

The alleged astragalar remains of *Didolodus* Ameghino, 1897 (Mammalia, Panameriungulata) and a critic of isolated bone association models

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Postcranial characters of South American native ungulates are important in order to analyze their relationships in the actual therian taxonomy, particularly to test their alleged afrotherian affinities. In this sense, the most primitive and oldest South American eutherians are represented by two endemic groups of “condylarths”, the Kollpaniinae and Didolodontidae. These forms, characterized by lower crowned bunodont dentition, have never been found in direct association with their postcranial remains. Even though, several skeletal elements have been assigned to some of forms, following different assumptions and criteria. Two distinct astragalar remains (MACN-CA 10737 and AMNH 117457) have been referred to the genus *Didolodus*, one of the most common didolodontids from early and middle Eocene Patagonian outcrops. Here we describe in detail and illustrate these materials. A critical analysis is made of several regression equation models which have been used in other cases to associate by size isolated postcranial elements to taxa defined by teeth. A new model was formulated based on 19 modern bunodont mammals with directly associated skeletons in order to test the accuracy of the regression equations. Although the results of the equation models failed to accurately assigned the isolated astragali to any of the *Didolodus* species, they can be used as a good tool to disprove the association hypothesis. A broad comparison with astragalar remains of South American native ungulates indicates that MACN-CA 10737 has notoungulate affinities, in contrast AMNH 117457 resembles the astragali assigned to didolodontids from São José de Itaboraí, Brazil, according to the models criticized here. The similitude is particularly due to the broad development of the cotylar fossa, a character proposed as an afrotherian synapomorphy, but probably developed independently in different groups. Improvement in knowledge regarding postcranial characters of the earliest South American native ungulates is necessary not only due to its importance in improving accuracy of phylogenetic relationships, but also for the inferences made on paleobiological features. • Key words: South America, Paleogene, Didolodontidae, astragali, regression equation models.

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The progressive fragmentation of Gondwana led to the isolation of South America during most of the Cenozoic (Simpson 1980, Pascual 1996, Benedetto 2010). On this island continent, therian mammals developed a great variety of autochthonous forms and particularly among eutherian mammals, a wide radiation of endemic ungulates can be recognized. South American native ungulates (SANU) were grouped into several orders – not all of them accepted by all authors –, but the most stable being Notoungulata, Litopterna, Astrapotheria, Xenungulata and Pyrotheria (Pascual & Ortíz Jaureguizar 2007). Monophyly of SANU was suggested by the Meridiungulata (McKenna 1975) one of the divisions of the Grandorder Ungulata, together with the Eparctocoryna

and Altungulata (McKenna & Bell 1997). But since molecular phylogenies split the Ungulata among Laurasiatheria and Afrotheria (Murphy *et al.* 2001, Waddell *et al.* 2001, Springer *et al.* 2007), the higher relationships between SANU remain uncertain. Agnolin & Chimento (2011) suggested a relationship among Afrotherian, Notoungulata and Astrapotheria based on a bibliographic revision of three morphological characters: the presence of a cotylar fossa in the astragali, the number of thoracolumbar vertebrae and the delayed dental eruption relative to skull growth. Despite several interpretative mistakes present in this work (Lopez *et al.* in press) at least there is no evidence for afrotherian-like delayed dental eruption among Notoungulata (Billet & Thomas 2011).

Alternatively, Panameriungulata was proposed as an order category combining Mioclaenidae, Didolodontidae and Litopterna (Muizon & Cifelli 2000), but was not supported by derived characters and only a very limited number of litoptern (*i.e.* Protolipternidae) were considered in the proposal. Panameriungulata was also considered, for practical purposes, not as an order (Gelfo 2006) but as node and as it is used here.

Traditionally it was proposed that some or all native ungulates evolved *in situ* from one of the North American “condylarths” which migrated to South America during the Late Cretaceous or earliest Paleocene (Simpson 1980). At least two group of “condylarths” were recorded in South America, the most primitive being the Kollpaniinae from the early Paleocene of Tiupampa, Bolivia (Muizon & Cifelli 2000, Gelfo *et al.* 2009), either considered as part of the North America Mioclaenidae (Muizon & Cifelli 2000) or an endemic group (Zack *et al.* 2005, Williamson & Carr 2007). The other group is the Didolodontidae, more derived in their bunodonty than the Kollpaniinae, and characterized as small to medium size ungulates, with brachyodont teeth, cusps with a wide base, which are never slender, lophoid or selenodont in structure (Gelfo 2006). The Didolodontid fossil record extends from the Selandian (middle Paleocene, Peligran South American Land Mammal Age – SALMA) until the Priabonian (late Eocene – Mustersan SALMA), plus one taxon tentatively referred to this family has been recorded in the late Oligocene (Deseadan SALMA) of Bolivia (Gelfo 2006). Didolodontids have been considered as closely related to South American native ungulates, particularly to Litopterna (*e.g.* Scott 1910, Simpson 1948, Muizon & Cifelli 2000, Soria 2001) and knowledge of this group is significant if the possible relationships and origins of native ungulates are to be understood.

