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## A SUBADULT MAXILLA OF A TYRANNOSAURIDAE FROM THE TWO MEDICINE FORMATION, MONTANA, UNITED STATES

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### ABSTRACT

*Daspletosaurus* is a Campanian genus of Tyrannosauridae from North America. This genus occupied the same geographic area of *Albertosaurus*, but remains of *Albertosaurus* are more abundant than *Daspletosaurus*. Here is described a subadult maxilla (AMNH FARB 5477) of *Daspletosaurus* sp. from Montana (USA) and possibly from the Two Medicine Formation. The description is based on Carr (1999) that described cranial ontogenetic variations in tyrannosaurids. The maxilla belongs to the ontogenetic Stage 3 sensu Carr (1999), in which the maxilla is thick, the lateral surface of the bone well sculptured, and the maxillary fenestra is subcircular and well separated from the anterior edge of antorbital fossa. Possibly there were more than one species of *Daspletosaurus* and the locality of the here described subadult specimen suggests that *Daspletosaurus* species occurred more southern than *Albertosaurus*.

KEY-WORDS: *Daspletosaurus*; Ontogeny; North America; Montana.

### INTRODUCTION

*Daspletosaurus* is a genus of non-avian theropod erected by Russell (1970) for many materials mainly from the Oldman Formation near Steeveville, Alberta. This genus is deeply nested within Tyrannosauridae (Brusatte *et al.*, 2010; Loewen *et al.*, 2013; Lü *et al.*, 2014) and occupied the same geographic area as *Albertosaurus*, although *Daspletosaurus* constitutes a much more robust form of Campanian tyrannosaurid than the latter taxon (Russell, 1970; Farlow & Planka, 2002). However, the remains of *Albertosaurus* are more abundant than *Daspletosaurus* even among juvenile individuals (Carr, 1999; Farlow & Planka, 2002; Currie, 2003). These two taxa occupied the northern of the continental area of Laramidia during the Late Cretaceous (Loewen *et al.*, 2013), but *Albertosaurus*

was more abundant further north than *Daspletosaurus* (Farlow & Planka, 2002; Currie, 2003). Farlow & Planka (2002) therefore suggested that *Albertosaurus* lived and nested within the northern regions of the continent whereas *Daspletosaurus* was restricted to more southern latitudes.

Carr (1999) described cranial ontogenetic variations in *Albertosaurus* and taxonomic differences among the tyrannosaurids *Albertosaurus*, *Daspletosaurus* and *Tyrannosaurus*. Carr (1999) identified four ontogenetic stages that can be recognized in the cranial elements. Though remains of juveniles and subadults of *Daspletosaurus* are scarcer compared to those of *Albertosaurus*, there are still abundant samplings of the former genus. Here I describe a new subadult maxilla of *Daspletosaurus* sp. from Montana, possibly from Two Medicine Formation.

