Wannagan Creek field crew in camp 1975. Left to right standing: T. O'Brien (chief preparator); M. O'Brien (student); B. Chuchel (student); C. Faraci (cook); B.R. Erickson (paleontologist); J. Guyer (student); R. Spading (photographer); C. Hudak (student); R.C. Melchior (paleobotanist). Left to right kneeling: T. McCutheon (student); P. Ganzel (student).
FLORA AND FAUNA OF
THE WANNAGAN CREEK QUARRY:
LATE PALEOCENE OF NORTH AMERICA

by

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INTRODUCTION

The Wannagan Creek Quarry flora and fauna make up one of the most complete assemblages of Paleocene megafossils in North America. It is significant that all classes of vertebrates and both aquatic and terrestrial plants are represented as well as a variety of invertebrates. It has taxonomic and ecologic similarity to the somewhat younger assemblages of Grube Messel and des Geiseltales in Germany and parallels may be drawn.

The quarry at Wannagan Creek was first excavated in 1970 after fragmentary surface evidence of fossil crocodilians was reported to the writer. During the ensuing 20 years, 18 seasonal expeditions to the site by the Paleontology Department of the Science Museum of Minnesota have produced a large suite of associated plant and animal fossils. All of these specimens were derived from a narrow zone some 60 centimeters thick at the excavation site. The assemblage, representing the Wannagan Creek biota, constitutes a major portion of a local community that now numbers several thousand specimens representing over 120 taxa.

Recovery rate of taxa previously unrecorded for this deposit began to diminish only in 1979 after ten years of intensive collecting. The assemblage is regarded as comprehensive of the megafossil component which has been preserved. It is unknown what percentage of the living community or biocoenose this represents as the sample has been undoubtedly strongly biased by selective preservation. Work, however, continues at the site with increasing efforts on taphonomic and ecological questions. The Wannagan Creek assemblage never has been reported in toto; therefore, current floral and faunal lists are presented herein for the record and for their potential application to the analysis of vicarious taxa or biotas of similar aspect. A bibliography of Wannagan Creek fossils is included in the text.

KEY WORDS: Wannagan Creek flora/fauna, Paleocene, Paleoenvironmental reconstruction.
FIGURE 1. Bird’s-eye view of Wannagan Creek Quarry, Little Missouri badlands, Billings County, North Dakota, USA.
GEOLOGICAL SETTING

Wannagan Creek Quarry occupies an area of approximately 35 x 50 meters within the upper part of the Bullion Creek (Tongue River) Formation, Tiffanian, Paleocene, Sec. 18, Tp. 141 N, R. 102 W, Billings County, North Dakota, U.S.A. (Erickson, 1976, 1982; Melchior and Hall, 1983). Classic “Badlands” erosion of the “upper breaks” of the Little Missouri River in this area originally exposed a fossiliferous zone on the western face of the small butte which has been since greatly reduced by activities resulting in the development of Wannagan Creek Quarry (fig. 1).

The primary lithotope of the fossiliferous zone is a lignitic, silty clay. Three thin beds of unequal thickness are productive of fossils and are defined as “Bed 1,” a gray, laminated, calcareous shale grading upward into “Bed 2,” a black, fissile shale in contact with overlying “Bed 3,” consisting of gray and buff silty shale. This sequence of sediments (fig. 2) appears to represent continuous deposition in a local floodbasin that was terminated by crevasse splays (Bed 4) of sand from nearby stream channels.

FIGURE 2. Stratigraphic profile of Wannagan Creek Quarry.
Fossil plants and invertebrates are well stratified among these sediments and characterize certain levels of the sequence. Vertebrates are somewhat less stratified, tending to span the entire sequence. The total assemblage, however, indicates a fluvial habitat for Bed 1, which is predominantly marl containing riparian mollusks, and a stream bank flora. Beds 2 and 3 represent somewhat more stable conditions having a floral admixture and faunal component indicative of a levee environment (Melchior and Hall, 1983). Beyond the quarry there is marked reduction in the occurrence of fossil remains except for a few isolated pockets with some exceptional vertebrate articulations (Erickson, 1982). These pockets are remnants of ponds and interfluves which were isolated locations. Abrupt lithofacies changes characterize the area.

