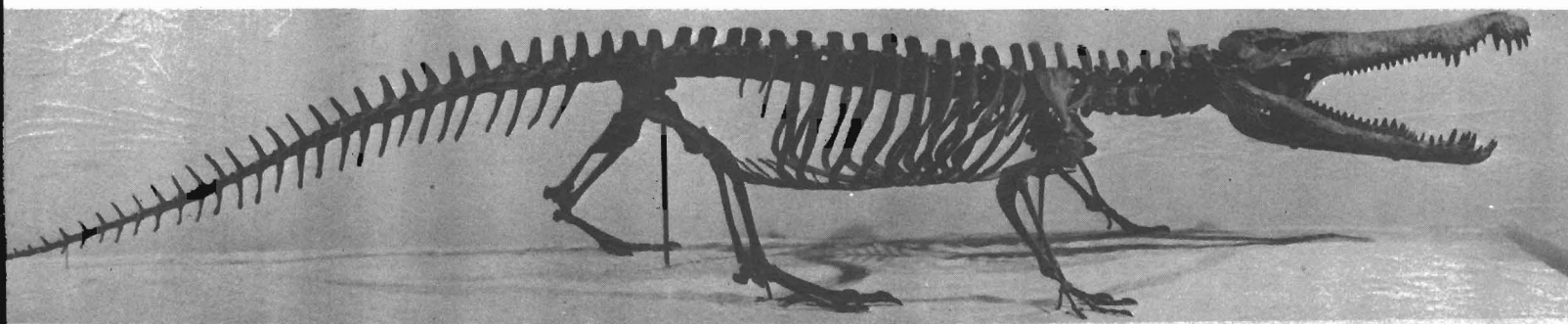


North Dakota Geological Survey
Report of Investigation No. 72

**THE WANNAGAN CREEK QUARRY AND ITS
REPTILIAN FAUNA
(BULLION CREEK FORMATION, PALEOCENE)
IN BILLINGS COUNTY, NORTH DAKOTA**

by

Bruce R. Erickson



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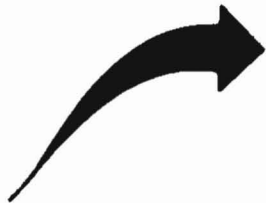
NORTH DAKOTA GEOLOGICAL SURVEY

Don L. Halvorson, State Geologist

1982



**WANNAGAN
CREEK
QUARRY**



NORTH DAKOTA

Location and aerial view (inset) of Wannagan Creek Quarry site looking east.

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INTRODUCTION

Historical Review

During the late summer of 1970 the author visited Paleocene exposures in western North Dakota to search for reported crocodile remains. Evidence of fossil crocodylians in the Dakota badlands is not, in itself, cause for surprise or even perhaps much interest, as their osteoscutes (bony plates) and vertebrae are among some of the oldest known and most common fossils of the West. The rather spectacular sample collection upon which the report was based, however, deserved more than casual consideration; for among some 40 odd pieces of weathered bone, which had been collected the year before, were six occipital condyles of large adult crocodiles. The occipital condyle is a heavy, solitary, bony structure at the back of the skull that articulates with the first vertebra of the backbone. Six of these meant that at least six individual crocodiles were represented--a rather high number for the limited sample. This initial collection was made by Evelyn Sheldrup in 1969 while vacationing in the area. It is not unusual in the annals of paleontology that significant discoveries have been made by nonpaleontologists who were not in search of fossils. Too frequently, however, such discoveries go unrecorded. In the present case, Mrs. Sheldrup is to be commended for bringing these materials to our attention.

After a brief search, the exposure from which the fossils were originally collected was located and an examination of the site was begun. The large number of bone fragments lying on the surface of the ground at first suggested a mere "bone bed"--a place where many bones had been deposited and disassociated from one another by the action of water currents. Upon closer investigation it was revealed that, even though most of the visible fragments were scattered at random, complete bones lying just beneath the surface were still intact and articulated with each other much as they had been in life. This indicated that perhaps a complete skeleton might be found if a careful excavation were undertaken.

In order to begin a scientific excavation, a grid system was employed to make a systematic collection

of all the broken and weathered surface materials for possible future reference. Included in the hundreds of pieces recovered by this method were many other crocodile bones and several more condyles as well as numerous turtle and fish fragments, some small mammal jaws, and a tiny bird bone. This survey clearly established the presence of a sizable group of animals and perhaps a potentially important paleoecological site.

Wannagan Creek Quarry was opened the following year in 1971, and it has been intensively worked each subsequent year. During this period, excavation has removed considerable overburden resulting in a quarry which presently encompasses some 1,500 square meters (13,500 square feet). This effort has yielded a remarkable fauna and flora *in situ*. It includes all classes of vertebrates, a modest number of invertebrates, and some interesting trace fossils in the form of burrows (Melchior and Erickson, 1979).

Large amounts of matrix are brought back from the quarry each year and subjected to a wet sieving treatment that separates the diminutive bones and teeth from the matrix and retains them in fine mesh baskets. The smaller jaw (fig. 1) is an example of such a microfossil that probably would have gone undiscovered if it had not been collected in a sieve.

Because the great majority (over 70 percent) of the vertebrate animals found here are previously unknown to science, the entire suite of specimens is collectively referred to as a "New Fauna" and will henceforth be called the Wannagan Creek Fauna.

Each year additional new species have been recovered. Until 1977 the rate of discovery of previously unidentified species rose each year. During that year alone nine new taxa were documented. Considering the scope of the biota and the investigating yet to be done, it is intended that this discussion serve primarily as an introduction to the Wannagan Creek Quarry community.

