

= Albertosaurus =

Albertosaurus (/ ælʔb??rt??s??r?s / ; meaning " Alberta lizard ") is a genus of tyrannosaurid theropod dinosaur that lived in western North America during the Late Cretaceous Period , about 70 million years ago . The type species , *A. sarcophagus* , was apparently restricted in range to the modern @-@ day Canadian province of Alberta , after which the genus is named . Scientists disagree on the content of the genus , with some recognizing *Gorgosaurus libratus* as a second species .

As a tyrannosaurid , Albertosaurus was a bipedal predator with tiny , two @-@ fingered hands and a massive head that had dozens of large , sharp teeth . It may have been at the top of the food chain in its local ecosystem . Although relatively large for a theropod , Albertosaurus was much smaller than its more famous relative *Tyrannosaurus* , probably weighing less than 2 metric tons .

Since the first discovery in 1884 , fossils of more than 30 individuals have been recovered , providing scientists with a more detailed knowledge of Albertosaurus anatomy than is available for most other tyrannosaurids . The discovery of 26 individuals at one site provides evidence of pack behaviour and allows studies of ontogeny and population biology , which are impossible with lesser @-@ known dinosaurs .

= = Description = =

Albertosaurus was smaller than some other tyrannosaurids , such as *Tarbosaurus* and *Tyrannosaurus* . Typical Albertosaurus adults measured up to 9 metres (30 feet) long , while rare individuals of great age could grow to be over 10 metres (33 feet) long . Several independent mass estimates , obtained by different methods , suggest that an adult Albertosaurus weighed between 1 @.@ 3 tonnes (1 @.@ 4 short tons) and 1 @.@ 7 tonnes (1 @.@ 9 tons) .

Albertosaurus shared a similar body appearance with all other tyrannosaurids . Typically for a theropod , Albertosaurus was bipedal and balanced the heavy head and torso with a long tail . However , tyrannosaurid forelimbs were extremely small for their body size and retained only two digits . The hind limbs were long and ended in a four @-@ toed foot on which the first digit , called the hallux , was short and did not reach the ground . The third digit was longer than the rest . Albertosaurus may have been able to reach walking speeds of 14 ? 21 kilometres per hour (8 ? 13 miles per hour) . At least for the younger individuals , a high running speed is plausible .

= = = Skull and teeth = = =

The massive skull of Albertosaurus , which was perched on a short , S @-@ shaped neck , was approximately 1 metre (3 @.@ 3 feet) long in the largest adults . Wide openings in the skull (fenestrae) reduced the weight of the head while also providing space for muscle attachment and sensory organs . Its long jaws contained , both sides combined , 58 or more banana @-@ shaped teeth ; larger tyrannosaurids possessed fewer teeth , *Gorgosaurus* at least sixty @-@ two . Unlike most theropods , Albertosaurus and other tyrannosaurids were heterodont , with teeth of different forms depending on their position in the mouth . The premaxillary teeth at the tip of the upper jaw , four per side , were much smaller than the rest , more closely packed , and D @-@ shaped in cross section . Like with *Tyrannosaurus* , the maxillary (cheek) teeth of Albertosaurus were adapted in general form to resist lateral forces exerted by a struggling prey . The bite force of Albertosaurus was less formidable , however , with the maximum force , by the hind teeth , reaching 3 @, @ 413 Newtons . Above the eyes were short bony crests that may have been brightly coloured in life and used in courtship to attract a mate .

William Abler observed in 2001 that Albertosaurus tooth serrations resemble a crack in the tooth ending in a round void called an ampulla . Tyrannosaurid teeth were used as holdfasts for pulling meat off a body , so when a tyrannosaur pulled back on a piece of meat , the tension could cause a purely crack @-@ like serration to spread through the tooth . However , the presence of the ampulla distributed these forces over a larger surface area , and lessened the risk of damage to the tooth

under strain . The presence of incisions ending in voids has parallels in human engineering . Guitar makers use incisions ending in voids to , as Abler describes , " impart alternating regions of flexibility and rigidity " to the wood they work with . The use of a drill to create an " ampulla " of sorts and prevent the propagation of cracks through material is also used to protect aircraft surfaces . Abler demonstrated that a plexiglass bar with incisions called " kerfs " and drilled holes was more than 25 % stronger than one with only regularly placed incisions . Unlike tyrannosaurs , ancient predators like phytosaurs and Dimetrodon had no adaptations to prevent the crack @-@ like serrations of their teeth from spreading when subjected to the forces of feeding .

