An Illustrated Guide to latest Cretaceous Vertebrate Microfossils of the Hell Creek Formation of northeastern Montana

By David G. DeMar, Jr.

Edited by Gregory P. Wilson and Blakely K. Tsurusaki

Version 1.0

Introduction

Vertebrate microfossil sites, or **microsites**, are concentrations of fossilized vertebrate bones and teeth of multiple individuals that are usually in the millimeter to centimeter size range. Microsites often contain many species of animals including fish, amphibians, reptiles, birds, and mammals.



A view of the Hell Creek Formation near Fort Peck Reservoir in Garfield County, northeastern Montana. Photo by David G. DeMar, Jr. (2011).

There have been several hundred microsites found in the Hell Creek Formation of Garfield County, northeastern Montana. The Hell Creek Formation is a geologic unit made up of rock strata that were deposited during the last chapter of the Dinosaur Era. More specifically, these rocks and the fossils found within them are from the latest Cretaceous, approximately 67 to 65 million years ago, when Montana and other western states were situated along the coast of a vast seaway. Hell Creek microsites have yielded thousands of fossils. This guide will help you to identify vertebrate **microfossils** from one such microsite. *Part 1* of the guide contains images of different body parts represented by the fossils found at microsites in the Hell Creek Formation, including vertebrae, teeth, jaws, and scales. *Part 2* is a primer on the comparative anatomy of vertebrate animals that will be useful in assigning the fossils to particular vertebrate groups (e.g., fish, amphibian, mammal, etc.). Words in **bold font** are defined in the glossary at the end of Part 2.

Anatomical directional terms are used throughout this guide to orient the reader. The terms are defined below and illustrated on the next page.

Anterior – towards the front or head. Posterior – towards the rear or tail.

Dorsal – towards the backbone or top. **Ventral** – towards the belly or bottom.

Lateral – away from the midline. **Medial** – towards the midline.

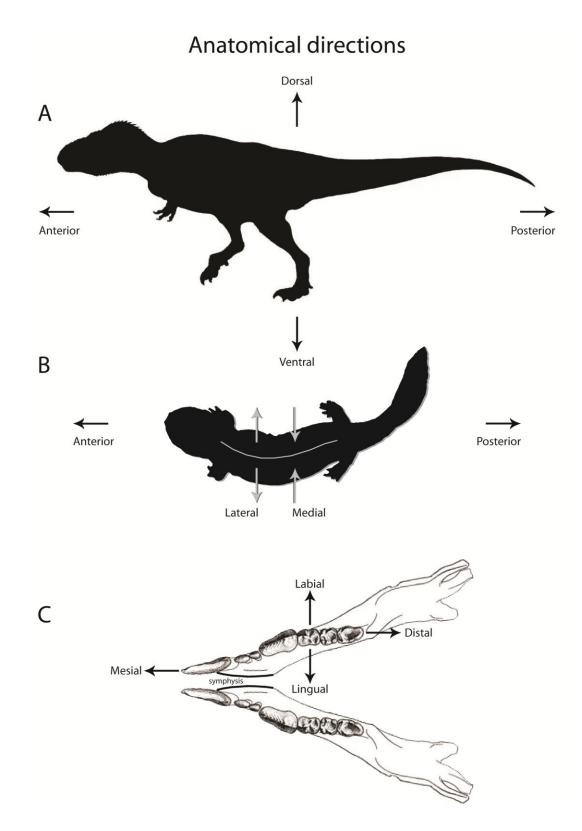
Lingual – towards the tongue or inside of mouth; refers to mouth only.

Labial – towards the lips or outside of mouth; refers to mouth only.

Mesial – towards the front of the mouth; refers to mouth only.

Distal – towards the back of the mouth; refers to mouth only.

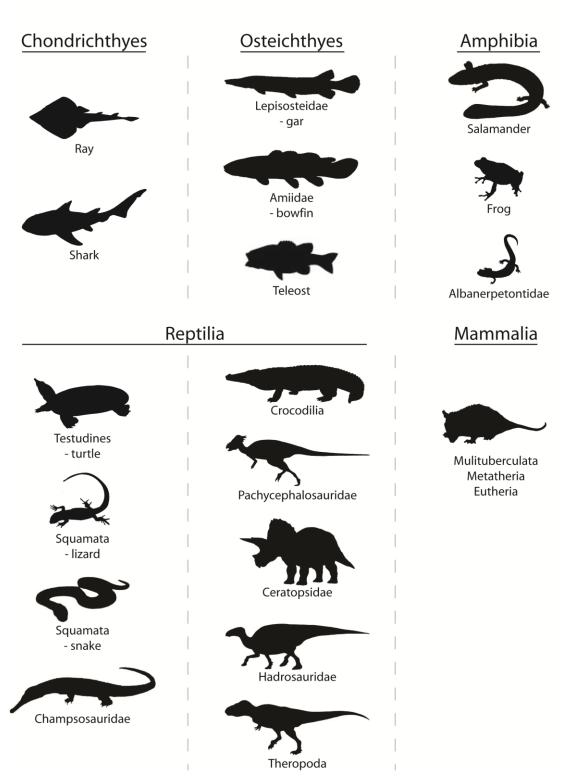
Occlusal – the grinding surface of a tooth; towards the top of the crown.



Anatomical directions: A) Tyrannosaur in lateral view; B) Salamander in dorsal view with the midline highlighted with a gray line; C) Mammal lower jaw in occlusal view. C modified from Bloch and Gingerich (1998).

PART 1

In **Plates 1** – **4**, silhouettes of vertebrate animals are placed next to fossil specimens to provide a quick reference for the reader. Below is a key to the animal silhouettes.



Guide to Animal Silhouettes

The fossil specimens in **Plates 1 – 4** are meant to provide a general guide for identifying major vertebrate groups, but note this guide is not comprehensive. Refer to Part 2 for explanations of the anatomical terms and descriptions. Additional information can also be found by consulting the recommended readings found at the end of this guide.

Plate 1. Vertebrae of vertebrates from the Hell Creek Formation. The presence/absence and condition (open/closed) of the notochordal foramen, the centrum type, and the presence/absence of the zygapophyses are features that help to assign a vertebra to a vertebrate group. Refer to Part 2 for explanations of these features. The white dot on the animal silhouette estimates the position of the vertebra shown. All scale bars equal 1 mm. Use the scale bar at the bottom of the plate to measure your specimens.

Plate 1.	Notochordal foramen	Centrum type	Zygapophyses
A . Amiidae (bowfin fish). Trunk centrum.	Yes, open	Amphicoelous	No
B . Lepisosteidae (gar fish). Trunk centrum.	No	Opisthocoelous	No
C . Teleostei (fish). Trunk centrum.	Yes, open	Amphicoelous	No
D . <i>Opisthotriton kayi</i> (salamander). Atlas vertebra.	Yes, closed	Posterior cotyle concave	Yes
E . <i>Scapherpeton tectum</i> (salamander). Trunk verte	bra. Yes, closed	Amphicoelous	Yes
F .Teiidae (lizard). Caudal vertebra.	No	Procoelous	Yes
G . <i>Coniophis precedens</i> (snake). Trunk vertebra.	No	Procoelous	Yes
H . <i>Champsosaurus</i> (semi-aquatic reptile). Trunk ve	ertebra. No	Acoelous	Yes
I. Crocodilidae (crocodilian). Cervical vertebra.	No	Procoelous	Yes

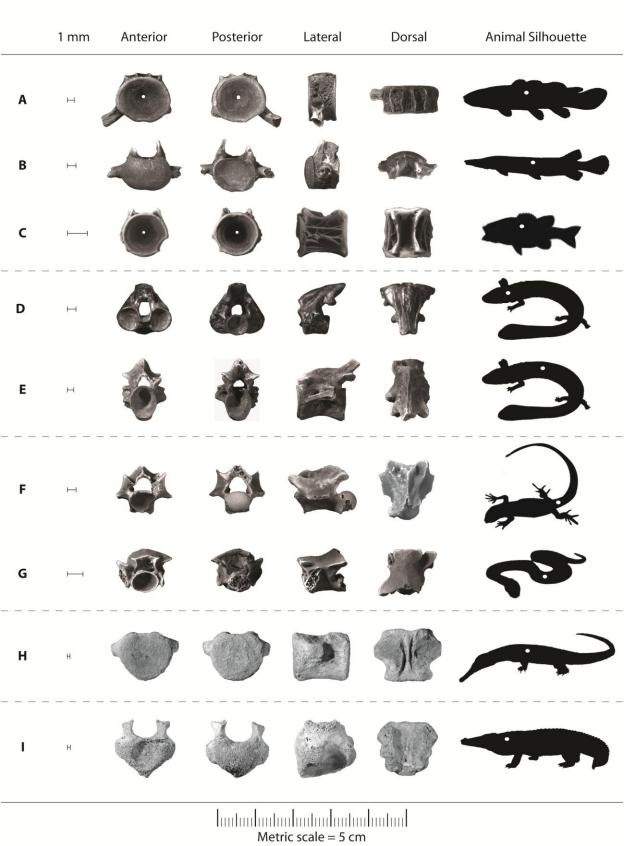


Plate 1: Vertebrae and Centra

Plate 2. Teeth of vertebrates from the Hell Creek Formation. The <u>Special</u> heading indicates a unique feature useful for identifying the specimen. All scale bars equal 1 mm. Use the scale bar at the bottom of the plate to measure your specimens.