Acknowledgments

The writer is grateful to W. Langston and J. Lang for helpful suggestions on fossil crocodylians and discussions of behavior in living crocodylians. Appreciation is extended to A.

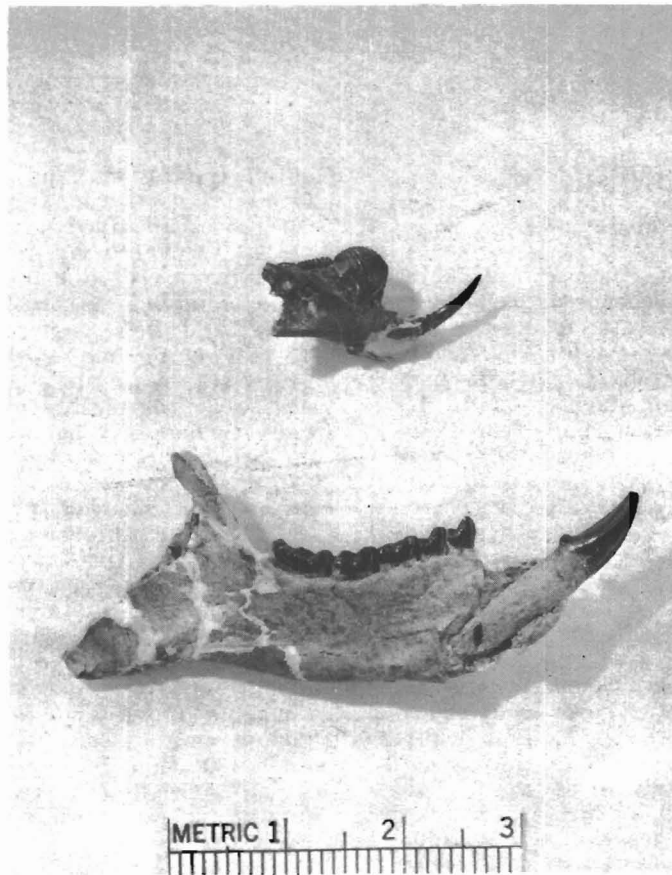


Figure 1. Lower jaw halves of a multituberculata, SMM P74.24.130 (top), and a primate, *Plesiadapis* SMM P78.14.61 (below) indicate the nature of the small mammal community of Wannagan Creek Quarry.

Cvancara and C. Carlson for important contributions to the text and to R. Melchior for reading the manuscript. K. Sander provided figure 4 and frontispiece and R. Spading provided all of the photographs. Much of the research related to this report was supported by the Geneste M. Anderson Paleontology Fund.

Geologic Setting

Wannagan Creek Quarry (frontispiece) is located in the "upper breaks" of the Little Missouri River in Billings County, North Dakota. Runoff water in the area is delivered to the river by numerous tributaries that have deeply eroded the bedrock and produced a badlands topography. One of the largest streams is Wannagan Creek from which the site takes its name. Steep vertical rock faces, slump blocks, and earthflows further characterize the area.

Badlands exposures here comprise Late Paleocene clastics (weakly consolidated sedimentary rocks) of the Bullion Creek (=Tongue River; Clayton et al., 1977) and Sentinel Butte Formations of the Fort Union Group. These rock units were derived from sediments carried eastward by streams flowing from the rising Rocky Mountains, and consist of fluvial and lacustrine sands, silts, clays, lignites, and limestones. The contact between the two formations is clearly marked by a prominent lignite bed (the HT lignite; Royse, 1972) which is traceable for considerable distances. Wannagan Creek Quarry occupies a stratigraphic position some 20 meters (66 feet) below this major lignite bed within the Bullion Creek Formation.

The quarry is on the summit of a ridge that is isolated on all sides but the south. It is in a remnant of a local flood basin in which sediments accumulated during a period of quiescence

and, therefore, form an uninterrupted sequence.

A lower gray silt containing many pelecypods (clams) and a few gastropods (snails) represents the initial phase in the development of a back-swamp environment. This is overlain by a dark lignitic shale primarily made up of locally produced organic material. It contains abundant crocodile and turtle bones in addition to many delicately preserved tree leaves. This bed grades upward into a fine gray silt that again contains many vertebrates, but fewer plant fossils. Crocodiles are still present at this horizon and several varieties of fishes and plants appear for the first time in the quarry sequence. These new species and the fine-grained sediments suggest that a lacustrine (lake) environment followed the paludal (swamp) habitat. An unconformity (erosional surface) marks the top of this final bed. Above this lies a massive layer of silty sand without fossils, which is interpreted as a crevasse splay (deposited during floods at breaks in the natural levee) from a nearby stream channel.

Within the quarry, the fossil-bearing beds have a dip that conforms to the morphology of the local flood basin. The dip is due south at 3-6°. A thick sand facies along the north edge of the quarry, where the dip is slightest, has formed a series of discrete cusps that are interpreted as beach features caused by gentle water movements. Minor intertonguing of sand and silt here demonstrates the presence of a beach zone throughout the duration of the existence of the swamp and lake phases. It further demonstrates that only slight fluctuations of the shoreline took place during this time with perhaps some periodic flooding of subaerial surfaces; however, neither waves nor currents of significance are indicated.

As preserved, the total thickness of these three fossil-producing beds is only about 60 centimeters (2 feet). This sequence contains the total record of the Wannagan Creek community. Beyond the limits of the quarry, correlations with surrounding strata show dramatic changes in lithofacies (rock record) and different habitats are implied. This is perhaps the principal explanation for the relative paucity of vertebrate fossils outside the quarry deposits.

