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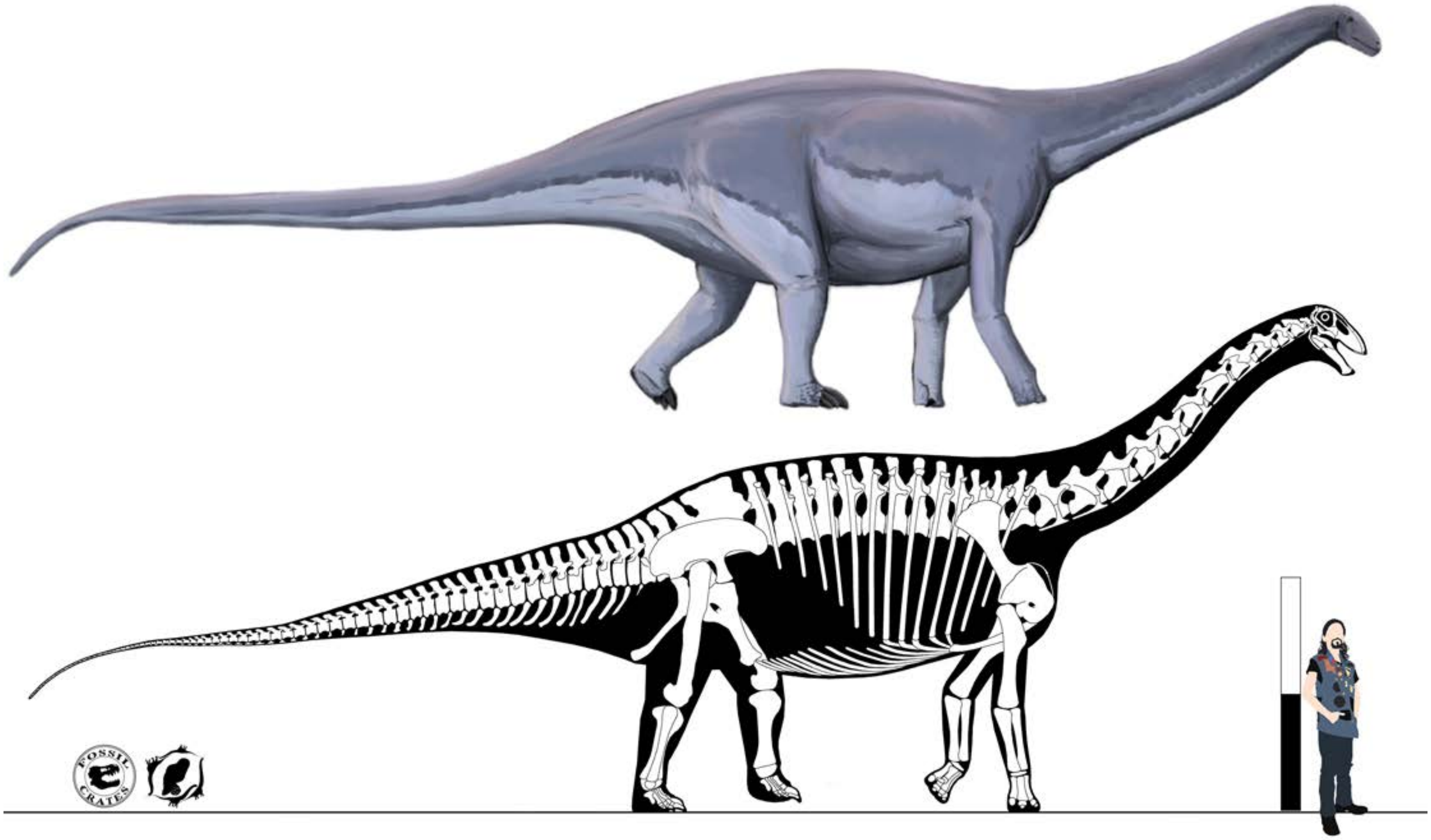
CENSUS OF CURRENTLY KNOWN SPECIMENS OF THE LATE JURASSIC SAUROPOD *HAPLOCANTHOSAURUS* FROM THE MORRISON FORMATION, USA

Colin Boisvert, Gunnar T. Bivens, Brian Curtice, Ray Wilhite, Mathew Wedel



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Cover

A skeletal reconstruction and life restoration of the enigmatic Late Jurassic Morrison Formation sauropod *Haplocanthosaurus* (scale is 2 m). Image of skeletal reconstruction is by Gunnar Bivens and image of life restoration is by Jun-Hyeok Jang.

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Census of Currently Known Specimens of the Late Jurassic Sauropod *Haplocanthosaurus* from the Morrison Formation, USA

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ABSTRACT

Currently known from two valid species, *Haplocanthosaurus priscus* and *H. delfsi*, the Late Jurassic sauropod *Haplocanthosaurus* (Morrison Formation, Western United States) has often been described as an enigmatic sauropod taxon due to its unstable phylogenetic position and paucity of specimens. Here, we quantify the number of *Haplocanthosaurus* specimens known from the literature and in collections. Although most regions of the postcranial skeleton are known, the most commonly found elements of *Haplocanthosaurus* are vertebrae (dorsals and caudals) and tibiae. Our investigation identified twelve individuals of *Haplocanthosaurus* from ten localities across four states, Colorado, Utah, Montana (private specimen), and Wyoming, making *Haplocanthosaurus* spatially widespread in the central part of the Morrison Formation. The existence of twelve individuals across four states indicates this genus was widely distributed and more abundant than historically thought. *Haplocanthosaurus* has been characterized as a 'primitive' sauropod restricted to the lower half of the Morrison Formation, but the identification of *Haplocanthosaurus* in the Dry Mesa Dinosaur Quarry confirms that the genus was also present within the upper part of the Morrison Formation.

INTRODUCTION

Haplocanthosaurus has long been considered among the most enigmatic of Late Jurassic Morrison Formation sauropods (McIntosh and Williams, 1988; Curtice et al., 2023). It has been recovered in several disparate positions, either as a basal macronarian (Upchurch, 1995; Wilson and Sereno, 1998; Upchurch et al., 2004b), a brachiosaurid (Riggs, 1904), a derived eusauropod outside Neosauropoda (Harris, 2006), or (the most well-supported position currently) a basal diplodocoid (Wilson 2002; Whitlock, 2011; Mannion et al., 2012; Tschopp et al., 2015a).

Hatcher (1903a) used the name *Haplocanthus priscus* for a partial skeleton recovered from Marsh-Felch Quarry 1 in Colorado (Cañon City Quarry 1 and Felch Quarry 1 are synonymous with Marsh-Felch Quarry 1; we use the latter designation throughout) (Figure 1). Later Hatcher (1903b) incorrectly believed his name was preoccupied by the acanthodian fish *Haplacanthus* (Agassiz, 1844), and proposed the replacement name *Haplocanthosaurus*. The two names were not, however, identical in either spelling or pronunciation and so *Haplocanthus* held priority over *Haplocanthosaurus* until the International Commission on Zoo-

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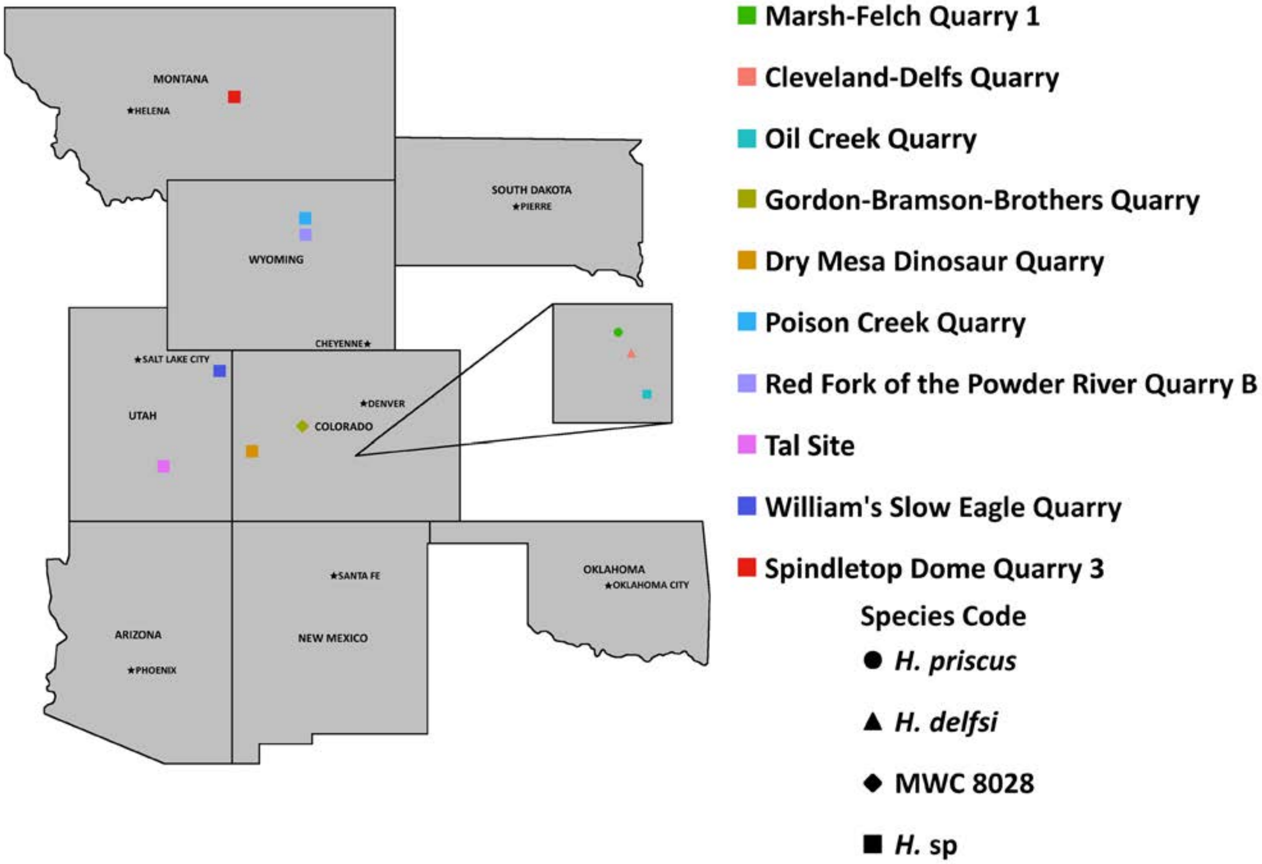

Figure 1. Spatial distribution map showing all confirmed *Haplocanthosaurus* locales, with the area around Garden Park, Colorado, inset zoomed in to show the comparative abundance of specimens found in this area. The states shown here contain surface exposures of the Morrison Formation.

logical Nomenclature ruled to suppress it (ICZN, 1991).