Plate 2.

A. *Myledaphus bipartitus* (ray). Tooth in mesial, labial or lingual, and occlusal views. Special: note the wrinkled texture and C-shaped groove on the top.

B. Orectolobidae (shark). Tooth in distal, mesial, and occlusal views. Special: note the tiny size of the tooth (actual size shown and in distal view) and the triangle-shaped top (crown).

C. Lepisosteidae (gar). Tooth in mesial, distal, and basal views. Special: note the slight constriction at the base of the tip of the tooth.

D. *Champsosaurus* (semi-aquatic reptile). Tooth in lingual, mesial or distal, and basal views. Special: note the ridges along the sides of the tooth.

E. Crocodilia. Tooth in lingual, mesial or distal, and basal views. Special: note the offset ridges along the sides of the tooth.

F. Pachycephalosauridae. Tooth in lingual, mesial or distal, and labial views. Special: note the large bumps (denticles) on the tooth tip and the vertical flat surface (wear facet) on the lingual side of the tooth.

G. Ceratopsidae. Tooth in labial, mesial or distal, and lingual views. Special: note the flat and worn crown of the tooth on the right versus the unworn leaf-shaped crown on the left. Also note the multiple ridges (carinae) on the outer (labial) side of the tooth and the offset middle ridge (carina).

H. Hadrosauridae. Tooth in labial, mesial or distal, and lingual views. Special: note the flat and worn crown of the tooth on the right versus the unworn diamond-shaped crown on the left. Also note the single midline ridge (carina) on the outer (labial) side of the tooth.

I. Tyrannosauridae. Tooth in lingual, labial, and basal views. Special: note the bumps (denticles) or serrations on the ridges (carinae) of the front (mesial) and back (distal) sides of the tooth.

J. Therian mammal. Lower molar in inner (lingual), outer (labial), and top (occlusal) views. Special: note the multiple bumps (cusps) on the top (occlusal) surface of the tooth.

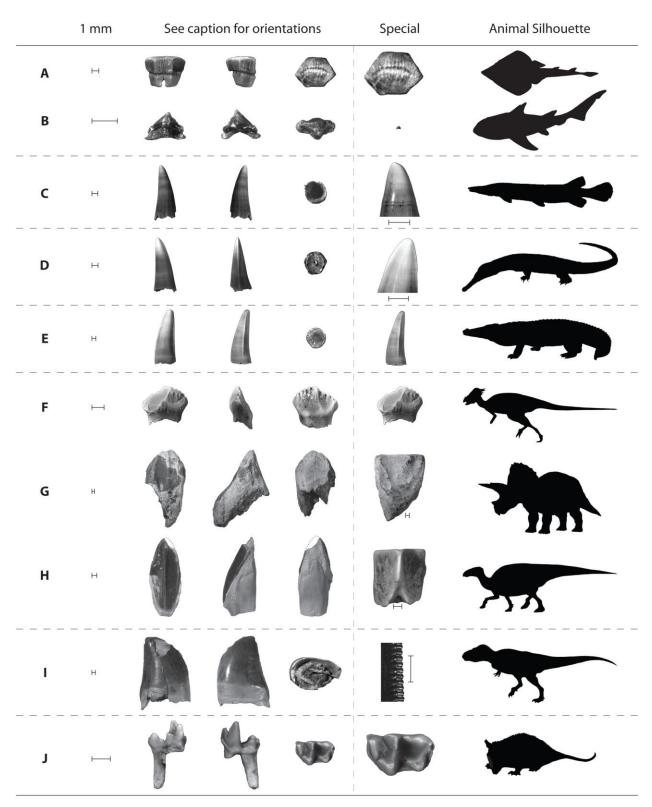
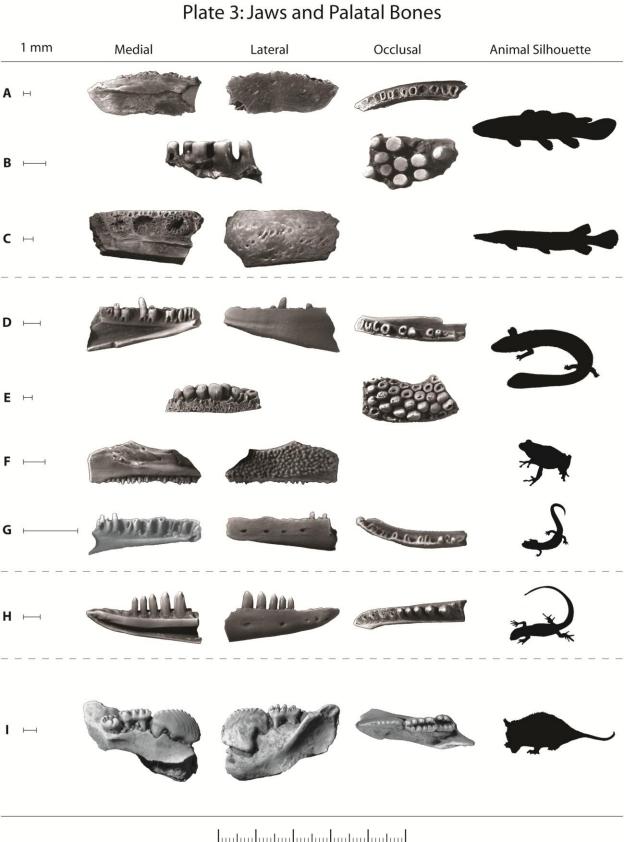


Plate 2: Teeth

Metric scale = 5 cm

Plate 3. Jaws and palatal bones of vertebrates from the Hell Creek Formation. How the teeth are attached to the bone (tooth attachment type) is a useful character for identifying major groups of vertebrates. For example, the tooth attachment type of fish is acrodont versus pleurodont in the jaw bones of most amphibians and lizards. See Part 2 for descriptions of tooth attachment types. All scale bars equal 1 mm. Use the scale bar at the bottom of the plate to measure your specimens.

Plate 3.	Tooth attachment type
A . Amiidae (bowfin fish). Right dentary. Note the oval attachment surfaces for the teeth.	Acrodont
B . <i>Cyclurus fragosus</i> (bowfin fish). Palatal bone. Note the flattened tube-like teeth.	Acrodont
C . Lepisosteidae (gar fish). Right dentary. Note the small round attachment surfaces for the outer row of teeth.	Acrodont
D . <i>Opisthotriton kayi</i> (salamander). Left dentary. Note the pedicellate teeth and the smooth outer surface of the bone.	Pleurodont
E . <i>Habrosaurus dilatus</i> (salamander). Palatine. Note the multiple rows of teeth.	Acrodont
F . <i>Scotiophyrne pustulosa</i> (frog). Right maxilla. Note the numerous small and tightly packed teeth and bumpy lateral surface of the bone.	Pleurodont
G . <i>Albanerpeton galaktion</i> (salamander-like amphibian). Left dentary. Note the small lateral holes (foramina) and tiny size.	
H . Teiidae (lizard). Right dentary. Note the holes (foramina) on the outside of the jaw.	Pleurodont
I. Multituberculate mammal. Left dentary. Note the large blade-like premolar and the numerous bumps on the molar teeth.	Thecodont



Metric scale = 5 cm

Plate 4. Scales and dermal bones of vertebrates from the Hell Creek Formation. These bones form within the dermis or skin of the animal. All scale bars equal 1 mm. Use the scale bar at the bottom of the plate to measure your specimens.

Plate 4

A. *Myledaphus bipartitus* (ray). Dermal denticle in anterior, lateral, and outer views. Note the tooth-like shape of the denticle and the deep vertical grooves and prominent ridges along the sides.

B. Lepisosteidae (gar fish). Ganoid scale in outer and inner views. Note the shiny enamel-like ganoid on the outer surface and the overall diamond shape of the scale.

C. Holostean A (fish). Ganoid scale in outer and inner views. Note the shiny ganoid on the outer surface and the triangular "peg and socket" best seen in inner view.

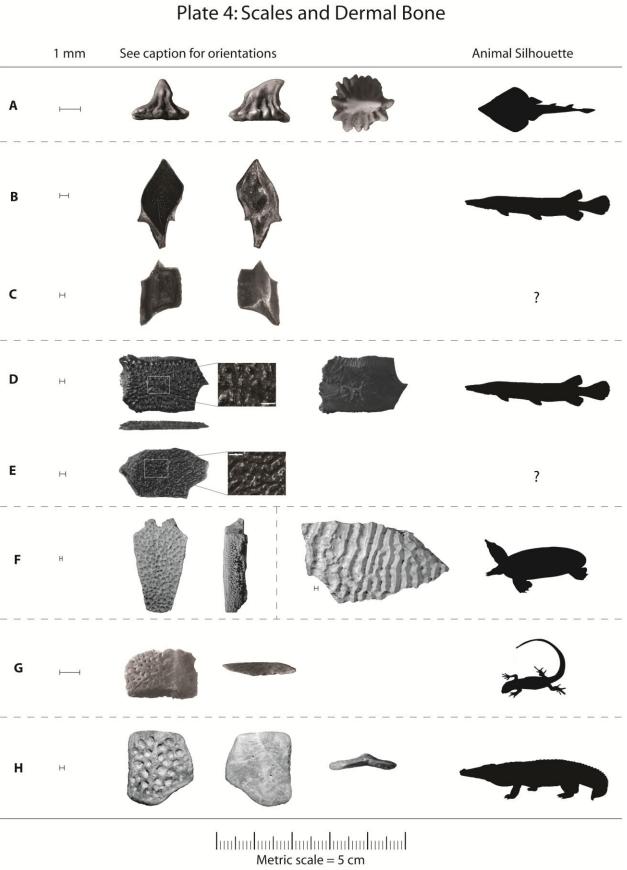
D. Lepisosteidae (gar). Dermal bone. Note the ganoid-covered tubercles on the outer surface (see magnified box) and the smooth inner surface of the bone. The side view displays how thin the bone is.