QUARRY SIGNIFICANCE

Wannagan Creek Assemblage

Wannagan Creek Quarry has yielded a diverse biota with a vertebrate biota that would rival that of any extant crocodile-dominated habitat except for an absence of large mammals. Smaller vertebrates are represented by more than 30 species comprising a variety of fishes, amphibians, birds, and mammals. Their abundant remains are found in the silt and clay sediment and are recovered through laboratory processing of that material.

There are several chelonians (turtles) in this fauna. These are represented by numerous individuals of various age groups. Chelydrids (snapping turtles) are most abundant, followed by emydids (pond tortoises) and a few trionychids (soft-shelled forms). Protochelydra (Erickson, 1973) is the most common chelonian, making up about half of the specimens. It is a somewhat unusual "snapper" in having a high-domed carapace (upper shell). Yet its cruciform plastron (lower shell) is of typical chelydrid design. The emydids, at least two species, have low-silhouette shells and by contrast are scarce. Least conspicuous because of their small size are the trionychids. The largest number of young turtles belong to this group, including some very small specimens and the site may have been a nesting area for turtles. Other reptiles, viz., lizards, were generally small. In spite of the fact that they are known from relatively few specimens, two forms have been so far identified, a varanid (Monitor) and two species of Amphisbaenidae. Among the remaining associated aquatic vertebrates are a gigantic salamander, Piceoerpeton, and several primitive kinds of fishes including Amia (bowfin or dogfish) and Lepisosteus (garfish).

The flora consists largely of leaf impressions and casts of fruiting bodies, although much wood is also present in the form of carbonized tree trunks and branches. There are 90 documented species including some new taxa (Melchior, 1976, 1977). Abundant plant remains indicate quiet water that was well shaded in places by large overhanging trees and vines, and exposed to open sunlight in other places. A lush mat of emergent and floating aquatic plants is clearly

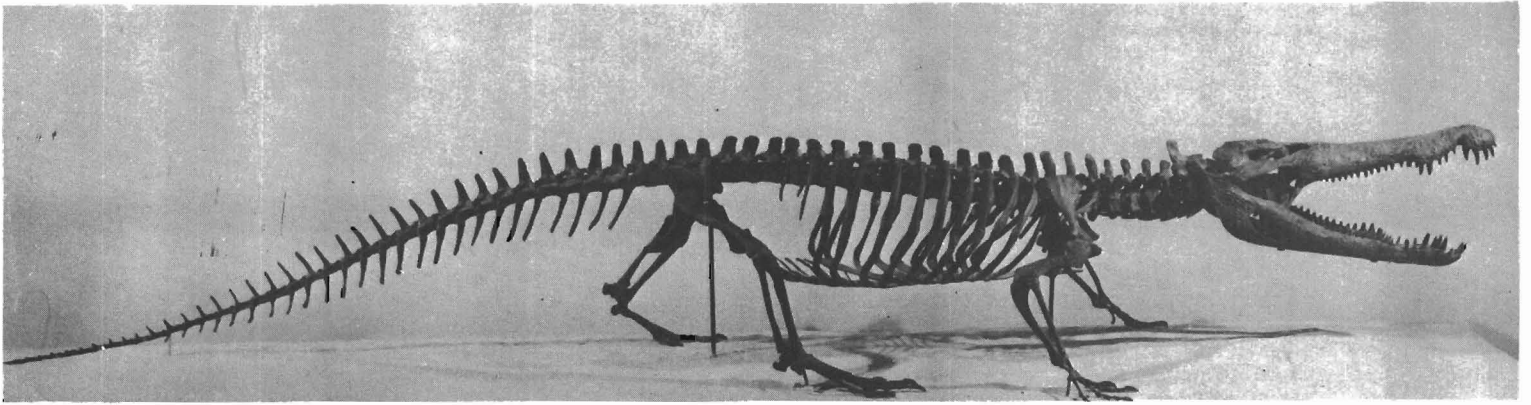


Figure 2. Articulated skeleton of *Leidyosuchus formidabilis*, SMM P74.24.6 length approximately 3.5 meters. Specimen collected from the lower level (swamp phase) of Wannagan Creek Quarry.

defined by the fossil record. These waters must have resembled some of Florida's present-day everglades and those of Chambri Lake in Papua, New Guinea, where the floating vegetation is so thick that man's fishing nets will not penetrate.

A few beetle elytra (wing cases) and two dragonfly wing imprints (as yet unnamed) are the principal remaining evidence of the insect life, which must have flourished here. There were undoubtedly many other soft-bodied forms that were not preserved. Rare forms that existed in limited numbers or for a very brief time may also have escaped detection. There were surely other species as well whose flying or arboreal (tree-climbing) habits allowed them to evade entrapment in the sediments that provide our collections.

These little known and seldom discovered forms add interesting details to the paleoecological interpretation, but it is the plants and larger vertebrates, namely the reptiles, that contribute the greatest amount of evidence regarding the paleoenvironment of 58 million years ago at the Wannagan Creek Quarry site. The variety and durability of their bony parts affords the best record of the inhabitants of this ancient community.

Reptiles of Wannagan Creek

The interest of the writer and the abundance of the reptilian remains leads to a more thorough examination of these elements of the Wannagan Creek biota. Most outstanding of these is the large eusuchian crocodile

Leidyosuchus formidabilis (Erickson, 1976) with over 50 individuals ranging in size from hatchlings 25 centimeters in length, to large adults over 4 meters long. Behavioral aspects of these animals are revealed by this ontogenetic series and offer a most unusual glimpse into a Late Paleocene community.

