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HINDLIMB ALLOMETRY IN THE LATE JURASSIC THEROPOD DINOSAUR *ALLOSAURUS*, WITH COMMENTS ON ITS ABUNDANCE AND DISTRIBUTION

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Abstract—A partial skeleton of a juvenile *Allosaurus*, from the Morrison Formation of the Black Hills of northeastern Wyoming, is the smallest associated skeleton of the genus yet reported (femur length = 274 mm). This specimen allows comparison of hindlimb proportions with sub-adult and adult specimens with articulated or associated hindlimb elements. Proportions of the femur, tibia, and metatarsal indicate that juvenile *Allosaurus* had relatively long effective leg lengths compared to adults. The tibia and metatarsal IV are each longer relative to the femur than in adult specimens, and the femur is longer relative to the ilium. The combined length of the femur, tibia, and metatarsal is 33% greater, relative to ilium length, than in adults. Higher cursoriality in juveniles may have assisted in competing with adults of small theropod species for small vertebrate prey, although longer relative leg lengths of juveniles of other reptiles indicate that this may not necessarily have been the only reason for the allometric growth of the limbs.

INTRODUCTION

The theropod genus *Allosaurus* is one of the more common members of the dinosaur fauna of the Upper Jurassic Morrison Formation of the western United States. *Allosaurus* is one of eleven theropod genera in the formation, but it accounts for nearly 75% of the theropod specimens (Foster and Chure, 1998). Although juvenile theropod specimens are relatively rare in the Morrison Formation, the Dry Mesa Quarry in Colorado has produced the proximal half of a very small femur of *Allosaurus* (17mm proximal width, BYU 12892). The Cleveland–Lloyd Quarry in Emery County, Utah, has yielded disarticulated juvenile *Allosaurus* material, including one of the smallest femora known for the genus (femur length 245 mm, UUVP 6023) (Madsen, 1976, p. 43, table 5). However, the disarticulation of the Cleveland–Lloyd material prevents positive association of elements from a specific age category and precludes examination of allometric differences in limb proportions between separate elements of different age categories.

A partial and disarticulated but associated specimen from the Black Hills of northeastern Wyoming is the most complete small juvenile *Allosaurus* yet discovered and provides insights to the relative proportions of the hindlimbs compared to larger individuals. We compared the lengths and proportions of the Black Hills juvenile to several articulated or associated sub-adult and adult *Allosaurus* specimens in order to determine to what degree the proportions of the hindlimb changed with increasing size.

Abbreviations: AMNH, American Museum of Natural History, New York; DINO, Dinosaur National Monument, Jensen; MCZ, Museum of Comparative Zoology, Cambridge; MOR, Museum of the Rockies, Bozeman; SDSM, South Dakota School of Mines & Technology, Rapid City; USNM, Smithsonian National Museum of Natural History, Washington, D.C.

MATERIALS

SAURISCHIA (Seeley, 1887)

THEROPODA (Marsh, 1881)

ALLOSAURIDAE (Marsh, 1879)

ALLOSAURUS SP. (Marsh, 1877)

Referred specimen.—SDSM 30510, partial skeleton including a tooth, partial basicranium (still in preparation), three cervical vertebrae, one dorsal vertebra, two sacral vertebrae, at least four caudal vertebrae, a manual phalanx and ungual, several ribs, both ilia, an ischium, femur, tibia, metatarsal IV, and several pedal phalanges and unguals (Fig. 1); from the Little Houston Quarry (SDSM locality V9138), Morrison Formation (Upper Jurassic), Crook County, Wyoming.

Comparative material.— AMNH 6125; USNM 4734; AMNH 680; MCZ 3897; MOR 693; and DINO 3984. These are *Allosaurus* specimens with hind limb elements, some with at least one ilium.

