

THE UTILITY OF CLAW CURVATURE IN ASSESSING THE ARBOREALITY OF FOSSIL REPTILES

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Abstract—Claw curvature is a metric that has been used by some workers to argue for arboreality in fossil taxa. Here, we measure and report the claw curvature of three drepanosaurids (*Megalanosaurus*, *Drepanosaurus* and *Vallesaurus*) that have been interpreted as arboreal based on their specialized postcrania. The claw curvature of these drepanosaurids is relatively low when compared with other arboreal fossil taxa and extant birds. This suggests that arboreal reptiles without postcranial specializations require a high degree of claw curvature in order to gain purchase on inclined substrates, while otherwise highly specialized arboreal reptiles do not require highly curved claws. Thus, claw curvature should be considered along with other skeletal modifications when arboreality is assessed.

INTRODUCTION

Claw curvature is an infrequently used metric in the morphologic analysis of fossil taxa. However, Feduccia (1993) and Spielmann et al. (2005) have used this metric to argue that the primitive bird *Archaeopteryx* and the archosauromorph *Trilophosaurus*, respectively, were arboreal. Feduccia (1993) examined the claw curvatures of numerous bird taxa and noted three distinct ranges of curvature based on the whether the taxon was terrestrial or arboreal: ground-based birds with relatively low claw curvature (~38° to 95°), perching birds with moderate claw curvature (~89° to 148°) and climbing birds with high claw curvatures (~147° to 176°). These ranges are based on the data from figure 3 of Feduccia (1993) and are not the species averages but encompass all the individual claw data plotted. Accommodating the overlap of these ranges, five claw curvature intervals can be established: (1) ground-based, (2) ground/perching, (3) perching, (4) perching/climbing, and (5) climbing. Because the manual claws of *Archaeopteryx* fall in the perching/climbing and climbing intervals and the pedal claws fall in the perching/climbing interval, Feduccia (1993) concluded that *Archaeopteryx* was arboreal. Spielmann et al. (2005) used a similar argument, noting that all isolated claws of *Trilophosaurus* fall within the perching-climbing intervals, and thus fall outside the curvature interval of ground-based birds, furthering the argument that *Trilophosaurus* was arboreal.

Renesto and colleagues (Renesto and Paganoni, 1995; Renesto, 2000; Renesto and Binelli, 2006) have interpreted numerous Late Triassic drepanosaurids (*Drepanosaurus unguicaudatus*, *Megalanosaurus preonensis* and *Vallesaurus cenensis*) from the Zorzino Limestone of northern Italy as being arboreal, based on two separate but related bodies of data: numerous specializations of their postcranial skeletons and their claw morphology, including curvature and possession of a flexor tubercle. To test the utility of claw curvature as an indicator of arboreality – to see whether or not it concurs with interpretation of arboreality based on other postcranial characters – and whether the data set compiled by Feduccia (1993) can be directly applied to fossil reptile taxa, we examined the claw curvature of these Italian arboreal Late Triassic reptiles and plotted them on a graph of the five claw curvature intervals.

Pike and Maitland (2004) noted that claw geometry can be used to predict mode of life in birds; however, they utilized body mass in their calculations, something beyond the range of this current study. Also, predatory non-avian theropods have a high degree of claw curvature with no indication of arboreality (Chiappe, 1997). Thus, when dealing with basal archosauromorphs, it may prove useful in the future to compare them to extant lizards, instead of extant birds, though no robust data set for lizard claw curvature across a large size range currently exists. Thus, Feduccia's (1993) claw curvature data set is currently the best available

for assessing arboreality in fossil reptiles.

In this paper, MBSN & MCSNB = Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy; MFSN = Museo Friulano di Storia Naturale, Udine, Friuli, Italy; MPUM = Museo di Paleontologia Università di Milano, Milano, Italy.

MATERIAL AND METHODS

The various Italian specimens were photographed by one of us (SR) in views as mediolateral as possible given their two-dimensional preservation, in part and counterpart. These photographs were then printed out and claw curvatures measured using the protocols of Feduccia (1993, p. 790, fig. 1). This measuring protocol (Fig. 1A) was described as:

"A perpendicular (CD) is drawn to bisect the chord (AB) of the inner arc, which is itself bisected at the point X. Perpendiculars are drawn (EE' and E'E'') to bisect the chords AX and XB. These perpendiculars, when extended, meet at the center (E') of the circle of which the arc is a part. The radii are then drawn to each end of the arc (AE' and BE'). The angle (Y) between these radii (read directly from a protractor) is a measure of the degrees of the arc."

To establish the inner arc of the claws, a drafting compass was used. This inner arc measurement is based on the anterior two-thirds of each claw, because the flexor tubercle truncates the posterior inner arc (compare Fig. 1A with fig. 1 of Feduccia, 1993).