E. Osteichthyes (bony fish). Dermal bone. Note the wrinkled texture and the lack of ganoid tubercles.

F. Trionychidae (soft-shelled turtle). Neural and costal fragment. Neural in dorsal and lateral view. Costal fragment in dorsal view. Note the coffin-shape of the neural and the round pits and ridges on the surface. In lateral view the bone is relatively thick and spongy internally. Note the long grooves and ridges of the costal.

G. *Odaxosaurus piger* (lizard). Dermal osteoscute in outer and side views. Note both the pitted and smooth surfaces of the outer surface of the bone. The front, back, and sides are angled for overlapping with adjacent osteoderms (see side view).

H. Crocodilidae. Dermal osteoscute in outer, inner, and anterior or posterior views. The outer surface has widely-spaced and deep pits and a low, central keel. The inner surface is smooth.

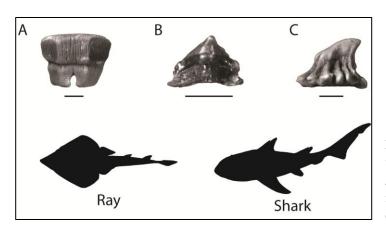


PART 2

FISHES

Chondrichthyes (cartilaginous fishes)

Modern Chondrichthyes (cartilaginous fishes) consist of two major groups, sharks and rays (elasmobranchs) and chimeras or rat fishes (holocephalans). Because the skeletons of chondrichthyans are made of cartilage, many of their parts do not regularly fossilize. The main part of the vertebra (**centrum**) can sometimes become hardened and preserve as a fossil. More commonly, chondrichthyans are recorded in the fossil record by their **teeth** and **placoid scales**. Although holocephalans are present in the Late Cretaceous of North America, they <u>do not</u> appear in the Hell Creek Formation. In contrast, sharks and rays <u>are found</u> in the Hell Creek Formation. The most common elasmobranch from the Hell Creek Formation is the ray *Myledaphus*



bipartitus. Its teeth are hexagonshaped in occlusal view and have split or double roots (Figure 1A; Plate 2A). Less common are the teeth of small sharks such as orectolobids (Fig. 1B; Plate 2B).

Figure 1. Ray and shark fossils. **A**) *Myledaphus* tooth; **B**) orectolobid shark tooth; **C**) *Myledaphus* placoid scale. Scale bars equal 1 mm. Fossils in lateral view. Silhouette of ray in dorsal view. Silhouette of shark in lateral view.

In life, placoid scales of sharks and rays are embedded in the skin of the animal. They are conical and can be hooked and pointed or flattened at their tips (Fig. 1C; Plate 4A). Placoid scales look like teeth but differ in having flat, smooth, and rootless bottoms. Placoid scales can also have deep grooves and ridges running up and down the sides from the base and sometimes to the tip of the scale. Some fish teeth also have vertical ridges but are far less prominent.

The spool-shaped centra (plural of centrum) of the ray *Myledaphus* are occasionally found in the Hell Creek Formation. Growth rings are easily seen in the centra when looking at them from the front or back.

Osteichthyes (bony fishes)

Remains of bony fishes (osteichthyans) are by far the most common fossils found in the Hell Creek Formation. They represent primitive fishes, such as the paddlefish, gar, and bowfin, and more advanced teleost fishes (Fig. 2). The remains include scales, vertebrae, jaws, teeth, and skull elements.

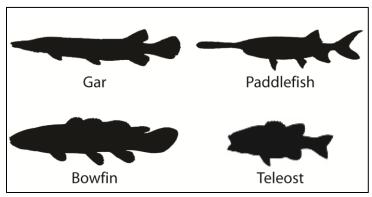


Figure 2. Silhouettes of common bony fishes found in the Hell Creek Formation.

Scales

Scales cover the body surface of fishes. They vary in form and composition, but are generally platelike. Scales of the gar (Family Lepisosteidae) are perhaps the most abundant fossil in the Hell Creek Formation. They are thick and diamond-shaped with a shiny, **enamel**like (ganoine) outer surface (Fig. 3; Plate 4B). Similar scales belonging to

an unnamed species of fish, Holostean A, are more rectangular in shape and have a prominent triangular-shaped peg and socket joint not present in gar scales (Fig. 3; Plate 4C). The scales of bowfins and other fish are often found broken because they are thin and lack the hard ganoine of gar and Holostean A scales. They also tend to have concentric rings on their surface.

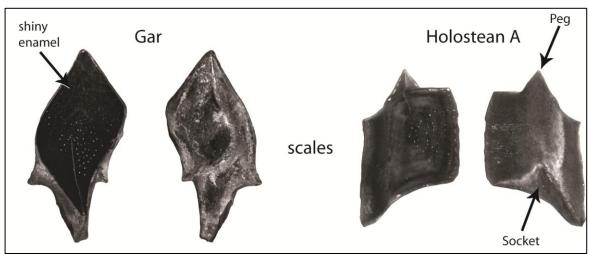
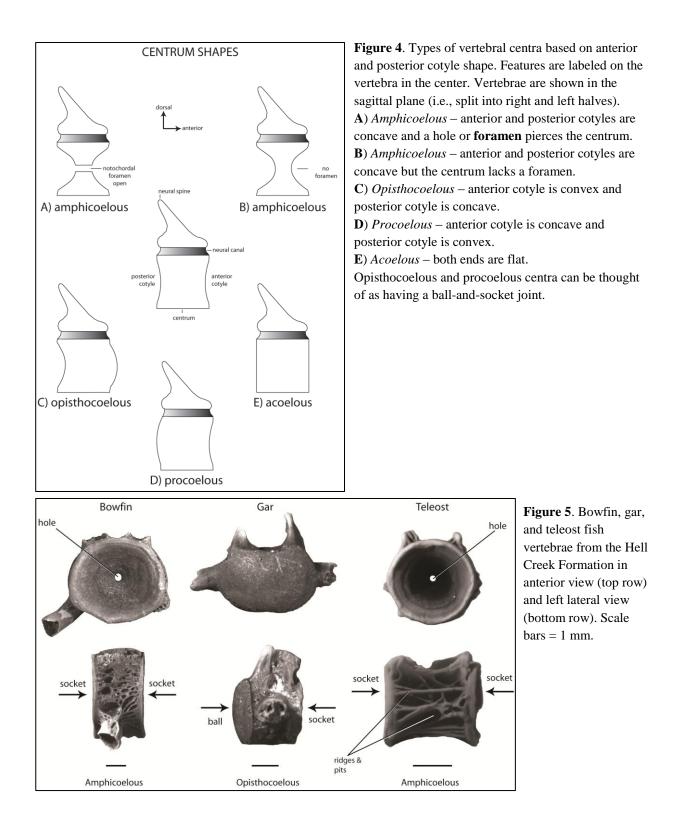


Figure 3. Gar and Holostean A scales from the Hell Creek Formation in outer and inner views.

Vertebrae

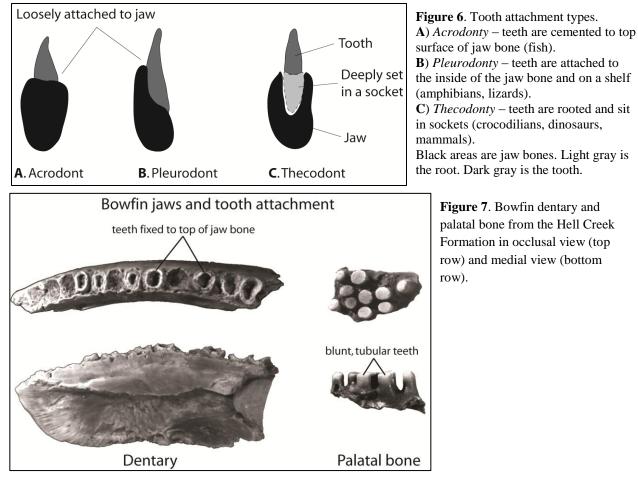
The vertebrae of bony fishes vary in form, but are generally more complex than the vertebrae of sharks and rays. The **centrum** (centra is plural), or the base of a vertebra, of a bony fish often has ridges and pits along the top, back, and/or sides (Fig. 5 right; Plate 1A–C). In most fishes, it is **amphicoelous** (front and back are concave; see Figs. 4 and 5 left and right) and short from front to back. A hole passes through the center of the centrum (the notochordal foramen; Fig. 4; Plate 1A, 1C) in many but not all fishes. Gar centra are unique among the fishes from the Hell Creek Formation in that they are **opisthocoelous** (convex in the front, concave in the back; Fig. 5 middle; Plate 1B).



