Ornithopod Dinosaurs from the Grand Staircase–Escalante National Monument Region, Utah, and Their Role in Paleobiogeographic and Macroevolutionary Studies

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ORNITHOPOD DINOSAURS WERE BIPEDAL, HERBIVOROUS dinosaurs represented in the Late Cretaceous of North America by basal ornithopods ("hypsilophodontids") and a clade of derived iguanodontians containing, in part, hadrosaurids. Recent research focused on the Cretaceous macrovertebrates of Grand Staircase–Escalante National Monument and surrounding areas of southern Utah has resulted in numerous discoveries of ornithopod dinosaur skeletons, complimenting the previous record based largely on teeth. The new collections are dominated by hadrosaurid material but include multiple basal ornithopod and indeterminate iguanodontian specimens. Several new taxa of hadrosaurids have been identified from these rocks along with one new species of basal ornithopod. Isolated teeth typify the majority of basal ornithopod remains currently known from the Straight Cliffs and Wahweap formations, with several skeletal specimens from the Kaiparowits Formation representing the hypodigm of a new taxon. The Straight Cliffs Formation has recently yielded several iguanodontian specimens with at least three taxa represented from Turonian, Coniacian, and Santonian strata. Hadrosaurid diversity within the Campanian Wahweap and Kaiparowits formations now includes five taxa, at least three of which appear to be new species. Hadrosaurids from the Kaiparowits Formation include one species of *Parasaurolophus* and two stratigraphically separated species of *Gryposaurus*. The recognition of this diverse ornithopod fauna within southern Utah provides a rare opportunity in North America to examine the transition from more basal iguanodontians to those taxa within Hadrosauridae. In addition, these sediments provide a testing ground for biogeographic hypotheses of basal ornithopods.

INTRODUCTION

Ornithopods were bipedal herbivorous dinosaurs that originated in the Late Jurassic (sensu Butler, Upchurch, and Norman, 2008) and diversified through the terminal Cretaceous period. Ornithopoda was first proposed by Marsh (1881), and more recently defined in a cladistic sense by Norman et al. (2004:393) as "all cerapodans closer to *Edmontosaurus* than to *Triceratops*." These dinosaurs were extremely widespread, with fossil remains discovered from every continent, including Antarctica (Case et al., 2000).

Though sporadic work on dinosaur paleontology by Brigham Young University began in what is now Grand Staircase–Escalante National Monument in the early 1970s, it was not until after the monument's creation in 1996 that expanding knowledge of the macrovertebrate fossil record from Upper Cretaceous formations started in earnest. (See Titus, this volume, Chapter 1, for an overview of paleontology history in Grand Staircase–Escalante National Monument.) This work was built upon a rich foundation of microvertebrate work spearheaded by Jeff Eaton and Rich Cifelli (Cifelli, 1987, 1990; Eaton, 1991, 2002). To date, dinosaur paleontology of the region has focused on the Kaiparowits Plateau where three stratigraphically contiguous terrestrial formations have all yielded diagnostic macroskeletal remains of dinosaurs. These are, in ascending order, the Straight Cliffs (see Titus et al., Chapter 2, this volume), Wahweap (see Jinnah, Chapter 4, this volume), and Kaiparowits (see Roberts et al., Chapter 6, this volume). The Cedar Mountain and Dakota Formations, and the Tropic Shale have not yielded diagnostic skeletal remains of dinosaurs and are not treated here, although teeth recovered by screen washing of microvertebrate samples demonstrates the presence of both basal ornithopods ("hypsilophodontids") and more advanced hadrosaurids or hadrosauromorphs. These same two clades of ornithopods occur through the remainder of the region's Cretaceous record, and they are generally the most common dinosaur fossils found in any given formation.

Basal ornithopods were small-bodied, bipedal, cursorial ornithopods ranging from 1 to 3 m in length (Norman et al., 2004). They have relatively small heads and leaf-shaped teeth, primitive characteristics in the ornithopod clade. In contrast, virtually all hadrosaurids are large-bodied animals, and some of those found within the Kaiparowits Formation were relatively gigantic, exceeding 10 m in length. Hadrosaurids are further distinguished from basal ornithopods in possessing large, elongate heads and densely packed, multiple rooted teeth in each socket that total more than 200 teeth in each jaw quadrant—a highly derived condition among dinosaurs. The hind limbs of hadrosaurids are massively built in order to support their enormous weight, more so than the forelimbs, which were used for facultative weight-bearing only during certain types of locomotion (Horner, Weishampel, and Forster, 2004). The clade Hadrosauridae consistently resolves into two subclades, the hollow-crested Lambeosaurinae and the non-hollow-crested Hadrosaurinae (Forster, 1997). Both subclades possessed highly modified skulls with cranial ornamentations, although lambeosaurines are extreme in this regard, forming an elaborate extension of the nasal cavity within hollow, bony crests composed mostly of nasals and premaxillae.

This chapter provides a brief overview of known ornithopod diversity within the Upper Cretaceous Straight Cliffs, Wahweap, and Kaiparowits formations in the Grand Staircase region, ultimately focusing on their biostratigraphic and biogeographic significance. This chapter is an updated and expanded version of a previous survey (Gates et al., 2010).

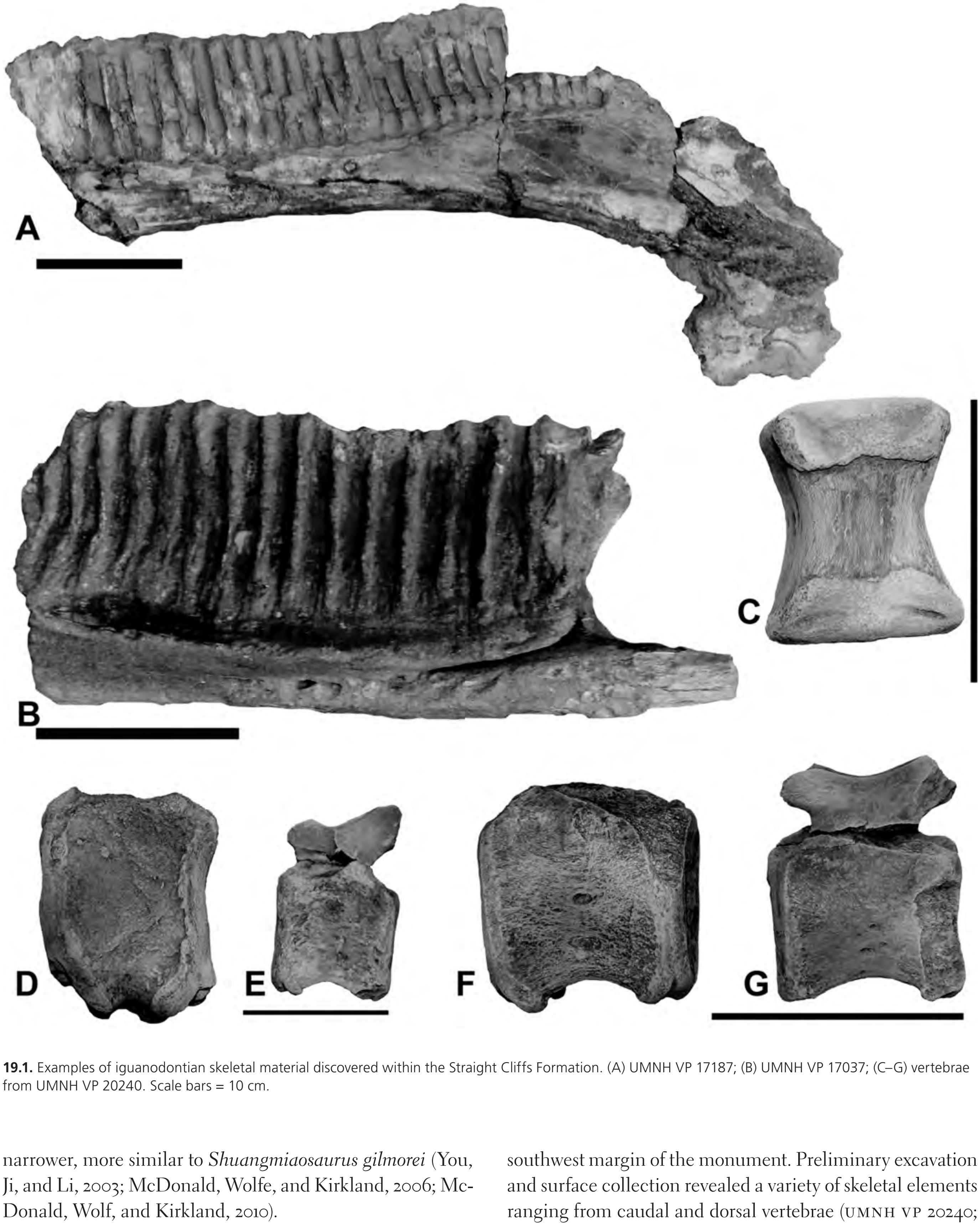
Institutional Abbreviations BYU, Brigham Young University, Provo, Utah; FMNH, Field Museum of Natural History, Chicago, Illinois; MNA, Museum of Northern Arizona, Flagstaff, Arizona; MOR, Museum of the Rockies, Bozeman, Montana; MSMP, Mesa Southwest Museum Paleontology Collection, Mesa, Arizona; RAM, Raymond M. Alf Museum, Claremont, California; ROM, Royal Ontario Museum, Toronto; UCMP, University of California Museum of Paleontology, Berkeley, California; UMNH, Natural History Museum of Utah, Salt Lake City, Utah; USNM, United States National Museum, Washington, D.C.

STRAIGHT CLIFFS FORMATION

The Smoky Hollow and John Henry members produce the majority of well-preserved nonmarine vertebrate taxa recovered from the Straight Cliffs Formation, whereas the Drip Tank Member contains mostly logs and scrappy bone fragments (Peterson, 1969; Eaton, 1991; Eaton et al., 1999; Cobban et al., 2000; Doelling et al., 2000). Most previous research has focused on screen washing microvertebrate localities, which resulted in the collection of abundant and diverse dinosaur teeth (Eaton et al., 1999; Parrish, 1999). Consequently, our current understanding of the taxonomic diversity of dinosaurs within the Straight Cliffs Formation is limited largely to inferences based on tooth morphology—a practice that generally produces only family-grade resolution.

More specific to the present review, taxonomic resolution of ornithopod diversity from the Straight Cliffs Formation is currently constrained to basal ornithopod and Hadrosauridae incertae sedis or *confer* (Eaton et al., 1999; Parrish, 1999). Parrish (1999) identified basal ornithopod teeth from the Smoky Hollow Member, comparing them to the Maastrichtian genus *Thescelosaurus*. On the basis of recent phylogenetic and stratigraphic analysis (Roberts, Deino, and Chan, 2005; Boyd et al., 2009), it appears that the clade of basal ornithopods containing *Thescelosaurus* did not exist until the Maastrichtian, making it more appropriate to compare the basal ornithopod material from the Straight Cliffs Formation to the taxa *Zephyrosaurus* or *Oryctodromeus*. No basal ornithopods have been identified from other portions of the formation.