= = Classification and systematics = =

Albertosaurus is a member of the theropod family Tyrannosauridae , in the subfamily Albertosaurinae . Its closest relative is the slightly older Gorgosaurus libratus (sometimes called Albertosaurus libratus ; see below) . These two species are the only described albertosaurines ; other undescribed species may exist . Thomas Holtz found Appalachiosaurus to be an albertosaurine in 2004 , but his more recent unpublished work locates it just outside Tyrannosauridae , in agreement with other authors .

The other major subfamily of tyrannosaurids is the Tyrannosaurinae , which includes Daspletosaurus , Tarbosaurus and Tyrannosaurus . Compared with these robust tyrannosaurines , albertosaurines had slender builds , with proportionately smaller skulls and longer bones of the lower leg (tibia) and feet (metatarsals and phalanges) .

Below is the cladogram of Tyrannosauridae based on the phylogenetic analysis conducted by Loewen et al. in 2013 .

= = Discovery and naming = =

= = = Naming = = =

Albertosaurus was named by Henry Fairfield Osborn in a one @-@ page note at the end of his 1905 description of Tyrannosaurus rex . The name honours Alberta , the Canadian province established the same year , in which the first remains were found . The generic name also incorporates the Greek term ?????? / sauros (" lizard ") , the most common suffix in dinosaur names . The type species is Albertosaurus sarcophagus ; the specific name is derived from Ancient Greek ?????????? (sarkophagos) meaning " flesh @-@ eating " and having the same etymology as the funeral container with which it shares its name : a combination of the Greek words ???? / sarx (" flesh ") and ?????? / phagein (" to eat ") . More than 30 specimens of all ages are known to science .

= = = Early discoveries = = =

The type specimen is a partial skull , collected in the summer of 1884 from an outcrop of the Horseshoe Canyon Formation alongside the Red Deer River , in Alberta . This specimen , found on June 9 , 1884 , was recovered by an expedition of the Geological Survey of Canada , led by the famous geologist Joseph Burr Tyrrell . Due to a lack of specialised equipment the almost complete skull could only be partially secured . In 1889 , Tyrrell 's colleague Thomas Chesmer Weston found an incomplete smaller skull associated with some skeletal material at a location nearby . The two skulls were assigned to the preexisting species Laelaps incrassatus by Edward Drinker Cope in 1892 , although the name Laelaps was preoccupied by a genus of mite and had been changed to Dryptosaurus in 1877 by Othniel Charles Marsh . Cope refused to recognize the new name created by his archrival Marsh . However , Lawrence Lambe used the name Dryptosaurus incrassatus instead of Laelaps incrassatus when he described the remains in detail in 1903 and 1904 , a combination first coined by Oliver Perry Hay in 1902 . Shortly later , Osborn pointed out that D.

incrassatus was based on generic tyrannosaurid teeth , so the two Horseshoe Canyon skulls could not be confidently referred to that species . The Horseshoe Canyon skulls also differed markedly from the remains of *D. aquilunguis* , type species of *Dryptosaurus* , so Osborn created the new name *Albertosaurus sarcophagus* for them in 1905 . He did not describe the remains in any great detail , citing Lambe 's complete description the year before . Both specimens (the holotype CMN 5600 and the paratype CMN 5601) are stored in the Canadian Museum of Nature in Ottawa . By the early twenty @-@ first century , some concerns had arisen that , due to the damaged state of the holotype , *Albertosaurus* might be a nomen dubium , a " dubious name " that could only be used for the type specimen itself because other fossils could not reliably be assigned to it . However , in 2010 , Thomas Carr established that the holotype , the paratype and comparable later finds all shared a single common unique trait or autapomorphy : the possession of an enlarged pneumatic opening in the back rim of the side of the palatine bone , proving that *Albertosaurus* was a valid taxon .

