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Is the Astragalar Index a Valid Character for the Study of Giraffid Phylogeny?

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Abstract

Astragali are one of the most recovered skeletal elements as it can be seen in several of the most complete giraffid fossil collections. Even in sites where all the skeletal elements are well represented they tend to be one of the more abundant, making them a very valuable element for the identification and study of the taxa they belong to. Recent studies have shed light on the phylogenetic importance of the morphological features of the astragalus but not valuable quantitative parameters have been described yet. In this study we analyze several giraffid astragal biometric parameters to find out its phylogenetic relevance, in cases were the preservation does not allow an accurate morphological description.

Keywords: Astragalus; Giraffidae; Vertebrate; Mammalia; Morphology; Phylogeny

Introduction

The Giraffidae is a relict family with only two extant genera: *Giraffa* [1] and *Okapia* [2] in the past was more abundant and diversified, with more than 40 taxa spanning the past 20 million years (since the beginning of the early Miocene) [3-6]. Nevertheless, until recently only a few studies approached the description of their phylogenetic relationships [4,5], due to the lack of appropriate materials to build a solid character matrix and the scarcity of complete fossil giraffid skulls as well as the high intra- and interspecific variability of most of giraffid teeth [7,4] the postcranial skeleton has probed key to giraffid identification [6,8-10].

Giraffid astragali are part of the hind limb, and together with the cubonavicular the calcaneus and the ento-ectomeso cuneiform form the articulation of the tibia with the metatarsal III-IV [11]. As in the rest of artiodactyls, the astragalus of giraffids has a double pulley structure [6] that dorsally articulate with the distal tibia, plantarly with the cubonavicular and laterally to the calcaneus. The recent remarkable study on their morphology by Solounias, et al. [10] pointed out the importance of the study of tarsal morphology to make accurate identifications in giraffids as each giraffid astragalus exhibits a unique combination of anatomical characteristics. They also describe highly valuable morphological features that are very helpful to phylogeny and reinforce previously established phylogenetic relationships.

However in some cases the preservation of fossils does not allow for accurate anatomical descriptions and some important features are lost, and given the abundance of astragali in giraffid collections internationally we want to analyze the biometric parameters of several giraffid taxa in order to assess their phylogenetic relevance, since previous studies have probed biometrical features of high value [9].

Materials and Methods

The giraffid astragali analyzed in this work comes from the fossil collections curated by the MNCN-CSIC (Madrid, Spain), the Institut Català de Paleontologia

(Sabadell, Spain), the Museo de Geologia de la Universidad de Valencia (Burjasot, Spain); the AMNH (New York, USA), the NHM (London, UK) and the MNHN (Paris, France).

They include the fossil giraffid taxa from the early to mid-Miocene Canthumeryx *sirtensis* from Libya; *Injanatherium arabicum* from Saudi Arabia; *Giraffokeryx punjabiensis* from *Pakistan* and India and Giraffokeryx *primaevus* from Kenya. From the late Miocene of the Iberian Peninsula *Decennatherium pachecoi*, *Decennatherium rex,* and *Birgerbohlinia schaubi.* From the early Turolian to late Pliocene of Greek-Iranian region *Samotherium major,* Samotherium *boissieri, Palaeotragus rouenii, Bohlinia attica. Helladotherium duvernoyi, Alcicephalus neumayri* and *Palaeotragus coelophrys*. Also from the same collections comes the data of the Chinese *Schansitherium tafeli*, *Honanotherium schlosseri* and *Samotherium sinense* from the late Miocene and early Pliocene of China. Finally, from the late Miocene of India and Pakistan *Bramatherium perimense* and *Bramatherium megacephalum* as well as the early Pleistocene *Sivatherium giganteum* and *Giraffa jumae* Turkey and Kenya; as well as the extant giraffids *Giraffa camelopardalis* and *Okapia johnstoni* from the collections of comparative anatomy of the MNCN-CSIC (Madrid, Spain) and the AMNH (New York, USA). Additional information on the specimens from this study is included in Appendix 1 as well as additional biometrical information that come from several publications, listed also on Appendix 1.