In recent years, the fossil record for large ornithopods within the Straight Cliffs Formation has improved, with several fragmentary skeletal elements and partial skeletons discovered. In 2006, one of us (J.G.E.) discovered the partial skeleton of a large ornithopod in the Middle Turonian Smoky Hollow Member west of the Kaiparowits Plateau and north of the town of Tropic; the specimen, subsequently excavated by the Utah Geological Survey, consists only of vertebrae and limb elements, allowing no further taxonomic assessment. In addition to the previous specimen, several others demonstrate a broadening diversity of ornithopods from the Straight Cliffs Formation. Thus far, dentary fragments provide evidence for at least two taxa of large ornithopods from the Coniacian–Santonian of southern Utah. The partial dentaries UMNH VP 17037 and UMNH VP 17187 (Fig. 19.1) from the Coniacian (less than 5 m above the base of the John Henry Member) both have near vertical tooth rows, whereas the Santonian-aged UMNH VP 17434 has distinctly more posteriorly angled tooth rows, demonstrating distinct morphotypes. Another locality discovered just to the west of Grand Staircase–Escalante National Monument in more terrestrial sediments of the Coniacian John Henry Member (less than 5 m above the base of the member; same area as above) represents a partial skeleton that has the potential to greatly increase understanding of Santonian large ornithopod diversity and hadrosaurid evolution. The only other large ornithopod known from this time period of the southwestern United States is a derived iguanodontian ornithopod from the Middle Turonian–aged lower Moreno Hill Formation in west-central New Mexico (McDonald, Wolfe, and Kirkland, 2006; McDonald, Wolf, and Kirkland, 2010). It is not possible to make detailed comparisons between the Moreno Hill taxon and the Straight Cliffs taxa, although the anterior dentary downturning of UMNH VP 17187 is similar to MSMP-4166 but the relative height of the MSMP-4166 tooth row is



19.1. Examples of iguanodontian skeletal material discovered within the Straight Cliffs Formation. (A) UMNH VP 17187; (B) UMNH VP 17037; (C–G) vertebrae from UMNH VP 20240. Scale bars = 10 cm.

narrower, more similar to *Shuangmiaosaurus gilmorei* (You, Ji, and Li, 2003; McDonald, Wolfe, and Kirkland, 2006; McDonald, Wolf, and Kirkland, 2010).

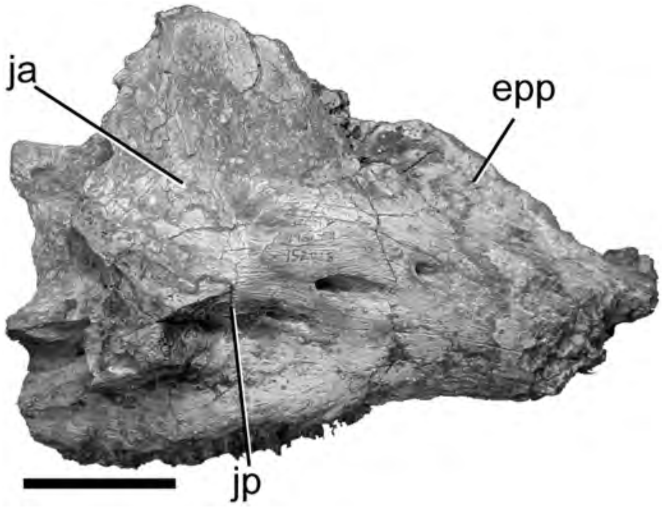
Most recently, a multi-individual bonebed was discovered by A. Titus in the Smoky Hollow Member located along the southwest margin of the monument. Preliminary excavation and surface collection revealed a variety of skeletal elements ranging from caudal and dorsal vertebrae (UMNH VP 20240; Fig. 19.1), chevrons, phalanges, and a partial dentary, all in partial articulation or close association. The dentary is the most taxonomically useful element available for study at this time, although it is still largely unprepared and more detailed description will be forthcoming. The middentary shows what appears to be an original height of the tooth-bearing portion only around 4–5 cm tall. Given that the element is not a hatchling or yearling, this height is not uncommon for most nonhadrosaurid iguanodontian ornithopods, but it seems that a critical characteristic of the ornithopod dentary is the overall length relative to height. Within North America, this is an easily recognizable characteristic of the Zuni Basin–derived iguanodontian MSMP-4166 (McDonald, Wolf, and Kirkland, 2010). It turns out that middle Turonian MSMP-4166 is penecontemporaneous with UMNH VP 20240, allowing speculation that the two specimens might represent the same species.

WAHWEAP FORMATION

Significant ornithopod localities yielding taxonomically informative specimens or an abundance of ornithopod fossils have been found in the lower three members – the lower (LM), middle (MM), and upper (UM) members – of the Wahweap Formation, although the MM is currently the most productive member. Unfortunately, to date, teeth comprise the only evidence of basal ornithopods within the formation (Eaton et al., 1999; Parrish, 1999). As with the Smoky Hollow Member teeth, Parrish (1999) compared the Wahweap ornithopod teeth with *Thescelosaurus*. Given that the thescelosaurid clade probably did not originate until the Maastrichtian, a more suitable comparison would be with the as yet unnamed basal ornithopod taxon from the Kaiparowits Formation.

Hadrosauridae

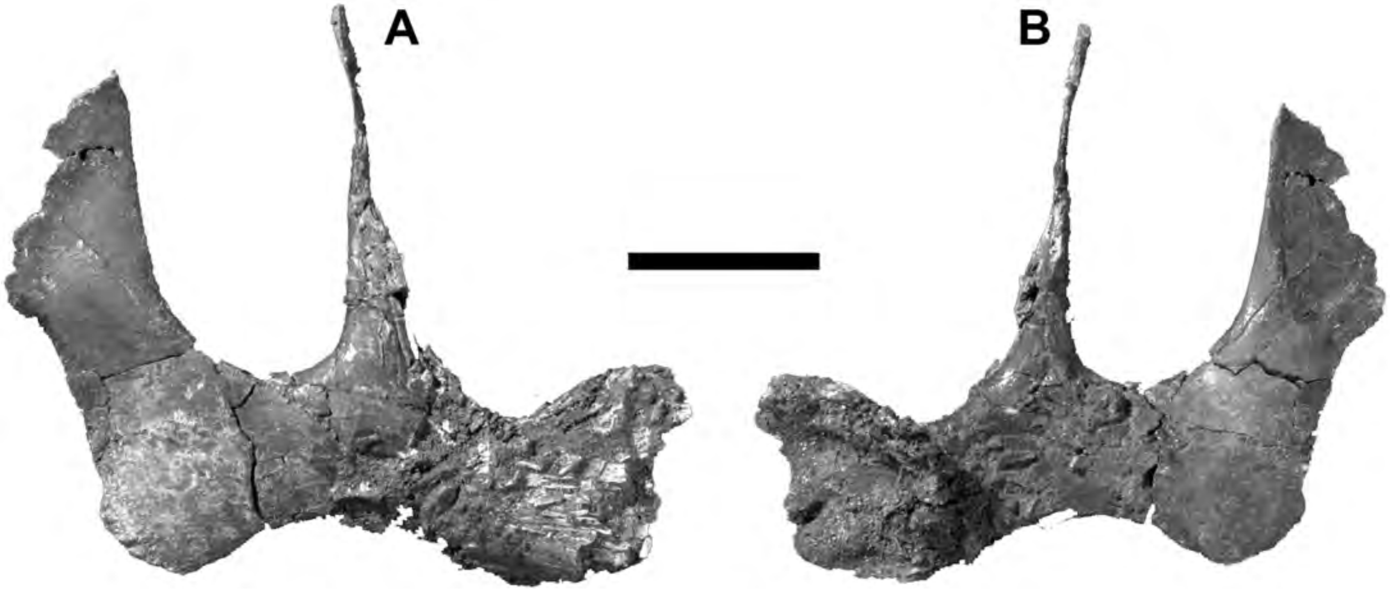
Hadrosaurids are more abundant than basal ornithopods, and numerous macroskeletal sites have been found throughout most of the Wahweap Formation. Beginning in the lowest portion of the stratigraphic section, several dozen fossils have been recovered from the hadrosaurid-dominated Tibbet Springs Quarry, located in highly indurated sandstone near the base of the LM. Multiple individuals are represented in this quarry by numerous limb and girdle elements, vertebrae, and a poorly preserved jaw. Some of this material likely represents partial associated skeletons, but more excavation at the difficult Tibbet Springs Quarry is required before further taphonomic information can be revealed. The Tibbet Springs Quarry has been the richest dinosaur locality found thus far in the lower member of the Wahweap Formation. Other hadrosaur sites occur nearby around Nipple Butte, but no diagnostic cranial material has been recovered.



19.2. Unidentified lambeosaurine maxilla (UCMP 152028) from the Wahweap Formation shown in lateral view. epp, expansion of the premaxillary process (maxillary shelf sensu Horner, Weishampel, and Forster, 2004); ja, jugal articulation; jp, jugal process. Scale bar = 5 cm.

All but one of the identifiable hadrosaurid specimens recovered thus far from the Wahweap Formation can be referred to the clade Hadrosaurinae. The single exception is an isolated lambeosaurine maxilla recovered from the UM (UCMP 152028; Fig. 19.2), making it the oldest lambeosaurine currently known in North America. Diagnosis of UCMP 152028 to Lambeosaurinae is based on the presence of the anterodorsal shelf that forms a flat, broad premaxillary shelf on the anterodorsal region of the maxilla (Prieto-Marquez, 2010:character 84, state 1), dorsal process of the maxilla dorsoventrally taller than it is wide, with a peaked and caudally inclined apex (Prieto-Marquez, 2010:character 91, state 1). The medial side of the preserved portion reveals similarities to an undescribed maxilla of *Parasaurolophus* sp. (UMNH VP 16666.1) from the Kaiparowits Formation, such as a dorsal expansion of the premaxillary process (maxillary shelf of Horner, Weishampel, and Forster, 2004; Fig. 2.19, epp). These same characteristics are muted in the crested hadrosaurs *Corythosaurus* and *Hypacrosaurus*. On the other hand, UCMP 152028 differs significantly from UMNH VP 16666.1 and all other known lambeosaurines, suggesting that this element pertains to a new taxon.

Published records of dinosaur faunas contemporaneous with those of the Wahweap Formation (81–76.1 Ma; Jinnah et al., 2009) do not include substantive descriptions of materials attributed to lambeosaurines. This interval corresponds in part to the Foremost and Oldman formations of Alberta, and the Judith River and lower part of the Two Medicine formations of Montana. An undescribed lambeosaurine has been reported to have been excavated from the Oldman Formation near Sandy Point, Alberta, Canada, by Horner,



19.3. Right juvenile hadrosaurine jugal (UMNH VP 16695) found in the Upper Sandstone Member of the Wahweap Formation shown in (A) lateral and (B) medial views. Scale bar = 5 cm.

Weishampel, and Forster (2004). However, recent relocation of the quarry reveals that the specimen originated from the base of the Dinosaur Park Formation.