The fossil record of “condylarths” in South America lacks any complete skeleton or even postcranial remains found in direct association with a skull. Thus, the whole taxonomy of kollpaniinae and didolodontids is based on dental characters. Ameghino (1904) referred several isolated astragali to didolodontids without an explicit justification for the associations. Among them, he described a left astragalus as belonging to *Didolodus*. This, as well as other astragali assigned by Ameghino (1904) to *Asmithwoodwardia*, *Argyrolambda* and *Lambdaconus*, was not considered by Simpson (1948) as valid as he understood them to have notoungulates or litoptern affinities. As part of a later article which was never published, Simpson (1948) discussed several astragali assigned to didolodontids, but without any illustration or repository number for the material considered. Simpson’s (1948) criteria for the astragali and teeth association is based on the similar relative abundance of these isolated astragali in comparison with didolodontid teeth relative to other mammal

teeth. Cifelli (1983a) mentioned an unassociated specimen from the Casamayoran of Chubut (Colhue-Huapi) in the AMNH collection of ?*Didolodus* without given the repository number, which was usually assumed to have been one of the astragali mentioned by Simpson (1948). This astragalus was compared and considered similar to one tentatively assigned to *Lamegoia conodonta* and those referred to *Paulacoutoia protocenica* (Cifelli, 1983a). Later, in a phylogenetic analysis including several Didolodontidae, nine astragalar characters were codified for the genus *Didolodus*, probably including the AMNH material (Cifelli 1993).

In contrast to Ameghino’s unknown criteria used in the assignment of astragalar remains to species only defined by teeth, a new approach was proposed considering explicit parameters. The proposal was based on the morphological features of postcranial remains, the relative size and abundance, and models using logarithmic equations relating different bones and dental measurements (Cifelli 1983a). These methods were applied to the disassociated postcranial bones and teeth from the fissure fills of the São José de Itaboraí Basin, Rio de Janeiro, Brazil, for which a number of associations have been proposed including several for didolodontids (Cifelli 1983a; Bergqvist 1996, 2008). Based in the high correlation between different body measurements and body mass (Kay 1975, Gingerich 1977, Gingerich *et al.* 1982, Damuth & MacFadden 1990), several logarithmic linear regression models were constructed, in order to support the association of isolated bones to fossil species known only by teeth (Cifelli 1983a, Bergqvist 1996).

Here we analyze the associations of the two morphologically different left astragali which were assigned historically to *Didolodus*: MACN-CA 10737 and AMNH 117457. The first mentioned by Ameghino (1904) and the second referred to by Cifelli (1983a, 1993) probably based on Simpson’s (1948) comments. We also review one of the criteria proposed by Cifelli (1983a) and followed by Bergqvist (1996, 2008), the linear regression models, and discuss the phylogenetic implications of the morphological characters of the tali.

Materials and methods

Institutional abbreviations. – AMNH – American Museum of Natural History, USA; CNHM – Field Museum Natural History, Chicago, USA; MACN-Ma – Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina, Colección de Mastozoología; MACN-CA – Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina, Colección Ameghino; MLP – Museo de La Plata, Argentina, Colección Mastozoología; MPEF – Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

Materials. – Two astragali assigned to *Didolodus* (MACN-CA 10737 and AMNH 117457) and Appendix 2.

Other abbreviations. – ln – natural logarithm; AL – astragalar maximum length; MLT – maximum length of the astragalar medial trochlea; Am2 – lower second molar tooth area; MRD – maximum residual differences; %PE – percent prediction error.

Nomenclature. – The characters described for the astragali, when available, follow the Acta Anatomica Veterinaria Nomenclature. However since no clear reference to the astragali orientation was given, and considering that this bone is not in the same position in all mammals (e.g. has the same axis as the tibia in Artiodactyla and is perpendicular to it in most Primates) we preliminarily follow Marivaux *et al.*'s (2003) orientation which is almost the same as that of Sisson & Grossman (1982) but instead of 'proximal' and 'distal', the terms 'posterior' and 'anterior', are respectively used.

Regression equations. – Two regression equations were taken from the literature in order to test the probable fit of these astragali to the teeth of *Didolodus*. (1) $\ln \text{Am2} = -0,77 + 1,55 * \ln \text{AL}$, (Cifelli, 1983a) and (2) $\ln \text{MLT} = -0,283 + 1,345 * \ln \sqrt{\text{Am2}}$ (Bergqvist 1996). Plus the two tali and several *Didolodus* teeth were measured to integrate this data with the equations (Appendix 1). All measurements were taken with a point digital caliper (Schwyz). A new sample of dental and astragalar measurements were taken from 19 modern bunodont mammals with directly associated skeletons, in order to test the accuracy of previous regression equation models and produce a new model (Appendix 2). Measurements taken from right and left sides were considered as independent data. The AL was measured as an imaginary line, perpendicular to the fixed jaw resting over the two trochlear crests, and the sliding jaw in contact with the astragalar head (Fig. 1). The MLT was considered as the maximum antero-posterior distance measured along the medial trochlear crest (Fig. 1). From the entire number of skeletons available, only 32 astragali were in optimal condition for measuring the AL but the complete sample was used for MLT. The Am2 was considered as the product of the maximum mesiodistal length plus the maximum labiolingual length of the second lower molar.

The maximum residual differences (the observed value minus the expected) given in the association hypothesis made by Cifelli (1983a) and Bergqvist (1996) are used here as comparison criterion in the absence of any proposed statistical error in these previous publications. The percent prediction error calculated as: $[(\text{Observed} - \text{Predicted}) / \text{Predicted}] \times 100$, (Van Valkenburgh 1990), and the residuals were analyzed for the new sample. A normality test was run for the residual analysis, and then standardized for interpretation purposes.

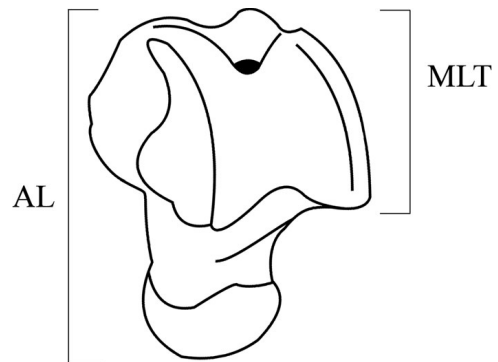


Figure 1. Astragali with the measurements used in the present study.