Leidyosuchus is a large eusuchian crocodile (fig. 2) measuring over 3.5 meters in length. The skull possesses a rather long snout and has the general habitus of the American crocodile *Crocodylus acutus* and the Nile crocodile *C. niloticus*, both of which attain lengths comparable to that of the fossil species. Outstanding features of the mandibles are its long symphyseal area (where the halves of the lower jaw contact one another at midline) and the presence of two enlarged caniniform teeth near the front on each side of the lower jaw. Lengthening of the symphysis is a structural modification for strengthening the bite, and the two enlarged teeth (3rd and 4th) were presumably a feeding adaptation as well. They are accommodated by a wide, deep crocodyloid notch in the skull when the jaws are occluded. In this feature there is a striking resemblance to *Diplocynodon* of the Eocene of North America (Mook, 1960) and Europe (Pomel, 1847).

The postcranial osteology of this crocodile is of typical design; however, the front legs are unusually long and suggest that it had better than average capabilities for terrestrial locomotion. Most crocodylians have much shorter forelegs and are belabored ambulators on solid ground; therefore, they are best suited to

swimming or moving about in the water where much of their body weight is buoyed.

A second noteworthy skeletal feature is the coat of heavy dermal osteoscutes (bony plates) that was borne by this animal. These bony plates, originally within the skin, are individually broad, flat, and without crests. The larger ones evidently overlapped one another in life. Such extensive development of dermal armor is usually a defensive adaptation associated with terrestrial rather than aquatic animals (Romer, 1956). The obvious protection afforded by this body armor, in any case, would seem to have been unjustified as there are no known Paleocene predators which would have been capable of "doing-in" such a large, formidable crocodile, except perhaps one of its own kind. The heavy scutellation may have had some function other than protection, or it may simply have been a persisting primitive character. In other structures this crocodile appears to have been amply equipped for an aquatic existence. Unlike many of the smaller vertebrates of Wannagan Creek Quarry, whose numbers probably misrepresent their actual relative abundance in this community because of their susceptibility to transport (Korth, 1979), the record of the large crocodile is judged to be indicative of the population size.

Some studies (Cott, 1961; Webb, 1977) have looked at size to sex relationships of crocodile communities. They show no obvious sexual dimorphism of contemporary forms so it is not possible to determine the sex of the collected specimens. However, it is assumed that the largest skulls and corresponding number of parts of the largest propodials (major limb bones) belong to males.

A single, nearly complete skeleton of a small species of alligator (estimated length of 1.2 meters) accounts for the only other crocodylian species so far known from the site. This form (as yet unnamed) is unique as it is the earliest known association of alligator and crocodile. Early alligator-crocodile associations are known in but a few places (Berg, 1966; Krumbiegel, 1959), and most associations that are suspected are based upon rather tenuous stratigraphic correlations. Therefore, this newly discovered evidence of coexistence is of considerable interest.

This small alligator bears a stronger resemblance to later alligators than any of its contemporaries or near-contemporaries of either Paleocene or Eocene age. It is, therefore, hypothesized that it may represent one of the earliest of the lineage leading to true alligators. It is characterized by its short broad skull and large bulbous rear teeth that are designed for crushing prey.

A second specimen regarded as conspecific (same species) is worthy of mention in that it preserves the greater part of the postcranial skeleton (fig. 3). It was collected from nearby deposits that are slightly older than those of the main quarry. Much of its osteodermal (bony armor) covering is preserved, and of special interest is the caudal (tail) section wherein osteoscutes apparently encircled the entire structure forming a tail sheath as in *Caiman* (Romer, 1956). Many of the body and caudal osteoscutes bear low dorsal crests similar to those possessed by the former specimen. The nuchal (nape of neck) and cervical (neck) osteoscutes of the quarry specimen show maximum development of these crests and a few of the forward ones have sharp, blade-like crests. A few other isolated osteoscutes were found within the main quarry indicating the presence of additional individuals.

Another important reptilian element of this fauna is the longirostrine (long-nosed) *Champsosaurus*. Together with the larger crocodile and the smaller alligator, three basic snout designs are established, each, no doubt, with its own special functional purpose. In spite of its fairly large size (average length of about 3 meters) bones of this highly specialized fish-eating reptile are found in limited quantity within the main quarry, whereas elsewhere it is abundantly represented. The implication is its preference for waters not inhabited by crocodylians, which may have preyed upon it. Throughout its history, *Champsosaurus* has maintained a constant association with crocodylians (Erickson, 1972). Its skull is superbly designed for capturing fishes (fig. 4). With its long, narrow jaws, lined with many small sharply pointed teeth, this predator adequately filled a role similar to that which was later so successfully assumed by long-nosed garfishes as a subordinate predator existing with



Figure 3. Field sketch of alligator skeleton, SMM P72.34.274 (posterior two-thirds) *in situ* showing extensive scutellation of the caudal region. Collected 100 yards north of Wannagan Creek Quarry at a slightly lower level.

crocodiles. The skull is a complicated structure, as well as fragile, due to its widely expanded cranial vault of thin bony bars and plates whose function is uncertain. Figure 4 illustrates its unusual construction.

There is a remote possibility that among the champsosaur remains, especially the numerous vertebral centra, some few elements belong to another reptile, *Simoedosaurus*. This closely allied genus has been recently discovered in North America (Russell and Baird, 1978). Although somewhat larger, its vertebrae, as well as some of its other bones, are remarkably similar to those of *Champsosaurus*. The resemblance has very likely contributed to its lack of recognition in the past. No evidence of a simoedosaur is yet

known from the quarry; however, research in progress by the writer suggests that *Champsosaurus* and *Simoedosaurus* coexisted but each occupied a very different niche. It is further suspected that the larger simoedosaur, even more so perhaps than the champsosaur, preferred an environment without large crocodiles because of the even greater likelihood of being preyed upon by the large crocodile.

