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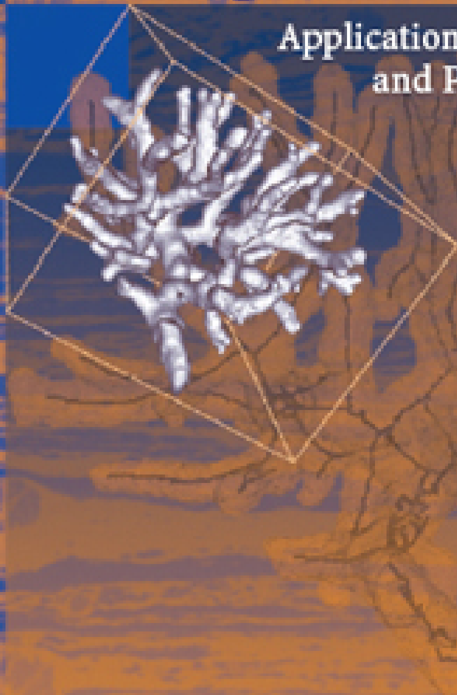

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10. Sauropod Tracks – a geometric morphometric study

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10.1 ABSTRACT

Geometric morphometrics are used to characterize shape variations in different *Sauropodomorpha* ichnotaxa and unclassified ichnites. Ten landmarks were collected from each of 30 specimens. Landmark configurations were superimposed, and residuals were modeled with the thin-plate spline interpolating function (to visualize shape changes). This group of techniques allows to discriminate tendencies in shape changes (providing quantitative descriptors).
The multivariate analysis of shape variables on the centroid size indicates the absence of allometry in our sample of *Sauropodomorpha* tracks.

Keywords: *Sauropoda pes* tracks; *Brontopodus*; Geometric morphometrics; allometry; Relative Warps

10.2 INTRODUCTION

Application of Geometric Morphometric (GM) techniques in the ichnological record haven't received much attention. Some applications have been made on dinosaur tracks particularly the *Theropoda* and *Ornithopoda* ichnological record (Rasskin 1995; Rasskin et al. 1997). This work presents the first GM study on the *Sauropodomorpha* ichnological record. Here we constrast a descriptive study based on four sauropod ichnological morphotypes with a geometric morphometric approach.

The discovery and documentation of many new sauropod tracksites in Portugal over the last ten years have yielded valuable information to better understand sauropod *manus* and *pes* prints morphologies. Nevertheless, well-preserved sauropod *manus* and *pes* prints are still rare in the general fossil record.

Until 1990 a small number of well-preserved specimens were known worldwide and few ichnogenus were considered valid scientific names. Middle Jurassic sauropod ichnites from Morocco were described as *Breviparopus taghbaloutensis* (Dutuit and Ouazzou 1980).

Brontopodus birdi was named on the basis of well-preserved sauropod trackways from Albian carbonates from Texas (Farlow et al. 1989). *Parabrontopodus mcintoshi* was proposed from narrow-gauge Upper Jurassic sauropod trackways (Lockley et al. 1994a)

The record of the ichnogenus *Brontopodus* is worldwide distributed - Portugal (Lockley et al. 1994a,b), Croatia (Mezga and Bajraktarevic 1999)**,** Switzerland (Meyer 1993), Spain (e.g. Moratalla 1993), Poland (Gierlinski 2002), United Kingdom (Romano et al. 1999), China (Lockley et al. 2002), South Korea (e.g. Lim et al. 1994), Australia (e.g. Thulborn et al. 1994), USA (Farlow et al. 1989).

More recently, Lower Cretaceous sauropod footprints from Croatia were described and named as *Titanosaurimanus nana* (Dalla Vecchia and Tarlao 2000).

In the present study were used *Sauropodomorpha* footprints outlines from several works (Table 1).

Most of the sauropod footprints are oval- or egg-shaped without diagnostic digit impressions, due to inadequate substrate conditions, and further unfavorable conservation factors (e.g. Leonardi 1987; Lockley 1991; Gatesy et al. 1999; Garcia-Ramos et al. 2000; Nadon 2001). Nevertheless, several of these poorly preserved ichnites have received formal names despite the fact that other well-preserved specimens have not (Lockley et al. 1986).