TAPHONOMIC BACKGROUND

The vegetational record is considerable (Melchior and Hall, 1983). Species are numerous and represented by leaves, fruits, and megaspores. Stems are merely carbon films or chunks in the case of tree trunks. Invertebrates are not abundant nor is their preservation remarkable. Most are either carbonized fragments or masserated shell material within the marl horizon. Bioturbation structures are present as burrows (Melchior and Erickson, 1979). Other trace fossils such as coprolites, which are primarily those of crocodiles (Sawyer, 1981), are present in large numbers indicating that feeding took place during deposition of these beds. They are especially abundant in the eutrophic lower level where conditions were most suitable for their preservation. Bioerosion structures are also found at this site as gnawed and bitten traces (Erickson, 1982; 1984).

By far the most abundant large form is the eusuchian crocodile _Leidyosuchus_ (Erickson, 1976; 1982). With some 70 individuals documented so far by basicranial count, this was the single dominant predator. Skull morphometrics and the paleoecology of this large crocodile are subjects of current research by the writer.

The taphonomic mode of Wannagan Creek vertebrates is complete skulls and partly complete postcranials amongst a preponderance of separate elements. This is in contrast with the remains found at Grube Messel (Bornhardt, 1975; Franzen, 1975; 1976) and des Geiseltales (Krumbiegel, 1959) wherein completely articulated skeletons are the rule. Bioturbation of bottom sediments principally due to the great concentration of large crocodiles accounts at least in part for this difference. In insular locations near the main quarry, such as noted above, large crocodiles were not present, therefore skeletons are mostly intact. One cannot, however, escape the similarities of Wannagan Creek, Grube Messel, and des Geiseltales. Because of the importance of these sites for Paleogene faunas, it seems appropriate to mention and briefly compare them here.

Many of the principal forms that occur at each of these sites are closely related taxa and in some instances identical at the generic level. The overall floral and faunal composition
for each is distinct, but a good deal of this distinction is size and relative abundance of various taxa. At Wannagan Creek, for example, the dogfish/mudfish (*Amia*) is abundant, whereas the gar (*Lepisosteus*) is relatively scarce. At Messel and des Geiseltales, on the other hand, *Lepisosteus* abounds and *Amia* is just fairly common (Franzen, 1977). Non-amphibious (landbewohnende) forms, such as water-loving birds and small mammals of the underbrush and trees, that occur at all of these sites further emphasize paleoenvironmental similarities. It is also not out of place to characterize these three Paleogene discrete stream and lakeshore sites as subtropical nesting grounds of crocodilians as all three sites have yielded fine and numerous examples of hatchling-size crocodilian remains and, for des Geiseltales, crocodile eggs (Krumbiegel, 1959).

The Wannagan Creek assemblage undoubtedly comprised an ecologically balanced biotope. Notions and inferences gathered from the collections and host sediments have resulted in an interpretation of the paleoenvironment shown in early stages of quarry development (fig. 3) and in later stages of quarry development (fig. 4). Further discussion of the flora and fauna is provided by Erickson (1973; 1975; 1985), Melchior (1976; 1977), Naylor and Krause (1981), and Lewis (1988). Also see Krumbiegel, 1959; Franzen, 1975; Maier, 1978; and Shipman, 1987, for discussions of paleoenvironmental reconstructions of des Geiseltales and Messel. The thanatocoenosis of Wannagan Creek Quarry is listed below. These preliminary lists were compiled with the assistance of R.C. Melchior (plants); J. Hartman (invertebrates); R.D. Benson (birds); and R. Holtzman (mammals).
TABLE 1. Flora of Wannagan Creek Quarry

Taxon (alphabetically arranged) and Distribution Indicated: (L) lower; (U) upper; (*) both levels