A second species, *Haplocanthosaurus 'utterbacki'*, was also named by Hatcher (1903c) for a second, more complete partial skeleton from the same quarry, and a third, *Haplocanthosaurus delfsi*, was named for a specimen that was both larger and stratigraphically older than either *H. priscus* or *H. 'utterbacki'* (McIntosh and Williams, 1988).

In addition to some less complete specimens found either at or in the vicinity of Marsh-Felch Quarry 1, new Colorado material was found both near the town of Snowmass (Foster and Wedel, 2014) and at the extensive Dry Mesa Dinosaur Quarry (Boisvert et al., 2024). Material has also been recovered from two different sites in Wyoming (Erickson, 2014; Tschopp et al., 2019), two in Utah (Bilbey et al., 2000; the other new to the literature), and finally a possible new specimen from Montana (Ronson, 2016). Contrary to previous statements, *Haplocanthosaurus* is more common than once thought (Wilson and Sereno, 1998; Foster and Wedel, 2014; Maidment, 2024).

This study provides a short description of eleven publicly held valid *Haplocanthosaurus* specimens from nine locales in three states and currently held in eight public collections with a note on other possible public specimens, as well as specimens that should not be identified as *Haplocanthosaurus*.

MATERIALS AND METHODS

Members of our team visited collections to examine as many specimens as possible firsthand. For the remaining specimens, we relied on published sources, unpublished photographs, and assistance from museum staff. Measurements were taken, when possible, for comparison. Identification to genus and/or species level was made using measurements and known autapomorphies. Diagnostic characters of the various *Haplocanthosaurus* specimens are given in Table 1, and information on the multiple specimens is provided in Table 2. We follow the terminology of Wilson (1999, 2012) for vertebral laminae and Wilson et al. (2011) for vertebral fossae. Furthermore, a map of the known *Haplocanthosaurus* specimens was produced (Figure 1).

Whereas it would be greatly beneficial to place all of the known *Haplocanthosaurus* specimens into a well-calibrated stratigraphic framework, unfortunately, such does not yet exist for the entirety of the Morrison Formation. On the northern part of the Colorado Plateau, the Morrison Formation can be divided into three distinct members (the Tidwell, Salt Wash, and Brushy Basin Members). Outside the Colorado Plateau, some local sections can be correlated to the Tidwell, Salt Wash, and Brushy Basin (e.g., the Oklahoma Panhandle, Richmond et al., 2020), but others show no clear correlation (e.g., the Black Hills of Wyoming, Foster et al., 2020). Long-distance correlations based on an inferred "clay change" (Turner and Peterson 1999) have not been supported by the absolute dates provided by radiometric dating (Trujillo 2006, Trujillo and Kowalis, 2015). In the absence of radiometric dates for most of the *Haplocanthosaurus* localities, we have placed the known specimens into relative correlation where possible (Table 3).

INSTITUTIONAL ABBREVIATIONS

BLM – Bureau of Land Management, Utah, USA
BYU – Brigham Young University, Provo, Utah, USA
CM – Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
CMNH – Cleveland Museum of Natural History, Cleveland, Ohio, USA
DMNS – Denver Museum of Nature and Science, Denver, Colorado, USA
FHPR – Utah Field House of Natural History State Park Museum, Vernal, Utah, USA
MWC – Dinosaur Journey, Museums of Western Colorado, Fruita, Colorado, USA
MMCh – Museo Municipal 'Ernesto Bachman', Villa El Chocón, Neuquén, Argentina
NCSM – North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA
SMM – Science Museum of Minnesota, St. Paul, Minnesota, USA
USNM – United States National Museum of Natural History, Washington, D.C., USA
YPM – Yale Peabody Museum of Natural History, New Haven, Connecticut, USA

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Diplodocoidea Upchurch, 1995
Haplocanthosaurus Hatcher, 1903b

Type species: *Haplocanthosaurus priscus* Hatcher, 1903a.

Revised Diagnosis

The genus *Haplocanthosaurus* is diagnosed by the following characters (autapomorphies marked with asterisks): (1) presacral centra pneumaticity—procamerate, (2) simple lateral pneumatic fossae in the cervical and dorsal vertebrae, (3) dorsal neural arches with elongate CPOLs* (unambiguous autapomorphy), (4) dorsal neural arches dorsoventrally heightened relative to total vertebral height, (5) mid-posterior dorsal diapophyses projecting dorsolaterally at 45° and approaching the dorsoventral height of the neural spines* (unambiguous autapomorphy), (6) large articular chevron facets on caudal vertebrae, (7) caudal vertebrae neural canals anteriorly inclined* (ambiguous autapomorphy), (8) scapular acromion process narrow, (9) scapular blade with a dorsally and ventrally expanded distal end, (10) large obturator foramen of pubis, (11) ambiens process absent (within Diplodocoidea, this state is only shared

Table 1. Diagnostic characters of *Haplocanthosaurus*, and the specimens in which they are visible.

Character	**Specimen(s)**	**Source**
Cervical ribs shorter than centra	CM 572, 879, CMNH 10380	Hatcher (1903c), Whitlock (2011)
Procamerate presacral vertebrae	BYU 11506, 17530, 17689, CM 572, 879, CMNH 10380, MWC 8028	Wedel (2003, 2005), Foster and Wedel (2014), Boisvert et al. (2024)
13 dorsal vertebrae	CM 879	Wilson (2002)
Long dorsal CPOLs	BYU 17530, 17531, CM 572, 879, CMNH 10725, 10380	Wilson (2002)
Dorsal diapophyses at 45°	BYU 11506, 17530, 17531, CM 572, 879, CMNH 10725, 10380, FHPR 1106	Hatcher (1903c), McIntosh and Williams (1988), Wilson (2002), Boisvert et al. (2024)
Dorsal PRSL formed by SPRLs	BYU 11506, 17530, CM 572, 879, CMNH 10380	Whitlock (2011)
Caudal vertebrae with large chevron facets	CM 572, 879, 36034, 36036, CMNH 10380, MWC 8028, SMM P 90.37.10	McIntosh and Williams (1988), Foster and Wedel (2014)
Scapular acromion narrow	CM 879	Wilson (2002)
Proportionally large obturator foramen	CM 572, CMNH 10380	Hatcher (1903c), personal observation
Scapular distal end expanded	CM 879, CMNH 10380	McIntosh and Williams (1988), Wilson (2002)
Tibia distal end flared	BYU 12865, CM 2043, CMNH 10725, USNM V 4275	McIntosh and Williams (1988), Boisvert et al. (2024)
Posterolaterally facing fibular facet of the astragalus	SMM P 90.37.10, USNM V 4275	Whitlock (2011)
Lack of ambiens process	CM 572, CMNH 10380, FHPR 1106	Hatcher (1903c), McIntosh and Williams (1988)
Dorsal neural arches dorsoventrally heightened relative to total vertebral height	BYU 11506, 17530, 17531, 17689, CM 572, 879, CMNH 10380, FHPR 1106, MWC 8028	Hatcher (1903c), McIntosh and Williams (1988), Foster and Wedel (2014), Boisvert et al. (2024)
Simple lateral pneumatic fossae in presacral vertebrae	BYU 11506, 17530, 17531, 17689, CM 572, 879, CMNH 10380, FHPR 1106, MWC 8028	Hatcher (1903c), McIntosh and Williams (1988), Foster and Wedel (2014), Boisvert et al. (2024)
Caudal vertebrae neural canals anteriorly inclined	CM 572, 879, CMNH 10380, FHPR 1106, MWC 8028, SMM P 90.37.10	Hatcher (1903c), McIntosh and Williams (1988), Foster and Wedel (2014), Erickson (2014)

with *Limaysaurus tessonei*), (12) proximal femur medial to the midshaft meridian (MMM) ratio about 75% (unique within Diplodocoidea, see Sassani and Bivens, 2017, Figure 9), and (13) tibia with a flared distal end. Additionally, *Haplocanthosaurus* can be assigned to Diplodocoidea based on the following shared apomorphies: (1) dorsal neural spine PRSL formed by conjoined SPRL (seen in all diplodocoids except *Supersaurus vivianae*), (2) cervical rib anteroposterior lengths shorter than respective centra, and (3) posterolaterally facing fibular facet of astragalus.

Other Diagnoses

Wilson and Sereno (1998) considered the proximal end of the tibia subcircular. However, our personal observation suggests this profile is more likely due to diagenetic distortion than a legitimate feature. Wilson (2002) also considered the presence of 13 dorsal vertebrae an autapomorphy of *Haplocanthosaurus* by way of reversal. Thirteen dorsal vertebrae, however, appear to be the plesiomorphic condition for Eusauropoda, with reduced vertebral counts in some mamenchis-

Table 2. Confirmed *Haplocanthosaurus* specimen information including stratigraphic age, location (discovery and curation), paper mention/description, and material available. RFPRB = Red Fork of the Powder River Quarry B.