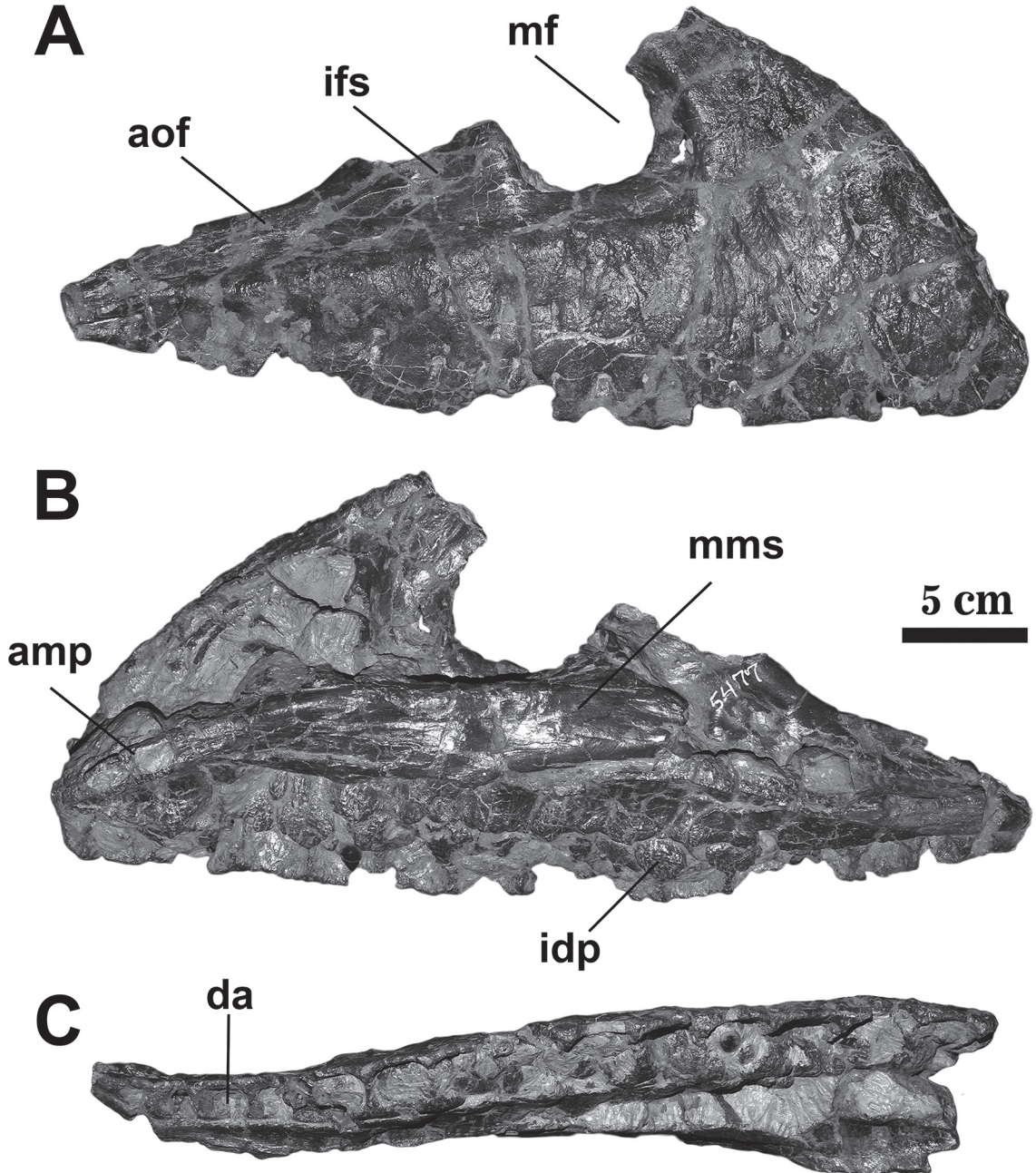
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### Institutional Abbreviations

**AMNH FARB**, American Museum of Natural History, New York; **BHI**, Black Hills Institute of Geological Research, Hill City, South Dakota; **BYU**, Brigham Young University Museum of Paleontology, Provo, Utah; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **GIN**,

Institute of Geology, Ulaanbaatar; **MOR**, Museum of the Rockies, Bozeman, Montana; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **TMP**, Royal Tyrell Museum of Paleontology, Drumheller, Alberta; **UMNH**, Utah Museum of Natural History, now the Natural History Museum of Utah, Salt Lake City, Utah; **USNM**, National Museum of Natural History, Smithsonian Institute, Washington DC.



**FIGURE 1:** Right maxilla of *Daspletosaurus* sp. (AMNH FARB 5477). In, (A) lateral, (B) medial and (C) ventral view. **amp**, anteromedial process; **aof**, anteorbital fossa; **da**, dentary alveoli; **idp**, interdentary plates; **ifs**, interfenestral strut; **mf**, maxillary fenestra; **mms**, medial maxillary shelf.

## SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842  
 Theropoda Marsh, 1881  
 Tyrannosauroida Walker, 1964  
 Tyrannosauridae Osborn, 1906  
*Daspletosaurus* sp. Russell, 1970

## Material

AMNH FARB 5477. An incomplete right maxilla, lacking the distal end of the ascending process and some areas of the jugal ramus (= horizontal ramus) (Figure 1).

## Locality

The exact locality of AMNH FARB 5477 is missing. However, it is known from AMNH number, that the maxilla came from Montana, USA. Montana has two Campanian formations: the Two Medicine and Judith River formations (Eberth, 1997) (Figure 2). Remains of *Daspletosaurus* were recovered only from the Two Medicine Formation in USA (Weishampel *et al.*, 2004). Thus, it is more plausible to suppose that AMNH FARB 5477 belongs to this unit. The Two Medicine Formation has yielded multiple *Daspletosaurus* specimens (Varricchio, 2001; Currie, 2003; Currie *et al.*, 2005).