Up to now, no Geometric Morphometric analysis of shape variation in a sample of *Dinosauria – Sauropodomorpha* footprints of the world ichnological record has been conducted and just only the preliminary results of the application of this methodological approach on 22 specimens were presented (Rodrigues and Santos 2003). The aim of this paper is to discuss the contribution of the Geometric Morphometrics analysis to improving the discrimination of *Sauropodomorpha* footprints and, possibly, to improving the characterization of ichnological shape variation.

In this paper we use GM analysis on *pes* prints attributed to *Sauropoda* and other marks attributed to *Prosauropoda* footprints in order to provide a contribution to *Sauropodomorpha* footprints discrimination. We chose a total of 30 *Sauropodomorpha pes* tracks from the world ichnological record (range of standard length 5.8–94.0 cm) (see Table 1).

10.3 Materials and methods

10.3.1 Samples

Good general preservation and presence of, at least, four digit impressions determined selection of specimens. With these selection criteria, we tried to reduce the taphonomical bias.

The descriptions of sauropod tracks were based on several features characteristics of *Sauropoda autopodia*. Concerning *pes* prints the following distinctive features were characteristic:

- subcircular/suboval/subtriangular shape of the *pes* print with asymmetrical expanded proximal portion (entaxonic);
- outward rotated;
- four or five digit impressions usually outward rotated or laterally oriented;
- strongly curved and usually triangular impressions;
- claws on digits I, II, III.

We grouped the specimens into four morphotypes, based on the ichnotaxonomy proposed by different authors in the literature. Morphotype 1 (MT1) – this morphotype gathers *Brontopodus birdi*/*Brontopodus* sp.; Morphotype 2 (MT2) – *Brontopodus* aff. *B. birdi* / *Brontopodus type* / *Brontopodus*; Morphotype 3 (MT3)– *Prosauropoda* ichnites (*Tetrasauropus*/ *Pseudotetrasauropus*/ *Paratetrasauropus*); Morphotype 4 (MT4) – miscellaneous and unidentified ichnites.

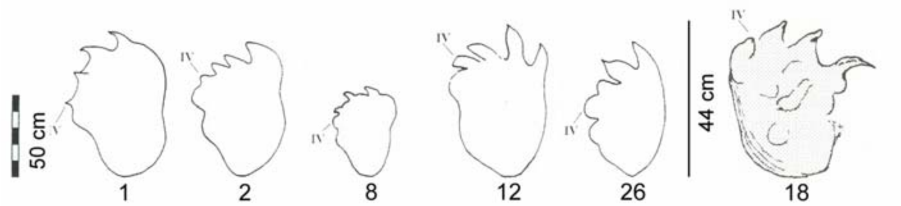

Fig. 1. Examples of specimens used in this study – Specimen 1 (Morphotype 1), Specimen 2 (Morphotype 2), Specimen 8 (Morphotype 4), Specimen 12 (Morphotype 1), Specimen 26 (Morphotype 2) and Specimen 18 (Morphotype 3). Parataxonomy and references in Table 1. IV – fourth digit. (Adapted from Lockley et al. 1994a, Santos et al. 1994, Thulborn 1990).

10.3.2 Obtaining Landmarks coordinates

Due the inherent characteristics of the materials analyzed in this study, the type of landmarks applied were Type III (Bookstein 1991).

Silhouettes and photos of *Sauropodomorha* footprints in literature were used and digitized with Hp 5470C scanner.

Images were treated digitally (digital clearness) using Paint Shop Pro 7.0 (Jasc Software 2002).

We assumed that all specimens were left *pes*. When only right *pes* existed, the specimens were reflected (mirror effect) using Paint Shop Pro 7.0 (Jasc Software 2002).

The coordinates of the specimens were determined with TpsDig 1.37 (Rohlf 2003a). Since we used figures from different literature sources, they presented different sizes. In order to correct this we used scale factor in every specimen.

Some of the specimens studied have been measured in terms of length and width, applying the measure tool on TpsDig 1.37 (Rohlf 2003a). This procedure was applied because those measurements are not mentioned in the literature.

10.3.3 Description of landmarks

1- maximum *hypex* of digit I; 2 - *hypex* between digits I and II; 3 - maximum *hypex* of digit II; 4 - *hypex* between digits II and III; 5 - maximum *hypex* of digit III; 6 - *hypex* between digits III and IV; 7 - maximum *hypex* of digit IV; 8 – intersection point between a perpendicular line (from mid point of landmark 7 and 9) and the ichnite contour; 9 – most posterior point of the print considering its axis; 10 - intersection point between a perpendicular line (from mid point of landmark 1 and 9) and the ichnite contour .
All ichnological terms and definitions follows Leonardi (1987) and Thulborn (1990). The long axis of the footprint employed in the landmarks 8, 9 and 10 follows the definition of Leonardi (1987).