Specimen Number	**Quarry**	**Strat Age**	**Species**	**Year Described**	**State**	**Known Elements**
USNM V 4275	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1896	CO	Left femur, right femur, both ischia, left tibia, left fibula, left astragalus
CM 572	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1903	CO	Two posterior cervicals, ten dorsals, five sacrals, both ilia, both ischia, and both pubes, nineteen anterior caudals, two chevrons, a nearly complete series of ribs, and a left femur
CM 879	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1903	CO	Ten cervical, thirteen dorsal, five sacral, and seven caudal vertebrae, several ribs, left scapula, right coracoid
CM 2043	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1981	CO	Right tibia, fibula, and astragalus
CM 2046	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1981	CO	Left tibia and fibula
CM 33995	Marsh-Felch Quarry 1	Morrison, age unknown	*H. priscus*	1981	CO	Left scapula
CMNH 10380	Cleveland-Delfs Quarry	Morrison, age unknown	*H. delfsi*	1988	CO	Four anterior cervicals, nine posterior dorsals with ribs on left side, five sacrals, fourteen anterior caudals, several chevrons, partial left scapula, possible fragmentary coracoid, right sternal plate, partial left radius and ulna, both ilia, left pubis, left femur, and left ischium
SMM P 90.37.10	Poison Creek Quarry	Morrison, age unknown	*H.* sp.	2014	WY	Left tibia, fibula, astragalus, calcaneum, and foot minus proximal phalanx of digit one, along with 30 articulated caudal vertebrae
SMM D14-77 P 78.21.20 P 78.21.36 P 84.15.72 P 87.14.6	Poison Creek Quarry	Morrison, age unknown	*H.* sp.	undescribed	WY	Tibiae, caudal vertebrae
FHPR 1106	William's Slow Eagle Quarry	Salt Wash (upper)	*H.* sp.	2000, paper in prep	UT	Cervical, dorsal, sacral, and caudal vertebrae, scapulocoracoid, humerus, radius, ulna, metapodial elements, femur, tibia, fibula, ribs, and pelvic material
MWC 8028	Gordon-Bramson-Brothers Quarry	Morrison, age unknown	*H.* sp.	2014	CO	Four dorsal centra, five partial ribs, sacrum, five caudal vertebrae, three chevrons, five partial neural spines, and bone fragments.
CM 312	RFPRB	Morrison, age unknown	*H.* sp.	2019	WY	Anterior caudal vertebrae, chevrons, partial ischium
CM 36034	RFPRB	Morrison, age unknown	*H.* sp.	2019	WY	Two middle caudal vertebrae
CM 36036	RFPRB	Morrison, age unknown	*H.* sp.	2019	WY	Middle caudal vertebra
BYU 9194, 11506, 12865, 17530-1, 17689	Dry Mesa Dinosaur Quarry	Brushy Basin (middle)	*H.* sp.	2024	CO	Seven dorsal vertebrae (three articulated, four disarticulated), right tibia
BLM field specimen	Tal Site	Salt Wash (upper)	*H.* sp.	undescribed	UT	Dorsal vertebra, ribs
CMNH 10725	Oil Creek Quarry	Morrison, age unknown	*H.* sp.	undescribed	CO	Two partial dorsal vertebrae, right tibia, and bone pieces

Table 3. Stratigraphic position of the known *Haplocanthosaurus* specimens within the Late Jurassic Morrison Formation. The asterisks refer to a potential *Haplocanthosaurus* specimen.

Stratigraphic Unit	**Quarry Name**	**State**
Brushy Basin Member (youngest strata)	Dry Mesa Quarry	Colorado
Salt Wash Member	William's Slow Eagle Quarry	Utah
	Tale Site	Utah
Tidwell Member (oldest strata)	None	
Morrison Formation, age unknown	Cleveland-Delfs Quarry	Colorado
	Como Bluff*	Wyoming
	Gordon-Bramson-Brothers Quarry	Colorado
	Marsh-Felch 1 Quarry	Colorado
	Oil Creek Quarry	Colorado
	Poison Creek Quarry	Wyoming
	Red Fork of the Powder River Quarry B	Wyoming

aurids (e.g., *"Omeisaurus" tianfuensis*, He et al., 1988; *Xinjiangtitan shanshanesis,* Zhang et al., 2022), all macronarians, and Flagellicaudata. Within Diplodocoidea, 13 dorsal vertebrae are seen in Rebbachisauridae (e.g., *Nigersaurus taqueti*, the unnamed specimen MMCh-Pv 49, see Vidal, 2019).

Haplocanthosaurus priscus Hatcher, 1903a =*Haplocanthus priscus* Hatcher, 1903a =*Haplocanthosaurus utterbacki* Hatcher, 1903c

Holotype: specimen CM 572.

Revised Diagnosis

Haplocanthosaurus priscus can be diagnosed by the following characters: (1) middle dorsal vertebrae mildly opisthocoelous, and (2) distal end of ischia fused (see discussion below).

Referred specimens: CM 2043, CM 2046, CM 879, CM 33995.

Haplocanthosaurus delfsi McIntosh and Williams, 1988

Holotype: specimen CMNH 10380.

Revised Diagnosis

Haplocanthosaurus delfsi can be diagnosed based on the following characters (autapomorphies marked with an asterisk): (1) middle dorsal vertebrae strongly opisthocoelous, (2) V-shaped anterolaterally projecting laminae present on mid-dorsal vertebral neural spines*, (3) posterior dorsal vertebral neural spines with greater development of median laminae compared to *H. priscus**, (4) pelvis and femur more robust than *H. priscus,* and (5) distal end of ischia unfused.

Other Diagnoses

McIntosh and Williams (1988) considered *H. delfsi* distinct from *H. priscus* based on its larger body size (roughly a third again as large, see below). However, size is variable within adult taxa of other dinosaur populations (e.g., *Allosaurus, Edmontosaurus, Plateosaurus*). Additionally, at least one other specimen attributable to *Haplocanthosaurus* (SMM P 90.37.10) is comparable in size to the *H. delfsi* holotype CMNH 10380 and does not appear to be referable to this species.

Haplocanthosaurus sp.

Referred specimens: BYU 9194, BYU 11506, BYU 12865, BYU 17530, BYU 17531, BYU 17689, CM 312, CM 36034, CM 36036, CMNH 10725, FHPR 1106, MWC 8028, SMM P 90.37.10, unnumbered BLM specimen, USNM V 4275.

Issues with Diagnosing *Haplocanthosaurus* Species

Whereas various specimens have been attributed to *Haplocanthosaurus* in the past, little has been done in the way of diagnosing the lower-level taxonomy of this genus. When initially described, *Haplocanthosaurus delfsi* was distinguished from *H. priscus* (McIntosh and Williams, 1988); however, little to no effort has been made in distinguishing the latter from the former or from other *Haplocanthosaurus* specimens. At least one character used by McIntosh and Williams (1988) to distinguish *H. delfsi* from *H. priscus*—the lack of fused ischia in the former—could represent ontogenetic or individual variation. Specimen USNM V 4275 was found in close proximity to the specimens of *H. priscus* and possessed fused ischia as in that taxon, yet the femoral least breadth to length measurements, as currently defined, imply closer affinities to *H. delfsi*. It is unclear which, if any, of these characters are more taxonomically informative.

Some characters that have been previously used to distinguish the species of *Haplocanthosaurus*, such as the level of co-ossification of sacral neural spines, are likely a result of individual variation, whereas others may be attributable to ontogeny or other factors (Hone et al., 2016). For example, specimen CM 572 exhibits a pneumatic fossa at least in the first caudal vertebra (Upchurch and Mannion, 2009; Wedel, 2009); although at this time it is unclear whether this is a result of individual variation or is more taxonomically significant. Other characters, such as a proportionally large obturator foramen for the genus, may be phylogenetically informative but have yet to be extensively discussed (Figure 2). Ontogeny and individual variation have long plagued sauropod taxonomy and phylogeny (Woodruff, 2019) and it is unclear how much these factors affect *Haplocanthosaurus*. Additional study and reevaluation, both of the original type specimens and new specimens, such as specimen FHPR 1106, will hopefully further elucidate the interrelationships of this genus.

SPECIMEN DESCRIPTIONS

Specimen CM 572

This specimen represents the holotype for the genus *Haplocanthosaurus* and of the species *H. priscus* (Hatcher 1903a, 1903b, 1903c). Specimen CM 572 was recovered from the Marsh-Felch Quarry 1 (Turner and Peterson, 1999) and includes two posterior cervical and

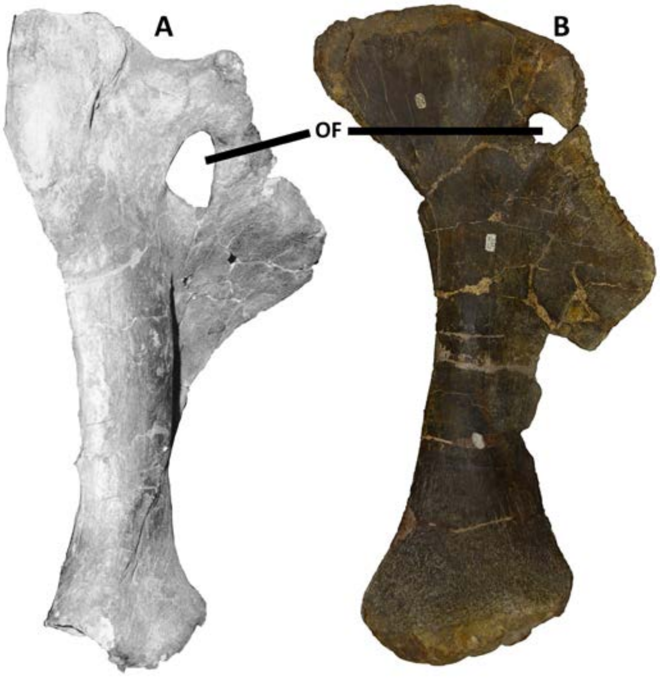

Figure 2. Comparative photographs of the large obturator foramen (OF) of *Haplocanthosaurus* based on specimens CM 572 (A) and Apatosaurinae indet. BYU 681-12915 (B). Image of CM 572 (not to scale) is modified from an unpublished image by John S. McIntosh (Wesleyan University), courtesy of Dan Chure (Dinosaur National Monument).

ten dorsal vertebrae, the sacrum and ilia, ischia and pubes, nineteen anterior caudal vertebrae, two chevrons, a nearly complete series of dorsal ribs, and a left femur (Figure 3). As the genoholotype of this taxon, it forms the basis for the generic diagnosis, including the tall neural arch pedicles, non-bifurcated neural spines, dorsally angled transverse processes, and simple amphicoelous caudal centra with large chevron facets (Hatcher, 1903c).

A right tibia, fibula, and astragalus cataloged as specimen CM 2043 likely belongs to *Haplocanthosaurus* (McIntosh, 1981) and possibly to the genoholotypic individual of *H. priscus* (contra McIntosh and Williams, 1988) due to the least breadth/length measurement of the tibia, tibial morphology, overall limb proportions, and its proximity to other bones in the quarry assigned to *Haplocanthosaurus*. There is also no overlap in elements with specimen CM 572, which further suggests such an association (Figure 3). The limb proportions also do not match specimen CM 879, providing evidence against it being assigned to that *Haplocanthosaurus* specimen. A left scapulocoracoid specimen CM 33995 and left tibia and fibula specimen CM 2046 also match the cross-scaled limb proportions for CM 572 and very likely also belong to this individual.