## Description and comparisons

The maxilla (AMNH FARB 5477) is incomplete, lacking the distal extremities of ascending ramus and jugal ramus (= horizontal ramus). The medial wall of the antorbital fossa is also partially preserved and, as a result, the borders of the maxillary foramen are incomplete. It has a preserved length of 38.42 centimeters and is dorsoventrally deep. The tooth row is convex in lateral view and moderately damaged, but all fifteen alveoli are preserved.

The maxilla is transversely thick especially in the anterior portion. The maxillary body is sculptured with large foramina and deep dorsoventral neurovascular sulci as seen in advanced ontogenetic stage of *Daspletosaurus* (Carr, 1999). The neurovascular sulci are concentrated on the anterior end of the jugal ramus and are more abundant than in *Albertosaurus libratus* (AMNH 5336; AMNH 5458; AMNH 5432), *Bistahieversor* (NMMNH 27469), *Teratophoneus* (BYU 8120/9402; UMNH VP 16690, Loewen *et al.*, 2013: fig. 3A) and *Lythronax* (Loewen *et al.*, 2013: fig. 2C), but similar to *Daspletosaurus* (FMNH PR 308; TMP 94.143.1 [Currie, 2003]; MOR 590, TMP 2001.36.1) and *Tyrannosaurus* (AMNH 2750; USNM 4811033; FMNH 2081; BHI 3033). There are two parallel rows of foramina dorsal to the alveolar margin, as occurs in *Albertosaurus*, *Alioramus*, *Daspletosaurus* and *Tyrannosaurus*

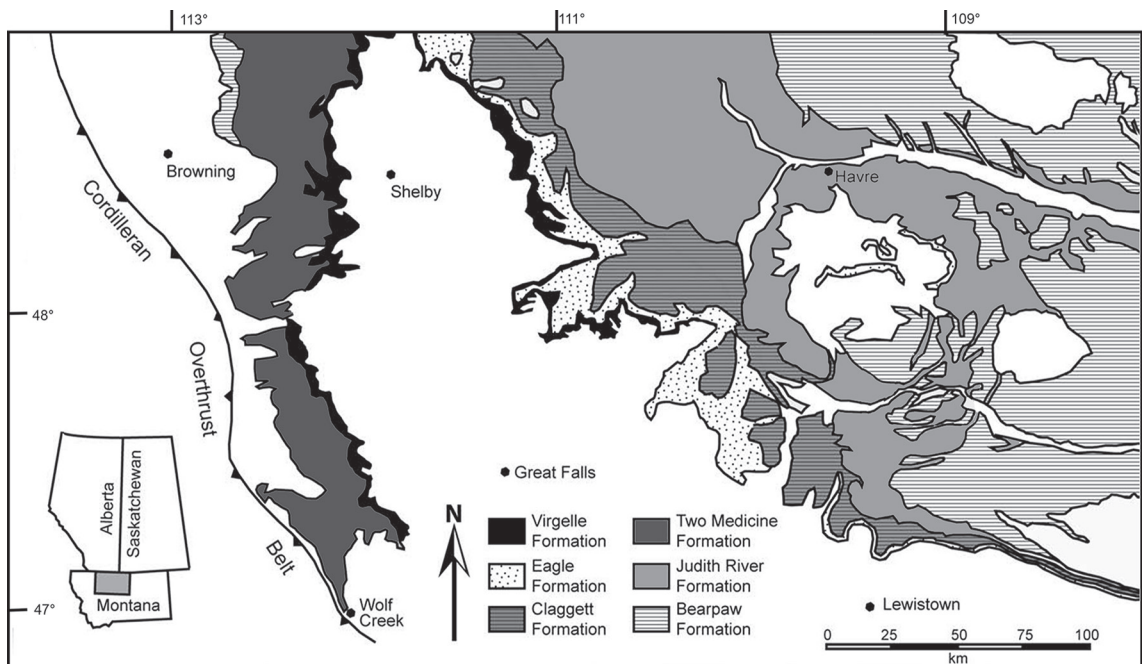


FIGURE 2: Map of Upper Cretaceous units in northwestern and north-central Montana showing the Two Medicine and Judith River formations (after Rogers *et al.*, 2010). The exact locality of AMNH FARB 5477 is missing, but possibly it belongs to the Two Medicine Formation (see text).



(Currie, 2003). The antorbital fossa is smooth as in other tyrannosaurids, with the lateral interfenestral strut being proportionally wider than that observed in *Albertosaurus*. This strut is damaged, reaching only the midpoint of the maxillary fenestra. However, its morphology resembles an hourglass shaped as in others tyrannosaurids.