Among hadrosaurines, a large bonebed, an associated skeleton, and a partial skull are the three most significant discoveries to date, all found within the Middle Mudstone member. A locality known as Jim's Hadrosaur Site has yielded a number of juvenile postcranial elements, including a large portion of the fore- and hind limbs, dorsal, and cervical vertebrae. This specimen was scattered amid abundant carbonized log sections and conifer branches, as well as a disarticulated turtle, unionid clams, and freshwater crab claws. Jim's Hadrosaur Site is located near the base of the MM and appears to preserve a single juvenile hadrosaur individual.

Another locality within the MM preserved in the same stratigraphic level and taphonomic style as Jim's Hadrosaur Site is a large bonebed near Camp Flats along the Smoky Mountain Road. Deposited in a back swamp environment, two hadrosaurine individuals, an adult and a juvenile, were completely disarticulated over an area of more than 18.5 m^2 (Jinnah, Getty, and Gates, 2009). Additional fossils found within the site include maniraptoran theropod teeth, fish bones, a turtle pelvis, and large freshwater xanthid (mud and stone crabs) or paguroid (hermit and coconut crabs) crab claws (A. Milner, pers. comm., 2010). The site also preserves abundant plant remains consisting of mostly plant hash and unidentified conifer leaves. However, an interesting aspect of the site is that numerous coalified tree trunks crisscross both above and below the hadrosaur specimens. The excavation has thus far revealed approximately 70–80% of the adult postcranium and numerous elements of a much smaller juvenile specimen (Jinnah, Getty, and Gates, 2009).

Unfortunately, the only skull material collected from this locality to date consists of a juvenile jugal, maxilla, and dentary, and an adult postorbital. Studies of taxonomic affinity are still underway, although the taxon does appear to be a new species but not in the same clade as the Wahweap hadrosaurine *Acristavus.* In addition to a set of possible autapomorphies, the taxon is likely diagnosable through a unique suite of characters involving at minimum the jugal, pubis, and caudal vertebrae. As such, it seems that the pubis is diagnosable enough to support the identification of the juvenile recovered from Jim's Hadrosaur Site to the same taxon as found at this locality. The site is extremely significant in that it has yielded the most complete dinosaur specimen known from the Wahweap Formation.

Other significant hadrosaur materials recovered from the MM include the following: (1) an isolated juvenile jugal diagnostic of brachylophosaurin hadrosaurines (UMNH VP 16695; Fig. 19.3; Gates et al., 2011); (2) a large partial pubis and two femora; (3) an associated hadrosaur scapula, proximal humerus, and dentary; and (4) a partial skull representing a new taxon of hadrosaurid dinosaur (UMNH VP 16607; Gates et al., 2011).

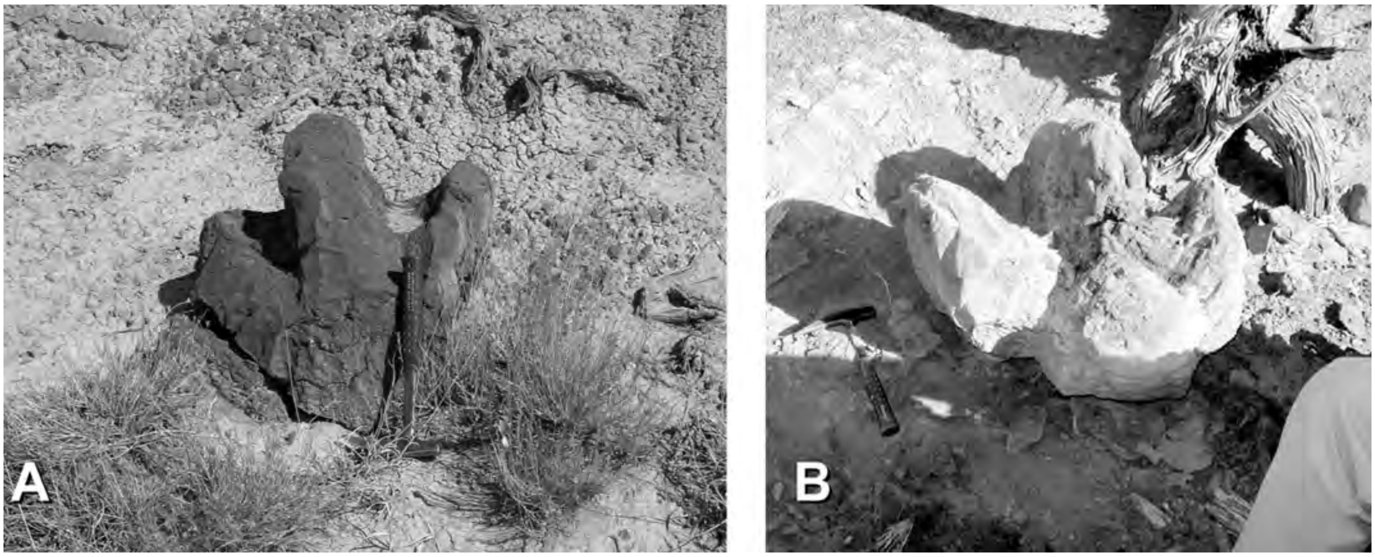
Currently, the most diagnostic hadrosaurid specimen discovered from the Wahweap Formation is the partial skull of a hadrosaurine (UMNH VP 16607) that pertains to a new genus also found in Montana (Gates et al., 2011). Dr. Riley Nelson (Brigham Young University) discovered the specimen in a massive sandstone at the top of the MM, just north of Right

19.4. Right maxillae (A) UMNH VP 9548 recovered from the Upper Sandstone Member of the Wahweap Formation, currently attributed to cf. *Brachylophosaurus* and (B) MOR 1071-8-13-92-559, *Brachylophosaurus canadensis,* shown in lateral view. Scale bar = 5 cm.

Hand Collett Canyon. The skull consists of a complete braincase and mostly complete posterior skull roof and lacrimals. UMNH VP 16607 clearly belongs to a clade of hadrosaurines that include *Brachylophosaurus* and *Maiasaura* to the exclusion of all other known hadrosaurids (interbasipterygoid ridge descends to level of ventral basipterygoid processes of basisphenoid; alar process of basisphenoid large and highly angled; Gates et al., 2011). A marked difference between *Acristavus gagslarsoni* and the former two taxa is the overall robustness of the skull elements. For instance, the lacrimal of UMNH VP 16607 is almost twice as broad posteriorly as a *Brachylophosaurus* lacrimal (MOR 1071 7-10-98-171) of comparative external size. Another interesting feature is that it possesses orbital rugosity in similar patterns to that seen on the Moreno Hill ornithopod (MSMP-4166; McDonald, Wolf, and Kirkland, 2010).

The stratigraphically highest bonebed in the Wahweap Formation occurs near the base of the UM in the area of the monument known as The Gut. This site yielded several postcranial elements from at least two individuals entombed within a silty mudstone; representative elements include a tibia, two ilia, a partial humerus, and ribs.

Another significant specimen, discovered within a sandstone unit of the UM on Death Ridge, includes partial limb bones and an isolated partial maxilla (UMNH VP 9548; Fig. 19.4) tentatively identified as cf. *Brachylophosaurus.* More material is required to verify the generic assignment. The maxilla more closely matches the morphology of *Brachylophosaurus* than of *Maiasaura*, *Acristavus*, or the taxon *Gryposaurus* commonly found in the overlying Kaiparowits Formation. This assessment is based on the more gracile appearance of the maxilla compared to the other taxa, the presence of a well-developed shelf on the medial side of the dorsal process (smaller shelf in *Maiasaura* and no shelf in *Acristavus*; Gates et al., 2011), long low jugal articular surface differing from *Gryposaurus* which possesses a more curved articulation surface that projects dorsally, and an anterodorsal process that appears to be as broad as seen on



19.5. Ornithopod footprints from the (A) Wahweap Formation and (B) Kaiparowits Formation.

Brachylophosaurus, but unfortunately is broken in UMNH VP 9548).

In addition to the body fossils discussed above, we have discovered a number of dinosaur tracksites in the Wahweap Formation (Fig. 19.5A). These tracksites consist primarily of natural casts associated with thin sandstone units most likely representing crevasse splays. The majority of these are large tridactyl tracks attributable to hadrosaurs. These tracks have been found in both the LM and MM, and are relatively abundant in the transition from the LM to the MM in the Wesses Cove and Wesses Canyon vicinity. We have noted a similar mode of track preservation in the Kaiparowits Formation. A more detailed examination and documentation of these tracksites is currently underway. Together, all of the above-mentioned specimens are providing a substantial foundation for the study of hadrosaurs within the Wahweap Formation, and the middle portion of the Campanian stage as a whole.