Jaws and Teeth

Fish teeth usually attach to the surface of the jaw bones (i.e., premaxillae, maxillae, dentaries). This type of tooth attachment, which is called **acrodonty**, differs from the types of tooth

attachment in most other vertebrates (Figs. 6a and 7 left). Because most fish teeth are only loosely attached to the jaws by a cement-like substance, they often break off during the burial or collecting process. Many fish also have rows or plates of teeth on the roof of their mouth; these teeth are also acrodont. Tooth plates of the bowfin *Cyclurus* are common in the Hell Creek Formation. The teeth are cylindrical with blunt tips (Fig. 7 right; Plate 3B). Teeth from the jaws of the teleost *Coriops* are conical and curved. Those of the large bowfin *Melvius* are arrowshaped with translucent tips. Gar teeth are conical, often have a clear tip, and grooves and ridges running up and down the sides of the tooth (see Fig. 27 below).



Dermal Bone

In addition to finding vertebrae, scales, teeth, and jaws of fish, you may also come across bones or fragments of bones from their skulls (dermal bone). Dermal bones are usually thin and platelike with fine surface sculpturing. Similar to their ganoid -covered scales, the dermal bone of gars often has an enamel-like surface covering (Fig. 8; Plate 4D) whereas other fish may lack it (Plate 4E).

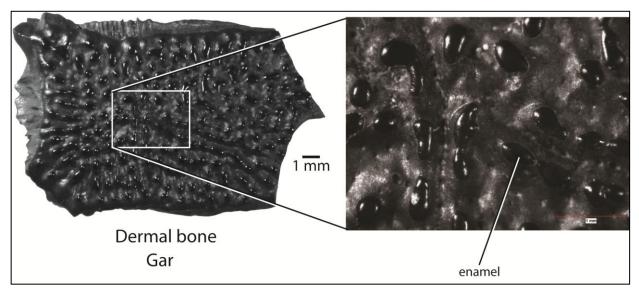


Figure 8. Gar dermal bone from the Hell Creek Formation with close up view on the right.

AMPHIBIANS

Modern amphibians, also known as Lissamphibia, comprise three major living groups and one that is now extinct. The living groups are frogs and toads (Anura), salamanders and newts (Urodela), and caecilians (Gymnophiona). The now-extinct group is the salamander-like Albanerpetontidae. The word amphibian comes from *Amphi*- meaning "double" and *-bios* meaning "life". The name refers to the two phases of their life. Most species have an early larval aquatic stage and later metamorphose into terrestrial adults. As a result, most modern amphibians are prone to drying out, or desiccation, and require wet or moist environments to survive.

Frogs, salamanders, and albanerpetontids were common inhabitants of the Late Cretaceous of North America, but caecilians are not known from North America at this time. *Opisthotriton kayi* and *Scapherpeton tectum* are two of the most common species found in the Hell Creek Formation. Salamanders and albanerpetontids are known mostly from teeth, jaws, and vertebrae, whereas frogs are known mostly from teeth, jaws, skull parts, and hip bones.

Teeth and Jaws

The teeth of most lissamphibians consist of a **crown** and a base (both lacking enamel) that are separated by a zone of weakness (pedicellate; Fig. 9 and 10; see also Plate 3D, F). Because the crowns of fossil salamanders and frogs easily break from the base of the tooth (pedicel), they will rarely be preserved with the jaw. The fossil sirenid salamander, *Habrosaurus*, and the Albanerpetontidae (Plate 3G) <u>do not</u> have a zone of weakness separating the crown from the pedicel (non-pedicellate teeth), so the teeth are sometimes preserved with the jaws. Teeth attached to the inside of the jaw bone and sit on a shelf are **pleurodont** (Fig. 6B). Teeth also occur on the roof of the mouth (palatal) and attach in an acrodont fashion (Plate 3E).

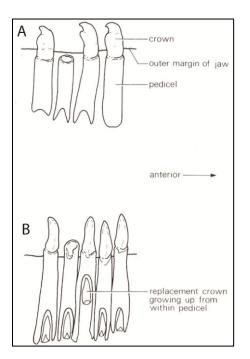


Figure 9. Pedicellate teeth in Lissamphibia.

A) Salamander.

B) Frog.

Image modified from Duellman and Trueb (1986; fig. 15-20).

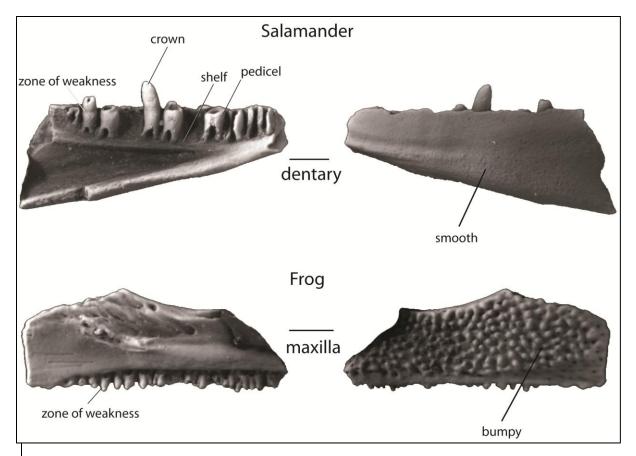


Figure 10. Salamander and frog jaws from the Hell Creek Formation. The jaws are shown in medial and lateral views. Note the smooth outer surface of the salamander jaw versus the bumpy texture of the frogs. Scale bars = 1 mm.

Vertebrae

The vertebrae of frogs, salamanders, and albanerpetontids and all other **tetrapods** (i.e., reptiles including birds, mammals) differ from their fish ancestors in having structures for supporting the body against the forces of gravity when on land. For example, dorsal to the centrum are bony processes called **prezygapophyses** and **postzygapophyses** (Fig 11). The centrum of salamanders is usually long, cylindrical, and thin at mid length. The notochordal foramen found in the vertebrae of most fish (e.g., Figs. 4a and 5 left and right; Plate 1A, C;) is absent in amphibians and all other tetrapods (e.g., Fig. 11a; Plate 1D–I).

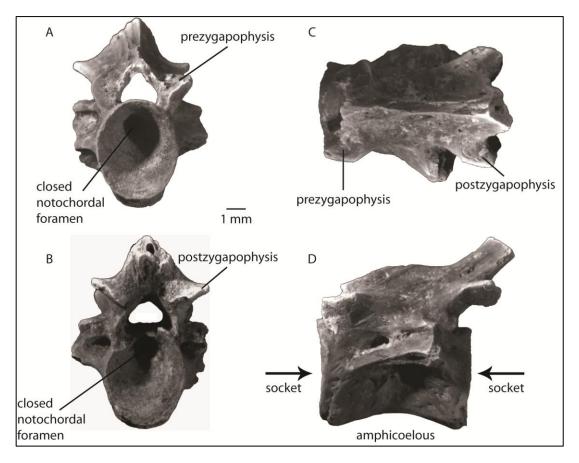
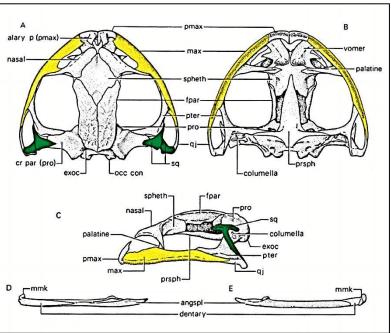


Figure 11. A salamander (*Scapherpeton tectum*) vertebra from the Hell Creek Formation in A) anterior, B) posterior, C) dorsal, and D) left lateral views.

FROGS (ANURA)

Skull and hip bones are the most commonly occurring and easily recognizable fossils of frogs (e.g., Figs. 10 and 12; Plate 3F). Less common fossils of frogs are vertebrae and limb bones (Fig. 13A and B).

Figure 12. Diagram of the skull (A - C) and lower jaw (D - E) of a modern frog, *Gastrotheca walkeri*, with the maxilla (upper jaw) in yellow and squamosal in green. A) Dorsal, (B) ventral, and C) left lateral views of the skull. D) Lateral and E) medial views of the dentary (lower jaw). Modified from Duellman and Trueb (1986; fig. 13-15, p. 311).



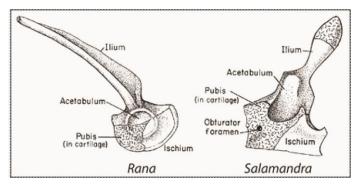


Figure 13. The hip girdle of a modern frog (*Rana*) and salamander (*Salamandra*) in lateral or side view. Modified from Romer (1962).

SALAMANDERS (URODELA)

Fossils of salamanders are much more common than frogs in the Hell Creek Formation. We also find more parts of their skeleton than we do for frogs. The most commonly found parts are from the backbone: the first neck vertebra (atlas; Figs. 14 and 15; Plate 1D) and trunk vertebrae (Figs. 16 and 17; Plate 1E). For some species, such as *Habrosaurus dilatus* and *Albanerpeton nexuousus*, we also find jaws and other tooth-bearing elements (e.g., Plate 3E and G, respectively).