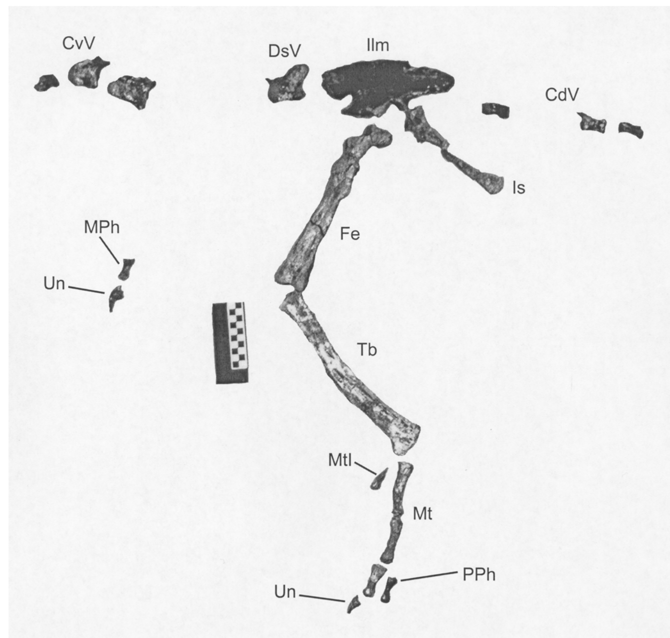

FIGURE 1. Elements of juvenile *Allosaurus*, SDSM 30510, showing relatively long hind limbs. CvV, cervical vertebrae; DsV, dorsal vertebrae; Ilm, ilium; CdV, caudal vertebrae; Is, ischium; Fe, femur; MPh, manual phalanx; Un, unguals; Tb, tibia; MtI, metatarsal I; Mt, metatarsal IV; PPh, pedal phalanges. Scale bar = 10cm.

Discussion.—SDSM 30510 (Fig. 1) was found in a gray-green, silty mudstone stratigraphically above and slightly lateral to an abandoned channel deposit at the Little Houston Quarry in the Morrison Formation of the northwestern Black Hills (unit 4 in a stratigraphic section by Foster and Martin, 1994). Associated taxa from the same excavation as the juvenile *Allosaurus* include turtles, elements of a juvenile sauropod, and the lungfish *Ceratodus*.

The disarticulated elements of the *Allosaurus* were found in an area slightly over 1m^2 (Fig. 2). Although other taxa were found at the same level less than 1m away, these were not significantly intermixed, and there was no repetition of *Allosaurus* elements. All elements matched in size and thus they belong to an associated skeleton of a single individual.

Preservation on SDSM 30510 varies from highly fractured ilia and femur to well preserved ischium, phalanges, and basicranium.

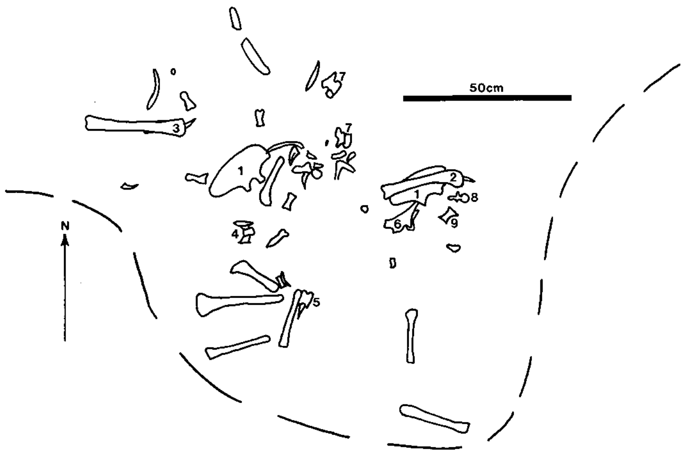

FIGURE 2. Quarry map of juvenile *Allosaurus* specimen SDSM 30510. Individual elements include: 1) Ilia, 2) Femur, 3) Tibia, 4) Sacral vertebra, 5) Basicranium, 6) Ischium, 7) Cervical vertebrae, 8) Dorsal vertebra, and 9) Caudal vertebra. Dashed line is edge of excavation.

The adult and sub-adult *Allosaurus* specimens used for comparison (Table 1) include two adults from Bone Cabin Quarry, an adult from Marsh-Felch Quarry, sub-adults from Dinosaur National Monument and northern Wyoming, and a juvenile from Utah. Most of these larger specimens are partial skeletons and contain nearly complete hindlimbs.