The maxillary fenestra of AMNH FARB 5477 is incomplete and seemingly was subcircular, contrasting with more elongated maxillary fenestra of *Daspletosaurus* (MOR 590, CM 8506, TMP 2001.36.1), but similar to TMP 94.1431, AMNH 5432, BHI 3033, UMNH VP 16690, NMMNH 27469 and *Appalachiosaurus* (Carr *et al.*, 2005: fig. 6A). It does not contact the anterior and posterior border of this fossa as seen in *Tyrannosaurus* and *Tarbosaurus* (Larson, 2013). As in *Daspletosaurus* (MOR 590, TMP 2001.36.1, CM 8506: Carr, 1999: fig. 2G), juvenile *Tarbosaurus* (GIN 100/177) and *Shanshanosaurus huoyanshanensis* (Carr & Williamsom, 2004) the maxillary fenestra of AMNH FARB 5477 is separated from the anterior edge by a narrow apron of bone. In *Appalachiosaurus*, *Albertosaurus* (Carr *et al.*, 2005), juveniles *Tyrannosaurus* and *Daspletosaurus* (Carr & Williamsom, 2004), *Bistahieversor*, *Alioramus altai* (Brusatte *et al.*, 2012), *Lythronax* and *Teraphoneus* (Loewen *et al.*, 2013) all display a maxillary fenestra that is separated from the border by a proportionally wider apron of bone.

The promaxillary fenestra is covert in lateral view by the lateral lamina of the ascending ramus, as in *Tyrannosaurus*, *Tarbosaurus*, *Daspletosaurus* and *Eotyrannus* (Brusatte *et al.*, 2010). Although this fenestra is filled with matrix and the anterior rim of the antorbital fossa is damaged, AMNH FARB 5477 shows a foramen-like promaxillary fenestra, as occurs in adults of *Daspletosaurus*, *Tyrannosaurus* and *Tarbosaurus*, whereas this fenestra is more developed in *Albertosaurus* and *Bistahieversor*.

The vestibular bulla, between the subnarial foramen ventrally and the contact surface for the premaxilla dorsally (broken in AMNH FARB 5477), is well developed and convex in transverse section as in *Daspletosaurus* and *Tyrannosaurus* whereas in juveniles and subadults of *Albertosaurus* is laterally flat or transversely convex (Carr, 1999). The subnarial foramen is a notch anterior to the row of foramina and dorsal to the margin of the premaxillary buttress as seen in others tyrannosaurids.

The medial surface of the bone is damaged, but preserves the anteromedial process, medial maxillary shelf and the interdental plates. The medial bounding wall of the maxillary antrum was lost after the death of the animal as it is in *Alioramus altai*, *Daspletosaurus*

(TMP 97.12.223) and *Albertosaurus* (ROM 1247), however, this wall is present in diverse tyrannosaurids (Brusatte *et al.*, 2012).

The interdental plates are large and unfused as in *Daspletosaurus* as showed by Carr (1999), *Alioramus altai* showed by Brusatte *et al.* (2012), *Tarbosaurus* showed by Hurum & Sabath (2003), *Tyrannosaurus*, *Raptorex* and *Albertosaurus*. The plates possess striations on its medial surface and become reduced triangles posteriorly and ventral to articular facet for palatine as seen in derivatives tyrannosaurids (Brusatte *et al.*, 2012).

The anteromedial process (= palatal process) is damaged and the grooves on its surface are poorly preserved. It starts ventrally to the third alveoli and a more ventral inclination is more accentuated in AMNH FARB 5477, *Daspletosaurus*, *Albertosaurus*, *Tarbosaurus*, *Tyrannosaurus* and *Appalachiosaurus* (Carr *et al.*, 2005: fig. 6) than in *A. altai* and *Raptorex*. The grooves progressively pinch out posteriorly merging to the medial maxillary shelf.

The medial shelf is robust, flat and well developed reaching, its greatest dorsoventral height below the maxillary fenestra as in others tyrannosaurids (*e.g.*, *Tarbosaurus*, *Daspletosaurus* and *Tyrannosaurus*). The medial shelf is preserved just in the midpoint of the interfenestral strut and reveals the posterior anteromaxillary fenestra ventral to the posterior edge of the antorbital fenestra. This fenestra is rounded and its diameter is nearly half of the anteroposteriorly length of the interfenestral strut.

The medial shelf becomes posteriorly the articular facet for the palatine (Brusatte *et al.*, 2012); however, in AMNH FARB 5477 this structure is not preserved, neither the jugal articulation of maxilla.