Data was recorded and analyzed using the programs PAST (version 2.0) and Microsoft Office Excel 2003 (version 11.8231.8172).

Results

There are no complete *Didolodontidae* skeletons or postcranial remains directly associated with teeth. Therefore there is a constraint on paleobiological inferences and the possible phylogenetic characters, due to availability of only teeth, on which all these species were based. However, several associations of isolated postcranial bones to *didolodontid* teeth were made, with (Cifelli 1983a, Bergqvist 1996) and without any explicit criteria (Ameghino 1904).

The astragali analyzed here were both assigned to *Didolodus* but, they show mutually exclusive morphology. The left astragali MACN-CA 10737 (Fig. 2A, B) came from upper *Notostylops* beds of Patagonia (Ameghino 1904), equivalent to Simpson's (1948) Casamayoran. No other reference regarding the geographic location was available for this specimen. The astragali were illustrated, described and compared particularly with two North American condylarths, *Periptychus rhabdodon* and *Ectaconus ditrigonus* (Ameghino 1904).

The only available information pertaining to the left astragali AMNH 117457 (Fig. 3A, B) can be found in the AMNH database, and it is indicated that it was found in Lake Colhue-Huapi, Chubut, Argentina. From this astragali several characters were acquired for a data matrix (Cifelli 1993), being the assumption that it belongs to *Didolodus* sp. It was briefly described and illustrated, but the assignation was also questioned (Gelfo 2006).

Morphological description

The tali could be clearly distinguished by their morphology, and thus the specimens cannot therefore be assigned

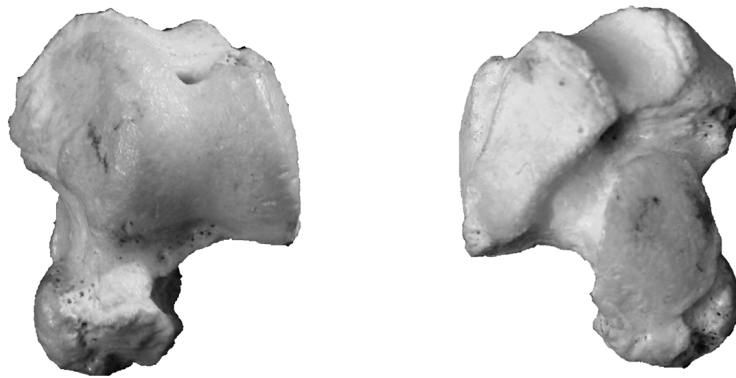
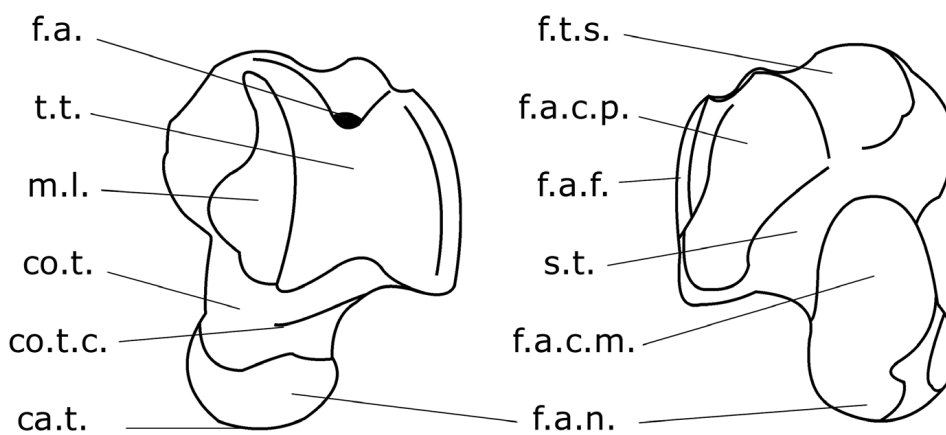


Figure 2. MACN-CA 10737 in dorsal (A and B) and plantar views (C and D). Abbreviations: astragalar foramen (a.f.), *caput tali* (ca.t.), *collum tali* (co.t.), *collum tali crest* (co.t.c.), *facies articularis fibularis* (f.a.f.), *facies articulares calcaneae: media* (f.a.c.m.), *facies articulares calcaneae: posterior* (f.a.c.p.), *facies articularis navicularis* (f.a.n.), flexor tendon sulcus (f.t.s.), *malleolous lateralis* (m.l.), *sulcus tali* (s.t.) and *trochlaea tali* (t.t.). Scale: 10 mm approximately.