Measurements

We follow the set of measurements illustrated in (Figure 1). All were taken with digital calipers and compiled in excel. Due to the extension they can be found on Appendix 1.

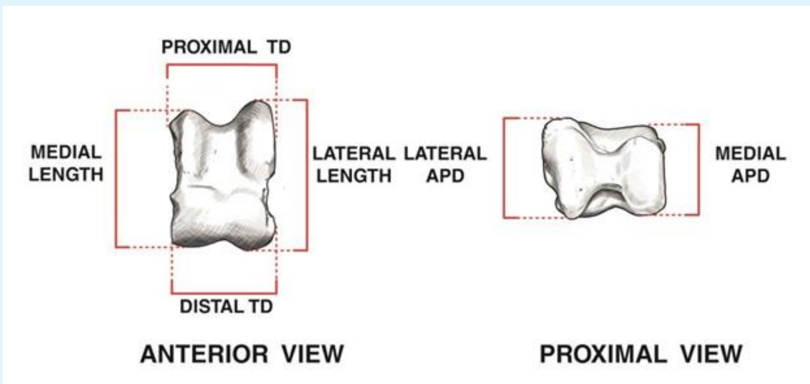

Figure 1: Astragalar measurements defined for this study based on a Decennatherium rex astragalus. Paleoillustration by Rubén Guerrero.

Nomenclature

We use the terminology of Barone [12] for anatomic nomenclature of the postcranial skeleton.

Institutional / Technical abbreviations

AMNH, American Museum of Natural History, New York, USA; ICP, Institut Català de Paleontologia- Miquel Crusafont, Barcelona, Spain; MGUV, Museu de Geologia de la Universitat de València; MNCN-CSIC, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; MNHN, Musèum national d'Histoire naturelle, Paris, France; NHM, Natural History Museum, London, UK.

Results

We analyzed three different Astragalar indexes that recover their biommetric variability and checked for their phylogenetic potential:
(1)Distal transverse diameter/Lateral length*100
(2)Medial anteroposterior diameter/Medial length*100
(3) Medial length / Lateral length*100

The results of the three can be seen in Figures 2-4 and Tables 1-3.

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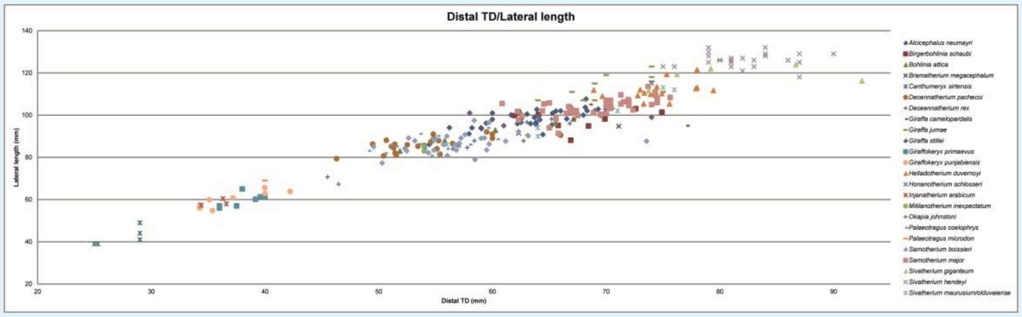

Figure 2: Dispersal plot showing the Index (1) of the giraffid taxa analyzed (measurements in mm.).

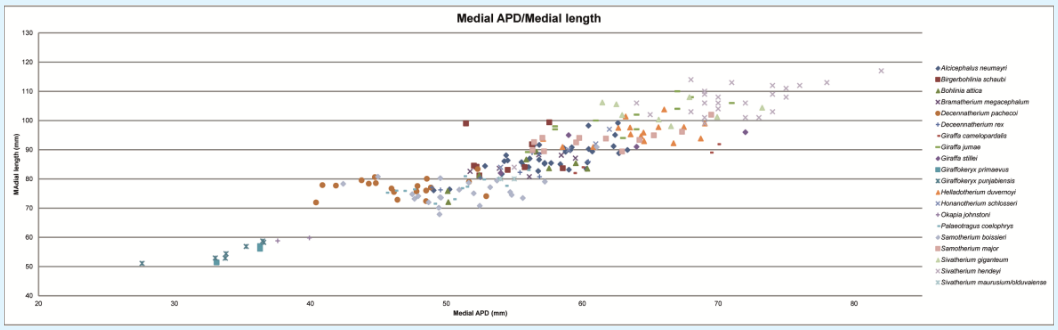

Figure 3: Dispersal plot showing the Index (2) of the giraffid taxa analyzed (measurements in mm.).