= = = Dry Island bonebed = = =

On 11 August 1910 , American paleontologist Barnum Brown discovered the remains of a large group of *Albertosaurus* at another quarry alongside the Red Deer River . Because of the large number of bones and the limited time available , Brown 's party did not collect every specimen , but made sure to collect remains from all of the individuals that they could identify in the bonebed . Among the bones deposited in the American Museum of Natural History collections in New York City are seven sets of right metatarsals , along with two isolated toe bones that did not match any of the metatarsals in size . This indicated the presence of at least nine individuals in the quarry . The Royal Tyrrell Museum of Palaeontology rediscovered the bonebed in 1997 and resumed fieldwork at the site , which is now located inside Dry Island Buffalo Jump Provincial Park . Further excavation from 1997 to 2005 turned up the remains of 13 more individuals of various ages , including a diminutive two @-@ year @-@ old and a very old individual estimated at over 10 metres (33 feet) in length . None of these individuals are known from complete skeletons , and most are represented by remains in both museums . Excavations continued until 2008 , when the minimum number of individuals present had been established at 12 , on the basis of preserved elements that occur only once in a skeleton , and at 26 if mirrored elements were counted when differing in size due to ontogeny . A total of 1 @,@ 128 *Albertosaurus* bones had been secured , the largest concentration of large theropod fossils known from the Cretaceous .

= = = *Gorgosaurus libratus* = = =

In 1913 , paleontologist Charles H. Sternberg recovered another tyrannosaurid skeleton from the slightly older Dinosaur Park Formation in Alberta . Lawrence Lambe named this dinosaur *Gorgosaurus libratus* in 1914 . Other specimens were later found in Alberta and the US state of Montana . Finding , largely due to a lack of good *Albertosaurus* skull material , no significant differences to separate the two taxa , Dale Russell declared the name *Gorgosaurus* a junior synonym of *Albertosaurus* , which had been named first , and *G. libratus* was renamed *Albertosaurus libratus* in 1970 . A species distinction was maintained because of the age difference . This addition extended the temporal range of the genus *Albertosaurus* backwards by several million years and its geographic range southwards by hundreds of kilometres .

In 2003 , Philip J. Currie , benefiting from much more extensive finds and a general increase in anatomical knowledge of theropods , compared several tyrannosaurid skulls and came to the conclusion that the two species are more distinct than previously thought . The decision to use one or two genera is rather arbitrary , as the two species are sister taxa , more closely related to each other than to any other species . Recognizing this , Currie nevertheless recommended that *Albertosaurus* and *Gorgosaurus* be retained as separate genera , as he concluded that they were no more similar than *Daspletosaurus* and *Tyrannosaurus* , which are almost always separated . In addition , several albertosaurine specimens have been recovered from Alaska and New Mexico ,

and Currie suggested that the *Albertosaurus* @-@ *Gorgosaurus* situation may be clarified once these are described fully . Most authors have followed Currie 's recommendation , but some have not .

== Other discoveries ==

In 1911 , Barnum Brown , during the second year of American Museum of Natural History operations in Alberta , uncovered a fragmentary partial *Albertosaurus* skull at the Red Deer River near Tolman Bridge , specimen AMNH 5222 .

William Parks described a new species in 1928 , *Albertosaurus arctunguis* , based on a partial skeleton lacking the skull excavated by Gus Lindblad and Ralph Hornell near the Red Deer River in 1923 , but this species has been considered identical to *A. sarcophagus* since 1970 . Parks ' specimen (ROM 807) is housed in the Royal Ontario Museum in Toronto .

Between 1926 and 1972 , no *Albertosaurus* fossils were found at all ; but , since the seventies , there has been a steady increase in the known material . Apart from the Dry Island bonebed , six more skulls and skeletons have since been discovered in Alberta and are housed in various Canadian museums : specimens RTMP 81 @.@ 010 @.@ 001 , found in 1978 by amateur paleontologist Maurice Stefanuk ; RTMP 85 @.@ 098 @.@ 001 , found by Stefanuk on 16 June 1985 ; RTMP 86 @.@ 64 @.@ 001 (December 1985) ; RTMP 86 @.@ 205 @.@ 001 (1986) ; RTMP 97 @.@ 058 @.@ 0001 (1996) ; and CMN 11315 . However , due to vandalism and accidents , no undamaged and complete skulls could be secured among these finds . Fossils have also been reported from the American states of Montana , New Mexico , and Wyoming , but these probably do not represent *A. sarcophagus* and may not even belong to the genus *Albertosaurus* .