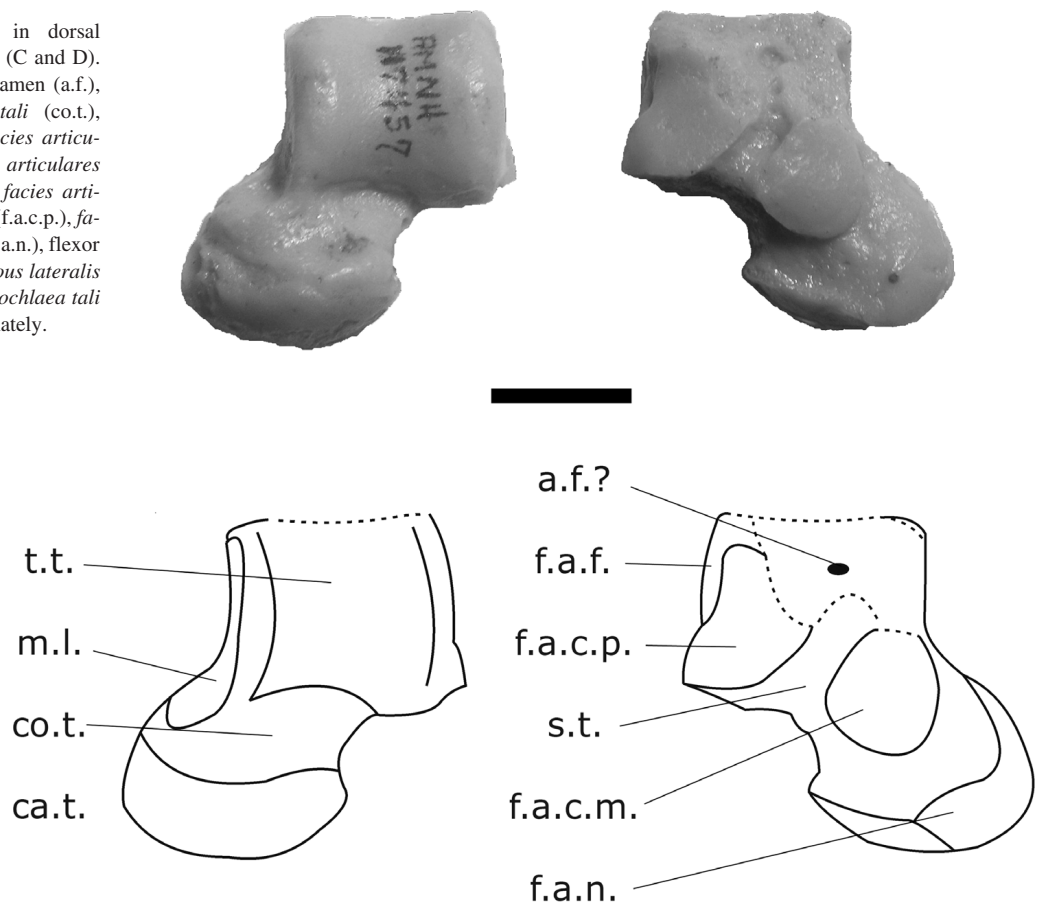


to the same taxon. The talus recorded as MACN-CA 10737 (Fig. 2C, D) is relatively slender, the length of the bone is greater than the width of the trochlea (*trochlaea tali*) and the ratio of total width to the talar length being 0.894. The talus neck (*collum tali*) is relatively short, ending in a well defined, rounded convex head (*capus tali*), which is not mediolaterally expanded. The head of the talus is mesiolaterally shorter than the trochlea is wide, and anteroposteriorly located on the same line as the medial trochlea crest. The navicular facet (*facies articularis navicularis*) is not expanded around the entire talus head. On the lateral side of the head there is smooth contact between the navicular and sustentacular facets (*facies articulares calcaneae: media*), but they are clearly separated by a furrow on the medial side of the head. The sustentacular facet is convex and oblong with the higher axis covering most of the plantar side of the talus neck. The ectal facet (*facies articulares calcaneae: posterior*) is concave and separated by a widely excavated sulcus (*sulcus tali*) originating from the sustentacular sulcus. In contrast to the sustentacular facet, the ectal facet is more obliquely orientated than in a plantar plane. The inferior astragalar foramen is present in plantar view inside the *sulcus tali*, near the contact between the ectal facet and the strong sulcus of the flexor tendon. Dorsally, the foramen is visible between the flexor tendon sul-

cus and the tibial trochlea (*trochlea talis distalis*). The sulcus of the flexor tendon is well excavated and produces a continuous groove joining the plantar and dorsal side of the talus. The medial and lateral crest of the tibial trochlea are not very sharp, as in litopterns, but are well defined and divergent anteriorly. The posterior edge of the trochlea shows a U-shaped groove where the superior astragalar foramen is situated. The limit of the anterior side of the trochlea and the neck of the talus is diffuse. A sharp crest is projected from the more anterior end of the lateral crest of the trochlea up to the mid point of the talus neck. The fibular facet (*facies articularis fibularis*) is limited by the lateral edge of the tibial trochlea and towards the plantar side by the well defined ectal facet. The fibular facet is not very prominent, but posteriorly and near the ectal facet, there is a pronounced deep scar in the fibular facet. The medial malleolus facet of the tibia (*malleolous lateralis*) is restricted to the talar body (*corpus tali*) and clearly separated from the short neck of the talus.

In contrast with the previously described talus, the left talus, AMNH 117457 (Fig. 3C, D) is incompletely preserved. Although in plantar view the anterior portion of the trochlea and the anteromedial side of the ectal facet are missing, the principal characteristics of the talus can be described. Compared with MACN-CA 10737, the talus is

Figure 3. AMNH 117457 in dorsal (A and B) and plantar views (C and D). Abbreviations: astragalar foramen (a.f.), *caput tali* (ca.t.), *collum tali* (co.t.), *collum tali crest* (co.t.c.), *facies articularis fibularis* (f.a.f.), *facies articulares calcaneae: media* (f.a.c.m.), *facies articulares calcaneae: posterior* (f.a.c.p.), *facies articularis navicularis* (f.a.n.), flexor tendon sulcus (f.t.s), *malleolus lateralis* (m.l.), *sulcus tali* (s.t.) and *trochlaea tali* (t.t.). Scale: 10 mm approximately.



wider, the ratio of total width to the length of the talus being 1.024. The neck of the talus is also short, but in contrast the talar head is not rounded and small, but strong and expanded mesiolaterally. The neck is oblique and the talus head is medially shifted, its lateral border corresponding with an imaginary anteroposterior line in the middle of the trochlea. The navicular facet is large and very convex anteriorly. On the posterior side of the head the navicular facet projects a dorsal shelf which is limited by the neck of the talus. The navicular facet is not expanded on the plantar side of the talus, but is in contact with a small facet probably related to the insertion of the medial collateral ligaments. The posteromedial limit of the sustentacular facet is broken. The preserved part is almost rounded, not expanded through the neck of the talus, and clearly separated from the astragalar head. The preserved portion of the ectal facet is separated from the sustentacular facet by a sulcus. The presence of an astragalar foramen could not be determined since part of the posterior side of the talus is missing. The crests of the tibial trochlea are almost parallel and smooth compared with MACN-CA 10737. The medial maleolar facet is not restricted to the trochlea, but expands on the medial side of the talus neck and bends almost 90° to form a shelf over the talus head. Both ends of the fibular facet are broken.