Vertebrae

The atlas is the first vertebra of the neck, right behind the skull. It is unique to tetrapods because fish do not have a true neck. Salamander atlantes (plural of atlas) have a projecting bony process on the front called the odontoid process, which has two cotyles (rounded cup-like structures) on either side of it (Fig. 14). Frog atlantes do not have an odontoid process. See the figures below for examples of atlantes of a modern (Fig. 14) and fossil (Fig. 15) salamander. The neural spine is usually not preserved in fossil salamander atlantes due to their delicate nature.

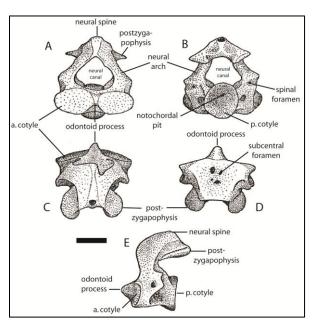


Figure 14. Atlas vertebra of the extant salamander *Necturus maculosus* (mud puppy) in A) Anterior (front) view.

- **B**) Posterior (back) view.
- C) Dorsal (top) view.
- **D**) Ventral (bottom) view.
- E) Left lateral (side) view.
- Modified from Naylor (1978, fig. 10, p. 667). Scale bar = 2 mm.

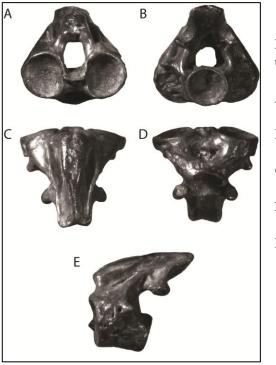


Figure 15. Atlas of a fossil salamander (*Opisthotriton kayi*) from the Tullock Formation, Montana.

- A) Anterior (front) view.
- **B**) Posterior (back) view.
- C) Dorsal (top) view.
- **D**) Ventral (bottom) view.
- E) Left lateral (side) view.

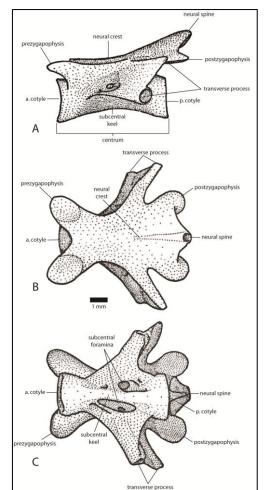


Figure 16. Labeled trunk vertebrae of the living salamander *Necturus maculosus*.

A) Left lateral (side) view.

B) Dorsal (top) view.

C) Ventral (bottom) view.

Scale bar = 1 mm. Figure modified from Naylor (1978, fig. 12A, p. 671).

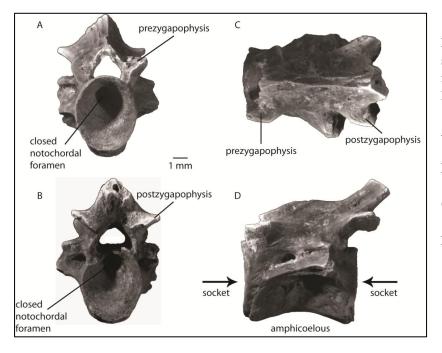


Figure 17. Trunk vertebra of a fossil salamander (*Scapherpeton tectum*) from the Hell Creek Formation, Montana.

A) Anterior (front) view.

B) Posterior (back) view.

C) Dorsal (top) view.

D) Left lateral (side) view.

REPTILIA

Extant or modern reptiles are a diverse group of vertebrates that include turtles, lizards, snakes, crocodilians, and birds. The Hell Creek Formation preserves fossils of all of these groups plus some extinct groups including the crocodile-like champsosaurs, the winged pterosaurs, and dinosaurs.

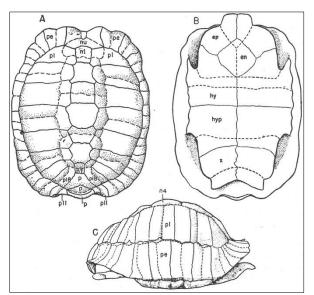
TURTLES (TESTUDINES)

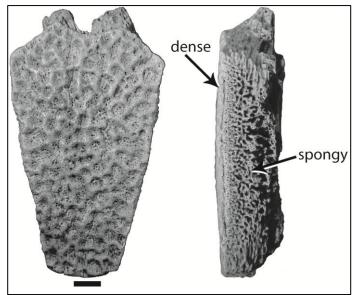
Carapace and Plastron (Shell)

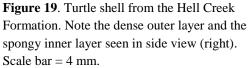
The turtle shell is made up of numerous bony parts (Fig. 9). The upper part of the shell is called the carapace and the lower part is the plastron. Because turtle shell is thick, it is very durable and more likely to become a fossil. Turtle shell pieces are some of the most commonly found fossils in the Hell Creek Formation. Turtle shell is characteristically flat and moderately thick. In cross section, turtle shell has dense outer layers that sandwich a porous or spongy middle layer (Fig. X).

Most shell fragments you will encounter are costals (Fig. 18; Plate 4F, right, fragment) from the lateral part of the carapace. The coffin-shaped neural bones from the midline of the carapace are common as well (Fig. 18 and 19; Plate 4F, left).

Figure 18. Diagram of a modern turtle shell in A) dorsal (carapace), B) ventral (plastron), and C) right lateral views. Abbreviations: n, neural; pe, peripherals; pl, costal. Image modified from Romer (1962).







The surface texture of turtle shell is often distinct and can be used to assign a piece of turtle shell to a family or genus. For example, the surface texture of the shell of *Compsemys* (Fig. 20) is made up of densely-packed, small, rounded, and flat bumps. The shell of *Basilemys*, in contrast, has rows of low triangular pits. The most common type of turtle in the Hell Creek Formation are the soft-shelled turtles (Trionychidae) which have a shell ornamentation with rounded pits that often merge to form long grooves (Fig. 19 versus 20; Plate 4F, left versus right).



LIZARDS AND SNAKES (SQUAMATES)

Jaws and Teeth

Lizards and snakes are relatively uncommon fossils of the Hell Creek Formation when compared to the groups discussed above (i.e., fish, amphibians, turtles). Fossil lizards have been described based mainly on tooth-bearing elements such as upper and lower jaws (see green and purple bones in Fig. 21 and Figs. 22 and 23). Lizards typically have teeth that sit on a shelf on the inside of the jaw (pleurodont; Fig. 6B) with only part of the tooth exposed above the rim of the jaw. This condition is also seen in amphibians. The teeth of lizards can be quite distinct. Teiids (Figs. 22 and 23; see also Plate 3H) often have teeth with several ridges or bumps (cusps), whereas other lizards have teeth that are curved backwards and serrated like a steak knife as in varanids (e.g., *Palaeosaniwa*). Other skull elements of lizards have also been described (pink and gray bones in Fig. 21) as well as vertebrae (Fig. 24; Plate 1F).

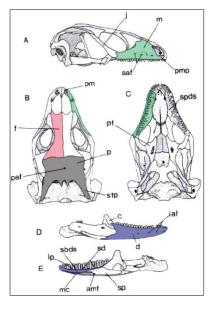


Figure 21. Living lizard (*Eumeces obsoletus*) skull (**A-C**) and lower jaw (**D-E**) with common fossil elements highlighted:

A) Right lateral (side) view.

- **B**) Dorsal (top) view.
- C) Ventral (bottom) view.
- **D**) Right lateral (side) view.
- E) Medial (inside) view.

The upper jaw or maxilla (m) is **green**. The lower jaw or dentary (d) is **blue**. The frontal (f) bone is **pink**. The parietal (p) is in dark **gray**. Image modified from Gao and Fox (1996, fig. 2, p. 5).

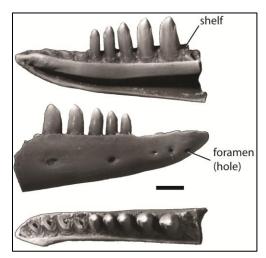


Figure 22. Lizard (Teiidae) right lower jaw (dentary) from the Hell Creek Formation, Montana. Scale bar = 1 mm.

Top in medial or inside view.

Middle in lateral or outside view.

Bottom in occlusal or top of teeth view.

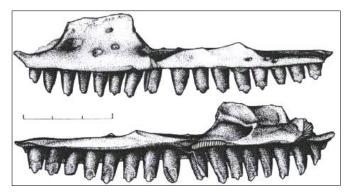


Figure 23. *Chamops segnis*. Partial left upper jaw (maxilla) bone. T

Top in left lateral (side) view.

Bottom in medial (inside) view.

Note the bumps (cusps) on the tips of the teeth. Scale bar equals 3 mm. Image modified from Gao and Fox (1996, fig. 6, p. 19).

Vertebrae

Fossil snakes, which are known mainly by vertebrae, are extremely rare in the Hell Creek Formation. The only named snake from the Hell Creek Formation is *Coniophis precedens* (Fig. 24; Plate 1G).