The only modification of this protocol was in the pes of *Drepanosaurus*, in which the claws do not terminate in well-defined points; instead, they end in divoted tips (Fig. 1B). In order to fully characterize this morphology, measurements were taken of both the inner and outer arcs of each claw (Figs. 1B, 2), the inner arc being defined as the posterior point of the divoted tip, and the outer arc being the anterior point of the divoted tip. These data are bracketed on the resulting graph. A difficulty in dealing with two-dimensionally preserved material is that a completely mediolateral view of the material is difficult to achieve, so the data we feel may not have yielded the most accurate measurements are marked with an asterisk in Figure 3.

Our measurements of the claws of *Drepanosaurus unguicaudatus*, *Megalanosaurus preonensis* and *Vallesaurus cenensis* are from the few specimens currently known. The *Drepanosaurus* measurements in this study are from the holotype (MCSNB 5728), a complete postcranial skeleton (Pinna, 1980, 1984). Unfortunately, only one manus is well preserved and visible in this specimen, and its digits overlap each other to such a degree that only the fourth and fifth unguals can be accurately

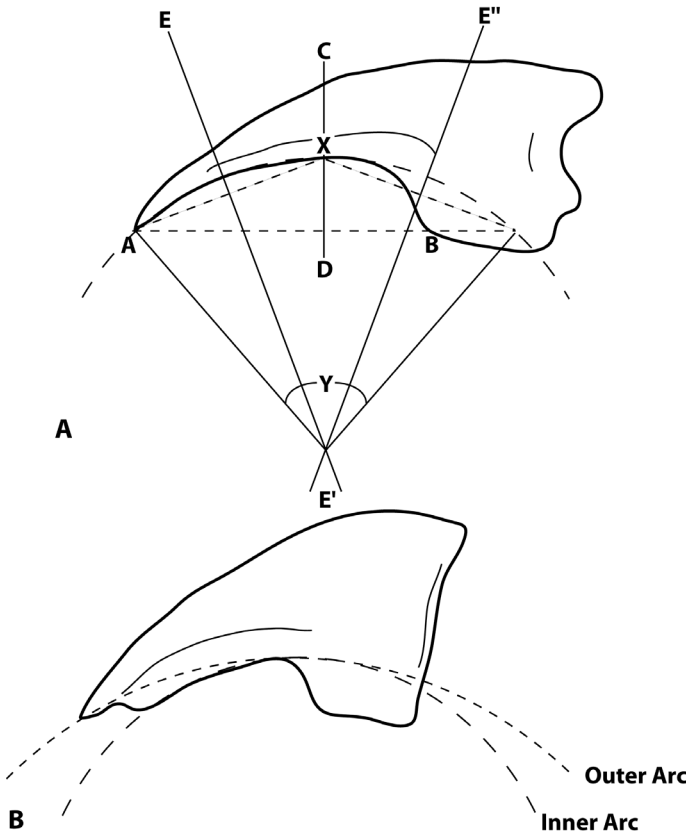


FIGURE 1. **A**, Claw curvature measuring protocols based on Feduccia (1993). Letters are explained in text. **B**, Modified measuring protocol for *Drepanosaurus* pedal unguals.

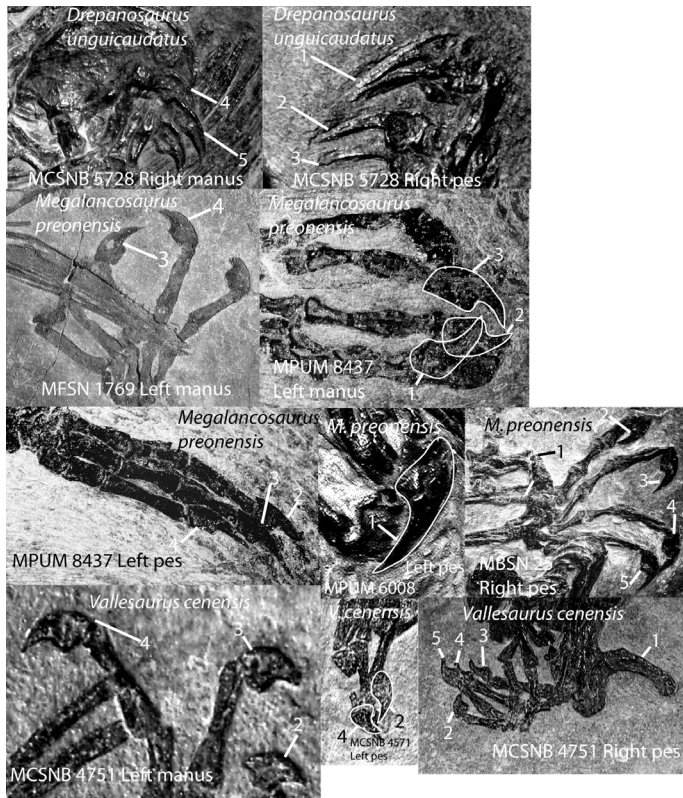


FIGURE 2. Visual atlas of all drepanosaur specimens examined in this study. Only those unguals measured or mentioned in text are labeled.