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alismaphyllites grandifolius (*)</td>
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</tr>
<tr>
<td>Amentotaxus campbelli (L)</td>
<td></td>
</tr>
<tr>
<td>Ampelopsis acerifolia (L)</td>
<td></td>
</tr>
<tr>
<td>Azolla stanleyii (*)</td>
<td></td>
</tr>
<tr>
<td>Cabomba inermis (L)</td>
<td></td>
</tr>
<tr>
<td>Canariophyllum ampla (U)</td>
<td></td>
</tr>
<tr>
<td>Carpolithes arcticus (L)</td>
<td></td>
</tr>
<tr>
<td>Carpolithes sp. - ca. 12 spp. (*)</td>
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</tr>
<tr>
<td>Carya antiquorum (*)</td>
<td></td>
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<tr>
<td>Castanea intermedia (*)</td>
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<tr>
<td>Celtis newberryi (U)</td>
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<tr>
<td>Celtis peracuminata (L)</td>
<td></td>
</tr>
<tr>
<td>Cercidiphyllum genetrix (*)</td>
<td></td>
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<tr>
<td>Cissus marginata (*)</td>
<td></td>
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<tr>
<td>Cocculus flabella (L)</td>
<td></td>
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<tr>
<td>Cornus hyperborea (*)</td>
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<tr>
<td>Corylus insignis cf. C. acutertiaria (L)</td>
<td></td>
</tr>
<tr>
<td>Cypericites sp. (*)</td>
<td></td>
</tr>
<tr>
<td>Dictyophyllum anaomolum (U)</td>
<td></td>
</tr>
<tr>
<td>Dictyophyllum hebronensis (U)</td>
<td></td>
</tr>
<tr>
<td>Equisetum sp. (L)</td>
<td></td>
</tr>
<tr>
<td>Ficus artocarpoides cf. Dictyophyllum (U)</td>
<td></td>
</tr>
<tr>
<td>Ficus minutidens cf. Dictyophyllum (U)</td>
<td></td>
</tr>
<tr>
<td>Ficus planistocata cf. Dictyophyllum sp. (L)</td>
<td></td>
</tr>
<tr>
<td>Ficus subtruncata cf. Dictyophyllum sp. (L)</td>
<td></td>
</tr>
<tr>
<td>Ginkgo adiantoides (U)</td>
<td></td>
</tr>
<tr>
<td>Glyptostrobus europaeus (U)</td>
<td></td>
</tr>
<tr>
<td>Glyptostrobus nordenskioldi (L)</td>
<td></td>
</tr>
<tr>
<td>Hammamelites inaequalis (U)</td>
<td></td>
</tr>
<tr>
<td>Hydrangea antica (L)</td>
<td></td>
</tr>
<tr>
<td>Isoetites horridus (*)</td>
<td></td>
</tr>
<tr>
<td>Juglans taurina (*)</td>
<td></td>
</tr>
<tr>
<td>Laurophyllum perseum (L)</td>
<td></td>
</tr>
<tr>
<td>Magnolia berryi (U)</td>
<td></td>
</tr>
<tr>
<td>Magnolia magnifolia (L)</td>
<td></td>
</tr>
<tr>
<td>Magnolia regalis (L)</td>
<td></td>
</tr>
<tr>
<td>Melastomites montanensis (L)</td>
<td></td>
</tr>
<tr>
<td>Metasequoia occidentalis (*)</td>
<td></td>
</tr>
</tbody>
</table>
Minostites coloradensis (L)
Morus montanensis (L)
Nelumbium tenuifolium (L)
Oreopanax dakotensis n. sp. (L)
Pensophyllum cordatum (U)
Persia brossiana (*)
Planera microphylla (L)
Platanus nobilis (*)
Platanus reynoldsii (*)
Polareodoxites plicatus (*)
Porosia verrucosa (*)
Prunus perita (L)
Pterocarya hispida (L)
Quercus sullyi (U)
Rhamnus cleburni (L)
Salix aquilina (L)
Sassafras thermate (L)
Sparganium stygium (*)
Taxodium olriki (U)
Ulmus rhamnifolia (L)
Viburnum antiquum (*)
Viburnum asperum (L)
Viburnum cupaneoides (*)
Vitis olriki (U)
Zamia coloradensis (L)
Zelkova planeroides (*)
Zizyphus fibrillosus (L)
TABLE 2. Invertebrate fauna of Wannagan Creek Quarry.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>GASTROPODA</td>
<td>Mesogastropoda</td>
<td>Hydrobiae</td>
<td>Hydrobia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Viviparidae</td>
<td>Viviparus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pleuroceridae</td>
<td>Lyoplacodes</td>
</tr>
<tr>
<td>PELECYPODA</td>
<td></td>
<td>Unionidae</td>
<td>undet. bivalves</td>
</tr>
<tr>
<td>INSECTA</td>
<td>Odonata</td>
<td>Gomphaeschna schrankii</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coleoptera</td>
<td>undet. coleopteran</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lepidoptera</td>
<td>undet. lepidopteran</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 3. Vertebrate fauna of Wannagan Creek Quarry.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHONDRICHTHYES</td>
<td>Batoidea</td>
<td>Myliobatis sp.</td>
</tr>
<tr>
<td>OSTEICHTHYES</td>
<td>Semionotiformes</td>
<td>Lepisosteus sp.</td>
</tr>
<tr>
<td></td>
<td>Amiiformes</td>
<td>Amia sp.</td>
</tr>
<tr>
<td></td>
<td>Clupeiformes</td>
<td>indet. clupeiform</td>
</tr>
</tbody>
</table>
Class AMPHIBIA
   Order Urodela
      *Piceoerpeton willoodense*
      *Scapherpeton* sp.
   Order Anura
      indet. anuran