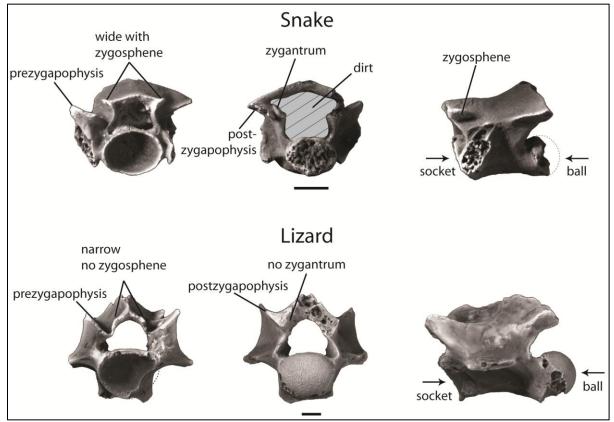


Figure 24. Snake (*Coniophis*) and lizard vertebrae from the Hell Creek Formation, Montana. From left to right the specimens are in anterior, posterior, and left lateral views.

The vertebrae of lizards and snakes have an anterior cup or socket and a posterior ball on the centrum (procoelous; Figs. 4 and 24; see also Plate 1F, G). The vertebrae of snakes differ from the vertebrae of most lizards in having additional bony processes between the zygapophyses. These structures are called the zygantrum and the zygosphene (Fig. 25; see also Fig. 24 above).

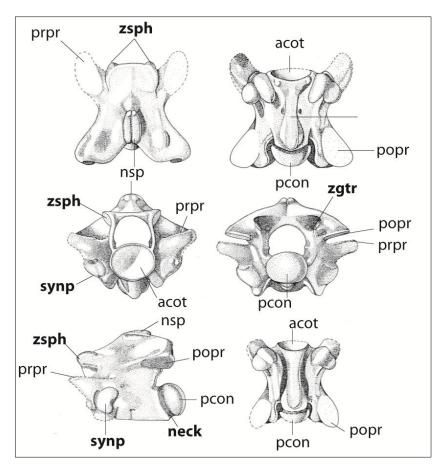


Figure 25. A snake vertebra with some important features in bold font.

Top row from left to right: dorsal and ventral views.

Middle row: anterior and posterior views.

Bottom row: left lateral and ventral views.

Abbreviations:

Nsp = neural spine

Popr = postzygapophyseal process

Prpr = prezygapophyseal process

Synp = synapophysis

Zgtr = zygantrum

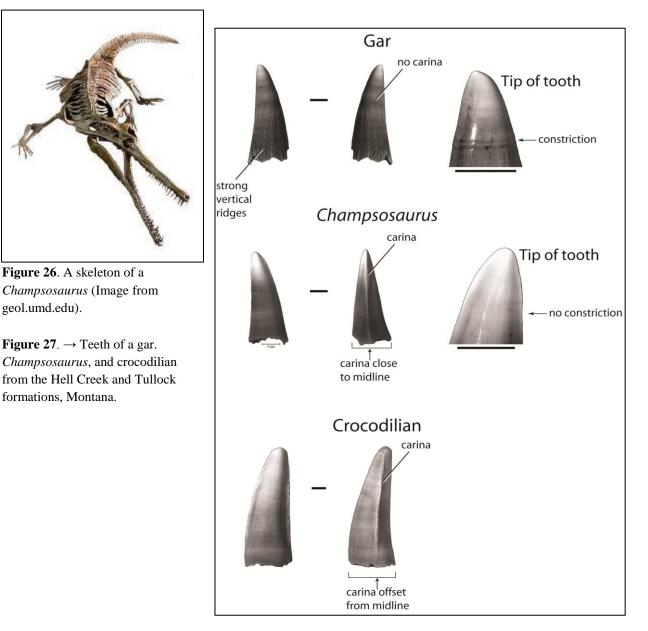
Zsph = zygosphene

Image modified from http://www.pjpellicane.com/Naturalscience2.htm.

CHAMPSOSAURS (CHORISTODERA)

Teeth

Champsosaurs are primarily aquatic, crocodile-like reptiles (Fig. 26) that went extinct approximately 50 million years ago. They are found mainly as teeth and vertebrae. The teeth of champsosaurs are similar in size and shape to that of gar fish (Fig. 27). Champsosaur teeth differ from gar teeth in having a thin ridge (**carina**) on opposite sides of the tooth and in lacking a constriction at the base of the tip of the tooth. Gar teeth also have numerous strong vertical ridges whereas the ridges on champsosaur teeth are weak (Fig. 27; Plate 2C versus 2D).



Vertebrae

The anterior and posterior cotyles of champsosaurs vertebrae are roughly flat or slightly concave (i.e., acoelous to slightly amphicoelous; Fig. 28; Plate 1H). The centrum usually separates from the upper parts (neural arch) of the vertebra during fossilization and resembles a square or rectangular barrel in lateral view (Fig. 28B). The bottom of the vertebra is often broadly rounded but can sometimes have a thin ridge or keel on its surface. The rib attachments can be found on the upper part of the side of the centrum. In dorsal view (Fig. 28C), the portion between the rib attachments is hourglass-shaped and has a thin midline ridge.

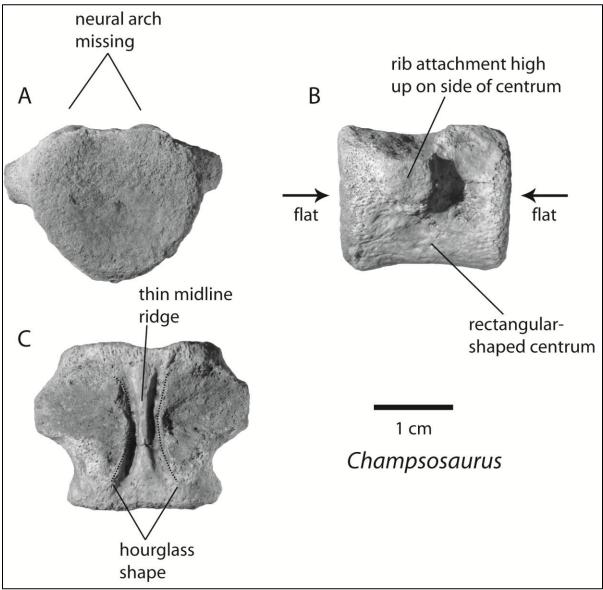


Figure 28. Champsosaurus vertebra from the Hell Creek Formation. A) anterior, B) left lateral, and C) dorsal views.

CROCODILIANS (CROCODILIA)

Teeth

Fossil microsites often preserve crocodilian teeth, scutes, and vertebrae. Teeth are usually conical. A pair of ridges (carinae) runs up opposite sides of the tooth. The ridges are offset to one side of the tooth, whereas in champsosaur teeth the ridges run along the midline (Fig. 27 above; Plate 2D versus 2E). On some teeth, the surface has a number of vertical ridges and the base of the tooth has a deep hole or pulp cavity. These teeth are generally from the front of the mouth whereas those from farther back in the mouth tend to become short (Fig. 29B), blunt, and pinched or constricted at their bases.

Scutes

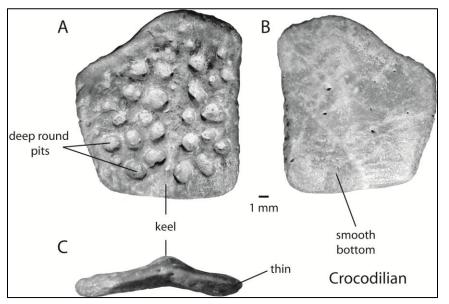


Figure 29. Bony plate (scute) of crocodile. A) Top, B) bottom, and C) front or back views.

Scutes of crocodilians are flat, plate-like bones embedded in the skin that are usually rectangular or oval (Figs. 29 and 30A; Plate 4H). Along the surface of the scute is a ridge or keel that can be short or tall. Crocodilian scutes are smooth on the bottom surface, and have

many widely-spaced, deep pits on the top surface. Crocodilian scutes differ from turtle shell in that they are thinner, not "layered", and the pits are deeper and more widely spaced (Fig. 29 vs. 19).

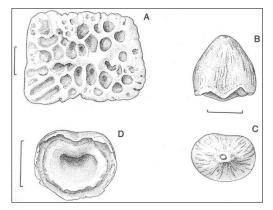


Figure 30. Crocodilian (Brachychampsa montana) scute and tooth.

Scute in **A**) Dorsal view. **Tooth** in **B**) Medial view. **C**) Occlusal (top of tooth) view. **D**) Basal view. Scale bars equal 1 cm. Image from Bryant (1989, fig. 14, p. 55).

Vertebrae

Vertebrae from the neck and back of crocodilians are concave in the front (socket) and convex (ball) in the back (procoelous) like in lizards and snakes but are generally much larger in size (Fig. 31 vs. 24; Plate 1I). The tail vertebrae range from concave on both sides (amphicoelous) to flat on both sides (acoelous).

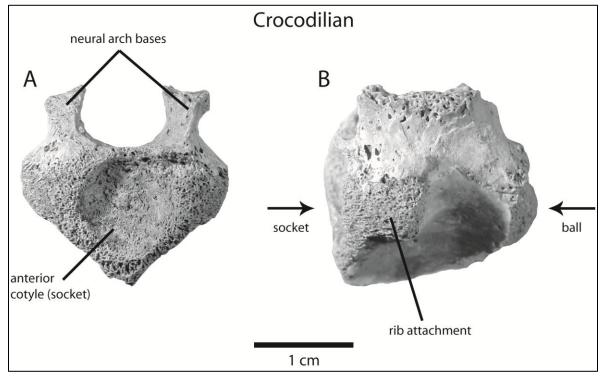


Figure 31. Crocodilian neck or cervical vertebra in A) anterior and B) left lateral views.