Analysis of the equation regression models

Beside the wide morphological variation in tooth structure, only three species, *Didolodus multicuspis*, *D. minor* and *D. magnus* were recognized as valid taxa (Gelfo 2006, 2010). These species cover an important wide range of sizes. They were found in several localities of Patagonia, including Lake Collhue-Huapi, Chubut, Argentina, where probably both assigned tali came from (Ameghino 1904, Simpson 1948).

The two tali exhibit similar observed and predicted values when Cifelli's (1983a) and Bergqvist's (1996, 2008) regression formulas were used. The major differences between these values are always for *D. magnus* (see Tables 1, 2). The residuals of *Didolodus minor* and *D. multicuspis* show lower values (< 0.37) than the maximum residual differences accepted in the previous associations made by Cifelli (1983a) and Bergqvist (1996, 2008) which were -1.44 and -0.43, respectively. But, as explained above, the two astragali are morphologically very different and cannot, therefore, be associated to the same genera.

The maximum residual difference (Tables 1, 2), which we use here as a comparison criterion, is not actually the best parameter to test an association hypothesis. Analysis

Table 1. Results of isolated teeth and tali association using Cifelli (1983b) regression formula ($\ln \text{Am2} = -0.77 + 1.55 * \ln \text{LA}$).

	<i>Didolodus multicuspis</i>		<i>Didolodus minor</i>		<i>Didolodus magnus</i>	
	AMNH 117457	MACN-CA 10737	AMNH 117457	MACN-CA 10737	AMNH 117457	MACN-CA 10737
AL (mm)	26.25	21.62	26.25	21.62	26.25	21.62
m ₂ area (mm ²)	66.63		50.82		186.05	
ln m ₂ area	4.199		3.93		7.33	
Expected ln m ₂ area	4.23	3.99	4.23	3.99	4.23	3.99
Difference between the observed and expected	-0.03	-0.205	0.37	0.07	1.0001	1.23
Maximum residual difference Cifelli (1983b)	-1.44					

Table 2. Results of isolated teeth and tali association using Bergqvist (1996, 2007) regression formula ($\ln \text{LMT} = -0.283 + 1.345 * \ln \sqrt{\text{Am2}}$).

	<i>Didolodus multicuspis</i>		<i>Didolodus minor</i>		<i>Didolodus magnus</i>	
	AMNH 117457	MACN-CA 10737	AMNH 117457	MACN-CA 10737	AMNH 117457	MACN-CA 10737
m ₂ area (mm ²)	66.63		50.82		186.05	
LMT (mm)	14.13	10.52	14.13	10.52	14.13	10.52
LMT ln	2.65	2.35	2.65	2.35	2.65	2.35
Expected LMT	2.54		2.38		3.23	
Difference between the observed and expected	0.11	-0.19	-0.27	0.03	-0.58	-0.88
Maximum residual difference Bergqvist (1996)	-0.43					

of the residuals (Packard & Boardman 2008) from the original models can provide better ways to analyze the variables. But, the absence of these analyses in the previous publications and the lack of the measurements these models were based on, do not allow recognition of the expected variation or to make a contrast with any association hypothesis. Also, the samples used previously are too small, $N = 10$ (Cifelli 1983a), $N = 7$ (Bergqvist 1996) or $N = 8$ (Bergqvist 2008), and, the tests for residual analysis need samples larger than $N = 20$ (e.g. normality tests). For this reason, a new comparative sample of 19 modern bunodont animals (Appendix 2) was used to make such analyses, using Am2 (Table 3) and LMT (Table 4) as dependent variables, following the proposals of Cifelli (1983a) and Bergqvist (1996). Despite the still limited sample, it at least allows residual analysis, using the right and left talus from the individual skeletons as independent data, thus both sides are represented and a bigger sample is available. We also considered the possibility that this can lead to data redundancy.

The sample yielded a lower Y intercept and a steeper slope for the astragalar length in comparison with Cifelli's (1983a) formula, and a higher Y intercept and shallower slope for the trochlear length than Bergqvist's (1996, 2008) formula. For both regressions, using this new sample, the %PE was less than 12% and residuals showed a normal distribution. The residuals of the two new regressions (Tables 3 and 4) showed a normal distribution (Table 5) and residuals were then standardized in order to facilitate the

interpretation. Considering the astragalar length, the regression indicated no preference for any association, but the best combination was between MACN-CA 10737 and *Didolodus multicuspis* (standardized residual -0.25; %PE = 2). Considering the lateral trochlear length, a greater difference was found between the two tali. The talus MACN-CA 10737 showed a greater residual standardized deviation (-2.91), surpassing slightly (for *Didolodus multicuspis*) the greater standardized residual found in the model sample (2.56). This contradicts the results of the astragalar length formula and can indicate that the MACN-CA 10737 talus is small for the size of *D. multicuspis* molars, but these results are insufficient to reject an association. None of the four formulas helped to discriminate between the two astragali or to indicate if according to their size one of them could match any of the *Didolodus* species considered.