Taphonomy

The term "taphonomy" as proposed by Efremov (1940) is that division of paleontology which treats the conversion of living animals to fossils. A number of assemblages have been

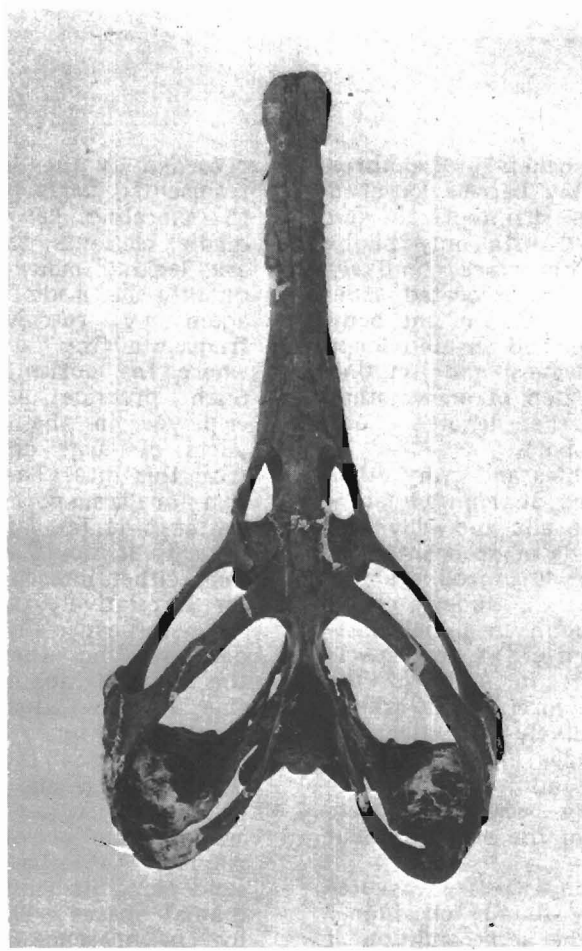


Figure 4. Skull of fish-eating Champsosaurus, SMM P77.33.24, showing the delicate cranial structures. Skull length 56 cm.

analyzed for their taphonomy. A common aspect of many taphonomic studies is "mass mortality" ascribed to a catastrophic event. The Wannagan Creek accumulation of crocodiles does not represent such a mass mortality. The remarkable size range of individuals, including hatchlings, and the vertical distribution of numerous individuals throughout the sediments, suggest that a community of some stability existed for a substantial length of time. The causes of individual death seem to have been due to more normal events such as natural attrition, and more traumatic causes, such as cannibalism, that were also operating to a considerable degree.

Twenty-seven complete skulls of crocodiles distributed over much of the site show a definite preference of positioning with respect to dorso-ventral orientation. Of these skulls, 7 are oriented with the dorsal surface up, 16 with the palatal surface up, and 4 with a lateral side up, i. e., on edge. Three skulls having their palates

up still retain their lower jaws in articulation, as does one of the skulls "on edge." The preference for an "overturned" position clearly reflects the floating posture of a bloated crocodile carcass, and the posture it is more likely to assume when settling to the bottom. It is further suspected that all of the present individuals, which were floating carcasses at some point, first contacted the bottom sediments in this position. Scavenging of these carcasses lying on the bottom, by other crocodiles, would have been a common event. During this process the lower jaws could have been easily separated and the heads overturned or partially overturned as is suggested in at least 4 specimens.

Individual integrity of most of the skeletons wherein postcranials, at least major portions thereof, remain proximal to their respective skulls, attests to a disturbance, but not to transport. About half of the skulls (30 of which are essentially complete) still contain most of their teeth within their respec-



Figure 6. Diagrammatic reconstruction of Wannagan Creek Quarry site during the Paleocene. Left to right: Champsosaurus, alligator (yet unnamed, and Leidyosuchus, each occupying a special niche. Flora represented here: Cercidiphyllum (Katsura tree), palm, palmetto, Metasequoia (in distance), Azolla (water fern), and Nelumbium (water lily).

waters. In rough water, the snout, with its narial disc, must necessarily be elevated at a rather high and awkward angle to keep from "shipping water." In doing so the animal is set off balance and founders, causing the head to slip backward underwater (Cott, 1961). In a place of congregation such as at Wannagan Creek Quarry, it is improbable that either strong currents or significant waves were anything but unusual conditions, occurring only perhaps during storms, and it is far more likely that the existing disarrangement of skeletal remains was primarily the result of direct disturbance by the large crocodiles themselves.

Paleoecology

Whereas the efforts of the ecologist are directed at understanding the interrelationships of organisms that live together, the work of the paleoecologist is concerned with reconstructing the extinct environment which associated organisms inhabited. Complexities of the paleoenvironment can only be imagined, and this attempted assessment of a few relationships emphasizes the great amount of lengthy analysis that is still needed for the reconstruction of the Wannagan Creek paleocommunity. In this discus-

sion the writer will consider, in detail, only some of those ecological factors that impinged directly upon the principal vertebrate, and to a lesser extent those that affected closely associated taxa. Some preliminary behavioral reconstructions will also be hypothesized.

The two crocodilians and Champsosaurus that inhabited the quarry site area exploited a paleoecosystem that embraced a wealth of potential prey species within a setting of dense vegetation typical of the North American Paleocene (Brown, 1962). Figure 6 depicts diagrammatically these three principal predators in their respective niches. A few of the more salient floral types that flourished in the immediate area are also indicated.