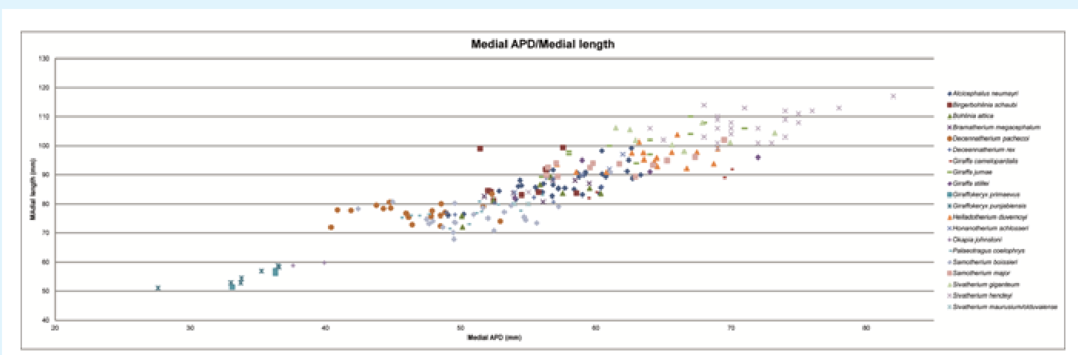

Figure 4: Dispersal plot showing the Index (3) of the giraffid taxa analyzed (measurements in mm.).

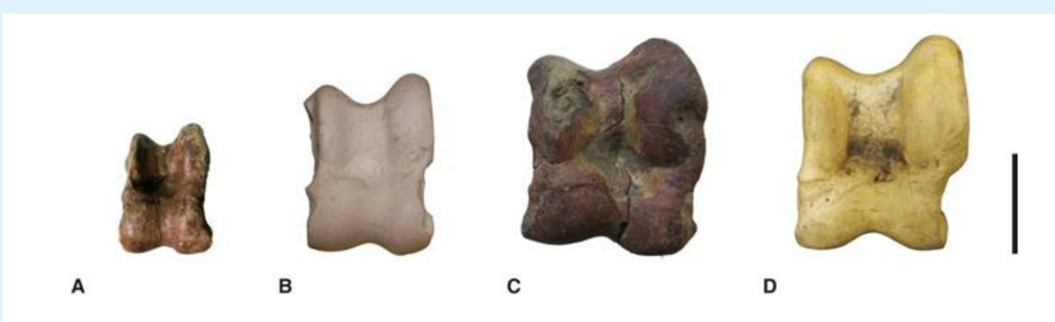

Figure 5: Dorsal views of giraffid astragali. A) Giraffokeryx punjabiensis , AMNH-19453; B) Decennatherium rex, BAT-10’09-G2-59; C) Sivatherium giganteum, NM OR-16998; D) Giraffa camelopardalis, AM-5354. Scale bar equals 5 mm.