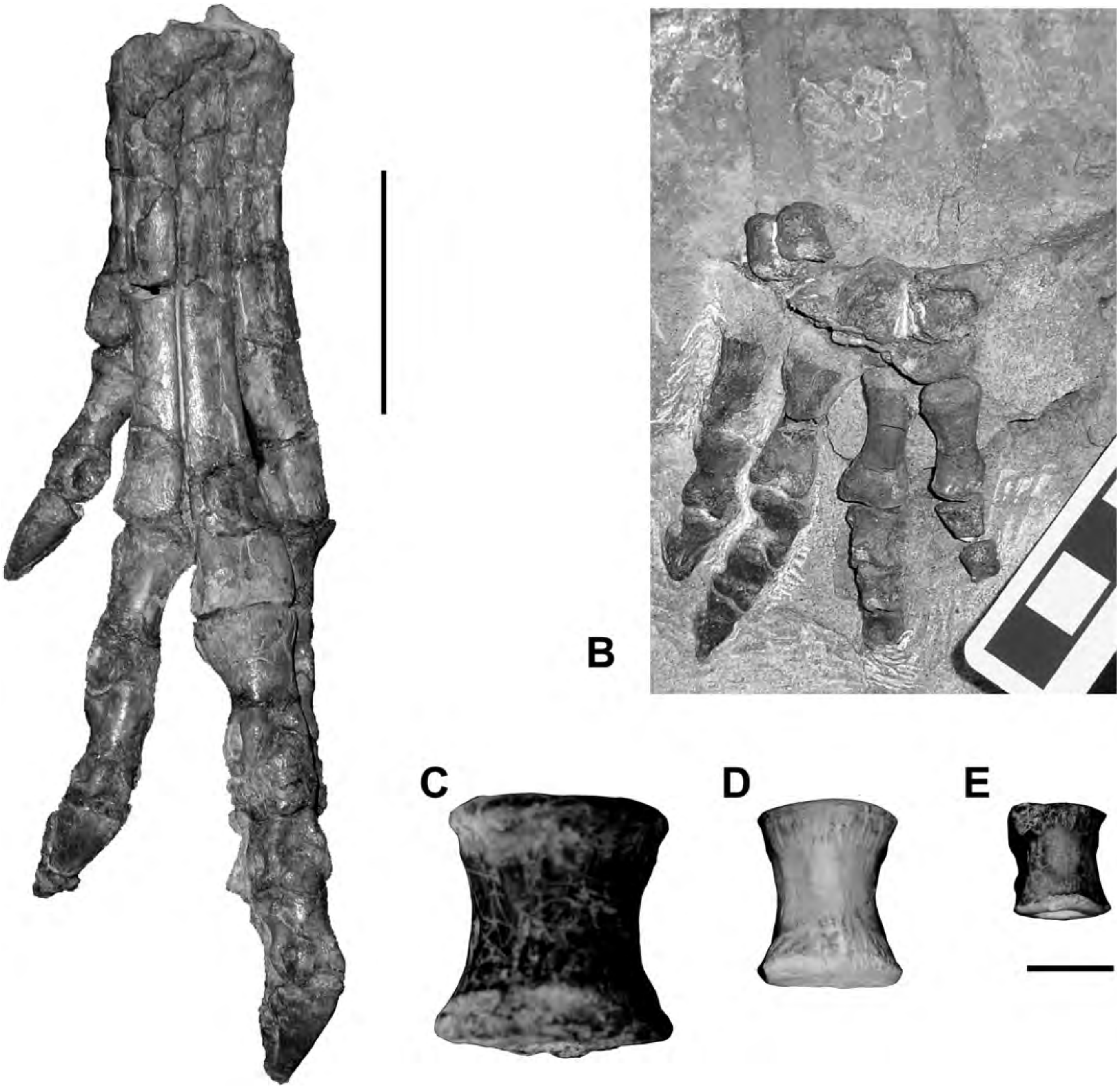
KAIPAROWITS FORMATION

Three informal units (lower, middle, and upper) subdivide the Kaiparowits Formation based on sandstone to mudstone ratios (Roberts, 2007). The vast majority of ornithopod specimens come from the lower and middle units, the former unit being composed mostly of sandstone and the latter being mudstone dominated. Most of the articulated ornithopod specimens collected to date have been recovered from fluvial sandstone bodies within the lower and middle units. Only a couple of basal ornithopods and a single hadrosaur have been recovered articulated from finer grained sediments, where disarticulation is much more common.

Basal Ornithopods

Over the past 10 years, at least eight basal ornithopod specimens (i.e., "hypsilophodontids") were recovered from the Kaiparowits Formation. Prior to these discoveries, basal ornithopods had not been reported from the formation. Nearly all of these specimens consist of concentrations of disarticulated elements, though two specimens from the lower unit preserve articulated portions of the skeleton (UMNH VP 12677, 16281). The basal ornithopod material from the Kaiparowits Formation displays a large range of size variation that is here interpreted as ontogenetic variation (Fig. 19.6). This interpretation is supported by the absence of fusion between the neural arches and the centra of isolated cervical, dorsal, and sacral vertebrae in all but the largest specimens and the lack of fusion between adjacent sacral vertebrae in smaller specimens (e.g., UMNH VP 12665 and 19470), features previously shown to be useful for assessing ontogenetic maturity in other archosaurian taxa (Brochu, 1996; Irmis, 2007).

Two morphologically and taxonomically informative specimens were recovered from the Lower unit of the Kaiparowits Formation. The first consists of articulated left and right feet from a single individual preserved in a sandy siltstone (UMNH VP 16281; Fig. 19.6A). The morphology of the pes is typical of most basal ornithopod taxa, except as noted. The medial distal tarsal is L shaped in proximal view, with a short process extending over the posterior portion of the dorsal surface of metatarsal II. The metatarsals are thin and elongate, with metatarsal III being more than twice as long as the combined transverse width of the proximal ends of metatarsals II through IV as in *Orodromeus*, *Oryctodromeus*,



19.6. Examples of basal ornithopod specimens from the lower unit of the Kaiparowits Formation. (A) Articulated right foot of UMNH VP 16281; (B) articulated left hand of UMNH VP 12677; (C–E) vertebrae showing variation in size of basal ornithopod specimens recovered. Scale bar = 5 cm in (A) and 1 cm in (C–E).

and *Zephyrosaurus*. This morphology differs from that of *Parksosaurus* and *Thescelosaurus*, where these three metatarsals are relatively shorter and more robust. Metatarsal V is a short, thin plate of bone appressed to the posterior surface of the lateral distal tarsal proximally and then curves ventromedially against the posterior surface of metatarsal IV. In *Orodromeus* metatarsal V is also a flattened plate of bone, but in *Thescelosaurus* it is more robust, though still greatly shortened. Digit III of the right pes of the Kaiparowits basal ornithopod measures 211 mm, which is ~60% larger than that of the contemporaneous *Orodromeus* (based on MOR 530; Scheetz, 1999), but ~25% smaller than that of the immature holotype of *Thescelosaurus* (USNM 7757; Gilmore, 1913). A second specimen recovered from the lower unit (UMNH VP 12677) consists of a mostly complete, well-preserved, articulated hand exposed in plantar view (Fig. 19.6B) and associated disarticulated vertebrae and limb fragments from a channel sandstone. The carpus is composed of five carpals as in *Thescelosaurus*, though their arrangement differs. Digits I through IV are present, but digit V is not preserved. The manual phalangeal formula is 2–3–(4?)–2–?, with the reduction from three to two phalanges in digit IV being autapomorphic among basal ornithopod taxa.

The most taxonomically informative specimen yet recovered was collected from an overbank mudstone within the middle unit (UMNH VP 19470; Fig. 19.7). This specimen consists of a partial disarticulated skull (including a partial jugal, frontal, dentary, pterygoid, and exoccipital–opisthotics) and fragmentary postcranial material. The jugal displays a prominent posterolaterally projecting boss that is present in *Orodromeus* and *Zephyrosaurus* (Varricchio, Martin, and Katsura, 2007). The morphology of the frontal more closely resembles *Orodromeus* than *Zephyrosaurus*, especially in that the articulation surface for the postorbital faces dorsolaterally rather than only laterally. The dorsal ramus of the jugal bears a dorsally oriented socket that received the ventral ramus of the postorbital. This condition is unknown in any described taxon, though in *Orodromeus* the dorsal ramus of the jugal bears a dorsoventrally oriented groove that received the postorbital. The cranial elements that are preserved in UMNH VP 19470 are slightly smaller than those preserved with the immature holotype of *Orodromeus* (MOR 294; Scheetz, 1999), and the presence of disarticulated dorsal vertebral centra that are unfused to their respective neural arches suggests that UMNH VP 19470 likely represents an immature individual (Brochu, 1996; Irmis, 2007).

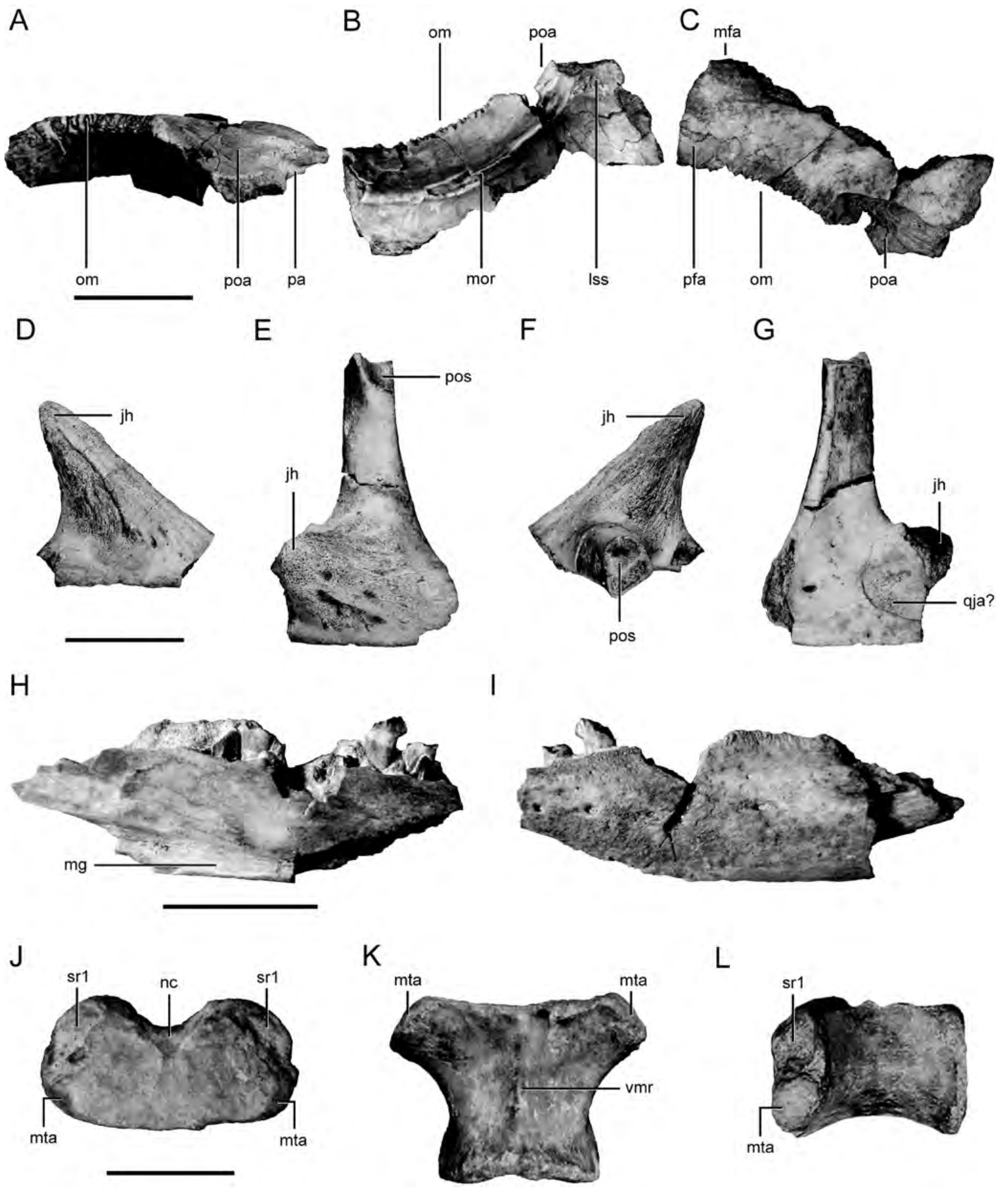
The most productive basal ornithopod site within the Kaiparowits Formation is located within a crevasse splay deposit in the Middle unit. This site has produced a substantial number of disarticulated elements representing at least three ontogenetically immature individuals of various sizes (UMNH VP 12665). This material consists largely of disarticulated vertebral centra and fragmentary fore and hind limb elements, though fragments of two dentaries and a partial maxilla were also recovered. Among the more important elements recovered is an isolated sacral centrum that displays prominent articulation facets on the anterolateral margin that directly supported the medial protuberance of the pubis (sensu Scheetz, 1999). This feature is apomorphic for a clade containing *Orodromeus*, *Oryctodromeus*, and *Zephyrosaurus* (Varricchio, Martin, and Katsura, 2007). Additionally, a fragmentary left coracoid collected from this site possesses an oblong foramen in the ventral margin of the sternal hook just anterior to the glenoid fossa, a characteristic unknown in any previously described basal ornithopod taxon.