A bit of insight into the role of the small alligatorine may be gained if one considers the peculiar niche it filled as a rather inconspicuous contemporary of a large group of aggressive crocodiles. Its general skull structure and tooth form suggest an omnivorous habit that may have included any of the numerous small vertebrates as well as invertebrates as prey species. The abundant vegetation, especially the emergent types growing in the shallows, would have provided suitable refuge and a productive

stalking territory. Its poor representation would indicate a sociality quite different from the apparent gregarious habits of the large crocodile. Like other early alligators, this new form inhabited a swampy realm that meant reduced visibility. Garrick and Lang (1977) discussed the need for vocalizing among extant alligators under such conditions, and further suggested the possibility of vocal signaling in extinct species. If such intraspecific communication became part of the basis for the remarkable adaptations and ultimate survival of this special group of crocodylians, it is possible that their early crocodile associations provided the pressures, which, in turn, evoked such innovative behavior. Distribution of the Alligatorinae by the Paleocene and Eocene is nearly world-wide (Sill, 1968) demonstrating their early success.

Evidence of Predation

In his lengthy analysis of feeding behavior of the Nile crocodile, Cott (1961) observes that crocodylians occupy no single niche, but many; therefore, they usually have a varied plentiful food source available to them. This includes predation up to one-half mile from the water. It is possible that the large Paleocene crocodile Leidyosuchus resembled the living form in this respect. If its terrestrial capabilities were as well-developed as its limbs and feet indicate, its hunting range could have exceeded this. Few large terrestrial prey species were available, however, and, unlike the Nile crocodile's diet, which includes numerous ungulate (large-hoofed) mammals, that of Leidyosuchus must have been limited to aquatic forms and resembled that of the American crocodile in its more piscivorous (fish-eating) habits.

The most conspicuous evidence that demonstrates predation by this large crocodile is a suite of turtle shells in different states of completeness, and representing several distinct species. Most exhibit perforations and surface scars in the posterior (rear) regions (fig. 7). These anomalies can be directly associated with the large caniniform teeth in the jaws of Leidyosuchus. The carapace (upper shell), rather than the plastron (lower shell), is more severely scarred. This is due presumably to the structure of the shell wherein the carapace over-

hangs the much smaller xiphiplastra (rear part of plastron) and is more easily "grabbed" by opposing jaws. Partial penetration of the bony carapace resulting from an unsuccessful capture attempt was evidently a frequent occurrence as most of the shells bearing wounds also show evidence of subsequent healing. Similar injuries are frequently observed in living turtles that are habitually associated with crocodylians.

Protochelydra remains appreciably outnumber those of other turtles in this deposit. Its carapace is rather highly domed for a snapping turtle (fig. 8) but is otherwise characteristically chelydrid in form. Aside from any other adaptive advantage (either aquatic or terrestrial) that this feature may have bestowed upon its possessor, its shape made it invulnerable to all but the largest of jaws that might securely seize it. Presumably a capable predator in its own right, Protochelydra successfully coexisted amongst a population of large crocodiles. Although not present in large numbers, Trionyx (soft-shelled turtle) may also have been a predator upon young crocodylians. Flower (1933) notes the heavy toll they inflict upon hatchling crocodiles today.

Scatological evidence shows that fishes were also part of the diet of Leidyosuchus. Among some 300 coprolites (fossil feces) examined in this regard, some 100 were rejected on size and shape as possibly belonging to other species, perhaps Champosaurus. Of those remaining, 21 were found to contain inclusions mostly of fragmented ganoid scales. These are plentiful enough to make the assumption that garfishes were relatively abundant and were a habitual part of the diet.

Regulation of population size in the living Nile crocodile is related to predation or cannibalism rather than food supply (Cott, 1961). Cannibalism is a normal practice for the Indo-Australian species (Webb, 1977), unknown in some caiman, even under the most adverse conditions of seasonal overcrowding (Lang, personal commun., 1979), and only suspected in others. From what can be discerned about the potential food source that was available, as well as the absence of any potential predator, cannibalism must be given serious consideration as a behavior for this fossil population also.

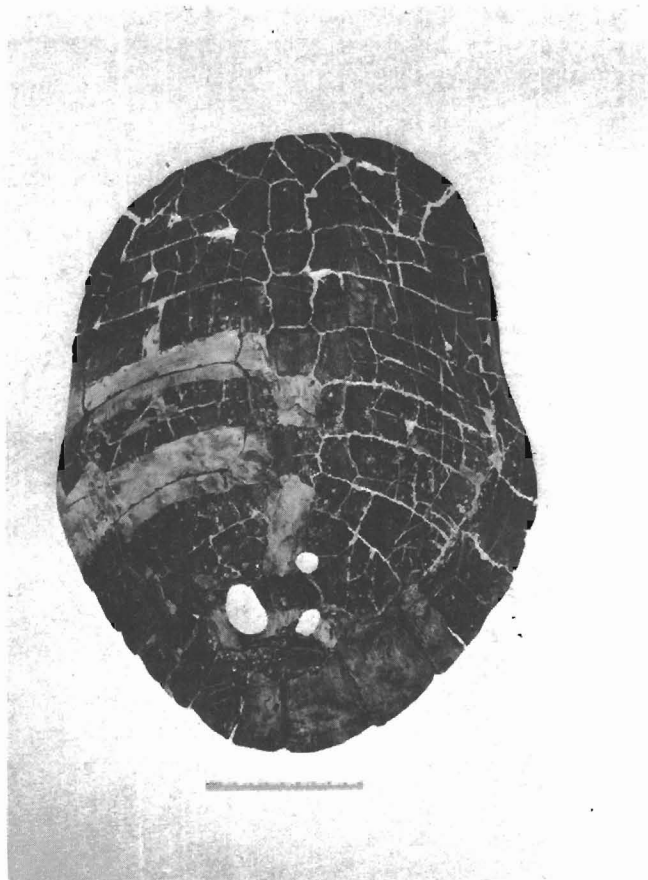


Figure 7. The carapace (upper shell) of *Protochelydra*, SMM P75.22.271 shows wounds inflicted by large crocodile teeth. Scale 10 cm.