Taxa	DISTAL TD/LATERAL LENGTH*100				
	Minimum	Mean	Maximum	Standard Deviation	Total N
Alcicephalus neumayri	59,406	64,657	70,946	2,764	43
Birgerbohlinia schaubi	62,125	70,027	75,916	4,191	13
Bohlinia attica	61,402	64,786	68,378	2,901	10
Bramatherium megacephalum	68,125	70,427	75,074	3,212	7
Canthumeryx sirtensis	59,184	64,960	70,732	4,133	5
Decennatherium pachecoi	57,330	63,076	72,928	3,690	32
Decennatherium rex	65,232	68,051	71,458	2,085	8
Giraffa camelopardalis	65,495	69,481	73,429	3,368	6
Giraffa jumae	58,824	62,573	67,568	2,754	13
Giraffa stillei	62,366	66,924	70,000	3,260	11
Giraffokeryx primaevus	58,462	63,770	65,789	2,478	8
Giraffokeryx punjabiensis	58,585	61,957	66,067	2,547	8
Helladotherium duvernoyi	61,631	66,910	71,776	2,865	23
Honanotherium schlosseri	64,348	64,497	64,646	,211	5
Injanatherium arabicum	60,035	61,079	63,103	1,753	3
Mitilanotherium inexpectatum	63529	64,295	65,060	1,082	6
Okapia johnstoni	64,356	66,713	69,070	3,333	2
Palaeotragus coelophrys	58,837	63,450	68,179	3,223	22
Palaeotragus microdon	57,971	57,971	57,971	.	2
Palaeotragus rouenii	61,619	62,782	63,946	1,645	2
Samotherium boissieri	58,267	65,936	83,932	5,206	35
Samotherium major	57,671	66,413	71,991	2,932	52
Sivatherium giganteum	63,930	68,910	79,632	6,413	10
Sivatherium hendeyi	59,848	65,311	73,729	3,303	38
Sivatherium maurusium/olduvaiense	65,116	68,025	71,111	2,157	9

Table 1: Descriptive parameters of the Astragalar Index (1).

Taxa	MEDIAL APD/MEDIAL LENGTH*100				
	Minimum	Mean	Maximum	Standard Deviation	Total N
Alcicephalus neumayri	100,324	104,922	114,190	3,666	43
Birgerbohlinia schaubi	85,816	95,854	108,866	5,897	13
Bohlinia attica	103,157	108,110	116,902	5,306	10
Bramatherium megacephalum	95,887	100,045	103,785	3,753	7
Decennatherium pachecoi	93,155	102,074	112,428	5,805	32
Decennatherium rex	100,159	105,501	111,819	4,615	8
Giraffa camelopardalis	116,390	116,390	116,390	.	6
Giraffokeryx primaevus	104,747	108,814	115,863	6,129	8
Giraffokeryx punjabiensis	91,245	96,476	101,696	4,728	8
Helladotherium duvernoyi	91,277	109,495	116,086	6,378	23
Okapia johnstoni	108,094	108,495	108,094	.	2
Palaeotragus coelophrys	104,107	106,348	111,812	2,321	22
Samotherium boissieri	89,244	103,162	120,986	9,433	35
Samotherium major	94,848	102,290	113,889	5,637	52
Sivatherium giganteum	95,640	104,098	112,500	5,504	10
Sivatherium maurusium/olduvaiense	112,698	113,380	114,063	,965	9

Table 2: Descriptive parameters of the Astragalar Index (2).

Taxa	MEDIAL LENGTH/LATERAL LENGTH*100				
	Minimum	Mean	Maximum	Standard Deviation	Total N
Alcicephalus neumayri	83,973	88,795	93,694	2,230	43
Birgerbohlinia schaubi	81,653	87,571	99,258	5,976	13
Bohlinia attica	86,288	87,237	88,264	,751	10
Bramatherium megacephalum	85,251	87,279	90,290	2,471	7
Decennatherium pachecoi	84,289	90,886	98,098	3,546	32
Decennatherium rex	89,495	90,986	91,970	,759	8
Giraffa camelopardalis	85,016	86,142	87,524	1,063	6
Giraffa jumae	84,127	88,847	92,437	2,612	13
Giraffa stillei	83,871	88,184	95,960	3,994	11
Giraffokeryx primaevus	90,175	91,737	93,157	1,362	8
Giraffokeryx punjabiensis	86,982	91,150	99,198	3,706	8
Helladotherium duvernoyi	81,958	86,141	90,918	2,377	23
Honanotherium schlosseri	84,348	84,598	84,848	,354	5
Injanatherium arabicum	87,417	90,605	93,019	2,880	3
Mitilanotherium inexpectatum	94,118	94,118	94,118	.	6
Okapia johnstoni	83,168	86,033	88,897	4,051	2
Palaeotragus coelophrys	81,025	88,377	93,135	3,617	22
Palaeotragus rouenii	88,435	88,435	88,435	.	2
Samotherium boissieri	84,077	88,935	103,720	3,964	35
Samotherium major	86,216	89,663	94,489	1,879	52
Sivatherium giganteum	82,212	86,026	89,909	3,677	10
Sivatherium hendeyi	80,303	85,711	90,909	2,914	38
Sivatherium maurusium/olduvaiense	85,106	87,930	93,023	3,164	9

Table 3: Descriptive parameters of the Astragalar Index (3).