Discussion

Some comments need to be made in relation to the different samples used for all the models considered here. Previous models used a sample of 10 North American condylarth species *Choeroclaenus turgidunculus*, *Anisonchus sectorius*, *Chriacus gallinae*, *Hyopsodus walcottianus*, *Meniscotherium chamense*, *Tetraclaenodon puercensis*, *Phenacodus wortmani*, *Periptychus rhabdodon*, *Arctocyon ferox*, and *Phenacodus primaevus* (Cifelli 1983a, fig. 2); and

5 North American condylarths *Phenacodus wortmani*, *Chriacus* sp., *Meniscotherium chamense*, *Meniscotherium robustum*, *Hyopsodus walcottianus*, plus two litopterns, *Diadiaphorus majusculus*, *Megadolodus molariformis* (Bergqvist 1996, table 6). In contrast to the last sample, the model by Bergqvist (2008, table 6.2) apparently included the talus of *Periptycus rhabdodon*, and despite the absence of the “–” sign in the talus regression equation, the equation is the same as Bergqvist’s (1996). But, the absence of measurements used in construction of the previous models (Cifelli 1983a; Bergqvist 1996, 2008) hindered recognition of the expected variation and the possibility to contrast the association hypothesis. For this reason, a new sample was obtained containing a larger number of extant bunodont mammals.

In correlations used for body size estimation, it has been suggested that the average Paleogene ungulate species has larger teeth for its body size than the average modern equivalent; if equations for body mass estimation were based on the ensemble of living species, the results could be overestimated (Damuth 1990). Even though it should be noted that the Paleogene sample considered by Damuth (1990) was restricted to 23 North American ungulates of which nine represented bunodont taxa, while in their extant sample it appears that from a total of 95 ungulates there were only four bunodont taxa. This sample could bias the observations of bunodont forms. Due to the lack of any living didolodontid relatives or any South American native ungulates, we selected extant mammals in order to produce a larger sample size. The selection was limited to bunodont mammals of different sizes and from different groups (*i.e.* primates, artiodactyls and carnivores). This taxonomic diversity seems to be more appropriate for testing the association of isolated material with didolodontids, since *prima facie* the only suitable analogy seems to be those with comparable dentition. Unfortunately, representatives of South American native ungulates with bunodont dentition found in direct association with astragali, are restricted to the litoptern *Megadolodus molariformis* (Protheroheriidae, Megadolodinae) from the Miocene of La Venta in Colombia (Cifelli & Villarroel 1997). We are aware that it is desirable to add this measurement into the analysis, but probably the impact on the regression equation presented here will be low within the context of the sample.

Taken into account the astragali considered in this study, the present regression equation model is not sufficient to justify their assignment to *Didolodus* species. Comparison with certain associated astragali of South American native ungulates could at least suggest possible affinities. The MLP collections house several isolated astragali, with the same morphology and proportions found in Casamayoran beds of the Cerro Guacho locality in the Chubut province, Argentina. Some of these materials were labeled as *Didolodus* (*i.e.* right tali MLP 59-II-24-215,

Table 3. Regression formula results ($\ln \text{Am2} = -2.0997 + 2.0223 * \ln \text{LA}$) with the new sample of modern bunodont mammals of Appendix 2, using variables as Cifelli (1983). $r = 0.81$; $p = 0.00000$

	%PE	Residuals	Standardized
Min.	0.43	0.02	0.07
Max.	11.51	0.58	1.78
Median	-0.43	-0.02	
Average	-0.51	0	
Standard deviation	-7.27	-0.02	
Standardized	<i>D. minor</i>	<i>D. multicuspis</i>	<i>D. magnus</i>
AMNH 117457	-1.49	-0.57	2.46
MACN-CA 10737	-0.67	0.25	3.38

Table 4. Regression formula results ($\ln \text{LMT} = 0.08884 + 0.8706 * \ln \sqrt{\text{Am2}}$) with the new sample of modern bunodont mammals of Appendix 2, using variables as Bergqvist (1996, 2007). $r = 0.93$; $p = 0.0000$

	%PE	Residuals	Standardized
Min.	0.07	0.002	0.01
Max.	-11.51	-0.32	2.56
Median	-0.04	0	
Average	-0.17	0	
Standard deviation	4.16	0.12	
Standardized	<i>D. minor</i>	<i>D. multicuspis</i>	<i>D. magnus</i>
AMNH 117457	0.4	-0.54	-4.14
MACN-CA 10737	-1.97	-2.91	-6.51

Table 5. Normality Tests for the new formulas as presented in Tables 3 and 4. α level = 0.05; the null hypothesis (the sample is normal) rejected when $p < 0.05$.

	$\ln \text{Am2} = -2.0997 + 2.0223 * \ln \text{LA}$	$\ln \text{LT} = 0.08884 + 0.8706 * \ln \sqrt{\text{Am2}}$
N	32	38
Shapiro-Wilk W	0.948	0.974
p(normal)	0.1268	0.5093
Jarque-Bera JB	1.898	0.9788
p(normal)	0.3871	0.613
p(Monte Carlo)	0.1978	0.5064
Chi ²	1.75	2
p(normal)	0.18588	0.1573
Chi ² OK (N > 20)	YES	YES

MLP 59-II-24-213 and MLP 59-II-24-578, and left MLP 59-II-24-504) and the rest were labeled as *Notostylops* (*i.e.* right tali MLP 56-XII-18-199, MLP 56-XII-18-200, and left MLP 56-XII-18-198, MLP 56-XII-18-201) following field notes. As previously suggested all these remains probably belonged to notoungulates (Gelfo & Picasso 2003, Gelfo 2006). These tali, as well as MACN-CA 10737 analyzed here, closely correspond in diversity with some of the known notoungulates tali. Despite a shorter neck and a

proportionally larger and somewhat more medially located head, the tali of the Mesotheriidae *Trachytherus* (e.g. MLP 61-IV-11-7, MLP 61-IV-11-5, MLP 61-IV-11-6, MLP 61-IV-11-8) shows a similar morphology. The similitude is also evident with several Isotemnidae, such as *Thomas-huxleya externa* and *Pleurostylodon similis* (see Shockey & Flynn 2007). In particular it should be noted that a crest is present extending from the more anterior end of the lateral crest of the trochlea up to the mid point of the talus neck. This crest, informally referred to as a “tibial stop”, was described as a distinctive derived character in Paleocene–Eocene notoungulates, and it appears to change its orientation to a more transverse position in later taxa such as toxodontid and interatheriid (Shockey & Flynn 2007). The possible phylogenetic value of this crest and its orientation needs to be tested on a wider sample, but it seems to be characteristic of other notoungulates.