As seen above AMNH FARB 5477 has 15 tooth positions. This number varies among derived tyrannosaurids. There are 11-12 alveoli in *Tyrannosaurus*, 12-13 in *Tarbosaurus*, 13-17 in *Daspletosaurus*, 13-15 in *Albertosaurus* (see Currie, 2003), 15 in *Appalachiosaurus* (Carr *et al.*, 2005), 12 in *Teratophoneus* (Carr *et al.*, 2011), 17 in *Alioramus altai* (see Brusatte *et al.*, 2012), and 11 in *Bistahieversor* and *Lythronax* (see Loewen *et al.*, 2013). There are preserved two replacement teeth on the third and the fifth alveoli. They are flattened labiolingually as seen in others tyrannosaurids. It is not possible to see others replacement teeth, however, it is possible that they are covered by matrix.

## DISCUSSION

AMNH FARB 5477 has more characters shared with *Daspletosaurus* than others tyrannosaurids. The

combination of abundance of anterior neurovascular sulci, number of maxillary teeth, promaxillary foramen-like covert, narrow separation between maxillary fenestra and anterior edge of antorbital fossa, wide interfenestral strut, and, finally, vestibular bulla well developed and convex in transverse section argues for referral of AMNH FARB 5477 to *Daspletosaurus* sp.

The estimated total length of AMNH FARB 5477 (~ 48 cm) suggests that it was an immature individual possibly in the ontogenetic Stage 3 of Carr (1999) with subcircular maxillary fenestra as in TMP 94.143.1 instead of elongated as in mature individuals (CM 8506, TMP 2001.36.1 and MOR 590), and greater distance from the anterior edge of antorbital fossa. However, AMNH FARB 5477 shows characters of mature individuals, such as maxilla thickened and lateral surface well sculptured (Carr, 1999).

*Daspletosaurus* and *Albertosaurus libratus* coexistent and occupied the northern of Laramidia whereas the others Campanian tyrannosaurs (*Bistahieversor*, *Lithronax* and *Teratophoneus*) occupied the southern region (Loewen *et al.*, 2013). AMNH FARB 5477 was recovered from Montana, but it was not possible to recognize the geological formation that this material belongs (Two Medicine Formation or Judith River Formations). Nevertheless, *Daspletosaurus* remains were recovered only in Two Medicine Formation so far (Weishampel *et al.*, 2004).

Possibly there were more than one species of *Daspletosaurus* (Farlow & Planka, 2002; Currie, 2003; Holtz, 2004) and seemingly the species from Oldman Formation, Dinosaur Park Formation (both from Alberta, Canada) and Two Medicine Formation (Montana, USA) were three different species (Currie, 2003). If there were at least three different species of *Daspletosaurus* and the fact that AMNH FARB 5477 is a subadult individual, shows that the *Daspletosaurus* species may have distributed more to the south than the others genus, whereas *Albertosaurus* lived and nested north, as suggested by Farlow & Planka (2002).

## CONCLUSIONS

The specimen AMNH FARB 5477 is here best considered as *Daspletosaurus* sp. The size, subcircular maxillary fenestra with greater distance from the anterior edge of antorbital fossa, and maxilla thickened and lateral surface well sculptured suggest that AMNH FARB 5477 was a subadult individual in ontogenetic Stage 3 of Carr (1999). The locality of the subadult specimen also suggests that this *Daspletosaurus* species nested southernmost than *Albertosaurus*.

## RESUMO

*Daspletosaurus* é um gênero de *Tyrannosauridae* do Campaniano da América do Norte. Esse táxon ocupou a mesma área geográfica que *Albertosaurus*, no entanto restos de *Albertosaurus* são mais abundantes que *Daspletosaurus*. Aqui é descrito um maxilar de um indivíduo sub-adulto (AMNH FARB 5477) do gênero *Daspletosaurus* sp. de Montana (EUA) e possivelmente da Formação Two Medicine. A descrição é baseada em Carr (1999) que descreveu a variação ontogenética craniana em tiranossaurídeos. O maxilar foi reconhecido como estágio ontogenético 3 de Carr (1999), o qual possui fenestra maxilar sub-circular com grande distância a partir da borda anterior da fossa anteorbital, e maxilar robusto com superfície lateral bem esculpida. Possivelmente existiram mais de uma espécie de *Daspletosaurus* e a localidade do espécime sub-adulto sugere que essa espécie de *Daspletosaurus* viveu mais ao sul *Albertosaurus*.

**PALAVRAS-CHAVE:** *Daspletosaurus*; Ontogeny; North America; Montana.

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