== Other species ==

Apart from *A. sarcophagus* , *A. arctunguis* and *A. libratus* , several other species of *Albertosaurus* have been named . All of these are today seen as younger synonyms of other species or as nomina dubia , and are not assigned to *Albertosaurus* .

In 1930 , Anatoly Nikolaevich Riabinin named *Albertosaurus pericolosus* based on a tooth from China , that probably belonged to *Tarbosaurus* . In 1932 , Friedrich von Huene renamed *Dryptosaurus incrassatus* , not considered a nomen dubium by him , to *Albertosaurus incrassatus* . Because he had identified *Gorgosaurus* with *Albertosaurus* , in 1970 , Russell also renamed *Gorgosaurus sternbergi* (Matthew & Brown 1922) into *Albertosaurus sternbergi* and *Gorgosaurus lancensis* (Gilmore 1946) into *Albertosaurus lancensis* . The former species is today seen as a juvenile form of *Gorgosaurus libratus* , the latter as either identical to *Tyrannosaurus* or representing a separate genus *Nanotyrannus* . In 1988 , Gregory S. Paul based *Albertosaurus megagracilis* on a small tyrannosaurid skeleton , specimen LACM 28345 , from the Hell Creek Formation of Montana . It was renamed *Dinotyrannus* in 1995 , but is now thought to represent a juvenile *Tyrannosaurus rex* . Also in 1988 , Paul renamed *Alectrosaurus olseni* (Gilmore 1933) into *Albertosaurus olseni* ; this has found no general acceptance . In 1989 , *Gorgosaurus novojilovi* (Maleev 1955) was renamed by Bryn Mader and Robert Bradley as *Albertosaurus novojilovi* ; today this is seen as a synonym of *Tarbosaurus* .

On two occasions , species based on valid *Albertosaurus* material were reassigned to a different genus : in 1922 William Diller Matthew renamed *A. sarcophagus* into *Deinodon sarcophagus* and in 1939 German paleontologist Oskar Kuhn renamed *A. arctunguis* into *Deinodon arctunguis* .

= Paleobiology =

== Growth pattern ==

Most age categories of *Albertosaurus* are represented in the fossil record . Using bone histology ,

the age of an individual animal at the time of death can often be determined , allowing growth rates to be estimated and compared with other species . The youngest known *Albertosaurus* is a two @-@ year @-@ old discovered in the Dry Island bonebed , which would have weighed about 50 kilograms (110 lb) and measured slightly more than 2 metres (6 @.@ 6 feet) in length . The 10 metres (33 feet) specimen from the same quarry is the oldest and largest known , at 28 years of age . When specimens of intermediate age and size are plotted on a graph , an S @-@ shaped growth curve results , with the most rapid growth occurring in a four @-@ year period ending around the sixteenth year of life , a pattern also seen in other tyrannosaurids . The growth rate during this phase was 122 kilograms (269 pounds) per year , based on an adult 1 @.@ 3 tonnes (1 @.@ 4 short tons) . Other studies have suggested higher adult weights ; this would affect the magnitude of the growth rate , but not the overall pattern . Tyrannosaurids similar in size to *Albertosaurus* had similar growth rates , although the much larger *Tyrannosaurus rex* grew at almost five times this rate (601 kilograms [1 @,@ 325 pounds] per year) at its peak . The end of the rapid growth phase suggests the onset of sexual maturity in *Albertosaurus* , although growth continued at a slower rate throughout the animals ' lives . Sexual maturation while still actively growing appears to be a shared trait among small and large dinosaurs as well as in large mammals such as humans and elephants . This pattern of relatively early sexual maturation differs strikingly from the pattern in birds , which delay their sexual maturity until after they have finished growing .

During growth , through thickening the tooth morphology changed so much that , had the association of young and adult skeletons on the Dry Island bonebed not proven they belonged to the same taxon , the teeth of juveniles would likely have been identified by statistical analysis as those of a different species .

= = = Life history = = =

Most known *Albertosaurus* individuals were aged 14 years or more at the time of death . Juvenile animals are rarely found as fossils for several reasons , mainly preservation bias , where the smaller bones of younger animals were less likely to be preserved by fossilization than the larger bones of adults , and collection bias , where smaller fossils are less likely to be noticed by collectors in the field . Young *Albertosaurus* are relatively large for juvenile animals , but their remains are still rare in the fossil record compared with adults . It has been suggested that this phenomenon is a consequence of life history , rather than bias , and that fossils of juvenile *Albertosaurus* are rare because they simply did not die as often as adults did .