Preliminary examination of all basal ornithopod specimens from the Kaiparowits Formation indicates the presence of at least one previously undescribed taxon. This conclusion is based on the recognition of three autapomorphic traits from three different specimens. However, the fragmentary nature of all known specimens makes it difficult to accurately resolve the taxonomic diversity these specimens represent. Thus far, only UMNH VP 12665 and 19470 from the middle unit of the Kaiparowits Formation can be confidently referred to a single taxon on the basis of shared character evidence (Boyd and Gates, unpubl. data). The combined presence of a prominent jugal boss in UMNH VP 19470 and the direct support of the pubis by the sacral centra demonstrated by UMNH VP 12665 suggest a close relationship between this new taxon and the North American basal ornithopod taxa *Orodromeus* and *Zephyrosaurus*.

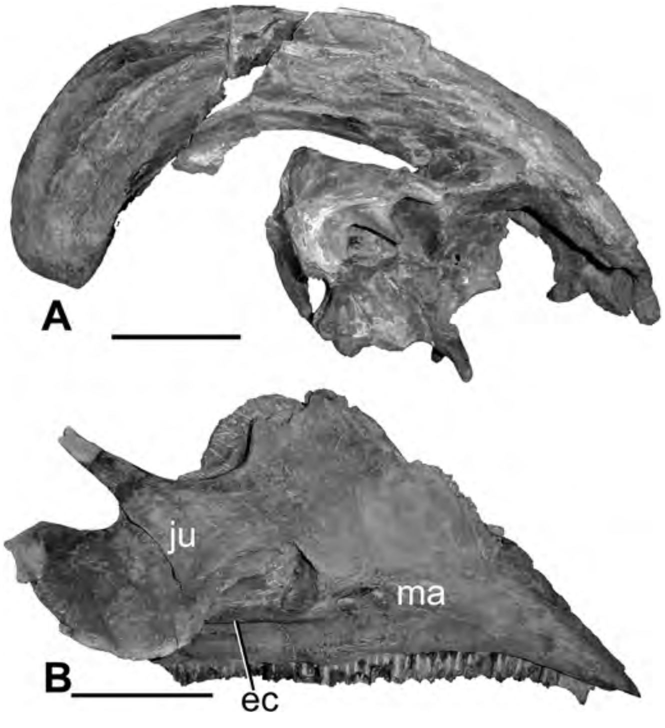
Hadrosauridae

Both lambeosaurine and hadrosaurine remains have been recovered from the Kaiparowits Formation. The lambeosaurine *Parasaurolophus* is the most distinctive hadrosaur from the formation, possessing a large, curved, hollow narial tube composed almost entirely of fused premaxillae (Fig. 19.8A). *Parasaurolophus* was the first dinosaur to be identified from the Kaiparowits Formation, based upon a highly eroded, partial skull (BYU 2467; Weishampel and Jensen, 1979). Sullivan and Williamson (1999) identified these materials and another, more complete specimen (UCMP 143270; Fig. 19.8A) as pertaining to *P. cyrtocristatus*, a taxon otherwise known only from the Fruitland Formation of New Mexico.

Recent work conducted by the KBP has yielded additional *Parasaurolophus* materials from this formation. Currently, the total sample consists of seven isolated partial skulls (BYU 2467, UCMP 143270, UMNH VP 16394, 16666, 16689 and two unnumbered unprepared UMNH specimens), a partial skeleton consisting of mostly the pelvic region (UMNH VP 19471), and fragmentary associated elements within a multitaxic bonebed, all collected from or closely associated with sandstone deposits in the middle unit of the Kaiparowits Formation. One of the recently collected partial skulls (UMNH VP 16666.1; Fig. 19.8B) includes a maxilla, jugal, palatine, ectopterygoid, and quadrate–elements unknown for any *P. cyrtocristatus* specimen or for any other *Parasaurolophus* specimen collected from the Kaiparowits. The best preserved *Parasaurolophus* specimen from the Kaiparowits Formation (UCMP 143270) differs from the holotype specimen of *P. cyrtocristatus* (FMNH P27393; Fruitland Formation, New Mexico) in the curvature of the snout and the degree of descent of the posterior portion of the crest. However, FMNH P27393 is much larger than UCMP 143270 and the observed differences may represent ontogenetic variation. In fact, all of the recovered Kaiparowits *Parasaurolophus* skull material, except UMNH VP 16666.1 and one unprepared skull, is smaller than the type specimen of *P. cyrtocristatus*. Whether or not this seemingly consistent size discrepancy is taxonomically important still remains a question. The excellently preserved,



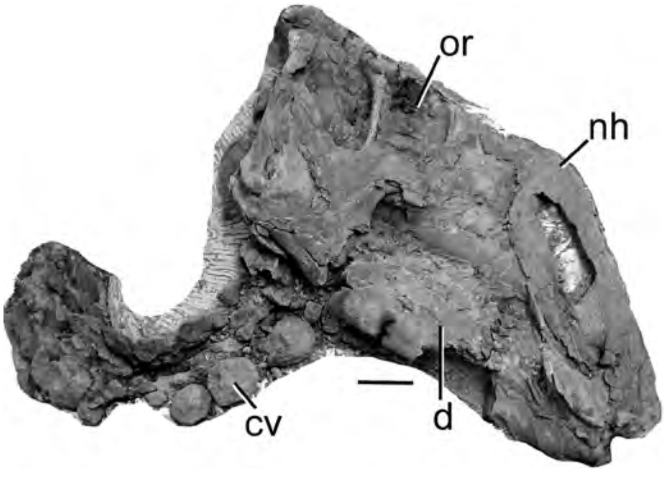
19.7. Examples of basal ornithopod material from the middle unit of the Kaiparowits Formation. (A–C) Left frontal from UMNH VP 19470 shown in lateral, ventral, and dorsal views, respectively. (D–G) Right jugal from UMNH VP 19470 shown in ventral, lateral, dorsal, and medial views, respectively. (H, I) Left dentary from UMNH VP 19470 shown in medial and lateral views, respectively. (J–L) First true sacral centrum from the same locality as UMNH VP 12665 (given its own specimen number: UMNH VP 21095) shown in anterior, ventral, and lateral views, respectively. All Scale bars = 1 cm and apply to its corresponding row of figures. jh, jugal horn; lss, laterosphenoid socket; mfa, medial frontal articulation; mg, Meckelian groove; mor, medial orbital ridge; mta, articulation for the medial tubercle of the pubis; nc, neural canal; om, orbital margin; pa, parietal articulation; pfa, prefrontal articulation; poa, postorbital articulation; pos, postorbital socket; qja, quadratojugal articulation; sr, sacral rib; vmr, ventral midline ridge.



19.8. Examples of *Parasaurolophus* specimens recovered from the Kaiparowits Formation. (A) Partial articulated *Parasaurolophus* skull UCMP 143270 shown in lateral view; (B) articulated *Parasaurolophus* maxillary complex shown in lateral view. et, ectopterygoid; ju, jugal; ma, maxilla. Scale bar = 10 cm.

uncrushed nature of the UCMP 143270 specimen reveals details of crest morphology including premaxillary and nasal sutural contacts unknown or controversially interpreted in all other specimens of *Parasaurolophus*. The Kaiparowits material will provide important new information that will contribute significantly to understanding the morphology and relationships of this iconic genus. All of these materials are currently under study in order to assess whether or not the Kaiparowits taxon corresponds to *P. cyrtocristatus*.

An articulated tail, partial pelvis, and left leg (MNA V8369) from a site in the lower unit was tentatively identified as a lambeosaurine hadrosaur by Titus, Gillette, and Albright (2001). However, more recent analysis of this specimen demonstrated that it is a hadrosaurine of unknown generic affinity, currently leaving lambeosaurines undocumented in the lower portion of the Kaiparowits Formation.

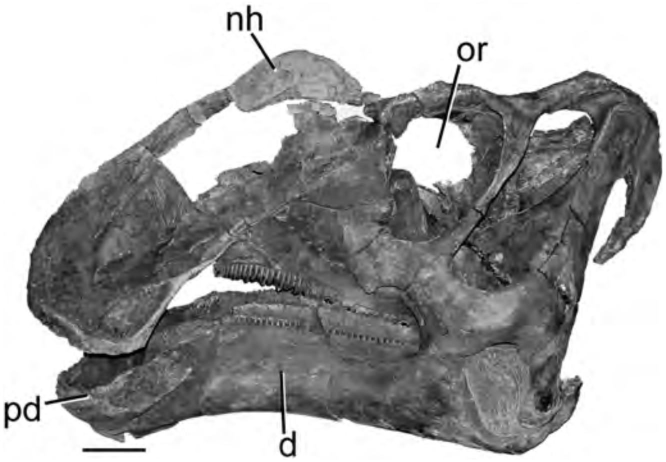


19.9. Lateral view of articulated skull of *Gryposaurus* sp. (UMNH VP 16667) recovered from of the lower unit of the Kaiparowits Formation. cv, cervical vertebrae; d, dentary; nh, nasal hump; or, orbit. Scale bar = 10 cm.

The most common hadrosaur fossils discovered in the Kaiparowits Formation are of the hadrosaurine genus *Gryposaurus*, the remains of which – including several associated partial skulls (UMNH VP 12265, 13831, 13970, 16669, 18568, 20181 and RAM 6797), three of which are associated with partial postcranial skeletons (UMNH VP 12265, 18568, and 20181) – have been collected at eight localities that range from near the base of the Kaiparowits through the top of the Middle unit. Significantly, those specimens found in the lower unit, near the base of the formation, are morphologically distinct from those found stratigraphically higher in the formation, indicating the presence of two successive species of *Gryposaurus*, and thus intergeneric faunal turnover.

The stratigraphically lowest occurring taxon, here termed *Gryposaurus* sp., is represented by several specimens, including a virtually complete articulated skull (UMNH VP 18568; Fig. 19.9) discovered by one of us (AT) within a massive sandstone near Wahweap Creek. The skull of this specimen exhibits the distinctive nasal "hump" of *Gryposaurus* but is almost 1 m long, exceeding that of any other previously described specimens attributable to this genus. Another more fragmentary skull from the Kaiparowits Formation (UMNH VP 16668), also attributable to *Gryposaurus* sp., is approximately 20% larger than UMNH VP 18568, suggesting that this taxon greatly exceeded the body size of more northern congeners. The proportions of the temporal region of the skull more closely resemble *Gryposaurus notabilis* from the Dinosaur Park Formation of Alberta, in contrast to the reduced size of the infratemporal fenestra in *G. monumentensis* (Gates and Sampson, 2007). In fact, there is no apparent morphological distinction aside from size that would infer the Kaiparowits *Gryposaurus* sp. to be classified in a different species from *Gryposaurus notabilis*. However, more detailed anatomical analysis and comparisons are required to determine if *Gryposaurus* sp. from the Kaiparowits is conspecific with the northern taxon, or if it represents a new, closely related species.