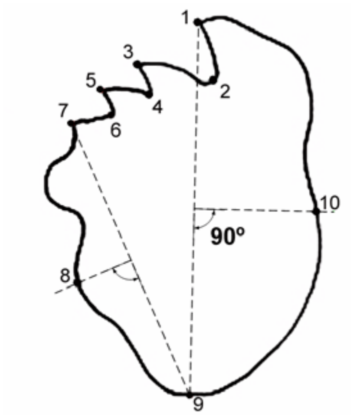

Fig. 2. – Orientation terminology and position of the 10 landmarks used in this study. Landmark 1 and 9 are in the anterior and posterior region of the track, respectively; landmark 8 and 10 are in the lateral and medial region of the track, respectively

The mid points between landmarks 1 and 9 and between 7 and 9 were calculated. Marking of a perpendicular line to the referred mid points and the point of intersection of that line with the contour of the footprint. These calculations were performed with Microsoft Visio 2000 (Microsoft Corporation 2000).

A full, detailed, mathematical description of the GM methodology used in this study is outside the range of this paper. Theoretical background of these methdologies are reviewed in different literature sources (e.g. Bookstein 1989a, b, 1990, 1991; Rohlf and Marcus 1993; Marcus et al. 1996; Rohlf and Bookstein 2003).

For each specimen, centroid size and weight matrix (with both uniform components appended) were computed. The weight matrix is the matrix of the partial warp scores. Centroid size was tested for differences by single classification analysis of variance (ANOVA) (Sokal and Rohlf 1995). All specimens were scaled to unit centroid size before alignment by the method of Generalized Procrustes Analysis (GPA) superimposition.

10.4 Relative warp analysis

The coordinates of all aligned specimens were used for thin-plate splines relative warp analysis (Bookstein 1991; Rohlf 1993).

The Relative Warps (RW) analysis was performed with the scaling option $\alpha=0$ (Rohlf 1993) that weights all landmarks equally, with the uniform component included - complement method (Rohlf and Bookstein 2003).

Relative warps analysis corresponds to a Principal Components Analysis of the covariance matrix of the partial warp scores, which are different scales of a thin-plate spline transformation of landmarks. The thin-plate spline is a smooth interpolation function that computes and visualizes transformations of Cartesian Coordinates in a way similar to D'Arcy Thompson's transformation grids (Thompson 1917). A rectangular grid is projected over Procrustes aligned landmark configurations and the bending of the grid visually depicts the difference in landmark locations between two configurations

The columns of the weight matrix represent the shape variables (Partial warps), being the last two columns the uniform shape components (Unif X, shearing, and Unif Y, stretching along the major axis of the consensus configuration). The first n-2 columns characterize more localized shape components (non uniform shape components).

10.5 Multiple Regression analysis

Centroid size, the square root of the sum of the squared distances between all homologous landmarks and the center of gravity of the landmarks, is commonly used as general size measure in geometric morphometrics.

To explore the existence of size allometry (i.e. shape change as a function of size), a multivariate regression of the weight matrix (with uniform components appended) onto log centroid size was performed. The log of centroid size was used as our size variable because most of shape change occurs early in ontogeny (e.g., Zeldich et al. 2000).

10.6 Software

Procrustes superimposition, weight matrix, graphical material and centroid size were performed using TPSRelw 1.35 (Rohlf 2003b); TPSRegr 1.26 (Rohlf 2003c). Statistical analysis and scatterplots – SPSS 10.0 (SPSS Inc., 2000).

10.7 RESULTS

Centroid size was tested for differences among specimens by ANOVA ($F= 4.126$, $p< 0.05$) and was significant. The centroid size is moderately correlated with the uniform component x ($r=-0.379$, $p<0.05$) and not correlated with uniform component y.