Specimen CM 879

Specimen CM 879 was originally designated the holotype of *Haplocanthosaurus 'utterbacki'* (Hatcher, 1903c). Also recovered from Marsh-Felch Quarry 1, this specimen consists of ten cervicals (likely representing cervical vertebrae two, three, and five through twelve), thirteen dorsal vertebrae, several dorsal ribs, the sacrum, the anterior seven caudal vertebrae, the left scapula, and right coracoid (Hatcher, 1903c). This individual was referred to *Haplocanthosaurus* based on tall neural arch pedicles, the simple non-bifurcated neural spines, and dorsally angled transverse processes (Hatcher, 1903c, and Figure 4).

Haplocanthosaurus 'utterbacki' was distinguished by Hatcher (1903c) solely based on the level of sacral neural spine fusion. However, this character was later recognized as ontogenetically variable, and as a result, this species was synonymized with *H. priscus* (McIntosh and Williams, 1988).

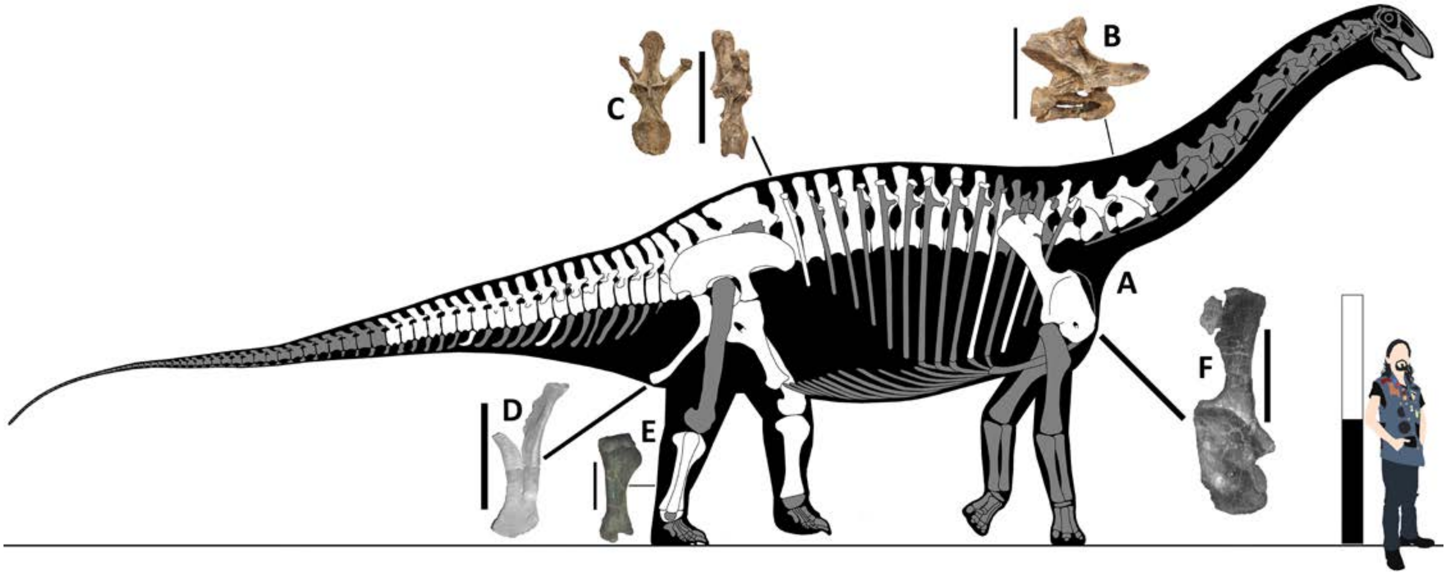

Figure 3. Skeletal reconstruction of composite type individual (A), with specimen CM 572 cervical eleven in right lateral (B), dorsal thirteen in posterior and right lateral views (C), fused ischia in posterior view (D), right tibia specimen CM 2043 in posterior view (D), and fused left scapulocoracoid specimen CM 33995 in left lateral view (F). Scale bars equal 2 m (A), 20 cm (B) and 50 cm (C, D, E, F). Scale individual for this and all skeletals is co-author GTB at his natural height of 165 cm. Photographs of ischia and scapulocoracoid modified from unpublished images by John S. McIntosh (Wesleyan University), courtesy of Dan Chure (Dinosaur National Momument).

Specimen CM 36034

Specimen CM 36034 was collected from the Red Fork of the Powder River Quarry B in Wyoming (Tschopp et al., 2019). CM 36034 consists of two mid-caudal vertebrae (Figure 5). Tschopp et al. (2019) considered this specimen to belong to an indeterminate neosauropod, as the prezygapophyses of these caudals are shorter proportionally than can be seen in other *Haplocanthosaurus* specimens (e.g., specimens CM 572, CM 879, CMNH 10380, SMM P 90.37.10). It is possible, however, that this is an artifact of taphonomic processes rather than a legitimate feature; and besides this morphological discrepancy, the remainder of the vertebral morphologies are consistent with *Haplocanthosaurus*. For example, the large chevron facets exceed those of *Camarasaurus*, but are consistent with those of *Haplocanthosaurus*; therefore, we recognize CM 36034 as *Haplocanthosaurus* sp.

Additionally, specimens CM 36036 and CM 312, also from the Red Fork of the Powder River Quarry B, preserve additional anterior and mid-caudal vertebrae, several chevrons, and a partial ischium. Whereas originally being assigned to separate individuals, this material likely belongs to the same individual as specimen CM 36034, based on the comparable size and morphology present in all the vertebrae. There may be additional *Haplocanthosaurus* material from this quarry as well (originally all cataloged as specimen CM 1256), although given the disarticulated nature of this quarry and lack of a quarry map (see Tschopp et al., 2019), it requires further study that is outside the scope of this review.

Specimen CMNH 10380

Specimen CMNH 10380 represents the holotype of *Haplocanthosaurus delfsi* (Mcintosh and Williams, 1988). CMNH 10380 comes from the Cleveland-Delfs Quarry (or "Delfs' Quarry" of Turner and Peterson, 1999). This specimen is represented by cervical vertebrae one through four, nine posterior dorsal vertebrae with left dorsal ribs, five sacral vertebrae, caudal vertebrae one through fourteen, several chevrons, shaft and distal end of left scapula, a possible fragmentary coracoid, right sternal plate, proximal ends of the left radius and ulna, both ilia, left pubis, left femur, and left ischium (McIntosh and Williams, 1988, and Figure 6). This specimen was referred to *Haplocanthosaurus* based on the tall neural arch pedicles, dorsally angled transverse processes, and a flared distal end of the tibia (McIntosh and Williams, 1988).

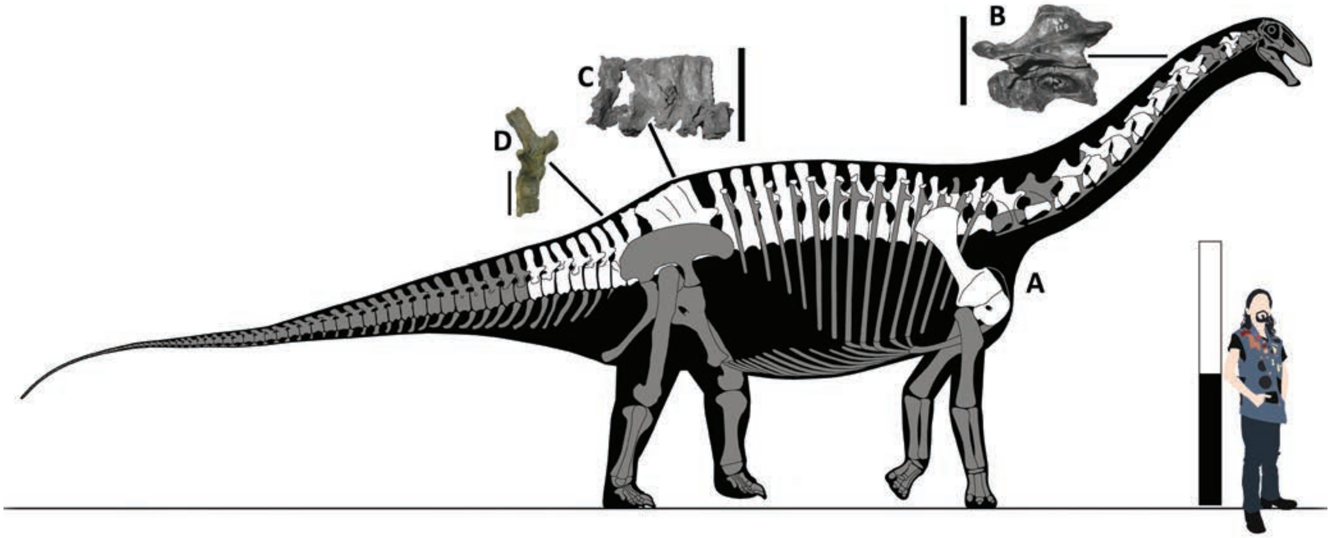

Figure 4. Skeletal reconstruction of specimen CM 879 (A), with fifth cervical in left lateral view (B), unfused sacral neural spines in right lateral view (C), and first caudal in right lateral view (D). Scale bars equal 2 m (A), 20 cm (B, D), and 50 cm (C). Images of cervical and sacrals modified from ones by John S. McIntosh (Wesleyan University), courtesy of Dan Chure (Dinosaur National Monument).