A hypothesis of *Albertosaurus* life history postulates that hatchlings died in large numbers , but have not been preserved in the fossil record due to their small size and fragile construction . After just two years , juveniles were larger than any other predator in the region aside from adult *Albertosaurus* , and more fleet of foot than most of their prey animals . This resulted in a dramatic decrease in their mortality rate and a corresponding rarity of fossil remains . Mortality rates doubled at age twelve , perhaps the result of the physiological demands of the rapid growth phase , and then doubled again with the onset of sexual maturity between the ages of fourteen and sixteen . This elevated mortality rate continued throughout adulthood , perhaps due to the high physiological demands of procreation , including stress and injuries received during intraspecific competition for mates and resources , and eventually , the ever @-@ increasing effects of senescence . The higher mortality rate in adults may explain their more common preservation . Very large animals were rare because few individuals survived long enough to attain such sizes . High infant mortality rates , followed by reduced mortality among juveniles and a sudden increase in mortality after sexual maturity , with very few animals reaching maximum size , is a pattern observed in many modern large mammals , including elephants , African buffalo , and rhinoceros . The same pattern is also seen in other tyrannosaurids . The comparison with modern animals and other tyrannosaurids lends support to this life history hypothesis , but bias in the fossil record may still play a large role , especially since more than two @-@ thirds of all *Albertosaurus* specimens are known from one locality .

== = Pack behaviour == =

The Dry Island bonebed discovered by Barnum Brown and his crew contains the remains of 26 *Albertosaurus*, the most individuals found in one locality of any large Cretaceous theropod, and the second @-@ most of any large theropod dinosaur behind the *Allosaurus* assemblage at the Cleveland Lloyd Dinosaur Quarry in Utah. The group seems to be composed of one very old adult; eight adults between 17 and 23 years old; seven sub @-@ adults undergoing their rapid growth phases at between 12 and 16 years old; and six juveniles between the ages of 2 and 11 years, who had not yet reached the growth phase.

The near @-@ absence of herbivore remains and the similar state of preservation common to the many individuals at the *Albertosaurus* bonebed quarry led Currie to conclude that the locality was not a predator trap like the La Brea Tar Pits in California, and that all of the preserved animals died at the same time. Currie claims this as evidence of pack behaviour. Other scientists are skeptical, observing that the animals may have been driven together by drought, flood or for other reasons.

There is plentiful evidence for gregarious behaviour among herbivorous dinosaurs, including ceratopsians and hadrosaurs. However, only rarely are so many dinosaurian predators found at the same site. Small theropods like *Deinonychus* and *Coelophysis* have been found in aggregations, as have larger predators like *Allosaurus* and *Mapusaurus*. There is some evidence of gregarious behaviour in other tyrannosaurids as well. Fragmentary remains of smaller individuals were found alongside "Sue", the *Tyrannosaurus* mounted in the Field Museum of Natural History in Chicago, and a bonebed in the Two Medicine Formation of Montana contains at least three specimens of *Daspletosaurus*, preserved alongside several hadrosaurs. These findings may corroborate the evidence for social behaviour in *Albertosaurus*, although some or all of the above localities may represent temporary or unnatural aggregations. Others have speculated that instead of social groups, at least some of these finds represent Komodo dragon @-@ like mobbing of carcasses, where aggressive competition leads to some of the predators being killed and cannibalized.

Currie also offers speculation on the pack @-@ hunting habits of *Albertosaurus*. The leg proportions of the smaller individuals were comparable to those of ornithomimids, which were probably among the fastest dinosaurs. Younger *Albertosaurus* were probably equally fleet @-@ footed, or at least faster than their prey. Currie hypothesized that the younger members of the pack may have been responsible for driving their prey towards the adults, who were larger and more powerful, but also slower. Juveniles may also have had different lifestyles than adults, filling predator niches between the enormous adults and the smaller contemporaneous theropods, the largest of which were two orders of magnitude smaller than adult *Albertosaurus* in mass. A similar situation is observed in modern Komodo dragons, with hatchlings beginning life as small insectivores before growing to become the dominant predators on their islands. However, as the preservation of behaviour in the fossil record is exceedingly rare, these ideas cannot readily be tested. In 2010, Currie, though still favouring the hunting pack hypothesis, admitted that the concentration could have been brought about by other causes, such as a slowly rising water level during an extended flood.