The second *Gryposaurus* species now recognized in the Kaiparowits Formation, *Gryposaurus monumentensis* (Gates and Sampson, 2007), occurs higher in section and is also represented by multiple specimens, including the mostly complete type skull (RAM 6797; Fig. 19.10) found in a muddy sand



19.10. Lateral view of articulated skull of *Gryposaurus monumentensis* (RAM 6797). d, dentary; nh, nasal hump; or, orbital rim; pd, predentary. Scale bar = 10 cm.

point bar deposit. *Gryposaurus monumentensis* possesses a number of unique characteristics, mostly related to the more robust nature of the skull and lower jaws (Gates and Sampson, 2007). A partial subadult skull attributed to this taxon (UMNH VP 13970) demonstrates that the extremely robust dentary present in adults developed prior to the onset of adult size. One of the more interesting features of *G. monumentensis* is the predentary, which possesses large, clover-shaped processes along the oral margin that are much more conspicuous than similar structures seen on the predentaries of other hadrosaurs (e.g., *Gryposaurus latidens* MOR 553s). Although the precise function of these structures is uncertain, other hadrosaur taxa show evidence of a keratinous beak adhered to the snout via small processes on the predentary oral margin (Morris, 1970), and it is perhaps likely that these features had a similar role.

Modifications to chewing appear to be the driving force behind the evolution of *G. monumentensis* especially when one considers the bony correlates of a large keratinous beak, robustness of the masticating skull elements, and the relative anteroposterior shortening of the posterior skull region (Gates and Sampson, 2007). More specifically, the infratemporal fenestra does not display the gaping morphology seen in all other species of *Gryposaurus*, but instead has a much narrower fenestra. This implies that the posterior region of the skull is shorter in this taxon. An independent confirmation of posterior shortening is the observation that the fenestra present between the surangular, jugal, and quadrate is round, nearly circular, in all *Gryposaurus* taxa except *G. monumentensis*, which displays a distinctly oval fenestra (Fig. 19.10). Overall shortening of the posterior skull would shorten the moment arm of the chewing lever and allow muscles of equivalent size as other *Gryposaurus* taxa apply more force to processing plant matter.

Recently, a crew from the Alf Museum found another important specimen higher in stratigraphic section than the *G. monumentensis* type specimen. RAM 12065 consists of a partial skull roof and partial braincase. According to A. Farke (unpubl. data, pers. comm. 2010), RAM 12065 is smaller than and possesses a slightly different morphology from the *G. monumentensis* type specimen such as a planar skull roof instead of the dorsally projecting posterior process of the postorbital seen in the latter taxon and *G. notabilis* (Herrero and Farke, 2010).

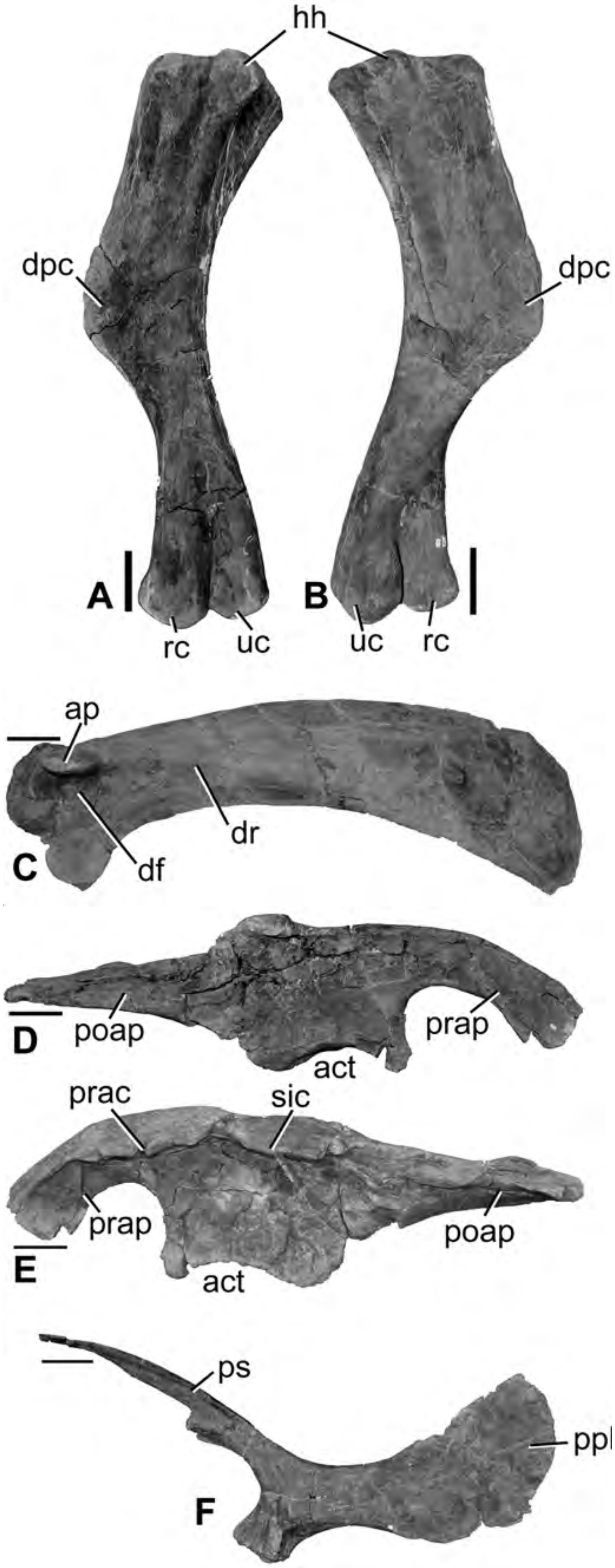
One of the most complete skeletons of *Gryposaurus monumentensis* (also one the most complete adult hadrosaur skeletons discovered to date from the Monument) is UMNH VP 12265 (Fig. 19.11), an exceptionally preserved specimen recovered from the middle unit in an expansive area of outcrop known as The Blues. Encased mostly in well-indurated sandstone, the associated and partially articulated skeleton includes a portion of the skull and lower jaws (maxillae, jugal, quadrate, dentary), most of the dorsal, sacral, and caudal vertebral series, fragmentary ribs, scapulae, coracoid, humerus, and the entire pelvis.

Gates and Sampson (2007) attributed UMNH VP 12265 to *G. monumentensis*, which is the only postcranial skeleton known for the species. The original description was based on the complete skull RAM 6797 and the authors neglected to describe the postcranial material preserved in UMNH VP 12265. Presented below is a short description of this partial skeleton.

The partial skeleton UMNH VP 12265 preserves most of the dorsal, sacral, and caudal vertebral series, a number of ribs, right scapula, right humerus, right radius and ulna, and a complete pelvis. This description focuses on the phylogenetically informative appendicular elements: humerus, scapula, ilium, and pubis (Fig. 19.11).

Humerus The UMNH VP 12265 humerus (Fig. 19.11A, B) is typical for hadrosaurine hadrosaurids with a deltopectoral crest that extends to nearly midshaft and a more gracile morphology compared to most lambeosaurines. The ulnar condyle is larger than the radial, which is an usual feature and has been speculated as being age related (Brett-Surman and Wagner, 2007). Among hadrosaurines, UMNH VP 12265 most closely resembles *Gryposaurus notabilis* (ROM 764, formerly *G. incurvimanus*) although the former is more robust. Increased robusticity is a characteristic of most skeletal elements associated with *G. monumentensis*, including the skull. As such, the humerus does not resemble the gracile elements seen in *Brachylophosaurus canadensis* (Prieto-Marquez, 2007) or even *Edmontosaurus* spp.

19.11. Postcranial elements of *Gryposaurus monumentensis* (UMNH VP 12265). (A, B) Humerus in posterior and anterior views; (C), scapula in lateral view; (D, E) ilium in medial and lateral views; (F) pubis. act, acetabulum; ap, acromion process; df, deltoid fossa; dpc, deltopectoral crest; dr, deltoid ridge; hh, humeral head; poap, postacetabular process; ppb, prepubic blade; prap, preacetabular process; ps, pubic shaft; rc, radial condyle; uc, ulnar condyle. Scale bar = 10 cm.



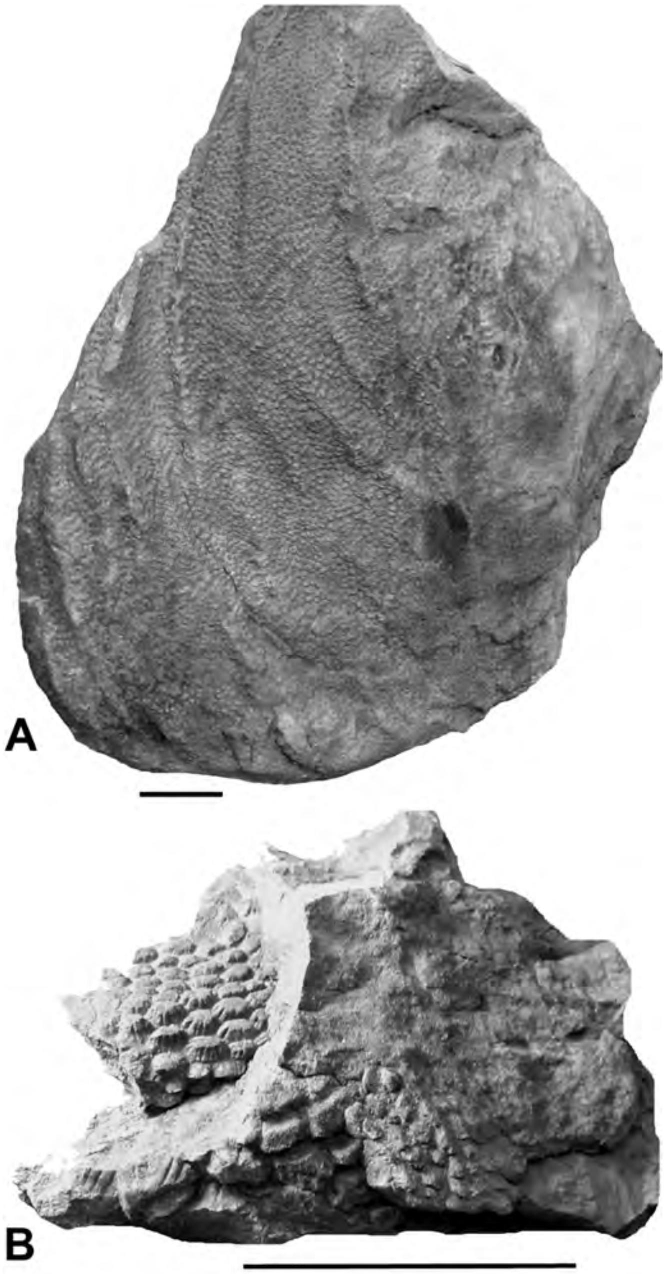
Scapula In general aspect, the shape of the scapula matches the long, narrow profile of hadrosaurines as opposed to the shorter, wider profile of lambeosaurines (Brett-Surman and Wagner, 2007). The distal end of the scapular blade is eroded so a ratio of length to width is unavailable. Proximally, as in other hadrosaurids, a convex deltoid fossa occupies the center of the proximal region (Fig. 19.11C). The acromion process protrudes laterally from the scapula. The deltoid ridge can be observed just dorsal to the acromion process extending posteroventrally to the ventral margin of the scapula, midway through its length. Angulation between the proximal scapula and the blade appears to be greater than that shown for *Brachylophosaurus* by Prieto-Marquez (2007); in other words, there is more curvature in the *Brachylophosaurus* scapula compared to *G. monumentensis.* The straighter scapula in *Gryposaurus* is confirmed by the nearly identical profile of the element preserved on *Gryposaurus notabilis* (ROM 764; formerly *G. incurvimanus*; see Prieto-Marquez, 2010).