In contrast to MACN-CA 10737, which seems to be comparable with already established notoungulates, AMNH 117457 is comparable to those isolated astragali assigned to “condylarths” from the Itaboraí Basin, Brazil. Among them, it particularly resembles MCT 1388M assigned to *Paulacoutoia protocenica* (Cifelli 1983a; Bergqvist 1996, 2008) and also MCN-PV 1359M and DGM 940M (previously recorded as DNPM LE443) which were assigned to *Lamegoia conodonta* (Cifelli 1983a; Bergqvist 1996, 2008). All these astragali share particularly what could be considered as a generalized morphology with a well defined neck and head, not very pronounced trochlear crest and the presence of an astragalar foramen. These features are present in several groups not necessary phylogenetically related such as several families of North American “condylarths”, basal notoungulates, artiodactyls, carnivores, etc. The Itaboraian tali shared the extension of the medial malleolar facet, distally expanded over the neck and reaching almost to the head of the astragalus (Cifelli 1983a). This character was considered a synapomorphy of Didolodontidae (Cifelli 1993, Bergqvist 1996) and so it could be predicted that this feature could be used to support the assignment of MACN-CA 10737 to *Didolodus*. However, the assignment of the astragalar remains to *Lamegoia* and *Paulacoutoia* is only through an association hypothesis linking isolated postcranial remains to species which were previously recognized and diagnosed only by dental characters. These interpretations are not completely accurate as it is possible that taxa known only from postcranial remains might not be represented by teeth (Wyss *et al.* 1994, Soria 2001). No associated skeleton is known for any South American “condylarth”, and as a consequence, independent evidence is not available to prove the postcranial hypotheses of *Lamegoia* and *Paulacoutoia*. Thus, the projection of the medial malleolar facet over the neck and the head of the astragalus should not be considered as a specific synapomorphy of didolodontids. It

should also be stated that the same form of the medial malleolar facet, but defined as a “cotylar fossa”, was identified in *Plesiorycteropus* (MacPhee 1994) and several but not exclusively, in afrotherian mammals (Tabuce *et al.* 2007).

Conclusion

The origin and affinities of SANU among placental mammals are still uncertain. Since very few associated skeletons are known for some of these Paleogene groups, they have been mostly and best described by their dentition. Even though, isolated postcranial remains are not absent in these outcrops, they are usually not subjected to a proper analyses which could integrate the information they preserved. In fact, knowledge of postcranial remains could be an important key for contrasting phylogenetic links between SANU groups and, among them and other placental mammals. The morphological characters used with molecular data in recent mammal phylogenies emphasize the increasing importance of generating a clear understanding of postcranial morphology of the oldest SANU. Up till now, both the Notoungulata and Astrapotheria have been postulated as afrotherian mammals (Agnolin & Chimento 2011) based on the alleged recognition of three characteristics: more than 19 thoracolumbar vertebrae (Sánchez-Villagra *et al.* 2007), late eruption of permanent dentition (Asher & Lehmann 2008) and the development of an astragalar cotylar fossa (Tabuce *et al.* 2007). But, there is no evidence that delayed dental eruption was the basal state among these animals (Billet & Thomas 2011, Kramarz *et al.* 2011) and the other afrotherian characters appear to be variable (Lorente *et al.* 2011, Lopez *et al.* in press). In particular, the astragalar cotylar fossa was alternatively considered as a synapomorphy for different groups: afrotherian mammals (Tabuce *et al.* 2007) and, described as the expansion of the malleolar facet over the neck and head of the astragali, for didolodontids (Cifelli 1983b, Bergqvist 1996). However, it was stated that it does not represent a clearly derived character in the Afrotheria, as it is lacking in chrysochlorids and most tenrecids (Salton & Szalay 2004), and it should also be remembered that is variably present among primates, laurasic “condylarths” (e.g. *Meniscotherium*), dinoce- rates (e.g. *Probathyopsis*), notoungulates (e.g. *Nesodon*) and macropodid marsupials (Zack *et al.* 2005, Lorente *et al.* 2011).

The two remains discussed here are particularly relevant since the “condylarths” and particularly the didolodontids were traditionally related to some of the SANU. Considering their morphology compared to already known SANU tali, several statements can be made. AMNH 117457 fits with a generalized astragalar type, but the development of the malleolar facet seems to have evolved

independently in different groups. So, this character could be a necessary condition to relate it to similar morphotypes (e.g. Itaboraian tali assigned to *Lamegoia* and *Paulacoutoia*) but not a sufficient condition to assign it to *Didolodus*. In particular several litopterns, such as Protolipternidae or Megadolodinae, also retained a bunodont dentition but were defined by a very different astragalar type (Cifelli 1983a, Cifelli & Villarroel 1997). In contrast, MACN-CA 10737 morphologically fits well with known notoungulates morphology, to which it is here referred due to the general similitude and particularly the presence of a crest or “tibial stop”.

