitted turtle shell from an area that produced numerous undamaged bones of tiny lizards and delicate mammal teeth. Similarly etched turtle bones have been encountered at Wannagan Creek Quarry among a multitude of tiny and large normal bones and teeth. That these are remnants of some crocodile's meal is debatable, since these unusual pieces of turtle are of the same size and mass as some etched crocodile centra and osteoscutes from the same location, possibly ingested to serve as "stomach stones" in the absence of more suitable objects (pebbles). See Erickson (1982) and Neill (1971) for discussion of this idea.

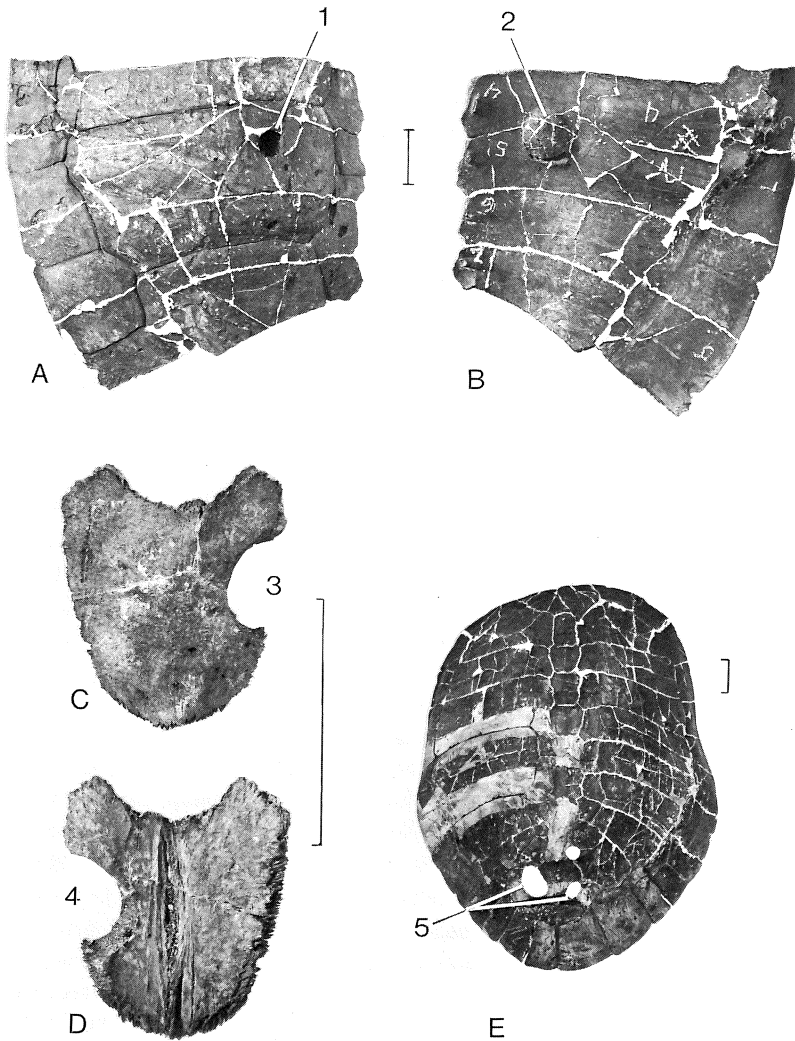


Figure 1. Shell injuries of *Protochelydra*. Positions indicated by white lines and numerals 1-5. A, SMM P76.28.258 dorsal surface of partly complete carapace with injury on suture of fourth and fifth costals, white line 1. B, Ventral view of same. Note area of new bone, white line 2. C, SMM P75.22.327 dorsal surface of neural with puncture wound, 3. D, Ventral view of same puncture wound, 4. E, SMM P75.22.328 carapace with three perforations in pygal region, white line 5. Scale equals 3 cm.