10.7.1 Relative warps analysis

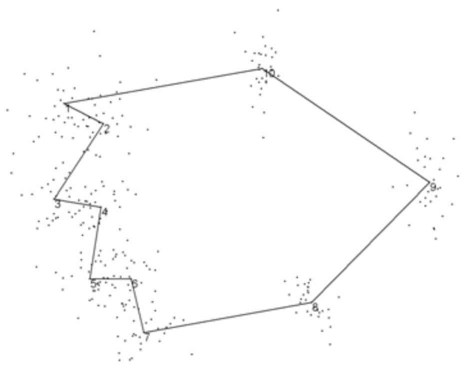

Fig. 3. Scatterplot of mean consensus configuration with individual specimens superimposed by Generalized Procrustes Analysis (GPA)

There is large variability in most of the landmarks as visualized in Fig. 3. In landmarks 8, 9 and 10 the observed variability is mostly latero-medial.

The first three relative warps account for 66.46% of the total variation of the specimens. RW1 accounts for 35.52% of total shape variability. There is a significant correlation between centroid size and the first relative warp (r=0.404, P <0.05).

RW2 accounts for 18.40% for shape variability and is not correlated with centroid size. RW3 explains 12,54% of shape variability and is not correlated with centroid size.

The distribution of the four morphotypes is presented in a scatterplot of Relative Warp 1 (RW1) and Relative Warp 2 (RW2) (Fig. 4).

Distribution of specimens presents some tendencies: specimens 16, 17 and 18 (*Prosauropoda* origin) clearly separated from other specimens; specimens 1, 2, 12, 24 and 26 are morphological related despite their different morphotype classification; Croatia specimens (27, 28, 29 and 30) are closely associated with the exception of specimen 30. This could be explained as probable misidentification of digit polarity. All other specimens present a distribution very similar with the consensus and without clear grouping.

Patterns of shape change along the two first relative warps are illustrated in Fig.5. Most of the variance from the consensus, along RW1 axis (negative to positive deviations), is due to the rotation of digits from an inward (medial) position to an outward (lateral) position. Similar tendency in relative shape change is observed in the heel region. This shape variation along this axis is also a consequence of a medial bending. In addition, we detected an antero-posterior shortening associated with digit rotation (both outward and inward). The correlation between centroid size and the first relative warp support this size shift.

RW2 differences from the consensus (negative to positive deviations) are due: 1- reduction in relative length of digits I and II; 2 – digits I, II and III becoming narrow.