Among the many separate skeletal elements of *Leidyosuchus* that were deposited along the shoreline, about a dozen or so belong to hatchlings. This occurrence indicates the possibility of nearby nesting sites. Very young crocodylian remains are virtually absent from the fossil record (Langston, 1978). Apart from the special conditions required for their preservation, their absence in the contemporary environment is well noted. This is believed due to a wide variety of accidents that befall them during the first year of life (Langston, 1978). Much predation upon the very young may be due to cannibalism by larger animals inhabiting the same area. In addition to hatchlings, the relative size and length of other young individuals found within the deposits of Wannagan Creek Quarry agrees, in general, with those of contemporary populations wherein animals of overall lengths around 1 to 1.5 meters are absent. From this it is hypothesized that

individuals within this general size range relocate themselves to avoid contact with larger animals.

Cannibalism is further indicated by the disassociation of postcranial skeletons. In looking at the distribution of the remains of *Leidyosuchus* within the limits of the site, it is apparent that the majority of skulls lack complete postcranial skeletons. A general disarticulation and scattering of bones is the rule and orientation seems random. A total of some 50 individuals have been so far recorded by skull count--a number consisting of basicrania alone. A total of only 705 vertebrae are accounted for, and 2930 osteoscutae have been recovered. This is obviously much less skeletal material than that which was originally present.

Little evidence exists of any water current that could have acted upon the assemblage as a transporting agent to carry bones either into the site or away from it. Carcass scavenging by crocodiles is established behavior. In

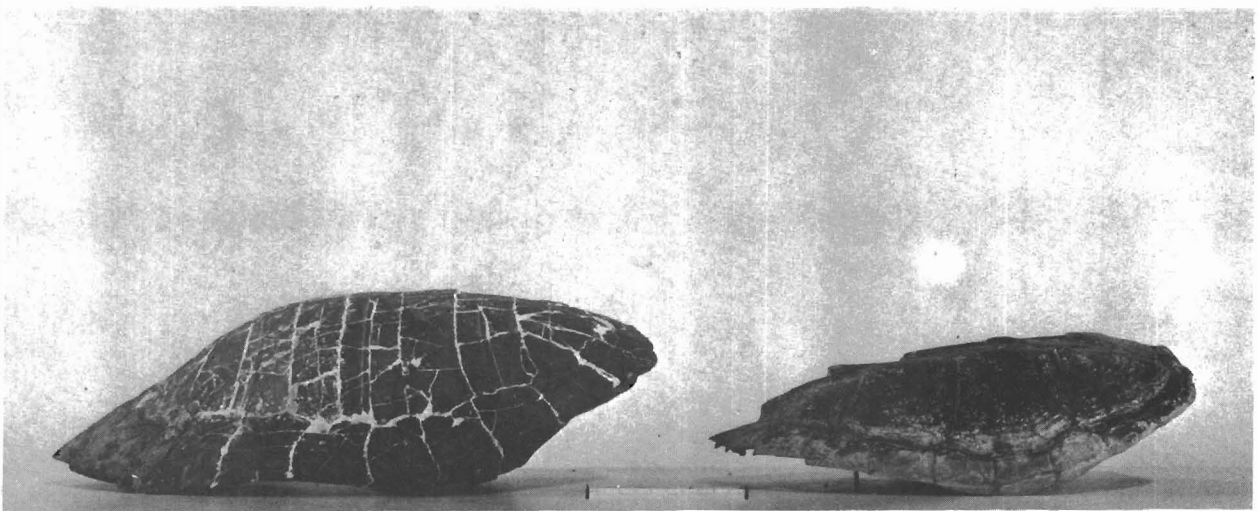


Figure 8. Shell differences in two snapping turtles, *Protochelydra*, SMM P75.22.271 (Paleocene) and *Chelydra* (recent common snapper), SMM uncatalogued specimen. The high-domed shell of the former is suspected to have had survival advantage in its association with large crocodiles. Scale 10 cm.

the process, many of the bones of dead animals are ingested and thereby removed from the system through the subsequent digestive processes. Bones that are too large to be ingested, such as skulls and mandibles are largely ignored and remain as part of the faunal record (Behrensmeyer, 1975). This probably accounts for the disparity of skull and skeletal material.

Pathological alterations of bones among the adults of the population are fairly common, consisting of fractures, punctures, various kinds of lesions, and plastic deformations. All but the latter condition were due largely to traumatic, nonfatal causes, as most show evidence of healing. These conditions are largely attributed to intra-specific encounters.

Least obvious of potential prey species are perhaps the diminutive mammals that existed in prodigious numbers and many varieties. Although none are thought to have been aquatic, some had a strong tendency toward arboreal niches. In spite of the large amount of small mammal remains that occur at this site, their relative numbers in life may have been somewhat fewer, as the effects of stream flow may concentrate these elements.

The occurrence of unabraded, and gnawed, crocodile bones (fig. 9), however, clearly demonstrates the presence of at least certain species of micromammals in the immediate area. Two characteristic mammalian types of the deposit are multituberculates and primates (fig. 1). Both are fairly well

represented and possibly may have been "gnawers." In light of this, and the arboreal habits suspected for some of these forms in the overhanging vegetation, it is likely that they were occasionally eaten by smaller crocodiles as well as alligators. Neill (1971) reports that food of the modern alligator, although diverse, should reflect the local abundance and availability of some particular prey organisms. Although there is no direct evidence of their predation by the small alligator, this rather rich fauna suggests that an ample food source was available in small mammals alone.