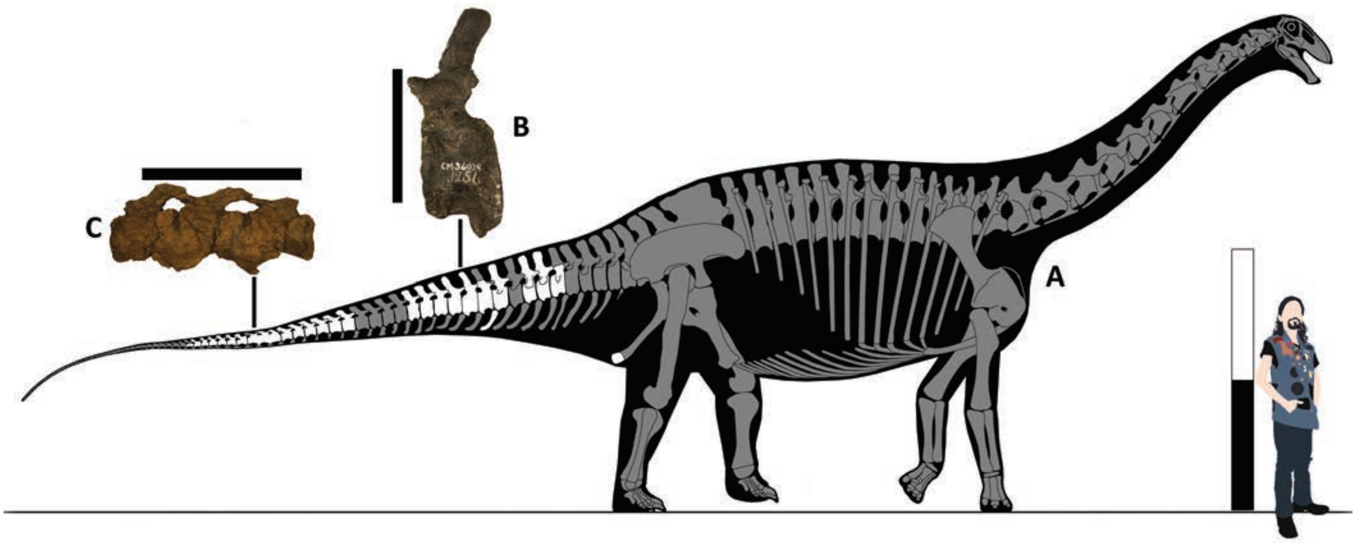

Figure 5. Skeletal reconstruction of the Red Fork of the Powder River Quarry B individual (A), with specimen CM 36034 twelfth caudal in left lateral view (B), and specimen CM 312 fused posterior caudals in left lateral view (C). Scale bars equal 2 m (A) and 20 cm (B, C). Photograph of fused caudals modified from Tschopp et al. (2019)

Specimen CMNH 10725

Specimen CMNH 10725 comes from the Oil Creek Quarry in Colorado. While CMNH 10725 awaits description, the specimen is represented by two dorsal vertebrae, a right tibia, and some unidentified fragments. The specimen was referred to *Haplocanthosaurus* based on the tall neural arch pedicles, dorsally angled transverse processes, and flared distal end of the tibia (Hatcher, 1903c, McIntosh and Williams, 1988, and Figure 7). CMNH 10725 was found in close proximity to the specimens from the Cleveland-Delfs and Marsh-Felch Quarries in Colorado (Figure 1), suggesting populations of *Haplocanthosaurus* were more numerous here than in other areas.

Specimen MWC 8028

Specimen MWC 8028 comes from the Gordon-Bramson-Brothers Quarry in undifferentiated Morrison strata in Colorado (Foster and Wedel, 2014), and includes four dorsal centra, five partial dorsal ribs, sacrum, five caudal vertebrae, three chevrons, and many unidentified fragments (Figure 8). MWC 8028 was identified as *Haplocanthosaurus* based on the amphicoelous caudal vertebrae with large chevron facets. Further studies have indicated that this individual had caudal vertebrae with unusually large neural canals and deeply amphicoelous centra (Wedel et al., 2021), and that these morphologies, in combination with other differences in the centra and neural spines, may indicate enough morphological disparity to warrant a new species within the genus.

Specimen USNM V 4275

Specimen USNM V 4275 comes from Marsh-Felch Quarry 1 in Colorado and is represented by a left femur, right femur, both ischia, left tibia, left fibula, and left astragalus. USNM V 4275 was referred to *Haplocanthosaurus* based on the least breadth to length measurement, flared distal end of the tibia, and fused ischia – as in *H. priscus* (McIntosh and Williams, 1988, and Figure 9).

Of historical note, specimen USNM V 4275 was described seven years before specimen CM 572. Marsh (1896; Pl. XVIII) originally figured the ischia of this specimen and assigned them to *Diplodocus longus*. However, Gilmore (1907) recognized that they were very different from ischia referred to *Diplodocus*, and reassigned these elements to "*Morosaurus*."

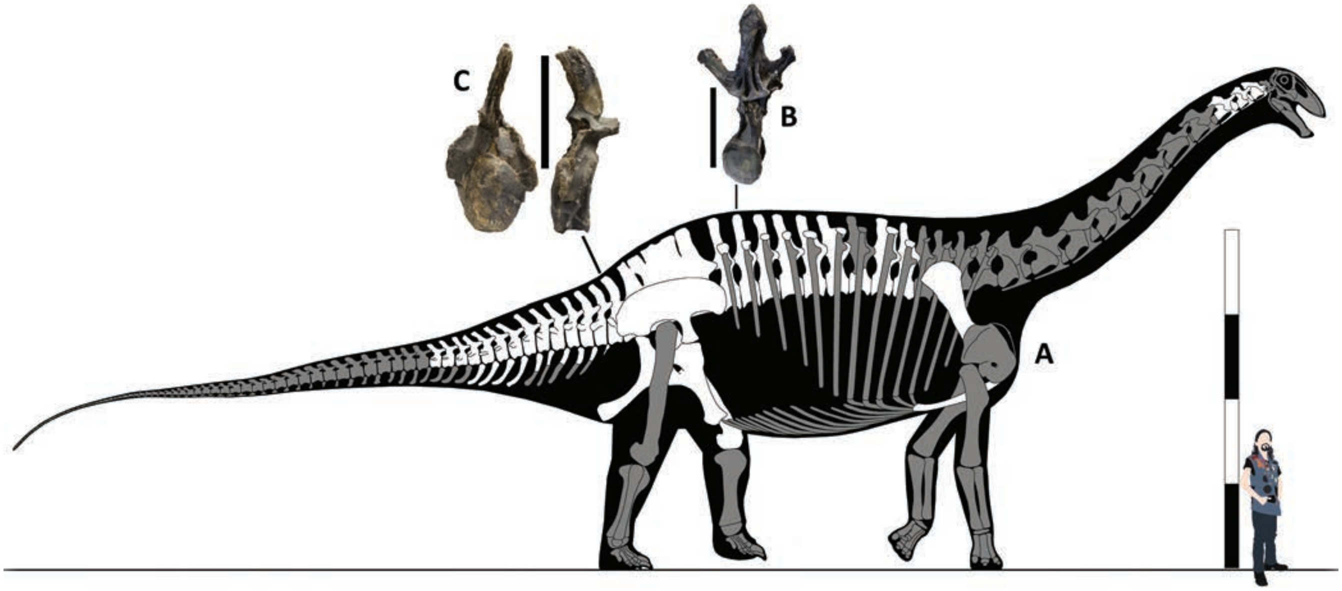

Figure 6. Skeletal reconstruction of specimen CMNH 10380 (A), with twelfth dorsal in posterior view (B), and first caudal in right lateral and posterior views (C). Scale bars equal 4 m (A) and 50 cm (B, C).

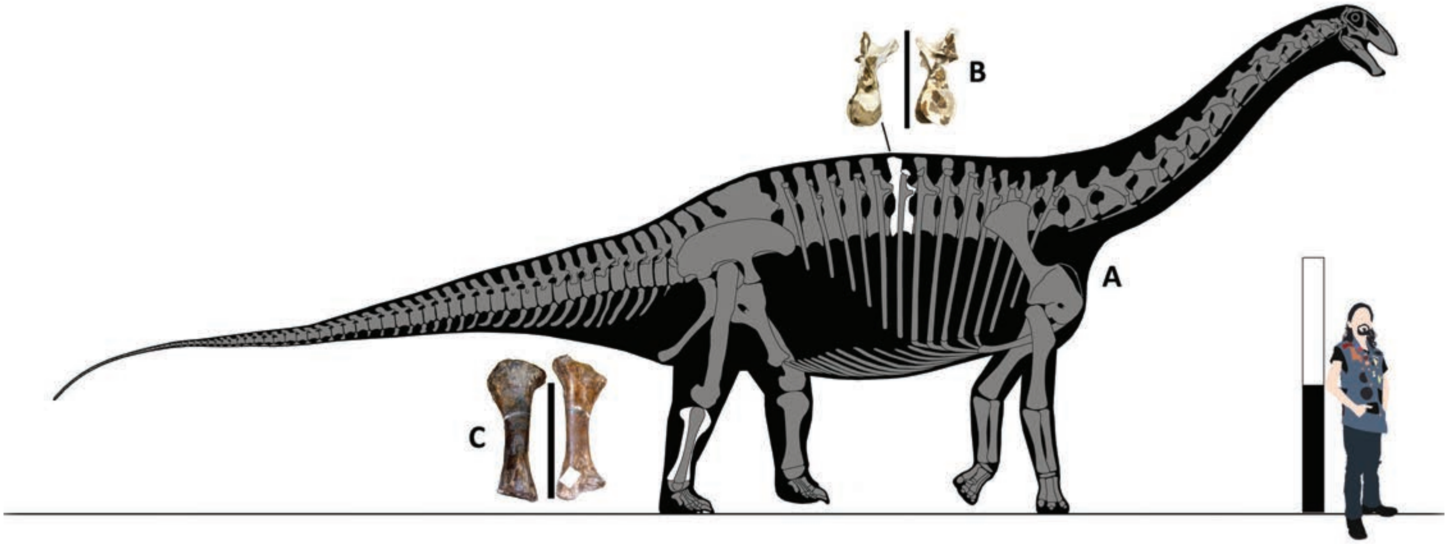

Figure 7. Skeletal reconstruction of specimen CMNH 10725 (A), with middle dorsal in anterior and left posteroventral views (B), and right tibia in medial and posterior views (C). Scale bars equal 2 m (A) and 50 cm (B, C).