RESULTS

The measurements of the specimens indicate a change in proportions of the hindlimb in *Allosaurus* during ontogeny. In particular, during growth into adulthood, the tibia becomes shorter relative to the femur and metatarsal IV becomes shorter relative to the tibia. Based on comparison with data in Coombs (1978), the proportions of the tibia, femur, and metatarsal in adult *Allosaurus* are roughly similar to those of modern subcursorial animals, whereas the proportions in young juvenile *Allosaurus* (SDSM 30510) are closer to those of modern quadrupedal cursorial animals (Fig. 3). The distribution of *Allosaurus* datum points in Figure 3 also shows the trend toward lower tibia/femur and metatarsal/tibia ratios in larger individuals, as those specimens to the lower left in the graph are larger overall than those above and to the right. Holtz (1994) plotted similar data for a number of different theropods on a graph also based on Coombs' modern data, and in this plot it is clear that adult members of the Allosauridae had the lowest tibia/femur and metatarsal/tibia ratios among theropods, suggesting low cursoriality. In Holtz's (1994) graph the Coelophysidae had ratios similar to those of SDSM 30510.

A schematic diagram of the hindlimb proportions of several of the *Allosaurus* specimens, all scaled to the same ilium length (Fig. 4), demonstrates the longer effective leg lengths of the juvenile specimen (SDSM 30510). In particular, the tibia and metatarsal are longer relative to the femur than in larger specimens. MCZ 3897 is missing the metatarsals but seems to have an unusually short femur and tibia relative to the ilium, and this specimen may be anomalous. It is, however, the next-smallest associated *Allosaurus* specimen with a well preserved hind limb after SDSM 30510, and if it instead had slightly longer hindlimb elements, similar in proportions to those of the adult specimens, it would seem to indicate that "adult" hindlimb proportions were reached in these theropods by a femur length of about 43 cm.

The *Allosaurus* specimen ratios were also plotted with the theropod dinosaur data of Coombs (1978) (Fig. 5). It is apparent that most *Allosaurus* specimens plot among the ratios of the large theropods, whereas SDSM 30510 is similar in ratios to *Coelophysis* and other small theropods. Coombs' data also indicate that the main difference in proportions of the hindlimb between large theropods and large ornithopods is the greater length

TABLE 1. Length measurements of *Allosaurus* specimens used in this study. In millimeters. *=Estimated.

Specimen	Quarry	Ilium	Femur	Tibia	Metatarsal IV
AMNH 6125	Bone Cabin	–	868	758	325
USNM 4734	Marsh-Felch	–	850	690	275
AMNH 680	Bone Cabin	808	1008	856	342
DINO 3984	Dino. Nat'l Mon.	–	605	555	254
MOR 693	Big Al	640	748	665	286
MCZ 3897	Willow Springs	398	428	371	~159*
SDSM 30510	Little Houston	200	274	295	148

of metatarsal III compared to the tibia in large theropods. The tibia/femur ratios in these two groups have a similar range.

DISCUSSION

The longer leg lengths (relative to ilium length) of SDSM 30510 compared with sub-adult and adult specimens suggests that young juveniles of *Allosaurus* were more cursorial. Relatively longer limbs have also been found in juveniles of the modern crocodilian *Alligator* (Dodson, 1975); these animals are more semi-aquatic as adults and are far less dependent on their hindlimbs than theropods would have been. Colbert (1989) found that smaller individuals of *Coelophysis* had longer hindlimbs relative to the presacral vertebral column than adults, and Russell (1970) has indicated that young albertosaurs likely had relatively long hind limbs as well, so the trend certainly is not unique to *Allosaurus* among theropods. The low tibia/femur and metatarsal III/tibia ratios of adult allosaurids (Holtz, 1994) indicate that, unlike juveniles, adult *Allosaurus* were among the least cursorial theropods. Christiansen (1999), in a study of long bone scaling, also noted that small and juvenile theropods were likely more highly cursorial than their larger adult counterparts. Loewen et al. (2002) found that young allosaurs also had more circular femoral cross-sections than their adult counterparts and suggested that this was due to differences in locomotor function. Specifically, the juvenile *Allosaurus* may have had more multi-directional loads and stresses on the hind limb, associated with agile running not just in a straight-forward direction. This would appear compatible with juveniles preying on small vertebrates.

The differences in limb proportions between juvenile and adult *Allosaurus* suggest different cursorial capabilities and possibly different predation strategies. Whereas juveniles, along with adults of smaller theropods such as *Ornitholestes* and *Coelurus*, were likely chasing small vertebrate prey, Christiansen (1999) has suggested that larger adult theropods such as *Allosaurus* may not have had a suspended stage to their stride, although this did not mean they necessarily were slow animals (Christiansen, 1998). It is possible therefore that *Allosaurus* may have been agile, cursorial hunters of small vertebrate prey as young juveniles, but as they became as large or larger than many of their presumed non-sauropod prey taxa, they may have switched to being more ambush-type predators. This probably occurred in early adulthood. Adults may have used short, forward dashes to catch mid-sized dinosaurs and may have employed their fore limbs extensively in securing prey items (the grasper-clutcher strategy of Carpenter, 2002). Therrien et al. (2005) found differences in the lower jaws of adult and juvenile *Allosaurus* also suggesting differences in feeding styles.