== = Paleopathology == =

In 2009, researchers hypothesized that smooth @-@ edged holes found in the fossil jaws of tyrannosaurid dinosaurs such as *Albertosaurus* were caused by a parasite similar to *Trichomonas gallinae*, which infects birds. They suggested that tyrannosaurids transmitted the infection by biting each other, and that the infection impaired their ability to eat food.

In 2001, Bruce Rothschild and others published a study examining evidence for stress fractures and tendon avulsions in theropod dinosaurs and the implications for their behavior. They found that only one of the 319 *Albertosaurus* foot bones checked for stress fractures actually had them and none of the four hand bones did. The scientists found that stress fractures were "significantly" less common in *Albertosaurus* than in the carnosaur *Allosaurus*. ROM 807, the holotype of *A. arctunguis* (now referred to *A. sarcophagus*), had a 2 @.@ 5 by 3 @.@ 5 cm (0 @.@ 98 by 1

@. @ 38 in) deep hole in the iliac blade , although the describer of the species did not recognize this as pathological . The specimen also contains some exostosis on the fourth left metatarsal . In 1970 , two of the five *Albertosaurus sarcophagus* specimens with humeri were reported by Dale Russel as having pathological damage to them .

In 2010 , the health of the Dry Island *Albertosaurus* assembly was reported upon . Most specimens showed no sign of disease . On three phalanges of the foot strange bony spurs , consisting of abnormal ossifications of the tendons , so @-@ called enthesophytes , were present , their cause unknown . Two ribs and a belly @-@ rib showed signs of breaking and healing . One adult specimen had a left lower jaw showing a puncture wound and both healed and unhealed bite marks . The low number of abnormalities compares favourably with the health condition of a *Majungasaurus* population of which it in 2007 was established that 19 % of individuals showed bone pathologies .

= = Paleoecology = =

All identifiable fossils of *Albertosaurus sarcophagus* are known from the upper Horseshoe Canyon Formation in Alberta . These younger units of this geologic formation date to the early Maastrichtian stage of the Late Cretaceous Period , 70 to 68 Ma (million years ago) . Immediately below this formation is the Bearpaw Shale , a marine formation representing a section of the Western Interior Seaway . The seaway was receding as the climate cooled and sea levels subsided towards the end of the Cretaceous , exposing land that had previously been underwater . It was not a smooth process , however , and the seaway would periodically rise to cover parts of the region throughout Horseshoe Canyon before finally receding altogether in the years after . Due to the changing sea levels , many different environments are represented in the Horseshoe Canyon Formation , including offshore and near @-@ shore marine habitats and coastal habitats like lagoons , estuaries and tidal flats . Numerous coal seams represent ancient peat swamps . Like most of the other vertebrate fossils from the formation , *Albertosaurus* remains are found in deposits laid down in the deltas and floodplains of large rivers during the later half of Horseshoe Canyon times .

The fauna of the Horseshoe Canyon Formation is well @-@ known , as vertebrate fossils , including those of dinosaurs , are quite common . Sharks , rays , sturgeons , bowfins , gars and the gar @-@ like *Aspidorhynchus* made up the fish fauna . Mammals included multituberculates and the marsupial *Didelphodon* . The saltwater plesiosaur *Leurospondylus* has been found in marine sediments in the Horseshoe Canyon , while freshwater environments were populated by turtles , *Champsosaurus* , and crocodilians like *Leidyosuchus* and *Stangerochampsia* . Dinosaurs dominate the fauna , especially hadrosaurs , which make up half of all dinosaurs known , including the genera *Edmontosaurus* , *Saurolophus* and *Hypacrosaurus* . Ceratopsians and ornithomimids were also very common , together making up another third of the known fauna . Along with much rarer ankylosaurians and pachycephalosaurs , all of these animals would have been prey for a diverse array of carnivorous theropods , including troodontids , dromaeosaurids , and caenagnathids . Intermingled with the *Albertosaurus* remains of the Dry Island bonebed , the bones of the small theropod *Albertonykus* were found . Adult *Albertosaurus* were the apex predators in this environment , with intermediate niches possibly filled by juvenile albertosaurs .