Specimen FHPR 1106

Specimen FHPR 1106 is the most complete *Haplocanthosaurus* known to date, with over 60% of the skeleton recovered (Bilbey et al., 2000). While currently under study, FHPR 1106 was recovered from the William's Slow Eagle Quarry in Utah within the upper Salt Wash Member of the Morrison Formation (Turner and Peterson, 1999; Maidment, 2024; Boisvert et al., 2024). FHPR 1106 is represented by a majority of the cervical, dorsal, sacral, and caudal vertebral series, a scapulocoracoid, numerous stylopodial, zeugopodial, and metapodial elements, dorsal ribs, and pelvic material (Bilbey et al., 2000, and Figure 10). The specimen has been tentatively

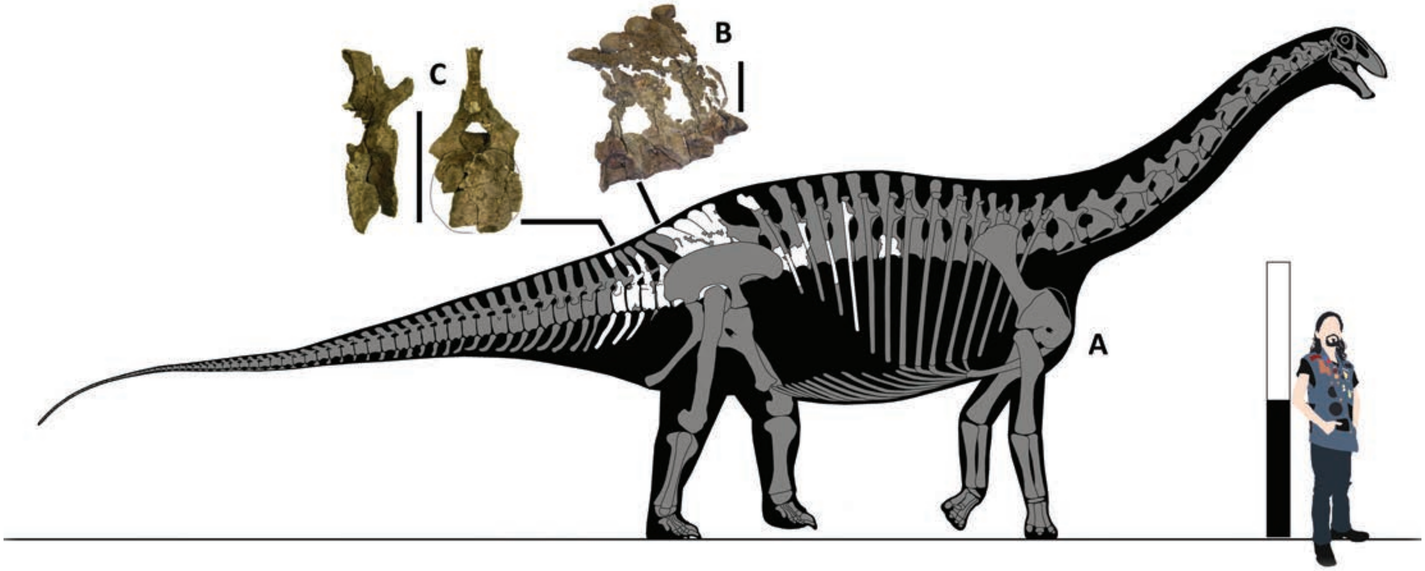

Figure 8. Skeletal reconstruction of specimen MWC 8028 (A), with sacrum in right lateral view (B), and third caudal in anterior and right lateral views (C). Scale bars equal 2 m (A) and 20 cm (B, C).

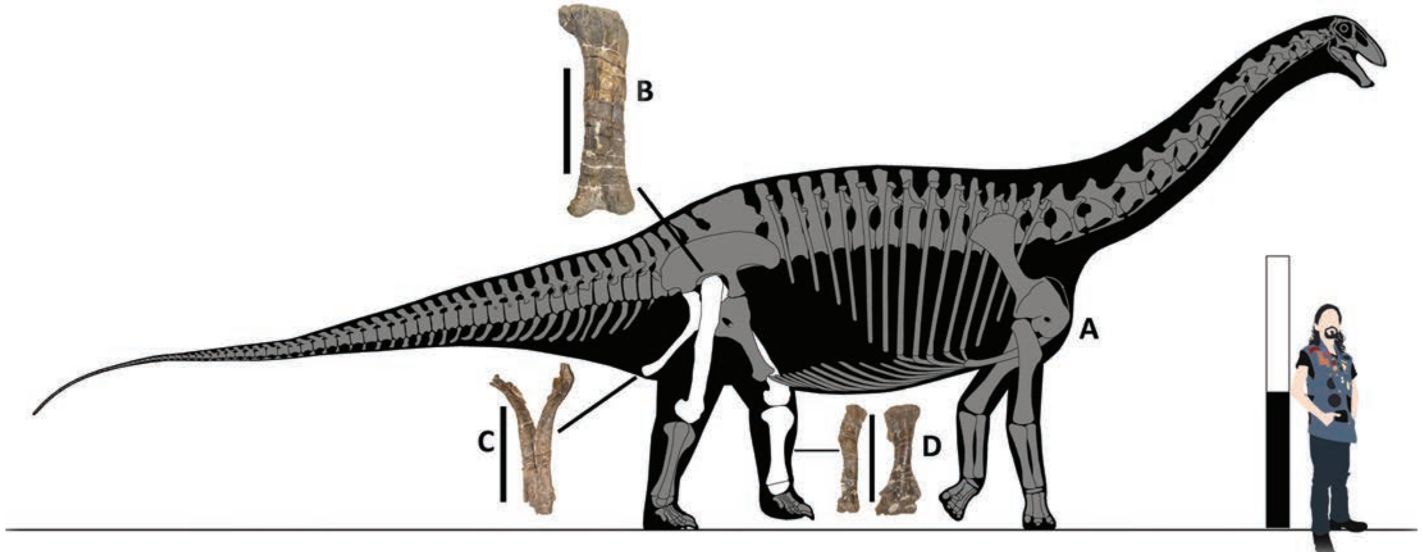

Figure 9. Skeletal reconstruction of specimen USNM V 4275 (A), with left femur in anterior view (B), fused ischia in posterior view (C), and left fibula, and fused tibia and astragalus in posterior view (D). Scale bars equal 2 m (A) and 50 cm (B, C, D).

identified as *Haplocanthosaurus* based on the tall neural arch pedicles, simple non-bifurcated neural spines in the dorsal vertebrae, and dorsally angled transverse processes (Hatcher, 1903c). The caudal vertebrae possess enlarged chevron facets. Due to its completeness, this specimen will be important in future phylogenetic and taxonomic analyses of *Haplocanthosaurus*.

Specimens SMM D14-77, P 78.21.20, P 78.21.36; P 84.15.72, P 87.14.6, P 90.37.10

Specimen SMM P 90.37.10 was discovered in Wyoming at the Poison Creek Quarry, and is represented by a lower left hind limb with a tibia, fibula, astragalus, calcaneum, pes (minus the proximal phalanx of digit 1),

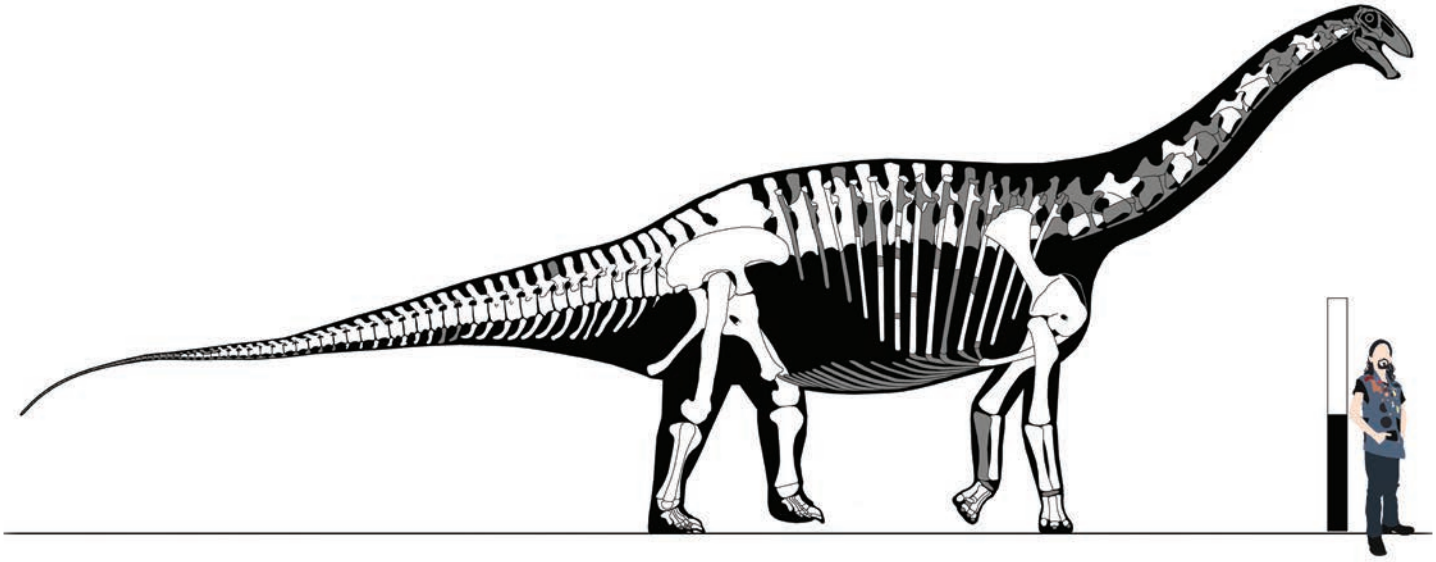

Figure 10. Skeletal inventory of specimen FHPR 1106. Scale bar equals 2 m.

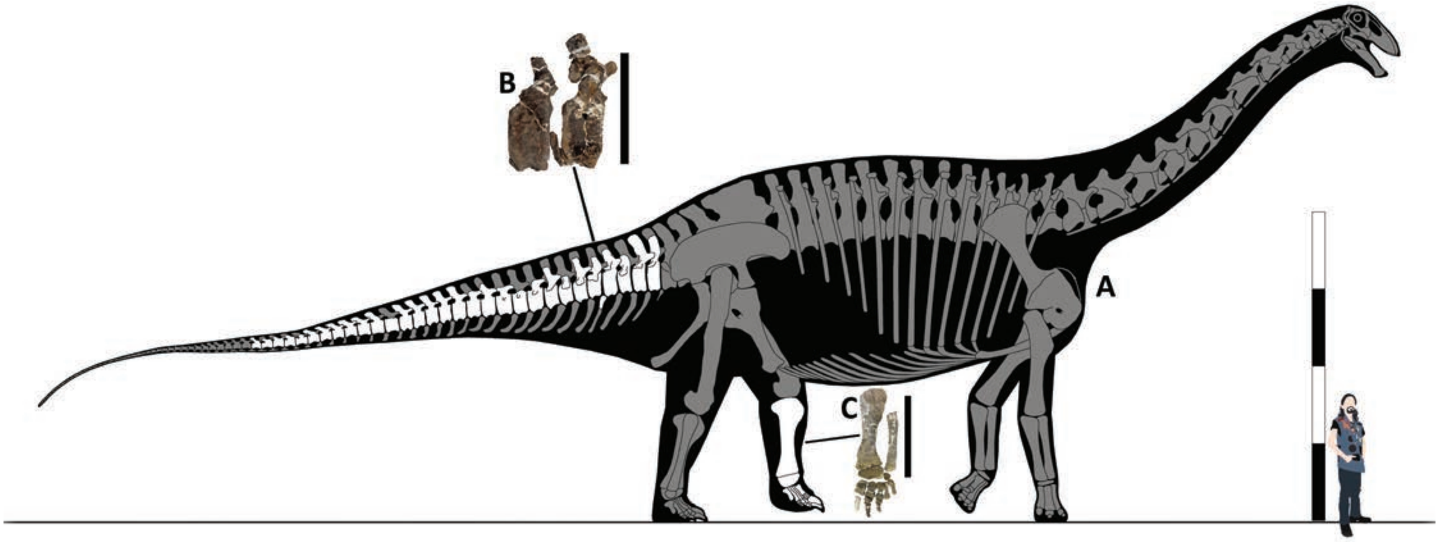

Figure 11. Skeletal reconstruction of specimen SMM P 90.37.10 (A), with caudals 5 and 6 in right lateral view (B), and left crus and pes in anterior view (C). Scale bars equal 4 m (A), 50 cm (B), and 1 m (C). Photograph of left limb modified from Erickson (2014).