Allosaurus is the only theropod genus to occur widely throughout the formation both stratigraphically and geographically. More than 150 specimens are known from a total of 100 localities in all but one of the states in which the Morrison is exposed. Other taxa are somewhat less

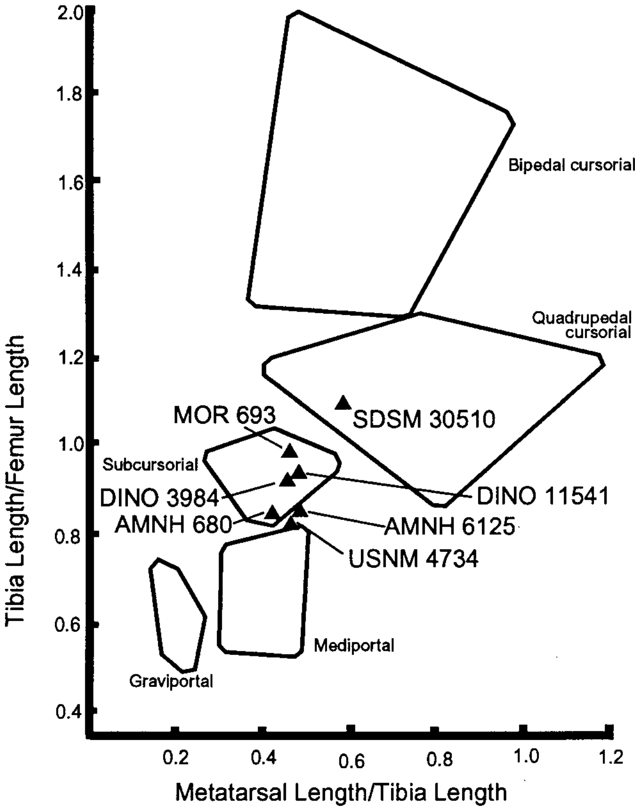

FIGURE 3. Hindlimb element ratios for *Allosaurus* specimens measured in this study compared to ranges for modern animals as graphed by Coombs (1978). SDSM 30510 x-axis ratio based on metatarsal IV (the only one preserved), others are metatarsal III.

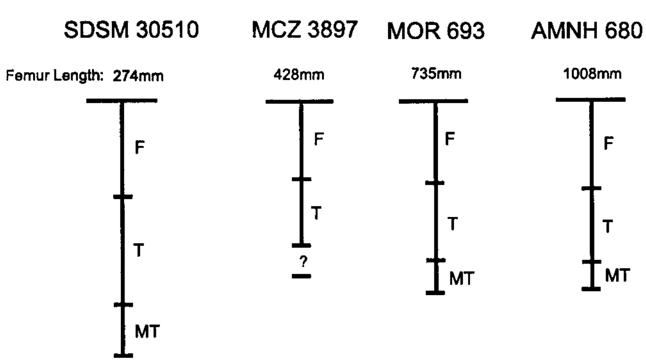

FIGURE 4. Schematic diagram representing hindlimb element lengths for juvenile to adult *Allosaurus*, all scaled to the same ilium length. Specimens are arranged smallest to largest left to right. Total effective leg length, tibia length, and metatarsal length are all greater relative to the ilium and femur in the smallest individual (SDSM 30510). The tibia:femur ratio is greater than 1 only in SDSM 30510. Ilium in each is top horizontal bar. F= femur; T= tibia; MT= metatarsal.

widespread and are numerically rare. Within all stratigraphic levels and depositional environments, *Allosaurus* has a relative abundance of approximately 70% of all theropod specimens (Foster and Chure, 1998) and constitutes approximately 13% of all dinosaur specimens in the Morrison. *Allosaurus* was by far the most common theropod in the Morrison fauna as represented by straight counts of specimens (70% of theropod sample), adjusted theropod population percent (49%), and adjusted theropod biomass percent (81%) (these latter two calculated using the method of Russell, 1989). After *Allosaurus*, the next most abundant theropods in the formation were *Coelurus*, *Torvosaurus*, and *Ceratosaurus*.