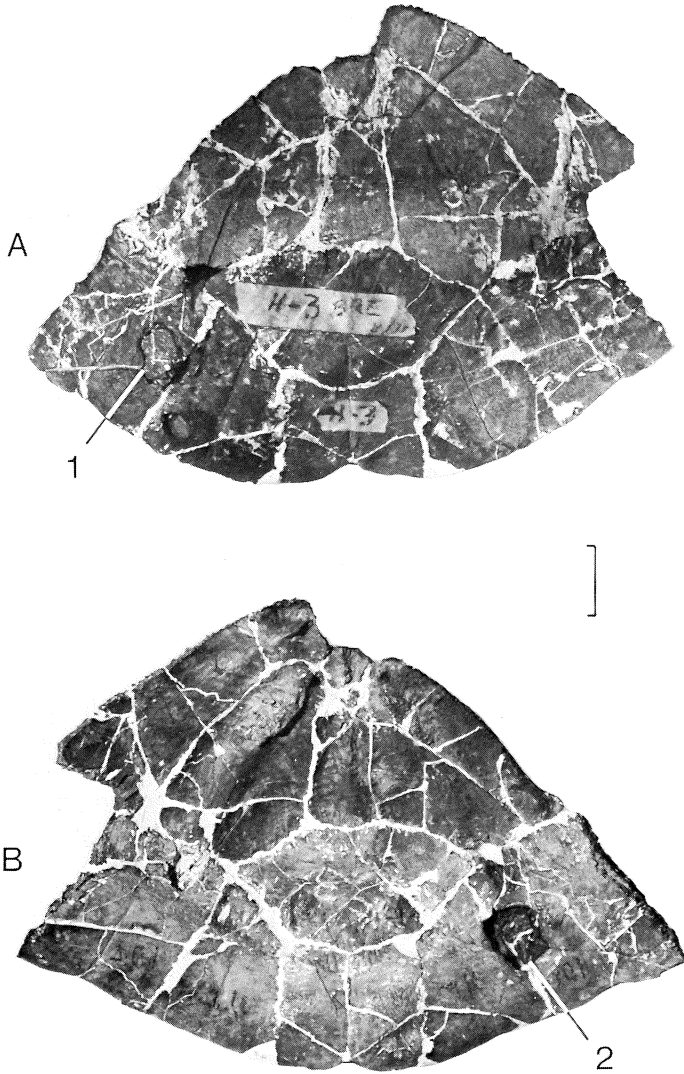


Figure 2. Shell injury of unidentified turtle SMM P73.25.134. A, Dorsal surface of partly complete carapace with injury on peripheral, white line 1. Note filling of puncture by regeneration. B, Ventral view of same, white line 2. Scale equals 3 cm.

## CONCLUSIONS

In a fossil assemblage it is not often that a specific predator-prey combination can be identified and so clearly illustrated. The evidence strongly indicates that *Leidyosuchus* preyed upon all of the turtles found in the vicinity. The turtle materials examined in connection with this investigation are, for the most part, remains of individuals that were captured but fortuitously avoided being eaten. This is apparent from the injuries which exhibit evidence of healing.

Feeding behavior of a large living crocodile, as determined by stomach analyses, is reported by Cott (1961), who demonstrates that the Nile crocodile sometimes feeds upon unlikely organisms because of their availability at a specific location. Jackson, et al (1974) discusses the relative importance of primary versus secondary ingestion and the resulting bias of prey selection. Inclusion of turtles in the diet of *Leidyosuchus* may have been circumstantial but hardly unintentional.

Whether or not the rear teeth of small brevirostrine crocodylians were evolved specifically for crushing the shells of small turtles is debatable. Perhaps an equally credible explanation for enlarged posterior teeth, considering the varied diets of living taxa (Neill, 1971), is that such specialization of the teeth would afford their owners simply a greater capability for handling any "hard" food. It follows that small, short-snouted species did not capture their prey, if indeed it included young turtles, in the manner described for *Leidyosuchus*, but instead had developed a tactic whereby its prey was "taken" towards the back of the jaws where it could be promptly crushed and ingested.

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