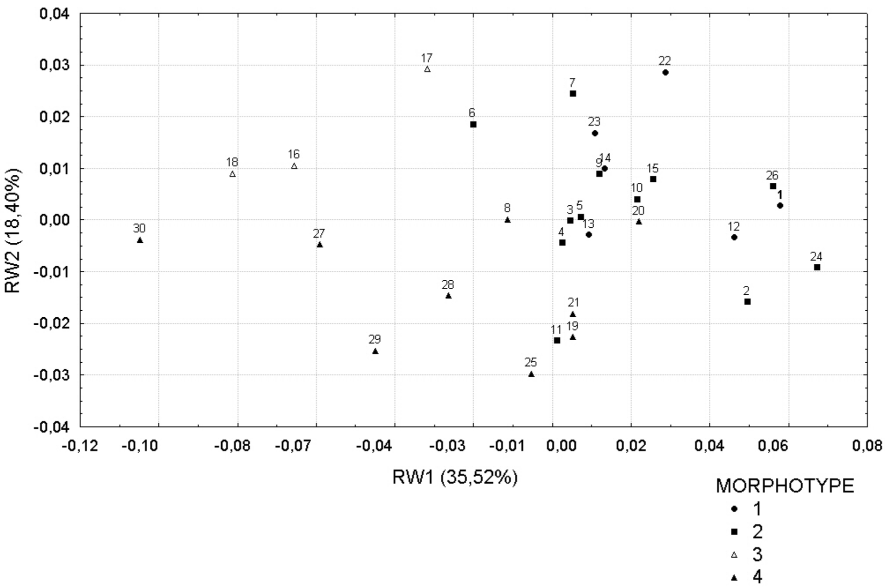

Fig. 4. Scatterplot of RW1 and RW2 of the specimens and respective Morphotypes

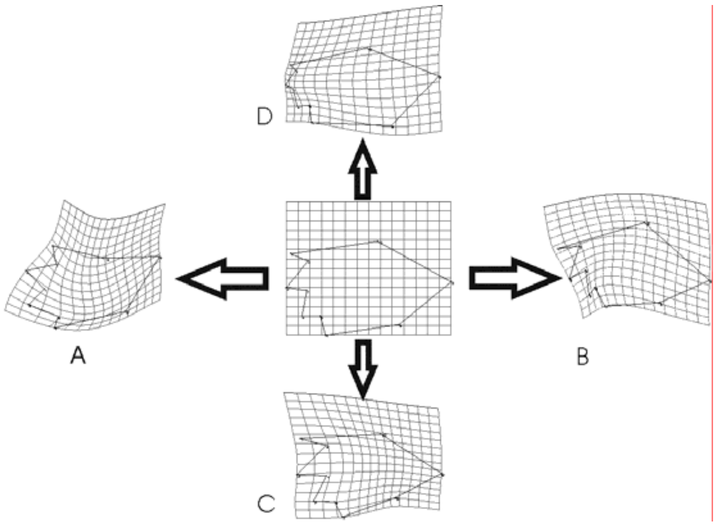

Fig. 5. Shape changes depicted by the RW1 and RW2. (A) Deformation relative to the mean shape toward the negative direction of RW1. (B) Deformation relative to the mean shape toward the positive direction of RW1. (C) Deformation relative to the mean shape toward the negative direction of RW2. (D) Deformation relative to the mean shape toward the positive direction of RW2

10.7.2 Multiple Regression analysis

Regressing the full set of partial warps on log centroid size showed no significant differences (Wilks' Lambda = 0.4372, F (16, 13) = 1.046, P>0.4). Size explains only 4.91% of the shape variation in our sample. Clearly, in our sample, shape is not a function of size.

The isometric growth of appendicular skeleton in sauropods has been noted (e.g. Carpenter and McIntosh 1994). For instance, the limbs of *Camarasaurus* show evidence of isometric growth with very little indication of allometry (Wilhite 1999, 2003). Some authors also noted isometric growth in the limbs of *Apatosaurus* (Carpenter and MacIntosh 1994).

10.8 DISCUSSION AND CONCLUSIONS

Ichnology can complement information from the dinosaur osteological record, for instance, by providing complementary data on *autopodia* shape and structure as well on limb posture. (Lockley and Hunt 1995; Gatesy et al. 1999; Wilson and Carrano 1999).

GM techniques were applied for the first time in the *Sauropodomorpha* ichnological record, as far as we are aware. This methodology allowed to descriminate between tendencies in shape changes in our sample as well as to confirm the absence of allometry.

The shape variation observed in our sample are caused by:

relative digit position (inward/medial to outward/lateral rotation);

medial region bending (directly associated with outward/lateral rotation of digits) and relative heel position (inward/medial to outward/lateral rotation).

We have observed and quantified that specimens attributed to prosauropods (*Tetrasauropus, Pseudotetrasauropus* and *Paratetrasauropus*) are closely related to each other in comparison to the mean shape and to specimens attributed to sauropods (i.e., there is a morphological discontinuity between the *Prosauropoda* and *Sauropoda* tracks). As a consequence of this GM analysis, we can maintain the idea of a *Prosauropoda* origin for Morphotype 3, which includes the above referred ichnogenus type *Tetrasauropus*. An opposite ichnotaxonomical proposal is the attribution of *Tetrasauropus* to the *Sauropoda* ichnological record (Lockley et al. 2001).

The general sauropod track record suggests that *pes* prints are slightly longer than wider and present a trend as an outward rotation of four or five externally rotated digit impressions (e.g. Farlow et al. 1989; Lockley 1991; Meyer et al. 1994). These features are reliable with character 64 on the sauropod phylogenetic hypothesis of Wilson and Sereno (1998) - "*Pedal unguals, orientation: aligned with (0), or deflected lateral to (1), digit axis*.".

Digit rotation is the most important factor in the shape variation in our sample. Despite this, there are other factors contributing to the variability of shape observed.

This analysis allows us to suggest that *Brontopodus birdi* present more outward rotated digits than the Portuguese specimens 3, 4, 5 and 8. These specimens present a digit rotation very similar to mean shape.

Specimens from Croatia (27, 28, 29 and 30) were attributed to a *Titanosauria* origin (Dalla Vecchia and Tarlao 2000). In this analysis, they are the most extreme specimens regarding inward digit rotation, which is close associated with Morphotype 3 (*Prosauropoda* origin) and distant to Morphotypes 1 and 2 (*Sauropoda* origin). This may suggest a slightest non-*sauropoda* origin hypothesis or digit misidentification (i.e., digit I could be digit IV, inverting the digit rotation course). This methodology could permit the recognition of misidentified tracks as long as other factors could be included (e.g. stratigraphical age, wide or narrow-gauge trackway).