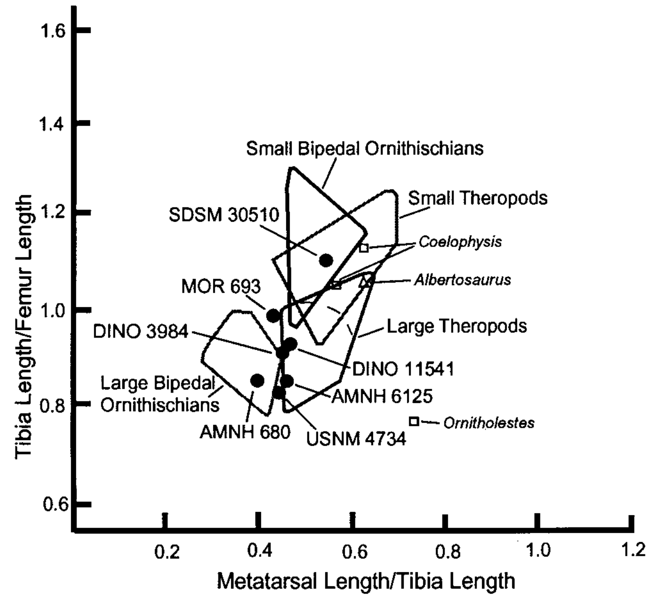

FIGURE 5. Hindlimb element ratios for *Allosaurus* specimens measured in this study compared to ranges for other dinosaur groups based on data in Coombs (1978). *Allosaurus* specimens are represented by filled circles with specimen numbers; size of the specimens generally decreases downward. SDSM 30510 x-axis ratio based on metatarsal IV (the only one preserved), others are metatarsal III.

The possibly drought-induced collection at the Cleveland-Lloyd Quarry (Gates, 2005; see also Hunt et al., this volume) has yielded about half the theropod genera known from the Morrison Formation (*Allosaurus*, *Ceratosaurus*, *Stokesosaurus*, *Marshosaurus*, *Torvosaurus*, and *Tanycolagreus*), suggesting that ecological segregation between these carnivores was weak. This is further supported by the fact that *Allosaurus* is commonly found in quarries yielding other rare theropods elsewhere in the Morrison Formation. In fact, the other main large theropods in the Morrison Formation are almost always found with *Allosaurus*. *Ceratosaurus*, for example, is found with *Allosaurus* in 77% of the localities from which *Ceratosaurus* is known, and at the only sites at which it occurs without *Allosaurus*, it is the only vertebrate specimen found in the quarry. These lone occurrences of *Ceratosaurus* are not unique because 23% of *Allosaurus* localities contain only isolated, single skeletons. *Torvosaurus* occurs with *Allosaurus* at 63% of *Torvosaurus* sites. *Ceratosaurus* and *Torvosaurus* have never been found together without *Allosaurus*. Those three genera have been found together at the Dry Mesa, Cleveland-Lloyd, and Dinosaur National Monument quarries. Shed teeth belonging to *Allosaurus* and *Ceratosaurus* have been found together at several sites, and at the Mygatt-Moore Quarry in western Colorado these teeth are in among numerous sauropod bones (some exhibiting tooth marks) and allosaur teeth far out number ceratosaur teeth. At all sites where *Allosaurus* and *Ceratosaurus* are found together, *Allosaurus* out-numbers *Ceratosaurus* by an average of approximately 7.5 to 1.

These data all suggest geographic and environmental overlap of *Allosaurus* and *Ceratosaurus* but that *Ceratosaurus* was simply rarer. There appears to be no area or paleoenvironment in which *Ceratosaurus* was more abundant. *Torvosaurus* is often found with *Allosaurus*. However, it shows some indication of having been slightly more ecologically separated from other theropods (occurring as the only large theropod at a site 38% of the time). The data appear to support predatory niche partitioning among large Morrison theropods (Henderson, 1998) but indicate that this partitioning was neither environmental nor geographic and may have related more to feeding behavior. Feeding behavioral differences are possibly evidenced by differences in forelimb, tooth, and skull proportions between *Allosaurus* and *Ceratosaurus*. However, similarities in general bite force profiles suggest competition for similar prey overall (Henderson, 1998; Therrien et al., 2005). Large Morrison theropods appear to have been living in the same areas and environments, hunting the same general types of prey dinosaurs, yet possibly attacking/feeding/specializing slightly differently.

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