TAXON	SPECIMEN NUMBER	MANUS/PES	LEFT/RIGHT	DIGIT	OUTLINE DRAWING	CLAW CURVATURE		
<i>Drepanosaurus unguicaudatus</i>	MCSNB 5728	Manus	Right	4		75*		
				5		95		
		Pes	Right	1		72/57		
				2		72/75		
				3		89/95		
<i>Megalancosaurus preonensis</i>	MFSN 1769	Manus	Left	3		86		
	MPUM 8437	Manus	Left	1		98*		
				2		105		
				3		92		
	MPUM 6008	Manus	Right	1		91		
				2		73		
				3		73		
	MBSN 25	Pes	Right	4		79		
				5		90		
				1		62*		
				2		50		
				3		54		
	<i>Vallesaurus cenensis</i>	MCSNB 4751	Manus	Left	2		100	
					3		98	
					4		95	
2						106*		
MCSNB 4751		Pes	Left	Left	4		109	
					Right	2		86
						3		104
			4			106		
			MCSNB 4751	Pes	Right	5		110

FIGURE 3. Chart of drepanosaurid claw information and curvature.

measured (Fig. 2). The digits of its pes likewise overlap, allowing only the first through third unguals to be measured (Fig. 2).

Four *Megalancosaurus preonensis* specimens were examined for this study: the holotype (MFSN 1769) and three others (MPUM 8437, MPUM 6008, MBSN 25) (Calzavara et al., 1981; Renesto, 1994, 2000). The holotype of *M. preonensis* is the anterior half of an individual. However, its first and second unguals are obscured by the lower jaw, and the fifth ungual is incomplete, leaving only the third and fourth unguals measurable (Fig. 2). MPUM 8437 preserves both a manus and pes. However, the third digit in both the manus and pes overlap the fourth

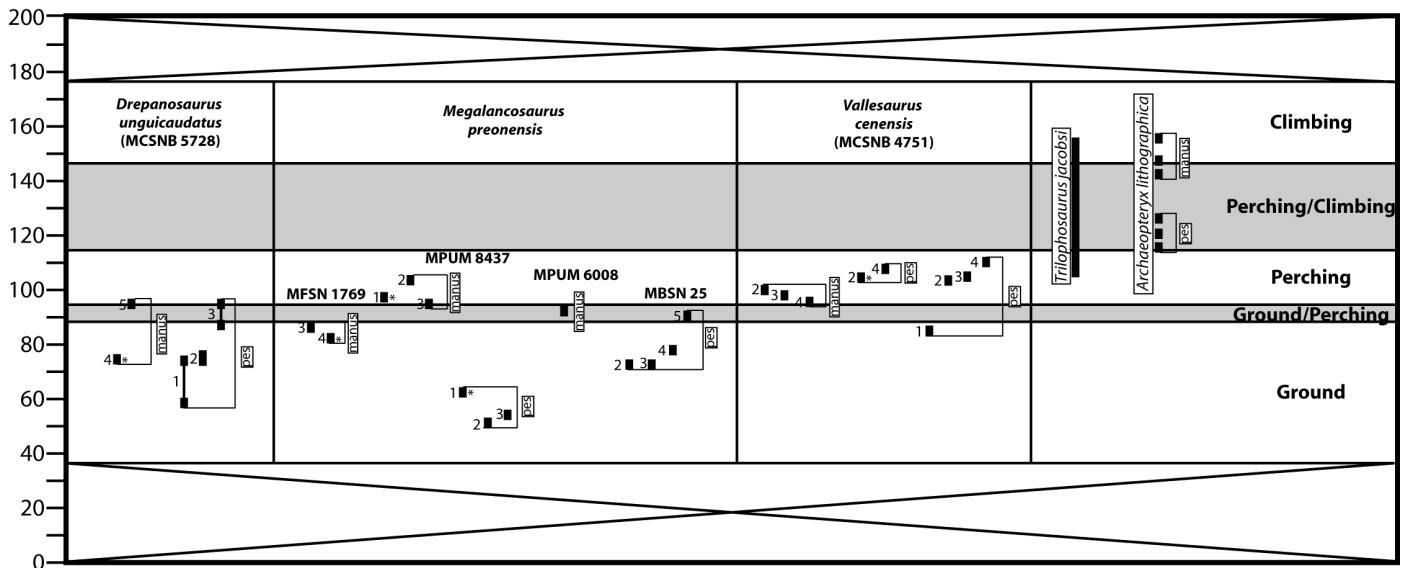


FIGURE 4. Graph of drepanosaurid claw curvatures plotted on curvature intervals of Feduccia (1993). The left column is the degree of curvature. Data points from a single manus or pes are grouped together, with the number next to each data point representing the digit.

and fifth digits, making only the first through third manual and pedal unguals measurable (Fig. 2). MPUM 6008 has a manus with digits that are so tangled that only the first ungual can be measured. MBSN 25 preserves a right pes in which the first pedal digit is modified, a condition seen in some *M. preonensis* specimens (Renesto, 2000), while the second through fifth unguals are measurable (Fig. 2).