and thirty articulated caudal vertebrae (Erickson, 2014). It was referred to *Haplocanthosaurus* based on the flared distal end of the tibia and large posterior chevron facets on the caudal vertebrae (McIntosh and Williams, 1988; Erickson, 2014; and Figure 11). This specimen marks the northernmost occurrence of the genus *Haplocanthosaurus* within a museum collection. Additional SMM specimens examined by the authors indicate at least three additional individuals of *Haplocanthosaurus* in the quarry, based on tibiae (specimens SMM field no. D14-77, SMM P 78.21.20, SMM P 84.15.72) and caudal vertebrae (specimens SMM P78.21.36, SMM P87.14.6).

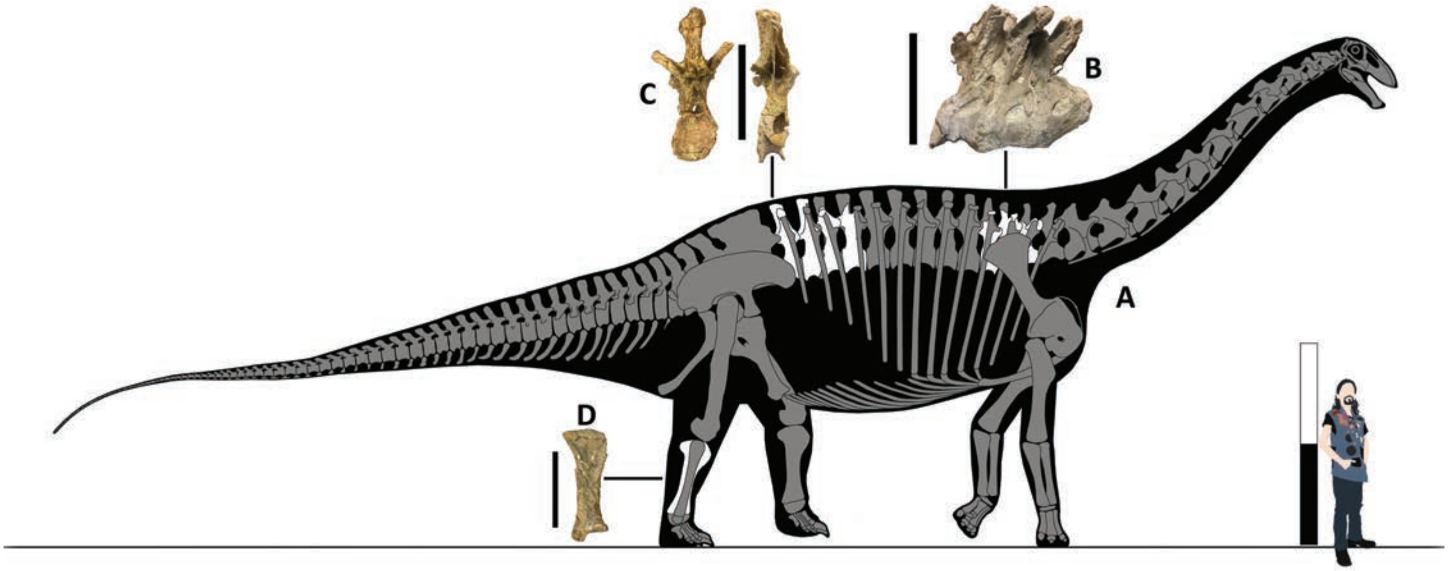

Figure 12. Skeletal reconstruction of the composite BYU individual (A), with conjoined anterior dorsals BYU 17531 in right lateral (B), dorsal thirteen in posterior and right lateral views (C), and right tibia from specimen BYU 12865 in anterior view (D). Scale bars equal 2 m (A), and 50 cm (B, C, D).

Specimens BYU 9194, 11506, 12865, 17530, 17531, and 17689

These specimens, probably representing a single individual, come from the Dry Mesa Dinosaur Quarry in the middle Brushy Basin Member of the Morrison Formation in Colorado (Turner and Peterson, 1999; Curtice et al., 2023; Boisvert et al., 2024; Maidment, 2024; and Figure 12). The BYU specimens are represented by three anterior dorsal vertebrae, four disarticulated posterior dorsal vertebrae, and a right tibia (Curtice et al., 2023; Boisvert et al., 2024). The specimens were referred to *Haplocanthosaurus* based on the tall neural arch pedicles, dorsally angle transverse processes, and the flared end of the distal tibia (Hatcher, 1903c; McIntosh and Williams, 1988).

These BYU specimens are also the geologically youngest *Haplocanthosaurus* specimens (Turner and Peterson, 1999), and suggest that *Haplocanthosaurus* may have temporally spanned a much longer part of the Morrison Formation than has traditionally been thought (Boisvert et al., 2024).

BLM Specimen

The BLM specimen was discovered on BLM land, known as the Tal Site, near the Brachiosaur Gulch Quarry (Foster et al., 2021, and Figure 1). It is still in the ground at the time of this paper's publication. The only material found was a single dorsal vertebra and associated partial ribs. It is identified as *Haplocanthosaurus* by the tall neural arch pedicles and dorsally angled transverse processes (Hatcher 1903c, and Figure 13). The locality is in the upper Salt Wash Member of the Morrison Formation (Foster et al., 2021; Boisvert et al., 2024). The specimen is currently under study for possible collection by FHPR.

Specimens Potentially Referable to *Haplocanthosaurus*

There is a large partial skeleton from Spindletop Dome Quarry 3 in central Montana that has been previously suggested to be *Haplocanthosaurus* (Woodruff and Foster, 2017; Richmond, 2023). This specimen is currently in private hands so further information was not gleaned from it (Ronson, 2016).

Figure 13. Mid-posterior dorsal of the unnumbered BLM specimen in situ. Scale bar equals 10 cm.

Specimen NCSM 28359

Specimen NCSM 28359 consists of a radius, ulna, manual ungual, left femur, phalanx, metapodial, and a fragmentary element that may belong to either a coracoid or sternal plate. It was found at Como Bluff in Wyoming (no more precise locality information is currently available). Much of the material is in poor condition and difficult to identify to a lower phylogenetic level. The femur is not incongruent with other *Haplocanthosaurus* femora but cannot reliably be distinguished from *Camarasaurus* either. Further research is needed on this specimen, which should be revisited once specimen FHPR 1106 is described, as more of the skeleton of *Haplocanthosaurus* will be known (including the radius and ulna, which cannot be compared to any confirmed *Haplocanthosaurus* specimens at the moment). If referable to *Haplocanthosaurus*, this would document the first occurrence of this genus within southern Wyoming.

Specimen USNM V 4264

Specimen USNM V 4264 consists of a partial left humerus, radius, ulna, and five left metacarpals from Marsh-Felch Quarry 1, which is cataloged in the USNM database as "*Haplocanthosaurus*? sp." These elements were not found in association with the partial skeletons of *Haplocanthosaurus* from this quarry. To date no associated *Haplocanthosaurus* forelimb has been described, so USNM V 4264 cannot be referred to *Haplocanthosaurus*.

Specimen USNM V 4267

Specimen USMN V 4267, consisting of a right humerus, radius, and ulna, is from Marsh-Felch Quarry 1 and is cataloged in the USNM database as "*Haplocanthosaurus*? sp." It is quite probable, given the similar ratios and overall size of the elements, that this is the opposite limb of specimen USNM V 4264.

Specimen YPM VP.001906

Specimen YPM VP.001906 consists of the left radius, ulna, metacarpals I-V, and manual phalanx V-1, and was recovered from Marsh-Felch Quarry 1. YPM VP.001906 was originally considered to belong to *"Morosaurus"*, then *Diplodocus longus* (Marsh, 1896), before being tentatively excluded by McIntosh and Carpenter (1998), who considered it possibly belonging to either *Apatosaurus* or *Haplocanthosaurus*. Tschopp et al. (2018) only assigned it as far as Diplodocoidea indet., noting it differed from both Apatosaurinae and Diplodocinae. The first metacarpals of specimen FHPR 1106 (the only confirmed *Haplocanthosaurus* specimen with a manus) are both incomplete, thus precluding comparison here to determine if it was proximodistally longer than metacarpal IV as in most apatosaurines (but see specimen NSMT-Pv 20375; Upchurch et al., 2004a). We agree with Tschopp et al. (2018) in tentatively identifying this specimen Diplodocoidea indet.

Specimens Not Referable to *Haplocanthosaurus*

Several additional specimens have been previously referred to the genus *Haplocanthosaurus*. Here, we briefly review these specimens and discuss issues with these referrals.

Specimen DMNS EPV.2909

Specimen DMNS EPV.2909 was recovered from DMNH Locality 582, the "*Haplocanthosaurus* Quarry," in Colorado. McIntosh and Carpenter (1998) considered DMNS EPV.2909, which consists of a dorsal vertebra, caudal vertebrae, and two femora, to belong to *Haplocanthosaurus*, and additionally referred specimen USNM V 4273 to this taxon as well (see below). The dorsal vertebral transverse processes are dorsoventrally short compared to the very dorsoventrally tall neural spines, and they do not project dorsally. Additionally, the chevron facets are small, and the femoral shafts are also slenderer than seen in other *Haplocanthosaurus* specimens (Figure 14). Taking all of these characters into account, we consider DMNS EPV.2909 to represent an indeterminate diplodocid.