DINOSAURIA

Dinosaur teeth are commonly found in vertebrate microsites. In fact, some species of carnivorous dinosaur (e.g., *Richardoestesia isosceles* [Fig. 32], *Paranychodon lacustris*) are only known by teeth from microsites.



Figure 32. Drawing of *Richardoestesia isosceles*. Modified drawing from Russell Hawley © 2006. Coloring by Nick Longrich (2008).

Most dinosaur teeth found at microsites were shed by the animal during its life. The crown of the tooth is what we usually find and the root is missing.

Two major dinosaur groups are found in the Hell Creek Formation: the Saurischia, or lizard-hipped dinosaurs, and the Ornithischia, or bird-hipped dinosaurs. The saurischian dinosaurs from the Hell Creek Formation are primarily carnivorous such as *Tyrannosaurus rex* and the raptors *Dromaeosaurus* and *Saurornitholestes*. The ostrich-mimic dinosaurs, or ornithomimids, do not have teeth. Ornithischian dinosaurs are the most common dinosaurs in the Hell Creek Formation. These include the ceratopsians, such as *Triceratops*, and the duck-billed hadrosaurs, such as *Edmontosaurus*. Less common ornithischians are the armored dinosaurs (ankylosaurs), and the dome-headed dinosaurs (pachycephalosaurs; Fig. 33).

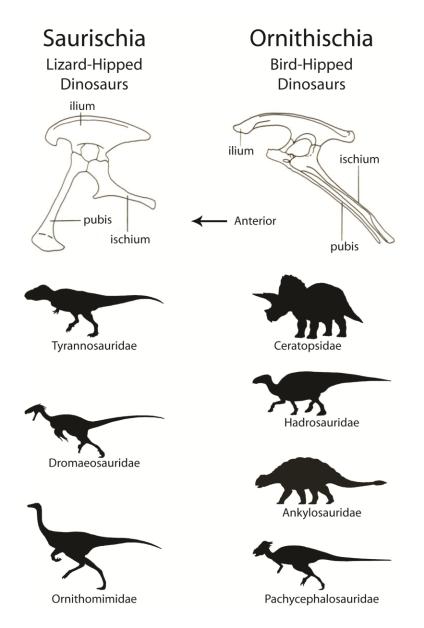


Figure 33. The two major types of dinosaurs from the Hell Creek Formation: Saurischia and Ornithischia. The pubis bone points forward in the Saurischia and backwards in the Ornithischia.

Ceratopsia (horned dinosaurs)

Teeth

Ceratopsian teeth are by far the most common dinosaur fossils found in Hell Creek Formation vertebrate microsites. The crown of an unworn tooth is leaf shaped and has multiple ridges (carinae) on the outer side (labial) of the tooth crown. The middle ridge (carina) is the largest and is offset from the midline of the tooth. The inner side (lingual) of the tooth has only a small amount of enamel on the top of the tooth (Fig. 34; Plate 2G). The enamel along the lateral margins of the tooth is wrinkled. Most shed teeth are worn flat on the top (apex) of the tooth (Fig. 34; see also Special in Plate 2G).

Hadrosauria (duck-billed dinosaurs) Teeth

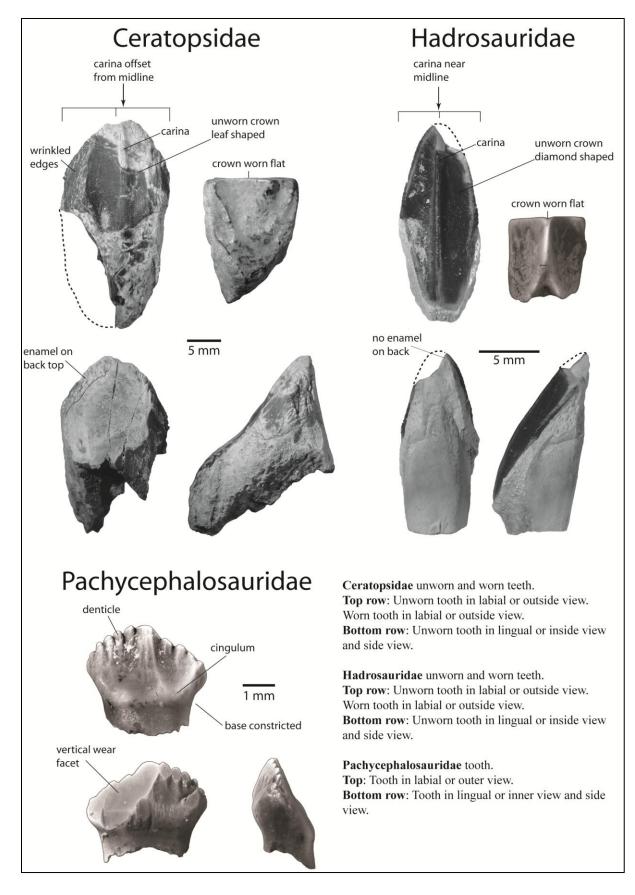
Hadrosaur teeth are similar to ceratopsian teeth in several ways but differ in a number of features (Fig. 34; Plate 2H). In lateral view, unworn crowns are diamond shaped and have a single midline ridge (carina). There is no enamel on the inside (lingual) side of the tooth. Wrinkled enamel is often found on the outer margins of the crown but not on the inner side (lingual) of the tooth. Most isolated and shed teeth are worn flat on the top of the tooth (Fig. 34; see also Special in Plate 2H).

Pachycephalosauridae (dome-headed dinosaurs)

Teeth

Pachycephalosaur teeth are uncommon but distinct when found. In general the crown is triangular to leaf shaped. The crown (Fig. 34; Plate 2F) has nine large and vertically oriented bumps (denticles) along the top of the crown. A large vertical flat surface (wear facet) is present (see Special in Plate 2F) and differs from the more horizontal flat surface seen in ceratopsian and hadrosaur teeth (Plate 2G and 2H, respectively). A prominent horizontal ridge (cingulum) is found at the base of the crown and the tooth has a single round root.

Figure 34. Teeth or Ceratopsia, Hadrosauria, and Pachycephalosauridae \rightarrow



Ankylosauria (armored dinosaurs)

Teeth

Ankylosaur teeth are similar to pachycephalosaur teeth in that they have large vertically-oriented bumps (denticles) and large ridges (cingula) at the base of the crown. The teeth of ankylosaurs are typically much larger than pachycephalosaur teeth.

Theropoda (mostly carnivorous dinosaurs)

Teeth

Most theropod teeth are blade like, curved or straight, and have small bumps (denticles or serrations) on the anterior and/or posterior ridges (carinae; Fig. 35). The shape and size of the denticles vary among species of theropod and some species lack **denticles** altogether. Tyrannosaurs have equally-sized anterior and posterior bumps (denticles) that are bluntly rounded at their tips (Fig. 35; Plate 2I Special).

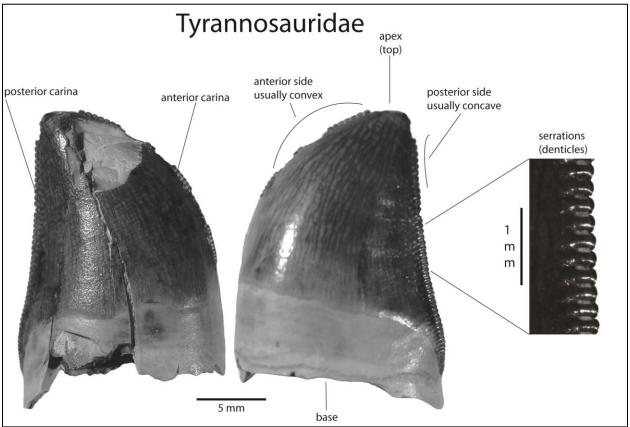


Figure 35. Tyrannosaur tooth in lingual and labial view. Serrations (denticles) of posterior carina.

MAMMALIA

Multituberculates, marsupials, and placentals

During the Late Cretaceous, mammals were small and had relatively fragile bones, so we rarely find much besides their teeth and jaw bones. Because mammals have high metabolic energy demands (essentially a fast-running motor), they must efficiently breakdown food in their mouth. As a result, their teeth can give us information about their diet. The posterior teeth or molars are also used in species identification. Tooth attachment type in mammals is **thecodonty** (Fig. 6C).

Three major mammal groups are known from the Hell Creek Formation: Multituberculata, Metatheria (e.g., marsupials), and Eutheria (e.g., placentals).

The name Multituberculata refers to the numerous tubercles, or bumps, on the molar teeth (Fig. 36; see teeth labeled as M or in dark gray). The now-extinct multituberculates were like modern rodents and likely played a similar ecological role. In the lower jaw of multituberculates is a large, blade-like premolar with curved and verticallyoriented ridges (Fig. 36C and D; see P₄ or light gray tooth). Premolars and molars have two roots that are often preserved with the crown, as mammals do not constantly shed their teeth like nonmammals often do (e.g., dinosaurs). See Fig.38 and Plate 3I for examples of multituberculate teeth and jaws.