Morphotypes 1 and 2 are morphologically comparable, which is confirmed by its parataxonomical origin affinity. This GM study corroborates the majority of previous ichnotaxonomical classifications.

The multivariate regression analysis on the centroid size supports the lack of allometry in different taxa of *Sauropoda* limbs (Wilhite 1999, 2003; Carpenter and MacIntosh 1994). This geometric study corroborates the osteological results on absence of allometry on *Sauropoda* appendicular structures.

Other multivariate analyses are currently under study using as independent variables: velocity; wide/narrow gauge trackway; geological/stratigraphical frame; illustration authors. This latter variable study is justified by the ichnological interpretation that precedes each track illustration. It means the author of the illustration is a very important variable in geometric morphometric studies that uses track contours.

Table 1. Reference, morphotype, parataxonomy, age, literature consulted and standard dimensions of the specimens analyzed. * - measurements made by the authors; ** - measurements made by the authors on the most external contour; LT- Late Triassic; J- Jurassic MJ- Middle Jurassic UJ- Upper Jurassic; LC – Lower Cretaceous.

Reference	Morphotype	Parataxonomy	Age	Authors	Length	Width
1	1	*Brontopodus birdi*	LC	Thulborn 1990, p. 170, fig. 6.16.a	89*	65*
2	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 249, fig. 6.15.9.	80	58
3	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 241, fig. 6.15.5.	72*	56*
4	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 241, fig. 6.15.5.	80	50
5	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 186, fig. 6.7.3.	85	68
6	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 186, fig. 6.7.3.	70	60
7	2	*Brontopodus aff. B. birdi*	UJ	Santos 2003, p. 188, fig. 6.7.4.	60	60
8	4	*Polyonichnus gomesi*	MJ	Santos 2003, p. 124, fig. 6.1.7.	90	60
9	2	*Brontopodus aff. B. birdi*	UJ	Lires 2000, p. 33	74*	56*
10	2	*Brontopodus aff. B. birdi*	UJ	Lires 2000, p. 34	62*	58*
11	2	*Brontopodus aff. B. birdi*	UJ	Lires 2000, pers. commun.	52	36
12	1	*Brontopodus sp.*	UJ	Lockley & Mickelson 1997, p. 136	60	46
13	1	*Brontopodus sp.*	UJ	Lockley & Mickelson 1997, p. 136	55	40
14	1	*Brontopodus sp.*	UJ	Lockley & Mickelson 1997, p. 136	55	40
15	2	*Brontopodus (?)*	LC	Thulborn 1990, p. 170, fig. 6.16.f	70	65*
16	3	*Pseudotetrasauropus*	LT	Thulborn, 1990, p. 178, fig. 6.23.b	49	39*
17	3	*Paratetrasauropus*	LT	Thulborn 1990, p. 178, fig. 6.23.e	28	22*
18	3	*Tetrasauropus*	LT	Thulborn 1990, p. 178, fig. 6.23.c	44	41*
19	4	Non-identified	J	Thulborn 1990, p. 170, fig. 6.16.e	80	51*
20	4	Non-identified	LC	Woodhams 1998, pers. commun.	58*	36*
21	4	Non-identified	LC	Woodhams 1998, pers. commun.	62*	51*
22	1	*Brontopodus birdi*	LC	Ray Stanford 2003, pers. commun.	5.8	5
23	1	*Brontopodus birdi*	LC	Ray Stanford 2003, pers. commun.	5.8	5
24	2	*Brontopodus type*	MJ	Romano et al. 1999, p. 365, fig. 3A	94	70
25	4	*Breviparopus type*	MJ	Romano et al. 1999, p. 365, fig. 3B	81	67
26	2	*Brontopodus type*	UJ	Lockley et al. 1994, p.143, fig. 6.b	83*	51*
27	4	*Titanosaurimanus nana*	LC	Dalla Vecchia & Tarlao, 2000, p. 261, fig. 29E	34.5**	32**
28	4	*Titanosaurimanus nana*	LC	Dalla Vecchia & Tarlao, 2000, p. 261, fig. 29G	33**	29**
29	4	*Titanosaurimanus nana*	LC	Dalla Vecchia & Tarlao, 2000, p. 261, fig. 29B	31**	23**
30	4	*Titanosaurimanus nana*	LC	Dalla Vecchia & Tarlao, 2000, p. 261, fig. 29F	34**	29**

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