Ilium The ilium (Fig. 19.11D, E) is the most distinctive skeletal element associated with *G. monumentensis* and contains features that make this element diagnostic of the species. The preacetabular process deflects ventrally as is seen in all hadrosaurid ilia, but the process does not taper anteriorly; instead, it increases in dorsoventral height. This feature is not known in other hadrosaurids. Additionally, the process is relatively shorter than most other taxa. The dorsal margin of the main iliac plate is flat. Other taxa have varying degrees of swelling of the pre- and postacetabular processes, yet *G. monumentensis* apparently displays none. A strongly overhanging ridge marks the dorsal boundary of the medial preacetabular process. The ridge is thick and extensive, continuing to the proximal margin of the postacetabular process. The supraacetabular crest is positioned dorsal to the iliac peduncle, and as preserved, it does not fold ventrally, as seen in ROM 764 or most other hadrosaurid specimens (Prieto-Marquez, 2010). Finally, the postacetabular process is distinctly triangular in lateral view, much more so than the squared to rounded posterior end seen in other hadrosaurids. This termination is different from that of *Gryposaurus notabilis* (ROM 764). As currently documented with known *G. monumentensis* ilia, characteristics that may be diagnostic to this species include distally expanded preacetabular process, nearly horizontal supraacetabular process, and triangular postacetabular process.

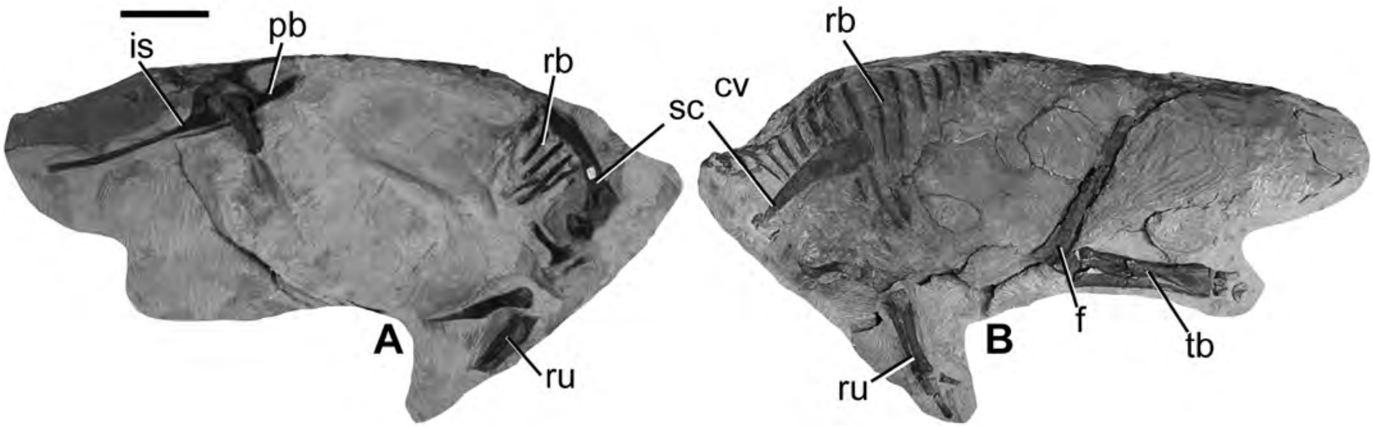
Pubis Pubic morphology varies substantially between hadrosaurid species, even between genera. This is true of *G. monumentensis* and *G. notabilis*, where the former has a ventrally deflected prepubic blade with a rounded dorsal margin (Fig. 19.11F) and the latter has a notched neck and square-like prepubic blade with rounded corners. However, it should be noted that an unknown portion of the dorsal prepubic blade of UMNH VP 12265 had eroded prior to excavation. The morphology of the prepubic blade is most similar to *Brachylophosaurus* (MOR 794).

Remarkably, UMNH VP 12265 also preserves more than 2.5 m^2 of fossilized skin impressions. Nonmineralized vertebrate tissues tend to be rare in the fossil record, because they are a rich source of nutrients for predators, scavengers, and microbes (Lund, 2006). Yet, more than 30 vertebrate localities preserving soft-tissue patterns have been recorded in the Kaiparowits Formation over the past six years, and all integument impressions are preserved within fine-to-coarse-grained, fluvial indurated sandstone. The majority of these localities preserve ornithopod, particularly hadrosaurid, skin impressions in both negative and positive relief. Impressions are known from nearly every portion of the body, although the best-preserved examples to date occur in association with the head, neck, and tail (Fig. 19.12). Tubercle density, shape, and size appear to vary along the body. Smaller, unornamented, circular tubercles cluster tightly around the head, whereas larger, ovoid, wider-spaced tubercles dominate along the back, tail, and limbs, many of the latter are ornamented with radiating ridges and grooves that converge at their apices. Tubercle size ranges from small (<3 mm) to large (>10 mm). The only exception is UMNH VP 12265, which preserves large, butterfly-shaped scales (~80 mm wide) and similarly sized ovoid scales found in direct association with each of the distal neural spines along the back and tail; a similar conformation has been described for a hadrosaur from the Hell Creek Formation (probably *Edmontosaurus*) (Horner, 1984). Overall, the hadrosaurid skin impressions known from Kaiparowits Formation compare favorably to others found in the Dinosaur Park Formation of Alberta, Canada, the Two Medicine and Judith River formations of Montana, and the Ringbone Formation of New Mexico (Lambe, 1914; Parks, 1920; Horner, 1984; Anderson et al., 1998; Negro and Prieto-Marquez, 2001; Evans and Reisz, 2007).

Finally, the most complete hadrosaurid specimen collected to date from Grand Staircase–Escalante National Monument (UMNH VP 16677; Fig. 19.13) consists of a juvenile specimen entombed in highly cemented sandstone. Other than the skull, lower jaws, hands, feet, and distal tail, the skeleton of this specimen appears to be complete. It is approximately 88 cm long and fully articulated except for the anteriormost cervical vertebrae that are just slightly separated from the remainder of the neck. On the basis of size-to-age comparisons by Horner, Ricqles, and Padian (2000), this individual is estimated to be approximately 3 months old, assuming that its growth rate was similar to that of *Maiasaura*. Definitive taxonomic identification is currently restricted to Hadrosaurinae, although given that only one genus of hadrosaurine has been discovered thus far from the Kaiparowits Formation, it seems



19.12. Specimens of hadrosaur skin impressions recovered from the Kaiparowits Formation. (A) Sandstone block containing large area of skin impression from near the neck region of UMNH VP 16667; (B) Close-up of skin impression, showing large tubercles with radiating ridges. Scale bar = 10 cm.



19.13. Articulated juvenile hadrosaur skeleton (UMNH VP 16677) found in the middle unit of the Kaiparowits Formation. cv, cervical vertebrae; f, femur; is, ischium; pb, pubis; rb, rib; ru, radius and ulna; sc, scapula; tb, tibia. Scale bar = 10 cm.

reasonable to suggest that UMNH VP 16677 is likely a species of *Gryposaurus*.

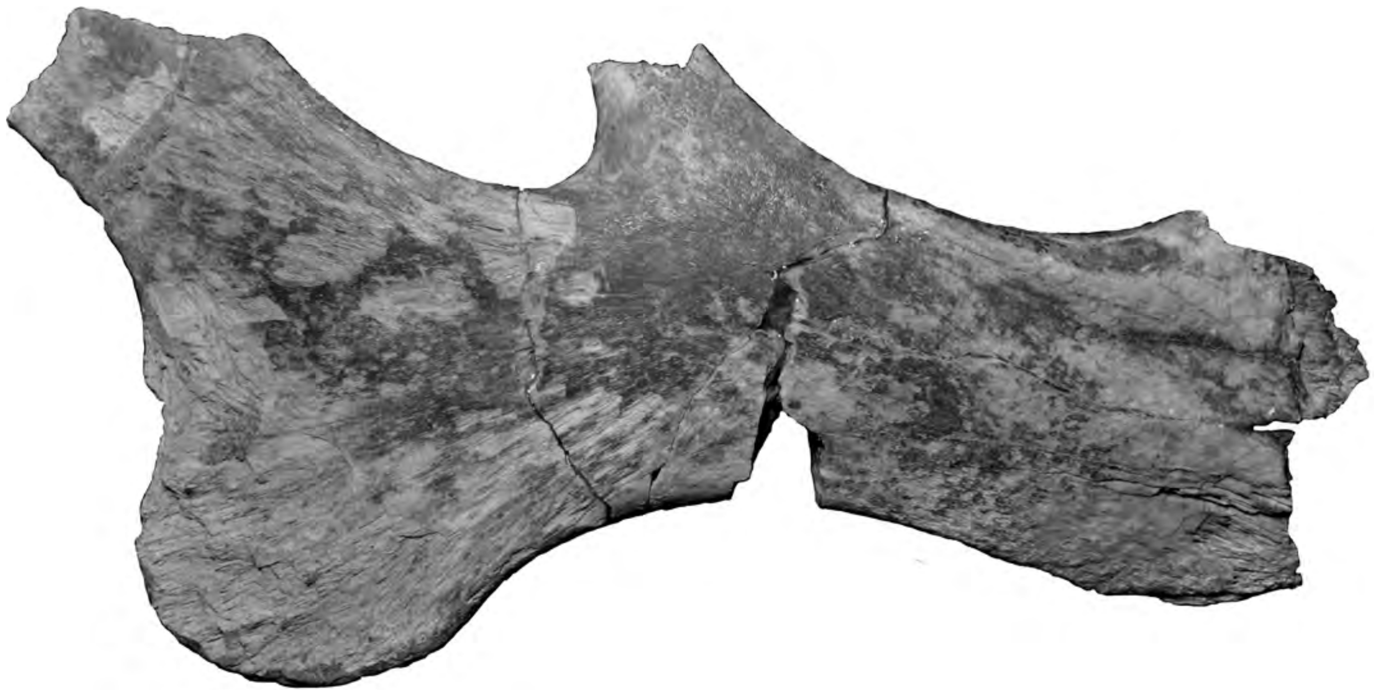
Ornithopod fossil foot traces are currently restricted to hadrosaurids. To date only isolated traces have been discovered, composed of sandstone and achieving sizes of 1 m in maximum width (Fig. 19.5). There has been no study of the morphology of the Kaiparowits Formation ornithopod tracks but some tracks such as that seen in Fig. 19.5 display asymmetry in pedal form.

IMPLICATIONS OF GRAND STAIRCASE–ESCALANTE NATIONAL MONUMENT FOSSIL RECORD

One of the greatest challenges within paleontology is discovering the nature of transition from one species or clade to a succeeding species or clade in terrestrial settings. More specific to the present ornithopod dinosaur survey is the transition from slightly more basal iguanodontians to those ornithopod taxa strictly within Hadrosauridae (as defined by Forster, 1997). Questions to be asked include: when did hadrosaurids arise in North America?; did hadrosaurids coexist with more basal iguanodontians in southern Utah?; if so, how long did they coexist before nonhadrosaurid iguanodontians became extinct?