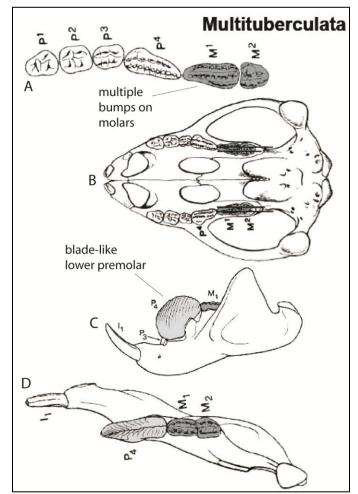


Figure 36. Multituberculata teeth and skull and lower jaw. **A**) Upper tooth row in occlusal view; **B**) skull in ventral view showing occlusal view of upper tooth rows; **C**) left dentary in outer (labial) view with blade-like fourth premolar in light gray and the first lower molar in dark gray; **D**) left dentary in occlusal view with blade-like fourth premolar in light gray and the lower molars in dark gray. A, C-D modified from Krause (1982). B modified from Wall and Krause (1992).

The upper molars of metatherians and eutherians are triangular shaped with three major cusps or bumps on the occlusal surface of the crown. The main differences between metatherian and eutherian upper molars are that metatherians have more small cusps on the outer side (labial) of the occlusal surface of the tooth and have a front to back (mesiodistal) longer tooth (Fig. 37

uppers). The lower molars are more complex and can be divided into two major parts: a triangular-shaped trigonid and a circular or oval talonid. In metatherians the talonid is more round and the cusps are less evenly spaced on the top of the crown (Fig. 37 lowers). See Figure 38 and Plate 2J for an example of a metatherian tooth.

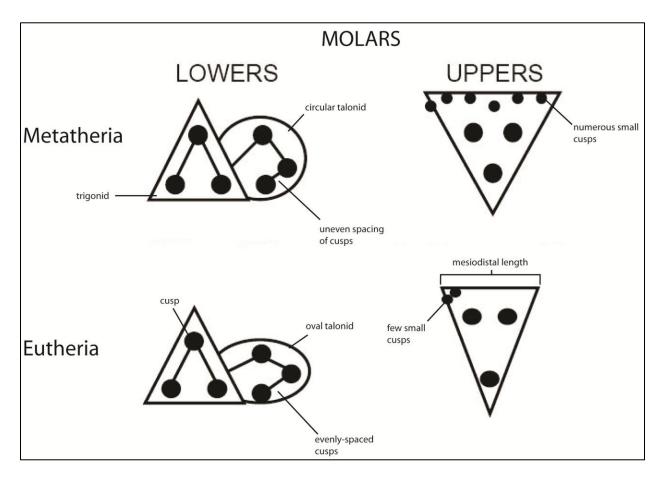


Figure 37. Graphical representation of metatherian and eutherian upper and lower molars. See text above for discussion.

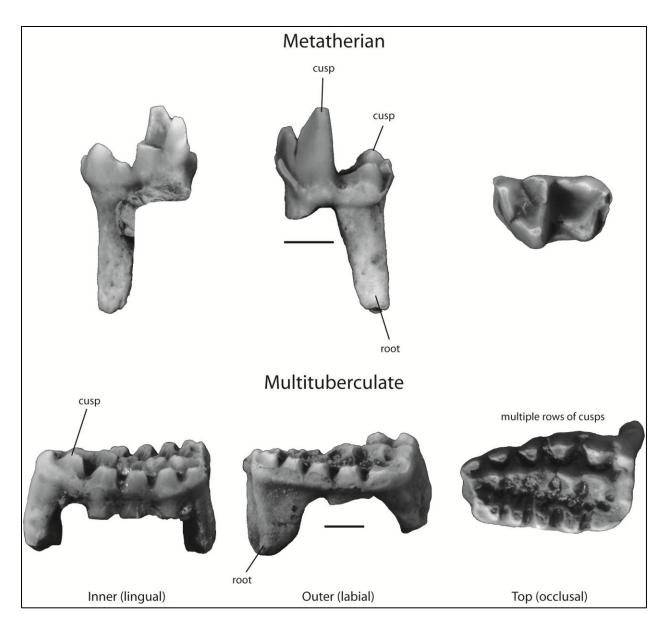


Figure 38. Metatherian (top) and multituberculate (bottom) mammal teeth (lower molars).

Jaws

Most mammal jaws from the Hell Creek and Tullock formations are small and often times one or all of the teeth are missing. The teeth sit in deep sockets (thecodont dentition; Fig. 3C). Small mammal jaws can easily be differentiated from similar sized vertebrates such as fish, amphibians, and lizards even if the teeth are missing because of this condition. See Plate 3I for an example of a mammal jaw.

Glossary of Terms

Acoelous – Type of vertebra having flat front and back cotyles.

Acrodonty – Type of tooth attachment where the teeth sit on top of the jaw bone.

Amphicoelous – Type of vertebra having concave front and back cotyles.

Carina – A ridge or keel that projects from a surface. Carinae is plural.

Centrum – The body or base of a vertebra.

Cotyle – A cuplike cavity. It is on the front or back of a centrum and they can be concave, convex, or flat.

Crown – Top of a tooth.

Denticle – A small tooth or tooth-like projection.

Enamel – Forms the top of most teeth and some fish scales. Hardest substance in the vertebrate body.

Foramen – A hole through a wall of tissue (e.g., a bone).

Ganoine – A type of enamel.

Microfossil – a fossil that requires a microscope to study.

Microsite – a common term used in place of a vertebrate microfossil assemblage.

Opisthocoelous – Type of vertebra having a ball or convex front cotyle and a socket or concave back cotyle.

Placoid scale – A tooth-like scale found in cartilaginous fishes such as sharks, skates, and rays.

Pleurodonty – Having teeth that attach to the inside of the jaw.

Prezygapophysis – An anterior or front zygapophysis.

Postzygapophysis – A posterior or back **zygapophysis**.

Procoelous – Type of vertebra having a socket or concave front cotyle and a ball or convex back cotyle.

Tetrapod – A vertebrate having four limbs.

Thecodonty – Having teeth with a root that fit in a cavity or socket.

Tooth – A hard, bonelike structure in the mouth used for biting or chewing food.

Vertebrate microfossil assemblage – concentrations of fossilized vertebrate bones and teeth of multiple individuals that are usually in the millimeter to centimeter size range.

Zygapophysis – A forward or backward projecting process that is above the centrum of a vertebra.

Recommended readings

- Archibald, J. D., 1982, A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana: University of California Publications in Geological Sciences, v. 122, p. 1-286.
- Archibald, J. D., 1996, Dinosaur Extinction and the End of an Era: What the Fossils Say: New York, Columbia University Press, 237 p.
- Archibald, J. D., 2011, Extinction and Radiation: How the Fall of Dinosaurs Led to the Rise of Mammals: Baltimore, The Johns Hopkins University Press, 108 p.
- Brinkman, D., 2008, An illustrated guide to the vertebrate microfossils from the Dinosaur Park Formation: revised and updated for the workshop on vertebrate microfossils Dinosaur Park Formation, May 13–18. Royal Tyrrell Museum of Palaeontology, Unpublished manuscript, p. 1-138.
- Bryant, L. J., 1989, Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana: University of California Publications in Geological Sciences, v. 134, p. 1-107.
- Clemens, W.A., 1966, Fossil mammals of the type Lance Formation, Wyoming. Part II. Marsupialia: University of California Publications in Geological Sciences, v. 62, p. 1-105.
- Clemens, W. A., 2002, Evolution of the mammalian fauna across the Cretaceous-Tertiary boundary in northeastern Montana and other areas of the Western Interior, *in* Hartman, J. H., Johnson, K. R., and Nichols, D. J., eds., The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous: Boulder, Colorado, Geological Society of America Special Paper 361, p. 217-245.
- Estes, R., 1964, Fossil vertebrates from the Late Cretaceous Lance Formation eastern Wyoming: University of California Publications in Geological Sciences, v. 49, p. 1-187.
- Gao, K., and Fox, R. C., 1996, Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from Western Canada: Bulletin of Carnegie Museum of Natural History, no. 33, p. 1-107.
- Holman, J. A., 2000, Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology: Bloomington, Indiana University Press, 357 p.
- Holman, J. A., 2003, Fossil Frogs and Toads of North America: Bloomington, Indiana University Press, 246 p.
- Holman, J. A., 2006, Fossil Salamanders of North America: Bloomington, Indiana University Press, 232 p.
- Kardong, K. V., 2009, Vertebrates: Comparative Anatomy, Function, Evolution, 5th ed.: New York, McGraw-Hill, 779 p.
- Krause, D. W., 1982, Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*: Paleobiology, v. 8, no. 3, p. 265-281.
- Peng, J., Russell, A. P., and Brinkman, D. B., 2001, Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide: Provincial Museum of Alberta, Natural History Occasional Paper, no. 25, 1-54 p.
- Sankey, J.T., and Baszio, S., eds., 2008, Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography: Bloomington, Indiana University Press, 278 p.

- Wall, C. E., and Krause, D. W., 1992, A biomechanical analysis of the masticatory apparatus of *Ptilodus* (Multituberculata): Journal of Vertebrate Paleontology, v. 12, p. 172-187.
- Wilson, G. P., 2005, Mammalian faunal dynamics during the last 1.8 million years of the Cretaceous in Garfield County, Montana: Journal of Mammalian Evolution, v. 12, no. 1/2, p. 53-75.