Class REPTilia
   Order Chelonia
      Superfamily Baenoidea?
         undet. baenid
      Superfamily Testudinoidea
         *Protochelydra zangerli*
      Superfamily Trionychoidea
         *Trionyx* sp.

Suborder Lacertilia
   Family Varanidae
   Family Amphisbaenidae

Order Choristodera
   *Champsosaurus gigas*
   *Champsosaurus* sp.

Order Crocodilia
   *Leidyosuchus formidabilis*
   *Wannaganosuchus brachymanus*

Class AVES
   Order Charradriiformes
      *Dakotornis cooperi*
      cf. Charadriidae
   Suborder Ralli
      cf. Rallidae

Class MAMMALIA
   Order Multituberculata
      *Ptilodus wyomingensis*
      *Ptilodus* sp.
      *Neoplagiaulax hazeni*
      *Neoplagiaulax* cf. *hunteri*
      *Neoplagiaulax mckinnai*
Order Polyprotodonta

*Peradectes* sp.

Order Proteutheria

cf. *Palaeoryctes* sp.
cf. *Pararyctis* sp.
*Propalaeosinopa* n. sp.
*Propalaeosinopa* sp.
*Labidolemur soricoides*
*Leptacodon* sp.

Order Lipotyphla

cf. *Leptacodon*
*Entomolestes* sp.

Order Primates

*Plesiadapis* cf. *fodinatus*
*Plesiadopis* sp.
*Ignacius* sp.
cf. *Phenacolemur*

Order Condylarthra

*Thryptacodon* cf. *australis*
*Thryptacodon* sp.
*Eotocion* sp.
*Phenacodus* sp.

Order Carnivora

*Protictis* cf. *Microlestes*
Paleoenvironmental reconstructions depicted by figures 3 and 4 suggest conditions as they may have been during deposition of Beds 2 and 3 (during upper level time, fig. 2). A number of plant taxa occur in both levels of the quarry (Table 1). Others that are recorded only from the lower level such as *Equisitum* and *Nelumbium* probably occur in upper level sediments as well. This is indicated in the reconstructions which portray a somewhat stable environment with big trees, a well-developed shoreline, and rather quiet, shallow water where plant debris rapidly accumulated on the bottom. During this time the large crocodile *Leidyosuchus* proliferated and perhaps utilized the seemingly well-suited shore habitat for nesting. Nesting behavior and hatchling crocodiles are shown along with a variety of other well-documented vertebrates.

Many questions remain unanswered. Some prime ones are: (1) If not for nesting, what might account for the great abundance (some 70 individuals at latest count) and apparent massing of the large crocodile? (2) What was the duration of sedimentation and occupation of the site by large vertebrates? (3) Is Wannagan Creek Quarry unique to the area? Current research is focused on the general area and region of Wannagan Creek Quarry in an effort to define a clearer picture of crocodile habitats in the Bullion Creek and Sentinel Butte formations.

ACKNOWLEDGEMENTS

The following persons are gratefully acknowledged for their assistance with this paper: T. Sawyer critically read the manuscript; R. Melchior, J. Hartman, R. Holtzman, and R. Benson provided lists of taxa; R. Spading, A. Hage, and K. Sander contributed the photography and illustrations (fig. 2 and figs. 3 and 4) respectively; S. Nowland did the typing and N. Petschauer the editing and proofreading.
FIGURE 3. Early paleoenvironmental reconstruction of Wannagan Creek Quarry site based on recorded taxa to 1979.
FIGURE 4. Late paleoenvironmental reconstruction of Wannagan Creek Quarry site based on recorded taxa to date.
REFERENCES