Specimen USNM V 4723

Specimen USNM V 4723 consists of a series of mid-posterior caudals from Marsh-Felch Quarry 1, and was originally referred to *Diplodocus longus* by Marsh at the advice of Marshal Felch. McIntosh and Carpenter (1998) questioned this assignment based on comparison to the caudal sequence CM 307 from the Red Fork of the Powder River Quarry B, and assigned USNM V 4723 to *Haplocanthosaurus* based on favorable comparison to that of specimen DMNS EPV.2909. As discussed above, the latter specimen is clearly not referable to *Haplocanthosaurus*, and as a result, we exclude USNM V 4723 as well, and consider it to be an indeterminate diplodocid.

Specimen USNM PAL 337859

Specimen USNM PAL 337859 includes several partial cervical vertebrae from Marsh-Felch Quarry 1. Regarding one of the middle cervical vertebrae, McIntosh and Carpenter (1998) wrote it "...has an undivided neural spine and probably belongs to *Haplocanthosaurus*." This specimen is listed as "cf. *Brachiosaurus* sp." in the USNM collections database. Personal observation by Mathew J. Wedel (Western University of Health Sciences, October 31, 2023) shows an anteroposteriorly long cervical centrum and pre- and post-zygapophyses that are set forward of their respective centrum ends, consistent with brachiosaurids and unlike those seen in *Haplocanthosaurus*, corroborating the USNM's database assignment.

Specimen YPM VP.004688

Specimen YPM VP.004688 consists of a right scapula, humerus, radius, and ulna from Marsh-Felch Quarry 1. It is currently cataloged as "?*Haplocanthosaurus* sp." in the collections database and was identified as such

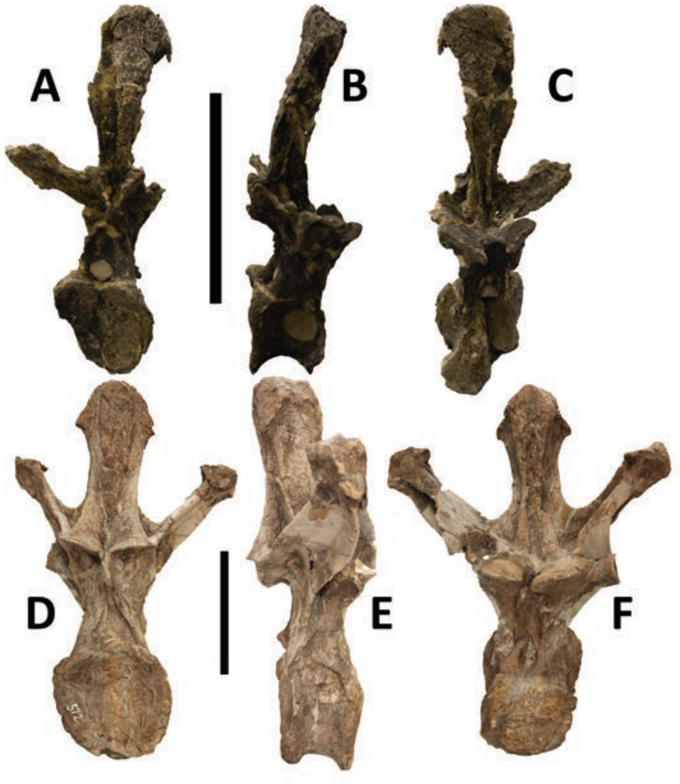

Figure 14. Diplodocinae indet. specimen DMNS EPV.2909 mid-posterior dorsal vertebra in posterior (A), right lateral (B), and anterior (C) views. *Haplocanthosaurus priscus* specimen CM 572 dorsal thirteen in posterior (D), right lateral (E), and anterior (F) views. Scale bars equal 20 cm.

by Carpenter (2019, Figure 1c). However, Tschopp et al. (2018) note that the radius possesses a distinct medial projection on the proximal articular surface, a morphology consistent in known brachiosaurid radii (e.g., *Cedarosaurus*, *Giraffatitan*, *Lusotitan*). The radius:humerus ratio of YPM VP.004688 also compares favorably to Brachiosauridae, although some diplodocoids possess a similar ratio (Table 4). The scapular morphology of YPM VP.004688 is similar to other brachiosaurids in the widely expanded distal end and slender shaft. Collectively, we find it most parsimonious that YPM VP.004688 represents Brachiosauridae indet.

Specimen YPM VP.059137

Specimen YPM VP.059137 consists of five right metatarsals from Marsh-Felch Quarry 1, was originally cataloged as part of specimen YPM VP.001920 (McIntosh and Carpenter, 1998), and was considered by them to belong to either *Brachiosaurus* or *Haplocanthosaurus*. As noted by Tschopp et al. (2018), this pes shares the synapomorphic brachiosaurid beveling of the distal end of metatarsal IV relative to its proximodistal long axis (Mannion et al., 2013; Maltese et al., 2018), and our current analysis agrees with their assignment of the specimen to Brachiosauridae.

DISCUSSION

Despite the proportionally low number of specimens compared to the coeval sauropods *Apatosaurus*, *Diplodocus*, or *Camarasaurus*, all of which are known from dozens or even hundreds of specimens (Foster, 2020), *Haplocanthosaurus* appears to be both geograph-

Table 4. Measurements (in mm) and radius:humerus ratios of various sauropod forelimbs.

Taxon	Specimen	Humerus	Radius	Ratio	Reference
Brachiosauridae indet.	YPM VP.004688	1700	985	0.58	Personal Observation
Haplocanthosaurus? sp.	USNM V 4264/4267	816/805	537/525	0.66	Personal Observation
Brachiosaurus altithorax	BYU 4744/USNM 21903	2060	1270	0.61	D'Emic and Carrano (2019)
Brachiosaurus sp.	Gyeryongsan Museum specimen	1530	940	0.61	Personal Observation
Giraffatitan brancai	MB.R.2181	2130	1240	0.58	Janensch (1961)
Cedarosaurus weiskopfae	DMNS 39045	1380	812	0.59	Tidwell et al. (1999)
Camarasaurus lewisi	NMZ 1000002	705	464	0.66	Tschopp et al. (2015b)
Camarasaurus grandis	YPM VP.001901	890	615	0.69	Vidal (2019)
Camarasaurus lentus	WDC B	1140	795	0.69	Ikejiri (2004)
Camarasaurus lewisi	BYU 9047	1018	720	0.71	McIntosh et al. (1996)
Apatosaurus louisae	CM 3018	1150	800	0.69	Gilmore (1936)
Brontosaurus excelsus	YPM VP.001980	1101	765	0.69	Personal Observation
Diplodocus hallorum	USNM V 10865	1010	690	0.68	Gilmore (1932)
Galeamopus pabsti	NMZ 1000011	870	601	0.69	Tschopp and Mateus (2017)
Barosaurus lentus	SDSM 25217	735	571	0.77	Foster (1996)

ically and temporally widespread, and potentially ecologically present across a wide expanse of the Morrison Formation based on latitudinal occurrences. Although rare demographically, it is possible that *Haplocanthosaurus* may be a part of the cosmopolitan Morrison Formation sauropod fauna represented by *Apatosaurus, Diplodocus*, and *Camarasaurus,* as these taxa are also found in Wyoming, Utah, Colorado, and Montana (Dodson et al., 1980; Woodruff and Foster, 2017; Foster, 2020; Boisvert et al., 2024). If *Haplocanthosaurus* contributed to this cosmopolitan fauna, it raises further ecological questions of how this basal sauropod survived throughout and across the Morrison Formation. As one example, co-occurrence with more numerous and derived sauropod taxa highlights a potentially complex series of ecological mechanisms necessary to concurrently sustain a high diversity and abundance of large-bodied terrestrial herbivores (Button et al., 2014).

The specimens listed above represent a census of known *Haplocanthosaurus* remains. The scarcity of published material and lack of complete skeletons (e.g., no skull material) have impacted nearly every aspect of our understanding of this genus. Hopefully as more specimens are identified and described, this will answer many of the questions surrounding this genus. Currently, there is support for at least three species within the genus; two are the previously described and valid *H. priscus* and *H. delfsi,* in addition to one currently under study (specimen MWC 8028 by Mathew J. Wedel). This raises other ecological questions regarding the species turnover rate in the Morrison Formation, as many taxa found in the Late Jurassic of North America have multiple species to a genus, especially the sauropods (Table 5).

Table 5. Valid Morrison Formation sauropod species as recognized at the time of writing.

Genus	**Species**	**Taxonomic authority**
Amphicoelias	*A. altus*	Cope (1877c)
Apatosaurus	*A. ajax, A. louisae*	Marsh (1877), Holland (1915)
Ardetosaurus	*A. viator*	van der Linden et al. (2024)
Barosaurus	*B. lentus*	Marsh (1890)
Brachiosaurus	*B. altithorax*	Riggs (1903)
Brontosaurus	*B. excelsus, B. parvus, B. yahnapin*	Marsh (1879), Peterson and Gilmore (1902), Filla and Redman (1994)
Camarasaurus	*C. grandis, C. lentus, C. lewisi, C. supremus*	Cope (1877b), Marsh (1877), Marsh (1889), Jensen (1988)
Diplodocus	*D. carnegii, D. hallorum, D. longus*	Marsh (1878), Hatcher (1901), Gillette (1994)
Dystrophaeus	*D. viaemalae*	Cope (1877a)
Galeamopus	*G. hayi, G. pabsti*	Holland (1924), Tschopp et al. (2015), Tschopp and Mateus (2017)
Haplocanthosaurus	*H. delfsi, H. priscus*	Hatcher (1903a), Hatcher (1903b), McIntosh and Williams (1988)
Kaatedocus	*K. siberi*	Tschopp and Mateus (2013)
Maraapunisaurus	*M. fragillimus*	Cope (1878), Carpenter (2018)
Smitanosaurus	*S. agilis*	Marsh (1889), Whitlock and Wilson (2020)
Supersaurus	*S. vivianae*	Jensen (1985)
Suuwassea	*S. emilieae*	Harris and Dodson (2004)

CONCLUSION

From the current paleobiological data, the sauropod genus *Haplocanthosaurus* is restricted to the northwestern and central regions of the Morrison Formation. Temporally, *Haplocanthosaurus* is known from the middle and upper parts of the defined Morrison Formation and potentially, based on undifferentiated strata (i.e., not able to be correlated within the Tidwell, Salt Wash, or Brushy Basin Members), may be found throughout nearly the entirety of the formation stratigraphically. Whereas more detailed description and identification of some of the aforementioned specimens are needed, the current evidence illustrates that *Haplocanthosaurus* was more geographically and stratigraphically widespread than previously known, and there is currently support for high species diversity within this genus.

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