Regression models do not provide support for the association hypothesis because they only indicate in what interval a variable can be linked to another variable. Animals of very different orders can have very similar sizes, and regressions cannot discriminate between them. For example, the talus of *Potamochoerus larvatus* (Artiodactyla, Suidae) from our sample can be associated with a large part of the sample, including *Sus scrofa* (Artiodactyla, Suidae), *Pan troglodytes* (Primates, Hominidae) and *Ursus arctos* (Carnivora, Ursidae). Associating postcranial remains to isolated teeth only by size can lead to inaccurate conclusions. Regression models can be a useful tool to complement other anatomical inferences and test an association hypothesis, but only if the residual analysis and the interval is clearly defined. The interval selected could be used to reject an association hypothesis or to identify an extremely abnormal individual or group which deviates significantly from that which is expected for a larger group of animals. Other criteria used to support the associations proposed by Bergqvist (1996) were the relative abundance of isolated teeth and postcranial remains, and bone morphology when the predicted size matched more than one taxa. Considering the associated postcranial bones mentioned above, Bergqvist (1996) proposed a morphological tendency exhibited by the astragalus of each order of SANU and thus, reinforced the associations suggested by the evolutionary trend recognised in the tali. This could be useful in groups where postcranial bones have already been found in association with teeth. Even though is important to emphasize the invalidity of this argument in providing support for problematic associations, for example as in the Sparnotheriodontidae or, Didolodontidae as discussed here. The main problem of these criteria is that the proposition to be proved is already assumed in the premises. How could the evolutionary trend be determined for the astragalus of an order or an equivalent taxonomic unit, in which no postcranial bone was ever found in association? In addition, it is not correct to link, *prima facie*, a taxa characterized by primitive dental features with primitive postcranial morphology. Selective pressures among different systems (i.e. digestive and locomotor) are not the same, and the ‘quantity’ of evolutionary change accumulated could be variable in different

systems. Consider, for example, the North American archaic ungulate, *Meniscotherium chamense*, with a more derived dentition than other phenacodontids (i.e. molarization of posterior premolars and lophodont-selenodont cheek teeth), but in contrast, having limbs retaining a relatively generalized pentadactyl structure.

In summary, it is methodologically incorrect to characterize the postcranial elements of a group known and defined only by teeth, and then use this generalization to associate other similar postcranial bones with this group. Particularly in the case of the astragali discussed here it is clearly not an acceptable criterion. Despite the obvious need for intersubjectivity in any scientific model, probably one of the most important observations related to the previous association of isolated postcranial remains to teeth, should be the quest for independent evidence to contrast statements and, in the particular case presented here, to avoid a dogmatic and incorrect use of regression equations.

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Appendix 1.

Dental measures of *Didolodus* species.

	N	Materials	m ₂ area (mm ²)	Average of m ₂ area (mm ²)
<i>Didolodus multicuspis</i>	7	MACN-A 10689	67.4478	66.63
		MACN-A 10725	61.824	
		MLP 52-X-4-1	58.9656	
		MLP 59-II-28-14	74.69	
		AMNH 28475	68.7425	
		AMNH 109618	58.5331	
		CNHM P13499	76.23	
<i>Didolodus minor</i>	1	AMNH 28472	50.82	50.82
<i>Didolodus magnus</i>	1	MPEF 7859	186.05	186.05

Appendix 2.

Species used in the new sample.

Order	Species	N	Materials	m ₂ area (mm ²)	LMT (mm)	LA (mm)	
Artiodactyla	<i>Potamochoerus larvatus</i>	2	MLP 1068	24.27	37.85	278.50	
				24.58	36.81	285.30	
			MACN 15–23	26.8	45.69	271.76	
				26.44	45.48	269.34	
	<i>Sus scrofa</i>	6	MV R9	31.39	–	289.81	
				32.16	–	330.37	
			MV R15	30.93	–	282.71	
				31.62	–	288.66	
	<i>Tayassu tajacu</i>	2	MLP 1177	16.08	26.21	143.88	
				16.04	25.94	158.82	
	<i>Tayassu pecari</i>	2	MLP 1072	27.32	–	217.87	
				27.23	–	207.01	
Carnivora	<i>Procyon cancrivorus</i>	2	MLP 1.IX.00.63	15.67	23.6	107.75	
				16.36	23.58	113.00	
	<i>Ursus arctos</i>	2	MACN 47-127	29.06	36.18	199.65	
				28.83	35.41	202.39	
Primates	<i>Alouatta caraya</i>	6	MACN 23457	13.32	20.56	51.60	
				13.07	18.59	47.46	
			MLP 20.V.02.4	12.34	22.5	47.45	
				12.33	22.61	45.60	
			MLP 204	13.11	20.71	51.50	
				13.03	20.73	42.55	
	<i>Cercopithecus</i> sp.	2	MACN 48–208	13.7	20.76	43.87	
				13.53	20.87	44.17	
	<i>Colobus</i> sp.	2	MACN 48-207	13.11	22.58	49.37	
				13.31	22.24	47.55	
	<i>Macacus</i> sp.	2	MACN 47–115	12.71	17.55	47.32	
				13.28	19	50.66	
	<i>Papio</i> sp.	6	MACN 23383	20.26	29.49	104.08	
				17.68	29.42	105.64	
			MACN 23384	25.71	38.09	116.40	
				24.37	38.76	119.52	
MACN 48–192			17.13	21.73	85.74		
			16.83	20.38	85.93		
<i>Pan troglodytes</i>			2	MACN 50–587	18.97	29.13	131.61
					17.39	28.67	129.05
<i>Semnopithecus</i> sp.	2	MACN 5–52	15.56	27.68	63.03		
			15.28	27.64	64.99		