The virtually continuous sequence of Upper Cretaceous sediments comprising the Straight Cliffs, Wahweap, and Kaiparowits formations provides an unparalleled opportunity to study the transitional zone between North American hadrosaurids and nonhadrosaurid iguanodontians and then the turnover of hadrosaurid taxa through the Campanian. On the basis of fossils collected thus far, it appears that nonhadrosaurid iguanodontians dominated the Smoky Hollow Member of the Straight Cliffs Formation, but forms that closely resemble hadrosaurids are preserved in the overlying John Henry Member. This assertion is based strictly on the apparently narrow dentary of the Coniacian specimens, and therefore the evolutionary interpretation could be changed once better material has been acquired. As more attention is devoted to the Straight Cliffs Formation, the fossil record of ornithopods will undoubtedly increase and, consequently, the understanding of hadrosaurid first occurrences in southern Utah. The diversity of morphologies among dentaries collected from the John Henry Member demonstrates multiple taxa living in the region. Yet the stratigraphic relationship of these specimens is not established and further discussion of the transition toward a hadrosaurid dominated dinosaurian fauna must await more data collection.

Nevertheless, a relatively comprehensive picture of hadrosaur diversity is developing for the upper Wahweap and Kaiparowits formations. The growing picture appears to be one of relatively rapid faunal turnover and replacement. Such resolved evolutionary patterns are relatively rare, and approximately coeval examples of within-lineage turnover are otherwise documented only from geologic formations in the northern portion of the Western Interior Basin (e.g., Dinosaur Park Formation, Two Medicine Formation; Horner, Varricchio, and Goodwin, 1992; Ryan and Evans, 2005). Recognition of this pattern in the Campanian of Utah is the direct result of the large number of hadrosaur specimens collected within Grand Staircase–Escalante National Monument. To date, dozens of highly significant hadrosaur localities have been identified within the monument, with some preserving multiple specimens of one species, exquisite examples of hadrosaurids preserving integument impressions and skeletal elements in articulation, as well as sites containing taxonomically informative material from stratigraphic areas that do not contain many known fossils across the continent, making these some of the most productive Campanian strata in North America for the recovery of ornithopod dinosaurs.



19.14. UMNH VP 16722 brachylophosaur-type hadrosaurine jugal found in the lower unit of the Kaiparowits Formation.

At present, the Wahweap and Kaiparowits formations preserve minimal evidence of faunal turnover within lambeosaurines. The new lambeosaurine taxon found in the Upper Sandstone Member of the Wahweap Formation is replaced by *Parasaurolophus* sp., which occurs in the Kaiparowits Formation. However, these two taxa are separated by a temporal gap of approximately 2–3 million years. More finely scaled faunal turnover can be documented for hadrosaurines as a result of better sampling in almost all of the subdivisions of the Wahweap and Kaiparowits. Beginning from a broader perspective, it is apparent that the "brachylophosaurs" are succeeded by the *Gryposaurus* clade. There are at least two "brachylophosaur" taxa in the Wahweap Formation and one other hadrosaurine taxon of unknown affinity. The Kaiparowits Formation has no substantial evidence of "brachylophosaur" hadrosaurs except one isolated jugal found near the base of the formation (UMNH VP 16722; Fig. 19.14). Nonetheless, this single element pushes the upper stratigraphic boundary of "brachylophosaur" hadrosaurines to younger than 76 million years, which is the latest known occurrence of this hadrosaurid clade. All other "brachylophosaurs" (*Acristavus*, *Maiasaura*, and *Brachylophosaurus*) are extinct elsewhere in the Western Interior Basin by around 76.5 million years ago (Horner et al., 2001; Gates et al., 2011).

Despite the three distinct hadrosaurines currently known from the Wahweap Formation, the exact stratigraphic distribution of these hadrosaurs is unknown and little can be said regarding turnover suffice to say that *Acristavus* may be replaced by cf. *Brachylophosaurus* over a course of 1–2 million years. More substantive evidence of faunal turnover is documented by the presence of two stratigraphically successive species of *Gryposaurus* within the Kaiparowits Formation. The large *Gryposaurus* sp. is currently only known from the lower unit of the Kaiparowits Formation whereas *G. monumentensis* is found in the middle unit. Exact timing of the interchange cannot be established at this time, as more specimens are needed to stratigraphically sandwich the turnover boundary, but the change likely took place over a course of a few hundred thousand years.

A series of recently obtained radiometric dates from Campanian-aged geologic formations within the Western Interior Basin (see Roberts, Deino, and Chan, 2005, for review) now permit time slice biogeographic comparisons. For example, the hadrosaurine *Acristavus* in the Wahweap Formation is approximately time correlative, with a specimen of the same species from the lower portion of the Two Medicine Formation of Montana and the cf. *Brachylophosaurus* sp. material found in the Upper Sandstone member of the Wahweap occurs at nearly the same time as *Brachylophosaurus canadensis* in the Judith River Formation of Montana.

Within the Kaiparowits Formation, two main time intervals are available for comparison, corresponding to the lower and middle units. The only hadrosaur genus in the lower unit is *Gryposaurus* sp. A radiometric date of 76.1 mya for the base of the formation indicates that this taxon is approximately coeval with *G. notabilis* from the lower Dinosaur Park Formation of Alberta, Canada (Ryan and Evans, 2005). Within the middle unit of the Kaiparowits Formation, *G. monumentensis* is probably contemporaneous with *Prosaurolophus maximus*, which has an extended stratigraphic range within the Dinosaur Park Formation and lower part of the marine Bearpaw Formation in Alberta, and the upper portion of the Two Medicine Formation in Montana (Horner, 1992; Gates and Evans, 2005; Ryan and Evans, 2005; Gates and Sampson, 2007; Prieto-Marquez, 2010).

The contemporaneous nature of the fossiliferous portion of the Kaiparowits and Dinosaur Park formations permits faunal comparisons over a large geographic transect in the Western Interior Basin. The Kaiparowits formation hadrosaurid fauna differs significantly from that of the contemporaneous Dinosaur Park Formation in that it is dominated by hadrosaurines. In this respect it is more typical of Late Cretaceous hadrosaur-dominated assemblages. The Dinosaur Park Formation is dominated by lambeosaurines, of which corythosaurian taxa are common and *Parasaurolophus*, although present, is rare (Ryan and Evans, 2005; Evans, Bavington, and Campione, 2009). Corythosaurian lambeosaurines, which are well documented in the series of Late Cretaceous assemblages of Alberta and Montana, are unknown from contemporaneous strata of Utah and New Mexico.

Also within the middle unit of the Kaiparowits Formation is *Parasaurolophus* sp., which is approximately contemporaneous with two northern lambeosaurines, *Hypacrosaurus stebingeri* in Montana and *Lambeosaurus lambei* in Alberta (Gates and Evans, 2005). The type and only confirmed specimen of *Parasaurolophus cyrtocristatus* occurs in the upper Fruitland Formation, in beds that are stratigraphically higher than all known occurrences of the Utah *Parasaurolophus*. Thus, if it turns out that the *Parasaurolophus* from the Kaiparowits Formation should be placed within *P. cyrtocristatus*, this finding would extend the stratigraphic distribution of the species. The other two species of *Parasaurolophus* (*P. walkeri* and *P. tubicen*) occur in the lower Dinosaur Park Formation in Alberta (~ 75.5 Ma) and in the Upper Kirtland Formation (~ 73.5 Ma) of New Mexico, respectively (Sullivan and Williamson, 1999; Gates and Evans, 2005; Ryan and Evans, 2005; Evans, Bavington, and Campione, 2009). On the basis of current evidence, none of the *Parasaurolophus* species appear to co-occur in time (Sullivan and Williamson, 1999; Evans, Bavington, and Campione, 2009). However, it is interesting to note that the geographic distribution of this genus correlates with its stratigraphic distribution, the earliest example of *Parasaurolophus*, *P. walker*, occurs in the north, whereas the youngest species occur in the southern region of the Western Interior Basin.

With regard to basal ornithopods, the only well-known basal ornithopod taxon from the late Campanian, *Orodromeus*, occurs stratigraphically higher within the Two Medicine Formation of Montana than the earliest known basal ornithopod specimen from the Grand Staircase–Escalante National Monument (UMNH VP 16281) that was recovered near the base of the Kaiparowits Formation. In fact, UMNH VP 16281 has no known stratigraphic equivalent in North America. In contrast, the basal ornithopod specimens collected from the younger middle unit of the Kaiparowits Formation (UMNH VP 12665 and 19470) appear to be approximately coeval with, though unequivocally different from, the more northerly occurring *Orodromeus*.

A single specimen of basal ornithopod collected from the lower unit of the Kaiparowits Formation (UMNH 12677) displays an autapomorphic trait of only two phalanges in the fourth digit, though the specimen is too fragmentary to accurately compare to the diagnostic specimens recovered from the middle unit (i.e., UMNH VP 12665 and 19470). This fact leaves open the possibility that the material from the lower and middle units of the Kaiparowits Formation may represent two distinct, temporally segregated basal ornithopod taxa. Alternatively, the lack of character conflict among all known specimens from the formation may indicate all of these specimens are referable to a single, previously undescribed taxon. Resolution of this taxonomic question will require the recovery of additional, diagnostic specimens from the lower unit of the Kaiparowits Formation, or a specimen with an articulated manus from the middle unit.

CONCLUSIONS

In summary, Upper Cretaceous (Campanian) sediments preserved within Grand Staircase–Escalante National Monument have yielded an abundance of ornithopod specimens that dramatically increase our knowledge of this clade, particularly for the southwestern region of the Western Interior Basin. The majority of these specimens have been recovered from the late Campanian Kaiparowits Formation, although the underlying Wahweap Formation has also produced several significant discoveries, including hadrosaur bonebeds and the partial skull of a new hadrosaurine. The Straight Cliffs Formation is producing significant specimens and will become an extremely important source of information regarding the transition between nonhadrosaurid iguanodontians and hadrosaurids.

Key specimens from the Kaiparowits Formation include several partial skulls and a partial skeleton of the lambeosaurine *Parasaurolophus* as well as multiple specimens (skulls and postcranial remains) pertaining to two species of *Gryposaurus*. Finally, several "hypsilophodontid" specimens have been recovered from the Kaiparowits Formation, the most significant of which includes partial skulls as well as manual and pedal elements representing an undescribed form (Boyd and Gates, unpubl. data). The acquisition of multiple radiometric dates from the Kaiparowits Formation permits relatively high-resolution temporal comparisons within a 2 million year window spanning approximately 76–74 Ma. Thus, for example, the *Gryposaurus* species discovered near the base of the Kaiparowits Formation (*Gryposaurus* sp.) appears to have been coeval with other species of *Gryposaurus* in the northern region of the Western Interior Basin. In contrast, *Gryposaurus monumentensis*, from the middle unit of the Kaiparowits Formation, corresponds temporally with the northern hadrosaurine genus *Prosaurolophus*. Together, these recent discoveries establish Grand Staircase–Escalante National Monument as one of the premier localities in North America for producing remains of ornithopod dinosaurs.

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