All living crocodiles possess gastroliths (stomach stones). Gastroliths, whether used for hydrostatic control (Cott, 1961), or as an aid in digestion, or both (Webb, 1977), are normally present where crocodile assemblages are found; however, none have been found at this site. Cott (1961) notes that swamp crocodiles lag somewhat in gathering stones because of bottom type, but do eventually acquire them. Remains from several deposits such as those from the Geiseltal contain "Magensteine" (Krumbiegel, 1959), as do those from Grube Messel (personal obser.). Even very young solitary individuals contain them (Langston, 1978). Assuming that stomach stones were originally present in this population, they either: (1) were removed subsequent to deposition of the carcasses, or (2) are present but unrecognized for what they are. Removal by transportation seems very



Figure 9. A fragmented crocodile metatarsal, SMM P74.22.329 from the beach facies of Wannagan Creek Quarry shows the telltale marks of gnawing, presumably by small scavenging mammals.

unlikely. Dissolution is a possibility if the objects selected, perforce from some convenient location away from the site, had the capability of performing and enduring, for a time, the functions of stomach stones, only to break down upon the demise of the animal. Yet this is highly unlikely, as some traces surely would remain in one of the lithologies of the site.

A more plausible explanation is the utilization of osteoscutes and other smaller bones, such as vertebral centra, as gastroliths, in lieu of more suitable objects. Cott (1961) notes that where crocodiles exist in numbers, they die in numbers, leaving their rotting carcasses as carrion, and also leaving numerous scutes and other bones to be ingested as gastroliths. It has been suggested that the relatively low counts of vertebrae and osteoscutes reflect the cannibalistic behavior of this crocodile.

In an attempt to determine the

relative durability of certain crocodile bones, three contemporary crocodile bones were placed together in a HCl solution (pH 1.5) and regularly agitated. After 10 weeks the vertebra and two large osteoscutes remained intact and showed only moderate erosion and softening of their surfaces. It is not unreasonable then to assume that some of the ingested bones may have been pressed into service as gastroliths. It is likely that such "stones" would not be as durable as those more commonly utilized (e.g., pebbles) and would need occasional replenishing.

Evidence of Nesting

A nesting site is suggested by the existence of diminutive crocodile bones (Erickson, 1976) which fall within the size range that would be expected in hatchlings of an animal comparable in size to the American and Nile crocodiles. Korth (1979) has shown the susceptibility of very small bones to

transport, and the unreliability of their presence as an indication of the faunal composition. Nevertheless, the environmental setting would favor them as an indigenous segment of the present fauna. The attempted partial reconstruction of the paleoenvironment of Wannagan Creek Quarry (fig. 6) incorporates salient features derived from the evidence at hand, and that established by Cott (1961), as being best suited for living crocodiles as nesting habitats.

Firstly, a persistent beach zone documents a rather stable condition with only minor fluctuations of the water's edge during the time which the Wannagan Creek fauna inhabited the flood basin. Mild abrasion is expressed by some bones occurring within the beach zone; therefore, it is likely that at times the beach was awash. A short distance inland, however, the sand must have stood high above the water's surface as here it is over a meter thick and contains animal burrows that are interpreted as those of decapods (crayfish). This would have been seemingly appropriate ground for nesting.

Nothing yet can be stated about the location or type of nest that may have been utilized. It is presumed that a "nest" as described by Greer (1971) was probably required for incubation of the eggs. Whether this was a mound of sand or vegetation, or a simple pit in the sand, is pure conjecture.

Secondly, the beach was situated with access to a fairly large body of deeper water, thereby explaining the presence of numerous, large (estimated lengths up to 1.5 meters) fishes.

Finally, a forest canopy of large trees including magnolia, walnut, cypress, and the prevalent Cercidiphyllum (katsura tree) overhanging the beach and various shrubs and vines formed a dense understory (Melchior, personal commun., 1980). This vegetation provided the shade that is invariably associated with the nesting sites of contemporary crocodiles.

SUMMARY

The Wannagan Creek Quarry site represents a unique look at a prolific fossil-bearing strata of Paleocene age. It is a remarkable site in the broad spectrum of species which have been preserved there, some of which are similar to younger fossils, and a few that are closely related to living kin. Since Paleocene strata have had rather limited study, this site has produced many new species and further excavations will likely add to the list. As of the end of 1980, 7 new species have been described and at least an additional 18 new taxa are believed to be present among all of the groups.

Reptiles account for the majority of the fossilized vertebrate remains. They also include the only complete skeletons from the site. So far they are represented by two crocodylian taxa, five chelonians, one champsosaurid, at least two species of lizard, and one possible snake. Among the mammals, multituberculates, insectivores, primates, and condylarths are represented by dozens of mandibles, solitary limb and girdle bones, and many isolated teeth. Dakotornis (Erickson, 1975) is one of at least three different species of birds. Several amphibians and fishes are present but only an estimate of about 10 different types can be made from their incomplete record.

The invertebrate fauna as yet is largely unstudied; however, current laboratory preparation of quarry matrix indicates the presence of a variety of insects and mollusks.

In addition to the expanded knowledge of the Paleocene biota that this site has provided, it offers a detailed look at a paleocommunity. Comparisons of the fossil record at Wannagan Creek and contemporary crocodile communities provides a means of reconstructing the climate and depositional setting in western North Dakota when the lignite-bearing strata of the Fort Union Group (Paleocene) were being deposited.

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