Discussion

Despite the Giraffidae being a relict family with only two extant genera it shows an extremely high past diversity with a wide arrange of shape and forms between all present and extinct giraffids [7,5]. This diversity is reflected in the giraffid astragalus through its morphology and proportions [10].

Given that Past studies have probed that biometrical features in metacarpals III-IV and metatarsals III-IV in giraffids are useful for giraffid identification [9] we found interesting to research Astragalus biometrical features as they have been exhaustively anatomically described [10] and are usually found in fossil sites, if not in pristine conditions at least preserving is overall form and size (they are a strong compact bone).

We took absolute standardized measurements and analyzed the astragalus shape with biometrical indexes and as we can see in the results section (Figures 2-4, Tables 1-3) some of the indexes tend to give more phylogenetic information about the giraffid taxa analyzed.

Index (1), which relates the distal transverse diameter to the lateral length, giving us information about the overall shape, it being squarer or more rectangular, probes to be a reliable biometrical feature. As we see in figure 2, the most primitive taxa as *Canthumeryx sirtensis, Giraffokeryx punjabiensis, Injanatherium arabicum* and *Giraffokeryx primaevus,* have smaller overall size and smaller index (1) value (the smallest being of 57, Table 1, Figure 5), meaning a more rectangular overall shape, whereas later and more derived taxa as *Samotherium boissieri, Samotherium major* and *Helladotherium duvernoyi* show a higher size and higher value indexes with the highest mean values being those of being the very large fossil taxa *Decennatherium rex, Sivatherium maurusium/olduvaiense, Bramatherium megacephalum, Birgerbohlinia schaubi* and *Sivatherium giganteum* which are all part of the Samotheriinae-Sivatheriinae clade and have robust limbs and the extant *Giraffa Camelopardalis,* the largest of the *Giraffa* genus and the more robust of them, and which shows some the most square-shaped astragali with index (1) values of over 73 (Table 1, Figure 5).

Index (2) which relates the medial anteroposterior diameter with the medial length, giving information on the shape of the medial side, or the medial thickness of the astragalus (Figure 3, Table 2). Figure 3 also shows the more primitive and older taxa on the left, as *Giraffokeryx punjabiensis,* as they have smaller overall size and a lower value of index (2), though most of the taxa plot together in the middle of the graph with similar index (2) values, making it hard to differentiate between each other and making it less useful. It is useful two for the large *Sivatherium maurusium/olduvaiense* and *Giraffa camelopardalis* which share means above 110, making them have greater thickness related to the height medially and easier to identify.

Index (3), which relates medial length to lateral length (Figure 4, Table 3) shows the difference in size between the two sides of the astragalus. AS in the indexes mentioned above, the graph separates very well the smaller and more primitive giraffids, as well as the largest ones but renders difficult to use for the identification of most giraffid taxa. Most giraffids also share a similar index (3) values (between 85-90) with only *Injanatherium arabicum, Mitilanotherium inexpectatum, Decennatherium pachecoi, Decennatherium rex, Giraffokeryx punjabiensis,* and *Giraffokeryx primaevus,* showing values above 90, meaning their lateral ridge of the trochlea is larger in relation to the medial dirge of the trochlea than in other giraffids.

Conclusions

Each giraffid astragalus exhibits a unique combination of biometrical characteristics and biometrical measurements can be very useful to identify giraffid taxa. However, most of late Miocene fossil giraffids fall within the same range of index values, and have overall similar shapes, rendering the use of the astragalar proportions as a tool for phylogenetic studies one to use with caution. That being said, the most derived and the most primitive taxa can be easily biometrically distinguished, so though limited, the use of standardized biometrical features can be of help in developing future phylogenetic character matrixes for the Giraffidae and can be helpful in cases where the state of the fossils don't allow for accurate morphological descriptions.

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