Vallesaurus cenensis data comes from the holotype, MCSNB 4751, a nearly complete skeleton and the only known drepanosaurid with the complete skull articulated with the body (Renesto and Binelli, 2006). The manus of *Vallesaurus* is partially obscured by its rib cage, rendering only its second through fourth unguals measurable (Fig. 2). The pes of *Vallesaurus* has a modified first digit, so only the second through fifth unguals of the right pes can be measured, whereas in the left pes, only the second and fourth unguals are measurable (Fig. 2).

RESULTS

Our claw curvature analysis found that all three of the drepanosaurid taxa (*Drepanosaurus unguicaudatus*, *Megalancosaurus preonensis*, *Vallesaurus cenensis*) have low claw curvatures compared to *Trilophosaurus* and *Archaeopteryx*.

The holotype of *Drepanosaurus unguicaudatus* (MCSNB 5728) has manual unguals with curvatures in the ground-based interval (fourth ungual) and the ground/perching interval (fifth ungual) (Figs. 3-4). The pedal unguals (first through third unguals) fall within the same range (Figs. 3-4). Within this, individual claw curvature increases from inner to outer unguals.

The four *Megalancosaurus preonensis* specimens (MFSN 1769, MPUM 8437, MPUM 6008, and MBSN 25) have manual unguals with curvatures that span the upper ground-based through the mid-perching intervals (Figs. 3-4). The pedal unguals have lower curvatures, ranging from the low to mid-ground through the low ground/perching interval (Figs. 3-4).

The holotype of *Vallesaurus cenensis* (MCSNB 4751) has manual unguals with claw curvatures in the perching interval and pedal claw curvatures that range from the ground to perching interval (Figs. 3-4). Overall, *Vallesaurus* has the highest claw curvature, with only one ungual (digit 2 on the right pes) falling within the ground or ground/perching intervals. Also, in the pes of the holotype, claw curvature increases from the inner to outer unguals.

DISCUSSION

All three Italian drepanosaurids have low claw curvatures. Only *Vallesaurus* has claw curvatures that, with the exception of one ungual,

fall entirely outside the ground-based interval. This suggests two possibilities: either the claws of fossil reptiles cannot be directly compared to those of extant birds or that non-avian claw curvature cannot be correlated directly with arboreality.

Zani (2000), in his study of lizard claw and toe morphology, noted that all vertebrate claws are similar enough to allow for comparisons between species; thus, this negates the first possibility. Alternatively, Mertens (1942), in his study of varanid species, noted that arboreal varanids have increased claw curvature when compared to terrestrial species; this seemingly negates the second possibility. How can this be resolved? We suggest, based on our study, that arboreal climbers with unspecialized postcrania, such as varanids and *Trilophosaurus*, require higher degrees of claw curvature in order to gain purchase on inclined substrates, whereas arboreal climbers with highly modified postcrania, such as drepanosaurids, have additional ways of gaining purchase and moving within trees, making claw curvature less important components of their climbing behaviors.

This is further evident in our results: *Vallesaurus* is the least postcranially specialized of the three drepanosaurids examined, lacking the hook-like terminal caudal vertebra and the opposing digits of the manus. It thus required (and has) the highest claw curvatures. Proportionally, among the drepanosaurids, *Vallesaurus* has the smallest claws with the highest curvature, while other drepanosaurids have longer but less curved claws. *Megalancosaurus* and *Drepanosaurus* while possessing lower claw curvatures, have postcranial specializations of the manus, pes and tail that made them particularly adept at maneuvering in trees (Renesto and Paganoni, 1995; Renesto, 2000; Renesto and Binelli, 2006). This also applies to the American drepanosaurids: the more advanced *Dolabrosaurus* possesses *Megalancosaurus*-like (elongate and low curvature) claws while the more basal *Hypuronektor* has smaller claws with high curvature.

In summary, while claw curvature cannot be directly correlated with arboreality in non-avian reptiles, it nevertheless provides a useful metric in assessing the potential for a taxon to be arboreal. Claw curvature alone should not be depended upon to determine whether or not a fossil non-avian taxon was arboreal; such measurements should be balanced against other postcranial morphological features that independently suggest arboreality.

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